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Effect of climate on recruitment success of clupeid stocks in the North Atlantic

M. Cardinale, J. Hjelm and M. Casini

Abstract
Environmental factors have recently been modelled to explain recruitment variability of fish stocks in different sea areas. Among those factors, temperature is often the principal variable investigated since temperature regulates the rate in many ecological and physiological processes. Temperature is assumed to influence recruitment directly, through egg and larval survival, or indirectly via its effects on productivity at lower trophic levels. Although several studies have investigated the effect of temperature on recruitment success of several gadoid species in the North Atlantic, a similar analysis is lacking for pelagic species in the same area. In this study, we explore spawning stock biomass and recruitment data for herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) stocks in the North Atlantic in relation to temperature and NAO (North Atlantic Oscillation) variation and their geographic distribution. We used a synthetic approach and argue that including several stocks and areas and long time series of both biotic and abiotic factors are needed to determine generality in biological processes. Our results suggest that recruitment and recruitment success of the Baltic stock-complex are positively related to temperature and NAO while the opposite applies for the North Sea stock-complex. In contrast, recruitment success was not related to temperature in any of the analysed North West Atlantic stocks. Our correlative analysis suggest that recruitment and recruitment success of the North West Atlantic stocks is more dependent on spawning stock biomass then on temperature and NAO compared to North East Atlantic stocks. This implies that the dynamic of North East Atlantic stocks is more dependent to climate shifts than in the North West part of the Atlantic.

Keywords: Pelagic fish; climate changes; population dynamic

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Introduction

The effects of climate variability on the recruitment dynamics of different fish stocks have recently received a great deal of attention (i.e. Daskalov 1999; Marshall et al. 2000; Jarre-Tiechmann et al. 2000; Saetre et al. 2002; Cardinale and Hjelm 2004). Although determining what factors control recruitment dynamics remains a difficult task (Myers and Barrowman 1996; Planque and Fredou 1999; Needle 2002 for a useful review), including climate variability into stock assessment models represents the next logical step to increase the predictability of stock dynamic and to improve management of fisheries resources. Nevertheless, testing the general hypothesis of environment-recruitment correlations should also include the correction for SSB since many trends in recruitment are also a result of changes in SSB (Myers and Barrowman 1996; Myers 1998; Cardinale and Hjelm 2004). In this context, the stock specific recruitment success (R_s) is considered a particularly valuable index of recruitment success of marine fishes when exploring possible environmentally mediated events (Beverton 2002; Cardinale and Hjelm 2004).
Temperature is often the principal variable investigated since temperature regulates many ecological and physiological processes. Temperature is assumed to influence recruitment directly, through egg and larval survival, or indirectly via its effects on productivity at lower trophic levels (Rothschild 1994). Alternatively, wind-induced

turbulence may also influence the larval growth and survival by affecting temperature and availability of zooplankton (i.e. prey encounter rate) (Ottersen and Sundby 1995) or via retention effect in areas characterised by unfavourable hydrographic conditions (Jarre-Teichmann et al. 2000; Hinrichsen et al. 2002).

Large-scale climatic oscillation, as reflected by NAO (Hurrel 1995), governs the pattern and strength of the wind, temperature and precipitation over the North Atlantic (Hurrel 1995). Thus, NAO is considered a proxy for climate stochasticity in the North Atlantic. NAO is strongly related to winter temperature, wind and precipitation particularly in Northern Europe and on the Northeast American coasts (Ottersen et al. 2001). At the same time, NAO is related to alterations in the direction of strength of oceanic surface currents that are governed by variable wind conditions (Ottersen et al. 2001). Variability in wind is known to affect both zooplankton production (Planque and Taylor 1998) and retentions and transport mechanisms of fish larvae (Ottersen et al. 2001) and in turn, it may contribute to regulate recruitment dynamic of fish species.

In this study, we focus on the effect of the variation in temperature and NAO on the recruitment success of clupeid (*Clupea harengus and Sprattus sprattus*) stocks in the North Atlantic. Although a number of studies have investigated the effect of temperature and NAO on recruitment dynamic of several gadoid species in the North Atlantic (e.g. Planque and Fredou 1999; Cardinale and Hjelm 2004), a similar analysis is lacking for pelagic species in this area. We limit the discussion to abiotic factors (temperature, wind, water inflow etc) although biotic factors (predation, competition, stock structure, food availability, etc) are also known to play a key role on recruitment processes. We argue that a synthetic approach including several stocks and areas and using long time series of both biotic and abiotic factors are needed to determine generality in these biological processes.

Materials and methods

Time series

Stock and recruitment

We compiled data available at the International Council for the Exploration of the Sea (ICES), <<http://www.ices.dk>>, the Northwest Atlantic Fisheries Organization (NAFO), <<http://www.nafo.ca>> and Ransom Myers web site, <<http://www.mscs.dal.ca/~myers/welcome.html>>. The time series used in the analysis included: herring (19) and sprat (2) stocks (Table 1). Their geographical distribution is shown in Figure 1. Yearly estimates of spawning stock biomass (SSB) and number of recruits (R) are given in tonnes and thousands of individuals, respectively. Values of SSB, R, natural mortality (M) and fishing mortality (F) are VPA (Virtual Population Analysis) model based and are the official estimates of ICES and NAFO.

Temperature and North Atlantic Oscillation (NAO) data

When using temperature data for correlation with stock parameters, we assume that these indices mirror the environment inhabited by the stock. This is obviously not the case since either the depth or the period of the year where the mechanistic effect of temperature acts on recruitment is highly species, stock and area dependent. Therefore, in order to cover the whole time-series and the whole North Atlantic, we were forced to use sea surface temperature (SST) data. Estimated mean SST values for the distribution area of each stock were compared with bottom temperature values

(i.e. stock ambient temperature) used in Brander (1995) for a similar study on cod. We are aware that SST is not stock ambient temperature but there is a strong correlation between bottom temperature and SST. Bottom temperature as used by Brander (1995) was strongly significantly correlated ($r^2 = 0.81$; $p < 0.01$) with SST used in this study. However, clupeids are pelagic species and therefore SST is reasonably a more reliable index of their ambient temperature than for cod. Temperature data for the different areas of the North Atlantic were available at <<http://sgi62.wwb.noaa.gov >>. Monthly average at the spatial resolution of 1 degree of latitude and 1 degree of longitude were available from 1854 to 2003.
We used the Hurrel´s winter (December to March) index of the NAO, measured as the difference in normalised air pressure at the sea level (SLP) between Ponta Delgades (Azores) and Reykjavik (Iceland) (Hurrel 1995; Hurrel et al. 2003). Strong positive phases of the NAO are often associated with above-normal temperatures and precipitation in the eastern United States and across northern Europe and below-normal temperatures and precipitation in Greenland and across southern Europe (Hurrel 1995). Opposite patterns of temperature and precipitation anomalies are typically observed during strong negative phases of the NAO. The NAO winter index data were available at http://www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html

Statistical analysis
Estimates of R are given for different age classes depending on the stock assessed. To allow for stock comparisons, we chose to estimate R as the number of age 1 individuals. For those stocks where the numbers of age 1 individual were not available the logistic equation (Hilborn and Walters 1992) was applied. The logistic equation is defined as:

$$N_t = N_{t+1} \cdot \exp^{(-F+M)}$$

where N_t is the number of individuals at age t, N_{t+1} is the number of individuals at age $t+1$, F is the fishing mortality and M is the natural mortality. M is age and stock specific (as within ICES and NAFO assessment framework) while F is the value estimated for the youngest age present in the assessment. Year-specific F values were used in the analysis. Those F values are VPA model estimated while M values are either MSVPA (Multi Species Virtual Population Analysis) estimates or defined by ICES and NAFO.
Moreover, to make the number comparable for spring and autumn spawners, the number of spring spawners as 1-ringer were negatively adjusted for a natural mortality of 0.075 per month for 2 months (see Toresen 2001).
The stock specific recruitment success (R_s) was estimated as *Ln* (R/SSB). Generally, because of the shape of the stock-recruitment curves, the R_s are improving as the stock falls. Thus, in time when the stocks are overexploited, R_s increases when the stock declines (Beverton 2002). However, in case of environmental mediated events, as it is the case of survival in the early life history, the situation is reversed. When the stock is declining, the effect of the environment on R_s is that it decreases at roughly the same rate as the stock decreases. This can result in that R_s instead of increasing may stay constant or even possibly decline slightly as the population density stabilize when the stock decreases. As a consequence, R_s is considered a particularly valuable index of recruitment success of marine fishes especially when investigating possible environmental mediated events (Beverton 2002). Mean value and 25% and 75% percentiles of R_s for each stock were estimated using a bootstrapping technique with

1000 replicates.

Climate and recruitment

The relationship between R_s and SSB is considered approximately linear (Hilborn and Walters 1992, Beverton 2002). As defined below, the variability around this relationship may be determined by the stochasticity in the environment (Beverton 2002). Thus, we fitted a simple deterministic linear model:

$R_s = \alpha - \beta \cdot SSB$ (1)

Where parameters α and β are respectively the intercept and slope of the linear regression. For those stocks where the slope of (1) was significant different (at 5% probability) from 0, the residuals from the fitted linear model were estimated. The residuals of the relationship between R_s and SSB are defined hereafter as recruitment anomalies (R_a). R_a values were correlated with temperature and NAO fitting a polynomial model of second order to allow the data to specify the functional form of the relationship. For those stocks where the relationship between R_s and SSB was not significant, the relationships between absolute values of R (without SSB correction) and temperature and between R and NAO were tested fitting a linear model.

Furthermore, we performed a Principal Component Analysis (PCA) based on covariances using the following variables for each stock: the correlation coefficients of the SSB - R_s relation, the correlation coefficients of the temperature and NAO - R_s and the average value of R_s.

We did not account for time-series autocorrelation in this study although autocorrelation might represent a serious problem here (see Needle 2002 for an useful discussion). At the same time, stock and recruits are commonly derived from the same catch-at-age analysis and thus cannot be considered as independent variables (Needle 2002). However, the scope of this analysis was not to develop the best stock-recruitment model for prediction but to compare the relationship between recruitment anomalies and temperature and NAO. Therefore in this context accounting for autocorrelation was not considered necessary. Statistical analysis was performed using Statistica (1995) and S-Plus (2001) computer softwares.

Results

The mean R_s for each clupeid stock with the 25% and 75% percentiles suggest that there is, on average, a difference in R_s between the west and east Atlantic and generally are the R_s kower for west Atlantic clupeids (Table 2). The relationship between R_s and SSB was not significant for four stocks (two herring and two sprat stock, 19 % of analysed stocks) (Table 3). The strength of the effect of spawning biomass on R_s was much larger (in terms of both the number of stocks where the relation was significant and strength of the correlation) for stocks in the North West than in the North East Atlantic. For those stocks where the relationship between R_s and SSB was significant (17 herring stocks), R_a were estimated and successively tested for correlation with the temperature and NAO (Figure 2). Generally, temperature was more related to recruitment anomalies and recruitment than NAO for those stocks were a significant relationship was found. A total of three stocks showed a significant ($p < 0.05$) relationship between temperature and recruitment anomalies while one stocks showed also a significant relationship between NAO and recruitment anomalies (Table 3). Among those, all belong to North East Atlantic stocks while

none of the North West Atlantic stocks showed a significant correlation between R_s and temperature or NAO. North Sea herring and Irish Sea herring showed a negative relation between R_s and temperature while Norwegian Spring spawning herring had a positive relation with higher recruitment success than expected associated with high temperature.
For those stocks (4) where the relationship between R_s and SSB was not significant, three belong to the Baltic stocks complex (Figure 3). Those stocks showed also a significant positive relation between recruitment (in absolute values) and both temperature and NAO (Table 2) while North Sea sprat is the only stock where recruitment success and recruitment are both independent from spawning biomass and climate variability.
The clear distinction in R_s for clupeids in the west and east Atlantic was also supported by a PCA that showed a clear separation between NEA and NWA stocks (Figure 4). The first factor explained 97% of the variance and we regressed this PC score against longitude, latitude (the centroid of the stock distribution) and average SST of each stock. The largest correlation was found with the longitude ($r^2 = 0.73$) of although also the relation between the first PC score and the latitude and SST were significant ($r^2 = 0.34$ and 0.36, respectively; $p < 0.05$).

Discussion

Overall, we found a similar effect (i.e. similar form of the functional relationship between recruitment and NAO or temperature) of temperature and NAO on recruitment dynamics of North Atlantic clupeid stocks. This fact is not an unexpected since temperature and NAO are strongly positively correlated (Hurrel et al. 2003). However, when a climate effect was present, temperature was more associated to recruitment than NAO in all stocks analysed. This implies that temperature should be used into modelling of climate effect on recruitment of clupeid stocks and thus we refer to temperature correlation only hereafter.
Our results suggest that recruitment and recruitment success of the Baltic clupeid stock-complex are positively related to temperature while the opposite applies for the North Sea clupeid stock-complex. In contrast, recruitment success was not related to temperature in any of the analysed North West Atlantic stocks. Our analysis suggest that recruitment and recruitment success of the North West Atlantic stocks is more dependent on spawning stock biomass then on temperature and NAO compared to North East Atlantic stocks. This implies that the dynamic of North East Atlantic stocks is more dependent to climate shifts than in the North West part of the Atlantic.
Previously, recruitment of Gulf of Riga herring has been found corrrelated to temperature (Kornilovs 1992). Similar temperature dependent recruitment has been suggested for Central Baltic herring (Axenrot and Hansson 2003) and Baltic sprat (Mackenzie and Köster 2004 and references therein) and hence it appears to be a general pattern of clupeid stocks recruitment in the Baltic Sea ecosystem (this study). Moreover, laboratory experiments have shown that eggs and larvae produced by sprat have a significant increased mortality at lower temperature (Nissling 2003). This may support the hypothesis of a positive effect of temperature on metabolism of eggs and larvae survival of clupeid in the Baltic area. Overall it can be suggested that the Baltic clupeid stock-complex is at it distribution boarder. The importance of temperature in determining large year class for the Baltic complex stocks is highlighted by the lack of relation between spawning biomass and recruitment success in three of five stocks analysed. In the North Sea clupeid complex, recruitment of Norwegian spring

spawning herring is showing a positive effect of temperature while recruitment a negative effected was found for North Sea herring. For Norwegian spring spawning herring, it can be suggested that this stock is at its distribution boarder similar to the Baltic clupeid stock-complex. The positive correlation between recruitment and temperature for this stock is in accordance with both correlative (e.g. Toresen 2001, Saetre et al. 2002) and laboratory studies (Fiksen and Folkvord 1999) although food availability seems to play an important role here (Fiksen and Folkvord 1999). For North Sea herring, there is contrasting information as both a positive (Toresen 2001) and a negative effect (Svendsen 1995) between recruitment and temperature has been suggested. However, in contrast to the Baltic complex, temperature effects are less pronounced for stocks in this area, as this complex is in a more central part of clupeid distribution. Nevertheless, the pattern observed may of course be related to other factors including biotic such as predation, competition, stock structure, food availability, although we deliberately have chosen to focus our study on abiotic factors only.

None of the stocks around the UK islands, except Irish Sea herring, showed a temperature effect on R_s and recruitment, which can also be explained by the fact that these stocks are in a more central part of the clupeid distribution. Unfortunately, there are no previous studies on the influence of climate on recruitment of those stocks. In contrast, recruitment success was not related to temperature in any of the analysed North West Atlantic clupeid stocks. On the other hand, similar studies conducted on herring and sprat stocks in other areas outside the Atlantic (i.e. Pacific Ocean and Black Sea) have shown an effect of temperature on year class strength (i.e. Daskalov 1999; Nagasawa 2001; Williams and Quinn 2000).

Management implications

The historical development of fish stocks is related to both natural external factors and anthropogenic influence of which fisheries is far the most important. The development of fisheries techniques may explain the rapid decline of several herring stocks during the 60´s (Toresen 2001), although an historical period of poor recruitment occurred at the same time, which can have affected the clupeid stocks (Toresen and Ostvedt 2000). In fact, it has been suggested that poor recruitment in combination with fisheries accelerated the already negative stock-size trend in several herring stocks including Norwegian spring spawning (Fiksen and Slotte 2002) and Georges Bank herring (Toresen 2001). However, stock productivity is also related to eggs numbers, and as a matter of fact, an effect of spawning biomass on recruitment success was evident for 81% of all stocks analysed in this study. This again stresses the fact that failing to account for spawning biomass effect in recruitment studies can mask any influence of climate variability on recruitment dynamic. Therefore, our approach, as advocated by Beverton (2002), is appropriate here because we are able to unravel stock productivity and climate by using the deviation from the theoretical relation between spawning biomass and recruitment success. This fact also indicate that previous studies, where absolute recruitment or recruitment success were used, are biased and not direct comparable to our study.

The link between recruitment and climate can be used to improve current deterministic or stochastic short term forecast used in stock assessment (MacKenzie and Köster 2004) as climatic shifts has a certain level of predictability (Marshall et al. 2001). In many cases, including abiotic variables in recruitment modelling of clupeid species, has lead to an improvement of the model fit (i.e. Daskalov 1999; Fiksen and Slotte 2002). Thus, the integration of consistent environmental proxies into stock

assessment models has the potential to increase our ability to manage fisheries resources and improve the predictability of the effect of fishing on exploited stocks. However, it is true that high (or low) temperature (or other climatic proxies) do not assure a large year class although it certainly increases the probability of eggs or larvae survival. Nevertheless, although specific mechanisms are not always fully understood, failing to include climatic shift into fisheries management may have implications that are often too serious to be ignored.
One final remark is that, in the last decade, several studies have suggested regime shift in the North Atlantic marine ecosystem (Worm and Myers 2003). Such shifts have obviously large ecological and socio-economic implications since they usually change both the relationship between marine organisms and the relative abundance of important commercial species. Even though regime shifts have been related to fisheries induced effect (Pauly et al. 2000) also large climatic changes can play a major role. For example, given the results presented here, a temperature increase in North East Atlantic result in better recruitment of the Baltic clupeid stock-complex whereas clupeid the North Sea stock-complex would experience a lower recruitment success. This could, in turn, have important implications for other throphic levels in the ecosystem.

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Table 1. The list of the stocks used in this study with the stock acronymous, the fishing area as defined by ICES and NAFO commissions, the latitude and longitude corresponding to the centroid of the distribution, the geographical location (i.e. side, NEA = North East Atlantic; NWA = North West Atlantic), the period of available data and the age of recruits to the fisheries. For details of the fishing areas refer to Figure 1.

Common name	Fishing area	Area	Stock acronym	Years	Age of recruits (years)	Lat	Long	Temp	CV temp
Central Baltic herring	**IIId (SDs25-29)**	NEA	**HCB**	**1974-2003**	**1**	57	21	8.82	4.98
Celtic Sea herring	**VIIe-j**	NEA	**HCS**	**1958-2001**	**1**	51	-5	12.94	2.96
Gulf of Riga herring	**IIId (SD 32)**	NEA	**HGR**	**1977-2003**	**1**	57.3	23.4	7.91	4.13
Irish Sea herring	**VIIaN**	NEA	**HIS**	**1961-2003**	**1**	54	-4.5	10.81	3.05
Iceland summer spawning herring	**Va**	NEA	**HISS**	**1981-2003**	**2**	63	-21	8.64	2.67
Northern Bothnian herring (SD 31)	**IIId (SD 31)**	NEA	**HNBB**	**1980-2003**	**1**	65	23	6.91	6.04
North Sea autumn spawners herring	**IV&VIId&IIIa**	NEA	**HNSA**	**1960-2003**	**1**	58	2	9.93	3.73
Norwegian spring spawning herring	**II&IVa**	NEA	**HNSS**	**1950-2003**	**1**	65	8	8.8	3.5
Southern Bothnian herring (SD 30)	**IIId (SD 30)**	NEA	**HSBB**	**1973-2003**	**1**	62	20	6.44	6.12
Western Baltic spring spawners herring	**IIIa&SDs 22-24**	NEA	**HWBSS**	**1991-2003**	**1**	55	12	8.83	5.14
West of Irland herring	**Via(S)&VIIb-c**	NEA	**HWI**	**1970-2003**	**1**	54.3	-12	12.14	2.79
Herring west of Scotland	**Via (N)**	NEA	**HWS**	**1958-2003**	**1**	57	-9	11.1	2.4
Baltic Sea sprat	**IIIb-d**	NEA	**SBS**	**1974-2001**	**1**	57	21	8.82	4.98
North Sea sprat	**IV**	NEA	**SNS**	**1984-2003**	**1**	58	2	9.93	3.73
Newfoundland herring Bonavista Bay&Trinity Bay	**3KL**	NWA	**HNFBBTB**	**1971-2001**	**2**	48.25	-52.45	5.48	7.6
Newfoundland herring St Mary´s Bay&Placentia Bay	**3KL**	NWA	**HNFMBPB**	**1970-2000**	**2**	46.4	-54	6.25	7.62
Newfoundland herring White Bay&Notre Dame Bay	**3KL**	NWA	**HNFWBNB**	**1971-2001**	**2**	50	-55	4.92	8.44
South Gulf of St Lawrence herring autumn spawners	**4T**	NWA	**HSSLAS**	**1978-2002**	**2**	47	-63	6.27	6.89
South Gulf of St Lawrence herring spring spawners	**4T**	NWA	**HSSLSS**	**1978-2002**	**2**	47	-63	6.27	6.89
West coast of Newfoundland herring spring spawners	**4R**	NWA	**HWNFSS**	**1965-2000**	**2**	49.25	-59	5.41	10.07
West coast of Newfoundland herring autumn spawners	**4R**	NWA	**HWNSAS**	**1965-1999**	**2**	49.25	-59	5.41	10.07

Table 2. The mean R_s for each stock with the 25% and 75% percentiles estimated with a bootstrapped technique with 1000 samples.

Common name	**Area**	**Stock acronym**	25%	75%	R_s
Norwegian spring spawning herring	NEA	HNSS	1.88	2.16	2.05
Iceland summer spawning herring	NEA	HISS	0.85	1.02	0.93
Herring west of Scotland	NEA	HWS	2.12	1.99	2.06
West of Irland herring	NEA	HWI	1.88	1.76	1.83
Celtic Sea herring	NEA	HCS	2.05	1.84	1.91
North Sea autumn spawners herring	NEA	HNSAS	3.06	2.93	3.01
Irish Sea herring	NEA	HIS	3.04	2.81	2.88
Western Baltic spring spawners herring	NEA	HWBSS	2.81	3.00	2.91
Central Baltic herring	NEA	HCB	3.04	2.95	3.00
Gulf of Riga herring	NEA	HGR	3.46	3.33	3.40
Southern Bothnian herring (SD 30)	NEA	HSBB	2.8	2.68	2.76
Northern Bothnian herring (SD 31)	NEA	HNBB	2.76	2.55	2.64
North Sea sprat	NEA	SNS	4.5	4.17	4.34
Baltic Sea sprat	NEA	SBS	4.41	4.21	4.32
West coast of Newfoundland herring spring spawners	NWA	HWNFSS	-0.45	-0.13	-0.31
West coast of Newfoundland herring autumn spawners	NWA	HWNSAS	-0.36	-0.62	-0.47
South Gulf of St Lawrence herring spring spawners	NWA	HSSLSS	1.07	1.34	1.19
South Gulf of St Lawrence herring autumn spawners	NWA	HSSLAS	1.47	1.23	1.34
Newfoundland herring White Bay&Notre Dame Bay	NWA	HNFWBNB	-0.73	-1.18	-0.97
Newfoundland herring Bonavista Bay&Trinity Bay	NWA	HNFBBTB	-0.49	-0.99	-0.76
Newfoundland herring St Mary´s Bay&Placentia Bay	NWA	HNFMBPB	-0.11	-0.39	-0.25

Table 3. Results of the regression analysis between R_s (recruitment success) and SSB (spawning stock biomass) (log-linear), recruitment (R) (in absolute numbers) against temperature and NAO (linear) and the residuals of the R_s - SSB regression (i.e. recruitment anomalies, R_a) against temperature and NAO (linear and second order polynomial, respectively) for all stocks analysed.

			SSB-R_s		R-temp linear		R-NAO linear		R_a-temp polynomial		R_a-NAO polynomial	
Common name	**Area**	**Stock acronym**	r^2	p	r^2	p	r^2	p	r^2	p	r^2	p
Norwegian spring spawning herring	NEA	HNSS	0.11	0.001					0.12	0.01	0.02	ns
Iceland summer spawning herring	NEA	HISS	0.15	0.05					0.02	ns	0.01	ns
Herring west of Scotland	NEA	HWS	0.20	0.002					0.02	ns	0.03	ns
West of Irland herring	NEA	HWI	0.35	< 0.001					0.03	ns	0.03	ns
Celtic Sea herring	NEA	HCS	0.15	< 0.001					0.10	ns	0.04	ns
North Sea autumn spawners herring	NEA	HNSAS	0.41	< 0.001					-0.11	0.03	0.01	ns
Irish Sea herring	NEA	HIS	0.14	0.015					-0.25	< 0.001	0.25	< 0.001
Western Baltic spring spawners herring	NEA	HWBSS	0.62	0.001					0.087	ns	0.01	ns
Central Baltic herring	NEA	HCB	0.31	0.001					0.03	ns	0.06	ns
Gulf of Riga herring	NEA	HGR	0.01	**ns**	0.47	< 0.001	0.27	0.003				
Southern Bothnian herring (SD 30)	NEA	HSBB	0.01	**ns**	0.51	0.002	0.14	0.03				
Northern Bothnian herring (SD 31)	NEA	HNBB	0.33	0.003					0.001	ns	0.001	ns
North Sea sprat	NEA	SNS	0.08	**ns**	0.007	**ns**	0.07	**ns**				
Baltic Sea sprat	NEA	SBS	0.10	**ns**	0.28	0.003	0.13	0.04				
West coast of Newfoundland herring spring spawners	NWA	HWNFSS	0.29	0.001					0.05	ns	0.10	ns
West coast of Newfoundland herring autumn spawners	NWA	HWNSAS	0.49	< 0.001					0.08	ns	0.01	ns
South Gulf of St Lawrence herring spring spawners	NWA	HSSLSS	0.64	< 0.001					0.06	ns	0.01	ns
South Gulf of St Lawrence herring autumn spawners	NWA	HSSLAS	0.67	< 0.001					0.01	ns	0.05	ns
Newfoundland herring White Bay&Notre Dame Bay	NWA	HNFWBNB	0.30	0.002					0.06	ns	0.01	ns
Newfoundland herring Bonavista Bay&Trinity Bay	NWA	HNFBBTB	0.59	< 0.001					0.04	ns	0.01	ns
Newfoundland herring St Mary´s Bay&Placentia Bay	NWA	HNFMBPB	0.33	0.001					0.01	ns	0.01	ns

Figure 1. Map of the ICES and NAFO fishing areas.

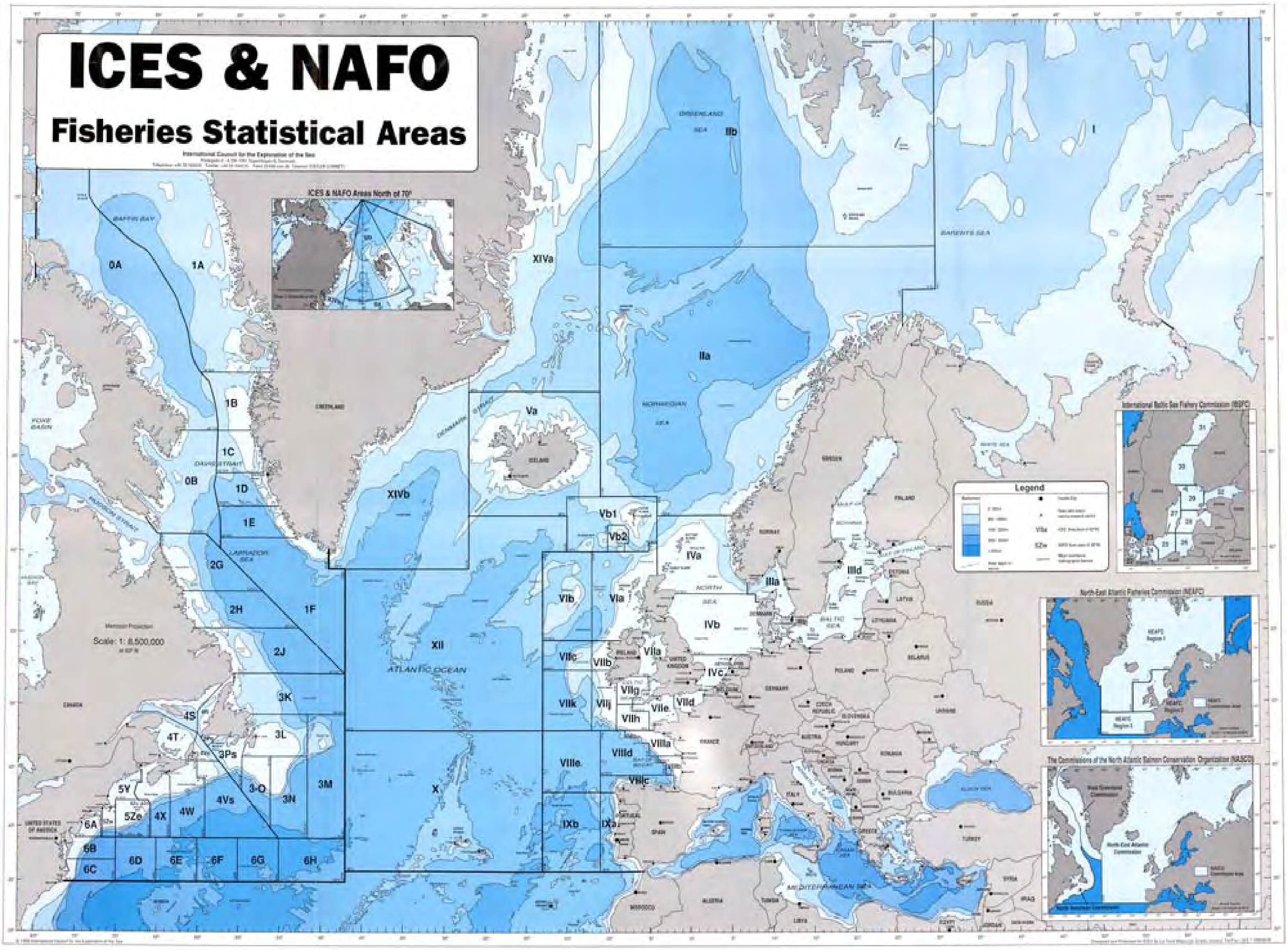

Figure 2. The relationship between recruitment (in thousands of individuals) and the NAO index estimated for those stocks where the $R_s \sim SSB$ regression was not significant. Only stocks with a significant (i.e. $p < 0.05$) relationship are shown. Superimposed lines are fitting from a linear regression or a second order polynomial model.

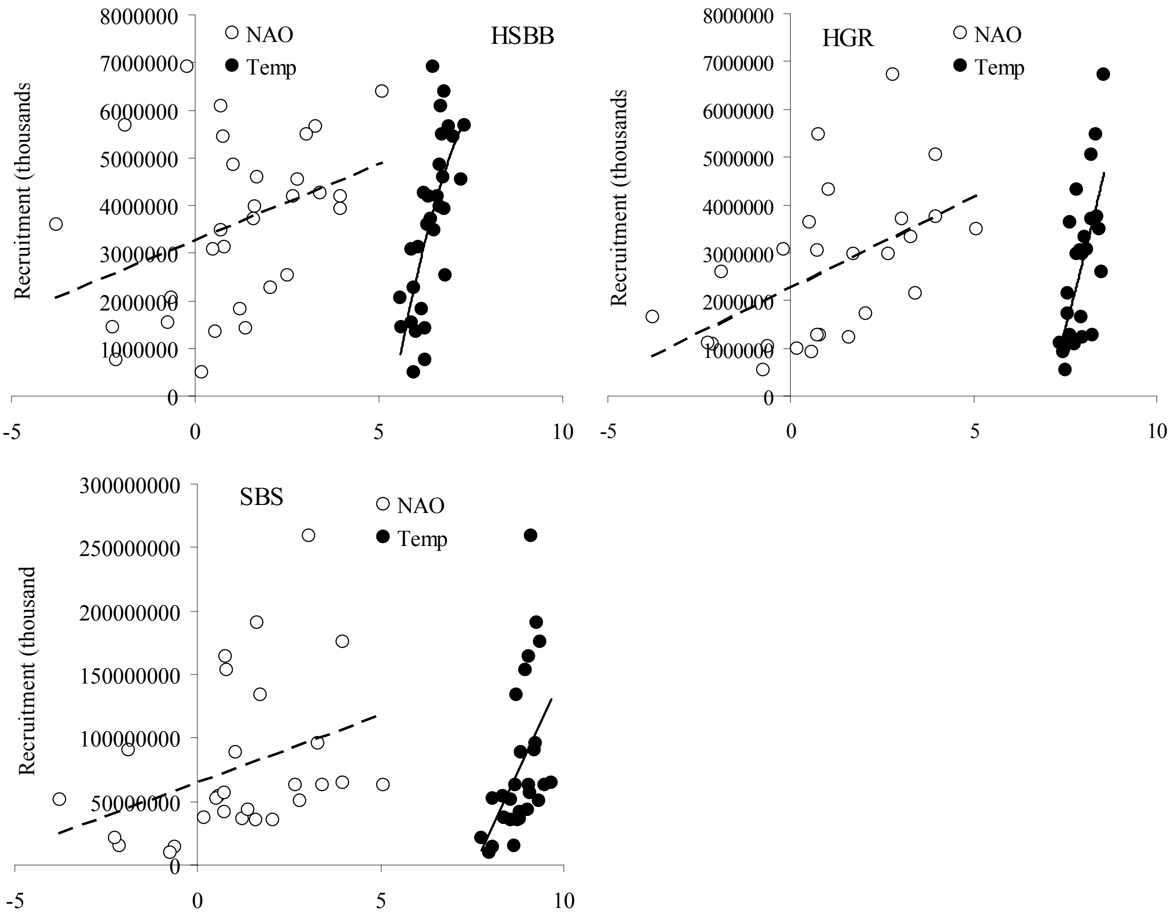

Figure 3. The relationship between the residuals of the $R_s \sim SSB$ regression (i.e. recruitment anomalies) and the NAO. Only stocks with a significant (i.e. $p < 0.05$) relationship are shown. Superimposed curves are fitting from a linear or second order polynomial model.

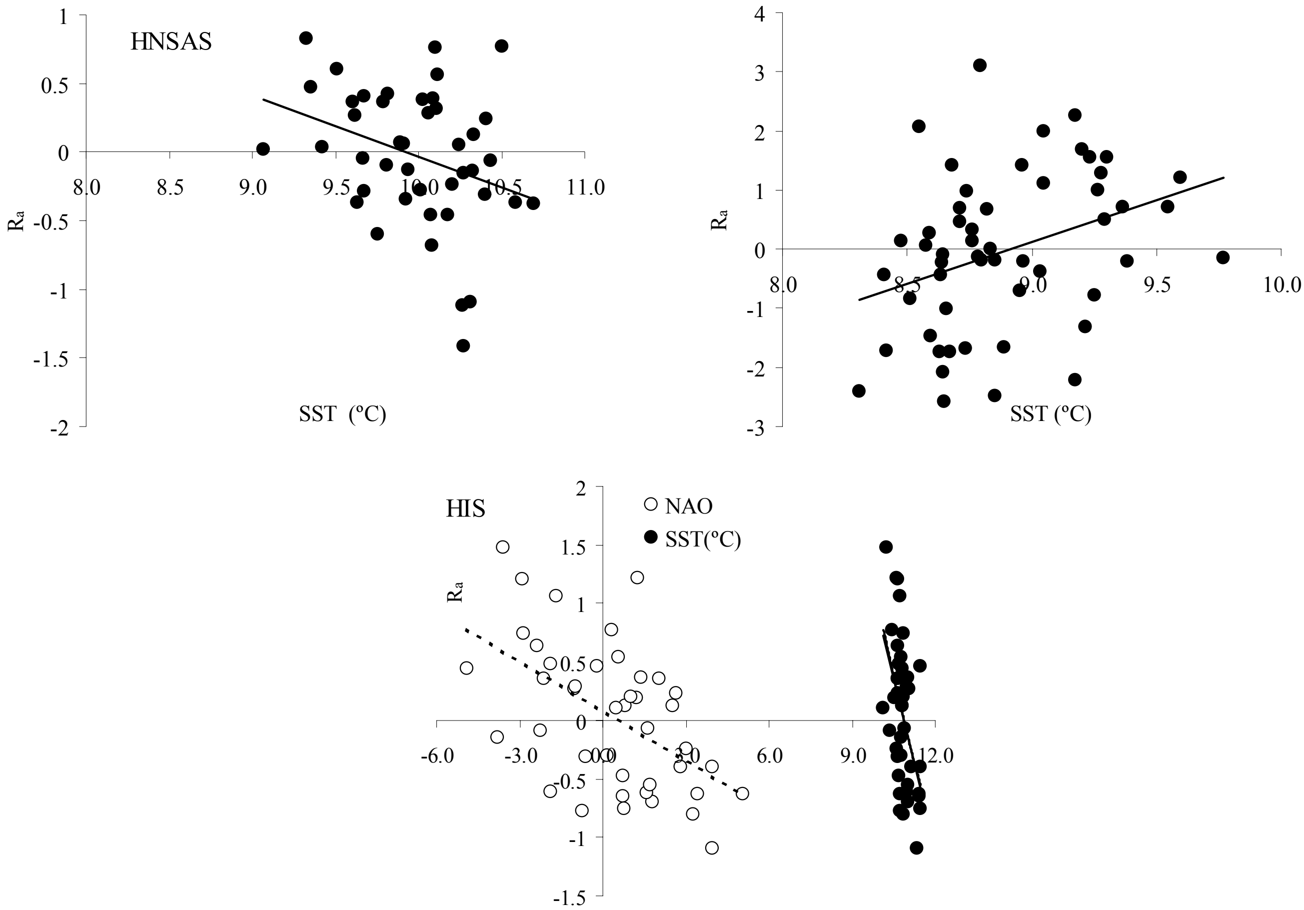

Figure 4. Principal Component Analysis (PCA) based on the correlation coefficients of the SSB - R_s relation, the correlation coefficients of the temperature and NAO - R_s and the average value of R_s of each stock.

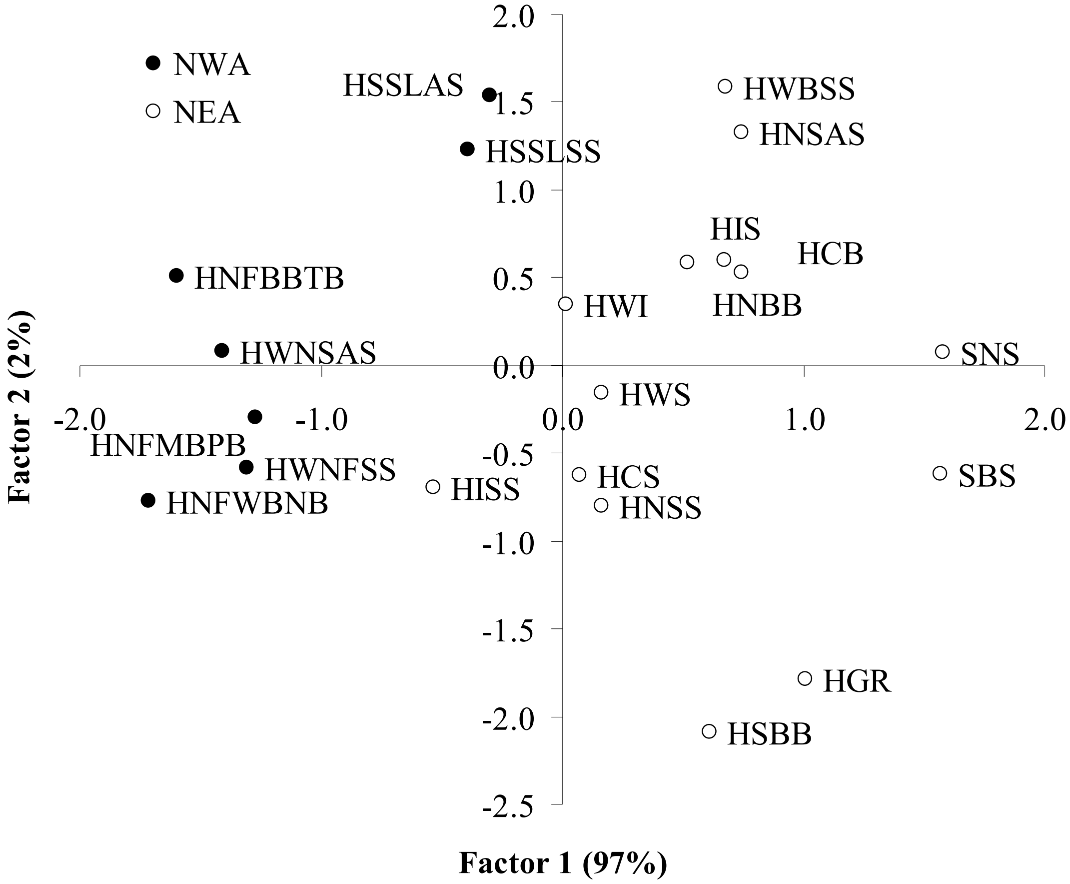

Figure 5. The relation between the first factor of the PCA and the longitude of the centroid of the stock distribution.