

Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod

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Abstract

Harvesting may be a potent driver of demographic change and contemporary evolution, which both may have great impacts on animal populations. Research has focused on changes in phenotypic traits that are easily quantifiable and for which time series exist, such as size, age, sex, or gonad size, whereas potential changes in behavioural traits have been under-studied. Here, we analyse potential drivers of long-term changes in a behavioural trait for the Northeast Arctic stock of Atlantic cod *Gadus morhua*, namely choice of spawning location. For 104 years (1866–1969), commercial catches were recorded annually and reported by county along the Norwegian coast. During this time period, spawning ground distribution has fluctuated with a trend towards more northerly spawning. Spawning location is analysed against a suite of explanatory factors including climate, fishing pressure, density dependence, and demography. We find that demography (age or age at maturation) had the highest explanatory power for variation in spawning location, while climate had a limited effect below statistical significance. As to potential mechanisms, some effects of climate may act through demography, and explanatory variables for demography may also have absorbed direct evolutionary change in migration distance for which proxies were unavailable. Despite these caveats, we argue that fishing mortality, either through demographic or evolutionary change, has served as an effective driver for changing spawning locations in cod, and that additional explanatory factors related to climate add no significant information.

Keywords: behaviour, climate, demography, fishing, *Gadus morhua*, migration, Northeast Arctic cod, trait

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Introduction

It is now a century since Hjort's classic book *Fluctuations in the great fisheries of northern Europe* (Hjort, 1914), and not only have abundance and yield continued to vary due to fluctuations in recruitment as he beautifully demonstrated, we now also know that many other traits are changing over time. Across species and stocks, it has been shown that growth, survival, and reproduction can be affected during all life stages, and the causes of these changes can broadly be attributed to variation in the physical or biological environment (e.g. Swain *et al.*, 2003) and to fishing (Beverton & Holt, 1957; Walsh *et al.*, 2006; Wright & Trippel, 2009). In the marine environment, water temperature has a particularly strong effect because fish are ectotherms and ambient temperature therefore has a direct influence on the rate of physiological processes including growth (e.g. Brander, 1995). Another important driver is indus-

trial fishing. The majority of the world's fisheries resources are either fully exploited or overexploited (FAO, 2014) and for demersal fish current fishing mortality several times higher than natural mortality (Mertz & Myers, 1998; Worm *et al.*, 2009). One direct consequence of fishing is the reduced probability of becoming old, and many exploited fish stocks show truncated distributions of size and age and thus a relative increase in small and young fish, both within a species (Borisov, 1978) and at the level of the community (Pauly *et al.*, 1998).

The traits that have received most focus are those that are physically observable, either directly as size or age or maturity status at capture, or indirectly in structures such as scales or otoliths that allow reconstruction of past phenotypic traits. Less is known about changes in behavioural traits, because these often are ephemeral, difficult to observe, standardized methodologies are lacking, and if a trait can be quantified time-series are normally nonexistent which prevents comparison across time. In this article, we overcome some of these challenges by using the observed location of fisheries landings to represent a behavioural trait: the spawning location for the Northeast Arctic (NEA) stock of Atlantic cod *Gadus morhua*.

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An important life history trait essential to the reproductive strategy of the NEA cod is its extensive southbound spawning migration from the feeding grounds in the Barents Sea to various spawning locations along the Norwegian coast. From the spawning grounds, the eggs and subsequently the developing larvae drift with the prevailing northbound currents back to the Barents Sea, where they eventually settle to the bottom as juveniles. Today, the majority of NEA cod spawn around and north of the Lofoten archipelago (Bogstad, 2009), roughly 750 km from the Barents Sea. In the period from 1866 to 1969 landings were registered by county and the catch statistics separated between the migratory Northeast Arctic stock and local stocks. These historical records suggest that spawning has taken place as far as 2000 km south of the Barents Sea, outside Vest-Agder at the southern tip of Norway (Opdal, 2010). Figure 1 shows the relative geographical distribution of the catch in three ten-year periods, and particularly catches at the southern and northern locations vary substantially over time. The truncation and northward shift of spawning ground distribution are well documented (Sund, 1939; Sætersdal & Hysten, 1964), although the reason has been attributed to both climate variability (Sundby & Nakken, 2008) and fishing (Opdal, 2010). Loss of historic spawning grounds has also been documented for North Sea cod (Fox *et al.*, 2008).

Extensive migrations have costs (Roff, 1988), not only directly in terms of the energetic cost of swimming, but there is also an opportunity cost as the fish spend considerable time away (Alexander, 1998) from the main

foraging areas in the Barents Sea at the time when the favoured prey, the capelin *Mallotus villosus*, is most accessible. From the focus on trade-offs in life history theory, one can infer that such behaviours would only be selected for by evolution if the migrating individuals obtained a comparable or larger benefit in return. The benefit need not target the spawning individuals directly, but can also be mediated through increased fitness to their progeny, essentially through increased survival probability (Smith & Fretwell, 1974; Trivers, 1974). In the case of the NEA cod, potential effects on offspring survival was investigated by Opdal *et al.* (2008, 2011) using general circulation models that track virtual fish eggs and larvae released at various spawning grounds along the Norwegian coast. From their drift trajectories towards the Barents Sea, it was evident that eggs and larvae released from more southerly spawning grounds experienced higher average temperatures, which led to faster growth, a shorter vulnerable larval stage, and consequently reduced mortality. In the simulation model, the latitudinal effect was much stronger than interannual variation in temperature due to natural climate variability (Opdal *et al.*, 2011). Climate may also affect spawning locations through other pathways. In a time series analysis of roe indices for NEA cod (1905–1976), Sundby & Nakken (2008) found a strong link between roe indices at spawning location and ocean temperature. They suggested several mechanisms through which higher temperatures might cause a northerly shifts in spawning ground distribution, including effects on offspring drift routes and adult

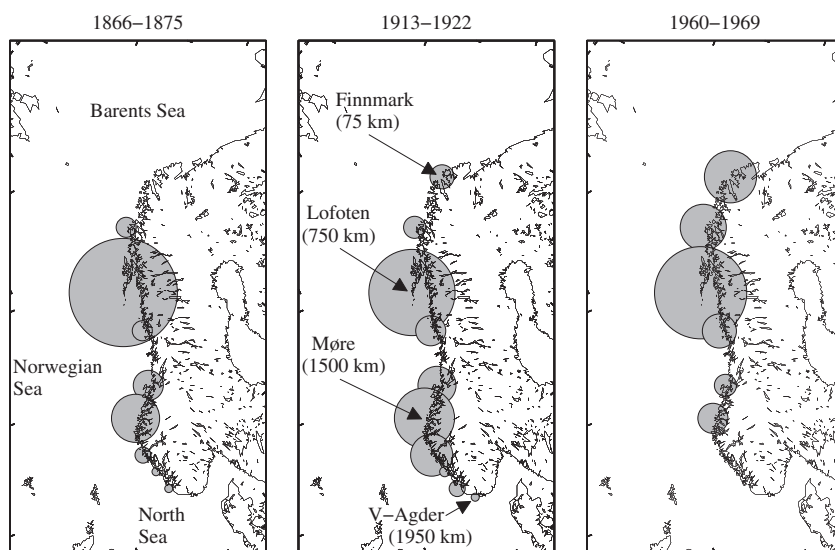


Fig. 1 Spawning ground distribution of NEA cod during three decades, based on commercial catches within the period 1866–1969. Circle diameter indicates relative total catch weights over the indicated time-periods. Also, the most important spawning ground Lofoten is indicated, as well as the historically relevant spawning grounds Finnmark, Møre and Vest-Agder. Distance to central Barents Sea is denoted in brackets.

distribution at the feeding areas. However, with a longer time series of commercial catch weights (1866–1969), Opdal (2010) found that the effect of climate was small, and fishing pressure was suggested as the key driver of changing spawning locations.

The effect of latitude on larval survival was incorporated in an evolutionary model for optimal maturation and migration in the NEA cod by assuming that the fitness of an egg spawned increased linearly with the parent's migration distance (Jørgensen *et al.*, 2008). Overall, the model predicted that individuals of large body size and in good condition gained higher fitness from longer spawning migrations compared to smaller individuals with less energy reserves. More interestingly, when simulating the historical exploitation pattern, the optimal life history strategy was large and late-maturing and with long migrations, whilst a contemporary trawl fishery, typically concentrated at the feeding areas in the Barents Sea, selected for small and early maturing fish with shorter optimal migration distances (Jørgensen *et al.*, 2008). That large-bodied fish migrate longer in the model corresponds to observations across species (Roff, 1988). A key mechanism underlying this effect of body size is the decreasing weight-specific cost of locomotion the larger the size of the fish (Alexander, 2003).

Spawning location may thus be influenced by temperature effects acting on the adult stage directly (but possibly tailored to maximize benefits for eggs or larvae), by fishing that truncates age- and size-distributions towards smaller fish with shorter optimal migration distances, or through evolutionary processes on migration behaviour itself or life history traits that affect demography. In this study we consolidate a suite of potential explanatory variables for the observed changes in spawning ground distribution and apply statistics to infer their impact. In particular, we investigate potential effects on spawning distribution of demography (age and age at maturation) and biomass of the spawning stock, fishing mortality, ocean temperature and the North Atlantic Oscillation (NAO) winter index.

Materials and methods

The main objective of this study is to identify likely drivers of the observed changes in mean spawning location of NEA cod, inferred from statistical models including temporally lagged effects.

Data sources

To obtain time-series of the population's average spawning location, we went through catch reports from the commercial

spawning ground fishery in winter/spring for the years 1866–1969, and use landing location (county) as a proxy for spawning location. The fisheries catch statistics (Anon, 1866–1969) has recorded for different cod populations separately, including NEA cod (*skrei*), coastal cod (*kysttorsk*), and also offshore cod (*banktorsk*), the latter being cod associated with feeding areas on banks off the Norwegian coast but which spawned at the coast although somewhat later than the coastal cod (Anon, 1866–1969).

A crucial assumption for our further analysis is that NEA cod are correctly distinguished from the other cod stocks. It is likely that this distinction has been made based on at least two main criteria; (i) time of capture; and (ii) morphological traits including size. With regards to time of capture, no fish caught outside the winter/spawner fishery between January and May (Brander, 1994) would have been recorded as NEA cod. However, as all the cod stocks spawn around the same time, morphological differences (reviewed in Nordeide *et al.*, 2011) have been used to separate them within the spawning season. An obvious feature is the skin colour. The NEA cod, having grown up in the Barents Sea, exhibits grey and bluish colours compared to the typically brownish coastal cod from Norwegian fjords (e.g. Pethon, 2005). Moreover, the overall body shape of the NEA cod is significantly slimmer and more elongated (Svåsand *et al.*, 1996), most likely as an adaptation to long migrations (Roff, 1988; Mclaughlin & Grant, 1994). The NEA cod are also overall larger (and older) at first spawning compared to coastal cod (Berg & Albert, 2003). At the time, most fishermen along the Norwegian coast would likely have participated several seasons in the spawner fishery for cod in Lofoten (Kolle & Kristiansen, 2014); then and now the most important spawning ground of NEA cod (Opdal, 2010). This would have given them first-hand experience on the characteristic morphological features of the NEA cod, making it possible to recognize NEA cod also when caught at their local fishing grounds. It is also likely that as fishing practices changed, the lack of first-hand knowledge of *skrei* led to the discontinuation of reporting cod by stock of origin in the official statistics in 1970.

We further assume that landing location accurately reflects spawning location because: (i) the NEA cod fishery was economically important throughout this period and was supervised by local county governors along the entire west coast of Norway, and catch statistics were rigorously kept by central authorities and published in the series Official Statistics of Norway (Anon, 1866–1969); (ii) up until the 1920s fishing was done from small open boats propelled by rowing or sail and cooling technology did not exist, so there was no alternative to landing the fish close to where it was caught, and while engines gradually made their appearance from 1920 the fleet consisted of small boats up until the end of the time series used and there were few exceptions to local landing; and (iii) cod are batch spawners with repeated releases of eggs over several weeks (Kjesbu *et al.*, 1996), in addition they may spend up to a month at a spawning site before they spawn, so the time spent migrating through a region is small compared to the time spent at its spawning site. Finally, the same data have been used to show changes in spawning ground distri-

bution in NEA cod for shorter (1914–1938; Sund, 1939) and longer (1866–1957; Sætersdal & Høyen, 1964), time periods. The complete time series (1866–1969), and further details of data collection can be found in Opdal (2010). From 1970 onwards NEA cod was no longer reported separately from local cod stocks, which effectively terminated the time series available for analysis. The reason for this is not mentioned in the statistical records, except as a note stating that supervision of the NEA cod fishery (excluding Lofoten) is no longer in operation.

The landed biomass ($w_{n,y}$; kg) was recorded for 10 counties n along the coast for each year y , and we attributed a specific spawning location d_n , for ease of interpretation quantified as the distance from the central Barents Sea to each county [Finnmark (75 km); Troms (350 km); Lofoten (750 km); Helgeland (950 km); Trøndelag (1150 km); Møre (1500 km); Sogn (1600 km); Hordaland (1700 km); Rogaland (1850 km); and Vest-Agder (1950 km)]. From these data, we each year calculated the relative annual biomass-weighted mean spawning location (D_y) for the entire spawning stock,

$$D_y = \sum_n \frac{w_{n,y}}{w_y} \cdot d_n,$$

where w_y (kg) is the total catch in year y .

Potential explanatory variables come from several sources (the raw data are shown in Fig. 2b–d). Fishing mortality (F_y), spawning stock biomass (SSB_y) and spawning stock age ($SSAge_y$) have been back-calculated from 1913 using virtual population analysis (VPA) by Høyen (2002). For $SSAge$ before 1932, age is estimated based on scales (and not otoliths as has been the preferred method after 1932) and later adjusted based on a scale-age/otolith-age key derived from a small sample ($n = 150$) of NEA cod in a single year (1932) with several age-classes (5, 6, and 7 year olds) missing (Høyen, 2002). Thus $SSAge$ for the years prior to 1932 should be treated with caution. Since 1932, the Institute of Marine Research (IMR, Bergen, Norway) has sampled ca. 400–4000 individual NEA cod each year from commercial landings in Lofoten during the spawning season (January–May). The data are accessible through the IMR. From these, age at capture and age at matu-

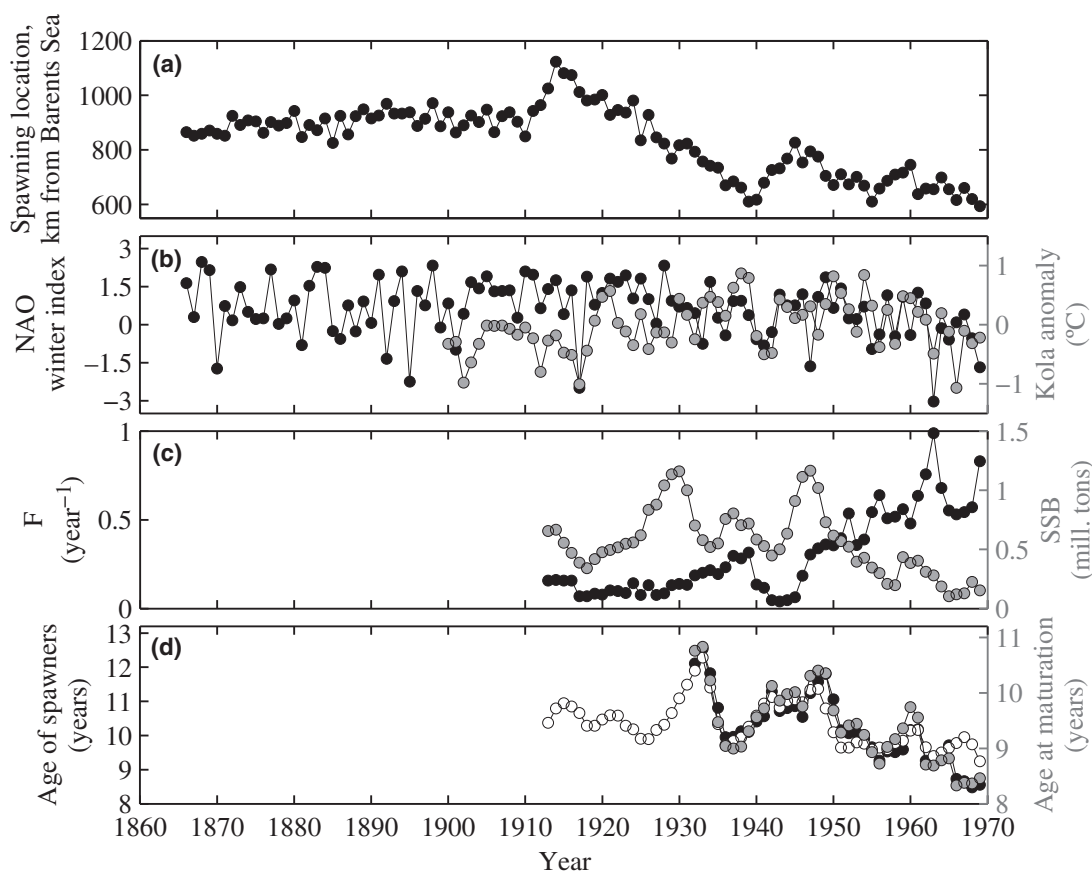


Fig. 2 Spawning location in NEA cod, and potential explanatory variables. (a) Mean spawning location (D_y , km; based on estimated distance from central Barents Sea) for the time period 1866–1969. (b) Climatic variation represented by the NAO winter index (NAO_y) for the time period 1866–1969 and the temperature anomalies ($Kola_y$, °C) from the Kola transect for the time period 1900–1969. (c) VPA estimates of fishing mortality (F_y , yr^{-1}) for the time period 1913–1969, and spawning stock biomass, (SSB_y , million tons) for the same time period. (d) Observed mean age of spawners (black dots; Age_y , years) for the time period 1932–1969 and observed mean age at maturation (grey dots; $AgeMat_y$, years) for the same time period. In addition, spawning stock age from VPA ($SSAge_y$, years) is plotted with open circles on the left y -axis.

ration have been inferred from annual zonation in the otoliths (Rollefsen, 1933; Høie *et al.*, 2009). Age at capture and age at maturation are highly correlated ($R^2 = 0.93$, $P < 0.001$), but since age at maturation had slightly higher explanatory power ($R^2 = 0.44$, $P < 0.001$) compared to age at capture ($R^2 = 0.41$, $P < 0.001$) we only show results for age at maturation ($AgeMat_y$) in the statistical analyses. As proxies for the physical environment we used the winter index of the North Atlantic Oscillation (NAO_y) (Jones *et al.*, 1997), available based on instrumental observations from 1821, as well as the sea temperature anomalies in the Barents Sea ($Kola_y$) from the Kola transect (0–200 m depth, 70°30′–72°30′N, 33°30′E) sampled since 1900 (Boitsov *et al.*, 2012).

Lagged effects (1–15 years) for the Kola section and NAO time series were tested using single linear regression analysis. Temperature data from the Kola section explained most variance when using a lag of 4 years ($Kola_{y-4}$) ($R^2 = 0.23$, $P < 0.001$); using the unlagged time series had correlation coefficient $R^2 = 0.12$, $P < 0.001$). Thus, $Kola_{y-4}$ was added in subsequent analyses. This may be biologically plausible as temperature can operate directly or indirectly through physiological processes related to growth several years prior to spawning, or have effects on the food base only after some time affect cod. Introducing a lag for NAO did not improve explanatory power.

Statistical models

To analyse the explanatory variables' influence on spawning location, we applied a generalized least squares (GLS) model correcting for first order autoregressive processes. Because the time-series of our explanatory variables start in different years (1866, 1900, 1913 and 1932), we had to run four separate analyses, one for each time period, to make use of all available data. For each time period, a null model ($M_0: D_y \sim 1$) was defined. Then, for each explanatory variable V_1 through V_i , consecutive models were set up trying to improve on model M_0 ($m_{0,i}: D_y \sim V_i$), and a model comparison test (ANOVA) was performed to assess change in the Akaike information criterion (ΔAIC) between M_0 and $m_{0,i}$. The single explanatory variable V_i with the largest reduction in ΔAIC was included in a new model M_1 , and the procedure was then repeated with M_1 as the new null model and adding one by one the $i - 1$ remaining explanatory variables. The analysis was performed using the procedure GLS in R version 2.15.2. All P -values assigned to models were inferred from ANOVAS.

Results

The mean spawning location fluctuated over the period 1866–1969, with the weighted mean spawning location being fairly stable prior to 1910, showing its southernmost distribution around 1916 and then shifting northwards (Fig. 2a; the potential explanatory variables are presented in Fig. 2b–d).

For the two time periods starting before 1913 (1866, 1900), only the models including *Year* perform

significantly better ($\Delta AIC < -3$, $P < 0.05$) than their respective null models ($M_0: D_y \sim 1$) (Table 1). This suggests that no significant information is gained by adding *NAO*, *Kola* (including lags), *F*, or *SSB*, neither to the null models nor to models including *Year* ($M_1: D_y \sim Year$).

When including variables from the VPA for the time period starting in 1913, models including either *Year* or *SSAge* perform significantly better than the null model, with the model including *Year* (*Year*; $\Delta AIC = -7.4$, $P < 0.001$) results in a larger reduction in AIC compared to the model including *SSAge* ($\Delta AIC = -1.92$, $P = 0.048$). Adding *SSAge* to the model including *Year* [$M_1(1913): D_y \sim Year$], gives a slight reduction in AIC (-0.18), although not significant ($P = 0.14$).

In the latest time-period, starting in 1932 when demographic data became more reliable (see Materials and methods), the model including *AgeMat* ($M_1[1932]: D_y \sim AgeMat$) performs significantly better ($\Delta AIC = -11.8$, $P < 0.001$) than the null model. The models including *SSAge* ($\Delta AIC = -8.9$, $P < 0.001$), *F* ($\Delta AIC = -6.21$, $P = 0.0042$) or *Year* ($\Delta AIC = -2.07$, $P = 0.044$) are also significantly better than the null model, but with less reduction in AIC than the model with *AgeMat*. No further fit is gained by adding additional variables beyond *AgeMat* to $M_1(1932)$ ($\Delta AIC > 0$). Variation in distance to spawning ground (D_y) and age at maturation (*AgeMat*) are plotted together over time (Fig. 3a). A simple linear regression model ($D_y \sim AgeMat$) gives a correlation coefficient, $R^2 = 0.45$ (ANOVA; P -value < 0.001), with normally distributed residuals (Fig. 3b).

Discussion

Demography has a strong influence on spawning location

Through statistical analyses of four time series of varying length we have shown that only year and 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. 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). Our analysis further suggests no effects of density dependence on spawning location, which were included through spawning stock biomass.

Table 1 Statistical results from four independent generalized least square (GLS) models for mean spawning location in NEA cod. A null model (M_0 ; $D_y \sim 1$) is defined for each time period (1866, 1900, 1913 and 1932), all with different available explanatory variables (V_i). Statistical difference between M_0 and models including each of the explanatory variables (M_i ; $D_y \sim V_i$) is indicated with P -value and change in the Akaike information criterion (ΔAIC). The variable with the greatest significant reduction in AIC compared to M_0 is typeset in bold, and is included in the next model (M_1) and denoted *

MODEL ID	AIC	Year P	ΔAIC	NAO P	ΔAIC	Kola P	ΔAIC	Kola _{y-4} P	ΔAIC	F P	ΔAIC	SSB P	ΔAIC	SSAge P	ΔAIC	AgeMat P	ΔAIC
M_0 (1866)	1108.65																
$m_{0,j}$ (1866)		0.017	-3.67	0.36	1.17												
M_1 (1866)	1104.98	*	*														
$m_{1,j}$				0.37	1.21												
M_0 (1900)	710.57																
$m_{0,j}$ (1900)		0.0047	-6.00	0.83	1.96	0.84	1.96	0.87	1.97								
M_1 (1900)	704.57	*	*														
$m_{1,j}$ (1900)				0.90	1.99	0.73	1.88	0.80	1.94								
M_0 (1913)	613.23																
$m_{0,j}$ (1913)		0.0022	-7.40	0.87	1.97	0.77	1.92	0.60	1.72	0.16	0.039	0.38	1.23	0.048	-1.92		
M_1 (1913)	605.83	*	*														
$m_{1,j}$ (1913)				0.36	1.99	0.61	1.8	0.36	1.53	0.54	1.64	0.38	1.99	0.14	-0.18		
M_0 (1932)	395.62																
$m_{0,i}$ (1932)		0.044	-	0.72	1.87	0.75	1.90	0.77	1.92	0.0042	-6.21	0.081	-1.04	0.001	-8.90	0.0002	-11.8
M_1 (1932)	383.82															*	*
$m_{1,i}$ (1932)		0.99	2.00	0.55	1.64	0.99	2.00	0.41	1.32	0.19	0.25	0.32	0.99	0.53	1.60		

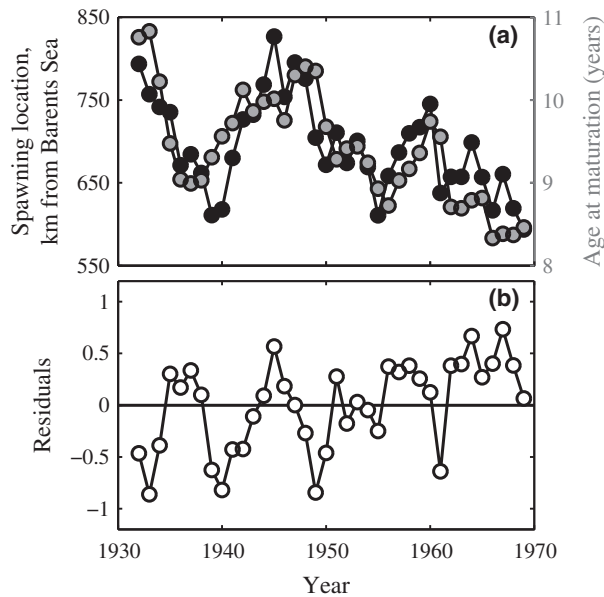


Fig. 3 (a) Mean spawning location of NEA cod (black dots, km), and mean age at maturation (grey dots, years). Correlation coefficient from single linear regression model, $R^2 = 0.45$ (ANOVA; P -value < 0.001), with (b) normally distributed residuals.

Although we find no measurable effect of climate on spawning location, climate is likely influencing other traits and characteristics of the NEA cod stock. Temporal variation in spawning stock biomass generally resembles fluctuations in temperature, sometimes with lagged effects (Hollowed & Sundby, 2014). A direct linear relationship between temperature and recruitment has been found (Sætersdal & Loeng, 1987; Drinkwater, 2005), but as these studies did not correct for stock-recruitment relationships the effect may have been caused by NEA cod utilizing a much larger feeding area in years with warm water in the Barents Sea, which allows for faster growth and increased production (Kjesbu *et al.*, 2014a) and better condition (Kjesbu *et al.*, 2014b). In contrast, we link the changing spawning distributions to changing demography and intense fishing, which means that the NEA cod stock might simultaneously be experiencing two anthropogenic pressures. To isolate, understand and potentially predict the consequences of climate change, it becomes necessary to also account for the concurrent effects of fishing.

Direct effect of climate on spawning location

Climate may influence NEA cod feeding distribution in the Barents Sea. During the last few years with warm water, cod have expanded their feeding distribution further north and east in the Barents Sea (Kjesbu *et al.*,

2014a), but it is not known whether such range expansion has been correlated with climate in earlier periods too. 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. Thus, distribution prior to onset of the spawning migration may influence spawning ground distribution as it affects migration distance (Sundby & Nakken, 2008). However, if feeding distribution is temperature-dependent, and spawning ground distribution depends on feeding distribution, then we should expect temperature or climate to explain more of the variation in spawning ground distribution than found by our analysis. Temperature may further have a direct positive effect on larval fitness (Pepin, 1991) at any given spawning location. This could make it optimal to spawn further south in warm years (Opdal *et al.*, 2011) while at the same time the higher temperature would increase the energetic cost of migration due to temperature-dependent metabolic rates. Climate-related variation in ocean circulation patterns (Toggweiler & Russell, 2008) may also alter drift routes of cod eggs and larvae (Harley *et al.*, 2006). In particular this has been shown in drift simulations of cod eggs and larvae along the Norwegian coast (Vikebø *et al.*, 2007).

We note that the above-mentioned temperature effects are all expected to cause a link between climate and spawning distribution, promoting more northerly spawning in warmer periods and vice versa. However, our analysis finds no evidence for any consistent effect of climate in the data tested. Climate may still influence spawning distribution more indirectly, although, by affecting demography.

Many factors may influence demography

Demography may be affected through a number of pathways, and we have attempted to summarize potential mechanisms through which demography may influence spawning location in Fig. 4.

It is worth noting that climate may affect demography through phenotypic plasticity of growth and maturation. Thus, when demographic parameters become available, the effect of climate that acts through demography may become attributed to demographic variables and no longer attributed to climate variables directly. This implies that climate may play a stronger effect than suggested by the analysis covering 1932–1969. Still, the effects of fishing on demography are pronounced, particularly at the intense rates of harvesting that this stock has experienced (Ottersen *et al.*, 2006).

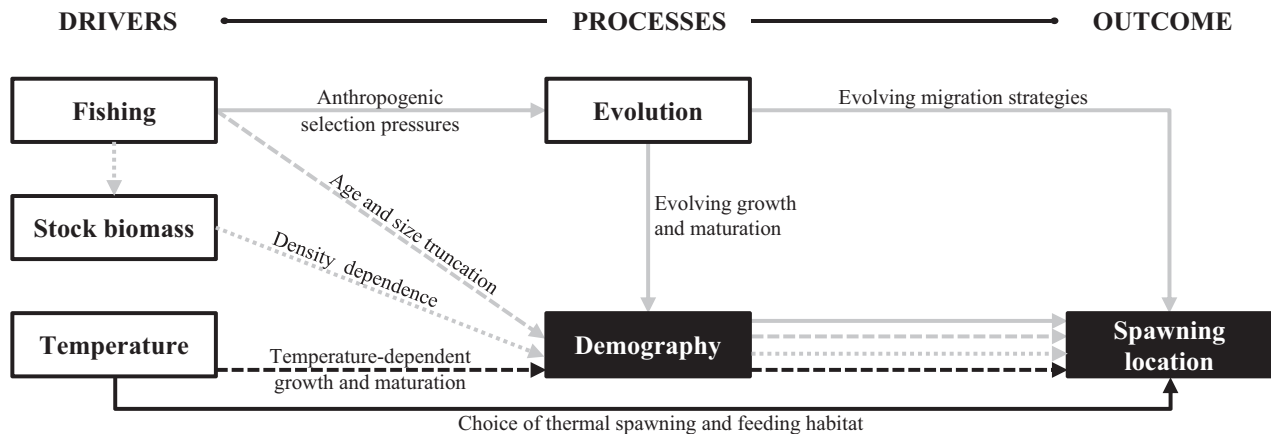


Fig. 4 The analysis in this article revealed a strong effect of demography on spawning location (black boxes) in Northeast Arctic cod over the period 1932–1969, but does not resolve which mechanisms (arrows) were involved. Demography may be influenced by the physical climate through phenotypic plasticity, by density dependence, by fishing-induced truncation of the stock's age distribution, or through fishing-induced evolution of life history parameters. In addition, there might be direct effects on spawning location not acting through demography, both from the physical climate or from evolution of migration behaviour.

Fishing may act on demography directly through demographic truncation or over time by fishing-induced evolution of demographic parameters including maturation (Heino *et al.*, 2002) and potentially also growth (Enberg *et al.*, 2012) and survival (Jørgensen & Fiksen, 2010). Our data did not allow us to separate between these mechanistic routes, although the fact that year was the only variable included in models prior to 1932, when demographic data became available, suggests a potential role for slowly accumulating effects such as evolution. There might, for example, be evolution of migration strategies themselves, independent of demographic parameters (Jørgensen *et al.*, 2008). If so, this would likely inflate the effect of demography, as such evolution most probably would be gradual and correlated with the long-term decline in mean maturation age. The lack of a temporal trend in residuals (Fig. 3b) does suggest that any evolution of migration strategies above that accounted for by evolution of demographic rates is likely insignificant.

A historical interpretation of changes

The fishery for NEA cod has a long history, with records of export to England dating back to 875 (Kurlansky, 1997). From that time and up until the early 1900s fishing was primarily conducted from small open boats close to the Norwegian coast during the spawning season, thus catching only mature individuals. With the development of an industrial trawl fishery at the feeding grounds in the Barents Sea beginning around 1910 (Hjort, 1914; Godø, 2003) two important transitions happened: the total harvest intensity

increased dramatically (Fig. 2c) and immature fish became exploited which particularly affected late-maturing fish (Law & Grey, 1989). Both changes would add to the truncation of age and size distributions of the stock.

From the historical development of the fishery one may reason that the demography of the stock likely has undergone relatively modest changes prior to the onset of trawling in 1910, while some demographic truncation likely happened before 1932. Most of the demographic change likely happened after 1932 and is therefore documented. The history of exploitation and the strong effect of demography suggested by our analyses correspond well with the relatively southern and stable spawning ground distribution prior to 1910 (Fig. 2a), as would be expected from relatively old and large individuals being abundant in the population (Jørgensen *et al.*, 2008).

From 1970, geographically resolved catch data are no longer available for the NEA cod, which prevents quantitative analysis of spawning location in the more recent decades. However, abundance and distribution of the NEA cod spawning stock indicate that most of the spawning takes place around Lofoten and northwards (Bogstad, 2009). This coincides with a continued decline of age and age at maturation of NEA cod (Law & Grey, 1989; Jørgensen, 1990; Heino *et al.*, 2002), although these have stabilized during the last decade (M. Heino, personal communications).

It is interesting that the harvest control rule implemented for Northeast Arctic cod in 2006 has lowered harvest rates, increased total abundance and SSB, and also restored the historical age structure of the stock,

with fish older than 11 years now making up roughly the same proportion as in the period 1946–1949 (Kjesbu *et al.*, 2014a). It would of course be interesting to see whether this causes NEA cod to again utilize spawning areas further south (indicating a reversible, demographic effect) or whether the current, more northerly spawning distribution has replaced the longer migrations of previous times (suggestive of loss of socially learned migration routes or an evolutionary change in migration strategies).

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