COMMENTARY on Frainer A et al. (2017) Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proc Natl Acad Sci USA*

Climate warming drives large-scale changes in ecosystem function

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The Barents Sea is the continental shelf sea to the north of Scandinavia and Northwest Russia and supports some of the richest fisheries in Europe. Until recently, the northern Barents Sea was dominated by small-sized, slow-growing fish species with specialized diets, mostly living in close association with the sea floor. Concomitant with rising sea temperatures and retreating sea ice, these fishes are being replaced by fast-growing, large-bodied generalists moving in from the south. In this week's issue of PNAS, Frainer et al. (1) document these changes and investigate consequences for ecosystem functioning, a topic of interest far beyond the Barents Sea.

Global climate change leads to a poleward displacement of species, with the fastest responses occurring in the oceans, where there are fewer physical barriers to movement than on land (2). All species do not move at the same pace, however, and hence, new species configurations emerge. These alterations in biogeographic patterns have unknown consequences for ecosystem functioning and services. The emerging scientific field of functional biogeography addresses this knowledge gap by integrating biogeographic information on species distributions with information on how species affect ecosystem functioning (3). Functional biogeography focuses on the traits that describe the ecological roles of organisms – such as feeding type and body size of animals. Focusing on functional traits instead of species can provide new insights into how climate and other factors affect ecosystem functioning. For example, using functional biogeography to study forests on a global scale, Reich et al. (4) demonstrated that the proportion of plant biomass in foliage relative to roots was higher in warm compared to cold climate zones, with implications for how climate change may impact carbon storage in forest ecosystems. However, few studies prior to Frainer et al.'s (1) have used functional biogeography to investigate how climate change affects ecosystem functioning at large geographic scales in marine environments. Moreover, the study of Frainer et al. (1) is the first to do so in the Arctic. This research is particularly timely as some of the world's highest temperature increases in recent decades have occurred in the Arctic (5), and the region can be seen as an early indicator of global change.

Based on abundance data from a bottom trawl survey conducted in the Barents Sea between 2004 and 2012, Frainer et al. (1) identified 52 fish species that could be described using 15 functional traits – including body size, longevity, fecundity, growth rate, habitat, diet characteristics and position in the food web. The authors first asked: what can the distribution of traits among species tell us about the Barents Sea fish community? They found that the majority of the species displayed traits typical of Arctic bottom fishes ("Arctic-like traits"): small body size, low growth rate and specialist diet mostly consisting of other organisms on the sea floor. Fishes with these traits were typically low in abundance, found in the northern part of the Barents Sea and included species like sculpins (*Icelus* spp, *Triglops* spp) and snailfish (*Liparis* spp). A smaller group of fish species had "boreal-like traits", such as larger body size, fast growth and a generalist diet including prey from both the sea floor and water column. Some of these species, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), were high in abundance, and the species were most dominant in the southwestern Barents Sea.

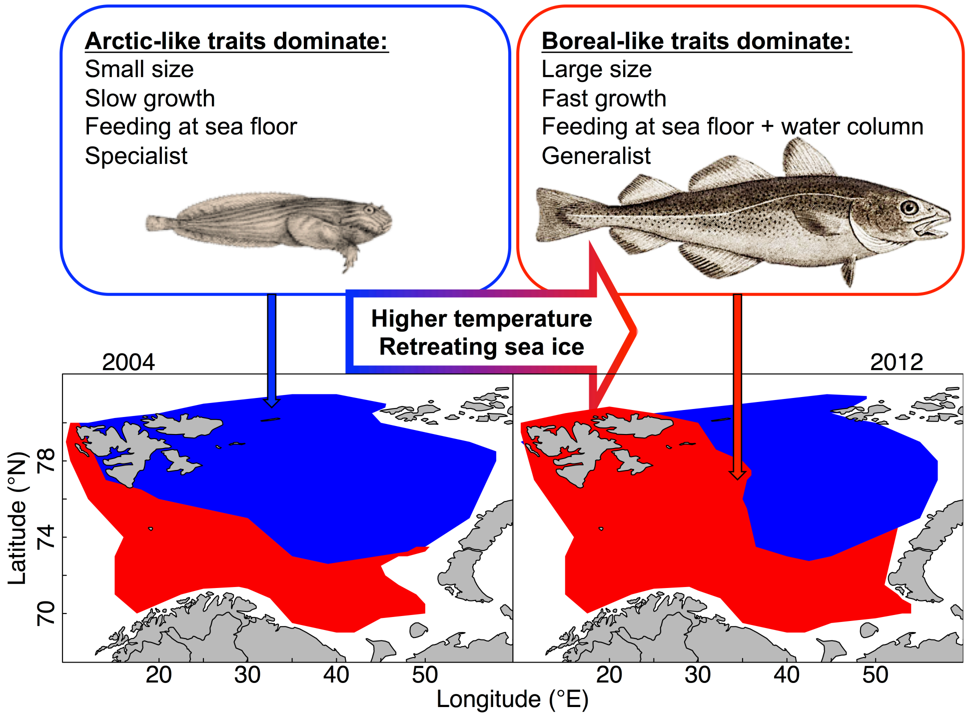

Figure 1. Climate change leads to large-scale changes in ecosystem functioning, as represented by functional trait distributions in bottom fish communities in the Barents Sea (1). The spatial distributions shown are simplified from Fig. 1 of Frainer et al. (1) and not exact in all details. Fish illustrations are from Wikimedia Commons. Arctic fish illustration: *Liparis liparis* by Samuel Garman, 1892, published in the U.S. before 1923 and public domain in the U.S. Boreal fish illustration: *Gadus morhua*, in the public domain because it contains materials that originally came from the U.S. National Oceanic and Atmospheric Administration, taken or made as part of an employee's official duties.

The period from 2004 to 2012 was characterized by a rapid temperature increase and sea ice retreat in this part of the Arctic. Hence, Frainer et al. (1) could investigate how such changes in climate influence ecosystem functioning, as represented by the spatial distribution of functional traits. The functional characteristics of the fish community at each station were quantified by average trait values across all fish species found at the station. Based on the trait distribution, the community was scored as more “Arctic-like” or “boreal-like”. The changes in trait distribution were dramatic. In 2004, Arctic-like traits were dominant in nearly 50 % of the Barents Sea, whereas by 2012, boreal-like traits dominated in more than 80 % of the area (Figure 1). A northward expansion of boreal fish and corresponding retraction of Arctic fish in the Barents Sea has been described before (6). The novelty of Frainer et al.’s (1) study was that these biogeographic changes were linked to functional traits.

By focusing on functional traits, studies like Frainer et al.’s (1) throw new light on possible causes and consequences of biogeographic shifts (3). For example, one of the changes occurring in the northern parts of the Barents Sea was an increase in fish body size. Large individuals require more energy to maintain metabolism compared to small individuals, and must therefore have higher per capita consumption rates. This is only possible if there is sufficient food, thus, an increase in food availability could drive these changes. In fact, changes in other traits also indicate improved feeding conditions in the northern Barents Sea: growth rates and fecundity rates have also increased. Another striking shift is that fish obtain more of their food from the water column, not only the sea floor.

To get closer to the mechanisms driving these changes, Frainer et al. (1) asked, which environmental variables associate with the spatial and temporal variation in functional traits? Results pointed to sea ice and bottom water temperature as key variables. The increased water temperature and reduced sea ice cover observed in the northern Barents Sea over the course of the study can indeed explain increased productivity over time. Over large parts of the Arctic, the length of the production season has increased due to fewer days with ice coverage, resulting in higher primary production (7). Where and when the production occurs is also changing: a longer period of open water causes a prolonged and less pulsed phytoplankton bloom, with a lower fraction of the production sinking to the sea floor and fuelling the organisms living there (8, 9). Together with the increased temperature, these changes create opportunities for large-bodied generalist species to move in from the south. This study is thus a good example of how functional biogeography, by synthesizing information from complex mosaics of species redistributions, allows scientists to highlight large-scale changes and identify mechanisms leading to these ecosystem reconfigurations.

What are the broader implications of the changes identified by Frainer et al. (1)? The shift from Arctic-like to boreal-like traits in the northern Barents Sea accords with the global trend of poleward shifts in species distributions (2). Organisms adapted to seasonally ice-covered Arctic shelf habitats, including Arctic fish in the northern Barents Sea, may in turn face local extinction if they are pushed north beyond the shelf edge (8). While most studies focus on the abiotic drivers behind poleward shifts, the findings by Frainer et al. (1) underscore the possible role of biotic environmental change in pushing Arctic species northwards: the increased dominance of boreal-like traits imply elevated consumption rates, and thereby higher overall predation rates, which can make it hard for species with slow growth and low fecundity to survive.

Another implication is that with increased dominance of generalists, the different parts of the ecosystem are more closely linked together, with the expected consequence that perturbations from climate and human impacts such as fishing spread faster and wider through the ecosystem (10). Furthermore, the changes in functional traits have implications for how energy and matter is channelled through the ecosystem, with, for example, increased feeding in the water column implying that the bottom fish community as a whole becomes less dependent on sedimented matter. The changes in functional traits also influence how much of the production ends up in harvestable resources. In the Barents Sea, we note that the commercially important cod and haddock are among the generalist boreal species expanding northwards and taking advantage of the increased production in the water column.

The paper by Frainer et al. (1) opens perspectives for new studies. We would like to see the approach expanded in different directions, including other compartments of Arctic marine ecosystems. For example, retreating sea ice may transform the present plankton community dominated by diatoms and large *Calanus* copepods to a less lipid rich system (11). This shift can negatively impact seabirds, baleen whales and other animals currently feeding on large, lipid-rich copepods (12). Moving the focus from species to functional traits, including traits related to lipid storage and transfer, can help to understand the mechanisms behind these changes. We also welcome corresponding analyses for other ecosystems globally to test if, as Frainer et al. hypothesize, expansion of motile, large-sized, generalists to higher latitudes is a general trend (1). If consistent associations between climate and functional traits emerge, we have a basis for projecting effects of climate change on ecosystem services (3). A trait-based approach can circumvent the difficulty in projecting climate effects on species interactions. Indeed, climate influences species more strongly indirectly through predators, prey and competitors, than by direct effects of physical variables on vital rates such as growth, fecundity and survival (13). These indirect effects of climate change on species distributions, biodiversity and ecosystem services such as fisheries yields are difficult to capture by traditional species-based approaches such as bioclimate envelope models (14-16). Functional biogeography may hence provide a highly valuable supplement to other modelling approaches to project ecological effects of climate change.

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Footnotes
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