

Long term synchronous trends in the recruitment of the North Eastern Atlantic fish populations related to climate change and exploitation.

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Synchrony in population fluctuations have commonly been observed among a variety of species. They are generally attributed to the effect of common environmental forcings on population dynamics. Here, we investigate long term synchrony in the recruitment variations of the North East Atlantic fish populations. A PCA (principal component analysis) was performed to extract the main patterns of variation. The most significant one reflects the synchronous decrease of the recruitment for the majority of gadoids populations, in the Baltic Sea, Kattegat, North Sea, Irish Sea and West of Scotland. The inverse pattern was observed for half of the herring populations. Plaice populations also exhibit synchronous recruitment trends, characterised by strong year classes during the 80's. Recruitment variations of saithe and sole populations never correlate with these general patterns. The analysis suggests that a regime shift occurred between 1982 and 1998 in the North East Atlantic. Actually, a step-like change was detected for most of the time series of recruitment and sea temperature at the end of the 80's. These changes in recruitment are concurrent with the regime shift observed in the North Sea and with the large scale changes reported for the plankton, which were both related to climate change. However, the analysis of the recruitment, stock biomass and fishing mortality time series indicates that the trends in recruitment for some populations could also result of the exploitation. We conclude that the variations of recruitment may reflect a regime shift in some areas of the North Eastern Atlantic, in response to climate change, but that exploitation is also responsible of a great part of the recruitment variations.

Keywords : climate change, North Eastern Atlantic, recruitment variations, regime shift, synchrony.

Introduction

Recent analysis of biological and hydroclimatical time series have shown that the North Sea ecosystem has experienced strong changes at the end of the 80's (Reid et al., 2001, Beaugrand, 2004). These changes have primarily been detected for the planktonic species in the CRP (Continuous Plankton Recorder) data. Since 1988, the phytoplankton biomass has

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strongly increased, profiting of a better growth during an extended growing season (Reid et al., 1998a, Edwards et al., 2001). The abundance and specific composition of the zooplankton community has also dramatically changed (Reid et al., 2001, Beaugrand, 2004). Northward biogeographical shifts for copepods species led to an increase of temperate water species to the detriment of sub arctic species, like *Calanus finmarchicus* (Beaugrand et al., 2002). Changes in biomass, abundance and diversity in the benthic community were also reported (Kröncke et al., 1998).

Fish populations of the North Sea have also exhibited strong long term changes in abundance during the last few decades. In the North Sea, the changes in the plankton were accompanied by an increase of horse mackerel catches (Reid et al., 2001), that have been linked to modifications in the species biogeography, due to an intensification of the northward shelf edge current. The increase of SST and the decrease in abundance of *Calanus finmarchicus* have also been detrimental to cod recruitment (Beaugrand et al., 2003). A marked decrease in the recruitment of the other species of Gadoid was also found (Beaugrand, 2004).

These changes, because of their extend and their abruptness, have been linked to an ecological regime shift (Reid et al., 2001, Beaugrand, 2004). This biological shift was accompanied by changes in the physical environment : increase of sea surface temperature in the North Sea after 1987, intensification of oceanic water inflows (Holliday and Reid, 2001) and reinforcement of winter westerly winds. The regime shift has been attributed to changes in the climate (Reid et al., 1998b, Beaugrand, 2004) that are apparent in the increase of the northern hemisphere temperature (NHT) anomalies and the prolonged positive phase of the North Atlantic Oscillation (NAO). For Beaugrand and Reid (2003), the North Sea ecosystem has shifted in 1988 from a cold to a warm dynamic regime.

The changes described in the plankton in the North Sea had in fact a greater geographical extension. The increase of primary production is obvious in the North Sea, but seems to have also taken place in more oceanic areas, like in the west of the British Islands (Reid and Planque, 2000). The changes in zooplankton species have occurred at the scale of the North Atlantic (Beaugrand et al., 2002). There are also assumptions of biological regime shifts in the Greenland (Buch et al., 2002) and in the Central Baltic Sea (Alheit et al., 2004). These ecological modifications correlate to large scale climatic indices, such as the NAO, or variability of the Gulf Stream. A question that should then be asked is to know whether or not the North Sea regime shift has occurred on a larger geographical scale in the North Atlantic.

Productivity of fish populations, i.e. recruitment, such as for other biological components of the ecosystem, is affected by regime shifts. The purpose of this paper is to see if long term variations of fish recruitment of the North East Atlantic are coherent with a large scale regime shift. This question is investigated by searching for synchronous changes in long term variations of fish recruitment. Large scale population synchronies are indicators of common forcings on population dynamics, via density independent factors (Moran, 1953). Such synchronies in recruitment variations have already been found, and ascribed to the influence of common environmental factors on reproduction success (Koslow, 1984, Hollwed et al., 1987).

Ecosystem regime shifts are due to external forcings. The North Sea shift was attributed to changes in the physical environment. However, considerable shifts have been described in the abundances of North Western Atlantic commercial species (groundfishes replaced by elasmobranches, or decapods). They were ascribed to the effect of

overexploitation, that passes through trophic levels by predator prey relationships (Worm and Myers, 2003, deYoung et al., 2004). Fishing seems to be an external forcing that can generate ecosystem regime shifts as well as climatic changes. The possible link between the observed trends in recruitment and the fishing activity was also investigated.

Materials and Methods

Data

Biological data

Data on fish populations were collected from the reports of the ICES working groups on stock assessment (<http://www.ices.dk/iceswork/workinggroups.asp>). For each stock, time series of populations abundance and fishing mortality for each age class are calculated by cohort analysis from commercial catches at age and survey abundance indices. Among all stocks assessed by ICES, those for which time series covers at least the 1970-1998 period were selected. The 40 populations following this criteria belong to 9 species and live from the Celtic Sea to Bering Sea.

Hydroclimatical data

Three large-scale indices were chosen to describe climatic variations during the 1970-1998 period.

The Northern Hemisphere Temperature anomaly (NHT) is a measure of the global variability of surface (sea and land) temperature. We used here the annual value of the index provided by Jones et al. (2001). This index is commonly used to characterise the global warming.

The North Atlantic Oscillation is the dominant mode of variation of sea level pressure over the north Atlantic (Dickson and Turrell, 2000). The winter NAO index used here is based on the difference of normalized sea level pressure between Lisbon, Portugal, and Reykjavik, Iceland for the winter months (Hurrell, 1995). It was obtained from the internet site <http://www.met.rdg.ac.uk/cag/NAO/index.html>.

The last index refers to the general circulation of the winds in the northern hemisphere. The Atmospheric Circulation Index (ACI) refers to the number of days of one year of zonal (west – east) or meridional (north – south) transport of air masses (Girs, 1971). These two forms of circulation are calculated from daily atmospheric pressure charts over northern Atlantic-Eurasian region. We used here the ACI WE (zonal component) index.

Data on SST were extracted from COADS (comprehensive ocean-atmosphere data set) for the period 1970-1997. As data were annual means for 2° lat × 2° long boxes, the annual mean for each ICES area was calculated. The boxes with missing data were excluded.

Statistical analysis

Synchrony in long term variations of fish recruitment

We first wanted see if the recruitment of marine fishes has experienced synchronous long term variations, and to identify the principal patterns of these variations. This was done by the mean of standardised Principal Component Analysis (PCA). The aim this technique is

to summarise the information (e.g. variability) of a large dataset into a small number of uncorrelated and possibly meaningful variables named principal components (PC). Each PC explains a fraction of the total data variance. The first PC explains the greatest amount of the total variability. The second one explains the greatest amount of the remaining variability, and so on, until there are as much PCs as variables in the dataset. The 2 or 3 first PCs generally summarise most of the information of a data set. A PCA was performed on fish recruitment data, on a matrix with log recruitment of each population in column, and years in rows. The log transformation of recruitment indices was performed to lessen the influence of exceptionally strong year classes of some populations on the calculation of the PCs. The firsts PCs will represent the most significant patterns of recruitment variability in the North East Atlantic. The correlations (loadings) with the PC indicates if a population follows the trend represented by the score of this PC. Groups of populations that would be well loaded on the same PC will hence have synchronous trends of recruitment.

Test of transitions

The next step of our analysis was to see if the long term variations detected in the biological and physical indices exhibit abrupt changes, characteristic of a regime shift. We used three different methods to investigate the temporal discontinuity in the data.

Cluster analysis was performed on the Euclidean distance matrix of fish recruitment data, using the hierarchical agglomerative clustering algorithm of Ward (minimising the intra-group variance). This method was used to see if different periods of similar recruitments characteristics could be isolated, corresponding to different regimes.

A second statistical method to detect transitions in multivariate time series is the average standard deviates (ADS) method employed by Ebbesmeyer et al. (1991). This allows to test the magnitude of a regime shift with an a priori hypothesis on the date of the shift. The method is detailed in Hare and Mantua (2000) but can be summarised as follow : 1) the time series of the dataset are standardised on the two periods corresponding to the hypothetical regimes, 2) these annual standard deviates are averaged to constitute an annual composite index of the state of the system, 3) the shift is significant if the composite index changes of sign between the two regimes and remains of the same sign within each regime. The ASD method was here applied on the recruitment dataset to test different dates for a potential regime shift, on the basis of the changes found with the cluster analysis.

Shifts were also searched in single time series by the mean of the cumulated sums method (Ibanez et al., 1993). For each year y , the cumulated sums time series is calculated as the sum from year 1 to y of the values of the original time series (centred on its mean). The cumulated sums plot is typically a broken line with breaking points corresponding to the dates of changes of mean level in the original series. Cumulated sums were calculated for each of the 40 recruitment time series, and differences in local means were tested with a Student test when a shift was suspected.

Effect of fishing

Trends in recruitment time series are usually related to both influence of human exploitation (Hutchings and Myers, 1994, Cook et al., 1997) and to long term climatic forcing (Klyashtorin, 1998, Ravier and Fromentin, 2004). As there exists to date no method to dissociate the environmental and human influence on stock dynamics, we made hypothesis on

what should be observed in the time series if recruitment trends were only caused by variations of fishing activity.

A negative influence of fishing pressure on stock size should be first observed, that would correspond to negative correlations between time series of spawning stock biomass (SSB) and fishing mortality (F). The relative value of the mean fishing mortality was also compared to F_{pa} (the precautionary approach reference point) and F_{lim} (the mortality above which stock extinction becomes highly probable), to see if overexploitation can explain the observed trends in stock size. An influence of the variations of the parent stock size on the recruitment is also expected. Stock - recruitment relationship was tested by calculating correlations between recruitment and SSB time series. However, as both recruitment and SSB time series are strongly autocorrelated, a positive correlation could reflect the influence of recruitment variation on stock size resulting from the maturation of the cohort (Sparholt, 1996). These “feedback” relationship could explain alone the stock – recruitment relationship. Correlations between recruitment and SSB were hence calculated with various lags to see the influence of cohort maturation. If the correlation with a lag corresponding to the age at maturity is greater than the non lagged correlation, the link between the two time series is more likely to arise from the cohort maturation than from the effect of the level of SSB on the subsequent recruitment.

Results

Long term changes in fish recruitment

Principal component analysis

The first two components of the analysis explain respectively 22 % and 14 % of the total variance of the 40 time series. As the other PCs explain each less than 9 % of the variance, only the PC1 and PC2 were considered as meaningful. The scores for this two PCs (i.e. their annual values) are illustrated on figure 1, and the correlations of population recruitment time series with these scores are given on figure 2 and 3.

The first principal component exhibit low frequency variations, with a positive period from 1970 until 1986 and a negative one after a relatively abrupt shift of 1986. Strong correlations ($|r| > 0.5$) occur for 15 populations, and moderate correlations ($0.3 < |r| < 0.5$) are found for other 15 populations. Most of the strong correlations on PC1 are positive (13 of the 15). In particular, six populations of cod are strongly positively correlated to the first component (with r ranging from 0.59 to 0.88), indicating that their recruitment have followed long term trends that are similar to the score of the PC1. These populations are Baltic Sea and Kattegat ones, as well as North Sea, West of Scotland and Irish Sea populations. Other cod populations have either negligible correlation (Iceland and Celtic Sea), or are weakly positively (Faroe) or negatively (N.E. Arctic) loaded. Strong loadings are also found for other gadoids, like whiting in the North Sea ($r = 0.70$) and in the West of Scotland ($r = 0.64$), North Sea haddock ($r = 0.57$) and Norway pout ($r = 0.51$). Two populations of plaice (in the Irish and Celtic Seas) and two of herring (Irish and Baltic Seas) are also highly loaded to PC1. The negative correlations with the first component are more scarce. The four strongest negative loadings are met among herring populations of the Iceland, N.E. Arctic, Gulf of Riga and North Sea. Finally, recruitment of saithe and sole is poorly related to the PC1.

The second principal component is also characterised by long term variations, with three distinct periods : negative values from 1970 to 1982, positive values from 1982 to 1988, values centred on 0 since 1989. Only six populations are highly loaded ($|r| > 0.5$), and 15 are moderately loaded ($0.3 < |r| < 0.5$) on PC2, with a majority of positive correlations. The strongest correlation with PC2 is observed for Celtic Sea cod, which was not correlated to PC1. Three plaice populations (English Channel, North Sea and Celtic Sea) are also strongly loaded. Other positive loadings are found among herring populations (in Iceland and North Sea).

PCA were also performed on data for single species or groups of species to see if coherent variations were found within species. Only the firsts PCs were considered, and are given in the figure 4. The PC1 for herring populations on one side, and for cod, whiting and haddock populations on the other, are highly significant of population recruitment trends as they explain respectively 34 % and 33 % of the variance for respectively 9 and 16 populations. This PCs shows a similar trend as the PC1 of the PCA on all species : both are characterised by two periods of low and high recruitment level, separated by rapid transition, occurring in 1982 for herring, and in 1987 for gadoids. For plaice populations, the PC1 shows temporal variations that are comparable to the second PC of the global analysis, with a period of good recruitment during the 80's. This PC is quite representative of the recruitment trends of plaice (58 % of the variance of the 5 populations). For saithe and sole, PC1 has high frequency variability, and no clear trend. Furthermore, these PC1s are not very representative of recruitment variations for this two species (38 % and 41 % of the variance for 4 populations).

Analysis of discontinuities

The dendrogram of the cluster analysis performed on the 40 recruitment time series (figure 5) was cut to form 3 groups of years. These groups are constituted of consecutive years, what indicates that they represent three distinct periods within which recruitment characteristics are relatively similar. The transition dates between these three periods are those which were also found for the PC2 : 1982 and 1988. The ADS method was applied for various hypothetical shift dates, between 1982 and 1988. The most important step change was found for a shift occurring in 1986 (figure 6).

The transition detected in 1987 between high and low recruitment periods for gadoid populations is confirmed by the analysis of the cumulated sums (table 1). For cod, most of the populations have experienced a significant transition from a high to a low level, occurring in 1986 or 1987 in the North Sea, Irish Sea, Eastern Baltic and West of Scotland, and around 1982-1983 in Iceland, Kattegat and Western Baltic. The shift is also significant in the recruitment of whiting and haddock in the North Sea between 1986 and 1988.

For herring, Celtic Sea, North Sea, Iceland and N.E. Arctic populations have shifted from low to high recruitment levels at the beginning of the 80's. The inverse transition is found at the same time in the Irish Sea and the Baltic Sea.

For other species, significant shifts are less frequent. A moderate decrease is found for plaice in the Celtic and Irish Seas in 1987, the recruitment of Norway Pout has decreased in 1983, Icelandic Saithe in 1986, whereas Faeroe's saithe increased in 1979.

Relationship between hydroclimatic changes and the trends in recruitment.

Time series of the climate indices are given on figure 7. The NHT anomalies and the ACI have increased over the 1970-1997 period, with a stabilisation for the ACI since 1990. The NAO index exhibits stronger high frequency variations, but has also an increasing trend till the 1996 strong negative anomaly.

For SST time series (figure 8), the trends are less apparent, but similar patterns are observed in several areas. For Eastern and Western Baltic, Kattegat, North Sea, Irish Sea and English Channel, cold temperatures were recorded between 1976 and 1987. Since 1987, higher temperatures are observed for all of these areas. The cumulated sums confirm that a change in SST occurred in 1987 or 1988 for these areas, although this change is not always significant. This warming is less obvious for other areas, but seems to have occurred in the Celtic Sea and in the West of Scotland at the same period. On the opposite, a cooling of the Icelandic waters is observed since the end of the 80's.

Correlations between principal components of fish recruitment and hydroclimatic variables are reported in the table 2. Both PC1 for all populations and for gadoid species are strongly negatively correlated to NHT and ACI. They are also negatively correlated to SST variations in the Celtic Sea, Irish Sea, North Sea and West of Scotland. The second component is positively correlated to the ACI, and negatively to the SST in Arctic and western Baltic Seas, and in south western areas. The herring PC1 is positively related to both ACI and NHT, but is independent of SST. Plaice recruitment is poorly linked to climatic indices, but correlates negatively to SST in Kattegat, English Channel, Irish Sea and North Sea. The first PC for sole shows not link with neither climate indices nor SST.

Effect of fishing

Comparisons of trends in recruitment, SSB, and fishing mortality were limited to the 10 populations which were highly positively correlated with the PC1, and the 5 most negatively correlated. The plots and correlation statistics are given in figure 9 and figure 10.

For half of the populations of the figure 9 the trends in SSB are significantly correlated to the fishing mortality. For instance, for cod in the Irish Sea and in the West of Scotland, the increase of fishing mortality is constant since 1970, what can explain the decrease in SSB. For other stocks, F is constant, or decreases, but remains at a high level. This is the case for North Sea cod for which fishing mortality is above F_{lim} since 1978. More generally, for all stocks for which F_{pa} was calculated, fishing mortality has remained above this reference point for most of the years. These populations have all supported a high exploitation that is likely to explain the decrease of SSB.

For the stocks of the figure 10, significant negative relationships between SSB and F are found for Arctic cod and Gulf of Riga herring, for which a decrease of the fishing mortality led to the beginning of the recovery of the stock. For herring in the North Sea and in the Arctic, the correlation is not significant, but the fishing mortality has been strongly reduced at the beginning of the series, what can explain the recovery of the stock.

Significant positive relationships between time series of recruitment and SSB with no lag were found for 9 populations. However, for 8 of them, a greater correlation was obtained when the time series were lagged, what suggests that much of the correlation between stock and recruitment is due to the link between the strength of a year class, and the SSB which is observed after maturation. For some populations, for which, correlation with lag is much

greater than correlation without lag, one can assume that the variations observed in the recruitment time series are poorly dependant on the variations of stock size. This is for instance the case for Eastern and Western Baltic cod populations, or North Sea herring. For these populations, together with those for which no link was found between recruitment and SSB (e.g. Irish Sea plaice and cod, West of Scotland whiting), fishing is unlikely to be the only cause of the long term recruitment trends observed.

For cod in the North Sea and in the Kattegat, and whiting in the North Sea, differences between lagged and no lagged correlations are weak and the recruitment variations are more likely to result of stock variations. For these three populations the heavy exploitation of the stock is likely to have resulted in recruitment overexploitation.

Discussion

The PCA has isolated the dominant patterns of recruitment variations of the North East Atlantic fish populations. The first dominant pattern correspond to a decrease of recruitment, with a positive and a negative period, separated by a relatively fast transition occurring in 1986. The second pattern correspond to an increase from a negative period to a positive one in 1982, and a stabilisation since 1988 to a medium level.

Few populations have experienced recruitment variations that completely match with one of these two patterns (i.e. strong loading on one PC and null on the other, like Eastern Baltic cod and North Sea cod and whiting). However, in a broader point of view, the majority of the populations, including most of the gadoids (10 populations), 2 of the 9 herring populations and 1 plaice population, are well correlated to the first PC. These populations have hence experienced a synchronous decrease of their recruitment. Most of them are located either in the North Sea, or in the Baltic Sea, West of Scotland, and Irish Sea. The inverse trend was found for two herring populations and one of cod, located in the Baltic Sea and the North East Arctic. Only three populations of plaice and one of cod had synchronous variations close to PC2. Populations of sole and saithe, did not follow the synchronous trends met for other species.

Most of the populations that exhibit this synchronous decrease in recruitment are heavily exploited. We found that high, or increasing fishing mortality, was a possible cause for this general fall of recruitment (figure 9). Furthermore, the reduction of exploitation, for stocks that had nearly collapsed, is also a possible explanation for the increasing trends that have been found (figure 10). The dominant pattern of recruitment trend that we observe is hence likely to be a consequence of the overexploitation for the majority of the stocks.

However, for some populations, an environmental control of population dynamics is more likely than an anthropic control through exploitation. This is obviously the case for the Eastern Baltic cod (figure 9), that produced strong recruitments in the 70's, when stock level was not very high. The decrease of recruitment occurred when the stock was at his highest level. Then, in the mid 80's, the a decrease of SSB followed that of recruitment. The good recruitments of the end of the 70's have been related to a favourable environment (in fact an, increase of the hydrological "spawning volume" defined by Sparholt, (1996)). Herring populations have since long time experience strong abundance fluctuations, with periods where it nearly disappeared and periods of outburst, that have been related to climate variations (Alheit and Hagen, 1997). For instance, the reduced inflow of oceanic water into

the northern North Sea was suspected to be responsible for the recruitment failure of herring during the 70's (Corten, 1990, Corten and de Kamp, 1992). The increase in recruitment of herring in the mid 80's correspond to the reappearance of two oceanic copepod species, that had declined since the period of reduced inflow that begun in the 60's (Corten, 1999).

Moreover, our analysis suggest that many populations have experienced concordant variations, and synchronous step-like changes of recruitment level. These strong changes were recorded between 1986 and 1988 for gadoids, and between 1979 and 1984 for herring. The end of the 80's is also characterised by an increase in SST in the Irish Sea, North Sea, English Channel, Baltic Sea, and to a lesser extend Celtic Sea and West of Scotland. However, if the timing of the shift in recruitment and SST is the same, the correlations displayed in the table 2 are weak. On the opposite, recruitment trends seem to be more related to the climatic indices. The decrease of gadoids is strongly correlated to the increase of NHT and ACI, as well as the first PC of the herrings. The influence of the NAO is non significant. The climate variations may not affect populations through a simple physical variable, such as SST. Global climatic indices may constitute proxies of the suite of changes of the physical environment that can influence biology in an ecosystem (Stenseth et al., 2003) and hence, better explain the ecological changes.

Furthermore, the changes in fish recruitment match with that detected in the plankton. Beaugrand and Reid (2003) showed that the main changes in the planktonic species were concurrent with the changes in SST and NHT and occurred between 1984 and 1988. These changes in the plankton were detected in the North Sea, but also in more oceanic area, such as west of Scotland. For phytoplankton, the changes for Faroe and Iceland are different than those of the areas around British Islands. Recruitment of fish populations of these to areas are not synchronous with other populations. These differences are also obvious in the variations of SST. Climate variability seems hence to have different local consequences both on physical environment and on population biology.

As our primarily question was to test the existence of a regime shift in the North East Atlantic, we have to see if the changes we show here follow the definition of deYoung et al.(2004) of a regime shift : “changes in marine system function that are relatively abrupt, persistent, occurring at a large spatial scale, observed at different trophic levels and related to climate forcing”. The changes that occurred in fish recruitment meet some of these criterions. They for instance concern all trophic levels, from the herring, to the cod and are concurrent with changes in the lower trophic levels of the plankton. According to ADS and cumulated sums methods, these changes occur relatively fast. This is particularly obvious in some time series of the figure 9. For North Sea cod, Irish Sea plaice or West of Scotland whiting, the step - like change is particularly clear in the time series. Changes in the recruitment of fishes seem to be well related to the global warming, the persistent positive anomalies of the NAO, and their local consequences on the weather. However, exploitation is an other potential forcing factor, that can as well explain the trends in recruitment. Furthermore, the spatial scale of the shift is restricted to the North Sea, Irish Sea and West of Scotland. The Baltic Sea, at least for cod, seems to have experienced the same changes. However, for Iceland, Faroe and Arctic on one side, and the Celtic Sea on the other, the changes in recruitment do not match with this shift. For other area, such as Bay of Biscay and the Iberian waters, the time series were too short to include the populations in the PCA. Finally, the two regimes that we distinguish are only 15 years long. A PCA performed on a restricted set of populations for the period 1960-1998 indicates that the first regime may have existed since at least the 60's. Time

series are for the moment too short to say if the shift in recruitment that occurred at the end of the 80's led to a stable new regime, or if this change goes on.

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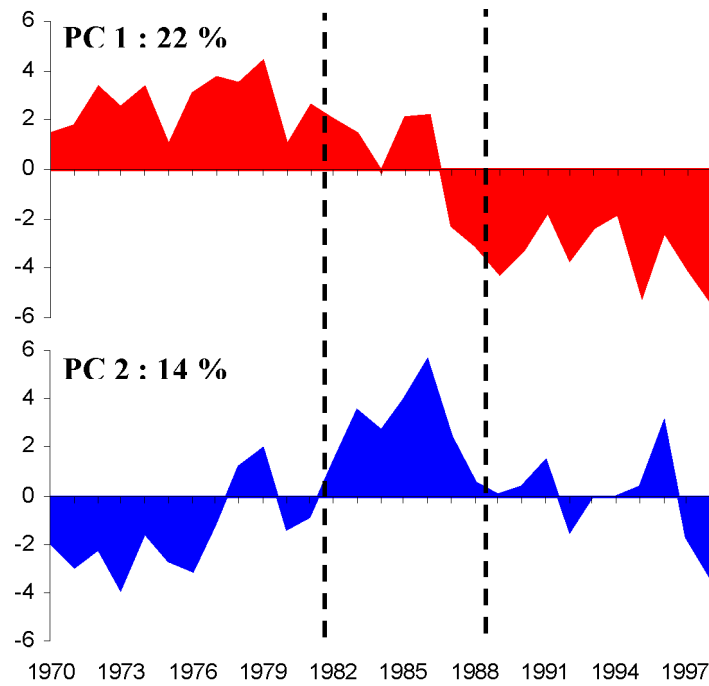


Figure 1 : The first and second principal components of a PCA performed on recruitment time series of the north Atlantic fish populations. Vertical bars show the 1982 and 1988 transitions detected by cluster analysis (see figure 5).

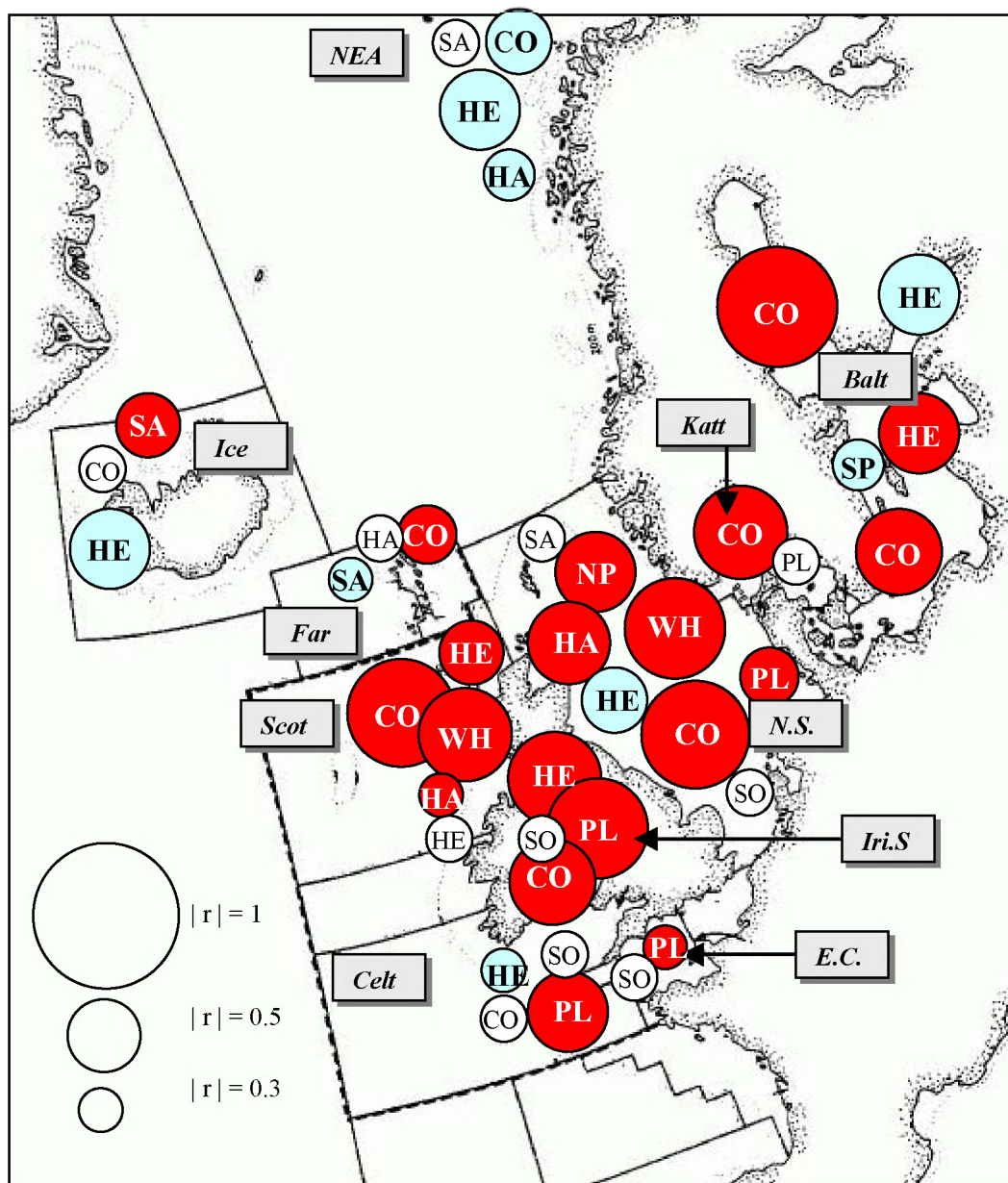


Figure 2 : correlations between population recruitment time series and PC1. The size of the circles is proportional to the absolute correlation value. White circles are for the weak correlations ($-0.3 < r < 0.3$), blue circles for negative correlations ($r < -0.3$) and red circles for positive correlations ($r > 0.3$). Codes for species are CO : cod, HA : haddock, HE : herring, NP : Norway pout, PL : plaice, SA : saithe, SO : sole, SP : sprat, WH : whiting. Codes for the ICES fishing areas are : *N.E.A.* : North East Arctic, *Balt* : Baltic Sea, *Ice* : Iceland, *Far* : Faroe, *Scot* : West of Scotland, *Katt* : Kattegat, *N.S.* : North Sea, *E.C.* : English Channel, *Iri.S.* : Irish Sea, *Celt* : Celtic Sea.

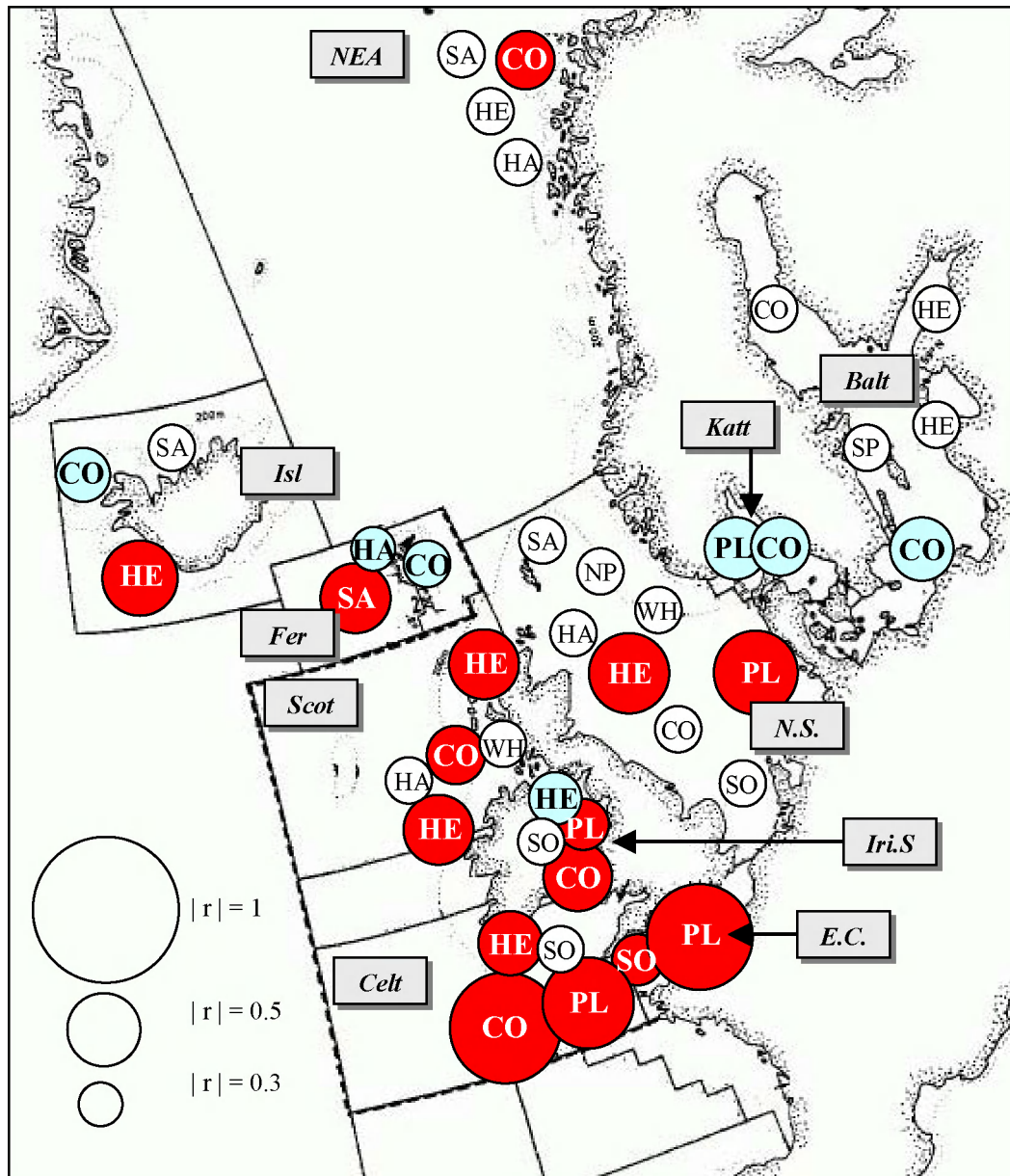


Figure 3 : correlations between population recruitment time series and PC2. Codes are the same as for figure 2.

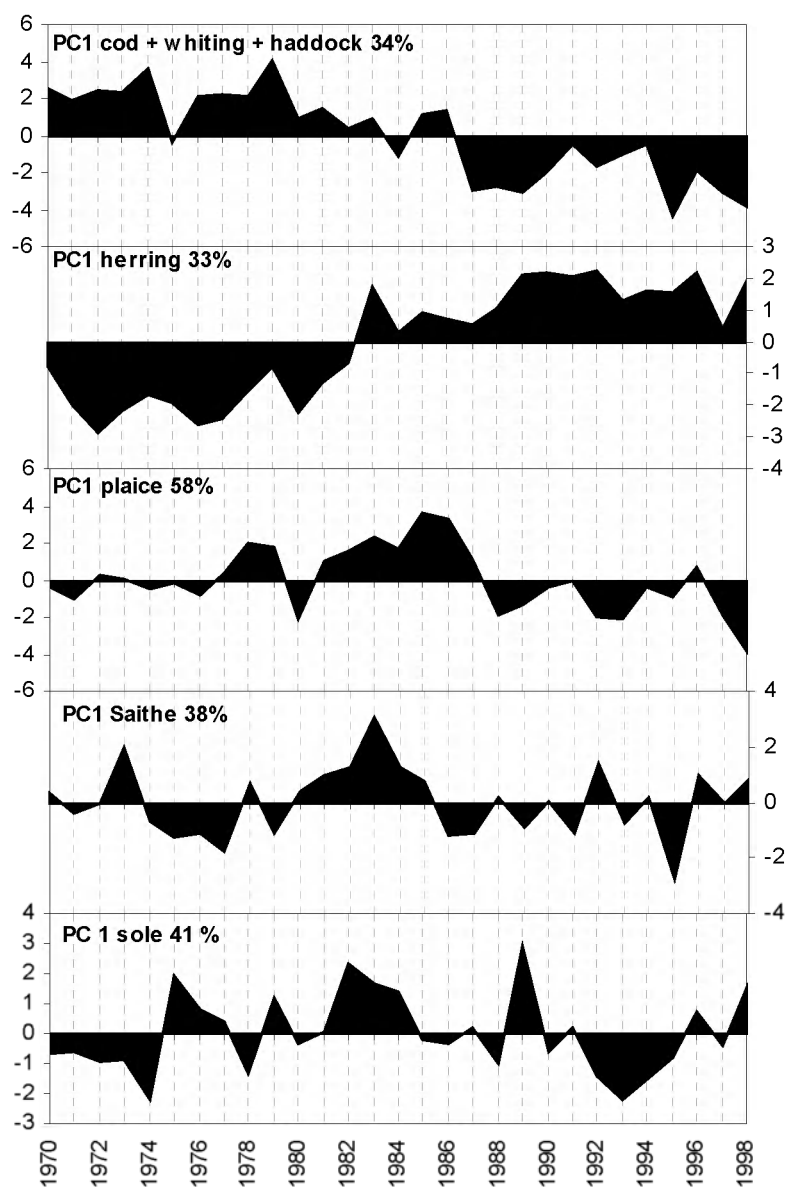


Figure 4 : first components of PCAs performed for each species or group of species.

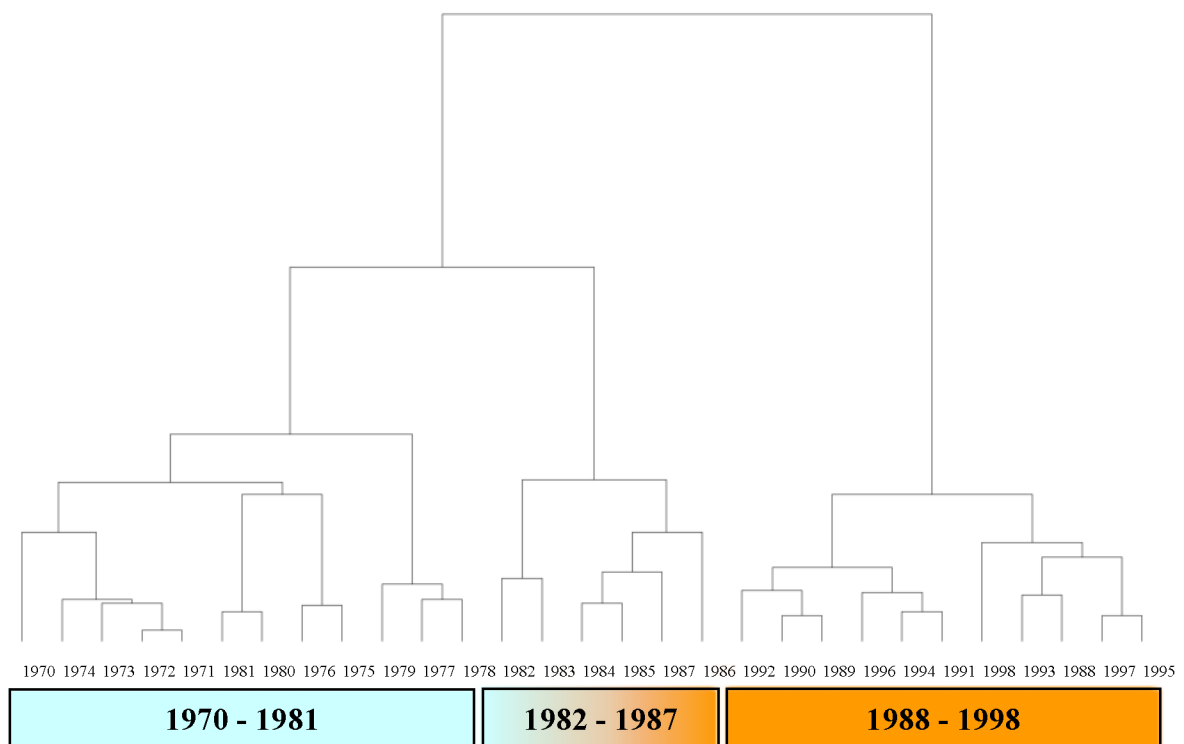


Figure 5 : Dendrogram of the cluster analysis performed on the recruitment time series of the 40 fish populations for the period 1970-1998.

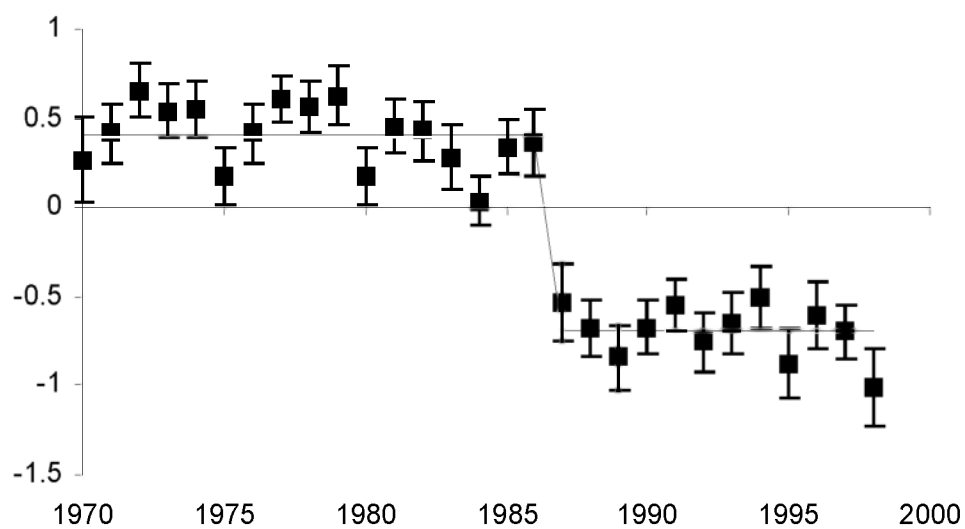


Figure 6 : composite indices (ASD method) of the 40 fish recruitment time series for an hypothetical regime shift occurring in 1986.

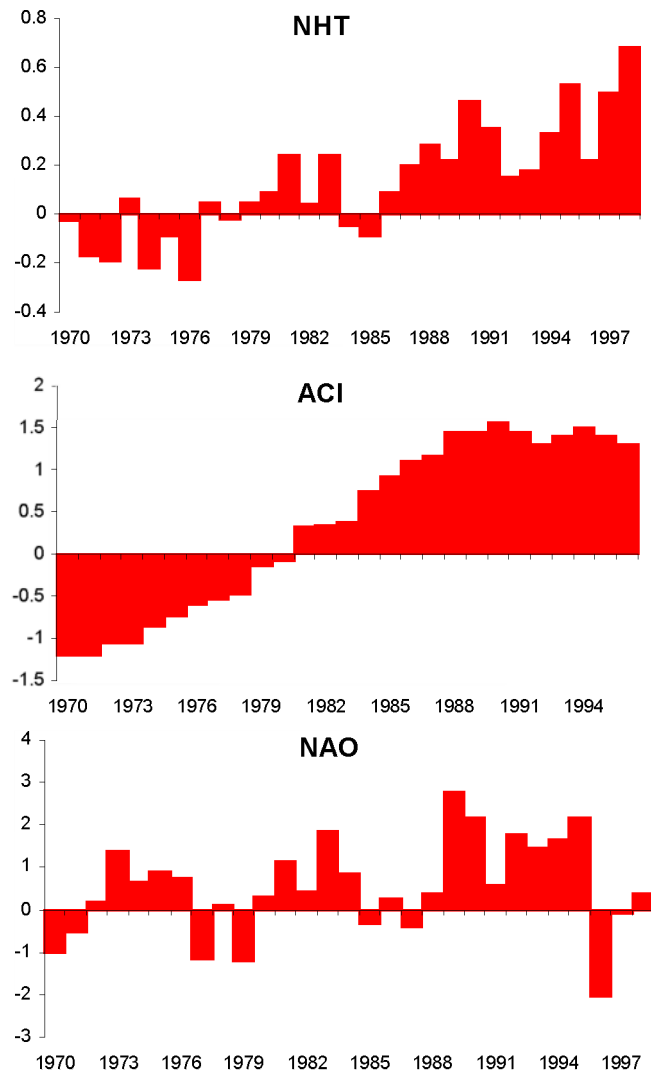


Figure 7 : time series of the climatic indices (NHT : north hemisphere temperature anomalies, ACI : atmospheric circulation index, NAO : north Atlantic oscillation).

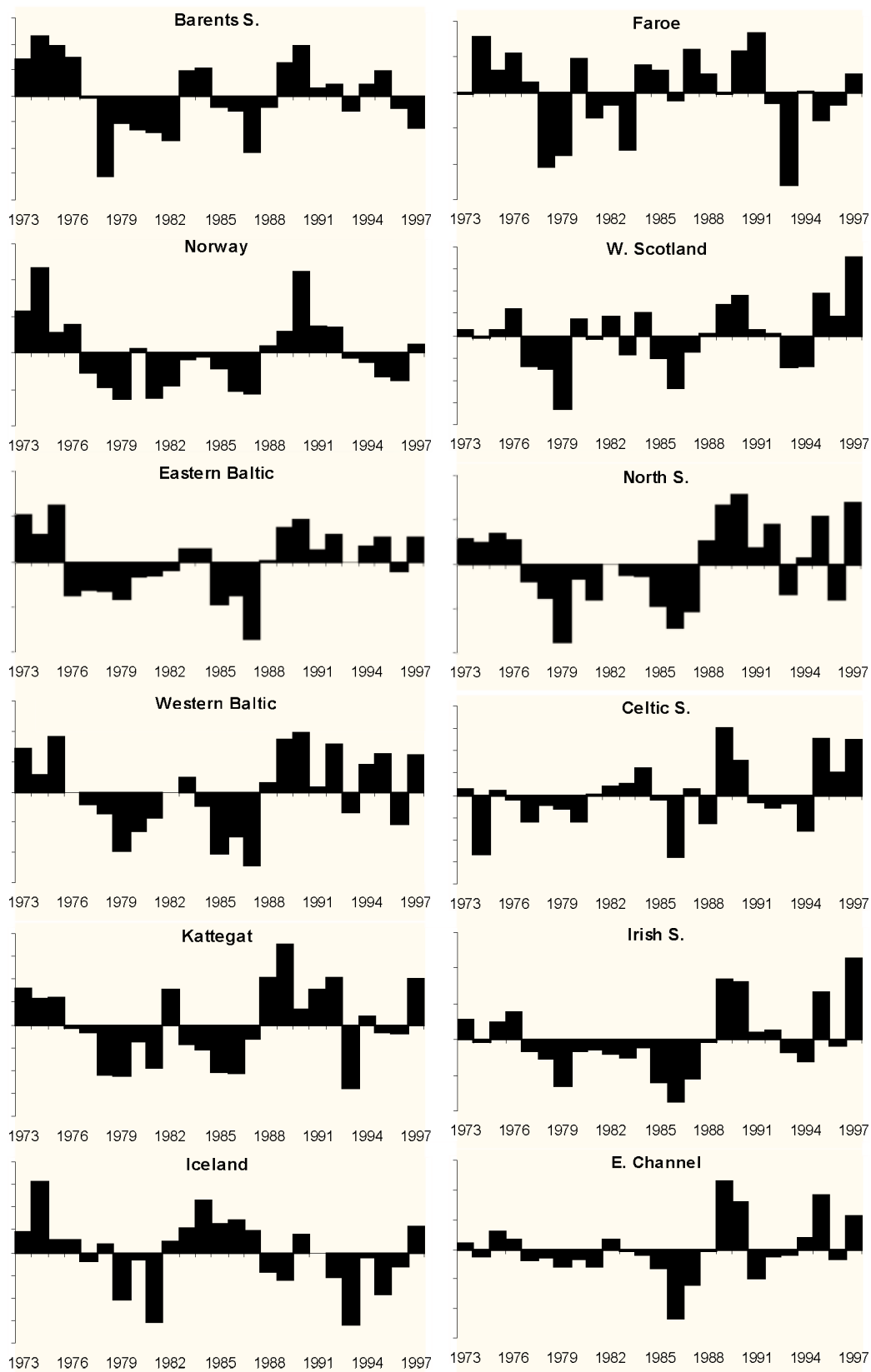


Figure 8 : time series of the annual SST anomalies for each ICES fishing area.

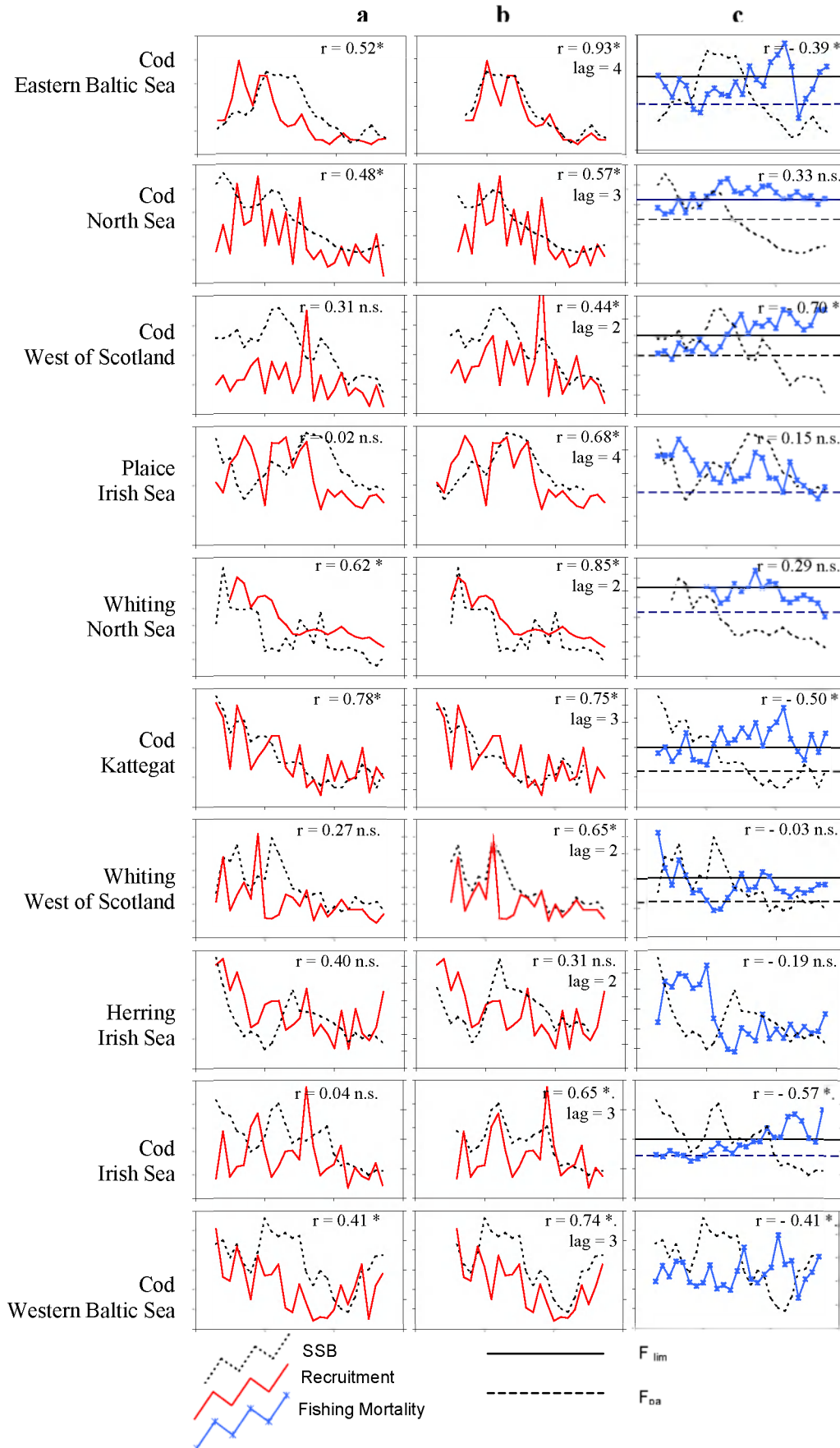


Figure 9 : relationship between recruitment, spawning stock biomass and fishing mortality time series for the populations positively loaded on PC1. a : SSB and subsequent recruitment time series, b: recruitment and SSB lagged to fine the maximal correlation, c : SSB and fishing mortality time series, with F_{lim} and F_{pa} .

* and n.s. correspond respectively to significant at the 1% level and non significant correlations.

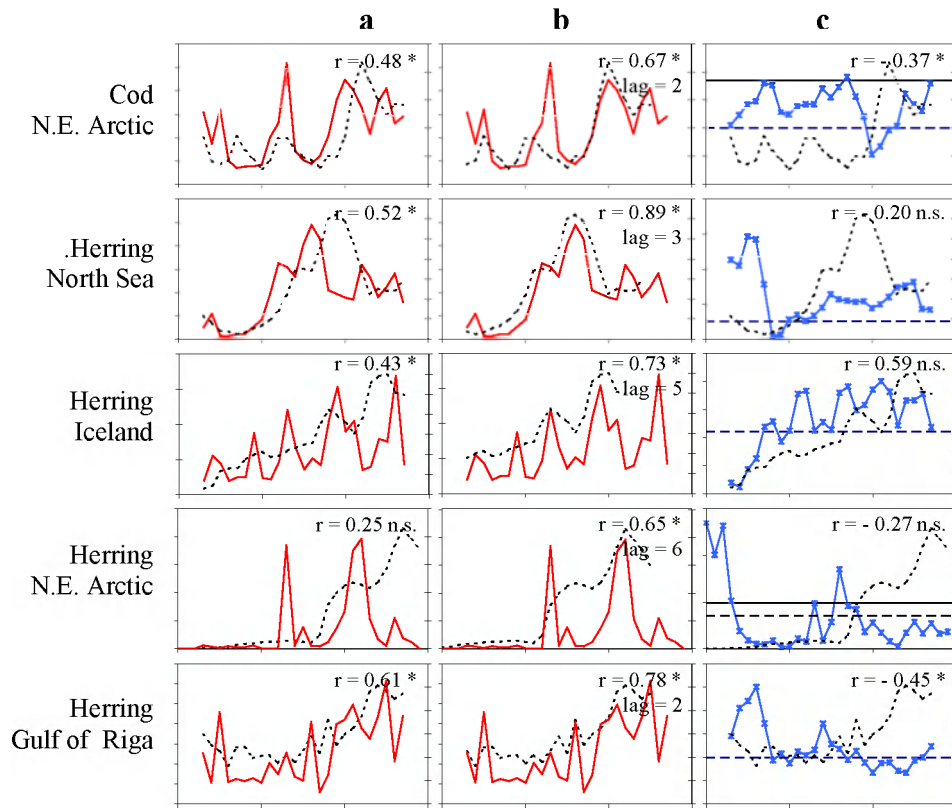


Figure 10 : relationship between recruitment, spawning stock biomass and fishing mortality time series for the populations negatively loaded on PC1.

Stock	Year of change	Mean recruitment		% of change (with probability)	
		First period	Second period		
Cod					
N.E. Arctic	1988	455	655	44%	*
Baltic Sea (West)	1982	109	53	-51%	***
Baltic Sea (East)	1986	410	122	-70%	***
North Sea	1986	480	216	-55%	***
Celtic Sea	1980	3	5	95%	***
Irish Sea	1987	9	5	-47%	***
Kattegat	1984	20	10	-52%	***
Iceland	1982	212	139	-34%	*
Faroe	1983	17	14	-17%	n.s.
West of Scotland	1986	12	8	-32%	*
Haddock					
N.E. Arctic	1981	75	160	113%	n.s.
North Sea	1986	46260	22142	-52%	*
Faroe					
West of Scotland					
Herring					
West of Scotland (North)	1986	1256	853	-32%	n.s.
Baltic Sea	1984	24255	15092	-38%	***
Celtic Sea	1979	266	531	100%	***
Baltic Sea (G. of Riga)	1988	1688	3399	101%	***
N.E. Arctic	1982	4959	104675	2011%	***
Iceland	1982	333	771	132%	***
North Sea	1980	15274	50539	231%	***
Irish Sea	1982	299	151	-50%	***
West of Scotland (South)					
Norway pout					
North Sea	1983	188017	101527	-46%	***
Plaice					
Celtic Sea	1987	7	4	-44%	***
Kattegat					
North Sea					
English Channel					
Irish Sea	1987	17	10	-42%	***
Saithe					
North Sea					
N.E. Arctic					
Iceland	1986	38	21	-45%	***
Faroe	1979	17	33	96%	***
Sole					
Celtic Sea					
North Sea					
Irish Sea					
English Channel	1989	5	4	-19%	n.s.
Sprat					
Baltic Sea	1987	54944	98720	80%	n.s.
Whiting					
North Sea	1988	32804	15504	-52 %	***
West of Scotland	1981	136	78	-43%	*

Table 1 : test of transition for individual populations. Transition dates were detected by application of cumulative sums (no data for populations when cumulated sums plot did not show any clear change). Differences in mean recruitment between the first and second periods were tested (Student test) to see the relevance of recruitment level change.

	PC1 all	PC2 all	PC1 gadoid	PC1 sole	PC1 plaice	PC1 herring
Climate index						
NHT	-0.79***	0.10	-0.75***	0.06	-0.39*	0.71***
ACI	-0.73***	0.61***	-0.79***	0.03	-0.03	0.90***
NAO	-0.37	-0.12	-0.35	-0.02	-0.25	0.33
SST anomalies						
E. Baltic Sea.	-0.38	-0.47*	-0.28			0.19
W. Baltic Sea.	-0.43*	-0.56***	-0.35			0.18
N.E. Arctic	-0.17	-0.52***	-0.02			0.01
Faroe	-0.11	-0.20	-0.13			-0.10
Iceland	-0.05	0.15	-0.05			0.03
Kattegat	-0.45*	-0.46*	-0.40*		-0.54***	
English Ch.	-0.49*	-0.45*		0.19	-0.52***	
Celtic Sea	-0.56***	-0.07	-0.63***	0.44*	-0.19	0.34
Irish Sea	-0.55***	-0.57***	-0.51***	0.07	-0.65***	0.13
North Sea	-0.55***	-0.58***	-0.49*	-0.03	-0.66***	0.18
W of Scotland	-0.55***	-0.39	-0.59***			0.13
Barents Sea	-0.13	-0.34	-0.04			0.09

Table 2 : correlations between fish recruitment (principal components 1 and 2 of PCA on all populations, and first component for species) and climate and SST (correlation significant at : *** : 1%, * : 5% level).