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Grand challenges at the frontiers of fish science

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We provide a review of what we consider to be grand research challenges for fish science in an era of human-induced rapid environmental change.

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1 Introduction

It is common knowledge that fishes are the most speciose of the vertebrates with the true bony fishes, the teleosts, having over 34,000 species and still counting. Fishes thrive in water bodies over the entire globe, from polar seawaters at sub-zero temperatures to continental soda springs at 40°C, and a huge diversity of aquatic habitats in between. They include species with extremely short life cycles, such as the azure killifish (*Notobranchus furzeri*) that inhabits seasonal puddles in equatorial Africa (1), and also the vertebrate with the longest known life span, the Greenland shark (*Somniosus microcephalus*) that lives in deep cold waters of the Northern Atlantic (2). The biology of fishes is so diverse and such a vast topic that each fish biologist may have their own opinion about what constitute the most interesting characteristics of fishes and the most important priorities for research.

1.1 Fishes and humans

Fishes are profoundly interwoven into the fabric of human societies with evidence of consumption by Pliocene hominins dating back almost 2 million years, and of fishing by *Homo sapiens* 40,000 years ago in the Upper Paleolithic (3, 4). They remain a pillar of food security for mankind, a source of high-quality protein and essential nutrients. Although aquaculture provides an increasing proportion of fishes for human consumption, wild populations continue to be extremely valuable resources. Emblematic examples include the bluefin tuna, where a single Pacific bluefin (*Thunnus orientalis*) individual weighing 278 kg commanded a price of over three million US dollars in 2019, or the beluga sturgeon (*Huso huso*) that is critically endangered because its caviar sells for thousands of dollars per kg. Human predation on fishes is, therefore, a major issue in fish science. Fishes also have an important role in human sense of wellbeing.

The beauty of fishes is a source of pleasure that supports major industries, especially in the Global South, whether it be tourism on coral reefs or the aquarium trade in ornamental marine and freshwater species. The joys of angling have been mused about for centuries and recreational fishing is a massive global industry (5). Mankind's interaction with fishes for pleasure is, however, complex. Eco-tourism interactions with fishes, even when these seem harmless, may actually influence their physiology and behavior in negative ways (6). At the same time, recreational fishing may be very stressful for fishes and its impacts on welfare require further research (7). The negative effects of ecotourism or angling on fish welfare seem, however, almost trivial when compared to the welfare concerns related to commercial fishing and intensive aquaculture, and to the unceasing anthropogenic pressure on fish populations worldwide, with the myriad facets of global change that can interact with harvesting pressure and harvest-induced evolution (8–10).

1.2 Fishes and the stability of aquatic ecosystems

Beyond the many services that fishes provide to humankind, they are a key component of aquatic biota with ecological roles that are essential for the stability of their ecosystems, with many of these roles remaining to be discovered. They contribute profoundly to nutrient cycling, with feeding strategies at all levels of the food web, from detritivores and planktivores up to apex predators (11). Their dead carcasses provide a source of nutrients to the base of the food web and, in marine systems, sinking carcasses sequester carbon dioxide into the abyss and contribute to the carbon biological pump in the deep sea (12). Marine fish produce and excrete precipitated (non-skeletal) calcium carbonate in various forms and thus they represent a significant source of carbonate sediments in the oceans (13). We are only beginning to understand patterns of biodiversity within fishes, at all biological levels from individuals to communities. For example, within fish assemblages, it is the functional diversity that plays a major role in the stability of aquatic ecosystems, not simply the species richness. While species richness is linked to several ecosystem processes such as productivity and the efficiency of resource use and nutrient cycling (14), fish species do not all contribute equally to the function of their ecosystems: the diversity of species functional attributes adds another important dimension to ecosystem understanding (15, 16). Such functional diversity enhances long-term stability, through functional redundancy and complementarity, and can help to buffer ecosystems against disturbances (17).

The modern sharks and rays, the Subclass Elasmobranchii, are worthy of a special mention. One of the most ancient and evolutionarily distinct vertebrate clades, comprising more than 1,200 species, sharks and rays are key functional components of marine ecosystems. They can only sustain relatively low levels of fishing mortality because of their particular life history traits, with late maturity and the production of few offspring. Many populations now show signs of rapid depletion and local extinctions, mainly due to overexploitation (18, 19). The Elasmobranchs have many ecological roles, that range from nutrient cycling to habitat engineering to controlling invasive species (20), and there are ongoing debates about whether their decline will ultimately induce trophic cascades in marine ecosystems (21).

2 The grand challenge

The greatest and overriding research challenge that we face is to increase our understanding of the biology of fishes in a context of human-induced rapid environmental change (HIREC). Increasing the knowledge base is our best strategy for understanding and predicting how fish populations, species, and communities will respond to ongoing global change and for identifying potential mitigation measures. This is not an argument against curiosity-driven research, quite the opposite. Basic knowledge is just as valuable as applied studies in, for example, ecotoxicology. The challenge is so vast that we can only provide a few examples of major research areas that, inevitably, reflect our own interests. At times this may betray elements of a checklist, as the diversity of themes defies the tracing of a unifying line of thought.

2.1 Experimental biology

Experimental biology holds the promise of providing a mechanistic understanding of how individual fishes are affected by conditions in their environment, whether these be biotic, abiotic, or xenobiotic. This could be of fundamental importance in projecting effects of HIREC on populations (22, 23) but is a major research challenge because fishes are so diverse and animal experimentation is so costly in terms of infrastructure and manpower. Currently, our knowledge of fish physiology and behavior is restricted to a few hundred mostly teleost species, with a profound bias toward temperate species from the Global North (24). A majority of fishes are, of course, extremely difficult to obtain alive to perform experimental biology, especially cryptic or deep-sea species. There is also a pervasive issue with the ecological validity of methods in experimental biology, and this is an active area of reflection (25, 26). One example would be that fish tend to be studied individually but often actually live in groups, where the physiology of the constituent individuals may be a major determinant of emergent group behaviors (27), for example phenotypic assortment may occur not just among but also within schools of fish (28). There is also a need to understand whether there are universal physiological and behavioral principles that underly how fishes respond to HIREC. For example, the major broadscale responses to global warming, namely changes in distribution, changes in phenology, and declines in adult size, but also responses to major environmental stressors such as heatwaves and hypoxia (25). A particular research effort is required to design experiments that can support robust mechanistic models to project how fishes will cope with current conditions and respond to future climates.

Most studies of the effects of environmental conditions on fishes focus on single species, limiting our forecasting ability to principles of autoecology (29), which aims at predicting how individuals of a given species respond to environmental change based on their specific environmental tolerance. While this approach has been used to model future distributions of ectotherms (30, 31) including those of co-occurring invasive and native species (32), interspecific interactions such as competition and predation are likely to exacerbate the effect of HIREC on fish communities (33, 34). This is particularly true for interacting species in which the effects of HIREC are driven by asymmetric responses (35). For this reason, a promising avenue to increase our predictive power on the ecological consequences of HIREC would be to focus on interacting species with different ecophysiological characteristics, especially of environmental tolerance.

Fish species with different physiologies will respond differently to climate change and this is even more marked when comparing endotherms (such as many predators of fishes, including birds and marine mammals) and ectotherms (such as fishes). For example, hypoxia and ocean acidification play no direct role in the ability of endotherms to prey on ectotherms, but likely cause decreased performance in the latter, increasing their vulnerability. The differential effects of HIREC on a predator vs. those on a prey is likely to shift the overall predator-prey balance with major consequence on species abundance and distribution, with obvious relevance for conservation (35–37). Some of these questions can be addressed by our increased ability to integrate experimental laboratory work with field observations, using techniques of biologging of physiological and behavioral traits, as well as the use of drones to monitor fish movement patterns in the wild.

2.2 Ecology: what fishes actually do in the wild

Among the myriad species of conservation concern and commercial importance, there is a critical knowledge gap about their movements and migration. It is surprising how little we know about the ecology and life cycles of species that we have been fishing for centuries, such as the bluefin tunas (38, 39). This is now becoming increasingly possible through acoustic telemetry networks, such as the European Tracking Network, the Integrated Marine Observing System or the Acoustic Tracking Array Platform, which now allow us to track fish migrations at continental scales. Simply coupling such information with biopsies, to estimate physiological variables such as energy reserves, this can provide much needed knowledge in the future. In fact, studying the physiology and behavior of fishes in their underwater environment remains a major challenge. The field of biologging and biotelemetry is undergoing exciting technological developments, including miniaturization and improved instrumentation, coupled with machine learning and Artificial Intelligence. The rapid development of these technologies will be particularly useful for studying the ecological roles of Elasmobranchs, in the few rare locations on Earth that have escaped the impacts of human activities (40, 41). This can provide a baseline from which to investigate their ability to cope with, and adapt to, areas subject to anthropogenic pressures. For almost all fish species, however, we are still not able to provide more than rough ballpark estimates of patterns of energy use in the wild (42, 43), information that is of great fundamental interest from an ecological viewpoint but also vital in understanding impacts of HIREC (44).

Amongst fishes, freshwater communities are a huge conservation concern related to HIREC, presenting severe population declines (45). Accessible freshwater habitats for fishes account for <0.01% of water on the planet, yet hold about half of all fish species (45, 46). The incessant human exploitation of freshwater, with an ever-increasing demand for agriculture, industrial uses, and drinking water, has led to scarcity, pollution, and massive damming of waterways. The consequent fragmentation limits not only productivity, but also connectivity among populations and habitats. Fish species that migrate over long distances and through different habitats have been hit by a multitude of these effects and have either declined severely or been extirpated (46, 47). These include such emblematic animals as the anadromous salmonids and sturgeons, and the catadromous eels. The importance of inland fisheries for human food security is underappreciated and underestimated, with very poor assessment by comparison to marine fisheries. Although two of the 14 UN Sustainability Goals specifically address water—N° 6 Clean Water and Sanitation, N° 14 Life Below Water—freshwater fishes and ecology are buried in N° 15, Life on Land. This has led some NGOs to describe the world's freshwater fishes as "forgotten" by decision-makers.

2.3 Understanding patterns of biodiversity toward conservation

Taxonomic knowledge is important to catalog and understand biodiversity, and is pivotal for measuring and achieving conservation goals. From a fundamental perspective, however, a pervasive problem for fish ecologists and fishery biologists has simply been knowing "what and how much is out there." This remains a challenge but, in the so-called "omics era," patterns of genomic diversity can now be examined and portrayed using cutting-edge and high-throughput DNA techniques and tools to identify fish stocks, assess migration between areas, and investigate local adaptations. Techniques of environmental DNA (eDNA) coupled to other non-destructive methods such as underwater visual census through ROV or AUV for visual species, and the use of deep-learning and automation processes for their recognition, promise advances that can expand the scale of observations at both spatial and temporal levels (48). Validation studies under controlled conditions provide promise in using eDNA to estimate abundance of species in their habitat. Such developments will be particularly useful for understudied freshwater ecosystems and in the vast marine deep-sea realm. Notably, deep-sea ecosystems (below 200 m depth) remain a particular mystery and there is now an urgency to study the "dark diversity" of their denizens, because of increased deep-sea fishery, with mesopelagic fishes as the last remaining frontier of marine fishery exploitation (49), coupled with growing pressure to expand deep-sea mining and oil and gas exploration, plus the creation of deep-sea reservoirs.

Although marine fisheries definitely receive more management attention than freshwater ones, overexploitation is recognized as a primary environmental and socioeconomic problem that menaces biodiversity and ecosystem functioning. Beyond factors such as a lack of political will and simply ignoring management advice, there were unsuitable fish stock management policies applied in the past because of insufficient description of subtle genetic structures in many exploited fish species. In fact, to manage wild populations and protect them from overfishing and climate change, we need to understand their genetic structure, breeding areas, and the factors associated with their adaptive diversity. In the marine environment, it is important to investigate how genetically distinct populations reflect the biogeographic and oceanographic history of a species, particularly the isolation of basins and the emergence of continental shelves during eras with low sea levels, such as during glacial maxima. Although present-day ecological and genetic connectivity among populations can be inferred from the duration of the pelagic larval phase, water's physicochemical characteristics and the sea-surface current patterns, we need to know more about potential inherited movement patterns for larval and juvenile stages. Some fish species can detect the earth's magnetic field to orient their migrations so exploring the contribution of inherited magnetic direction to larval dispersal is a challenging but interesting avenue to complement traditional modeling studies (50, 51).

Understanding the molecular mechanisms of adaptation is a major research challenge, both for fundamental evolutionary biology and for effective conservation of biodiversity. There is a need to determine the genomic background of important fitness traits for survival and reproduction over short evolutionary timescales, and how differences in evolution of gene expression among natural populations are due to genetic and/or environmental influences. Gene expression is highly sensitive to the environment, it is vital to understand how genotype-by-environment interactions elicit variations in gene expression that underly plasticity and can facilitate the early stages of adaptation and/or colonization of new environments. A species may experience spatially variable selection pressure from bioclimatic and/or environmental variables, which may drive adaptive divergence at the genomic level and reveal ecological trade-offs. This is the fascinating world of landscape and seascape genomics, exploring how the terrestrial and marine environment, respectively, influence the genomic diversity and connectivity of organisms, including fishes (52, 53).

Global change is expected to negatively impact fisheries and aquaculture, so research is underway to prepare these sectors for future challenges. This includes abiotic factors such as increased temperatures, but also biotic factors such as the non-indigenous species and viral, microbial and parasitic infections that are expected to thrive in the warmer environments. Non-indigenous species (NIS), especially invasive ones linked to ongoing climate change, represent a major research challenge. New routes for dispersal are being created by warming waters in temperate areas coupled with ice melting, which exacerbates the effects of human activities such as shipping and canal development (54, 55). There are socio-economic implications to the problems of non-indigenous species because, although escapes from aquaculture and the ornamental fish trade are frequently reported, these economic sectors provide a livelihood for many people. In addition, recent work has shown that non-native species are more resistant to extreme weather (56), stressing the importance of studying the relative performance of co-occurring native and non-native species in order to allow for predictions of their future potential habitat suitability (32, 57).

2.4 Integrating across scales of biological organization

An important theme that emerges from this brief review is the need for research that integrates across biological levels, from the genomic basis of individual function to outcomes and predictions at an ecological scale. That is, to develop multidisciplinary approaches that can explore how effects at the level of individuals translate up levels of organization to affect ecosystem processes. A couple of examples are mentioned here. One fruitful research avenue could be the development of databases of functional traits both among and within species, such as metabolic rates and environmental tolerances, to improve understanding of the ecological significance of patterns of phenotypic diversity (58). Innovative mechanistically-based modeling approaches are also beginning to link from individual function to population outcomes, including development of eco-genetic models to integrate information about heritability of traits of environmental adaptation to project short-term evolutionary responses (59–61).

3 Conclusions and the purpose of *Frontiers in Fish Science*

This partial view of global research priorities in fish science reveals just how vast the challenge is, and the broad scope for progression. There has never been a more important time to support the dissemination of research into the biology of fishes. *Frontiers in Fish Science* provides a conduit for rapid and open dissemination of high-quality research on all facets of the biology of fishes, from experimental studies on individuals to understanding and modeling processes at ecological and evolutionary levels. In so doing, *Frontiers in Fish Science* will foster an improved understanding of patterns of biodiversity in fishes, toward sustainable management of fishes and the ecosystems that they inhabit. We are particularly interested in helping to redress global imbalances in research focus, so we hope to promote publications in fish biology from the Global South and in freshwater ecosystems. We are committed to supporting principles of equity, diversity, and inclusion in our global community.

Author contributions

DM: Conceptualization, Writing – original draft, Writing – review & editing. KA: Writing – original draft, Writing – review & editing. PD: Writing – original draft, Writing – review & editing. EF: Writing – original draft, Writing – review & editing. JM: Writing – original draft, Writing – review & editing. CT: Writing – original draft, Writing – review & editing.

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