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Combined effects of exploitation and temperature on fish stocks in the Northeast Atlantic

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Abstract :

Fish stock fluctuations are affected by two potentially confounding forces: the removal of individuals by fisheries and climatic variations affecting the productivity of fish populations. Disentangling the relative importance of these forces has thus been a question of primary importance for fisheries management and conservation. Through the analysis of long-term time-series for 27 fish stocks from the Northeast Atlantic, the present study shows that the sign and intensity of the effect of temperature on biomass are dependent on the geographical location: the stocks located at the southernmost and northernmost latitudes of our study displayed stronger associations with temperature than the stocks located in the middle range of latitudes. As a consequence, the investigation of the combined effects of exploitation and the environment revealed that the stocks at the northern/southern boundaries of the spatial extent of the species were more prone to combined effects. The interplay between geographic location, climate and exploitation thus plays a significant role in fish stock productivity, which is generally ignored during assessment, thus affecting management procedures.

Keywords : combined climate/exploitation effect, exploitation, fish stocks, Northeast Atlantic, response to climate, time-series

INTRODUCTION

In fish stock assessment, exploitation is often defined as the key driving force acting on population size. Climatic and other environmental factors are most often perceived as additional random white noise generating variations in biological processes, such as growth or recruitment. In marine ecology the general paradigm has been similar (i.e. additive processes), but somehow reversed, as environmental changes were shown to be crucial to understand the patterns of variations in exploited fish populations (Alheit and Bakun, 2010; Lehodey *et al.*, 2006). The variability of oceanographic variables is dominated by slow, long-term fluctuations (Halley, 1996; Rouyer *et al.*, 2010; Vasseur and Yodzis, 2004) and have thus been proposed as a potential force driving the long-term fluctuations in fish stocks (Lawton, 1988; Steele, 1984). Such environmental variations have been advocated to explain long-term changes in the overall level of fish populations (Alheit and Hagen, 1997; Toresen and Østvedt, 2000), while historical time series have revealed that fish populations display substantially large fluctuations even in the absence of intensive exploitation (Baumgartner *et al.*, 1992; Ravier and Fromentin, 2004). Environmental conditions impact recruitment strength during the early life stages of fishes, which affect the level of the stock as it flows through the age-classes of the population over its lifetime (Hjort, 1914, 1926). Abiotic variations also impact other key biological/ecological processes of wild fish populations, such as growth (Brander, 1995) or migratory behavior (Fromentin, 2009). Nonetheless, the response of fish stocks to environmental fluctuations depends on their life-history characteristics and on the time scales at which the environment fluctuates (Johst and Wissel, 1997; Nisbet and Gurney, 1993; Petchey, 2000). Furthermore, the sensitivity to the environment is not uniform across populations as it may depend upon their geographical location within the range of the species' repartition (Miller *et al.*, 1991). For instance, the intensity of the temperature effect on the recruitment of Atlantic cod (*Gadus morhua*) has been shown to be stronger for stocks located at the boundaries of the species geographical distribution, but also opposed between its northern and southern edges (Planque and Fox, 1998; Planque and Frédou, 1999; Stige *et al.*, 2006).

Understanding the driving forces of population fluctuations has been the source of an intensive ongoing research effort that attracted a particular interest in the field of fisheries ecology for its implications in conservation and management in the context of global change. This question has remained much debated because of the complex nature of these fluctuations, originating from the interplay between deterministic and stochastic forces (Bjørnstad and Grenfell, 2001). Particularly, the effects of environmental changes and exploitation on fish populations have been seen until very recently as additive, but growing evidence shows that they have in fact important combined effects. Substantial changes in stock productivity associated to climate fluctuations can create the conditions for the over-exploitation of a given stock under an otherwise acceptable fishing effort, because the level of exploitation cannot be sustained anymore under the new environmental conditions (Perry *et al.*, 2010; Planque *et al.*, 2010). Here, we investigated a set of long-term total biomass time series for 27 commercial fish stocks from the Northeast Atlantic, to test (i) whether combined effects of climate and exploitation could be detected in their long-term fluctuations and (ii) how those effects depend on the stocks geographical location.

MATERIALS AND METHODS

Fisheries time series

Recruitment, total biomass and fishing mortality time series were extracted from reports made available by the relevant working groups at the International Council for the exploration of the Sea (ICES, http://www.ices.dk/indexfla.asp). Among the 40 fish stocks comprised in the data set, we selected 27 stocks (Table 1) for which long-term and age-structured data of abundance, weight, maturity and fishing mortality were available. Because the length of time series is a key parameter for the robustness of the analysis, only fish stocks displaying at least 30 years of continuous data were selected. The Baltic Sea stocks were voluntarily left out from the analyses as the environmental driver associated to the regime shift that drastically changed its composition is believed to be salinity rather than temperature (Möllmann *et al.*, 2008). However, the analyses proved robust to the inclusion of those stocks. For two stocks, the Northeast Arctic cod and the Norwegian Spring-spawning herring, exceptionally long data was available (94 and 100 years, respectively). For those, the ICES data have been extended back using the historical analyses of (Hylen, 2002) for the Northeast Arctic cod and (Toresen and Østvedt, 2000) for the Norwegian Spring-spawning herring, further details are available in (Rouyer *et al.*, 2011). These stocks from 9 different species are located in contrasting geographical areas and display various life history traits and exploitation histories

Fishing mortality was used to quantify the effects of the variations in exploitation on total biomass, while temperature was used to assess the effect of changing environmental conditions on total biomass. Total biomass has the advantage to be more directly linked to temperature than the spawning stock biomass, for which a lag equal to the age at maturity has to be accounted for and that is plagued by two problems. First, age at maturity can substantially vary over time, which was observed for some stocks (e.g., Northeast Arctic cod). Second, introducing a lag implies removing as many data points as the number of delays introduced, which reduces the length of the time series.

The relative latitudinal position of each stock within the species range was obtained by the following approach. The centre of the latitudinal distribution for each stock was estimated on maps of the stocks distribution. The positions were then rescaled so that a “0” indicates a stock at the southern end of the distribution and “1” a stock at the northern end, using data on fish species distribution extracted from FishBase (http://www.fishbase.org).

Temperature time series

Temperature time series were extracted over each stock distribution area from the extended reconstructed sea surface temperature (*NOAA_ERSST_V3*) data set provided by the *NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their web-site at* http://www.esrl.noaa.gov/psd/ and available from 1880 to 2009. This data set is constructed using the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) Sea Surface Temperature data and improved statistical methods. The extracted time series were averaged over space and months in order to obtain one yearly time series per stock matching the length of the fisheries data. For Arctic stocks, the temperature in the Barents Sea from 1921 until 2006 from the Kola meridian transect (33°30' E, 70°30'-72°30' N) was used (34). The recruitment age in the age-structured data used to compute total biomass time series varied among stocks. Thus, the time series of temperature were lagged so that the first data point of the first age-class was aligned with the temperature the year before its birth.

Extracting long-term fluctuations from temperature and fishing mortality time series

Long-term fluctuations were defined in the present study as fluctuations occurring at time scales above 5 years. This empirical limit was set to capture and focus on long-lasting periods of high/low values in fishing mortality/temperature, while being consistent with the length of the time series. The wavelet approach was used to decompose time series and extract long-term fluctuations (Cazelles *et al.*, 2008; Lau and Weng, 1995; Torrence and Compo, 1998). The wavelet transform decomposes the variability of time series in both time and frequency and allows to cope with non-stationarity and transients. The reversibility property of the wavelet transform was used to extract the short-term fluctuations in the time series, defined as the fluctuations below 5 years. The long-term fluctuations in temperature and fishing mortality were then obtained by subtracting the filtered signal from the original time series and removing the residual variability by a low-pass filter.

Testing associations

On the contrary to exploitation, which is expected to be negatively associated with total biomass, the association between temperature and total biomass is likely to vary in sign and intensity across species and stock locations (Brunel and Boucher, 2007; Planque and Frédou, 1999). The association between temperature and total biomass/recruitment were thus investigated. As it is more robust to outliers and does not require Gaussian distributions, the non-parametric Spearman correlation coefficient was used to quantify the associations between the long-term fluctuations in temperature and in total biomass/recruitment. Dealing with autocorrelation for assessing the statistical significance of associations is a classical challenge in ecology (Pyper and Peterman, 1998). To cope with this, the Fourier surrogate technique was used (Rouyer *et al.*, 2008b; Royer and Fromentin, 2006; Schreiber and Schmitz, 2000). Through spectral synthesis, Fourier surrogates generate random time series that preserve the power spectrum of the original time series and therefore its autocorrelation structure. Surrogate time series thus display exactly the same fluctuations than the original series, but occurring at random times. This technique was then used to generate an empirical distribution for each Spearman correlation coefficient, allowing to test whether or not the correlation could be produced by chance while formally accounting for autocorrelation.

Semi-quantitative approach

Detecting the combined effects of two variables upon a third one can be done within the classical generalized modelling framework (GLMs), which also provides ways to control for autocorrelation. However for most of the stocks the number of events for which total biomass, temperature and fishing mortality were all in a high/low period was relatively low, which was thus equivalent to an unbalanced dataset. This therefore limited the ability of GLMs to quantify such events. In addition, the raw total biomass time series displayed a high degree of autocorrelation and the inclusion of auto-regressive terms to 'clean-up' the autocorrelation in the residuals was found inoperative. Including autoregressive terms often lead to explain most of the trend in the time series, which can impair the detection of external effects (Pyper and Peterman, 1998). To overcome these limitations a test was designed using a semi-quantitative method, intuitive yet powerful, inspired from Brander (2005). For each time series of raw total biomass and for each time series of long-term fluctuations in temperature and fishing mortality, the points were ranked into categories of 'low' and 'high' levels. For each variable and each time series, the years of 'low' and 'high' levels were defined as the values below the 33rd and above the 66th percentiles of the distribution, respectively. Attempts to use higher percentiles, such as the 20th and the 80th, critically reduced the number of observations within the 'low' and 'high' levels. Since the sign of the effect of temperature on recruitment varies across latitudes and stocks (Brunel and Boucher, 2007; Planque and Frédou, 1999), the ranking of temperature for stocks displaying a negative correlation between recruitment and temperature was inverted so that 'low temperature' could be interpreted as 'unfavourable conditions' and 'high temperature' could be interpreted as 'favourable conditions' for all stocks (regardless of the significance of the correlation). The effect of exploitation, temperature and the combined effect of both on total biomass were quantified by comparing the number of years following the “expected behaviour” to the number of years following the “unexpected behaviour”. The “expected” and “unexpected” behaviours were defined as follows. For exploitation the expected behaviour corresponded to a year of low total biomass with a high fishing mortality, or to a year of high total biomass with a low fishing mortality. Conversely the unexpected behaviour corresponded to a year of low total biomass with a low fishing mortality, or to a year of high total biomass with a high fishing mortality. Similarly, the expected behaviour for temperature was a high total biomass with a favourable temperature or a low total biomass with an unfavourable temperature. The unexpected behaviour was thus defined as a low total biomass with a favourable temperature or a high biomass with an unfavourable temperature. Finally, the expected behaviour for the combined effect of temperature and fishing mortality corresponded to a year of low total biomass with a high fishing mortality and an unfavourable temperature, or to a year of high total biomass with a low fishing mortality and a favourable temperature. The unexpected behaviour was thus a year of low total biomass with a low fishing mortality and a favourable temperature or a year of high total biomass with a high fishing mortality and an unfavourable temperature. Note that this test did not directly address counteracting effects between temperature and exploitation on biomass, as such effects are more likely to range around the median of the biomass (i.e., not in the 'low'/'high' levels). For a given stock, the strength of the effect was quantified through the percentage of years conform to the expected behaviour. An effect was considered meaningful if at least 50% of the years displayed an expected behaviour. However, this proportion is largely affected by the fact that in autocorrelated time series two consecutive points will have a high probability to belong to the same category. To assess whether or not the proportions observed were higher than those obtained by chance, a test based on the surrogates approach was performed. For each stock, 1000 Fourier surrogates (see *Testing associations*) of the raw total biomass time series were produced. These allowed to compute the distribution of the unexpected and expected behaviours for each effect. For a given effect, the proportion of years displaying an expected behaviour was considered significant when the observed proportion was higher than for 90% of the surrogates.

RESULTS

The association between recruitment and temperature was found similar in sign and intensity to the association between total biomass and temperature (Pearson correlation coefficient C=0.81, p<0.0001, Fig. 1a). Stocks for which a weak association between recruitment and temperature was found also displayed a weak association between biomass and temperature. However, significant associations with temperature were only found for a reduced number of stocks for both recruitment (11 stocks) and total biomass (6 stocks). The association between total biomass and temperature was found variable in sign and intensity over the species latitudinal range (Fig. 1b) as it was also the case for the association between recruitment and temperature (Fig. 1c), suggesting a difference in sensitivity to temperature across the range of the species distribution. Correlations were generally aligned along a latitudinal gradient, but this pattern often disappeared at the species level. The biomass/temperature and recruitment/temperature correlations were significantly associated to the mean latitude of the stock's geographical location (Pearson correlation coefficient C=0.44, p=0.02, Fig. 1b and Pearson correlation coefficient C=0.68, p<0.0001, Fig. 1c, respectively).

Figure 1 around here

They were generally negative for the stocks located at lower latitudes, whereas they were positive for the stocks located at higher latitudes. In the middle range of latitudes the correlations were weaker and the few significant correlations between biomass and temperature were only found in the northernmost and southernmost areas. Comparable fluctuations were also noticed between stocks with different life history traits and exploitation histories, but located in the northernmost and southernmost areas of the study. This was particularly clear for the North-east Arctic cod, the Arctic haddock and the Norwegian Spring Spawning herring that displayed common periods of low and high biomass consistent with the long-term fluctuations in temperature at the Kola section (Fig. 2a). Likewise, the more southern Irish Sea cod and sole stocks both displayed common long-term fluctuations consistent with their negative relationship to temperature (Fig. 2b).

Figure 2 around here

The long-term fluctuations in fishing mortality also often displayed patterns opposite to those of biomass, such as for the Northeast Arctic cod, the Irish Sea cod, the Icelandic haddock, the Northern hake, the Arctic Saithe and the Celtic Sea sole (Fig. 3). This illustrated the difficulty to disentangle the relative effects of temperature and fishing mortality on total biomass, as both variables seemed to have substantial effects on the stocks.

Figure 3 around here

The effect of temperature and exploitation on biomass were then investigated by analysing co-occurrences of periods of low/high biomass with periods of high/low levels in the long-term fluctuations of temperature and exploitation. The long-term fluctuations of temperature and fishing mortality were obtained by filtering the time series above a 5 years threshold (Table 1). The raw time series of both fishing mortality and temperature were dominated by long-term fluctuations, which explained between 51.4% and 93.7% of the total variance for fishing mortality (77% on average) and between 52.2% and 86.7% of the total variance for temperature (73.7% on average, Table 1).

Table 1 around here

The effects of temperature and exploitation were difficult to rank as when pooling all stocks, the percentage of expected events for these factors was 67% and 68%, respectively. Furthermore, significant temperature effects were found for 8 stocks, whereas 9 stocks displayed a significant effect of exploitation (Fig. 4). In contrast, although the pool of points with a combined effect was smaller in comparison, the percentage of expected events was found higher (79%) than for exploitation or temperature alone. Among 27 stocks, 8 were found to display significant combined effects between temperature and exploitation (Fig.4). For 5 stocks the proportion of expected combined effects was found to be 100%, whereas the effect was not significant (Faroe cod, West Scotland cod, Icelandic haddock, North Sea saithe and Celtic sole, Fig. 4). This was due to the small amount of points with a combined effect (below 6) that was easily reproduced in the test by random time series displaying similar fluctuations (i.e. surrogates). As expected, significant combined effects were found for stocks that displayed a significant effect of exploitation and/or temperature. Therefore, the geographical location of stocks appeared important as stocks in the southernmost and northernmost latitudes, which displayed higher correlations with temperature, were thus more prone to undergo stronger combined effects.

Figure 4 around here

A couple of examples from the northernmost latitudes provided a clear illustration of periods with combined effects, albeit with slight differences (Fig. 5). For instance, the North-east Arctic cod has been fully to over-exploited since the late 1950s, but the total biomass remained at relatively high levels and mostly dropped during the mid-1970s and mid-1980s, when the temperature decreased and possibly drove the recruitment to low levels (Fig. 5a). The Norwegian Spring spawning herring case is even more striking, as the crash of this population in the 1970s coincided with a large peak in fishing mortality that followed a prolonged period of unfavourable temperature associated to consecutive years of poor recruitment. The later rebuilding of this population corresponded to favourable temperature while fishing mortality remained at average levels (Fig. 5b).

DISCUSSION

Long-term effects of climate on recruitment have already been documented for a large number of commercial stocks from the North-east Atlantic (Beaugrand *et al.*, 2003; Brunel and Boucher, 2007) and are likely to be associated to substantial changes in productivity (Alheit and Hagen, 1997; Toresen and Østvedt, 2000; Vert-pre *et al.*, 2013). Here we showed that the fluctuations in temperature were associated to those in recruitment and total biomass with a comparable sign and intensity (Fig. 1a) and that those associations varied with the latitudinal location of the stocks (Fig. 1b,c). Such a spatial pattern has already been documented for the recruitment of Atlantic cod stocks (Planque and Fox, 1998; Planque and Frédou, 1999; Stige *et al.*, 2006) and has been generalized to a broad range of species (Brunel and Boucher, 2006). In accordance with the species range hypothesis (Miller *et al.*, 1991), these studies showed that the recruitment of stocks located at the limits of the species' geographical distribution were more prone to be affected by environmental variability than stocks in the middle range, while the sign of this effect was opposed between the northernmost and southernmost stocks. Even though the present data set did not cover the total range of the species repartition, consistently with these studies the results showed that such a pattern could also be detected in biomass fluctuations (Fig. 1b). The importance of the geographical location was further stressed by the common features in the long-term fluctuations of stocks with different life-history traits and exploitation history but located close to each other (Fig. 2). This appeared clearly for the Irish Sea cod and sole stocks, but also for three stocks from the Barents Sea area for which the environmental link has already been put forward to explain the relative synchrony of their recruitment dynamics (Ottersen and Loeng, 2000). With the current climate change, such a geographical effect could have great consequences. The raise of the sea surface temperature over the North-east Atlantic during the past 30 years could have contrasted effects on the productivity of northern and southern fish stock. Averaging the standardized biomass time series of the northernmost and southernmost stocks illustrated this (Fig. 6). Whereas the trend in biomass of the northernmost stocks indicates a slight increase during this period, it indicates a clear decrease for the southernmost ones (Fig. 6). Indeed, such a general figure has to be interpreted carefully because it does not account for the variability in management efficiency across stocks and areas and also because our dataset does not cover the total species' distribution.

Figure 6 around here

In our database, even though the longest available time series were used, most of them began long after the development of the fisheries and therefore integrated long periods of overfishing. The percentage of points above the fishing mortality of the precautionary approach was on average equal to 61% when pooling the stocks together and ranged from 8% to 100%. Furthermore, 70% of the stocks displayed more than 50% of years above the fishing mortality of the precautionary approach, illustrating the general state of over-exploitation of the North-east Atlantic stocks during the studied period. The lack of contrast in the state of exploitation of the stocks, due to the relative shortness of the time series, was thus a limit that impaired the detection of combined effects. The procedure detected synchronous events based on 'high' and 'low' levels, which were defined by the distribution of the time series and not by an objective baseline. Therefore, in the case of stocks for which relatively short time series were available but that have been overexploited for a long time, 'high' biomass may in fact represent medium to low levels of biomass relatively to virgin biomass, which is difficult to estimate precisely. It was therefore not surprising that the clearest examples were found for the stocks for which the longest data were available (Fig. 5). This underlines the importance of past levels to define baselines and assess the current state of stocks. Finally, it has to be noted that our results were based upon the analysis of SST in the North-East Atlantic, but that other environmental variables in other areas are known to be important drivers of fish stock productivity (Möllmann *et al.*, 2008).

Little doubt can be cast over the crucial contribution of exploitation on the decline of commercial fish stocks from the North Atlantic (Christensen *et al.*, 2003) and our results documented clear effects of fishing mortality on the variations of total biomass of fish stocks. However, our results also show that substantial changes in fish stock productivity induced by long-term changes in the environment have probably amplified or dampened the impacts of exploitation, increasing the risk of depletion during periods of unfavourable environmental conditions, or stabilizing the biomass during periods of favourable conditions. The combined effects seemed overall stock-specific as stocks from common areas seemed to have been affected differently. For instance, the decline of the North-east Arctic cod seemed to be primarily due to a long period of overfishing, enhanced by a period of unfavourable temperatures inducing poor recruitment that drove the whole stock to its lowest level. The collapse of the Norwegian Spring Spawning herring stock in the 1970s seemed to correspond to a prolonged period of unfavourable temperatures that have probably translated into consecutive years of poor recruitment during a period of moderate exploitation. Then, the dramatic and sharp increase in fishing mortality in the early 1960s seems to have been enhanced by the constant exploitation level while the stock was declining. These two examples suggest that fishing could have amplified the effects of temperature in the case of the Norwegian Spring herring, whereas temperature could have amplified the effect of fishing in the case of the Northeast Arctic cod. Interplays between geographical location, environment and exploitation have already been noted for tuna and tuna-like species (Rouyer *et al.*, 2008a) and question the management of stocks using stable reference points. As suggested by the Norwegian Spring herring case, maintaining an otherwise acceptable level of exploitation during prolonged periods of unfavourable conditions could induce dramatic stock declines.

Our results highlight the spatial and temporal scales as key parameters to understand fish stocks dynamics and emphasize that combined effects of climate and exploitation appear to have substantial effects on the long-term fluctuations of exploited fish stocks. This stresses the importance of studying the dynamics of exploited fish populations within the context of global warming, because over-exploitation has been shown to be related to poor governance, the *common-pool* nature of these resources and the globalization of sea food markets (Garcia and Grainger, 2005; Hilborn *et al.*, 2005; Sethi *et al.*, 2010).

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FIGURE LEGENDS

Figure 1: Recruitment/temperature correlations $r_{(Rec,Temp)}$ against the biomass/temperature correlations $r_{(TotBiom,Temp)}$ (a). Black dots indicate statistical significance of $r_{(Rec,Temp)}$ at the 10% level. Average latitude of the stock against $r_{(TotBiom,Temp)}$ (b). Black dots indicate statistical significance of $r_{(TotBiom,Temp)}$ at the 10% level. Average latitude of the stock against $r_{(Rec,Temp)}$ (c). Black dots indicate statistical significance of $r_{(TotBiom,Temp)}$ at the 10% level. All correlations were Spearman correlation coefficients computed on the raw time series and their significance was assessed using the surrogates method (see Materials and Methods).

Figure 2: Common features in the fluctuations exhibited by the raw total biomass time series and the filtered temperature series for a) the North-east Arctic cod, the Arctic haddock and the Norwegian Spring-Spawning herring stocks and for b) the Irish Sea cod and sole stocks.

Figure 3: Opposite fluctuations in the raw total biomass time series (black line and black circles) and the filtered fishing mortality time series (solid line) for the North-east Arctic cod (a), the Irish Sea cod (b), the Icelandic haddock (c), the Northern hake (d), the Norwegian Spring-Spawning herring (d) and the Arctic saithe (e) stocks.

Figure 4: Histograms of the proportion of years displaying an expected behaviour for the exploitation (Exp.), temperature (temp.) and combined (comb.) effects. The numbers above the bars indicate the

proportion of years displaying an expected behaviour and a black bar indicates that this proportion is significantly higher than found by chance. For each stock this test was realised by computing the proportion of years displaying an expected behaviour for 1000 surrogates time series; a proportion was considered significant when the observed proportion was found higher than for 90% of the surrogates.

Figure 5: Combined effects for a) the North-east Arctic cod (top three panels), b) the Norwegian Spring Spawning herring (bottom three panels). The left panels represent the effect of exploitation, the plain line represents fishing mortality and the grey broken line represents the total biomass. The middle panels depict the effect of temperature, the plain line represents temperature and the grey broken line represents the total biomass. The right panels depict combined effects and the plain line represents the total biomass. Horizontal lines depict the limits between the levels of fishing mortality, temperature and total biomass for the left, middle and right panels, respectively. Years complying with expected cases for fishing mortality, temperature and combined effects are identified with white squares, whereas black diamonds identify unexpected cases.

Figure 6: Standardized time series of biomass for the northernmost and southernmost stocks (plain line white circles and plain line with black squares, respectively) and time series of the average temperature over the North-east Atlantic (grey line). The northernmost and southernmost stocks were selected as the stocks above the 66th percentile and below the 33rd percentile of the distribution of the mean latitude of the stocks, respectively. The time series were computed as the average of the standardized time series of total biomass over the period 1979-2006 and re-standardized. The North-east Atlantic temperature was obtained by averaging over space and years time series extracted between 30°W and 30°E, and 45°N and 80°N. The resulting time series was standardized over 1900-2006.

TABLES

Table 1: Available period of data for the studied stocks, percentage of variance explained by the long-term fluctuations (above 5 years) in the fishing mortality and temperature time series.

Species	Stock	Data period	Variance (%) fishing mortality	Variance (%) temperature
cod	Northeast_Arctic	1913-2006	93.7	52.2
cod	Faroe	1961-2008	61	86.2
cod	Iceland	1955-2009	83.1	81.4
cod	North_Sea	1963-2008	72.5	75.9
cod	West_scotland	1978-2007	51.4	85.7
cod	Irish_Sea	1968-2007	79.4	70.1
cod	Celtic_Sea	1971-2007	74.1	68.3
haddock	Northeast_Arctic	1950-2008	73.7	58.9
haddock	Faroe	1957-2008	86	86.7
haddock	Iceland	1979-2008	74.4	75.9
haddock	North_Sea	1963-2008	82.2	75.9
haddock	West_scotland_a	1978-2007	51.7	84.5
hake	northern	1978-2008	79.9	78.7
herring	North_Sea	1960-2008	82.4	76.2
herring	Northeast_Arctic	1907-2006	83.1	52.2
herring	West_scotland_a	1957-2008	78.7	85.3
plaice	North_Sea	1957-2008	79.8	74.4
plaice	Irish_Sea	1964-2007	83.1	70
plaice	Channel_West	1976-2007	66.4	70.5
saithe	Arctic	1960-2008	93.3	64.5
saithe	Faroe	1961-2008	79.5	86.2
saithe	Iceland	1974-2008	79.4	75.6
saithe	North_Sea	1967-2008	89.9	78.1
sole	North_Sea	1957-2008	87.8	74.4
sole	Irish_Sea	1970-2006	58.9	66.8
sole	Channel_West	1969-2007	82.3	68.3
sole	Celtic_Sea	1971-2007	83.7	67.1

FIGURES

FIGURE 1

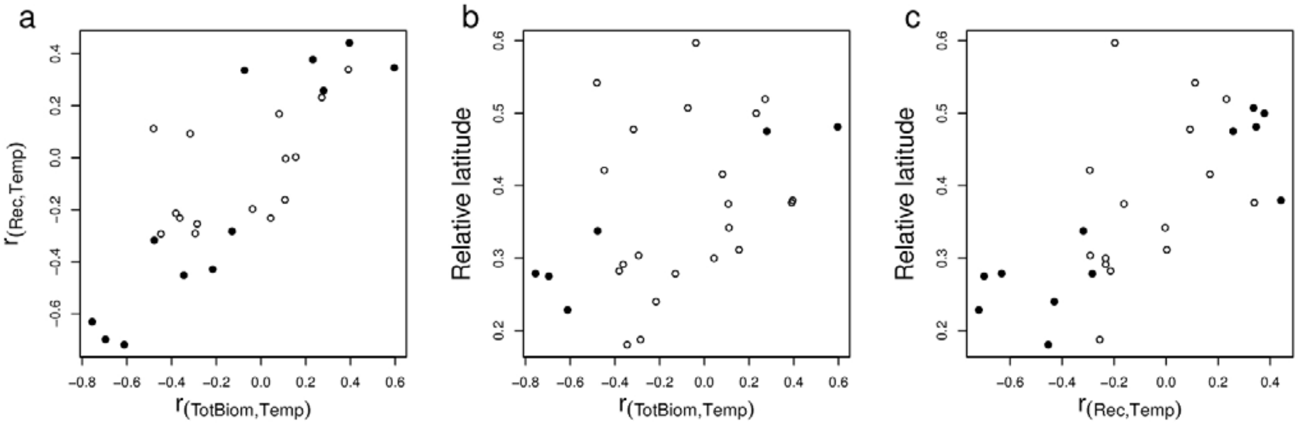


FIGURE 2

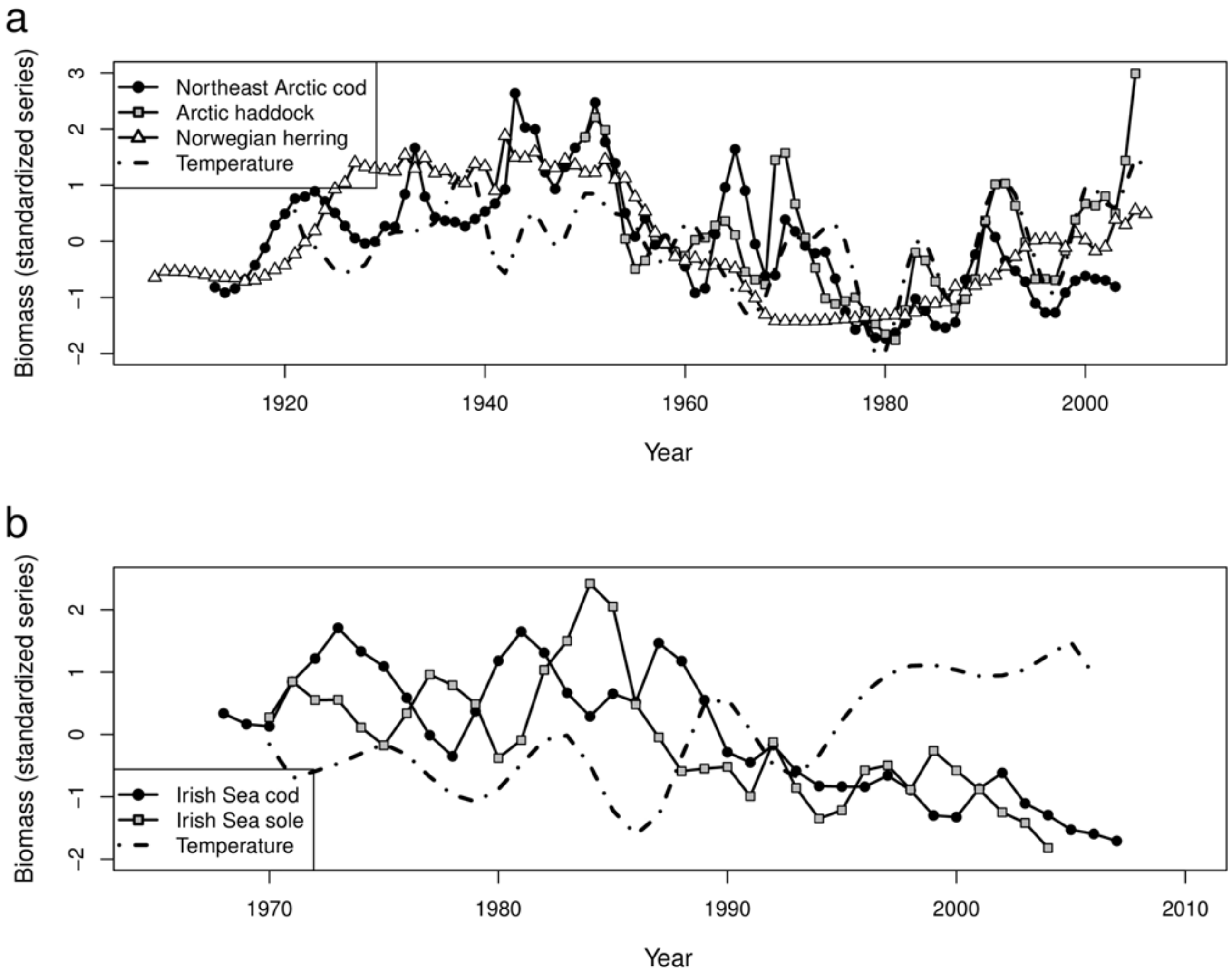

a
Northeast Arctic cod
Arctic haddock
Norwegian herring
Temperature
Biomass (standardized series)
3
2
1
0
−1
−2
1920
1940
1960
1980
2000
Year
b
Irish Sea cod
Irish Sea sole
Temperature
Biomass (standardized series)
2
1
0
−1
−2
1970
1980
1990
2000
2010
Year

FIGURE 3

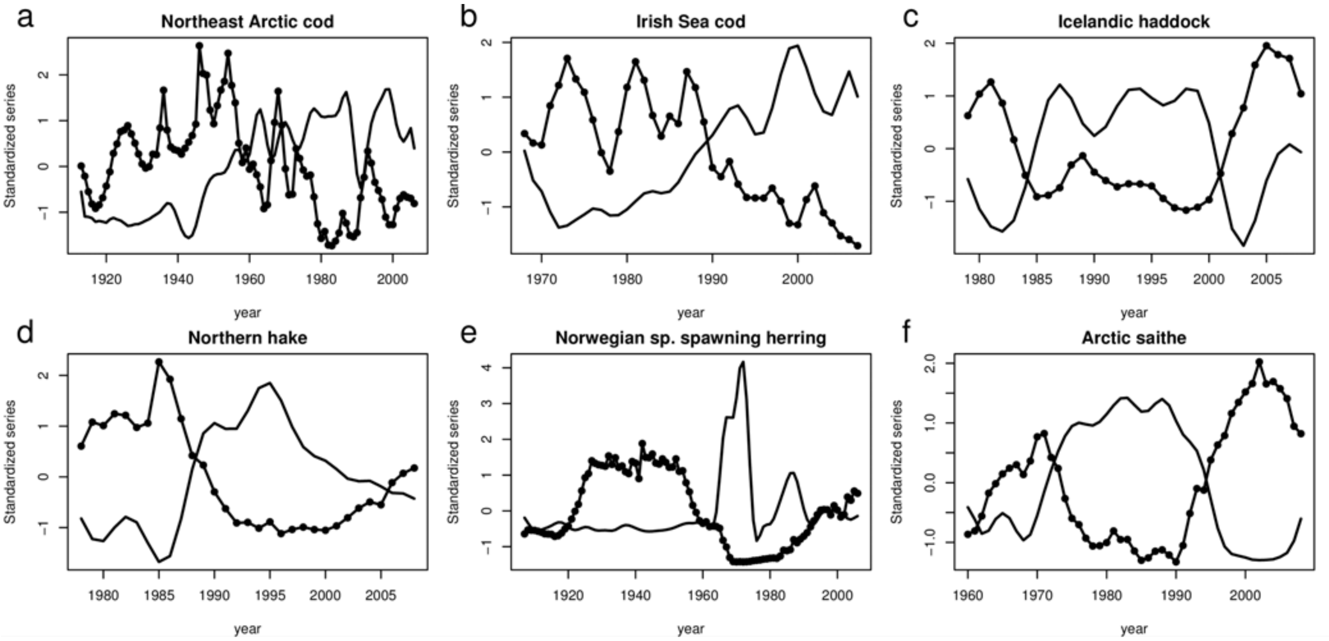

a
Northeast Arctic cod
Standardized series
−1
0
1
2
1920
1940
1960
1980
2000
year
b
Irish Sea cod
Standardized series
−1
0
1
2
1970
1980
1990
2000
year
c
Icelandic haddock
Standardized series
−1
0
1
2
1980
1985
1990
1995
2000
2005
year
d
Northern hake
Standardized series
−1
0
1
2
1980
1985
1990
1995
2000
2005
year
e
Norwegian sp. spawning herring
Standardized series
−1
0
1
2
3
4
1920
1940
1960
1980
2000
year
f
Arctic saithe
Standardized series
−1.0
0.0
1.0
2.0
1960
1970
1980
1990
2000
year

FIGURE 4

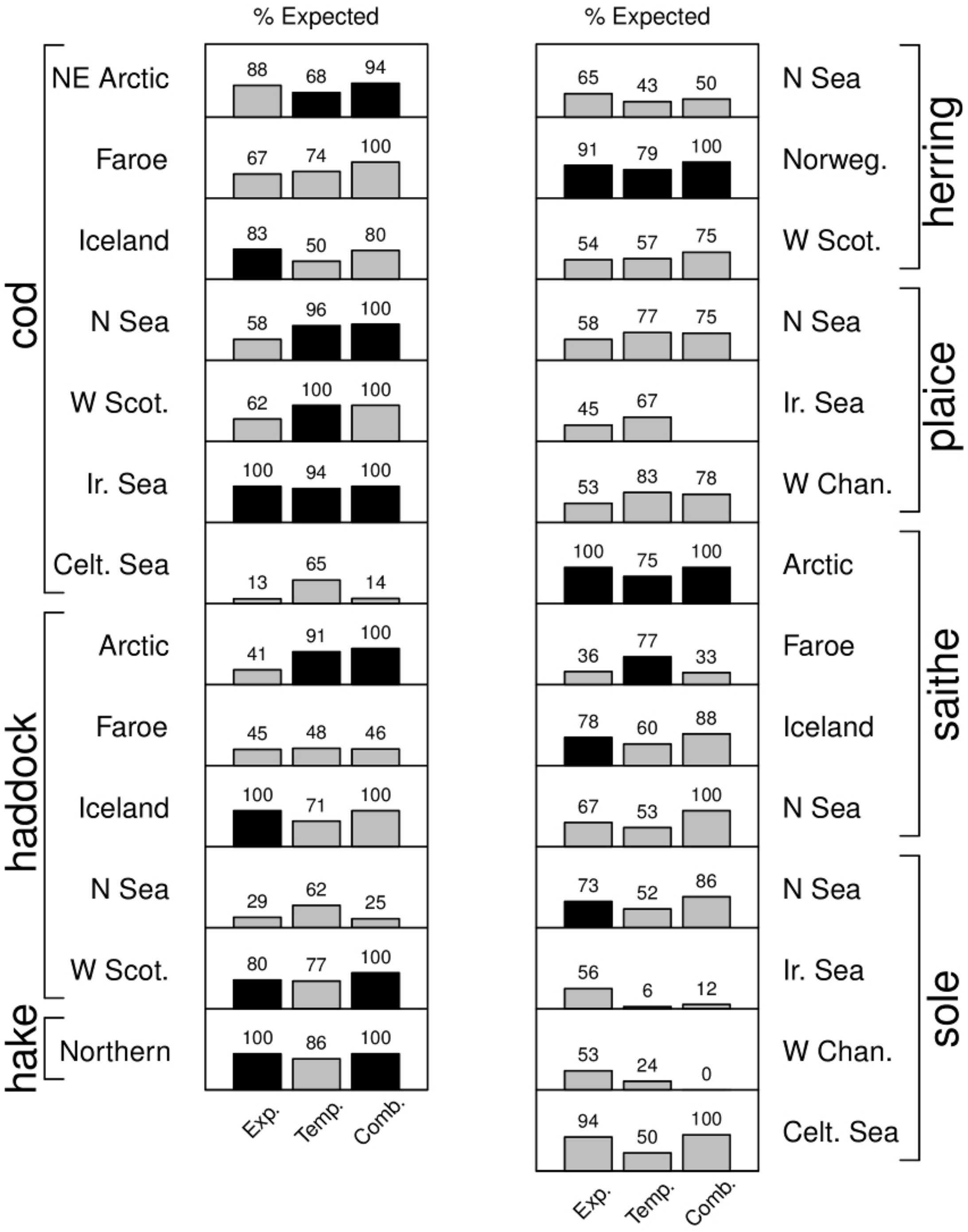
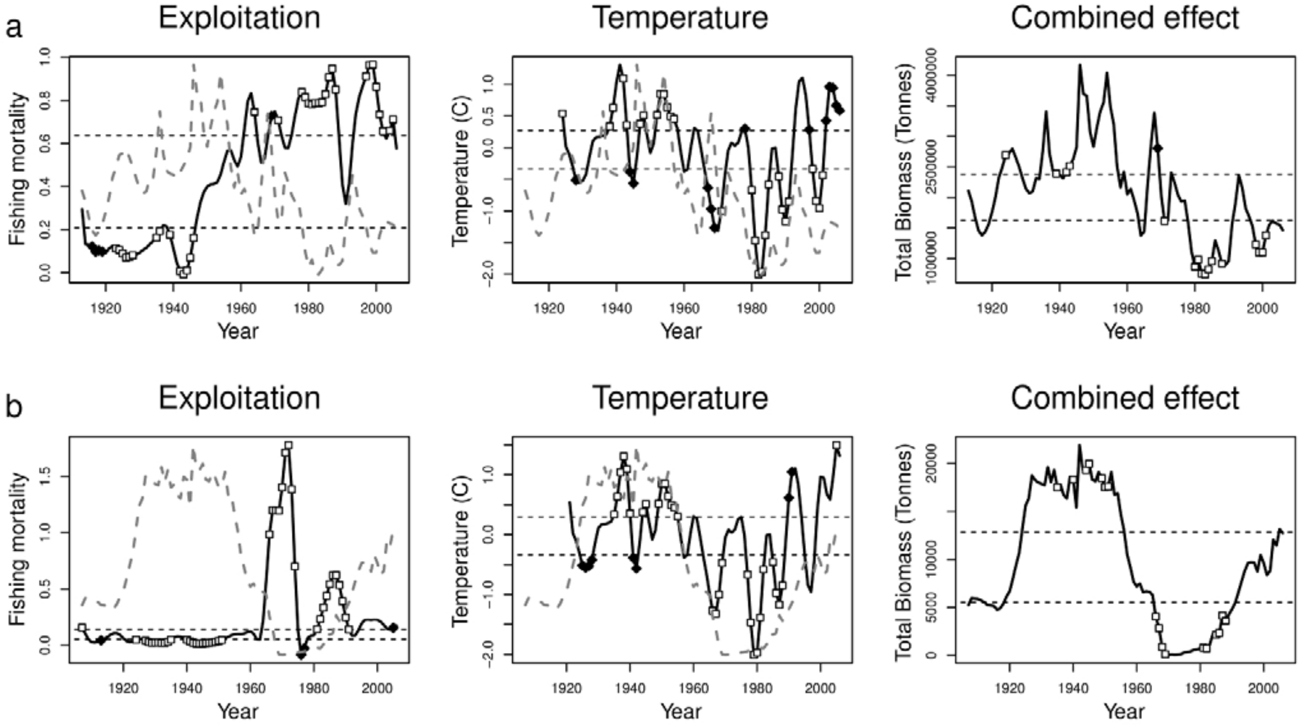
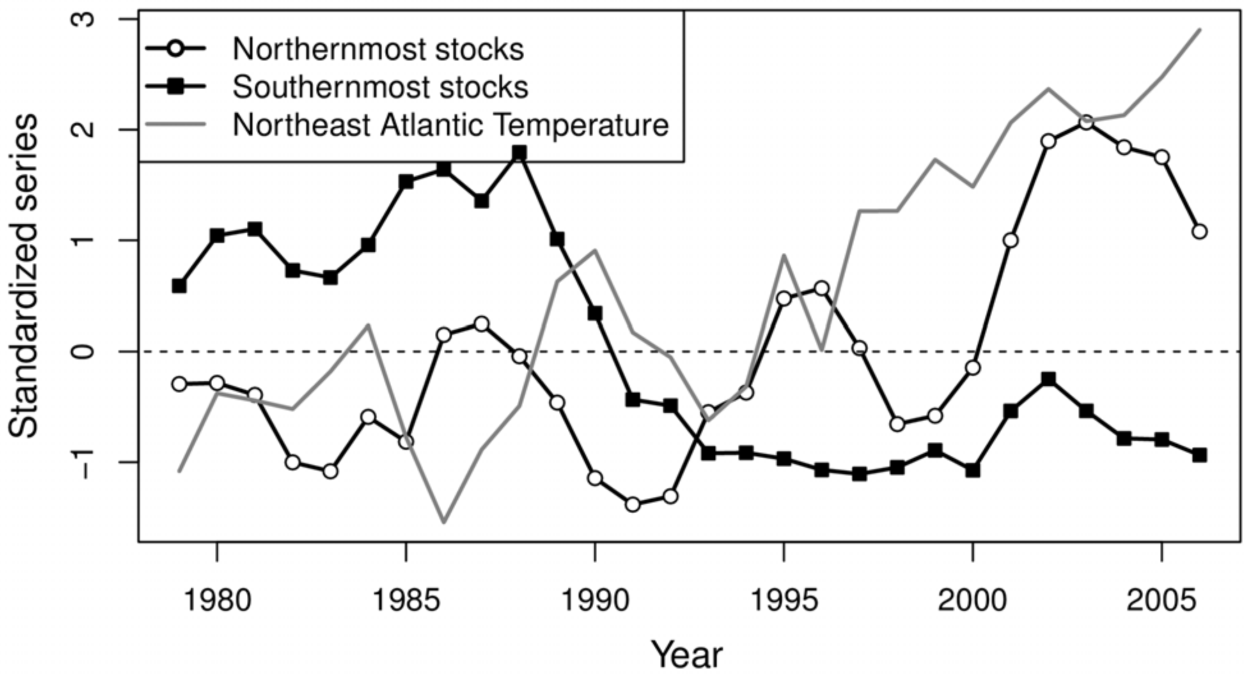

% Expected
% Expected
cod
NE Arctic 88 68 94
Faroe 67 74 100
Iceland 83 50 80
N Sea 58 96 100
W Scot. 62 100 100
Ir. Sea 100 94 100
Celt. Sea 13 65 14
haddock
Arctic 41 91 100
Faroe 45 48 46
Iceland 100 71 100
N Sea 29 62 25
W Scot. 80 77 100
hake
Northern 100 86 100
Exp.
Temp.
Comb.
herring
N Sea 65 43 50
Norweg. 91 79 100
W Scot. 54 57 75
plaice
N Sea 58 77 75
Ir. Sea 45 67
W Chan. 53 83 78
saithe
Arctic 100 75 100
Faroe 36 77 33
Iceland 78 60 88
N Sea 67 53 100
sole
N Sea 73 52 86
Ir. Sea 56 6 12
W Chan. 53 24 0
Celt. Sea 94 50 100
Exp.
Temp.
Comb.

FIGURE 5


a
Exploitation
Fishing mortality
0.0
0.2
0.4
0.6
0.8
1.0
1920
1940
1960
1980
2000
Year
Temperature
Temperature (C)
−2.0
−1.0
0.0
0.5
1.0
Combined effect
Total Biomass (Tonnes)
1000000
2500000
4000000
b
Exploitation
Fishing mortality
0.0
0.5
1.0
1.5
Temperature
Temperature (C)
−2.0
−1.0
0.0
1.0
Combined effect
Total Biomass (Tonnes)
0
5000
10000
20000

439 FIGURE 6



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