



Biological geography of the European seas: results from the MacroBen database

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ABSTRACT: This study examines whether or not biogeographical and/or managerial divisions across the European seas can be validated using soft-bottom macrobenthic community data. The faunal groups used were: all macrobenthos groups, polychaetes, molluscs, crustaceans, echinoderms, sipunculans and the last 5 groups combined. In order to test the discriminating power of these groups, 3 criteria were used: (1) proximity, which refers to the expected closer faunal resemblance of adjacent areas relative to more distant ones; (2) randomness, which in the present context is a measure of the degree to which the inventories of the various sectors, provinces or regions may in each case be considered as a random sample of the inventory of the next largest province or region in a hierarchy of geographic scales; and (3) differentiation, which provides a measure of the uniqueness of the pattern. Results show that only polychaetes fulfill all 3 criteria and that the only marine biogeographic system supported by the analyses is the one proposed by Longhurst (1998). Energy fluxes and other interactions between the planktonic and benthic domains, acting over evolutionary time scales, can be associated with the multivariate pattern derived from the macrobenthos datasets. Third-stage multi-dimensional scaling ordination reveals that polychaetes produce a unique pattern when all systems are under consideration. Average island distance from the nearest coast, number of islands and the island surface area were the geographic variables best correlated with the community patterns produced by polychaetes. Biogeographic patterns suggest a vicariance model dominating over the founder-dispersal model except for the semi-closed regional seas, where a model substantially modified from the second option could be supported.

KEY WORDS: Marine biodiversity · Biogeography · Macrobenthos · Polychaetes · Europe

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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

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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 Common Environmental Policy (McCormick 2001).

Large-scale biodiversity patterns are the central issue in Theme 1 of the European Network of Excellence 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 regulatory 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 empirical 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 hydrography of the regions. The study used information on both planktonic and benthic species, such as cnidarians, crustaceans, molluscs, polychaetes, echinoderms, chordates, nemerteans, 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 attempt 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 ecosystems (LME) concept of Sherman (1992), which divides the oceans into relatively large regions (ca. 200 000 km²) characterized by bathymetry, hydrography, productivity, and trophic groups, is another example of the systems included in this category. In addition, Longhurst (1998) suggested a division of the seas based on the oceanographic characteristics of large water masses and their associated plankton communities. 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 conservation 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 suggested 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 Exploration 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 important species. Finally, the International Hydrographic Organization (IHO 1953), actively engaging all interested 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 patterns 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 benthic ecosystem, against pre-determined criteria. The patterns so derived can serve as background information 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 Mediterranean Sea, respectively, and treating them as separate 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 Mediterranean 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 example, 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

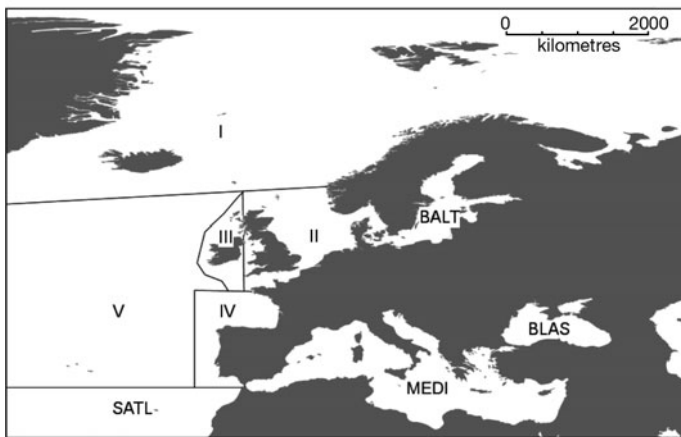


Fig. 1. European marine provinces defined by the Oslo-Paris Commission (OSPAR) and modified for the purposes of the present study. I: Arctic waters, II: Greater North Sea, III: Celtic Seas, IV: Bay of Biscay and Iberian Coast, V: Wider Atlantic, SATL: South European Atlantic, BALT: Baltic Sea, MEDI: Mediterranean, BLAS: Black Sea

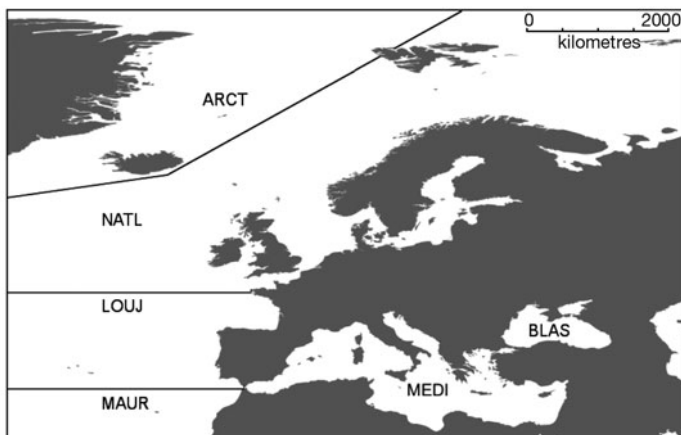


Fig. 2. European marine provinces defined by Fredj (1974) and modified for the purposes of the present study. ARCT: Arctic province, NATL: North Atlantic, LOUJ: Lousitanian, MAUR: Mauretania; remaining provinces as in Fig. 1

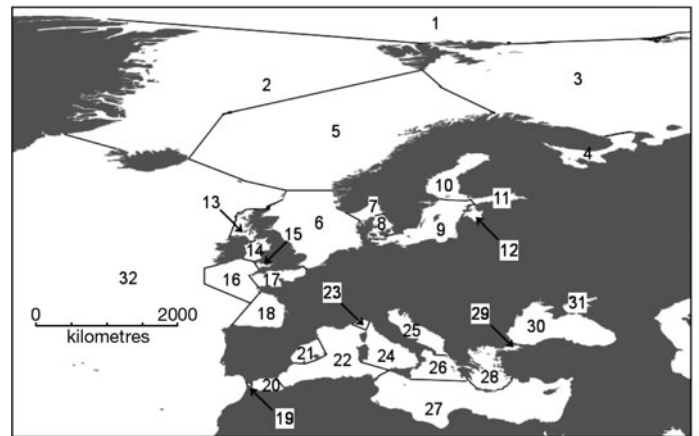


Fig. 3. European marine provinces defined by the International Hydrographic Organization (IHO). 1: Arctic Ocean, 2: Greenland Sea, 3: Barents Sea, 4: White Sea, 5: Norwegian Sea, 6: North Sea, 7: Skagerrak, 8: Kattegat, 9: Baltic Sea, 10: Gulf of Bothnia, 11: Gulf of Finland, 12: Gulf of Riga, 13: Inner Sea off the west coast of Scotland, 14: Irish Sea and St. George's Channel, 15: Bristol Channel, 16: Celtic Sea, 17: English Channel, 18: Bay of Biscay, 19: Strait of Gibraltar, 20: Alboran Sea, 21: Balearic Sea, 22: Mediterranean Sea–Western Basin, 23: Ligurian Sea, 24: Tyrrhenian Sea, 25: Adriatic Sea, 26: Ionian Sea, 27: Mediterranean Sea–Eastern Basin, 28: Aegean Sea, 29: Sea of Marmara, 30: Black Sea, 31: Sea of Azov, 32: North Atlantic Ocean

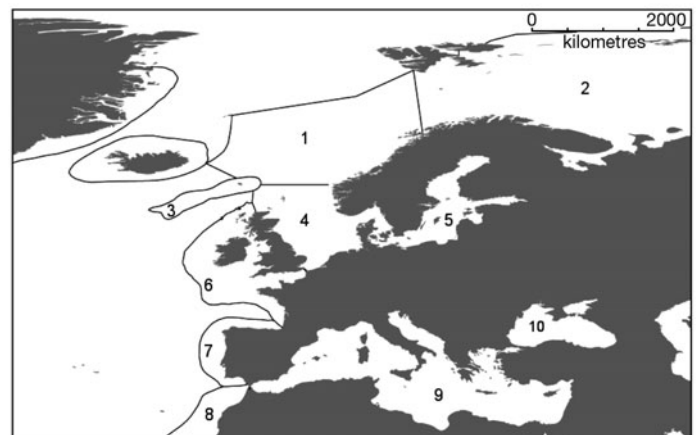


Fig. 4. European marine provinces defined in the Large Marine Ecosystems concept. 1: Norwegian Sea, 2: Barents Sea, 3: Faroe Plateau, 4: North Sea, 5: Baltic Sea, 6: Celtic-Biscay Shelf, 7: Iberian coastal, 8: Canary current, 9: Mediterranean Sea, 10: Black Sea

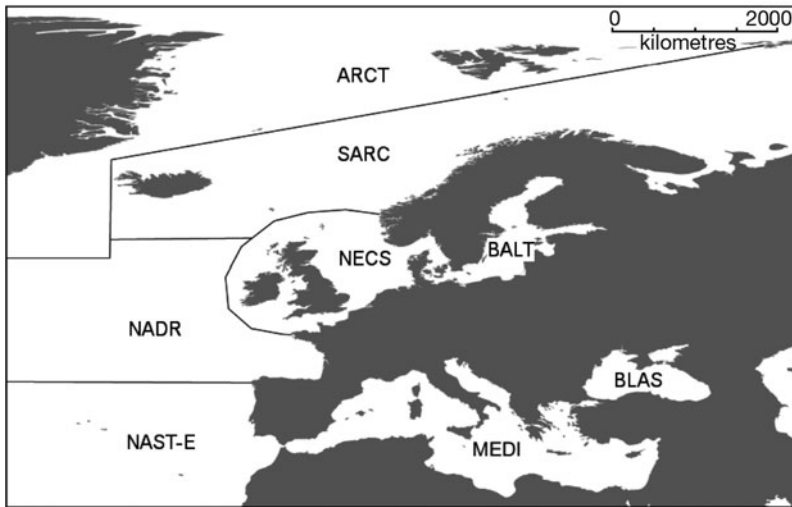


Fig. 5. European marine provinces defined by Longhurst (1998) and modified for the purposes of the present study. ARCT: Arctic, SARC: Subarctic, NECS: North-east Atlantic Shelf, NADR: North Atlantic Drift, NAST-E: North Atlantic Sub-tropical Gyre, East, MEDI: Mediterranean, BLAS: Black Sea, BALT: Baltic Sea

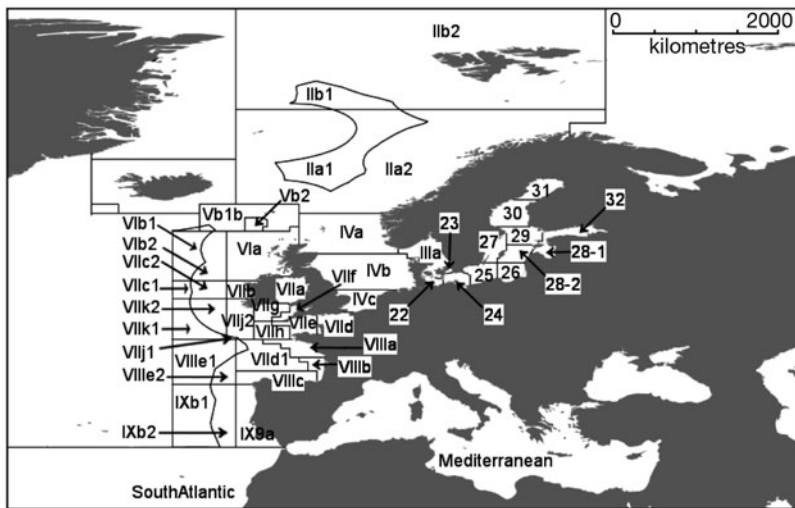


Fig. 6. Rectangles defined by the International Council for the Exploration of the Sea (ICES) for the European seas

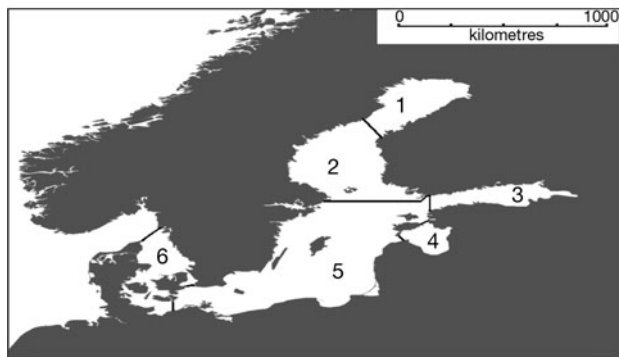


Fig. 7. Baltic Sea marine sectors defined by the Helsinki Commission (HELCOM). 1: Bothnian Bay, 2: Bothnian Sea, 3: Gulf of Finland, 4: Gulf of Riga, 5: Baltic Proper, 6: Kattegat Sound

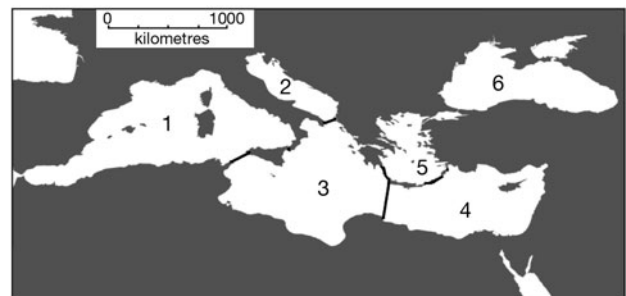


Fig. 8. Mediterranean and Black Seas marine sectors defined by Por (1989). 1: Western Mediterranean, 2: Adriatic Sea, 3: Central Basin, 4: Levantine Basin, 5: Aegean Sea, 6: Black Sea

(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-

ronmental 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),

$$\Delta^+ = [\sum_{i < j} \omega_{ij}] / [s(s-1) / 2] \quad (1)$$

where ω_{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, Λ^+), as defined by Clarke & Warwick (2001)

$$\Lambda^+ = [(\sum_{i \neq j} \omega_{ij}^2) / \{s(s-1) / 2\}] - (\Delta^+)^2 \quad (2)$$

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 (Olsford 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

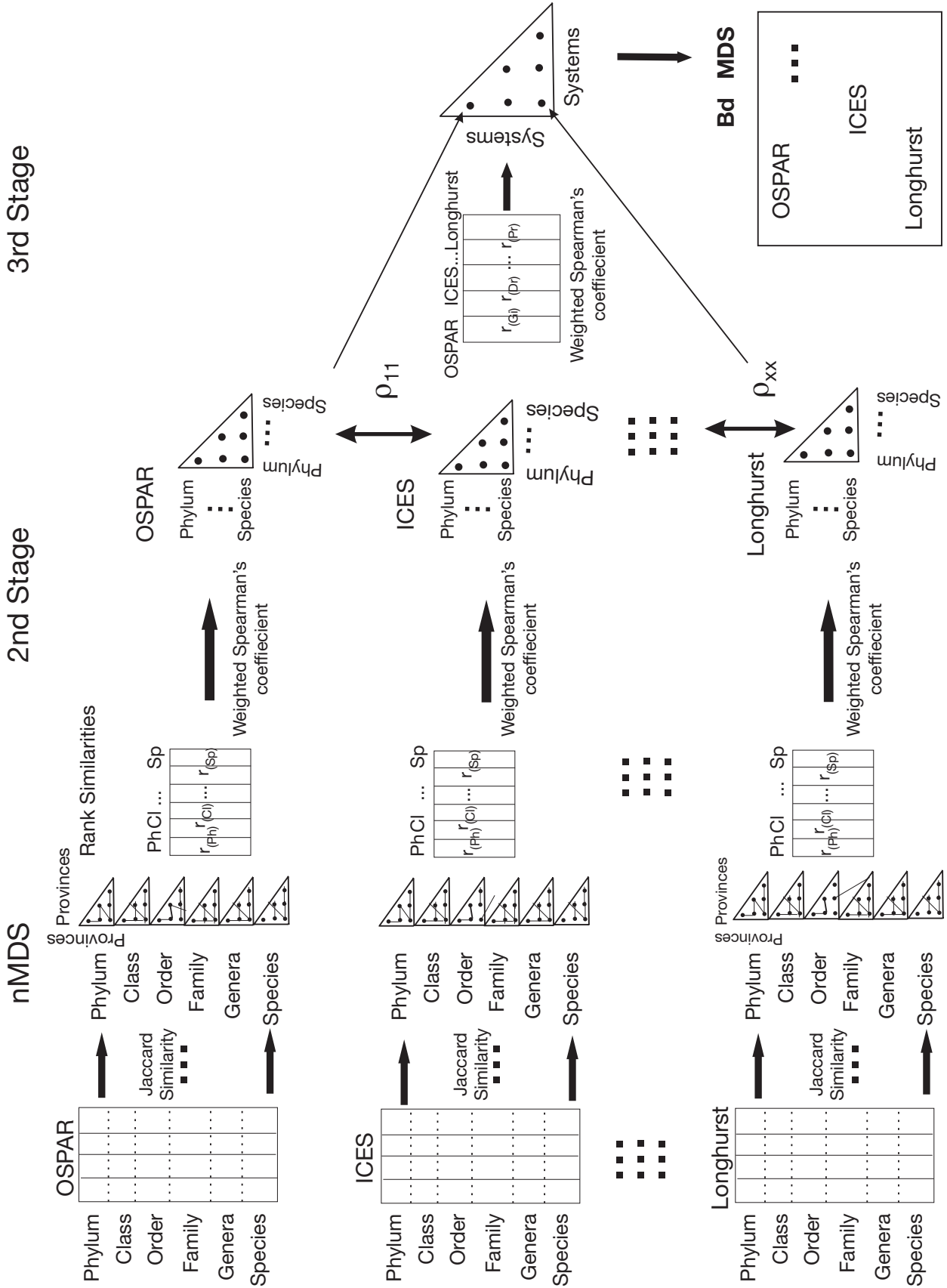


Fig. 9. Schematic representation of the third-stage non-metric multidimensional scaling (NMDS) approach (modified from Arvanitidis et al. 2009)

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 ($H_{2,18} = 4.01$; $p = 0.13$) and for the categories of order and class ($H_{1,12} = 2.6$; $p = 0.11$) were tested.

Table 1. Distribution of taxa for each macrobenthic group

	Species	Genera	Families	Orders	Classes	Phyla
All macrobenthos	5012	2196	768	149	42	18
Crustacea	1413	523	174	12	3	1
Mollusca	1285	579	223	34	5	1
Polychaeta	971	407	57	10	3	1
Echinodermata	300	171	72	32	4	1
Sipuncula	41	9	5	3	2	1

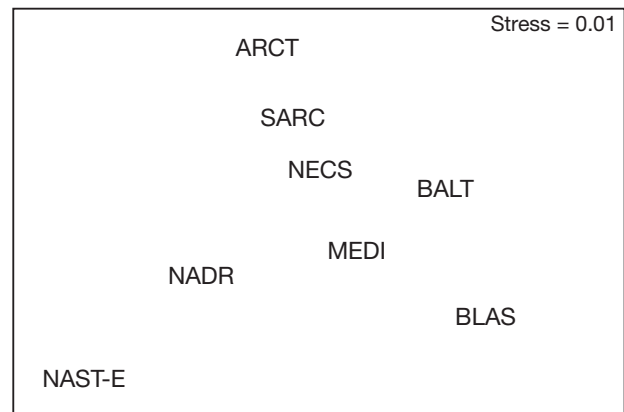


Fig. 10. Non-metric multidimensional scaling (NMDS) ordination plot resulting from the resemblance matrix of the provinces defined by Longhurst (1998), based on the Jaccard coefficient calculated from the soft-bottom macrobenthic inventories (the plot from polychaete inventories, not shown, is identical). 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 (Δ^+ , Λ^+) 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 Δ^+ and Λ^+ values as calculated from the species lists of the 8 provinces and regional seas. All provinces except NADR show lower than expected Δ^+ values and Λ^+ 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 Δ^+ 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 Λ^+ 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 Λ^+ 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 Δ^+ values and the MEDI region showed Δ^+ 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

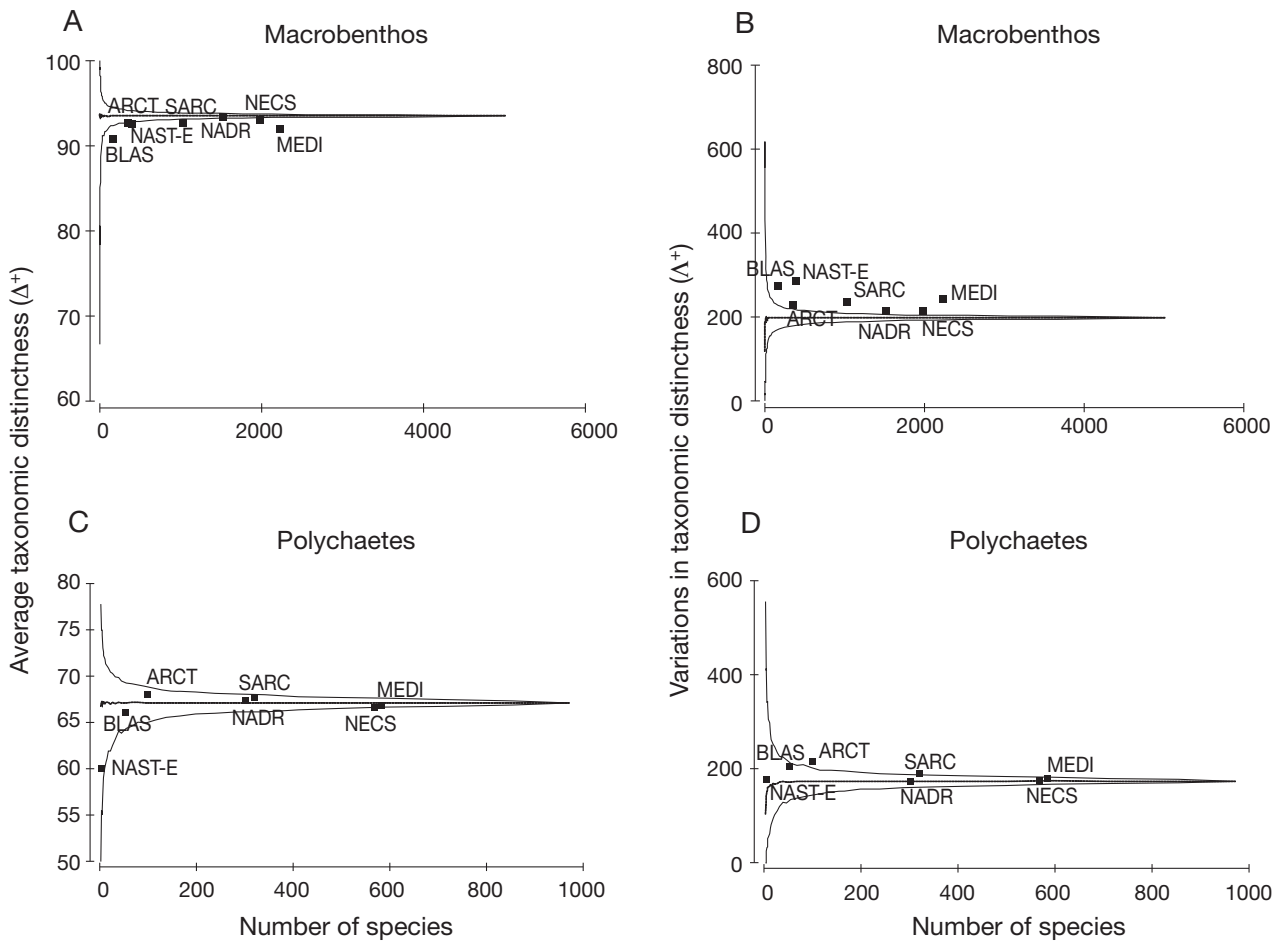


Fig. 11. 95% probability funnel for taxonomic distinctness (Δ^+ , Λ^+) for (A, B) macrobenthos and (C, D) polychaetes, as calculated for Longhurst (1998) provinces. Expected average indicated by the straight line in the middle of the funnel. Abbreviations as in Fig. 5

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).

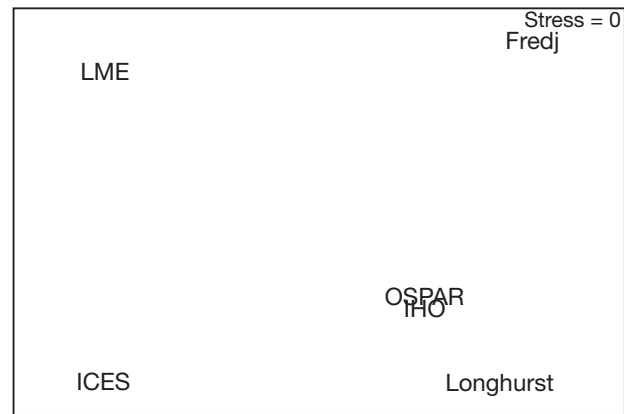


Fig. 12. Third-stage ordinations of ranked inter-matrix correlations between the systems of division of the European Seas, based on their polychaete inventories and the classification of the species to higher categories

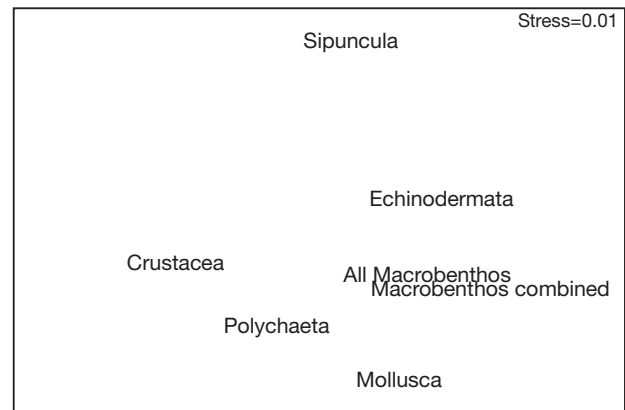


Fig. 13. Third-stage ordinations of ranked inter-matrix correlations between the benthic groups used in the analyses, based on their inventories and the classification of the species to higher categories, for Longhurst's (1998) system

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 polychaete 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-

Table 2. Summary of results from the application of guidelines used in the present study. Columns correspond to the (bio)geographic divisions proposed for the European seas. Numbers represent the criteria met. See 'Data and methods' for definition of biogeographic divisions and biodiversity criteria. Crustacea, Mollusca, Echinodermata and Sipuncula met none of the criteria set in the context of this study and are omitted from the table

	LMEs	OSPAR	ICES	IHO	Fredj	Longhurst	HELCOM (Baltic)	ICES (Baltic)	IHO (MEDI)	Por (MEDI)
All macrobenthos	–	–	–	–	–	1	1, 2	1	–	–
Macrobenthos combined	–	–	–	–	–	1	–	–	–	–
Polychaeta	–	2	2	2	2	1, 2, 3	–	–	1	1, 2

Table 3. Environmental variables best correlated with the distribution pattern of the benthic polychaetes in the European provinces, as defined by Longhurst (1998). AIDC: average island distance from nearest continent; IID: Inter-island distance; TSA: total sea surface area of the province; SSA: shelf surface area of the province; NIs: number of islands included in each of the province; ISA: total island surface area; ρ_w harmonic rank coefficient

AIDC	IID	TSA	SSA	NIs	ISA	ρ_w
x				x		0.62
x						0.61
x					x	0.59
x				x	x	0.59
x	x			x		0.53
x		x				0.53
x	x					0.52
x		x		x		0.50
x		x			x	0.49
x	x		x			0.48

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,

class, phylum) to which species are assigned, rather arbitrarily, by taxonomists. Thus, higher categories in different groups, which are treated by different taxonomists, may have a different status depending on the taxonomist's own classification practices. The latter is essential for testing of the second criterion, which is depicted by the taxonomic distinctness funnels. Potential problems with the macrofaunal inventories used here may emerge from the fact that classifications are more stable within groups that have undergone recent phylogenetic analysis than in others with Linnaean classifications. A family within the polychaetes does not necessarily correspond to a molluscan or a crustacean family. Such difficulties are supposed to be resolved when the entire 'tree of life' is assembled by phylogenetic analysis (Cracraft & Donoghue 2004). Therefore, the fact that polychaetes have undergone a recent phylogenetic review down to the family level (Rouse & Pleijel 2001), the resulting classification of which has been used in the present study, may largely account for the fitness of this group to the criterion of randomness.

The third criterion requires comparison of the distribution patterns derived from the same macrofaunal group across systems or of the patterns across macrofaunal groups within each of the systems. These patterns are derived from multi-species distribution matrices. However, the different numbers of provinces and sectors defined in each of the systems considered cause serious problems for the comparison of the resulting multivariate patterns. By applying the 3 successive steps of the third-stage MDS, it is possible to compare systems that differ in numbers of provinces or sectors. The basis of these comparisons has been altered in this step; as information is aggregated to higher taxonomic categories, systems with similar changes in multi-taxon distribution patterns will appear closer to each other in the third-stage MDS plots. In this way, the third-stage MDS may be considered as the multivariate analogue of the taxonomic distinctness. Consequently, its performance would also be influenced by the existence of a consistent taxonomy. The only system that met all 3 criteria is that proposed by Longhurst (1998). This system was developed to interpret plankton multi-species distribution patterns as a function of regional oceanographic characteristics. However, benthic–pelagic coupling can be very strong (Graf 1989, 1992, Boero et al. 1996, Raffaelli et al. 2003). In a review by Wilson (1991), 64.5% of polychaete species studied worldwide develop pelagic larvae. In earlier reviews, 70% of macrobenthic invertebrate species were reported as having pelagic development (e.g. Mileikovsky 1972). Warwick (1989) showed potential ways through which meiobenthos may have influenced the development of pelagic lar-

vae 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 datasets 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 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 Mysidacea), 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

- Arvanitidis C, Bellan G, Drakopoulos P, Valavanis V, Dounas C, Koukouras A, Eleftheriou A (2002) Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes. *Mar Ecol Prog Ser* 244:139–152
- Arvanitidis C, Somerfield PJ, Chatzigeorgiou G, Reizopoulou S, Kevrekidis T, Eleftheriou A (2009) Do multivariate analyses incorporating changes in pattern across taxonomic levels reveal anthropogenic stress in Mediterranean lagoons? *J Exp Mar Biol Ecol* 369:100–109
- Berg A (1999) Implementing and enforcing European fisheries law: the implementation and the enforcement of the Common Fisheries Policy in the Netherlands and in the United Kingdom. Martinus Nijhoff Publishers, Leiden
- Boero F, Belmonte G, Fanelli G, Piraino S, Rubino F (1996) The continuity of living matter and the discontinuities of its constituents: Do plankton and benthos really exist? *Trends Ecol Evol* 11:177–180
- Briggs JC (1995) *Global biogeography*. Elsevier, Amsterdam
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Clarke KR, Ainsworth M (1993) A method for linking multivariate community structure to environmental variables. *Mar Ecol Prog Ser* 92:205–209
- Clarke KR, Gorley RN (2001) *PRIMER v5: User Manual/Tutorial*. PRIMER-E, Plymouth
- Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. *Mar Ecol Prog Ser* 46:213–226
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth
- Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. *J Appl Ecol* 35:523–531
- Clarke KR, Warwick RM (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar Ecol Prog Ser* 216:265–278
- Cracraft J, Donoghue MJ (2004) *Assembling the tree of life*. Oxford University Press, Oxford
- Croizat L (1958) *Panbiogeography*, 3 volumes. Caracas: published by the author
- Croizat L (1968) Introduction raisonnée à la biogéographie de l'Afrique. *Mem Soc Broter [Coimbra]* 20:1–451
- Darwin C (1859) *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. Murray, London
- Deprez T (2006) *Taxonomy and biogeography of the Mysida (Peracarida, Crustacea): a global approach through the biological information system NeMys*. PhD Thesis, Universiteit Gent
- Ekman S (1967) *Zoogeography of the sea*. Sidgwick & Jackson, London
- Ellingsen KE, Gray JS (2002) Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *J Anim Ecol* 71:373–389
- Ellingsen KE, Clarke KR, Somerfield PJ, Warwick RM (2005) Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *J Anim Ecol* 74:1069–1079
- ESRI (1994) *ARC Macro Language*. Environmental Systems Research Institute, Redlands, CA
- Fauchald K (1984) Polychaete distribution patterns, or: can animals with Palaeozoic cousins show large-scale geographical patterns. In: Hutchings PA (ed) *Proc 1st Int Polychaete Conf*. Linnean Society of New South Wales, Sydney, p 1–6
- Fauchald K, Jumars P (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Fredj G (1974) *Stockage et exploitation des données en écologie marine. C: Considerations biogéographiques sur les peuplements benthiques de la Méditerranée*. *Mém Inst Océanogr Monaco* 7:1–88
- Garraffoni ARS, Nihei SS, Da Cunha Lana P (2006) Distribution patterns of Terebellidae (Annelida: Polychaeta): an application of Parsimony Analysis of Endemicity (PAE). In: Sardá R, San Martín G, López E, Martín D, George D (eds) *Scientific advances in polychaete research*. *Sci Mar, Barcelona* p 269–276
- Glasby CJ (2005) Polychaete distribution patterns revisited: an historical explanation. *PSZNI: Mar Ecol* 26:235–245
- Graf G (1989) Benthic-pelagic coupling in a deep-sea benthic community. *Nature* 341:437–439
- Graf G (1992) Benthic-pelagic coupling: a benthic view. *Oceanogr Mar Biol Annu Rev* 30:149–190
- Heads M (2005) Towards a panbiogeography of the seas. *Biol J Linn Soc* 84:675–723
- HELCOM (2007) *Towards favourable conservation status of Baltic Sea biodiversity*. HELCOM Ministerial Meeting, Krakow
- IHO (1953) *Limits of oceans and seas*, International Hydrographic Organization. Imprimerie Monegasque, Monaco
- Jolly MT, Viard F, Gentil F, Thiébaud F, Jollivet D (2006) Comparative phylogeography of two coastal polychaete tube-worms in the Northeast Atlantic supports shared history and vicariant events. *Mol Ecol* 15:1841–1855
- Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. *J Am Stat Assoc* 47:583–621
- Kruskal JB, Wish M (1978) *Multidimensional scaling*. Sage, Beverly Hills, CA
- Legendre P, Legendre L (1998) *Numerical ecology. Developments in environmental modelling*. Elsevier, Amsterdam
- Longhurst A (1998) *Ecological geography of the sea*. Academic Press, San Diego

- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ
- McCormick J (2001) Environmental policy in the European Union. The European Series, Macmillan, London
- McKenzie JA (1999) From desert to deluge in the Mediterranean. *Nature* 400:613–614
- Mees J, Jones MB (1997) The hyperbenthos. *Oceanogr Mar Biol Annu Rev* 35:221–255
- Mileikovsky SA (1972) The 'pelagic larvaton' and its role in the biology of the world ocean, with special reference to pelagic larvae of marine bottom invertebrates. *Mar Biol* 16:13–21
- Olsgard F, Somerfield PJ, Carr MR (1997) Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. *Mar Ecol Prog Ser* 149:173–181
- OSPAR (2003) Strategies of the OSPAR Commission for the protection of the marine environment of the North-East Atlantic. Ministerial Meeting of the OSPAR Commission, Bremen
- Pierrot-Bults AC, Nair VR (1991) Distribution patterns in Chaetognatha. In: Bone Q, Kapp H, Pierrot-Bults AC (eds) The biology of chaetognaths. Oxford University Press, New York, p 86–116
- Pleijel F, Rouse GW (2003) Ceci n'est pas une pipe: names, clades and phylogenetic nomenclature. *J Zoological Syst Evol Res* 41:162–174
- Por FD (1989) The legacy of Tethys. An aquatic biogeography of the levant. Kluwer, Dordrecht
- Raffaelli D (2006) Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Mar Ecol Prog Ser* 311:285–294
- Raffaelli D, Bell E, Weithoff G, Matsumoto A and others (2003) The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. *J Exp Mar Biol Ecol* 285-286:191–203
- Richter TO, Lassen S, van Weering TJCE, de Haas H (2001) Magnetic susceptibility patterns and provenance of ice-rafted material at Feni Drift, Rockall Trough: implications for the history of the British-Irish ice sheet. *Mar Geol* 173:37–54
- Rouse GW, Pleijel F (2001) Polychaetes. Oxford University Press, Oxford
- Rozwadowski HM (2002) The sea knows no boundaries. A century of marine science under ICES. University of Washington Press, Seattle, WA
- Sherman K (1992) Large marine ecosystems: patterns, processes and yields. American Association for the Advancement of Science, Washington, DC
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- Somerfield PJ, Clarke KR (1995) Taxonomic levels in marine community studies, revisited. *Mar Ecol Prog Ser* 127: 113–119
- Somerfield PJ, Arvanitidis C, Faulwetter S, Chatzigeorgiou G and others (2009) Assessing evidence for random assembly of marine benthic communities from regional species pools. *Mar Ecol Prog Ser* 382:279–286
- Stewart JR, Lister A (2001) Cryptic northern refugia and the origins of the modern biota. *Trends Ecol Evol* 16:608–613
- Vanden Berghe E, Claus S, Appeltans W, Faulwetter S, and others (2009) MacroBen integrated database on benthic invertebrates of European continental shelves: a tool for large-scale analysis across Europe. *Mar Ecol Prog Ser* 382: 225–238
- Van Soest RWM, Hajdu E (1997) Marine area relationships from twenty sponge phylogenies. A comparison of methods from coding strategies. *Cladistics* 13: 1–20
- Wallace AR (1860) On the zoological geography of the Malay Archipelago. *Proc Zool J Linn Soc Lond* 4:173–184
- Warwick RM (1989) The role of meiofauna in the marine ecosystem: evolutionary considerations. *Zool J Linn Soc* 96:229–241
- Warwick RM, Clarke KR (1998) Taxonomic distinctness and environmental assessment. *J Appl Ecol* 35:532–543
- Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. *Oceanogr Mar Biol Annu Rev* 39:207–231
- Wilson WH (1991) Sexual reproductive modes in polychaetes: classification and diversity. *Bull Mar Sci* 48:500–516

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