INTRODUCTION

Biogeography is useful for identifying patterns of biological diversity and mechanisms (e.g. vicariance vs. founder-dispersal), determining their occurrence on many scales, from local to continental or even larger (e.g. Croizat 1958, MacArthur & Wilson 1967, Heads 2005). By integrating knowledge from the disciplines of ecology and taxonomy, biogeography is equipped to play a central role in exploring the relationship between biodiversity and ecosystem functioning through identifying large-scale background patterns.
against which some of the hypotheses formulated in
the context of the proposed relationships (e.g. Solan et al. 2004, Raffaelli 2006) can be tested. Large-scale
approaches are particularly useful for European Union
policies, which usually have to be implemented on
scales larger than the ecosystem. Examples include the
Common Fisheries Policy (Berg 1999) and the Com-
mon Environmental Policy (McCormick 2001).

Large-scale biodiversity patterns are the central
issue in Theme 1 of the European Network of Excel-
lence on marine biodiversity, Marine Biodiversity and
Ecosystem Functioning (MarBEF) (www.marbef.org).
A suite of (bio)geographic systems dividing the seas of
the globe into sectors, regions and provinces has been
proposed by various scientists and by several regulat-
ory organizations. These systems can be divided into 2
broad categories if one takes into account the basis on
which they have been proposed.

(1) Systems proposed largely on the basis of empiri-
cal relationships between the distribution of taxa and
environmental (geological, hydrographical, physical)
variables. Into this category fall systems such as those
proposed by Ekman (1967) and by Fredj (1974). Ekman
(1967) summarized the knowledge on the distribution
and reproductive physiology of individual species and
tried to integrate this information with the hydro-
graphy of the regions. The study used information on
both planktonic and benthic species, such as cnidari-
ans, crustaceans, molluscs, polychaetes, echinoderms,
chordates, nemertean, rotifers and bryozoans, and
considered that temperature was the main factor in
influencing multi-species distributions, in association
with salinity and depth. Nevertheless, he did not at-
tempt to set the limits of the provinces and sectors he
proposed. Fredj (1974) focused on the influence of
depth on benthic communities, rather than individual
species, and set geographic limits to the provinces
defined by Ekman (1967). The large marine eco-
systems (LME) concept of Sherman (1992), which
divides the oceans into relatively large regions (ca.
200 000 km²) characterized by bathymetry, hydrogra-
phy, productivity, and trophic groups, is another exam-
ple of the systems included in this category. In addi-
tion, Longhurst (1998) suggested a division of the seas
based on the oceanographic characteristics of large
water masses and their associated plankton com-
munities. Finally, Por (1989) proposed a division of the
Mediterranean and Black Sea region into sectors
based on relationships between geological formations,
hydrographic and physical/chemical variables and
faunal distributions.

(2) Systems that, at least implicitly, acknowledge a
political as well as a scientific dimension to the setting
of geographical boundaries aimed at promoting the con-
servation and protection of the marine environment, for the
safeguarding of human health and for the sustainable
use of resources. Into this category fall the systems sug-
gested by the Oslo-Paris Commission (OSPAR 2003) for
the European seas and by the Helsinki Commission
(www.helcom.fi, HELCOM 2007), for the Baltic Sea. On
a larger scale, the International Council for the Explo-
ration of the Seas (ICES) (www.ices.dk/abouts/icesareas.
asp, Rozwadowski 2002) has adopted a grid of rectangles
for the reporting of the catch data of commercially im-
portant species. Finally, the International Hydrographic
Organization (IHO 1953), actively engaging all inter-
ested states to improve maritime safety and efficiency
in support of the protection and sustainable use of
the marine environment, divides the world seas into
sectors according to their physical characteristics.

Until recently, most scientific efforts to explain pat-
terns of multi-species distributions were, with very few
exceptions — such as Ekman (1967), Fredj (1974), Por
(1989), and Longhurst (1998) — directed towards the
experts’ favoured taxon. For example, the provinces of
Briggs (1995) were primarily defined using fish species
distributions, those of Pierrot-Bults & Nair (1991) using
chaetognaths, whereas Van Soest & Hajdu (1997) used
sponges, Glasby (2005) used polychaetes, and Deprez
(2006) used hyperbenthic mysids. However, even in
the studies using multi-taxon distributions, rigorous
hypothesis testing to validate findings has rarely been
attempted.

The objective of the present study was to test the
validity of the proposed systems for the division of the
European seas based on soft-bottom macrobenthic
community data, an important component of the ben-
thic ecosystem, against pre-determined criteria. The
patterns so derived can serve as background informa-
tion for further testing of hypotheses concerning links
between biodiversity and ecosystem functioning.

DATA AND METHODS

Biogeographic systems. The system of Longhurst
(1998) was tested both as originally defined and in a
slightly modified version by excluding the Baltic and
Black Seas from their corresponding provinces of the
Northeast Atlantic continental shelves and the Medi-
terranean Sea, respectively, and treating them as sep-
ate regional seas. The same modification was also
followed in the case of the systems used by OSPAR,
while in the case of the ICES rectangles, the Medi-
terranean and the Black Seas were taken as separate
provinces, since ICES does not include these 2 regional
seas. This modification to the biogeographic provinces
was made in order to emphasize the distinctive nature
of the above sea areas when characterized, for exam-
ple, according to salinity or temperature gradients.
Consequently, the present study deals with 6 systems that have profoundly influenced the (bio)geographic division of the European seas: OSPAR (Fig. 1), Fredj (1974) (Fig. 2), IHO (Fig. 3), LME (Fig. 4), Longhurst (1998) (Fig. 5) and ICES (Fig. 6). Additionally, more detailed systems were employed for the Baltic, Mediterranean, and Black Seas: those proposed by HELCOM (Fig. 7) and the ICES rectangles for the Baltic and those proposed by Por (1989) and IHO (Fig. 8) for the Mediterranean and Black Seas.

**Data.** Two types of data were used in the analyses: (1) species distribution data derived from the entire MacroBen database (Vanden Berghe et al. 2009, this Theme Section); and (2) geographic variables, such as total sea surface area (per province/region/sector), shelf surface area, number of islands, island surface area, island distance from the nearest coastline, and shortest inter-island distance. These variables were selected because of their correlation with biogeographic patterns in the Mediterranean and the Black Sea region, as documented in previous studies (Arvanitidis et al. 2002).

The above geographic variables were calculated using standard Geographical Information Systems (GIS) procedures. Using ArcGIS software (ESRI 1994), all...
(bio)geographic systems were digitized and geo-referenced according to world shoreline (scale 1:250,000). Following this, distance and area ArcGIS macro-routines were used upon selected geographic features for the calculation of different geographic variables.

The phylogenetic/taxonomic classification of the taxa taken into account for the present study follows that of the European Register of Marine Species (ERMS 2.0) (www.marbef.org/data/erms.php). However, polychaete taxonomy follows that recently suggested by Rouse & Pleijel (2001).

Binary matrices were initially constructed in which species presence/absence in the sectors, defined by each of the biogeographic systems considered, was marked as 1 or 0, respectively. Seven major macrofaunal groups were examined during this study: (1) all macrobenthos groups, (2) combined groups including only those taxa for which taxonomic expertise is equally distributed across Europe (which includes all of the following groups), (3) crustaceans, (4) molluscs, (5) polychaetes, (6) echinoderms, (7) sipunculans. Consequently, the 7-groups-by-6-systems made up a total of 42 matrices for analyses. Taking into account the 4 detailed systems considered for the Baltic, the Mediterranean and Black Seas, an additional 28 matrices were included. In addition, depending on the hypotheses tested, scientific criteria and methods, additional matrices were constructed (see below). The same types of matrices were constructed for the envi-
vironmental variables, but the difference here was that the values entered were average, maximum, minimum and the range of the variables instead of presence/absence.

Criteria. A large number of biodiversity patterns may result from a study starting with 7-groups-by-6-systems, which could hamper the selection of the most plausible pattern. However, selection can be aided by using simple, hierarchically applied criteria such as:

1) Proximity: biodiversity patterns in adjacent provinces (regions/sectors) should appear close to each other along gradients, unless there appears an obvious reason for this not to be the case. Following this criterion, for instance, a region in the Arctic is not expected to be placed near the Black Sea region on a biodiversity gradient.

2) Randomness: since the biodiversity patterns in this experiment are derived from species inventories at the scale of sector or larger, it is anticipated that the inventories of the sectors, as defined in a biogeographic system, would be random samples of either the regional inventory in which the sectors are included or of the total European inventory, respectively. This is because, on these large spatial scales, conservative structural patterns, determined by regional processes such as evolutionary mechanisms (Warwick 1989, Somerfield et al. 2009, this Theme Section), are assumed to prevail.

3) Differentiation: provided that the first 2 criteria are fulfilled, when biodiversity patterns derived from the distribution of each taxon in relation to the (bio)geographic systems considered are compared, they should be different from one another. The same result should occur when patterns derived from all taxa within the same biogeographic system are compared. Consequently, this criterion should provide a measure of uniqueness in the taxon/taxa and system(s) chosen from the application of the former 2 criteria.

Hierarchical application of the above criteria should offer a rigorous selection procedure with respect to the observed patterns.

Analyses. The non-parametric ANOVA or Kruskal-Wallis statistic (Kruskal & Wallis 1952) was applied to test for any significant difference in: (1) the distribution of number of taxa across the higher taxonomic categories for each of the 7 groups considered, and (2) the distribution of taxa across the groups considered, for each of the 6 taxonomic categories (species to phylum).

The following mathematical analyses provide the means for the selection of the patterns, consistent with the criteria above. Their presentation closely follows these criteria:

1) To derive resemblance patterns between the sectors or regions, as defined in each biogeographic system, the Jaccard coefficient was used (Legendre & Legendre 1998). The resulting resemblance matrices were used for non-metric multidimensional scaling (NMDS), as suggested by Field et al. (1982) and Clarke & Warwick (1994). The goodness-of-fit of the resulting 2-dimensional plots was measured using Kruskal’s stress formula I (Kruskal & Wish 1978, Clarke & Green 1988).

2) We used 2 recently developed indices to compare the biodiversity of the various sectors and regions of the (bio)geographic systems proposed for the European seas: average taxonomic distinctness (AvTD, Δ+) as defined by Clarke & Warwick (1998),

\[ Δ^+ = \frac{[\sum_{i<j} o_{ij}]}{[s(s-1)/2]} \] (1)

where \( o_{ij} \) is the phylogenetic/taxonomic path length between species \( i \) and \( j \), and \( s \) is the number of species, and variation in taxonomic distinctness (VarTD, \( \Lambda^+ \)), as defined by Clarke & Warwick (2001)

\[ \Lambda^+ = \frac{[\sum_{i<j} o_{ij}^2]}{[s(s-1)/2]} - (\Delta^+)^2 \] (2)

By constructing a simulation distribution (funnel) from random subsets of species from the regional (European) inventories, both AvTD and VarTD statistics, calculated from the species lists of the areas considered, can be tested for departure from expectation (Clarke & Warwick 2001, Warwick & Clarke 2001). Values of AvTD and VarTD located within the 95% probability funnel indicate that species diversity in the corresponding areas falls within the expected range and thus provides a way of testing for the second criterion of randomness. These indices allow for both sample-size/sample-effort free diversity comparisons and the use of the inventories in ‘biological effects’ monitoring studies in the future.

3) Multivariate patterns derived from all taxonomic levels (from species to phylum) and for each group across the biogeographic systems or patterns derived from the various taxa in each of the systems considered were compared using the methods described by Somerfield & Clarke (1995). Following their mathematical approach, a rank correlation, using the harmonic rank correlation coefficient (Clarke & Ainsworth 1993), was computed between every pair of the resemblance matrices produced by each taxonomic level in each of the taxa across all systems or by all taxa in each of the systems. In all cases, a final triangular resemblance matrix was constructed, containing the resulting values of the harmonic rank correlation coefficient. These correlation values were first ranked and subsequently subjected to ‘second-stage’ MDS (Olsgard et al. 1997). Accordingly, to display interrelationships between biogeographic systems based on a single taxon or between groups within each of the systems (that is, to show how similar they are with respect to how patterns change across taxonomic levels or across taxa), an
Fig. 9. Schematic representation of the third-stage non-metric multidimensional scaling (NMDS) approach (modified from Arvanitidis et al. 2009)
additional second-stage resemblance matrix (here termed a third-stage resemblance matrix) (Arvanitidis et al. 2009) was constructed using rank correlations between corresponding elements in the set of second-stage matrices (Fig. 9). This third-stage matrix was ordinated using a third-stage MDS in which systems showing similar changes in pattern as information on species is aggregated to higher taxonomic levels will group together. Similarly, groups within the same biogeographic system showing like patterns, will also group together.

Finally, the correlations between multivariate patterns derived from the resemblance matrices of the taxa and systems that met the above criteria, and the various combinations of the geographical variables, were examined using the BIO-ENV analysis (Clarke & Ainsworth 1993). The PRIMER package (Clarke & Gorley 2001) was used for these analyses.

RESULTS

European benthic fauna

Overall, the European macrobenthic fauna, at least as derived from the MacroBen database, includes 5012 species belonging to 2196 genera, 768 families, 149 orders, 42 classes and 18 phyla. Crustaceans were the most numerous taxon, accounting for 28.2% of the total number of macrofaunal species, followed by molluscs (25.6%), polychaetes (19.4%), echinoderms (6.0%) and sipunculans (0.8%). Numbers of taxa in each of the major groups used in this study are provided in Table 1. In the above numbers, colonial species and non-macrobenthic species (e.g. demersal fish) are not included.

The distribution of taxa across taxonomic categories for each of the groups studied (benthos to sipunculans) did not appear to be different. The Kruskal-Wallis test gave a value of 7.92 for the statistic $H_{5,36}$ ($p = 0.16$). This was also the case when distributions of taxa across groups for each of the categories of species, genus and family ($H_{5,18} = 4.01; p = 0.13$) and for the categories of order and class ($H_{5,12} = 2.6; p = 0.11$) were tested.

Table 1. Distribution of taxa for each macrobenthic group

<table>
<thead>
<tr>
<th>All macrobenthos</th>
<th>Species</th>
<th>Genera</th>
<th>Families</th>
<th>Orders</th>
<th>Classes</th>
<th>Phyla</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustacea</td>
<td>1413</td>
<td>523</td>
<td>174</td>
<td>12</td>
<td>42</td>
<td>1</td>
</tr>
<tr>
<td>Mollusca</td>
<td>1285</td>
<td>579</td>
<td>223</td>
<td>34</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>971</td>
<td>407</td>
<td>57</td>
<td>10</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>300</td>
<td>171</td>
<td>72</td>
<td>32</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Sipuncula</td>
<td>41</td>
<td>9</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Fig. 10. Non-metric multidimensional scaling (NMDS) ordination plot resulting from the resemblance matrix of the provinces defined by Longhurst (1998), based on the Jaccard coefficient calculated from the soft-bottom macrobenthic inventories (the plot from polychaete inventories, not shown, is identical). Abbreviations as in Fig. 5

Multivariate pattern

The MDS plot in Fig. 10 shows a gradient of the European seas as derived by species inventories of the provinces defined by Longhurst (1998). In this gradient, provinces are primarily arranged along the vertical axis, which corresponds to a geographic North–South gradient. Two additional groups of provinces are arranged along the horizontal axis of the plot: the first includes the Baltic Sea (BALT), and the second includes the Black Sea (BLAS). Both have salinity and temperature regimes that differ from their neighbouring regional seas. When the inventories of the BALT and BLAS were included in their respective neighbouring provinces, NECS and MEDI, as originally proposed by Longhurst (1998), there was no change in this gradient (not shown). Polychaete inventories from the provinces suggested by Longhurst (1998) resulted in an identical MDS plot (not shown). Sectors within the MEDI and BLAS regions, as defined both by IHO and Por (1989), were arranged on an East–West gradient when compared on the basis of their polychaete inventories. Benthic species inventories produced similar East–West trends in the BALT sectors, as defined by either HELCOM or ICES (not shown).

Benthic macrofaunal diversity

The 95% funnels for the simulated distribution of average and variation in taxonomic distinctness ($A^*, A^+$) for random subsets of fixed numbers of ben-
thic species from the European species list, as derived by the MacroBen database and the system suggested by Longhurst (1998), are displayed in Fig. 11A,B. Superimposed on these funnels are the $\Lambda^*$ and $\Delta^*$ values as calculated from the species lists of the 8 provinces and regional seas. All provinces except NADR show lower than expected $\Delta^*$ values and $\Lambda^*$ values well beyond the upper limit of the simulated distribution.

The corresponding funnels for the polychaete species lists are shown in Fig. 11C,D. Here, all provinces and regional Seas show $\Delta^*$ values located within the 95% limits, whereas in the funnels showing the variation in taxonomic distinctness, only the ARCT and SARC provinces show higher than expected $\Lambda^*$ values.

Provinces defined by OSPAR were random samples of the European inventory as far as polychaetes are concerned, since all provinces were located inside the simulated funnels produced by both the average and variation in taxonomic distinctness simulated values. Similar results using polychaetes were obtained for the systems of Fredj (1974), ICES rectangles and IHO, with the exception of a few rectangles and regions with higher than expected $\Lambda^*$ values in the funnels produced for the last 2 systems. For the Fredj (1974) system, mollusc inventories produced funnels in which only the North Atlantic province (NECS) showed higher than expected $\Delta^*$ values and the MEDI region showed $\Delta^*$ values below the limit of the funnel. The latter was unexpected for a regional sea with such high species diversity. In contrast, only the Arctic and the North Atlantic provinces were located inside the funnels simulated for the variation in taxonomic distinctness by the mollusc inventories, whereas the remaining provinces were located beyond the upper limit in the Fredj (1974) system. For the HELCOM system, only the category ‘all macrobenthos’ gave values within the expected distribution in the case of average taxonomic distinctness, while the Gulf of Finland had a higher

![Fig. 11. 95% probability funnel for taxonomic distinctness ($\Delta^*$, $\Lambda^*$) for (A, B) macrobenthos and (C, D) polychaetes, as calculated for Longhurst (1998) provinces. Expected average indicated by the straight line in the middle of the funnel. Abbreviations as in Fig. 5](image-url)
than expected value in the funnel simulated by the variation in taxonomic distinctness values. Again, the only taxon that produced diversity values as high or higher than expected in the MEDI and BLAS regions, according to the system of Por (1989), were the polychaetes. In this case, 2 of the sectors (Central Basin and Levantine Sea) were located above the upper limit of the funnel simulated for the average taxonomic distinctness. Funnels other than for ‘all macrobenthos’ and polychaetes for the Longhurst (1998) system are not shown for brevity.

Overall, only polychaete inventories met the second criterion in the provinces defined by Longhurst (1998), OSPAR, Fredj (1974), ICES, and IHO biogeographic systems; that is, according to the simulated funnels, they can be considered as random samples of the European polychaete inventory.

**System–taxon interrelationships**

Since the application of the second criterion (randomness) indicated polychaetes to be the only successful taxon, it was necessary to use this taxon to determine conformity with the third criterion. Accordingly, the patterns derived from every taxonomic level (from species to class in this case) in every system were compared by means of the second-stage MDS and their interrelation between every pair of biogeographic systems were compared by means of the third-stage MDS. The final third-stage MDS plot demonstrates that the 4 systems are well separated on the basis of their taxonomic structure and, specifically, how patterns derived from each taxonomic level change as the information is aggregated from species to class in each of the systems (the differentiation criterion). Accordingly, the systems found to be well separated are those proposed by Fredj (1974), LME, ICES and Longhurst (1998) (Fig. 12). In contrast, the OSPAR system could not be separated from the IHO system.

The final step, to check for the third criterion, was to look for interrelations between patterns derived from different taxa in the system by Longhurst (1998). All taxa were separated from the group composed of the total macrobenthos and the combined macrobenthos (Fig. 13). Again, it should be kept in mind that these taxa are now compared on the basis of changes in the patterns derived from the multiple taxonomic levels, as the information is aggregated from species to phylum, and not solely from the species composition matrices.

A comparison of the results of the taxa and systems tested against the 3 criteria is provided in Table 2. All criteria were met only for patterns derived from polychaete inventories and only for the biogeographic system proposed by Longhurst (1998).

**Associated geographic variables**

Table 3 summarizes the results from the BIO-ENV analysis. Only the polychaete multivariate pattern for the Longhurst (1998) system was used since this was the only taxon/system combination that met all 3 criteria. The best correlated geographic variables were island distance from the nearest coastline and number of islands; Spearman’s weighted correlation coefficient between polychaetae pattern and pattern deriving from these variables was estimated at 0.62. The second best correlated variable was the island distance from the nearest coastline alone (0.61), while in the third best correlation, the island surface area (0.59) was also included. Insular variables are exclusively and syner-
gistically associated with the polychaete pattern up to the fifth best correlation (0.53), whereas variables indicative of the overall dimension of the provinces, such as total sea surface area and shelf surface area, are added to the aforementioned ones with much lower correlation values, down to the tenth place.

### DISCUSSION

#### Choice of system and taxon

Only polychaete inventories derived from the provinces defined by the Longhurst (1998) system met all 3 criteria. Although ranked third in species richness over the entire European macrobenthos inventory, the dominance of polychaetes in the majority of soft-bottom habitats may explain why they meet the first criterion, namely greater similarity with adjacent provinces or sectors relative to more distant ones. Adjacent provinces or sectors are expected to share more habitats and communities than more distant ones; thus, the multivariate patterns derived by the most dominant taxa should demonstrate their proximity.

Testing of the randomness criterion involved a large number of simulated distributions that form the confidence limits of the expected distribution (funnels). Here, another type of information is used: the taxonomic identity of the species, which deals not only with its presence or absence but also with its classification to higher categories. The average path length of the taxonomic/phylogenetic tree and the variations occurring in these lengths are used as measures of taxonomic distinctness. Consequently, provinces hosting, on average, inventories with path lengths similar to the overall inventory will probably show taxonomic distinctness values inside the expected range (funnels).

Based on this concept, 2 main characteristics of the polychaetes appear to strengthen their potential for a better fit with the second criterion:

1. Almost all feeding methods (from sarcophagy to parasitism) occur in this taxon (Fauchald & Jumars 1979, Rouse & Pleijel 2001). Feeding diversity is indicative of the functioning of communities in terms of efficient use of the available resources (Brown et al. 2004). On the other hand, species within trophic groups are likely to possess similar feeding structures and mechanisms which, in turn, are likely to be reflected in close associations at higher taxonomic levels (e.g. species classified under the same family). As a result, the more diverse a group is with respect to feeding methods, the more likely are species with varying degrees of taxonomic affinity included. The latter tends to produce taxonomic distinctness values within the expected range of the simulated funnel, whereas groups with closely related species tend to fall under the funnel.

2. Parsimony, applied to species-by-characters matrices, is expected to produce more classifications (phylogenies) that are more natural (Pleijel & Rouse 2003) compared to the former Linnaean classification. Higher taxonomic categories identified by the phylogenetic approach and placed at the same level have equal status; that is, a certain family corresponds hierarchically to any other family recognized on the phylogenetic tree or an order to any other order and so on. The Linnaean system, instead, provides a fixed number of higher categories (e.g. genus, family, order, etc.).
showed potential ways through which meiofauna may have influenced the development of pelagic larvae. In earlier reviews, 70% of macrofaunal invertebrate species were reported as having pelagic development (e.g. Mileikovsky 1972). Warwick (1989) showed potential ways through which meiofauna may have influenced the development of pelagic larvae of macrobenthic species over evolutionary time. From this follows that the fact that macrobenthos groups validate a biogeographic system based on regional water masses and plankton multi-species distribution is not at all surprising.

**Patterns in aggregated information**

Up to now, results from the application of taxonomic distinctness indices at sea-wide scales were available only from a study focused on the benthic polychaete diversity in the MEDI and the BLAS regions (Arvanitidis et al. 2002). Results from both areas show congruent patterns in the taxonomic distinctness funnels and all sectors were located within the expected range. However, the results published by Arvanitidis et al. (2002) were based on data from the entire literature on benthic polychaetes, while the source of data for the present study were certain qualitative and quantitative datasets collected in the various sectors of the province. The fact that both studies provide congruent patterns may be important for 2 reasons. (1) The databases used in the context of the current study are representative of the one collected from the entire body of the relevant literature on the taxon from the region. By scaling up and taking into account that more datasets have been collected from most of the remaining European provinces and sectors than from the MEDI and BLAS, it could be assumed that, overall, the inventories derived from the European soft-bottom datasets are representative of those derived from the relevant literature. (2) By considering the studies of Warwick & Clarke (1998) and Clarke & Warwick (2001), in which departures of the taxonomic distinctness values from the expected range (funnels) are indicative of severe community degradation, the results of the polychaete taxonomic distinctness funnels from the current study do not, as a whole, suggest any severe degradation of the provinces and sectors considered. Consequently, these inventories could serve as the reference lists for future comparisons by means of taxonomic distinctness in ‘anthropogenic effects’ studies carried out on smaller scales.

Finally, the non-parametric ANOVA shows homogeneity in taxon distribution, which means that distribution of polychaete taxa to higher taxonomic categories is the same as for other benthic macrofaunal groups (e.g. crustaceans, molluscs). However, taxonomic distinctness funnels demonstrate that polychaete inventories can place provinces and sectors inside the expected range of biodiversity values while, in most cases, the other groups do not perform in this way. The origin of these differences must be sought in the data used for the 2 approaches: Kruskal-Wallis
ANOVA uses only numbers of taxa, while taxonomic distinctness uses the identity of the taxa in addition to the numbers.

**Synergy of the geographic variables**

The best correlated variables are those indicative of habitat diversification and fragmentation, i.e. the insular variables. These variables were also mostly correlated with the multivariate polychaete pattern in Arvanitidis et al. (2002), which focused on the Mediterranean and Black Seas (MEDI and BLAS). However, one might anticipate that many more unmeasured variables would be better correlated with the resulting pattern (Clarke & Ainsworth 1993).

In the current study, the absence of suitable abiotic data over evolutionary time scales (e.g. detailed stratigraphic data) constrains the potential of the analysis. In any case, these obstacles are likely to be solved in the future as new geological data are accumulated, and of any case, these obstacles are likely to be solved in the future as new geological data are accumulated, and of population genetics may also contribute to finding answers for the critical questions (e.g. Jolly et al. 2006).

**Comparisons with available knowledge**

Up to now, the work of Deprez (2006) was the most complete study in European marine biogeography; however, it is focused on a single taxon, the Mysida (formerly Mysidaeace), which are a component of the hyperbenthos (Mees & Jones 1997). The multivariate pattern derived from the mysid inventories across the European sectors defined by IHO is tentatively interpreted as a latitudinal gradient; sectors are arranged according to their geographic proximity from South to North along the diagonal of the MDS plot (Deprez 2006). The same gradient for the Longhurst (1998) provinces was evidenced by the macrobenthos and polychaete distribution information, although an additional feature was depicted on the corresponding MDS plots of the present study: provinces with temperature/salinity gradients were placed along the horizontal axis of the plots. This gradient was produced by the polychaete inventories of the Mediterranean and Black Sea sectors and described as a zoogeocline (Arvanitidis et al. 2002).

Our findings show that soft-bottom polychaetes perform better in producing multivariate patterns on a European scale than the other macroinvertebrate groups. This contrasts with previous studies (Fauchald 1984), in which polychaete genera or families were found to be poor biogeographic indicators. Instead, it agrees well with results from recent studies based on phylogenetic analysis on a global scale (Glasby 2005, Garraffoni et al. 2006).

At smaller scales (regional/sectoral), soft-bottom benthic communities of the Norwegian continental shelf are among the most recently studied datasets (Ellingsen & Gray 2002, Ellingsen et al. 2005). By applying a different methodology, Ellingsen & Gray (2002) could not find any convincing evidence of latitudinal clines in alpha, beta or gamma diversity. However, Ellingsen et al. (2005) found that average taxonomic distinctness decreased with both latitude and depth for benthic macroinvertebrates as a whole and increased as a function of the same variables for the annelids and crustaceans. The results of the current study (BIO-ENV) do not support such a relationship between taxonomic distinctness values and latitude or depth.

**Evidence for vicariance?**

Have the European biogeographic regions identified by Longhurst (1998) been shaped by processes or by phenomena under the founder-dispersal or under the vicariance (panbiogeography) models? The former model predicts that taxa evolve at a point centre of origin and expand their distribution by physical movement (Darwin 1859, Wallace 1860). The latter model declares that taxa develop by vicariance or allopatry and there is no point centre of origin (Croizat 1958, 1968).

The evidence may be assessed using the testing framework of Glasby (2005) in a modified form, i.e.: (1) if the former model is responsible for the shaping of the major biogeographic zones in the European Seas, then their grouping in multivariate outputs would include provinces or sectors which do not necessarily share a common geological history; (2) if the latter model is predominant, then close faunal relationships would appear between provinces sharing a common history. This was tested through the application of the first criterion (proximity). Indeed, in Glasby’s (2005) minimal length area cladograms, the Mediterranean and Northeastern Atlantic appear closer to each other than to the Arctic and the Boreal Eastern Atlantic group. Although derived from a different approach, the results of the present study follow this trend: adjacent provinces, i.e. those most probably sharing a common history, appear close to each other on the MDS plots. Therefore, these results tend to support the vicariance model.

Recent evidence from molecular data (mitochondrial cytochrome oxidase I gene) enhances the vicariance model over the founder-dispersal model. Jolly et al. (2006) found congruent patterns in the timing of cladogenic events between populations of the polychaete genera Pectinaria and Owenia in European waters, a finding which suggests a common geological history.
They interpreted their results by considering vicariant events during glacial periods, which were followed by range expansion pulses of these species through remnant populations in refugia both in the North and the South Atlantic and in the Mediterranean (Por 1989, McKenzie 1999, Richter et al. 2001, Stewart & Lister 2001).

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LITERATURE CITED

Croizat L (1958) Panbiogeography, 3 volumes. Caracas: published by the author
ESRI (1994) ARC Macro Language. Environmental Systems Research Institute, Redlands, CA
IHO (1953) Limits of oceans and seas, International Hydrographic Organization. Imprimerie Monegasque, Monaco

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