Global Change Biology

Global Change Biology (2016) 22, 965–967, doi: 10.1111/gcb.12977

RESPONSE TO EDITOR

Response: Demography affects spawning location in Northeast Arctic cod, but what affects demography?

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In a letter to the editor, Sundby (2015) expresses concerns about our study of changing spawning locations of the Northeast Arctic (NEA) stock of Atlantic cod over the period 1866–1969, where we identified statistically significant effects of the stock's demography whereas various climate indices all fell below statistical significance. Our conclusion on the role ascribed to climate disagrees with that of Sundby & Nakken (2008), which, based on a subset of our data and without considering demography, concluded that spawning was shifted northwards in warm periods.

Sundby's (2015) criticism boils down to four points that we will address in turn.

A: 'the calculated spawning migration distance (. . .) is based on incorrect assumptions' (quote from abstract, covered by points 1–3 in Sundby's letter)

In our analysis, we never did calculate spawning migration distance because the data did not allow it. From the data, a time-series of regional statistics of the cod spawner fishery, we could only quantify spawning *location*. We thus only know the endpoint of the spawning migration, and as there are no data on where in the Barents Sea migration began we could not, and did not, calculate migration *distance*. It is unclear to us how this misreading of our paper originated. In fact, we explicitly raise this issue, for example in this quote (Opdal & Jørgensen, 2015, page 1527):

> It is also known that younger cod tend to be distributed in colder water further north and east in the Barents Sea than older, larger cod (Ottersen *et al.*, 1998). This has the implication that one cannot infer from spawning location how far an individual has migrated to get there.

Instead of using metrics of latitude and longitude, we quantified spawning location as distance from a central point in the Barents Sea. This is only a technical issue of presentation and does not make assumptions or inferences about migration distance.

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B. An alternative hypothesis is that feeding distribution in the Barents Sea explains spawning location (point 3 in Sundby's letter)

Sundby (2015) proposes the hypothesis 'that the spawning migration distance is constant, since the distributions during the feeding in the Barents Sea and at the spawning areas are fluctuating with the similar amplitude (i.e. 250-300 km) on decadal scale' (see fig. 1 in Sundby, 2015). He also notes that 'data is not available to test this'. However, Sundby (2015) also refers to several studies showing that feeding cod move further north and east in the Barents Sea during warm years (e.g. Kjesbu *et al.*, 2014). With temperature-dependent feeding location and constant migration distance, a prediction from his hypothesis is thus that spawning location would shift north in warm years, which is exactly the effect that our statistical analysis finds no support for.

C. We are using irrelevant climate indices (point 1 in Sundby's letter)

Sundby stresses that the North Atlantic Oscillation (NAO) is an atmospheric pressure index and not a measure of water temperature, which is what likely would have the strongest effect on fish. We are of course aware of this, and included NAO only because direct observations of sea temperature (the Kola section) were initiated in 1900 and therefore not available for the first 34 years of our data. Neither NAO nor Kola sea temperature significantly explained variations in spawning location in our study. The use of NAO is not completely unwarranted, however, as NAO has been found to correlate with oceanography and ecology of cod in the Barents Sea (Ottersen & Stenseth, 2001). More generally, pressure indices describe large-scale physical drivers, with influences on the dynamics of both terrestrial and marine ecosystems (Stenseth *et al.*, 2002).

Sundby & Nakken (2008) further stressed multidecadal climate fluctuations and used running mean Kola temperature in the 5 years prior to the observation of cod spawning, because of the considerable inertia of both the marine physical environment as well as cod population dynamics. When we repeat our statistical analysis with five-year running mean Kola temperature, temperature is sometimes retained as a significant explanatory variable. The role of temperature is even more significant when we correlate it with the five-year running mean spawning location. However, when we use five-year running mean of demographic indices too, the statistically favoured model only includes demography while temperature falls below statistical significance again. Thus, it is the smoothing itself that brings out stronger and more significant correlations, likely because the smoothed data better reflect the temporal trend in the system or because the smoothing cancels out measurement error and other random fluctuations and therefore results in a more accurate quantification of the state of the natural system. As long as the same smoothing is applied to all variables, demography still describes most of the variation in spawning location and our conclusions are unaffected.

D. There have been changes after 1969 that contradict our findings (covered by points 2 and 4 in Sundby's letter)

Sundby (2015) refers to several interesting observations which indicate altered population and spawning dynamics of NEA cod after the data series we studied was terminated in 1969. Prominent changes have particularly occurred during the most recent decade, which is almost half a century later than our data allow us to make inferences about.

A main motivation for us was to show that environment–species relationships may be fluid and transform over time, as indicated by time being a statistically significant factor (a nonspecific trend) in several of the statistical models. The well-documented decline in maturation age (Jørgensen, 1990; Heino *et al.*, 2002) was further identified as affecting spawning location in our data, indicating drivers other than the physical climate. Changes after 1969 do not negate the effects we found, but could suggest that relationships governing the dynamics of cod have continued to transform. This has the implication that statistical approaches, such as ours, have clear limitations when environmental and anthropogenic drivers move outside their historical range, when one instead would depend on a mechanistic understanding to describe and predict biological dynamics.

Causes for the apparent conflict

While Sundby & Nakken (2008) portrayed a system driven by temperature, our study (Opdal & Jørgensen, 2015) highlighted a role for demography. If one takes a step back, there is actually little conflict between these apparently opposing perspectives, which can be understood by considering how spawning was quantified.

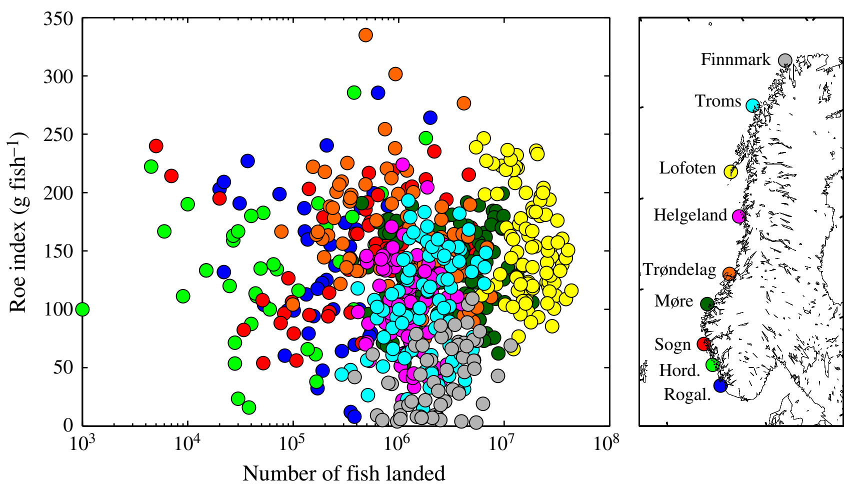

Fig. 1 Roe index, as used by Sundby & Nakken (2008), is not consistently related to the amount of fish landed (1877–1969): depending on region, the correlation is sometimes positive (Finnmark and Hordaland), sometimes negative (Lofoten and Trøndelag) and often insignificant (remaining regions). While they used the unit 'litres of roe per 1000 fish', we converted this to 'grams per fish' by assuming that 1 ml of gonads weighs 1 g. With this new unit, it is easier to appreciate how the roe index is an individual measure, roughly amounting to half the size an average female gonad and carries little information about the regional variation in numbers of spawning fish.

We used the total biomass fished per region to describe the local spawning component (nonspawners remain in the Barents Sea) and discuss why fisheries landings likely are representative of the total spawning taking place in a given region (Opdal & Jørgensen, 2015). In contrast, Sundby & Nakken (2008) quantified what they termed 'spawning intensity' using a roe index: for each fishing region, total volume of landed roe was divided by the number of landed fish. They found a positive correlation between the roe index and temperature, except for a southern spawning location where the correlation was negative. We do not question this finding, but their interpretation. If one assumes an equal sex ratio, the roe index amounts to half the size of an average female gonad. When Sundby & Nakken (2008) discuss 'spawning intensity', it is thus the intensity at which the average spawning female reproduces, not a measure of the size of the spawning population in that region. Simply put, the roe index is independent of the size of the regional spawning population and cannot be used to make inferences about it (Fig. 1).

In terms of mechanisms, it is well known that for the temperature range in the Barents Sea, cod grow faster when it is warm (Bjørnsson *et al*., 2001). Higher temperatures also allow faster gonad growth and larger gonads for a given body size (Kjesbu *et al*., 1998). These individual responses strongly influence the roe index, which as a consequence is expected to have higher values in warm years. Taken together, the analysis of Opdal & Jørgensen (2015) suggests that demography influences spawning location, while the analysis of Sundby & Nakken (2008) suggests that temperature influences demography through effects on somatic and gonadic growth. Beyond this, there are probably other factors which influence demography, such as the long-term trend towards earlier maturation likely attributable to fishing-induced evolution (Heino *et al*., 2002), as well as factors beyond demography that influence spawning location; these are discussed in Opdal & Jørgensen (2015).

Acknowledgements

We thank Dag L. Aksnes and Katja Enberg for carefully commenting on the text.

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