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Molecular methods for assessing temporal adaptive changes in fish populations; a case study employing historical analysis of Pan I in cod (*Gadus morhua*).

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At present most population genetic studies of marine fishes are conducted employing non-coding DNA markers, i.e. markers not subject to natural selection. Neutral markers are ideally suited for making inferences on the demographics of marine fish populations by providing evidence of population structure, estimates of genetic isolation (migration rates) and genetically effective population sizes. State of the art genetic markers are microsatellites, which besides providing evidence on population structure; allow for assigning individual fish to population as well as estimating the contribution of different populations to a mixed fishery. However, neutral markers have a number of shortcomings, which are particularly evident in marine fish populations. In marine fishes the build up process of neutral genetic differentiation is generally very slow due to high migration rates and large effective population sizes. In contrast natural selection acts very fast in large populations facilitating rapid build up of large genetic differences. For instance, the level of genetic differentiation between cod in the North Sea and Baltic Sea is about 10 times higher for haemoglobin gene than for microsatellites. Also, by temporal monitoring of genetic marker genes suspected to be subject to environmental selection, the genetic impact of global change can be assessed. A particular strong case can be built when a combination of neutral and selected markers are employed enabling separation of demographic from selective changes.

The Pan I gene in cod has shown much elevated levels of genetic differentiation compared to microsatellites. The general hypothesis is that the frequency of the two allele classes found at this locus, the Pan I^A and the Pan I^B alleles respectively, are subject to temperature selection, since the Pan I^B allele is most common northern latitudes. However, many other environmental variables are correlated with latitude, so one possible test for temperature selection at this gene could be to study changes in the frequency of the two alleles over time and correlate that to temporal changes in temperature.

Accordingly, we investigated temporal genetic differentiation at the Pan I locus in four cod populations from the southeastern part of the species distribution: the Baltic Sea, the North Sea, the Faeroe Plateau and the Faeroe Bank. Historical otolith collections enabled investigation of allele

frequency variation over time periods up to 69 years employing Pan I primers specifically designed for partially degraded DNA. Small and non-significant temporal changes in Pan I allele frequencies were observed in the four populations. We employed simultaneous microsatellite analysis to correct for demographic changes, revealing similar temporal genetic stability with temporal F_{ST}´s ranging from 0 – 0.006 suggesting limited changes. Sea surface temperature (SST), which has been suggested as the primary driver for the geographical distribution of Pan I alleles in cod, showed no long-term trend although temperature has increased since the mid-1990s. Our study demonstrates that populations in the south-eastern part of the species range have been characterized by very high frequencies of the Pan I^A allele for many decades.

We recommend further studies for elucidating the evolutionary drivers responsible for the distribution of Pan I alleles and suggest including populations from regions with more Pan I variability and regions which have experienced a significant change in temperature. We also recommend the application of many more genes under selection in order to better understand the process of local adaptation, thereby enabling prediction of future population distribution and size in a scenario of global change.

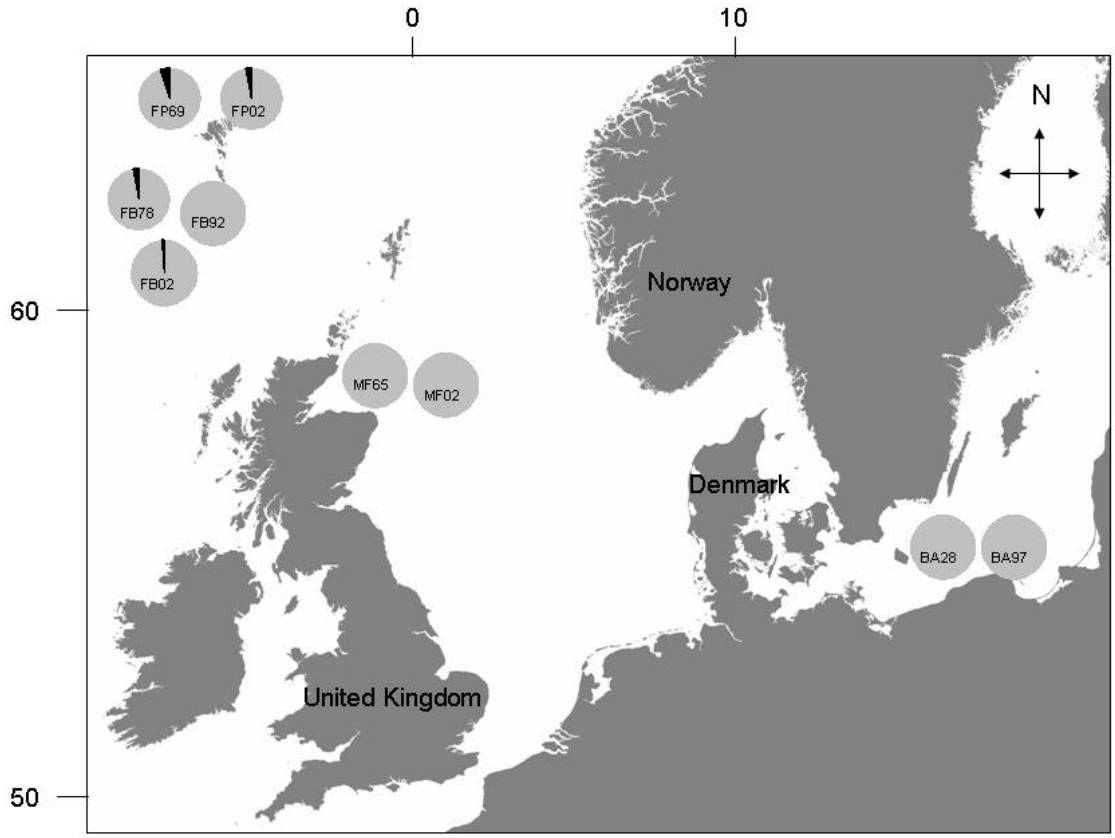

Fig. 1. Location of temporal cod samples and Pan I allele frequencies. Grey: Pan I^A; black: Pan I^B.

Keywords: Atlantic cod, population genetics, archived samples, Pan I, temperature

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