

On the challenges and opportunities facing fish biology: a discussion of five key knowledge gaps

A. JACOBS*†, C. DORAN‡, D. S. MURRAY§, J. DUFFILL TELSNIG||, K. L. LASKOWSKI‡, N. A. R. JONES¶, S. K. AUER* AND K. PRÆBEL**

Institute of Biodiversity, Animal Health & Comparative Medicine, College of Medical, Veterinary & Life Sciences, University of Glasgow, Glasgow, G12 8QQ, U.K.*, ‡*Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology & Inland Fisheries, Müggelseedamm 310, Berlin, 12587, Germany*, §*School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, U.K.*, ||*School of Marine Science & Technology, University of Newcastle, Newcastle upon Tyne, NE1 7RU, U.K.*, ¶*Scottish Oceans Institute, School of Biology, University of St. Andrews, St. Andrews, KY16 9TH, U.K.* and *Faculty of Biosciences, Fisheries and Economics, The Norwegian College of Fishery Science, UiT The Arctic University of Norway, N-9037, Tromsø, Norway*

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 synthesize and summarize 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, U.K., 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; behaviour; data analysis; food security; integrative approaches; trait correlations.

INTRODUCTION

Similar to most fields in the biological sciences, fish and fisheries biology have advanced rapidly over the past 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). A deeper understanding of the biology of fish is more important than ever, however, as global challenges such as climate change, overfishing, intensive aquaculture systems and other anthropogenic stressors have effects that may prove increasingly challenging to many fish species (Ficke *et al.*, 2007; Halpern *et al.*, 2008).

†Author to whom correspondence should be addressed. Tel.: +44 141 330 6637; email: a.jacobs.1@research.gla.ac.uk

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

KEY QUESTIONS AND OPPORTUNITIES IN FISH BIOLOGY

HOW CAN WE USE FISH BIOLOGY TO INFORM AQUACULTURE AND WILD FISHERIES IN ORDER TO SECURE FOOD FOR A GROWING POPULATION?

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

In aquaculture, feed sustainability, disease and gamete quality are a growing concern. Systematic biological approaches involving multiple aspects of fish biology can help resolve these problems. As an example, the microbiome is one field of fish biology that may dramatically facilitate aquaculture's growth. Our growing understanding of a fish's second genome and our ability to manipulate microbiomes can improve aquaculture's understanding of nutritional requirements, pathogen resistance, sexual maturation and survivorship in farmed fish (Llewellyn *et al.*, 2014). For example, the use of plant-based products to feed predominantly carnivorous teleosts is a key issue (Murray *et al.*, 2014). Fishes are unable to process insoluble carbohydrates and fibre, commonly found within plant-based diets. Therefore, this huge, yet largely indigestible, source of nutrients is quickly excreted (Llewellyn *et al.*, 2014). A considerable step towards sustainable aquaculture would be to: use our knowledge of fish microbiomes to improve predictions regarding interactions between plant-based sustainable feed sources and the digestive systems of farmed fish; to manipulate fish microbiomes to efficiently process and utilize previously indigestible nutrients.

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

As a caveat to these and other examples of future research priorities within aquaculture and fisheries, scientists must also continue to develop their core understanding of fish biology. Despite the wealth of knowledge accrued during decades of aquaculture and fisheries research, fundamental biological research continues to provide new insights on the basic biology of fish. For example, the genetic bases underlying ecologically important traits (Barson *et al.*, 2015) or intraspecific variability in physiological traits (Burton *et al.*, 2011), enable scientists to fully investigate behavioural, physiological or genomic changes from accurate biological baselines.

HOW CAN WE USE EVOLUTIONARY BIOLOGY TO PREDICT CONTEMPORARY RESPONSES TO CLIMATE CHANGE, HARVESTING AND OTHER ANTHROPOGENIC STRESSORS?

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

Species may be able to cope with environmental change by either shifting their distributions, coping with new environments *via* phenotypic plasticity, or adapting to novel environmental conditions (Crozier & Hutchings, 2014; Campbell *et al.*, 2017). Therefore, more detailed knowledge of evolutionary responses and the underlying mechanisms, on different time scales and in different environments and species are needed to enhance our understanding of how fishes will respond to different stressors. For example, studies on the effects of strong harvesting pressures on fish populations, *e.g.* through long term declines in population size and genetic diversity (Pinsky & Palumbi, 2014) or through short-term changes in gene expression (Uusi-Heikkilä *et al.*, 2017), have already given us a better understanding of how harvesting pressure might affect the evolutionary potential of fish populations. Furthermore, evolutionary studies, *e.g.* in combination with detailed ecological and developmental approaches, can illuminate questions of interest for conservation, regarding *e.g.* the effects of reduced genetic diversity on population persistence and adaptive potential (Pauls *et al.*, 2013), the flexibility of evolution (Elmer & Meyer, 2011), or in locating species refugia and drivers of diversity (Dornburg *et al.*, 2017).

We therefore argue for more collaborative studies that combine a wide range of information on populations and species that differ in distribution, ecology, genetic and

phenotypic diversity, adaptive potential and evolutionary history. This will help to generate more generic information about the potential of populations, species or biomes to respond to environmental and anthropogenic stressors.

CAN KNOWLEDGE OF CORRELATED TRAITS IMPROVE PREDICTIONS FOR FISH POPULATION RESPONSES TO ENVIRONMENTAL CHANGE?

For simplicity and clarity as fish biologists, we often consider our trait of interest, such as reproductive effort, morphological specialization, or migration tendencies, as independent or at least in isolation from other traits of that same individual. It is clear, however, that the expression and function of all traits within an individual are, to some extent, dependent on each other. Whole suites of traits can be correlated due to either mechanistic constraints [*e.g.* genetic correlations (Steppan *et al.*, 2002)] or because they work well together and increase the fitness of the individual [*i.e.* correlational selection (Sinervo & Svensson, 2002)]. A more complete and explicit consideration of these connections among traits is therefore needed to improve our predictions of how individuals and thus populations, will respond to changes in their environments.

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

HOW CAN WE USE EXISTING DATASETS IN COMBINATION WITH NEW ANALYTICAL APPROACHES TO GAIN NOVEL INSIGHTS INTO THE BIOLOGY OF FISHES?

Within the past decade scientists have accumulated vast amounts of genomic, phenotypic and ecological data for many fish species, mainly due to technological advances in data generation and rapidly decreasing monetary costs (Muir *et al.*, 2016). Collection and synthesis of existing data provides a great opportunity to understand better the biology of fish populations and communities without the need to generate more information. Analytical approaches, however, for large datasets are still lacking due to the low accessibility of data or challenges in combining different types of data. Therefore, it is important that the scientific community increases their efforts in developing new approaches for extracting, combining and analysing existing data. One promising

avenue for fish biology is that of machine learning. While machine learning approaches, *e.g.* the decision-tree based random-forest approach (Breiman, 2001; Boulesteix *et al.*, 2012), have been popular in many fields such as biomedical science or agriculture, they are now becoming more popular for analysing complex datasets in many other fields, especially for datasets with many indicators and small sample sizes (Chen & Ishwaran, 2012; Bernatchez, 2016). Random-forest approaches have been used successfully in a variety of studies analysing population genomic and phenotype datasets, *e.g.* for predicting adaptive phenotypes related to climate (Holliday *et al.*, 2012), determining genetic loci distinguishing ecotypes (Pavey *et al.*, 2015), detecting intra-generational selection through pollutants (Laporte *et al.*, 2016), improving stock assignments in complex or mostly panmictic populations (Sylvester *et al.*, 2018), or predicting of fish ages from otolith morphometric data (Williams *et al.*, 2015). These are all situations in which classical approaches have lower power or have failed. Random-forest algorithms have also proven useful for the analysis of stable-isotope datasets, using regression or classification approaches to model interactions between predictor variables and imputing missing data (Cutler *et al.*, 2007). While a detailed review is outside the scope of this article, there are many other promising analytical frameworks and solutions that could be used to tackle complex biological datasets. In order to make such large-scale studies feasible, data have to be collected and compiled in an accessible and unified way. Such databases exist for some types of data or are in the process of being built, *e.g.* GenBank or IsoBank (NCBI, 2017; Pauli *et al.*, 2017), but more effort is needed to develop a common reporting format that permits integration of different types of data, such as phenotype and genotype data.

HOW CAN WE USE ANIMAL COLLECTIVE BEHAVIOUR TO BETTER UNDERSTAND THE GROUP LEVEL IMPACTS OF ENVIRONMENTAL STRESSORS?

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

Group living provides the opportunity for social learning and in many cases this benefits individuals within groups, thereby allowing the spread of learnt behaviours or knowledge through social transmission and avoiding potentially costlier trial and error

learning (Rendell *et al.*, 2010). Social learning also enables cross-generational transmission of information like migratory routes (Helfman & Schultz, 1984). Traditions and social learning strategies, however, may lead to maladaptive outcomes; traditions may become deleterious when disadvantageous environmental changes arise or when naive fish follow leaders down sub-optimal routes (Laland & Williams, 1998). The potential consequence of group movement where leaders or specific phenotypes may be selectively removed or affected by global stressors is poorly understood.

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

CONCLUDING REMARKS

Challenges and opportunities facing various themes within fish biology are analytical in nature. The methods proposed to solve these different issues, however, 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 & Tocher, 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 revolutionize 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 (GLEON; www.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.

The authors thank the organizing committee of the 50th Anniversary Meeting of The Fisheries Society of the British Isles for organizing and facilitating the discussion leading to this opinion piece. We also thank the delegates for excellent presentations and discussions during the week in Exeter. Finally, the authors would like to thank their respective funding bodies: A.J. was supported by an FSBI conference registration bursary, N.J. is supported by an FSBI studentship,

J.D.T is supported by NERC and Cefas, K.L.L. is supported by the Deutsche Forschungsgemeinschaft (LA 3778/1-1) and D.S.M. is supported by BBSRC.

References

- Alava, J. J., Cheung, W. W. L., Ross, P. S. & Sumaila, U. R. (2017). Climate change-contaminant interactions in marine food webs: toward a conceptual framework. *Global Change Biology* **23**, 3984–4001. <https://doi.org/10.1111/gcb.13667>
- Arlinghaus, R., Laskowski, K., Alós, J., Klefoth, T., Monk, C., Nakayama, S. & Schröder, A. (2017). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* **18**, 360–373. <https://doi.org/10.1111/faf.12176>
- Barson, N., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G., Fiske, P., Jacq, C., Jensen, A., Johnston, S., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Næsje, T. F., Orell, P., Romakkaniemi, A., Sægvog, H., Urdal, K., Erkinaro, J., Lien, S. & Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature* **528**, 405–408.
- Bernatchez, L. (2016). On the maintenance of genetic variation and adaptation to environmental change: considerations from population genomics in fishes. *Journal of Fish Biology* **89**, 2519–2556. <https://doi.org/10.1111/jfb.13145>
- Bernatchez, L., Wellenreuther, M., Araneda, C., Ashton, D., Barth, J., Beacham, T., Maes, G., Martinsohn, J., Miller, K., Naish, K., Ovenden, J. R., Primmer, C. R., Young Suk, H., Therkildsen, N. O. & Withler, R. E. (2017). Harnessing the power of genomics to secure the future of seafood. *Trends in Ecology & Evolution* **32**, 665–680.
- Boulesteix, A., Janitza, S., Kruppa, J. & König, I. (2012). Overview of random forest methodology and practical guidance with emphasis on computational biology and bioinformatics. *Wiley Interdisciplinary Reviews: Data Mining and Knowledge Discovery* **2**, 493–507. <https://doi.org/10.1002/widm.1072>
- Breiman, L. (2001). Random forests. *Machine Learning* **1**, 5–32. <https://doi.org/10.1023/A:1010933404324>
- Burton, T., Killen, S. S., Armstrong, J. D. & Metcalfe, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B* **278**, 3465–3473. <https://doi.org/10.1098/rspb.2011.1778>
- Campbell, C., Adams, C., Bean, C. & Parsons, K. (2017). Conservation evo-devo: preserving biodiversity by understanding its origins. *Trends in Ecology & Evolution* **32**, 746–759. <https://doi.org/10.1016/j.tree.2017.07.002>
- Chen, X. & Ishwaran, H. (2012). Random forests for genomic data analysis. *Genomics* **99**, 323–329. <https://doi.org/10.1016/j.ygeno.2012.04.003>
- Côté, I. M. & Poulin, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behavioural Ecology* **6**, 159–165. <https://doi.org/10.1093/beheco/6.2.159>
- Crozier, L. & Hutchings, J. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* **7**, 68–87. <https://doi.org/10.1111/eva.12135>
- Cutler, R., Edwards, T., Beard, K., Cutler, A., Hess, K., Gibson, J. & Lawler, J. (2007). Random forests for classification in ecology. *Ecology* **88**, 2783–2792. <https://doi.org/10.1890/07-0539.1>
- Dornburg, A., Federman, S., Lamb, A., Jones, C. & Near, T. (2017). Cradles and museums of Antarctic teleost biodiversity. *Nature Ecology & Evolution* **1**, 1379–1384. <https://doi.org/10.1038/s41559-017-0239-y>
- Elmer, K. & Meyer, A. (2011). Adaptation in the age of ecological genomics: insights from parallelism and convergence. *Trends in Ecology & Evolution* **26**, 298–306. <https://doi.org/10.1016/j.tree.2011.02.008>
- Ficke, A. D., Myrick, C. A. & Hansen, L. J. (2007). Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries* **17**, 581–613. <https://doi.org/10.1007/s11160-007-9059-5>
- Halpern, B., Walbridge, S., Selkoe, K., Kappel, C., Micheli, F., D'Agrosa, C., Bruno, J., Casey, K., Ebert, C., Fox, H., Fujita, R., Heinemann, D., Lenihan, H., Madin, E., Perry, M., Selig,

- E., Spalding, M., Steneck, R. & Watson, R. (2008). A global map of human impact on marine ecosystems. *Science* **319**, 948–952. <https://doi.org/10.1126/science.1149345>
- Helfman, G. & Schultz, E. (1984). Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour* **32**, 379–384. [https://doi.org/10.1016/S0003-3472\(84\)80272-9](https://doi.org/10.1016/S0003-3472(84)80272-9)
- Holliday, J., Wang, T. & Aitken, S. (2012). Predicting adaptive phenotypes from multilocus genotypes in sitka spruce (*Picea sitchensis*) using random forest. *G3: Genes|Genomes|Genetics* **2**, 1085–1093. <https://doi.org/10.1534/g3.112.002733>
- Hutchings, J. & Fraser, D. (2008). The nature of fisheries and farming-induced evolution. *Molecular Ecology* **17**, 294–313. <https://doi.org/10.1111/j.1365-294X.2007.03485.x>
- Krause, J., Hoare, D. J., Croft, D., Lawrence, J., Ward, A., Ruxton, G. D., Godin, J. G. J. & James, R. (2000). Fish shoal composition: mechanisms and constraints. *Proceedings of the Royal Society B* **267**, 2011–2017. <https://doi.org/10.1098/rspb.2000.1243>
- Laland, K. & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology* **9**, 493–499. <https://doi.org/10.1093/beheco/9.5.493>
- Laporte, M., Pavey, S. A., Rougeux, C., Pierron, F., Lauzent, M., Budzinski, H., Labadie, P., Geneste, E., Couture, P., Baudrimont, M. & Bernatchez, L. (2016). RAD sequencing reveals within-generation polygenic selection in response to anthropogenic organic and metal contamination in North Atlantic eels. *Molecular Ecology* **25**, 219–237. <https://doi.org/10.1111/mec.13466>
- Llewellyn, M. S., Boutin, S., Hoseinifar, S. H. & Derome, N. (2014). Teleost microbiomes: the state of the art in their characterization, manipulation and importance in aquaculture and fisheries. *Frontiers in Microbiology* **5**, 207. <https://doi.org/10.3389/fmicb.2014.00207>
- Muir, P., Li, S., Lou, S., Wang, D., Spakowicz, D., Salichos, L., Zhang, J., Weinstock, G., Isaacs, F., Rozowsky, J. & Gerstein, M. (2016). The real cost of sequencing: scaling computation to keep pace with data generation. *Genome Biology* **17**, 53. <https://doi.org/10.1186/s13059-016-0917-0>
- Murray, D. S., Hager, H., Tocher, D. R. & Kainz, M. J. (2014). Effect of partial replacement of dietary fish meal and oil by pumpkin kernel cake and rapeseed oil on fatty acid composition and metabolism in Arctic charr (*Salvelinus alpinus*). *Aquaculture* **431**, 85–91. <https://doi.org/10.1016/j.aquaculture.2014.03.039>
- NCBI (2017). Database resources of the National Center for biotechnology information. *Nucleic Acids Research* **45**, D12–D17. <https://doi.org/10.1093/nar/gkw1071>
- Pauli, J., Newsome, S., Cook, J., Harrod, C., Steffan, S., Baker, C., Ben-David, M., Bloom, D., Bowen, G., Cerling, T., Cicero, C., Cook, C., Dohm, M., Dharampal, P. S., Graves, G., Gropp, R., Hobson, K. A., Jordan, C., MacFadden, B., Birch, S., Poelen, J., Ratnasingham, S., Russell, L., Stricker, C. A., Uhen, M. D., Yarnes, C. T. & Hayden, B. (2017). Opinion: why we need a centralized repository for isotopic data. *Proceedings of the National Academy of Sciences* **114**, 2997–3001. <https://doi.org/10.1073/pnas.1701742114>
- Pauls, S., Nowak, C., Bálint, M. & Pfenninger, M. (2013). The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology* **22**, 925–946. <https://doi.org/10.1111/mec.12152>
- Pavey, S., Gaudin, J., Normandeau, E., Dionne, M., Castonguay, M., Audet, C. & Bernatchez, L. (2015). RAD sequencing highlights polygenic discrimination of habitat ecotypes in the panmictic American eel. *Current Biology* **25**, 1666–1671. <https://doi.org/10.1016/j.cub.2015.04.062>
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B. & Falconi, L. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, 9214. <https://doi.org/10.1126/science.aai9214>
- Pelé, M. & Sueur, C. (2013). Decision-making theories: linking the disparate research areas of individual and collective cognition. *Animal Cognition* **16**, 543–556. <https://doi.org/10.1007/s10071-013-0631-1>
- Pinsky, M. & Palumbi, S. (2014). Meta-analysis reveals lower genetic diversity in overfished populations. *Molecular Ecology* **23**, 29–39. <https://doi.org/10.1111/mec.12509>
- Rassweiler, A., Costello, C., Hilborn, R. & Siegel, D. (2014). Integrating scientific guidance into marine spatial planning. *Proceedings of the Royal Society B* **281**, 20132252. <https://doi.org/10.1098/rspb.2013.2252>

- Réale, D., Garant, D., Humphries, M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B* **365**, 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>
- Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T. & Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science* **328**, 208–213. <https://doi.org/10.1126/science.1184719>
- Schinegger, R., Palt, M., Segurado, P. & Schmutz, S. (2016). Science of the total environment untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. *Science of the Total Environment* **573**, 1079–1088. <https://doi.org/10.1016/j.scitotenv.2016.08.143>
- Sinervo, B. & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity* **89**, 329–338. <https://doi.org/10.1038/sj.hdy.6800148>
- Sprague, R. J. R. & Tocher, D. R. (2016). Impact of sustainable feeds on omega-3 long-chain fatty acid levels in farmed Atlantic salmon, 2006–2015. *Scientific Reports* **6**, 21892. <https://doi.org/10.1038/srep21892>
- Steppan, S., Phillips, P. & Houle, D. (2002). Comparative quantitative genetics: evolution of the G matrix. *Trends in Ecology & Evolution* **17**, 320–327. [https://doi.org/10.1016/S0169-5347\(02\)02505-3](https://doi.org/10.1016/S0169-5347(02)02505-3)
- Sutter, D., Suski, C., Philipp, D., Klefoth, T., Wahl, D., Kersten, P., Cooke, S. & Arlinghaus, R. (2012). Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences* **109**, 20960–20965. <https://doi.org/10.1073/pnas.1212536109>
- Sylvester, E., Bentzen, P., Bradbury, I., Clément, M., Pearce, J., Horne, J. & Beiko, R. (2018). Applications of random forest feature selection for fine-scale genetic population assignment. *Evolutionary Applications* **11**, 153–165. <https://doi.org/10.1111/eva.12524>
- Thorson, J., Jannot, J. & Somers, K. (2017). Using spatio-temporal models of population growth and movement to monitor overlap between human impacts and fish populations. *Journal of Applied Ecology* **54**, 577–587. <https://doi.org/10.1111/1365-2664.12664>
- Troell, M., Naylor, R., Metian, M., Beveridge, M., Tyedmers, P., Folke, C., Arrow, K., Barrett, S., Crépin, A.-S., Ehrlich, P., Gren, A., Kautsk, N., Levin, S. A., Nyborg, K., Österblom, H., Polasky, S., Scheffer, M., Walker, B. H., Xepapadeas, T. & de Zeeuw, A. (2014). Does aquaculture add resilience to the global food system? *Proceedings of the National Academy of Sciences* **111**, 13257–13263. <https://doi.org/10.1073/pnas.1404067111>
- Uusi-Heikkilä, S., Wolter, C., Klefoth, T. & Arlinghaus, R. (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution* **23**, 419–421. <https://doi.org/10.1016/j.tree.2008.04.006>
- Uusi-Heikkilä, S., Sävilampi, T., Leder, E., Arlinghaus, R. & Primmer, C. (2017). Rapid, broad-scale gene expression evolution in experimentally harvested fish populations. *Molecular Ecology* **26**, 3954–3967. <https://doi.org/10.1111/mec.14179>
- Ward, A. & Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals*, pp. 111–124. Heidelberg: Springer. https://doi.org/10.1007/978-3-319-28585-6_6
- Williams, A., Newman, S., Wakefield, C., Bunel, M., Halafih, T., Kaltavara, J. & Nicol, S. (2015). Evaluating the performance of otolith morphometrics in deriving age compositions and mortality rates for assessment of data-poor tropical fisheries. *ICES Journal of Marine Science* **72**, 2098–2109. <https://doi.org/10.1093/icesjms/fsv042>