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

Running title: Tools for understanding fish populations

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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., 2006). In light of the increasing challenges presented by climate change and other natural and anthropogenic stressors (Gordon et al., 2017), 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 advancements 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, to better understand and protect wild fish populations.

Tagging and telemetry

A significant problem hampering the study of marine fish is that of determining their geographical locations at fine scales, over long durations and, in particular, for benthic species. Tagging and telemetry involves the application of external and or internal tags or devices to manually or passively track fish movement (Cooke et al., 2013). Both forms can be particularly challenging in the marine environment, though

manual tracking can work at feeding grounds and at spawning aggregations (e.g. Murchie et al., 2015), while passive tracking has valuable applications along known migration routes (Dahlgren et al., 2016), for example, as anadromous/catadromous species migrate in and out of river estuaries (e.g. Lauridsen et al., 2017). Suites of tools exist for such tasks (e.g. acoustic transmitters, PIT and Floy™ tags, radio, archival, etc.) and have been routinely used to understand the spatial ecology of a range of fish taxa (Bograd et al., 2010). With technological improvements in tags and tracking equipment, the field has grown vastly in recent decades (see reviews by Pine et al., 2003; Bograd et al., 2010; Jepsen et al., 2015). We briefly highlight some of the tags and telemetry options commonly used by researchers along with a discussion of some of the limitations and challenges associated with these tools.

Data storage tags (DSTs), which collect data on both the internal and/or external environments of fish are the only method available to assess internal states (e.g. bioenergetics, Cooke et al., 2016). However, DSTs currently only provide information on the environment experienced by the tagged fish if the tag is recovered, meaning these data are lost if fish recapture rates are low, often the case in fish tagging surveys. Communication History Acoustic Tags (so called 'CHATs'), which transmit data to nearby transponder receivers are a promising alternative. Since there have been relatively few uses of this tag type (Voegeli et al., 2001; Hight & Lowe, 2007), there is potential for development in this area.

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

105 behaviour (Methling et al., 2011). Additionally, battery failure, antenna damage, or
106 mechanical failure may limit registration or transmission of data (Musyl et al., 2011).
107 PSAT technology is relatively new, so future reductions in size and weight and also
108 improvement in reliability can be expected. In terms of software, PSATs currently
109 only transmit limited amounts of data due to transmission costs and the short time
110 that the receiving satellite is above the horizon. Future software development is
111 required to reduce transmission costs, optimise data transmission and provide more
112 flexibility for users to tailor controls to provide higher resolution data at the desired
113 temporal scale. An increase in the number of satellite platforms that can receive
114 PSAT data would help to improve reception issues. Interference on frequencies
115 selected for tags at certain geographical locations (see Musyl et al., 2011) also
116 requires consideration.

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

125 Organisations such as the Ocean Tracking Network (Whoriskey et al., 2015), (OTN;
126 http://oceantrackingnetwork.org) and the Australian Animal Tracking Network both
127 maintain acoustic infra-structure in the form of deployed receivers (arrays or curtains)
128 in key ecological areas into which researchers are free to release tagged animals.

These initiatives substantially reduce the cost and risk associated with acoustic tracking projects and similar approaches can be applied globally. Furthermore, integration of data standardised repositories along with a comprehensive set of analytical tools to ensure rapid and sophisticated analysis of acoustic array data would lead to new insights into the spatial ecology of fish. Further technological developments such as the use of AUVs to perform routine data download operations, or even complement fixed acoustic receivers (Davis et al., 2016), will make acoustic telemetry increasingly affordable and accessible to more researchers. Continued collaborations with established regional and international tracking networks, together with the ever-increasing sophistication, miniaturisation, durability and cost reduction of tags promises an increasingly important role for acoustic telemetry in our understanding of fish ecology.

Molecular tools

Population genetics and genomics

Using genetic tools to understand fish genetic diversity and population structure has wide-ranging applications for evolutionary biology, and the conservation and 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; Abdul-Muneer, 2014). 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 (https://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) and *de novo* eukaryotic genomes (including fish) are in progress (Jansen et al., 2017).

Alongside population genetic studies, research based on whole genome data is emerging, and the genomes of several commercially important species have now been published (e.g. Atlantic cod (*Gadus morhua*), Star et al., 2011; Atlantic salmon (*Salmo salar*), Lien et al., 2016). However, while the ever-reducing cost of whole

176 genome sequencing provides opportunities to sequence and publish more fish
177 genomes, in our view, the key priority is not simply publishing genomes, but also
178 high-quality genome annotation. Gene annotation and accurate knowledge of the
179 function of different identified regions is of extreme importance if genomic tools are to
180 be used reliably in conservation and management (Ekblom & Wolf, 2014). Therefore,
181 projects such as the 'Functional Annotation of All Salmonid Genomes' (Macqueen et
182 al., 2017) should be encouraged and developed. It is also important not to
183 underestimate or neglect the computing power and bioinformatics expertise required
184 to produce high quality genome scaffolds and annotations, and also to recognise and
185 account for biases in next generation sequencing data (see Benestan et al., 2016).

186 Furthermore, population genetic approaches are usually focused on a single species.
187 Consequently, there is a mismatch between studies of a single species genotyped at
188 high resolution, but generally at small spatial scales (e.g. population genetics, often
189 using hundreds to thousands of markers through GBS or GWAS) and studies of
190 multiple species at larger spatial scales but using lower resolution markers (e.g.
191 phylogeography or biodiversity assessments using metabarcoding or mtDNA
192 sequencing). Nonetheless, the widespread application of molecular resources has
193 led to the accumulation of rich datasets across a broad range of species,
194 geographical regions and time periods (Blanchet et al., 2017). Accordingly, we
195 anticipate that this aggregation of data may allow the underlying processes that drive
196 genetic variability across these regions and times to be revealed, enabling a broader
197 testing of theories in population genetics and evolution (Ellegren & Galtier, 2016;
198 Pauls et al., 2014).

Such studies will require combining high genetic resolution markers across large spatial scales, which is a non-trivial task, especially when dealing with non-model species. Three challenges arise in such cases: firstly, the financial investment required to obtain reliable datasets for several species remains significant. Despite reductions in sequencing costs, it may be financially sensible to rely on more classical markers such as microsatellites or small subsets of single nucleotide polymorphisms (SNPs). Secondly, there is a need for a standardised framework in order to make datasets comparable across different species and regions. This standardisation must occur when collecting samples, characterising markers (e.g. Ellis et al., 2011; Helyar et al*.,* 2011) and during the subsequent data analysis to streamline user choices (Paris et al*.,* 2017), which may bias the biological interpretation of data, see Rodríguez-Ezpeleta et al*.* (2016). It is therefore important that researchers use common methods to isolate and characterise markers for entire sets of focal species, and/or provide full access to detailed analyses when datasets are generated. Finally, as multi-species approaches remain scarce, there is a need to define hypotheses at the beginning of such investigations. The integration of mathematical and statistical models with fish population genetics would be useful for revealing genotype-phenotype interactions (Ritchie et al., 2015), evolutionary signatures (Stark et al., 2007), functional DNA elements (Schrider & Kern, 2014), and spatial dynamics (Guillot et al*.,* 2009).

eDNA

The use of environmental DNA, or eDNA, to identify the presence and understand the distribution of fish has expanded rapidly in the last decade. eDNA is a polydisperse mixture (Turner et al., 2014; Wilcox et al., 2015) of various biological

material ranging from entire cellular fragments to extracellular DNA, which is isolated from environmental samples such as water or sediment. Such techniques are used for species identification and food security purposes. Universal primers that target mitochondrial DNA can be applied for identifying species presence (Yamamoto et al., 2016) or to gain information about species natural history (e.g. food web construction, Sousa et al. (2016)).

An important component of this work is validating the results from eDNA surveys with traditional fish survey methods. In both freshwater and marine environments, eDNA has compared favourably to traditional fish survey methods (Eichmiller et al., 2014; Sigsgaard et al., 2017). However, eDNA was found to be less effective compared to experienced snorkel surveys (Ulibarri et al., 2017). This underpins the importance of validation with traditional techniques, especially in spatially heterogeneous and complex aquatic environments (Shogren et al., 2017).

The development of effective PCR primers is central to the successful application of eDNA (e.g. Freeland, 2016; MacDonald & Sarre, 2017). As a result, a vast range of primer sets are available for fishes (e.g. Clusa et al., 2017; Gargan et al., 2017; Doi et al., 2015). Metabarcoding primers, that simultaneously amplify eDNA from many fish species, have also been developed for monitoring entire fish communities (Miya et al., 2015; Valentini et al., 2016).

Beyond inferring if a fish species is present in the sampled location, researchers have begun to investigate if eDNA can provide further information regarding fish populations. The use of eDNA to infer population level variation has been demonstrated (Sigsgaard et al., 2016; Uchii et al., 2015), but is still in its infancy.

Similarly, several attempts have been made to link eDNA concentration and fish biomass (Lacoursière-Rousse et al., 2016; Thomsen et al., 2016; Yamamoto et al., 2016), producing encouraging results. Further development is required to use this tool to more accurately estimate fish abundance and biomass.

However, for techniques utilising eDNA to be optimised, preexisting molecular information needs to be accessible. A number of publicly available databases (e.g. NCBI Genbank and BOLD - boldsystems.org) hold a vast array of molecular data but there is still a need for further mitochondrial genome sequencing to allow optimal usage of molecular identification techniques (but see Deiner et al., 2017).

Microbiomes

Analysis of a microbiome can provide novel insights into the health and biology of fish populations. Traditional culture-dependent tools used to map the commensal microbiota community in teleost fish are often time-consuming, expensive and subjected to bias as only 0.1-10% of bacteria can be cultured *in vitro* (Amann et al*.,* 1995; Austin, 2006). More recently, rapid culture-independent tools such as 16S rRNA targeted sequencing have been utilised to provide detailed profiles of the structure and diversity of the microbiota residing on the mucosal surface of fish (Ghanbari et al*.,* 2015).

The gut microbiome composition has also become an important biomarker for understanding the influence of stress in fish (Llewellyn et al., 2014), as numerous stressful stimuli have been shown to alter the microbiome composition (Xia et al*.,* 2014; Gaulke et al*.,* 2016). The gut microbiome composition can provide insights into the ecology and physiology of fish in a range of areas such as ecological speciation

(Sevellec et al., 2014), the biology of migratory fish (Llewellyn et al., 2016), trophic interactions within ecosystems (Ingerslev et al., 2014) and adaptation to extreme environments (Song et al., 2016).

There are a number of challenges currently facing fish microbiome research. At present, the majority of data regarding the microbiome composition in wild teleost fish originates from laboratory models (Tarnecki et al., 2017). More studies are required to see if captive-reared animals provide a reliable analogue for wild populations. Standardised protocols for collecting and generating microbiome data are also lacking, which could restrict progress as several processes have the potential to introduce differential bias in microbiota profiles (e.g. Salipante et al., 2014; Hart et al., 2015; Lyons et al., 2017). Adopting a framework of robust, quality-controlled protocols (e.g. similar to human microbiome research Methé et al., (2012)) would be of great benefit. In addition, there is currently a lack of non-invasive protocols for conducting longitudinal or repeated sampling of the gut microbial community in individual fish over time. The application of rectal swabs (Budding et al., 2014) for sampling the vent of fish could provide a non-invasive strategy for collecting microbiome data from individuals over time. Finally, time-series data could also enhance our knowledge in terms of the functional aspects of host lifecycles and the stability and resilience of microbiota (Goodrich et al., 2014).

Survey Tools

Field-based surveys

Fish population assessments are conducted using a wide range of techniques; the advantages, limitations, personnel requirements and health and safety

292 considerations of each are presented in Table 1. It is encouraging to note that even
293 well-established methods such as hydro-acoustics are continually being improved,
294 while emerging tools such as eDNA (see above) are beginning to be included in
295 routine monitoring. We suggest that integrating methods and data series are key
296 priorities for future research in this field.

297 In large and complex habitats it is often the case that a suite of survey methodologies
298 has to be employed to sample different times, places and fish species effectively.
299 Indeed, an advantage of field-based surveys is the ability to generate information
300 from both fishery-independent (Nash et al., 2016) and fishery-dependent (Shin et al.,
301 2010) data. However, this need, and the availability of a diversity of methodologies,
302 can make the task of assessment in these habitats even more costly; issues also
303 remain over how to use often disparate data types to develop a sound understanding
304 of a fishery. Integrating methods represents a key means of improving data resolution
305 from such field surveys. For instance, methods such as eDNA and hydro-acoustic
306 sampling provide comparatively fast and non-invasive estimates of fish community
307 structure and biomass. However, to obtain a thorough understanding of fish
308 populations, this information must be combined with fish age, size and health data
309 obtained via destructive sampling (e.g. gill netting). As yet, there are no structured,
310 universally agreed guidelines on which methods should be integrated to obtain a
311 thorough assessment of population dynamics from a specific habitat type.

312 Fish survey methodologies are typically determined at a national level, making
313 international comparisons of data extremely challenging. In recent years,
314 standardised protocols initiated through the EU Water Framework Directive have
315 facilitated Europe-wide assessments of fish community structure. Such international

316 standardisation is essential when assessing the impact of anthropogenic effects on
317 fish (see Gordon et al., this issue), and we recommend that efforts are made to make
318 national datasets available using standardised metadata and biodiversity information,
319 ideally via open sharing platforms (e.g. http://www.freshwaterplatform.eu/).

320 *Historical records*

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

335 **Statistical and modelling tools**

336 *Bayesian methods* - Reliable estimates of demographic parameters (e.g. abundance,
337 survival, growth rates and fecundity) and an understanding of the processes that
338 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, 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, 2015) 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: http://derekogle.com/fishR/packages) and programmable environments (e.g. NetLogo; https://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

364 and statistical backgrounds would be advantageous. For more robust future
365 application of IBMs within fisheries science, there is a need for more assessment of
366 the relative strengths and weaknesses (and potential availability and future
367 development) of the different models.

368 Integration with environmental data is a pertinent issue when modelling and is
369 becoming easier through developments in GIS and other programming environments
370 (such as R), which now include procedures and libraries for use in ecological work.
371 One example is the use of food web models that integrate environmental data (e.g.
372 Christensen & Walters, 2004) and coral reef ecosystem modelling methods (e.g.
373 Rogers et al., 2014; Weijerman et al., 2015). A hindrance to the integration of
374 environmental data into fisheries science is that it can be difficult to find and access
375 data sources, although availability and accessibility of such data is improving (e.g.
376 worldclim.org). The existence of a central node or hub with paths to these data
377 sources would be useful.

378 **Tissue analysis**

379 *Stable isotope ecology*

380 Stable isotopes are now routinely used to quantify the trophic ecology (Boecklen et
381 al., 2011) and migration history (Trueman et al., 2012) of fishes, or to identify
382 community level patterns in food web structure and resource use (Layman et al.,
383 2012). Although the technique is still in its relative infancy, stable isotope ecology has
384 advanced much in recent decades. Below we outline four areas of rapid development
385 with potential to enhance the applicability of this tool to studies of fish biology.

386 *Biochemical mechanism:* The relationship between the isotopic composition of a
387 consumer's tissues and that of its prey is fundamental to all applications of stable
388 isotopes in ecology. However, while general principles are clear (i.e. faster reaction
389 rates and preferential incorporation of light isotopes into excretory metabolites a
390 process termed trophic fractionation (DeNiro & Epstein, 1977)), the precise
391 mechanisms leading to fractionation and, particularly, the extent of isotopic
392 fractionation expected under differing physiological conditions cannot currently be
393 predicted, primarily due to the complexity of amino acid biochemistry. Uncertainties
394 associated with the isotopic expression of tissue composition, and relative rates of
395 tissue growth and regeneration further complicate the interpretation of stable isotope
396 values in ecology. However, recent information gained from compound-specific
397 isotope analysis (i.e. assessing isotopic compositions of single amino acids) is
398 beginning to shed light on the fractionation process (McMahon & McCarthy, 2016).

399 *Population-level data:* The distribution of isotopic compositions of individuals within a
400 population (often termed the 'isotopic niche', Newsome et al., 2007) has been
401 proposed as a powerful comparative measure of population-level ecological
402 characters. However, in addition to individual variability in consumers, the distribution
403 of isotopic compositions in a population is influenced by spatial and temporal
404 variations in the isotopic composition of primary production, temporal variability within
405 trophic linkages and differential rates of growth and isotopic assimilation. Very few
406 studies have attempted to combine ecological and food web theory with isotope
407 systematics to explore the sensitivity of community isotopic metrics to changes in
408 food web structure and function.

IsoBank: To date, applications of stable isotopes to fish biology have predominantly focussed on analyses of specific populations or communities. The absence of a centralised, open-access repository for stable isotope data restricts the opportunity for syntheses or meta-analyses of stable isotope data (Pauli et al., 2017). Recent efforts to address this have found broad support from the stable isotope research community (Pauli et al., 2017) and would be especially beneficial to fish biologists due to the large amount of fish isotope data currently available. Defining an ontology of stable isotope metadata, information required to describe and interpret isotope data, for fish biologists is an immediate requirement in this regard.

Marine isoscapes: The stable isotope ratios of a consumer's tissue encode the resources (water, air, prey etc.) it was using when that tissue was formed. As such, provided one has access to a suite of isotopic baseline measurements (e.g. water, plants and primary consumers), it is possible to trace an organisms route through space and time up to the point of capture (Trueman et al., 2012). Creation of a practically useful isoscape requires relatively dense sampling of a reference organism across space (and potentially time). Bulk stable isotope analyses are now routine, commonly available globally, and relatively cheap, and regional marine isoscape models are being developed at a rapid rate (MacKenzie et al., 2014; Kurle & McWhorter, 2017). In the open ocean, sample-based isoscapes are difficult to develop, but progress is being made in isotope-enabled global biogeochemical models (Magozzi et al., 2017), offering temporal and spatial models of expected isotopic variability at global scales. Improving the precision, accuracy and availability of these baseline measurements will increase the robustness and precision of isotope based estimates animal position.

433

434 *Archaeological material*

435 Archaeological material can allow an otherwise impossible snapshot into past
436 populations. Traditional morphological approaches can provide age distributions and
437 species ranges, and with the explosion in the past 20 years of biomolecular
438 archaeology, many of the techniques used to explore modern populations can now
439 be used to look into the past. From ancient DNA to proteomics, and isotopes to lipids,
440 a wide range of biomolecules have been recovered and explored from archaeological
441 material (Orton, 2016). For example, compound-specific isotope analysis has the
442 potential to track trophic level changes through time (McClelland & Montoya, 2002;
443 Naito et al., 2016). Population genetics of extinct populations have been successfully
444 explored in terrestrial animals (Chang & Shapiro, 2016; Murray et al., 2017) and
445 these same techniques can be used on fish bones to reconstruct past genetics
446 (Iwamoto et al., 2012; Ólafsdóttir et al*.,* 2014). Ideally these data will be used to
447 understand environmental and anthropogenic effects on fish populations and how
448 modern fish populations might respond to climate change and fishing pressures.

449 A major barrier to the use of archaeological fish material is the fact that less than
450 10% of fish bones are identified to species (Wheeler & Jones, 1989; Gobalet, 2001)
451 and much of what is identified is buried in the 'grey literature' of archaeological
452 reports that are often not digitised and printed in small quantities (Linden & Webley,
453 2012). This makes the material relevant to an ecological question very difficult to find.
454 Archaeologists are working towards ways to improve the amount of bones identified
455 by better reference collections and education on fish bones (National

Zooarchaeological Reference Resource, Nottingham's Archaeological Fish Resource, Vertebra@UWF) and on creating searchable databases of archaeological material (Callou, 2009; Kansa, 2010). In addition, new ZooMS (Zooarchaeology by Mass Spectrometry) techniques are being explored to quickly identify even small bones and scales to species using peptide mass fingerprinting (Richter et al., 2011) which will allow even more material to be identified in a useful way for those working on understanding fish populations. In the near future, it should be possible for modern fish biologists, in conjunction with archaeologists, to ask direct questions of past populations (Van Neer & Ervynck, 2010).

General topics identified as applicable across all themes

Management of data: integration, calibration and standardisation

Progression of an integrated management framework for data classification, characterisation, storage and accessibility would be a valuable resource for fish and fisheries biologists. FishBase, which at the time of writing contains information regarding 33,600 fishes, involving 2290 collaborators, and receives over 600,000 visits per month, is an example of the potential for such a resource (see: fishbase.org; Froese & Pauly, 2017). A single database for all types of fish data (for example, DNA, tagging, isotopes, diet) is probably unworkable, but the advent of application programming interfaces (API) and analytical software which allows automated querying across multiple databases represents an unprecedented opportunity to access a wealth of global data. Indeed, we suggest that more data (such as those discussed here) could be integrated into FishBase. However, such

478 resources require significant funding and long-term commitment from governments
479 and trans-national organisations, e.g. NASCO.

480 *Public engagement, education and outreach*

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

489 In addition to funding science, the public can also actively engage in the process of
490 research directly through citizen science projects. Whilst research conducted by non-
491 professionals is certainly not a new concept, the numbers of projects involving citizen
492 scientists are growing, especially in the fields of environmental science and ecology
493 (Silverton, 2009). Through catch records of amateur anglers and commercial net
494 fishery data extending back many years, research into fish and fisheries is uniquely
495 placed to benefit from citizen science projects (Stuart-Smith et al., 2013), which have
496 effectively spanned generations of contributors. Similarly, REEF (reef.org) has been
497 collecting reef fish diversity and abundance data from trained volunteer divers for 27
498 years, and the data have been successfully leveraged in hundreds of publications
499 (e.g. Stallings, 2009; Serafy et al., 2015). Citizen science can also help achieve
500 important social outcomes, e.g. in establishing sustainable fisheries and marine

protected areas, MPAs (Bonney et al., 2014). And, as with crowdfunding, the best examples of citizen science typically encourage deeper engagement with the public, and offer a pathway to the democratisation of science.

Fisheries policy and governance

Conserving critical habitats is central to the sustainable management of fish species and populations. Marine Protected Areas (MPAs), networks of MPAs and Marine Conservation Zones (MCZs) are widely accepted management tools for fish and other marine organisms that have been established in many countries (Harborne et al., 2008; OSPAR, 2013). However, the design of MPA networks could benefit greatly from the integration of traditional survey data, along with modelling and connectivity data (Botsford et al., 2009; Grüss et al., 2014). From a social science perspective, there is a need to better understand public perceptions of marine-related conservation issues, e.g. fishery regulations, MPAs and MCZs, and to incorporate these data into fisheries policy and governance frameworks. For example, there is high public support for MPAs, with surveys showing that people desire around 40% of the UK's marine waters to be protected (Hawkins et al., 2016). But, while the public appears to realise that in reality levels of coverage are well below 40%, there is still a substantial disconnect between perceived coverage of highly protected UK MPAs (11%) and actual MPA coverage (<0.1%); ultimately, this means that people believe the UK oceans receive a higher level of conservation than in reality they do (Hawkins et al., 2016). Developing and implementing effective policies for fisheries management remains challenging because of the complexities of fisheries and the socio-political landscape under which they typically operate (Jentoft & Chuenpagdee, 2009). However, the establishment of guidelines or frameworks for fisheries policy

525 and governance (e.g. FAO Voluntary Guidelines for Securing Sustainable Small-
526 Scale Fisheries) have the potential to better address these challenges and provide
527 appropriate implementable solutions.

528

529 **Conclusions**

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

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

548 important that both traditional and emerging tools remain in the toolbox of fish biology
549 research.

550 Likewise, when genetic-based assignment became popular, many researchers
551 naively believed the days of tagging fish were over. It is now realised that due to the
552 many stochastic drivers of population structure, genetic stock identification-based
553 methodologies such as genetic assignment, do not always succeed. In such cases,
554 there remains a significant role for tagging in fisheries research. As tag sizes
555 decrease, and the deleterious effects of tag insertions on fish also decrease, we can
556 anticipate that genetics and tagging will both continue to have a role to play. The
557 importance of the relative roles of each technique will depend on the questions being
558 addressed, the population structure of the study species, and the scale of the
559 questions being assessed.

560 A final example, which highlights the importance of applying inter-disciplinary and
561 complimentary tools for understanding fish populations, was a five-year, multi-
562 agency, EU-funded project investigating the migration and distribution of Atlantic
563 salmon (*Salmo salar* L.) in the north-east Atlantic (the SALSEA project; NASCO
564 2008). The purpose was to understand not just where salmon go, but what they eat,
565 migration routes to feeding grounds, and which waters and regions they pass
566 through. The SALSEA project used a combination of genetics (microsatellites), stable
567 isotope analysis, at-sea trawls, tagging and gut contents analysis to assess the
568 movements and diet of Atlantic salmon across the north-east Atlantic Ocean. As a
569 result of applying these combined approaches, salmon post-smolt movements have
570 been confidently ascertained (Gilbey et al., 2017). Nonetheless, even while this
571 comprehensive study was being finalised, a similarly broad-ranging study was also
572 being undertaken using SNPs (Bourret et al., 2013). Arguably, this method offers

both the potential for finer levels of stock discrimination and the ability to better explore patterns among functional loci, which may make microsatellite-based analysis redundant within a short period of time (though see Narum et al., 2008).

Thus, the authors consider the continued development of emerging tools, together with the use of multiple methodologies and inter-disciplinary approaches, to represent the best avenues for further improving our understanding of fish populations. We implore scientists from unrelated fields to collaborate on such projects. The FSBI 50th Anniversary Symposium represented one such event, where fish-focused researchers across diverse fields, came together to advance the state of fish biology.

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