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1                                   **On the challenges and opportunities facing fish biology:**

2                                   **a discussion of five key knowledge gaps**

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14  
15   Running title: Challenges and opportunities in fish biology

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## Abstract

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Many fish species face increasing challenges associated with climate change and overfishing. At the same time, aquaculture is becoming vital for food security. Gaining a deeper understanding of the basic biology of fish is therefore more important than ever. Here we synthesise and summarise key questions, opportunities, and challenges in fish biology highlighted during a round-table discussion at the 50th Anniversary Symposium of The Fisheries Society of the British Isles, held at the University of Exeter, UK, in July 2017. We identified several knowledge gaps but also key opportunities for fish biology to inform food security, for collective behaviour, evolutionary history, and trait correlations to predict responses to environmental change, and for novel analytical approaches to mine existing data sets. Overall, more integrative approaches through stronger collaborations across different fields are needed to advance our understanding of the basic biology of fish.

Key words: Aquaculture; Integrative approaches; Behaviour; Food Security; Data analysis; Trait correlations

## Introduction

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Similar to most fields in the biological sciences, fish and fisheries biology have advanced rapidly over the last decade due to technological improvements in computer science, Next Generation Sequencing in genetics, and novel analytical approaches such as the decision-tree based random forest approach (Breiman 2001, Boulesteix *et al.*, 2012). However, a deeper understanding of the biology of fish is more important than ever, as global challenges such as climate change, overfishing, intensive aquaculture systems, and other anthropogenic stressors have impacts that may prove increasingly challenging to many fish species (Ficke *et al.* 2007; Halpern *et al.*, 2008). Gaps in our knowledge of the basic biology of many species prevent us from fully understanding and predicting how fish species and fish communities are responding and will respond to these challenges. Filling these gaps is crucial if we want to maintain healthy ecosystems and provide food security for an ever-growing human population.

Here we outline five key knowledge gaps that will be important for advancing the field of fish biology in the near future. These outstanding questions and potential avenues for their resolution were identified as part of a discussion organized at the 50th Anniversary Symposium of The Fisheries Society of the British Isles held at The University of Exeter, UK, in July 2017. They range from issues in aquaculture and fisheries, to physiology, behaviour and life history, and to problems in bioinformatics and analytical approaches. The overarching conclusion of this discussion was that more integrative studies are needed to understand fish responses to environmental change. In addition, available aquatic resources must be used responsibly in order to provide food security for future generations. In the following sections, we elaborate on each knowledge gap, outline

66 potential ways to fill each, and then conclude with a short synthesis. This article is not a  
67 comprehensive review of the field, but rather a starting point for future discussions.

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## 69 **Key questions and opportunities in fish biology**

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71 *1. How can we use fish biology to inform aquaculture and wild fisheries in order to secure*  
72 *food for a growing population?*

73

74 Incentives for sustainable aquaculture and fisheries have risen exponentially within the  
75 last decade due a projected increase of 3 billion people by 2050 (Sprague *et al.*, 2016).  
76 Even though fish is already a primary source of protein for millions of people and the  
77 contribution of aquaculture is approaching the level of fisheries, both the aquaculture and  
78 fisheries industries are expected to play an increasingly important role in providing  
79 sustainable sources of essential nutrients to humans (Troell *et al.*, 2014; Sprague *et al.*,  
80 2016; Bernatchez *et al.*, 2017).

81

82 In aquaculture, feed sustainability, disease, and gamete quality are a growing concern.  
83 Systematic biological approaches involving multiple aspects of fish biology can help  
84 resolve these problems. As an example, the microbiome is one field of fish biology that  
85 may dramatically facilitate aquaculture's growth. Our growing understanding of a fish's  
86 'second genome' and our ability to manipulate microbiomes can improve aquaculture's  
87 understanding of nutritional requirements, pathogen resistance, sexual maturation and  
88 survivorship in farmed fish (Llewellyn *et al.*, 2014). For example, the use of plant-based  
89 products to feed predominantly carnivorous teleosts is a key issue (Murray *et al.*, 2014).  
90 Fish are unable to process insoluble carbohydrates and fibre, commonly found within

91 plant-based diets. Therefore, this huge, yet largely indigestible, source of nutrients is  
92 quickly excreted (Llewellyn *et al.*, 2014). A considerable step towards sustainable  
93 aquaculture would be to 1) use our knowledge of fish microbiomes to improve  
94 predictions regarding interactions between plant-based sustainable feed sources and the  
95 digestive systems of farmed fish, and 2) manipulate fish microbiomes to efficiently  
96 process and utilise previously indigestible nutrients.

97

98 There is also a dire need to prevent further declines in wild fisheries and to manage  
99 fisheries sustainably. However, this is hindered by a lack of information and  
100 understanding in three key areas: target species' biology and their spatial and temporal  
101 distribution across all life stages; the effect of multiple stressors on fish populations; and  
102 the effectiveness of fisheries management in maintaining sustainable populations  
103 (Rassweiler *et al.*, 2014; Schinegger *et al.*, 2016). Integrative work connecting these areas  
104 is crucial when pursuing sustainability goals. For example, understanding the spatial and  
105 temporal overlap between population densities and distributions and how they are  
106 shaped by anthropogenic factors is imperative when assessing sustainable management  
107 measures (Alava *et al.*, 2017; Bernatchez *et al.*, 2017; Thorson *et al.*, 2017).

108

109 As a caveat to these and other examples of future research priorities within aquaculture  
110 and fisheries, scientists must also continue to develop their core understanding of fish  
111 biology. Despite the wealth of knowledge accrued during decades of aquaculture and  
112 fisheries research, fundamental biological research continues to provide new insights on  
113 the basic biology of fish. For example, the genetic bases underlying ecologically important  
114 traits (Barson *et al.*, 2015) or intraspecific variability in physiological traits (Burton *et al.*,

115 2011), enable scientists to fully investigate behavioural, physiological or genomic  
116 changes from accurate biological baselines.

117

118 *2. How can we use evolutionary biology to predict contemporary responses to climate*  
119 *change, harvesting, and other anthropogenic stressors?*

120

121 Understanding and predicting the response of a particular species to environmental  
122 change, or other stressors, is difficult without having a detailed baseline knowledge of its  
123 evolutionary history or its ability to respond through phenotypic changes to  
124 environmental challenges. Since phenotypic responses can be either heritable or plastic,  
125 accurate baselines must be obtained for both populations and species. Ultimately, by  
126 combining knowledge of evolutionary histories with other types of data we can gain a  
127 better understanding of the evolutionary potential of populations and species and better  
128 inform conservation efforts.

129

130 Species may be able to cope with environmental change by either shifting their  
131 distributions, coping with new environments via phenotypic plasticity, or adapting to  
132 novel environmental conditions (Crozier & Hutchings, 2014; Campbell *et al.*, 2017).  
133 Therefore, more detailed knowledge of evolutionary responses, and the underlying  
134 mechanisms, on different time scales, and in different environments and species are  
135 needed to enhance our understanding of how fishes will respond to different stressors.  
136 For example, studies on the effects of strong harvesting pressures on fish populations,  
137 e.g. through long term declines in population size and genetic diversity (Pinsky &  
138 Palumbi, 2014) or through short-term changes in gene expression (Uusi-Heikkilä *et al.*,  
139 2017), have already given us a better understanding of how harvesting pressure might

140 affect the evolutionary potential of fish populations. Furthermore, evolutionary studies,  
141 e.g. in combination with detailed ecological and developmental approaches, can  
142 illuminate questions of interest for conservation, regarding e.g. the effects of reduced  
143 genetic diversity on population persistence and adaptive potential (Pauls *et al.*, 2013),  
144 the flexibility of evolution (Elmer & Meyer, 2011), or in locating species refugia and  
145 drivers of diversity (Dornburg *et al.*, 2017).

146

147 We therefore argue for more collaborative studies that combine a wide range of  
148 information on populations and species that differ in distribution, ecology, genetic and  
149 phenotypic diversity, adaptive potential, and evolutionary history. This will help to  
150 generate more generic information about the potential of populations, species or biomes  
151 to respond to environmental and anthropogenic stressors.

152

153 *3. Can knowledge of correlated traits improve predictions for fish population responses to*  
154 *environmental change?*

155

156 For simplicity and clarity, we as fish biologists often consider our trait of interest - for  
157 example reproductive effort, morphological specialization, or migration tendencies - as  
158 independent or at least in isolation from other traits of that same individual. However, it  
159 is clear that the expression and function of all traits within an individual are, to some  
160 extent, dependent on each other. Whole suites of traits can be correlated due to either  
161 mechanistic constraints (e.g. genetic correlations, Steppan *et al.*, (2002)) or because they  
162 work well together and increase the fitness of the individual (i.e. correlational selection,  
163 Sinervo & Svensson, 2002). A more complete and explicit consideration of these



164 connections among traits is therefore needed to improve our predictions of how  
165 individuals, and thus populations, will respond to changes in their environments.

166

167 A prime example of the importance of understanding trait correlations is the life-history,  
168 morphological, and behavioural changes observed in fish populations heavily exploited  
169 by fishing (Hutchings & Fraser, 2008, Uusi-Heikkilä *et al.*, 2008). Many harvesting  
170 regulations are size selective, so individuals are removed from the population based  
171 (more or less) solely on their morphology, that is, their body size. However, as we now  
172 know, individual growth rates are correlated with a whole suite of physiological,  
173 behavioural, and life-history traits (Réale *et al.*, 2010; Uusi-Heikkilä *et al.*, 2008; Sutter *et*  
174 *al.*, 2012; Arlinghaus *et al.*, 2017). Therefore, highly selective harvesting will ultimately  
175 have consequences at the population level, leading to changes in recruitment, population  
176 recovery, and sustainable yields (Hutchings & Fraser, 2008). Disentangling how direct  
177 and indirect selection shapes these trait correlations, and the genetic mechanisms  
178 underlying their coupling, has led to a better understanding of how and why fish  
179 populations respond to harvesting as they do (Hutchings & Fraser, 2008). Similar  
180 approaches should now be used to understand how environmental change and other  
181 stressors, such as ocean acidification, anthropogenic noise, and warmer temperatures,  
182 will impact fish populations globally.

183

184 *4. How can we use existing datasets in combination with new analytical approaches to gain*  
185 *novel insights into the biology of fishes?*

186

187 Within the last decade scientists have accumulated vast amounts of genomic, phenotypic  
188 and ecological data for many fish species, mainly due to technological advances in data

189 generation and rapidly decreasing monetary costs (Muir *et al.*, 2016). Collection and  
190 synthesis of existing data provides a great opportunity to understand better the biology  
191 of fish populations and communities without the need to generate more information.  
192 However, analytical approaches for jointly analysing large datasets are still lacking due  
193 to the low accessibility of data or challenges in combining different types of data.  
194 Therefore, it is important that the scientific community increases their efforts in  
195 developing new approaches for extracting, combining, and analysing existing data. One  
196 promising avenue for fish biology is that of machine learning. While machine learning  
197 approaches, e.g. the decision-tree based random forest approach (Breiman 2001,  
198 Boulesteix *et al.* 2012), have been popular in many fields such as biomedical science or  
199 agriculture, they are now becoming more popular for analysing complex datasets in many  
200 other fields, especially for datasets with many indicators and small sample sizes (Chen &  
201 Ishwaran, 2012; Bernatchez, 2016). Random forest approaches have been successfully  
202 used in a variety of studies analysing population genomic and phenotype datasets, e.g. for  
203 predicting adaptive phenotypes related to climate (Holliday *et al.*, 2012), determining  
204 genetic loci distinguishing ecotypes (Pavey *et al.*, 2015), detecting intra-generational  
205 selection through pollutants (Laporte *et al.*, 2016), improving stock assignments in  
206 complex or mostly panmictic populations (Sylvester *et al.*, 2017), or predicting of fish  
207 ages from otolith morphometric data (Williams *et al.*, 2015). These are all situations in  
208 which classical approaches have lower power or have failed. Random forest algorithms  
209 have also proven useful for the analysis of stable isotope datasets, using regression or  
210 classification approaches to model interactions between predictor variables, and  
211 imputing missing data (Cutler *et al.*, 2007). While a detailed review is outside the scope  
212 of this article, there are many other promising analytical frameworks and solutions that  
213 could be used to tackle complex biological datasets. In order to make such large scale

214 studies feasible, data have to be collected and compiled in an accessible and unified way.  
215 Such databases exist for some types of data or are in the process of being built, e.g.  
216 GenBank or IsoBank (NCBI Resource Coordinators, 2017; Pauli *et al.*, 2017), but more  
217 effort is needed to develop a common reporting format that permits integration of  
218 different types of data, such as phenotype and genotype data.

219

220 *5. How can we use animal collective behaviour to better understand the group level impacts*  
221 *of environmental stressors?*

222

223 As in most animal groups, fish benefit from social living in a variety of ways. These  
224 advantages can influence individual fitness directly, such as increased protection against  
225 predators, enhanced foraging success, better access to reproductive partners, and  
226 transmission of behaviour and information between individuals (Ward & Webster,  
227 2016). However, there are also costs associated with group living, for example, increased  
228 chances of parasitism (Côté & Poulin, 1995) and increased competition (Krause *et al.*,  
229 2000). Trade-offs arising from these costs and benefits are likely to be influenced by large  
230 scale environmental stressors, including, but not limited to increases in water  
231 temperatures, ocean acidification, and fishing pressure. There has been considerable  
232 research on the effects of these stressors showing for example species range shifts due to  
233 climate change (Pecl *et al.*, 2017). However, while considerable information is available  
234 at the individual and population level, few studies seek to explain or understand how fish  
235 respond to perturbations or stressors at the more ecologically relevant scale of group,  
236 shoal, or school. A large proportion of fish species live in such groups, and in order to fully  
237 understand the impacts of global change on fish, studies of group level effects on animal  
238 collective behaviour may be paramount.

239

240 Group living provides the opportunity for social learning and in many cases this benefits  
241 individuals within groups, thereby allowing the spread of learnt behaviours or  
242 knowledge through social transmission and avoiding potentially costlier trial and error  
243 learning (Rendell *et al.*, 2010). Social learning also enables cross-generational  
244 transmission of information like migratory routes (Helfman & Schultz, 1984). However,  
245 traditions and social learning strategies may lead to maladaptive outcomes; traditions  
246 may become deleterious when disadvantageous environmental changes arise or when  
247 naive fish follow leaders down sub-optimal routes (Laland & Williams, 1998). The  
248 potential consequences of group movement where leaders or specific phenotypes may  
249 be selectively removed or impacted by global stressors is poorly understood.

250

251 The argument to move from studies focused on factors which affect behaviour at an  
252 individual level to consider group level collective behaviour has been raised before. For  
253 example, previous studies have suggested combining cognitive studies at the individual  
254 level with similar questions posed at the collective level (Pelé & Sueur, 2013). However,  
255 attempts at developing a cohesive approach that incorporates individual behaviour into  
256 collective decision making at the shoal or school level are limited. With recent and rapid  
257 technical advancements allowing improved video and tag-tracking abilities, questions on  
258 the importance of variation at the individual level in group responses to stressors or on  
259 the effect of environmental change on collective motion, are becoming more tractable.

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## Concluding remarks

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Challenges and opportunities facing various themes within fish biology are analytical in nature. However, the methods proposed to solve these different issues are in many cases interchangeable, highlighting the need and possibility for stronger collaborative networks between fish biologists working within different disciplines. For example, data on the changing dietary constituents of fish feed and their corresponding effect on the nutritional quality of farmed fish have been collected for decades and, while some effort has been made to analyse patterns within these datasets and link them to human nutritional trends (Sprague *et al.*, 2016), accessibility and data formatting issues have prevented more powerful analyses. Collaboration among scientists involved in aquaculture and those researching analytical approaches, such as machine learning algorithms, could revolutionise predictive modelling of nutrient budgets within farmed systems, resulting in more accurate predictions for future nutritional availability. Other scientific fields are beginning to turn towards these highly diverse collaborations. For example, the Global Lake Ecological Observatory Network or GLEON ([gleon.org](http://gleon.org)) is an international group of limnologists and ecologists working to understand, predict and communicate the response of lake ecosystems to a changing global environment. This network of scientists shares resources, and near constant monitoring of limnological variables from lakes in over 50 countries, allows near real-time, web-accessible databases for rapid data transfers, facilitating international collaborations. Whether as part of a formal or informal network, many of the challenges discussed within this paper could benefit from more wide-ranging collaborations, thereby ensuring a productive future for research on fish biology.

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