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Pseudocollapse and rebuilding of North Sea mackerel (*Scomber scombrus*)

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The largest observed change in mackerel (*Scomber scombrus*) abundance in the North Atlantic happened when the so-called “North Sea mackerel” collapsed due to overfishing. Despite protection, it has remained in a depleted state. Central to this interpretation was that the “North Sea mackerel” was considered to be a distinct spawning component. However, a recent study has shown that this is not likely. In the light of this study, a review of the history of mackerel spawning in the North Sea found that the traditional explanation of the collapse did not account for a range of unfavourable environmental changes: high fishing pressure was followed by decreasing temperatures that reduced the spawning migration into the North Sea. This was further supplemented by unfavourable changes in food and wind-induced turbulence. On the population level, this was, therefore, not a local stock collapse, but a southwest shift in spawning distribution combined with a reduction in that portion of the population cline with an affinity for spawning in the northeastern part of the spawning area, including the North Sea. No indication of irreversible genetic or behavioural losses caused by the events was found. The previously unexplained lack of rebuilding of spawning in the North Sea consequently seems related to two environmental factors that have remained unfavourable: (i) zooplankton concentration, and (ii) wind-induced turbulence. Furthermore, the large commercial autumn–winter fishery in the North Sea continues to land unknown quantities of mackerel that have an affinity for spawning in the northeastern part of the spawning area, including the North Sea.

Keywords: distribution, environment, mackerel, migration, North Sea, overfishing, stock collapse, stock rebuilding.

Introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory pelagic fish species in the Northeast Atlantic, where it is caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes (ICES, 2011). Long migrations expand the population to its maximum range during summer, when it is distributed from Morocco to Norway and from Greenland to the western Baltic Sea. In the cold season, mackerel school along the European continental shelf edge until spawning commences in February off the Iberian Peninsula. Spawning continues until early July when it ends in the northern areas, such as the North Sea (Figure 1) (ICES, 2013). During the last century, large changes in abundance and distribution have been observed in the northern parts of its distribution area, especially in the North Sea (ICES, 2011; Jansen *et al.*, 2012a, 2012b). The reasons for these changes have been widely discussed, but are poorly understood (ICES, 2011). These changes have had significant ecological and economic impacts. The political and direct economic impacts are easily observed and are well known (Bazilchuk, 2010;

Cendrowicz, 2010). The ecological impacts are more difficult to observe, but include altered predation pressures on zooplankton and pelagic larval and juvenile stages of fish, including a number of commercially important fish stocks. It is, therefore, important to study these changes and understand the mackerel dynamics. In this paper, the causes of the largest known change in the history of Atlantic mackerel are examined by reviewing the substantial body of literature on the subject in light of recent changes in our perception of mackerel population dynamics and new time-series of environmental data.

The historic collapse in the North Sea

The most dramatic change in mackerel observed by scientists was the collapse in the North Sea in the 1970s (Jansen *et al.*, 2012b). Mackerel were highly abundant in the North Sea in the 1950s and 1960s. Larval surveys showed that spawning intensity varied greatly from year to year, but was generally on a very high level (Jansen *et al.*, 2012b). During the same decades, annual commercial landings of mackerel in the North Sea increased from <50 000 to 50 000–100 000 t as

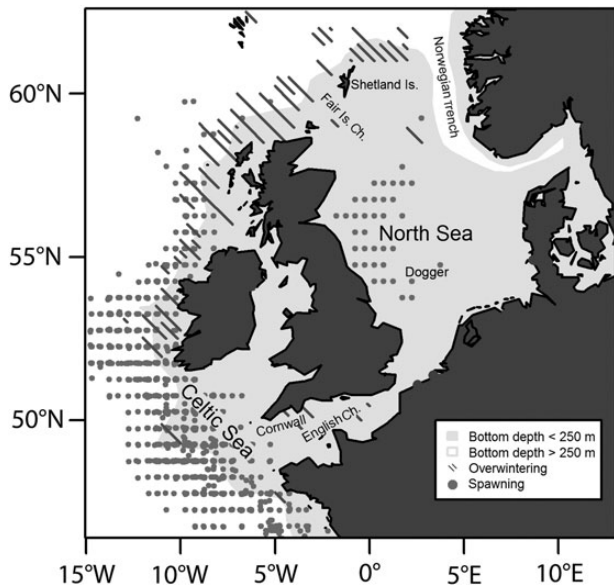


Figure 1. Recent mackerel distribution around the northwest European shelf. Continental shelf marked in grey (bottom depth < 250 m). Spawning indicated by dots. Each dot marks an observation of $50+$ eggs $m^{-2} d^{-1}$ [data from international mackerel egg surveys in the North Sea 2002–2011 (ICES, 2005, 2008, 2010) and western areas 1977–2007 (ICES WGMEGS)]. Stripes mark the distribution of mackerel before spawning (based on commercial catch data in January–March 1985–2010) (Jansen *et al.*, 2012a).

the traditional line and driftnet fisheries for mackerel were supplemented by a Dutch trawl fishery (Postuma, 1972; Lockwood, 1988). In the late 1960s, commercial fishermen on Norwegian purse-seiners realized that mackerel had very low target strength (acoustic reflectivity), which meant that the schools they were observing with the newly developed sonar actually represented a very large resource (Hamre, 1980). This discovery led to a targeted fishery utilizing novel techniques such as power blocks and single-vessel purse-seining. Landings consequently increased rapidly to a peak of approximately 900 000 t in 1967 (Figure 2) (Hamre, 1978; Lockwood, 1988). Even in 2012, this is unparalleled in numbers because the catch consisted of a high proportion of juveniles that were landed for industrial reduction (Revheim and Hamre, 1968; Hamre, 1970). The massive landings were followed by a collapse in the 1970s (Hamre, 1978). It was, therefore, concluded that fishing pressure in the North Sea was too high and had caused the local stock to collapse (Hamre, 1978; Lockwood, 1988). From 1970, the Norwegian commercial fishery was regulated with quotas and later with a minimum landing size. However, the relatively high fishing pressure continued in the 1970s, supplemented by a new large pelagic trawl fishery that developed in the Celtic Sea off Cornwall, where juveniles also constituted a significant part of the landings (Lockwood and Dann, 1976; Lockwood and Shepherd, 1984; ICES, 1984a). Despite subsequent regulations that were designed specifically to protect the North Sea “component”, mackerel spawning never rebuilt to precollapse levels. In the last decade (2000s), the biomass of mackerel spawning inside the North Sea was 150 000–230 000 t (ICES, 2011), which is significantly lower than before 1970 (Jansen *et al.*, 2012b). It is currently unknown why spawning in the North Sea has not rebuilt to former levels (Jansen *et al.*, 2012b). Outside the spawning season, millions of tonnes of mackerel started to spend autumn and winter in the northern North Sea in the 1990s (Jansen *et al.*, 2012a).

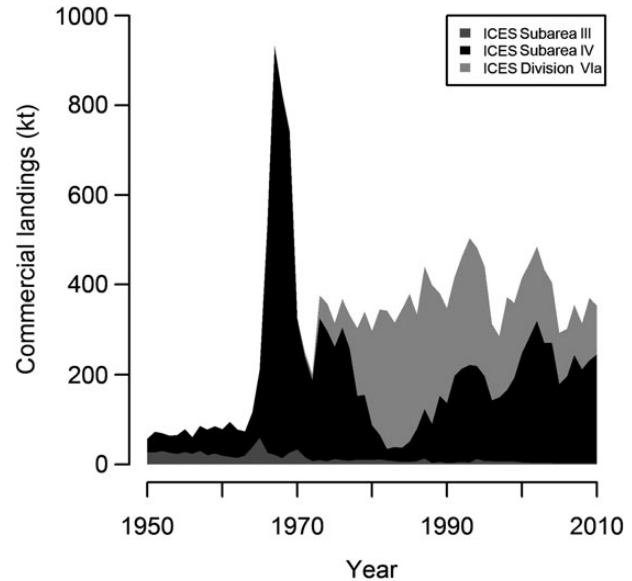


Figure 2. Commercial landings of mackerel in the North Sea (ICES Subarea IV), Kattegat–Skagerrak (Subarea III), and West of Scotland (Division VIa). Data from 1945–1949 from Postuma (1972). Data from 1950–2010 from Lassen *et al.* (2012).

The North Sea component – just a corner of a “dynamic cline”

The ICES assessments of the North Sea component and the scientific community’s perception of a local stock collapse caused by overfishing were based on the hypothesis of a separate North Sea spawning component. This hypothesis has recently been questioned, as an alternative population structure has been suggested and shown to be consistent with observations of age distributions and larval data (Jansen and Gislason, 2013). The “dynamic cline” hypothesis describes a more dynamic spatio-temporal spawning distribution than the traditional hypothesis of three spawning components. The cline is the result of interplay between conservative repeated migration behaviour and environmentally forced straying.

A conceptual population model from the perspective of spawning in the North Sea is shown in Figure 3. The cline is illustrated by the colour transition from the North Sea to areas towards the southwest. The abundance of mackerel with a tendency to spawn in the North Sea (blue/light grey) varies, with straying farther down the cline (green/black), mortality, and local recruitment. Each year the spawning migration into the North Sea is regulated by the environment (Jansen *et al.*, 2013; Jansen and Gislason, 2013).

This conceptual model is used to discuss the history of spawning in the North Sea in relation to a series of anthropogenic and environmental factors that are known to affect mackerel spawning and recruitment, namely temperature effects on the spawning migration, zooplankton (food), and wind-induced turbulence during spawning.

Material and methods

Environment

An average spring sea surface temperature (Spr T) was selected to reflect temperature conditions prior to and during spawning in North Sea surface waters. Yearly average spring sea surface temperature was estimated as the average of monthly values in April–June in $2 \times 4^\circ$ rectangles and for the area 56 – $62^\circ N$ 0 – $4^\circ E$. Observations

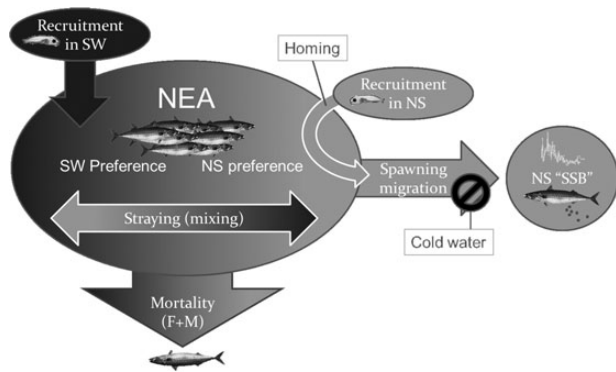


Figure 3. Conceptual model of spawning–stock biomass (SSB) in the North Sea (NS, light grey) and areas farther southwest (SW, black). Mortality can be due to fisheries (F) or natural causes (M) such as predation and disease.

originated from depths of <10 m from CTD, bottles, underway, pump, and moorings and were obtained from the ICES hydrographic database (ICES, 2012).

The temperature in the continental shelf edge current that flows along the western edge of the Norwegian trench (Figures 1–2 in Jansen *et al.*, 2012a) was selected to represent the conditions experienced by mackerel through winter (Win T). Mackerel distribution during winter is related to this temperature, possibly with a propagating effect on spawning (Jansen *et al.*, 2012a). Details of this modelled temperature time-series have previously been published (Jansen *et al.*, 2012a). In this paper, the same approach was followed, and the time-series was extended back to 1951 with available temperature profiles from CTD stations and bottle sampling between November and January obtained from the ICES hydrographic database (ICES, 2012).

Turbulence may affect the suitability of spawning sites and has been found to correlate with recruitment (Borja *et al.*, 2002). Turbulence was proxied by wind stress (= cube wind speed). The wind speed data “esrlcoads2ge” was downloaded as gridded (2° latitude \times 2° longitude) monthly averages from the NOAA ICOADS website (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/esrlcoads2ge.html>). Seasonal means were calculated for the spawning season and area in 1948–2010 in the North Sea (May–June, 50 – 60° N 4° W– 8° E).

Zooplankton data from Continuous Plankton Recorder (CPR) surveys during 1958–1974 were obtained from the database managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) as abundance by species by sample. Data for 1948–1957 were unavailable by species. Biomass by sample was calculated using the mean dry weight by species provided in Pitois and Fox (2006). Mean zooplankton density (g m^{-3}) by year was calculated as a simple average of all samples in the North Sea (50 – 60° N 4° W– 8° E) during the peak spawning season (June). Biomass was used instead of abundance because mackerel in all life stages are size-selective feeders and prefer larger Calanoid copepods over smaller Cyclopoid copepods (Pepin *et al.*, 1987, 1988; Ringuelette *et al.*, 2002; Langoy *et al.*, 2006; Robert *et al.*, 2008). The CPR is known to undersample in some situations, which mostly affects smaller species, and was, therefore, ignored (Pitois and Fox, 2006).

Recruitment

Four time-series of recruitment in the North Sea were used to identify strong year classes: (i) catch rates of 4-year-old mackerel from

the 1955–1961 year classes from the Dutch trawl fishery, assuming that these were fully recruited to the fishery (Postuma, 1972); (ii) number of 1-year-old mackerel from the 1962–1970 year classes from a landings- and tagging-based assessment (Hamre, 1978); (iii) catch rates of first-winter juveniles from the ICES International Bottom Trawl Survey (IBTS) in the first quarter of 1968–1979 from ICES (1979); and (iv) catch rates of first-winter juveniles in the first quarter of 1973–2010 from the ICES DATRAS database (<http://datras.ices.dk>). The four recruitment indices were thus not on the same absolute scales. In order to visualize the strong year classes within the same plot, the values in each dataset were standardized to the mean of each time-series. The last time-series of catch rates was further downscaled by an arbitrary factor of 0.2.

Proxies for spawning mackerel in the North Sea

Geostatistically modelled abundance time-series based on larval observations in the CPR survey were obtained from Jansen *et al.* (2012a). The mackerel larvae observations were obtained from the SAHFOS database. Jansen *et al.* (2012a) described the data and the model.

Total number of eggs spent in the North Sea per year was provided in the annual reports from the 1982–2012 ICES Working Group on Mackerel and Horse Mackerel Egg Surveys (WGMEGS).

Results and discussion

Temperature effects on the first part of the spawning migration during autumn and winter

Winter temperature in the shelf edge current where mackerel overwinter affects the distribution of the first part of the spawning migration, with a possible secondary knock-on effect into the spawning season (Jansen *et al.*, 2012a).

When Northeast Atlantic mackerel return from the feeding areas on the European shelf and in the Nordic seas in late summer, they aggregate along the continental shelf edge west of the British Isles and up to the North Sea, where they stay throughout autumn and early winter and are targeted by commercial trawlers and purse-seiners (ICES, 2011; Jansen *et al.*, 2012a). Later in winter, the commercial fleets and fishery-independent bottom trawl surveys find the mackerel farther southwest. The path of the migration, as suggested by the location of commercial and survey catches, coincides with the location of the relatively warm high-saline eastern Atlantic water flowing northeast on and along the continental shelf edge, flanked by cooler water masses. The timing of the southwest migration is related to the long-term temperature fluctuations of this current, most likely because the mackerel population is forced to seek warmer waters upstream as the current cools down during winter. Mackerel were thus found farther southwest during the relatively cold winters in the late 1970s and early 1980s than in the 1990s and early 2000s (Figure 4a) (Jansen *et al.*, 2012a).

In this paper, the temperature time-series has been expanded farther back in time to the 1950s and 1960s. This revealed a warmer period prior to the “collapse” (Figure 4a). If temperature had similar effects on the overwintering distribution of the mackerel in those decades, as it had on the whole main Northeast Atlantic population in recent decades, then the effect of cooling might have added to the reduction in spawning in the North Sea by moving the mackerel, that had an affinity for spawning in the North Sea, away from this area prior to spawning.

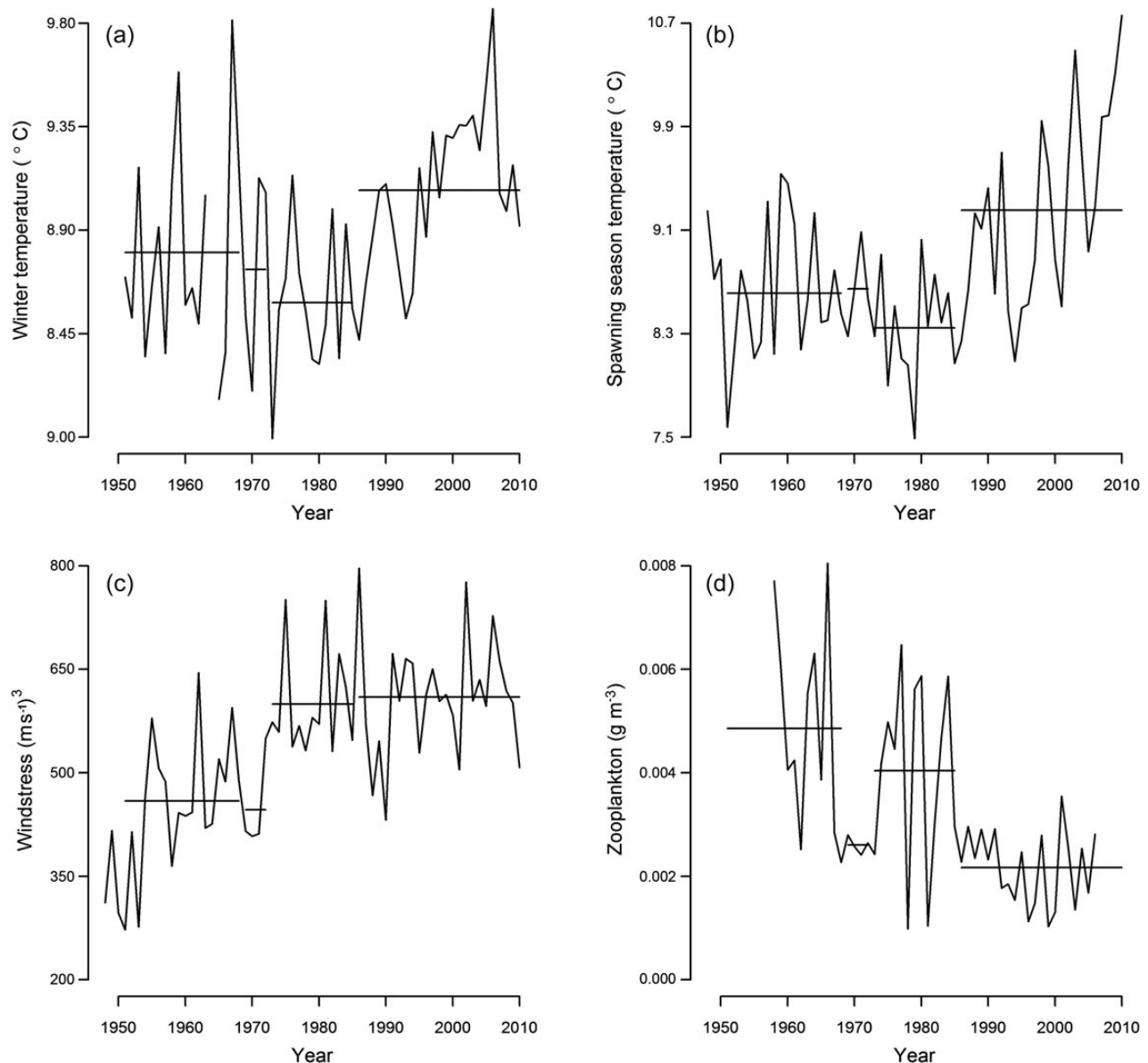


Figure 4. Time-series of the four environmental variables that are known to affect spatio-temporal mackerel population dynamics and/or spawning in the North Sea. Horizontal lines show average over multiple years. (a) Sea temperature in autumn – winter (November – January). (b) Sea surface temperature in the early spawning season (April – June). (c) Wind-induced turbulence in the early spawning season (May – June). (d) Mean zooplankton concentration in CPR samples during spawning in June (g m^{-3}).

Spatially disaggregated catch and survey data, as used by Jansen *et al.* (2012a) for analysing winter distributions during 1977–2010, were not available for the period 1950–1976. Literature was, therefore, reviewed to seek descriptions of winter distributions that could support or reject the notion of a winter temperature effect in these years. Three sources were found to be informative.

(i) Based on Norwegian data, Nederlec (1958) wrote that mackerel overwinter either in the deep waters along the continental shelf break (around 120–200 m), and also in local aggregations on the shelf, such as: “. . . the central deep of the English Channel, Eastern Channel, and southern North Sea”. Note, however, that in the North Sea from November to January, the scarcity of mackerel in the trawl seems to be explained by a migration out of the North Sea to the Atlantic slope of the continental shelf

or, which seems less likely, by vertical migration to intermediate depths (Nederlec, 1958).

(ii) On the commercial winter fishery in the Norwegian Trench (inside the North Sea), Hamre (1980) wrote that it “fluctuated considerably, owing to varying availability of the schools to the purse seiners. The mackerel were distributed in deeper water layers during winter, often below the range of the purse net, in order to avoid the winter-cooled surface layers. The winter fishery was therefore of minor importance to the purse-seine fleet”.

(iii) Age distributions of the mackerel caught in November 1976, 1978, and 1979 northwest of Scotland (outside the North Sea) showed relatively large fractions of mackerel from the 1969 year class, an indicator of North Sea origin (see Figure 5).

The described avoidance of cool surface waters in the northeast North Sea fits the observations in the 1990s, where mackerel schools were found to concentrate in the core of relatively warm water flowing into the North Sea along the western edge of the Norwegian trench (Reid *et al.*, 2001). Hamre (1980) furthermore describes the varying availability of mackerel during winter inside the North Sea. This could be explained by a westward emigration driven by cooling events. Indeed, the data from Walsh (1981) show that mackerel of North Sea origin were observed outside the North Sea in the late 1970s where the shelf edge current was relatively cold (Figure 4a) (Walsh, 1981).

Information from the literature, therefore, supports rather than rejects the hypothesis that the distribution of mackerel with an affinity for spawning in the North Sea was affected by winter temperatures in the shelf edge current. This suggests a tendency for more mackerel to be in the northern North Sea during winter in the 1950–1960s than during the subsequent decline in the 1970s. This environmentally driven change in winter distribution that appeared simultaneously with the “collapse” thus pushed mackerel away from the North Sea prior to spawning.

Temperature effects on the last part of the spawning migration during spring

Spawning migrations into the North Sea vary considerably in strength and timing (Jansen and Gislason, 2011, 2013). During the decades leading up to the “collapse”, spawning in the North Sea was highly correlated with temperature in the surface waters of the North Sea-bound currents. In warm years, mackerel spawning was intensified in the North Sea and slightly reduced in the Celtic Sea, indicating that temperature affected the choice by mackerel of a spawning area (Jansen and Gislason, 2013). It is, therefore, noteworthy that temperature in spring and early summer developed similarly to winter temperature, with cooling during the collapse in the 1970s and a warming during recent decades (Figure 4b). This suggests that the unfavourable cooling of the North Sea in the 1970s could have changed the spawning distribution, leading to a reduction in spawning in the North Sea.

Food and turbulence

Wind-induced turbulence probably affects the suitability of spawning sites, since it has been found to be negatively correlated with recruitment (Borja *et al.*, 2002; Villamor *et al.*, 2011). Turbulent mixing may disrupt food aggregations and the vertical distribution of eggs, larvae, and juveniles, but the actual mechanisms behind the correlation between turbulence and recruitment remains unknown (Borja *et al.*, 2002).

Since adult mackerel feed through the spawning season (Mehl and Westgård, 1983; Daan, 1989), spawning mackerel are likely to be attracted to areas with high concentrations of zooplankton. Insufficient zooplankton concentrations (and high turbulence) in the North Sea may, therefore, reduce the spawning migration into the North Sea.

In the longer term, increased recruitment due to good feeding opportunities and/or low levels of turbulence would increase the numbers of mackerel with an affinity for spawning in the North Sea, due to their natal homing behaviour. This would have an effect on the spawner biomass and spawning intensity after 2–3 years, when the recruits mature. Zooplankton is important as food for both adults and larvae (Trenkel *et al.*, 2013). It is, therefore, possible that turbulence and zooplankton concentrations affect

spawning distribution of Northeast Atlantic mackerel through several processes.

Both zooplankton and wind changed in unfavourable directions during the collapse (Figure 4c and d); it is, therefore, possible that this added to the other negative changes in this period through any of the suggested pathways.

Drivers of the change

The traditional explanation of the historic development of spawning in the North Sea seems to have overlooked a range of unfavourable environmental changes that might have added to the problems caused by high fishing pressure. Quantifying and ranking the importance of each effect and their interactions is currently impossible, because sufficient data are unavailable for a full quantitative model of all the involved processes. Furthermore, some predictors are clearly confounded. However, it is possible to provide a holistic view of the available information about the key variables.

The summary plot (Figure 6) shows the larval index as a proxy for biomass of mackerel that spawn in the North Sea, overlain with information on the environment, recruitment, and commercial catch. The plot illustrates how the period before the collapse was characterized by favourable or intermediate environmental conditions, good recruitment, and very low fishing mortality. Then, in the late 1960s, landings increased radically, environmental conditions changed in unfavourable directions, and recruitment was minimal after the last good year class in 1969. The first two negative effects (overfishing and poorer feeding conditions) correspond with the radical drop in spawning in 1970–1972. After an uncertain short rebuilding in 1972–1974, possibly related to good recruitment from the 1969–1971 year classes (ICES, 1978), spawning in the North Sea as well as in the Celtic Sea continued to decrease (ICES, 1984b). Through the 1970s, substantial cooling was observed. The cool winters (Figure 4a) most likely forced mackerel away from the North Sea, and the cool springs (Figure 4b) likely reduced and delayed the spawning migration into the North Sea. The increase in zooplankton concentration from around 1975 to the early 1980s (Figure 4d), apparently did not counter the combined effects of low temperature, lack of recruitment, and continued fishing, as spawning in the North Sea continued to decrease. Then, large year classes in 1979, 1980, and especially in 1981 and 1984 originating from the west increased the population in the Northeast Atlantic (ICES, 2011). However, no substantial straying effect seemed to support spawning in the North Sea. From the late 1980s, temperatures increased to a level that, in most years, matched or exceeded the early decades. But, at the same time, zooplankton concentrations had decreased to the lowest level in the time-series, and turbulence remained high. These conditions likely kept recruitment and spawning in the North Sea at very low levels until the early 2000s, when an increase in recruitment was observed, whereas spawning remained at a relatively low level. Egg survey data suggest a slight increase in spawning during the last decade, but the larvae index is too uncertain in the latter decades to confirm this development (Jansen *et al.*, 2012b).

The notorious “collapse of the North Sea component” thus seems to be a result of the combined effects and possible interactions between high fishing pressure and environmental conditions acting to reduce recruitment and spawning migration into the area. The word “collapse”, therefore, seems misleading when acknowledging that (i) the North Sea mackerel never were a separate stock, and (ii) the decline in abundance appeared more dramatic in the North Sea than it actually was for mackerel in the Northeast

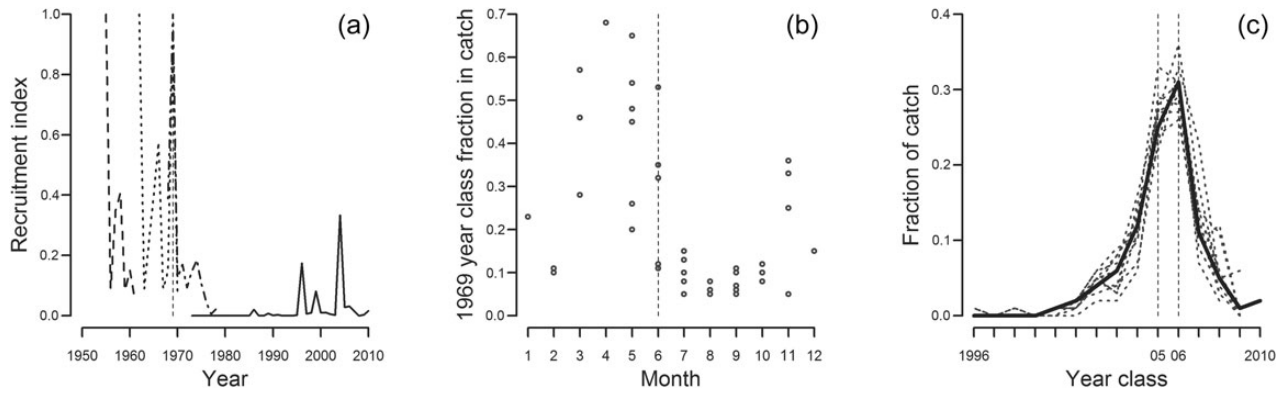


Figure 5. Age distributions and recruitment. (a) Time-series of recruitment in the North Sea indicating strong year classes. Please note that time-series are not in scale. (b) Fraction of 1969 year class by month in 1974–1979 from commercial fisheries in the area between the Outer Hebrides and Cape Butt. (c) Age distributions in commercial catches in January–March 2010 by ICES division (stippled lines) and for all areas combined in July–September (bold line). (This figure is Figure 7 from Jansen and Gislason (2013)).

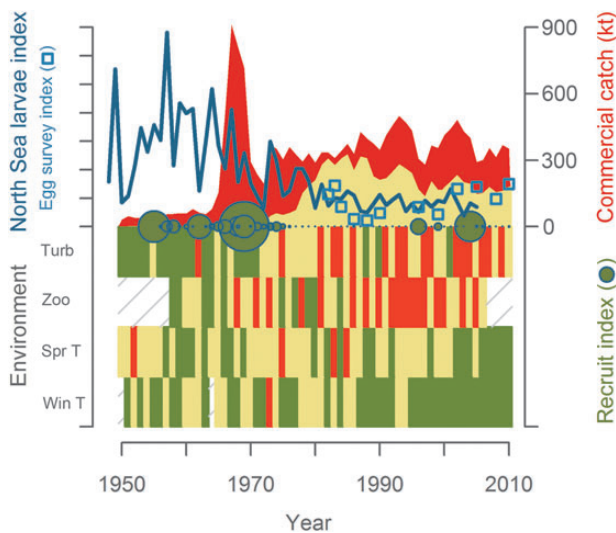


Figure 6. Summary plot combining information from the North Sea on the development of local mackerel SSB [proxied by the larvae index (blue/black line) and egg index (blue/black squares)] with potential causal variables. Upper half: commercial catch [red/grey: North Sea (Subarea IV), beige/light grey: west of the British Isles (Division VIa)]. Mid: recruitment index (green/grey circles). Lower half: four variables as traffic light plots: winter temperature (Win T), spring temperature (Spr T), zooplankton concentration (Zoo), and wind-induced turbulence (Turb). Traffic light colors indicate favourable (green/light grey), neutral (beige/grey), and unfavourable conditions (red/black). Annual values are favourable when exceeding the mean, neutral when exceeding the minimum, and unfavourable below the minimum of the period of high mackerel abundance (1955–1967). The scale for wind-induced turbulence was reversed because still low values are favourable. Missing information is indicated by grey stripes.

Atlantic (because it coincided with a change in distribution). In the following text, this event is referred to as “pseudocollapse”.

Rebuilding

The return of massive spawning in the North Sea would thus depend on an increase in numbers of mackerel with a tendency to spawn in

the North Sea, combined with environmental conditions that favour the spawning migration to and recruitment in the North Sea.

However, this would only be possible if there were no irreversible consequences of the events around the 1970s. Irreversible consequences could be loss of gene variants linked to the tendency to spawn in the northeastern parts of the spawning area or linked to increased survival of recruits in the North Sea. If mackerel have genetically based preferences for natal homing to certain areas or environments, then they are weak and can be overruled by other stimuli. This has been shown by massive straying of the 2005 year class (Jansen and Gislason, 2013). That this is not a post-collapse phenomenon can be seen in the high-amplitude, high-frequency switching between spawning in the North Sea and farther southwest that occurred before the pseudocollapse (Jansen and Gislason, 2013). A consequence of this dynamic spawning migration is that the genes from the mackerel that tended to spawn in the North Sea before the pseudocollapse must have been represented to a fair degree in the mackerel that tended to spawn farther southwest. Therefore, it is suggested that the pseudocollapse in the North Sea may have changed some gene frequencies in the Northeast Atlantic, but did not lead to an extinction of major gene variants.

In the case that natal homing is based on learned recognition of certain environmental cues experienced during the first year, as with salmon (*Oncorhynchus* spp.) (Lohmann et al., 2008), then the high mortality of the pseudocollapse and subsequent poor local recruitment have led to a significant behavioural loss. A behavioural loss of this type is not permanent, and rebuilding could follow a reduction in mortality and substantial straying if the environment still allows for life-cycle closure (Petitgas et al., 2010). It can even be expected to happen faster than in cases where collapses result in the breakdown of socially transmitted traditions, as for herring (*Clupea harengus*) and cod (*Gadus morhua*) (Petitgas et al., 2010). There is no evidence of such a complex behaviour of later entrainment of recruit (first-time) spawners in mackerel, as has been proposed for herring (Petitgas et al., 2010). The tendency for homing shown by Jansen et al. (2013) does not indicate this type of learning, as the growth patterns that appeared in the first year disappeared in the second before reappearing at spawning time throughout the adult life span. Furthermore, since mackerel are not divided into somewhat distinct contingents, like herring, it is assumed that this behaviour is of minor importance or not existing.

Rebuilding is, therefore, not prevented by permanent historic losses, but depends on straying, mortality, and environment.

The previously unexplained lack of rebuilding of spawning in the North Sea then seems related to two environmental factors that have remained unfavourable: (i) wind-induced turbulence, and (ii) zooplankton concentration (especially of the larger Calanoid copepods such as *Calanus* spp.) (Figure 4c and d). Furthermore, the large commercial autumn–winter fishery in the North Sea and west of the Hebrides continues to land unknown quantities of mackerel with an affinity for spawning in the North Sea. Given the evidence discussed above, it can be assumed that mackerel with an affinity to spawn in the North Sea are among the last to leave the northern North Sea and migrate along the continental shelf edge to west of the British Isles. This being the case, these mackerel may have been more heavily exploited in recent years. For example, in 2009, parts of the fishing fleet were restricted to fishing their very large quotas in the northern North Sea, even though most mackerel had migrated west due to increasing temperatures (Jansen *et al.*, 2012a).

It is impossible to forecast fish population abundance more than a few years ahead due to the difficulties in predicting recruitment. This is also the case for mackerel (ICES, 2011). However, some reflections can be made on future prospects for environmental conditions that may support increased spawning in the North Sea.

The environmental conditions that have remained unfavourable since the pseudocollapse are zooplankton biomass and wind-induced turbulence.

Confidence in predictions of wind speeds in the future is low. Several model studies have suggested increased average and/or extreme wind speeds in Europe, but some studies point in the opposite direction (Solomon *et al.*, 2007).

The long-term reduction in zooplankton biomass was mostly due to a reduction in larger copepods observed by CPR sampling, especially *Calanus finmarchicus* in the northern North Sea. This is in accordance with previously published analyses of the same dataset (Heath *et al.*, 1999; Pitois and Fox, 2006). Abundance dynamics of *C. finmarchicus* in the North Sea in spring are driven by a combination of wind patterns and the volume of cold bottom water in the Faroe–Shetland Channel. In winter at depths >600 m, the bottom water flowing south from the Norwegian Sea basin contains large numbers (up to 650 m⁻³) of hibernating *C. finmarchicus* (Heath *et al.*, 1999). In spring, these copepods ascend to surface waters where advection transports parts of the population into the North Sea (Heath *et al.*, 1999). The bottom water in the Norwegian Sea is formed at high latitudes in the Greenland Sea by a process of cooling at the sea surface and sinking. Since the 1960s, the intensity of this process has been decreasing due to warming and increasing freshwater inputs from Arctic rivers and ice melt (Dickson *et al.*, 1996). The further transport into the North Sea appears to depend on wind strength and direction, factors that also changed in an unfavourable direction (Heath *et al.*, 1999). The additive combination of these physical changes is the likely reason for the decrease in spring abundance of *C. finmarchicus* in the North Sea (Heath *et al.*, 1999). *Calanus finmarchicus* have furthermore been observed to seek the cooler waters below the thermocline when surface waters become too warm (Jónasdóttir and Koski, 2011). This is also below the CPR sampling depths of ~7 m (Hays and Warner, 1993; Batten *et al.*, 2003) and below the habitat of the smaller larvae (Röpke, 1989; Hillgruber and Kloppmann, 2001). However, this latter effect is more pronounced in the warm months after spawning. Anticipated future warming of the climate system has the potential to further weaken the thermohaline circulation by reducing surface

water density in the areas where the North Atlantic Deep Water is formed through both high-latitude warming and enhanced poleward moisture transport in the atmosphere (Manabe and Stouffer, 1993; Houghton *et al.*, 2001). Assuming unchanged transport mechanisms of *C. finmarchicus* into the North Sea, this would not lead to any improvements in the possibilities for an increase in mackerel production in the North Sea in the future. However, mackerel are opportunistic feeders, and the larvae also seek other large species of zooplankton, so a major increase in mackerel spawning in the North Sea could happen if other preferred zooplankton species should increase in abundance.

Conclusion

In light of new knowledge about the population structure of mackerel in the Northeast Atlantic, the most dramatic observed change in mackerel history, namely the so-called collapse of the North Sea mackerel in the 1970s, was reviewed. It was found that the traditional explanation did not account for a range of unfavourable environmental changes that likely added to the effect of high fishing pressure by reducing recruitment and spawning migration into the North Sea. These parameters were the following.

Temperature effects on the first part of the spawning migration during autumn and winter

Information from the literature supported rather than rejected the hypothesis that the spawning distribution of mackerel, with an affinity for spawning in the North Sea, was affected by decreasing winter temperatures in the shelf edge current. This environmentally driven change in winter distribution appeared simultaneously with the pseudocollapse, pushing mackerel away from the North Sea prior to spawning.

Temperature effects on the last part of the spawning migration during spring

The link between temperature and spawning migration in late spring and early summer indicates that the unfavourable cooling of the North Sea in the 1970s changed the spawning distribution away from the North Sea.

Zooplankton (food) and wind-induced turbulence during spawning

Both zooplankton and wind changed in unfavourable directions during the pseudocollapse; it is, therefore, possible that this has added to the other negative changes in this period through effects on spawning migration and/or recruitment.

No indications were found for any irreversible genetic or behavioural losses caused by the pseudocollapse. The previously unexplained lack of rebuilding of spawning in the North Sea consequently seems related to two environmental factors that have remained unfavourable: (i) wind-induced turbulence, and (ii) zooplankton concentration (especially of the larger Calanoid copepods such as *Calanus* spp.). Furthermore, the large commercial autumn–winter fishery in the northern North Sea continues to land unknown quantities of mackerel with an affinity for spawning in the North Sea. Rebuilding of spawning to a precollapse level, therefore, seems possible under favourable environmental conditions and sufficient conservation of mackerel with an affinity for spawning in the North Sea.

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