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

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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 Symposium of The Fisheries Society of the British Isles at the University of Exeter, UK, in July 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: tagging and telemetry; molecular tools; survey tools; statistical and modelling tools; 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

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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; stable isotopes; surveys; 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. In July 2017, The Fisheries Society of the British Isles held its 50th Anniversary Symposium at the University of Exeter, UK, under the broad umbrella of 'Understanding Fish Populations'. To highlight key knowledge gaps and opportunities, we report 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 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 well at feeding grounds and at spawning aggregations (Murchie *et al.,* 2015), while passive tracking has valuable applications along known migration routes (Dahlgren *et al.,* 2016), for example, as anadromous and catadromous species migrate in and out of river estuaries (Lauridsen *et al.,* 2017). Suites of tools exist for such tasks [*e.g.* acoustic transmitters, passive information transponder (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 (Pine *et al.,* 2003; 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.

Archival data storage tags (DST), which can collect data on both the internal and external environments of fish are the only method available to assess internal states (*e.g.* bioenergetics; Cooke *et al.,* 2016). DSTs, however, currently only provide information on the environment experienced by the tagged fish if the tag is recovered, meaning these data are lost if recapture rates are low, as is often the case in fish tagging surveys. Communication history acoustic tags (CHAT), 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-off DSTs are also becoming available and may alleviate several of these concerns once problems associated with size and recoverability are resolved.

Pop-up Satellite Archival Tags (PSAT), 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 fish habitat use, activity patterns and resource partitioning (Hussey *et al.,* 2015). Acoustic arrays have been used in many studies elucidating fish movements (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, in the significant cost and effort involved in deploying and maintaining acoustic arrays.

Organizations such as the Ocean Tracking Network (OTN; oceantrackingnetwork.org; Whoriskey, 2015) and the Integrated Marine Observing System (IMOS) animal tracking database Australian Animal Tracking Network (www.imos.org.au/facilities/animaltracking) both maintain acoustic infra-structure in the form of deployed receivers (arrays or curtains) 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 (*e.g.* a European tracking network is currently being developed). Furthermore, integration of standardised data repositories along with a comprehensive set of analytical tools to ensure rapid and sophisticated analysis of acoustic array data (Lea *et al.,* 2016) would lead to new insights into the spatial ecology of fish. Further technological developments such as the use of autonomous underwater vehicles (AUV) 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 molecular 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 (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 (Davey & Blaxter, 2011) and RNAseq (Wang *et al.,* 2009)], has revolutionized the fields of population and conservation genetics (Allendorf *et al.,* 2010). It is, however, important to appreciate 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. Emerging technologies, *e.g*. the MinION USB sequencer (www.nanoporetech.com/products/minion), have the potential to revolutionize 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 been 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* L. 1758; Star *et al.,* 2011; Atlantic salmon *Salmo salar* L. 1758; Lien *et al.,* 2016). While the ever-reducing cost of whole genome sequencing provides opportunities to sequence and publish more fish genomes, in our view, the key priority is not simply publishing genomes, but also attaining high-quality genome annotation. Gene annotation and accurate knowledge of the function of different identified regions is of extreme importance if genomic tools are to be used reliably in conservation and management (Ekblom & Wolf, 2014). Therefore, projects such as the 'Functional Annotation of All Salmonid Genomes' (Macqueen *et al.,* 2017) should be encouraged and developed. It is also important not to underestimate or neglect the computing power and bioinformatics expertise required to produce high quality genome scaffolds and annotations, and also to recognise and account for biases in next generation sequencing data (Benestan *et al.,* 2017).

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

Such studies will require the combination of 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 standardization must occur when collecting samples, characterising markers (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 (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 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. In this respect, simulation tools (Laval & Excoffier, 2004; Peng & Kimmal, 2005; Neuenschwander, 2006) are particularly useful for testing complex hypotheses and also for predictive purposes. Moreover, 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), spatial dynamics (Guillot *et al.,* 2009) and species-genetic diversity correlations (SGDC; Vellend, 2003; Vellend *et al.,* 2014).

ENVIRONMENTAL DNA

The use of environmental (e)DNA to identify the presence and understand the distribution of fish has expanded rapidly in the past 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 mtDNA can be applied for identifying species presence (Yamamoto *et al.,* 2016) or to gain information about species interactions (*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 with traditional fish survey methods (Thomsen *et al.,* 2012; Hänfling *et al.,* 2016). eDNA, however, was found to be less effective compared with 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 (Freeland, 2016; MacDonald & Sarre, 2017). As a result, a vast range of primer sets are available for fishes (Doi *et al.,* 2015; Clusa *et al.,* 2017). 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 (Uchii *et al.,* 2016; Sigsgaard *et al.,* 2016), but is still in its infancy. Similarly, although attempts to link eDNA concentration and fish biomass have shown promising results (Lacoursière-Roussel *et al.,* 2016; Yamamoto *et al.,* 2016), further development is required to improve the accuracy of these measurements. However, for applications utilising eDNA to be optimised, preexisting molecular information needs to be accessible. A number of publicly available databases [*e.g.* NCBI Genbank (www.ncbi.nlm.nih.gov/genbank/) and BOLD (www.boldsystems.org)] hold a vast array of molecular data, but there is still a need for further mitochondrial genome sequencing to allow for optimal usage of molecular identification techniques.

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 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 ribosomal (r)RNA targeted sequencing have been used 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 (Salipante *et al.,* 2014; Hart *et al.,* 2015). 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 such data. 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 considerations of each are presented in Table I. It is encouraging to note that even well-established methods such as hydroacoustics are continually being improved, while emerging tools such as eDNA are beginning to be included in routine monitoring. We suggest that integrating methods and data series are key priorities for future research in this field.

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

Fish-survey methodologies are typically determined at a national level, making international comparisons of data extremely challenging. In recent years, standardised protocols initiated through the European Union Water Framework Directive (E.C., 2000) have facilitated Europe-wide assessments of fish community structure. Such international standardisation is essential when assessing anthropogenic effects on fish (Gordon *et al.,* 2018) and we recommend that efforts are made to make national datasets available using standardised metadata and biodiversity information, ideally *via* open sharing platforms (*e.g.* www.freshwaterplatform.eu).

HISTORICAL RECORDS

Historical records (*e.g.* catch records) can also be useful in helping to extrapolate population data back into the recent past. Libraries and historical societies often hold picture archives and these images can in some instances be used as a form of historical

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

Method	Advantages	Limitations	Personnel requirement	Health & safety consideration
Electric fishing	Can be used in flowing and still water, among macrophytes and obstructions; relatively unselective; can be used quantitatively	Inefficient in water >1–1·5 m depth or in wide reaches; limited by water and bed conductivity; can be harmful to sensitive fish species and life stages; invasive	Significant to high	High
Seine netting	Can be used quantitatively; efficiency well-understood; relatively unselective	Limited effectiveness in very deep or very shallow water; limited effectiveness where there are macrophytes, obstructions, or soft sediment; restricted to use in low velocity water bodies; invasive	High	Significant
Trawling	Large areas of deep water can be surveyed efficiently	Restricted to use in relatively open continuous stretches of water of >2 m depth; cannot be used where there are dense growths of macrophytes, very variable bed profiles or large debris; requires sizeable boats and launching facilities; invasive	High	High
Gill netting	Can be used in a wide variety of environments among debris and macrophytes, in almost any depth	Invasive–destructive; limited ability to assess absolute fish abundance	Significant	Significant
Hydroacoustics	Huge expanses of water can be surveyed efficiently; non-invasive; quantitative abundance estimates possible	Limited effectiveness in turbulent environments; can only sample relatively open water so unsuitable to use for sampling in marginal habitats; lacks capacity to differentiate between species; cannot assess age, condition and health of fish	Significant	Significant

TABLE I. Continued

Method	Advantages	Limitations	Personnel requirement	Health & safety consideration
Fyke netting and trapping	Can be deployed in a variety of Environments; can be effective for some species difficult to sample by other methods	Very species and size-selective; limited ability to assess absolute fish abundance	Significant	Significant
Fry surveys: micromesh seine, handnet & traps	Focuses on margins of rivers and lakes, therefore less resource intensive, simple equipment only; assesses a key life stage; relatively unselective	Only assesses juvenile populations; invasive as very young fish are unlikely to survive capture	Significant	Significant
Fish counters & fixed traps: sometimes accompanied by cameras (video recorder)	Good for assessing highly mobile fish with relatively predictable migration patterns	Resource intensive, high capital costs, maintenance; quantitative assessment for migratory species only; often only operational under certain environmental conditions	High	Significant
Rod-and-line	Adaptable, can be deployed almost anywhere; amenable to volunteers and citizen-science participation	Very effort-dependent (quantity and quality); strongly influenced by conditions; very selective for species and size of fish; limited capability to assess absolute fish abundance; very noisy data	High	Low
Commercial catch monitoring	Enables large volumes of data collected over large spatial and temporal scales; relatively inexpensive as fish are being caught anyway	Can only happen where commercial fisheries exist; little control over changes in effort and methodology, which are driven by market forces; strongly influenced by conditions	Low	Low
Visual surveys: snorkelling, diving, counting from the bank	Relatively non-invasive; enables observation of fish in their surroundings	Only applicable in high water clarity and over short ranges; mostly applicable to species with distinct individual home range, typically associated with physical habitat features	Moderate	Significant to high

TABLE I. Continued

Method	Advantages	Limitations	Personnel requirement	Health & safety consideration
Methods under development				
eDNA: single-target and meta barcoding	Very adaptable, deployable anywhere; non-invasive; non-selective; low field manpower requirement	Currently can only establish fish presence and abundance of species relative to each other, absolute abundance remains a challenge; cannot assess age, size, condition or health; uncertainty around the source of eDNA in lotic environments; high laboratory time requirement	Significant	Significant
DIDSON*–ARIS#high resolution sonar	Can be used in turbid water, among obstructions; can be used in a variety of depths and flows except very turbulent water; enables visualization of target fish, species identification; quantitative estimates possible; species (some) and size of fish can be identified; observations of fish behaviour possible; non-invasive	Mobile deployment currently challenging; limited ability to assess whole water-body abundance; limited species identification capability; high data-processing requirement; cannot assess age, condition and health of fish	Significant	Significant

*Dual-frequency IDentification *SONar*.
#Adaptive Resolution Imaging Sonar.

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 *et al.,* 2010; Thurstan & Roberts, 2010). Catch reconstruction approaches can also provide useful insights into fishery trends that may not be apparent from data reported only by the U.N. Food and Agriculture Organization (FAO, 2015; 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, this can provide a unique way to extrapolate population data back in time.

STATISTICAL AND MODELLING TOOLS

BAYESIAN METHODS

Reliable estimates of demographic variables (*e.g.* abundance, survival, growth rates and fecundity) and an understanding of the processes that regulate these variables are fundamental for sustainable management of fish populations. To understand the ecological processes in order to truly inform policy, however, 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. 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). To develop the use of this specific framework in fish ecology and management, however, there is a need to educate and train fish biologists in the use of Bayesian principles and methods.

INDIVIDUAL-BASED MODELS

Individual-based models (IBM) are process-based mechanistic computer models that simulate emergent properties of fish biology, behaviour, traits or group characteristics, based on simple heuristic functions. The use of IBMs in fish research has grown exponentially (DeAngelis & Mooij, 2005) as computational power has increased (DeAngelis & Grimm, 2014). Several IBMs were presented at the 50th Anniversary Symposium of The Fisheries Society of the British Isles, 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 (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 (www.r-project.org) and programmable environments (*e.g.* NetLogo; www.ccl.northwestern.edu/netlogo). Programmes such as R, however, 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 a more robust future application of IBMs within fisheries science, there is a need for further assessment of the relative strengths and weaknesses (and potential availability and future development) of the different models.

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

TISSUE ANALYSIS

STABLE-ISOTOPE ECOLOGY

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

BIOCHEMICAL MECHANISM

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

POPULATION-LEVEL DATA

The distribution of isotopic compositions of individuals within a population (often termed the isotopic niche; Newsome *et al.,* 2007) has been proposed as a powerful comparative measure of population-level ecological characters. In addition to individual variability in consumers, however, the distribution of isotopic compositions in a population is influenced by spatial and temporal variations in the isotopic composition of primary production, temporal variability within trophic linkages and differential rates of growth and isotopic assimilation (Gorokhova, 2017). Very few studies have attempted to combine ecological and food web theory with isotope systematics to explore the sensitivity of community isotopic metrics to changes in 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.

ARCHAEOLOGICAL MATERIAL

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

A major barrier to the use of archaeological fish material is the fact that less than 10% of fish bones are identified to species level (Wheeler & Jones, 1989; Gobalet, 2001) and much of what is identified is buried in the grey literature of archaeological reports that are often printed in small quantities and not digitised (Linden & Webley, 2012). This makes the material relevant to an ecological question very difficult to find. Archaeologists are working towards ways to improve the amount of bones identified 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 STANDARDIZATION

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, receiving over 600 000 visits per month, is an example of the potential for such a resource (www.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. Such resources, however, require significant funding and long-term commitment from governments and trans-national organizations, *e.g.* the North Atlantic Salmon Conservation Organization (NASCO).

PUBLIC ENGAGEMENT, EDUCATION AND OUTREACH

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

In addition to funding science, the public can also actively engage in the process of research directly through citizen science projects. Whilst research conducted by non-professionals is certainly not a new concept, the numbers of projects involving citizen scientists are growing, especially in the fields of environmental science and ecology (Silvertown, 2009). Through catch records of amateur anglers and commercial net-fishery data extending back many years, research into fish and fisheries is uniquely placed to benefit from citizen science projects (Stuart-Smith *et al.,* 2013), which have effectively spanned generations of contributors. Similarly, REEF (www.reef.org) has been collecting reef-fish diversity and abundance data from trained volunteer divers for 27 years and the data have been successfully leveraged in hundreds of publications (Stallings, 2009; Serafy *et al.,* 2015). Citizen science can also help achieve important social outcomes, *e.g.* in establishing sustainable fisheries and marine protected areas (MPA) (Bonney *et al.,* 2014). As with crowdfunding, the best examples of citizen science typically encourage deeper engagement with the public and offer a pathway to the democratization of science.

FISHERIES POLICY AND GOVERNANCE

Conserving critical habitats is central to the sustainable management of fish species and populations. MPAs, networks of MPAs and marine conservation zones (MCZ) are widely accepted management tools for fish and other marine organisms that have been established in many countries (Harborne *et al.,* 2008; OSPAR Convention, 2013). The design of MPA networks could, however, benefit greatly from the integration of traditional survey data, along with modelling and connectivity data (Botsford *et al.,* 2009; *Gruss 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 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 (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). The establishment of guidelines or frameworks for fisheries policy and governance (FAO, 2015), however, 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. It should be noted, however, that not infrequently, revolutionary methods have been promoted 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 [*e.g*. 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 (Goodwin *et al.,* 2016; Nielsen *et al.,* 2017), the marriage of which can provide a new angle for researching challenging biological problems. It is important that both traditional and emerging tools remain in the toolbox of fish biology research.

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

A final example, which highlights the importance of applying inter-disciplinary and complimentary tools for understanding fish populations, was a five-year, multi-agency, E.U. funded project investigating the migration and distribution of *S salar* in the north-east Atlantic (the SALSEA project; NASCO, 2008). The purpose was to understand not just where *S. salar* go, but what they eat, migration routes to feeding grounds and which waters and regions they pass through. The SALSEA project used a combination of genetics (microsatellites), SIA, at-sea trawls, tagging and gut contents analysis to assess the movements and diet of this species across the north-east Atlantic Ocean. As a result of applying these combined approaches, *S. salar* post-smolt movements have been confidently ascertained (Gilbey *et al.,* 2017). Nonetheless, even while this comprehensive study was being finalised, a similarly broad-ranging study was also 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 (although 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 50th Anniversary Symposium of The Fisheries Society of the British Isles represented one such event, where fish-focused researchers across diverse fields, came together to advance the state of fish biology.

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