

# Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene

Wilkes, M, Birnie-Gauvin, K, Franklin, P & Aarestrup, K

Author post-print (accepted) deposited by Coventry University's Repository

**Original citation & hyperlink:**

Wilkes, M, Birnie-Gauvin, K, Franklin, P & Aarestrup, K 2018, 'Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene' *Aquatic Conservation: Marine and Freshwater Ecosystems*, vol (In-Press), pp. (In-Press).

ISSN 1052-7613

ESSN 1099-0755

Publisher: Wiley

**This is the peer reviewed version of the following article Wilkes, M, Birnie-Gauvin, K, Franklin, P & Aarestrup, K 2018, 'Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene' *Aquatic Conservation: Marine and Freshwater Ecosystems*, vol (In-Press), pp. (In-Press). This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.**

**Copyright © and Moral Rights are retained by the author(s) and/ or other copyright owners. A copy can be downloaded for personal non-commercial research or study, without prior permission or charge. This item cannot be reproduced or quoted extensively from without first obtaining permission in writing from the copyright holder(s). The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the copyright holders.**

**This document is the author's post-print version, incorporating any revisions agreed during the peer-review process. Some differences between the published version and this version may remain and you are advised to consult the published version if you wish to cite from it.**

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25

**Moving beyond fitting fish into equations: Progressing the fish passage debate in the  
Anthropocene**

*Accepted in Aquatic Conservation (supplemental issue: Freshwater Ecosystems in the  
Anthropocene)*

Kim Birnie-Gauvin<sup>1</sup>, Paul Franklin<sup>2</sup>, Martin Wilkes<sup>3</sup> and Kim Aarestrup<sup>1</sup>

<sup>1</sup> Section for Freshwater Fisheries and Ecology, National Institute of Aquatic Resources,  
Technical University of Denmark, Vejlsovej 39, 8600 Silkeborg, Denmark

<sup>2</sup> National Institute of Water and Atmospheric Research, Gate 10 Silverdale Road, Hamilton,  
New Zealand

<sup>3</sup> Centre for Agroecology, Water and Resilience, Coventry University, Ryton Organic  
Gardens, Wolston Lane, Ryton-on-Dunsmore, United Kingdom, CV8 3LG

**Author for correspondence:** K. Birnie-Gauvin, [kbir@aqu.dtu.dk](mailto:kbir@aqu.dtu.dk)

26 **Abstract**

27 1. Realization of the importance of fish passage for migratory species has led to the  
28 development of innovative and creative solutions to mitigate the effects of artificial barriers  
29 in freshwater systems in the last few decades ('fishways').

30 2. In many instances, however, the first move has been to attempt to engineer a solution to the  
31 problem, thus attempting to "fit fish into an equation". These fishways are often derived from  
32 designs targeting salmonids in the Northern Hemisphere. They are rarely adequate, even for  
33 these strong-swimming fish, and certainly appear to be unsuitable for most other species, not  
34 the least for those of tropical regions.

35 3. Fishway design criteria do not adequately account for natural variation among individuals,  
36 populations and species. Moreover, engineered solutions cannot reinstate the natural habitat  
37 and geomorphological properties of the river, objectives that have been largely ignored.

38 4. Here, we discuss the most prominent issues with the current management and conservation  
39 of freshwater ecosystems as it pertains to fish passage. This paper is not intended as a review  
40 on fish passage, but rather a perspective paper on the issues related to fishways, as seen by  
41 practitioners.

42

43 **Keywords:** biodiversity, conservation, dams, ecological engineering, habitat, hydropower,  
44 fishways, freshwater, management, weirs

45

46

47

48

49

50

## 51 **1. Introduction**

52 Fragmentation of freshwater ecosystems has been identified as one of numerous global river  
53 syndromes characteristic of the Anthropocene (Meybeck, 2003). Continued human  
54 population growth will only serve to increase pressures on water resources, driving further  
55 investment in infrastructure to support water, food and energy security, and to protect land  
56 and property from flooding (Vörösmarty et al., 2010; Garcia-Moreno et al., 2014). For  
57 example, at least 3,700 major hydropower dams (capacity >1MW) are planned or under  
58 construction worldwide, and the number of smaller dams (<1MW) planned is likely to  
59 significantly exceed this (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015).

60 While ensuring access to food, energy and potable water is fundamental for  
61 supporting the future of human societies, freshwater biodiversity in the Anthropocene is  
62 under great threat due to unsustainable river basin development (Vörösmarty et al., 2010;  
63 Garcia-Moreno et al., 2014; Poff, 2014). Ongoing river fragmentation and dam construction  
64 presents one of the greatest global threats to freshwater biodiversity and ecosystem  
65 functioning (Dudgeon et al., 2006). Disruptions to river connectivity threaten ecosystem  
66 structure and function by interrupting movements of migratory species (Winemiller et al.,  
67 2016), blocking the exchange of individuals and genetic information between populations  
68 (Wofford, Gresswell, & Banks 2005; Raeymaekers et al., 2008), modifying aquatic habitats  
69 and altering flow and sediment transport regimes (Bunn & Arthington, 2002). Unfortunately,  
70 consideration of biodiversity and ecosystem functioning tends to take a distant second place  
71 to engineering solutions that meet immediate human needs (Garcia-Moreno et al., 2014). This  
72 is despite the increasing recognition that biodiversity loss impairs and fundamentally alters  
73 the functioning of ecosystems upon which society depends for food, energy and water  
74 security (Vignieri, 2014).

75 Globally, freshwater fish are a critical food resource and support economically and  
76 culturally important fisheries (e.g. Winemiller et al., 2016). As a result, the loss of fish  
77 populations during the Anthropocene has probably received greater global attention than any  
78 other freshwater group. Connectivity is fundamental to the structure and functioning of  
79 freshwater fish communities and aquatic ecosystems worldwide, and is active along the  
80 longitudinal, vertical, lateral and temporal dimensions (Tockner, Schiemer, & Ward 1998).  
81 Instream structures, such as dams, weirs, tide gates and culverts, interrupt connectivity in all  
82 dimensions, with the repercussions being observed as species and/or population declines and  
83 extirpations in river systems across the globe (Table 1).

84 The impact of instream structures on the movements and migration of fish has long  
85 been recognized. In Northern Europe, fishways were already being established by the mid-  
86 18th century. Though these early fishways were inefficient (Francis, 1870), their presence  
87 indicates the recognition of connectivity issues. At that time, the main concern was the  
88 upstream passage of Atlantic salmon, *Salmo salar*, mostly due to its high economic and  
89 recreational value (Katopodis & Williams, 2012). Despite the ever-increasing awareness of  
90 barrier impacts on other fish species (Raeymaekers et al., 2008; Perkin et al., 2015; Branco,  
91 Amaral, Ferreira, & Santos, 2017; Wilkes, McKenzie, & Webb, 2018), contemporary  
92 approaches to fish passage research and management continue to be dominated by salmonid-  
93 centric methods, solutions and thinking, and continue to focus on the upstream passage of  
94 fish at larger structures, giving relatively little attention to equally important downstream  
95 movements and small structures.

96 Increasing realisation of the importance of effective fish passage for sustaining  
97 migratory species has led to the development of innovative and creative solutions to mitigate  
98 the effects of artificial barriers in freshwater systems over recent decades, but management of  
99 fish passage continues to be dominated by an 'impair-then-repair' approach (Vörösmarty,

100 Pahl-Woslt, Bunn, & Lawford, 2013). For most dams and other instream infrastructure,  
101 fishways continue to be considered an add-on ‘fix’ once the standard structural design is  
102 complete (Katopodis & Williams, 2012). Furthermore, fish passage tends to be treated on a  
103 site-by-site basis, focused only on getting fish from one side of the structure to the other, and  
104 effectiveness monitoring is often absent. Rarely is consideration given to the broader  
105 catchment context of fish passage, or the impacts on aquatic habitats and ecosystem processes  
106 (Pelicice & Agostinho, 2008; Pompeu, Agostinho, & Pelicice, 2012; McLaughlin et al., 2013;  
107 Kemp, 2016; Silva et al., 2018). We argue that this reductionist approach is symptomatic of  
108 the origins of fish passage research, embedded in a philosophy of engineering our way out of  
109 the problems created by human modifications of the riverscape.

110 A characteristic of the dominant engineering approach to fish passage is determinism  
111 (*e.g.* ‘the species can swim at  $x$  velocity for  $t$  time’). A general failure to consider the bigger  
112 picture and a continued focus on trying to ‘fit fish into equations’ cannot account for the  
113 natural variation among individuals, populations and species that is an essential characteristic  
114 of sustainable aquatic ecosystems. We believe that to improve outcomes for freshwater  
115 biodiversity, fish passage research and its applications must embrace this natural variability.  
116 To achieve this there is a need to confront what we view as inherent biases in fish passage  
117 research, policy and practice that derive from the overwhelming dominance of research on  
118 the salmonid species of the temperate Northern Hemisphere. The field of fish passage as a  
119 whole needs rethinking, with the objective of helping fish move up and down rivers with no  
120 adverse effects.

121 The intent of this paper, therefore, is to contribute to the ongoing debate on fish  
122 passage (*e.g.* Bunt, Castro-Santos, & Haro, 2016; Kemp, 2016; Williams & Katopodis, 2016;  
123 Silva et al., 2018) by providing a perspective on what we view to be among the most crucial  
124 issues related to the prevailing paradigm of fish passage research and management at a global

125 scale. In particular, we consider the question of whether the current approach to the fish  
126 passage problem is fit-for-purpose and suitable for effectively tackling the freshwater  
127 biodiversity crisis of the Anthropocene. We finish by proposing some potential approaches to  
128 progress the fish passage debate by moving beyond some of the biases we identify, and  
129 pursuing a more holistic approach to fish passage research and applications.

130

## 131 **2. Biases in fish passage research and application**

132

### 133 *2.1 Long standing focus on salmonids and upstream passage*

134 Much of the knowledge we have about the effects of instream barriers, fishways, and the  
135 ability of fish to pass them is derived from studies based on anadromous salmonids in the  
136 temperate Northern Hemisphere. This focus emerged due to the well-documented declines in  
137 salmonid stocks in river systems around the globe arising from anthropogenic interruptions to  
138 migration routes (*e.g.* Yeakley, Maas-Hebner, & Hughes, 2014). Due to the economic and  
139 cultural importance of salmonid populations, and often supported by local legislative  
140 requirements, efforts to ‘fix’ the problem emerged. Despite these efforts, there remains a  
141 focus on upstream movements, with less consideration given to getting fish back downstream  
142 (though efforts to address downstream movement have risen in recent years, *e.g.* Arnekleiv,  
143 Kraabøl, & Museth, 2007; Birnie-Gauvin, Candee et al. in press).

144       Adult salmonids have very particular needs given their highly directed and relatively  
145 synchronized migration. Salmonid migratory behaviours are some of the most studied,  
146 though downstream movements have received considerably less attention. The behaviour of  
147 downstream migrating salmonid smolts is often simplified and believed to be addressed by  
148 designing screens and bypasses that screen fish only near the water surface (Arnekleiv et al.,  
149 2007). In our experience however, a significant proportion of smolts move below the screen,

150 with evidence of individuals migrating near the bottom (Svendsen, Eskesen, Aarestrup, Koed,  
151 & Jordan, 2007). Our lack of focus (and knowledge) on this downstream movement,  
152 combined with the observation of highly synchronous upstream migrations, have led to the  
153 perception that these fish have relatively narrow and well-defined needs, with characteristics  
154 that suit the reductionist approach of the engineering discipline.

155 Historically, designing effective fish passage solutions was challenged by the  
156 constraints (primarily space, cost and flow) typically imposed by having to retrospectively  
157 append fishways to existing structures. Solutions inevitably became a balancing act between  
158 overcoming the fall height created by the obstruction, minimising fishway length, and  
159 maintaining hydraulic conditions in the fishway within the capabilities of the target species  
160 and life stage, and only generating marginal changes to the function of the obstacle in  
161 question. Adult salmonids are agile and highly capable swimmers as they swim upstream  
162 and, thus, have a greater ability to overcome more hydraulically challenging environments  
163 than many other species. This has had a strong influence on the type and hydraulic  
164 performance standards of most fishway designs that exist today (Mallen-Cooper & Brand,  
165 2007).

166 Fish passage research remains largely entrenched in the early paradigm of salmonid  
167 biology. This long-standing focus has resulted in the same approach being perpetuated all  
168 over the globe, for all species, in all geographical contexts, rather than taking a step back and  
169 rethinking whether it is the right approach in a particular location (e.g. Link & Habit, 2015;  
170 Mallen-Cooper & Brand, 2007; Wilkes et al. in press). Despite the significant differences  
171 between the requirements of salmonids and most other fishes (e.g. Figure 1), including those  
172 from the tropics and temperate Southern Hemisphere, the knowledge, techniques, thinking  
173 and solutions developed from studies of salmonids have been widely transferred to fish  
174 passage design and management elsewhere (Silva et al., 2018). Application of these



175 approaches to freshwater systems with native species that have completely different needs  
176 has contributed to repeated failures and poor performance of fishways around the world (Lira  
177 et al., 2017; Wilkes et al., 2018). For example, Mallen-Cooper and Brand (2007) showed very  
178 poor passage of native Australian fish species through a salmonid fishway on the Murray  
179 River, with <1% of the most abundant species ascending. The continued underwhelming  
180 performance of many salmonid fishways (Brown et al., 2013), and ongoing unsuccessful  
181 application of salmonid-centric solutions to non-salmonid species has led some to suggest  
182 that, in a global sense, fishways are a technology in decline (Kemp, 2016).

183

## 184 *2.2 Engineering our way out of the problem*

185 The fundamental dichotomy of the fish passage problem is the need to balance the trade-offs  
186 between doing what would be best ecologically (i.e. remove all barriers), and trying to  
187 engineer our way out of the problem where there is a need for essential infrastructure (*e.g.*  
188 Nieminen, Hyytiäinen, & Lindroos, 2017). In too many instances, engineered solutions  
189 continue to be the default first step to solving fish passage issues. We suggest this bias has  
190 emerged from the emphasis of early fish passage research on retrospectively engineering site  
191 scale solutions to fix problems for individual species at existing infrastructure. This has  
192 embedded the idea of fish passage solutions as an ‘add on’ to structural designs, rather than  
193 an integral component of the design to be considered from the outset. However, inappropriate  
194 transfer of technological solutions and increasing evidence of the unintended consequences of  
195 providing fish passage (Pelicice & Agostinho, 2008; McLaughlin et al., 2013; Pelicice,  
196 Pompeu, & Agostinho, 2015), along with the broader ecosystem changes (Birnie-Gauvin,  
197 Aarestrup, Riis, Jepsen, & Koed, 2017), raise questions over the continued suitability of this  
198 approach.

199 Obviously, there are instances where instream infrastructure is necessary, and hence  
200 there will always be cases where engineered solutions are required. However, current design  
201 philosophies tend to force ecologists to take a reductionist approach, trying to fit fish into  
202 equations suitable for engineers to work out a solution that fits the appropriate hydraulic  
203 design envelope and minimizes costs. This approach has undoubtedly contributed to the less  
204 than satisfactory success of many fish passage solutions, as evidenced in multiple reviews  
205 (Roscoe & Hinch, 2010; Bunt, Castro-Santos, & Haro, 2012; Noonan, Grant, & Jackson,  
206 2012; Lira et al., 2017). The simplified representations of reality required by this approach,  
207 while convenient, inevitably fail to capture the natural variation that is characteristic of all  
208 organisms, ecological communities and ecosystems. Furthermore, the ability to effectively  
209 characterise the full range of hydraulic requirements of multiple species and life stages of fish  
210 in sufficient detail to provide effective hydraulic design criteria is impractical, particularly  
211 when considering ‘megadiverse’ fish communities such as those typical of tropical regions  
212 (Winemiller et al., 2016).

213 We encourage a more holistic approach, planning infrastructure and designing  
214 structures from the outset with a view to maintaining ecosystem processes and functioning,  
215 including aiming for the seamless movement of organisms. Doing so requires a change in  
216 design philosophy and a shift in expectations of how things should be done at every level.  
217 Scientists, engineers and managers must realise that the difference between removing (or not  
218 installing) a barrier and constructing a fishway is huge; fishways will *never* be as effective as  
219 the complete absence of barriers for providing fish with sufficient habitat and allowing safe  
220 movement. We argue that the first question we should always ask ourselves (perhaps twice)  
221 is whether that barrier is necessary at all, and if so, whether a fishway will contribute to the  
222 maintenance of viable populations upstream and downstream of the structure (*e.g.* Pompeu et  
223 al., 2012). There is strong evidence that removing artificial barriers to migration can be cost-

224 effective and result in rapid recovery of freshwater biodiversity and ecosystem processes, as  
225 seen for American eel (*Anguilla rostrata*; Hitt, Eyster, & Wofford, 2012), sea lampreys  
226 (*Petromyzon marinus*; Hogg, Coghlan, & Zydlewski, 2013), brown trout (*Salmo trutta*;  
227 Birnie-Gauvin, Larsen, Nielsen, & Aarestrup, 2017; Birnie-Gauvin, Candee et al. in press) as  
228 well as other species (O'Connor, Duda, & Grant, 2015;), yet barrier removal remains  
229 relatively uncommon, even where structures are redundant. Consequently, despite the  
230 growing use of fishways, which are supposedly designed to allow migrating fish to bypass  
231 barriers and reach suitable habitat in which to grow and reproduce, these structures remain  
232 mere pacifiers of the underlying ecological problems (Roscoe & Hinch, 2010; Bunt et al.,  
233 2012, 2016; Noonan et al., 2012; Lira et al., 2017).

234

### 235 *2.3 Requirement mismatches and ignoring natural variation*

236 The dominance of salmonid studies and reductionist engineering design approaches have  
237 combined to result in a situation where consideration of natural variations in fish behaviour  
238 and dispersal capabilities are minimised. Migration is a concept which has been known and  
239 studied for centuries. Its occurrence is widespread across all major taxonomic groups and has  
240 piqued the interest and curiosity of scientists for as long as it has been known. For decades,  
241 we have tried to understand its underpinning mechanisms and drivers, making a point of  
242 protecting migratory species as they usually depend on at least two types of environments to  
243 thrive (*e.g.* eels growing in freshwater and migrating to saltwater to spawn). While many of  
244 the overarching concepts of migration are well known, and largely accepted, the focus on a  
245 relatively narrow range of high status species has biased management actions towards  
246 particular life history strategies. Furthermore, it has led us to stop questioning some of the  
247 basic information we have regarding migration.

248           The majority of fish passage solutions have been designed to cater for anadromous  
249 life histories. However, even within the well-studied salmonid species, there is growing  
250 evidence that salmonid smolt migrations occur throughout the year rather than during a single  
251 peak period (Winter, Tummers, Aarestrup, Baktoft, & Lucas, 2016; Aarestrup, Birnie-  
252 Gauvin, & Larsen, 2018). Despite this, current fish passage management strategies, such as  
253 spillway opening and dam/weir closure periods, typically only occur during the peak spring  
254 migration for smolts, neglecting to cater for fish that do not fit the currently accepted  
255 salmonid paradigm (Aarestrup et al., 2018).

256           Another important consideration is the ‘migratory’ versus ‘non-migratory’ or  
257 ‘resident’ terminology; it creates the perception that non-migratory or resident fish do not  
258 move, yet they do (Schlosser & Angermeier, 1995; Jepsen & Berg, 2002; Radinger & Wolter,  
259 2014), and they may be impacted by barriers more than is traditionally recognised (*e.g.*  
260 Branco et al., 2017). The whole fish passage issue has largely focused on obligate migrants,  
261 sometimes classifying facultative migratory species as non-migratory for the purpose of  
262 passage needs. The functional explanations for movement of ‘non-migratory’ or ‘resident’  
263 fish are manifold, and may involve distances of the same order of magnitude to those  
264 characteristic of ‘migratory’ species. The reasons include: (i) to avoid unpredictable resource  
265 scarcity and perturbances (*e.g.* Falke, Fausch, Bestgen, & Bailey, 2010); (ii) to repopulate  
266 habitats previously affected by disturbance or disease (*e.g.* Perkin et al., 2015); (iii) to shift  
267 distribution gradually in response to large-scale environmental change, including climate  
268 change (Hari, Livingstone, Siber, Burkhardt-Holm, & Guttinger, 2006); and (iv) to exchange  
269 adaptive genetic information in the face of environmental change (*e.g.* Brauer, Hammer, &  
270 Beheregaray, 2016). We stipulate unpredictability in some of the instances listed above  
271 because if the phenomena were predictable the species may well be considered migratory.  
272 Such ‘unpredictability’ also encompasses the effects of climate change, so movement for

273 resident fish is likely to become even more important. There is a need in the first instance,  
274 therefore, to recognise this diversity of movements that occur within and between species and  
275 over time, and to cater for this diversity of movements in fish passage research and  
276 applications. There is also a need to consider variation at the individual level.

277         Individuals vary in their ability and motivation to overcome barriers (Agostinho et al.,  
278 2007; Bunt et al., 2012). There also exists variation amongst populations of the same species  
279 (Birnie-Gauvin, Larsen, Thomassen & Aarestrup, 2018; Figure 1). The reductionist approach  
280 typically adopted for fishway design means that this natural variation is often neglected  
281 completely, or is at least poorly accounted for (but see Wilkes et al. in press). Variation in  
282 fish behaviour and requirements is wide-ranging, and often discounted in modelling  
283 exercises, potentially rendering the outcomes invalid when we apply them to real-life  
284 situations. Whilst modelling is a valuable tool, explicit considerations of the uncertainty  
285 created by natural variation need to be implemented. Most modelling approaches in fish  
286 passage research, at their core, are equations. This means that fish must be fitted into a  
287 mathematical phrase, essentially collapsing all natural variation into one ‘magic’ number,  
288 even in situations where swimming behaviour between populations is strongly divergent (*e.g.*  
289 Link et al., 2017). Whilst the biologist would be calling for explicit recognition of this  
290 divergent swimming behaviour in fishway design, the engineer may instead consider an  
291 equation that does away with this variability.

292         The requirement to fit fish into equations in a way that is consistent with typical  
293 engineering design practices has seen an emphasis on efforts to quantify fish swimming  
294 speeds. The most convenient way of achieving this is through controlled laboratory  
295 swimming tests. Water velocity design criteria for fishways are typically determined through  
296 controlled swimming tests that force fish to swim at a fixed mean velocity (endurance tests)  
297 or at an incrementally increasing velocity (critical swimming tests) (Beamish, 1978). While

298 practical, this raises several issues related to individual variability, for example: turbulence  
299 and fish acceleration and deceleration are often ignored (but see *e.g.* Plew, Nikora, Larned,  
300 Sykes, & Cooper, 2007); the difference between different measures of swimming  
301 performance remains unclear (Peake, 2004); variations in swimming performance at different  
302 temperatures or under varying water quality are often not considered (but see *e.g.* Bannon &  
303 Ling, 2003); and species and individuals that do not ‘cooperate’ by swimming in the  
304 laboratory are often selected out rather than being considered a separate behaviour class to be  
305 accounted for (*e.g.* Santos, Pompeu, & Martinez, 2007). Furthermore, the behaviour of fish in  
306 an artificial laboratory set-up is unlikely to be natural due to the stress of handling and the  
307 change in behaviour that comes with being held in captivity for long periods, as well as the  
308 absence of natural environmental heterogeneity or migration cues (*e.g.* Vrieze, Bjerselius &  
309 Sorensen, 2010). This has led some authors to suggest that volitional swimming speed tests,  
310 for example measured in open channel flumes, are more appropriate (Haro, Castro-Santos,  
311 Noreika, & Odeh, 2004). However, while this may improve the biological realism of fish  
312 swimming performance evaluations, it still does not overcome the challenge of effectively  
313 characterising the natural variability in performance between individuals and populations and  
314 translating them in to practical design criteria that account for this uncertainty. While general  
315 relationships between hydraulics and swimming behaviour can be investigated, and are  
316 essential for supporting development of hydraulic design criteria, laboratory studies alone are  
317 insufficient for developing absolute criteria and much greater effort should be placed on  
318 incorporating natural variation and uncertainty into results.

319         As attention in fish passage research begins to move towards catering for multi-  
320 species assemblages, a further challenge emerges in trying to also account for the variation  
321 between and among species and life stages. In all but the most extreme cases, fish passage  
322 must be available for more than a single species, each with potentially different requirements,

323 at different life stages. How can we accommodate the range of individuals that must  
324 overcome barriers? A mature female on her way to spawn is full of eggs. Are her swimming  
325 abilities reduced? How can fish passage infrastructures accommodate her?

326

#### 327 *2.4 Ignoring small-scale barriers*

328 The impacts of large dams have been well documented and have often been the primary focus  
329 of fish passage research. However, in most river basins, small-scale structures such as weirs  
330 and culverts frequently make up the vast majority of obstructions (Gibson, Haedrich, &  
331 Wernerheim, 2011). Small structures, with fall heights as little as 50 mm, can be a complete  
332 barrier for some fish species (Baker, 2003), particularly the small-bodied species  
333 characteristic of many Southern Hemisphere fish communities (Link & Habit, 2015). Despite  
334 their widespread distribution, these smaller barriers continue to receive relatively little  
335 attention, as individually they are often deemed to have small effects (Branco et al., 2017).  
336 However, there is increasing evidence of their impacts on fish movements (Lucas, Bubb,  
337 Jang, Ha, & Masters, 2009; Branco et al., 2017), and it has been suggested that the  
338 cumulative effects of multiple barriers can be at least as severe as large dams (Cooke et al.,  
339 2005).

340 Fish passage through culverts has received some attention, again focussed almost  
341 exclusively on salmonids. Early work investigated the hydraulic effects of culvert baffling  
342 (Rajaratnam, Katapodis, & Lodewyk, 1988; Ead, Rajaratnam, & Katapodis, 2002), and more  
343 recent studies have included observations of fish behaviour during culvert passage (Goerig,  
344 Bergeron, & Castro-Santos, 2017). However, there is a need to develop solutions appropriate  
345 to the target species. For example, David, Tonkin, Taipeti, & Hokianga (2014) investigated a  
346 novel approach for facilitating upstream passage of small-bodied fish through culverts using  
347 mussel spat ropes as a baffling media, showing that culvert passage success could be

348 significantly improved. We suggest that increased focus on fish passage at small-scale  
349 structures has the potential for rapid and cost-effective biodiversity gains. For example, there  
350 are several studies from Australia and New Zealand describing positive outcomes for non-  
351 salmonid fish species richness and abundance resulting from retrofitting fish passage  
352 solutions to culverts (David & Hamer, 2012; Franklin & Bartels, 2012; Amtstaetter,  
353 O'Connor, Borg, Stuart, & Moloney, 2017). Erkinaro, Erkinaro, & Niemelä (2017) also  
354 demonstrated increases in the distribution of juvenile Atlantic salmon following the  
355 restoration of impassable road culverts in Finland. However, these approaches remain  
356 embedded in the philosophy of trying to engineer a fix to be applied to a structure rather than  
357 taking a more holistic approach to fish passage management.

358 We suggest that, more importantly, small-scale barriers also offer the best opportunity  
359 for overcoming the bias towards engineered fish passage fixes. Many small-scale structures  
360 are now redundant, no longer serving their original purpose, but are seen as valuable parts of  
361 cultural heritage. There are obvious opportunities for removal here yet fish passage  
362 frequently takes a back seat to cultural interests. Very often, the basis of local arguments that  
363 can be observed or noticed in some way (*e.g.* the sound of a waterfall, a bridge over a dam, or  
364 a reservoir) win over the problems that cannot be seen by the naked eye (*i.e.* the fish). But  
365 what benefits are conferred from enjoying the sound of a waterfall? Should these arguments  
366 take precedence over the protection of freshwater biodiversity? The sad reality is that in the  
367 case of small barriers, these arguments will often hold. Removal of such barriers is often  
368 achievable and cost-effective, and should be a priority for achieving rapid, sustained recovery  
369 of freshwater communities (though we acknowledge that dams can sometimes serve as a  
370 barrier to the spread of non-native species; Gangloff, 2013). Removal also has the advantage  
371 of restoring physical habitat and ecosystem processes (Birnie-Gauvin, Aarestrup et al., 2017;



372 Birnie-Gauvin, Tummers, Lucas, & Aarestrup, 2017; Timm, Higgins, Stanovick, Kolka, &  
373 Eggert, 2017).

374 Under circumstances where removal is not an option, it is also feasible and practicable  
375 to rethink design approaches to better accommodate the unhindered movement of organisms  
376 and maintain ecosystem processes. A good example has been the adoption of the stream  
377 simulation approach to culvert design (Forest Service Stream-Simulation Working Group,  
378 2008). The stream simulation approach adopts a more holistic method with the objective of  
379 maintaining continuity of physical habitat and ecosystem processes between the upstream and  
380 downstream reaches. As such, the conditions inside the culvert replicate adjacent stream  
381 reaches and represent no greater impediment to the movement of organisms than progress  
382 through the normal stream environment. Studies of culverts built using this approach indicate  
383 that not only do they provide effective fish passage, but they are also more effective at  
384 maintaining sediment transport (Timm et al., 2017), and are more resilient to large flood  
385 events than traditional hydraulic culvert designs (Gillespie et al., 2014; Barnard, Yokers,  
386 Nagygyor, & Quinn, 2015). It has also been shown that the relatively modest increases in  
387 initial investment to implement stream simulation designs can yield substantial societal and  
388 economic benefits in the long term (Gillespie et al., 2014).

389

### 390 *2.5 More than just safe passage: Critical habitat availability and distribution*

391 Barriers have received so much attention largely because they hinder the movements of fish  
392 by reducing connectivity (Wheeler, Angermeier, & Rosenberger, 2005), and also because  
393 they alter hydrological and thermal processes (Bergkamp, McCartney, Dugan, McNeely, &  
394 Acreman, 2000). However, the modification and loss of aquatic habitats caused by the  
395 presence of barriers is an impact that is often neglected (Franklin & Hodges, 2015; Birnie-  
396 Gauvin, Aarestrup et al., 2017). Whilst the knowledge that habitat alterations are in fact

397 induced by barriers is common, addressing the implications of losing ecologically-relevant  
398 habitat is rare. Because dams are most often established in river reaches with high-gradient,  
399 there can be a disproportionate loss of rheophilic (i.e., fast-flowing and highly-oxygenated  
400 water) habitat. These areas are essential for rheophilic fish species such as salmonids and eels  
401 that depend on these ‘critical habitats’ to complete their life-cycles. Consequently, even if  
402 those species can overcome a barrier, population viability is still compromised due to the loss  
403 of adequate habitat (Birnie-Gauvin, Aarestrup et al., 2017). Tide gates also have a significant  
404 impact on physical habitats, reducing hydrological exchange and interrupting natural salinity  
405 gradients, in addition to blocking fish movements (Boys, Kroon, Glasby, & Wilkinson, 2012;  
406 Franklin and Hodges, 2015). Fish survival is also severely reduced due to habitat  
407 modifications. Large predatory species, such as the pike (*Esox lucius*), can thrive in  
408 impoundments, with younger fish as a source of food (Jepsen, Aarestrup, Økland, &  
409 Rasmussen, 1998). Habitat loss should, therefore, be addressed through hydrological and  
410 morphological mitigation, either before or simultaneously (at the very least) with the issue of  
411 fish passage (Birnie-Gauvin, Aarestrup et al., 2017).

412         The complexity of the fish passage problem in Neotropical South America, Southeast  
413 Asia and Africa, reflecting the diversity of native species assemblages and the wide range of  
414 fish life-histories there, has highlighted the need to consider the distribution of critical  
415 habitats on either side of a barrier (Pompeu et al., 2012). This broader approach was  
416 necessary because fishways were found to be failing as a conservation tool; high percentages  
417 of fish approaching the fishway were passing only to be ‘trapped’ without access to critical  
418 habitats upstream due to reservoirs or the presence of other barriers without fishways  
419 (Pelicice & Agostinho, 2008; Pelicice et al., 2015). In Brazil, therefore, far from protecting  
420 fish populations, policies that require the provision of fish passage at dams have in some  
421 cases been the main threat to their viability (Pelicice et al., 2017).

422

423 *2.6 Lack of post-implementation monitoring: how well does it work?*

424 In many cases, monitoring the effectiveness of fishways is not implemented or is not a  
425 licencing requirement. In other words, asking how well it works is not part of fulfilling  
426 requirements, and thus post-implementation monitoring remains unaccomplished. This is a  
427 major reason for the unsustainable policies prevailing in Brazil, as introduced in the previous  
428 example (Pelicice et al., 2017), and likely many other parts of the world. Part of the answer to  
429 this paradox relates to the deterministic tradition of engineering, as we have previously  
430 discussed. If the effectiveness of fishways is pre-determined, monitoring and adaptive  
431 management is optional. There is rarely a statutory obligation to prove that the fishway is  
432 really achieving its overall goal of sustaining viable fish populations, although it may be  
433 achieving other goals, such as those associated with corporate social responsibility. However,  
434 what difference does it make to have measures in place for fish passage if you do not know  
435 the answer to how many individuals get through and whether that is sufficient to sustain fish  
436 communities?

437       Herein lies a critical challenge for both fish passage scientists and practitioners; how  
438 do we define objectives for fishways (or more broadly for maintaining connectivity) that are  
439 ecologically meaningful, but are also practical (i.e. specific and measurable)? The lack of  
440 post-implementation monitoring is a lost opportunity. Understanding how existing mitigation  
441 efforts work and do not work may offer significant learnings that will help improve future  
442 rehabilitation efforts (Birnie-Gauvin, Tummers et al., 2017). However, to achieve this there is  
443 a need to provide guidance on what to monitor and how, and this is reliant on having clearly  
444 defined objectives. Definitions such as 'effective' or 'free' fish passage can be ambiguous,  
445 open to interpretation and/or unachievable. The term 'free', for example, is frequently used to  
446 describe fish passage targets, but this is highly unlikely to be measurable given the general

447 lack of knowledge on how many fish attempted to pass versus how many fish actually passed  
448 a structure. Furthermore, the term “free” would require that fish are not delayed, which is  
449 seldom the case. Delay may in fact have carryover effects that may lead to future adverse  
450 consequences (McCormick, Lerner, Monette, Nieves-Puigdoller, Kelly, & Björnsson, 2009).  
451 So can fish passage ever be free? Yes, if the barrier is removed, but no if a fishway is present.

452         Perhaps the correct scientific question to ask is thus “How many individuals who  
453 attempt to pass actually pass?” Along similar lines, the appropriate management question to  
454 ask may be “How many individuals need to get through to meet ecological objectives and  
455 ensure population viability?” Despite their necessity in the context of fish passage, these  
456 questions are almost never inquired, let alone answered. Instead there is almost invariably a  
457 focus on the movement of individual fish in the immediate vicinity of the structure to be  
458 passed. This focus is made possible through the use of biotelemetry, which has emerged as  
459 the ‘gold standard’ in fish passage research (Bunt et al., 2012; Silva et al., 2018). Use of these  
460 techniques have undoubtedly resulted in significant advances in fish passage science by  
461 improving understanding of behavioural and motivational aspects of fish movements  
462 (Aarestrup, Lucas, & Hansen, 2003). However, while ongoing miniaturisation of the tags  
463 used in biotelemetry studies has broadened the size range of fish to which this technology can  
464 been applied (e.g. Baker, Reeve, Baars, Jellyman, & Franklin, 2017), small-bodied fish and  
465 fish that migrate during early life stages (larval and juvenile) remain outside the reach of  
466 these technologies. Consequently, if biotelemetry methods continue to be upheld as the  
467 standard by which fish passage success is to be measured there is a risk of yet again  
468 perpetuating the focus on larger fish species at the expense of considering all parts of the fish  
469 community and all life stages.

470

### 471 **3. Discussion**

472 Awareness of the impacts of instream infrastructure on fish movements, and hence fish  
473 populations, has increased considerably over the last couple of decades. Despite this, the  
474 reductionist, salmonid-centric, impair-then-repair approach to infrastructure design largely  
475 continues to prevail, and continues to be biased towards upstream movement. We suggest  
476 that this stems from the roots of fish passage research emerging from attempts to  
477 retrospectively engineer fishways as fixes for moving individual iconic species upstream at  
478 existing infrastructure to mitigate for an emerging problem. While we acknowledge the  
479 significant progress that has been made in restoring fish passage following this approach,  
480 including the benefits of studying salmonids in this context, the effectiveness of many of  
481 these structures remains too small to be ecologically meaningful. For example, several recent  
482 meta-analyses have attempted to evaluate the effectiveness and performance of fishways  
483 (Roscoe & Hinch, 2010; Bunt et al., 2012; Noonan et al., 2012). The most consistent  
484 messages that emerge from these reviews are the overwhelming dominance of studies  
485 focusing on anadromous salmonids, and the high variability (ranging from near 0 to near  
486 100%) in fishway performance. As focus has increasingly turned to non-salmonid fishes and  
487 catering for multi-species assemblages in fishways, evidence of failures in the current fish  
488 passage paradigm continues to mount. Largely precipitated by the direct transfer of findings  
489 from the Northern Hemisphere to diverse geographical and ecological contexts, repeated  
490 failures and the emergence of unintended consequences has undermined confidence and the  
491 willingness of practitioners to invest in implementing fish passage solutions (Harris,  
492 Kingsford, Peirson, & Baumgartner, 2016).

493         While potentially disheartening, we believe that this reflects a failure in the discipline  
494 to adequately recognise and move beyond inherent biases in methods and ways of thinking,  
495 rather than a flaw in the concept of fish passage itself. We are encouraged by recent  
496 contributions to the fish passage debate, particularly emerging from the Southern Hemisphere

497 and the tropics, which challenge some of these biases. Pompeu et al. (2012), for example,  
498 propose that fishway efficiency should be assessed based on the capability of the structure to  
499 maintain viable fish populations, rather than a simple metric of the proportion of fish that  
500 ascend a structure. Traditional passage efficiency metrics may have been suitable for species  
501 similar to salmonids that exhibit relatively synchronous, seasonal and highly directed  
502 movements between clearly separated critical habitats (Kemp, 2016), but transferring these  
503 metrics to species and populations with more diverse life-histories and behaviours may not be  
504 the most appropriate measure of fish passage success. Impoundments upstream of dams can  
505 act as ecological traps (Pelicice & Agostinho, 2008; Pelicice et al., 2015) preventing  
506 downstream movement of eggs and larvae necessary to complete fish life cycles. Providing  
507 effective upstream passage for adults past dams, therefore, acts as a population sink with  
508 negative consequences for the long-term sustainability of fish populations (Pelicice &  
509 Agostinho, 2008). Likewise, in New Zealand, juvenile eels (*Anguilla dieffenbachii* and *A.*  
510 *australis*) are regularly transferred upstream of hydropower dams to seed upstream  
511 populations, but in most cases there is no, or only very limited, facility for subsequent  
512 downstream passage of migrant adults through the dams (Jellyman, 2007). Thus, while they  
513 do support fisheries, the long-term value to biodiversity conservation may be questionable.

514 Harris et al. (2016), in a review of barrier mitigation efforts in Australia, also  
515 highlight the challenges of catering for a mixture of life-history strategies across freshwater  
516 fish communities. They propose that there is a need for river basin-scale management  
517 strategies that integrate fishway construction, where appropriate, with other approaches such  
518 as barrier removal, improved barrier management, environmental flow provision and strategic  
519 prioritisation of mitigation efforts. Furthermore, they also support the idea of broader  
520 definitions of fishway success and the need for performance to be assessed against  
521 predetermined, comprehensive biological criteria including considerations for cumulative

522 effects of multiple barriers. The concept of river basin-scale decision making is also  
523 emphasised by Winemiller et al. (2016), who suggest we should strive for more integrated  
524 and strategic planning of dams that also takes in to account the cumulative effects of multiple  
525 structures on hydrology, sediment dynamics, ecosystem productivity, fisheries and  
526 biodiversity.

527         We echo these calls for the need to take a step back and consider strategies for  
528 managing connectivity at a broader scale, rather than thinking about fish passage on a site-by-  
529 site basis in isolation from the wider catchment context, as is commonly done today. Crucial  
530 to progressing the fish passage debate is also the need to move beyond the idea that fishways  
531 provide a universal solution to mitigating the impacts of instream structures on aquatic  
532 communities (Brown et al., 2013; Kemp, 2016). While we do not disagree with the view of  
533 Williams, Armstrong, Katapodis, Larinier, & Travade (2012) that with sufficient investment  
534 in ecohydraulic research effective fishways can be engineered, this belief is still predicated on  
535 the anthropocentric impair-then-repair approach, and the assumption that providing fish  
536 passage at instream infrastructure is inherently good. Additionally, as Kemp (2016) rightly  
537 identifies, in many cases and for the majority of species, knowledge is currently far short of  
538 being able to develop such technical solutions (*e.g.* Wilkes et al., 2018), and that sufficient  
539 funding and many years of research will be required to fill those knowledge gaps. In the  
540 meantime, we propose some recommendations to address the biases currently limiting fish  
541 passage in Table 2. We emphasise in the first instance the need to avoid creating new  
542 barriers. New structures should be planned in a catchment or regional context and, where  
543 deemed necessary from a socioeconomic perspective, be built in a manner that avoids or  
544 minimises impacts on fish movements. We recognise that remediation of existing structures  
545 can be more challenging due to existing site constraints and legacies, but we highlight the

546 need for removal to become the go-to option and for a more holistic approach to finding  
547 solutions where removal is not practicable.

548

#### 549 **4. Conclusion**

550 In river ecosystems, fragmentation is a key driver of the Anthropocene biodiversity crisis  
551 (Meybeck, 2003), raising alarm bells in the midst of a global boom in dam building (Zarfl et  
552 al., 2015). Paradoxically, because biodiversity and ecosystem function are inextricably  
553 linked, river basin development aimed at supporting food, energy and water security may  
554 actually be having the opposite effect. The uncritical application of fishway technology has  
555 traditionally been the measure of choice to mitigate connectivity losses, but it is increasingly  
556 seen as a technology in decline. As is typically the case when a solution is not working, the  
557 reasons why lie in its historical development. Early fishways were conceived in response to  
558 the collapse of salmonid stocks due to a proliferation of migration barriers in Northern  
559 Europe. The migratory characteristics of salmonid species meant that application of  
560 traditional, deterministic engineering approaches came to dominate, specifically focusing on  
561 upstream migration. With the realisation that connectivity is important for taxa other than  
562 salmonids, and the sharp increase in dam building outside of the temperate Northern  
563 Hemisphere, came the erroneous assumption that salmonid-type fishways would work  
564 everywhere for all species. Evidence to the contrary is now overwhelming but, as is usual  
565 with a paradigm shift, the response lags behind. However, the debate is rapidly intensifying,  
566 supported by the emergence of revised thinking, particularly from outside of the temperate  
567 Northern Hemisphere, and by increasingly interdisciplinary training of practitioners. We have  
568 attempted to contribute to this debate in the hope that continued discourse will lead to better  
569 conservation of fish biodiversity in the near future. We have highlighted examples that we



570 believe represent progress and proposed guiding principles for helping to advance the fish  
571 passage discipline. However, if we fail to address these issues, we will never reverse the loss.

572

### 573 **Acknowledgements**

574 This contribution was funded by the European Union AMBER project (Adaptive  
575 Management of Barriers in European Rivers, #689682), the Danish Fishing License Funds  
576 and the New Zealand Ministry for Business, Innovation and Employment contract  
577 C01X1615. It was further supported by the European Commission through the Marie  
578 Sklodowska-Curie action, 'Knowledge Exchange for Efficient Passage of Fish in the  
579 Southern Hemisphere' (RISE-2015-690857-KEEPFISH).

### 580 **References**

- 581 Aarestrup, K., Lucas, M. C., & Hansen, J. A. (2003). Efficiency of a nature-like bypass  
582 channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT  
583 telemetry. *Ecology of Freshwater Fish*, 12, 160-168.
- 584 Aarestrup, K., Birnie-Gauvin, K., & Larsen, M.H. (2018) Another paradigm lost? Autumn  
585 downstream migration of juvenile brown trout: Evidence for a presmolt migration.  
586 *Ecology of Freshwater Fish*, 27, 513-516.
- 587 Agostinho, C.S., Pereira, C.R., Oliveira, R.J.D., Freitas, I.S., & Marques, E.E. (2007)  
588 Movements through a fish ladder: temporal patterns and motivations to move upstream.  
589 *Neotropical Ichthyology*, 5, 161-167.
- 590 Amtstaetter, F., O'Connor, J., Borg, D., Stuart, I., & Moloney, P. (2017) Remediation of  
591 upstream passage for migrating *Galaxias* (Family: Galaxiidae) through a pipe culvert.  
592 *Fisheries Management and Ecology*, 24, 186-192.
- 593 Arnekleiv, J.V., Kraabøl, M., & Museth, J. (2007). Efforts to aid downstream migration  
594 brown trout (*Salmo trutta* L.) kelts and smolts passing a hydroelectric dam and a  
595 spillway. *Hydrobiologia*, 582, 5-15.
- 596 Baird, I.G., (2006) *Probarbus jullieni* and *Probarbus labeamajor*: the management and  
597 conservation of two of the largest fish species in the Mekong River in southern Laos.  
598 *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16, 517-532.
- 599 Baker, C.F. (2003) Effect of fall height and notch shape on the passage of inanga (*Galaxias*  
600 *maculatus*) and common bullies (*Gobiomorphus cotidianus*) over an experimental weir.  
601 *New Zealand Journal of Marine and Freshwater Research*, 37, 283-290.
- 602 Baker, C.F., Reeve, K., Baars, D., Jellyman, D., & Franklin, P. (2017) Efficacy of 12-mm  
603 half-duplex passive integrated transponder tags in monitoring fish movements through  
604 stationary antenna systems. *North American Journal of Fisheries Management*, 37,  
605 1289-1298.
- 606 Bannon, H.J., & Ling, N. (2003) Running the unseen, lowland gauntlet: Compounding effects  
607 of temperature, hypoxia and exercise for diadromous fishes. In Rupp, G., & White, M.D.  
608 (Eds.), *Seventh International Symposium on Fish Physiology, Toxicology and Water*  
609 *Quality* (pp. 207-218), Tallinn, Estonia: USEPA.

610 Barnard, R.J., Yokers, S., Nagygyor, A., & Quinn, T. (2015). An evaluation of the stream  
611 simulation culvert design method in Washington State. *River Research and*  
612 *Applications*, 31, 1376–1387.

613 Beamish, F.W.H. (1978) Swimming capacity. In Hoar, W.S., & Randall, D.J. (Eds), *Fish*  
614 *physiology VII* (pp. 101-187), New York, USA: Academic Press.

615 Bergkamp, G., McCartney, M., Dugan, P., McNeely, J., & Acreman, M.C. (2000). *Dams,*  
616 *ecosystem functions and environmental restoration*. Cape Town, World Commission on  
617 Dams.

618 Birnie-Gauvin, K., Aarestrup, K., Riis, T.M.O., Jepsen, N., & Koed, A. (2017). Shining a  
619 light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence  
620 of barriers, and its implications for management. *Aquatic Conservation: Marine and*  
621 *Freshwater Ecosystems*. DOI: 10.1002/aqc.2795.

622 Birnie-Gauvin, K., Tummers, J.S., Lucas, M.C., & Aarestrup, K. (2017) Adaptive  
623 management in the context of barriers in European freshwater ecosystems. *Journal of*  
624 *Environmental Management*, 204, 436-431.

625 Birnie-Gauvin, K., Larsen, M.H., Nielsen, J., & Aarestrup, K. (2017) 30 years of data reveal  
626 a dramatic increase in abundance of brown trout following the removal of a small  
627 hydrodam. *Journal of Environmental Management*, 204, 467-471.

628 Birnie-Gauvin, K., Candee, M.M., Baktoft, H., Larsen, M.H., Koed, A., & Aarestrup, K. (in  
629 press). River connectivity reestablished: effects and implications of six weir removals on  
630 brown trout smolt migration. *River Research and Applications*.

631 Birnie-Gauvin, K., Larsen, M.H., Thomassen, S.T., & Aarestrup, K. (2018) Testing three  
632 common stocking methods: differences in smolt size, migration rate and timing of two  
633 strains of stocked Atlantic salmon (*Salmo salar*). *Aquaculture*, 483, 163-168.

634 Boys, C.A., Kroon, F.J., Glasby, T.M., & Wilkinson, K. (2012) Improved fish and crustacean  
635 passage in tidal creeks following floodgate remediation. *Journal of Applied Ecology*, 49,  
636 223–233.

637 Branco, P., Amaral, S.D., Ferreira, M.T., & Santos, J.M. (2017) Do small barriers affect the  
638 movement of freshwater fish by increasing residency? *Science of The Total*  
639 *Environment*, 581, 486–494.

640 Brauer, C.J., Hammer, M.P. & Beheregaray, L.B. (2016) Riverscape genomics of a  
641 threatened fish across a hydroclimatically heterogeneous river basin. *Molecular*  
642 *Ecology*, 25, 5093-5113.

643 Brown, J.J., Limburg, K.E., Waldman, J.R., Stephenson, K., Glenn, E.P., Juanes, F., &  
644 Jordaan, A. (2013) Fish and hydropower on the U.S. Atlantic coast: failed fisheries  
645 policies from half-way technologies. *Conservation Letters*, 6, 280–286.

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

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

650 Bunt, C.M., Castro-Santos, T., & Haro, A. (2016) Reinforcement and validation of the  
651 analyses and conclusions related to fishway evaluation data from *Bunt et al.*:  
652 ‘Performance of fish passage structures at upstream barriers to migration’. *River*  
653 *Research and Applications*, 32, 2125–2137.

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

658 Colavecchia, M., Katopodis, C., Goosney, R., Scruton, D.A., & McKinley, R.S. (1998).  
659 Measurement of burst swimming performance in wild Atlantic salmon (*Salmo salar* L.)

660 using digital telemetry. *Regulated Rivers: Research & Management*, 14, 41-51.

661 David, B.O., & Hamer, M.P. (2012). Remediation of a perched stream culvert with ropes  
662 improves fish passage. *Marine and Freshwater Research*, 63, 440–449.

663 David, B.O., Tonkin, J.D., Taipeti, K.W.T., & Hokianga, H.T. (2014) Learning the ropes:  
664 Mussel spat ropes improve fish and shrimp passage through culverts. *Journal of Applied  
665 Ecology*, 51, 214–223.

666 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C.,  
667 ... Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and  
668 conservation challenges. *Biological Reviews*, 81, 163-182.

669 Ead, S.A., Rajaratnam, N., & Katopodis, C. (2002). Generalized Study of Hydraulics of  
670 Culvert Fishways. *Journal of Hydraulic Engineering*, 128, 1018–1022.

671 Erkinaro, J., Erkinaro, H., & Niemelä, E. (2017) Road culvert restoration expands the habitat  
672 connectivity and production area of juvenile Atlantic salmon in a large subarctic river  
673 system. *Fisheries Management and Ecology*, 24, 73–81.

674 Falke, J.A., Fausch, K.D., Bestgen, K.R., & Bailey, L.L. (2010). Spawning phenology and  
675 habitat use in a Great Plains, USA, stream fish assemblage: an occupancy estimation  
676 approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1942-1956.

677 Forest Service Stream-Simulation Working Group. (2008) Stream simulation: An ecological  
678 approach to providing passage for aquatic organisms at road-stream crossings. San  
679 Dimas, CA: U.S. Department of Agriculture.

680 Francis, F. (1870) *Reports on salmon ladders: with original drawings, plans and sections*.  
681 Horace Cox, London.

682 Franklin, P.A., & Bartels, B. (2012) Restoring connectivity for migratory native fish in a New  
683 Zealand stream: Effectiveness of retrofitting a pipe culvert. *Aquatic Conservation:  
684 Marine and Freshwater Ecosystems*, 22, 489–497.

685 Franklin, P.A., & Hodges, M. (2015) Modified tide gate management for enhancing instream  
686 habitat for native fish upstream of the saline limit. *Ecological Engineering*, 81, 233–242.

687 Froese, R., & Pauly, D. (Eds.) (2016) FishBase. [www.fishbase.org](http://www.fishbase.org)

688 Gangloff, M. M. (2013). Taxonomic and ecological tradeoffs associated with small dam  
689 removals. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 475-480.

690 Garcia-Moreno, J., Harrison, I.J., Dudgeon, D., Clausnitzer, V., Darwall, W., Farrell, T., ...  
691 Tubbs, N. (2014) Sustaining freshwater biodiversity in the Anthropocene. In Bhaduri,  
692 A., Bogardi, J., Leentvaar, J., & Marx, S. (Eds.), *The Global Water System in the  
693 Anthropocene* (pp. 247-270). Springer, Cham: Springer International Publishing.

694 Gibson, R.J., Haedrich, R.L., & Wernerheim, C.M. (2011) Loss of Fish Habitat as a  
695 Consequence of Inappropriately Constructed Stream Crossings. *Fisheries*, 30, 10-17.

696 Gillespie, N., Unthank, A., Campbell, L., Anderson, P., Gubernick, R., Weinhold, M., ...  
697 Kim, R. (2014) Flood effects on road–stream crossing infrastructure: economic and  
698 ecological benefits of stream simulation designs. *Fisheries*, 39, 62–76.

699 Goerig, E., Bergeron, N.E., & Castro-Santos, T. (2017) Swimming behaviour and ascent  
700 paths of brook trout in a corrugated culvert. *River Research and Applications*, 33, 1463-  
701 1471.

702 Hari, R.E., Livingstone, D.M., Siber, R., Burkhardt-Holm, P., & Guttinger, H. (2006)  
703 Consequences of climatic change for water temperature and brown trout populations in  
704 Alpine rivers and streams. *Global Change Biology*, 12, 10–26.

705 Haro, A., Castro-Santos, T., Noreika, J., & Odeh, M. (2004) Swimming performance of  
706 upstream migrant fishes in open-channel flow: a new approach to predicting passage  
707 through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences*, 61,  
708 1590–1601.

709 Harris, J.H., Kingsford, R.T., Peirson, W., & Baumgartner, L.J. (2016) Mitigating the effects

710 of barriers to freshwater fish migrations: the Australian experience. *Marine and*  
711 *Freshwater Research*, 10, 687–696.

712 Hitt, N.P., Eyster, S., & Wofford, J.E.B. (2012) Dam removal increases American eel  
713 abundance in distant headwater streams. *Transactions of the American Fisheries Society*,  
714 141, 1171–1179.

715 Hogg, R., Coghlan, S.M., & Zydlewski, J. (2013) Anadromous sea lampreys recolonize a  
716 Maine coastal river tributary after dam removal. *Transactions of the American Fisheries*  
717 *Society*, 142, 1381–1394.

718 Jellyman, D.J. (2007) Status of New Zealand fresh-water eel stocks and management  
719 initiatives. *ICES Journal of Marine Science*, 64, 1379–1386.

720 Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998) Survival of radiotagged  
721 Atlantic salmon (*Salmo salar* L.)–and trout (*Salmo trutta* L.) smolts passing a reservoir  
722 during seaward migration. *Hydrobiologia*, 371, 347–353.

723 Jepsen, N., & Berg, S. (2002) The use of winter refuges by roach tagged with miniature radio  
724 transmitters. In Thorstad, E.B., Fleming, I.A., & Næsje, T.F. (Eds.), *Aquatic Telemetry*  
725 (pp. 167–173). Springer: Netherlands.

726 Katopodis, C., & Williams, J.G. (2012) The development of fish passage research in a  
727 historical context. *Ecological Engineering*, 48, 8–18.

728 Kemp, P.S. (2016) Meta-analyses, metrics and motivation: mixed messages in the fish  
729 passage debate. *River Research and Applications*, 32, 2116–2124.

730 Link, O., & Habit, E. (2015) Requirements and boundary conditions for fish passes of non-  
731 sport fish species based on Chilean experiences. *Reviews in Environmental Science and*  
732 *Bio/Technology*, 14, 9–21.

733 Link, O., Sanhueza, C., Arriagada, P., Brevis, W., Laborde, A., González, A., ... Habit, E.  
734 (2017) The fish Strouhal number as a criterion for hydraulic fishway design. *Ecological*  
735 *Engineering*, 103, 118–126.

736 Lira, N.A., Pompeu, P.S., Agostinho, C.S., Agostinho, A.A., Arcifa, M.S., & Pelicice, F.M.  
737 (2017) Fish passages in South America: an overview of studied facilities and research  
738 effort. *Neotropical Ichthyology*, 15, e160139.

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

742 Mallen-Cooper, M., & Brand, D.A. (2007) Non-salmonids in a salmonid fishway: what do 50  
743 years of data tell us about past and future fish passage? *Fisheries Management and*  
744 *Ecology*, 14, 319–332.

745 McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdoller, K., Kelly, J.T., &  
746 Björnsson, B.T. (2009) Taking it with you when you go: How perturbations to the  
747 freshwater environment, including temperature, dams, and contaminants, affect marine  
748 survival of salmon. *American Fisheries Society Symposium*, 69, 195–214.

749 McLaughlin, R.L., Smyth, E.R.B., Castro-Santos, T., Jones, M.L., Koops, M.A., Pratt, T.C.,  
750 & Vélez-Espino, L.-A. (2013) Unintended consequences and trade-offs of fish passage.  
751 *Fish and Fisheries*, 14, 580–604.

752 Meybeck, M. (2003) Global analysis of river systems: from Earth system controls to  
753 Anthropocene syndromes. *Philosophical transactions of the Royal Society of London.*  
754 *Series B, Biological Sciences*, 358, 1935–1955.

755 Morita, K., & Yamamoto, S. (2002). Effects of habitat fragmentation by damming on the  
756 persistence of stream-dwelling charr populations. *Conservation Biology*, 16, 1318–1323.

757 Nehlsen, W., Williams, J.E., & Lichatowich, J.A. (1991) Pacific salmon at the crossroads:  
758 stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, 16, 4–21.

759 Nieminen, E., Hyttiäinen, K., & Lindroos, M. (2017) Economic and policy considerations

760 regarding hydropower and migratory fish. *Fish and Fisheries*, 18, 54–78.

761 Nikora, V.I., Aberle, J., Biggs, B.J.F., Jowett, I.G., & Sykes, J.R.E. (2003). Effects of fish  
762 size, time-to-fatigue and turbulence on swimming performance: a case study of *Galaxias*  
763 *maculatus*. *Journal of Fish Biology*, 63, 1365-1382.

764 Noonan, M.J., Grant, J.W.A., & Jackson, C.D. (2012) A quantitative assessment of fish  
765 passage efficiency. *Fish and Fisheries*, 13, 450–464.

766 O'Connor, J.E., Duda, J.J., & Grant, G.E. (2015) Ecology. 1000 dams down and counting.  
767 *Science*, 348, 496–497.

768 Peake, S. (2004) An evaluation of the use of critical swimming speed for determination of  
769 culvert water velocity criteria for smallmouth bass. *Transactions of the American*  
770 *Fisheries Society*, 133, 1472–1479.

771 Pelicice, F.M., & Agostinho, A.A. (2008) Fish-passage facilities as ecological traps in large  
772 Neotropical rivers. *Conservation Biology*, 22, 180–188.

773 Pelicice, F.M., Pompeu, P.S., & Agostinho, A.A. (2015) Large reservoirs as ecological  
774 barriers to downstream movements of Neotropical migratory fish. *Fish and Fisheries*,  
775 16, 697–715.

776 Pelicice, F.M., Azevedo-Santos, V.M., Vitule, J.R., Orsi, M.L., Lima Junior, D.P.,  
777 Magalhães, A.L., ... Agostinho, A.A. (2017). Neotropical freshwater fishes imperilled  
778 by unsustainable policies. *Fish and Fisheries*, 18, 1119-1133.

779 Perkin, J.S., Gido, K.B., Cooper, A.R., Turner, T.F., Osborne, M.J., Johnson, E.R. & Mayes,  
780 K.B. (2015) Fragmentation and dewatering transform Great Plains stream fish  
781 communities. *Ecological Monographs*, 85, 73-92.

782 Plew, D.R., Nikora, V.I., Larned, S.T., Sykes, J.R. & Cooper, G.G. (2007). Fish swimming  
783 speed variability at constant flow: *Galaxias maculatus*. *New Zealand Journal of Marine*  
784 *and Freshwater Research*, 41, 185-195.

785 Poff, N.L. (2014) Rivers of the anthropocene? *Frontiers in Ecology and the Environment*, 12,  
786 427.

787 Pompeu, P.S., Agostinho, A.A., & Pelicice, F.M. (2012) Existing and future challenges: the  
788 concept of successful fish passage in South America. *River Research and Applications*,  
789 28, 504–512.

790 Porcher, J.P., & Travade, F. (1992) Les dispositifs de franchissement : bases biologiques,  
791 limites et rappels réglementaires. *Bulletin Français de la Pêche et de la Pisciculture*,  
792 326-327, 5–14.

793 Radinger, J., & Wolter, C. (2014) Patterns and predictors of fish dispersal in rivers. *Fish and*  
794 *Fisheries*, 15, 456-473.

795 Rajaratnam, N., Katopodis, C., & Lodewyk, S. (1988) Hydraulics of offset baffle culvert  
796 fishways. *Canadian Journal of Civil Engineering*, 15, 1043–1051.

797 Raeymaekers, J.A., Maes, G.E., Geldof, S., Hontis, I., Nackaerts, K. & Volckaert, F.A.  
798 (2008) Modeling genetic connectivity in sticklebacks as a guideline for river restoration.  
799 *Evolutionary Applications*, 1, 475-488.

800 Rodgers, E.M., Cramp, R.L., Gordos, M., Weier, A., Fairfall, S., Riches, M., & Franklin,  
801 C.E. (2014). Facilitating upstream passage of small-bodied fishes: linking the thermal  
802 dependence of swimming ability to culvert design. *Marine and Freshwater Research*,  
803 65, 710-719.

804 Roscoe, D.W., & Hinch, S.G. (2010) Effectiveness monitoring of fish passage facilities:  
805 historical trends, geographic patterns and future directions. *Fish and Fisheries*, 11, 12–  
806 33.

807 Santos, H., Pompeu, P.S., & Martinez, C.B. (2007). Swimming performance of the migratory  
808 Neotropical fish *Leporinus reinhardti* (Characiformes: Anostomidae). *Neotropical*  
809 *Ichthyology*, 5, 139-146.

- 810 Schlosser, I.J., & Angermeier, P.L. (1995) Spatial variation in demographic processes in lotic  
811 fishes: Conceptual models, empirical evidence, and implications for conservation.  
812 *American Fisheries Society Symposium*, 17 360–370.
- 813 Silva, A.T., Lucas, M.C., Castro-Santos, T., Katapodis, C., Baumgartner, L.J., Thiem, J.D.,  
814 ... Cooke, S.J. (2018) The future of fish passage science, engineering, and practice. *Fish*  
815 *and Fisheries*. 19, 340-362.
- 816 Starrs, D., Ebner, B.C., Lintermans, M., & Fulton, C.J. (2011). Using sprint swimming  
817 performance to predict upstream passage of the endangered Macquarie perch in a highly  
818 regulated river. *Fisheries Management and Ecology*, 18, 360-374.
- 819 Svendsen, J. C., Eskesen, A. O., Aarestrup, K., Koed, A., & Jordan, A. D. (2007) Evidence  
820 for non-random spatial positioning of migrating smolts (Salmonidae) in a small lowland  
821 stream. *Freshwater Biology*, 52, 1147-1158.
- 822 Timm, A., Higgins, D., Stanovick, J., Kolka, R., & Eggert, S. (2017). Quantifying fish habitat  
823 associated with stream simulation design culverts in Northern Wisconsin. *River*  
824 *Research and Applications*, 33, 567-577.
- 825 Tockner, K., Schiemer, F., & Ward, J.V. (1998) Conservation by restoration: the  
826 management concept for a river-floodplain system on the Danube River in Austria.  
827 *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 71–86.
- 828 Tudorache, C., Viaene, P., Blust, R., Vereecken, H., & De Boeck, G. (2008). A comparison  
829 of swimming capacity and energy use in seven European freshwater fish species.  
830 *Ecology of Freshwater Fish*, 17, 284-291.
- 831 Vignieri, S. (2014) Vanishing fauna. Introduction. *Science*, 345, 392–395.
- 832 Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P.,  
833 ...Davies, P.M. (2010) Global threats to human water security and river biodiversity.  
834 *Nature*, 467, 555–561.
- 835 Vörösmarty, C.J., Pahl-Wostl, C., Bunn, S.E., & Lawford, R. (2013) Global water, the  
836 anthropocene and the transformation of a science. *Current Opinion in Environmental*  
837 *Sustainability*, 5, 539–550.
- 838 Vrieze, L.A., Bjerselius, R., & Sorensen, P.W. (2010) Importance of the olfactory sense to  
839 migratory sea lampreys *Petromyzon marinus* seeking riverine spawning habitat. *Journal*  
840 *of Fish Biology*, 76, 949–964.
- 841 Wan, Q., Fan, S., & Li, Y. (2003) The loss of diversity in Dabry's Sturgeon (*Acipenser*  
842 *dabryanus Dumeril*) as revealed by DNA fingerprinting. *Aquatic Conservation: Marine*  
843 *and Freshwater Ecosystems*, 13, 225–231.
- 844 Wei, Q., Ke, F., Zhang, J., Zhuang, P., Lou, J., Zhou, R., & Wang, W. (1997) Biology,  
845 fisheries, and conservation of freshwater biodiversity 181 sturgeons and paddlefish in  
846 China. *Environmental Biology of Fishes*, 48, 241–255.
- 847 Wei, Q., He, D., Yang, D., Zhang, W., & Li, L. (2004) Status of sturgeon aquaculture and  
848 sturgeon trade in China: a review based on two recent nationwide surveys. *Journal of*  
849 *Applied Ichthyology*, 20, 321–332.
- 850 Welcomme, R.L. (1985). River fisheries. FAO Fisheries Technical Paper (262), pp 30.
- 851 Wheeler, A.P., Angermeier, P.L., & Rosenberger, A.E. (2005) Impacts of new highways and  
852 subsequent landscape urbanization on stream habitat and biota. *Reviews in Fisheries*  
853 *Science*, 13, 141–164.
- 854 Wilkes, M.A., Mckenzie, M., & Webb, J.A. (2018) Fish passage design for sustainable  
855 hydropower in the temperate Southern Hemisphere: an evidence review. *Reviews in Fish*  
856 *Biology and Fisheries*, 28, 117–135. DOI 10.1007/s11160-017-9496-8.
- 857 Wilkes, M.A., Baumgartner, L., Boys, C., Silva, L.G.M., O'Connor, J., Jones, M., Stuart, I.,  
858 Habit, E., Link, O. & Webb, J.A. (in press) Fish-Net: Probabilistic models for fishway  
859 planning, design and monitoring to support environmentally sustainable hydropower.

860 *Fish & Fisheries*. doi: 10.1111/faf.12282  
861 Williams, J.G., & Katopodis, C. (2016). Commentary: Incorrect application of data negates  
862 some meta-analysis results in Bunt et al. (2012). *River Research and Applications*, 32,  
863 2109–2115.  
864 Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. (2012) Thinking  
865 like a fish: A key ingredient for development of effective fish passage facilities at river  
866 obstructions. *River Research and Applications*, 28, 407–417.  
867 Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S.,  
868 ... Sáenz, L. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and  
869 Mekong. *Science*, 351, 128–9.  
870 Winter, E.R., Tummers, J.S., Aarestrup, K., Baktoft, H., & Lucas, M.C. (2016) Investigating  
871 the phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two  
872 European populations. *Hydrobiologia*, 775, 139–151.  
873 Wofford, J.E., Gresswell, R.E. & Banks, M.A. (2005) Influence of barriers to movement on  
874 within-watershed genetic variation of coastal cutthroat trout. *Ecological Applications*,  
875 15, 628-637.  
876 Yeakley, J.A., Maas-Hebner, K.G., & Hughes, R.M. (2014). *Wild Salmonids in the*  
877 *Urbanizing Pacific Northwest*. New York, USA: Springer.  
878 Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015) A global boom  
879 in hydropower dam construction. *Aquatic Sciences*, 77, 161–170.

880  
881  
882  
883  
884  
885  
886  
887  
888  
889  
890  
891  
892  
893  
894  
895  
896  
897  
898  
899  
900  
901  
902  
903  
904  
905  
906  
907  
908

909 **Table 1.** Examples of fish population declines and local extinctions ascribed to river  
 910 fragmentation.  
 911

<b>Species</b>	<b>Location</b>	<b>Fragmentation impacts</b>	<b>References</b>
Atlantic salmon; <i>Salmo salar</i>	Rhine, Seine and Garonne basins, France Gudena River, Denmark	Disappearance of whole stocks	Porcher & Travade (1992); Jepsen et al. (1998)
Pacific salmon; <i>Oncorhynchus</i> <i>spp.</i>	Pacific Coast, USA	101 stocks at high risk of extinction	Nehlsen, Williams & Lichatowich. (1991)
Whitespotted char; <i>Salvelinus</i> <i>leucomaeni</i>	Hokkaido, Japan	Local extinction at 17 sites upstream of dams	Morita & Yamamoto (2002)
Dabry's sturgeon; <i>Acipenser</i> <i>dabryanus</i>	Yangtze River	Critically endangered (possibly extinct)	Wei et al. (1997, 2004); Wan, Fan & Li (2003)
Spotted sorubim; <i>Pseudoplatystoma</i> <i>coruscans</i>	São Paulo state, Brazil	Rapid local extinction after dam construction	Welcomme (1985)
Jullien's golden carp; <i>Probarbus</i> <i>jullieni</i>	Northern Malaysia	Possibly local extinction (Pahang River) and significant population decline (Perak River)	Baird (2006); Dudgeon et al. (2006)

912  
 913  
 914  
 915  
 916  
 917  
 918  
 919  
 920  
 921  
 922  
 923  
 924  
 925  
 926  
 927  
 928  
 929  
 930  
 931  
 932  
 933  
 934



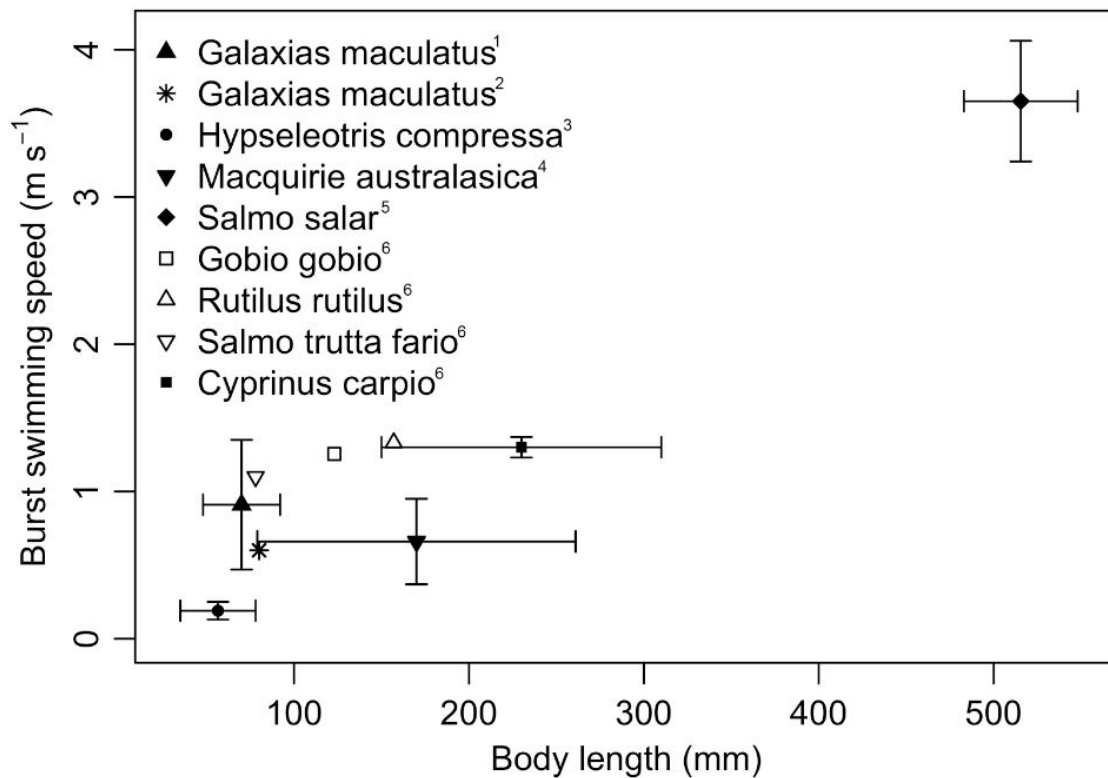
935  
936

**Table 2.** Recommendations to address biases in fish passage research and applications.

1. Avoid building new barriers whenever possible; if unavoidable, build the dam/weir/culvert such that it is not a barrier
2. First choice should always be to remove existing structures rather than to engineer a solution
3. Reconsider removing barrier (#2)
4. Recognise and embrace diversity of fish movement ecology
5. Integrate natural variation and build in uncertainty to designs
6. Use a more holistic approach including the consideration of geomorphic and hydrological processes
7. Stop recommending absolute design criteria from laboratory swimming tests. Laboratory experiments are excellent tools for comparative studies, but lack biological and environmental realism
8. Use an evidence-based approach

937  
938  
939  
940  
941  
942  
943  
944  
945  
946  
947  
948  
949  
950  
951  
952

Accepted



953

954 **Figure 1.** Burst swimming speeds (the maximum swimming velocity that a fish is capable of  
 955 sustaining for up to 20 s) of salmonids and other migratory fish with characteristic body  
 956 lengths at the time of upstream migration. All species listed are defined as diadromous or  
 957 potamodromous in FishBase (Froese & Pauly, 2016). All studies listed sampled burst  
 958 swimming speeds in laboratory flumes. Symbols show modes. Whiskers show range from  
 959 selected studies to demonstrate population-level variation. Examples cited: <sup>1</sup>Nikora, Aberle,  
 960 Biggs, Jowett & Sykes. (2003); <sup>2</sup>Plew, Nikora, Larned, Sykes, & Cooper (2007); <sup>3</sup>Rodgers et  
 961 al. (2014); <sup>4</sup>Starrs, Ebner, Lintermans & Fulton (2011); <sup>5</sup>Colavecchia, Katopodis, Goosney,  
 962 Scruton & McKinley (1998); and <sup>6</sup>Tudorache, Viaene, Blust, Vereecken & De Boeck (2008).

963