

Persistence and Variation in the Distribution of Bottom-trawl Fish Assemblages over the Flemish Cap

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Abstract

The aim of this study is to test the variability of the assemblages defined in the Flemish Cap area. Data from 951 bottom hauls were analysed, covering depths between 126 and 740 m in the years 1995–2002. The fish fauna in Flemish Cap appears distributed in a persistent structural zonation defined in three assemblages. The first three factors of a Principal Component Analysis explained the 78.4% of the variance in distribution species, and they are consistent with the results of a cluster analysis. The three characteristic assemblages show a temporal persistence, but some changes appear in this period, for instance: displacements of the assemblages limits towards shallower waters, and some changes in relative position of the dominant species in each assemblage. These changes can be related with the constant decrease of the biomass of the main demersal fish species like Atlantic cod and American plaice. The species of *Genus Sebastes* appear as dominant fish species in the area.

Key words: Demersal, dominance, ecosystem, *Gadus morhua*, *Hippoglossoides platessoides*, north-west Atlantic, *Sebastes*

Introduction

In recent years, attention has started to shift towards determining the role of species in their ecosystem and the likely impacts of fishing on them. As our knowledge on ecosystem interactions and processes increases, fisheries management is likely to move away from single-species approaches towards ecosystem-based strategies (Kendrick and Francis, 2002).

Fish represent the major biomass component of marine ecosystems. Interactions among fish species, and between fish and their physical environment, are important to define the structure, diversity and stability of marine ecosystems. Therefore, the study of fish assemblages is an important step in this study. However, interactions are difficult to observe in practice. The simplest way to assess potential interactions may be to identify "fish assemblages", which are defined here as groups of spatially and temporally co-occurring fish.

Numerous attempts have been made worldwide to identify fish assemblages (Bianchi, 1991, 1992; Koslow, 1993; Fujita *et al.*, 1995; Gomes *et al.*, 1995; Fariña *et al.*, 1997; Mahon *et al.*, 1998; Bergstad *et al.*, 1999; Francis *et al.*, 2002; Beentjes *et al.*, 2002; Gaernet *et al.*, 1999; Jay, 1996). A common approach involves multivariate analysis of abundance or presence-absence data from bottom trawl surveys. Some fish assemblages are stable on a time scale of decades (Musick *et al.*, 1996).

The Flemish Cap is located in NAFO Division 3M and centred at about 47°N 45°W (Fig. 1). Templeman (1976) provides a background of the biology and hydrography of the Flemish Cap area. Stein's (1996) presented an overview of the oceanography of the zone.

Fish assemblages, their structure and temporal persistence have been recently under analysis in several zones of the North Atlantic (Musick *et al.*, 1996); the Northwest Atlantic (Mahon *et al.*, 1998; Lee and Sampson, 2000) and other intensely exploited areas: New Zealand, (Francis *et al.*, 2002); Norwegian Sea (Bergstad *et al.*, 1999); Portugal shelf (Gomes *et al.*, 2001). However, these aspects have hardly been studied in Flemish Cap.

Several studies have described the biology and ecology of Flemish Cap fish species (Rodríguez-Marín *et al.*, MS 1994; Rodríguez-Marín and De Cárdenas, MS 1997; Saborido-Rey and Junquera, 1999 a,b; Murua, MS 2000; Saborido-Rey, MS 2001; Alpoim *et al.*, MS 2002). Most previous works concerned single species and species-specific spatial distributions, population dynamics or biology. However, in this study we have focused on the assemblages of fish species. A similar approach can be found in Paz and Casas (1996).

A bottom trawl survey on Flemish Cap has been performed by the European Union since 1988 (Vázquez, MS 2000; MS 2002). The results are useful to describe

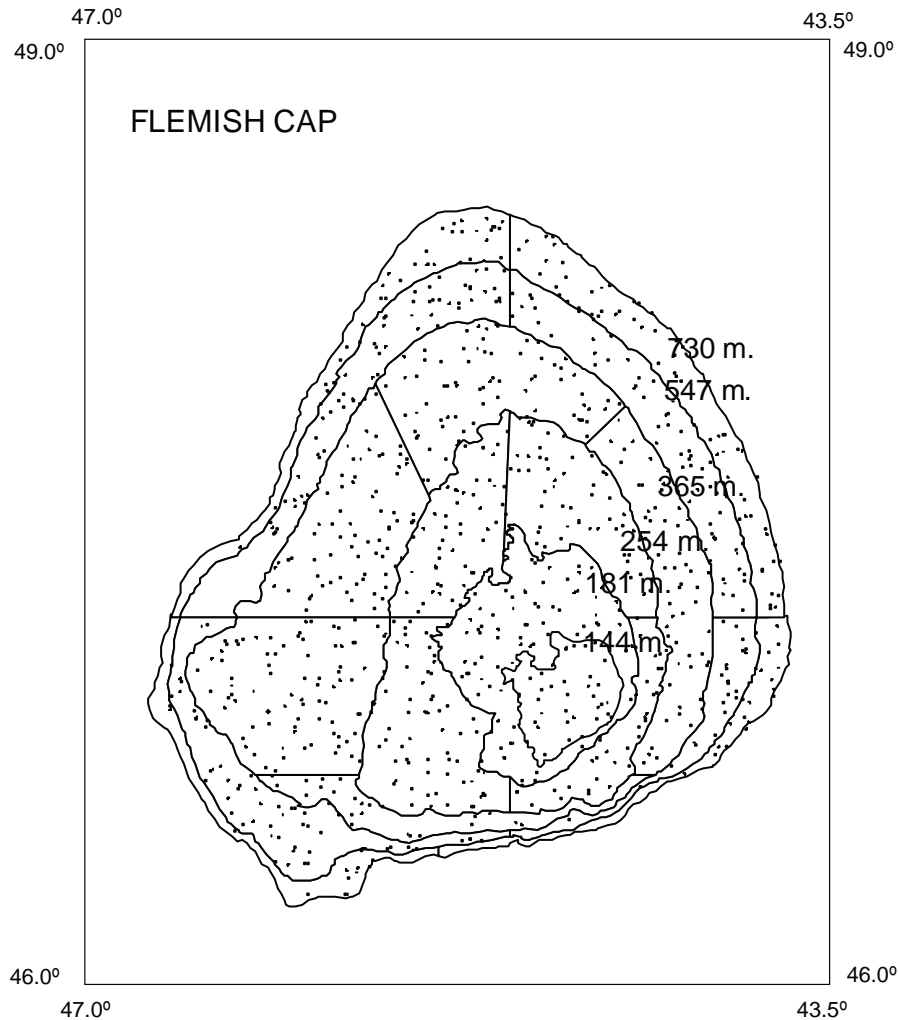


Fig. 1. Chart showing the positions of bottom trawl stations on Flemish Cap area between the years 1995 and 2002 with the approximate isobaths.

the abundance and spatial distribution of demersal and mesopelagic fish species.

The biomass and abundance of some commercial fish stocks in Flemish Cap have strongly decreased in the last years according to EU survey results (Fig. 2). The cod biomass was 103 644 tons in 1989, 24 062 tons in 1994 and 2 270 tons in 2002. The stock has been under a fishing moratorium since 1999, and little improvement is expected in the near future given the absence of recruitment after 1992. American plaice has also been under a fishing moratorium since 1996; its biomass was 11 887 tons in 1988, 6 173 tons in 1994 and 1 536 tons in 2002, with a minimum of 1 204 tons in 2000. Both stock biomass and spawning stock biomass are at very low levels and there is no sign of recovery due to the

consistent year-to-year recruitment failure since the beginning of the 1990s. For redfish, abundance remained stable from 1996 to 2001, and increased afterwards due to the recruitment of the above average 1998–2000 year-classes. In 2004, SSB was still well below the 1990's level, which produced a strong recruitment. The current fishery is targeting shrimp and redfish in depth less than 700m and Greenland halibut in depths more than 700 m (Casas and González-Tronoso, 2003; NAFO, 2004; 2005).

The changes in abundance of some dominant species should have consequences on their distribution and aggregation pattern. The objective of this paper is to describe the homogeneity and heterogeneity of dominant fish fauna in Flemish Cap for the period 1995–2002 and

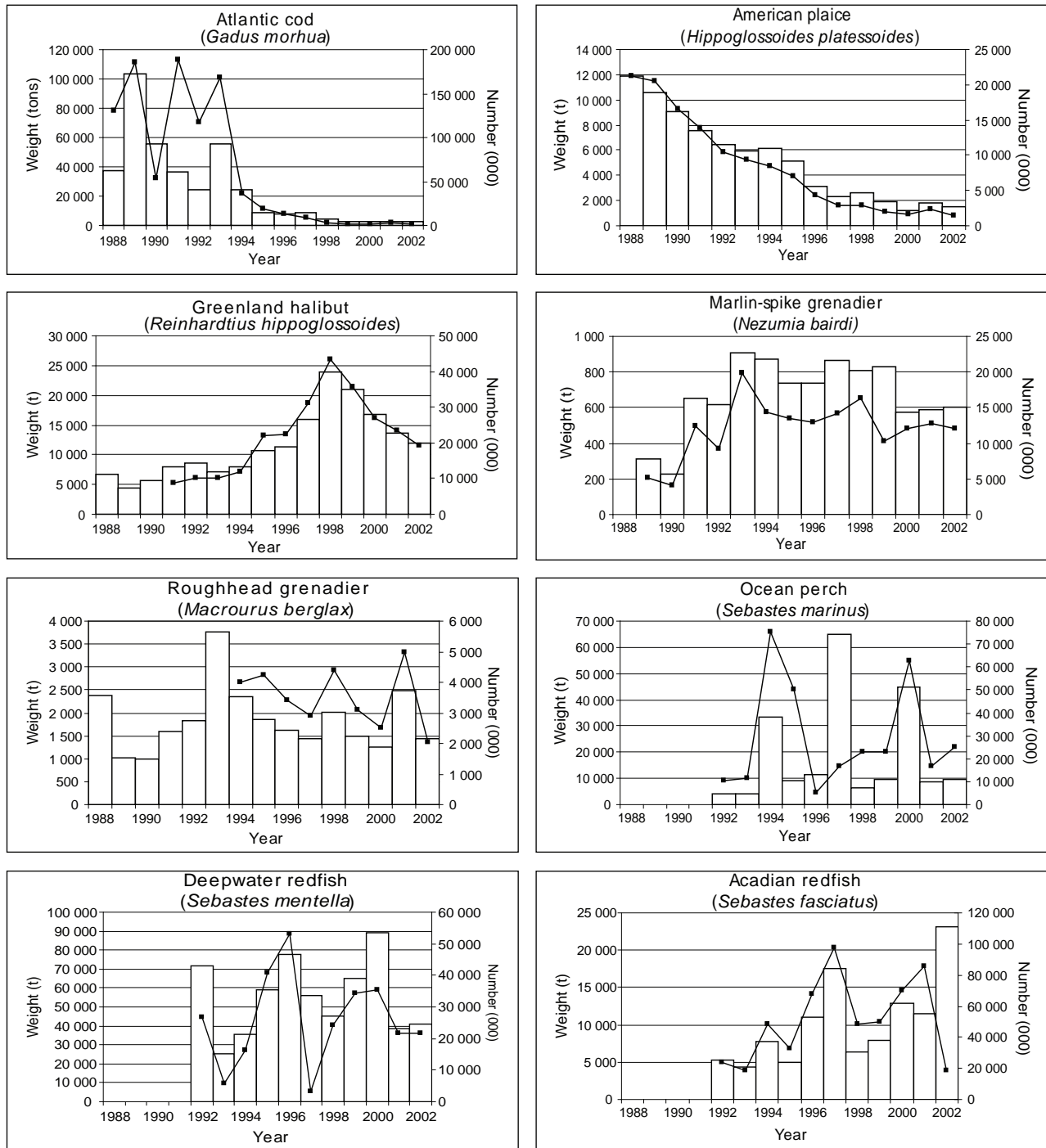


Fig. 2. Weight (bars) in metric tons and abundance (lines) in thousands of the principal captured species in Flemish Cap in years 1988–2002.

to explore the possible changes that took place in the communities as described in previous works (Paz and Casas, 1996).

We have tried to know firstly the structure and specific composition of the population in assemblages by

depth. We have also tried to find out the relative importance of the considered dominant species in order to see the relation between the possible changes with fishing effects in the interspecific structures and the evolution of the abundance of each population. To do this, we have used in this paper four different analysis: Empirical

cumulative distribution function, cluster analysis via Bray-Curtis measure, Correspondence analysis and Principal Component analysis.

In order to better understand the interaction of the different species found in Flemish Cap, we have included a table in the Appendix with a complete list of the studied species. In this table the family, the common name, the type of habitat, the maximum length, the trophic level and the depth of each species are shown. The species in this table are ordered firstly by habitat type, and secondly by trophic level (upward).

Material and Methods

The period studied in this paper is 1995–2002. The data base corresponds to the sampling results from standard groundfish research trawl survey conducted by the European Union in summer between 1988 and 2002. The survey used a stratified random sampling design, with strata based on depth boundaries of 144, 181, 254, 365, 547 and 730 m (80, 100, 200, 300 and 400 fathoms) (Fig. 1). A description of the demersal sampling gear used can be found in Vázquez (MS 2000); it was the same throughout the study period. The survey sample unit was defined as the swept area by a Lofoten trawl towed at a constant speed of 1.8 ms⁻¹ (3.5 knots) for 30 min.

In each survey the sets were allocated to strata according to area, with all strata containing at least two sets. Details of the survey are described by Vázquez (MS 2002). Some information about the surveys is shown in Table 1.

A species was not considered when its weight was less than 15 grams or only one specimen was found. These criteria were not applied to the mesopelagic

TABLE 1. Number of trips and hauls made during Flemish Cap EU bottom Trawl Surveys on R/V *Cornide de Saavedra*. NAFO Divisions 3M: 1995–2002.

Year	Valid hauls	Depth range
1995	121	126–721
1996	117	135–710
1997	117	133–720
1998	119	137–712
1999	117	133–718
2000	120	135–704
2001	120	132–720
2002	120	130–740
Total	951	126–740

species (*Serrivomer beani*, *Chaulodius sloani* and *Stomias boa*) due to the small size and low frequency of appearance, because of their low catchability with the gear used.

Twenty-two demersal and three mesopelagic species were included in the analysis. They consisted of commercial and non-commercial species, but they were potentially dominant species in a given region, or potential forage for other species. The species of genus *Sebastes* were identified every year and three species were considered in the analysis: *Sebastes marinus*, *S. mentella* and *S. fasciatus*. These 25 species amounted more than 89% of the catch. All species were present at least in 8.4% of the total observed tows, except *Synphobranchus kaupi* (2.6%). All strata were sampled with sufficient intensity to assess their composition.

As a preliminary analysis to establish whether zonation was present, an application of the chi-square test (Gardiner and Haedrich, 1978) was used. This method is applied to the presence or absence of the species. To apply it, the bottom trawl available hauls were arranged in order of increasing depth, the area studied was randomly divided into seven depth regions of 100 m depth ranges (≤ 150 m, 151–250 m, 251–350 m, 351–450 m, 451–550 m, 551–650 m, and ≥ 651 m) and the number of species that appeared for the first time in each region (upslope boundaries; they had not appeared before in any region) were recorded. This method tests the distribution across the area of upslope boundaries using the formula:

$$\chi^2 = \frac{Q}{K} \left(V - \frac{K^2}{Q} \right) \quad \text{with } Q-1 \text{ degrees of freedom}$$

where: Q = numbers of regions into which the area was randomly divided,

K = total number of species, and

V = sum of squares over all regions of the number of upslope boundaries.

The null hypothesis is that the locations of upslope boundaries are uniformly distributed along the gradient, and that there is no tendency towards clustering. In order to reject this null hypothesis with a significant level of α , a two-tailed test is performed using the chi-square statistic with $Q-1$ degrees of freedom and values of $\alpha/2$ at each tail. So, values of the index were compared with those in a chi-square table for $Q-1$ degrees of freedom. If the calculated value exceeded the value obtained from the table, the upslope boundaries were considered to be distributed non-randomly, i.e., they are zoned.

The preliminary explorations were made to identify associations among the catches of the 25 selected species. Cumulative distributions of the number of the specimens caught by species were compared with the empirical cumulative distribution of the depths of the hauls. The numbers of hauls in each stratum were strictly proportional to stratum area, so that the different size of the strata can be ignored (Perry and Smith, 1994).

If there was no particular association between fish distribution and depth within the area surveyed, e. g., if the fish were randomly distributed with respect to depth, then the cumulative distribution function for each species would be almost identical to the function for depth. Conversely, when the fish were associated with a small depth range, then these functions would be very different.

These cumulative distribution functions were plotted (Fig. 3) and the potential boundaries were examined by calculating the percentage similarity between the regions involved. Percentage similarity is a commonly-used measure of faunal overlap and was calculated according to the formula of Whittaker and Fairbanks (1958):

$$PS = 100(1.0 - 0.5 \sum |P_{ia} - P_{ib}|)$$

where P_{ia} = the proportion assumed by species in sample, and

P_{ib} = the proportion assumed by species in sample.

Percentage similarity is an insensitive index to sample size, but it is in fact highly sensitive to the relative number of species among the regions involved (e.g., if the sample size varies excessively among strata and the species number is closely related to sample size, it will lead to a downwardly biased perception of affinities among strata (Koslow, 1993)). In the current work, the narrow depth range analysed showed small differences in the species number recorded and little relation with the sample size.

Cluster analysis was used to assess faunal change with depth and to contrast with the results based on analysis of the percentage similarity data. We used the commonest type of cluster analysis, joining analysis, in which samples were arranged into groups where each had a similar biotic composition.

To reduce the large number of sets (951) for the 1995–2002 period, the sets were grouped into class depth of 50 m for every two years. These class-depths or strata were labelled with the maximum depth value of the class. Therefore, for every two years (1995–96,

1997–98, 1999–2000, 2001–02) there were 13 strata named: 150, 200, 250, ..., 750, i.e., we have a total of 52 strata.

The classification and ordination analysis were based on a matrix of similarity coefficients among strata. To calculate the similarity coefficients we used the mean numbers of specimen per strata for each species.

The data (number of specimens for each species) were previously root-root transformed ($\times^{1/4}$). This transformation has the effect of scaling down the scores of abundant species to avoid swamping the other data (Field *et al.*, 1982). Moreover, the root-root transformation has the advantage that, when similarity is assessed by the Bray-Curtis measure, the similarity coefficient is invariant to a scale change (Stephenson and Burges, 1980).

We have adopted the Bray and Curtis measure of similarity because it is not affected by joint absences (Field and McFarlane, 1968) and is, therefore, sufficiently robust for marine survey data where many of the species are absent from the majority of the samples, while it gives more importance to abundant species (in comparing samples) than to rare ones.

The Bray-Curtis measure has the form:

$$\delta_{jk} = \frac{\sum_{i=1}^s |Y_{ij} - Y_{ik}|}{\sum_{i=1}^s (Y_{ij} + Y_{ik})}$$

where: Y_{it} = score for the species in the sample, and

δ_{jk} = dissimilarity between the and the samples summed over all species.

The dissimilarity matrix of the data was calculated in Matlab (The MathWorks, Inc., 2002).

The clustering strategy is the hierarchical weighted group-average sorting, which joins two groups of samples together at the average level of similarity between all members of one group and all members of the other. Analyses were carried out with Statistica (StatSoft, Inc., 2005).

To corroborate the results of the cluster analysis, we used two more multivariate techniques: correspondence analysis and principal components. The data used in these analyses were the same used in the cluster analysis.

Correspondence analysis is an ordination method in which each site is located at the centre of gravity of

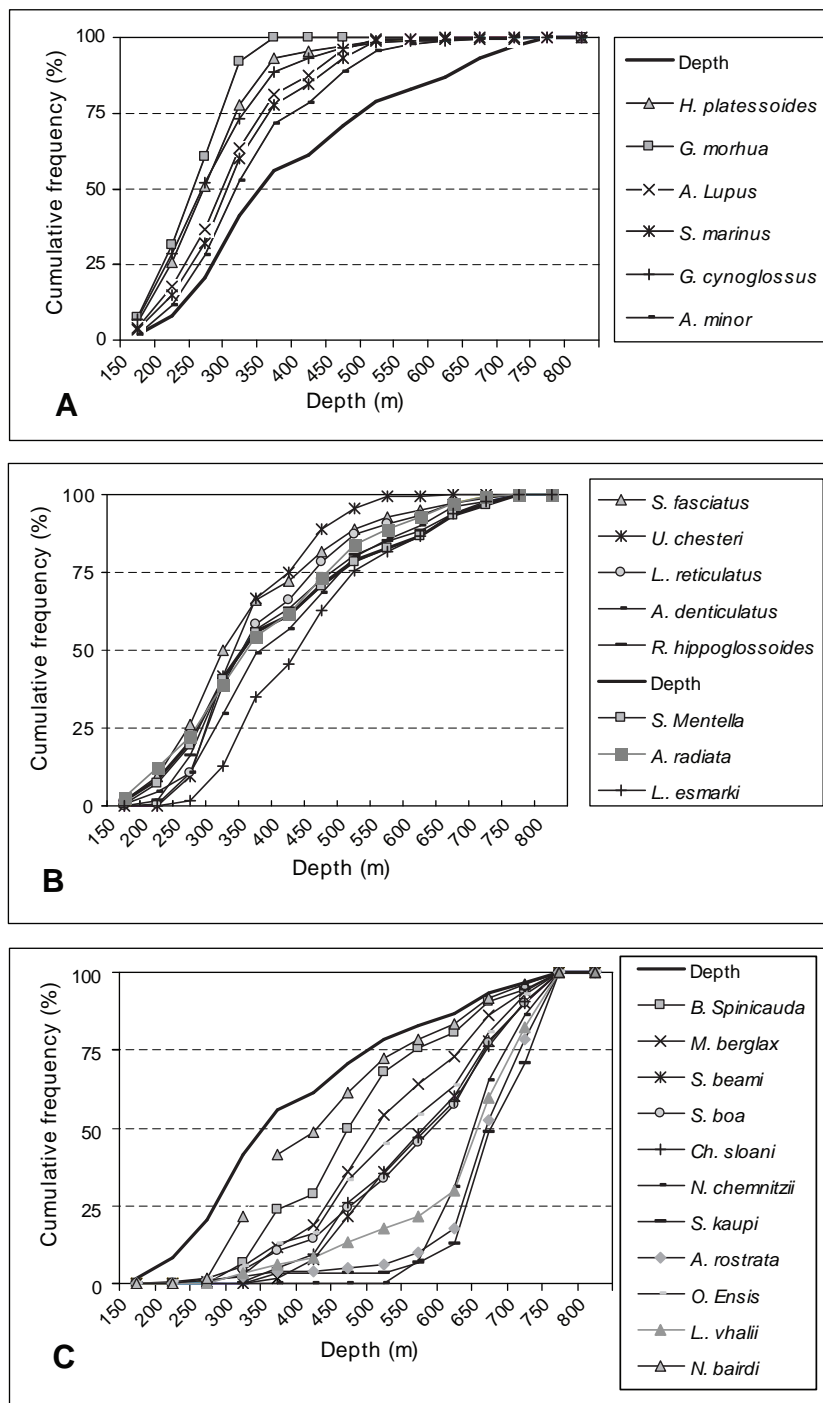


Fig. 3. Cumulative frequency distributions of depth variable and depths as weighted by number of the specimens caught for each species on Flemish Cap in summer 1995–2002. (A) Shelf group species; (B) Upper continental slope group species; (C) Middle continental slope group species

the species that occur there. This method is unaffected by double-zero, i.e., tows in which both species being compared are absent (Gauch, 1982; Jackson and Harvey, 1989; Kendrick and Francis, 2002).

Principal component analysis was also used to test the results obtained in the cluster and correspondence analysis. Species loadings of principal components were used to identify groups of species that tend to co-occur

(i.e., assemblages). The eigenvalue associated with a Principal Component indicates the relative importance of that component. Principal components with eigenvalues >1 are considered to represent statistically significant assemblages (Jolliffe, 1986). VARIMAX rotation was used for the data, and performed by Statistica program. The data used were the same used for the cluster and correspondence analysis (Mahon *et al.*, 1998).

Diversity, H , for the resultant depth zone was calculated using the information function (Shannon and Weaver, 1963):

$$H = -\sum p_i \ln p_i$$

where p_i = fraction of the total comprised by species in a region.

Regressions were performed on individual species to establish whether a correlation between size and depth existed. The size was estimated by calculating the mean weight for each species and set from the total weight of the species and the specimen number in the set.

Results

A complete list of species considered for the period studied 1995–2002 is given in Table 2. This table shows the depth range, weight and number of specimens in the total sets by species. Each species showed an unique vertical depth range. The data are for all valid hauls (951).

The chi-square test was run on all sets for the years from 1995 to 2002, grouped into regions of 100 m depth intervals. The value of chi-square, $\chi^2_{\text{upslope}} = 28.48$, exceeded the 0.01 significance level for 6 d. f. ($\chi^2 = 18.55$). This showed that, in the period considered, the distribution was zoned between 127 and 730 m. However, the fact that the survey sampling did not completely cover the depth range of all species made it difficult to set up the zonation with certainty, because some species have a larger depth distribution, deeper than the range sampled.

Figure 3 shows cumulative distribution functions for observed depth and depths weighted by the number of specimens caught of each species. We constructed three graphs where the species were grouped according to similarity behaviour with respect to depth.

Basically, we found three groups of species. Group A (Fig. 3a) comprised the species with cumulative occurrence percentages higher than 50% in depths less than 300 m, except *Sebastes mentella* that shows an almost identical frequency to that of the depth (40.7% at 300 m

versus 41.3% of the depth). In group B (Fig. 3b), the species present showed no particular association between fish distribution and the depth within the area surveyed, with a random distribution with respect to the depth. Group C (Fig. 3c) is composed of species with cumulative occurrence percentage higher than 68% in depth greater than 500 m.

Nezumia bairdi, *Lycodes smarki* and *Bathiraja spinicauda* do not appear clearly located, between the groups B and C. To assign them into a group the respective graph of the capture was drawn concerning the bottom (Fig. 4). In this figure we represent the minimum, the maximum and the quartiles (25%, median and 75%) of the non-zero value for each year. The biggest captures in *Lycodes* were concentrated between 350 and 450 m (group B) (Fig. 4a); in the case of *Nezumia* and *Bathiraja spinicauda* the biggest captures were carried out around 500 m (Fig. 4b and 4c), between group B and C. We assigned them to group C.

The potential boundaries appear to be at 300 and 500 m (Fig. 3). These potential boundaries were examined by calculating the percentage similarities between regions involved. PS measured across the 300 m level was 55.26% and across 500 m level was 28.34%. These data thus suggest that the distribution is zoned between 127 and 730 m.

To contrast this result, a cluster analysis was also performed. Figure 5 is the resulting dendrogram showing sample affinities based on the mean root-root transformed abundance (mean number of specimens in each stratum) of the 25 species studied, using the Bray Curtis measure of similarity and group average sorting. Three main zones or clusters were distinguished at an arbitrary dissimilarity level of 35%. Cluster I comprised the strata with depth lesser than 300 m; cluster II comprised the transition depth strata between 300 m and 500 m, and cluster III the depth strata greater than 500 m. The results showed grouping of species with similar biotic character and comparable depth preferences.

Besides, we conducted two more multivariate analyses in order to confirm the results. Cluster analysis made three exclusive groups in agreement with the three groups made by the cumulative distribution functions (Fig. 6) except for the *Bathiraja spinicauda*, which appears in group II instead of group III.

We made a principal components analysis. We found three components with eigenvalues greater than 1, which explains more than the 78% of the total variance (Table 3). When we graphed the two first components (Fig. 7),

TABLE 2. Vertical depth ranges and catch data for fish species taken by bottom trawls on the Flemish Cap surveys 1995–2002 including all valid hauls. In brackets, the 1988–94 values, except for *Sebastes marinus* (1990–94 values), *Sebastes fasciatus* and *Sebastes mentella* (1992–94 values)².

Maine Fish Species	FAO Code	Depth Range	Weight (kg)	No. of Specimens	No. of Stations
<i>Gadus morhua</i>	COD	126–343 (126–631)	6 332 (48 500)	8 008 (119 979)	382 (459)
<i>Anarhichas lupus</i>	CAA	126–716 (130–497)	4 911 (4 950)	17 860 (100 063)	706 (498)
<i>Sebastes marinus</i>	REG	126–643 (130–441)	25 065 (6 810)	64 611 (16 220)	674 (253)
<i>Glyptocephalus cynoglossus</i>	WIT	126–677 (130–738)	496 (540)	1 056 (1 242)	289 (249)
<i>Sebastes fasciatus</i>	REN	126–740 (151–660)	13 846 (2 340)	92 196 (12 675)	781 (214)
<i>Anarhichas minor</i>	CAS	126–703 (129–605)	6 053 (2 590)	4 201 (1 752)	600 (302)
<i>Amblyraja radiata</i>	RJR	126–718 (126–717)	1 430 (1 950)	891 (1 071)	381 (385)
<i>Sebastes mentella</i>	REB	145–740 (249–738)	66 958 (17 100)	379 133 (65 618)	763 (186)
<i>Hippoglossoides platessoides</i>	PLA	126–716 (126–519)	3 027 (6 910)	3 840 (12 412)	420 (456)
<i>Urophycis chesteri</i>	GPE	213–703 (280–638)	190 (112)	3 694 (1 295)	327 (168)
<i>Lycodes reticulatus</i>	LCT	179–716 (155–683)	1 295 (975)	13 951 (5 607)	571 (281)
<i>Bathyraja spinicauda</i>	RJQ	256–719 (149–717)	685 (853)	157 (192)	114 (118)
<i>Anarhichas denticulatus</i>	CAB	144–740 (130–738)	1 786 (1 130)	605 (295)	324 (167)
<i>Reinhardtius hippoglossoides</i>	GHL	154–740 (221–753)	18 093 (5 550)	32 539 (6 821)	799 (383)
<i>Lycodes esmarki</i>	SP1 ¹	218–714 (242–738)	239 (143)	1 256 (458)	254 (73)
<i>Nezumia bairdi</i>	NZB	201–740 (249–753)	780 (460)	14 718 (8 991)	432 (290)
<i>Macrourus berglax</i>	RHG	227–740 (249–753)	1 853 (1 440)	3 957 (2 656)	318 (179)
<i>Serrivomer beani</i>	ASB	316–720 (249–738)	37 (13)	403 (151)	115 (44)
<i>Stomias boa</i>	SBB	244–740 (313–738)	15 (4)	836 (151)	110 (30)
<i>Chauliodus sloani</i>	CDN	284–720 (263–753)	34 (19)	994 (67)	121 (60)
<i>Notacanthus chemnitzii</i>	NNN	501–721 (424–753)	183 (311)	249 (363)	95 (65)
<i>Synaphobranchus kaupii</i>	SSK	300–740 (466–753)	12 (445)	71 (351)	25 (72)
<i>Antimora rostrata</i>	ANT	201–740 (524–753)	348 (389)	4 014 (3 366)	93 (69)
<i>Gaidropsarus ensis</i>	GDE	240–740 (575–738)	67 (24)	501 (99)	130 (29)
<i>Lycodes vahlii</i>	SP2 ¹	269–721 (533–738)	88 (89)	518 (372)	80 (38)

¹ non-FAO codes

² The values in brackets are from Paz and Casas, 1996

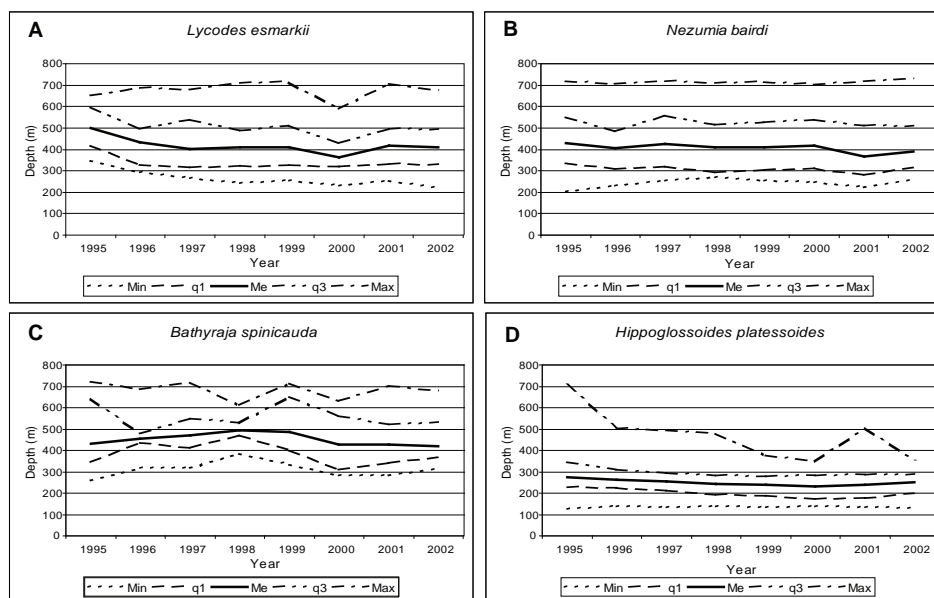


Fig. 4. Depth range of occurrence for *Lycodes esmarkii*, *Nezumia bairdi*, *Bathyraja spinicauda* and *Hippoglossoides platessoides* in years 1995–2002: minimum (*Min*); 25% quartile (*q1*); median (50% quartile) (*Me*); 75% quartile (*q3*) and maximum (*Max*).

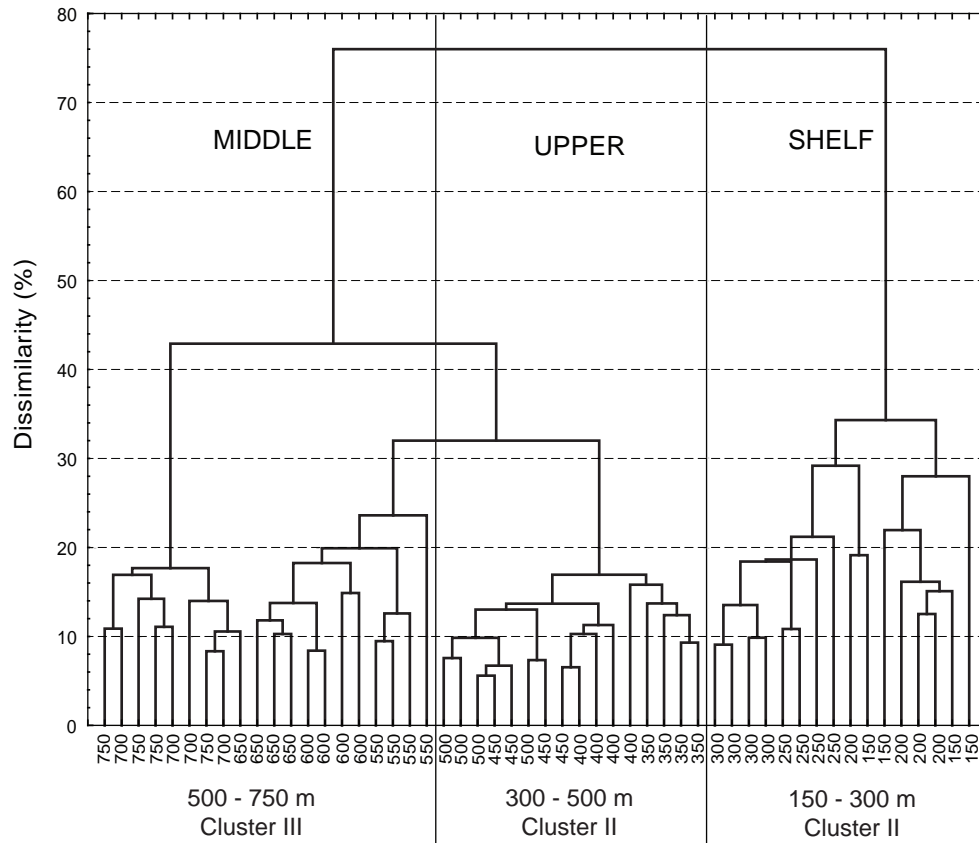


Fig. 5. Dendrogram showing classification of 951 sets grouped in 13 depth class of 50 m by two years (1995–96, 1997–98, 1999–2000, 2001–02) based on mean abundance of fish fauna species composition by depth class. Abundance were root-root transformed before comparing stations using the Bray-Curtis measure, and the dendrogram formed by group-average sorting. Three main cluster are distinguished at an arbitrary dissimilarity level of 35%.

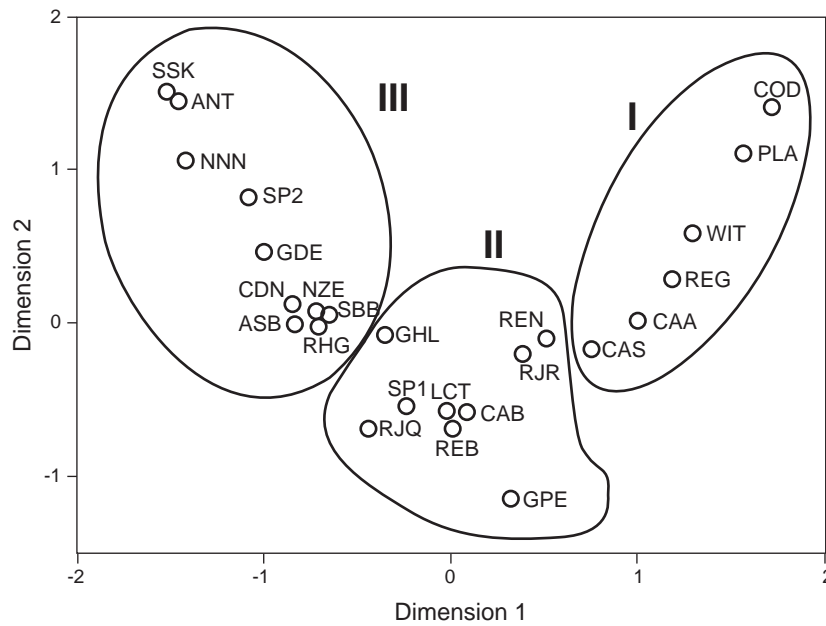


Fig. 6. Results of the Analysis of Correspondence for the 25 species used in the analysis.

TABLE 3. Eigenvalues from the principal components analysis performed on root-root transformed data.

Value	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative %
1	12.5103	50.0410	12.5103	50.0410
2	5.9707	23.8828	18.4810	73.9238
3	1.1250	4.5001	19.6060	78.4240

we found the same three groups of species than in the analysis below, although group I and group II superimpose with *Anarhichas minor* and *Sebastes fasciatus*.

In order to quantify the differences between these three zones: Shelf group (comprising sets shallower than 300 m), Upper Continental Slope group (comprising sets between 300 and 500 m) and Middle Continental Slope (comprising sets deeper than 500 m). Tables 4 and 5 show, respectively, the overall community parameters and the most abundant demersal species (like percentage of total number and total biomass) in the three depth zones considered and the corresponding values for the years 1992–94 (Paz and Casas, 1996).

No species was dominant over the whole depth sampling range (Table 5). *Sebastes mentella* and *Reinhardtius hippoglossoides* were the only species present in all depth strata, standing out into upper continental slope.

Regression analysis of mean weight per individual for each species versus depth was performed (Table 6). Some species like *Urophycis chesteri*, *Reinhardtius hippoglossoides* and *Sebastes mentella* showed a well marked "bigger-deeper" distribution. Another species, like *Macrourus berglax*, *Stomias boa*, *Sebastes marinus*, *Nezumia bairdi*, *Sebastes fasciatus* and *Serrivomer beani* showed a less-marked "bigger-deeper" trend in distribution.

Others authors also observed this "bigger-deeper" trend in other areas for several species studied here. Poltoni *et al.* (1979) and Snelgrove and Haedrich (1985) reported the "bigger-deeper" phenomenon, on the South of Newfoundland's continental slope, for *Antimora rostrata*, *Synphobranchus kaupi* and *Nezumia bairdi*.

Discussion

Analysis of eight years of EU trawl survey data from the Flemish Cap area identified three main fish assemblages of 25 studied species. A similar approach with the same group of species of Flemish Cap can be found in Paz and Casas (1996). In that paper, the authors established three assemblages between 300 and 600 m in a study of the data obtained in the EU surveys in the years 1989–94. These assemblages are consistent with the identified in this paper, although three "problematic" species (*Lycodes smarki*, *Nezumia bairdi* and *Bathiraja spinicauda*) were assigned to another groups in that

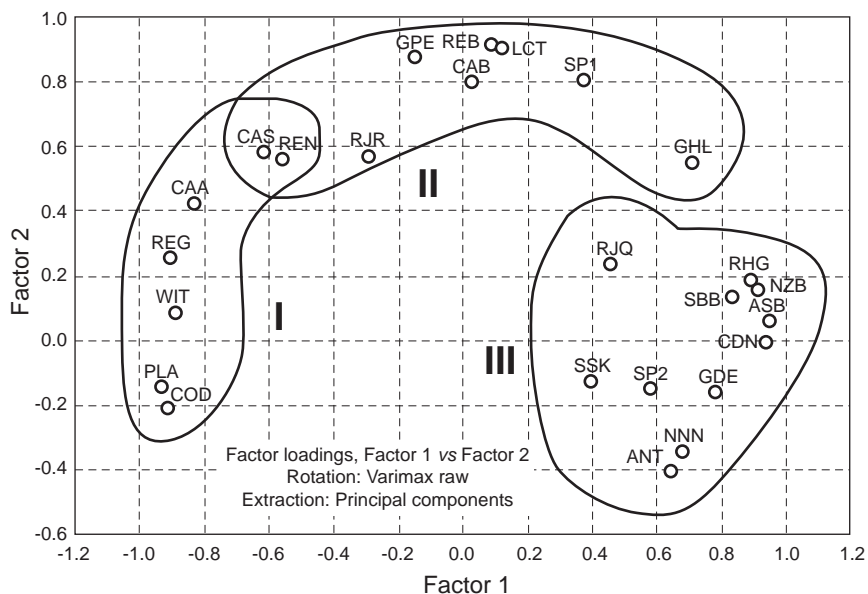


Fig. 7. Results of the Principal Components Analysis for the 25 species used in the analysis.

TABLE 4. Community parameters and catch rates for fish assemblages by depth strata on the Flemish Cap in the years 1995–2002. The 1992–94 values are in parentheses.

	Depth strata (m)					
	127–300 (126–300)		301–500 (301–600)		501–730 (601–753)	
Number of species	21	(19)	23	(25)	21	(20)
Diversity, <i>H</i>	1.74	(1.4)	0.98	(1.2)	1.97	(2.1)
Number of specimens	205 002	(83 611)	404 002	(79 053)	39 290	(10 761)
Number of stations	468	(177)	324	(123)	159	(34)
Specimens 0.5 h ⁻¹	438	(472)	1247	(643)	1 247	(316)
Total biomass (Catch kg)	54 067	(31 400)	83 843	(23 000)	13 401	(4 170)
Biomass (kg 0.5 h ⁻¹)	116	(177)	259	(187)	84	(123)

TABLE 5. The most abundant demersal fish species at the three depth zones considered. Values are percentages of total number and of total biomass.

Species	1995–2002		Species	1992–94	
	Number (%)	Biomass (%)		Number (%)	Biomass (%)
Dominant species in depths <300 m			Dominant species in depths <300 m		
<i>Sebastes mentella</i>	32.13	14.3	<i>Gadus morhua</i>	60.50	55.70
<i>Sebastes marinus</i>	25.76	37.77	<i>Sebastes marinus</i>	14.50	17.20
<i>Sebastes fasciatus</i>	22.40	12.37	<i>Sebastes mentella</i>	8.00	4.80
<i>Anarhichas lupus</i>	5.73	6.33	<i>Sebastes fasciatus</i>	6.10	3.10
<i>Reinhardtius hippoglossoides</i>	3.99	5.02	<i>Anarhichas lupus</i>	4.50	5.90
<i>Gadus morhua</i>	3.84	11.22	<i>Hippoglossoides platessoides</i>	3.90	6.80
Total	93.85	87.02	Total	97.50	93.50
Dominant species in depths between 301 and 500 m			Dominant species in depths between 301 and 600 m		
<i>Sebastes mentella</i>	75.63	66.55	<i>Sebastes mentella</i>	72.00	63.60
<i>Sebastes fasciatus</i>	11.34	8.45	<i>Sebastes fasciatus</i>	9.50	5.90
<i>Reinhardtius hippoglossoides</i>	3.84	10.57	<i>Nezumia bairdi</i>	3.10	0.50
<i>Sebastes marinus</i>	2.90	5.50	<i>Reinhardtius hippoglossoides</i>	2.80	6.30
<i>Lycodes reticulatus</i>	2.07	0.82	<i>Lycodes reticulatus</i>	2.60	1.70
<i>Anarhichas lupus</i>	1.50	1.74	<i>Anarhichas lupus</i>	2.40	3.30
Total	97.28	93.64	Total	92.40	81.30
Dominant species in depths >500 m			Dominant species in depths >600 m		
<i>Nezumia bairdi</i>	28.57	4.90	<i>Nezumia bairdi</i>	25.60	4.40
<i>Reinhardtius hippoglossoides</i>	22.44	48.53	<i>Sebastes mentella</i>	18.40	24.00
<i>Sebastes mentella</i>	19.54	25.12	<i>Antimora rostrata</i>	15.50	5.60
<i>Antimora rostrata</i>	10.09	2.57	<i>Reinhardtius hippoglossoides</i>	13.80	33.60
<i>Macrourus berglax</i>	7.01	10.22	<i>Macrourus berglax</i>	10.90	16.20
<i>Chauliodus sloani</i>	2.23	0.22	<i>Chauliodus sloani</i>	3.00	0.30
Total	89.89	91.57	Total	87.20	84.10

paper, and the same happened with *Anarhichas minor*. Besides, it seems there is a tendency to less-deeper waters in all the species. This can be noted in the clus-

ter analysis, which had established the limit between the second and the third cluster in 500 m, instead of 600 m. We can also note this phenomenon in Table 2. In this

TABLE 6. Regression parameters of mean weight per individual by species *versus* depth where the regression was significant.

Species	No. of Cases	Correlation coefficient	Significance	Parameters of Equation $y = ax + b$	
				<i>a</i>	<i>b</i>
<i>Anarhichas minor</i>	506	-0.1782	<0.001	2.3356	-0.0202
<i>Macrourus berglax</i>	303	0.2126	<0.001	0.2065	0.00047
<i>Anarhichas lupus</i>	674	-0.2621	<0.001	0.5245	-0.00073
<i>Stomias boa</i>	175	0.3152	<0.001	0.0065	0.00002
<i>Hippoglossoides platessoides</i>	320	-0.3474	<0.001	1.1355	-0.00155
<i>Sebastes marinus</i>	639	0.3564	<0.001	0.1402	0.00058
<i>Nezumia bairdi</i>	472	0.3800	<0.001	0.0138	0.00007
<i>Glyptocephalus cynoglossus</i>	188	-0.3807	<0.001	0.6990	-0.00106
<i>Sebastes fasciatus</i>	780	0.3868	<0.001	0.0885	0.00015
<i>Serrivomer beani</i>	165	0.4398	<0.001	-0.0284	0.00021
<i>Reinhardtius hippoglossoides</i>	782	0.6527	<0.001	0.1153	0.00113
<i>Urophycis chesteri</i>	342	0.7680	<0.001	-0.0645	0.00035
<i>Sebastes mentella</i>	736	0.8476	<0.001	-0.1533	0.00096

table, we can see the differences over the two periods (in parentheses, the data of the period 1989–94 appears). For instance, the cod depth range in years 1989–94 was 126–631, instead of the 126–343 range in years 1995–2002. The bathymetric pattern of cod during the feeding season was related to their abundance: during periods of high abundance, densities tended to be higher at intermediate depths. However, in periods of low abundance, density was either unrelated to depth or higher in shallow waters (Swam, 1993; Chouinard and Swan, 2002). For *Antimora rostrata*, the depth range for 1989–94 was 524–753, and in 1995–2002, 201–740. Quite the same occurs for *Gaidropsarus ensis* and *Lycodes valhii*. On the other hand, there are species that extend their depth range, as for example *Hippoglossoides platessoides* or *Sebastes marinus*. But this effect can be caused by a punctual catch, because if we graph the preferred depths of, for example, *Hippoglossoides platessoides*, we can see that its depth range was decreasing in the last years (Fig. 4d).

Main changes in the relative abundance were observed in the shelf assemblage. The constant decrease in the biomass of some demersal species (Vázquez, MS 2002), traditional target species for fishing in the area, as cod and American plaice, can be the cause of changes in the composition of that assemblage. Thus, American plaice no longer appears as a dominant species, and cod loses importance in that assemblage (Table 5). The genus *Sebastes*, despite of its abundance decrease with regard to historical levels, is still the dominant species. This is probably because its relative presence is very high in the

groundfish due to the great decrease of some of the other dominant species.

The zones (<300 m; 300–500 m, and >500 m), established from cluster analysis, coincide with the zones defined in the calculation of the Percentage similarity index. The agreement in the results of two independent methods is an important requirement for assemblage validity. Moreover, these results coincide with Haedrich *et al.* (1980) for the depth range studied here compared to the deep sea South New England. These authors found distinct faunal assemblages on the shelf continental slope (40–264 m), upper continental slope (283–650 m) and middle continental slope (653–1 290 m).

Both abundance and biomass declined on the middle continental slope. In this region, however, the diversity was greater than in the other zones (Table 4). This fact has an important effect on fish community structure and eventually on the traditional fisheries (Gordon *et al.*, 1994). The commercially important species tend to be present in low diversity communities where they are a significant proportion of the total biomass (Haedrich, 1994). In agreement with this assertion, the shelf and upper continental slope presented the smallest diversity and were the regions where the traditional commercial species exploited in the area, such as *Gadus morhua* and *Sebastes* spp., were the most important species in terms of both number and biomass. In the shelf and upper continental slope, *Sebastes mentella* is the most abundant species. In the upper continental slope, that species represents more than 75% of the specimen numbers and

more than 66% of the specimen catches. In the shelf continental slope, the three species of *genus Sebastes* represent more than 80% of the specimen numbers and more than 64% of the specimens catches (Table 5).

The representative species of the middle continental slope were more homogeneously represented. *Reinhardtius hippoglossoides*, *Sebastes mentella* and *Macrourus berglax* comprise the 84% of caught biomass and make up the target fish species of the most recent fisheries in the area.

Conclusions

The fish fauna in Flemish Cap appears distributed in a persistent structural zonation defined in three assemblages. In the period 1995–2002 the bathymetric distribution of the species shows three previously defined assemblages. The specific composition remains with very few changes. The most important changes that have taken place since that first period studied are:

- Split of the limits among (between) assemblages toward less depth due to the concentration of some species in shallower waters.
- Changes in the dominant species in the shelf assemblage due to the strong decrease in the biomass of the corresponding species (Cod, American plaice).
- The species of the genus *Sebastes* appears as dominant species in shelf and upper continental slope groups in the last years in Flemish Cap.

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APPENDIX TABLE 1. Some characteristics of the described species.

Name	Family	Common name	Habitat type	L_{max}	Trophic Level	Depth
<i>Lycodes esmarkii</i>	<i>Zoarcidae</i>	Greater eelpout	Bathydemersal	75	3.40	251–500
<i>Lycodes vahliei</i>	<i>Zoarcidae</i>	Vahl's eelpout	Bathydemersal	52	3.44	65–540
<i>Lycodes reticulatus</i>	<i>Zoarcidae</i>	Artic eelpout	Bathydemersal	36	3.49	100–380
<i>Bathyraja spinicauda</i>	<i>Rajidae</i>	Spinetail ray	Bathydemersal	170	3.50	140–800
<i>Synaphobranchus kaupi</i>	<i>Synaphobranchidae</i>	Kaup's arrowtooth eel	Bathydemersal	100	4.09	236–3 200
<i>Chauliodus sloani</i>	<i>Stomiidae</i>	Sloane's viperfish	Bathypelagic	35		1–1 800
<i>Serrivomer beani</i>	<i>Serrivomeridae</i>	Bean's sawtoothed eel	Bathypelagic	78		10–4 550
<i>Stomias boa</i>	<i>Stomiidae</i>	Scaly dragonfish	Bathypelagic	32.5		200–1 500
<i>Antimora rostrata</i>	<i>Moridae</i>	Blue antimora	Bathypelagic	92	3.58	350–3 000
<i>Sebastes mentella</i>	<i>Sebastidae</i>	Deepwater redfish	Bathypelagic	55	3.65	300–1 000
<i>Urophycis chesteri</i>	<i>Phycidae</i>	Longfin hake	Benthopelagic	40	3.17	90–1 400
<i>Gaidropsarus ensis</i>	<i>Lotidae</i>	Threadfin rockling	Benthopelagic	40	3.38	
<i>Notacanthus chemnitzii</i>	<i>Notacanthidae</i>	Spiny eel	Benthopelagic	120	3.50	125–2 500
<i>Nezumia bairdi</i>	<i>Macrouridae</i>	Marlin-spike grenadier	Benthopelagic	40	3.57	16–700
<i>Anarhichas denticulatus</i>	<i>Anarhichadidae</i>	Northern wolffish	Benthopelagic	180	3.75	60–900
<i>Gadus morhua</i>	<i>Gadidae</i>	Atlantic cod	Benthopelagic	200	4.42	1–600
<i>Macrourus berglax</i>	<i>Macrouridae</i>	Roughhead grenadier	Benthopelagic	110	4.48	100–1 000
<i>Reinhardtius hippoglossoides</i>	<i>Pleuronectidae</i>	Greenland halibut	Benthopelagic	120	4.48	1–2000
<i>Sebastes fasciatus</i>	<i>Sebastidae</i>	Acadian redfish	Demersal	30		70–500
<i>Glyptocephalus cynoglossus</i>	<i>Pleuronectidae</i>	Witch flounder	Demersal	74	3.14	45–1 460
<i>Anarhichas lupus</i>	<i>Anarhichadidae</i>	Wolffish	Demersal	150	3.24	1–500
<i>Anarhichas minor</i>	<i>Anarhichadidae</i>	Spotted wolffish	Demersal	180	3.45	25–600
<i>Hippoglossoides platessoides</i>	<i>Pleuronectidae</i>	American plaice	Demersal	82	3.65	10–400
<i>Amblyraja radiata</i>	<i>Rajidae</i>	Thorny skate	Demersal	100	4.02	20–1 000
<i>Sebastes marinus</i>	<i>Sebastidae</i>	Ocean perch	Pelagic	100	4.04	100–1 000

Sources: Froese and Pauli, 2005 (Fishbase); Leim and Scott, 1966

