



Changes and trends in the demersal fish community of the Flemish Cap, Northwest Atlantic, in the period 1988–2008

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The Flemish Cap fish community (NAFO Division 3M) has been fished since the 1950s, and major changes in the biomass and abundance of its most important commercial species have been reported since the late 1980s. Variations in oceanographic conditions at the Cap, with alternating periods of cold and warm weather, have also been described. This work examines the existence of common trends in the biomass levels of the main demersal species over time using dynamic factor analysis, and the occurrence of “occasional species” was explored in relation to temperature conditions. Overall, there have been significant changes in community structure involving both commercial and non-commercial species. Common trends among species were identified and overall fishing pressure, environmental conditions (represented by a moving average of the North Atlantic Oscillation, NAO), and predation pressure (represented by the abundance of piscivorous fish) emerged as important drivers of the temporal dynamics. The NAO influence in the dynamics of most species was in agreement with their temperature preference. For occasional species, their pattern of occurrence appears also to be linked to changes in temperature regimes.

Keywords: demersal fish, environmental conditions, fisheries, Flemish Cap, NAO, Northwest Atlantic, predation.

Introduction

The Flemish Cap is an isolated bank located in the Northwest Atlantic, between 46 and 49°N and 43 and 47°W. It is separated from the Newfoundland shelf by the Flemish Pass (Figure 1), a channel characterized by depths >1100 m. The Cap is a deep-water seamount, with an area of 10 555 square miles up to 730 m deep, with the shallowest part of the bank (120 m depth) located in the southeastern quadrant. The Flemish Pass hinders migration to and from the Grand Banks of relatively shallow demersal fish species, such as Atlantic cod *Gadus morhua* (Templeman and Fleming, 1963; Konstantinov, 1970) and American plaice *Hippoglossoides platessoides* (Morgan and Bowering, 2004), although some migration does take place (de Cardenas *et al.*, 1993). In relation to eggs and larvae, a quasi-permanent anticyclonic gyre over the Cap produces a retention effect that hinders exchange with adjacent populations, although current transport from the adjacent Grand Banks has been described (Frank *et al.*, 1996; Borovkov *et al.*, 2006).

It has been suggested that fish recruitment on the Flemish Cap depends on the integrity of its anticyclonic gyre, whose weakening can produce the dispersion of eggs and larvae from the Cap to the open ocean (Kudlo *et al.*, 1984; Borovkov *et al.*, 2006).

The strength and temperature of this gyre is related to the extent of the Labrador Current (Stein, 1995), which in turn is stronger with lower values of the North Atlantic Oscillation (NAO; Marsh, 2000). On the Newfoundland–Labrador (NL) shelf and the Flemish Cap, strong NW winds, as well as cold temperatures and low salinity, have been associated with a strongly positive NAO (Drinkwater, 1994; Petrie, 2007).

Predation on juvenile stages may also be an important regulatory mechanism for fish stocks on the Flemish Cap. Predation by *G. morhua* has been suggested as a controlling factor for *Sebastes* spp. populations (Lilly, 1983), although other important predatory fish such as *Reinhardtius hippoglossoides* and wolffish (*Anarhichas* spp.) also prey on juvenile fish (Pérez-Rodríguez *et al.*, 2011a).

Compared with adjacent fishing grounds, intensive fishing started late on the Flemish Cap because of its geographic isolation (>300 nautical miles from Newfoundland to the centre of the Cap) and large mean depth. These drawbacks were overcome with the arrival of engine-powered trawlers in the mid 20th century. However, the most critical event determining the increase in fishing the Flemish Cap was the establishment of a 200-mile exclusive economic zone (EEZ) by Canada in 1978, which moved most of the international fishing fleet outside the EEZ (Wells

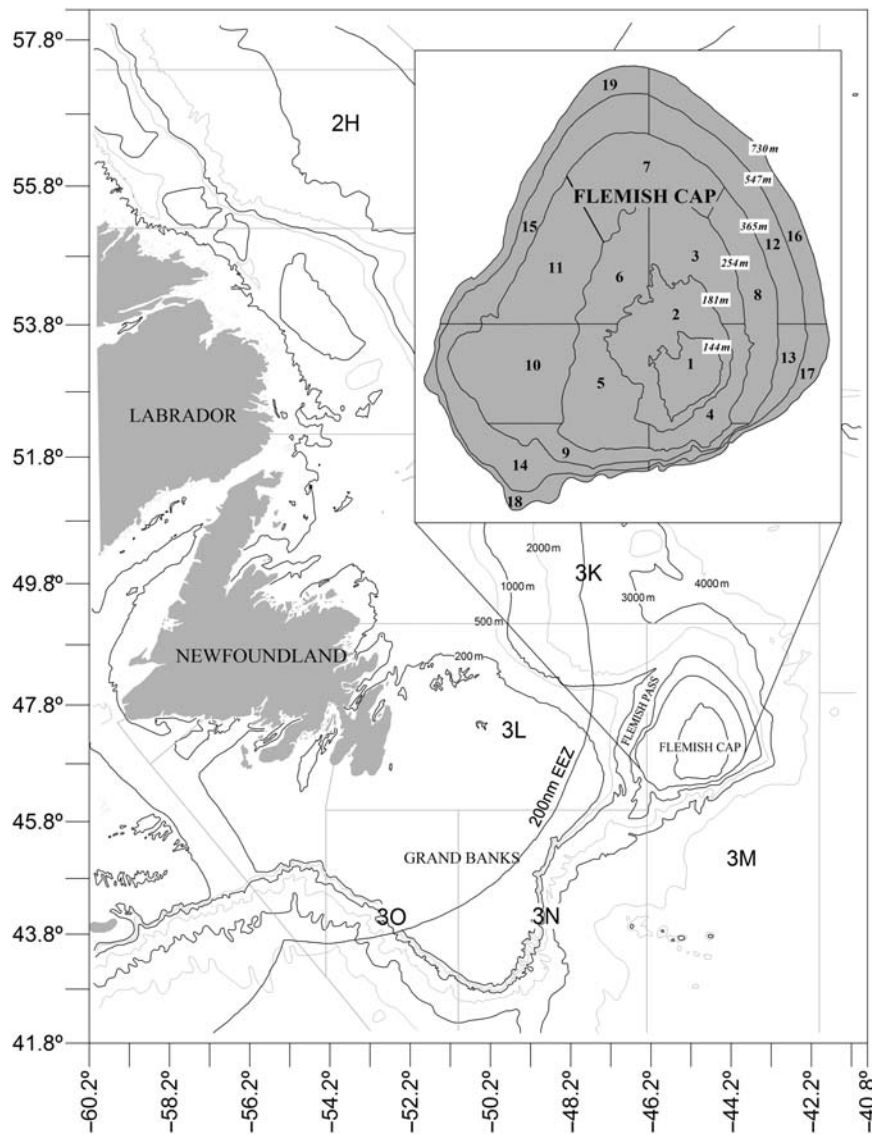


Figure 1. Map of a part of the NAFO regulatory area showing the Flemish Cap separated from the Grand Banks by the Flemish Pass. The inset shows the Flemish Cap area shallower than 730 m with the 19 strata surveyed during the period 1988–2008.

et al., 1984). During that period, fishing mainly focused on *G. morhua* and *Sebastes* spp. until the early 1990s, when those stocks suffered steep declines (Vázquez, 2010). In 1998, with the collapse of *G. morhua* on the Flemish Cap, a fishing moratorium was established. This event was contemporary with the collapses in other Northwest Atlantic cod stocks, and fishing was advanced as the main driver (Myers *et al.*, 1996; Fogarty and Murawski, 1998; Vázquez and Cerviño, 2002). Since the mid 1990s, fishing on the Flemish Cap has mainly focused on an increasing population of *Pandalus borealis* and *R. hippoglossoides* (Anon., 2002; Casas-Sánchez, 2010).

Since the start of regular research surveys on the Flemish Cap during the late 1980s, most research has focused on commercial species and been driven by the need to provide single-species management advice (Vázquez, 2010). However, current efforts towards developing ecosystem approaches to fisheries within the Northwest Atlantic Fisheries Organization (NAFO, 2010a, b) require the development of a more holistic view of the Flemish Cap system. In

this context, the objectives of this paper are to seek common patterns in the trajectories of species in the demersal fish community of the Flemish Cap and to link such commonalities with biological and environmental drivers, then by doing so to shed some light on the mechanisms that might regulate the dynamics of the Flemish Cap fish community.

Material and methods

Data on biomass and abundance for each fish species in the demersal assemblage, as well as the corresponding bottom and surface temperatures, were obtained from the EU July bottom-trawl survey of the Flemish Cap in the period 1988–2008. That survey uses Lofoten-type bottom-trawl gear and follows a stratified random survey design as recommended by NAFO specifications (Alpoim *et al.*, 2002). The standard swept-area calculation for stratified random sampling designs (Gunderson, 1993) was used to estimate the index of biomass for all 65 demersal fish species caught during this period, as well as of *P. borealis* and *Illex*

illecebrosus. These indices were calculated using the first 19 strata in the survey (from the top of the Cap out to 730 m deep). Each survey was designed to encompass a total of 120 fishing trawls (between 2 and 12 sets per stratum, depending on the total stratum area). However, owing to unexpected circumstances, this number was lower in some years (Alpoim *et al.*, 2002). The research vessel employed in the surveys was changed in 2003, so conversion factors were applied to correct for vessel replacement (Pérez-Rodríguez and Koen-Alonso, 2010).

Surface and bottom temperatures were based on CTD (conductivity, temperature, depth) casts made during the July survey. Mean surface and bottom temperatures were calculated as the average of all CTD data from the top and the bottom 10 m, respectively.

For most species, annual declared fisheries catches were obtained from the STATLANT 21A database compiled by NAFO (available at the NAFO website, www.nafo.int). For *G. morhua*, the estimated catches used for stock-assessment purposes were considered instead (González-Troncoso and Vázquez, 2010), because declared catches were recognized to be well below the real catches during the late 1980s and the early 1990s (Vázquez, 1991). The annual mean NAO index was calculated from monthly NAO values obtained from the National Oceanic and Atmospheric Administration (NOAA) website, <http://www.cpc.noaa.gov>.

Based on their occurrence and biomass, species in the demersal assemblage were separated into three groups for analysis. Group I consisted of species observed in all years and which accounted for >0.5% of the total demersal assemblage biomass in at least one of those years. Group II consisted of species observed in most years (>15) and represented small fractions of the total biomass (<0.5%), and group III species observed in the surveys at frequency and biomass (<15 years, and consistently <0.5% of the total demersal assemblage biomass, respectively).

Common trends in the biomass trajectories were studied using dynamic factor analysis (DFA), an exploratory multivariate time-series technique that estimates common trends in a set of short time-series (Zuur *et al.*, 2003). In addition to common trends, DFA also allows for consideration of explanatory variables in the model. A general expression in matrix notation for a DFA model can be written as

$$\mathbf{Y}_\tau = \mathbf{Z}\boldsymbol{\alpha}_\tau + \mathbf{D}\mathbf{x}_\tau + \mathbf{c} + \boldsymbol{\varepsilon}_\tau, \quad (1)$$

where \mathbf{Y}_τ is an $N \times 1$ vector containing the values of the N time-series at time t , \mathbf{Z} a matrix of dimensions $N \times M$ with factor loadings of each trend for each time-series, $\boldsymbol{\alpha}_\tau$ a vector that contains the values of the M common trends at time t , \mathbf{D} an $N \times L$ matrix containing regression coefficients, \mathbf{x}_τ a vector with the values of the L explanatory variables at time t , \mathbf{c} a constant parameter of dimension $N \times 1$, and $\boldsymbol{\varepsilon}_\tau$ an $N \times 1$ noise component assumed to be normally distributed with mean 0 and covariance matrix \mathbf{R} . \mathbf{R} was modelled as a symmetric positive-definite matrix (Zuur *et al.*, 2003). Approximate t -tests were used to explore the significance of the regression coefficients; t -values >2 suggest that coefficients are significantly different from zero.

DFA was used to explore the biomass trajectories of species in groups I and II. For each group, multiple models involving different combinations of explanatory variables and number of common trends were developed. Among the alternative DFA models for each group, model selection was carried out using

the Akaike Information Criterion (AIC; Burnham and Anderson, 2002). The explanatory variables considered in the DFA models were intended to represent key processes that can influence the dynamics of the species studied: recruitment, where oceanographic features can have a large impact; and mortality, where both predation and fishing can be important drivers.

To represent the environmental conditions that, in a general sense, may have potentially influenced recruitment success for the demersal fish community, the moving average of the NAO index in the period between 4 and 7 previous years was employed (interval t_{-4} to t_{-7}). This range was used because, on average, 50% of the biomass of commercial species (the only species for which age data are available) in any given year is constituted by fish of ages 4–7. Therefore, the average environmental conditions during recruitment for a given year would be coarsely described by the moving average of the NAO during the interval t_{-4} to t_{-7} .

The fishery index (Koen-Alonso *et al.*, 2010) is a measure of relative exploitation attributable to fishing for the demersal community as a whole, and it was estimated as

$$\text{Fishery index} = \frac{\text{Total catches}}{\text{Total fish biomass EU survey index}}. \quad (2)$$

As the EU surveys are conducted in July, but declared catches are reported for the entire calendar year, there is a mismatch between the timing of the catches and the biomass involved in calculating the index. Catches affecting the biomass in July will be those made after July of the previous year. To compensate for this mismatch, the actual variable considered in the DFA analysis was not the fishery index itself, but the moving average of the fishery index (AFI) between the given and the previous year.

As a proxy for predation pressure, the abundance of the main piscivorous species on the Flemish Cap (i.e. *G. morhua*, *R. hippoglossoides*, *Anarhichas denticulatus*, *A. lupus*, and *A. minor*) was employed. First, for each of these piscivorous species, the size from which fish became an important part of the diet was determined using the results of Pérez-Rodríguez *et al.* (2011a, b). These size limits were established at 50, 30, 65, 40, and 40 cm, respectively, for the five species above. Second, the predation pressure index was estimated annually as the sum of the indices of abundance (from the EU survey) for each species larger than these sizes. The sum of abundance was employed instead of the sum of biomass because no data on biomass by size range were available from the EU surveys. On the other hand, the correlation between total biomass and total abundance for each of these species was always >0.8 (average value 0.89).

Given the sparse nature of the data for species in group III, differences in species composition (biomass) over time were studied using non-metric multidimensional scaling (MDS), as well as permutational analysis of variance and dispersion (PERMANOVA and PERMDISP, respectively). The aim of MDS is to represent samples in low-dimensional space (typically two-dimensional or three-dimensional), with the distance between points in the same rank order as the relative value of any similarity measure between samples (Clarke and Gorley, 2006). PERMANOVA is a multivariate technique designed to test the difference between two or more multivariate datasets in relation to one or more factors based on the measure of a similarity matrix (Anderson, 2001). The factor considered in this analysis was bottom-water temperature. Each year in the time-series was labelled “positive” or “negative” depending on whether its mean bottom temperature

was above or below the average for the entire period 1988–2008, and differences between groups in terms of species composition and biomass were evaluated with PERMANOVA. As in ANOVA, PERMANOVA requires homogeneity of variance between groups, which was tested using the other permutation method, PERMDISP (Anderson *et al.*, 2008).

Results

Environmental and biomass time-series

During the study period, local environmental conditions on the Flemish Cap were characterized by cold water in the early to mid-1990s (bottom 3.1°C; surface 5°C), followed by a warmer period starting in the late 1990s (bottom 4.1°C; surface 13.5°C). The average monthly NAO in the year and a half before the survey followed an opposite pattern, showing negative correlations with surface and bottom-water temperature ($r = -0.59$ and $r = -0.61$, respectively, $p < 0.1$).

The average monthly NAO index in the interval $t_{-4}-t_{-7}$, the AFI, and the piscivorous fish abundance are shown in Figure 2. The NAO was highest in the mid-1990s and lowest in the early 2000s. The AFI exhibited a pattern consistent with the highest catches on *G. morhua* in the early 1990s and *P. borealis* in the early 2000s. The piscivorous index showed two different peaks, one in the late 1980s, corresponding to the maximum abundance of large *G. morhua* in the time-series, and the second in the late 1990s, as a response to the increase in *R. hippoglossoides* abundance.

Of the demersal assemblage, group I contained 17 species and included all the commercial species of the Flemish Cap. Species such as *G. morhua*, *H. platessoides*, and *Bathyraxa spinicauda* exhibited a sustained decline in biomass from the late 1980s (Figure 3). The three species of the genus *Anarhichas* (*A. denticulatus*, *A. minor*, and *A. lupus*) followed similar dome-shaped patterns with peak biomass in the mid-1990s; *R. hippoglossoides* exhibited a similar pattern but with a peak in the late 1990s. *Pandalus borealis* showed a notable increase in biomass in the late 1990s and remained at that high biomass until 2005, when it started to decrease. The biggest change in biomass was observed for *Sebastes fasciatus* and *S. marinus*, which had exhibited a sudden increase in biomass in 2004.

Group II consisted of 14 species. Some species in the group, e.g. *Notacanthus chemnitzii* and *Synaphobranchus kaupii*, experienced notable declines in biomass in the early to mid-1990s, whereas

others such as *Gaidropsarus ensis* and *Urophycis chesteri* followed an opposing trend, with biomass highest in the later part of the time-series (Figure 4). *Lycodes vahli* and *L. esmarki* biomasses were highest during the 1990s, whereas those of other species, e.g. *Malacoraja senta* and *Coryphaenoides rupestris*, peaked in the early and late years of the period analysed.

With 36 fish species, group III contained the largest number of species, but all the species are low in biomass and were inconsistent in terms of occurrence in the survey (Figure 5). Despite this, within the group there also appear to be temporal patterns. Some species had higher biomasses in the early and later years with a period somewhere around the mid-1990s with no catch (e.g. *Melanogrammus aeglefinus*, *Urophycis tenuis*, and *Argentina silus*). Others had higher biomasses in the intermediate years (e.g. *Squalus acanthias*, *Leptagonus decagonus*). Some species appeared mainly in later years (e.g. *Lycodonus flagellicauda* and *Lophius americanus*), others in earlier years (e.g. *Etmopterus princeps*).

DFA with only common trends

For group I, the DFA model with the lowest AIC included three common trends (Table 1). Globally, the species in this group were influenced by one of these three trends (Table 2). Common trend 1, of a notable increase from the late 1990s (Figure 6), showed factor loadings >0.2 for *Glyptocephalus cynoglossus*, *I. illecebrosus*, *S. fasciatus*, and *S. marinus* (Table 2). Common trend 2 exhibited a dome-shaped form peaking in 1996 and was followed by the three species of the genus *Anarhichas*. *Gadus morhua*, *H. platessoides*, and *B. spinicauda* had factor loadings >0.2 for common trend 3, which was a declining trend from 1988 to 2000, and a very slight recovery after 2000. *Pandalus borealis* was the only species clearly influenced by all three common trends, showing negative factor loadings close to -0.2 .

In group II, the DFA model with the lowest AIC included only two common trends (Table 1). Common trend 1 was of a slight increase from 1988 to mid-1990s, followed by a decline (Figure 6), and characterized *Enchelyopus cimbrius*, *G. ensis*, *L. vahli*, *N. chemnitzii*, and *U. chesteri* (Table 2). Common trend 2 was of a steady decline from 1988 to the late 1990s, followed by a period of slight increase until 2008; this common trend was followed by *C. rupestris*, *M. senta*, and *S. kaupii*, and <0.2 for *Triglops murrayi*. Common trends 3 and 2 in groups I and II, respectively, were highly correlated ($r = 0.92$, $p < 0.01$).

DFA with explanatory variables

Groups I and II had the lowest AIC for the same structural model containing just one common trend and all three explanatory variables (NAO, AFI, and piscivorous abundance; Table 1). For group I, and based on the differences in AIC between models ($\Delta AIC < 10$), only the model with all three explanatory variables but two common trends was plausible (Table 1). For group II, plausible models included that with all explanatory variables and two common trends, but two other models, both including NAO and piscivorous abundance, and with one or two common trends, were also found to be within the realm of possibility (Table 1). These results indicate that environmental condition and predation pressure appear to be important drivers for all species, whereas the effects of fishing are definitely important, but more so for the group containing all commercial species than for one containing low-biomass non-commercial species.

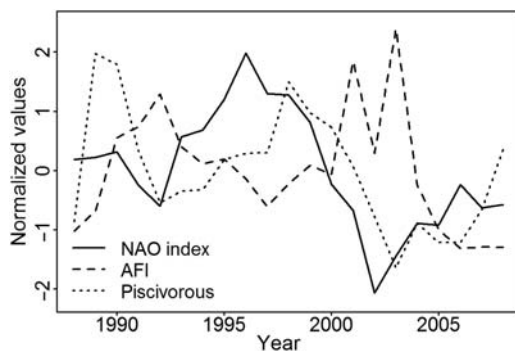


Figure 2. Normalized values of the annual NAO averaged over years $t_{-4}-t_{-7}$, plotted along with the moving AFI between the given and the previous year t and the abundance of piscivorous species in year t .

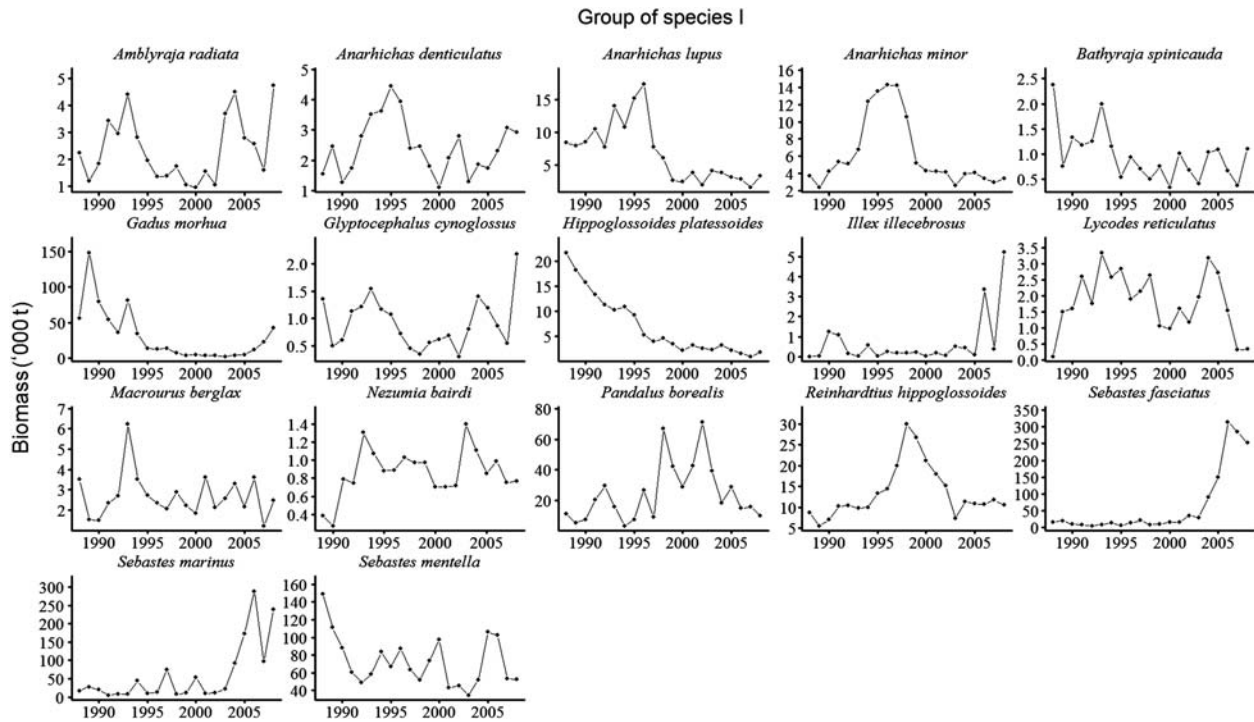


Figure 3. Survey-based biomass indices for species in group I estimated from the EU surveys of the Flemish Cap.

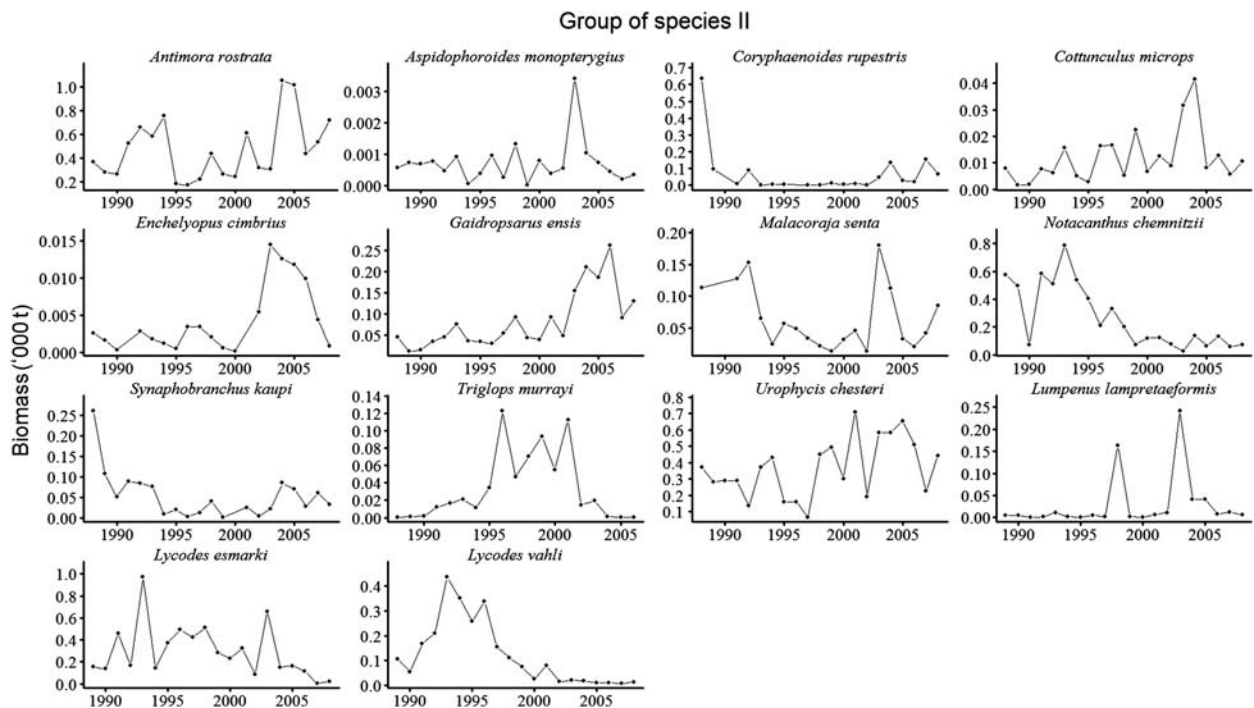


Figure 4. Survey-based biomass indices for species in group II estimated from the EU surveys of the Flemish Cap.

In terms of the effects of the explanatory variables, the abundance of piscivorous species had a generalized negative effect (i.e. negative coefficients) in both groups (25 of 31 species), except *G. morhua*, *H. platessoides*, *P. borealis*, and *R. hippoglossoides* in group I, and *T. murrayi* and *M. senta* in

group II. The AFI exhibited a variable effect depending on the species; it was positive in 18 of 31 species (Table 2). The NAO also had a variable effect, although it was mainly positive for species in group I and negative for species in group II (Table 2).

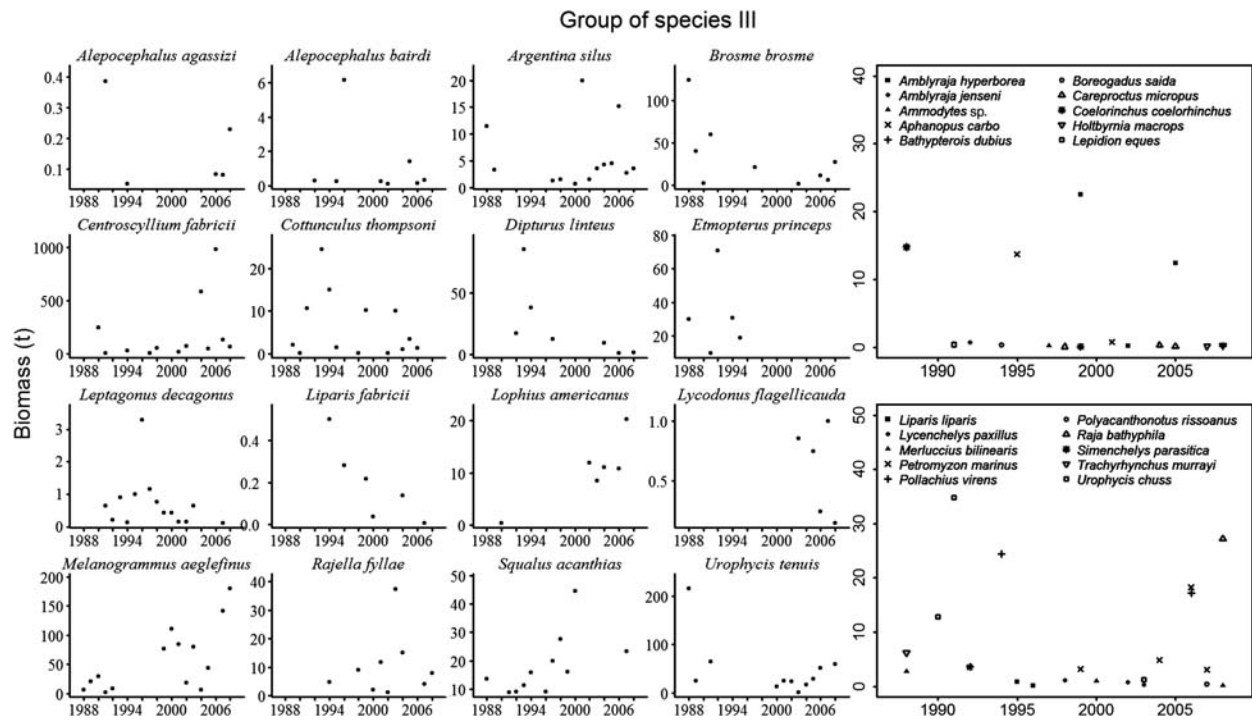


Figure 5. Index of biomass for species of group III. The most common species in the group are displayed in independent graphs, and the less common ones together in the top and bottom right panels.

Table 1. Difference in the AIC value between the best fit (model 8) and the remaining models.

Model	DFA model	Group I			Group II		
		Trend 1	Trend 2	Trend 3	Trend 1	Trend 2	Trend 3
1	Only common trends	227.6	217.9	215.3	47.7	39	45.9
2	NAO	195.4	184.6	193.3	36.8	41.3	46.6
3	AFI	193.4	180.2	191.5	52.1	44.5	45.4
4	Piscivorous	179.1	176.5	168.7	17.8	13.4	24.7
5	NAO + AFI	129.6	135.6	139.4	33.4	39.4	41.6
6	NAO + Piscivorous	94.4	87.4	103.7	2.6	5.1	15.2
7	AFI + Piscivorous	101.6	92.3	111.9	17.9	14.4	20.3
8	NAO + AFI + Piscivorous	0	6.6	27.8	0	3.7	11.2

To evaluate whether the signs of the estimated coefficients for the NAO were consistent with fish temperature preferences, the average preferred temperature for each fish species was estimated from the information gathered by Scott and Scott (1988). For each species, we determined whether the estimated average preferred temperature was higher or lower than the mean bottom temperature in July during the period 1988–2008 (3.6°C), classifying each species as having a “warmer” or a “colder” preference, respectively (Table 2). For *I. illecebrosus*, *E. cimbricus*, and *T. murrayi*, temperature preferences were approximated from distribution maps from FishBase (<http://www.fishbase.org/search.php>). Given the negative correlation between NAO and temperature at the Flemish Cap, a species with a “warmer” preference would be expected to have a negative DFA coefficient for NAO, and *vice versa* when the preference was “colder”. Following this criterion, 26 of the 31

species from groups I and II showed the expected sign in the NAO coefficient.

Multivariate analysis

The average water temperature from 1988 to 2008 was 3.6°C. The years 1989–1997 and 2003 were below this average value (negative years), whereas 1988, 1998–2002, and 2004–2008 were above the average (positive years). The PERMANOVA analysis found significant differences in the species composition of group III between years with the positive and negative temperature anomaly ($p < 0.01$). Results from the PERMDISP analysis did not find significant differences in dispersion between groups of positive and negative years ($p > 0.05$), supporting the conclusion that the differences between both groups of years were actually attributable to differences in their species composition and not to differences in dispersion. Results from the MDS analysis also supported the

Table 2. Outputs from the DFA model fitting with and without explanatory variables for groups I and II.

Species	DFA without explanatory variables			DFA with explanatory variables					
	Factor loadings			Factor loadings (trend 1)	Coefficients (significance)			Average ^a	Preference ^b
	Trend 1	Trend 2	Trend 3		NAO	AFI	Piscivorous		
<i>Reinhardtius hippoglossoides</i>	-0.189	0.065	-0.238	-0.236	0.32	0.277	0.439*	2.25	Colder
<i>Pandalus borealis</i>	-0.179	-0.186	-0.196	-0.177	-0.262	0.622*	0.365	5.2	Warmer
<i>Nezumia bairdii</i>	0.037	0.102	-0.169	-0.145	0.534**	0.517*	-0.569**	5.5	Warmer
<i>Anarhichas minor</i>	-0.058	0.416	-0.065	-0.071	1.004***	0.384*	-0.204	1.825	Colder
<i>Sebastes marinus</i>	0.29	0.02	-0.04	-0.047	-0.218	-1.207***	-0.383*	5	Warmer
<i>Sebastes fasciatus</i>	0.318	0.002	-0.035	-0.038	-0.291**	-1.273***	-0.448***	5.55	Warmer
<i>Lycodes reticulatus</i>	-0.047	0.099	-0.024	-0.022	0.463*	0.796**	-0.136	1.3	Colder
<i>Anarhichas denticulatus</i>	0.126	0.386	-0.002	-0.011	0.605*	-0.027	-0.338	2.8	Colder
<i>Illex illecebrosus</i>	0.246	0.043	0.015	-0.008	-0.285	-0.846**	-0.028	-	Warmer
<i>Macrourus berglax</i>	-0.003	0.037	0.015	0.038	0.447*	0.511	-0.515*	2.75	Colder
<i>Amblyraja radiata</i>	0.195	-0.024	0.072	0.072	-0.079	0.088	-0.441	6	Warmer
<i>Glyptocephalus cynoglossus</i>	0.206	0.06	0.105	0.103	0.028	-0.193	-0.478*	4	Warmer
<i>Anarhichas lupus</i>	-0.033	0.323	0.136	0.125	0.830***	0.51**	-0.259*	1.8	Colder
<i>Sebastes mentella</i>	-0.023	0.003	0.159	0.16	0.205	-0.659*	-0.276	0	Colder
<i>Bathyraja spinicauda</i>	0.006	-0.017	0.211	0.221	0.172	0.154	-0.398*	0.9	Colder
<i>Gadus morhua</i>	0.016	-0.01	0.272	0.244	-0.241	-0.298	0.311*	4.75	Warmer
<i>Hippoglossoides platessoides</i>	-0.086	0.008	0.296	0.287	0.077	0.138	0.037	1	Colder
<i>Triglops murrayi</i>	0.084	-0.232	-	-0.211	0.579**	0.63**	0.244	-	Colder
<i>Cottunculus microps</i>	-0.15	-0.067	-	-0.126	0.145	0.583*	-0.32	2	Colder
<i>Lumpenus lampretaeformis</i>	-0.12	-0.025	-	-0.098	-0.042	0.329	-0.065	1.25	Colder
<i>Gaidropsarus ensis</i>	-0.252	-0.022	-	-0.096	-0.159	-0.51**	-0.555**	1.25	Colder
<i>Urophycis chesteri</i>	-0.214	0.025	-	-0.078	-0.268	-0.028	-0.094	5.65	Warmer
<i>Enchelyopus cimbrius</i>	-0.26	0.044	-	-0.058	-0.188	-0.042	-0.594**	-	Warmer
<i>Lycodes esmarki</i>	0.147	-0.133	-	-0.037	0.602**	0.876**	-0.131	2	Colder
<i>Aspidophoroides monopterygius</i>	-0.111	0.057	-	-0.026	-0.097	0.552	-0.082	0.75	Colder
<i>Antimora rostrata</i>	-0.099	-0.024	-	0.025	-0.291	-0.147	-0.311	3.35	Colder
<i>Lycodes vahli</i>	0.333	-0.145	-	0.098	0.838***	0.634**	-0.29*	2.75	Colder
<i>Coryphaenoides rupestris</i>	-0.061	0.28	-	0.198	-0.063	-0.361	-0.376	4	Warmer
<i>Malacoraja senta</i>	-0.008	0.253	-	0.21	-0.36	0.414	0.096	5.5	Warmer
<i>Notacanthus chemnitzii</i>	0.267	0.061	-	0.232	0.414*	0.383	-0.225	3	Colder
<i>Synaphobranchus kaupii</i>	-0.024	0.321	-	0.264	-0.152	-0.246	-0.247	5.5	Warmer

Species with absolute factor loadings >0.2 were considered to be notably influenced by the trend (bold values).

^aAverage value of the temperature range for each species, obtained from Scott and Scott (1988).

^bTemperature preference in relation to the average bottom temperature on the Flemish Cap in the period 1988–2008.

* $p \leq 0.05$, $2.09 < t < 2.85$.

** $p \leq 0.01$, $2.85 < t < 3.85$.

*** $p \leq 0.001$, $t > 3.85$.

PERMANOVA results (Figure 7); positive and negative years appear to be fairly segregated in two-dimensional space.

Discussion

The results from the analyses clearly reveal important and generalized changes in the demersal fish community of the Flemish Cap since the late 1980s. DFA analyses identified common trends in the trajectories of many of the fish species in groups I and II. Also, the explanatory variables considered in the analyses appeared to be consistently important, suggesting that environmental conditions, along with predation and fishing mortality, are significant drivers of the Flemish Cap fish community. After including these explanatory variables in the DFA analysis, the remaining common trend was similar between both groups of species ($r = 0.98$, $p < 0.01$), strongly suggesting that the dynamics of the main demersal species in the Flemish Cap (groups I and II) are interconnected, and can be summarized by a few common patterns.

The NAO index is considered a good indicator of the global climate in the North Atlantic (Hurrell *et al.*, 2003) and is linked with the dynamics of primary production and zooplankton communities (Fromentin and Planque, 1996), as well as the recruitment success of groundfish stocks such as *G. morhua*, *Limanda ferruginea*, and *M. aeglefinus* (Brodziak and Ó'Brien, 2005; Stige *et al.*, 2006), and alternating *Clupea harengus* and *Sardina pilchardus* strength in European waters (Alheit and Hagen, 1997). We used a multiyear average of this index as a proxy for environmental conditions. The DFA results indicate that the environmental effects we detected appeared to be linked to the temperature preferences of the fish species, suggesting that temperature regimes have an important role in determining recruitment success, growth, survival, and species interactions in the Flemish Cap system.

The link between temperature regimes and fish temperature preferences, as represented by the DFA coefficients for the NAO variable, is shown clearly by the results obtained for the genus

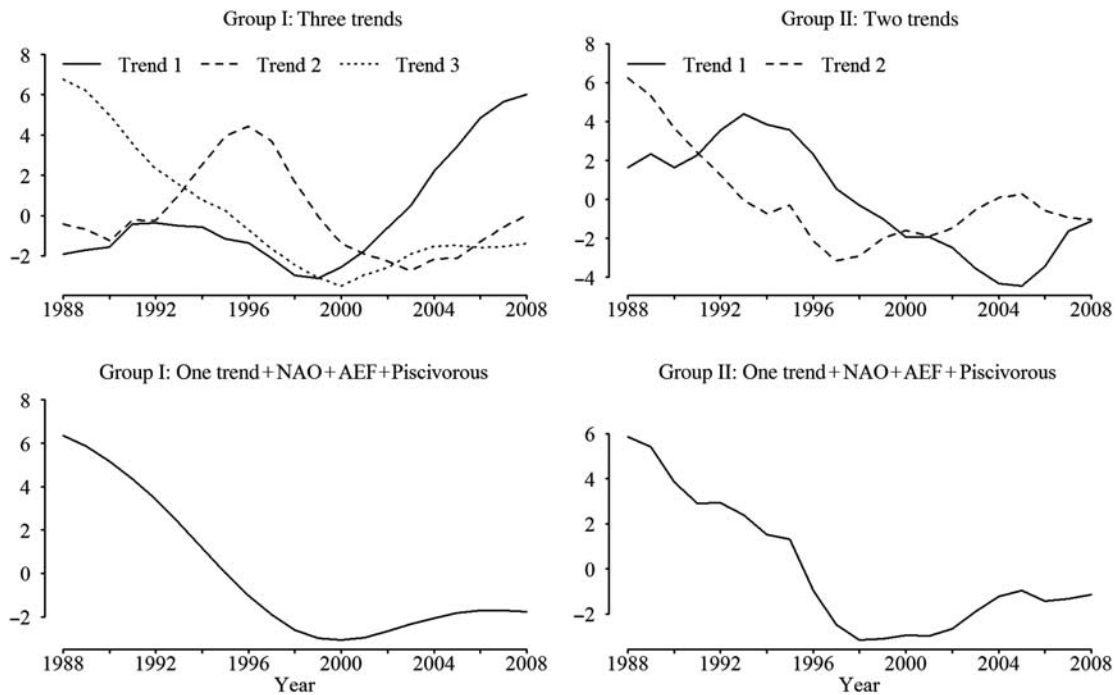


Figure 6. (Upper panels) Common trends for groups I and II from the best DFA models without explanatory variables. (Lower panels) The single common trend for each of these groups obtained from the best DFA model when explanatory variables were included in the analysis. The variables included in the best DFA models were the NAO index, the AFI, and the piscivorous abundance for both groups.

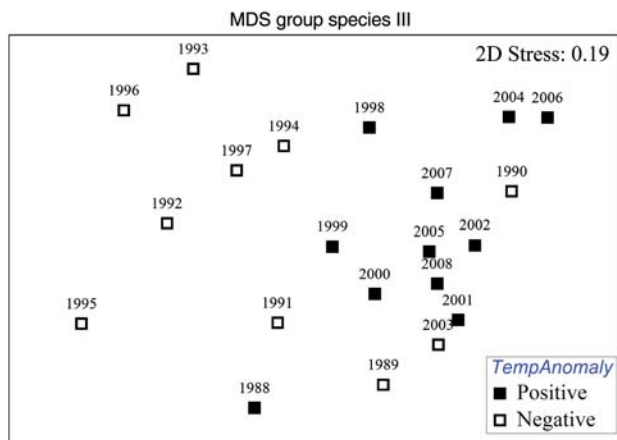


Figure 7. A two-dimensional MDS plot for species of group III. The black squares represent the years with bottom temperature above the average during the period 1988–2008, and the open squares the years with bottom temperatures below this average.

Sebastes. There are three species of that genus on the Flemish Cap, *S. mentella*, *S. marinus*, and *S. fasciatus*. Although the three species overlap extensively, there are differences in their distribution, revealing a gradient in both depth and latitude. *Sebastes mentella* tends to be found more in northern, deeper water, whereas *S. fasciatus* tends to occupy more the southern, shallower water, with *S. marinus* somewhere in between (Saborido-Rey, 1994). This gradient in distribution also implies a gradient in the temperature environment, *S. mentella* inhabiting the cooler water and *S. fasciatus* the warmer water. The influence of the NAO found in the DFA analysis showed this relationship, with a positive

coefficient for *S. mentella*, a negative one for *S. marinus*, and an even more negative coefficient for *S. fasciatus*.

On the Flemish Cap, fishing has been considered the main driver for the decrease in commercial species such as *G. morhua* and *P. borealis* (Casas-Sánchez, 2010; González-Troncoso and Vázquez, 2010). In agreement with this perspective, the DFA results here also indicated a strong influence of fishing in the dynamics of all species, but more so for group I, where commercial species are included, than for group II, which consists of mainly non-commercial species. The most commonly expected mechanism for this type of effect on non-commercial species is bycatch mortality (Jennings and Kaiser, 1998; Hall, 1999).

The results also showed that, instead of the expected widespread negative influence, the AFI variable often had positive coefficients. These positive effects could be a reflection of indirect mechanisms resulting from complex interactions between species (e.g. trophic cascades, competition, and/or predation release). For example, several studies in the Northwest Atlantic have suggested that the increase in *P. borealis* was a consequence of predation release attributable to the collapse of such groundfish stocks as *G. morhua* (Lilly *et al.*, 2000; Worm and Myers, 2003; Frank *et al.*, 2005). The AFI yielded negative coefficients for *G. morhua* and *Sebastes* spp., which could explain the positive coefficients found for *P. borealis*, potential cod prey species such as *Lumpenus lampretaeformis* and *Lycodes reticulatus*, and other relatively small fish species. Skates, as well as *Anarhichas* spp. and *R. hippoglossoides*, share their main prey items with *G. morhua* during early life (Pérez-Rodríguez *et al.*, 2011a). In these cases, competition release from *G. morhua* and other dominant demersal fish species (e.g. *Sebastes* spp.) may help to explain the positive coefficients found for AFI for these species; competition release mechanisms have been proposed for other

systems in the Northwest Atlantic (Fogarty and Murawski, 1998; Myers *et al.*, 2007).

Overall, although the AFI is admittedly coarse and general and does not pretend to capture species-specific detail (e.g. gear type and target-specific fishing behaviour), it still emerges as a useful indicator for investigating the overall fishing pressure to which the demersal fish assemblage has been exposed, and in conjunction with analyses such as DFA, seems to provide an avenue to discriminate potentially between the direct and indirect effects of fishing.

Although it can be argued that fishing has a greater impact on larger individuals of commercial species, predation influences fish population dynamics through its impact on eggs, larvae, and juvenile stages, often exceeding the effect of fishing (Bax, 1998; Wootton, 1998). In this study, we used the abundance of large piscivorous fish as a proxy for this type of predation pressure. The results from the DFA analyses demonstrate that this variable was not only important, but also that its coefficients consistently showed the negative sign expected from a predation-related variable, suggesting that predation by large piscivorous fish influences not only the juveniles of *Sebastes* spp. (in agreement with the suggestion of Lilly, 1983), but the structure and dynamics of the entire demersal assemblage on the Flemish Cap.

Despite the evidence pointing towards predation effects, *P. borealis*, one of the most important prey species for the fish demersal community of the Flemish Cap, showed a nearly significant positive coefficient for piscivorous abundance. Several studies have argued that the sudden increase in *P. borealis* populations in the Northwest Atlantic is a consequence of predation release (Lilly *et al.*, 2000; Worm and Myers, 2003; Frank *et al.*, 2005), so a negative effect between piscivorous abundance and *P. borealis* was expected. One way for interpreting this contradictory result is to consider the characteristics of the predators of *P. borealis*. Although the piscivorous fish included in the piscivorous index prey upon *P. borealis*, they do so mainly as juveniles, becoming more piscivorous as they grow, whereas many other smaller fish species also feed on shrimp (Pérez-Rodríguez *et al.*, 2011a). Therefore, the positive trend in *P. borealis* biomass could be thought of as a trophic cascade effect negatively influencing the abundance of the smaller fish preying more intensively on northern shrimp.

Our analysis also suggests that competitive interactions may also be at play between two important species in the Flemish Cap system. *Reinhardtius hippoglossoides* and *G. morhua* have similar feeding habits there (Pérez-Rodríguez *et al.*, 2011a). When no explanatory variables are included in the DFA analysis, these two species were associated with the same common trend but with opposite sign; this relationship was maintained even after all explanatory variables were included in the DFA analysis, suggesting a competitive link between the two species. This interpretation finds additional support from the observation that *R. hippoglossoides* expanded its range to shallowest areas, traditionally occupied by *G. morhua*, when the population of the latter declined (Hendrickson and Vázquez, 2005).

Overall, when the explanatory variables were included in the DFA models, the initial number of common trends were reduced to just one; and these single common trends were highly correlated between groups I and II. The reduction in the number of common trends, from models without explanatory variables and models that included them, indicates that signals initially represented by common trends were well captured by explanatory variables. However, even after including explanatory

variables, species such as *G. morhua* still showed important common trend loadings, suggesting that one or more latent variables may still remain unknown or that the types of driver currently included may be acting at multiple levels (and not necessarily in a linear fashion). For example, Stige *et al.* (2006) suggested that the effect of NAO on cod recruitment is mediated through local variables such as temperature, salinity, and oxygen, so it would be conceivable that these local variables can affect recruitment not just in terms of the survival of eggs and larvae, but also in terms of their effects on the reproductive potential of the stock. Although comprehensive studies on reproductive parameters for demersal species on the Flemish Cap are lacking, it has been argued recently that the reproductive potential of *G. morhua* on the Flemish Cap has dropped since the early 1990s (Pérez-Rodríguez *et al.*, 2011b), potentially leading to a decreased capacity to react under adverse environmental conditions.

Many factors can influence the dynamics of a species, and the distribution observed is the outcome of these different forces acting at once (Margalef, 1998). In our case, for species included in groups I and II, the Flemish Cap could be considered as a reasonably suitable area for their biological requirements, because they have a long and consistent record of occupancy of the region. On the other hand, for species included in group III, characterized by sporadic occurrence and low biomass, the Flemish Cap may be an area with suboptimal (for them) conditions, on the fringe of their distributions, and where they may be less competitive. In this context, the results of the PERMANOVA and MDS analyses clearly show that the species composition in group III changes with temperature. During the 1980s, the water temperature on the Flemish Cap was above average for most years, but then followed by the coldest period ever registered in the early to mid-1990s, then warming again in the late 1990s (Colbourne, 2006). This means that the start of our study, 1988, was at the end of the warm period of the 1980s. Hence, the recent temperature history of the system since the 1980s can be described in terms of three periods, an initial warm period in the 1980s, a cooler period until the mid- to late 1990s, and a second warm period since the late 1990s. Given this temperature pattern, and the location of the transition years (warm-to-cold 1988–1991, cold-to-warm 1997–1999) in the MDS plot (Figure 7), the differences in species composition of group III are most likely related to recruitment processes rather than migration events.

The location of the transition years between colder and warmer years suggests a gradual change in species composition, as opposed to a sudden appearance of species, as would be expected under a migration hypothesis. This interpretation would be coherent with the current understanding of the Flemish Cap as a semi-closed system (Konstantinov, 1970; de Cardenas *et al.*, 1993; Morgan and Bowering, 2004), but where advection processes still can potentially bring larvae from the Newfoundland shelf to the Flemish Cap (Konstantinov *et al.*, 1985), and which, if environmental conditions are suitable, can survive and settle. Another plausible explanation could simply be that the rare species are always present on the Flemish Cap, but with biomass levels so low that they are scarcely detected by the survey. However, when environmental conditions are good (either warm or cold), the consequent increases in recruitment and survival would drive the stocks to levels where they can then be detected by the survey.

On the NL shelf, environmental variables such as the NAO index, sea surface temperature, and a composite environmental index, together with the fishing pressure, were also important

drivers in the trajectories of five key fish species during the period 1981–2008 (Koen-Alonso *et al.*, 2010). In addition, changes in the NL marine community, such as the collapse of groundfish stocks and the rise of *P. borealis* during the late 1980s and early to mid-1990s, also bear many similarities with the pattern observed on the Flemish Cap. In the Gulf of Maine marine ecosystem, synchrony in fish population dynamics of various fish species was suggested to be partly attributable to environmental influence in recruitment success, although fishing at the adult stage was also important for the synchrony (Nye *et al.*, 2010). These observations suggest that demersal communities in these regions may share sufficient functional structures to respond similar to major driving forces, at least during the period considered here.

From an integrated management perspective, the results of this study have provided some basic foundations for further developing the science needed for an ecosystem approach to the fisheries of the Flemish Cap. The results suggest that the dynamics of the fish stocks are regulated by both bottom-up and top-down mechanisms at different stages. As explored here, environmental conditions emerge as important factors influencing recruitment success, and mortality by piscivorous predators emerges as an important driver for juvenile and/or smaller fish. Large predatory fish, which are responsible for the top-down predation control, are in turn also subject to mortality by fishing, making fisheries another important regulatory force shaping the Flemish Cap fish community. The rare, low-biomass species in the system also seem to respond to changes in temperature through varying their recruitment success on the Flemish Cap; this type of change may be a hint for what we should expect to see as climate change progresses. Overall, the study provides a reasonable template for developing a general understanding of the major forces regulating the structure and dynamics of the Flemish Cap fish community, but translating this general understanding into practical tools and a framework for management application would require refinement, and further testing, of many of the ideas and hypotheses outlined.

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