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LETTER

Comment to 'Opdal AF, Jørgensen C (2015) Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod. *Global Change Biology*, 21:4, 1521–1530, doi: 10.1111/gcb.12773'

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The Northeast Arctic (NEA) cod is the largest cod stock in the Atlantic Ocean with feeding area in the Barents Sea and spawning areas along the Norwegian coast. The mature population undertakes spawning migration during winter and spawns in March and April along a 1500-km coastline with core spawning area in Lofoten around 68°N.

In Opdahl & Jørgensen (2015) 'Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod'. Global Change Biology, 21, 1521–1530, doi: 10.1111/gcb.12773, hereafter termed O&J, they conclude that only 'demography contributed with statistical significance towards explaining temporal variation in spawning ground distribution in NEA cod, and that climate indicators such as the NAO winter index and ocean temperature from the Kola transect only had effects below statistical significance'.

Moreover, 'This emphasis of the role of demography agrees with earlier empirical analyses (Opdal, 2010) and is consistent with the strong effect of fishing on optimal migration distances found through evolutionary modelling (Jørgensen *et al.*, 2008), but contradicts conclusions from other studies where climate has been found to play a more important role (Sundby & Nakken, 2008)'.

Their conclusions are problematic of four reasons:

(i) Sundby & Nakken (2008), hereafter termed S&N, addressed change in spawning intensities along the coast and found that it varied proportional to the multidecadal temperature signal at the northern spawning fringe and inversely proportional to that signal at the southern spawning fringe. S&N *explicitly emphasized and discussed the multidecadal temperature signal as the link between changes in temperature and spawning intensity*, in contrast to the interannual to decadal signal partly related to the NAO index that is an *atmospheric pressure index* and not a *temperature index*. S&N *did not* consider spawning migration distance as O&J do, because it is not possible to calculate that distance in any reliable way. O&J's data analysis and conclusion rely entirely on their estimate of spawning migration distance and that estimate is basically incorrect because, (ii) the stock of NEA cod, including the spawning stock, undergoes interannual, decadal, and multidecadal shifts in their distribution in the Barents Sea documented in a number of publications since Nakken & Raknes (1987). Ottersen *et al.* (1998) found that the centre of gravity of the older age classes (5, 6, and 7 years) of NEA cod changed by 250–300 km during 1988–1995 (right panel of Fig. 1). Similar quantitative data for distributional shifts for the earlier period considered by O&J are lacking. However, the northwards shift of species towards the Arctic during the warming period from the 1920 to the late 1940s is qualitatively well documented (Rollefsen & Ahlmann, 1948). This northward shift of species was not only confined to the north-east Atlantic but happened for a number of fish stocks around the North Atlantic (Drinkwater, 2006). Parallel to the recent warming (1980-present) in high latitudes, a substantial northward shift in the NEA cod feeding areas and increase in spawning-stock biomass have occurred (Hollowed & Sundby, 2014; Kjesbu *et al.*, 2014). Similar feature is evident for another Barents Sea gadoid species, the NEA haddock (Landa *et al.*, 2014). In conclusion, the distribution of the adult NEA cod at the feeding areas in the Barents Sea is shifting south-west to north-east on various timescales from interannual to multidecadal. This dynamical distribution of NEA cod at the feeding areas in the Barents Sea and at the spawning areas along the Norwegian coast was discussed in detail by S&N. Therefore, (iii) calculating the spawning migration distances from a fixed geometrical average in the Barents Sea and applying those distances to show the strong correlation with age at maturity (Fig. 3) is incorrect. In contrast, one could, as well, hypothesize that the spawning migration distance is constant, as the distributions during the feeding in the Barents Sea and

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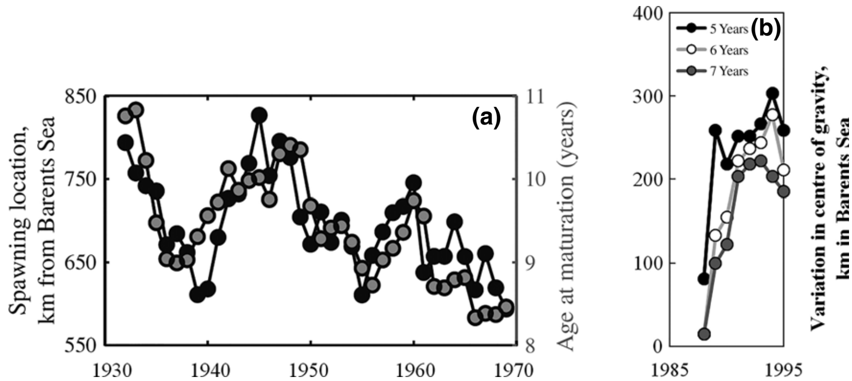

Fig. 1 Spawning migration does not start from a fixed geographical point in the Barents Sea. Left panel (a): Fig. 3 of Opdahl & Jørgensen (2014) showing the covariation between mean age at maturation of NEA cod and a calculated spawning migration distance. The calculation of the spawning migration distance is based on the distance between a fixed geographical point in the Barents Sea and the spawning area. Right panel (b): after Ottersen *et al.* (1998), Fig. 10, showing west–east interannual variation (1988–1995) in centre of gravity of the age classes 5, 6, and 7 years. The interannual variation in the centre of gravity [panel (b)] is larger than the calculated variation in spawning migration distance [panel (a)].

at the spawning areas are fluctuating with the similar amplitude (i.e. 250–300 km) on decadal scale. However, data are not available to test this, because one would need additional tagging data to explore where in the distributional area a fish is migrating to a specific spawning area. Besides, the fluctuations of the distribution on interannual to decadal scales would also make it problematic to test either of these mechanisms. Moreover, (iv) the subsequent 45-year period after the 1970s shows substantial changes in the NEA cod life history that further contradict O&J's conclusions. Along with the multidecadal temperature increase, the stock started to increase from its minimum in the late 1970s (Kjesbu *et al.*, 2014). Since 2003, the NEA cod started to spawn again at the coast of East Finnmark (S&N) close to feeding area of the adult cod. The long-term trend in age at maturation still decreased after the 1970s, but from the late 1980s also age at maturation started to increase (ICES, 2013). From 2002, the age structure has increased monotonically, but the cod continues to spawn adjacent to the feeding area in the Barents Sea (S&N), also in contrast to the conclusions of O&J.

Even though it might be a reasonable hypothesis to assume that also demography will influence the spawning migration distance, there are no real data to support their conclusion. In a subarctic ecosystem like the Barents Sea, there are a number of interacting processes causing changes in distribution of gadoids age classes such as (i) growth and survival of the early life stages along the drift route from the spawning areas, (ii) time of settlement from the pelagic juvenile stage to bottom-dwelling young fish, (iii) age and weight at maturation, (iv) inflow of warm Atlantic water associated with productivity at lower trophic levels, particularly zooplankton, (v) abundance and distribution of main prey such as capelin, prawns, and euphausiids, and (vi) position of ice edge. The changing temperature influences all these processes in different ways. Disentangling the quantitative contributing for each of these factors is more complicated than inferred by O&J.

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