

Effective monitoring of freshwater fish

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34 **Abstract**

35 Freshwater ecosystems constitute only a small fraction of the planet's water resources,
36 yet support much of its diversity, with freshwater fish accounting for more species than
37 birds, mammals, amphibians, or reptiles. Fresh waters are, however, particularly
38 vulnerable to anthropogenic impacts, including habitat loss, climate and land use change,
39 nutrient enrichment, and biological invasions. This environmental degradation, combined
40 with unprecedented rates of biodiversity change, highlights the importance of robust and
41 replicable programmes to monitor freshwater fish assemblages. Such monitoring
42 programmes can have diverse aims, including confirming the presence of a single species
43 (e.g. early detection of alien species), tracking changes in the abundance of threatened
44 species, or documenting long-term temporal changes in entire communities. Irrespective
45 of their motivation, monitoring programmes are only fit for purpose if they have clearly
46 articulated aims and collect data that can meet those aims. This review, therefore,
47 highlights the importance of identifying the key aims in monitoring programmes, and
48 outlines the different methods of sampling freshwater fish that can be used to meet these
49 aims. We emphasise that investigators must address issues around sampling design,
50 statistical power, species' detectability, taxonomy, and ethics in their monitoring
51 programmes. Additionally, programmes must ensure that high-quality monitoring data
52 are properly curated and deposited in repositories that will endure. Through fostering
53 improved practice in freshwater fish monitoring, this review aims to help programmes
54 improve understanding of the processes that shape the Earth's freshwater ecosystems, and
55 help protect these systems in face of rapid environmental change.

56 **Keywords:** Biodiversity Targets; Ecological Monitoring; Environmental Assessment;
57 Environmental Management; Rivers; Sampling Design

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82

83 **1. Introduction**

84 Human-driven environmental changes continue to raise substantial concerns for
85 biodiversity conservation and have led to the development and implementation of many
86 ecological monitoring programmes around the world (Nichols & Williams, 2006). These
87 programmes generally aim to understand and manage the interactions of environmental
88 change with biodiversity (Fölster et al., 2014). Given the increasing seriousness of
89 environmental degradation, the need for effective ecological and biodiversity monitoring
90 programmes has never been higher (Lindenmayer & Likens, 2010). Freshwater
91 ecosystems are particularly imperilled by anthropogenic activities worldwide. Although
92 fresh waters cover less than 1% of the earth's surface, they support high levels of
93 biodiversity (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Extinction rates of
94 freshwater taxa are considerably higher than terrestrial species (Sala et al., 2000), due to
95 issues including habitat loss, climate and land use change, pollution, and biological
96 invasions (Ormerod et al., 2010; Stendera et al., 2012). At approximately 13,000 species,
97 freshwater fish represent 40-45% of global fish diversity (Lévêque et al., 2008), with this
98 highly diverse group including some of the most imperilled animals on the planet (Cooke
99 et al., 2012).

100 Freshwater fishes also provide ecosystem services of major economic, nutritional,
101 scientific, historical, and cultural importance (IUCN FFSG, 2015). For example,
102 freshwater and marine fisheries jointly constitute the largest extractive use of wildlife in
103 the world and contribute to overall economic wellbeing by means of export commodity
104 trade, tourism, and recreation (Santhanam, 2015). Freshwater fish provide a major source
105 of protein for humans and support the livelihoods of many people (Holmlund & Hammer,
106 1999), particularly in the Global South. However, there are serious threats to this valuable

107 resource related to over-exploitation and other anthropogenic stressors (Allan et al., 2005;
108 de Kerckhove et al., 2015).

109 The wide range of responses of freshwater fishes to anthropogenic stressors make
110 fish valuable indicators for assessing the biological and ecological integrity of fresh
111 waters and their catchments (Fausch et al., 1984; Magurran et al., 2018; Schiemer, 2000).
112 The breadth of fundamental information on ecology and taxonomy, combined with their
113 higher societal importance compared to other freshwater taxa, makes freshwater fish a
114 popular target taxon in assessments of ecological integrity (Simon & Evans, 2017).
115 Correspondingly, freshwater fishes are commonly used for evaluating the functioning and
116 status of freshwater ecosystems and habitat quality. These assessments, however, are only
117 as good as the data that underpin them. For this reason, effective and meaningful
118 monitoring of fish populations and communities in freshwater habitats is essential.

119 The need for effective monitoring in ecological research is well-recognized and
120 there are many monitoring programmes that have provided important scientific advances
121 and crucial information for environmental policy (Lovett et al., 2007). For example,
122 freshwater fish monitoring has highlighted changes in species diversity and species status
123 in rivers and lakes (e.g. Counihan et al., 2018; Holmgren et al., 2016; Wagner et al.,
124 2014), played a central role in fish-based assessment systems (e.g. for the European
125 Water Framework Directive, Pont et al., 2007), and resulted in guidelines on standardized
126 fish sampling methods (e.g. Bonar et al., 2009).

127 There remains a series of issues and knowledge gaps with how these programmes
128 are designed and implemented. In particular, freshwater fish monitoring that has been
129 poorly planned and lacks focus results in ineffective programmes that rarely meet their
130 aims (Lindenmayer & Likens, 2009, 2010; Marsh & Trenham, 2008; Nichols &

131 Williams, 2006). Moreover, there is considerable disparity across developed and
132 developing regions in how monitoring schemes are implemented. This is an acute
133 problem, as developing regions are often characterised by high levels of fish diversity but
134 limited resources for research (e.g. Vörösmarty et al., 2010). Where monitoring
135 programmes are in place, there are almost inevitably trade-offs in temporal and spatial
136 scales of measurement (Pollock et al., 2002), but these trade-offs are often poorly
137 quantified or justified, resulting in long-term data lacking statistical power. Finally, there
138 are inherent issues over programmes being either question driven or mandated, with the
139 latter often lacking rigour in design resulting in their provision of only coarse-level
140 summaries of change (Lindenmayer & Likens, 2010).

141 In this review, we examine these issues and knowledge gaps, and make
142 recommendations about how they can be addressed within monitoring programmes. Our
143 aim is to foster improved practices by: a) summarizing key questions that monitoring can
144 address when aims are clear, and the approach is rigorous (Section 3 and 4); b)
145 synthesising issues related to sampling design and statistical models, and indicating how
146 they might be overcome (Section 5); c) reviewing different monitoring and sampling
147 approaches (Section 6); d) considering challenges related to species' detectability,
148 taxonomy, economical costs, and ethics (Section 7); and, e) discussing the importance of
149 the appropriate management of monitoring data (Section 8).

150

151 **2. History of fish monitoring**

152 The long history of monitoring programmes is reflected in the scientific literature
153 (Fig. S1.1). Early, though presumably less systematic, efforts in freshwater fish
154 monitoring recorded temporal changes in fisheries, such as reports of Atlantic salmon
155 *Salmo salar* declines in a central European river that date back to the 18th century
156 (reviewed by Wolter, 2015). The 20th century marked a shift towards systematic
157 sampling with the majority of fish monitoring programmes being established before 1979
158 (Mihoub et al., 2017). Despite this and in contrast to other taxonomic groups such as
159 birds, mammals, and many plants, freshwater fish are generally under-represented in
160 contemporary biodiversity studies and monitoring programmes (Mihoub et al., 2017;
161 Troudet et al., 2017). This underrepresentation of fish, despite their high diversity, might
162 be explained partly by the fact that they occur in aquatic environments. Thus, in contrast
163 to many terrestrial biota, which can be monitored by visual observations and where
164 community scientists (also known as citizen scientists) can be easily recruited (Thomas,
165 1996), fish require more specialized sampling methods. However, one feature shared with
166 other taxa is that the spatial extent of fish monitoring is highly biased, being concentrated
167 in the Global North (Fig. 1). Freshwater ecosystems (e.g. lacustrine and fluvial habitats)
168 are also generally neglected in fish monitoring programmes, compared to the marine
169 environments (Fig. 1). A further issue is that even when freshwater fish are monitored,
170 the resulting data are often not published or electronically archived, and thus are often
171 inaccessible to the broader scientific community (Lindenmayer & Likens, 2009; Revenga
172 et al., 2005).

173

174

[Fig. 1]

175 **3. Aims of effective monitoring**

176 As it is now widely recognised, ecological communities experience continuous
177 temporal turnover, i.e. change in species composition and abundances (e.g. Darwin,
178 1859; MacArthur & Wilson, 1967). Some degree of temporal turnover is necessary to
179 maintain ecosystem functions and properties. However, the rate of temporal turnover in
180 contemporary assemblages exceeds the baseline predicted by ecological theory (Dornelas
181 et al., 2014). Consequently, the overall goal in effective monitoring of freshwater fish
182 should not be limited to documenting change *per se*, but should also address the drivers
183 of the observed change (thereby identifying potential remedies).

184 There are a number of definitions of monitoring in conservation, ecological, and
185 aquatic contexts (Supporting Information Table S1.1). Here, we define **freshwater fish**
186 **monitoring as repeated, field-based measurements of fish that are collected in a**
187 **systematic manner, allowing the potential detection of important shifts at**
188 **population or community levels.** Therefore, effective monitoring requires a clear set of
189 specific objectives linked to the overall goal of detecting systemic shifts in fish
190 populations or communities over time and space, and so should utilise methodologies and
191 sampling effort that provide the data and statistical power sufficient to meet these
192 objectives.

193

194

195 **4. Different questions lead to different monitoring approaches**

196 Monitoring programmes need a rigorous design and protocol for collection of data
197 over a sufficiently long period to ensure sufficient statistical power to detect trends or

198 changes and to enable the answering of the motivating questions (Lindenmayer & Likens,
199 2010; Nichols & Williams, 2006). Irrespective of the motivating question, freshwater fish
200 monitoring should generally help to advance ecosystem understanding and provide
201 information needed to identify potential remedies, requiring the detection of significant
202 changes at the community level (e.g. quantifying trends in species richness, temporal α -
203 and β -diversity, functional diversity, food web structure), and/or at the population level
204 (e.g. quantifying trends in population size and dynamics, abundance of keystone,
205 threatened or non-native species, genetic diversity, species ranges, fisheries stocks, size
206 and age structure, behaviour, phenology, growth, shape, and/or condition). An exception
207 to this might be in mandated-monitoring programmes where highly specific data (e.g. on
208 species presence, abundance, and/or age structure) are compared against predetermined
209 standards (Alexander, 2008; Hellawell, 1991; Hurford, 2010), such as in the Water
210 Framework Directive of the European Union (Birk et al., 2012). In a restoration context,
211 monitoring often aims at assessing the success of implemented measures (Kershner,
212 1997). Thereby, monitoring is not a stand-alone activity; it contributes to conservation
213 oriented-science and is used to inform a structured decision-making processes in
214 conservation management (Nichols & Williams, 2006).

215

216

217 It is the question(s) that determine the design of a monitoring programme. Some
218 questions can be addressed with species-specific presence-only data, while others might
219 require sampling of an entire community (Table 1). The latter case may utilise a range of
220 capture methods (Zale et al., 2012) that can, in turn, help assess the spatial behaviour,
221 trophic ecology, and genetic characteristics of individuals (Lucas & Baras, 2000;

222 Lundqvist et al., 2010). Alternative sampling methods include more recent approaches
223 such as community science and the use of social media/crowd-sourced science (Section
224 6). The data needs associated with a suite of key monitoring questions are summarised in
225 Table 1. We stress the importance of programmes clearly articulating their questions as
226 this ensures that the sampling design can generate the data required to answer them. As a
227 minimum, there should be identification of what needs to be measured (e.g. fish
228 abundance, fish attributes), the spatial and temporal scope of the programme (e.g.
229 duration, scale; *cf.* Dixon & Chiswell, 1996); the criteria for reliability (e.g. precision,
230 power); and the practical constraints (e.g. human resources, costs, social conflicts).

231

[Table 1]

232 **5. Sampling and network design, and statistical models**

233 Sampling design relates to the temporal frequency of sampling within a designed
234 network that comprises a series of spatially segregated sites. As such, decisions need to
235 be made regarding how to allocate monitoring effort within and among years, and across
236 sites (Larsen et al., 2001). Two major principles, the avoidance of bias in the selection
237 procedure and achievement of high precision, should underlie the design (Crawford,
238 1997). A sampling design can be based on probabilistic or non-probabilistic methods.
239 Probabilistic designs include simple random sampling, systematic sampling, and
240 stratified random sampling, with the latter two being more appropriate for heterogeneous,
241 hierarchically-structured aquatic environments, such as river drainages (Lowe et al.,
242 2006; Thorp et al., 2006). However, in fish monitoring, sample sites are frequently
243 selected non-probabilistically, often based on judgment or convenience (Pope et al.,
244 2010; Wilde & Fisher, 1996). Irrespective of this, decisions on the design of the

245 programme should be based on *a priori* defined statistical models that can reliably
246 answer the questions motivating the monitoring programme, such as those related to
247 quantifying community structure, species abundance or other population parameters (e.g.
248 age structure). These questions require consideration during design phases as well as
249 additional resources and time, separate from the monitoring programme itself, for
250 completion.

251 Where the aims are to detect changes related to (local) management actions such
252 as habitat restoration, or to impact assessment, before-after control-impact (BACI)
253 designs are frequently used (Osenberg et al., 2006; Stewart-Oaten & Bence, 2001;
254 Thiault et al., 2017). Here, *a priori* power analyses (Legg & Nagy, 2006; Marsh &
255 Trenham, 2008; Maxwell & Jennings, 2005; Peterman, 1990) can guide the estimation of
256 the minimum number of samples needed to detect a certain effect size (or minimum
257 detectable difference) according to a desired level of significance (Peterman, 1990; Steidl
258 et al., 1997).

259 However, as fish monitoring programmes are typically undertaken to detect
260 temporal changes in populations over potentially larger scales (Cowx et al., 2009),
261 statistical control and replication designs are often unfeasible (Carpenter et al., 1989;
262 Hargrove & Pickering, 1992; Schindler, 1998; Turner et al., 2001). Advanced Bayesian
263 (hierarchical) models (Hobbs & Hooten, 2015) offer useful alternatives, especially when
264 working with imperfect datasets and/or uncertainty associated with sampling and
265 observation, as it is often the case in fish monitoring. For example, Wenger et al. (2017)
266 applied a Bayesian approach to predict the viability of multiple (potentially isolated)
267 populations of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*); this approach
268 enabled predictions to be made in minimally-sampled or even un-sampled populations.

269 Other applications of Bayesian models to analyse monitoring data include estimations of
270 occupancy and richness of fish while accounting for imperfect detection (Bayley &
271 Peterson, 2001; Coggins et al., 2014), and for relating environmental drivers to stream
272 fish population dynamics (Letcher et al., 2015; Wheeler et al., 2018).

273 The spatial structure of dendritic networks, and their associated connectivity and
274 directionality, make river systems particularly challenging for monitoring. The effect of
275 spatial variability can be reduced by stratified random sampling, i.e. the proportional
276 sampling of strata that represent different habitat units (Downes et al., 2002) and is
277 widely used in aquatic ecosystems (Dukerschein et al., 2011; Haxton, 2011; Wilde &
278 Fisher, 1996). More recently, Spatial Stream Network models (SSN) have been
279 developed to better capture the continuous nature of rivers (Fausch et al., 2002) and to
280 account for the spatially autocorrelated relationships between locations within a stream
281 network (Isaak et al., 2014). For example, Isaak et al. (2017) analysed a large fish density
282 dataset using SSN models to obtain population estimates for trout species from 108 sites
283 in a 735 km river network. The SSN methodology is accessible via the statistical tools
284 ‘STARS’ (Peterson & Ver Hoef, 2014) and ‘SSN’ (Ver Hoef et al., 2014).

285 In a systematic sampling design, the first sample site is chosen randomly and all
286 subsequent samples are regularly placed in space or time (Conroy & Carroll, 2009; Quinn
287 & Keough, 2002). A systematic design is useful when investigating effects of
288 environmental gradients. A recent development in this context is the Generalized
289 Random Tessellation Stratified design (GRTS) (Stevens & Olsen, 2003, 2004), available
290 from the statistical package ‘spsurvey’ (Kincaid & Olsen, 2016). GRTS allows design-
291 based inferences to entire areas based on spatially-balanced samples, i.e. a spatial
292 distribution of sample locations that balances the advantages of simple or stratified

293 random samples or systematic samples (Larsen et al., 2008). GRTS has been evaluated as
294 reliable and cost-effective, for example, for monitoring North American salmonids
295 (Gallagher et al., 2010).

296 The adaptive approach (Box 1) argues that the sampling design should be re-
297 evaluated and re-designed as necessary as data are gathered and their variability analysed.
298 An analysis of the components of variance and their influence on trend detection
299 capability can help in preparing design-efficient trend monitoring networks (Larsen et al.,
300 2001). This ensures that changes in the chemical, physical, or biological conditions are
301 accounted for in the sampling design (Buckland et al., 2012; Strobl & Robillard, 2008).

302

303 **Box 1. Adaptive monitoring**

304 There is often high uncertainty and complexity in the drivers of fish community
305 change that can range from global environmental change (e.g. climate change; Graham &
306 Harrod, 2009; Radinger et al., 2016) to more local issues (e.g. altered flow regimes;
307 Harby et al., 2007). Monitoring programmes must be capable of providing data suitable
308 for the continued management of the resources (Polasky et al., 2011). The informed
309 decision-making process of adaptive monitoring (sensu Lindenmayer & Likens, 2009)
310 enables monitoring programmes to evolve in response to new questions, information,
311 situations, or conditions or the development of new protocols (Lindenmayer et al., 2011).
312 Adaptive monitoring is considered a long-term activity closely related to scientific
313 research and management. The ultimate aim of any adaptive monitoring programme is to
314 demonstrate that new insights gained through its application will improve management
315 practices (Lindenmayer et al., 2011), potentially leading to increases in the effectiveness
316 of monitoring for conservation.

317 An example of adaptive monitoring is outlined by Fölster et al. (2014) for
318 Swedish fresh waters. At the outset the early naturalists measured specific and localized
319 natural phenomena such as the relationship between macrophytes and lake water
320 chemistry (Lohammar, 1938). However, the scope of the freshwater monitoring
321 programme in Sweden and the number of monitored sites increased along with the
322 emergence of new challenges related to, for example, eutrophication in the 1960s, acid
323 rain in the 1970s, and the EU Water Framework Directive in 2000. Today, the program
324 consists of regular long-term monitoring of water chemistry and biodiversity (including
325 freshwater fish) in 114 streams and 110 lakes (Fölster et al., 2014). This example not only
326 illustrates the value of adaptive monitoring by providing long-term data to understand
327 and overcome many of the emerging environmental problems, but also emphasizes its
328 potential to investigate future challenges, e.g. related to climate change, testing resilience
329 theory, or predicting regime shifts and tipping points.

330 **6. Approaches to fish monitoring**

331 **6.1. Monitoring questions versus sampling methods**

332 The numerous sampling methods that can be utilised for fish monitoring,
333 including capture and non-capture techniques, have been extensively reviewed (e.g.
334 Bonar et al., 2009; Joy et al., 2013; Zale et al., 2012). Capture methods involve the
335 physical removal of fish from the water to enable species identification, and the
336 collection of biometric data (e.g. length, weight) and hard structures (e.g. scales) for
337 ageing the fish to determine population demographics and dynamics. The most common
338 methods available for capturing freshwater fish include electrofishing, netting, and

339 trapping (Bonar et al., 2009). Non-capture methods (e.g. hydroacoustic surveys) can
340 provide data complementary to capture techniques. They can also be used where capture
341 methods lack sufficient power to provide robust estimates of population abundances
342 (Hughes, 1998; Lyons, 1998). However, a feature of some non-capture methods is their
343 taxonomic ambiguity due to either their lack of fish capture (Boswell et al., 2007)
344 (Section 6.4) or through erroneous identification of specimens (Section 7.2).

345 The application of a sampling method in monitoring might differ markedly
346 according to the programme's aims. For example, electrofishing can be applied within
347 point abundance sampling designs that can be effective for monitoring the diel activity of
348 (small) fishes (reviewed by Copp, 2010) or the status of rare species (e.g. the critically
349 endangered European eel, *Anguilla anguilla*; Laffaille et al., 2005). However, capturing
350 fish in longer river reaches using electrofishing might be more suitable where the
351 monitoring aim is to assess biological/ecological integrity, as biotic indices require data
352 at multiple organization levels, from size structure to assemblage richness (e.g. Noble et
353 al., 2007; Pont et al., 2007; Schmutz et al., 2000), often in conjunction with data on
354 habitat quality (e.g. Van Liefferinge et al., 2010; Milner et al., 1998).

355 **6.2. Capture techniques and application within monitoring programmes**

356 The challenge of ensuring that capture methods are fit for purpose, such as
357 evaluating the composition of an assemblage (details in Box 2) (e.g. Zale et al., 2012),
358 has resulted in a series of standardised protocols being made available for sampling
359 inland fish populations in many areas of the world, including Europe, North America, and
360 New Zealand (Bonar et al., 2009; CEN, 2003, 2006; Joy et al., 2013; Table S4.1).
361 Standardization not only refers to the equipment used or how it is used, but also to the
362 timing of sampling, the habitats that are sampled, and effort applied (Bonar et al., 2011).

363 Standardizing the collection and reporting of fish monitoring data offers many
364 advantages including an improved ability to compare data across regions or time,
365 improved communication across political boundaries, and the control of bias associated
366 with different sampling techniques (Cooke et al., 2016). Standardization in fish sampling
367 has been considered an important step forward in managing long-term data and assessing
368 efficacy of large spatial scale management strategies (Bonar et al., 2017). This is of
369 particular relevance in monitoring programmes where many researchers combine datasets
370 to jointly address questions over time and space. For a comprehensive overview on
371 standardisation of fish sampling across sampling gears and aquatic environments, see
372 Bonar et al. (2009).

373 Two fundamental concepts have emerged in relation to the application of capture
374 techniques and protocols to fish monitoring: the importance of sampling design
375 (discussed earlier in Section 5) and response design (Stevens & Urquhart, 2000).

376 Response design incorporates decisions about how to measure the fish community
377 and population metrics with accuracy and precision (Pollock et al., 2002). For example,
378 where assessments of age structure, growth rates, and recruitment are required, then
379 decisions are needed on the ageing method, such as whether to rely on length-frequency
380 analyses or collect hard structures, such as scales, from captured fishes (e.g. Hamidan &
381 Britton, 2015). If scales are collected, then decisions are needed regarding how many
382 individual fish need to be sampled and over what size range (Busst & Britton, 2014). In
383 addition, where hard structures are being used for ageing, the frequency of annulus
384 formation might need validating to maximise accuracy (Beamish & McFarlane, 1983),
385 requiring regular sampling throughout the year or mark-recapture methods (Britton et al.,
386 2010; Chisnall & Kalish, 1993). Scale samples for fish ageing, and tissue samples for

387 genetic and stable isotope analyses, can be collected from fish captured by anglers to
388 complement on-going monitoring (Gutmann Roberts et al., 2017).

389

390 **Box 2: Sampling effort and biodiversity estimation**

391 Decisions about the spatial extent and duration of sampling have important
392 implications. If the goal is to quantify an attribute of a population of interest, then, all
393 other things being equal, estimates of abundance will scale predictably with effort. There
394 are a range of statistical techniques, such as removal sampling (Southwood & Henderson,
395 2000), that can be used to estimate population size and/or to ensure that effort is adequate
396 for the intended purpose. It is relatively straightforward, therefore, to compute trends for
397 single populations.

398 If, on the other hand, the aim is to quantify compositional turnover (temporal β
399 diversity), or to calculate a metric of α diversity, such as assemblage richness, it is
400 essential that any temporal or spatial comparisons take account of the inherent
401 unevenness of ecological assemblages. Although the number of individuals (across all
402 species) will typically increase linearly if an assemblage is sampled over a longer time
403 period, or the area sampled is increased, the species accumulation curve will gradually
404 flatten (Fig. 2). As a result, any metrics that either explicitly or implicitly depend on
405 richness cannot be scaled by simple multiplication or division. Species richness is the
406 metric most obviously influenced by this, but most biodiversity indices, including, for
407 example, the Berger-Parker dominance metric (Magurran, 2004, 2011; Magurran &
408 McGill, 2011) and Jaccard similarity (Baselga, 2010), are also affected.

409 Fortunately, there are statistical solutions to this problem. Rarefaction is the
410 traditional way of making fair comparisons across assemblages or of community

411 diversity over space or time (Gotelli & Colwell, 2001, 2011). In essence, the samples (or
412 assemblages) are rarefied to the smallest common sampling effort. Rarefaction can be
413 computed in relation to the minimum number of individuals sampled, or to the smallest
414 number of sampling units. While most rarefaction analyses focus on species richness, in
415 principle many different biodiversity metrics can be rarefied. In the case of temporal or
416 spatial β diversity comparisons, the investigator should use sample-based rarefaction as
417 this automatically retains the identity of the species involved. A recent innovation is to
418 extrapolate to the largest sample size rather than rarefy to the smallest one (Chao et al.,
419 2014; Hsieh et al., 2016). Rarefaction can also be used to make informed comparisons
420 about community structure and composition using null model approaches (Cayuela et al.,
421 2015; Cayuela & Gotelli, 2014). In summary then, any computation of trends in
422 community α diversity or β diversity should either be based on sampling that has been
423 rigorously standardized or data that have been statistically standardized (by rarefaction or
424 similar) – see Fig. 2 for an example.

425 [Fig. 2]

427 **6.3. Capture and release methods**

428 It is often desirable to release captured fish, unharmed, to the site of capture,
429 without further intervention. However, attaching tracking devices or marking fish, prior
430 to release, can substantially increase the amount of information obtained. For example,
431 biotelemetry using acoustic, radio, or passive integrated transponder tags (Cooke et al.,
432 2011; Thiem et al., 2011) can reveal individual variability in movements and behaviours
433 within and between populations (Lucas & Batley, 1996), elucidate population mixing and
434 gene flow (Huey et al., 2011), assess the effects of connectivity and habitat fragmentation

435 on river fishes (Capra et al., 2017; Lin et al., 2018), and help evaluate management units
436 for fisheries or conservation (Funk et al., 2012).

437 Mark-recapture studies can also strongly complement fish monitoring by providing
438 alternative estimates of population size and fish ages (Hamel et al., 2015; Sass et al.,
439 2010). They can also reveal the extent of migrations of individual fish between habitats
440 within specific populations (Sandlund et al., 2016).

441 **6.4. Non-capture monitoring techniques**

442 Non-capture monitoring methods to complement capture data include
443 environmental DNA and hydroacoustic assessments. These methods are often applied
444 within monitoring programmes to provide data on different components of the
445 community or population, and are especially useful for larger water bodies where capture
446 techniques are often difficult to apply or are inefficient.

447 Environmental DNA ('eDNA' hereafter) is based on the presence DNA of fishes
448 in water samples originating from mucus and faeces, the sloughing off of cells from their
449 gut lining, and the decomposition of dead individuals (Davison et al., 2016; Jerde et al.,
450 2011; Turner et al., 2015). DNA is extracted from water samples, and polymerase chain
451 reaction (PCR) used in conjunction with species-specific genetic markers to amplify
452 DNA fragments to indicate the presence of target species (Turner et al., 2015). The
453 method is increasingly being applied to the monitoring of freshwater species (Fig. S1.1),
454 including those of conservation importance (Takahara et al., 2012; Thomsen et al., 2012).

455 There are two basic ways that eDNA can be applied in a fish monitoring
456 programme. Water samples can be analysed to detect the presence of a specific species,
457 or can be screened for whole communities of organisms using 'eDNA metabarcoding'
458 (Hänfling et al., 2016; Lawson Handley, 2015). Recent refinements have improved the

459 reliability of species' detection (Hänfling et al., 2016), but some questions remain, for
460 example, on factors affecting the rate of DNA breakdown in the environment (Barnes et
461 al., 2014). However, the non-detection of species-specific DNA fragments in a sample of
462 river water does not necessarily imply the absence of the target species, nor does a
463 positive signal necessarily imply that the species is present, as eDNA could have been
464 transported from upstream areas (Roussel et al., 2015). Nevertheless, as refinements in
465 the technique continue, it should increasingly provide a strong complement to capture
466 methods, especially in regions where knowledge on the species likely to be present is
467 available. Although issues over the reliability of eDNA to provide estimates of
468 abundance are being addressed, they remain highly challenging (Lacoursière-Roussel et
469 al., 2016). One important consideration will be the integration of data collected using
470 traditional methods with inferences about fish communities obtained using eDNA (see
471 6.6 below).

472 Hydroacoustic assessments involve the application of an acoustic beam from a
473 transducer through the water. Any fish within the beam returns a signal, with the target
474 strength of the returning signal indicating the relative size of the fish. Whilst the method
475 generates data on fish density, there is high taxonomic ambiguity in terms of species
476 present, with no biometric data collected (other than conversion of target strengths to
477 approximate fish lengths) (Boswell et al., 2007). Nevertheless, hydroacoustic assessments
478 have been used extensively for fish monitoring, especially in lakes where sampling
479 strategies have been developed (e.g. Guillard & Vergès, 2007), with target strengths
480 related to species-specific attributes to increase knowledge on community composition
481 (Frouzova et al., 2005). In lowland rivers, such as the River Thames and River Trent in
482 England, mobile hydroacoustic techniques have been applied to monitor the spatial and

483 temporal distributions of fish communities (Hughes, 1998; Lyons, 1998). The method has
484 also been applied to assessing the status of endangered fishes (Zhang et al., 2009).

485 **6.5. Anglers' data and data mining**

486 Statistics on angler catch rates and species composition have been applied to the
487 monitoring of fish community composition of large lowland rivers where other fish
488 capture methods are either difficult to apply or inefficient (Jones et al., 1995). For
489 example, in the River Trent, England, angler catch statistics monitored changes in the fish
490 assemblage in relation to improvements in water quality (Cooper & Wheatley, 1981;
491 Cowx & Broughton, 1986). More recently, catch statistics from individual anglers were
492 used to assess the population status of mahseer fishes (*Tor* spp.) in the River Cauvery,
493 India (Pinder et al., 2015a,b). An issue with angler-based data is that they tend to be
494 biased for specific species and size ranges (Amat Trigo et al., 2017).

495 Data mining, where spatial and temporal data on species are gathered through
496 information available from on-line sources, is a different non-capture technique for
497 monitoring changes in the distribution of species. Databases including the Global
498 Biodiversity Information Facility (GBIF; www.gbif.org/), the Global Population
499 Dynamics Database (GPDD; www.imperial.ac.uk/cpb/gpdd2/secure/login.aspx), or
500 VertNet.org enable users to access global distribution records of species via directed
501 searches that provide records with location coordinates for use within GIS. The GPDD
502 also provides data on population dynamics, rather than just distribution data. The
503 FishBase database (Froese & Pauly, 2018) provides species-level information gathered
504 from the literature, including occurrences and a wide range of ecological data.

505 An alternative method to using these online databases is monitoring the
506 distribution of fishes via community science, particularly via social media platforms.

507 Indeed, the application of community science and crowd sourcing to the collection of
508 biological data is increasingly frequent (e.g. www.inaturalist.org, Fig. S1.1), thanks to
509 many smartphones now having GPS, high-resolution cameras, and continuous internet
510 connection (Bik & Goldstein, 2013; Di Minin et al., 2015). For example, for monitoring
511 distributions of non-native fish, a number of smartphone ‘apps’ are available, with these
512 generally enabling the user to send a geo-referenced image of the species to a specific
513 organisation for validation and recording. Current examples include ‘*That’s Invasive*’
514 (<http://www.rinse-europe.eu/resources/smartphone-apps/>) and ‘*AquaInvaders*’
515 (<http://naturelocator.org/aquainvaders.html>). Both of these ‘apps’ also provide users with
516 information and images on specific invaders to facilitate their identification of species.
517 Venturelli et al. (2017) have recently reviewed the opportunities and challenges
518 associated with angler ‘apps’.

519 Data can also be sourced from user-generated content on various social media
520 platforms (Di Minin et al., 2015). By data-mining these non-biological sources, such as
521 via searches of specific social media sources (e.g. <https://www.youtube.com/>),
522 recreational fisheries forums and blogs, and news-media channels, fish distribution and
523 dispersal data can be generated. For example, this approach has been applied successfully
524 to assessments of non-native fish invasions, such as perch *Perca fluviatilis* and channel
525 catfish *Ictalurus punctatus* in Portugal (Banha et al., 2015, 2017). Increasingly, these
526 searches can be automated through use of computer code. For example, geo-referenced
527 images and video of specific species within image and video hosting websites (e.g. flickr)
528 can be searched, with GIS interfaces enabling distribution maps to be constructed (see
529 Fig. 3) and thus temporal and spatial distribution patterns better understood (Coding
530 Club, 2018).

531

532

[Fig. 3]

533

534 **6.6. Complementarity of capture and non-capture methods**

535 Data acquired from capture and non-capture methods within the same monitoring
536 programme need to be integrated effectively. For example, fish monitoring in
537 Windermere, England, a relatively large and deep glacial lake, has recently been
538 complemented by application of eDNA that recorded the presence of 14 of 16 fish
539 species known to be present, when concomitant gill net surveys only captured four fish
540 species (Hänfling et al., 2016). Windermere has also been monitored regularly for over
541 60 years by other methods, including fish traps, gillnets, hydroacoustics, and piscivorous
542 fish diet composition (Langangen et al., 2011; Winfield et al., 2008, 2012). The high
543 complementarity of these datasets has improved understanding of environmental (e.g.
544 nutrient enrichment, warming) and other changes (e.g. invasive fishes), and illustrated
545 their potential for monitoring other systems (e.g. Vindenes et al., 2014; Winfield et al.,
546 2010).

547 **7. Major challenges in fish monitoring**

548 **7.1. Detectability**

549 Many evaluations of biodiversity, including those of freshwater fishes (Magurran,
550 2004; Southwood & Henderson, 2000), assume that individuals have been sampled
551 randomly from the assemblage (Buckland et al., 2011; Pielou, 1975). This is rarely
552 achievable in nature (Pielou, 1975). In many cases, the problem arises because it is

553 difficult (or impossible) to know if a species that is absent from a site or sample is truly
554 absent, or is missing through the ineffectiveness of the sampling method. Thus, it is
555 important to thoroughly consider observation error and capture probabilities and to
556 address issues of detectability and detection bias also in fish monitoring. Potential
557 solutions to issues of detectability have been extensively discussed elsewhere and include
558 modelling occupancy (Bayley & Peterson, 2001; Iknayan et al., 2014; MacKenzie et al.,
559 2002, 2006; Royle & Link, 2006; Wenger & Freeman, 2008), estimating the probability
560 of detection of species (and/or individuals) through mark-recapture (Borchers et al., 2002,
561 2015; Buckland et al., 2011) or distance sampling (Buckland et al., 2001, 2004, 2011),
562 and/or demonstrating that the data are sufficiently robust to address the question posed
563 without further correction (Buckland et al., 2011; Magurran et al., 2018).

564 **7.2. Taxonomy**

565 Taxonomic issues can often emerge in biological monitoring programmes, with
566 the most obvious one being taxonomic uncertainty and the risk of species
567 misidentification in the field or the laboratory. For example, Daan (2001) reported
568 extensive species misidentifications in a marine fish database and there are many other
569 cases in the freshwater fish literature (e.g. Hänfling et al., 2005; Serrao et al., 2014; Vidal
570 et al., 2010). Nevertheless, a well-appreciated advantage of fish is that their taxonomy is
571 better known and easier than in most other freshwater groups, such as invertebrates or
572 algae, and thus fish can often be identified in the field without sacrificing individuals.
573 However, this is less likely to be the case in species-rich regions such as the tropics,
574 where the taxonomy is less well known, compared to regions with well-characterised fish
575 faunas.

576 The extent of species misidentification in more taxonomically challenging groups,
577 such as stream invertebrates, receives greater attention than in freshwater fish. For
578 example, Stribling et al. (2008) compared taxonomic identification of stream macro-
579 invertebrates across eight U.S. laboratories and found means of 21% taxonomic
580 disagreement. These kinds of errors might also occur in fish monitoring, especially in
581 samples with high species richness or in samples from regions where taxonomy is poorly
582 described. These studies reinforce the importance of adequate training and experience,
583 documentation of standard procedures, and routine quality control (Stribling et al., 2003,
584 2008). Species misidentification is even more important when fishers are interviewed to
585 obtain local knowledge data. Here, thorough validation procedures are essential (Poizat &
586 Baran, 1997; Valbo-Jørgensen & Poulsen, 2000).

587 A similar problem is when taxonomy changes and it is recognised that a single
588 species in fact comprises several cryptic species. This problem is increasingly frequent
589 given the increasing power of molecular tools (e.g. April et al., 2011; Lara et al., 2010;
590 Young et al., 2013). For example, Young et al. (2013) found that the majority of species-
591 level taxonomic units of the genus *Cottus* as evaluated by DNA barcoding did not assign
592 to previously recognized species in this region. New taxonomic alignments hinder
593 comparison with old samples if no specimens were preserved. In addition, the same
594 species names may have had different synonyms in the past, meaning that databases need
595 to be carefully revised for inconsistencies and errors. Erroneous sequences and
596 misidentifications are also frequent in GenBank and similar sequence databases (Harris,
597 2003). It has been estimated that up to 56% of German freshwater fish species may be
598 incorrectly identified to species level in some databases (Kneibelsberger et al., 2015).
599 Consequently, errors in genetics databases might have major adverse impacts on eDNA

600 as a robust technique. It is likely that the frequency of such taxonomic problems in data is
601 more prevalent in monitoring of freshwater fish than in research (Stribling et al., 2003). It
602 is thus important to fully reference the taxonomic resources used in studies, not just as a
603 quality check on methodology, but also to recognize the importance of taxonomy and the
604 work of taxonomists (Santos & Branco, 2012; Vink et al., 2012; Wägele et al., 2011).

605 **7.3. Economic costs**

606 For a monitoring programme to be effective, successful and sustainable over the
607 longer-term, it must not only be ecologically relevant and statistically credible, but also
608 cost efficient, i.e. the perceived benefits of ecological monitoring (e.g. information on
609 trends or status changes) must justify its cost (Caughlan & Oakley, 2001; Charles et al.,
610 2016; Hinds, 1984). As financial limitations always apply, sustained monitoring requires
611 a proper selection of relevant variables that need to be measured (Braun & Reynolds,
612 2012). Often the true costs of monitoring are not recognized and likely underestimated
613 (Caughlan & Oakley, 2001), and its benefits depend on the value that society gives to the
614 long-term sustainability of freshwater ecosystems. Hence, costs of monitoring need to be
615 contrasted with the costs of not monitoring. These include increased uncertainty in
616 evaluating outcomes and future projections, and the possibility that managers may not
617 detect important shifts until it is too late to effectively address them.

618 Caughlan & Oakley (2001) provided a breakdown of monitoring costs,
619 comprising of budgetary expenses related to, for example, data collection, data
620 management, quality assessment, data analysis, reporting and scientific oversight,
621 opportunity costs (i.e. other benefits forgone by allocating resources to monitoring), and
622 external costs (i.e. costs not directly covered by the monitoring programme budget). The
623 costs for data collection – which are frequently the largest – may vary depending on the

624 methods applied. While established methods in fish monitoring, such as field-based
625 capture methods (e.g. electrofishing, netting, trapping), are commonly labour intensive in
626 the field and thus costly, the financial costs of emerging methods, such as use of eDNA,
627 the automatized collection of data (e.g. hydroacoustic assessments), and the use of
628 community science and data mining, are often related to post-processing, managing and
629 analysing big data (Section 6.4). A detailed review of the costs associated with ecological
630 monitoring can be found elsewhere (e.g. Caughlan & Oakley, 2001).

631 **7.4. Fish welfare and ethics in monitoring**

632 The importance of ethical issues relating to biological fieldwork and the need to
633 minimize harm to species and ecosystems has repeatedly been emphasized (e.g. Bennett
634 et al., 2016; Costello et al., 2016; Farnsworth & Rosovsky, 1993); a detailed
635 consideration of these matters is beyond the scope of this review. We note, however, that
636 fish welfare issues have received much attention (e.g. Sloman et al., 2019), often centred
637 around the question of whether fish are sentient and can experience pain and suffering
638 (e.g. Arlinghaus et al., 2007; Braithwaite, 2010; Huntingford et al., 2006, 2007; Rose et
639 al., 2014) – a challenging question that has a number of implications in a scientific,
640 ethical, and legal context (Browman et al., 2019). Browman et al. (2019) argue for a
641 pragmatic approach using objective indicators of stress, health status, and behaviour to
642 inform about fish well-being.

643 Irrespective of the scientific debate on fish-welfare, institutional requirements and
644 legal regulations need to be considered during freshwater fish monitoring. Fish sampling
645 usually requires specific permits from responsible authorities, particularly when working
646 with protected species or in protected areas. Depending on the aim and sampling method,
647 fish monitoring might involve the capture and treatment of fish or might even require

648 methods of destructive sampling, i.e. the killing of fish (e.g. Blessing et al., 2010), such
649 as when individuals require taxonomic identification in the laboratory, including where
650 voucher specimens are required (Bortolus, 2008; Rocha et al., 2014; Section 7.2).
651 However, alternative methods of identification should be used to avoid collection of rare
652 species (Costello et al., 2016; Minter et al., 2014). Protocols for fieldwork (e.g. Barbour
653 et al., 1999; Brenkman et al., 2008; CCME, 2011; Cowx et al., 2009; Cowx & Fraser,
654 2003; Joy et al., 2013) typically provide guidelines on appropriate and least invasive
655 techniques (e.g. non-capture techniques such as hydroacoustics and eDNA where
656 applicable, Section 6.4) and are designed to minimize stress or damage caused by
657 catching, handling, and holding. Developmental stage and species differences are also
658 taken into account. The sampling method and design should consider trade-offs of the
659 potential harm to fish versus the quality of the obtained data in relation to sampling
660 efficiency. In particular, when capture techniques are applied, potential cumulative
661 effects should be paid specific attention as fish monitoring involves repeated sampling of
662 species that can be long-lived (> 20 years) and is often targeted for protected or
663 endangered species (Benejam et al., 2012). For example, an efficient and common
664 capture technique such as electrofishing might cause sub-lethal injuries that are often not
665 externally obvious and possibly fatal (Snyder, 2003). Moreover, ethical issues related to
666 fish monitoring extend beyond fish-welfare and must also consider impacts on non-target
667 species and ecosystems or the potential transmission of pests and/or invasive species
668 (Costello et al., 2016).

669 **8. Management of monitoring data**

670 For the sustainable success of a monitoring programme and to potentially infer
671 future changes, policies and procedures that guarantee the quality of data capture,
672 documentation, and preservation for long-term use is required (Michener, 2015;
673 Michener & Jones, 2012; Rüegg et al., 2014; Sutter et al., 2015). For example, Vines et
674 al. (2014) found that the availability of research data declines with article age, with the
675 probability of finding the dataset decreasing by 17% per year.

676 Although the importance of integrating data management into long-term
677 ecological (monitoring) projects has been emphasized repeatedly in previous papers
678 (Costello & Wieczorek, 2014; Sutter et al., 2015), this is often a neglected area in
679 freshwater fish studies (but see Moe et al., 2013; Peterson et al., 2013 for some
680 examples). Thoroughly considering data management to preserve data for long-term use
681 and accessibility (even beyond the lifetime of the work that generated them) will require
682 more time and resources to fish monitoring programmes and should be considered at the
683 earliest stages and accounted for in budgetary plans.

684 Data management is not limited to ‘what’ was collected (i.e. fish sampling data);
685 many other data often associated with sampling, such as geospatial information,
686 multimedia content, voucher specimens, associated environmental variables, and other
687 biological data, also need to be considered (Costello & Wieczorek, 2014). Furthermore,
688 to ensure the utility of a dataset, it must be accompanied by metadata, i.e., a detailed
689 description of who created the data, when and where the data were collected and stored,
690 how and why the data were generated, processed, and analysed (Michener, 2006).

691 Data management is a key element in freshwater fish monitoring programmes. A
692 detailed discussion of challenges and opportunities of data management, as well as

693 practices of how it can or should be implemented in fish monitoring is provided
694 elsewhere (Costello et al., 2013; Costello & Wieczorek, 2014; Michener & Brunt, 2000;
695 Reichman et al., 2011; Sutter et al., 2015).

696 **9. Conclusions**

697 Given the rapid environmental degradation of the Earth's freshwater ecosystems and
698 associated unprecedented rates of biodiversity change, the importance of robust,
699 replicable, and effective programmes to monitor freshwater fish has never been higher.
700 Future challenges related to habitat degradation, climate and land use change, and
701 biological invasions necessitate monitoring programmes that systematically collect
702 quality data allowing the potential detection of systemic shifts of populations or
703 communities and thereby improve our understanding of ecosystem responses to
704 environmental change. There is a pressing need for effective monitoring to
705 comprehensibly quantify biodiversity change and to inform evidence-based
706 environmental decision-making.

707 At a minimum, when establishing a monitoring programme, clear articulation of
708 the monitoring aim(s) is essential and should address: (i) what should be monitored and
709 how; (ii) how to allocate effort within time and across sites; (iii) establish criteria for data
710 reliability; and (iv) identify practical constraints.

711 Monitoring must also take into account issues related to the detectability of
712 species, taxonomy, and animal welfare. Additionally, monitoring programmes must
713 integrate data management practices that ensure the quality of data capture,
714 documentation, and preservation of information for long-term use and re-use.

715 In summary, careful reflection on aims(s) and the extent to which the data
716 collected will meet these aims will greatly improve the quality and usefulness of
717 monitoring data. Consistently high monitoring standards will improve data comparability
718 within and amongst countries and systems. Finally, effective monitoring of freshwater
719 fish will advance our overall understanding of freshwater ecosystems and contribute to
720 the preservation and management of freshwater fish diversity while helping mitigate
721 anthropogenic impacts.
722

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1345

1347 **Tables**

1348 **Table 1.** Overview of key questions in fish monitoring programs, associated data needs and applicable sampling methods.

1349 Sampling method: 1 electrofishing, 2 netting, 3 trapping, 4 telemetry (e.g. acoustic, radio or passive integrated transponder tags), 5 mark-

1350 recapture, 6 environmental DNA, 7 hydroacoustic assessment, 8 angler catch statistics, 9 data-mining, 10 community science. -/orange = no,

1351 yellow = maybe, green = yes, na not applicable.

	Key questions in freshwater fish monitoring Detecting relevant changes/shifts/trends in ...															
	Non-native species	Species distributional range	Phenology	Fish as ecological indicators	Food web structure	Fish behaviour	Species richness	Temporal Alpha-Diversity	Temporal Beta-Diversity	Population size and recruitment	Fishery performance	Productivity	Fish trait metrics	Genetic diversity	Diseases, Parasites	Size and/or age structure
Population / single-species																
Occupancy (presence only)	1-3,6,8-10	1-3,6,8-10	1-3,6,8-10	1-3,6,8	na	1-3	na	na	na	-	-	-	-	-	-	-
Presence / Absence	1-3,6	1-3,6	1-3,7	1-3,6	na	1-3	na	na	na	-	-	-	-	-	-	-
Counts, uncorrected for effort	1-3,7,8	1-3,8	1-3,7,8	1-3,7,8	na	1-3	na	na	na	1-3,5,7,8	1-3,5,7,8	1-3,7	-	-	-	-
Abundance estimate	1,2,5,7	1,2	1,2,5,7	1,2,5,7	na	1,2,5	na	na	na	1,2,5,7	1,2,5,7	1,2,7	-	-	-	-
Individual attributes	1-5	1-3	1-5	1-5	na	1-5	na	na	na	1-3,5	1-3,5	1-3	1-3	1-3	1-3	1-3,5
Community / multi-species																
Occupancy (presence only)	1-3,6	1-3,6	1-3	1-3,6	1-3,6	1-3	1,2,6	1,2,6	-	-	-	-	-	-	-	-
Presence / Absence	1-3,6	1-3,6	1-3	1-3,6	1-3,6	1-3	1,2,6	1,2,6	1,2,6	-	-	-	-	-	-	-
Counts, uncorrected for effort	1-3	1-3	1-3	1-3	1-3	1-3	1,2	1,2	1,2	1-3,5,7,8	1-3,5,7,8	1-3,7	-	-	-	-
Abundance estimate	1,2	1,2	1,2	1,2	1,2	1,2,5	1,2	1,2	1,2	1,2,5,7	1,2,5,7	1,2,7	-	-	-	-
Individual attributes	1-5	1-3	1-5	1-5	1-3	1-5	1,2	1,2	1,2	1-3,5	1-3,5	1-3	1-3	1-3	1-3	1-3,5

1352 **Figure legends**

1353 **Fig. 1.** Overview of fish monitoring programmes across global regions (A),
1354 taxonomic orders (B), and biotope types (C) based on records of the taxonomic order
1355 Osteichthyes ($n = 543$) in the Global Population Dynamics Database (GPDD, version
1356 2.0, released 2010, www.imperial.ac.uk/cpb/gpdd2, NERC Centre for Population
1357 Biology, Imperial College, 2010). Note: The apparent lack of monitoring in, for
1358 example, Africa and Australia might reflect a limitation of the database rather than an
1359 actual lack of monitoring.

1360 **Fig. 2.** Illustration of the variation of the number of species (species richness) and
1361 numerical abundance with sampling effort. The data are for two river sites in Trinidad
1362 (top – (A) Lower Aripo, bottom – (B) Maracas, sampled four times annually for five
1363 years. The data are described in Magurran *et al.* (2018). In each case the species (and
1364 numerical abundance) accumulation curves are constructed by randomly shuffling the
1365 temporal order of the samples a 1000 times. The open points represent the median
1366 value of the randomised accumulation curves; their 95% confidence limits (0.025 and
1367 0.975 quantiles) are also shown (species richness – left column; numerical abundance
1368 – right column).

1369 **Fig. 3.** The distribution of (A) Northern pike (*Esox lucius*) and (B) Zander (*Sander*
1370 *luciperca*) in the UK, between 1986 and 2016, based on data from GBIF
1371 (www.gbif.org). The R code (R Core Team, 2017) used to construct the figure was
1372 adopted from the Coding Club
1373 (<https://ourcodingclub.github.io/2017/03/20/secc.html>).

1374