Disentangling the Effect of Adult Biomass and Temperature on the Recruitment Dynamics of Fishes

**Massimiliano Cardinale, Joakim Hjelm,
and Michele Casini**

*National Board of Fisheries, Institute of
Marine Research, Lysekil, Sweden*

Abstract

Here we analyzed the relation between recruitment dynamic (recruitment or recruitment success) and temperature of 57 commercial fish stocks of the North Atlantic. We showed that, although the effect of temperature was generally significant, spawning biomass is the main factor governing recruitment dynamic. A significant effect of spawning biomass was evident for 67% of all stocks analyzed in this study. For gadoids, the effect of spawning biomass was larger than the effect of temperature (both in terms of number of stocks and proportion of variance explained). For clupeids, spawning biomass was more important than temperature for a higher number of stocks, but the strength of the two effects, when present, was similar. Also, stocks living in colder and warmer areas showed, respectively, a positive and negative response to temperature for both families. Our results highlight that failing to account for spawning biomass effect in climate-recruitment studies could mask the influence of climate variability on recruitment dynamic. In this context, although management of several exploited fish populations cannot be entirely decoupled from the effect of climate on stock reproductive success, it is likely that the observed changes in exploited fish population dynamics are mainly the consequences of an unsustainable human impact and not climate changes.

Introduction

The physical environment has been long recognized as an essential factor in the regulation of fish population in marine ecosystems (Cushing

1982, Steele 1985). Among environmental factors, temperature is often the principal variable investigated since it regulates the rate in many ecological and physiological processes (Brett 1979). Therefore, there are strong justifications for studying the link between fish recruitment and temperature, and this information may be crucial for the management of marine resources and to predict the long-term consequence of climate changes on fisheries (Myers 1998). It is now recognized that the twenty-first century will show a significant global warming trend induced by an increase in atmospheric greenhouse effect (Houghton et al. 2001). This will also imply that a global change in the oceanic climate may propagate to the upper level of the food webs (Sarmineto et al. 1998) and consequently affect important marine resources (i.e., Loukos et al. 2003, Drinkwater 2005). Therefore, there is an increasing interest on the relation between climate and fisheries, both at the ecological and economic level (Bopp et al. 2001, Eide and Heen 2002), and evidence suggests that there is a direct link between climate and fish population dynamics (Marshall et al. 2001, Bakun and Broad 2002). In this context, life history traits might constitute a powerful means to unravel the interaction between climate and fish population. Among those, the number of recruits per unit of spawning stock biomass (SSB), i.e., the stock recruitment success (R_s), is one of the most important parameter proxies for population productivity (MacKenzie et al. 2003, Stige et al. 2006).

In this study we explored recruitment data in relation to spawning stock biomass and temperature for exploited fish stocks in the North Atlantic—57 selected demersal gadoids (cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; saithe, *Pollachius virens*; and whiting, *Merlangius merlangus*) and pelagic clupeids (herring, *Clupea harengus*; and sprat, *Sprattus sprattus*). Common patterns in life histories and population dynamics are evident only after data from several stocks, species, and areas are combined and standardized in ways that enable fair and unbiased comparisons (Myers 1998, MacKenzie et al. 2003). First, we revised available information to disentangle the effect of spawning stock biomass and temperature on R_s for the selected stocks. Successively, we investigated the potential differences in the strength and sign of these effects between families (gadoids and clupeids) and areas. We deliberately limited the analysis to SSB and temperature, although we were aware that other abiotic factors (i.e., precipitation, wind direction, currents, ice cover, etc.) and biotic factors (i.e., predation, competition, stock structure, food availability, fecundity, condition of the spawners, etc.) play an important role on recruitment processes.

Materials and methods

Time series

Stock and recruitment data

We compiled data of spawning stock biomass (*SSB*) and number of recruits (*R*) available at the International Council for the Exploration of the Sea (ICES), www.ices.dk, at the Northwest Atlantic Fisheries Organization (NAFO), www.nafo.ca, and the Ransom Myers Web site, www.msos.dal.ca/~myers/welcome.html (Table 1). For geographical distribution the reader can refer to www.ices.dk and www.nafo.ca. All estimates are derived from VPA (virtual population analysis) models and thus do not include any assumptions on the form of stock-recruitment curve.

Temperature data

The temperature data appropriate for comparisons of North Atlantic stocks should fulfill several requirements (Planque and Frédou 1999): they must be available for every stock, be consistent and sufficiently long, and correspond to large oceanic areas to be representative of the change in temperature experienced by the stock over its area of distribution. It is well known (see discussion in Ottersen et al. 1998) that environmental temperature does not strictly correspond to “ambient” temperature, although the population generally experiences higher temperature in warm years and vice versa (Planque and Frédou 1999). At the same time, it is likely that sea surface temperature (*SST*) reflects more closely ambient temperature of pelagic fish than demersal species. Anyhow, to accomplish all listed criteria, we used sea surface temperature data from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) available at www.cdc.noaa.gov/coads/coads_cdc_netcdf.shtml. Monthly average at the spatial resolution of 2 degrees of latitude and 2 degrees of longitude were available for all stocks from 1800. For each stock, we calculated the annual average (*SST*) and the average temperature of the time series at the geographical centroid of the stock distribution (*SST-A*) (available at www.msos.dal.ca/~myers/welcome.html) (Table 1). The latter was used as a proxy for the mean ambient temperature occurring in the area of distribution of each stock.

Statistical analysis

To allow for stock comparisons, we chose to estimate *R* as the number of age 1 individual. For those stocks for which the numbers of age 1 individuals were not available, the logistic equation (Hilborn and Walters 1992) was applied using values of natural and fishing mortality estimated for the adjacent age class. In order to make comparable spring and autumn herring spawners, the number of 1-year-old individuals of

Table 1. List of the stocks used in this study with the stock acronyms, the fishing area as defined by ICES and NAFO, latitude and longitude corresponding to the centroid of the stock distribution, the geographical location (i.e., area, NEA = Northeast Atlantic; NWA = Northwest Atlantic), and the age of recruitment to the fisheries and the period of available data. SST-A is the average temperature experienced by the stock in the time-series, measured at the centroid of the stock distribution.

Acronym	Fishing area	Latitude	Longitude	Area	SST-A	Age of recruits (year)	Years
CA	I&II	68	15	NEA	7.6	3	1946-2003
CEB	IIIId	56	19	NEA	8.8	2	1966-2003
CF	Vb	62	-8	NEA	11.0	2	1961-2003
CI	Va	63	-21	NEA	8.6	3	1955-2003
CK	IIIa	57	12	NEA	9.0	1	1971-2003
CNS	IV	55	4	NEA	9.9	1	1963-2003
CWB	IIIc&d	55	13.5	NEA	8.8	1	1970-2003
CVIA	VIa	58.5	-6	NEA	10.8	1	1966-2003
CVIIA	VIIa	54	-5	NEA	10.8	0	1968-2003
CVIIIEK	VIIe-k	51	-5	NEA	13.0	1	1971-2003
HA	I&II	68	15	NEA	7.6	3	1950-2003
HF	Vb	62	-8	NEA	11.0	2	1961-2003
HI	Va	63	-21	NEA	8.6	2	1981-2003
HNS	IV	55	4	NEA	9.9	0	1963-2003
HVIB	Vb	57.25	-15	NEA	11.0	3	1985-2003
SA	I&II	68	15	NEA	7.6	3	1960-2003
SF	Vb	62	-8	NEA	11.0	3	1961-2003
SI	Va	63	-21	NEA	8.6	3	1962-2003
SNS	IIIa&IV&VI	55	4	NEA	9.9	3	1967-2003
WNS	IV	55	4	NEA	9.9	1	1980-2003
WVIA	VIa	58.5	-6	NEA	10.8	1	1978-2003
WVIIA	VIIa	54	-5	NEA	10.8	1	1980-2003
WVIIIEK	VIIe-k	51	-5	NEA	13.0	0	1982-2003
CESS	4W-4Vs	44	-59	NWA	8.8	1	1958-1993
CFC	3M	47	-45	NWA	8.4	1	1972-2001
CG	1	59	-44	NWA	5.4	3	1952-1992
CGEO	5Ze	41	-67	NWA	12.8	1	1977-1998
CLAB	2J-3KL	50	-52	NWA	4.1	3	1959-1992
CNSL	3Pn-4SR	49	-60	NWA	5.7	3	1974-1997
CSGB	3NO	44.5	-51.5	NWA	8.5	3	1956-1993
CSSL	4T-Vn	47.5	-63.5	NWA	6.2	3	1947-1993
CSTP	3Ps	46	-55.5	NWA	6.6	3	1956-1993

Table 1. (continued.)

Acronym	Fishing area	Latitude	Longitude	Area	SST-A	Age of recruits (year)	Years
CWSS	4X	43	-65.5	NWA	9.4	1	1948-1994
HGEO	5Ze	41	-67	NWA	12.8	1	1931-1998
HWSS	4X	43	-65.5	NWA	9.4	1	1970-1998
SESS	4VWX5Zc	44	-59	NWA	8.8	1	1982-2002
HCB	IIId (SDs25-29)	57	21	NEA	8.8	1	1974-2003
HCS	VIIe-j	51	-5	NEA	12.9	1	1958-2003
HGR	IIId (SD 32)	57.3	23.4	NEA	7.9	1	1977-2003
HIS	VIIaN	54	-4.5	NEA	10.8	1	1961-2003
HISS	Va	63	-21	NEA	8.6	2	1981-2003
HNBB	IIId (SD 31)	65	23	NEA	6.9	1	1980-2003
HNSAS	IV&VIIId&IIIa	58	2	NEA	9.9	1	1960-2003
HNSS	II&IVa	65	8	NEA	8.8	1	1950-2003
HSBB	IIId (SD 30)	62	20	NEA	6.4	1	1973-2003
HWBSS	IIIa&SDs 22-24	55	12	NEA	8.8	1	1991-2003
HWI	Via(S)&VIIb-c	54.3	-12	NEA	12.1	1	1970-2003
HWS	Via (N)	57	-9	NEA	11.1	1	1958-2003
SBS	IIIb-d	57	21	NEA	8.8	1	1974-2003
SNS	IV	58	2	NEA	9.9	1	1984-2003
HNFB BTB	3KL	48.25	-52.45	NWA	5.5	2	1971-2002
HNFM BPB	3KL	46.4	-54	NWA	6.3	2	1970-2002
HNFW BNB	3KL	50	-55	NWA	4.9	2	1971-2002
HSSLAS	4T	47	-63	NWA	6.3	2	1978-2002
HSSLSS	4T	47	-63	NWA	6.3	2	1978-2002
HWNFSS	4R	49.25	-59	NWA	5.4	2	1965-2002
HWNSAS	4R	49.25	-59	NWA	5.4	2	1965-2002

spring spawner stocks was negatively adjusted for a natural mortality of 0.075 per month for 2 months as in Toresen (2001).

The annual stock-specific recruitment success (R_s) was estimated for each stock and year as the natural logarithm of the ratio between R_y and SSB_{y-1} (Hilborn and Walters 1992, Beverton 2002). We are aware that SSB does not completely reflect the reproductive potential of a stock. For example, stock structure (i.e., proportion of older individuals, see Marshall et al. 1998; Cardinale and Arrhenius 2000) and/or variability in fecundity or condition of the spawners (e.g., Olsen et al. 2005, Scott et al. 2006) are not included in SSB estimation, although they are known to affect the reproductive output of the stock. However, SSB is the only estimate of the reproductive potential that is available for every stock, has a sufficiently long time series, and is consistently calculated to allow for comparisons among North Atlantic fish species.

Here we followed the procedure suggested by Cardinale and Hjelm (2006) and Stige et al. (2006). The first step is to test for and disentangle the SSB effect on R . In one of his last lectures at Woods Hole, Beverton (2002) suggested an approach for exploring this relationship. Because of the biological mechanisms behind the classical SSB - R relationships, recruitment success (R_s) should improve as SSB decreases (Fig. 1 in Cardinale and Hjelm 2006). However, if recruitment is also mediated by physical environmental events, this negative relationship may not be as obvious. For example, when the stock is declining, a negative effect of climate on R will result in a decrease in R_s ; this is reversed in the case of a positive effect of climate on R . Therefore, the variability around the relationship between R_s and SSB can be considered as a proxy for recruitment anomalies (R_a) and it is assumed to be partially determined by the stochasticity in the physical environment (Beverton 2002). However, it is worth it to emphasize that R_a can be used in climate-recruitment analysis only when a significant effect of SSB on R_s can be demonstrated. Conversely, when SSB has no significant effect on R_s , climate variables can be directly correlated to recruitment (R). It is also important to highlight that, if SSB has no effect on R_s , using R_a instead of R can actually mask any recruitment-climate relationship. The rationale behind these assumptions is mathematically formalized in the classical Ricker (1954) or Beverton and Holt (1995) recruitment functions, which are in turn based on sound ecological mechanisms (e.g., cannibalism and predation). Being that R_s is an index of recruitment scaled by SSB , the properties of R and R_s and their relationships with SSB are mathematically very different and cannot be directly compared.

The number of recruits in a fish species is generally related to egg production or SSB that is, in turn, considered a proxy of egg production (Myers and Barrowman 1996). Thus, we fitted a simple deterministic linear model:

Figure 1. Example (Irish Sea herring stock) of the procedure used in the analysis. (a) relationship R_s -SSB with residuals (R_a); (b) trends in R_a over time, and (c) relationship R_a -SST.

$$R_s = \alpha - \beta \times SSB \quad (\text{Eq. 1})$$

For those stocks where the slope of β was significantly different from 0, the residuals were estimated. The residuals from Eq. 1 are defined hereafter as annual recruitment anomalies (R_a). R_a values were successively tested for correlation with annual average SST for each stock. For those stocks where the relationship between R_s and SSB was not significant, the relationships between R (in numbers of individuals) and SST were tested fitting a simple deterministic linear model as for Eq. 1. Trends in R_a and R are defined as recruitment dynamic thereafter. An example of the procedure described above is shown in Fig. 1 for the Irish Sea herring stock.

In our analysis we also investigated the following.

1. The proportion of stocks with an effect of SSB on R_s and the proportion of stocks with an effect of SST on R_a (or R for those stocks where an SSB effect was not evident). Differences between and within families were calculated using the Fisher exact test.
2. The strength (i.e., r^2 in absolute terms) of the effect of SSB on the R_s and of the effect of SST on R_a (or R for those stocks where an SSB effect was not evident). Differences between and within families were calculated using the Kruskal-Wallis test.

We also investigated the proportion of stocks with a positive sign in the effect of SST on R_a (or R for those stocks where an SSB effect was not evident) and the difference in the strength of the SSB effect compared to that of SST between and within families.

Finally, we plotted the r^2 of those stocks for which a significant effect of SST on R_a (or R for stocks where an SSB effect was not found) was demonstrated against the average ambient temperature in the area of distribution of each stock during the time series ($SST-A$) for gadoids and clupeids separately.

The models used do not take temporal autocorrelation into account. The level of significance was set at 5% for all the statistical tests used in this study. Statistical analysis was performed using S-PLUS (Insightful Corporation 2005) and Statistica (Statsoft Inc. 2003) computer software.

Results

There were no statistically significant differences (Fisher exact test) between families (gadoids against clupeids) in the proportion of stocks with an SSB effect on R_s (test 1) as well as a SST effect on R_a (or R depending on the stocks) (test 2; Table 2). There was also no statistical

Table 2. Results of the Fisher exact test. Between: between-family (gadoids and clupeids) differences in the proportion of stocks with an effect of *SSB* on R_s (test 1), in the proportion of stocks with an effect of *SST* on R_a (or R) (test 2), and in the sign of the effect of *SST* on R_a (or R) (test 3). Within: within-family (gadoids and clupeids) differences in the proportion of stocks with an effect of *SSB* on R_s compared to the effect of *SST* on R_a (or R) (tests 4 and 5). All stocks: differences in the proportion of stocks with an effect of *SSB* on R_s compared to the effect of *SST* on R_a (or R) (test 6); p is the significance value of the tests and n the number of stocks used in the analysis.

Fisher test							
		Variable	Gadoids	Clupeids	p	n	Test
Between		Proportion of stock with an effect of <i>SSB</i> on R_s	61%	76%	0.27	38	1
		Proportion of stock with an effect of <i>SST</i> on R_a (or R)	31%	29%	0.87	17	2
		Proportion of stocks with a positive effect of <i>SST</i> on R_a (or R)	36%	67%	0.24	17	3
			<i>SSB</i>	<i>SST</i>			
Within	Gadoids	Proportion of stocks with <i>SSB</i> compared to <i>SST</i> effect	61%	31%	<0.01	33	4
	Clupeids	"	76%	29%	<0.001	22	5
All stocks		"	69%	31%	<0.001	55	6

difference between families concerning the sign of *SST* effect on R_a (or R depending on the stocks) (test 3).

On the other hand, there was a statistical difference in the proportion of stocks with an *SSB* effect on R_s compared to those with an *SST* effect on R_a (or R) for both gadoids and clupeids (tests 4 and 5) with a statistically larger proportion of stocks with a *SSB* effect on R_s (tests 4-6; Table 2).

There was no difference (Kruskall-Wallis test) concerning the strength of the *SSB* effect on R_s (test 7) and *SST* effect on R_a (or R depending on the stocks) (test 8) between families (Table 3). On the other hand, there was a statistical difference in the strength of the *SSB* effect compared to the *SST* effect for gadoids (test 9) and for all stocks combined (test 11), while the same was not found for clupeids (test 10; Table 3).

We plotted the r^2 of the *SST* effect on R_a (or R) against the average temperature in the area of distribution of each stock during the time series (*SST-A*) (see Table 1). Only those stocks where a significant effect of *SST* on recruitment dynamic was found were used (see Table 4). The

Table 3. Results of the Kruskal-Wallis test. Between: between-family (gadoids and clupeids) difference in the strength (r^2) of the effect of *SSB* on R_s (test 7) and in the strength of the effect of *SST* on R_a (or R) (test 8). Within: within-family (gadoids and clupeids) differences in the strength of the effect of *SSB* on R_s compared to the strength of the effect of *SST* on R_a (or R) (test 9 and 10). All stocks: differences in the strength of the effect of *SSB* on R_s compared to the strength of the effect of *SST* on R_a (or R) (test 11). The strength of the relationships is shown as median of r^2 ; p is the significance value of the tests and n the number of stocks used in the analysis.

			Kruskall-Wallis test				
Between	Strength [r^2]		Gadoids	Clupeids	p	n	Test
	Effect of SSB on R_s		0.31	0.33	0.89	38	7
	Effect of SST on R_a (or R)		0.16	0.26	0.61	17	8
			SSB	SST			
Within	Gadoids	SSB compared to SST effect	0.31	0.16	<0.01	33	9
	Clupeids	"	0.33	0.26	0.25	22	10
All stocks		"	0.32	0.19	<0.01	55	11

analysis showed that stocks living in colder areas present a positive effect of *SST* on R_a (or R), and vice versa, for both families (Fig. 2).

Discussion

Recruitment (R) is considered generally related to egg numbers or stock spawning biomass (*SSB*) (a proxy for egg numbers) (Myers and Barrowman 1996) and this was confirmed in our study by the fact that a significant effect of *SSB* on recruitment success (R_s) was evident for 67% of all stocks analyzed. This again highlights that failing to account for the *SSB* effect in climate-recruitment studies could mask the influence of climate variability on recruitment dynamic (Myers 1998, Cardinale and Hjelm 2006). Therefore, our approach, as advocated by Beverton (2002) and previously used by Cardinale and Hjelm (2006) and Stige et al. (2006), is able to unravel stock productivity and climate by using the deviation from the theoretical relation between *SSB* and R_s . During the last decade, most of the published papers on meta-analysis of fish and climate (for instance, see ICES Journal of Marine Science 58(5) and 62(7) and references herein) have used some climate proxy to explain observed variability in R or R_s without exploring and disentangling the effect of adult biomass on recruitment. This makes difficult a comparison between previous studies and our analysis (see Cardinale and Hjelm 2006 for a useful discussion). Also, R_s and recruitment is not the same

Figure 2. Relationships (both significant at $p < 0.01$) between the average SST experienced by the stock in its area of distribution during the time series and the correlation coefficient (r^2) of the SST effect on R_a (or recruitment depending on the stock) for gadoids (a) and clupeids (b). Only stocks where the relationship between SST and R_a (or recruitment depending on the stock) was statistically significant were used in the analysis.

Table 4. Results of linear regression analysis between R_s and SSB ; between the residuals of the R_s - SSB regression (i.e., recruitment anomalies, R_a) and SST ; and between R and SST for all stocks analyzed. ns = not significant relationship. The sign in front of r^2 indicate whether the relationship is negative or positive.

Stock	$R_s \sim SSB$		$R_s \sim SST$		$R \sim SST$	
	r^2	p	r^2	p	r^2	p
Northeast arctic cod	-0.26	<0.01	0.05	ns	-	-
Eastern Baltic cod	-0.18	<0.01	-0.023716	ns	-	-
Faroe cod	-0.42	<0.01	-0.047089	ns	-	-
Iceland cod	-0.48	<0.01	0.01	ns	-	-
Kattegat cod	-0.09	ns	-	-	0.01	ns
North Sea cod	-0.1	<0.05	-0.269361	<0.01	-	-
Western Baltic cod	-0.06	ns	-	-	-0.031329	ns
Scotland cod	-0.28	<0.01	-0.521284	<0.01	-	-
Irish cod	-0.2	<0.01	-0.297025	<0.01	-	-
Celtic cod	-0.01	ns	-	-	-0.082369	ns
Northeast arctic haddock	-0.01	ns	-	-	0.12	0.02
Faroe haddock	-0.21	<0.01	-0.054756	ns	-	-
Iceland haddock	-0.12	ns	-	-	0.09	ns
North Sea haddock	-0.13	<0.05	-0.01	ns	-	-
Northeast arctic saithe	-0.52	<0.01	-0.01	ns	-	-
Rockall haddock	-0.25	<0.05	-0.083521	ns	-	-
Faroe saithe	-0.45	<0.01	-0.01	ns	-	-
Iceland saithe	-0.3	<0.01	0.13	0.02	-	-
North Sea saithe	-0.49	<0.01	0.08	ns	-	-
North Sea whiting	-0.29	<0.01	-0.04	ns	-	-
Scotland whiting	-0.44	<0.01	-0.01	ns	-	-
Irish whiting	-0.66	<0.01	-0.01	ns	-	-
Celtic whiting	-0.46	<0.01	-0.01	ns	-	-
Eastern Scotian Shelf cod	-0.41	<0.01	-0.192721	<0.01	-	-
Flemish Cap cod	-0.11	ns	-	-	-0.186624	0.02
Greenland cod	-0.01	ns	-	-	0.15	0.02
Georges Bank cod	-0.09	ns	-	-	0.01	ns
Labrador Grand Bank cod	-0.02	ns	-	-	0.14	0.04
North Gulf of St. Lawrence cod	-0.01	ns	-	-	0.08	ns
Southern Grand Bank cod	-0.01	ns	-	-	-0.016129	ns
South Gulf of St. Lawrence cod	-0.35	<0.01	-0.03	ns	-	-

Table 4. (continued.)

Stock	$R_s \sim SSB$		$R_s \sim SST$		$R \sim SST$	
	r^2	p	r^2	p	r^2	p
St. Pierre Bank cod	-0.31	<0.01	-0.16	0.02	-	-
Western Scotian Shelf cod	-0.28	<0.01	-0.142129	<0.01	-	-
Georges Bank haddock	-0.01	ns	-	-	0.01	ns
Western Scotian Shelf Haddock	-0.02	ns	-	-	0.08	ns
Eastern Scotian Shelf Saithe	-0.2	ns	-	-	0.13	ns
Central Baltic herring	-0.31	0.001	0.03	ns	-	-
Celtic Sea herring	-0.15	<0.001	0.10	ns	-	-
Gulf of Riga herring	-0.01	ns	-	-	0.47	<0.001
Irish Sea herring	-0.14	0.015	-0.25	<0.001	-	-
Iceland summer spawning herring	-0.1	ns	-	-	0.06	ns
Northern Bothnian herring (SD 31)	-0.33	0.003	0.01	ns	-	-
North Sea autumn spawners herring	-0.41	<0.001	-0.11	0.03	-	-
Norwegian spring spawning herring	-0.11	0.001	0.12	0.01	-	-
Southern Bothnian herring (SD 30)	-0.01	ns	-	-	0.51	0.002
Western Baltic spring spawners herring	-0.62	0.001	0.08	ns	-	-
West of Ireland herring	-0.35	<0.001	0.04	ns	-	-
Herring west of Scotland	-0.2	0.002	0.02	ns		
Baltic Sea sprat	-0.1	ns	-	-	0.28	0.003
North Sea sprat	-0.08	ns	-	-	0.007	ns
Newfoundland herring Bonavista Bay & Trinity Bay	-0.59	<0.001	0.04	ns	-	-
Newfoundland herring St. Mary's Bay & Placentia Bay	-0.33	0.001	0.01	ns	-	-
Newfoundland herring White Bay & Notre Dame Bay	-0.3	0.002	0.06	ns	-	-
South Gulf of St Lawrence herring autumn spawners	-0.67	<0.001	0.01	ns	-	
South Gulf of St Lawrence herring spring spawners	-0.64	<0.001	0.06	ns	-	-

Table 4. (continued.)

Stock	$R_s \sim SSB$		$R_s \sim SST$		$R \sim SST$	
	r^2	p	r^2	p	r^2	p
West coast of Newfoundland herring spring spawners	−0.29	0.001	0.05	ns	—	—
West coast of Newfoundland herring autumn spawners	−0.49	<0.001	0.08	ns	—	—

thing. Recruitment success is in a linearized form and therefore, in this different numerical context, properties of R and R_s against SSB are mathematical very different and cannot be comparable. Thus, a lack of relationship between R_s and SSB does not contradict the fact that a significant relationship has been found for the same stock in other studies using R in absolute numbers (i.e., Rätz and Lloret 2005). Nevertheless, it is also important to stress that part of the observed variability around the relationship between SSB and R_s might be dependent on other factors, as structure of the stock (i.e., maternal effect; Marshall et al. 1998), changes in fecundity and conditions of the spawners (Olsen et al. 2005, Scott et al. 2006) and Allee effect (Frank and Brickman 2000), although the investigation of these factors was beyond the scope of the paper.

The historical dynamic of fish stocks is usually related to both natural external factors and anthropogenic influences, among which fishery is generally considered the most important (Myers and Worm 2003). For instance, the high fishing mortality in coincidence of a period of poor recruitment may explain the rapid decline in several herring commercial stocks during the 1960s (Toresen and Oestvedt 2000, Toresen 2001). A similar trend has been observed for some cod stocks in the Northwest Atlantic, with a rapid decline of the populations in coincidence with the development of fisheries techniques intertwined with unfavorable condition for survival of juvenile cod (Drinkwater 2003). A classical explanation is that the coincidence of those two factors accelerated the declining process (Fiksen and Slotte 2002; Toresen 2001). Here we show that the proportion of stocks with a significant SSB effect on R_s was significantly larger than the proportion of stocks with a significant SST effect on R_a (or R) for both gadoids and clupeids. Moreover, for gadoids, the strength of the relationships $SSB-R_s$ was significantly higher than the strength $SST-R_a$ (or R). Results as shown here underline that although the effect of temperature on recruitment dynamic is significant for some stocks spawning biomass has generally a much larger impact than climate on the recruitment dynamic of North Atlantic fish.

There were no significant differences between demersal gadoids and pelagic clupeids concerning the sign of the effect of *SST* on R_a (or R), although a difference was evident (36% against 67% stocks with a positive effect of *SST*). The lack of significance is possibly due to the low numbers of stocks where a *SST* effect was found and thus the low sample size used in the Fisher test. Anyhow, a clear relationship was found between the sign of the effect of the *SST* on R_a (or R) and the average temperature in the distribution area of the stocks, with stocks living in colder areas responding positively to increasing temperature, and vice versa, for both families. Gadoids showed an average ideal *SST* around 7-8°C for optimal R_s , whereas for clupeid this value was around 9-10°C. Those results are generally in accordance with other studies for cod (Planque and Frédou 1999, Rätz and Lloret 2005, Drinkwater 2005) (i.e., variation in R with temperature for cod stocks at the border of the species distribution), while the same pattern has never been demonstrated for clupeids. Interestingly, the relationship is much stronger for clupeids compared to gadoids. This might be explained by the existence of a stronger coupling between temperature and recruitment for pelagic fishes, but it could also be due to the fact that *SST* reflects more closely the ambient temperature experienced by the pelagic stocks.

Conclusions

It has been argued that resilience to climate changes in unexploited populations is significantly larger than in highly exploited or overfished stocks (Brander 2005). Nevertheless, we showed that spawning biomass play the fundamental role in the regulation of the dynamic of fish stocks. Therefore, although management of exploited fish populations cannot be decoupled from the effect of temperature on their reproductive success, it is likely that the observed shifts in exploited fish communities are mainly the consequences of an unsustainable fishing mortality (Pauly et al. 1997, Myers and Worm 2003, Hutchings 2004) and not of a climate changes.

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