



Influences of large- and regional-scale climate on fish recruitment in the Skagerrak–Kattegat over the last century



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ABSTRACT

Dynamics of commercial fish stocks are generally associated with fishing pressure and climate variability. Due to short time series, past studies of the relationships between fish stock dynamics and climate have mainly been restricted to the last few decades. Here we analyzed a century-long time series of plaice, cod and haddock from the Skagerrak–Kattegat, to assess the long-term influence of climate on recruitment. Recruitment success (R_s) was compared against sea-surface temperature (SST) and atmospheric circulation indices on large (North Atlantic) and regional (Skagerrak–Kattegat) scales. Our results show that the influence of climate on R_s was more pronounced on longer, than on shorter timescales. Over the century-long period, a shift from low to high climate sensitivity was seen from the early to the late part for plaice and cod, while the opposite was found for haddock. This shift suggests that the increasing fishing pressure and the climate change in the Skagerrak–Kattegat have resulted in an increased sensitivity of R_s to climate for plaice and cod. The diminishing of climate sensitivity in haddock R_s , on the other hand, may be linked to the early twentieth century collapse of the stock in the region. While no long-term relationship between R_s and the Atlantic Multidecadal Oscillation (AMO) could be found, large R_s fluctuations during the positive phase of the AMO (1935–1960), relative to the cold phases, suggests a changed pattern in recruitment during warm periods. On the other hand, this could be due to the increased fishing pressure in the area. Thus, reported correlations between climate and fish may be caused by strong trends in climate in the late-twentieth century, and coincident reduction in fish stocks caused by intense fishing, rather than a stable relationship between climate and fish recruitment per se.

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1. Introduction

Since the industrialization of fisheries at the end of the nineteenth century, fish stocks have been largely exploited worldwide (Myers and Worm, 2003). In the North Eastern Atlantic, several cod stocks have strongly declined in the last decades due to high fishing pressure (Sparholt et al., 2007). In some cases, such as the coastal aggregations of cod in the Kattegat, exploitation has driven them to the verge of extinction (Bartolino et al., 2012; Svedäng and Bardon, 2003; Svedäng et al., 2010). Nevertheless, marine ecosystems also change naturally in a variety of time scales, from seasonal to centennial and longer, as a response to climate variability (Lehodey et al., 2006). Thus, in order to assess the human impact on the temporal fluctuation of commercially exploited species, their response to changing natural environment and climate must be understood. However, it is difficult to determine how

much of the recent population variability is due to fishing pressure and how much is instead a response to climate and environmental change (e.g. Cardinale et al., 2008; ICES, 2010). Understanding the link between fish recruitment and climate variability is crucial for the management of marine ecosystems, and for the economical perspective of having sustainable fisheries.

Temperature is one of the most important environmental variables associated with marine life and its variability. Temperature has an impact on marine productivity in general (e.g. Behrenfeld et al., 2006), and it affects multiple processes that regulate fish populations. The direct implication of temperature on the survival of early life stages (Genner et al., 2009), on growth (Brander, 1995) and maturity and time of spawning (Page and Frank, 1989) has been demonstrated (Ottersen et al., 2001; Sundby, 2000). Recent studies have proposed recruitment success as a key process for understanding the effects of climate variability on fish populations (Stige et al., 2006), because it integrates the effects of environmental changes on the productivity and survival of the early life stages (i.e. eggs and larvae) and on the quality and extension of nursery habitats (Rijnsdorp et al., 2009). Recruitment

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in fish stocks located at the latitudinal limits of the species distribution appears to be more influenced by temperature (Brunel and Boucher, 2006; Grebmeier et al., 2006; Leggett and Frank, 1997; O'Brien et al., 2000; Philippart et al., 1998). Thus, increasing temperatures can be favorable for stocks at the northern limit of their distribution, but may be detrimental for those at the southern limit (Brunel and Boucher, 2007; Mantzouni et al., 2010; Planque and Frédou, 1999; Righton et al., 2010).

However, since the driving mechanisms behind fluctuations in fish populations are a multifaceted mix of climatic and biological factors, where fishing adds complexity to the impact of these factors, it can be difficult, if not impossible, to disentangle the effect of single environmental variables on fish stock fluctuations. In this context, large-scale integrative climate features, such as the atmospheric circulation or basin-wide sea-surface temperature (SST) variability, may provide valuable insight into the complex climate–fish associations. It is well established that the atmospheric circulation over the North Atlantic region, defined as the North Atlantic Oscillation (NAO), has a significant impact on regional climate, e.g. temperature, precipitation, storms and cloudiness, (Chen and Hellström, 1999; Folland et al., 2009; Hurrell et al., 2003), and from a marine ecosystem point of view, the NAO induces variations not only in temperature but also in salinity, vertical mixing, circulation patterns and ice formation of the North Atlantic Ocean (Visbeck et al., 2003). Consequently, late-twentieth century changes in marine ecosystems have been related to the NAO (e.g. Ottersen et al., 2006; Rosenzweig et al., 2007; Stige et al., 2006).

Regarding large-scale SST variations, several studies in recent years have suggested effects of relatively long-term (decadal-to-multidecadal) changes in ocean temperatures on fish abundance and recruitment, such

as the Atlantic Multidecadal Oscillation (AMO) (Condon et al., 2005; Gröger et al., 2010; Nye et al., 2011) or the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997), where the long-term SST fluctuations are associated with shifts in the limits of distribution of different species. Naturally, these “oscillations” in the ocean and the atmosphere cannot be regarded as independent influences on ecosystems, since they are strongly influenced by each other.

In this paper, a hundred year-long time series of fish-survey data is used to investigate the association between fish recruitment and atmospheric circulation and SST variability in the Skagerrak–Kattegat region of the eastern North Sea. Our aim is to assess the relative importance of the chosen climate variables on the recruitment of three commercially important fish species, European plaice (*Pleuronectes platessa*), haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*), during 1904–2004. Given the large temporal coverage, we could investigate changes in the association between recruitment and climate along with global warming and increasing fishing pressure, as well as the influence of climate on two different temporal scales; decadal and inter-annual. Moreover, by using climate indices representing different spatial scales, the importance of large and regional-scale influences on recruitment success was evaluated.

2. Material and methods

2.1. Study area

The Skagerrak–Kattegat is an area of transition between the North Sea and the Baltic Sea (Fig. 1). The region is influenced by the inflow from the Atlantic Ocean and the large-scale atmospheric circulation, where the westerly winds have a strong effect on water transport and distribution, vertical mixing and surface heat flux, all which are important for marine productivity, recruitment, growth and distribution of fish stocks (Svendsen et al., 1995). The Skagerrak basin is rather deep (average depth 210 m) and it is considerably deeper than adjacent parts of both the North Sea and the Kattegat, with the largest portion of the water body of Atlantic origin (Gustafsson, 1999). Under normal conditions water of higher salinity from the North Sea flows near the bottom into the Skagerrak while water from the Baltic Sea of lower salinity flows in the opposite direction in the surface layers (Alheit and Hagen, 1997). The relative proportions of North Sea and Baltic Sea water fluctuates widely depending on the water level in the Baltic Sea, wind direction and wind stress (Gustafsson and Andersson, 2001; Gustafsson and Stigebrandt, 1996).

2.2. Fish data

A database was established by compiling all known archived otter trawl surveys carried out in the Kattegat–Skagerrak (Fig. 1) from 1904 to 2007 by the Institute of Marine Research, Sweden, and its predecessors. Trawl station information included date, haul duration, towing speed and gear opening (i.e. to compute the swept area), setting and hauling position (latitude and longitude; prior to the use of a Geographical Position System those were reconstructed from detailed fishing area information included in the archived haul information) and depth (meters). Hauls used in the analysis were conducted exclusively during daylight hours. For each haul, number of individuals caught and fish total length (cm) were recorded for plaice, cod and haddock. For each haul, we calculated the density in number of small fish ($n \cdot km^{-2}$) and the density in biomass of large fish ($kg \cdot km^{-2}$) as local estimates of recruitment (R) and spawning stock biomass (SSB), respectively. Recruits were individuals between 20 and 30 cm for cod and haddock (mostly individuals aged 1 year) and 16 and 20 cm for plaice (individuals 1 and 2 years old). SSB was represented by individuals larger than the size at which 50% of fish in the population are mature (i.e., 40 cm for cod, 35 cm for haddock, 25 cm for plaice), and converting numbers

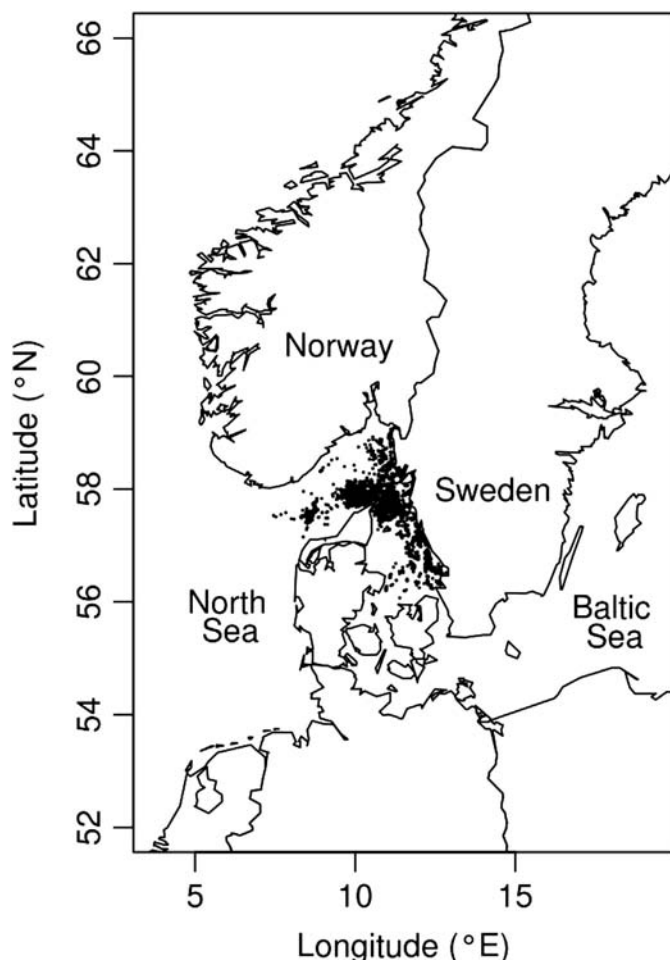


Fig. 1. Map of the Skagerrak–Kattegat, with the location of fish survey points.

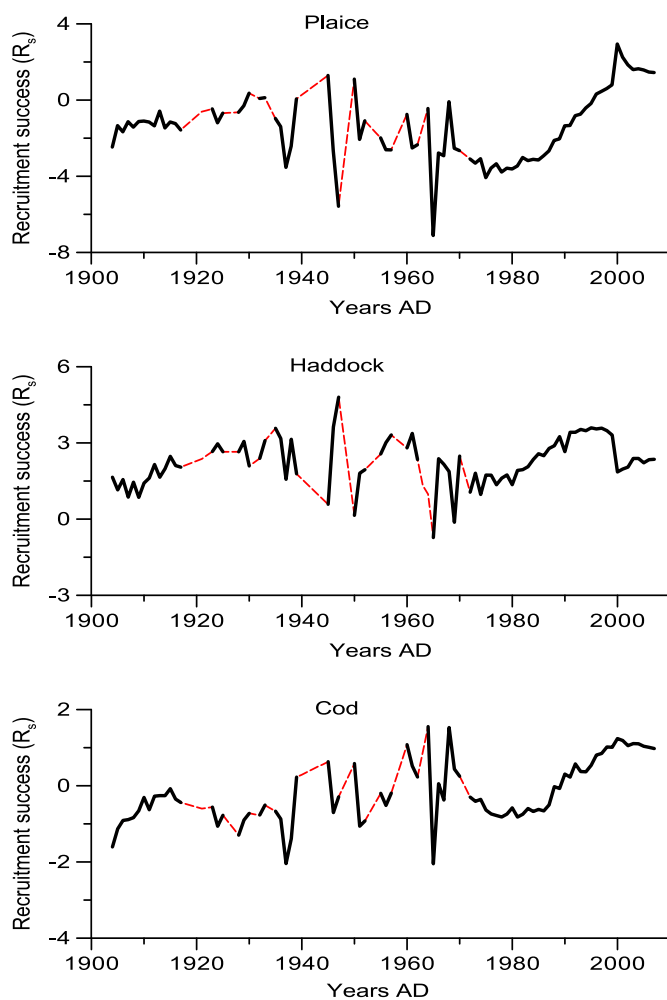


Fig. 2. Recruitment success (R_s) time series for a) plaice; b) haddock and c) cod. The dotted red lines shows the interpolated values of R_s for all species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

into biomasses using a length–weight power relationship (weight = $a \cdot \text{length}^b$) (see Cardinale et al., 2009, 2012 for details).

A generalized additive model (GAM, Hastie and Tibshirani, 1990) was used to standardize R and SSB to account for differences in month, geographical position, and depth of the sampling among years (see Maunder and Punt, 2004 for a useful review of different standardization approaches). Hence, standardized estimates of annual R and SSB were derived from the model for each species, and used to calculate the logarithm of their recruitment success, i.e. the ratio between R and SSB (R_s ; Cardinale and Hjelm, 2006; Stige et al., 2006). R_s is a measure of the number of recruits produced by a unit biomass of spawners, hence it is independent from the size of the adult population. This is particularly relevant for the long time frame of our analysis, during which the size of the adult populations of the three species investigated has certainly experienced wide variations. Because of the targeting behavior of the fisheries mainly directed towards adult fish, fisheries exploitation has a direct impact on the SSB. For this reason the use of R_s instead of R is a way to account for the major effect of fishing on the recruitment variability via reduction of the reproductive portion of the stock. Moreover, the use of biomass for standardizing recruitment on the size of the reproductive component, has also the potentiality to account for the size selectivity of the fishery and the consequent size truncation in the adult fish populations that has been related to intense fishing exploitation in the area (Cardinale et al., 2012). The R_s time series are shown in Fig. 2. For more details on sampling and standardization procedures, see

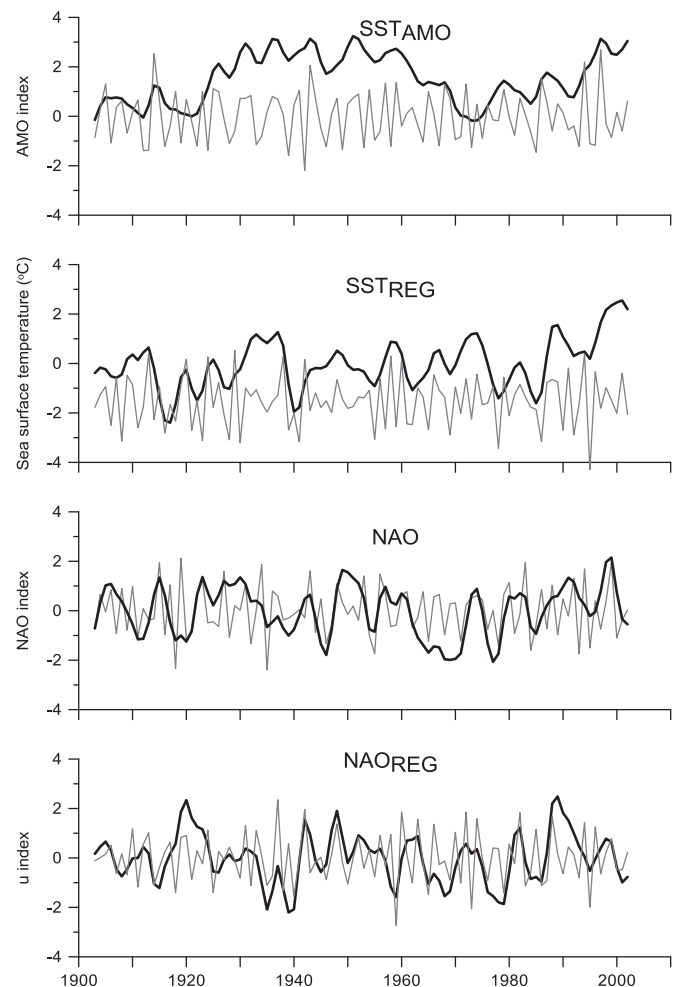


Fig. 3. Normalized annual average time series of the climate indices used in the study: a) SST_{AMO}; b) SST_{REG}; c) NAO and d) NAO_{REG}. Thick black lines represent low-pass filtered data, thin gray high-pass filtered data. See text for sources of data.

the Appendix and supplementary materials in Cardinale et al. (2009, 2010). Recruitment time series of plaice and of SSB for cod, haddock and plaice have been recently published (Bartolino et al., 2012; Cardinale et al., 2010, 2012) and the reader is referred to these publications for further details.

2.3. Climate data

To assess the long-term effect of climate on R_s , we chose two variables, sea-surface temperature (SST) and the NAO index, which have been linked with fish variability previously (e.g. Buch et al., 2005; Drinkwater, 2005; Lehodey et al., 2006; Ottersen et al., 2001; Wegner et al., 2003). To assess the influence of scale, we used both large-scale (North Atlantic Ocean) and regional (Skagerrak–Kattegat) climate indices. An annual AMO index, which represents multidecadal variability of SST in the North Atlantic, was chosen to represent large-scale SST variability. The AMO has been shown to influence temperatures and rainfall over much of the Northern Hemisphere, particularly in North America and Europe (Knight et al., 2006; Sutton and Hodson, 2005). When the AMO is in its positive (warm) phase, summers in North Western Europe are milder and wetter, while the opposite is true for the negative (cold) phase of the AMO (Folland et al., 2009). The AMO index was calculated from the Kaplan SST dataset (Kaplan et al., 1998), and is henceforth referred to as SST_{AMO}. The index (Fig. 3a), was obtained from the NOAA Earth System Laboratory webpage (<http://www.cdc.noaa.gov/data/timeseries/AMO/>). The AMO time series is usually

computed as the area weighted average of SST over the North Atlantic from 0° to 70°N which is then detrended to remove the effects of global warming (e.g. Enfield et al., 2001). To highlight the low frequency variability, the AMO index is usually smoothed, but here we used the unfiltered version of the index. More details about the AMO index can be found in Enfield et al. (2001).

Data from the gridded Hadley Centre SST data set (HadSST2), obtained from <http://hadobs.metoffice.com/hadsst2/>, was used to create a regional SST index. The HadSST2 dataset is based on quality checked in-situ measurements, where calculated monthly anomalies are averaged on a 5° by 5° grid. After gridding the anomalies, bias corrections are applied to remove spurious trends caused by changes in measuring practices before 1942. For more detailed description of the dataset, the reader should refer to Rayner et al. (2006). In this study we utilized SST data from 5 to 15°E and 55 to 60°N covering the region where the fish data were collected. Regional SST (Fig. 3b) is henceforth referred to as SST_{REG}.

The NAO index can be defined as either the pressure difference between two stations (e.g. at the Azores and Iceland), or the leading mode of sea level pressure (SLP) over the North Atlantic (Hurrell et al., 2003). The nodes of the NAO shifts spatially over time (Allan and Ansell, 2006), so using empirical orthogonal functions (EOF) to define the NAO may be more appropriate (Hurrell et al., 2003). We used a NAO index defined as the principal component (PC) time series of the leading EOF of the mean sea level pressure (MSLP) in the Atlantic Sector (20°N–70°N and 90°W–40°E) calculated over the period 1880–2007. The MSLP data are taken from the EMLP data set (Ansell et al., 2006) and extended with data from the National Center for Environmental Prediction (NCEP) up to 2007 (Kanamitsu et al., 2002) (Fig. 3c).

To interpret climate-related processes in regional ecosystems, circulation indices calculated over smaller regions may be more appropriate than using large-scale ones (Blenckner and Chen, 2003). Here we used a set of regional circulation indices for Scandinavia based on a 5° latitude × 10° longitude grid-point dataset for the Northern Hemisphere developed by Chen (2000). This set contains a range of variables, like geostrophic vorticity and wind speed, related to the atmospheric circulation, but we only used the westerly (zonal) component of the wind as a regional (as opposed to the entire North Atlantic region) version of the NAO and refer to it as NAO_{REG}. Although very similar to the NAO, the regional circulation index has been shown to be more strongly associated with regional climate than its large-scale counterpart (e.g. Blenckner and Chen, 2003). The indices we used were calculated for the area 10°–20°E and 55°–65°N. From 1904 to 1995 the indices were based on MSLP data from the ADVICE project (Jones et al., 1999), and after 1995 on NCEP data (Kanamitsu et al., 2002) (Fig. 3d).

2.4. Climate–fish analyses

Unfortunately, there are some gaps in the fish data, associated e.g. with the two World Wars. Thus, the fish data series contain 21 (22 for haddock) years of missing data: 1918–1920; 1922; 1926–1927; 1931; 1934; 1940–1944; 1948–1949; 1953–1954; 1958–1959; 1963; 1964 (only haddock) and 1971. However, to have continuous time series to facilitate the analyses, missing data in the time-series were linearly interpolated, irrespective of how many years of missing values were present. This shortcoming should be kept in mind when interpreting the results. We made statistical analyses over the full period, but also on two contrasting periods, in terms of assumed fishing pressure; one 36-year period in the beginning of the record, and one of similar length at the end. Finally, we analyzed the fish–climate relationships in one positive (1935–1960) and one negative (1965–1990) AMO phase.

To assess the association between climate and recruitment during the twentieth century, simple correlation analyses (Pearson's, two-tailed) between R_S and the selected climate indices were used. As we

were interested in the fish–climate association on both short and long time scales, the correlation analyses were performed both on high- and low-pass filtered climate and R_S time series. We used a 5-term Gaussian-type filter (González and Woods, 2002), to extract the long-term variations from the time series since power spectrum analysis showed periodicity of ≤ 5 years, which was common to all fish data series analyzed here (not shown). The low-pass filtered data was then used to represent the longer timescales. To get the high-frequency variability, the low-frequency signal described above was subtracted from the raw R_S time series. Annual values of R_S were compared to seasonal averages of the selected climate variables: December–February (DJF); March–May (MAM); June–August (JJA) and September–November (SON). Since one year is needed for haddock and cod to reach the size at estimated recruitment, and one to two years for plaice, the correlations were made with lagged climate data: t-1 for haddock and cod and t-1 and t-2 for plaice. The significance of the correlations was estimated using two sided t-tests, and the minimum level for significance was set at $p < 0.05$ for all statistical tests performed in this analysis. The large autocorrelation inherent in smoothed time series needs to be taken into account when estimating the significance of correlations, since there is otherwise an increased chance of getting spurious significant correlations. However, since we at this stage were interested in the low-frequency variability, rather than removing the autocorrelation by e.g. first difference or pre whitening, which may decrease the probability to find important relationships between long-term climate variables and fish population dynamics (Pyper and Peterman, 1998), a Monte Carlo technique (Livezey and Chen, 1983) was used to determine if the correlations were significant. In order to do so, two random time series, with 600,000 samples each, were generated, and then the specified length (e.g. 101 which indicates the 101 year case, 1904–2004) time series was subsequently picked out and low-pass filtered to get the correlation coefficient between the two. This was been done for 5000 times and repeated with 100 random time series. The 95th (99th) percentile of the resulting correlation coefficients was then selected to represent significant values at the 0.05 (0.01) level.

3. Results

3.1. Climate–fish R_S relationships 1904–2004

First, we investigated the fish R_S –climate associations for the whole analyzed period (1904–2004). The results from the correlation analysis are given in Table 1. A general observation is that the low-pass filtered fish time series show a stronger relationship with the selected climate variables compared to the high-pass filtered ones. Moreover, the correlation analysis suggests that R_S of all three species is more strongly related to SST than to the NAO.

Looking at the last century, the low-pass filtered data for plaice R_S is significantly positively correlated with SST_{AMO} in all seasons, with the highest significance ($p < 0.01$) found in MAM through SON (t + 1) and JJA–SON (t + 2). Significant positive correlations with SST_{REG} were found in MAM and JJA ($p = 0.01$), but they were weaker than those for the regional SST indices. The few significant correlations with NAO did not show the same consistency between t-1 and t-2 as for SST. However, significant correlations with NAO_{REG} occurred in DJF (positive) and SON (negative, $p = 0.01$) in both years. Weak, but significant, correlations when the high-pass filtered data was analyzed were found only with SST_{REG} in SON, being negative in t-1 and positive in t-2.

The only significant correlations between haddock R_S and climate were found in JJA, with SST_{AMO} for low-pass data and NAO_{REG} for high-pass data. The correlation patterns for cod R_S were similar to those of plaice, but showed a slightly stronger association to regional SST. Significant correlations with SST_{AMO} were found in all seasons except JJA, being highly significant ($p = 0.01$) in DJF and MAM, while the only season without a significant correlation with SST_{REG} was DJF. The most significant correlations ($p = 0.01$) with SST_{REG} were found

in JJA and SON. Significant correlations with NAO_{REG} were found in spring and autumn, being positive in MAM and negative in SON. No significant correlation was found when the high-pass filtered data was analyzed.

3.2. Climate and fish R_S 1904–1939 vs. 1968–2003

To assess the influence on the climate– R_S relationship of an increased fishing pressure (Sparholt et al., 2007) and global warming (IPCC, 2007) in the latter part of the twentieth century, we also applied correlation analyses to two separate 36-year periods, one in the earliest part of the twentieth century (1904–1939; lower fishing pressure, less warming) and one in the latter part of the records (1968–2003; higher fishing pressure, more warming). By doing so, we could have a rough estimate of potential changes in the sensitivity of the studied fish stocks to climate from the combined effects of increasing fishing pressure and climate change, and here we used the definition of sensitivity from Perry et al. (2010), where it is a measure of the strength of the relation between the fish stocks and climate variables. From Table 2, it is quite clear that changes

Table 1

Correlations (Pearson's, two tailed) between fish recruitment success (R_S), and selected climate variables, 1904 to 2004. Correlations were calculated for years t-1 and t-2 (plaice only). PLA is plaice, HAD is haddock and COD is cod. (low) = low-pass filtered data, containing low-frequency information, and (high) = high-pass filtered time series (see main text). Bold numbers indicate significant values, where * denotes significance at the 0.05 level, and ** at the 0.01 level. (For significance of smoothed data, see main text). The correlations with SST variables are shaded for easier comparison. See text for the explanation of the climate variables.

			PLA	PLA	HAD	HAD	COD	COD
			(low)	(high)	(low)	(high)	(low)	(high)
t-1	SST _{AMO}	DJF	.364*	.067	.158	.025	.398**	-.041
		MAM	.396**	.021	.254	.040	.405**	.023
		JJA	.454**	-.053	.295*	-.009	.269	-.001
		SON	.529**	-.020	.267	.104	.346*	.028
	SST _{REG}	DJF	-.027	-.041	.172	-.159	.033	-.031
		MAM	.322*	.141	.287	-.110	.327*	.086
		JJA	.376**	.058	.240	-.026	.486**	.178
		SON	.195	-.200*	.114	.131	.416**	-.129
	NAO	DJF	.268	.004	.229	-.050	.041	-.112
		MAM	.147	-.144	-.010	-.027	-.041	-.094
		JJA	.361*	.073	-.029	-.090	.028	.109
		SON	.140	-.015	.166	.030	.008	-.150
	NAO _{REG}	DJF	.297*	.045	.204	-.114	.139	-.013
		MAM	.190	.047	.081	.188	.343*	.031
		JJA	.226	-.064	-.034	.228*	-.108	-.133
		SON	-.495**	-.155	-.050	.074	-.356*	-.114
t-2	SST _{AMO}	DJF	.294*	.107				
		MAM	.328*	.042				
		JJA	.421**	.063				
		SON	.479**	.070				
	SST _{REG}	DJF	.002	-.011				
		MAM	.341*	-.140				
		JJA	.312*	.037				
		SON	.191	.238*				
	NAO	DJF	.310*	.091				
		MAM	.113	-.032				
		JJA	.286	.008				
		SON	.175	.154				
	NAO _{REG}	DJF	.293*	.046				
		MAM	.199	.115				
		JJA	.234	-.057				
		SON	-.439**	.019				

in the associations between R_S and climate occurred for all three species from the early to the late period. For plaice R_S , no significant correlations are found for the low-pass data in the early period, but when the high-pass data are concerned, significant correlations are found with SST_{AMO} in SON (t-1, negative), SST_{REG} in DJF (t-1, positive) and NAO_{REG} in MAM (t-2, positive, $p = 0.01$). In the latter period, there is a distinct change in the associations between the low-pass filtered data and climate, where significant and highly significant positive correlations are found with both SST_{AMO} and SST_{REG} in all seasons except DJF (SST_{REG}). Significant correlations are found with NAO in JJA (positive) and NAO_{REG} in MAM (t + 1, positive) and SON (negative, $p = 0.01$). Turning to the high-pass filtered data, significant correlations are found with SST_{REG} in SON (t + 2, positive, $p = 0.01$), NAO in JJA (t + 2, negative) and NAO_{REG} in Son (t + 1, negative, $p = 0.01$).

When low-pass filtered haddock data is concerned, there is seemingly a change in the association with SST from strong to weak between the two periods. In the early periods, significant positive correlations are found with SST_{AMO} in all seasons, while in the later period the only significant correlation is found in JJA. When the high-pass filtered haddock R_S data is concerned, more significant associations with the NAO than SST are found in the early period, where significant correlations are found with SST_{AMO} in MAM (positive), NAO in DJF (negative) and NAO_{REG} in DJF (negative, $p = 0.01$) and MAM (positive, $p = 0.01$). In the later period, only SST_{AMO} in JJA is significantly correlated with low-pass filtered haddock R_S , while an increased association with the NAO is observed; significant positive correlations with NAO in DJF and JJA, and with NAO_{REG} in DJF and MAM. No significant correlations were found when the high-pass filtered haddock R_S was analyzed.

Also cod R_S shows distinct changes in climate associations between the periods. In the early period the only significant correlation was found with NAO_{REG} in SON (negative) for high-pass filtered data. However, while the high-pass correlation remains in the later period, there is a distinct change in the correlations for the low-pass filtered data, where the mainly negative (but not significant) correlations with SST in the early period have turned positive and significant; both sets of SST indices in all seasons except DJF (SST_{REG}) display high correlations ($p = 0.01$) with cod R_S . Moreover, significant correlations with NAO_{REG} are seen in MAM (positive) and SON (negative, $p = 0.01$).

3.3. Fish recruitment and AMO variability

To investigate the possible influence of the phase of the AMO on R_S , we applied the same correlation analyses as above, to one warm (1935–1960) and one cold (1965–1990) phase. From Table 3, no distinct patterns can be readily seen. Regarding low-pass plaice R_S , a change from negative correlations with SST_{REG} in all seasons, being significant in DJF in the warm phase turns positive (but not significant) in the cold phase. The only significant association between low-pass plaice R_S and SST_{AMO} is found in SON (t-2) in the cold phase. Also in the cold phase there are significant positive correlations with NAO_{REG} in MAM, suggesting a stronger influence of spring atmospheric circulation during this phase. The only significant correlation in the high-pass analysis is found with NAO_{REG} in DJF (t-2) in the warm phase. For low-pass haddock R_S , correlations with SST_{AMO} turns from negative (not significant) in the warm phase to positive in the cold phase, being significant in JJA. However, correlations with SST_{REG} go from higher (significant in DJF) in the warm phase to lower or even negative (not significant) in the cold phase. The association with both NAO indices is mainly weak and negative in the warm phase, but it turns positive in most seasons in the cold phase, with the significant ($p = 0.01$) negative correlation with NAO_{REG} in MAM being one exception. The high-pass analysis shows similar patterns, although a highly significant ($p = 0.01$) correlation with NAO_{REG} is found in JJA during the warm phase. During the cold phase significant correlations are found with SST_{AMO} in JJA (positive) and NAO in MAM (negative, $p = 0.01$). Low-pass cod R_S shows similar tendencies as plaice, with mainly negative (not significant) SST correlations in the

warm phase, which turns positive in the cold phase (significant only in SON for SST_{REG}). The most obvious change when it comes to the atmospheric circulation, is the change from a positive and significant correlation with NAO_{REG} in JJA ($p = 0.01$) during the warm phase, which turns negative (but not significant) in the cold phase. No significant correlations were found for the high-pass filtered data.

4. Discussion

4.1. The importance of long data series

Having a century-long fish data series provides an opportunity to better understand the role of natural climate variability on fish dynamics, as these relationships can be studied prior to recent global warming

and intensified fishing, but also to assess the importance of climate on fish variability at different time scales. This is especially important when assessing the synergistic impact of climate change and fishery activities on fish stocks (e.g. Brander, 2010), as it increases the number of replicates in terms of occurrence of cold and warm periods. This knowledge is highly useful when implementing long-term strategies for sustainable management of exploited fish stocks. Previously, a number of studies on climate/fish relationships have been restricted to the latter half of the twentieth century due to shortness of available fish time series (Klyashtorin, 1998; Poulard and Blanchard, 2005; Stige et al., 2006; Wieland, 2005). Thus, suggested associations between climate and fish may be simply an artifact of strong trends in the climate, such as the positive phase of the NAO in the late-twentieth century, and coincident reduction in fish stocks caused by intensive fishing, rather than being a

Table 2

Same as for Table 2, but for two different periods Correlation analyses were performed over two periods: 1904–1939, and 1968–2003.

			1904–1939						1968–2003					
			PLA (low)	PLA (high)	HAD (low)	HAD (high)	COD (low)	COD (high)	PLA (low)	PLA (high)	HAD (low)	HAD (high)	COD (low)	COD (high)
t-1	SST _{AMO}	DJF	.190	.039	.491*	.251	-.303	-.032	.815**	-.310	.353	-.043	.788**	-.219
		MAM	.217	-.014	.523*	.331*	-.306	.024	.765**	-.284	.459	-.125	.714**	-.150
		JJA	.122	-.191	.475*	-.157	-.335	-.179	.764**	-.319	.544*	.036	.652**	-.140
		SON	.275	-.376*	.501*	.049	-.290	-.279	.875**	-.143	.441	.085	.787**	-.008
	SST _{REG}	DJF	.066	.340*	.061	-.162	-.181	.314	.230	-.080	-.005	-.209	.264	.080
		MAM	-.002	.207	.150	-.010	.096	.214	.661**	.256	.321	-.154	.610**	.208
		JJA	-.166	-.038	.203	-.113	-.082	.122	.827**	-.098	.284	.049	.814**	.083
		SON	-.102	-.071	.153	-.060	-.266	-.195	.651**	-.186	-.082	.143	.654**	-.123
	NAO	DJF	.132	-.020	-.382	-.394*	-.075	-.203	.284	.088	.541*	.291	.184	.058
		MAM	.234	-.151	.343	-.142	-.087	-.206	.072	-.172	-.252	-.004	.124	-.009
		JJA	.119	-.003	-.356	.015	-.192	.134	.558*	.225	.488*	-.020	.439	.267
		SON	.200	-.097	.509*	.216	-.146	-.281	.161	.178	.116	-.111	-.015	-.149
	NAO _{REG}	DJF	.284	.012	-.231	-.430**	.028	-.131	.350	.079	.533*	.138	.329	.088
		MAM	-.002	-.109	-.102	.635**	.303	-.013	.520*	.228	.481*	.175	.548*	.095
		JJA	.243	.021	.156	.295	-.255	-.153	.289	-.139	.213	.221	.235	-.147
		SON	.135	-.322	.334	.123	.004	-.421**	-.697**	-.493**	-.353	-.088	-.694**	-.366*
t-2	SST _{AMO}	DJF	.131	-.007					.789**	.212				
		MAM	.165	.035					.760**	-.026				
		JJA	.126	-.122					.767**	.018				
		SON	.308	.091					.876**	-.104				
	SST _{REG}	DJF	-.088	-.060					.316	.087				
		MAM	-.106	-.001					.665**	-.005				
		JJA	-.216	-.056					.788**	.069				
		SON	-.135	.054					.564*	.471**				
	NAO	DJF	.028	-.021					.390	.311				
		MAM	.228	.014					.063	-.068				
		JJA	-.029	-.058					.491*	-.403*				
		SON	.217	.173					.219	.141				
	NAO _{REG}	DJF	.014	-.103					.441	.132				
		MAM	.084	.510**					.462	.145				
		JJA	.357	.047					.341	.304				
		SON	.278	.132					-.675**	.300				

stable relationship between climate and fish productivity per se. Also, such short time series makes it difficult to assess the influence of climate variability on multidecadal time scales, e.g. from the AMO. In this context, century-long records provide opportunities to better understand the role of natural climate variability on fish dynamics, and these relationships can be studied prior to recent global warming and intensified

fishing. It should, however, be noted that while using recruitment success (R_S) allowed us to account for a large part of the fishing effect, the effects from selective fishing in terms of size will still remain, which may be of importance for the fish response to climate. It is important to note that the average size of the analyzed species has significantly declined over time (Cardinale et al., 2010, 2012). This does not affect the

Table 3

Same as Tables 1 and 2, but for two distinct phases of the AMO, one warm (1935–1960) and one cold (1965–1990).

			Warm					Cold						
			PLA (low)	PLA (high)	HAD (low)	HAD (high)	COD (low)	COD (high)	PLA (low)	PLA (high)	HAD (low)	HAD (high)	COD (low)	COD (high)
t-1	SST _{AMO}	DJF	.313	.358	-.403	-.067	.096	.057	.351	-.005	.006	.056	.440	-.033
		MAM	.294	.154	-.273	-.030	-.048	.026	.373	-.046	.200	-.014	.314	.038
		JJA	.281	-.060	-.374	-.259	-.491	-.052	.435	-.022	.646*	.080	.117	.060
		SON	.447	-.129	-.521	-.023	-.143	-.163	.493	.227	.412	.269	.343	.283
	SST _{REG}	DJF	-.552	.121	.585*	.091	-.471	.130	.269	-.388	.104	-.366	.297	-.298
		MAM	-.287	.313	.220	-.165	-.298	.153	.224	-.036	.133	-.174	.169	-.054
		JJA	-.073	.161	.034	-.350	-.297	.343	.449	.206	-.027	.130	.499	.279
		SON	-.319	-.358	.408	.215	-.107	-.182	.416	-.085	-.150	.067	.603*	-.130
	NAO	DJF	.254	.071	-.430	-.243	.085	-.186	.184	-.142	.540	.202	-.139	-.140
		MAM	.172	-.211	-.105	.015	-.172	-.088	-.421	-.143	-.702**	-.141	-.054	-.022
		JJA	.230	.187	-.217	-.196	.650*	.252	-.070	.159	.221	-.094	-.201	.208
		SON	.037	-.069	-.108	.297	-.211	-.165	-.068	-.041	.312	-.037	-.373	-.190
	NAO _{REG}	DJF	.164	.057	-.247	-.220	.138	-.085	.199	-.144	.325	.062	.035	-.096
		MAM	.082	.083	-.311	.208	.392	.047	.631*	.064	.294	.179	.530	-.017
		JJA	.339	-.118	-.484	.513**	-.060	-.262	-.189	-.210	-.177	.170	-.063	-.260
		SON	-.511	-.246	.340	.189	-.300	-.226	-.095	-.135	.271	-.047	-.295	-.093
t-2	SST _{AMO}	DJF	-.023	.066					.356	.134				
		MAM	-.079	.155					.432	.005				
		JJA	.284	.235					.538	.031				
		SON	.436	.266					.607*	.043				
	SST _{REG}	DJF	-.471	.290					.050	.104				
		MAM	-.178	.016					.068	-.080				
		JJA	-.161	-.161					.239	-.005				
		SON	-.045	.384					.334	.227				
	NAO	DJF	.153	.337					.097	.175				
		MAM	.073	-.027					-.474	-.062				
		JJA	.240	-.030					.028	-.097				
		SON	.115	.292					.041	.176				
	NAO _{REG}	DJF	.078	.421*					-.095	-.029				
		MAM	.099	.153					.657*	.134				
		JJA	.212	.069					-.217	.010				
		SON	-.321	-.052					-.015	-.040				

classification of R or SSB as they are the same over the time series (i.e. they are based on the same size limit over the time series), but it might have affected the estimate of the spawning potential and reproductive output over time as smaller fish may produce few and/or less viable eggs (i.e. Kjesbu et al., 1996; Marshall et al., 1998, but see also Morgan et al., 2007). Currently, no information is available to quantitatively include this in our models. Here instead we have chosen the approach used by ICES for estimating SSB, which does not explicitly account for the size structure in the population more than on the fact that large fish are heavier and contribute more to the SSB. Although R_S is used with the intent to standardize R in relation to SSB, it has to be noted that some level of dependency between these two quantities still exists. As it is formulated, R_S decreases as stock size increases, which may account for density-dependent effects on recruitment at large stock size, including the potential occurrence of cannibalism. However, R_S does not account for deviations at low stock size which could be related to the Allee effect or overcompensation. Moreover, the whole framework presented for detecting signals of climate effect on the recruitment of several fish species is based on a single-species approach which means that climate variability is assumed to be the main driver of fish recruit survival. In this case, ecosystem effects on R_S such as species interactions are taken into account only if linked to the direct impact of climate.

Another caveat is of course the lack of R_S data in some years, especially in the early parts of the records, which may hamper the correlation results. However, a comparison of correlation values between the interpolated and raw R_S data with gaps showed generally small differences, especially when the analyses cover the whole century (not shown). Still, some care should be taken when interpreting the results of the early periods.

4.2. Climate and recruitment success in a century perspective

Over the full period (1904–2004), the results showed that the strongest R_S -climate association (in terms of the number of significantly correlated months) was found using the low-pass filtered data rather than the high-pass filtered data. This suggests that the relationship between R_S and climate is more discernible over periods of several years. On the inter-annual timescale, other processes, such as internal population dynamics or interactions with other species (Lehodey et al., 2006), may be more relevant. Of the three studied species, the recruitment success of both plaice and cod show some similarities in their associations to climate, showing strong links with SST. From the analyses, it may be tentatively inferred that plaice have a stronger relation to large-scale SST compared to cod, which showed higher correlations to regional SST. Moreover, the results for plaice and cod suggest that the influence of SST, on both large and regional scales, is more coherent than that of the NAO. However, it should be noted that SST changes are gradual over the year, resulting in stronger correlations among seasons, especially when the low-pass filtered data is concerned, while the atmospheric variability, as described by the NAO index, is more dynamic, resulting in far less coherency among the seasons.

Comparing the early and late periods, a shift in the correlation patterns is evident. In the early part of the twentieth century (1904–1939), the most striking feature is the general lack of significant correlations between R_S and SST for plaice and cod, independent of filtering. The low-pass filtered haddock data, on the other hand, displays strong and significant correlation with the large-scale SST throughout the year during this period, while the influence of the regional SST is much weaker (see discussion of haddock below). In the latter period (1968–2003), there is a clear change towards positive (and significant) association between R_S and SST for cod and plaice when it comes to the low-pass filtered data. This is especially true for SST_{REG} where the associations in the early part were weakly negative (although not significant), but turning highly positive in the latter part. For haddock on the other hand, there is a decrease in the SST association. Thus, our result show responses in the long term dynamics of

the recruitment success of the three species, although haddock differs from cod and plaice, to increased fishing pressure and the observed warming trend during the last two decades of the century in the Skagerrak–Kattegat and in the whole North Atlantic. It has been argued that a heavy exploitation may increase the sensitivity of fish populations to climate, i.e. that they are more strongly associated with climate (Perry et al., 2010), e.g. through depletion of large fish (Hsieh et al., 2006; Planque et al., 2010), and by altering key processes of fish life cycles (Rijnsdorp et al., 2009). Thus, the increase in fishing pressure in Skagerrak–Kattegat (Cardinale et al., 2010, 2012) that determined the disappearance of large fish and thus the truncation of the size structure (Cardinale et al., 2009, 2012) over the last century, particularly in the latter half, is likely the reason for an increased sensitivity of recruitment success to temperature. The positive trend in plaice and cod R_S suggests a beneficial effect of increased SST, which for cod is in disagreement with the general conclusions of the effect of temperature on recruitment in the area (e.g. Olsen et al., 2012 and references therein), but the leveling out of the trend in cod R_S around 2000 may indicate that there is a threshold for the positive association with temperatures also for this particular stock. Thus, persisting warm temperatures in Skagerrak–Kattegat may ultimately have negative effects on the recruitment of cod, which is partly in agreement with the conclusion by Rogers et al. (2011), who studied cod size and climate along the Norwegian Skagerrak coast. They concluded that rising temperatures associated with global warming could cause coastal Skagerrak to become ill-suited for Atlantic cod.

4.3. The effect of the AMO on recruitment success

Since the role of long-term SST variability in the North Atlantic on influencing regional to global climates was highlighted some years ago (Knight et al., 2006; Sutton and Hodson, 2005), several studies have linked marine-ecosystem variability to the AMO (e.g. Condrón et al., 2005; Edwards et al., 2013; Gröger and Fogarty, 2011; Gröger et al., 2010; Kane, 2011; Nye et al., 2013). For instance, it has been shown that the abundance of North American Atlantic salmon (Condrón et al., 2005), Norwegian herring stock biomass (Edwards et al., 2013) and Arcto-Norwegian cod spawning intensity (Nye et al., 2013) covaried with the phase of the AMO during the twentieth century. However, we did not find any clear relationships from the correlation analyses of the studied Skagerrak–Kattegat species. While plaice showed positive correlations to SST_{AMO} but negative correlations to SST_{REG} in the cold phase, the pattern was opposite for haddock. It should be noted though that since this period (1935–60) contains a number of missing data in the R_S series, the correlations may be biased both in strength and signs. In the cold phase there seems to be more consistency among the species, where most SST correlations are positive, although only a few were significant.

A comparison of the R_S of cod, plaice and haddock in Skagerrak–Kattegat and the AMO is shown in Fig. 4. From this figure it is evident that there is no clear relationship between R_S of the studied species and the AMO. All three species show more or less opposite trends to the AMO in its cold phase in the beginning of the century (ca. 1900–1930), most pronounced in cod. During the subsequent warm phase (ca. 1930–1960), there are some increases in R_S for all species, but the most noteworthy observation is that this period is categorized by a very high R_S variability in all species. Since this period coincides with a period of many missing years in the data, it may possibly be an effect of sampling or data treatment. However, the fact that also the Norwegian herring stock biomass seemed to undergo large fluctuations during this period (see Fig. 3 in Edwards et al., 2013) suggests that at least some of this variability is real and not an artifact. Since the interannual R_S variability was much lower during the cold AMO periods (which corresponds to Norwegian herring biomass), possibly the AMO plays some role in the sensitivity of fish populations to climate by affecting their variance. Provided that the species are situated close to their limit of distribution, it is likely that

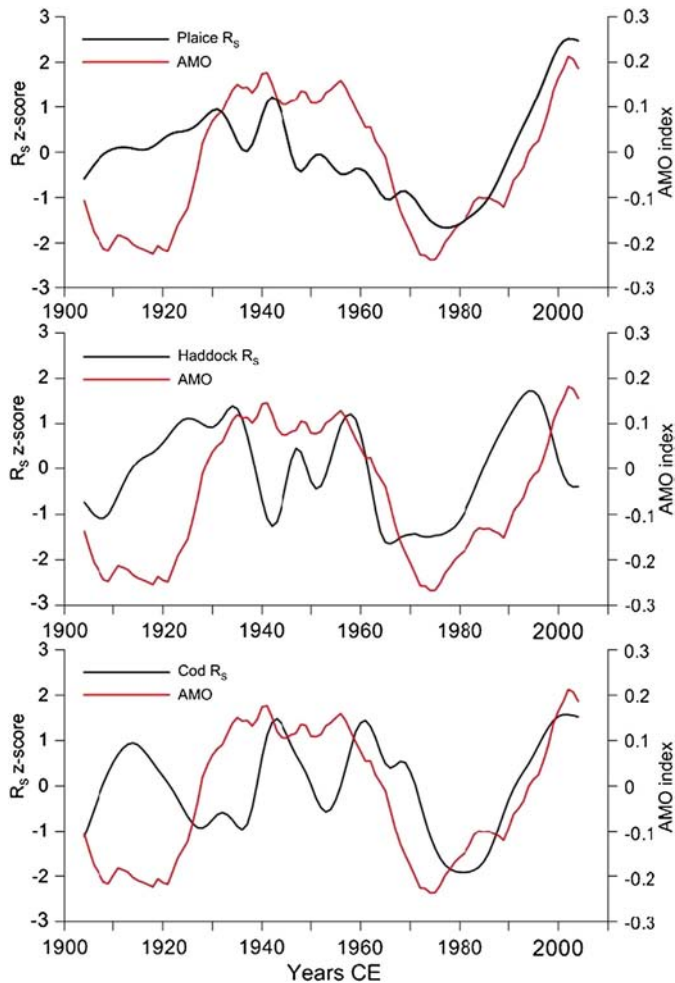


Fig. 4. Comparison between the AMO (red lines) and low-pass filtered (to highlight the decadal variability) recruitment success (R_S) of plaice, haddock and cod (black lines). The AMO is based on the Kaplan SST dataset (Kaplan et al., 1998), where the weighted average over the North Atlantic ($0-70^\circ\text{N}$) was computed, detrended and smoothed with a 121 month smoother. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

they get more sensitive during warm periods so that the R_S variability is an effect of habitat shifts (e.g. Nye et al., 2009). In the subsequent cool AMO phase, the variability becomes low again and the R_S trend of the three species quite closely follows that of the AMO, which, according to the reasoning above, could be an effect of the increased sensitivity to SST in the latter half of the century. The sudden drop in the association between haddock R_S and AMO in the 1990s is likely due to the collapse of that stock (Cardinale et al., 2012).

Another possible explanation for the high R_S variability between ca. 1930 and 1960 could be that it is a function of increased fishing pressure. It has been argued that exploited populations exhibit greater variability (Perry et al., 2010), so the large observed R_S fluctuations in Skagerrak–Kattegat could indicate an increasing fishing pressure in the mid-twentieth century. However, then it is difficult to explain the return to the much lower R_S variability in the subsequent decades. Maybe it is a sign of continuously increased fishing pressure, combined with climate warming, causing the R_S to be more sensitive to climate but exhibit less variations? More research is needed to better understand this.

4.4. Haddock – insensitive to climate?

From our analyses, haddock seems to be less sensitive to climate on long timescales than the other two species, especially in the latter part

of the analyzed century. Because most fish stocks are expected to be more sensitive to climate variability when the fishing pressure is high, the strong associations between haddock R_S and SST_{AMO} in the early part of the twentieth century may be related to the fact that the Skagerrak–Kattegat haddock stocks were already heavily exploited at this time. Indeed, Cardinale et al. (2012) argue that the fishing pressure on haddock in Skagerrak–Kattegat started earlier than for cod and plaice, where very high landings of haddock occurred in the first three decades of the twentieth century (Fig. 3a in Cardinale et al. (2012)). Thus, the low response to climate in the latter half of the analyzed period can be related to the collapse of the haddock stock in this region since the early 1940s (Cardinale et al., 2012). Since haddock fluctuated around very low biomass levels during most of the second half of the century, this may have increased the relevance of stochastic processes in the haddock dynamics and affected the likelihood of local unfavorable environmental conditions and recruitment failure, which may explain the low response of haddock to regional and large scale climate variability. Consequently, our results indicate different thresholds in fish recruitment responses to climate, on timescales above 5 years, where a healthy stock is less dependent on climate, whereas heavy exploitation increases the influence of climate on recruitment.

5. Conclusion

Our study of the association between climate and recruitment success (R_S) of three commercial species in Skagerrak–Kattegat over the last century revealed that:

- The commercial stocks of the studied species show much stronger associations with climate on long (>5 year) timescales than on shorter ones, suggesting that other factors than those investigated are more important for the year-to-year variations.
- Plaice and cod R_S have strong and positive association with large-scale and local SST over the whole of the last century. However, comparing the first and last parts of the century, significant correlations were only found in the latter part. Correlations with the atmospheric circulation are stronger for the regional than the Atlantic wide indices.
- Haddock R_S show opposite patterns, with significant positive correlations to large-scale SST only in the early twentieth century. The lack of SST/NAO sensitivity in the latter part is likely due to the collapse of the stock in the early 1940s and an increased importance of other processes/factors that were not considered in this study.
- In contrast to recent literature, cod recruitment success in this stock seems to be positively associated with higher temperature in the latter part of the twentieth century.
- The shift from low to high climate sensitivity in the stocks seen from the early to the late part of last century may be associated with the increased fishing pressure/climate change and related changes in fish size structure.
- There is no clear-cut relationship between R_S and the AMO for any of the studied species except for the last ~40 years. However, the relatively large fluctuations in R_S during the positive AMO phase suggest a changed behavior of the stocks during warmer SST conditions. On the other hand, these may be forced by progressively increasing fishing pressure and climate change.

In summary, the results highlight the need to take long-term climate forcing on fish stocks into account when implementing sustainable management strategies.

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