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OPINION

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Twenty-five emerging questions when detecting, understanding, and predicting future fish distributions in a changing climate

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Abstract
The 2023 Annual Symposium of the Fisheries Society of the British Isles hosted opportunities for researchers, scientists, and policy makers to reflect on the state of art of predicting fish distributions and consider the implications to the marine and aquatic environments of a changing climate. The outcome of one special interest group at the Symposium was a collection of questions, organized under five themes, which begin to capture the state of the field and identify priorities for research and management over the coming years. The five themes were Physiology, Mechanisms, Detect and Measure, Manage, and Wider Ecosystems. The questions, 25 of them, addressed concepts which remain poorly understood, are data deficient, and/or are likely to be impacted in measurable or profound ways by climate change. Moving from the first to the last theme, the questions expanded in the scope of their considerations, from specific processes within the individual to ecosystem-wide impacts, but no one question is bigger than any other: each is important in detecting, understanding, and predicting fish distributions, and each will be impacted by an aspect of climate change. In this way, our questions, particularly those concerning unknown mechanisms and data deficiencies, aimed to offer a guide to other researchers, managers, and policy makers in the prioritization of future work as a changing climate is expected to have complex and disperse impacts on fish populations and distributions that will require a coordinated effort to address.

KEYWORDS
climate change, conservation, ecosystems, management, physiology, species distributions

1 | INTRODUCTION

Under shifting climates, features of aquatic systems such as temperature (Abraham et al., 2013; van Vliet et al., 2013), dissolved oxygen (Keeling et al., 2010; Vedor et al. 2021), varying water level (Winfield et al., 2016), and storm frequency or intensity (Marcos et al., 2011) all continue to change. Whether in marine or freshwater environments, teleosts and elasmobranchs are likely to respond to these environmental changes with physiological and behavioral modifications (Galappaththi et al., 2021; Lam et al., 2016). For many species, this may include distribution shifts (e.g. Last et al., 2011; Townhill et al., 2023), further discussed here as an outward or inward adjustment of historical ranges driven by physiological or mechanistic constraints imposed by the prevailing climatic regime and, in some cases, the arrival and establishment of non-native species that potentially can become invasive (e.g. D'Amen & Azzurro, 2020). These range shifts may have broadscale consequences for species monitoring (Rooper et al., 2021), conservation (Stuart-Smith et al., 2021), and fisheries management (Mendenhall et al., 2020), ranging from challenges to our understanding of basal biological responses to climate effects, like ocean warming, to wider ecosystem effects (e.g. Perry et al., 2005).

At the 2023 Fisheries Society of the British Isles Annual Symposium (Symposium 2023 – Fisheries Society of the British Isles [fsbi.org.uk]) 2023, a dedicated Special Interest Group identified 25 emerging questions under five themes that reflect challenges and selected current and upcoming research opportunities for detecting, understanding, and predicting fish distributions under a changing climate. The themes were as follows: Physiology, Mechanisms, Detect and Measure, Manage, and Wider Ecosystems. Under each theme, we discussed the context of each topic concerning climate change impacts and the challenges associated with predicting future and/or understanding present fish distributions. We then identified the key questions relevant to the theme, which, if answered, could provide considerable insights for improved management and conservation purposes. In the context of a changing climate, we hope to help advance our understanding and capacity to respond to changing fish predictions in a sustainable way.

2 | THEME 1: PHYSIOLOGY

Changes in climate conditions are predicted to induce physiological responses in fishes, for example the ability to regulate homeostasis under stress, which can then affect higher-level functions, including growth, reproduction, behavior, and distribution patterns (Little et al., 2020; Mitra et al., 2023). The scope for physiological plasticity and acclimation varies among individuals, species, and populations, ultimately determining their resilience to changing climate (Bailey et al., 2022; Petitgas et al., 2013), and this scope can vary by populations within species and among species. While immediate, resultant, or long-term adaptative physiological responses of fishes to singular climate change impacts are becoming more apparent (Nagelkerken et al., 2023), it remains uncertain how synergistic impacts influence species' distribution and capacity for physiological acclimatization. The impacts of climate change on aquatic vertebrates begin with changes in the abiotic features of the environment, chief among these for fish are the arriving changes in temperature, ocean acidification, and oxygen saturation. Under tropicalization (Osland et al., 2021; Zarzyczny et al., 2024) and borealization (Siwertsson et al., 2024; von Biela et al., 2023) scenarios, long-term exposure may either buffer or intensify the direction of co-occurring climate effects on fish physiological and behavioral traits. Increasing temperatures can increase the physiological performance of tropical fishes at the leading edge of their distribution (Figueira & Booth, 2010), potentially providing thermally suitable habitats at higher latitudes, whereas boreal and temperate species face physiologically unfavorable conditions at their trailing range edge (Coni et al., 2021; Enzor & Place, 2014). Warming can also have interactive effects with ocean acidification on the physiological traits of fishes (Heuer & Grosell, 2014; Mitchell et al., 2022), which may, in turn, modify the pace of range shifts of non-native and native species (Coni et al., 2021). Novel species interactions can facilitate the coexistence of range-shifting tropical herbivores and native temperate species, offering several physiological benefits such as reduced predation risk, increased growth, and prey access, as was the case for the reef community following seasonal invasion and assimilation of a planktivorous damselfish (Smith et al., 2018). These benefits are expected to be short-lived under future climatic conditions because the recruits of range-shifting species often fail to survive through winter (Mitchell et al., 2023) because seasonal changes in temperature, energetics, light, and prey can halt the establishment of species entering novel environments, and work defining a climate risk index has identified that under high emission scenarios 85% of marine species will experience impacts across their native distributions (Boyce et al., 2022). One example of such widespread ecological shifts in oceanographic suitability is the deoxygenation of the oceans, predicted to increase with rising water temperatures (Keeling et al., 2010; Townhill et al., 2017), with serious implications for species already observed at key demographic bottlenecks (Alderdice et al., 1958; Sear et al., 2014). For example, this has already been observed in large-bodied pelagic predators and as individuals are forced into shrinking oxygenated surface levels they are at higher risk of exploitation from fisheries (Vedor et al., 2021).

These changing climate phenomena are likely to impact trophic levels in different ways and at different scales: higher trophic levels are suggested to be more susceptible to negative trends in stock biomass and growth rate (Erauskin-Extramiana et al., 2023). In particular, freshwater food webs may be more susceptible to climate change due to a stronger reliance on size-structured systems (Woodward et al., 2010). Furthermore, increasing temperatures may shift growth–mortality trade-offs in favor of smaller, faster body sizes (Niu et al., 2023; Petchey et al., 1999). Trophic organization is also likely to be impacted, with higher trophic positions fading out and middle levels taking over the upper echelon of food webs (Tanentzap et al., 2020; Townhill et al., 2017).

These impacts of climate change are likely to have synergistic impacts on life-history traits. For example, ocean acidification can harm embryonic development or larval behavior, threatening species' survival (Pankhurst & Munday, 2011), and warming temperatures can trigger earlier migration, negatively impacting migration timing (Peer & Miller, 2014), drive variability in morphological development of key sensory organs (Peele et al., 2023), and/or shorten or delay spawning events leading to phase-shifts or failure to reproduce (Pankhurst & Munday, 2011). Without individual and collective assessments on the effect of such phenomena, we cannot appreciate the global impact on species´ demography, survival, and resultant distribution (Somero, 2010; Wild et al., 2023). Although life history may influence these physiological impacts of climate change through behavioral plasticity, this is not necessarily the case for all fish species, therefore it is important to identify the extent to which physiological traits can vary to cope with changing climate conditions (Somero, 2010).

1. What traits will benefit under tropicalization versus borealization? What traits will be lost?
2. How does life history interact with changing climate to create winners and losers? What life-history traits will determine winners and losers?
3. What is the effect of climate change on the ontogenetic development of individuals?
4. How will climate trends and shifting habitat suitability affect the predictability of migratory patterns?
5. Where and with what magnitude will deoxygenation impact distributions? What are the realized impacts of expanding oxygen minimum zones?
6. What are the physiological ways in which populations will adapt to climate change?
7. How will climate interact with the phenological timing of life-history stage dependent physiological demands?

3 | THEME 2: MECHANISMS

A changing climate will have complex mechanistic interactions across ecosystems, where organismal traits interact with the changing environment to produce species-level variation in distribution in response to climate change (Donelson et al., 2019; Lefevre et al., 2021). Many phenomena will result in changes to fish distributions through mechanistic channels such as habitat alteration through eutrophication (e.g. Lindegren et al., 2012), overfishing in marine ecosystems (e.g. Litzow et al., 2014), and aquatic food web and functional trait diversity alteration through immigration (e.g. Tekwa et al., 2022), emigration, and local extinctions. However, identifying those mechanistic tipping points for species demography and ecosystem functioning, and assessing their variation to changing climate against a noisy background of density dependence and natural variation is a complex challenge (e.g. Denechaud et al., 2020).

Climate-driven ecological shifts in ecosystems can drive declines in abundances of native species via interspecific competition with non-native species or reduction of habitat availability (Aprahamian et al., 2021). This can emerge from invasive species spread triggered by eutrophication events, which provide the foothold to colonization for non-native species through many means (Effler et al., 1996; McElarney et al., 2021). Abiotically, rising air temperature will threaten small freshwater fishes inhabiting small and shallow water bodies, for example lake minnow *Rhynchocypris percnura* (Pallas 1814), which can be prone to dramatic drying, forcing alteration of historic distributions through the removal of suitable habitat (Wolnicki & Sikorska, 2019). Furthermore, climate change can interact with human activities, for example fishing, to have a large impact on the survival and distribution of species: overfishing can cause fish populations to become more vulnerable to short-term natural climate variability (e.g. Ottersen et al., 2006) by making such populations less able to "buffer" against the effects of the occasional poor year classes. Long-term climate change can make stocks more vulnerable to fishing through two main mechanisms: (1) reducing the overall productivity of the stock such that the same level of fishing pressure might not be sustained and (2) preventing recovery of stocks to levels observed in the past (Winter et al., 2019). To understand the ways these mechanistic changes may play out, we must begin to explore species distributions from mechanistic perspectives by incorporating knowledge of species physiology, and not simply rely on correlative species distribution modeling (Muhling et al., 2020).

None of these phenomena act alone, and the mechanistic concerns of future fish distributions will be increasingly interconnected as climate change exacerbates existing and introduces new pressures on fish biology and ecology (e.g. Muhling et al., 2020). Describing and quantifying these interactions will improve our capacity to account for the mechanistic impact of climate change.

8. How can we untangle the various synergistic potential mechanistic drivers of distribution changes?
9. What is the impact of commercial harvesting on species distributions?
10. How can we distinguish density dependence effects from climate change?
11. What is the functional effect of non-natives spreading due to climate change on native species?

4 | THEME 3: DETECT AND MEASURE

The practicality and capacity for detecting and measuring species distributions are fundamental to the task of predicting future distributions and implementing effective conservation management strategies (Bates et al., 2015; Dahms & Killen, 2023; Fogarty et al., 2017; Kirk & Rahel, 2023). Key areas of research for improving our capacity to "detect" and "measure" stem from limited data availability or, more pertinently, the reliability of available data or the absence of data (Taheri et al., 2021), for example unknown historical "baselines" (Pauly, 2019). Current detection, and therefore prediction, depend on fisheries-dependent sampling and limited fisheries-independent surveys, constraining our understanding of global spatial and temporal fish distribution patterns.

Using long-term and large-scale retrospective data allows us to characterize and measure past distributions, abundances, and ecosystem processes, and contextualize concepts like "shifting baselines". Some examples of these types of data include fisheries records, oral histories (local and traditional ecological knowledge), and archaeological and paleontological information (Gervais et al., 2021; Pinnegar & Engelhard, 2008), but it can often be difficult to separate natural variation from anthropogenic changes when elucidating long-term patterns. In addition, molecular and isotope technique developments have increasingly enabled the detailed reconstruction of past distributions (Chakona et al., 2020).

Given methodological constraints on contemporary technological capacity, we can turn in some cases to alternative technologies: environmental DNA technology (eDNA) has been successful at detecting species fronts in fresh water (e.g. Muha et al., 2021) and has potential merit if applied in marine systems as an alternative sampling approach for estimating relative species abundance (Liu et al., 2022; Thomsen & Willerslev, 2015), species distributions (Budd et al., 2021), community composition (Muha et al., 2021), and population genetic variation (Dugal et al., 2022). Recent efforts link eDNA outputs with trawls (Maiello et al., 2022; Stoeckle et al., 2021) and acoustic survey data (Shelton et al., 2022) to improve information provided by traditional fisheries survey methods. As is the case with many novel technologies, there are caveats and limitations to deployment, but if limitations are kept in mind, tools like eDNA sampling can be effective complementary tools for monitoring species distributions (Dunn et al., 2023; Nagarajan et al., 2022; Yao et al., 2022). Additionally, incorporating various data sources, such as historical ecology or eDNA, into actionable datasets is crucial for modeling future distributions amidst changing political and ecological seascapes. For example, combining commercial (fisheries-dependent) and survey-based (fisheries-independent) data, complemented with information from citizen science, are considered to address gaps in data coverage to improve species distribution mapping and modeling (Braun et al., 2023; Karp et al., 2023; Rufener et al., 2021).

As we address the limitation of sparse data availability in the face of climate change, a key priority is to address the unequal geographical distribution of documented range-shift studies, with current research showing a northern hemisphere bias (Melo-Merino et al., 2020). This hemispheric bias leaves much of the southern hemisphere (with the exception of Australia) as a data-deficient zone and less prepared to deal with changing distributions. To summarize, under climate change our methods for detecting and measuring fish distributions will have to be flexible and novel to overcome the absence of data and the phenomena of shifting baselines.

12. How can we integrate knowledge of shifted baselines from variable resolutions into distribution predictions?
13. Do we have enough temporal coverage to quantify the extent of changes in distributions and be able to predict into the future?
14. What models can temporally and spatially cope with the datasets that exist both commercially and non-commercially and how comparable are these different types of data?
15. What models can spatially and temporally cope with datasets that comprise limited time series or only cover very recent time periods or that have implicit bias in collection methods?
16. How can we study distributions and detect range shifts from data-poor species?
17. How do you monitor the extent/edges of tropicalization versus borealization?
18. What are the best approaches for detecting species range boundaries and identifying the middle ranges?
19. When governance imposes restrictions on the capacity to monitor areas, for example marine protected areas, how can we methodologically and statistically correct this imposed lack of information in datasets?
20. What is the role of alternative relative methods, for example environmental DNA technology, in monitoring populations and their distributions?

5 | THEME 4: MANAGE

Climate change has been shown to drive changes in distribution of both freshwater and marine fishes to the extent that they may shift over political boundaries, for example Exclusive Economic Zones (EEZs), or into areas where different management regimes exist (Barbarossa et al., 2021; Hollowed et al., 2013). In the past, competition over the right to access shared stocks has triggered international conflicts, such as the well-known "Cod Wars" of the 1970s (Steinsson, 2016). In the early 2000s the United Nations Fish Stocks Agreement came into force with the aim of ensuring the long-term conservation and sustainable use of straddling and highly migratory fish stocks within the framework of the United Nations Convention on the Law of the Sea (https://www.fao.org/iuu-fishing/international-framework/un-fish-stocks-agreement/en/). However, when species distributions shift across a political boundary or into international waters there is still potential and realized disruption to quota sharing or access arrangements (Madin et al., 2012), where pelagic fish stocks often make the most complicated cases (Hooker et al., 2011).

In a global modeling study of stock distributions over time, it was estimated that by 2030 nearly a quarter of the world's transboundary fish stocks will have shifted, and 78% of the world's EEZs will have experienced at least one shifting stock (Palacios-Abrantes et al., 2021). Even in a data-rich stock, such as the Northeast Atlantic mackerel (*Scomber scombrus*), a dynamic species distribution can generate the conditions for political disputes and unresolved quota agreements (ICES, 2023b; Østhagen et al., 2022). In theory, quotas or catch shares should be tailored to match the share of the fish stock biomass present within a country's EEZ, a concept known as "Zonal Attachment", and furthermore that in the face of climate change fish stocks in northern Europe would benefit from scientific approaches where zonal boundaries are periodically reassessed, with catch shares adjusting accordingly (Fernandes & Fallon, 2020), but whether political institutions have the capacity to put aside practices of quota allocations based on the stocks baseline from 1973 to 1978 in exchange for this adaptable-zonal attachment method is yet to be determined.

Marine protected areas (MPAs) are likely to also be affected by climate-driven shifts in fish distributions and may make dedicated no-trawl zones less effective if the species they are designed to protect no longer persist in an area (Cashion et al., 2020; Gaines et al., 2018; ICES, 2023b). For example, the North Sea "plaice box" is now considered much less effective relative to when it was established because of climate-associated north-westward distribution shifts in juvenile plaice (*Pleuronectes platessa*) (van Keeken et al., 2007). Under climate change, MPA boundaries, for example those associated with the "plaice box", may benefit from spatially "adaptive" measures, also referred as Dynamic Ocean Management, in response to changes in the distribution of the species they are intended to protect and/or manage (Grüss et al., 2011; Lewison et al., 2015).

21. When species or population distributions cross or leave political boundaries, how do you define or adjust quotas belonging to different fishing communities and stakeholders?
22. In response to fish distribution shifts, how should we approach spatial planning? Can marine protected areas be made "adaptive" to climate change: should they "follow the fish" or be deselected when the key species no longer persist?

6 | THEME 5: WIDER ECOSYSTEMS

Studying the spatiotemporal scales of community functional traits is crucial for understanding the resilience of wider ecosystems to disturbances under climate change and potential modification to ecological functions and ecosystem services (Thompson et al., 2020, 2023).

Regarding fish distributions and global warming, the immigration and emigration of different species can drive changes in the wider trophic dynamics, biodiversity patterns, trait composition and functioning of fish assemblages, and ecosystem phase shifts (Bosch et al., 2022; Pinsky et al., 2020; Sunday et al., 2015; Vergés et al., 2014). In this sense, functional trait redundancy, which is related to community stability and resilience against disturbances, can sometimes buffer the impact of "lost" species on biodiversity and ecological functions and services because populations within species and species within a community can perform similar functions (Biggs et al., 2020; Micheli & Halpern, 2005; Mouillot et al., 2013, 2014; Ricotta et al., 2016).

In highly diverse assemblages of low functional trait redundancy, ecosystem functions depend on complementary trait composition, typically maintained via species niche differentiation and resource partitioning (Guillemont et al., 2011; Loreau, 2004; Mouillot et al., 2014). Here, novel species in a system can drive important changes in the community's functional organization (Bosch et al., 2022), for example large-scale habitat feature shift from algae forests to barrens following climate-mediated immigration into a Mediterranean Sea community by a tropical herbivore (Vergés et al., 2014). Therefore, understanding the relationship between fish trait biodiversity and community ecology is crucial for predicting species' functional niches in areas where fish expanded their distribution range. This will require better knowledge of fish species' traits, their role in ecosystem functioning and services, environmental gradients, and drivers of global change (Beukhof et al., 2019; Pinsky et al., 2020; Villéger et al., 2017). To date, research into these aspects of fish biology and ecology has been mostly conducted in the northern Atlantic Ocean (e.g., Beukhof et al., 2019; Dulvy et al., 2008; Fredston et al., 2021; ICES, 2023a), with a need for a higher scientific effort in the southern hemisphere and northern Pacific (Beukhof et al., 2019).

Notably, there are discrepancies in the long-term application of trait-based approaches in the southern hemisphere compared to recent findings of tropicalization in South America (Galván et al., 2022; Luza et al., 2022, 2023; Pinheiro et al., 2018; Silva et al., 2023). Some work is ongoing to address these gaps and evaluate, for example, the structural change of reef fish systems in Australia following novel trait invasion (Stuart-Smith et al., 2021, 2022; Sunday et al., 2015), but in many regions large knowledge gaps persist where trait-based approaches could help understand the climate-driven changes in coastal marine fish range shifts (Lloyd et al., 2012; Whitfield et al., 2021; Yemane et al., 2014; Degen et al., 2018).

Filling the global knowledge gaps in data-limited areas would require (1) documenting "long-term" changes in fish species composition and biological traits, including using information from peer-review and gray local or regional literature (often available in native languages only), and (2) establishing systematic biodiversity monitoring frameworks and protocols for appropriate data management. While these are only a few suggested ways to improve our understanding of fish distributions under climate change, there are other considerations needed regarding how such non-English texts are handled and available to management and decision-making processes (Hunter et al., 2021; Amano, et al., 2016; 2023). These efforts may require international collaboration among scientists and capacity building to fill data and knowledge gaps in the field of fish biology and fisheries in the Global South (Harden-Davies et al., 2022; Nyboer et al., 2023).

23. How will a species or population shift trigger indirect ecosystem-level synergistic consequences?
24. Particularly in the southern hemisphere, what will the functional impact be on ecosystem level or range shifts? Will distribution shifts decrease ecosystem services?
25. How can we adapt and manage to support ecosystem functioning and services in the face of distribution shifts across political boundaries?

7 | DISCUSSION

The 2023 Fisheries Society of the British Isles Annual Symposium provided a forum to identify and document topics that delegates consider to be the major frontiers in predicting fish distributions under a changing climate and agree that the effects of climate change cannot solely be studied in isolation, but require improved knowledge and better understanding of a multitude of scientific disciplines related to fish biology.

Like the omnipresent effects of climate change, the current limitations in predicting future fish distributions are shared across the themes outlined in this paper. The Symposium offered a forum to discuss issues related to of data deficiencies (see also Murray et al. [2024], this issue), the complex interconnectedness of ecosystem functioning, and geo-political divisions. Where data are sparse, be that spatially, temporally, or flatly unavailable for underrepresented regions, our approaches to "filling" these gaps would require creativity and a multidisciplinary approach.

The capacity for measuring, modeling, and interpreting fishes' distributions has dramatically increased in recent decades towards meeting the curiosity of scientists and demands from managers, policymakers, the fishing industry, and environmental non-governmental organizations. Here, an international group of scientists have outlined 25 questions aiming to progress the science behind the predictions of future fish distributions under different global change scenarios and the understanding of some aspects of fish biology and fisheries science. By no means are these five themes and 25 questions exhaustive, but we hope they provide the seeds for further research which will romote the fields of fish biology, ecology, and fisheries management.

AUTHOR CONTRIBUTIONS

All authors attended the special interest group workshop for Predicting Fish Distributions at the 2023 Fisheries Society of the British Isles Annual Symposium at the University of Essex, in July 2023. During the workshop, the concept was identified, including solidification of the five themes. M.P.R.-D. transcribed notes from initial workshops. Further work on the manuscript was conducted during video meetings and through collaborative documents hosted on online platforms. Management and coordination of the manuscript was done by M.M.K. All authors at the time of meetings attended at least one of the video meetings organized by M.M.K. Following the workshop, M.M.K. and G.L.H. used the notes from M.P.R.-D. to generate the 25 questions and concepts for each theme. All authors contributed to the initial writing of the themes within the manuscript. Specifically, authors contributed to themes based on expertise, as follows: G.L.H. and J.S.M. contributed to Themes 1 and 2; M.M.K., A.K.S., G.L.H., and S.F. contributed to Theme 3; J.K.P., J.W.W., R.D.M.N., and M.E.S. contributed to Theme 4; and M.P.R.-D., J.K.P., and M.P.-G. contributed to Theme 5. Theme groups met separately to produce drafts of the theme-specific text. M.M.K. and G.L.H. conceptualized the broad content of the introduction and discussion; M.M.K. wrote the introduction and discussion, with final draft feedback and contributions from all authors. M.M.K. was responsible for reviewing, editing, and submitting the work in its entirety. All authors contributed to the conceptualization and in some part to the writing of the manuscript. All drafts were approved by all authors. M.E.S. received support from the European Union, Horizon 2020, Marie Skłodowska-Curie Action, PinkSIES project, grant agreement no. 101026030. G.L.H. was supported by the PREDICT (Predicting seasonal movement of marine top predators using fish migration routes and autonomous platforms) project funded by Ørsted (https://www.abdn.ac.uk/sbs/research/predict-938.php). M.M.K. received funding from the University of Exeter - Cornwall.

CONFLICT OF INTEREST STATEMENT

Authors declare no conflicts of interest.

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