Please cite the Published Version

Additional Information: This is an Author Accepted Manuscript of a paper accepted for publication in Journal of Fish Biology, published by and copyright Wiley.

Manuscript Number:	SP 17-012R1
Full Title:	Understanding and managing fish populations: keeping the toolbox fit for purpose
Short Title:	Tools for understanding fish populations
Article Type:	FSBI Symposium SI Review Paper
Keywords:	archaeology, genetics, modelling, surveys, stable isotopes, telemetry
Corresponding Author:	Josephine Paris University of Exeter Exeter, UNITED KINGDOM
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	University of Exeter
Corresponding Author's Secondary Institution:	
First Author:	Josephine Paris
First Author Secondary Information:	
Order of Authors:	Josephine Paris
	Krista Sherman
	Brian Hayden, PhD
	Jamie Stevens, PhD
Order of Authors Secondary Information:	
Manuscript Region of Origin:	UNITED KINGDOM
Abstract:	Wild fish populations are currently experiencing unprecedented pressures, which are projected to intensify in the coming decades. Developing a thorough understanding of the influences of both biotic and abiotic factors on fish populations is a salient issue in contemporary fish conservation and management. During the 50th Anniversary of the Fisheries Society of the British Isles, University of Exeter, 2017, scientists from diverse research backgrounds gathered to discuss key topics under the broad umbrella of 'Understanding Fish Populations'. Below, the output of one such discussion group is detailed, focusing on tools used to investigate natural fish populations. Five main groups of approaches were identified: (i) Tagging and telemetry; (ii) Molecular tools; (iii) Survey tools; (iv) Statistical and modelling tools; and (v) Tissue analyses. The appraisal covered current challenges and potential solutions for each of these topics. In addition, three key themes were identified as applicable across all tool-based applications. These included data management, public engagement, and fisheries policy and governance. The continued innovation of tools and capacity to integrate interdisciplinary approaches into the future assessment and management of fish populations is highlighted as an important focus for the next 50 years of fisheries research.

[Type text] [Type text] 14/07/15 Ethics Questionnaire for JFB

Submitted manuscripts will only be considered if the experimental methods employed are ethically justified. Please answer all questions. If you have answered 'yes' to questions 4 to 7, you should include an Ethics *paragraph in the Methods section of your manuscript which justifies your methods used. You should complete this questionnaire based on all fishes used in your experiment. For example, if you used live fishes as prey in predation experiments, this is a lethal endpoint for the prey fish (see Questions 5 & 6). Please read the Editorial published in JFB* 68*, 1-2, for full information on JFB ethics. PLEASE SUBMIT THE COMPLETED QUESTIONNAIRE WITH YOUR MANUSCRIPT ONLINE THROUGH EDITORIAL MANAGER.*

Corresponding author's name: Dr Jamie Stevens

Question 1*: Were fishes collected as part of faunal surveys? NO*

Question 2*: If you have undertaken experimental work, has the care and use of experimental animals complied with local and or national animal welfare laws, guidelines and policies? NO*

If 'Yes', state these and provide suitable evidence (e.g. for the U.K. a Home Office PPL number is sufficient), both here and in the manuscript, that protocols have undergone an ethical review process by an institutional animal care and use (or similar) committee, a local ethics committee, or by appropriately qualified scientific and lay colleagues.

[Type text] [Type text] 14/07/15

If 'No', because these laws do not exist in your country, please state this. Alternatively, if you carried out purely observational work so ethical permission was not considered necessary please state this both here and in the manuscript.

Purely observational work

```



```

Question 3*: Were fishes killed during or at the end of your experiment (e.g. for tissue sampling)? NO*

If 'Yes', what method was used? Please provide details both here and in the manuscript.

```



```

Question 4: Have you performed surgical procedures? NO If 'Yes', please give brief details of the surgery here. Full details should be given in the manuscript. If the procedures caused more than slight pain or distress, did you use appropriate sedation, analgesia and anaesthesia, with post-operative care? Please provide full details and justification both here and within the manuscript including type and concentration of anaesthetic.

```



```

Question 5*: Did you use experimental conditions that severely distressed any fishes involved in your experiments? NO*

If 'Yes', state the conditions and how they can be justified. What humane endpoints were used to minimise the effects? Please provide full justification within the methods section of your manuscript.

Question 6*: Did any of the experimental procedures, particularly those that involve lethal endpoints (e.g. predation studies, toxicity testing), cause lasting harm to sentient fishes? NO*

If 'Yes', provide details both here and in the methods section of your manuscript. Normally these procedures will be considered unacceptable by JFB unless any harm caused can be justified against the benefits gained.

Question 7*: Did any of your procedures involve sentient, un-anaesthetised animals paralysed by chemical agents such as muscle relaxants? NO*

If 'Yes', provide details both here and in the methods section of your manuscript. Normally these procedures will be considered unacceptable by JFB*.*

1   **Title:** Understanding and managing fish populations: keeping the toolbox fit for

2   purpose

3   **Running title:** Tools for understanding fish populations

4   **Authors** Paris, J.R.[1]*, Sherman, K.D.[1]*, Bell, E.[2], Boulenger, C.[3], Delord, C.[3], El-

5   Mahdi, M.B.M.[4], Fairfield, E.A.[2], Griffiths, A.M.[1], Gutmann Roberts[5], C., Hedger,

6   R.D.[6], Holman, L.E.[7], Hooper, L.H.[1], Humphries, N.E.[8], Katsiadaki, I.[9], King, R.A.[1],

7   Lemopoulos, A.[10], Payne, C.J.[11], Peirson, G.[12], Richter, K.K.[13], Taylor, M.I.[2],

8   Trueman, C.N.[7], Hayden, B.[14]† & Stevens, J.R. [1]†

9   * Joint first authors; † Joint senior authors

10   [1] Biosciences, University of Exeter, Stocker Road, Exeter, Devon EX4 4QD, UK

11   [2] School of Biological Science, University of East Anglia, Norwich Research Park,

12   Norwich, UK

13   [3] ESE, Ecology and Ecosystem Health, Agrocampus Ouest, INRA, Rennes, France

14   [4] Faculty of Science, Laboratory of Molecular Genetics and Molecular Biology,

15   Zoology Department, South Valley University, Qena 83523, Egypt

16   [5] Department of Life and Environmental Sciences, Faculty of Science and

17   Technology, Bournemouth University, Bournemouth, BH12 5BB, UK

18   [6] Norwegian Institute for Nature Research, Trondheim, NO-7485, Norway

19 [7] Ocean and Earth Science, National Oceanography Centre, University of

20 Southampton, European Way, Southampton SO14 3ZH

21 [8] Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill,

22 Plymouth PL1 2PB, UK

23 [9] Cefas, Weymouth Laboratory, Weymouth, Dorset, DT4 8UB, UK

24 [10a] Department of Environmental and Biological Sciences, University of Eastern

25 Finland, P.O. Box 111, FI-80101 Joensuu, Finland.

26 [10b] Department of Biology, University of Turku, FI- 20014, Turku, Finland.

27 [11] Institute of Aquaculture, Faculty of Natural Sciences, University of Stirling, Stirling,

28 UK

29 [12] Environment Agency, Research Analysis and Evaluation, Mance House,

30 Kidderminster, UK

31 [13] BioArCh, Department of Archaeology, University of York, York YO10 5DD, UK

32 [14] Biology Department, Canadian Rivers Institute, University of New Brunswick,

33 Fredericton, NB, E3B 5A3, Canada

34

35 **Corresponding Author:** Jamie R. Stevens, j.r.stevens@exeter.ac.uk 01392 723 775

36

Abstract

Wild fish populations are currently experiencing unprecedented pressures, which are projected to intensify in the coming decades. Developing a thorough understanding of the influences of both biotic and abiotic factors on fish populations is a salient issue in contemporary fish conservation and management. During the 50th Anniversary of the Fisheries Society of the British Isles, University of Exeter, 2017, scientists from diverse research backgrounds gathered to discuss key topics under the broad umbrella of 'Understanding Fish Populations'. Below, the output of one such discussion group is detailed, focusing on tools used to investigate natural fish populations. Five main groups of approaches were identified: (i) Tagging and telemetry; (ii) Molecular tools; (iii) Survey tools; (iv) Statistical and modelling tools; and (v) Tissue analyses. The appraisal covered current challenges and potential solutions for each of these topics. In addition, three key themes were identified as applicable across all tool-based applications. These included data management, public engagement, and fisheries policy and governance. The continued innovation of tools and capacity to integrate interdisciplinary approaches into the future assessment and management of fish populations is highlighted as an important focus for the next 50 years of fisheries research.

Key words: archaeology, genetics, modelling, surveys, stable isotopes, telemetry

Introduction

Approximately 30% of fish species have been overexploited (FAO, 2014), representing significant losses to biodiversity, ecosystem services and socioeconomic contributions (Worm et al., 2009). In light of the increasing challenges presented by climate change and other natural and anthropogenic stressors (Gordon et al., 2018), an improved understanding of fish populations is critical to facilitate effective management and conservation initiatives. During the summer of 2017, the Fisheries Society of the British Isles (FSBI) held its 50th Anniversary Symposium under the broad umbrella of 'Understanding Fish Populations'. To highlight key knowledge gaps and opportunities, we detail the outcome of a working group convened at the symposium, which was tasked with considering the theme of 'Tools for understanding fish populations'. The scope of the discussion spanned diverse areas including spatial ecology and migration patterns, genetics and evolutionary biology, physiology, trophic ecology, and developmental and population biology. In this article, we consider major advances in the use of tools across broad areas of fish biology, and identify knowledge gaps and potential solutions in each area in order to guide and inform future research, and to better understand and protect wild fish populations.

Tagging and telemetry

A significant problem hampering the study of fish, marine benthic species in particular, is that of determining their geographical locations at fine scales, over long durations. Tagging and telemetry involves the application of external and or internal

4

80 tags or devices to manually or passively track fish movement (Cooke et al., 2013).

81 Both forms can be particularly challenging in the marine environment, though manual

82 tracking can work well at feeding grounds and at spawning aggregations (e.g.

83 Murchie et al., 2015), while passive tracking has valuable applications along known

84 migration routes (Dahlgren et al., 2016), for example, as anadromous/catadromous

85 species migrate in and out of river estuaries (Lauridsen et al., 2017). Suites of tools

86 exist for such tasks (e.g. acoustic transmitters, PIT and Floy™ tags, radio, archival,

87 etc.) and have been routinely used to understand the spatial ecology of a range of

88 fish taxa (Bograd et al., 2010). With technological improvements in tags and tracking

89 equipment, the field has grown vastly in recent decades (see reviews by Pine et al.,

90 2003; Jepsen et al., 2015). We briefly highlight some of the tags and telemetry

91 options commonly used by researchers along with a discussion of some of the

92 limitations and challenges associated with these tools.

93 Archival data storage tags (DSTs), which collect data on both the internal and/or

94 external environments of fish are the only method available to assess internal states

95 (e.g. bioenergetics, Cooke et al., 2016). However, DSTs currently only provide

96 information on the environment experienced by the tagged fish if the tag is

97 recovered, meaning these data are lost if recapture rates are low, often the case in

98 fish tagging surveys. Communication History Acoustic Tags (so called 'CHATs'),

99 which transmit data to nearby transponder receivers are a promising alternative.

100 Since there have been relatively few uses of this tag type (Voegeli et al., 2001; Hight

101 & Lowe, 2007), there is potential for development in this area. Pop-off DSTs are also

102 becoming available and will no doubt prove very useful once problems associated

103 with size and recoverability are resolved.

Commented [JP1]: DSTs are perhaps the only tool to look at internal states, and recovery is possible for territorial species or those that converge in one place. A good reference here would be Cooke, S. J., Brownscombe, J. W., Raby, G. D., Broell, F., Hinch, S. G., Clark, T. D., & Semmens, J. M. (2016). Remote bioenergetics measurements in wild fish: opportunities and challenges. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 202, 23-37.

Pop-up satellite archival tags (PSATs), which detach from the tagged fish after some time at sea and transmit telemetry data to overpassing satellites, are currently limited in terms of hardware, software and satellite reception. PSATs are large, so are limited in use for larger, often highly migratory individuals, and may also affect fish behaviour (Methling et al., 2011). Additionally, battery failure, antenna damage, or mechanical failure may limit registration or transmission of data (Hays et al., 2007; Musyl et al., 2011). PSAT technology is relatively new, so future reductions in size and weight and also improvement in reliability can be expected. In terms of software, PSATs currently only transmit limited amounts of data due to transmission costs and the short time that the receiving satellite is above the horizon. Future software development is required to reduce transmission costs, optimise data transmission and provide more flexibility for users to tailor controls, in order to provide higher resolution data at the desired temporal scale. An increase in the number of satellite platforms that can receive PSAT data would help to improve reception issues. Interference on frequencies selected for tags at certain geographical locations (see Musyl et al., 2011) also requires consideration.

Acoustic telemetry offers autonomous, continuous monitoring (Heupel et al., 2006) and has the potential to significantly enhance our understanding of marine predator habitat use, activity patterns and resource partitioning (Hussey et al., 2015). Acoustic arrays have been used in many studies in elucidating fish movements (e.g. Papastamatiou et al., 2013; Lea et al., 2016), and transmitters have been used more innovatively to measure trophic interactions (Halfyard et al., 2017). Issues remain however, for example, in the significant cost and effort involved in deploying and maintaining acoustic arrays.

Commented [JP2]:
also the potential to measure trophic interactions eg Halfyard, E. A., Webber, D., Del Papa, J., Leadley, T., Kessel, S. T., Colborne, S. F. and Fisk, A. T. (2017), Evaluation of an acoustic telemetry transmitter designed to identify predation events. Methods Ecol Evol. doi:10.1111/2041-210X.12726

6

128   Organisations such as the Ocean Tracking Network (Whoriskey et al., 2015), (OTN;

129   oceantrackingnetwork.org) and the Australian Animal Tracking Network both maintain

130   acoustic infra-structure in the form of deployed receivers (arrays or curtains) in key

131   ecological areas into which researchers are free to release tagged animals. These

132   initiatives substantially reduce the cost and risk associated with acoustic tracking

133   projects and similar approaches can be applied globally (for example, a European

134   tracking network is currently being developed). Furthermore, integration of

135   standardised data repositories along with a comprehensive set of analytical tools to

136   ensure rapid and sophisticated analysis of acoustic array data (Lea et al., 2016)

137   would lead to new insights into the spatial ecology of fish. Further technological

138   developments such as the use of AUVs to perform routine data download

139   operations, or even complement fixed acoustic receivers (Davis et al., 2016), will

140   make acoustic telemetry increasingly affordable and accessible to more researchers.

141   Continued collaborations with established regional and international tracking

142   networks, together with the ever-increasing sophistication, miniaturisation, durability

143   and cost reduction of tags promises an increasingly important role for acoustic

144   telemetry in our understanding of fish ecology.

145

146   **Molecular tools**

147   *Population genetics and genomics*

148   Using genetic tools to understand fish genetic diversity and population structure has

149   wide-ranging applications for evolutionary biology, and the conservation and

7

management of fish stocks. Until recently, molecular techniques such as mitochondrial sequencing and the analysis of microsatellite loci have been used most commonly to explore intra-specific variation in fish and many other organisms (e.g. Ferguson & Danzmann, 1998; Chistiakov et al., 2006). More recently, however, the increased availability and cost efficiency of high-throughput sequencing, which is capable of producing millions of sequencing reads (e.g. RADseq, RNAseq), has revolutionised the fields of population and conservation genetics (Allendorf et al*.,* 2010). It is however important to understand what extra information high-throughput sequencing data can provide, the biases involved in study design and data generation, and also how its usage might be optimised. Here, we seek to identify knowledge gaps in the field of fish population genetics, and contemplate how this area of research may evolve in the future.

Attaining high quality, clean DNA for large numbers of individuals is paramount for downstream sequencing processes, but in some cases can be challenging. Biological samples can often be compromised during sampling or transport, potentially rendering field efforts futile. Population genetic studies on fish frequently require sampling from river transects or remote locations at sea, and so portable laboratories for sampling, storing and extracting DNA would be welcomed. At the same time, emerging technologies, e.g. the MinION USB sequencer (nanoporetech.com/products/minion), have the potential to revolutionise when and where genetic data can be generated. Most new technologies are currently restricted to sequencing small genomes, such as those of bacteria, but with on-going improvements, these technologies open up the possibility of being able to sequence DNA in real-time in the field (Hayden, 2015). Recently, the MinION technology has started to be used in hybrid assemblies with Illumina short reads (Austin et al., 2017)

175 and *de novo* eukaryotic genomes (including fish) are in progress (Jansen et al.,
176 2017).

177 Alongside population genetic studies, research based on whole genome data is
178 emerging, and the genomes of several commercially important species have now
179 been published (e.g. Atlantic cod (*Gadus morhua*), Star et al., 2011; Atlantic salmon
180 (*Salmo salar*), Lien et al., 2016). However, while the ever-reducing cost of whole
181 genome sequencing provides opportunities to sequence and publish more fish
182 genomes, in our view, the key priority is not simply publishing genomes, but also
183 high-quality genome annotation. Gene annotation and accurate knowledge of the
184 function of different identified regions is of extreme importance if genomic tools are
185 to be used reliably in conservation and management (Ekblom & Wolf, 2014).
186 Therefore, projects such as the 'Functional Annotation of All Salmonid Genomes'
187 (Macqueen et al., 2017) should be encouraged and developed. It is also important
188 not to underestimate or neglect the computing power and bioinformatics expertise
189 required to produce high quality genome scaffolds and annotations, and also to
190 recognise and account for biases in next generation sequencing data (see Benestan
191 et al., 2017).

192 Furthermore, population genetic approaches are usually focused on a single
193 species. Consequently, there is a mismatch between studies of a single species
194 genotyped at high resolution, but generally at small spatial scales (e.g. population
195 genetics, often using hundreds to thousands of markers through GBS or GWAS) and
196 studies of multiple species at larger spatial scales but using lower resolution markers
197 (e.g. phylogeography or biodiversity assessments using metabarcoding or mtDNA
198 sequencing). Nonetheless, the widespread application of molecular resources has

199 led to the accumulation of rich datasets across a broad range of species,

200 geographical regions and time periods (Blanchet et al., 2017). Accordingly, we

201 anticipate that this aggregation of data may allow the underlying processes that drive

202 genetic variability across these regions and times to be revealed, enabling a broader

203 testing of theories in population genetics and evolution (Ellegren & Galtier, 2016;

204 Pauls et al., 2014).

205 Such studies will require the combination of high genetic resolution markers across

206 large spatial scales, which is a non-trivial task, especially when dealing with non-

207 model species. Three challenges arise in such cases: firstly, the financial investment

208 required to obtain reliable datasets for several species remains significant. Despite

209 reductions in sequencing costs, it may be financially sensible to rely on more

210 classical markers such as microsatellites or small subsets of single nucleotide

211 polymorphisms (SNPs). Secondly, there is a need for a standardised framework in

212 order to make datasets comparable across different species and regions. This

213 standardisation must occur when collecting samples, characterising markers (e.g.

214 Ellis et al., 2011; Helyar et al., 2011) and during the subsequent data analysis to

215 streamline user choices (Paris et al., 2017), which may bias the biological

216 interpretation of data, see Rodríguez-Ezpeleta et al. (2016). It is therefore important

217 that researchers use common methods to isolate and characterise markers for entire

218 sets of focal species, and/or provide full access to detailed analyses when datasets

219 are generated.

220 Finally, as multi-species approaches remain scarce, there is a need to define

221 hypotheses at the beginning of such investigations. In this respect, simulation tools

222 (e.g. Laval & Excoffier, 2004; Peng & Kimmal, 2005; Neuenschwander, 2006) are

223 particularly useful for testing complex hypotheses and also for predictive purposes.

224 Moreover, the integration of mathematical and statistical models with fish population

225 genetics would be useful for revealing genotype-phenotype interactions (Ritchie et

226 al., 2015), evolutionary signatures (Stark et al., 2007), functional DNA elements

227 (Schrider & Kern, 2014), spatial dynamics (Guillot et al*.,* 2009) and species-genetic

228 diversity correlations (SGDC; Vellend 2003; Vellend et al., 2014).

229

230 *Environmental DNA*

231 The use of environmental DNA (eDNA) to identify the presence and understand the

232 distribution of fish has expanded rapidly in the last decade. eDNA is a polydisperse

233 mixture (Turner et al., 2014; Wilcox et al., 2015) of various biological material

234 ranging from entire cellular fragments to extracellular DNA, which is isolated from

235 environmental samples such as water or sediment. Such techniques are used for

236 species identification and food security purposes. Universal primers that target

237 mitochondrial DNA can be applied for identifying species presence (Yamamoto et al.,

238 2016) or to gain information about species natural history (e.g. food web

239 construction, Sousa et al. (2016)).

240 An important component of this work is validating the results from eDNA surveys

241 with traditional fish survey methods. In both freshwater and marine environments,

242 eDNA has compared favourably to traditional fish survey methods (Thomsen et al.,

243 2012; Hänfling et al., 2016). However, eDNA was found to be less effective

244 compared to experienced snorkel surveys (Ulibarri et al., 2017). This underpins the

245 importance of validation with traditional techniques, especially in spatially

246 heterogeneous and complex aquatic environments (Shogren et al., 2017).

247   The development of effective PCR primers is central to the successful application of

248   eDNA (e.g. Freeland, 2016; MacDonald & Sarre, 2017). As a result, a vast range of

249   primer sets are available for fishes (e.g. Doi et al., 2015; Clusa et al., 2017).

250   Metabarcoding primers, that simultaneously amplify eDNA from many fish species,

251   have also been developed for monitoring entire fish communities (Miya et al., 2015;

252   Valentini et al., 2016).

253   Beyond inferring if a fish species is present in the sampled location, researchers

254   have begun to investigate if eDNA can provide further information regarding fish

255   populations. The use of eDNA to infer population level variation has been

256   demonstrated (Uchii et al., 2015; Sigsgaard et al., 2016), but is still in its infancy.

257   Similarly, although attempts to link eDNA concentration and fish biomass have

258   shown promising results (Lacoursière-Rousse et al., 2016; Yamamoto et al., 2016),

259   further development is required to improve the accuracy of these measurements.

260   However, for techniques utilising eDNA to be optimised, preexisting molecular

261   information needs to be accessible. A number of publicly available databases (e.g.

262   NCBI Genbank and BOLD - boldsystems.org) hold a vast array of molecular data but

263   there is still a need for further mitochondrial genome sequencing to allow optimal

264   usage of molecular identification techniques.

265

266   *Microbiomes*

267   Analysis of a microbiome can provide novel insights into the health and biology of

268   fish populations. Traditional culture-dependent tools used to map the commensal

269 microbiota community in teleost fish are often time-consuming, expensive and

270 subjected to bias as only 0.1-10% of bacteria can be cultured *in vitro* (Amann et al*.,*

271 1995; Austin, 2006). More recently, rapid culture-independent tools such as 16S

272 rRNA targeted sequencing have been utilised to provide detailed profiles of the

273 structure and diversity of the microbiota residing on the mucosal surface of fish

274 (Ghanbari et al*.,* 2015).

275 The gut microbiome composition has also become an important biomarker for

276 understanding the influence of stress in fish (Llewellyn et al., 2014), as numerous

277 stressful stimuli have been shown to alter the microbiome composition (Xia et al*.,*

278 2014; Gaulke et al*.,* 2016). The gut microbiome composition can provide insights into

279 the ecology and physiology of fish in a range of areas such as ecological speciation

280 (Sevellec et al*.,* 2014), the biology of migratory fish (Llewellyn et al., 2016), trophic

281 interactions within ecosystems (Ingerslev et al., 2014) and adaptation to extreme

282 environments (Song et al*.,* 2016).

283 There are a number of challenges currently facing fish microbiome research. At

284 present, the majority of data regarding the microbiome composition in wild teleost

285 fish originates from laboratory models (Tarnecki et al*.,* 2017). More studies are

286 required to see if captive-reared animals provide a reliable analogue for wild

287 populations. Standardised protocols for collecting and generating microbiome data

288 are also lacking, which could restrict progress as several processes have the

289 potential to introduce differential bias in microbiota profiles (e.g. Salipante et al.,

290 2014; Hart et al., 2015). Adopting a framework of robust, quality-controlled protocols

291 (e.g. similar to human microbiome research Methé et al*.,* (2012)) would be of great

292 benefit. In addition, there is currently a lack of non-invasive protocols for conducting

293 longitudinal or repeated sampling of the gut microbial community in individual fish
294 over time. The application of rectal swabs (Budding et al., 2014) for sampling the
295 vent of fish could provide a non-invasive strategy for collecting microbiome data from
296 individuals over time. Finally, time-series data could also enhance our knowledge in
297 terms of the functional aspects of host lifecycles and the stability and resilience of
298 microbiota (Goodrich et al., 2014).

299

300 **Survey Tools**

301 *Field-based surveys*

302 Fish population assessments are conducted using a wide range of techniques; the
303 advantages, limitations, personnel requirements and health and safety
304 considerations of each are presented in Table 1. It is encouraging to note that even
305 well-established methods such as hydro-acoustics are continually being improved,
306 while emerging tools such as eDNA (see above) are beginning to be included in
307 routine monitoring. We suggest that integrating methods and data series are key
308 priorities for future research in this field.

309 In large and complex habitats it is often the case that a suite of survey
310 methodologies has to be employed to sample different times, habitats and species
311 effectively. Indeed, an advantage of field-based surveys is the ability to generate
312 information from both fishery-independent (Nash et al., 2016) and fishery-dependent
313 (Shin et al., 2010) data. However, the availability of a diversity of methodologies, can
314 make the task of assessment in these habitats even more costly; issues also remain

14

Commented [JRP3]: This is now a main table

315 over how to use often disparate data types to develop a sound understanding of a

316 fishery. Integrating methods represents a key means of improving data resolution

317 from such field surveys. For instance, methods such as eDNA and hydro-acoustic

318 sampling provide comparatively fast and non-invasive estimates of fish community

319 structure and biomass. However, to obtain a thorough understanding of fish

320 populations, this information must be combined with fish age, size and health data

321 obtained via destructive sampling (e.g. gill netting). As yet, there are no structured,

322 universally agreed guidelines on which methods should be integrated to obtain a

323 thorough assessment of population dynamics from a specific habitat type.

324 Fish survey methodologies are typically determined at a national level, making

325 international comparisons of data extremely challenging. In recent years,

326 standardised protocols initiated through the EU Water Framework Directive have

327 facilitated Europe-wide assessments of fish community structure. Such international

328 standardisation is essential when assessing the impact of anthropogenic effects on

329 fish (see Gordon et al., 2018), and we recommend that efforts are made to make

330 national datasets available using standardised metadata and biodiversity

331 information, ideally via open sharing platforms (e.g. freshwaterplatform.eu).

332

333 *Historical records*

334 Historical records (e.g. catch records) can also be useful in helping to extrapolate

335 population data back into the recent past. Libraries and historical societies often hold

336 picture archives and these images can in some instances be used as a form of

15

historical survey data to provide information on past community composition and size distributions (McClenachan, 2009). Historical records of catch data are typically held by government agencies or can be found in local archives (e.g. angling club logs) and corporate records. Such data have been used successfully to reconstruct fish populations back to the late 1800s (Thurstan & Roberts, 2010; Thurstan et al., 2010). Catch reconstruction approaches can also provide useful insights into fishery trends that may not be apparent from Food and Agriculture Organization (FAO) reported data alone (Smith & Zeller, 2015; Zeller et al., 2015). Although limited to the information that is still available and subject to the often-unidentifiable biases of the individuals who originally recorded the data, such data can provide a unique way to extrapolate population data back in time.

Statistical and modelling tools

Bayesian methods - Reliable estimates of demographic parameters (e.g. abundance, survival, growth rates and fecundity) and an understanding of the processes that regulate these parameters are fundamental for sustainable management of fish populations. However, to understand the ecological processes and to truly inform policy, researchers must use multiple data sources, provide links between management actions and population responses and also estimate uncertainty as a prerequisite to making forecasts that provide useful information. Bayesian methods in ecology and conservation biology are now increasingly being used to explore these links, for example, in stable isotope analyses (see below). Indeed, the Bayesian framework provides an intuitive method for estimating parameters,

Commented [JP4]: Bayesian techniques are also being used for SIA analyses, and this would provide a link into the next section.

expressing uncertainty in these estimates and allows for the incorporation of as much or as little existing data or prior knowledge that is available (Ellison, 2004). However, to develop the use of this specific framework in fish ecology and management, there is a need to educate and train fish biologists in the use of Bayesian principles and methods.

Individual-based models (IBMs) are process-based mechanistic computer models that simulate emergent properties of fish biology, behaviour, traits or group characteristics, based on simple heuristic functions, and their use has grown exponentially (e.g. DeAngelis & Mooij, 2005) as computational power has increased (DeAngelis & Grimm, 2014). Several separate individual-based models were presented at the 50th Symposium of the FSBI, and, with continued increases in computational power, IBMs look set to offer powerful new avenues for population research (DeAngelis & Grimm, 2014) in computationally challenging multifactor systems such as fish ecotoxicology (e.g. Mintram et al., 2017). Additionally, a variety of tools now exist which provide for the easier creation of new models, such as various R packages (see: derekogle.com/fishR/packages) and programmable environments (e.g. NetLogo; ccl.northwestern.edu/netlogo). However, programs such as R are sometimes not intuitive to new users, and so additional training for fisheries scientists and collaborations between scientists from different computational and statistical backgrounds would be advantageous. For more robust future application of IBMs within fisheries science, there is a need for more assessment of the relative strengths and weaknesses (and potential availability and future development) of the different models.

Commented [JP5]: be good to also highlight NetLogo https://ccl.northwestern.edu/netlogo/

Commented [JP6]: I think this section could include a short paragraph on the availability of cutting-edge frequentist statistical tools within freeware such as R. Example citation could be
Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution, 24, 127-135.

383   Integration with environmental data is a pertinent issue when modelling and is

384   becoming easier through developments in geographic information systems (GIS) and

385   other programming environments (such as R), which now include procedures and

386   libraries for use in ecological work. One example is the use of food web models that

387   integrate environmental data (e.g. Christensen & Walters, 2004) and coral reef

388   ecosystem modelling methods (e.g. Rogers et al., 2014; Weijerman et al., 2015). A

389   hindrance to the integration of environmental data into fisheries science is that it can

390   be difficult to find and access data sources, although availability and accessibility of

391   such data is improving (e.g. worldclim.org). The existence of a central node or hub

392   with paths to these data sources would be useful.

393

394   **Tissue analysis**

395   *Stable isotope ecology*

396   Stable isotopes are now routinely used to quantify the trophic ecology (Boecklen et

397   al., 2011) and migration history (Trueman et al., 2012) of fishes, or to identify

398   community level patterns in food web structure and resource use (Layman et al.,

399   2012). Although the technique is still in its relative infancy, stable isotope ecology

400   has advanced much in recent decades. Below we outline four areas of rapid

401   development with potential to enhance the applicability of this tool to studies of fish

402   biology.

403   *Biochemical mechanism:* The relationship between the isotopic composition of a

404   consumer's tissues and that of its prey is fundamental to all applications of stable

Commented [JP7]: Also you could highlight the use of food web models to integrate data eg Christensen, V. & Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172, 109-139.
Weijerman, M., Fulton, E.A., Kaplan, I.C., Gorton, R., Leemans, R., Mooij, W.M. & Brainard, R.E. (2015) An integrated coral reef ecosystem model to support resource management under a changing climate. PLoS ONE, 10, e0144165.
Rogers, A., Blanchard, J.L. & Mumby, P.J. (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Current Biology, 24, 1000-1005.

18

405　isotopes in ecology. However, while general principles are clear (i.e. faster reaction

406　rates and preferential incorporation of light isotopes into excretory metabolites a

407　process termed trophic fractionation (DeNiro & Epstein, 1977)), the precise

408　mechanisms leading to fractionation and, particularly, the extent of isotopic

409　fractionation expected under differing physiological conditions cannot currently be

410　predicted, primarily due to the complexity of amino acid biochemistry. Uncertainties

411　associated with the isotopic expression of tissue composition, and relative rates of

412　tissue growth and regeneration further complicate the interpretation of stable isotope

413　values in ecology. However, recent information gained from compound-specific

414　isotope analysis (i.e. assessing isotopic compositions of single amino acids) is

415　beginning to shed light on the fractionation process (McMahon & McCarthy, 2016).

416　*Population-level data:* The distribution of isotopic compositions of individuals within a

417　population (often termed the 'isotopic niche', Newsome et al., 2007) has been

418　proposed as a powerful comparative measure of population-level ecological

419　characters. However, in addition to individual variability in consumers, the distribution

420　of isotopic compositions in a population is influenced by spatial and temporal

421　variations in the isotopic composition of primary production, temporal variability

422　within trophic linkages and differential rates of growth and isotopic assimilation

423　(Gorokhova, 2017). Very few studies have attempted to combine ecological and food

424　web theory with isotope systematics to explore the sensitivity of community isotopic

425　metrics to changes in food web structure and function.

426　*IsoBank:* To date, applications of stable isotopes to fish biology have predominantly

427　focussed on analyses of specific populations or communities. The absence of a

428　centralised, open-access repository for stable isotope data restricts the opportunity

429 for syntheses or meta-analyses of stable isotope data (Pauli et al., 2017). Recent

430 efforts to address this have found broad support from the stable isotope research

431 community (Pauli et al., 2017) and would be especially beneficial to fish biologists

432 due to the large amount of fish isotope data currently available. Defining an ontology

433 of stable isotope metadata, information required to describe and interpret isotope

434 data, for fish biologists is an immediate requirement in this regard.

435 *Marine isoscapes:* The stable isotope ratios of a consumer's tissue encode the

436 resources (water, air, prey etc.) it was using when that tissue was formed. As such,

437 provided one has access to a suite of isotopic baseline measurements (e.g. water,

438 plants and primary consumers), it is possible to trace an organisms route through

439 space and time up to the point of capture (Trueman et al., 2012). Creation of a

440 practically useful isoscape requires relatively dense sampling of a reference

441 organism across space (and potentially time). Bulk stable isotope analyses are now

442 routine, commonly available globally, and relatively cheap, and regional marine

443 isoscape models are being developed at a rapid rate (MacKenzie et al., 2014; Kurle

444 & McWhorter, 2017). In the open ocean, sample-based isoscapes are difficult to

445 develop, but progress is being made in isotope-enabled global biogeochemical

446 models (Magozzi et al., 2017), offering temporal and spatial models of expected

447 isotopic variability at global scales. Improving the precision, accuracy and availability

448 of these baseline measurements will increase the robustness and precision of

449 isotope based estimates animal position.

450

451 *Archaeological material*

452 Archaeological material can allow an otherwise impossible snapshot into past
453 populations. Traditional morphological approaches can provide age distributions and
454 species ranges, and, with the rapid development of biomolecular archaeology in the
455 past 20 years, many of the techniques used to explore modern fish populations can
456 now be used to look into the past. From ancient DNA to proteomics, and isotopes to
457 lipids, a wide range of biomolecules have been recovered and explored from
458 archaeological material (Orton, 2016). For example, compound-specific isotope
459 analysis has the potential to track trophic level changes through time (McClelland &
460 Montoya, 2002; Naito et al., 2016). Population genetics of extinct populations have
461 been successfully explored in terrestrial animals (Chang & Shapiro, 2016; Murray et
462 al., 2017) and these same techniques can be used on fish bones to reconstruct past
463 genetics (Iwamoto et al., 2012; Ólafsdóttir et al., 2014). Ideally these data will be
464 used to understand environmental and anthropogenic effects on fish populations and
465 how modern fish populations might respond to climate change and fishing pressures.

466 A major barrier to the use of archaeological fish material is the fact that less than
467 10% of fish bones are identified to species (Wheeler & Jones, 1989; Gobalet, 2001)
468 and much of what is identified is buried in the 'grey literature' of archaeological
469 reports that are often not digitised and printed in small quantities (Linden & Webley,
470 2012). This makes the material relevant to an ecological question very difficult to
471 find. Archaeologists are working towards ways to improve the amount of bones
472 identified by better reference collections and education on fish bones (National
473 Zooarchaeological Reference Resource, Nottingham's Archaeological Fish
474 Resource, Vertebra@UWF) and on creating searchable databases of archaeological
475 material (Callou, 2009; Kansa, 2010). In addition, new ZooMS (Zooarchaeology by
476 Mass Spectrometry) techniques are being explored to quickly identify even small

477   bones and scales to species using peptide mass fingerprinting (Richter et al.*, 2011)

478   which will allow even more material to be identified in a useful way for those working

479   on understanding fish populations. In the near future, it should be possible for

480   modern fish biologists, in conjunction with archaeologists, to ask direct questions of

481   past populations (Van Neer & Ervynck, 2010).

482

General topics identified as applicable across all themes

Management of data: integration, calibration and standardisation

485   Progression of an integrated management framework for data classification,

486   characterisation, storage and accessibility would be a valuable resource for fish and

487   fisheries biologists. FishBase, which at the time of writing contains information

488   regarding 33,600 fishes, involving 2290 collaborators, and receives over 600,000

489   visits per month, is an example of the potential for such a resource (see: fishbase.org;

490   Froese & Pauly, 2017). A single database for all types of fish data (for example,

491   DNA, tagging, isotopes, diet) is probably unworkable, but the advent of application

492   programming interfaces (API) and analytical software which allows automated

493   querying across multiple databases represents an unprecedented opportunity to

494   access a wealth of global data. Indeed, we suggest that more data (such as those

495   discussed here) could be integrated into FishBase. However, such resources require

496   significant funding and long-term commitment from governments and trans-national

497   organisations, e.g. NASCO.

498

Commented [JRS8]: why not suggest the integration of these data into Fishbase?

499 *Public engagement, education and outreach*

500 Scientific engagement with the public is essential to effect meaningful societal
501 change or to ensure a wider consensus is made around new discoveries or ethical
502 considerations. Additionally, however, the power of the public as a "tool" in science is
503 also being increasingly recognised. 'Crowdfunding', whereby a scientist requests
504 small amounts of money from a large number of interested individuals to
505 successfully launch a project, potentially provides a powerful new way to raise funds,
506 overcoming some of the difficulties of raising money from traditional grant bodies,
507 especially for early career researchers or those in developing countries (Wheat et al.,
508 2013).

509 In addition to funding science, the public can also actively engage in the process of
510 research directly through citizen science projects. Whilst research conducted by non-
511 professionals is certainly not a new concept, the numbers of projects involving citizen
512 scientists are growing, especially in the fields of environmental science and ecology
513 (Silverton, 2009). Through catch records of amateur anglers and commercial net
514 fishery data extending back many years, research into fish and fisheries is uniquely
515 placed to benefit from citizen science projects (Stuart-Smith et al., 2013), which have
516 effectively spanned generations of contributors. Similarly, REEF (reef.org) has been
517 collecting reef fish diversity and abundance data from trained volunteer divers for 27
518 years, and the data have been successfully leveraged in hundreds of publications
519 (e.g. Stallings, 2009; Serafy et al., 2015). Citizen science can also help achieve
520 important social outcomes, e.g. in establishing sustainable fisheries and marine
521 protected areas, MPAs (Bonney et al., 2014). And, as with crowdfunding, the best

522 examples of citizen science typically encourage deeper engagement with the public,

523 and offer a pathway to the democratisation of science.

524

525 *Fisheries policy and governance*

526 Conserving critical habitats is central to the sustainable management of fish species

527 and populations. Marine Protected Areas (MPAs), networks of MPAs and Marine

528 Conservation Zones (MCZs) are widely accepted management tools for fish and

529 other marine organisms that have been established in many countries (Harborne et

530 al., 2008; OSPAR, 2013). However, the design of MPA networks could benefit

531 greatly from the integration of traditional survey data, along with modelling and

532 connectivity data (Botsford et al., 2009; Grüss et al., 2014). From a social science

533 perspective, there is a need to better understand public perceptions of marine-

534 related conservation issues, e.g. fishery regulations, MPAs and MCZs, and to

535 incorporate these data into fisheries policy and governance frameworks. For

536 example, there is high public support for MPAs, with surveys showing that people

537 desire around 40% of the UK's marine waters to be protected (Hawkins et al., 2016).

538 But, while the public appears to realise that in reality levels of coverage are well

539 below 40%, there is still a substantial disconnect between perceived coverage of

540 highly protected UK MPAs (11%) and actual MPA coverage (<0.1%); ultimately, this

541 means that people believe the UK oceans receive a higher level of conservation than

542 in reality they do (Hawkins et al., 2016). Developing and implementing effective

543 policies for fisheries management remains challenging because of the complexities

544 of fisheries and the socio-political landscape under which they typically operate

24

Commented [JP9]: I felt this section and the next (Aquaculture) felt out of place for the scope of the paper, and could be cut. The paper has a nice focus on tools for studying fish and fisheries, and these sections move towards conservation science. Each is a huge topic that can only be covered very briefly, and the reader is left wondering why the authors don't address quotas, gear restrictions, management of migrating species and so on.

Commented [JS10]: I know what Ref 2 means, but I'd like to keep it in. Certainly, from one view point, MPAs do constitute an important tool in fisheries conservation and management.

(Jentoft & Chuenpagdee, 2009). However, the establishment of guidelines or frameworks for fisheries policy and governance (e.g. FAO Voluntary Guidelines for Securing Sustainable Small-Scale Fisheries) have the potential to better address these challenges and provide appropriate implementable solutions.

Conclusions

Across all five of the research themes identified here, it is clear that innovative and novel tools are being employed to understand all aspects of the biology of fish populations. Notwithstanding, the authors call for the continued development of these new and emerging techniques. In particular, there is a need for better integration of these methods and resulting data, to inform scientifically sound management and conservation of fish populations.

However, it should be noted that, not infrequently, revolutionary methods have been pedestalled as providing the ability to offer unprecedented novel answers to long-standing practical problems. Unfortunately, the danger is that such methods can (by their novelty and the excitement surrounding them), blinker scientists into posing questions that showcase the methodology, rather than the biology (for example, the plethora of papers that emerged in the early 1990s extolling the virtues of the random amplified polymorphic DNA (RAPD) technique). The potentially reduced power of using any technique on its own (new or otherwise), in isolation of other apparently 'antiquated' methods can turn out to be unnecessarily restrictive. Every technique has its limitations, but often the restrictions of one tool can be substantially alleviated by the inclusion of another approach (e.g. Goodwin et al., 2016; Nielson et al., 2017), the marriage of which can provide a new angle for researching

25

Commented [JRS11]: Entire Aquaculture section deleted.

Commented [JP12]: the conclusions make some interesting points about combining techniques, but I think it also needs to call for the continued development of new and emerging techniques, since this is a focus of the paper.

569 challenging biological problems. It is important that both traditional and emerging

570 tools remain in the toolbox of fish biology research.

571 Likewise, when genetic-based assignment became popular, many researchers

572 naively believed the days of tagging fish were over. It is now realised that due to the

573 many stochastic drivers of population structure, genetic stock identification-based

574 methodologies such as genetic assignment, do not always succeed. In such cases,

575 there remains a significant role for tagging in fisheries research. As tag sizes

576 decrease, and the deleterious effects of tag insertions on fish also decrease, we can

577 anticipate that genetics and tagging will both continue to have a role to play. The

578 importance of the relative roles of each technique will depend on the questions being

579 addressed, the population structure of the study species, and the scale of the

580 questions being assessed.

581 A final example, which highlights the importance of applying inter-disciplinary and

582 complimentary tools for understanding fish populations, was a five-year, multi-

583 agency, EU-funded project investigating the migration and distribution of Atlantic

584 salmon (*Salmo salar* L.) in the north-east Atlantic (the SALSEA project; NASCO

585 2008). The purpose was to understand not just where salmon go, but what they eat,

586 migration routes to feeding grounds, and which waters and regions they pass

587 through. The SALSEA project used a combination of genetics (microsatellites),

588 stable isotope analysis, at-sea trawls, tagging and gut contents analysis to assess

589 the movements and diet of Atlantic salmon across the north-east Atlantic Ocean. As

590 a result of applying these combined approaches, salmon post-smolt movements

591 have been confidently ascertained (Gilbey et al., 2017). Nonetheless, even while this

592 comprehensive study was being finalised, a similarly broad-ranging study was also

593 being undertaken using SNPs (Bourret et al., 2013). Arguably, this method offers

594 both the potential for finer levels of stock discrimination and the ability to better

595 explore patterns among functional loci, which may make microsatellite-based

596 analysis redundant within a short period of time (though see Narum et al., 2008).

597 Thus, the authors consider the continued development of emerging tools, together

598 with the use of multiple methodologies and inter-disciplinary approaches, to

599 represent the best avenues for further improving our understanding of fish

600 populations. We implore scientists from unrelated fields to collaborate on such

601 projects. The FSBI 50th Anniversary Symposium represented one such event, where

602 fish-focused researchers across diverse fields, came together to advance the state

603 of fish biology.

604 **Acknowledgements**

609

References

610 **References**

611 Allendorf, F. W., Hohenlohe, P. A. & Luikart, G. (2010). Genomics and the future of
612 conservation genetics. *Nature Reviews Genetics,* **11**, 697–709. doi:10.1038/nrg2844

613 Amann, R. I., Ludwig, W. & Schleifer, K. H. (1995). Phylogenetic identification and in
614 situ detection of individual microbial cells without cultivation. *Microbiological*
615 *Reviews*, **59** 143-169.

616 Austin, B. (2006). The bacterial microflora of fish, revised. *The Scientific World*
617 *Journal* **6**, 931-945. doi: 10.1100/tsw.2006.181.

618 Austin, C. B., Hua Tan, M., Harrisson, K. A., Peng Lee, Y., Croft, L. J., Sunnucks,
619 P., Pavlova, A. & Ming Gan, H. (2017). *De novo* genome assembly and annotation
620 of Australia's largest freshwater fish, the Murray cod (*Maccullochella peelii*) from
621 Illumina and Nanopore sequencing reads. *Gigascience* gix063. doi:
622 10.1093/gigascience/gix063.

623 Benestan L, Moore J-S, Sutherland BJG, *et al.* (2017). Sex matters in massive
624 parallel sequencing: Evidence for biases in genetic parameter estimation and
625 investigation of sex determination systems. *Molecular Ecology,* 00:1–17.
626 https://doi.org/10.1111/mec.14217.

627 Blanchet, S., Prunier, J. G. & De Kort, H. (2017). Time to go bigger: emerging
628 patterns in macrogenetics. *Trends in Genetics*, (Online) doi:
629 10.1016/j.tig.2017.06.007

630 Boecklen, W. J., Yarnes, C. T., Cook, B. A., & James, A. C. (2011). On the Use of
631 Stable Isotopes in Trophic Ecology. *Annual Review of Ecology, Evolution, and*
632 *Systematics*, **42**, 411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726.

633 Bograd, S. J., Block, B. A., Costa, D. P. & Godley, B. J. (2010). Biologging
634 technologies: New tools for conservation. Introduction. *Endangered Species*
635 *Research* **10**, 1-7. doi: 10.3354/esr00269.

636 Bonney, R., Shirk, J. L., Phillips, T. B., Wiggins, A., Ballard, H. L., Miller-Rushing, A.
637 J. & Parrish, J. K. (2014). Next steps for citizen science. *Science* **343**, 1436-1437.
638 doi: 10.1126/science.1251554.

639 Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B. Largier, J., O'Farell, M.
640 R., Ralston, S., Soulanile, E. & Wespestad, V. (2009). Connectivity, sustainability,
641 and yield: bridging the gap between conventional fisheries management and marine
642 protected areas. *Reviews in Fish Biology Fisheries* **19,** 69−95. doi: 10.1007/s11160-
643 008-9092-z.

644 Bourret, V., Kent, M.P., Primmer, C. R. et al. (2013). SNP-array reveals genome-
645 wide patterns of geographical and potential adaptive divergence across the natural
646 range of Atlantic salmon (*Salmo salar*). *Molecular Ecology*, **22**, 532–551.

647 Budding, A. E., Grasman, M. E., Eck, A., Bogaards, J. A., Vandenbroucke-Grauls, C.
648 M., van Bodegraven, A. A. & Savelkoul, P. H. (2014). Rectal swabs for analysis of
649 the   intestinal   microbiota.   *PLoS   One*   **9**(7):   e101344.
650 https://doi.org/10.1371/journal.pone.0101344.

651   Callou, C. (2009). Inventaires archéozoologiques et archéobotaniques de France

652   (Inventaire National Du Patrimoine Naturel). *Muséum National d'Histoire Naturelle*.

653   Chang, D., and Shapiro, B. (2016). Using ancient DNA and coalescent-based

654   methods to infer extinction. *Biology Letters*, **12**(2), 20150822.

655   Chistiakov, D. A., Hellemans, B. & Volckaert, F.A.M. (2006). Microsatellites and their

656   genomic distribution, evolution, function and applications: A review with special

657   reference to fish genetics. *Aquaculture*, **255**, 1–29.

658   Christensen, V. & Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities

659   and limitations. *Ecological Modelling*, **172**, 109-139.

660   Clusa, L., Ardura, A., Fernández, S., Roca, A. A. & García-Vázquez, E. (2017). An

661   extremely sensitive nested PCR-RFLP mitochondrial marker for detection and

662   identification of salmonids in eDNA from water samples. *PeerJ* **5**, p.e3045.

663   Cooke, S. J., Brownscombe, J. W., Raby, G. D., Broell, F., Hinch, S. G., Clark, T. D.,

664   & Semmens, J. M. (2016). Remote bioenergetics measurements in wild fish:

665   opportunities and challenges. *Comparative Biochemistry and Physiology Part A:*

666   *Molecular & Integrative Physiology*, **202**, 23-37.

667   Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B.,

668   Eiler, J., Holbrook, C. & Ebner, B. C. (2013). Tracking animals in freshwater with

669   electronic tags: past, present and future. *Animal Biotelemetry*, **1**, 5.

670 Dahlgren, C. P., Buch, K., Rechisky E. & Hixon M. A. (2016). Multiyear tracking of
671 Nassau grouper spawning migrations. *Marine and Coastal Fisheries: Dynamics,*
672 *Management, and Ecosystem Science*, **8**, 522–535. DOI:
673 10.1080/19425120.2016.1223233.

674 Davis, R. M., Baumgartner, A. Comeau, D. Cunningham, K. Davies, A. Furlong, H.
675 Johnson, S. L'Orsa, T. Ross, C. Taggart, F. Whoriskey & Ieee. (2016). Tracking
676 whales on the Scotian Shelf using passive acoustic monitoring on ocean gliders.
677 Oceans 2016 Mts/Ieee Monterey.

678 DeAngelis D. L. & Grimm, V. (2014). Individual-based models in ecology after four
679 decades. *F1000Prime Reports*, **6**, 39 (doi:10.12703/P6-39)

680 DeAngelis, D. L. & Mooij, W. M. (2005). Individual-based modelling of ecological and
681 evolutionary processes. 1. *Annual Review of Ecology, Evolution, and Systematics*,
682 **36**, 147–168.

683 DeNiro, M. J. & Epstein, S. (1977). Mechanism of carbon isotope fractionation
684 associated with lipid synthesis. *Science,* **197**, 261–263.

685 Doi, H., Uchii, K., Takahara, T., Matsuhashi, S., Yamanaka, H. & Minamoto, T.,
686 (2015). Use of droplet digital PCR for estimation of fish abundance and biomass in
687 environmental DNA surveys. *PLoS One* **10**, p.e0122763.

688 Ekblom, R. & Wolf, J. B. W. (2014). A field guide to whole-genome sequencing,
689 assembly and annotation. *Evolutionary Applications,* **7**, 1026–1042.

690   Ellegren, H. & Galtier, N. (2016). Determinants of genetic diversity. *Nature Reviews*
691   *Genetics,* **17**, 422–433. https://doi.org/10.1038/nrg.2016.58.

692   Ellis, J. S., Gilbey, J., Armstrong, A., Balstad, T., Cauwelier, E., Cherbonnel, C.,
693   Consuegra, S. et al. (2011). Microsatellite standardization and evaluation of
694   genotyping error in a large multi-partner research programme for conservation of
695   Atlantic salmon (*Salmo salar* L.). *Genetica*, **139**, 353–367.

696   Ellison, A. M. (2004). Bayesian Inference in Ecology. *Ecology Letters,* **7**, 509–520.

697   FAO. (2014). The state of world fisheries and aquaculture opportunities and
698   challenges FAO, Rome. p. 7.

699   Ferguson, M.M. & Danzmann, R.G. (1998). Role of genetic markers in fisheries and
700   aquaculture: useful tools or stamp collecting? *Canadian Journal of Fisheries and*
701   *Aquatic Sciences*, **55**, 1553-1563.

702   Freeland, J. R. (2016). The importance of molecular markers and primer design
703   when characterizing biodiversity from environmental DNA. *Genome,* **60**, 358-374.

704   Froese, R. & Pauly, D. (2017) Editors. FishBase. World Wide Web electronic
705   publication: www.fishbase.org, (06/2017).

706   Gaulke, C. A., Barton, C. L., Proffitt, S., Tanguay, R. L. & Sharpton, T. J. (2016).
707   Triclosan exposure is associated with rapid restructuring of the microbiome in adult
708   zebrafish. *PloS One*, **11**. doi: 10.1371/journal.pone.0154632

709 Ghanbari, M., Kneifel, W. & Domig, K. J. (2015). A new view of the fish gut
710 microbiome: advances from next-generation sequencing. *Aquaculture,* **448**, 464-475.
711 doi: 10.1016/j.aquaculture.2015.06.033

712 Gilbey J., Coughlan, J., Wennevik, V., Prodöhl, P. Stevens, J. R., Garcia de Leaniz,
713 C., Ensing, D., Cauwelier, E., Cherbonnel, C., Consuegra, S., Coulson, M. W.,
714 Cross, T. F., Crozier, W., Dillane, E., Ellis, J. S., García-Vázquez, E., Griffiths, A. M.,
715 Gudjonsson, S., Hindar, K., Karlsson, S., Knox, D., Machado-Schiaffino, G.,
716 Meldrup, D., Nielsen, E. E., Ólafsson, K., Primmer, C. R., Prusov, S., Stradmeyer, L.,
717 Vähä, J.-P., Veselov, A. J., Webster, L. M. I., McGinnity, P. & Verspoor, E. (2017) A
718 microsatellite baseline for genetic stock identification of European Atlantic salmon
719 (*Salmo salar* L.). *ICES journal of Marine Science*, fsx184,
720 https://doi.org/10.1093/icesjms/fsx184.

721 Gobalet, K.W. (2001). A critique of faunal analysis; inconsistency among experts in
722 blind tests. *Journal of Archaeological Science*, **28**, 377e386.

723 Goodrich, J. K., Di Rienzi, S. C., Poole, A. C., Koren, O., Walters, W. A., Caporaso,
724 J. G., Knight, R. & Ley, R. E. (2014). Conducting a microbiome study. *Cell* **158**, 250-
725 262. doi: 10.1016/j.cell.2014.06.037.

726 Goodwin, J. C. A., Andrew King, R., Iwan Jones, J., Ibbotson, A. & Stevens, J. R.
727 (2016). A small number of anadromous females drive reproduction in a brown trout
728 (*Salmo trutta*) population in an English chalk stream. *Freshwater Biology,* **61**, 1075–
729 1089.

730 Gordon, T.A.C., Harding, H.R., Clever, F.K., Davidson, I.K., Davison, W.,
731 Montgomery, D.W., Nedelec, S.L., Weatherhead, R.C., Windsor, F.M., Armstrong,

732 J.D., Bardonnet, A., Bergman, E., Britton, J.R., Côté, I.M., D'Agostino, D.,
733 Greenberg, L.A., Harborne, A.R., Kahilainen, K.K., Metcalfe, N.B., Mills, S.C., Milner,
734 N.J., Mittermayer, F.H., Montorio, L., Prokkola, L.A., Rutterford, L.A., Salvanes,
735 A.G.V., Simpson, S.D., Vainikka, A., Pinnegar, J.K., Santos, E.M. (2018). Fishes in a
736 changing world: learning from the past to promote sustainability of fish populations.
737 *Journal of Fish Biology,* (In review, this issue).

738 Gorokhova E. (2017). Individual growth as a non-dietary determinant of the isotopic
739 niche metrics. *Methods Ecol Evol,* 00,1–9. https://doi.org/10.1111/2041-210X.12887.

740 Gruss, A., Robinson, J., Heppell, S. S., Heppell, S. A., & Semmens, B. X. (2014).
741 Conservation and fisheries effects of spawning aggregation marine protected areas:
742 What we know, where we should go, and what we need to get there. *ICES Journal of
743 Marine Science*, **71**, 1515–1534. https://doi.org/10.1093/icesjms/fsu038

744 Guillot, G., Leblois, R., Coulon, A. & Frantz, A. C. (2009). Statistical methods in
745 spatial genetics. *Molecular Ecology,* **18***, 4734–4756.* doi:10.1111/j.1365-
746 294X.2009.04410.x.

747 Halfyard, E. A., Webber, D., Del Papa, J., Leadley, T., Kessel, S. T., Colborne, S. F.
748 and Fisk, A. T. (2017), Evaluation of an acoustic telemetry transmitter designed to
749 identify predation events. *Methods Ecol Evol*. doi:10.1111/2041-210X.12726.

750 Hänfling, B., Lawson Handley, L., Read, D.S., Hahn, C., Li, J., Nichols, P.,
751 Blackman, R.C., Oliver, A. and Winfield, I.J., 2016. Environmental DNA
752 metabarcoding of lake fish communities reflects long‐term data from established
753 survey methods. *Molecular Ecology*, **25**, 3101-3119.

34

754 Harborne, A. R., Mumby, P. J., Cappel, C. V., Dahlgren, C. P., Micheli, F., Holmes,
755 K. E., Sanchirico, J. E., Broad, K., Elliot, I. A., Brumbaugh, D. R. (2008) Reserve
756 effects and natural variation in coral reef communities. *Journal of Applied Ecology*
757 **45**, 1010–1018.

758 Hart, M. L., Meyer, A., Johnson, P. J. & Ericsson, A. C. (2015). Comparative
759 evaluation of DNA extraction methods from feces of multiple host species for
760 downstream next-generation sequencing. *PloS ONE*, **10**, e0143334. doi:
761 10.1371/journal.pone.0143334.

762 Hawkins, J. P., O'Leary, B. C., Bassett, N., Peters, H., Rakowski, S., Reeve, G., and
763 Roberts, C. M. (2016). Public awareness and attitudes towards marine protection in
764 the United Kingdom. *Marine Pollution Bulletin*, **111**, 231–236.

765 Hayden, E. C. (2015). Pint-sized DNA sequencer impresses first users. *Nature,* **521**,
766 15-16.

767 Hays, G. C., C. J. A. Bradshaw, M. C. James, P. Lovell, and D. W. Sims. (2007).
768 Why do Argos satellite tags deployed on marine animals stop transmitting? *Journal*
769 *of Experimental Marine Biology and Ecology*, **349**:52-60.

770 Helyar, S. J., Hemmer-Hansen, J., Bekkevold, D., Taylor, M. I., Ogden, R., Limborg,
771 M. T., Cariani, A., Maes, G. E., Dopere, E., Carvalho, G. & Nielsen, E. E. (2011).
772 Application of SNPs for population genetics of nonmodel organisms: new
773 opportunities and challenges: analytical approaches. *Molecular Ecology Resources*
774 **11**, 123–136.

775 Heupel, M.R., Semmens, J.M. & Hobday, A.J. (2006) Automated acoustic tracking of

776 aquatic animals: scales, design and deployment of listening station arrays. *Marine*

777 *and Freshwater Research*, **57**, 1-13.

778 Hight, B. V. & Lowe, C. G. (2007). Elevated body temperatures of adult female

779 leopard sharks, Triakis semifasciata, while aggregating in shallow nearshore

780 embayments: Evidence for behavioral thermoregulation? *Journal of Experimental*

781 *Marine Biology and Ecology* **352**, 114-128.

782 Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T.,

783 Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Flemming, J. E. M. &

784 Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the

785 underwater world. *Science* **348**, 1221- 1255642. doi: 10.1126/science.1255642.

786 Ingerslev, H. C., von Gersdorff Jørgensen, L., Strube, M. L., Larsen, N., Dalsgaard,

787 I., Boye, M. & Madsen, L. (2014). The development of the gut microbiota in rainbow

788 trout (*Oncorhynchus mykiss*) is affected by first feeding and diet type. *Aquaculture*,

789 **424**, 24-34. doi: 10.1016/j.aquaculture.2013.12.032

790 Iwamoto, E. M., Myers, J. M., and Gustafson, R. G. (2012). Resurrecting an extinct

791 salmon evolutionary significant unit: archived scales, historical DNA and implication

792 for restoration. *Molecular Ecology*, **21**, 1567-1582.

793 Jansen, H.J., M., Liem, S. A., Jong-Raadsen, S., Dufour, F-A., Weltzien, W.,

794 Swinkels, A., Koelewijn, A. P., Palstra, B., Pelster, H. P., Spaink, G. E., Van den

795 Thillart, Dirks, R. P. & Henkel, C. V. (2017). Rapid de novo assembly of the

European eel genome from nanopore sequencing reads. *bioRxiv* 101907. doi: 10.1101/101907.

Jentoft, S., & Chuenpagdee, R. (2009). Fisheries and coastal governance as a wicked problem. *Marine Policy,* **33**, 553-560. doi: 10.1016/j.marpol.2008.12.002.

Jepsen, N., Thorstad, E. B., Havn, T. & Lucas, M. C. (2015). The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Animal Biotelemetry,* **3**, 49. 10.1186/s40317-015-0086-z.

Kansa, E. C. (2010). Open context in context: Cyberinfrastructure and distributed approaches to publish and preserve archaeological data. *The SAA Archaeological Record*, **10**, 12–16.

Kurle, C. M. & McWhorter, J. (2017) Spatial and temporal variability within marine isoscaes: implications for interpreting stable isotope data from marine systems. *Marine Ecology Progress Series,* **568**, 31-45. doi 10.3354/meps12045.

Lacoursière-Roussel, A., Rosabal, M. & Bernatchez, L. (2016). Estimating fish abundance and biomass from eDNA concentrations: variability among capture methods and environmental conditions. *Molecular Ecology Resources*, **16**, 1401-1414.

Lauridsen, R. B., Moore, A., Privitera, L. Gregory, S. D., Beaumont, W. R. C. & Kavanagh, A. J. (2017). Migration behaviour and loss rate of trout smolts in the transitional zone between freshwater and saltwater In: *Sea Trout: Science &*

816 *Management*. (Graeme Harris, *Ed.*). *Proceedings of the 2nd International Sea Trout*

817 *Symposium, October 2015, Dundalk, Ireland*, 292-307.

818 Laval, G. & Excoffier, L. (2004). SIMCOAL 2.0: a program to simulate genomic

819 diversity over large recombining regions in a subdivided population with a complex

820 history. *Bioinformatics*, **20,** 2485-7. DOI: 10.1093/bioinformatics/bth264.

821 Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E.,

822 Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M. &

823 Bearhop, S. (2012), Applying stable isotopes to examine food-web structure: an

824 overview of analytical tools. *Biological Reviews* **87**, 545–562. doi:10.1111/j.1469-

825 185X.2011.00208.x.

826 Lea, J. S. E., N. E. Humphries, R. G. von Brandis, C. R. Clarke & D. W. Sims.

827 (2016). Acoustic telemetry and network analysis reveal the space use of multiple reef

828 predators and enhance marine protected area design. *Proceedings of the Royal*

829 *Society of London B: Biological Sciences* **283.**

830 Lien, S., Koop, B. F., Sandve, S. R., Miller, J. R., Matthew, P., Leong, J. S., Minkley,

831 D. R., Zimin, A., Grammes, F., Grove, H. et al. (2016) The Atlantic salmon genome

832 provides insights into rediploidization. *Nature,* **533**, 200–205.

833 Linden, M. V. & Webley, L. (2012). Introduction: Development-led Archaeology in

834 North-West Europe. In R. Bradley, C. Haselgrove, M. V. Linden & L. Webley (Eds.),

835 *Development-led Archaeology in North-West Europe*. Oxbow Books.

836 Llewellyn, M. S., Boutin, S., Hoseinifar, S. H. & Derome, N. (2014). Teleost

837 microbiomes: the state of the art in their characterization, manipulation and

importance in aquaculture and fisheries. *Frontiers in Microbiology,* **5**. doi: 10.3389/fmicb.2014.00207.

Llewellyn, M. S., McGinnity, P., Dionne, M., Letourneau, J., Thonier, F., Carvalho, G. R., Creer, S. & Derome, N. (2016). The biogeography of the Atlantic salmon (*Salmo salar*) gut microbiome. *The ISME journal* **10**, 1280-1284. doi: 10.1038/ismej.2015.189.

MacDonald, A. J. & Sarre, S. D. (2017). A framework for developing and validating taxon‐specific primers for specimen identification from environmental DNA. *Molecular Ecology Resources,* **17**, 708-720.

MacKenzie, K. M., Longmore, C., Preece, C., Lucas, C. H., Trueman, C. N. (2014). Testing the long-term stability of marine isoscapes in shelf seas using jellyfish tissues. *Biogeochemistry,* **121**, 441-454. doi: 10.1007/s10533-014-0011-1.

Macqueen, D. J., Primmer, C. R., Houston, R. D., Nowak, B. F., Bernatchez, L., Bergseth, S., Davidson, W. S., Gallardo-escárate, C., Goldammer, T., Guiguen, Y., et al. (2017). Functional Annotation of All Salmonid Genomes (FAASG): An international initiative supporting future salmonid research, conservation and aquaculture. *BMC Genomics,* **18**, 1–9.

Magozzi, S. Yool, A., VanderZanden, H.B., Wunder, M.B., Trueman, C.N. (2017). Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere,* **8**, e01763. doi: 10.1002/ecs2.1763.

39

858   McClelland, J. W., and Montoya, J. P. (2002). Trophic relationships and the nitrogen

859   isotopic composition of amino acids in plankton. *Ecology*, **83**(8), 2173-2180.

860   McClenachan, L. (2009). Documenting loss of large trophy fish from the Florida Keys

861   with historical photographs. *Conservation Biology*, **23**(3), 636–643.

862   McMahon, K. W. & McCarthy, M. D. (2016). Embracing variability in amino acid δ^{15}N

863   fractionation: mechanisms, implications, and applications for trophic tcology.

864   *Ecosphere* **7**, e01511.

865   Methé, B. A., Nelson, K. E., Pop, M., Creasy, H. H., Giglio, M. G., Huttenhower, C.,

866   Gevers, D., Petrosino, J. F., Abubucker, S., Badger, J. H. & Chinwalla, A.T. (2012).

867   A framework for human microbiome research. *Nature,* **486**, 215-221. doi:

868   10.1038/nature11209.

869   Methling, C., Tudorache, C., Skov, P. V. & Steffensen, J. F. (2011). Pop Up Satellite

870   Tags Impair Swimming Performance and Energetics of the European Eel (*Anguilla

871   anguilla*). *Plos One,* **6**, e20797. doi: 10.1371/journal.pone.0020797.

872   Mintram, K. S., Brown, A. R., Maynard, S. K., Thorbek, P. & Tyler, C. R. (2017).

873   Capturing ecology in modeling approaches applied to environmental risk assessment

874   of endocrine active chemicals in fish. *Critical Reviews in Toxicology*, DOI:

875   10.1080/10408444.2017.1367756

876   Miya, M., Sato, Y., Fukunaga, T., Sado, T., Poulsen, J.Y., Sato, K., Minamoto, T.,

877   Yamamoto, S., Yamanaka, H., Araki, H. & Kondoh, M. (2015). MiFish, a set of

878   universal PCR primers for metabarcoding environmental DNA from fishes: detection

879   of more than 230 subtropical marine species. *Open Science* **2**, 150088. DOI:

880   Murchie, K.J., Shultz, A.D., Stein, J.A. et al. (2015). Defining adult bonefish (*Albula*

881   *vulpes*) movement corridors around Grand Bahama in the Bahamian Archipelago

882   *Environmental Biology of Fishes*, **98**, 2203–2212. https://doi.org/10.1007/s10641-

883   015-0422-4

884   Murray, G. G. R., Soares, A. E. R., Novak, B. J., Schaefer, N. K., Cahill, J. A., Baker,

885   A. J., Shapiro, B. (2017). Natural selection shaped the rise and fall of passenger

886   pigeon genomic diversity. *bioRxiv*. https://doi.org/10.1101/154294.

887   Musyl, M.K., Domeier, M.L., Nasby-Lucase, N.., Brill, R.W., McNaughton, L.M.,

888   Swimmer, J.Y., Lutcavage, M.S., Wilson, S.G., Galuardi, B., Liddle, J.B. (2011).

889   Performance of pop-up satellite archival tags. *Marine Ecology Progress Series*, **433**,

890   1-28.

891   Naito, Y. I., Chikaraishi, Y., Drucker, D. G., Ohkouchi, N., Semal, P., Wißing, C., and

892   Bocherens, H. (2016). Ecological niche of Neanderthals from Spy Cave revealed by

893   nitrogen isotopes of individual amino acids in collagen. *Journal of Human Evolution*,

894   **93**, 82–90.

895   Narum, S. R., Banks, M., Beacham, T. D., Bellinger, M. R., Campbell, M. R.,

896   DeKoning, J., Elz, A., Guthrie III, C. M., Kozfkay, C., Miller, K. M., Moran, P., Phillips,

897   R., Seeb, L. W., Smith, C. T., Warheit, K., Young, S. F. & Garza, J. C. (2008).

898   Differentiating salmon populations at broad and fine geographic scales with

899   microsatellites and SNPs. *Molecular Ecology,* **17**, 3464–3477.

NASCO (2008) *Salmon at Sea – SALSEA – An International Cooperative Research Programme on Salmon at Sea*. NASCO Report: SAL 04(5). http://www.nasco.int/sas/pdf/archive/other_reports/salsea_programme.pdf (accessed 31st October 2017).

Nash, K.L., Bijoux, J., Robinson, J., Wilson, S.K. & Graham, N.A.J. (2016) Harnessing fishery-independent indicators to aid management of data-poor fisheries: weighing habitat and fishing effects. *Ecosphere*, **7**, e01362.

Nielsen, J.M*.,* Clare, E.L.*,* Hayden, B.*,* Brett, M.T.*,* Kratina, P. (2017). Diet tracing in ecology: Method comparison and selection. *Methods Ecol Evol.* 00*:*1–14*.* https://doi.org/10.1111/2041-210X.12869.

Neuenschwander, S. (2006) AQUASPLATCHE: a program to simulate genetic diversity in populations living in linear habitats. *Molecular Ecology Notes*, **6** 583-585.

Newsome, S. D., del Rio, C. M., Bearhop, S. & Philiips D. L. (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, **5**, 429-436.

Ólafsdóttir, G. Á., Westfall, K. M., Edvardsson, R. & Pálsson, S. (2014). Historical DNA reveals the demographic history of Atlantic cod (*Gadus morhua*) in medieval and early modern Iceland. *Proceedings of the Royal Society B*, **281**, 20132976.

Orton, D. C. (2016). Archaeology as a tool for understanding past marine resource use and its impact. In *Perspectives on Oceans Past* (pp. 47–69). Springer, Dordrecht.

920 OSPAR Convention. (2013). An assessment of the Ecological coherence of the
921 OSPAR Network of Marine Protected Areas in 2012. OSPAR Commission, London,
922 UK, ISBN 978-1-909159-52-5.

923 Papastamatiou, Y. P., C. G. Meyer, F. Carvalho, J. J. Dale, M. R. Hutchinson & K. N.
924 Holland. (2013). Telemetry and random-walk models reveal complex patterns of
925 partial migration in a large marine predator. *Ecology,* **94**, 2595-2606.

926 Paris, J. R., Stevens, J. R. & Catchen, J. M. (2017). Lost in parameter space: a road
927 map for stacks. *Methods in Ecology and Evolution,* **8**, 1360–1373.
928 doi.org/10.1111/2041-210X.12775

929 Pauli, J. N., Newsome, S. D., Cook, J. A., Harrod, C., Steffan, S. A., Baker, C. J. O.,
930 Ben-David, M., Bloom, D., Bowen, G. J., Cerling, T. E. et al. (2017). Opinion: why we
931 need a centralized repository for isotopic data. *Proceedings of the National Academy*
932 *of Sciences* **114**, 2997–3001. doi: 10.1073/pnas.1701742114.

933 Pauls, S. U., Alp, M., Bálint, M., Bernabò, P., Čiampor, F., Čiamporová-Zaťovičová,
934 Z., Finn, D. S., Kohout, J., Leese, F., Lencioni, V., Paz-Vinas, I., Monaghan, M. T.
935 (2014). Integrating molecular tools into freshwater ecology: developments and
936 opportunities. *Freshwater Biology,* **59**, 1559–1576.
937 https://doi.org/10.1111/fwb.12381.

938 Peng, B., & Kimmal, M. (2005). simuPOP: a forward-time population genetics
939 simulation environment. *Bioinformatics*, **21**, 3686-3687.

940 Pine, W. E., Pollock, K. H., Hightower, J. E., Kwak, T. J., Rice, J. A. (2003) A review
941 of tagging methods for estimating fish population size and components of mortality.
942 *Fisheries,* **28**, 10-3, doi: 10.1577/1548-8446(2003)28.

943 Richter, K. K., Wilson, J., Jones, A. K. G., Buckley, M., van Doorn, N., and Collins,
944 M. J. (2011). Fish 'n chips: ZooMS peptide mass fingerprinting in a 96 well plate
945 format to identify fish bone fragments. *Journal of Archaeological Science*, **38**, 1502–
946 1510.

947 Ritchie, M. D., Holzinger, E. R., Li, R., Pendergrass, S. A. & Kim, D. (2015). Methods
948 of integrating data to uncover genotype-phenotype interactions. *Nature Reviews*
949 *Genetics*, **16**, 85–97. doi:10.1038/nrg3868

950 Rodríguez-Ezpeleta, N., Bradbury, I. R., Mendibil, I., Álvarez, P., Cotano, U. &
951 Irigoien, X. (2016). Population structure of Atlantic mackerel inferred from RAD-seq-
952 derived SNP markers: effects of sequence clustering parameters and hierarchical
953 SNP selection. *Molecular Ecology Resources,* **16**, 991–1001. doi: 10.1111/1755-
954 0998.12518.

955 Rogers, A., Blanchard, J.L. & Mumby, P.J. (2014) Vulnerability of coral reef fisheries
956 to a loss of structural complexity. *Current Biology*, **24**, 1000-1005.

957 Salipante, S. J., Kawashima, T., Rosenthal, C., Hoogestraat, D. R., Cummings, L. A.,
958 Sengupta, D. J., Harkins, T. T., Cookson, B. T. & Hoffman, N. G. (2014).
959 Performance comparison of Illumina and ion torrent next-generation sequencing
960 platforms for 16S rRNA-based bacterial community profiling. *Applied and*
961 *Environmental Microbiology,* **80**, 7583-7591. doi: 10.1128/AEM.02206-14.

Schrider, D. R. & Kern, A. D. (2014). Discovering functional DNA elements using population genomic information: A proof of concept using human mtDNA. *Genome Biology and Evolution*, **6**, 1542–1548. http://doi.org/10.1093/gbe/evu116.

Serafy J.E., Shideler G.S., Araújo R.J., Nagelkerken I. (2015). Mangroves enhance reef fish abundance at the Caribbean regional scale. *PLOS ONE*, **10**, e0142022. https://doi.org/10.1371/journal.pone.0142022.

Sevellec, M., Pavey, S. A., Boutin, S., Filteau, M., Derome, N. & Bernatchez, L. (2014). Microbiome investigation in the ecological speciation context of lake whitefish (*Coregonus clupeaformis*) using next-generation sequencing. *Journal of Evolutionary Biology,* **27**, 1029-1046. doi: 10.1111/jeb.12374.

Silvertown, J. (2009). A new dawn for citizen science. *Trends in Ecology & Evolution*, **24**, 467–471. https://doi.org/10.1016/j.tree.2009.03.017.

Shin, Y.-J., Shannon, L.J., Bundy, A., Coll, M., Aydin, K., Bez, N., Blanchard, J.L., Borges, M.d.F., Diallo, I., Diaz, E., Heymans, J.J., Hill, L., Johannesen, E., Jouffre, D., Kifani, S., Labrosse, P., Link, J.S., Mackinson, S., Masski, H., Möllmann, C., Neira, S., Ojaveer, H., Abdallahi, K.O.M., Perry, I., Thiao, D., Yemane, D. & Cury, P.M. (2010) Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science*, **67**, 692-716.

Shogren, A. J., Tank, J. L., Andruszkiewicz, E., Olds, B., Mahon, A. R., Jerde, C. L. & Bolster, D. (2017). Controls on eDNA movement in streams: transport, retention, and resuspension. *Scientific Reports, 7*, 5065. doi: 10.1038/s41598-017-05223-1.

984 Sigsgaard, E. E., Nielsen, I. B., Bach, S. S., Lorenzen, E. D., Robinson, D. P.,
985 Knudsen, S. W., Pedersen, M. W., Al Jaidah, M., Orlando, L., Willerslev, E. & Møller,
986 P.R. (2016). Population characteristics of a large whale shark aggregation inferred
987 from seawater environmental DNA. *Nature Ecology & Evolution,* **1**,0004.

988 Smith, N. S. & Zeller, D. K. (2015) Unreported catch and tourist demand on local
989 fisheries of small island states: these case of The Bahamas, 1950-2010. *Fishery*
990 *Bulletin,* **114**, 117-131. doi: 10.7755FB.114.1.10.

991 Song, W., Li, L., Huang, H., Jiang, K., Zhang, F., Chen, X., Zhao, M. & Ma, L. (2016).
992 The Gut Microbial Community of Antarctic Fish Detected by 16S rRNA Gene
993 Sequence Analysis. *BioMedical Research International*, doi: 10.1155/2016/3241529.

994 Sousa, L. L., Xavier, R., Costa, V., Humphries, N. E., Trueman, C., Rosa, R., Sims,
995 D.W. & Queiroz, N. (2016). DNA barcoding identifies a cosmopolitan diet in the
996 ocean sunfish. *Scientific Reports*, **6**, 1–9.

997 Stallings, C.D. (2009). Fishery-independent data reveal negative effect of human
998 population density on Caribbean predatory fish communities. *PLOS ONE,* **4**, e5333.
999 https://doi.org/10.1371/journal.pone.0005333.

1000 Star, B., Nederbragt, A. J., Jentoft, S., Grimholt, U., Malmstrom, M., Greger, T. F.,
1001 Rounge, T. B., Paulsen, J., Solbakken, M. H., Sharma, A. et al. (2011). The genome
1002 sequence of Atlantic cod reveals a unique immune system. *Nature,* **477**, 207–210.

1003 Stark, A., Lin, M. F., Kheradpour, P., Pedersen, J. S., Parts, L., Carlson, J. W. et al.
1004 (2007). Discovery of functional elements in 12 Drosophila genomes using
1005 evolutionary signatures. *Nature*, **450**, 219–232. https://doi.org/10.1038/nature06340.
46

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., Hill, N. A., Kininmonth, S. J., Airoldi, L. et al. (2013) Integrating Abundance and Functional Traits Reveals New Global Hotspots of Fish Diversity. *Nature* **501**, 539–542.

Tarnecki, A.M., Burgos, F.A., Ray, C.L. and Arias, C.R. (2017). Fish intestinal microbiome: diversity and symbiosis unravelled by metagenomics. *Journal of Applied Microbiology,* **123**. doi: 10.1111/jam.13415.

Thomsen, P.F., Kielgast, J., Iversen, L.L., Møller, P.R., Rasmussen, M. and Willerslev, E., 2012. Detection of a diverse marine fish fauna using environmental DNA from seawater samples. *PLoS one*, *7*(8), p.e41732.

Thurstan, R. H., Brockington, S. & Roberts, C. M. (2010). The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nature Communications*, **1**, 15.

Thurstan, R. H. & Roberts, C. M. (2010). Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. *PloS One*, **5**, e11767.

Trueman, C. N., MacKenzie, K. M. & Palmer, M. R. (2012) Identifying migrations in marine fishes through stable-isotope analysis. *Journal of Fish Biology* **81**, 826–847.

Turner, C. R., Barnes, M. A., Xu, C. C., Jones, S. E., Jerde, C. L. & Lodge, D. M. (2014). Particle size distribution and optimal capture of aqueous macrobial eDNA. *Methods in Ecology and Evolution,* **5**, 676-684.

1026 Uchii, K., Doi, H. & Minamoto, T. (2016). A novel environmental DNA approach to
1027 quantify the cryptic invasion of non-native genotypes. *Molecular Ecology Resources,*
1028 **16**, 415-422.

1029 Ulibarri, R. M., Bonar, S. A., Rees, C., Amberg, J., Ladell, B. & Jackson, C. (2017).
1030 comparing efficiency of American Fisheries Society standard snorkeling techniques
1031 to environmental DNA sampling techniques. *North American Journal of Fisheries*
1032 *Management* **37**, 644-651.

1033 Valentini, A., Taberlet, P., Miaud, C., Civade, R., Herder, J., Thomsen, P.F.,
1034 Bellemain, E., Besnard, A., Coissac, E., Boyer, F. & Gaboriaud, C. (2016). Next-
1035 generation monitoring of aquatic biodiversity using environmental DNA
1036 metabarcoding. *Molecular Ecology,* **25**, 929-942.

1037 Van Neer, W. & Ervynck, A. (2010). Defining "natural" fish communities for fishery
1038 management purposes: biological, historical, and archaeological approaches. In
1039 *Ecologies and Economies in Medieval and Early Modern Europe* (pp. 188–218). Brill.

1040 Vellend, M. (2003). Island biogeography of genes and species. *The American*
1041 *Naturalist*, **162**, 358-365.

1042 Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S. W. and Garant, D. (2014),
1043 Drawing ecological inferences from coincident patterns of population- and
1044 community-level biodiversity. *Molecular Ecology*, **23**, 2890–2901.
1045 doi: 10.1111/mec.12756.

1046 Voegeli, F. A., Smale, M. J., Webber, D. M., Andrade, Y. & O'Dor, R. K. (2001).
1047 Ultrasonic telemetry, tracking and automated monitoring technology for sharks.
1048 *Environmental Biology of Fishes,* **60**, 267-281.

1049 Weijerman, M., Fulton, E.A., Kaplan, I.C., Gorton, R., Leemans, R., Mooij, W.M. &
1050 Brainard, R.E. (2015) An integrated coral reef ecosystem model to support resource
1051 management under a changing climate. *PLoS ONE*, **10**, e0144165.

1052 Wheat, R. E., Wang, Y., Byrnes, J. E. & Ranganathan, J. (2013). Raising money for
1053 scientific research through crowdfunding. *Trends in Ecology & Evolution* **28**, 71–2.
1054 doi: 10.1016/j.tree.2012.11.001.

1055 Wheeler, A. & Jones, A.K.G. (1989). *Fishes. Cambridge Manuals in Archaeology.*
1056 Cambridge University Press, Cambridge, UK.

1057 Whoriskey, F. G. (2015). The Ocean Tracking Network: A global partnership uses
1058 electronic tagging technologies to track the movements of aquatic animals, answer
1059 science questions, stimulate new technology development and assist with
1060 sustainable development of the ocean. *Oceans 2015* - Mts/Ieee Washington. Ieee,
1061 New York. Development and International Law **47**, 221-232.

1062 Wilcox, T. M., McKelvey, K. S., Young, M. K., Lowe, W. H. & Schwartz, M. K. (2015).
1063 Environmental DNA particle size distribution from Brook Trout (*Salvelinus fontinalis*).
1064 *Conservation Genetics Resources,* **7**, 639-641.

1065 Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C. et al.
1066 (2009). Rebuilding Global Fisheries. *Science*, **325**, 578–585.
1067 https://doi.org/10.1126/science.1173146.

49

1068 Xia, J. H., Lin, G., Fu, G. H., Wan, Z. Y., Lee, M., Wang, L., Liu, X. J. & Yue, G. H.

1069 (2014). The intestinal microbiome of fish under starvation. *BMC Genomics*, **15**, doi:

1070 10.1186/1471-2164-15-266.

1071 Yamamoto, S., Minami, K., Fukaya, K., Takahashi, K., Sawada, H., Murakami, H.,

1072 Tsuji, S., Hashizume, H., Kubonaga, S., Horiuchi, T. & Hongo, M. (2016).

1073 Environmental DNA as a 'snapshot' of fish distribution: A case study of Japanese

1074 jack mackerel in Maizuru Bay, Sea of Japan. *PloS One,* **11**, p.e0149786.

1075 Zeller, D., Harper, S., Zylich, K., and Pauly, D. (2015). Synthesis of underreported

1076 small -scale fisheries catch in Pacific island waters. *Coral Reefs*, **34**, 25-39.

1077

Table 1. Summary of popular current and emerging methods used for fish surveys along with the associated advantages and limitations of each method.

Method	Advantages	Limitations	Manpower requirement	Health & Safety consideration
Electric fishing	1. Can be used in flowing and still water, amongst macrophytes and obstructions 2. Relatively unselective 3. Can be used quantitatively	1. Inefficient in water > 1 – 1.5m or in wide reaches 2. Limited by water and bed conductivity 3. Can be harmful to sensitive fish species and life stages 4. Invasive	Significant to high	High
Seine netting	1. Can be used quantitatively 2. Efficiency well-understood 3. Relatively unselective	1. Limited effectiveness in very deep or very shallow water 2. Limited effectiveness where there are macrophytes, obstructions, or soft sediment 3. Restricted to use in low velocity water bodies. 4. Invasive.	High	Significant
Trawling	1. Large areas of deep water can be surveyed efficiently	1. Restricted to use in relatively open continuous stretches of water of > 2m in depth. 2. Cannot be used where there are dense macrophytes, very variable bed profiles or large	High	High

		3. debris. Requires sizeable boats and launching facilities. 4. Invasive.		
Gill-netting	1. Can be used in a wide variety of environments amongst debris and macrophytes, in almost any depth	1. Invasive / destructive 2. Limited ability to assess absolute fish abundance	Significant	Significant
Hydro-acoustics	1. Huge expanses of water can be surveyed efficiently 2. Non-invasive 3. Quantitative abundance estimates possible	1. Limited effectiveness in turbulent environments 2. Can only sample relatively open water so unsuitable to use for sampling in marginal habitats 3. Lacks capacity to differentiate between species 4. Cannot assess age, condition and health of fish	Significant	Significant
Fyke netting and trapping	1. Can be deployed in a variety of environments, 2. Can be effective for some species difficult to sample by other methods	1. Very species and size-selective 2. Limited ability to assess absolute fish abundance	Significant	Significant
Fry surveys – micromesh seine/handnet/ traps	1. Focuses on margins of rivers and lakes, therefore less resource intensive, simple equipment only 2. Assesses a key life stage 3. Relatively unselective	1. Only assesses juvenile populations 2. Invasive – very young fish unlikely to survive capture	Significant	Significant
Fish counters /fixed traps	1. Good for assessing highly mobile fish with relatively	1. Resource intensive – high capital costs, maintenance 2. Quantitative assessment for	High	Significant

(sometimes accompanied by camera/video recorder	predictable migration patterns	migratory species only 3. Often only operational under certain environmental conditions		
Rod-and-line	1. Adaptable, can be deployed almost anywhere 2. Amenable to volunteer/citizen science participation	1. Very effort-dependent (quantity and quality) 2. Strongly influenced by conditions 3. Very selective for species and size of fish 4. Limited capability to assess absolute fish abundance 5. Very noisy data	High	Low
Commercial fish catch monitoring	1. Enables large volumes of data collected over large spatial and temporal scales. 2. Relatively cheap – fish are being caught anyway	1. Can only happen where commercial fisheries exist. 2. Little control over changes in effort and methodology – driven by market forces 3. Strongly influenced by conditions	Low	Low
Visual surveys (snorkelling, counting from the bank)	1. Relatively non-invasive 2. Enables observation of fish in their surroundings	1. Only applicable in high water clarity and over short ranges 2. Mostly applicable to species with distinct individual home range, typically associated with physical habitat features.	Moderate	Significant to High
Methods under development				
eDNA (single-	1. Very adaptable, deployable	1. Currently can only establish fish presence and abundance of	Significant	Significant

target and meta barcoding)	2. Non-invasive 3. Non-selective 4. Low field manpower requirement	species relative to each other – absolute abundance remains a challenge 2. Cannot assess age, size, condition or health 3. Uncertainty around the source of eDNA in lotic environments 4. High laboratory time requirement		
DIDSON /ARIS – high resolution sonar	1. Can be used in turbid water, amongst obstructions 2. Can be used in a variety of depths and flows except very turbulent water Enables visualisation of target fish, species identification 3. Quantitative estimates possible Species (some) and size of fish can be identified 4. Observations of fish behaviour permissible 5. Non-invasive	1. Mobile deployment currently challenging 2. Limited ability to assess whole water body abundance 3. Limited species identification ability 4. High data-processing requirement 5. Cannot assess age, condition and health of fish	Significant	Significant