

A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France)

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This new numerical approach proposes a solution to a fundamental and difficult question in ecology, consisting of the correct geographical representation of multidimensional structures. Firstly, transformation was applied to the original matrix (n sites \times q variables) in order to satisfy the condition of multinormality. Then, a hierarchical cluster analysis was used and each hierarchical level was studied and characterised by a certain probability level. For each cut off level an algorithm based on the computation of the Bayesian probabilities produced a smaller matrix (n sites \times c groups). These conditional probabilities measure the chance that each site has in belonging to a predefined group of sites. Spatial distributions of these probability values for each group of sites were mapped using kriging interpolation. Finally, the maps were used to define homogenous zones on a single map by superimposing one map on the other. The maximal value of interpolated probability was used as criterion to assign each point of the map to the zones predefined by this classification.

This method was applied to map demersal fish habitats by using a dataset from bottom trawl surveys in the Bay of Biscay (France) during October 1990. The boundaries between habitats were identified objectively. Then, the indicator species and species assemblages characterising the different habitats were identified by using an indicator value index. This index integrates the specificity and the fidelity quantities calculated for each species in each habitat. The obtained results showed that this method presented a robust tool to describe the habitat of exploited species. The obtained habitats were validated by their correspondence with depth strata, sediment type and also by the biological characteristics of the indicator species.

The proposed method is useful in the study of temporal variations of habitats with regards to species assemblages and can also be generalised to other multivariate databases of different descriptors (physical, chemical, biological, etc.).

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INTRODUCTION

Considerable developments have occurred in both data acquisition and in the modelling of spatial patterns of marine systems (Ault & al. 1999). Generally however, spatialized data bases covering long periods of time are still often treated separately from one another. This has led to a necessary development of adequate numerical

methods resulting in better understanding of the spatial and temporal variability in marine ecosystems. Moreover, the need for marine habitat classification and mapping is important as a result of increasing activities of the international conventions on Biodiversity (Rio), the Protection of Species and Habitat (OSPAR), the FAO Code of Conduct for Responsible Fisheries (Cancun), and the Jakarta Mandate for Marine Protected Areas.



Consequently, the rich source of ecological information available from scientific surveys carried out in different exploited areas has been increasingly analysed to define habitat and species changes after anthropogenic or environmental impact (Greenstreet & Hall 1996; Greenstreet & al. 1999; Jennings & al. 1999a, b; Rogers & Ellis 2000).

Recently Mahon & al. (1998) used a large data set collected by demersal research trawl surveys from 1970 to 1994 on the east coast of North America in order to study assemblages and biogeography of demersal fishes. The approach of pooling all the data from different surveys together in order to carry out multivariate analysis can however be confusing as both spatial and temporal factors are mixed. It is thus necessary to map each trawl survey fish habitat separately in order to efficiently assess spatial and temporal effects (Gaertner & al. 1998). Moreover, species assemblages should be considered in order to define the habitat dynamics.

Multivariate regionalization techniques are necessary in the study of spatial structure of large datasets. Several methods have been developed in spatialized disciplines (e.g. geology, climatology, terrestrial vegetation, etc.) including Principal Components Analysis (Richman & Lamb 1985; Boyer & al. 1997; Comrie & Glenn 1998), multivariate classification (Oliver & Webster 1989; Bourgault & al. 1992; Souissi & al. 2000). However until now, visual appreciation has been the primary means by which groups of sites have been assimilated to ecosystem regions after using regionalization methods. Spatial contiguity is not necessarily the rule in marine ecology especially when characterised by high levels of spatial heterogeneity due to accidental topography and to non-linear hydrodynamical properties. Therefore, the constrained cluster analysis often used in terrestrial ecology (Dufrière & Legendre 1991) may not be necessarily justified in marine habitat studies.

This paper describes a new algorithm combining both multivariate hierarchical classification techniques and spatial models of regionalized variables. This combination goes further than the separation of groups of sites as with ordinary classification since interpolation is used resulting in a more refined mapping. A one year bottom trawl survey in the bay of Biscay is used as an example to illustrate the different steps and results obtained with this algorithm. This study of demersal species habitats has four main aims: 1) to identify the spatial structure of demersal communities at different scales. 2) To establish how the definition of the boundaries between these sub-areas can be carried out objectively. 3) To define the characteristic species assemblages for each area. 4) To assess the ecological interpretations after using this method.

The data set was first subdivided into two matrices representing the dominant species and the secondary

species. A classification of sites after hierarchical cluster analysis was applied to the matrix of dominant species. Then, successive levels of hierarchical classification were considered. For each regionalization level, the study area was divided into different habitats corresponding to the number of clusters. The interpolation of each point within its identified habitat was obtained by using the theory of regionalized variables based on a Bayesian probability. These techniques were initially developed for geological applications (Harff & Davis 1990; Harff & al. 1993). Finally, the indicator species for each group of sites were identified by computing the indicator value index proposed by Dufrière & Legendre (1997).

MATERIAL AND METHODS

DATA SOURCES

The developed method was applied to a set of data collected during the groundfish survey carried out by IFREMER in the Bay of Biscay. The EVHOE survey series began in 1987 (Poulard 1989; ICES 1991, 1997; Amara & al. 1998). The survey area was between 48°30'N in the north and the northern margin of Gouf de Cap Breton in the south. The area was stratified according to latitude and depth. A 36/47 GOV trawl was used with a 20 mm mesh codend liner. The haul duration was 30 minutes long with a towing speed of 4 knots. Fishing was mainly restricted to daylight hours. Catch weights and catch numbers were recorded for all species, all finfish and a selection of shellfish were measured. The data obtained from the 135 hauls carried out between 25 September and 25 October 1990 were used to illustrate the different steps of the method. The biology of the species, alimentary diet, behaviour and habitat, is given by the FAO world fish fauna (Fisher & al. 1987).

SPECIES SELECTION AND MATHEMATICAL TRANSFORMATION

The abundance indices of pelagic species are better estimated by acoustic surveys (Massé 1996) and pelagic trawls than bottom trawls, so these species (e.g. anchovy, sardine, mackerel, etc.) were eliminated from this analysis. Species present in more than 5 % of the tows were retained (Fig. 1A). The data was transformed by a double square root for two reasons, firstly to minimise the effects of high values and secondly to satisfy the multinormality of the data, a required condition before using the regionalized variables (Harff & Davis 1990). In order to accomplish the latter condition, the sum of the total abundances for each selected species was computed. After this, species were ranked following their contribution to the global sum of the data (Fig. 1B). The contribution level of 0.5 % separated the species into two groups: the dominant species (Table 1) and the secondary species (Table 2).



The multinormality of transformed data was tested with the Dagnelie method (Dagnelie 1975 in Legendre & Legendre 1998) based on the Mahalanobis generalized distance (see Eq. 6). Generalized distances are computed between each object (site) and the multidimensional mean of all objects. Then the values of the skewness and kurtosis were computed and their deviation compared to a theoretical normal distribution was tested (CEA 1986; Legendre & Legendre 1998). The null hypothesis of normality of the distribution of both parameters tested could not be rejected ($p = 0.289$ and 0.122 for skewness and kurtosis, respectively). Thus the multinormality of the data was confirmed.

METHOD

The different steps of the numerical method are shown in Fig. 2. Only the stages after species selection have been detailed. In this case the inputs of the analysis are the sites-species matrices A and B (Fig. 2), corresponding to dominant species and secondary species, respectively.

Step 1: cluster analysis

The matrix A was used in a cluster analysis. First, the species abundances were transformed ($x^{0.25}$) before computing a similarity coefficient between sites (matrix S). The Bray-Curtis similarity coefficient and clustering strategy of flexible links with beta set at the value of -0.25 (Legendre & Legendre 1998) were used.

Instead of studying one spatial configuration with a fixed number of clusters, a hierarchical tree with successive cutting off levels was used. Consequently, for the same data set different spatial organization patterns of assemblages were studied.

Step 2: expression of conditional probabilities

For each level of the hierarchical classification a number of clusters was obtained. The level of heterogeneity between each site and properties of each group was assessed with one value of a conditional Bayesian probability. This method, originally developed in geology (Harff & Davis 1990; Harff & al. 1993), was adapted for the purposes of this study.

Each object (site) X_i is a q -dimensional variable, where q is the number of the selected dominant species (A in Fig. 2):

$$X_i = \{x_{i,1}, x_{i,2}, \dots, x_{i,j}, \dots, x_{i,q}\} \tag{1}$$

where $x_{i,j}$ is the transformed abundance of species j in the site i .

For each cut off level (c) of the hierarchical tree, a partition Z_c^G of groups of sites G_j can be considered,

$$Z_c^G = \{G_1, G_2, \dots, G_j, \dots, G_c\} \tag{2}$$

of which each element is defined by a number of sites

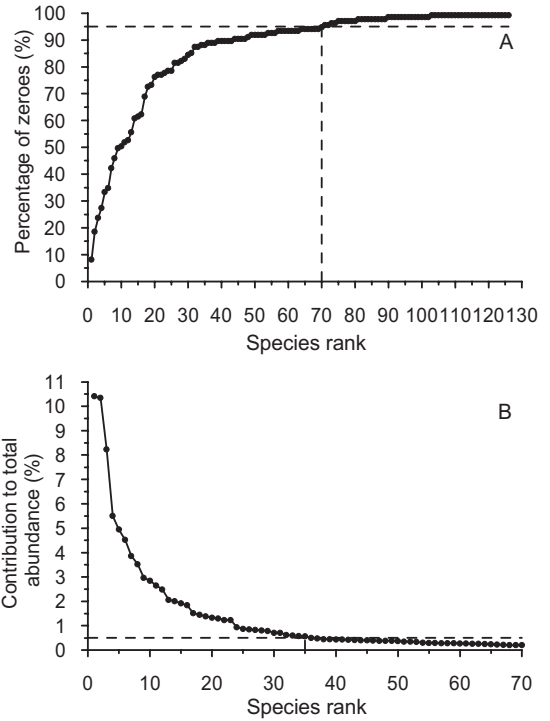


Fig. 1. Numerical criteria of species selection. A) the percentage of zeroes in the 135 sites for different species are sorted in ascending order. The threshold level of 95 % is considered. B) Contribution of each selected species in the total abundance. The 70 species selected in the step (A) are ranked according their contribution. At the level of 0.5 % the selected species are subdivided into two groups: the dominant species (Table 1) and the secondary species (Table 2).

n_j^G , a centroid of the group m_j^G and a covariance matrix Σ_j :

$$G_j : (n_j^G, m_j^G, \Sigma_j) \quad j \in I^c, I^c = \{1, \dots, c\} \tag{3}$$

Where j is a group of sites obtained from a hierarchical classification and I^c is the set of groups of sites containing c elements, where c is the cut off level. The centroid is the data point (vector) that is the mean of the abundance values of each species among the sites belonging to the considered group. The covariance matrix represents the within dispersion of a group G_j .

The partition Z_c^G is termed the model and each one of its elements G_j is termed a j -model (Harff & Davis 1990). It should be noted that the number of elements in each partition depends on the level c of the hierarchical classification (Fig. 2). In general, the spatial coherence of a j -model emerges from the contagiousness of the ecological processes involved. In this case this concerns the habitats of demersal species characterising a typical spe-



cies association. Depending on the composition of each site X_i (Eq. 1), its conditional probability of membership to a j -model is expressed by Bayes' relationship (Harff & al. 1993):

$$P(X_i \in G_j) = \frac{p_j |\Sigma_j|^{-1/2} \exp(-d_j^2(i)/2)}{\sum_{k \in C} p_k |\Sigma_k|^{-1/2} \exp(-d_k^2(i)/2)} \quad (4)$$

where p_j is an *a priori* probability of the j -model, which represents the proportion of the number of sites in the cluster j versus the total number of sites:

$$p_j = \frac{n_j^G}{\sum_{k \in C} n_k^G} \quad (5)$$

and $d_j^2(i)$ is the generalised Mahalanobis distance between G_j and X_i :

$$d_j^2(i) = (X_i - m_j^G)' \Sigma_j^{-1} (X_i - m_j^G) \quad (6)$$

Assuming that the dispersion matrices are equal (Harff & Davis, 1990),

$$\sum_i = \sum_j = \sum_0 \quad \forall i, j \in I^K$$

Table 1. List of dominant demersal species selected for mapping their habitats in the Bay of Biscay and the South Celtic Sea. All species were present in the 135 stations selected from the autumn survey of 1990 with a frequency greater than 5 % and a total abundance contribution greater than 0.5 %. The species are subdivided into 4 groups: Sharks and Rays, Bony fishes, Crustacea and Cephalopoda.

Group & Family	Label	(%)	Species
Sharks and Rays			
Scyliorhinidae	SCYLCAN	2.48	<i>Scyliorhinus canicula</i> (Linné., 1758)
Rajidae	RAJANAE	0.70	<i>Raja naevus</i> Müller & Henle, 1841
Bony fishes			
Argentinidae	ARGESIL	0.87	<i>Argentina silus</i> (Ascanius, 1775)
Argentinidae	ARGESP	4.52	<i>Argentina sphyraena</i> Linné, 1758
Gadidae	GADIARG	3.86	<i>Gadiculus argenteus</i> Guichenot, 1850
Gadidae	MERLMNG	1.38	<i>Merlangius merlangus</i> (Linné, 1758)
Gadidae	MICRPOU	10.35	<i>Micromesistius poutassou</i> (Risso, 1827)
Gadidae	TRISLUS	2.97	<i>Trisopterus luscus</i> (Linné, 1758)
Gadidae	TRISMIN	10.42	<i>Trisopterus minutus</i> (Linné, 1758)
Lotidae	MOLVMOL	0.56	<i>Molva molva</i> (Linné, 1758)
Merlucciidae	MERLMCC	8.23	<i>Merluccius merluccius</i> (Linné, 1758)
Zeidae	ZEUSFAB	0.78	<i>Zeus faber</i> Linné, 1758
Caproidae	CAPRAPE	2.84	<i>Capros aper</i> (Linné, 1758)
Triglidae	ASPICUC	2.01	<i>Aspitrigla cuculus</i> (Linné, 1758)
Sparidae	SPONCAN	0.80	<i>Spondyliosoma cantharus</i> (Linné, 1758)
Mullidae	MULLSUR	0.58	<i>Mullus surmuletus</i> Linné, 1758
Callionymidae	CALLLYR	2.65	<i>Callionymus lyra</i> Linné, 1758
Callionymidae	CALLMAC	1.29	<i>Callionymus maculatus</i> Rafinesque, 1810
Gobiidae	LESUFRI	0.83	<i>Lesueurigobius friesii</i> (Malm, 1874)
Gobiidae	POMAMIN	0.71	<i>Pomatoschistus minutus</i> (Pallas (ex Gronovius), 1770)
Scophthalmidae	LEPIWHI	1.92	<i>Lepidorhombus whiffiagonis</i> (Walbaum, 1792)
Bothidae	ARNOIMP	1.23	<i>Arnoglossus imperialis</i> (Rafinesque, 1810)
Bothidae	ARNOLAT	1.22	<i>Arnoglossus laterna</i> (Walbaum, 1792)
Soleidae	MICRVAR	0.93	<i>Microchirus variegatus</i> (Donovan, 1808)
Crustacea			
Nephropidae	NEPHNOR	1.32	<i>Nephrops norvegicus</i> (Linné, 1758)
Galatheidae	MUNIBAM	1.51	<i>Munida bamffia</i> (Pennant, 1777)
Cancridae	CANCPAG	0.62	<i>Cancer pagurus</i> Linné, 1758
Cephalopoda			
Sepiidae	SEPIELE	1.45	<i>Sepia elegans</i> Blainville, 1827
Sepiidae	SEPIORB	0.60	<i>Sepia orbignyana</i> Ferussac, 1826
Sepiolidae	SEPIISP	2.05	<i>Sepiola</i> spp. & <i>Sepietta</i> spp.
Loliginidae	ALLOSPP	5.50	<i>Alloteuthis</i> spp.
Loliginidae	LOLIFOR	3.52	<i>Loligo forbesi</i> Steenstrup, 1856
Loliginidae	LOLIVUL	1.84	<i>Loligo vulgaris</i> Lamarck, 1798
Ommastrephidae	ILLECOI	4.95	<i>Illex coindetii</i> (Verany, 1839)
Ommastrephidae	TODAEBL	0.84	<i>Todaropsis eblanae</i> (Ball, 1841)



a pooled variance-covariance matrix Σ_p (Cooley & Lohnes 1971; Legendre & Legendre 1998) was used as a substitute of the normal dispersion matrix Σ in the d^2 computation.

Step 3: cartography of regionalized variables

Harff & al. (1993) considered that the conditional probability (Eq. 4) may be treated as a regionalized variable, because the stochastic features of X_i were retained. Thus geostatistical tools can be applied to matrices P_c of con-

ditional probabilities (Fig. 2). In this way the spatial distributions of the conditional probability for each group of sites were mapped. An interpolated regular grid of 0.025 longitude by 0.025 latitude degrees corresponding to the study area limits was obtained by using a spherical variogram model and the kriging method (Matheron 1962). The probability data are assumed to be isotropic. For each point z in space (one node of the regular interpolated grid) a vector of conditional probabilities obtained by interpolation can be associated:

Table 2. List of secondary demersal species considered in the study of indicator species at the local scale when habitats are identified using the dominant species shown in Table 1. All species were present in the 135 stations selected from the autumn survey of 1990 with a frequency greater than 5 % and a contribution to total abundances of under 0.5 %. The selected species are subdivided into 5 groups: Sharks and Rays, Bony fishes, Crustacea, Cephalopoda and Bivalves.

Group & Family	Label	(%)	Species
Sharks and Rays			
Rajidae	RAJACLA	0.30	<i>Raja clavata</i> Linnaeus, 1758
Rajidae	RAJAMON	0.22	<i>Raja montagui</i> Fowler, 1910
Scyliorhinidae	GALEMEL	0.45	<i>Galeus melastomus</i> Rafinesque, 1810
Bony fishes			
Congridae	CONGCON	0.39	<i>Conger conger</i> (Linnaeus, 1758)
Lophiidae	LOPHBUD	0.20	<i>Lophius budegassa</i> Spinola, 1807
Lophiidae	LOPHPIS	0.39	<i>Lophius piscatorius</i> Linnaeus, 1758
Sebastidae	HELIDAC	0.43	<i>Helicolenus dactylopterus</i> (Delaroche, 1809)
Triglidae	EUTRGUR	0.42	<i>Eutrigla gurnardus</i> (Linnaeus, 1758)
Triglidae	TRIGLUC	0.20	<i>Trigla lucerna</i> Linnaeus, 1758
Cepolidae	CEPORUB	0.44	<i>Cepola rubescens</i> Linnaeus, 1766
Pleuronectidae	MICRKIT	0.39	<i>Microstomus kitt</i> (Walbaum, 1792)
Pleuronectidae	PLEUPLA	0.27	<i>Pleuronectes platessa</i> Linnaeus, 1758
Pleuronectidae	LIMALIM	0.26	<i>Limanda limanda</i> (Linnaeus, 1758)
Soleidae	SOLEVUL	0.38	<i>Solea vulgaris</i> Quensel, 1806
Soleidae	BUGLLUT	0.29	<i>Buglossidium luteum</i> (Risso, 1810)
Soleidae	DICOCUN	0.22	<i>Dicologlossa cuneata</i> (Moreau, 1881)
Trachinidae	TRACDRA	0.42	<i>Trachinus draco</i> Linnaeus, 1758
Trachinidae	ECHIVIP	0.45	<i>Echiichthys vipera</i> (Cuvier, 1829)
Bothidae	LEPIBOS	0.40	<i>Lepidorhombus boscii</i> (Risso, 1810)
Gadidae	PHYCBLE	0.35	<i>Phycis blennoides</i> (Brünnich, 1768)
Gadidae	POLLPOL	0.26	<i>Pollachius pollachius</i> (Linnaeus, 1758)
Gadidae	ENCHCIM	0.29	<i>Enchelyopus cimbrius</i> (Linnaeus, 1758)
Moronidae	DICELAB	0.34	<i>Dicentrarchus labrax</i> (Linnaeus, 1758)
Sparidae	BOOPBOO	0.25	<i>Boops boops</i> (Linnaeus, 1758)
Ammodytidae	AMMOTOB	0.53	<i>Ammodytes tobianus</i> (Linnaeus, 1758)
Ammodytidae	HYPELAN	0.27	<i>Hyperoplus lanceolatus</i> (Le Sauvage, 1824)
Mugilidae	LIZARAM	0.47	<i>Liza ramada</i> (Risso, 1826)
Macrouridae	MALALAE	0.28	<i>Malacocephalus laevis</i> (Lowe, 1843)
Crustacea			
Portunidae	MACRPUB	0.38	<i>Macropipus puber</i> (Linnaeus, 1758)
Crangonidae	CRANCRA	0.35	<i>Crangon crangon</i> (Linnaeus, 1758)
Cephalopoda			
Octopodidae	ELEDCIR	0.23	<i>Eledone cirrhosa</i> (Lamarck, 1798)
Octopodidae	OCTOSPP	0.28	<i>Octopus</i> sp.
Sepiidae	SEPIOFF	0.37	<i>Sepia officinalis</i> Linnaeus, 1758
Ommastrephidae	TODASAG	0.29	<i>Todarodes sagittatus</i> (Lamarck, 1798)
Bivalves			
Pectinidae	PECTMAX	0.20	<i>Pecten maximus</i> (Linnaeus, 1758)

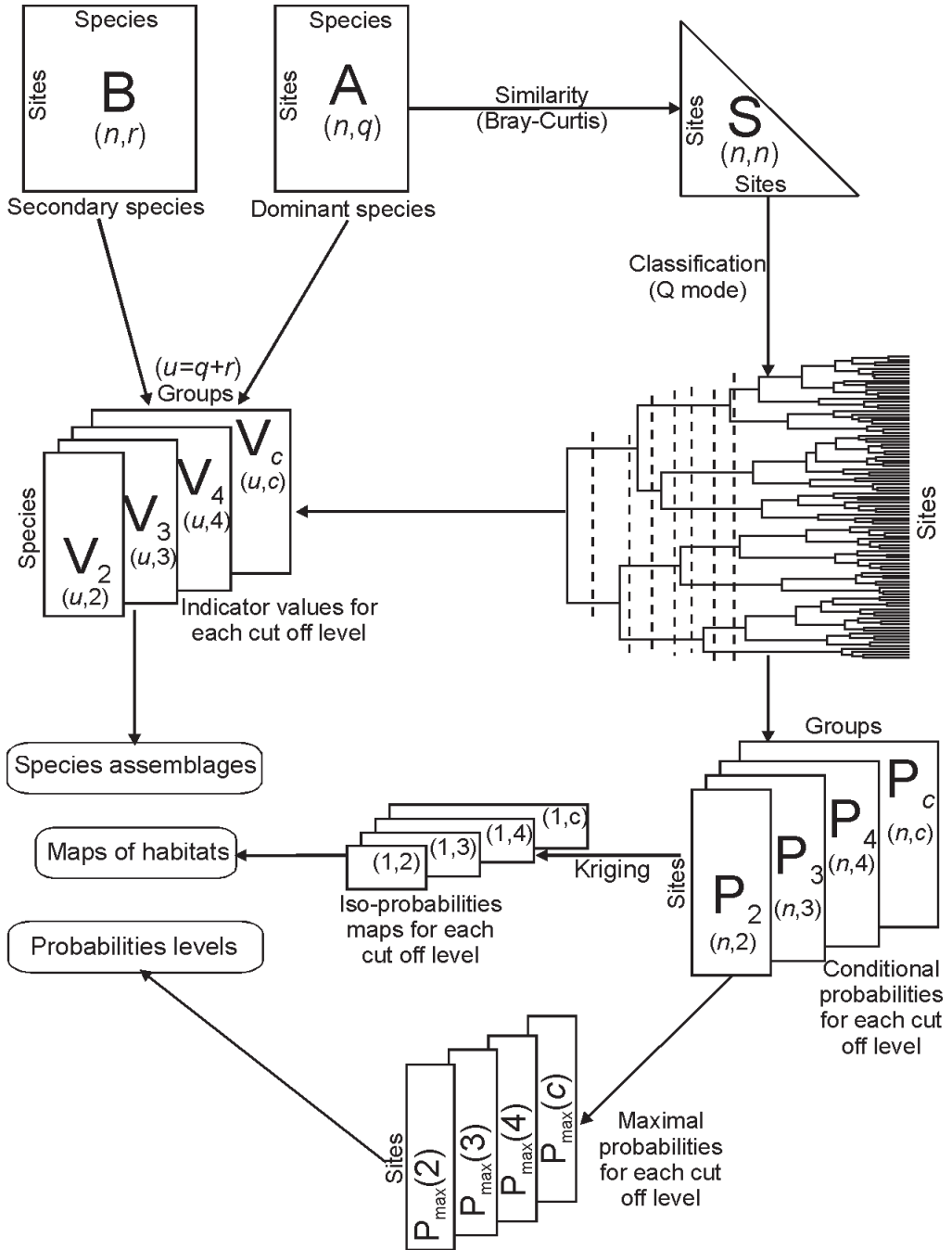


Fig. 2. Diagram of the analysis steps for the multivariate mapping method. The different steps explaining the connections between the input matrices $A(n: \text{sites}, q: \text{dominant species})$ and $B(n: \text{sites}, r: \text{secondary species})$ and the final resulting map of fish habitats and indicator species for each hierarchical level. The different steps of the diagram are detailed in Materials and Methods section.



$$p_z = \{p_z(1), p_z(2), \dots, p_z(c)\} \tag{7}$$

So z belongs to the area j representative of the group of sites G_j if its conditional probability is the largest for that group (Eq. 8).

$$p_z(j) = \max(p_z) \tag{8}$$

Step 4: characterisation of the different zones

After mapping the different habitat zones, it is necessary to identify the species that characterise each habitat. The indicator value index proposed by Dufrene & Legendre (1997) was used to identify the indicator species and the significant assemblages for each habitat and spatial organization (Fig. 2). The specificity and fidelity of each species s compared to each cluster of sites G_j can be measured by the values $SP_{j,s}$ and $FI_{j,s}$, respectively:

$$\begin{cases} SP_{j,s} = NI_{j,s} / NI_{+j} \\ FI_{j,s} = NS_{j,s} / NS_{+j} \end{cases} \tag{9}$$

where $NI_{j,s}$ is the mean abundance of species s across the sites relating to G_j , NI_{+j} which is the sum of the mean abundances of species s within the various groups in the partition. At the same time $NS_{j,s}$ is the number of sites in G_j where the species s is present and NS_{+j} is the total number of sites in that group. The specificity value ($SP_{j,s}$) is maximum when species s is present in group G_j only, whereas the fidelity value ($FI_{j,s}$) is maximum when species s is present in all sites of G_j . The specificity and fidelity represent information independently from one another, their product multiplied by 100 produces a percentage of the indicator value $IV_{j,s}$:

$$IV_{j,s} = 100SP_{j,s}FI_{j,s} \tag{10}$$

Dufrene & Legendre (1997) proposed to retain the maximum indicator value for each species s among all groups.

$$IV_j = \max(IV_{j,s}) \tag{11}$$

For this study, only species having an indicator value greater than 25 %, being the threshold level used by Dufrene & Legendre (1997), were retained in the assemblages. Furthermore, the indicator value indices were computed for each level of the hierarchical classification. The analysis of the variation of indicator value as the number of groups increased point out the characteristic species for each hierarchical level. For the highest hierarchical levels, when the indicator values of all species are decreasing, the clustering method does not often offer any additional information. So, this analysis provides an *a posteriori* criterion to define the highest significant hierarchical level (Dufrene & Legendre 1997).

Moreover, a new criterion for characterising each hierarchical level by one probability value was added. For each probability matrix (P_k , $k = 2$ to c in Fig. 2) a vector $P_{\max}(k)$ representing the maximal probability for each site was computed.

$$P_{\max}(k) = \max(P'_k) \tag{12}$$

where P'_k is the transposed sites-probabilities matrix for the cutoff level k .

Then each level of hierarchical classification k was characterised by one probability value $P_M(k)$ estimated from the median of the vector $P_{\max}(k)$:

$$P_M(k) = \text{median}(P_{\max}(k)) \tag{13}$$

$P_M(k)$ can be interpreted as being an average measure of the within-groups homogeneity for each hierarchical level.

The different steps of the method (shown in Fig. 2) were programmed with Matlab Software.

RESULTS

GLOBAL ANALYSIS OF SITE GROUPS AT DIFFERENT HIERARCHICAL LEVELS

Nineteen different partitions of groups of sites corresponding to increasing levels from 2 to 20 clusters were considered after hierarchical classification (Fig. 3). The corresponding $P_M(k)$ (Eq. 13) quantities were computed, and then plotted in Fig. 4. The median probability that a site belongs to its group of sites for the first cut off level was equal to 0.86. Then, $P_M(3)$ increased to the value of 0.89. For the next aggregation level, with 4 site groups, the median probability $P_M(4)$ decreased slightly to the value of 0.88. The highest amplitude of increase in P_M values was obtained for the five site group hierarchical level, where the associated probability ($P_M(5)$) overcame the threshold of 0.9. Then, the values of P_M increased slightly for the next levels 6 and 7. The threshold value of 0.95 was first reached for the eight cluster aggregation (Fig. 4). The probabilities P_M continued increasing with the number of clusters showing a plateau around 1.0 for the highest number of clusters. According to this first characterisation, the spatial organization patterns of species assemblages for the first seven partitions (from 2 to 8 clusters indicated with discontinuous lines in Fig. 3) were arbitrarily retained for the following detailed analyses.

Mapping of the different zones

Starting with the second hierarchical level, a matrix of conditional probabilities (135 sites × 2 site groups) was computed. The maps of the iso-probability contours for each zone are shown in Fig. 5A-B. The probability levels are shown by a colour scale increasing from white to one characteristic colour. For example the median depth of the first zone (Fig. 5A) is equal to 62 m, which corresponds to the green colour according to the depth colour scale. This representation facilitates the interpretation of the geographical representation of habitat zones and their

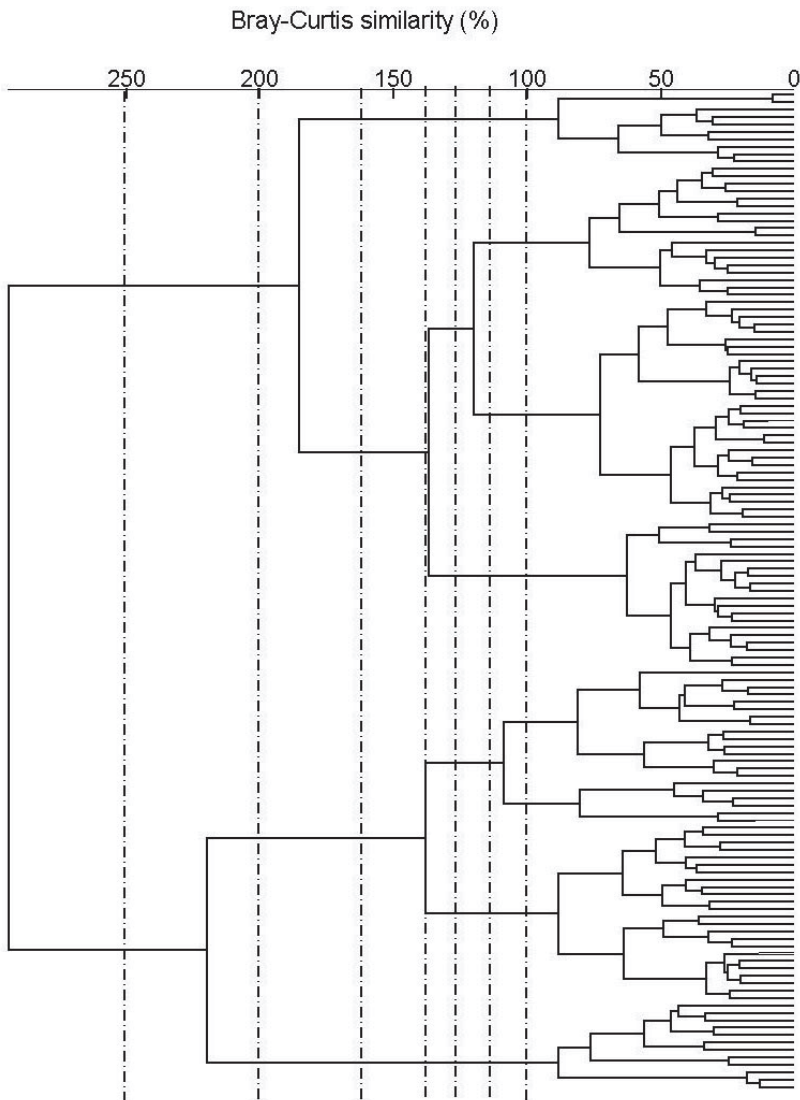


Fig. 3. Classification of the sampling sites for the bottom trawl survey carried out between 25 September and 25 October 1990, using Bray-Curtis dissimilarity coefficient and clustering strategy of flexible links with beta equal to -0.25 . The first seven hierarchical levels giving from 2 to 8 site groups were indicated with discontinuous lines.

average depth properties. The probability of correct classification of each point within a zone is assessed by applying the maximal probability value criterion (Eq. 8). Fig. 5C shows the final map of both habitats. The method does not introduce any spatial contiguity constraints, however the obtained zones are contiguous. They clearly represent a separation between the coastal zone in the bay of Biscay and the rest of the study area including the southern part of the Celtic Sea.

Fig. 6 shows the final maps obtained for a number of habitats starting from 3 and continuing up to 8. The first

habitats identified from the hierarchical classification are those of the bay of Biscay shallow water (Fig. 6A) and the slope of the shelf-break (Fig. 6B). It must be pointed out however that the resulting mapped group formations from one level to the next one, may subtly differ (particularly at group boundaries) from the groups formed after IndVal calculation using hierarchical clustering since interpolation is used. In fact the boundaries may change altogether, this is particularly noticeable for sites occurring near the borders of each group. An example is shown for the passage from 4 zones (Fig. 8B) to 5



zones (Fig. 8C). The newly appeared zone III (Fig. 8C) is represented by two separate areas. This is directly due to the procedure of computing new conditional probabilities and identifying, through interpolation, new boundaries between the different zones.

The subdivision of the studied area into 6 groups is characterised by a clearcut separation between the central bay of Biscay zone and the southern Celtic Sea zone (Fig. 6D). By increasing the number of habitats, we obtain first a separation between the central Bay of Biscay zone (zone IV in Fig. 6E) and the continental slope zone (zone VI in Fig. 6E). The last subdivision concerns the coastal area, which is characterised by 4 different habitats for the 8 site groups level (Fig. 6F).

The increase of the number of zones resulted in a decrease of both spatial heterogeneity (in terms of average probability, Fig. 4) and spatial contiguity between zones (Fig. 6).

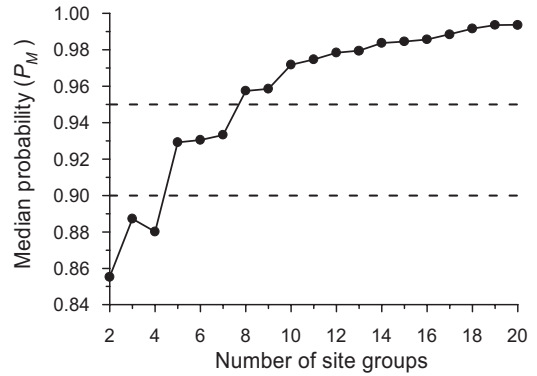


Fig. 4. Variation of the median probability (P_M) as a function of the number of site groups. Vectors of maximal probabilities (P_{max} in Fig. 2) were used in the computation of P_M at the considered 19 hierarchical levels. The probability levels of 0.9 and 0.95 are shown with discontinuous horizontal lines.

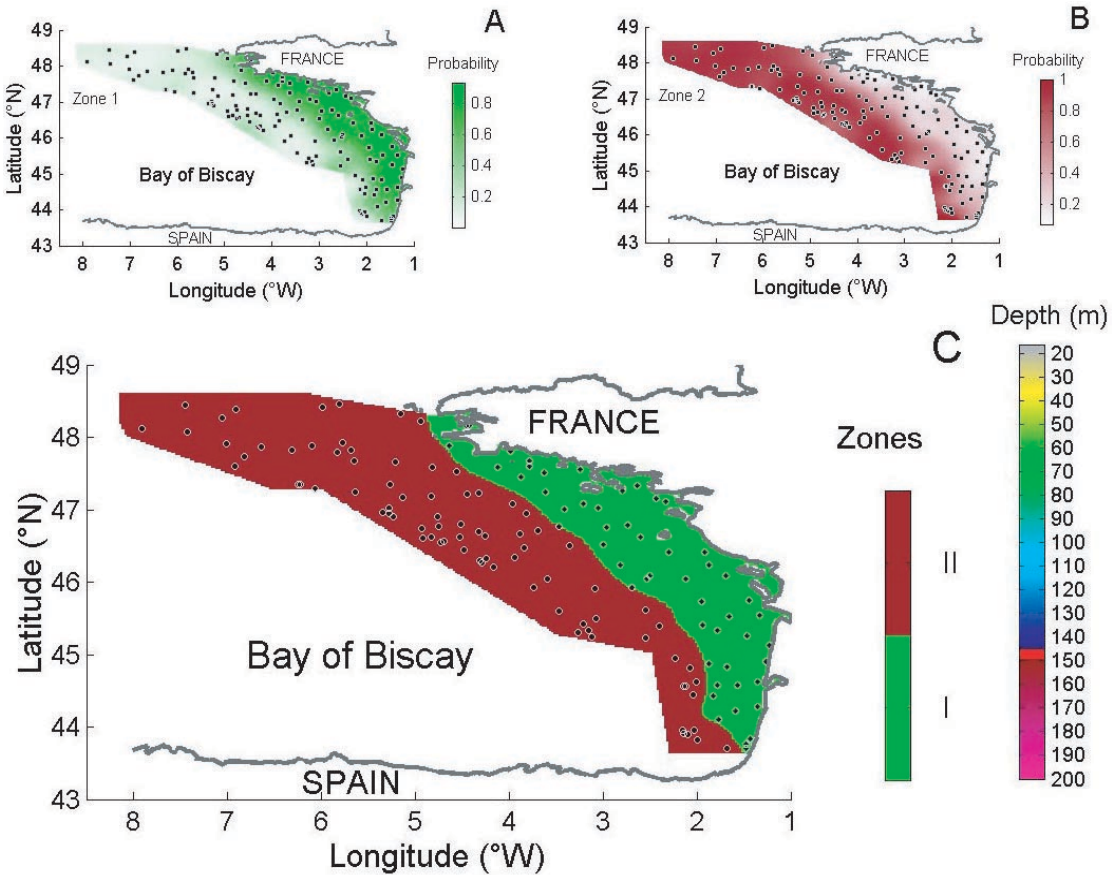


Fig. 5. Iso-probability maps for the coastal zone (A) and the offshore zone (B). Each map represents a spatial distribution of the probabilities of being a member of one group of sites identified in Fig. 3 for the two site groups hierarchical level. The probability levels are represented by a colour scale bar increasing from white ($P=0$) to a characteristic colour ($P=1$) depending on the median depth of the site group. The depth colour bar shown in (C) was truncated over 200 m depth. C) Final map of the two habitats zones. The positions of the sampling sites in the Bay of Biscay are indicated by black symbols.

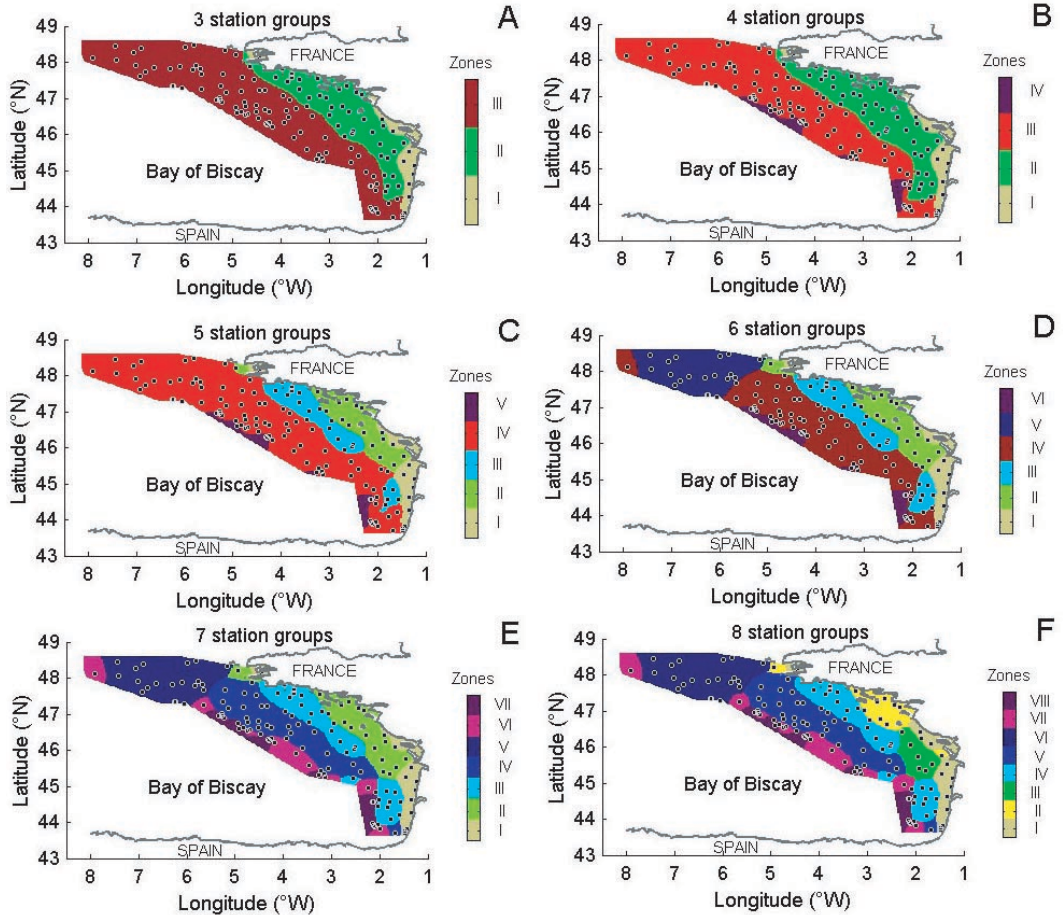


Fig. 6. Maps of the different habitat zones for the following hierarchical levels: 3(A), 4(B), 5(C), 6(D), 7(E) and 8(F). Each colour represents the median depth according to colour scale bar of Fig. 5. Dark violet colour indicates the deeper sites (median depth = 375 m).

BATHYMETRIC REGIONALIZATION OF THE SAMPLED AREA

As a first criterion for characterising the spatial patterns of site groups, the average depth distributions were calculated for different site groups using Box-and-whiskers plots (Fig. 7). When only two groups of sites were considered, their depths were distributed around two median values: 62 m and 150 m. For this level, the boxes of depth-distribution did not overlap (Fig. 7), so, the bathymetry can be considered as a good discriminator between these habitats. When increasing the hierarchical level, the more heterogeneous group was split into two new site groups. For example, the third hierarchical level was characterised by the isolation of the shallow coastal and estuarine site group (25 m median depth) from the other coastal sites of intermediate depths (77 m median depth). The group of deepest sites, characterised by a high variability of depths around a median of 375 m corresponding to the slope of the shelf-break, formed

the next cut off level (Fig. 7). The four identified site groups were sorted according to a bathymetric gradient. Five depth strata were distinguished around the following median values: 25 m, 51 m, 99 m, 145 m and 375 m. The higher hierarchical levels of 6 and 7 groups, showed a subdivision of the 145 m deep group. This group was subdivided into two groups with similar depth distributions (Fig. 7), one of these groups (141 m median depth) was then further subdivided into shallower sites (132 m median depth) and deeper sites (172 m median depth). The last subdivision concerned the coastal group of median depth 51 m, which was split into two groups having 36 m and 62 m median depths, respectively. While bathymetry appeared to be a good structuring factor, additional information was derived from the study of the assemblages and indicator species for each aggregation level.



INDICATOR SPECIES AND SPECIES ASSEMBLAGES

The indicator values (Eq. 11) for both dominant species (Table 1) and secondary species (Table 2) were computed for the seven levels of the hierarchical structure of site clustering. The threshold level of 25 % for the index

chosen by Dufrière & Legendre (1997) was used in this analysis. The characteristic species for each site group and the values of the index are shown in Table 3. For the first hierarchical subdivision in two groups, only 69 % of the total number of the dominant species were retained

Table 3. Variations of the indicator value (Eq. 10) with hierarchical levels shown in Fig. 3. Only species having indicator values greater than 25 % were retained. Species labels for dominant species and rare species are those of Tables 1 and 2, respectively. The indicator value is shown between parentheses and preceded by the number of the site group.

Species label	Number of site groups						
	2	3	4	5	6	7	8
Dominant species							
ALLOSPP	I(68)	II(69)	II(67)	III(44);II(32)	III(42);II(31)	III(39);II(29)	III(42)
ARGESIL			IV(48)	V(48)	VI(44)	VII(31)	VIII(31)
ARGESPH	II(70)	III(67)	III(77)	IV(67)	IV(55)	VI(38);IV(31)	VII(35);V(29)
ARNOIMP	II(46)	III(46)	III(53)	IV(52)	V(72)	V(61)	VI(61)
ARNOLAT	I(27)	II(32)	II(31)	III(29)	III(27)		III(37)
ASPICUC	II(46)	III(40)	III(44)	IV(38)	V(65)	V(57)	VI(54)
CALLLYR	I(51)	II(38)	II(37)	II(73)	II(64)	II(63)	II(63)
CALLMAC	II(25)		III(28)		IV(27)	IV(27)	
CAPRAPE	II(74)	III(74)	III(77)	IV(77)	V(67)	V(46);VI(33)	VI(46);VII(33)
GADIARG	II(62)	III(61)	IV(86)	V(84)	VI(80)	VII(70)	VIII(69)
ILLECOI	II(83)	III(82)	III(76)	IV(72)	IV(67)	VI(70)	VII(69)
LEPIWHI	II(63)	III(61)	III(39)	IV(37)	IV(30)	VI(32)	VII(32)
LESUFRI	I(31)	II(35)	II(35)	III(59)	III(59)	III(59)	IV(58)
LOLIFOR	II(58)	III(53)	III(41)	IV(35)	V(62)	V(59)	VI(58)
LOLIVUL	I(44)	I(80)	I(80)	I(66)	I(66)	I(66)	I(54);II(26)
MERLMCC	I(69)	II(76)	II(72)	III(74)	III(69)	III(61)	IV(58)
MERLMNG	I(49)	I(25)	I(25)	II(54)	II(54)	II(54)	II(53)
MICRPOU	II(97)	III(97)	III(72)	IV(71)	IV(74)	VI(83)	VII(83)
MOLVMOL					V(43)	V(40)	VI(40)
MULLSUR		I(56)	I(56)	I(48)	I(48)	I(47)	I(43)
MUNIBAM	II(26)	III(26)	IV(47)	V(46)	VI(45)	VII(42)	VIII(42)
NEPHNOR		II(28)		III(47)	III(44)	III(40)	IV(40)
POMAMIN		II(26)	II(26)	II(46)	II(46)	II(46)	II(39)
RAJANAE	II(32)	III(32)			V(36)	V(30)	VI(30)
SCYLCAN	II(49)	III(27)	III(27)				
SEPIELE	II(44)	III(42)	III(49)	IV(40)	V(49)	V(41)	VI(33)
SEPISSP				III(30)	III(26)	IV(25)	
SPONCAN	I(30)	I(81)	I(81)	I(71)	I(71)	I(71)	I(65)
TRISLUS	I(50)	I(41)	I(41)	I(32);II(27)	I(31);II(26)	I(30);II(25)	II(40);I(26)
TRISMIN	I(55)	II(70)	II(68);III(25)	II(61)	II(49)	II(47)	II(57)
Secondary species							
BOOPBOO		I(57)	I(57)	I(55)	I(55)	I(55)	I(53)
CEPORUB		II(27)	II(26)	III(28)	III(27)	III(26)	
ELEDCIR					V(33)	V(32)	VI(32)
GALEMEL			IV(89)	V(89)	VI(89)	VII(85)	VIII(85)
HELIDAC			IV(53)	V(53)	VI(47)	VII(41)	VIII(41)
HYPELAN		I(36)	I(36)	I(30)	I(30)	I(30)	
LEPIBOS			IV(54)	V(54)	VI(52)	VII(44)	VIII(44)
LIMALIM				II(32)	II(32)	II(32)	II(45)
LIZARAM		I(55)	I(55)	I(53)	I(53)	I(53)	I(50)
MALALAE			IV(66)	V(66)	VI(64)	VII(58)	VIII(58)
OCTOSPP			IV(33)	V(32)	VI(31)	VII(28)	VIII(27)
PHYCBLE			IV(58)	V(57)	VI(57)	VII(56)	VIII(56)
SOLESOL		I(28)	I(28)				II(27)
TODASAG			IV(45)	V(45)	VI(43)	VII(36)	VIII(36)
TRACDRA		I(38)	I(38)	I(34)	I(34)	I(34)	I(32)

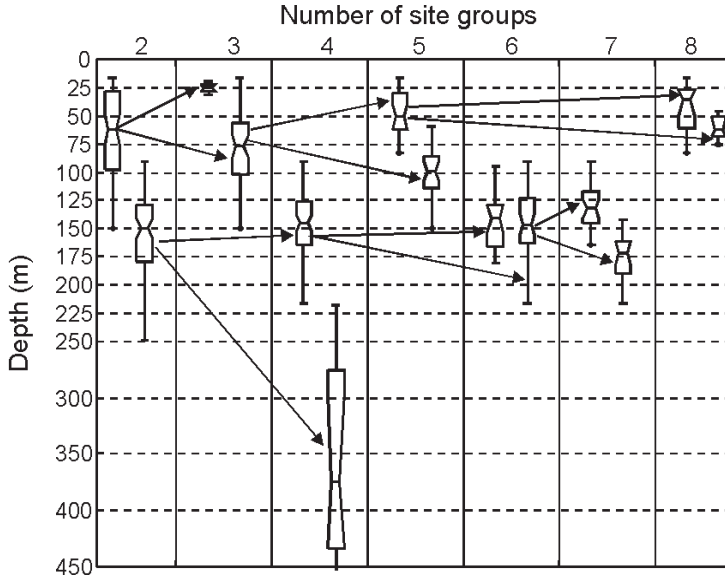


Fig. 7. Detailed representation of depth distributions of the two newly obtained groups of sites at each hierarchical level using box-and-whisker plots. For each aggregation level only the two newly obtained groups of sites were shown. Arrows indicated the hierarchical link between the different groups.

The box has lines at the lower quartile, median, and upper quartile values (representing the 25th, 50th and 75th percentiles of the sample, respectively). The whiskers are lines extending from each end of the box to show the extent of the rest of the data.

(see Table 1). Both zones (Fig. 5C) were dominated by species with wider spatial distribution patterns, such as blue whiting *Micromesistius poutassou* with an index value of 97 % for the second zone (Table 3). Almost all the blue whiting individuals were in the offshore zone and were present in all of these sites. This species is associated with *Illex coindetii*, *Capros aper*, *Argentina sphyraena*, *Lepidorhombus whiffiagonis*, *Gadiculus argenteus* and *Loligo forbesi*. The indicator values of these species were equal to or greater than 58 %. Another group of seven species (*Scyliorhinus canicula*, *Aspitrigla cuculus*, *Arnoglossus imperialis*, *Sepia elegans*, *Raja naevus*, *Munida bamffia* and *Callionymus maculatus*) with lower indicator values for the same zone was also distinguished. On the other hand, ten species characterised the coastal zone (Table 3). The highest indicator value of 69 % was obtained for hake *Merluccius merluccius*. The maximum indicator value for most characteristic species was obtained for higher hierarchical levels, this is an indication of the heterogeneity of the coastal habitats. For example, the species association of *Spondyliosoma cantharus*, *Loligo vulgaris* and *Mullus surmuletus* characterised the shallow water habitat for the third hierarchical level. For the same level, the indicator values of three characteristic species (*Merluccius*

merluccius, *Trisopterus minutus* and *Alloteuthis* spp.) of the second coastal zone reached their maximum. The isolation of smaller site groups made the apparition of secondary species in the list of indicator species possible (Table 3). For example, after the third hierarchical level, seven secondary species (*Boops boops*, *Liza ramada*, *Trachinus draco*, *Hyperoplus lanceolatus*, *Dicologlossa cuneata*, *Trigla lucerna* and *Solea solea*) were identified as indicators of the shallow coastal zone.

The first subdivision of the offshore zone isolated the break-shelf sites, characterised by the association of three dominant species (*Gadiculus argenteus*, *Argentina silus* and *Munida bamffia*) with seven secondary species (Table 3). The highest indicator value for this group was obtained for the secondary species *Galeus melastomus* (89 %). The characteristic species of zone III (Fig. 6B) were *Capros aper* and *Argentina sphyraena*, as their maximal indicator value (77 %) was reached at this level. The characteristic species of the next hierarchical level (5 site groups) were indicators of the newly isolated groups: *Callionymus lyra* for zone II (Fig. 6C) and *Lesueurigobius friesii* for zone III (Fig. 6C). The separation between the Southern Celtic Sea and the Bay of Biscay habitats occurred in the sixth hierarchical level (Fig. 6D). Table 3 shows the difference between these



zones in terms of assemblages of indicator species. With the exception of the species *Capros aper*, the maximal indicator values for the Southern Celtic Sea zone were obtained at this hierarchical level (Table 3).

The next levels did not result in any increase of indicator values for any of the species. So, it was assumed that the highest significant hierarchical level was attained for the six site groups.

DISCUSSION

The development of remote sensing techniques has significantly globalised approaches in spatially orientated ocean research. Considering the development of techniques using ocean colour detectors to estimate the primary productivity (Antoine & al. 1995) and water circulation (Taupier-Lepage & Millot 1988), extrapolation to estimate the productivity of the higher trophic levels (in particular the exploited resources) remains currently difficult. All mono-species and non spatialized approaches used in the past for fisheries management have shown their limitations (Gunderson & al. 1995; Parsons 1995), as an alternative the integrated ecosystem approaches (Christensen & al. 1996; Larkin 1996) and spatially based approaches (Ault & al. 1999) have been developed. In order to improve these approaches, it is necessary to develop broad scale monitoring and surveys of marine resources. At present, there is an increasing demand to study species assemblages in relationships with their habitats and to study their temporal evolution or change with respect to both fishing pressure and environmental change (Gomes & al. 1995; Mahon & al. 1998). However the current techniques used to analyse the databases coming from bottom trawl surveys or catch data are based on strong assumptions. These assumptions can go from sampling programs involving *a priori* selected areas (Iglesias 1981) up to the visual delimitation of homogenous regions after random sampling (Gomes & al. 1995). In the absence of an objective statistical approach to separate spatially homogenous zones according to their species assemblages, the comparison of the temporal evolution of these habitats and their biodiversity remains unsatisfactory.

The regionalization of habitats based on the properties of their inhabitants is a classical approach in ecology (Dufrene & Legendre 1997). However, this approach is limited because it relies too much on ecologically meaningful descriptors, because the species compositions and spatial distributions of species populations do not only vary with the habitat type. The other direct approach consisting in the description of all the characteristics of a habitat is also limited as much by the knowledge of the relevant characteristics of these habitats as that of the volume of work needed. Until now, both approaches have

come up against difficulties in geographically representing the properties defined in a multidimensional mathematical space. Mahon & al. (1998) used principal component analysis (PCA) and cluster analysis (CA) to map fish assemblages from large spatio-temporal datasets. In their study, assemblages were identified using arbitrary threshold levels of species loadings on the principal components (PCs). The top 5 % of the site scores for each PC, were also arbitrarily used in identifying the main sites of each assemblage. So, the same site can belong to more than one map, increasing the difficulty in defining clear boundaries between the biogeographical zones (see Fig. 3 in Mahon & al. 1998). Moreover, the authors did not perform any statistical tests showing the robustness of their results based on the use of one random subset of 10 % of the data in CA. Mahon & al. (1998) considered their results as being too preliminary to permit them to conclude with serious management implications. They also showed the necessity of the use of such results (assemblage maps) in the definition of boundaries for large marine ecosystems. Although the notion of boundaries is important, it is difficult to separate these objectively in the previous studies, especially if the number of site groups is low. Colvocoresses & Musick (1984) performed CA on a pooled sites-species matrix constructed from bottom trawl surveys over a 9-year period. They used different symbols to map the various site groups. This classically used representation is also limited when clear boundaries have to be drawn or if seasonal (or inter-annual) comparison between maps is to be made (for example see figs 4 & 6 in Colvocoresses & Musick 1984).

In this paper the proposed method overcomes these limitations and proposes an objective technique for defining boundaries after regionalization of spatialised databases. The first originality of the method is the application of the regionalized variables theory to map demersal species habitats. These techniques developed for geological applications (Harff & Davis 1990; Harff & al. 1993) are powerful tools for use in answering a host of ecological questions that deal with the mapping of multivariate databases. The computation of conditional Bayesian probabilities for each site showed several advantages. Firstly, it was used to assess the level of within-group heterogeneity. For example, for homogenous site groups, each site is characterised by high conditional probabilities of belonging to the same site groups. In other situations, when one or more sites again show high probabilities but this time in other site groups, the technique reallocates them. In other words, the conditional probability is a measure of the power of belonging of a site to a particular site group. In this paper, the vectors of maximal probabilities of sites were used to characterise each level of hierarchical classification by an average probability value (see Figs 3-4). Another advantage of the



use of conditional probabilities came from the objective method in the establishment of boundaries between the different zones (Fig. 5).

The method can be separated into three steps: i) the clustering of site groups, ii) the calculation of conditional probabilities, and, iii) the identification of assemblages and indicator species. The last two steps were applied to each hierarchical level. Each single step of the method is not new in itself, however, the combination between these different multivariate techniques developed for different disciplines may be considered as a new applied approach. This originality is further strengthened by the flexibility of the algorithm and the numerous extensions possible not to mention the use of various powerful multivariate analyses. For this application, a hierarchical cluster analysis was used in the first step to classify the different sites. However, all methods which are able to produce a partition of sites into groups, such as k-means or probabilistic clustering for example, may be used in the first step of this method (see Legendre & Legendre 1998). It is also possible to include partitions obtained from other environmental data sets (Souissi & al. 2000) or at least *a priori* partitions. In all cases, the homogeneity of biological characteristics (e.g. demersal assemblages in this paper) in the initial spatial partition can be assessed by the computation of conditional probabilities. In the example shown here, since the first regionalization level (2 site groups), the computed average probability was relatively high (Fig. 3).

Several methods for regionalization have been developed in other spatially oriented disciplines e.g. soil science (Goovaerts 1992), climate science (Comrie & Glenn 1998), water quality management (Boyer & al. 1997) and recently in the monitoring of coastal ecosystems (Souissi & al. 2000). The present algorithm can be further applied to these studies. However, only multinormally distributed data can be used in order to compute the conditional probabilities (Harff & Davis 1990). Several mathematical transformation are proposed for hydrological and physical parameters (Hernandez Encinas 1994; Sokal & Rohlf 1995). When species catches data were used (e.g. the present application) only dominant species (low percentage of zeroes) were used to compute conditional probabilities. In most multivariate analyses, the elimination of secondary species is frequent (Ibanez & al. 1993; Fromentin & al. 1997; Dufrêne & Legendre 1997; and others). In this application, the secondary species matrix was also used in identifying indicator species. It was shown that some secondary species were indicators of the shallower coastal habitats while others characterised the deeper habitat (see Table 3). This remains a good demonstration of the role of considering both global and local scales in studying the spatial organisation of demersal and benthic communities.

Instead of using the same cluster analysis approach in the R mode (classification of species), indicator values were used to discriminate between abundance in all sites and the spatial heterogeneity of species distributions. The added advantages of using indicator values are discussed in Dufrêne & Legendre (1997).

The objective choice of cut off level of a dendrogram is a common asked question in ecology. Few methods are proposed in terms of numerical techniques (Feoli & Lausi 1980; Legendre & Legendre 1998), and the common protocol is to use visual criteria and *a priori* knowledge of the system studied (Hosie & al. 1997). In the present study the solution of studying several successive hierarchical levels was adopted (Dufrêne & Legendre 1991). The first analysis of variation in average probability value as a function of the hierarchical level (Fig. 4) allowed for the selection of levels 2 to 8 site groups to take place. Then, the indicator value criteria showed that the only significant hierarchical levels were those from 2 to 6 site groups (Table 3). The bathymetry seems to have been the most structuring factor for the demersal species habitats, with the exception of the isolation of the southern Celtic Sea group (Fig. 7). According to the indicator values (Table 3), the last group was mainly characterised by 5 demersal fish species (*Arnoglossus imperialis*, *Capros aper* and *Aspitrigla cuculus*, *Molva molva* and *Raja naevus*). The first two and the fifth are subtropical species, the third is a temperate one and the fourth is boreal. As southern and northern species coexist in this group, biogeography may obviously not justify the separation of this group from the other groups of the Bay of Biscay. So, an explanation must be sought at the ecological level. These 5 species are most often associated with hard substrate bottoms such as rock, gravel and sand (in FishBase, Froese and Pauly 2001). The bottoms of the Bay of Biscay are mainly muddy while hard bottoms dominate in the Celtic Sea probably because of the strong hydrodynamical properties of this sea. Perhaps these species are found in the Celtic Sea rather than in the Bay of Biscay as a result of their bottom preferences. The characterisation of the southern Celtic Sea area by this group of species may therefore provide evidence for an ecological pattern so far unnoticed.

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