



Original Article

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

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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 knowledge of environmental changes was shown to be crucial in understanding the patterns of variations in exploited fish populations (Lehodey *et al.*, 2006; Alheit and Bakun, 2010). Changes in oceanographic variables are predominantly slow and characterized by long-term fluctuations (Halley, 1996; Vasseur and Yodzis, 2004; Rouyer *et al.*, 2010), and they have thus been proposed as a potential force driving the long-term fluctuations in fish stocks (Steele, 1984; Lawton, 1988). Such environmental variations have been used to explain long-term changes in the overall levels 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 affect recruitment strength during the early life stages of fish, which in turn affects the level of the stock as it flows through the age-classes of the population (Hjort, 1914, 1926). Abiotic variations also affect other key biological/ecological processes in wild fish populations, such as growth (Brander, 1995) and migratory behaviour (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 (Nisbet and Gurney, 1993; Johst and Wissel, 1997; Petchey, 2000). Furthermore, 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 aim of an intensive ongoing research effort that has attracted particular interest in the field of fisheries ecology for its implications in conservation and management in the context of global change. The complex nature of these fluctuations has created much debate regarding how they originate from the interplay between deterministic and stochastic forces (Bjørnstad and Grenfell, 2001). In particular, 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 with climate fluctuations can create the conditions for overexploitation of a given stock under an otherwise acceptable fishing effort, because the level of exploitation can no longer be sustained 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 geographical location of the stocks.

Material 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> (last accessed January 2014)]. Among the 40 fish stocks comprising the dataset, 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 intentionally left out of the analyses, as the environmental driver associated with the regime shift that drastically changed their 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 Hylan (2002) for the Northeast Arctic cod and Toresen and Østved (2000) for the Norwegian spring-spawning herring; further details are available in Rouyer *et al.* (2011). These stocks, from nine 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 variation 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 of being more directly linked to temperature than spawning stock biomass, for which a lag equal to the age at maturity has to be taken into account, and which is plagued by two problems. First, age at maturity can substantially vary over time, as observed for some stocks (e.g. Northeast Arctic cod). Second, introducing a lag implies removing as many datapoints as the number of delays introduced, which reduces the length of the time-series.

Table 1. Available period of data for the studied stocks and percentage of variance explained by long-term fluctuations (>5 years) in 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

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 a map of the stock’s 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> (last accessed January 2014)].

Temperature time-series

Temperature time-series were extracted over each stock distribution area from the extended reconstructed sea surface temperature (SST) (NOAA_ERSST_V3) dataset provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at <http://www.esrl.noaa.gov/psd> (last accessed January 2014) and available from 1880–2009. This dataset is constructed using the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST 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 age of recruitment in the age-structured data used to compute the total biomass time-series varied among stocks. Thus, the time-series of temperature were lagged so that the first datapoint 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 >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 (Lau and Weng, 1995; Torrence and Compo, 1998; Cazelles *et al.*, 2008). The wavelet transform decomposes the variability of time-series in both time and frequency and allows for 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 of period <5 years. 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 with 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 (Planque and Frédou, 1999; Brunel and Boucher, 2007). The associations 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 associations between long-term fluctuations in temperature and 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 (Schreiber and Schmitz, 2000; Royer and Fromentin, 2006; Rouyer *et al.*, 2008b). 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 as the original series, but they occur at random times. This technique was then used to generate an empirical distribution for each Spearman correlation coefficient, allowing us 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 linear 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 explains most of the trends in the studied time-series, which can impair the detection of external effects (Pyper and Peterman, 1998). To overcome these limitations, a test was designed using an intuitive yet powerful semi-quantitative method [inspired by 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 (Planque and Frédou, 1999; Brunel and Boucher, 2007), 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” with the number of years following the “unexpected behaviour”. The “expected” and “unexpected” behaviours were defined as follows. For exploitation, 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, 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, expected behaviour was a high total biomass with a favourable temperature, or a low total biomass with an unfavourable temperature. Unexpected behaviour was thus defined as a low total biomass with a favourable temperature, or a high biomass with an unfavourable temperature. Finally, 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. 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 conforming 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 of belonging 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 us 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 $C = 0.81$, $p < 0.0001$, Figure 1a). Stocks for which a weak association

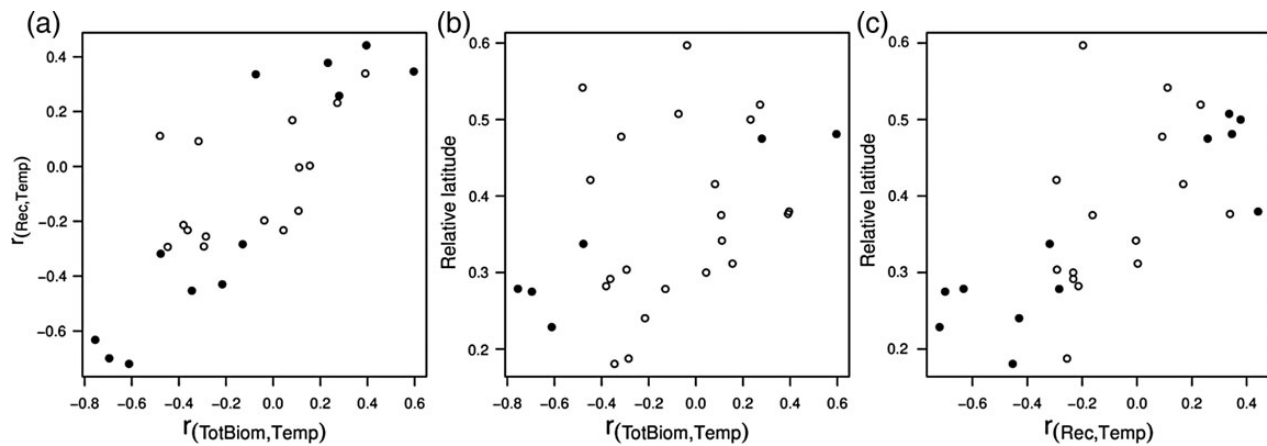


Figure 1. Recruitment/temperature correlations $r_{(Rec,Temp)}$ against the biomass/temperature correlations $r_{(TotBiom,Temp)}$. (a) Black dots indicate statistical significance of $r_{(Rec,Temp)}$ at the 10% level. Average latitude of the stock against $r_{(TotBiom,Temp)}$ (b). Black dots indicate 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 *Material and methods*).

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 (six stocks). The association between total biomass and temperature was found variable in sign and intensity over the species' latitudinal range (Figure 1b), as was also the case for the association between recruitment and temperature (Figure 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 with the mean latitude of the stock's geographical location (Pearson correlation coefficient $C = 0.44$, $p = 0.02$, Figure 1b, and Pearson correlation coefficient $C = 0.68$, $p < 0.0001$, Figure 1c, respectively).

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 Northeast Arctic cod, the Arctic haddock and the Norwegian spring-spawning herring, all of which displayed common periods of low and high biomass consistent with the long-term fluctuations in temperature at the Kola section (Figure 2a). Likewise, the more southern Irish Sea cod and sole stocks both displayed common long-term fluctuations consistent with their negative relationship to temperature (Figure 2b).

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 (Figure 3). This illustrated the difficulty of disentangling the relative effects of temperature and fishing mortality on total biomass, as both variables seemed to have substantial effects on the stocks.

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 in temperature and fishing mortality were obtained by filtering the time-series above a 5-year threshold (Table 1). The raw time-series of both fishing mortality and temperature were dominated by long-term fluctuations, which explained from 51.4–93.7% of the total variance for fishing mortality (77% on average) and from 52.2–86.7% of the total variance for temperature (73.7% on average, Table 1).

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 eight stocks, whereas nine stocks displayed a significant effect associated with exploitation (Figure 4). In contrast, although the pool of points with a combined effect was smaller in comparison, the percentage of expected events found was higher (79%) than for exploitation or temperature alone. Among 27 stocks, eight were found to display significant combined effects from temperature and exploitation (Figure 4). For five stocks, the proportion of expected combined effects was found to be 100%, however, the effect was not significant (Faroe cod, West Scotland cod, Icelandic haddock, North Sea saithe and Celtic sole, Figure 4). This was due to the small number of points with a combined effect (≤ 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 associated with exploitation and/or temperature. Therefore, the geographical location of stocks appeared to be important, as stocks in the southernmost and northernmost latitudes, which displayed higher correlations with temperature, were thus more prone to undergo stronger combined effects.

A couple of examples from the northernmost latitudes provided a clear illustration of periods with combined effects, albeit with slight differences (Figure 5). For instance, the Northeast Arctic cod has been fully exploited to overexploited since the late 1950s,

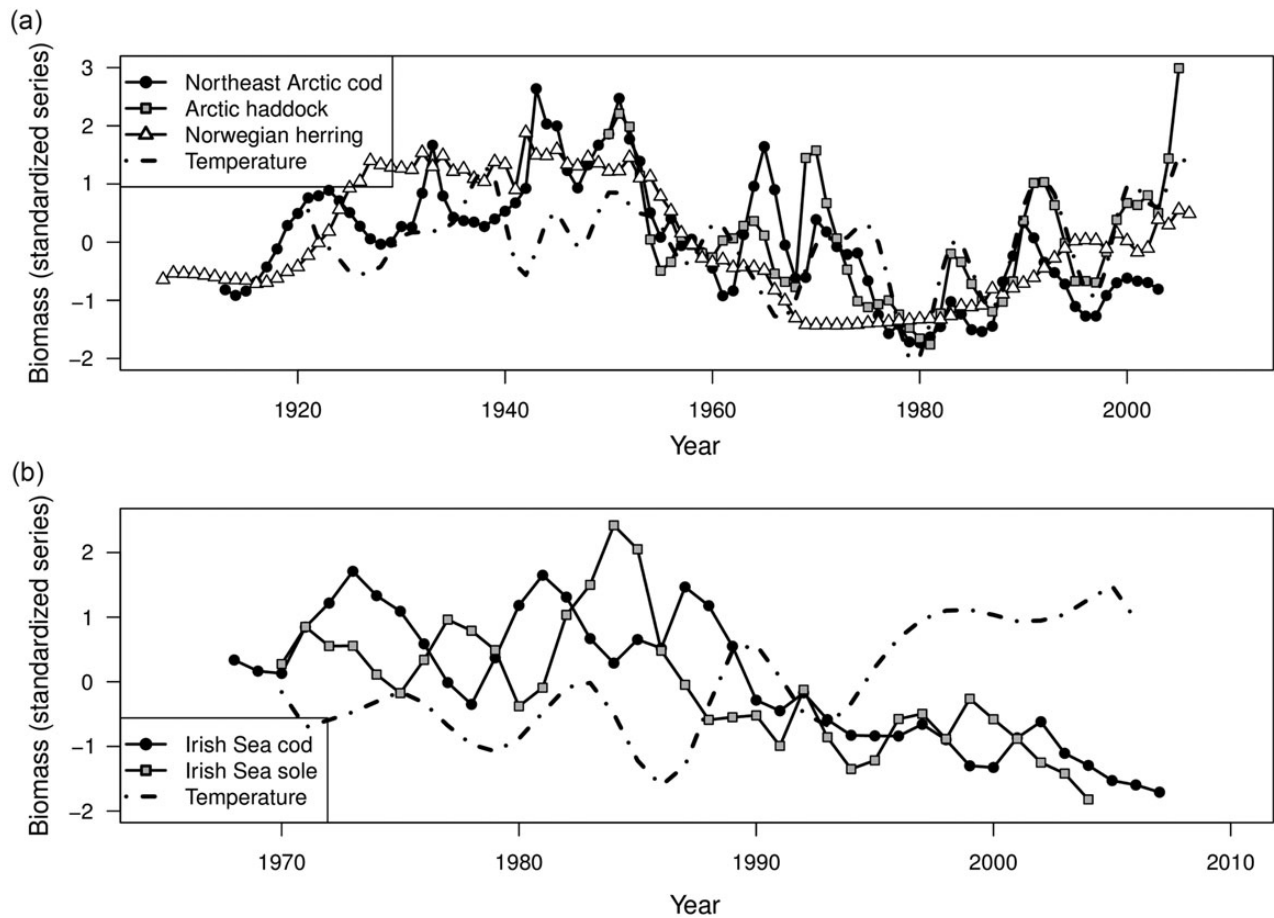


Figure 2. Common features in the fluctuations exhibited by the raw total biomass time-series and the filtered temperature series for (a) the Northeast Arctic cod, the Arctic haddock and the Norwegian spring-spawning herring stocks, and for (b) the Irish Sea cod and sole stocks.

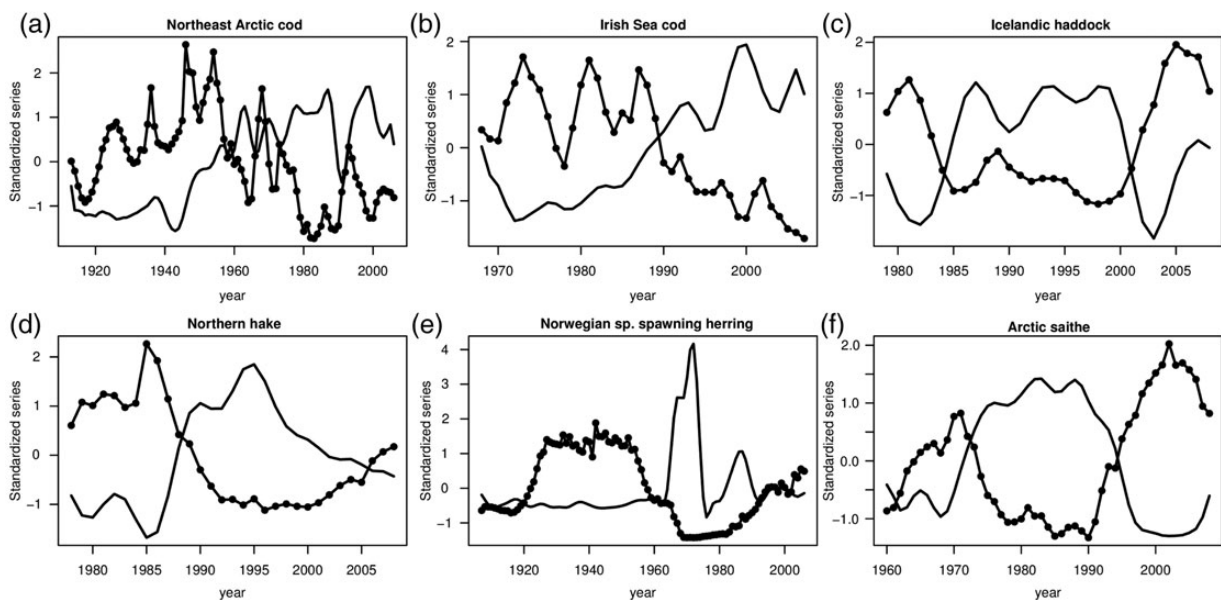


Figure 3. Opposite fluctuations in the raw total biomass time-series (black line and black circles) and the filtered fishing mortality time-series (solid line) for the Northeast Arctic cod (a), the Irish Sea cod (b), the Icelandic haddock (c), the Northern hake (d), the Norwegian spring-spawning herring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

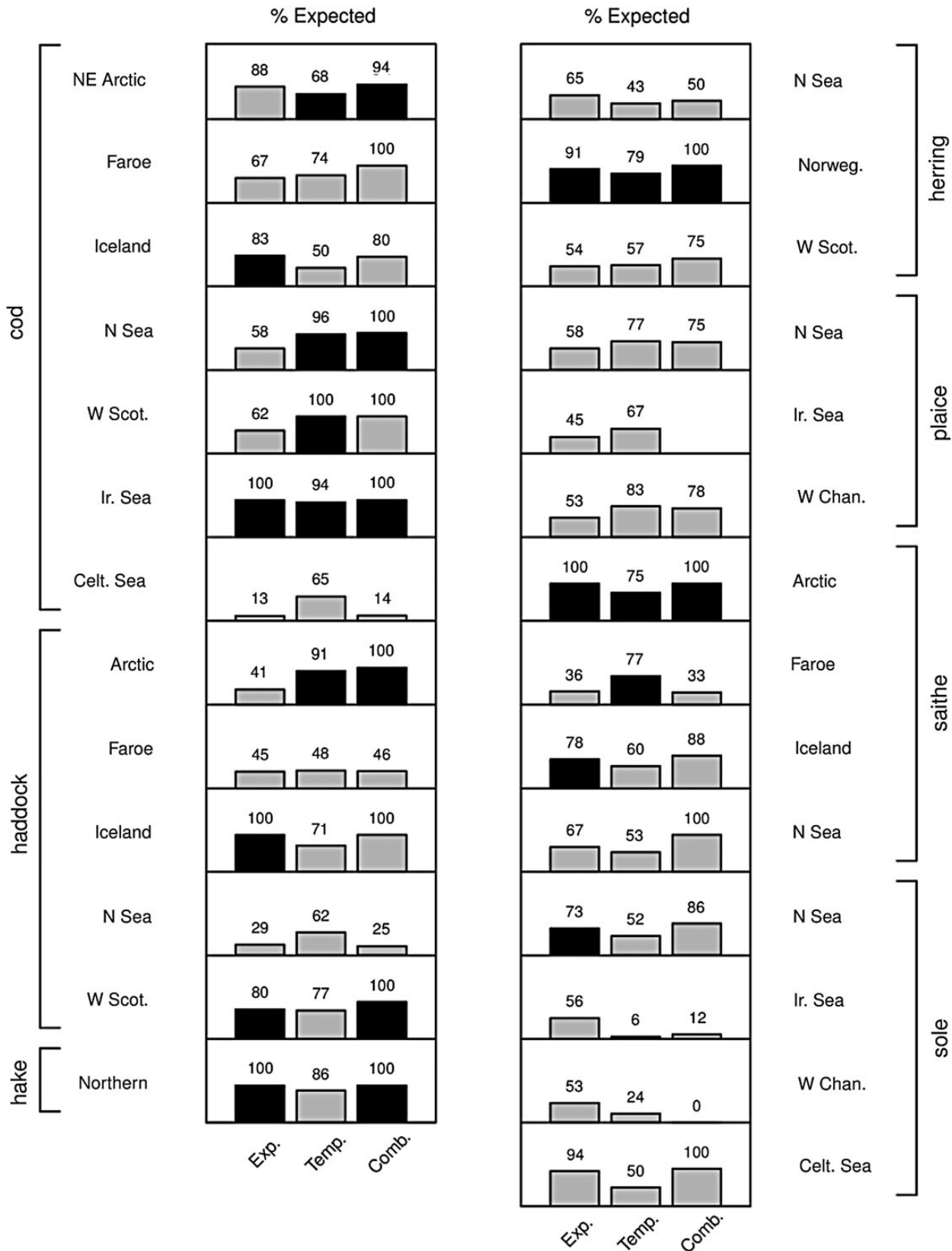


Figure 4. Histograms of the proportion of years displaying an expected behaviour for the exploitation (Exp.), temperature (temp.) and combined (comb.) effects. The numbers above the bars indicate the proportion of years displaying an expected behaviour, and a black bar indicates that this proportion is significantly higher than found by chance. For each stock this test was realized by computing the proportion of years displaying an expected behaviour for a 1000 surrogates time-series; a proportion was considered significant when the observed proportion was found to be >90% of the surrogates.

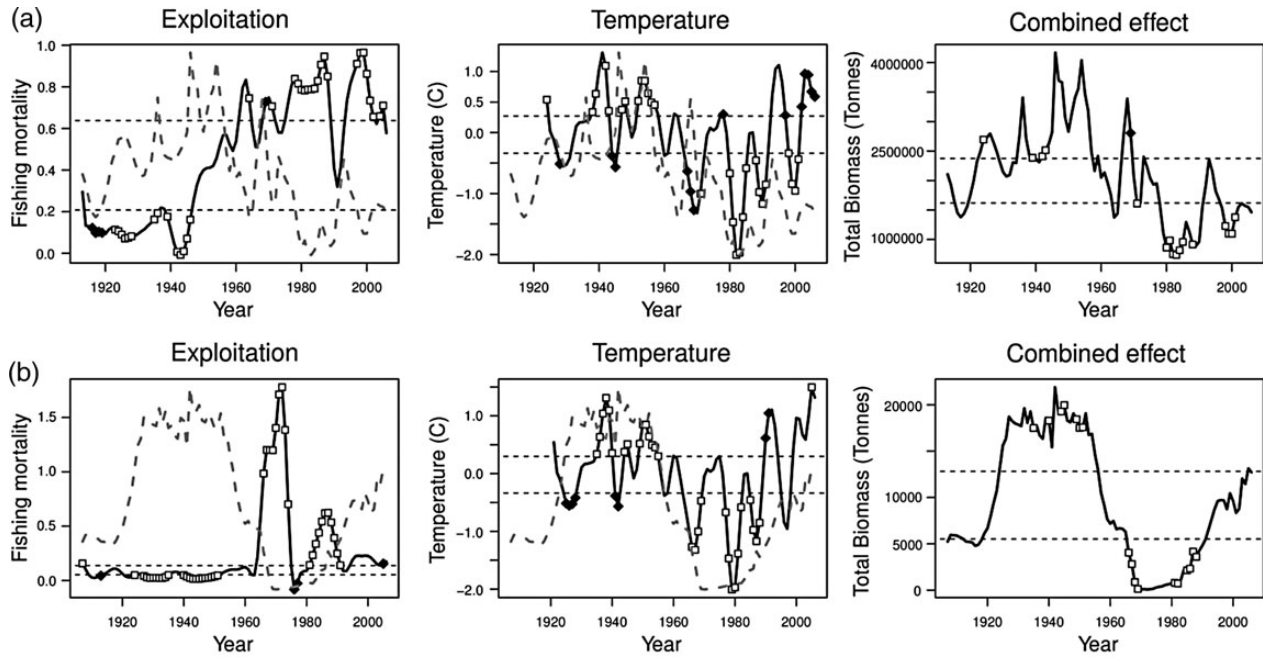


Figure 5. Combined effects for (a) the Northeast Arctic cod (top three panels), and (b) the Norwegian spring-spawning herring (bottom three panels). The left panels represent the effect of exploitation, the plain line represents fishing mortality, and the grey broken line represents the total biomass. 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; 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.

but the total biomass remained at relatively high levels till it mostly dropped during the mid-1970s and mid-1980s, when the temperature decreased and possibly drove the recruitment to low levels (Figure 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 with consecutive years of poor recruitment. The later rebuilding of this population corresponded to favourable temperature while fishing mortality remained at average levels (Figure 5b).

Discussion

Long-term effects of climate on recruitment have already been documented for a large number of commercial stocks from the Northeast Atlantic (Beaugrand *et al.*, 2003; Brunel and Boucher, 2007) and are likely to be associated with 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 with fluctuations in recruitment and total biomass with a comparable sign and intensity (Figure 1a) and that those associations varied with the latitudinal location of the stocks (Figure 1b and 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

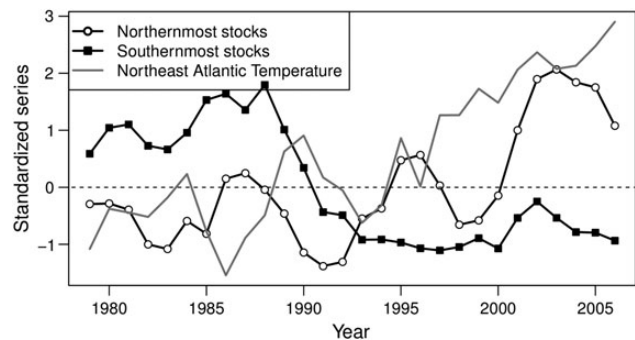


Figure 6. Standardized time-series of biomass for the northernmost and southernmost stocks (plain line with white circles and plain line with black squares, respectively) and a time-series of the average temperature over the Northeast Atlantic (grey line). The northernmost and southernmost stocks were 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 restandardized. The Northeast 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.

opposed between the northernmost and southernmost stocks. Even though the present dataset 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 (Figure 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 (Figure 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 rise of the SST over the Northeast Atlantic during the past 30 years could have had contrasting effects on the productivity of northern and southern fish stock. Averaging the standardized biomass time-series of the northernmost and southernmost stocks illustrated this (Figure 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 (Figure 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, but also because our dataset does not cover the total species' distribution.

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 8–100%. Furthermore, 70% of the stocks displayed >50% of years above the fishing mortality of the precautionary approach, illustrating the general state of overexploitation of the Northeast 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 that 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 (Figure 5). This underlines the importance of past levels in defining baselines and assessing the current state of stocks. Finally, it has to be noted that our results were based upon the analysis of SST in the Northeast 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 to 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 impact 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 to be stock-specific, as stocks from common areas seemed to have been affected differently. For instance, the decline of the Northeast Arctic cod seemed to be primarily due to a long period of overfishing, enhanced by a period of unfavourable temperatures that induced poor recruitment and drove the whole stock to its lowest level. The collapse of the Norwegian spring-spawning herring stock in the 1970s seemed to correspond with 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-spawning 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 challenge the practice of management of stocks using stable reference points. As suggested by the Norwegian spring-spawning herring case, maintaining an otherwise acceptable level of exploitation during prolonged periods of unfavourable conditions could induce dramatic stock declines.

Our results highlight the use of spatial and temporal scales as key parameters in understanding 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 overexploitation has been shown to be related to poor governance, the common-pool nature of these resources, and the globalization of seafood markets (Garcia and Grainger, 2005; Hilborn *et al.*, 2005; Sethi *et al.*, 2010).

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