Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography

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ABSTRACT: Present-day patterns in pelagic biodiversity are the result of the interaction of many factors acting at different scales. Developing an understanding of the processes that regulate the diversity of oceanic ecosystems is thus challenging. In this study, diversity of calanoid copepods was decomposed into species associations by means of the recent 'indicator value method' and multivariate analyses. For the first time, at an oceanic basin scale and with a spatial resolution approaching the mesoscale, species associations of calanoid copepods have been identified. Nine species associations were determined and have enabled us, (1) to improve the ecological partitioning of this region, and (2) to identify the main factors that regulate pelagic biodiversity in this area. It is shown that temperature, hydrodynamics, stratification and seasonal variability of the environment are likely to be the main factors contributing to the ecological regulation of diversity of calanoid copepods. The similar geographical pattern evident between currents/water masses and the species associations suggest that the species groups may be used as an environmental indicator to evaluate long-term changes in the marine environment related to climate change and other increasing human-induced influences.

KEY WORDS: Pelagic diversity · Species associations · Calanoid copepods · Continuous Plankton Recorder (CPR) survey · Multivariate analyses

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INTRODUCTION

Factors that contribute to the biodiversity in the pelagic realm are numerous and concern a large range of temporal and spatial scales (Mann & Lazier 1996, Angel 1997, Haury & McGowan 1998). Geological events that have modified the distribution of continents, opening or closure of seaways and changes in the general thermohaline circulation have led to speciation. Climatic oscillations have involved modifications in the geographic distribution of species (Gee 1991, Crame 1993, Molfino 1994) and in sea levels, which have been shown to contribute to evolution in certain circumstances (Fleminger 1986, Cronin & Schneider 1990). At a smaller scale, ecological factors influence the physiology of species and can contribute to the spatial-temporal regulation of diversity. All these factors have contributed synergistically to speciation and the shape of present day patterns of pelagic biodiversity.

Recently, a map of the pelagic diversity of calanoid copepods has been produced for the North Atlantic and the North Sea based on data historically collected by the Continuous Plankton Recorder (CPR) survey (Beaugrand et al. 2000a). Based on a large amount of data (about 18 million data points), this map shows an east-west asymmetry in plankton diversity throughout

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the northern North Atlantic Ocean and adjacent seas with pronounced local variability. Multivariate analyses and a diversity index were used at both diel and seasonal scales to distinguish major biological regions with a relatively small spatial resolution (Beaugrand et al. 2001). Currents were clearly shown to play an important role in the regulation of pelagic biodiversity at both meso- and macroscales. The warm North Atlantic Current and the European shelf edge current and undercurrent have emerged as important parameters for the maintenance and regulation of biodiversity in the Bay of Biscay and west of the British Isles (Beaugrand et al. 2001).

However, in these recent studies, information on taxa or assemblages that contributed to the diversity in a region of the survey area was not investigated. This represents a major gap in our understanding of the factors that maintain diversity at an ocean basin scale. Individual distributional ranges of many pelagic organisms has been determined, especially in the northern North Atlantic and the North Sea (Edinburgh Oceanographic Laboratory 1973). A number of aspects limit the application of this atlas. Firstly, it was only based on samples collected during the period from 1958 to 1968, with a restricted number of samples (about 45 000 in contrast to about 170 000 at present). Secondly, only the common species were divided into 3 categories of abundance; less common species were indicated as present. Thirdly, the presentation used a Mercator plane projection, which highly distorts the spatial pattern with changing latitude (Planque 1996, Planque et al. 1997).

Basing the partition of a region on the distribution of individual species or monitoring changes in ecosystems from a single species may be quite arbitrary as variable features related to factors such as aggregation or dispersal as well as mortality or survival may influence the distribution of a pelagic organism (Colebrook et al. 1961). These latter authors stressed that the use

Fig. 1. Main area (in grey) sampled by the Continuous Plankton Recorder survey from 1958 to 1997

of indicator associations may reduce such uncertainties. However, despite attempts realised by Colebrook et al. (1961) and Colebrook (1964) around the British Isles, research on species associations has not been undertaken on the CPR dataset at this scale.

The purpose of this study was to decompose diversity of calanoid copepods into species associations. The abundance of about 100 species of calanoid copepod was first regularised on a regular spatial grid and homogeneous time period at both diel and seasonal scales. Then, the recently proposed 'indicator value method' (Dufrêne & Legendre 1997) and multivariate analyses were applied to identify indicator species and associations. The detected associations are fully described and are then used, (1) to refine the recent partition proposed by Longhurst (1998) and Beaugrand et al. (2001), and (2) to improve understanding of factors implied in the regulation of diversity at this scale. Finally, it is argued that these associations represent a valuable tool to record environmental change and to evaluate the effects of climate change and increasing human-induced influences on marine eco-systems.

MATERIALS AND METHODS

Sampling. Data used in this study come from the Continuous Plankton Recorder (CPR) survey. This monitoring programme has sampled plankton monthly over the North Atlantic and the North Sea since 1948. Samples are collected by a high speed recorder (about 20 km h^{-1}) towed behind voluntary merchant ships at a standard depth of about 6.5 m (Hays 1994). Plankton is retained by a continuously moving band of silk, which has an average mesh size of 270 µm, corresponding to about 3 m^3 of seawater filtered (Hays 1994, Beaugrand et al. 2000b). On return of the CPRs to the laboratory, silks are unwound and plankton is counted according to a methodology described by Colebrook (1960, 1975) and Warner & Hays (1994). For this study, information on the abundance of calanoid copepods (108 taxa) was extracted from the CPR database for the period from 1958 to 1997. The investigated area is indicated in Fig. 1. Calanoid copepods were used because the CPR sampling and identification is optimal with this taxa. Indeed, in most cases (92.5%) identification is carried out to species level, except for small species which may be identified to genus and the group *Para-Pseudocalanus* which amalgamates the genera *Paracalanus* and *Pseudocalanus* (Beaugrand et al. 2001).

Pre-processing and analyses. Fig. 2 summarises the different steps that led to the identification of indicator species assemblages.

Step 1. Calculation of taxonomic richness: Taxonomic richness, which corresponds here to the number
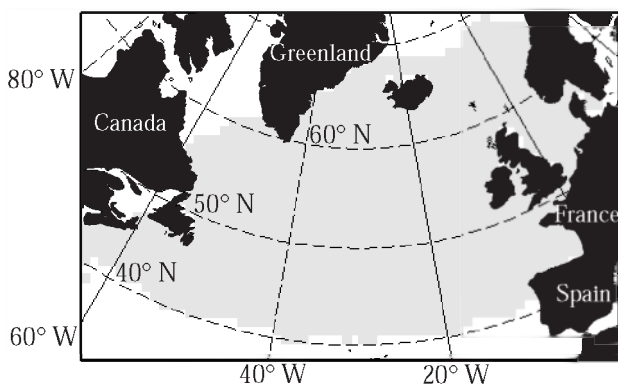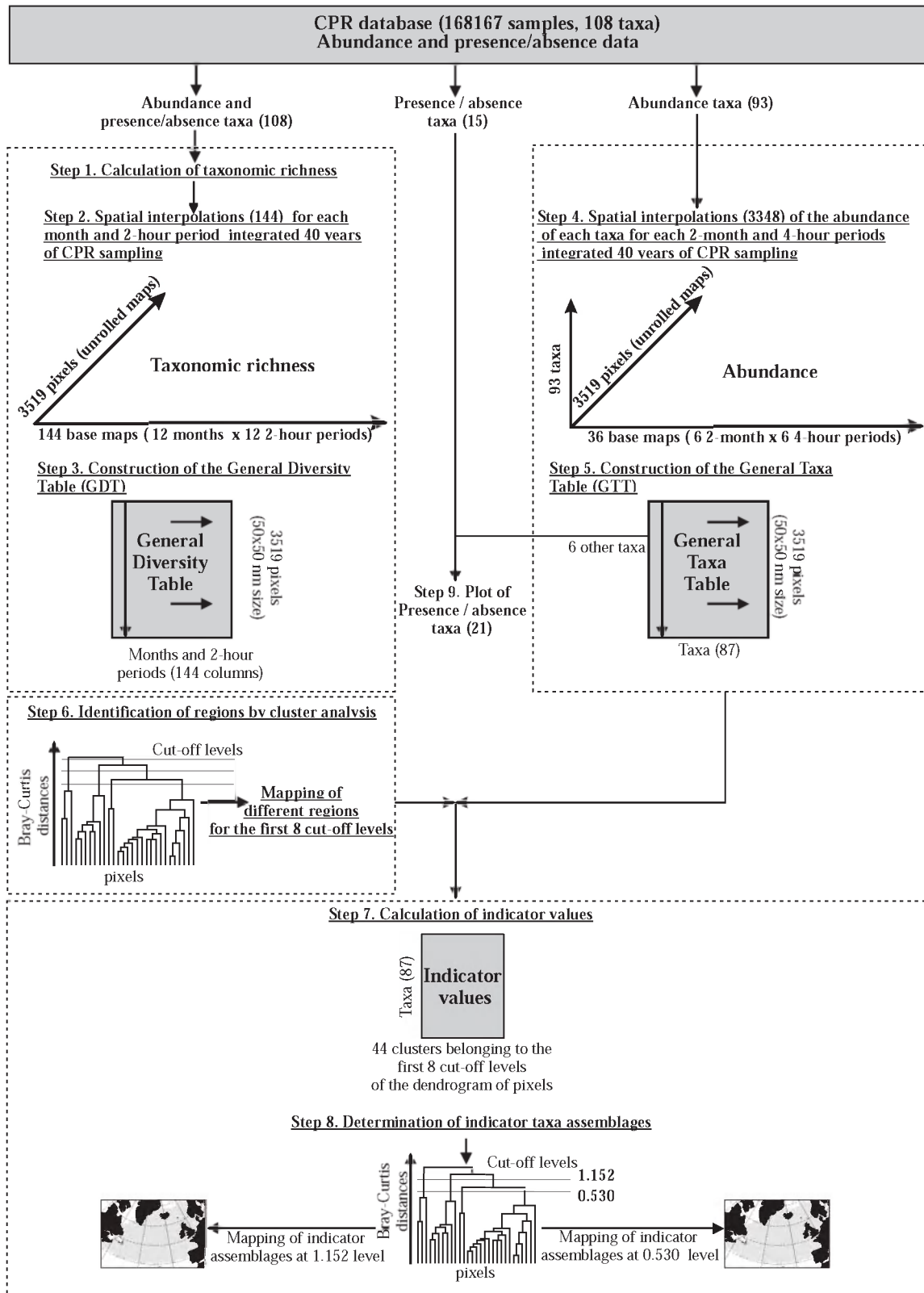
Fig. 2. Diagram of the analysis steps that led to the detection of regions, indicator taxa and associations of calanoid copepods into the North Atlantic and adjacent seas

of taxa per CPR sample, was calculated from the original matrix. This index was selected in this case instead of more robust estimators such as the Simpson or Shannon index because the original matrix also integrated presence/absence data for many taxa.

Step 2. Spatial interpolation of taxonomic richness: Before performing numerical analyses, it was necessary to take into account that the CPR survey does not follow a grid sampling system. In addition, samples are collected at different times of the day and the geographical location of samples varies from one month to another. Thus, the primary procedure was to rearrange the data in time and space and to generate 2 different data tables following a procedure described in Beaugrand et al. (2001).

The following procedure allows diel vertical migration and seasonal variations of many calanoid taxa to be taken into account. From 168 162 CPR samples, data were clustered by 2 h periods from 00:00 to 24:00 h, for each month, integrating 40 years of sampling. For each subgroup (12 mo × twelve 2 h periods = 144 subgroups), taxonomic richness was re-estimated on a regular grid of 50 × 50 nautical miles (n mile), using the inverse squared distance method (Lam 1983). As taxonomic richness is an index that is very sensitive to sampling size, a similar number of neighbours, fixed to 10, was used to realise spatial interpolations. The search radius corresponded to 250 n mile.

Step 3. Construction of general diversity table (GDT): Then, data for each subgroup were combined to generate a GDT (3519 pixels × 144 seasonal and diel periods) with estimated values for each pixel in row and time period in column. To give an example, rows of column 8 contained an estimation of diversity for the month of January and the period 14:00 to 16:00 h. This matrix corresponds to that analysed by principal component analysis in Beaugrand et al. (2001).

Step 4. Spatio-temporal regularisation of abundance of taxa: A similar protocol was used to estimate the average abundance of each calanoid taxon. Spatial regulations were performed for each taxa for 2 mo and 4 h periods in order to limit the number of spatial interpolations needed to integrate 40 years of CPR sampling (six 2 mo × six 4 h periods × 93 taxa = 3348 spatial interpolations).

Step 5. Construction of general taxa table (GTT): Then, an average of the 36 estimations (six 2 mo × six 4 h periods = 36) of the abundance was calculated for each taxon and data were combined to build the GTT (3519 pixels × 93 taxa), which thus contained the average abundance of each taxa (in column) for each pixel (in row). Six very rare species (e.g. *Labidocera aestiva*, *Candacia tenuimana*), for which the interpolation method did not work, were removed from this matrix and were not considered further in the analyses (3519 pixels × 87 taxa). No missing data were permitted in the calculation of the average abundance value of each taxa to induce no difference related to the weakness of the sampling in an area.

Step 6. Identification of regions by cluster analysis: From the general diversity table, a matrix of distances between pixels was calculated using the Bray & Curtis coefficient (Bray & Curtis 1957). This coefficient was used because (1) it is robust and (2) its properties have become well known due to its extensive use in ecology (Clarke 1993). Then, a hierarchical complete linkage clustering method was applied to distinguish regions that show different seasonal and diel patterns. The complete linkage was chosen because it is more difficult to add an element to a group when it grows in size (Legendre & Legendre 1998). This property tends to reduce the effects of spatial autocorrelation involved in the use of spatial interpolation. To take into account the hierarchy of the method, several cut-off levels were retained by examining associated indicator values (see below). This constitutes a necessary step in the application of the indicator value method (Dufrêne & Legendre 1997).

Step 7. Calculation of indicator values: The indicator value method (Dufrêne & Legendre 1997) enables the species characterising a region to be identified. It is calculated by combining a measure of specificity and of fidelity. The former, A_{ij} (specificity) computes the ratio of the average abundance of species i in the pixels of group j (Nindividuals$_{ij}$) to the sum of the mean abundance of the species i in all groups:

$$A_{ij} = \frac{N_{\mathrm{ind}_{ij}}}{N_{\mathrm{ind}_i}} \qquad (1)$$

The latter, B_{ij} (fidelity) is the ratio of the number of pixels where the species i in the group j is present ($N_{\mathrm{sites}_{ij}}$) to the total number of pixels in this group:

$$B_{ij} = \frac{N_{\mathrm{sites}_{ij}}}{N_{\mathrm{sites}_j}} \qquad (2)$$

Finally, the indicator value (INDVAL$_{ij}$) is reached by multiplying the specificity and fidelity indices as the 2 quantities represent independent information (Dufrêne & Legendre 1997).

$$\mathrm{INDVAL}_{ij} = A_{ij} \times B_{ij} \times 100 \qquad (3)$$

Indicator values for each taxa (see GTT) were calculated for the first 8 cut-off levels of the pixel dendrogram (see step 4), which encompassed a total of 44 groups. For example, 2 regions were identified at the first cut-off level of the dendrogram while 8 regions were detected at the 7th level of the dendrogram. Then, indicator value results were combined in a single data table (87 taxa × 44 groups) with the species or

taxa in rows and the indicator values in columns. Dufrêne & Legendre (1997) proposed to retain the maximum indicator value for each species among all groups.

$$INDVAL_i = \max[INDVAL_{ij}] \qquad (4)$$

Step 8. Detection of indicator associations: Instead of only considering maximum values (see Step 5), the matrix of indicator values (87 × 44) was also transformed into a distance between-species matrix using the Bray & Curtis coefficient. Then, the 'hierarchical flexible clustering method' (Lance & Williams 1967) was used to detect taxa indicator assemblages. The resulting dendrogram was analysed considering the distance cut-off levels 1.152 and 0.530. These 2 levels were selected because they represented the best compromise between high distance levels in the dendrogram where groups still included heterogeneous taxa and low distance levels for which the differences between groups were due to minor change in the geographical distribution of species. In contrast to Step 5, where the goal was to identify indicator taxa or species, the objective of this step was to detect indicator species groups.

Step 9. Representation of presence/absence species: The above analyses could not be performed on 21 taxa either because only presence/absence data were available (15 taxa) or because of the low abundance (6 taxa). Plots of the occurrence of these rarer taxa were produced.
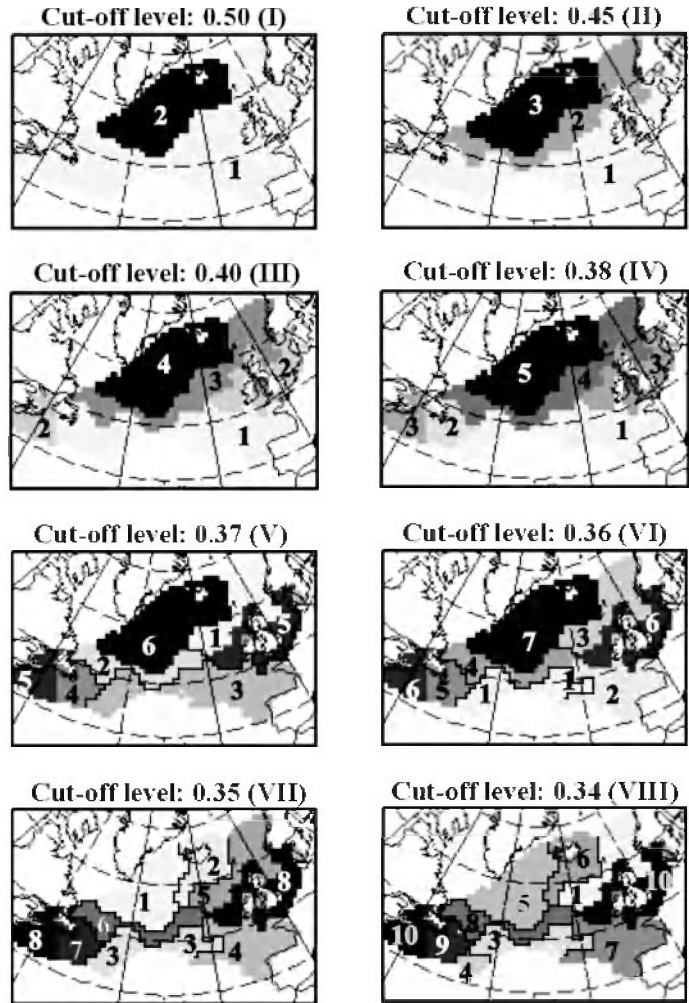

Fig. 3. Mapping of geographic clusters (regions) for the first 8 levels of the dendrogram of pixel (not shown). Roman numerals denote the number of the cut-off level of the dendrogram and normal numerals identify groups for a partition level

RESULTS

Identification of regions

Differing regional breakdown in the temporal changes of calanoid diversity were distinguished using the first 8 cut-off levels of the dendrogram (Fig. 3). The Atlantic Arctic biome and the Atlantic Westerly Winds Biome (Longhurst 1998) are separated in the first map (Fig. 3). A transitional region was detected at the next level. The level of 0.40 splits shallower from deeper regions with the exception of the Grand Banks of Newfoundland which were identified at level 0.38. The next level divided the transitional region into a western and eastern component. The level 0.36 splits the southern oceanic region of the survey area at the mid-Atlantic ridge. At level 0.35, the Atlantic Arctic Biome was separated into 2, one region influenced by subarctic water and another influenced by the path of the

North Atlantic Current. The last level identified 10 different clusters, one of which was ignored as it only comprised one pixel. This level splits the western oceanic part into 2, the Gulf Stream extension and another to the east. Thus, a total of 44 groups (regions) were identifiable at the 8th cut-off level of the dendrogram.

Indicator values were calculated for all species or taxa and for all 44 regions detected above (see Fig. 3), giving a total of 87 × 44 = 3828 values. Only indicator values ≥25% should be considered. Dufrêne & Legendre (1997) arbitrarily used this level, which means that a taxa occurs in at least 50% of the pixels in a region and that its relative abundance reaches at least 50%. We used the number of significant (indicator values (25%) maximal indicator values (see Step 5 in Fig. 2 and Eq. 4 in 'Materials and methods') detected in the 1st cut-off levels in the dendrogram as a criteria to
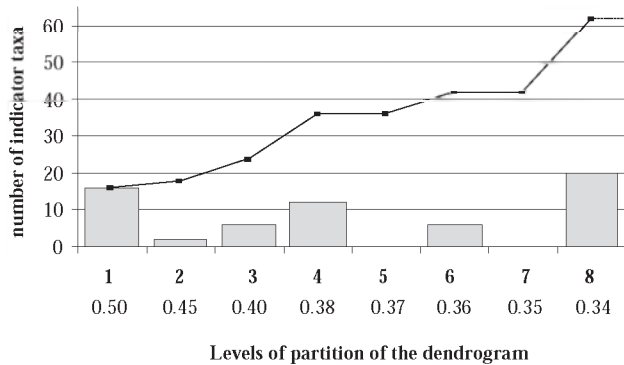
Fig. 4. Plot of the number of significant species indicator values calculated from the 8 successive hierarchical clustering levels (from 0.5 to 0.34). Number of taxa that have a maximal indicator value superior to 25% (see Fig. 3) are represented by histograms and the cumulated number of significant indicator taxa are indicated by a curve

select the different partition levels in the dendrogram. Fig. 4 shows the number of significant indicator values for the first 8 cut-off levels. For example, the last partition level of the dendrogram (0.34 in Fig. 3) was important to take into account, as it allowed 21 indicator species to be detected. Only the first 8 levels were chosen, as lower cut-off levels (0.33 to 0.30), which included 60 other groups, did not increase the number of indicator values and interpretation of the geographical regions was difficult. Intermediate levels (5 and 7, Fig. 4) for which no maximal indicator values were found were retained, as many of these values were still >25%.

Indicator value of species or taxa

Maximal indicator values found for each taxa in a specific pixel cluster and each cut-off level of the dendrogram of pixels are displayed in Fig. 5. In the analysis, 71.26% (62) of 87 taxa had an indicator value higher than the threshold of 25%. This also includes *Ctenocalanus vanus*, which has a value of 24.71.

A striking contrast exists between the diversity of the Atlantic Arctic biome, which only has 4 indicator species (e.g. *Euchaeta norvegica*), and the Atlantic Westerly Winds and Coastal Biomes with 58 taxa (Fig. 5). Taxa with the maximal indicator value for Region I.1 (see Fig. 3) are eurytopic (e.g. *Pseudocalanus* spp., *Calanus helgolandicus*) and can be found in neritic and temperate oceanic water. Some species such as *Candacia armata* and *Centropages typicus* occur preferentially above the continental shelf break. Neritic regions (Region III.2 in Fig. 5) only have few (4) indicator taxa such as *Temora longicornis* and *Centropages hamatus*. This contrasts with the many taxa found in the southern oceanic and Gulf Stream Extension re-

gions (Regions IV.1, VI.1 and VIII.4 in Fig. 5). *Calanoides carinatus* and *Euchaeta hebes* are characteristic of the Bay of Biscay region and the southern part of the European shelf break (Region VI.2).

Detection of indicator species or taxa assemblages

Two cut-off levels in the taxa dendrogram (Step 8 in 'Materials and methods') were used to interpret species clusters. At a threshold of 1.152, 10 clusters were detected (Fig. 6). A cut-off level at 0.53 allowed a finer breakdown of some clusters. Each subgroup is identified by the letters A, B, C and a number corresponding to the group to which it belongs. For some species clusters (1 to 2, 6 to 10), the division into subgroups did not show significant variations in the geographic distribution but rather a gradient. For these subgroups, figures will not be presented.

Fig. 7 shows the spatial distribution of the species groups at a partition level of 1.152 on the dendrogram of taxa (Fig. 6). To produce this figure, the mean abundance table of each species (see Step 2 in 'Materials and methods') for each group was converted into 0 (absence) and 1 (presence). Then, the different tables were added and the percentage of species present in each group was computed for all pixels.

Cluster 1 gathers together 16 warm-temperate oceanic taxa, which have a high average indicator value (64.03) and encompasses most of the indicator taxa of the Southern Oceanic region such as *Pleuromamma xiphias* and the 2 genera *Calocalanus* and *Clausocalanus* (Fig. 5). The boundary of this association is sharp and their geographic range is restricted to a depth >200 m (Fig. 7). The influence of the Oceanic Polar Front (Dietrich 1964; 52 to 53°N) on the latitudinal distribution of this association is strong between the Northwest Corner (51°N, 44°W; Worthington 1976) and the mid-Atlantic ridge. Then, this latitudinal front becomes meridional and the association extends to the north until about 58°N south of Iceland and 55°N west of Ireland. Examination of individual charts (not shown here) indicate that species belonging to Subgroup 1A (Fig. 7) such as *Pleuromamma borealis*, *P. gracilis* and *P. abdominalis* may extend further to the north in autumn.

Cluster 2 comprises pseudo-oceanic taxa that are mostly found over the southern part of the European continental shelf break and in the Bay of Biscay region (Fig. 7, see also indicator taxa of the region VI.2 in Fig. 5). Its average indicator value is high (52.19). *Euchaeta hebes* appears to spread further north than any of the other species in this group.

Cluster 3, which has an average indicator value of 71.85, encompasses taxa that have maximum indicator

All habitats

I

1 → **Atlantic Westerly Winds and Coastal biomes (12 taxa)**

Pseudocalanus adult (**95.49**), *Para-Pseudocalanus* spp. (**91.54**),
Centropages typicus (**89.73**), *Calanus helgolandicus* (**81.76**),
Candacia armata (**78.53**), *Metridia lucens* (**76.01**),
Acartia spp. (**64.81**), *Pleuromamma borealis* (**61.84**),
Pleuromamma robusta (**54.87**), *Rhincalanus nasutus* (**51.27**),
Mesocalanus tenuicornis (**45.49**), *Eucalanus crassus* (**35.18**)

2 → **Atlantic Subarctic biome (4 taxa)**

Euchaeta norvegica (**77.37**)
Calanus finmarchicus (**69.30**)
Scolecithricella spp. (**49.28**)
Heterorhabdus norvegicus (**43.79**)

VII 1 → **Atlantic Subarctic biome without area influenced by the Irminger Current**

Euchaeta glacialis (4.75)
Pseudochirella spp. (1.09)

II 2 → **Transitional region between the Atlantic Arctic and Westerly Winds Biomes (1 taxa)**
Calanus hyperboreus (**36.35**)

II 1 → **Southern oceanic and neritic regions (1 taxa)**
Nannocalanus minor (**68.85**)
Acartia longiremis (9.57)

V 2 → **Southern transitional region**
Scottocalanus persecans (7.25)

V 1 → **Northern transitional region**
Euchaeta tonsa (10.23)

III 1 → **Southern oceanic region and the Grand Banks (2 taxa)**

Mecynocera clausi (**46.77**)
Centropages bradyi (**46.65**)

III 2 → **neritic region (4 taxa)**

Temora longicornis (**60.12**), *Centropages hamatus* (**63.03**),
Labidocera wollastoni (**28.63**), *Anomalocera patersoni* (**25.21**),
Isias clavipes (18.88), *Parapontella brevicornis* (6.81),
Haloptilus longicornis (3.81), *Diaixis hibernica* (0.52)

IV 1 → **Southern oceanic region (9 taxa)**

Euchaeta acuta (**81.42**), *Clausocalanus* spp. (**78.71**),
Euchirella rostrata (**75.25**), *Undeuchaeta plumosa* (**73.56**),
Neocalanus gracilis (**71.52**), *Pleuromamma gracilis* (**64.64**),
Pleuromamma abdominalis (**61.14**), *Heterorhabdus papilliger* (**58.26**),
Calocalanus spp. (**47.72**), *Uudeuchaeta major* (19.35),
Scaphocalanus echinatus (13.11), *Euchirella curticauda* (7.83)

IV 2 → **The Grand Banks of Newfoundland (2 taxa)**

Calanus glacialis (**65.96**)
Metridia longa (**58.23**)
Candacia bipinnata (11.26)
Euchaeta spinosa (11.05)

VI 1 → **Southern central oceanic and Gulf Stream Extension region (3 taxa)**

Pleuromamma piseki (**79.30**), *Pleuromamma xiphias* (**63.42**),
Euchaeta gracilis (**36.51**), *Candacia curta* (11.48)

VI 2 → **Bay of Biscay and southern European shelf edge regions (3 taxa)**

Calanoides carinatus (**77.38**), *Euchaeta hebes* (**70.19**),
Ctenocalanus vanus (**24.71**), *Phaenna spinifera* (10.03),
Diaixis pygmoea (5.29), *Temora turbinata* (2.62),
Heterorhabdus clausii (1.76), *Neocalanus robustior* (1.18)

VIII 3 → **Southern central oceanic region**

Scolecithrix bradyi (11.28)

VIII 4 → **Gulf Stream Extension region (21 taxa)**

Euchaeta marina (**89.08**), *Euchaeta pubera* (**73.54**), *Eucalanus attenuatus* (**73.49**),
Temora stylifera (**71.58**), *Candacia ethiopica* (**71.57**), *Candacia pachydactyla* (**67.19**),
Scolecithrix danae (**65.25**), *Rhincalanus cornutus* (**54.44**), *Eucalanus elongatus* (**48.52**),
Eucalanus monachus (**47.56**), *Acartia danae* (**41.84**), *Euchaeta media* (**41.65**),
Centropages violaceus (**38.24**), *Lucicutia* spp. (**36.89**), *Xanthocalanus* spp. (**36.36**),
Paracandacia bispinosa (**35.13**), *Eucalanus pileatus* (**31.82**), *Candacia norvegica* (**29.96**),
Aetideus armatus (**26.61**), *Pontellina plumata* (**26.08**), *Heterorhabdus abyssalis* (**26.04**),
Candacia longimana (23.17), *Microcalanus* spp. (16.19), *Euchirella pulchra* (13.81),
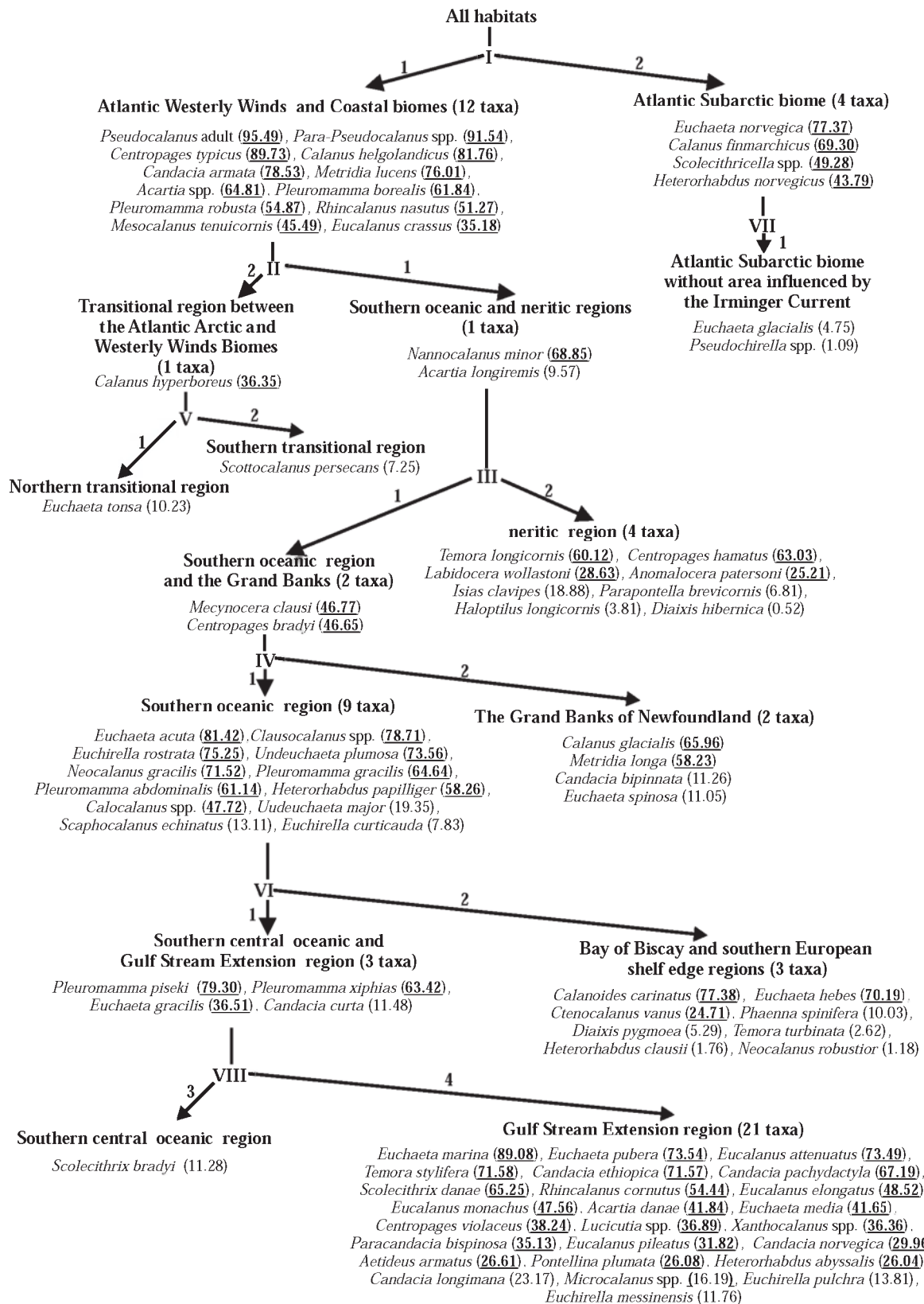*Euchirella messinensis* (11.76)

Fig. 5. Representation of taxa in the regions in which they have their maximum indicator value. Values above 25 (and 24.71 for *Ctenocalanus vanus*) are underlined and in bold. Roman and normal numerals correspond to those in Fig. 3
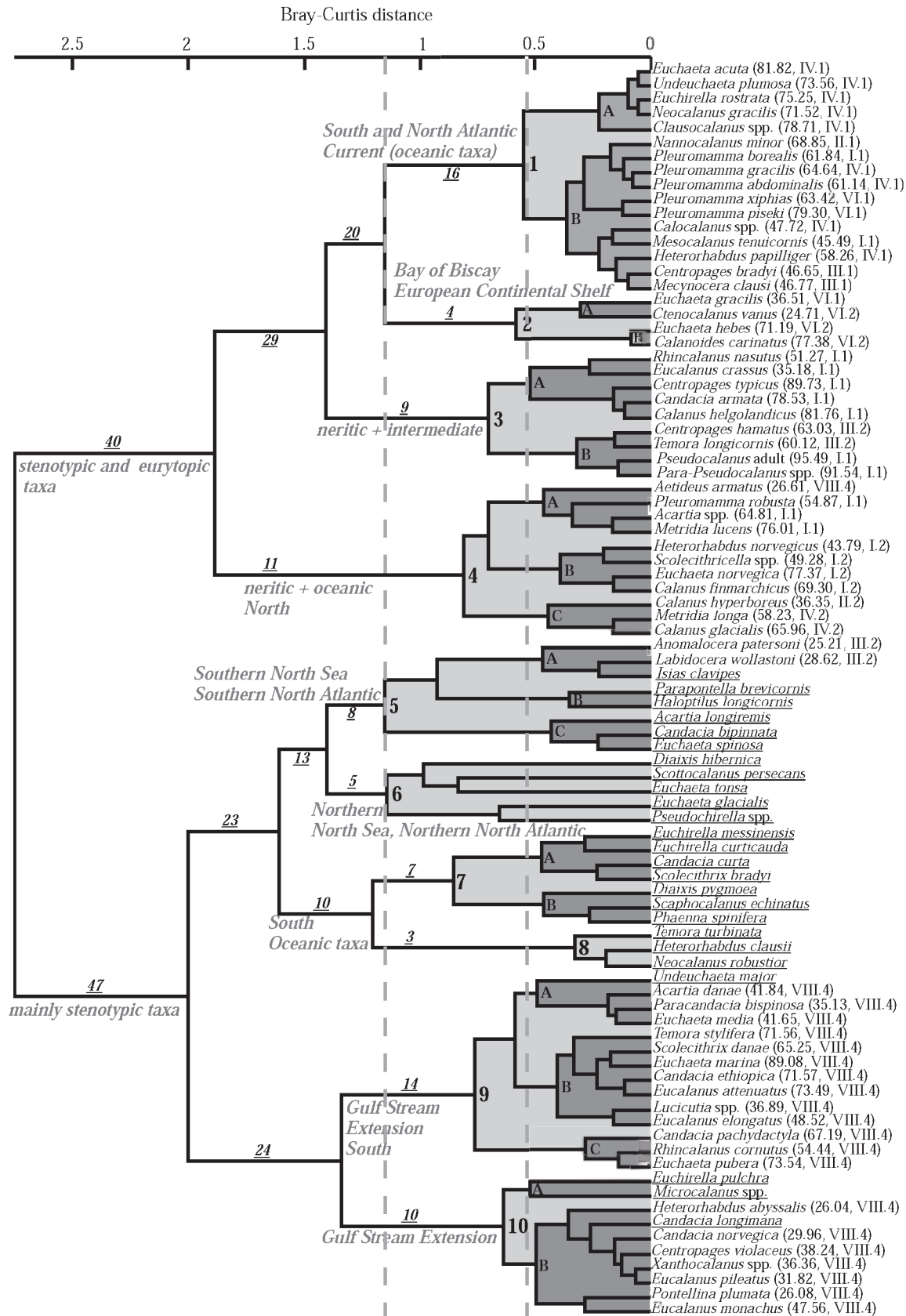
Fig. 6. Dendrogram of taxa resulting from a flexible hierarchical clustering method. Underlined taxa have indicator values lower than 25 %. Groups (at the distance cut-off level of 1.152; dashed line) are indicated in pale grey. Subgroups (distance cut-off level of 0.53; dashed line) are indicated in dark grey. Numbers underlined and in italic represent the number of taxa for each group. Some characteristics of each group are given in grey and italic. Maximum indicator values and the location to which they belong are displayed for each species when these values are significant
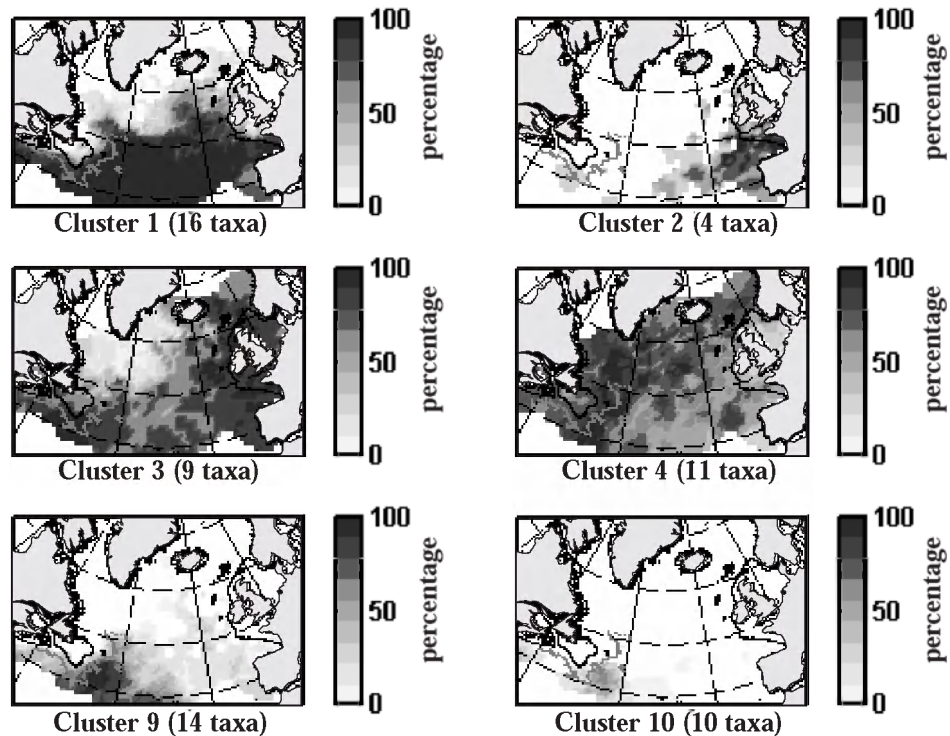
Fig. 7. Mapping of the percentage of occurrence of taxa per pixel for Clusters 1 to 4. Clusters 9 and 10 are defined at the parti-
tion level of 1.152 (see Fig. 6). Data come from the general taxa table (see Step 2 in Fig. 2). Abundance data were transformed
into presence/absence data. Then, the percentage of present taxa per pixel belonging to each group was calculated. When this
percentage is high, it denotes a high spatial aggregation of taxa and conversely. A blank pixel inside the survey area (see Fig. 1)
means the absence of a group. Number of taxa for each association is indicated into brackets

values over the Atlantic Westerly Winds and Coastal
Biomes (see regions I.1, III.2 in Fig. 5). At a weaker
level (0.53), this cluster is divided into 2 subgroups
(Fig. 8). The first one (Subgroup 3A) includes taxa or
species such as *Candacia armata* and *Centropages
typicus*. It is composed of eurytopic taxa that can be
found everywhere south or east of the Oceanic Polar
Front but are mainly present over the shelf edge. They
can be detected in both neritic and oceanic regions
(Fig. 8). The second one (Subgroup 3B) is made up of
neritic species such as *Temora longicornis* and *Cen-
tropages hamatus* which occur in the southern part of
the North Sea, off Nova Scotia and over the Grand
Banks of Newfoundland.

Cluster 4 brings cold-temperate, subarctic and arctic
taxa together. Its average indicator value is high
(56.59). Taxa are mostly present along the American
shelf break, in the Labrador Sea and the North Atlantic
Drift, Arctic and Subarctic provinces (Longhurst 1998).
This cluster is divided into 3 subgroups at a level of
0.530. Fig. 9 indicates that the first 2 subgroups (4A
and 4B) are broadly distributed; the first one is centred
over the northern and eastern part of the North
Atlantic Drift Province while the second mainly occurs
along the American shelf break, the Labrador Sea and

the Atlantic Arctic province (Fig. 9). Subgroup 4C is
centred around the Labrador Sea, the northern Cana-
dian part of the continental shelf break and the New-
foundland region. Some taxa are also found in the
Atlantic Subarctic Province (Longhurst 1998). These 2
last subgroups (4.B, 4.C) coexist over the Labrador
basin.

Cluster 5 comprises species with a patchy spatial dis-
tribution over the Atlantic Westerly Winds and Coastal
Biomes (Fig. 6). This cluster has a low indicator value
(14.40). At a level of 0.53, a small association was
detected (Cluster 5.A), which mainly occurs in the
southern North Sea. It has a higher indicator value
(24.24) and includes species such as *Isias clavipes* and
Labidocera wollastoni with significant indicator values
in the shallow region of the North Sea (see Region III.2
in Fig. 5). At the same level, a second small species
cluster (5.B) is made up of the species *Parapontella
brevicornis* and *Haloptilus longicornis*, mostly col-
lected over the European continental shelf. Subgroup
5.C occurs in the Atlantic Westerly Winds and Coastal
Biomes. The species within Clusters 5.B and 5.C are
rare or have restricted distributions.

Clusters 6 to 8 gather taxa having no significant indi-
cator value for the survey area. Taxa in the 6th cluster

are mostly present to the north of the survey although the 7th and 8th cluster is mainly composed of warm-temperate or subtropical oceanic taxa.

Cluster 9 includes mostly subtropical oceanic or pseudo-oceanic taxa such as *Euchaeta marina*, *Centropages violaceus* and *Candacia ethiopica*. Its average indicator value is high (56.39). This cluster has a major centre of distribution in the Gulf Stream extension east of the 4000 m isobath and can spread northwards as far as Flemish Cap. Some species can also reach Worthington's Northwest Corner but are not able to go further to the northeast or to cross the Oceanic Polar Front. Cluster 10 comprises taxa mainly present in the Gulf Stream Extension but its average indicator value is far lower than the previous one.

Most of the remaining 21 taxa were only found on single records (total 33 records) during the period from 1958 to 1997. The majority were found along continental shelf breaks and from the American continental shelf to the Mid-Atlantic Ridge at about 40° N.

Cluster 3.A (5 taxa)

Cluster 3.B (4 taxa)
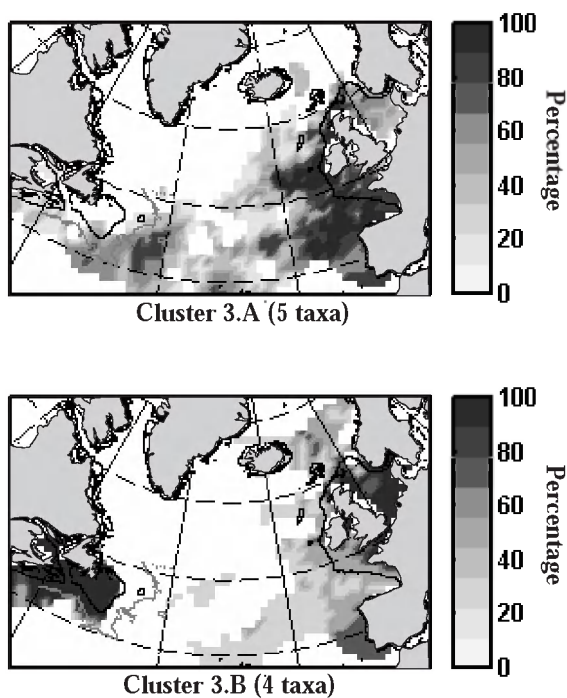
Fig. 8. Mapping of the 2 subgroups belonging to Taxa Cluster 3. The partition of this cluster was fixed at the level 0.53 (see Fig. 6). Data come from the general taxa table (see step 2 in Fig. 2). Abundance data were transformed into presence/absence. Data was coded in 2 states: 0 when the abundance of the taxa was lower than half its mean; 1 when the abundance was higher than half its mean. Then, the percentage of species in 1 square was calculated. This transformation allowed main centre of occurrence of taxa inside a group to be detected

Cluster 4.A (4 taxa)

Cluster 4.B (4 taxa)

Cluster 4.C (3 taxa)
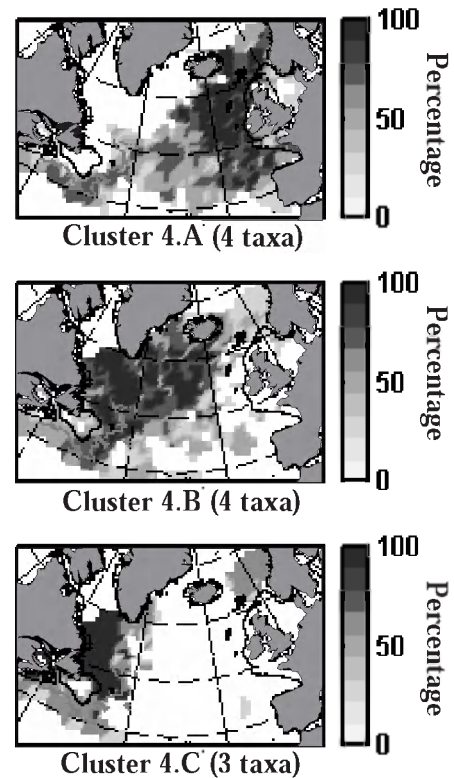
Fig. 9. Mapping of the 3 subgroups belonging to taxa cluster 4. The partition of this cluster was fixed at the level 0.53 of the taxa dendrogram (see Fig. 8). Data come from the general taxa table (see step 2 in Fig. 2). Abundance data were transformed into presence/absence. The same transformation as in Fig. 8 was applied

DISCUSSION

In the pelagic ocean, investigation of factors that maintain diversity is challenging (Angel 1993, Krause & Angel 1994, van der Spoel 1994b). Three factors have limited our understanding of the processes that regulate diversity. The first is a lack of strict physical barriers to the horizontal spread of marine organisms. Thus, the spatial distribution of species overlaps in often large transitional areas (Angel 1998, Boltovskoy 1998) and it is difficult to identify centres of distribution of organisms. This problem is emphasised by the 3-dimensional nature of the pelagic realm. Beaugrand et al. (2001) have shown the importance of considering diel and ontogenic seasonal vertical migration of calanoid copepods in the examination of spatial distributions of diversity. The third feature, probably the most important, is the problem of scales of variability (e.g. Levin 1992, Mann & Lazier 1996, Haury & McGowan 1998). All these features are often interwoven and it was crucial in this study to take them into consideration. This has been done by using a regular

spatial grid for each taxa, based exactly on the same number of CPR samples and taking into consideration both diel and seasonal scales, which represent a very high source of variability (van der Spoel 1994c, Piontkovski et al. 1999). Until now, most studies at an oceanic basin scale have been conducted at a coarse spatial resolution, which has implied large uncertainty in the identification of oceanic boundaries, ecosystems or ecotones (van der Spoel 1994c). The large database used in this study allowed us to examine mesoscale spatial resolution. Furthermore, the indicator value method (Dufrêne & Legendre 1997) has proved to be robust to the phenomenon of expatriation in the pelagic realm. A cluster analysis, which considers all indicator values, enabled biological associations to be detected. The use of a different code to represent species groups allowed the centre of distribution of certain associations to be clarified (see Fig. 8).

Species association: composition, distributional range and boundary

A total of 9 major species associations are proposed (Table 1). Their spatial distribution and boundaries are summarised by Fig. 10. With the exception of the subgroup 5A (southern North Sea), taxa belonging to Groups 5 to 8 did not show spatial aggregation but rather a patchy distribution and, therefore, do not represent species associations. This can be mainly explained by 3 factors. Firstly, most of these species are mesopelagic (e.g. species of the genus *Pseudochirella*, *Haloptilus longicornis*), bathypelagic (e.g. species of the genus *Scottocalanus* in groups 6 and 7) or benthopelagic (e.g. *Diaxis hibernica* in group 6, Boltovskoy 1999) and thus not normally sampled by the subsurface CPR sampling. Secondly, some calanoid species (e.g. *Diaxis pygmoea*) are very small and may have been undersampled. Lastly, subtropical species (e.g. *Candacia bipinnata*) were only occasionally found in the survey area.

Biodiversity region of the northern North Atlantic Ocean and adjacent seas

Based on the centre of distribution of organisms (Fig. 10), the recent partition of the northern North Atlantic Ocean outlined by Longhurst (1998) and Beaugrand et al. (2001) can be refined. The former mainly used ecological factors such as parameters of the Sverdrup model to identify biogeochemical biomes and provinces across the world ocean while the latter was based on changes in the diversity of calanoid copepods at seasonal and diel scales.

According to van der Spoel (1994a), an ecosystem or an ecotone is composed of: (1) a stable biotope component (geographically stable) in which a primary related community lives; and (2) a substrate biotope component (depending on the water mass) characterised by a secondary related community (mixed primary community, Beklemishev 1961). A pelagic ecosystem is mainly characterised by a primary related community linked to a stable biotope component although an ecotone is more distinguished by a secondary related community depending on water masses. Some authors also argue that an ecotone can also be characterised by its own biological composition (Frontier & Pichot-Viale 1993, Ramade 1994). These terms will be used in the subdivision of the studied area (Fig. 10, Table 2). As information contained in Fig. 10 and Table 2 is self-explanatory, this will not be commented on here. This closely corresponds to the recent partition proposed and fully discussed by Beaugrand et al. (2001). Boundaries are voluntarily not indicated as they can change seasonally, especially west of the European continental shelf. The position of the regions indicated by numbers in Fig. 10 should be understood as reflecting the position of the nodal points-of-stress (centre of ecosystems) and nodal points-of-flux (centre of ecotones) (van der Spoel 1994a).

Towards a better understanding of factors that contribute to the regulation of pelagic diversity

The effects of the polar tropical difference in diversity (Ruddiman 1969, Pierrot-Bults 1997) have been clearly detected even if our area is comprised between 40 and 60° N. The subtropical association (24 species if Groups 9 and 10 are gathered together) is more diverse than the warm-temperate (16 species), the cold-temperate (4 species), the subpolar (4 species) and polar associations (3 species) (Figs. 5 & 6). Numerous hypotheses have been proposed to explain this feature, e.g. the species-energy hypothesis (Currie 1991) Rapoport's rule (Stevens 1989) the species-area's hypothesis (Rosenzweig 1995) and the mid-domain effect (Colwell & Lees 2000). This has been set up at an evolutionary scale and it is not the purpose of this study to attempt an explanation of this feature that probably explains a large part of the difference in diversity detected between Ecosystems II and IX (Fig. 10). Instead, emphasis is given to ecological factors or mechanisms that are responsible for the pronounced local spatial variation in diversity as well as the East-West asymmetry recently detected in this region (Beaugrand et al. 2000a). In the surveyed area, the main factor that may regulate or maintain pelagic diversity of calanoids could be related to the rate and

Table 1. Biological composition of species associations. Numbers come from the identification of species groups at a cut-off level of 1.152 in the species dendrogram and subgroups at a cut-off level of 0.530 (see Fig. 6). The different types of distributions are neritic, oceanic and pseudo-oceanic (above the shelf edge). Seasonal charts were produced (not shown) to examine seasonal changes in the composition and aggregation of associations. This information is summarised in the 3rd column. In the 4th column, number in brackets denotes groups (or subgroups) that can be associated with the core group. Only the biological composition of the core group is indicated. E: epipelagic species. M: mesopelagic species. B: bathypelagic (from Rose 1933, Bradford-Grieve 1994, 1999, Boltovskoy 1999). Species marked with an asterisk also have pronounced warm-temperate affinity. *Centropages violaceus* was originally found to belong to Group 10 but was re-arranged in Association 1 after examination of individual charts. The *Para-pseudocalanus* group is mainly present in neritic regions but is also found in oceanic areas

| Associations	Distribution	Seasonal maximum of aggregation of taxa	Groups or subgroups	Biological composition
1: Subtropical and warm temperate association	Oceanic Pseudo-oceanic	Autumn	9	*Undeuchaeta major* * (MB), *Acartia danae* (E), *Paracandacia bispinosa* (E), *Euchaeta media* (E), *Temora stylifera* (E), *Scolecithrix danae* (E), *Euchaeta marina* (E), *Candacia ethiopica* (EM), *Eucalanus attenuatus* * (E), *Lucicutia* spp.* (MB), *Eucalanus elongatus* * (E), *Candacia pachydactyla* (EM), *Rhincalanus cornutus* (E), *Euchaeta pubera* (E), *Centropages violaceus* (E)
2: Warm temperate association	Oceanic	From spring to autumn south of 50° N In autumn, north of 50° N	1 (7, 5C)	*Euchaeta acuta* (E), *Undeuchaeta plumosa* (E), *Euchirella rostrata* (E), *Neocalanus gracilis* (E), *Clausocalanus* spp. (E), *Nannocalanus minor* (E), *Pleuromamma borealis* (EM), *P. gracilis* (EM), *P. abdominalis* (EM), *P. xiphias* (EM), *P. piseki* (EM), *Calocalanus* spp. (E), *Mesocalanus tenuicornis* (E), *Heterorhabdus papilliger* (M), *Centropages bradyi* (E), *Mecynocera clausi* (E)
3: Bay of Biscay and southern European shelf edge association	Pseudo-oceanic	From spring to autumn	2	*Euchaeta gracilis* (M), *Euchaeta hebes* (EM), *Ctenocalanus vanus* (E), *Calanoides carinatus* (EM)
4: European shelf edge association	Neritic Oceanic Pseudo-oceanic	From spring (south) to autumn (north)	3A	*Rhincalanus nasutus* (E), *Eucalanus crassus* (E), *Centropages typicus* (E), *Candacia armata* (E), *Calanus helgolandicus* (EM)
5: Shelf sea association	Neritic (oceanic)	From spring (south) to autumn (north)	3B, (5B)	*Centropages hamatus* (E), *Temora longicornis* (E), *Pseudocalanus* adult (E), *Para-Pseudocalanus* spp. (E)
6: Coastal association	Neritic	Mid-summer and early autumn	5A	*Isias clavipes* (E), *Anomalocera patersoni* (E), *Labidocera wollastoni* (E)
7: Temperate association	Transitional water Oceanic (neritic)	From spring (south) to Autumn (north) From spring to autumn between 50 and 60° N	4A	*Aetideus armatus* (EM), *Pleuromamma robusta* (EM), *Acartia* spp. (E), *Metridia lucens* (EM)
8: Subarctic association	Oceanic (neritic)	South of Newfoundland: Jan to Jun North to 52° N: May to Oct	4B (6)	*Heterorhabdus norvegicus* (M), *Scolecithricella* spp. (MB), *Euchaeta norvegica* (EM), *Calanus finmarchicus* (ME)
9: Arctic association	Oceanic (neritic)	May to Jun	4C (6)	*Calanus hyperboreus* (M), *Metridia longa* (M), *Calanus glacialis* (EM)
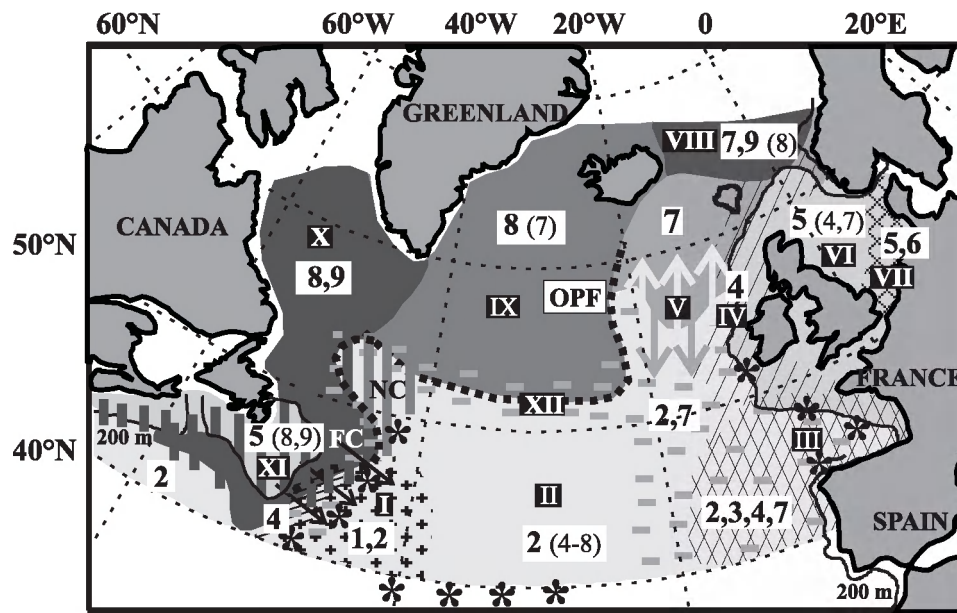
Fig. 10. Scheme of the geographical position of centres of distribution of the associations, ecosystems and ecotones. A number corresponding to those displayed in Table 1 identifies each association. In some areas such as in the Bay of Biscay, several associations overlap. The black cross symbol indicates the position of Species Association 9 (Gulf Stream Extension), which is superimposed on species association 2 (southern oceanic association). Single hatched line locates the centre of distribution of Species Association 4 (along shelf edges) and double hatched line locates Species Association 3 (Bay of Biscay). Dotted double hatched lines indicate the centre of distribution of Species Association 6 (southern North Sea), which also corresponds to a part of the geographical position of species association 5 (neritic association). Grey horizontal rectangles indicate the overlapping of species association 7 with other associations. Grey vertical bars denote the overlapping of Species Associations 2, 8 and 9. The asterisk indicates the location where very rare species were found during the 40 years CPR sampling. Grey arrows (west of Great Britain) denote the seasonal change in the northern position of Species Association 2. Black arrows (above the Canadian shelf) indicate that extrusion of water related to the high hydrodynamic activity of this region occurs and leads to expatriation of species belonging to Species Associations 4, 5, 8 and 9 towards the Gulf Stream Extension region. The thick black dotted line indicates the position of the Oceanic Polar Front. Numbers in brackets indicate the possibility of finding species belonging to adjacent species association. OPF: Oceanic Polar Front; FC: Flemish Cap; NC: Worthington's Northern Corner. Species Associations 4 and 7 seasonally progress northwards with a high aggregation of species in the south in spring and in the north in autumn. Roman numbers denote the different centres of ecosystems or ecotones identified and commented in the 'Discussion' and Table 2

the frequency of energy supply. This energy is supplied by a stable biotope (e.g. solar radiation) and substrate biotope components (warm current and undercurrents). Temperature, hydrodynamics, stratification, and seasonal variability of the environment are crucial variables that control pelagic diversity. These factors are often interwoven, also act at different scales and their contribution geographically varies (Fig. 10, Table 2). Other more secondary factors are also indicated in Table 2.

The North Atlantic Current, the Intermediate Shelf Edge and Mediterranean Intermediate Currents, which all transport heat towards Europe (e.g. Bigg 2000, Hansen & Osterhus 2000) are important in maintaining pelagic diversity. Ruddiman (1969) in the North Atlantic Ocean also detected an influence of currents on diversity. He even stressed that these currents (Subtropical North Atlantic Gyre in his case) could eliminate the effect of the polar tropical gradient in diver-

sity. Here, warm currents are enable many species of the warm-temperate association to be present east of the mid-Atlantic ridge and north to 52° N (Figs. 7 & 10) which could explain the west-east asymmetry clearly found by Beaugrand et al. (2000a). This factor might also play a role in the high diversity detected in the Celtic Sea, the western part of the English Channel and the southern part of the North Sea (Beaugrand et al. 2000a).

Superimposed on the effects of heat transported by the Gulf Stream extension, hydrodynamics also acts as a regulator of diversity east of the Canadian Shelf Edge. Hydrodynamics is important in this area (Dengg et al. 1996, Stammer & Böning 1996, Ducet et al. 2000). Restriction of the highly diverse subtropical association (Table 1) south of Flemish Cap (Fig. 10) tends to confirm mechanisms advanced by Beaugrand et al. (2001). Indeed, they attributed this feature to the presence of high pressure cells that may lead to the opening of

Table 2. Main characteristics of regions. Boundaries of ecosystems and ecotones are not specified as they change at a seasonal scale, especially west to the European continental shelf. Thus, only the position of nodal points-of-stress (centre of ecosystems) and nodal points-of-flux (centre of ecotones) (see van der Spoel 1994a) are indicated and correspond to location of numbers in Fig. 10. Type 1: primary related community; Type 2: secondary related community; BC: biotope component (see text for explanations)

Regions (see Fig. 10)	Main associations (see Table 1)	Other important associations	Ecological characteristics	Community characteristics	Biotope component (BC)	Primary factors	Secondary factors
I. The Gulf Stream extension	1	2, 4, 5, 7, 8, 9	Ecotone (hydrodynamics)	Type 2	Substrate BC (Stable BC)	Gulf stream extension current High hydrodynamics	Life history of organisms
II. The centre of North Atlantic Drift Province (Longhurst 1998)	2	–	Ecosystem	Type 1	Stable BC	Large-scale polar-tropical difference in diversity Temperature and stratification	Weaker seasonal variations
III. The Bay of Biscay and the southern European shelf edge	3	2, 4, 5, 7	Ecotone (topography and hydrodynamics)	Types 1 and 2	Substrate and stable BC	Intermediate Mediterranean Current and Shelf Edge Intermediate Current topography	Weaker seasonal variations
IV. The northern European shelf edge	4	5, 7 (2 in the south)	Ecotone (topography)	Types 1 and 2	Substrate and stable BC	Shelf Edge Current High seasonal variability Topography	–
V. The east to the OPF and above 50° N	7	2: south 4: shelf edge 8–9: north	Ecotone (high seasonal variability)	Types 1 and 2	Substrate and stable BC	North Atlantic Current Shelf Edge Current High seasonal variability	–
VI. The European continental shelf	5	Bounded by 3, 4, 6, 7	Ecosystem (bounded south, north and west by ecotones)	Types 1 and 2	Stable BC Substrate BC	Northern North Sea: influenced by boreal water and warmer water coming from the shelf edge Southern North Sea and English Channel: warm temperate water	Freshwater and nutrient inputs
VII. The southern North Sea	6	5	Ecosystem	Type 1	Stable BC	Warm temperate water	Shallow region, nutrient and freshwater inputs
VIII. North to Faeroe Isle and east of Iceland	8, 9	7	Ecotone (hydrodynamics)	Type 2	Substrate BC	High seasonal variability	–
IX. The subarctic region	8	7: eastern and southern part	Ecosystem	Type 1	Stable BC	Large-scale polar-tropical difference in diversity cold water	High seasonal variability
X. The arctic region	8, 9	–	Ecotone (hydrodynamics)	Type 2	Substrate BC	Large-scale polar-tropical difference in diversity cold water	–
XI. The Newfoundland continental shelf	5	8, 9	Ecotone (hydrodynamics)	Types 1 and 2	Substrate and stable BC	Influence of the Labrador Current (cold water)	High seasonal variability
XII. The Oceanic Polar Front	7	2, 8	Ecotone (hydrodynamics)	Type 2	Substrate BC	Strength or path of the North Atlantic Current	–

paths for the North Atlantic Current near Flemish Cap and imply significant return flow of water towards the Azores current (Käse & Krauss 1996). This mechanism, probably in conjunction with life history of organisms, is believed to reduce dispersal northwards (Beaugrand et al. 2001). However, the presence of cold water species *Candacia norvegica*, the genus *Microcalanus* (mostly *M. pygmaeus* and *M. pusillus*) and species of arctic and subarctic associations (associations 8 to 9) indicate that extrusion of Newfoundland and Labrador Sea water toward the Gulf Stream extension occurs, due to the high eddy activity in this region (Krauss 1986), also contributes to increase diversity (Fig. 10). Organisms such as species belonging to pseudo-oceanic and temperate associations (Table 1) can also be found augmenting the complexity of the area.

The Oceanic Polar Front (Dietrich 1964) also illustrates well the importance of hydrodynamics for the spatial regulation of diversity. However, its role differs in function of the considered associations, a feature that has been also observed by some authors (e.g. Brandt & Wadley 1981, Sournia et al. 1990, Sournia 1994). It acts as a sharp boundary for subtropical, shelf edge and warm-temperate species associations (Associations 2, 4 and 9; see Figs. 7, 8 & 9) limiting dispersal northwards. In contrast, colder species belonging to subarctic and cold-temperate associations are not so restricted to the north of this front and can often be detected in the south (see Fig. 9). This front also acts as a concentration site for some species such as *Metridia lucens* belonging to association 7 which was clearly detected along this front (Fig. 9).

Superimposed on the effect of temperature, stratification may also be important in the regulation of diversity. This has been recently recognised as an important factor that may explain the global polar tropical difference in diversity of foraminifers (Rutherford et al. 1999). Following the relationship between the number of vegetation levels and species richness of birds in a forest (MacArthur & MacArthur 1961), Rutherford et al. (1999) suggested that thermal structure, by its effect on vertical niche availability, could explain that tropics are richer in species than poles. Temperature and its vertical structure may account for the contrast between Ecosystems II (higher stratification) and IX (lesser stratification). However, it is likely that this factor might also play a role at a regional scale (Table 2).

Warm currents allow Species Association 2 to spread to the North West of the British Isles. However, the environment, which becomes very variable on a seasonal basis (Angel 1997), limits dispersal of this association northwards. This was clearly detected in the recent study of diversity of calanoids by Beaugrand et al. (2001, and see Figs. 4 & 6). Indeed, the centre of Ecotone V represents the transitional area between the south oceanic part of the survey area characterised by a higher diel and lower seasonal variations in diversity, and the northern oceanic part where seasonal variation becomes stronger and diel variation weaker.

CONCLUSION

For the first time at an oceanic basin scale and at a spatial resolution approaching the mesoscale, species associations of calanoid copepods have been identified. This result has been based on 40 yr of monthly CPR sampling, considering also diel and seasonal variations. The clear spatial centre of distributions of all these associations have allowed biogeochemical and biological partitions outlined by Longhurst (1998) and Beaugrand et al. (2001) to be refined. Examination of the zoocoenoses of the North Atlantic Drift Province has shown that this province can not be considered as an homogeneous system but rather as a central ecosystem south of the Oceanic Polar Front over the mid-Atlantic ridge, bounded by 5 ecotones. Moreover, species associations have allowed a better understanding of species that contribute to the diversity in this area and an improvement of factors and processes that regulate pelagic biodiversity. Factors linked to the rate and the frequency to which energy is supplied appear to be important in the ecological regulation of pelagic diversity in the investigated region. These factors depend on both stable and substrate biotope components. The pronounced local spatial variability as well as the east-west asymmetry found by Beaugrand et al. (2000a) are highly affected by the latter while the polar tropical difference in diversity is more influenced by the former.

Beaugrand et al. (2001) and this present study have clearly detected the influence of the warm currents on diversity and thus functional characteristics of ecotones west of Europe and over the Gulf Stream extension. Relationships between species associations and water masses or currents are strong. These associations, therefore, represent an important tool as an environmental indicator to monitor marine ecosystems and to evaluate the impact of climate change and other increasing human-induced influences. For example, species of the warm-temperate association (association 2) could be used as a proxy to evaluate the strength of the North Atlantic Current east of the Oceanic Polar Front, which is of high importance in the rate of heat transfer to Europe and its climate (e.g. Lehman & Keigwin 1992, Bigg 2000, Ganopolski & Rahmstorf 2001, Paillard 2001). A long-term decrease in the diversity of this association west of Europe could mean a change in the trajectory or strength of the North Atlantic Current. The oceanic warm-temperate association could also be

used to test oceanic advection over the Celtic Sea to the English Channel (Russell 1939, 1973). These topics are currently being investigated.

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