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

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Anthropocene)*

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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

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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

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909 **Table 1.** Examples of fish population declines and local extinctions ascribed to river
 910 fragmentation.
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Species	Location	Fragmentation impacts	References
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 spp.</i>	Pacific Coast, USA	101 stocks at high risk of extinction	Nehlsen, Williams & Lichatowich. (1991)
Whitespotted char; <i>Salvelinus leucomaeni</i>	Hokkaido, Japan	Local extinction at 17 sites upstream of dams	Morita & Yamamoto (2002)
Dabry's sturgeon; <i>Acipenser dabryanus</i>	Yangtze River	Critically endangered (possibly extinct)	Wei et al. (1997, 2004); Wan, Fan & Li (2003)
Spotted sorubim; <i>Pseudoplatystoma coruscans</i>	São Paulo state, Brazil	Rapid local extinction after dam construction	Welcomme (1985)
Jullien's golden carp; <i>Probarbus jullieni</i>	Northern Malaysia	Possibly local extinction (Pahang River) and significant population decline (Perak River)	Baird (2006); Dudgeon et al. (2006)

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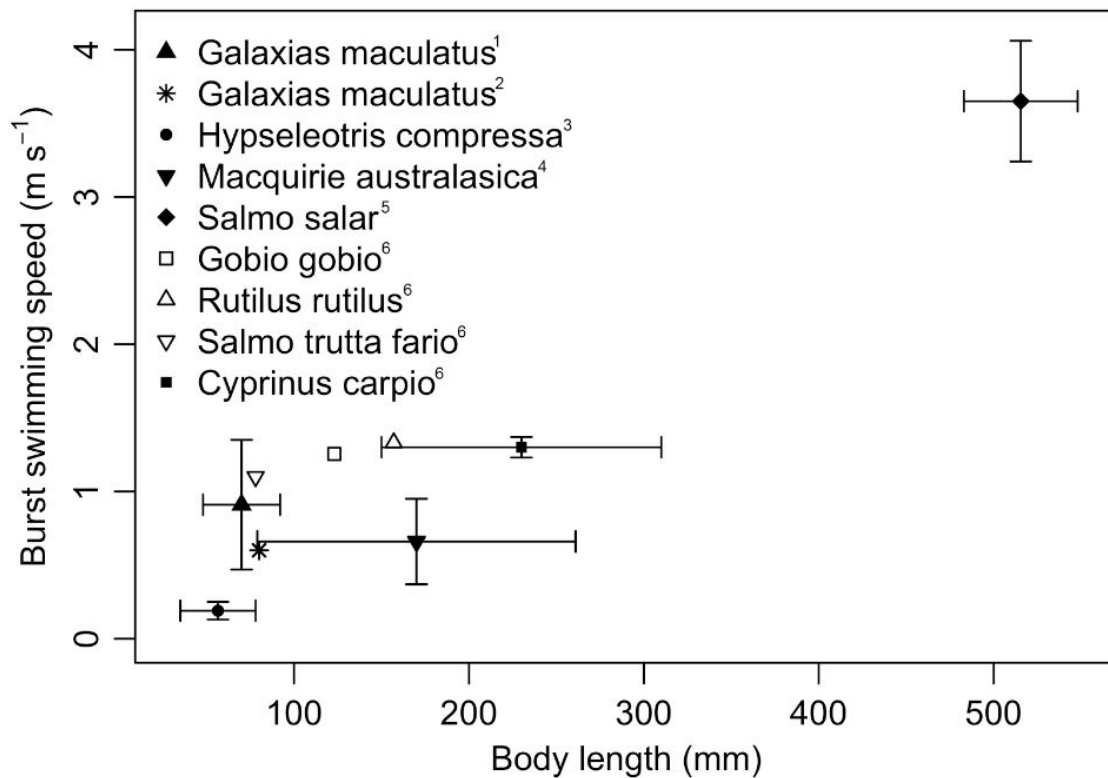
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Table 2. Recommendations to address biases in fish passage research and applications.

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

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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: ¹Nikora, Aberle,
 960 Biggs, Jowett & Sykes. (2003); ²Plew, Nikora, Larned, Sykes, & Cooper (2007); ³Rodgers et
 961 al. (2014); ⁴Starrs, Ebner, Lintermans & Fulton (2011); ⁵Colavecchia, Katopodis, Goosney,
 962 Scruton & McKinley (1998); and ⁶Tudorache, Viaene, Blust, Vereecken & De Boeck (2008).

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