Novel Ecosystems: Altering Fish Assemblages in Warming Waters

The effects of increasing sea temperatures extend far beyond changes in species' distributions. By altering local fish abundances, temperature changes will have profound effects on the structure, functioning and services of marine ecosystems.

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Temperature has a pervasive effect on the biology and ecology of organisms, and natural environmental cycles have driven changes across a range of ecosystems. Some of the most striking examples of these biological cycles have been documented in marine ecosystems. For example, the Russell Cycle in the English Channel describes transitions between periods of cold water with a planktonic assemblage that supports herring, and warmer periods with a different plankton assemblage that supports pilchards [1]. Indeed, climatic oscillations spanning several decades have made the North Atlantic a particularly fertile laboratory for studying the effects of temperature fluctuations on the movement of organisms between warmer sub-tropical regions in the south and colder boreal regions to the north [2].

Concerns over the impacts of anthropogenic climate change have intensified the interest in the responses of organisms to rising temperature. As scientists struggle to envisage how climate change will drive current species assemblages into the 'novel ecosystems' of the future, much attention has focused on the alteration of species' ranges. Natural ranges are typically delineated from the presence and absence of species in different locations, and are fairly tractable to study because they can be compiled from a variety of widely available, disparate data sources. One frequently used tool to explain such ranges is climate envelope modelling, which builds statistical relationships between environmental factors and the present distribution of species, and can then project the results into the future under various climate-change scenarios [3]. However, a new study in *Current Biology* [4] reminds us that changes in the abundance of species can be far more dramatic than changes in species' distributions, which are the main preserve of climate envelope modelling. The new paper by Simpson *et al.* [4] stems from the well-studied northeast Atlantic where sea temperatures have risen 0.04°C per year in the last three decades. Despite relatively minor changes in the ranges of fishes, the authors find that 72% of common fish species have exhibited a significant change in abundance. While some species increased in abundance others declined. Such changes are likely to have much greater impacts on the ecology and exploitation of these fish assemblages than any range extensions or contractions.

The basis of the Simpson *et al.* [4] study is a detailed series of biological surveys comprising more than 100 million fishes from 177 species, and covering an area exceeding a million square kilometres. When data were reduced to the presence or absence of species, the authors found 12 biogeographically distinct fish assemblages, whose distributions remained relatively stable over time. In contrast, the abundance of 36 of the 50 commonest species is correlated with temperature, and the relationships varied across the assemblage; the abundance of 9 species declined as the water warmed, compared to a majority of 27 species that became more abundant. The latter species tend to be smaller and have ranges that are centred in lower latitudes (i.e., they naturally favour warmer water) than species that became less abundant. The authors also provide evidence that commercial fishing in the region reflects the fisheries-independent data set: catches increased for species that became more abundant and decreased for species that become less abundant.

The two lines of evidence from both fisheries-independent and fisheries-dependent data make a convincing case that fundamental changes in fish abundances have occurred in the northeast Atlantic during the last 30 years of warming. These changes have occurred while alterations of species distributions have been relatively modest, as demonstrated by previous work [5]. The results make two important points. First, while it is axiomatic that abundance data will be more insightful than data on presence or absence, we must remember that climate envelope models might mask important changes in abundance that have great ecological and economic value; second, modelling shifts in both range and abundance will require coordinated studies of the natural history, biology and ecology of the communities (Figure 1). To paraphrase Niels Bohr: predictions are very difficult, especially about the future, and especially with only a few parameters.

Having documented the changes to the northeast Atlantic fish assemblage, two major questions remain. First, why have they occurred? The mechanisms altering fish abundance are likely to be multifaceted and species-specific, but can be loosely separated into biological processes and ecological interactions, plus the level of exploitation (Figure 1). Biological considerations, such as whether an organism can survive or reproduce successfully at a particular temperature, may be relatively straightforward [6,7]. Indeed, the tighter correlation between changes in abundance and sea-surface temperatures, compared to bottom-surface temperatures, may indicate that warming is having an effect on the pelagic larvae of fishes [4]. This conclusion is consistent with studies across a range of marine taxa demonstrating reduced pelagic dispersal with increasing temperature [8]. Ecological drivers are likely to be more complex, to vary across life stages and to involve changes to prey, predators and competitive interactions. Previous research on the effects of temperature provides mechanistic clues for some fish species: for example, cod recruitment success is closely linked to the composition and phenology of plankton communities, which in turn are driven by temperature cycles [9]. Alternatively, temperature rise may lead to trophic imbalance as the overlap in distribution becomes

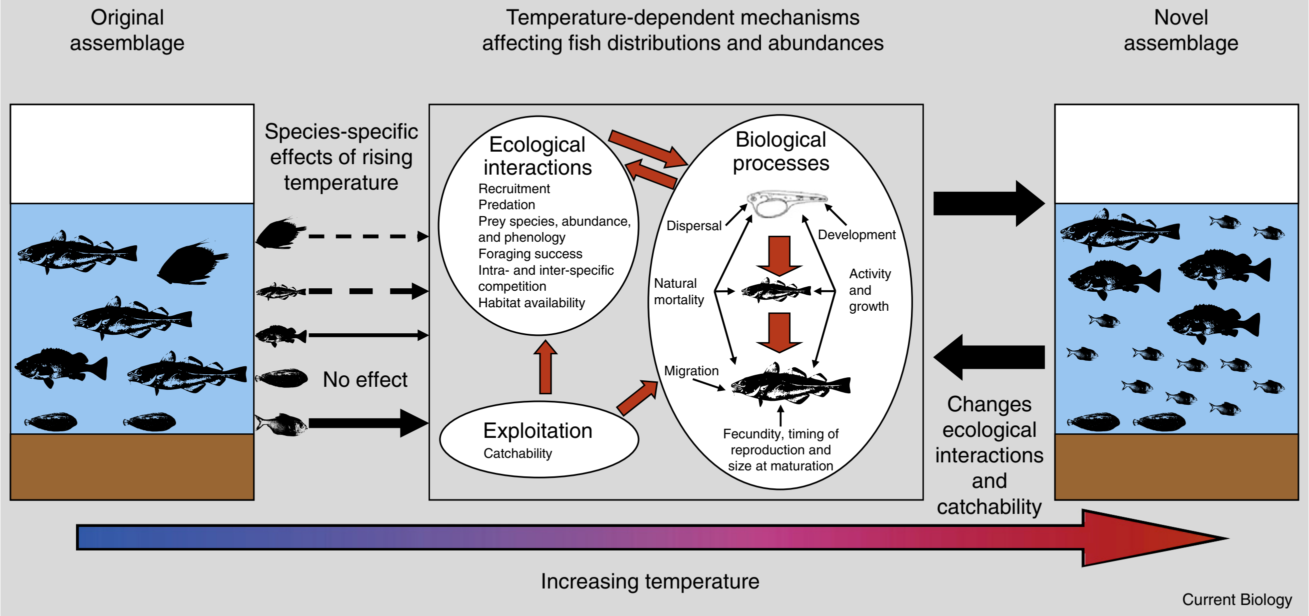

Figure 1. Changing assemblages.

The complexity of factors influencing the response of a fish assemblage to rising sea temperature, including biological processes, ecological interactions, human exploitation, and feedbacks. Species-specific differences in the overall response to temperature are represented by arrow style (dashed: abundances decreasing; solid: abundances increasing; arrow width indicates differences in the strength of response).

reduced between some predators and their prey [10]. However, limited data on the biology and ecology of many Atlantic species mean that it is difficult to move far beyond speculation over the factors that cause the changes reported in the Simpson *et al.* [4] study.

The second question concerns the impacts of changing fish assemblages on the wider community and fisheries. If understanding how temperature affects the abundance of individual species is already difficult, trying to establish these wider implications seems a Sisyphean task. Simpson *et al.* [4] show that individual fish species respond differently to rising temperatures, but such changes will be mirrored by other taxa in the ecosystem. This myriad of varying responses to increased temperature will result in novel assortments of species, and changes in their relative abundance (Figure 1). The study of such novel ecosystems is an emerging field of research [11,12], although most examples to date concern invasive terrestrial species. Extending this work into marine ecosystems will be particularly challenging, in part because species have such great potential for dispersal during their larval stages [13].

Yet, if we are to harvest novel marine ecosystems responsibly, it is important to understand their functioning. It is tempting to imagine that increased temperature could lead to increased productivity of large-bodied fishes because of the higher abundance of smaller fish prey, faster growth rates and reduced intra-guild competition. However, such speculation must also consider the response of the rest of the ecosystem, including factors such as the balance between heterotrophy and autotrophy as temperature changes [14]. Forecasting the full consequences of altered food webs in novel ecosystems requires us to embrace the metabolic theory of ecology, which explicitly considers the interactions among temperature, body size and resource availability [15]. Recent studies have attempted to incorporate aspects of this theory into simple food web models [16], but theoretical studies into the impacts of temperature on key properties of food webs remain in their infancy [17]. While assessing the effects of temperature on the persistence and functioning of food webs is challenging, it is clearly more than an academic exercise for critical fisheries such as the northeast Atlantic. Managing a region characterised by a labyrinthine fisheries policy that spans many countries, species, political agendas and market demands is difficult enough, but we now face a moving target. As climate changes, we rapidly need to understand how productivity of the new fishery will change, and how it can be harvested sustainably [18]. It took sampling of over 100 million fishes to document changing fish assemblages in the northeast Atlantic. It will be even harder to understand the structure, functioning, and implications of an entirely novel ecosystem.

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