



THEME SECTION

Large-scale studies of the European benthos: the MacroBen database

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MarBEF, databases, and the legacy of John Gray

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ABSTRACT: Within the European Network of Excellence (NoE) on Marine Biodiversity and Ecosystem Functioning (MarBEF), marine biodiversity scientists from across Europe have been brought together to focus on 3 broad themes. Theme 1 describes large-scale (and long-term) distribution patterns of marine biodiversity, Theme 2 examines the consequences of changes in marine biodiversity for the functioning of marine ecosystems, and Theme 3 explores and disseminates the socio-economic consequences of changes in marine biodiversity and biodiversity-mediated processes. Within MarBEF Theme 1, a large collaborative effort has produced an integrated database of species occurrence information (MacroBen), which contains data of quantitative samples of soft-sediment benthic infauna collected in European continental waters, from the Arctic to the Black Sea. Papers in this Theme Section describe initial studies based on the database. The late Prof. John S. Gray led activities within MarBEF Theme 1 for the first 2.5 yr, during which time the majority of the work described in this Theme Section was set in motion, and he continued to be involved in the work until his untimely death. We dedicate this body of work to his memory.

KEY WORDS: Marine biodiversity · Macrobenthos · Large-scale patterns · Science integration · MacroBen

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INTRODUCTION

In early 2003, a group of scientists from across Europe put a proposal to the European Commission to set up a network of institutes with expertise in different aspects of marine biodiversity research, under the then new Framework Programme VI instrument of a Network of Excellence (NoE). The proposal was accepted, and the NoE, entitled Marine Biodiversity and Ecosystem Functioning (MarBEF), began operating in 2004. An inaugural meeting took place in Bruges in March of that year. Institutes from Norway, Sweden, Finland, Lithuania, Poland, Germany, Denmark, the Netherlands, Belgium, France, the United Kingdom, Ireland, Portugal, Spain, Italy, Slovenia and Greece were represented. The framework of activities and provisional timetables for 5 yr of operation had been laid out in the original proposal document, but this was the first chance for members of the network to meet together to plan the practicalities of delivering the proposed programme.

A wide range of activities was included in MarBEF with the aim of integrating marine biodiversity research within Europe (see www.MarBEF.org). Although the primary goal of a NoE had to be integration rather than research, a programme of collaborative research was included in MarBEF as a means to promote integration. The proposed science was grouped into 3 themes. Broadly, Theme 1 addresses large-scale and long-term patterns in marine biodiversity, Theme 2 brings together researchers to examine relationships between biodiversity and ecosystem functioning, and Theme 3 explores and describes the socio-economic consequences of changes in marine biodiversity and biodiversity-mediated processes. The delivery mechanism for research within these core themes was workshop-based, with researchers coming together to discuss and undertake activities. In addition to the 3 scientific themes, several integrating activities shared by these themes were included in MarBEF's programme of activities, including data management.

Although the science proposed within Theme 1 had several elements, a major thrust was to use MarBEF's data management infrastructure and geographical spread of people and institutions to combine, integrate and analyse existing data to address large-scale patterns in species occurrence and community structure. A major motivation of this work was to attempt to address the mismatch in spatial scales between the scales of sampling (e.g. grabs with an area of 0.1 m², collected m or km apart) and the scales at which marine management and policy decisions are implemented (e.g. regional seas). In this Theme Section we describe initial scientific outcomes from MarBEF Theme 1.

MARBEF THEME 1

MarBEF had the ideal person to chair Theme 1 in Prof. John S. Gray (Fig. 1) of Oslo University, who agreed to take on the role for 2.5 yr. The well-attended Theme 1 'kick-off' meeting was held in Oslo in June 2004, at which MarBEF scientists discussed the practicalities of delivering the planned science programme. Friendships were forged and reforged, ideas were aired, shared and discussed, and all those involved left with work to do. An initial aim was to collect and make available existing data from samples collected in European waters. Data from across Europe were provided to the data management team, checked, organised, and added to a database. In parallel, ideas were formulated concerning analyses that could be carried out using the database. Within Theme 1, the decision was taken to focus initially on soft-sediment macrobenthos. Working with the data management team, scientists began to develop a subset (MacroBen) of the main MarBEF database, described by Vanden Berghe et al. (2009, this Theme Section). The second Theme 1 meeting was held in Oslo in March 2005, at which various analyses were discussed and trialed, and the teams that would collaborate to deliver them were formed. Discussions held during the second MarBEF General Assembly meeting in Porto during March 2005, led to the Declaration of Mutual Understanding (DMU) for data sharing within MarBEF Theme 1 (available from www.medobis.org/MarbefDMU.doc). Work continued through the summer of 2005, leading up to the highly successful workshop held in Crete in October 2005 at which an analysis and publication plan, which marked the genesis of this Theme Section, was agreed upon.

The DMU was also finalized at the Crete workshop, but difficulties of working in large multi-partner pro-



John Gray (1945–2007)

jects, and with large-scale sharing of data and resources, became manifest. Overcoming these required hard work and a detailed strategy to contact and engage those who could provide data (managers, stewards) both inside and outside MarBEF. The DMU lays out (1) the principles upon which the rules for sharing data within Theme 1 are based, and (2) the rights and obligations of the contracted parties, i.e. between the leader of the data management team (who acts for the MarBEF consortium), and the data providers. There are 3 main principles: (1) data custodians have formal agreements in place before sharing data; (2) the resulting database is open only to people sharing data within MarBEF Theme 1; and (3) scientists whose data are used should be involved in the creative process of hypothesis generation and testing. The data policy is assumed to be successful as almost of those contacted agreed to share their datasets in the context of the Theme 1 activities. All data providers wishing to access and analyse the database must first sign up to the DMU. Each of them can then exploit the dataset as a whole in order to test their own hypotheses. Studies involving only single datasets can only be undertaken after negotiations between the respective data providers. One of the consequences of the DMU (and the agreements explicit within it) is that data providers are, unless they state otherwise, included as authors on papers that use their data. This makes clear the scope of the collaborations involved in putting together and analysing the data. The results of each study in this Theme Section were communicated to the relevant data providers, who had the opportunity to add analyses or text or decline their right to co-authorship.

Professor Gray's term as chair of Theme 1 came to an end in 2006, following the MarBEF General Assembly meeting in Lecce in May. For many people in MarBEF, this was the last time that they saw him. Although further smaller workshops were held to develop specific aspects of the work, overall progress slowed as resources within MarBEF were focused on a series of Responsive Mode Programmes. It is to the credit of a small number of committed individuals, including Prof. Gray, who worked hard to maintain progress, that this work progressed to the stage where a series of manuscripts were in preparation in 2007.

PRELIMINARY OUTPUTS FROM THE MACROBEN DATABASE

Data sharing and integration were central to the work described in this Theme Section. Datasets and their associated metadata were sent to the Flanders Marine Institute where they were converted into a common format and integrated into the MacroBen

database. The datasets, the processes applied to them, and the resultant database are described by Vanden Berghe et al. (2009).

Renaud et al. (2009, this Theme Section) use samples from the database to describe large-scale patterns in benthic soft-sediment infaunal assemblages on European continental shelves, ranging from the high Arctic to the Black Sea. Escaravage et al. (2009, this Theme Section) analyse relationships between species accumulation and area. Both Renaud et al. (2009) and Escaravage et al. (2009) conclude that processes associated with local pelagic production are important determinants of infaunal community structure and that there are no strong differences between different regions in the way in which communities are structured. Coastal seas and oceans are partitioned according to different schemes for a range of purposes, e.g. science, management, politics, or simply convenience. The extent to which different schemes reflect genuine differences in the benthos is examined by Arvanitidis et al. (2009, this Theme Section) who conclude that a scheme based on regional differences in pelagic productivity reflects biogeographic differences in benthic infaunal assemblages.

The usefulness of a large-scale database such as MacroBen for addressing ecological questions is demonstrated by the next 2 papers. Sommerfield et al. (2009, this Theme Section) examine whether local macroinfaunal communities may be assembled at random from regional species pools at a range of spatial scales, concluding that this is not the case and that regional processes probably influence community assembly. Different processes determine the assembly of whole communities and of the polychaete component of those communities. Polychaete assemblages, on the local scale, appear to be a randomly assembled subset from the regional species pool. The large scale of the MacroBen database allowed Webb et al. (2009, this Theme Section) to apply techniques from the field of macroecology to marine benthic data for the first time. They show that there are important similarities and differences between macroecological patterns on land and on the seabed.

Finally, Grémare et al. (2009, this Theme Section) use the large-scale taxonomic and geographic coverage of the database to assess how 2 different indices proposed for monitoring the implementation of the European Water Framework Directive compare when the data used to calculate them come from different parts of the European coast.

It must be stressed that these papers are only first steps. New data may be added to the database, as there are large gaps in the geographic coverage, and even in areas where coverage is relatively good there are large distances between individual samples in both

space and time. Using the database as it is, there are many new questions that can be addressed, and the data provide new ways to address existing questions over a range of geographic scales. Linking the occurrence information in MacroBen to information about the species, such as functional traits (Bremner 2008), physiology, or information about the species' tolerances to chemicals, pollution, temperature, or climate change would allow whole new analyses aimed at understanding large-scale changes (e.g. Somerfield et al. 2008), and assessment of existing analyses at larger spatial scales (e.g. Grémare et al. 2009). Effort is already being made within MarBEF to integrate and synthesise time-series data, and a similar database to MacroBen for meiofauna (Vandepitte et al. 2009) is currently being analysed (e.g. Schratzberger et al. 2009).

PROFESSOR JOHN STUART GRAY

John Gray's terminal illness was diagnosed in 2006, and the MarBEF General Assembly in Poland in 2007 took place without him. Although John no longer attended meetings, he was active in MarBEF until the very end. It was with great sadness that we heard of his passing on 21 October 2007, aged only 66. His life and work have been covered in this journal (Warwick et al. 2008a) and elsewhere (Richardson et al. 2008, Warwick et al. 2008b). We present in this Theme Section a body of work that exemplifies John's belief that data always have value above and beyond the reasons for which the data were originally collected. Criticism has been levelled against John for being more a user of other people's data rather than a collector of original data, but we share his view that data represent information that can never be re-gathered. To make the best use of datasets (once the original purpose for the data collection is completed), it benefits everyone if the information is made available widely. The data collector benefits from the exposure of the original collection effort (and receives citations if the work was good enough to be published), and questions can be addressed that could never be addressed by new sampling programmes, no matter how much money is made available for conducting them. John believed in the approach adopted by MarBEF, and worked hard to make it a success. We acknowledge his contribution, are thankful for it, and dedicate the work presented here to his memory.

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MacroBen integrated database on benthic invertebrates of European continental shelves: a tool for large-scale analysis across Europe

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ABSTRACT: We describe an integrated database on European macrobenthic fauna, developed within the framework of the European Network of Excellence MarBEF, and the data and data integration exercise that provided its content. A total of 44 datasets including 465 354 distribution records from soft-bottom macrobenthic species were uploaded into the relational MacroBen database, corresponding to 22 897 sampled stations from all European seas, and 7203 valid taxa. All taxonomic names were linked to the European Register of Marine Species, which was used as the taxonomic reference to standardise spelling and harmonise synonymy. An interface was created, allowing the user to explore, subselect, export and analyse the data by calculating different indices. Although the sampling techniques and intended use of the datasets varied tremendously, the integrated database proved to be robust, and an important tool for studying and understanding large-scale long-term distributions and abundances of marine benthic life. Crucial in the process was the willingness and the positive data-sharing attitude of the different data contributors. Development of a data policy that is highly aware of sensitivities and ownership issues of data providers was essential in the creation of this goodwill.

KEY WORDS: Macrofauna · Biogeography · Integrated database · Data management · Data rescue

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INTRODUCTION

Often marine biological data are the result of projects with a limited temporal and spatial cover (Floen et al. 1993). Taken in isolation, datasets resulting from these projects are only of limited use in the interpretation of large-scale phenomena. More specifically, they fail to

be informative on a scale commensurate with the problems of global change that humankind is confronted with (Costello & Vanden Berghe 2006). Individual studies are restricted in the amount of data they can generate; but by combining the results from many studies, massive databases can be created that make analyses on a much-enhanced scale possible (Grassle 2000).

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Such data have never been of greater importance considering the recent observation of major shifts of marine species due to global change. A recent report from the Marine Board of the European Science Foundation shows clear evidence of northward migrations of several marine-species populations from European seas (Philippart et al. 2007). Increasingly, vast thematic databases are being created, made possible by advances in computer technology. The Ocean Biogeographic Information System (OBIS), the data-integration component of the Census of Marine Life (CoML), assesses and explains the diversity and distribution of marine life through a network of linked databases (Grassle 2000). The Marine Biodiversity and Ecosystem Functioning (MarBEF) initiative includes implementation and networking of large-scale biodiversity research in Europe; part of this forms a contribution to the OBIS network through its European node, EurOBIS. Within the MarBEF working group Global Patterns of Marine Biodiversity across Ecosystems (Theme 1), an integrated database (MacroBen) on soft-bottom macrobenthos was compiled. The present paper describes the content, data integration, standardisation and functionalities of the MacroBen database.

CONSTITUENT DATASETS

Each dataset (Table 1) was archived and described in detail at the data centre of the Flanders Marine Institute (VLIZ). Describing datasets in a standardised way made it possible to create a searchable metadata inventory, thus facilitating data discovery and sharing. These metadata include information needed to decide on the relevance of a dataset in a particular context, e.g. where and when the data were collected, what the intended use of the dataset was, how data were collected, who played a role in the collection and the management of the data, where the data are stored and in what format and under which conditions they are available. All metadata descriptions are publicly available through the MarBEF website (www.marbef.org/data/dataset.php). Archiving the datasets prevents them from being lost by ensuring the long-term integrity of the data. The Integrated Marine Information System (IMIS), the metadata system maintained by VLIZ (Cattrijsse et al. 2006), was used as a tool for metadata management; this system is also used to manage information on behalf of the MarBEF network.

A unique citation, brief explanation of the original dataset objective and derived publications from each of the contributing datasets are listed in Appendix 1, together with a link to the extended metadata description available in IMIS. In Appendix 1, we also propose a standard dataset citation including title, dataset

collector(s) or custodian(s) (equivalent to author[s] or editor[s]), dataset owner (equivalent to publisher) and final year of sampling. We hope that this standard citation, or an equivalent one, will stimulate formal recognition of data sources in future re-use of the data.

DATA INTEGRATION

The MacroBen database integrates datasets on soft-bottom macrobenthic fauna from all European seas. A total of 44 datasets was collected, harmonised and integrated into a relational Access database. The integrated database includes both quantitative and qualitative data on organisms and several abiotic parameters ranging from the northeast Atlantic and the North Sea, Norwegian Sea and Arctic Ocean, the Baltic Sea and the Mediterranean and Black seas.

One of the main difficulties in integrating and comparing different datasets from various data providers is the harmonisation of the data; 3 types of harmonisation were performed: (1) taxonomic, (2) geographical, and (3) sampling methodology. All geographical coordinates were converted to decimal degrees. All datasets in which information on the datum was available used the WGS84 coordinate system. We assumed that this was also the case for those datasets where this information was missing.

Taxonomic names as recorded in the constituent datasets were matched with the European Register of Marine Species (ERMS). This authoritative taxonomic register provides a list of species occurring in the European marine environment, defined as up to the strand-line or splash zone above the high-tide mark and down to 0.5 salinity (Costello et al. 2001). Spelling mistakes were corrected, information on gender and life stage removed and stored in the appropriate fields, and the taxonomic name as recorded in the dataset was linked to the name as included as valid in the ERMS. Many names in the constituent datasets proved to be omissions in the ERMS, and were, in consultation with the ERMS taxonomic editors, subsequently added to the ERMS. A further description of the ERMS can be found in Cuvelier et al. (2006), and on the MarBEF website (www.marbef.org/data/erms).

Various sampling tools and methods were used over the different datasets. About 50% of the data was derived from sampling with Van Veen grabs. To a lesser extent the data were derived from sampling with a Smith-McIntyre, Ponar or APN grab, cores or other hand-operated devices. Two datasets provided data from museum collections. Overall, 33% of the data were qualitative in nature, while 30% contained not only specimen counts but also biomass data (Table 2). The sampling area from the quantitative datasets

Table 1. Datasets included in the MacroBen database with 2-letter station code. The ID refers to the metadata of the datasets stored in the Register of Resources

ID	Code	Dataset	Geographical area	Total no. of records	Total no. of stations	Temporal cover
North Sea and northeast Atlantic Ocean						
345	bi	BioMar survey of Ireland	Irish coastal zone	86 359	2397	1972–1996
1600	o5	BIOMÖR 1 dataset	Southern Irish, Celtic seas	5166	51	1989–1991
615	np	National Marine Monitoring Programme	North Sea, English Channel Celtic Sea	1161	40	2002–2003
534	pl	Plymouth Sound dataset	Plymouth Sound, English Channel	1343	44	1995
597	ba	Benthos Gironde Estuary	Gironde Estuary, Biscay	3019	13	1979–2004
599	ni	BIS dataset of SW Netherlands (1985–2004)	Southern part of Dutch continental shelf, North Sea	136 677	15 564	1974–2005
633	ug	MacroDat Belgium	Belgian part of North Sea	33 995	1801	1977–2003
67	ns	North Sea Benthos Survey	North Sea	11 820	231	1985–1986
999	o3	Offshore reference stations, North/ Norwegian seas	North Sea	9904	30	1990–2002
Norwegian Sea and Arctic Ocean						
997	o4	Offshore reference stations, Norwegian/ Barents seas	North Sea, Norwegian Sea, Barents Sea	59 710	184	1991–2001
243	hs	Polish Arctic Marine Programme	Spitsbergen, Greenland Sea	603	34	2002
614	ko	Soft bottom community structure and diversity in Arctic Kongsfjorden	Spitsbergen, Greenland Sea	210	6	2003
533	ar	Arctic soft-sediment macrobenthos	Barents Sea and Arctic Ocean	1005	22	1991
998	o6	Offshore reference stations, Finnmark	Norwegian, Barents seas	11 898	53	1998–2000
12	o2	Northern Barents Sea 1992	Barents Sea	1919	10	1992
11	o8	Benthic fauna around Franz Josef Land	Barents Sea	2630	9	1992
461	o7	Benthic fauna around Pechora Sea	Barents Sea	2964	15	1992
Skagerrak and Baltic Sea						
601	ze	Macrozoobenthos Baltic Sea (1980–2005) as part of IOW Monitoring	Baltic Sea	3589	19	1980–2005
611	pu	Bay of Puck dataset	Baltic Sea	539	29	1996
612	gd	Gulf of Gdansk dataset	Baltic Sea	87	13	1995–2002
617	n3	N3 data of Kiel Bay	Baltic Sea	8944	1	1986–2004
618	70	Kiel Bay intercalibration dataset	Baltic Sea	1144	1	1995
11	of	Oslofjord 93–94	Skagerrak	1469	34	1993–1994
618	of	Oslofjord 96–97	Skagerrak	1096	23	1996–1997
Mediterranean and Black Sea						
603	bl	Soft Bottom of the Bay of Blanes	Balearic Sea	3754	2	1992–1997
213	gr	Redit dataset	Western Mediterranean	5642	92	1998
597	fb	Fauna Biontica dataset	Adriatic Sea	2418	380	1934–1936
602	lm	LBMRev dataset	Adriatic Sea	9321	28	1985–2004
600	oc	Cesenatico dataset	Adriatic Sea	963	1	1996–2002
630	o1	Northern Aegean dataset	Aegean, Ionian seas	7277	419	1937
595	ap	Aegean polychaetes dataset	Aegean Sea	2215	70	1937–2000
613	ka	Cretan shelf macrofauna and macro- fauna of Greek polluted sites	Aegean, Ionian seas	11 861	199	1986–1997
598	do	Mop Crete dataset	Aegean Sea	2670	56	1988
622	M2	Aegean Sea coastal benthic communities, Geras Gulf (Mytilini)	Aegean Sea	4634	9	1986–1988
289	M3	Seasonal zoobenthos, Saronikos	Aegean Sea	2050	6	1989–1990
623	M6	Kalamitsi dataset	Ionian Sea	2037	22	1990–1991
624	M7	Kerkyra dataset	Ionian Sea	1015	12	1991–1992
625	M8	Zoobenthos Kyklades, Aegean Sea dataset	Aegean Sea	882	14	1986
272	M0	Gialova 1	Aegean, Ionian seas	1216	7	1995–1996
626	M1	MegFeod-Black Sea dataset – IBSS, Sevastopol	Black Sea	169	24	1986
627	M4	Strelbay-Black Sea dataset – IBSS, Sevastopol	Black Sea	297	18	1993
628	M5	Yalta-Black Sea dataset – IBSS, Sevastopol	Black Sea	308	26	1979–1986
629	M9	Laspibay-Black Sea dataset – IBSS, Sevastopol	Black Sea	689	33	1996
490	bo	Biocean dataset	Atlantic, Arctic, Baltic, Mediterranean seas	18 685	1071	1967–2001

ranged from 0.008 to 1.2 m² with 0.1 m² being the most common. In 23 % of the distribution records, replicate samples were taken.

CONCEPTUAL MODEL

The structure and concept of the MacroBen database and data management was based on an earlier system, created for a similar initiative: the North Sea Benthos Project 2000 (NSBP), an activity of ICES (Rees et al. 2007). In the NSBP initiative, data from the North Sea from various sources was brought together and analysed jointly. The data management for the NSBP was described in Vanden Berghe et al. (2007). The data management of both NSBP and MacroBen is based on a series of Access databases: 1 for each constituent dataset, and 1 to contain the integrated data. The latter also contains tools and a simple user interface to work with the data. At any point, the integrated data could be recompiled from the individual databases. This system made it possible to manage the data from individual datasets separately, and go through an iterative process of data cleaning and harmonisation. The structure of the Access databases containing the individual datasets depended on the formats employed by the data providers, and will not be discussed further here. Each of these individual databases contained a query that wrote a standard table that was then available for the integrator Access file to read.

The basic structure of the integrator database (Fig. 1) is based on a relatively limited number of tables: distribution records, taxonomic information, georeferenced sampling stations, abiotic data and metadata. Since the data were not edited in this database, no attempt was made at complete normalisation; the normalisation was done at the level of the Access databases containing the constituent datasets. Before analysis, the data structure was even further simplified, to a single flat table. This way, users were not forced to study the structure of the database before analysing the data. It also made export of the data to other programs such as spreadsheets trivial.

Both qualitative and quantitative distribution records were integrated into the distribution record (dr) table. This table stores the station name and a unique station code, code of the replicate sample, latitude and longitude, date, depth, surface area sampled, sampling depth, sediment type, mesh size, count and biomass, life stage, the original dataset code (db), a code for the standardised species name (aphiaID) and a free note. Species name, latitude and longitude, and a description of the origin of the data were the only mandatory fields; but extra information was available for many of the constituent datasets.

Table 2. Sampled area and equipment used over the different datasets. na = not applicable

Code	Area (m ²)	Equipment
bi	na (qualitative data)	Direct observation on seashores and by SCUBA divers
o5	0.1	Van Veen grab
np	0.1	Day grab
pl	0.008	Diver-operated cores
ba	Variable	Several (hand-corer [intertidal] and Smith-McIntyre grab [subtidal], suction grab and quantitative Sanders sledge)
ni	Variable	Several (cores, box-corer, Van Veen grabs, Flushing sampler)
ug	0.1026 and 1.2	Van Veen grab
ns	Variable	Van Veen grab
o3	0.1	Modified Van Veen grab (APN grab, patent Akvaplan-niva)
o4	0.1	Modified Van Veen grab (APN grab, patent Akvaplan-niva)
hs	0.1	Van Veen grab
ko	0.2	Diver-operated airlift system/corer
ar	0.1	Box-corer
o6	0.1	Modified Van Veen grab (APN grab, patent Akvaplan-niva)
o2	0.1	Van Veen grab
o8	0.1	Van Veen grab
o7	0.1	Van Veen grab
ze	0.1	Van Veen grab, dredge with 5 mm mesh size (qualitative)
pu	0.01	Eckman grab
gd	0.1	Van Veen grab
n3	0.1	Van Veen grab
70	0.1	Van Veen grab
of	0.1	Van Veen grab
of	0.1	Van Veen grab
bl	0.06	Van Veen grab
gr	0.1	Van Veen grab
fb	0.1 and 0.2	Petersen dredge
lm	0.1	Van Veen grab
oc	0.24	Van Veen grab
o1	Variable	Variable (museum collection)
ap	Variable	Variable (museum collection)
ka	0.1 and 0.035	Smith-McIntyre grab/core
do	0.1	Smith-McIntyre grab
M2	0.045	Van Veen grab, hand-operated
M3	0.05	Ponar grab
M6	0.05 and 0.1	Several (Ponar grab, Smith-McIntyre and Veen grab)
M7	0.2	Van Veen grab, hand-operated
M8	0.1	Smith-McIntyre sampler, hand-operated
M0	0.05	Van Veen grab, hand-operated
M1	0.25	'Ocean' grab
M4	0.08	Van Veen grab, hand-operated
M5	0.25	'Ocean' grab
M9	0.04	Van Veen grab
bo	na (qualitative data)	Variable

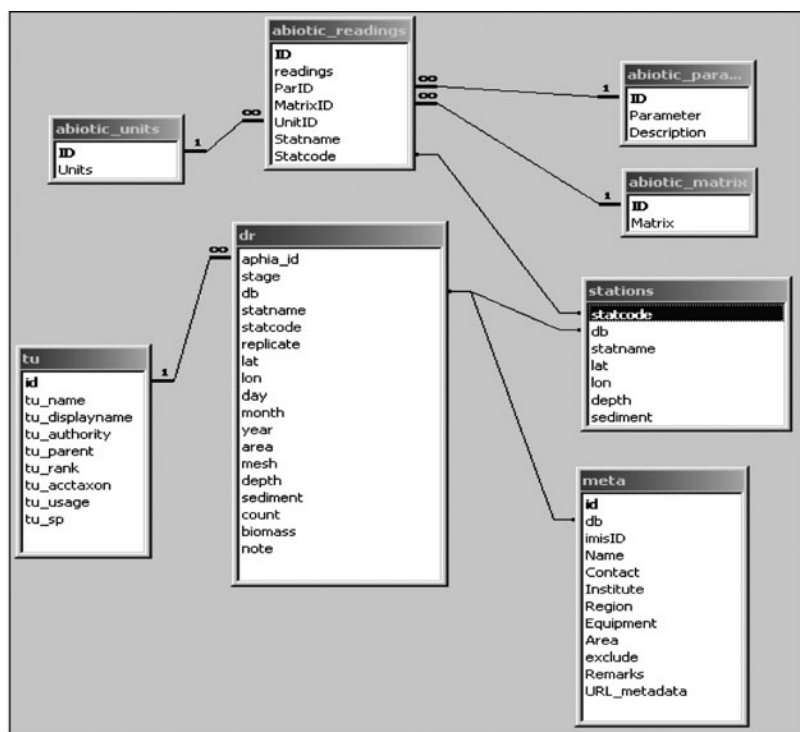


Fig. 1. Relational structure of the MacroBen database. Most table names and field names are self-explanatory; dr - distribution records; tu - taxonomic units; id - unique identifier for a record in that table. Lines show the relationships between the tables, with '1' and infinity signs indicating that one record in the first table can have many related records in the second table (e.g. one taxonomic unit has many distribution records)

A snapshot of ERMS was included in the MacroBen database, in the taxonomic unit (tu) table. The classification that is included in ERMS was used to create mechanisms to combine taxa into taxa of higher rank and to calculate several taxonomic variance measurements (Vanden Berghe 2006).

Abiotic variables measured at the stations, such as temperature, salinity and sediment type, were standardised and are stored in the table *abiotic_readings*. The measured parameters, the matrix and the units are stored in the tables *abiotic_parameters*, *abiotic_matrix* and *abiotic_units*.

The descriptive metadata of the different datasets are stored in the table called *meta* and linked with the biogeographical information through the unique dataset code (db). In the *meta* table, information was recorded that was essential for the interpretation of the data, especially information on sample sizes and methodology. Table 1 gives an overview of the datasets included in MacroBen, and was created on the basis of a report extracted from IMIS. Unique identifiers for each of the datasets are listed in the table, and can be used to find the relevant record in IMIS.

The database interface can be made available upon request, for similar initiatives, or to re-utilise some of

the coding to calculate the biodiversity measures. The Manuela Project, part of MarBEF, made use of the same database structure and tools (Vandepitte et al. 2007). Future work within Theme 1 of MarBEF will also make use of the system.

FUNCTIONALITIES

An interface was built on the integrated database, allowing users to manipulate data prior to analysis and allowing subselection of data at the level of dataset, species, or individual distribution records (Fig. 2).

The MacroBen database stores a set of built-in functions for calculation of taxonomic and diversity indices. Various options can be chosen for subselecting part of the data for analysis, such as the inclusion or exclusion of several datasets, selecting only the qualitative or quantitative data, only observations on adult specimens, restricting the data to a single taxonomic group or an identification rank or excluding manually non-macrobenic taxa. Temporal or spatial selections can

also be made. By indicating the proportion of samples in which a taxon has to be present and the minimum number of individuals in a sample to force the species to be present, rare species can be excluded from the selection. Excluding rare species has the effect of reducing the data matrix to a more manageable size (depending on the analytical objectives); it also minimises the effects of rare, possibly vagrant species, on the analysis (Gray 1981). Though the facility to conduct such filtering was considered important, the use of this feature is not necessarily recommended: modern computers and software are able to handle large matrices; a suitable choice of algorithms should make sure that the analysis demonstrates main effects, rather than those resulting from chance encounters of rare species.

The interface facilitates pooling of records using different criteria: replicates, taxonomy and life stages. For taxonomy, there were different lumping strategies: species level, genus level, family level, valid taxon or original name. The species-level lumping strategy keeps the highest taxonomic precision but sample size will decrease, since all incomplete identifications will be discarded. Aggregating records at genus or family level will decrease the taxonomic precision but will allow the inclusion of records only identified to genus or family,

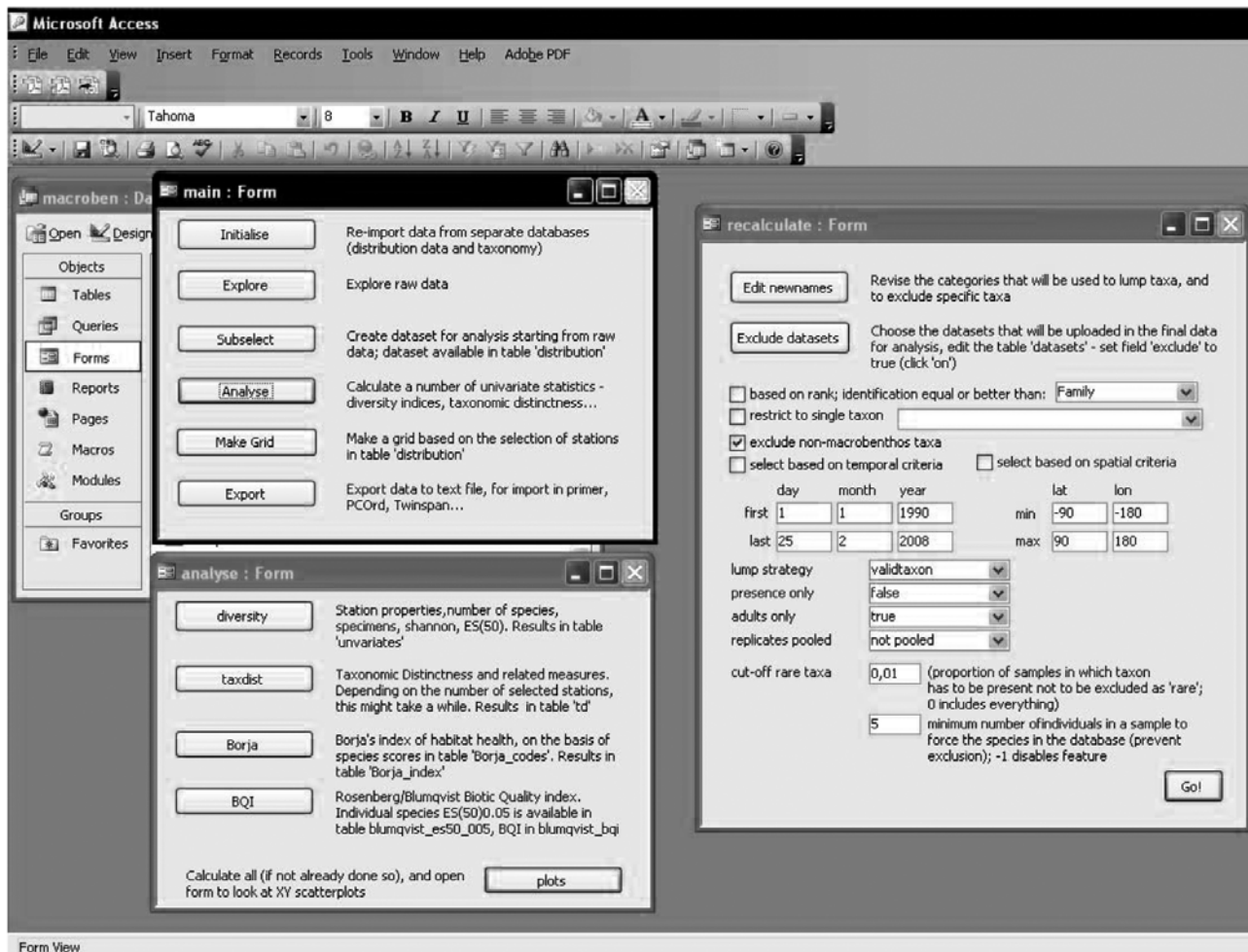


Fig. 2. User interface of the MacroBen database

respectively, thus increasing the number of records available for analysis. The main reason to include the taxonomic lumping was to increase the robustness of the conclusions based on the analysis. Aggregating to a higher taxonomic level has the advantage that resulting analyses become more robust, and less dependent on the potential problems posed by differences in identifications by different research groups.

After selection of the data for inclusion and pooling strategies, an intermediate table with density values (ind. m^{-2}) will be created, from which a variety of frequently used diversity and taxonomic indices can be calculated such as: (1) the Shannon-Wiener diversity index (Magurran 1998), (2) the Hurlbert diversity index calculated for 50 individuals, $E(S_{50})$ (Hurlbert 1971), (3) the Biotic Quality Index (Rosenberg et al. 2004), (4) AMBI indices of habitat health (Borja et al. 2000, 2003) and (5) taxonomic distinctness coefficients and related measures (Hurlbert 1971, Clarke & Warwick 1998, 1999, 2001). A graphic interface of the database allows 2-dimensional plotting of the calculated indices.

The different stations used in the selection can be projected (converted from latitude and longitude to distance in m north and east from a reference point) using the Lambert Azimuthal Equal Area or the Azimuthal Equidistant projection. This allows calculating distances between positions of stations, and aggregating data in grid cells, with the size of the cells controlled by the user.

After selection, calculation of the different indices and projection, the MacroBen database allows export of the species \times Station matrix to a delimited text file, which can be imported into additional statistical analysis software, such as TWINSPLAN (Hill 1979) or PRIMER (Clarke & Warwick 2001). Both density and count data can be exported; densities are scaled to 1 m^2 and counts are the actual number of specimens counted. Possible export file types are in condensed format (.con), which can be imported in the TWINSPLAN package, an ASCII tab-delimited list (e.g. PCOrd) or an ASCII tab-delimited table (e.g. PRIMER). Another possible export is the taxonomic hierarchy, which can be used as an aggregation file in PRIMER.

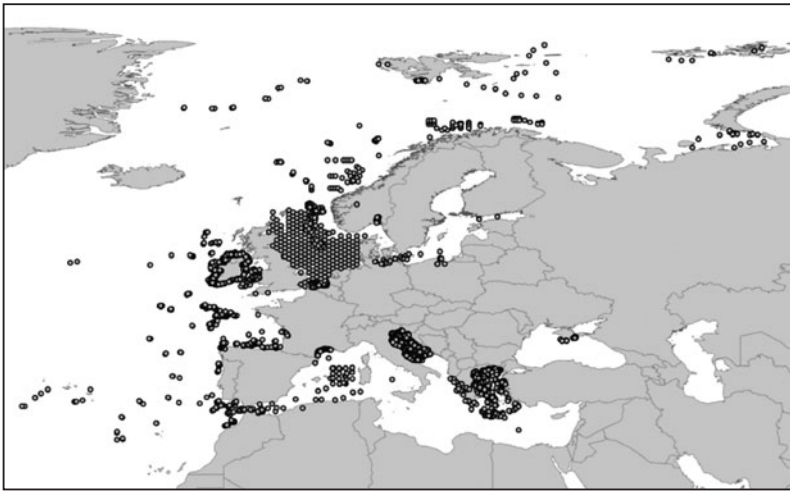


Fig. 3. Distribution map of the sampling stations of the integrated MacroBen database

CONTENT OF THE DATABASE

The MacroBen database contains data from 1937 to 2005 from different research and monitoring programmes and includes 22 897 sampled stations and 465 354 distribution records (Table 1). Depth is available for 416 312 distribution records (86%). There are 7481 taxa, of which 7203 were valid. The database contains 40 766 abiotic readings from 75 different parameters from both the sediment and water; 46 datasets provided by 24 European institutes were collected and integrated into the MacroBen database. The samples range geographically from 32° 2' 48" N to 81° 27' N and from 42° 55' 1" W to 58° 56' 35" E (Fig. 3).

The North Sea and northeast Atlantic region has the highest sampling density. Datasets from the Belgian part of the North Sea and the southern part of the Dutch continental shelf account for 37% of the total biotic records, while <0.05% of the total records in MacroBen are from the Skagerrak and Baltic Sea region. It is essential to allow for these strongly unequal sampling densities across the different geographical regions in evaluating the ecological basis for any observed patterns.

DATA POLICY

All data stored in the MacroBen database are subject to the declaration of mutual understanding for data sharing within MarBEF Theme 1. The policy implies that the participating institutes, organisations and/or the collector of the dataset remain owners of their contributed dataset, and in control of the conditions under which datasets can be used by a third party. Metadata,

as an essential tool for data discovery, is publicly available for all datasets, and includes the conditions of use. A description of the process that led to the policy, as well as a more complete description of the policy itself, is given in the introduction to this Theme Section. (Somerfield et al. 2008).

CONCLUSION

Probably the most challenging aspect in creating an integrated database is to convince data owners or custodians to contribute data. A relationship based on trust between data manager and data owner is therefore essential. Through networking activities (MarBEF Network of Excellence) at the European scale, an

unambiguous data policy stating the restrictions and future use of data was drafted. Part of the discussions on the data policy and terms of use of the data consisted of a discussion of what the future availability of the data should be. It was agreed to make at least presence/absence data available as soon as a first round of papers based on the combined database was published. Data would be published through EurOBIS (www.marbef.org/data/eurobis), one of the activities of the MarBEF network. From there, the data would be available for inclusion in the International Portal of OBIS (www.iobis.org) and the Global Biodiversity Information Facility (GBIF, www.gbif.org).

Compiling an integrated database on soft-bottom macrobenthic fauna is a time-consuming effort which requires sound and professional data management. However, costs are relatively low, compared to the costs (ship time, sampling, identification) of obtaining the data. A cost-comparison described by Zeller et al. (2005) indicated that recovering paper-based, archived data and then creating electronic databases is much cheaper than the actual survey itself: the price for recovery would only be 0.2 to 0.5% of the original survey costs. As analysis of these integrated data can lead to new scientific insights, data from different sources, obtained for different uses can, in combination, provide substantial added value. An important task when integrating different data is the standardisation of taxonomic, geographical and sampling information. An essential element of this standardisation is the adoption of controlled vocabularies for various aspects of the data, including sampling methodology, gazetteer and taxonomic reference lists. Ideally, these would be used by the scientist while collecting the data. Also, the scientist should be aware

of potential re-use of the data collected; all too often raw data are discarded, or information essential to other uses of the data are not written down. In general, there is a lack of training in, and understanding of, data management issues. The curriculum of environmental sciences (and other data-intensive sciences) should include instruction in proper data management procedures, just like students are now exposed to courses in statistical analysis.

Working with an integrated database such as MacroBen has its pitfalls: combining data from different sources causes extra variability and biases. For such large databases, it might be better to aggregate some of the data, sacrificing precision for accuracy. Since identifications were done by very many different groups, it is impossible to verify whether these identifications were done consistently—this would require ring-testing, or comparable inter-comparison exercises, for which no time or resources were available. It might therefore be beneficial to work at the level of genus or even higher, rather than at the more precise but possibly inaccurate level of species. Nevertheless, the result of the MacroBen data integration was the production of a very large dataset which, with suitable adjustments for inconsistencies in the data, provided enhanced statistical power in the identification of significant patterns. Also, the larger ‘footprint’ of the data (i.e. the larger taxonomic, geographical and temporal cover) should, in practice, result in the presence of stronger signals in the data. This increase in power and in signal should more than compensate for any loss in precision.

Of course, integration of existing data from disparate sources will rarely match the outcome of collaborative international research and monitoring programmes in terms of precision and accuracy. In the present integrated database, distribution of the data is dictated by research needs of the individual studies, and results in strong geographical and temporal bias. Large differences in sample size and replication restrict the type of analysis that can meaningfully be applied to the data. However, integrating all available data seems to be the only way, for the time being, to build databases that are needed to inform environmental management at and above sea-wide scales. Opportunistic re-use of available data can lead to problems, but the papers in this Theme Section prove that useful insights can be gained from them.

The MacroBen database and publications are only a first step in an ongoing process. MarBEF is now integrating datasets on hard-bottom biota, and planktonic datasets; a first round of papers on an integrated database on meiofauna was published (Vandepitte et al. 2009). Eventually, these activities will demonstrate the scientific and societal value of building collaborative

databases. Undoubtedly, better science would be done if all data were made publicly available after the publication of the reports and articles that refer to them. Many journals have a policy that ensures public availability of the involved datasets but in practice it seems to be poorly enforced (with the exception of genetic sequence data, which are routinely made available through GenBank). Scientists who are custodians of relevant data are urged to contact the MarBEF data management team and explore possible collaboration.

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Appendix 1. Datasets included in the MarBEF database

Aleffi I.F., 2004: LBMRev dataset. Marine Biology Laboratory, University of Trieste, Italy.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=602

The primary aim for this data collection was to build a database and to apply GIS techniques in the Gulf of Trieste and North Adriatic Sea (Aleffi et al. 1992, 1996, 2003, Aleffi & Bettoso 2001, Solis-Weiss et al. 2001). *Dataset code: Im.*

Arvanitidis C., 2000: Aegean polychaetes dataset. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=595

The Hellenic Centre for Marine Research collected samples in the context of a number of National and EU-funded projects. The datasets provide qualitative temporal information on polychaete worms in the Aegean and Ionian Sea (Arvanitidis 2000, Arvanitidis et al. 2002, 2006). *Dataset code: ap.*

Bachelet G., 2004: Benthos Gironde Estuary. Université Bordeaux 1, Station Marine d'Arcachon, Laboratoire d'Océanographie Biologique, France.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=597

The data are from 3 sources, namely the impact of dredging on benthic macrofauna (1979 data), a comparison of macrobenthos between major European tidal estuaries (1991–1992 data) and ecological monitoring of macrobenthos in an area affected by the effluents of a nuclear power plant (2004 data) (Bachelet 1981). *Dataset code: ba.*

Craeymeersh J.A., Kingston P., Rachor E., Duineveld G., Heip C.H.R., Vanden Berghe E., 1986: North Sea Benthos Survey.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=67

The data are the result of the 1986 North Sea Benthos Survey, an activity of the Benthos Ecology Working Group of ICES. Benthic samples were taken in a standardised way, on a regular grid covering the whole of the North Sea, and analysed by scientists from 10 laboratories. Extensive work was done to standardise taxonomy and identifications across the different laboratories (Heip et al. 1992, Craeymeersch et al. 1997). *Dataset code: ns.*

Dahle S., Cochrane S.J., 1992: Northern Barents Sea 1992.

Appendix 1. (continued)

Akvaplan-niva, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=12

Benthic fauna in the Northern Barents Sea was mapped in July 1992 by Akvaplan-niva (Cochrane et al. 1998). *Dataset code: o2.*

Dahle S., Palerud R., Anisimova N., 1992: Benthic fauna around Franz-Josef Land. Akvaplan-niva, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=11

Benthic fauna in the Franz-Josef Land was mapped in August 1992 by Akvaplan-niva (Dahle et al. 2009). *Dataset code: o8.*

Dahle S., Cochrane S.J., Denisenko S., 1992: Benthic fauna around Pechora Sea. Akvaplan-niva, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=461

Benthic fauna in the Pechora Sea was mapped in July 1992 by Akvaplan-niva (Dahle et al. 1992). *Dataset code: o7.*

Degraer S., Van Hoey G., Willems W., Speybroeck J., Vincx M., 2003: MacroDat Belgium. Macrobenthic data from the Belgian part of the North Sea from 1976 onwards. Ghent University, Biology Department, Marine Biology Section, Belgium.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=633

All data on macrobenthos of the Belgian part of the North Sea collected within several projects of the University of Ghent are integrated into this dataset. It was originally compiled to assure a proper data management of all physically separated datasets on macrobenthos (Van Hoey et al. 2004, 2005, 2007, Speybroeck et al. 2005, Rabaut et al. 2007, Van Hoey et al. 2007, Degraer et al. 2008, Willems et al. 2008). *Dataset code: ug.*

Dounas C., 1988: Benthos Cretan Continental Shelf. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=598

This pilot benthic study was carried out during the summer of 1988 on the continental Cretan shelf (Koutsoubas et al. 1990, Karakassis & Eleftheriou 1997, 1998). *Dataset code: do.*

Dounas C., 1996: Environmental impact assessment of oil pollution accident in Gialova lagoon and Navarino Bay. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=272

This dataset was part of a national project on the consequences of the Navarino oil spill in 1994 at the Gialova Lagoon, Ionian Sea (Arvanitidis et al. 1999, Koutsoubas et al. 2000, Triantafyllou et al. 2000). *Dataset code: M0.*

Fabri M.C., 2001: Biocean dataset. IFREMER France.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=490

This dataset combines information on deep sea benthic fauna collected during several IFREMER cruises from 1967 to 2001. Due to its large geographical scope and the deep sea habitat, this dataset can be considered to some extent as an outlier of the MacroBen database (Fabri et al. 2004, 2006). *Dataset code: bo.*

Gray J.S., 1997: Oslofjord 96-97. University of Oslo, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=1148

Unpublished soft bottom benthic data collected in the Oslofjord within the framework of a PhD study. *Dataset code: of.*

Grémare A., Amouroux J.M., Labrune C., 1998: Redit dataset. Observatoire Océanologique de Banyuls-Sur-Mer, Laboratoire d'Océanographie Biologique, France.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=213

This dataset describes the benthic macrofauna in the Gulf of Lyons. It was collected in order to assess the spatial scale of the increase of the polychaete *Ditrupa arietina*. *Dataset code: gr.*

Herrmann M., Laudien J., 2004: Soft bottom community structure and diversity in Arctic Kongsfjorden. Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Germany.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=614

The data were collected as part of a diver-operated shallow-water (5-30m) research study of the soft bottom benthic community in Arctic Kongsfjord/Spitsbergen (Laudien et al. 2004, Herrmann 2004). *Dataset code: ko.*

Hummel H., Sijm W.C.H., Escaravage V., 2004: BIS dataset of the south-western part of Netherlands (1985-2004). Benthos information System, Monitor Taskforce - NIOO-CEME, Netherlands.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=599

This was the largest contributing dataset (about 130 000 distribution records), over 95% of which was sourced from several Dutch monitoring programmes carried out in the Dutch Delta area (Eastern- & Western Scheldt Estuary, Lake Grevelingen, Lake Veere) and the Dutch coastal zone (Voordelta). *Dataset code: ni.*

Janas U., 2002: Gulf of Gdansk dataset. University of Gdansk, Institute of Oceanography, Department of Marine Biology and Ecology, Poland.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=612

The datasets relate to 2 studies in the Gulf of Gdansk, one in 1995 to study the influence of hypoxia and hydrogen sulphide on the macrofauna and the other in 2002 to analyse the distribution of the macrofauna (Janas 1998). *Dataset code: gd.*

Karakassis I., 1997: Cretan shelf macrofauna and macrofauna of Greek polluted sites. Biology Department, University of Crete, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=613

The original objective of the Cretan Shelf dataset was to unravel the structure of the benthic ecosystem of the continental shelf of Crete; the macrofauna of Greek polluted sites gathered data on the benthic effects of fish farming (Karakassis & Eleftheriou 1997, 1998, Karakassis et al. 1999, 2000, 2002, Karakassis & Hatzizanni 2000, Hyland et al. 2005). *Dataset code: ka.*

Kendall M.A., 1996: Arctic soft-sediment macrobenthos. Plymouth Marine Laboratory, UK.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=533

Samples of the macrobenthic fauna of soft sediments were collected from around Svalbard during the 1991 Arctic EPOS

Appendix 1. (continued)

cruise of RV Polarstern (Kendall 1995). *Dataset code: ar.*

Kendall M.A., Widdicombe S., 1999: Plymouth Sound dataset. Soft sediment macrobenthos from the Plymouth Sound from 1995. Plymouth Marine Laboratory, UK. Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=534

The intended use of this dataset of the Plymouth Sound was the description of small-scale spatial patterns in soft sediment fauna (Kendall & Widdicombe 1999). *Dataset code: pl.*

Kotwicki L., 1996: Bay of Puck dataset. Polish Academy of Sciences, Institute of Oceanology, Department of Marine Ecology, Poland.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=611

The dataset was collected in July 1996 for habitat mapping of the Bay of Puck. *Dataset code: pu.*

Koukouras A., 2000: Northern Aegean dataset. Aristotelian University of Thessaloniki Department of Zoology and Zoological Museum, School of Biology, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=630

The dataset consists of a museum collection of long term qualitative macrobenthic data from the Aegean and Ionian Sea. An extensive list of peer-reviewed articles was derived from this dataset. *Dataset code: o1.*

Mackie A.S.Y., Oliver P.G., Rees E.I.S., 1991: Biomôr 1 dataset. Benthic data from the Southern Irish Sea from 1989–1991. National Museum and galleries of Wales, Cardiff, UK. Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=1600

Surveys of benthic invertebrates of the Southern Irish Sea were carried out in 1989 and 1991. Both quantitative and qualitative samples were taken for faunal and sediment analysis (Mackie et al. 1995). *Dataset code: o5.*

Nevrova H., Petrov A., Revkov N., 1996: Laspibay-Black Sea dataset — IBSS, Sevastopol. Institute of Biology of the Southern Seas (IBSS), Ukraine.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=629

The dataset arose from an investigation of the structure of macrozoobenthos and microphytobenthos assemblages in relation to recreation and marifarming development in Laspibay (SW Crimea, the Black Sea) (Petrov 2000, Revkov & Nikolaenko 2002, Revkov 2003a,b, Revkov & Sergeeva 2004). *Dataset code: m9.*

Occhipinti-Ambrogi A., 2002: Cesenatico dataset. Department of Ecologia del Territorio, University of Pavia, Italy.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=600

This dataset was compiled in order to monitor long-term responses of the macrobenthos community to environmental quality changes in the Northern Adriatic Sea (Occhipinti-Ambrogi et al. 2005). *Dataset code: oc.*

Olsgard F., 1994: Oslofjord 93-94. Akvaplan-niva, Norway. Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=1152

Unpublished data collected as part of a general environmental investigation of the Oslofjord. *Dataset code: of.*

Petrov A., Revkov N., 1986: MegFeod-Black Sea dataset — IBSS, Sevastopol. Institute of Biology of the Southern Seas

(IBSS), Ukraine.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=626

The dataset arose from a comparative investigation of the structure and spatial patterns of macrozoobenthic assemblages along the coast of southeastern Crimea (Sergeeva & Mikhailova 1989a, Mironov et al. 1992, Petrov 1999, 2000, Hyland et al. 2005). *Dataset code: m1.*

Petrov A., Revkov N., 1993: Strelbay-Black Sea dataset — IBSS, Sevastopol. Institute of Biology of the Southern Seas (IBSS), Ukraine.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=627

The dataset arose from an investigation of the structure and condition of macrozoobenthos assemblages under persistent anthropogenic impact (Kisseleva et al. 1999, Petrov 2000, Revkov 2003a,b, Petrov & Revkov 2003, 2005). *Dataset code: m4.*

Petrov A., Revkov N., 1986: Jalta-Black Sea dataset — IBSS, Sevastopol. Institute of Biology of the Southern Seas (IBSS), Ukraine.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=628

The dataset arose from comparative studies of the condition of macro- and meio-zoobenthos around Jalta Gulf under the influence of domestic sewage discharge and recreation activity (Sergeeva 1992, Mikhailova 1989, Petrov 1999, 2000). *Dataset code: m5.*

Picton B.E., Emblow C.S., Morrow C.C., Sides E.M., Tierney P., McGrath D., McGeough G., McCrea M., Dinneen P., Falvey J., Dempsey S., Dowse J., Costello M.J., 1999: Marine sites, habitats and species data collected during the BioMar survey of Ireland. Environmental Sciences Unit, Trinity College, Dublin, Ireland.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=345

Through marine habitat and biotope surveys, the Biomar project (1992–1996) aimed at improved management of coastal ecosystems in Britain and Northern Ireland. Qualitative benthic data from 200 littoral and 700 sublittoral sites around the Republic of Ireland were collected both by direct observations on seashores and by SCUBA divers (Sides et al. 1995, Costello et al. 1996, Connor et al. 1999, McGrath et al. 2000). *Dataset code: bi.*

Rumohr H., 1995: Kiel Bay intercalibration dataset. Leibniz Institute of Marine Sciences, Marine Ecology Division, Germany.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=618

The ICES/HELCOM Intercalibration Exercise provided a series of replicate samples from 1 station in Kiel Bay from May 1995 (Rumohr et al. 2001). *Dataset code: 70.*

Rumohr H., Fleischer D., 2004: N3 data of Kiel Bay. Leibniz Institute of Marine Sciences, Marine Ecology Division, Germany.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=617

Long term monitoring of all invertebrate species of station N3 in Kiel Bay in the Western Baltic was conducted between 1986 and 2004. *Dataset code: n3.*

Sardá R., 1997: Soft Bottom Communities of the Bay of

Appendix 1. (continued)

Blanes. Centre d'Estudis Avançats de Blanes (CEAB) Consejo Superior de Investigaciones Científica (CSIC), Spain.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=603

Soft bottom communities of the Bay of Blanes in Girona were sampled from 1992 to 1997 in the framework of 2 Spanish national projects analysing the regulation of biological production in the Mediterranean littoral (Pinedo et al. 1996, 1997, Sarda et al. 1999, 2000). *Dataset code: bl*.

The Norwegian Oil Industry Association, 2001: Offshore reference stations, North/Norwegian sea. The Norwegian Oil Industry Association (OLF), Akvaplan-niva and Det Norske Veritas, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=999

The dataset is a compilation of selected reference stations from large-scale annual surveys of the benthic fauna in the vicinity of petroleum installations, funded by the Norwegian Oil Industry Association. *Dataset code: o3*.

The Norwegian Oil Industry Association, 2002: Offshore reference stations, Norwegian/Barents Sea. The Norwegian Oil Industry Association (OLF), Akvaplan-niva and Det Norske Veritas, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=997

Compilation of selected reference stations from large-scale annual surveys of the benthic fauna in the vicinity of petroleum installations, funded by the Norwegian Oil Industry Association. *Dataset code: o4*.

The Norwegian Oil Industry Association, 2000: Offshore reference stations, Finnmark. The Norwegian Oil Industry Association (OLF), Akvaplan-niva and Det Norske Veritas, Norway.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=998

Compilation of selected reference stations from large-scale annual surveys of the benthic fauna in the vicinity of petroleum installations, funded by the Norwegian Oil Industry Association. *Dataset code: o6*.

Vatova A., 1936: Fauna Bentonica dataset, Instituto di Biologia Marine per l'Adriatico, Venezia, Italy.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=596

These data were collected between 1934 and 1936 as part of a PhD study. Scientists from the Hellenic Centre for Marine Research computed the dataset afterwards (Vatova 1949). *Dataset code: fb*.

Węśławski J.M., Malec E., Jaskuła R., Włodarska-Kowalczyk M., Kędra M., 2002: Polish Arctic Marine Programme. Macro-benthic data from Hornsund from 2002. Polish Academy of Sciences, Institute of Oceanology, Poland.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=243

This dataset was collected as part of an All Taxa Biodiversity Inventory (ATBI). *Dataset code: hs*.

Whomersley P., 2003: National Marine Monitoring Programme. Benthos data of the North Sea, Irish Sea, English Channel from 2002–2003. Centre for environment, fisheries and aquaculture science, Burnham-on-Crouch, UK.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=615

The data were generated as part of the UK's mandatory monitoring requirements under the OSPAR Joint Assessment and Monitoring Programme (JAMP) and to monitor long-term trends at selected temporal stations around the UK. *Dataset code: np*.

Zenetos A., 1986: Zoobenthos Kyklades, Aegean Sea dataset. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=625

Under the framework of the project 'Oceanographic studies in open Seas', a survey of the benthic fauna of the Central Aegean Sea was performed in July 1986 (Van Aartsen & Zenetos 1987, Zenetos et al. 1991, 1993, Kallonas et al. 1999). *Dataset code: m8*.

Zenetos A., 1987: Aegean Sea coastal benthic communities, Geras Gulf (Mytilini), chemical pollution (tannery effluents). Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=622

An impact study of a tannery effluent on the benthic community was conducted over 2 and a half years in the Geras Gulf (Papathanassiou et al. 1989, Zenetos & Papathanassiou 1989, Pancucci & Zenetos 1990, Zenetos et al. 1992, Papathanassiou & Zenetos 1993, Bogdanos et al. 2002). *Dataset code: m2*.

Zenetos A., 1990: Seasonal zoobenthos, Saronikos. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=289

This dataset was collected under the framework of 2 different projects, recording biological parameters and an investigation of the effects of a wastewater treatment plant on the zoobenthos in Saronikos Gulf. (Nicolaidou et al. 1993, Zenetos et al. 1994, 1999, Simboura et al. 1995, Simboura & Zenetos 2002). *Dataset code: m3*.

Zenetos A., 1991: Kalamitsi dataset. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=623

The dataset arose from a survey of the Kalamitsi area of the Ionian Sea (Zenetos et al. 1997). *Dataset code: m6*.

Zenetos A., Bogdanos C., 1992: Kerkyra dataset. Hellenic Centre for Marine Research, Greece.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=624

The dataset arose from a survey of the Kerkyra area of the Ionian Sea. *Dataset code: m7*.

Zettler M.L., 2005: Macrozoobenthos Baltic Sea (1980–2005) as part of the IOW-Monitoring. Institut für Ostseeforschung Warnemünde, Germany.

Available at: www.marbef.org/modules.php?name=People&lvl=Data&show=html&dasid=601

This time-series study of species composition and biomass or abundance of macrozoobenthos in the Belt Sea and the Baltic proper provide data from 1979 to 2005 as part of the HELCOM monitoring programme (Wasmund et al. 2004). *Dataset code: ze*.



Continental-scale patterns in benthic invertebrate diversity: insights from the MacroBen database

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ABSTRACT: Latitudinal clines in species diversity in limnic and terrestrial habitats have been noted for well over a century and are consistent across many taxonomic groups. However, studies in marine systems over the past 2 to 3 decades have yielded equivocal results. We conducted initial analyses of the MarBEF (EU Network of Excellence for Marine Biodiversity and Ecosystem Function) database to test for trends in local and regional diversity over the latitudinal extent of European continental-shelf waters (36° to 81° N). Soft-sediment benthic macrofauna exhibit little evidence of a latitudinal cline in local (α -) diversity measures. Relationships with water depth were relatively strong and complex. Statistically significant latitudinal trends were small and positive, suggesting a modest increase in diversity with latitude once water-depth covariates were removed. These results are consistent regardless of whether subsets of the database were used, replicates were pooled, or component taxonomical groups were evaluated separately. Local and regional diversity measures were significantly and positively correlated. Scientific cooperation through data-sharing is a powerful tool with which to address fundamental ecological and evolutionary questions relating to large-scale patterns and processes.

KEY WORDS: Biodiversity · North Atlantic · Mediterranean · Arctic · Baltic · Continental shelf · Benthos · Latitude

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INTRODUCTION

Biodiversity research has expanded in the past 2 to 3 decades from the realm of systematics and biology to the fields of biogeography and evolution. This trend has resulted in renewed interest in describing and recording taxa, with corresponding studies describing regional and global biodiversity patterns, developing new techniques with which to measure diversity, proposing mechanisms responsible for generation and maintenance of these patterns, and experimentally investigating the functional significance of biodiversity

(e.g. Clarke & Warwick 1998, Willig et al. 2003, Gage 2004, Hillebrand 2004, Solan et al. 2006, and references therein). These timely studies come as the earth's ecosystems are confronted with natural and human-induced environmental change and its impact on biotic systems. Informed management and conservation strategies require a solid understanding of underlying biodiversity patterns and their consequences for system functioning.

Renewed efforts to document marine biodiversity were probably initiated by Grassle & Maciolek (1992), who suggested that there may be as many as 10 million

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benthic infaunal species yet to be identified in the deep sea. Since then, there have been many studies investigating diversity patterns, with special focus on how biodiversity varies with water depth and latitude. Many studies have identified an increase in diversity with water depth through the bathyal zone, followed by a decrease in abyssal and hadal zones (e.g. Rex 1981, Levin et al. 2001). Latitudinal patterns have been less clear, but, in general, diversity of benthic communities or of component groups has been shown to decline with increasing latitude in the northern hemisphere (Rex et al. 1993, 2000, Boucher & Lamshead 1995, Culver & Buzas 2000, Mokievsky & Azovsky 2002, Gage et al. 2004, Hillebrand 2004, Witman et al. 2004, Renaud et al. 2006). Other regional studies, however, have failed to detect this pattern or even showed regionally opposite trends (Heip et al. 1992, Kendall & Aschan 1993, Dauvin et al. 1994, Kendall 1996, Clarke & Lidgard 2000, Lamshead et al. 2000, Ellingsen & Gray 2002, Rees et al. 2007), and patterns in some taxonomic or trophic groups are not replicated in others (Azovsky 2000, Ellingsen 2001, Hillebrand 2004, Karakassis et al. 2006).

These conflicting results suggest that multiple factors are responsible for generating and maintaining biodiversity of the benthos. Instead of being viewed as a problem, these varying patterns can be used to help detect which factors/mechanisms are important for different conditions, scales, and taxa. Proposed mechanisms can be divided into 2 principle categories: ecological and evolutionary. Ecological mechanisms include temperature, primary productivity, sediment heterogeneity, and life-history strategy (e.g. Huston 1979, Etter & Grassle 1992, Lamshead et al. 2000, 2002, Roy et al. 2000, Levin et al. 2001, Renaud et al. 2006), while evolutionary factors include tectonic history, climate fluctuation, and the ages of taxonomic clades (e.g. Svavarsson et al. 1993, Crame 1997, 2001, Culver & Buzas 2000, Clarke & Crame 2003, Gage 2004, Włodarska-Kowalczyk et al. 2004). Spatial variability in these mechanisms determine biodiversity patterns, and varying degrees of interaction among them may be responsible for the differing observations recorded in the literature.

Patterns of species richness in the global avifauna appear to be well explained by models incorporating both spatial variation in available energy and the likelihood of a species reaching potentially suitable areas (Storch et al. 2006). Simple geometrical constraints may also play a role in concentrating species richness towards the midpoint of a domain (the 'mid-domain effect' or MDE, reviewed in Colwell et al. 2004). However, the predictive power of MDE models is critically dependent on *a priori* divisions between domains and knowledge of species ranges (Hawkins et al. 2005,

Zapata et al. 2005, Storch et al. 2006). They are, therefore, likely to be of limited utility in marine systems where such information is largely absent. Determining the relative importance of ecological, evolutionary, and statistical (geometrical) factors to the generation and maintenance of observed patterns in species richness remains a fundamental challenge for biodiversity studies.

Before mechanisms can be assessed, however, it is critical to evaluate the basis for the patterns that have been observed. Some studies have included extensive local sampling and meta-analysis, while others are based on limited sampling. Sample-collection techniques have not always been comparable, and intensive sampling may be restricted over narrow geographical ranges. An appropriate dataset must contain many samples collected by comparable procedures across a wide geographical domain: an effort not afforded through normal research projects—or even many careers. Marine Biodiversity and Ecosystem Functioning (MarBEF: www.marbef.org), an EU Network of Excellence, has made major strides to remedy these biases by compiling a database (MacroBen) comprised of datasets from across the European domain. These datasets from marine benthic studies can be used for a variety of investigations of biodiversity-related questions.

In the present study, we perform initial analyses of this database in reference to European-scale gradients in benthic biodiversity. With the power of such a large collection of comparable data, we can investigate whether there is support for previously identified trends in local (α -) biodiversity with water depth and latitude. We will pursue this for the entire benthic faunal communities, and for important component groups. In the process, we test for the effects of variable sampling effort represented in the database. Confidently identifying latitudinal or depth patterns can inform future investigations of underlying mechanisms responsible for their generation and maintenance.

DATA AND METHODS

MacroBen database. Integrating individual datasets into large databases, to enable analysis on Europe-wide scales, was one of the core objectives of the MarBEF network. Different databases were planned, each to capture comparable data for integrative analyses. The initial database included with data from soft-bottom benthic biotopes. A major effort was undertaken to harmonize the taxonomy across the different datasets: all names were matched, both for spelling and synonymy, with the European Register of Marine Species (ERMS) (Vanden Berghe et al. 2009, this

Theme Section). Raw data were retained whenever possible to allow maximum flexibility during analyses. Most data providers also furnished geographical and physical data.

The finalized dataset was distributed as an Access file to all data providers. Included in the database were several tools to extract data and to calculate basic statistics and diversity coefficients. The final database contained 465 354 distribution records, from 7481 taxa and 23 113 stations. There were 43 individual datasets. A full description of the database is given in Vanden Berghe et al. (2009).

Latitudinal-gradient database. In effort to work with the most inclusive, yet most comparable dataset possible, we performed initial filtering on the MacroBen database. The extracted working database for latitudinal-gradient studies of soft-sediment benthos included: (1) quantitative data, (2) non-juvenile animal taxa, (3) organisms identified to species level, (4) non-colonial animals (Bryozoa, Hydrozoa, Porifera excluded), (5) samples collected after 1980 (for taxonomic comparability reasons), (6) subtidal stations only, (7) samples collected with 0.1 m² grabs only, (8) samples sieved on max. 1 mm mesh, and (9) multiple records from the same location, if available.

While these criteria do not eliminate some potential problems (e.g. unequal effort per sampling location or latitude), they do make initial analyses more straightforward. Preliminary analyses of even this modified database suggested that some analyses should be performed following additional filtering (e.g. Fig. 1A,C).

Initially, samples were pooled for each 1° of latitude. This retains information contained in the database and allows calculation of a 'γ-richness' estimate for each 1° of latitude. Species-area and species accumulation curves were then constructed by plotting pooled 'γ-richness' by 2 measures of sampling effort, area sampled and number of individuals collected, for each 1° of latitude. These are not the traditional species-area or species accumulation curves, but instead are plotted in this way to test for effects of sampling intensity. 'γ-richness' residuals of least-squares regressions (log-transformed variables) were plotted against latitude to determine whether regional γ-diversity changed with latitude after accounting for sampling intensity (Clarke & Lidgard 2000). A multiple linear regression technique was also used to test for effect of latitude on regional diversity accounting for latitudinal differences in area and number of individuals sampled.

The 2 α-diversity indices that we based most of our analyses on are the number of species, S , and Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$. Species richness is better than equitability indices in the study of large-scale patterns, and $E(S_n)$ is robust to sample size variations (Boucher &

Lambhead 1995). In addition, $E(S_n)$ incorporates some of the evenness component of diversity. Analyses were conducted for each sample in the database for the entire faunal assemblage, and initially on samples pooled by 5° increments of latitude.

S and $E(S_{50})$ were plotted against latitude and water depth to determine whether relationships prevalent in the literature were consistent with our data. We tested for these relationships in several ways. First, linear and quadratic (unimodal) models were fitted to the plots of S and $E(S_{50})$ with latitude and water depth. LOWESS (locally-weighted scatterplot smoothing) functions (Quinn & Keough 2002) were also fitted to these data, with α set to 0.75 (i.e. the neighborhood for each locally weighted regression includes 3/4 of all points). The shape of the LOWESS smooth is useful for characterizing the shape of the relationship, and for assessing whether the fitted linear or quadratic model adequately captures this shape. After finding that the water-depth distribution of our sample locations was not random with respect to latitude, we controlled for this covariance by running multiple linear regressions with water depth and latitude as factors. This works well if the underlying relationship is linear, but because quadratic regressions had a better fit for much of the data, we also plotted the residuals from the quadratic regressions of each diversity index with water depth against the quadratic residuals of latitude with water depth. Similar analyses have been performed using residuals from linear regressions (Lambhead et al. 2001, Renaud et al. 2006). Since the Baltic Sea exhibited relatively low biodiversity compared to other areas at that latitude, we performed a second filtering of the dataset by excluding Baltic stations to determine whether this biased our findings for or against identifying latitudinal trends. We then repeated the regression analyses on the dataset with the Baltic data excluded, and on major taxonomic groups (polychaetes, mollusks, and arthropods) from this new dataset.

In addition to species richness and evenness, it is also relevant to ask whether variation in different axes of diversity may be contributing to observed patterns. Taxonomic distinctness, Δ^+ , a measure of relatedness among species (Warwick & Clarke 2001), was calculated for the subset of samples containing 5 or more species. Taxonomic relationships were determined from ERMS. Values were calculated for whole assemblages, annelids, crustaceans, and mollusks, and analyzed using linear and multiple linear regression.

Finally, we wanted to ensure the validity of using α-diversity statistics to evaluate regional diversity patterns. Therefore, we calculated Chao1 and Chao2, and S_{obs} γ-diversity estimators for each dataset and plotted those values against the average S value for those

datasets. If these indices are positively correlated, then local diversity patterns are likely to reflect diversity on regional scales. Analyses were performed using the JMP-In (SAS Institute), PRIMER (Clarke & Gorley 2006), Statistica (StatSoft), R (R Development Core Team 2005), and EstimateS (Colwell 1997) software packages.

Table 1. Summary statistics on component datasets. For additional information see Vanden Berghe et al. (2009, this Theme Section)

Dataset	Location	Depth (m)	No. of records
Baltic Sea			
70	Baltic Sea	23	998
Gd	Baltic Sea	30–100	87
Ze	Baltic Sea	11–90	3433
Ze	Gulf of Finland		7
Mediterranean Sea			
Do	Aegean Sea	10–60	2057
Do	Eastern Basin		453
Gr	Western Basin	10–50	4912
Lm	Adriatic Sea	5–25	6838
North Atlantic Ocean			
Hs	Hornsund, Svalbard	25–203	375
NP	Celtic Sea	35–96	252
NP	English Channel		309
NP	North Sea		365
o2	Barents Sea	59–379	1403
o4	North Sea	71–434	26 166
o4	Norwegian Sea		19 585
o5	Celtic Sea	7–130	1018
o5	Irish Sea/St. George's Channel		2936
o6	Barents Sea	160–374	2262
o6	Norwegian Sea		7460
o7	Pechora Sea	7–207	2106
o8	Franz Josef Land	52–312	1717
Ug	North Sea	35–40	6626
North Sea			
o3	North Sea	65–91	7951

RESULTS

Initial filtering of the MarBEF database resulted in a file containing over 3200 samples and over 1 million individuals from nearly 2200 species. This represents 16 individual datasets covering areas of the Adriatic, Mediterranean, Baltic, Irish, North, Barents, and Pechora Seas, as well as the European Atlantic coast (Table 1), from 36° to 81°N. Depths of stations varied considerably with latitude, with stations in low and high latitudes being generally shallower than stations at mid-latitudes (Table 2). Sample water depth was not recorded for one of the datasets, so samples sizes for regressions (Table 3) against water depth were slightly lower than diversity–latitude relationships.

Regional (by latitude) species diversity varied significantly with the area and number of individuals sampled ($p < 0.05$; $r^2 = 0.58$ and 0.60 , respectively; Fig. 1A,C). Plots of the diversity residuals from these regressions against latitude showed that γ -diversity did not vary with latitude ($p > 0.98$ and $p > 0.27$, respectively; Fig. 1B,D). Multiple linear regression analysis also indicated that this measure of regional diversity did not vary with latitude after controlling for area or number of individuals sampled ($p > 0.98$ and $p > 0.19$, respectively).

Both S and $E(S_{50})$ showed unimodal trends with water depth, with maximum values occurring at intermediate water depths ($r^2 = 0.22$ and 0.41 , $p < 0.0001$, respectively; Table 3, Fig. 2A,B). This trend was the same, whether models were fitted to point data or to data pooled into 50 m depth increments, and the LOWESS smooths show that the second-order polynomial models capture the shape of the relationships well. Unimodal relationships, albeit fairly weak, were also suggested between latitude and both S and $E(S_{50})$ ($r^2 = 0.21$ and 0.33 , $p < 0.0001$ respectively; Fig. 2C,D, Table 3), although the shapes of both the fitted polynomial models and the LOWESS smooths suggest that

Table 2. Number of stations sampled by depth and latitude zone

Depth (m)	Latitude (°N)									
	35–40	40–45	45–50	50–55	55–60	60–65	65–70	70–75	75–80	>80
0–50	55	76	148	518	107	4	4	0	13	0
50–90	1	16	0	40	81	2	1	5	11	4
90–150	0	0	0	32	44	100	0	1	17	0
150–200	0	0	0	0	0	14	2	7	2	1
200–250	0	0	0	0	0	7	6	5	1	1
250–300	0	0	0	0	0	18	7	22	0	0
300–350	0	0	0	0	0	40	13	22	2	1
350–400	0	0	0	0	0	9	11	3	0	0
400–450	0	0	0	0	0	0	2	0	0	0
Total	56	92	148	590	232	194	46	65	46	7

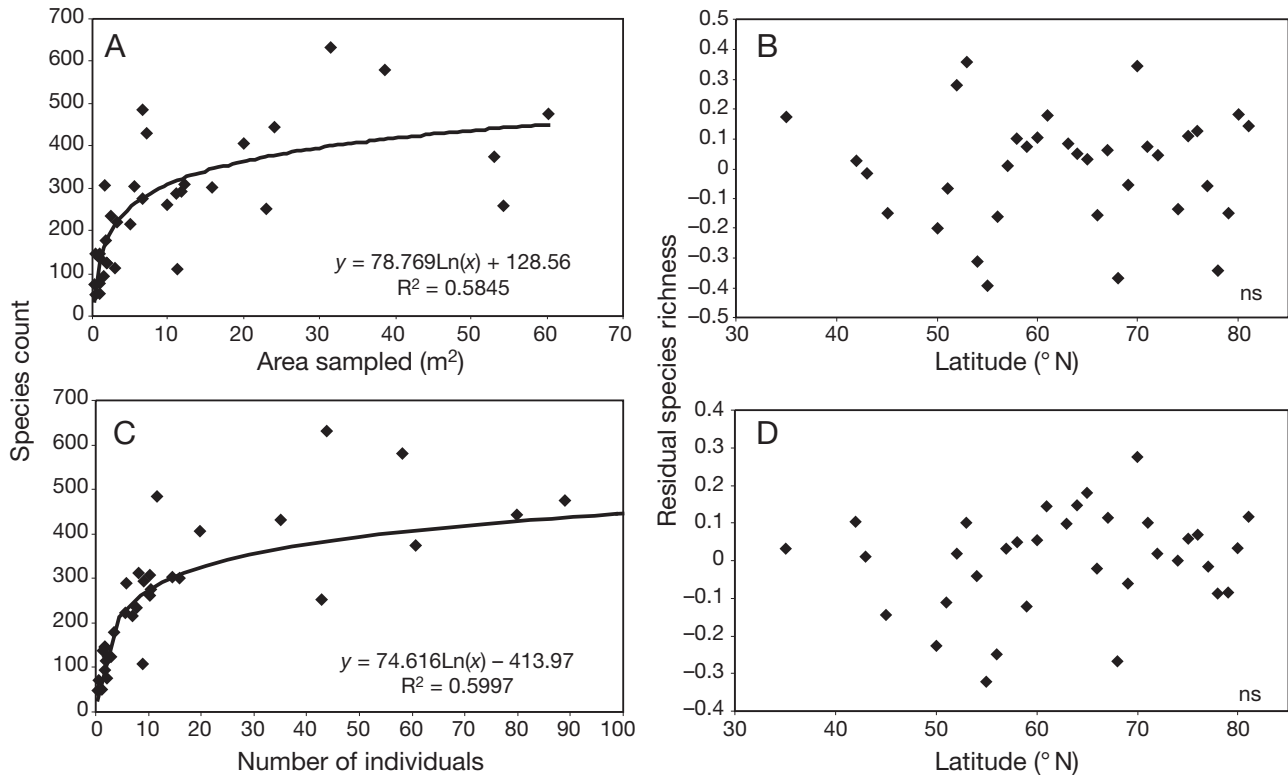


Fig. 1. Regional species richness (species count) pooled by degree of latitude plotted against 2 measures of sampling efforts (A): area sampled and (C) number of individuals sampled. Linear regression of log-transformed data in these 2 plots was performed and the residuals are plotted against latitude in (B) and (D)

Table 3. Linear, quadratic, and multiple linear regression (MLR) analyses of total number of species, S , and Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$, against depth and latitude. r^2 values are presented for each model, or for each predictor in MLR. Regressions of diversity–depth residuals in latitude–depth residuals are also presented. Since quadratic relationships explained most of the variation, residuals (resid) of these regressions (and not the linear regressions) are used. p -values for quadratic regressions are for the quadratic term in the equation; na: not applicable

Regression	Type	Entire dataset		Baltic removed	
		p	r^2	p	r^2
$S \times$ latitude	Linear	0.0001	0.184	0.0001	0.178
$S \times$ latitude	Quadratic	0.0001	0.211	0.0001	0.212
$S \times$ depth	Linear	0.0001	0.028	0.0001	0.013
$S \times$ depth	Quadratic	0.0001	0.218	0.0001	0.185
$S \times$ latitude, depth	MLR	0.0001	0.095, 0.003	0.0001	0.082, 0.009
Quadratic resid: $S -$ depth \times latitude – depth	Linear	0.0008	0.005	0.0001	0.007
$E(S_{50}) \times$ latitude	Linear	0.0001	0.300	0.0001	0.297
$E(S_{50}) \times$ latitude	Quadratic	0.0001	0.331	0.0001	0.337
$E(S_{50}) \times$ depth	Linear	0.0001	0.267	0.0001	0.235
$E(S_{50}) \times$ depth	Quadratic	0.0001	0.413	0.0001	0.376
$E(S_{50}) \times$ latitude, depth	MLR	0.0001	0.032, 0.267	0.0001	0.037, 0.236
Quadratic resid: $E(S_{50}) -$ depth \times latitude – depth	Linear	0.801	na	0.779	na

the main pattern is a relatively abrupt increase north of about 55°, with little change thereafter. Results were similar when the data were pooled into 5° increments of latitude. To remove the potentially confounding effect of water depth on the latitudinal trend, 2 techniques were employed. (1) Multiple linear regression

analyses were performed, and these indicated that both water depth and latitude contributed significantly, but latitude only explained 9.5 and 3.2% of the variability in S and $E(S_{50})$, respectively, while water depth explained 0.3 and 27%, respectively ($p < 0.02$ for all relationships; Table 3). (2) To remove the effect of

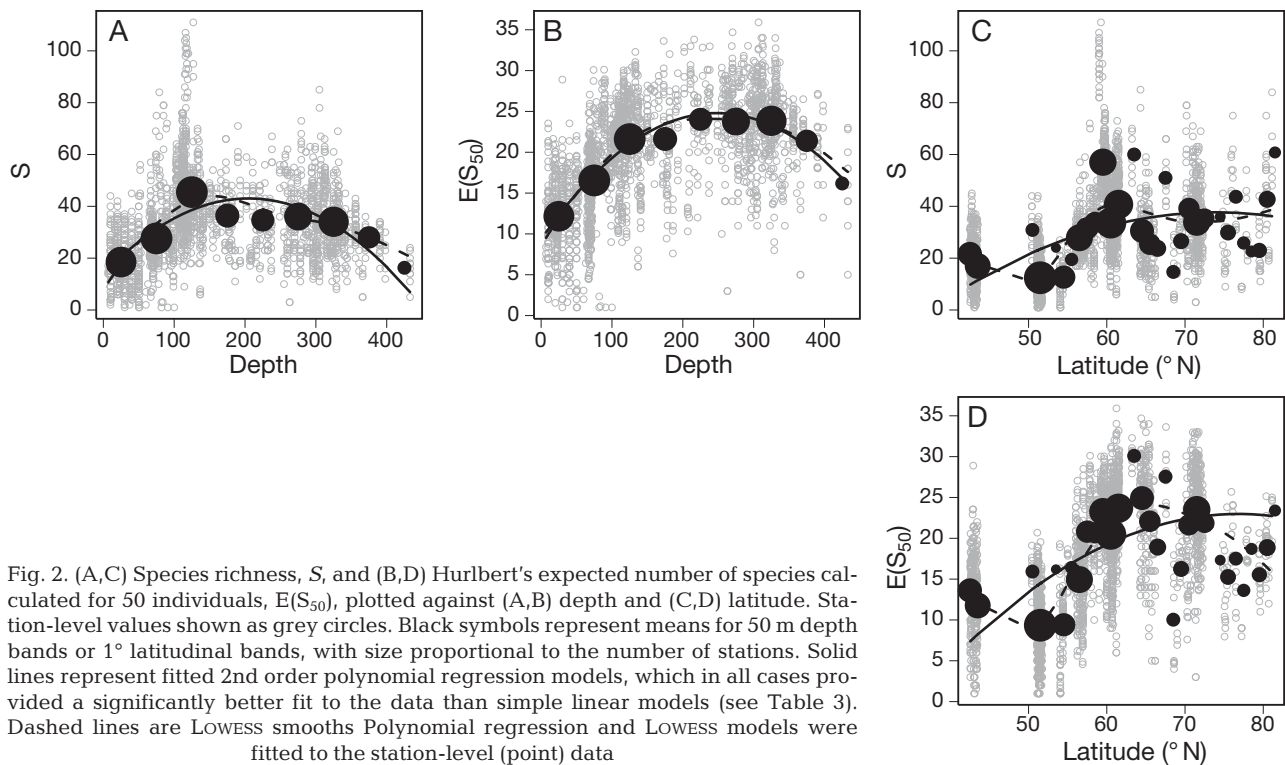


Fig. 2. (A,C) Species richness, S , and (B,D) Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$, plotted against (A,B) depth and (C,D) latitude. Station-level values shown as grey circles. Black symbols represent means for 50 m depth bands or 1° latitudinal bands, with size proportional to the number of stations. Solid lines represent fitted 2nd order polynomial regression models, which in all cases provided a significantly better fit to the data than simple linear models (see Table 3). Dashed lines are LOWESS smooths. Polynomial regression and LOWESS models were fitted to the station-level (point) data

water depth for quadratic relationships, residuals of the diversity–depth (quadratic) relationships were plotted against the latitude–depth (quadratic) residuals. This result indicated that latitude had little or no effect on either S or $E(S_{50})$. The linear regression of the residuals for S was significant ($p < 0.0001$; Table 3) but had $r^2 < 0.005$, while for $E(S_{50})$ the regression was not significant ($p > 0.80$; Table 3).

Both S and $E(S_{50})$ for the Baltic datasets were significantly lower than that for the other datasets (Fig. 3; ANOVA followed by Tukey-Cramer HSD: $p < 0.05$). The multiple regression analyses and residual plots were recalculated after omitting the Baltic datasets, with nearly identical results: little effect of latitude was seen on either diversity measure (Fig. 4, Table 3). Similar analyses of the 3 most abundant taxonomic groups indicated weak or no latitudinal pattern in diversity following residual regressions (Fig. 5, Table 4). Results varied for the different taxonomic groups, with water depth having a much greater effect on polychaete and arthropod diversity than on mollusk diversity (Table 4). Multiple linear regression showed a significant relationship with water depth for these 2 groups, with r^2 ranging from 0.21 to 0.39 (Table 4). Similar analyses showed that latitude did explain almost 20% of the variability in mollusk diversity (Table 4). In all these analyses, the explanatory power of latitude was very weak, but where significant, slopes were positive, i.e. suggesting increasing α -diversity with latitude.

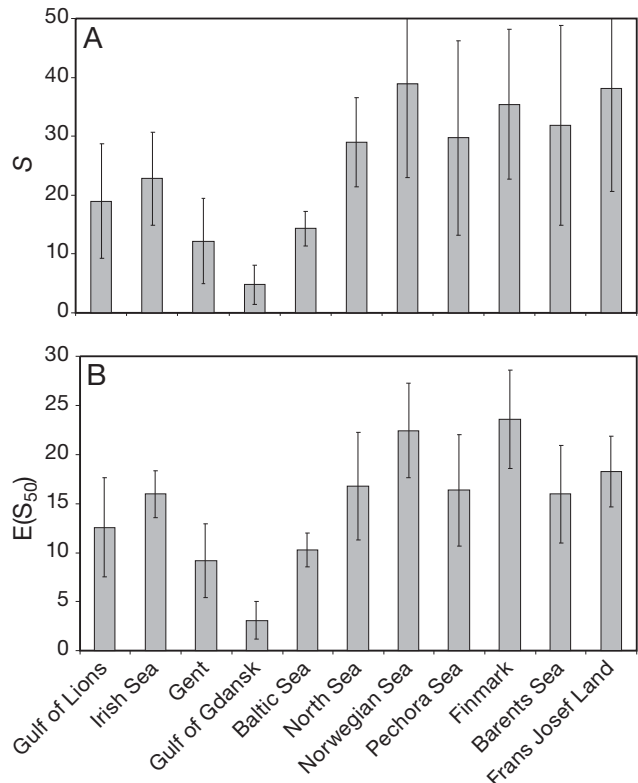


Fig. 3. (A) Total species richness, S , and (B) Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$, in order of increasing latitude. Note low values for Baltic Sea datasets (Gulf of Gdansk, Baltic Sea). Error bars represent SD

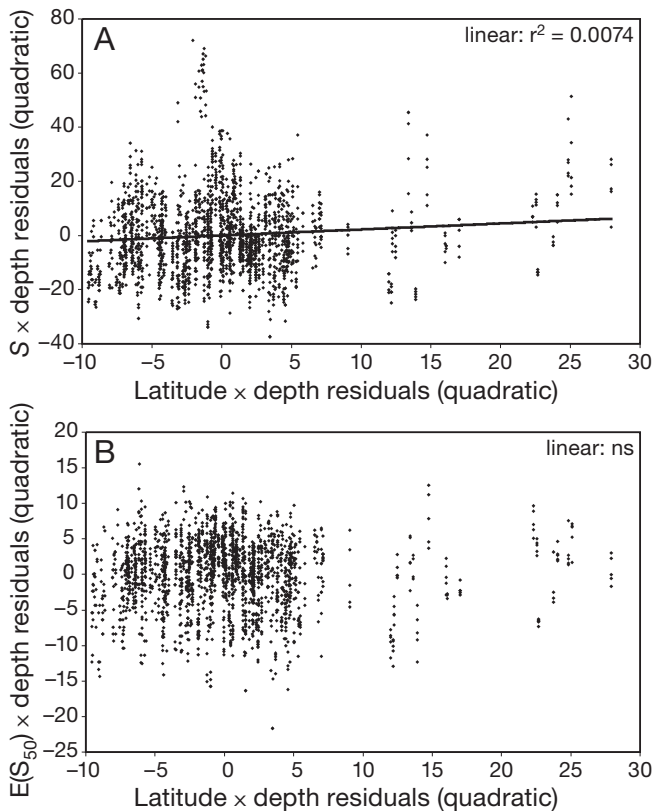


Fig. 4. (A) Residuals of the species richness, S , and (B) Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$, vs. depth regression against the residuals of the latitude vs. depth regression. Residuals are taken from the quadratic regressions. Baltic Sea stations removed. ns = linear regression not significant

Taxonomic distinctness also showed a weak but significant relationship with water depth ($r^2 = 0.041$), with samples from the middle of the range tending to have lower values (Fig. 6), rather than higher values as shown by S and $E(S_{50})$. The p -values for this, and all results for taxonomic distinctness, were <0.001 . After this effect was removed, the residuals showed a weak but significant ($r^2 = 0.025$) increasing trend with latitude (Fig. 6). The extent to which these patterns reflect subtle shifts in the phyletic composition of assemblages is difficult to assess, but different phyla show different patterns (Ellingsen et al. 2005). While annelids showed a positive relationship with water depth ($r^2 = 0.212$), tending to be lower at mid-depths, the remaining relationship with latitude, while significant ($r^2 = 0.035$), was one of decreased values in the middle of the latitudinal range (Fig. 7). Weaker but similar patterns ($r^2 = 0.15$ and 0.012 , respectively) were apparent for crustaceans (data not shown). In contrast, mollusks showed weak relationships with both water depth ($r^2 = 0.009$) and latitude ($r^2 = 0.045$), and indicated a tendency to increase towards the north (Fig. 7).

The Chao1 γ -diversity estimator and the mean (by dataset) α -diversity index, S , showed a positive relationship ($p < 0.05$; $r^2 = 0.39$; Fig. 8). Chao 1 was also highly correlated with S_{obs} and Chao 2 γ -diversity estimators ($p < 0.05$; $r^2 > 0.98$, data not shown).

DISCUSSION

Large-scale patterns in biodiversity

Initial analyses of the MarBEF database indicated little evidence for strong latitudinal trends in diversity (S , $E[S_{50}]$, or Δ^+) of benthic shelf fauna along the European continental shelf. Where statistically significant trends existed, they were generally weak ($r^2 < 0.1$) and positive, i.e. diversity increased with latitude (Figs. 2, 4, 5 & 6; Table 3). Findings were consistent whether interactive effects with water depth were removed by multiple linear regression or through regressions of residuals. Lack of a decline in diversity with latitude on continental-shelf soft substrates has also been documented by others (Kendall & Aschan 1993, Dauvin et al. 1994, Kendall 1996, Ellingsen & Gray 2002), but contradicts findings from the deep Arctic basin by Deubel (2000) and Renaud et al. (2006). The last 2 studies were conducted over shorter latitudinal ranges or beyond the depth range of the present study, however, and with generally low sample density. The present results agree with the observation of Thorson (1957) that, while there may be a latitudinal gradient in diversity for hard-substrate epifauna, similar patterns for soft-sediment benthos are not well-founded. Hillebrand (2004) found the latitudinal gradients in diversity to be particularly weak for benthic infauna in a meta-analysis of >100 marine studies from around the world and from shallow water to the deep sea. Extrapolating results from diversity studies of epifauna to infaunal communities has also proven to be untenable with respect to Antarctic shelf fauna (Włodarska-Kowalczyk et al. 2006).

The trend toward a poleward decrease in marine biodiversity has gained widespread acceptance over the past 30 yr, with similar results observed from deep-sea, estuarine tidal flat, and shallow subtidal hard-substrate communities, and from taxonomic groups as diverse as foraminifera, nematodes, gastropods, bivalves, and crustaceans (e.g. Rex et al. 1993, 2000, Boucher & Lambshead 1995, Roy et al. 1998, Crame 2000, Culver & Buzas 2000, Attrill et al. 2001, Gage et al. 2004, Witman et al. 2004). Patterns are not simple in all of these studies, however (e.g. peaks in diversity at mid-latitude in both Atlantic and Pacific gastropods, Roy et al. 1998; eastern versus western North Atlantic diversity levels in a variety of fish and invertebrates,

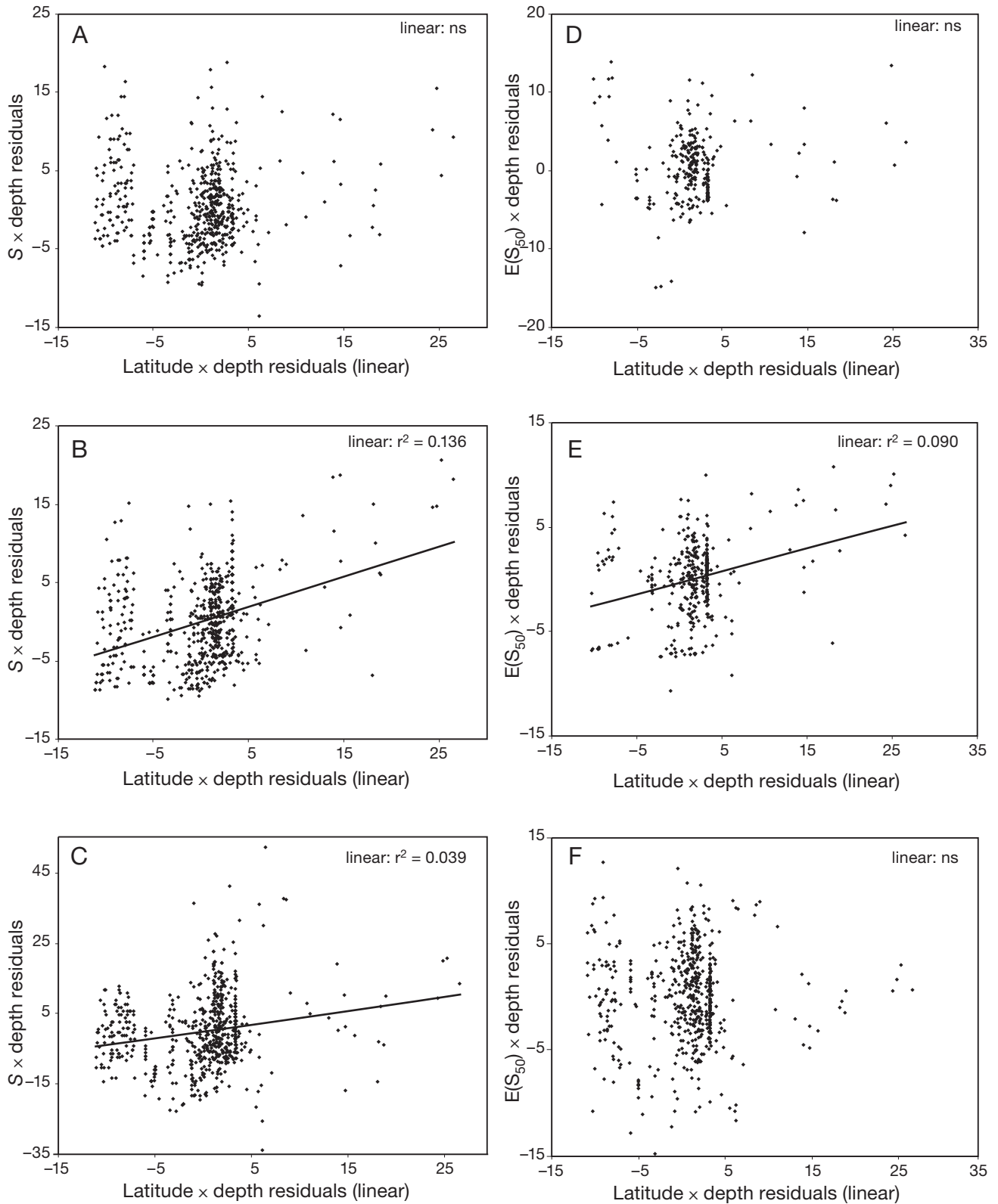


Fig. 5. (A–C) Residuals of the species richness, S , and (D–F) Hurlbert's expected number of species calculated for 50 individuals, $E(S_{50})$, vs. depth regression against the residuals of the latitude vs. depth regression. Data exclude Baltic Sea samples and are for the 3 most common taxonomic groups: (A,D) arthropods, (B, E) mollusks, and (C,F) polychaetes. Regression results expressed as in Table 4

Table 4. Statistical results for linear regressions of diversity indices on latitude and depth for the 3 most common taxonomic groups: polychaetes, arthropods, and mollusks. Analyses were performed following removal of Baltic data. Regressions of linear residuals (Resid) are also shown, as in Table 3. *S* = species richness; *E*(*S*₅₀) = Hurlbert's expected number of species calculated for 50 individuals; MLR = multiple linear regression; ns = not significant

Regression	Type	Polychaetes		Arthropods		Mollusks	
		p	r ²	p	r ²	p	r ²
<i>S</i> × latitude	Linear	0.0001	0.326	0.0001	0.137	0.0001	0.209
<i>S</i> × depth	Linear	0.0001	0.384	0.0001	0.246	0.0001	0.089
<i>S</i> × latitude, depth	MLR	0.0001	0.024, 0.385	0.0001	ns, 0.247	0.0001	0.210, 0.005
Resid: <i>S</i> - depth × latitude - depth	Linear	0.0001	0.039	0.860	ns	0.0001	0.137
<i>E</i> (<i>S</i> ₅₀) × latitude	Linear	0.0001	0.194	0.0001	0.173	0.0001	0.200
<i>E</i> (<i>S</i> ₅₀) × depth	Linear	0.0001	0.321	0.0001	0.304	0.0001	0.118
<i>E</i> (<i>S</i> ₅₀) × latitude, depth	MLR	0.0001	ns, 0.322	0.0001	ns, 0.307	0.0001	0.202, ns
Resid: <i>E</i> (<i>S</i> ₅₀) - depth × latitude - depth	Linear	0.777	ns	0.996	ns	0.0001	0.090

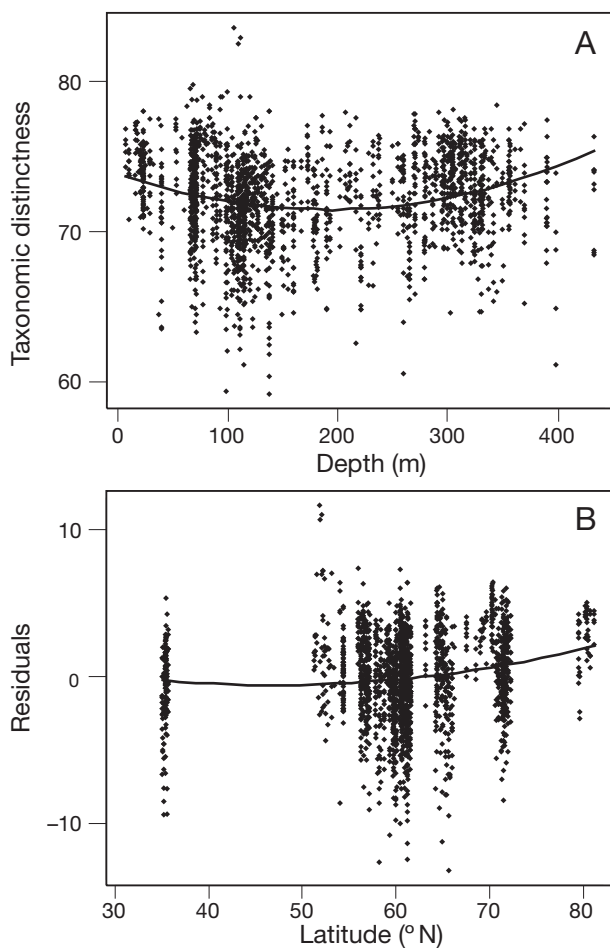


Fig. 6. (A) Average taxonomic distinctness against depth and (B) the residuals from this relationship plotted against latitude. Fitted lines from polynomial regressions

MacPherson 2002). Why then are the results from soft-sediment shelf habitats so equivocal, and perhaps even opposite? First, this may be a consequence of the limited latitudinal range observed in the present study, spanning only about 45° of latitude, while many of

the other studies sampled sites from the equator or even further south. Roy et al. (1998) identified a strong decrease in mollusk diversity with latitude, but much of that decrease took place between the equator and 35° N, a zone we miss entirely with our sampling range. Conversely, few of the other studies cover stations north of around 60° N, whereas the present study has fully half of its stations above that latitude. Sampling high-latitude areas is critical to evaluating not only patterns, but also mechanisms, as several theories postulate history of ice cover and connectivity of ocean basins as contributing to the observed pattern (e.g. Rex et al. 1993, Crame 1997, Gray 2002). Finally, several studies showing decreasing diversity with latitude in different taxonomic groups sampled the same stations (Rex et al. 1993, 2000, Gage et al. 2004), suggesting the possibility that the similar results represent a feature of the combination of stations sampled and perhaps not an underlying global pattern. Sampling density in the present study is unprecedented compared with other studies, reducing the potential problem of site-specific features having disproportionately large effects on observed patterns.

Investigation of biodiversity patterns over such a large spatial scale does present some problem in interpretation of the results. Some of the most obvious comparisons to be made are with high-resolution surveys of smaller components of this range. These smaller, regional studies (e.g. Heip et al. 1992, Ellingsen 2001, Ellingsen & Gray 2002, Rees et al. 2007), however, examine, implicitly or explicitly, impacts of environmental or ecological gradients on community assemblage from a single species pool. For example, there is an increase in biodiversity from south to north in the North Sea (Heip et al. 1992, Rees et al. 2007). The North Sea results, from stations spanning >11° latitude, are consistent in repeated surveys, and coincide with gradients in depth, bottom temperature, and salinity. Communities in the North Sea, however, are likely assembled from a regional species pool that is distinct from the pool sup-

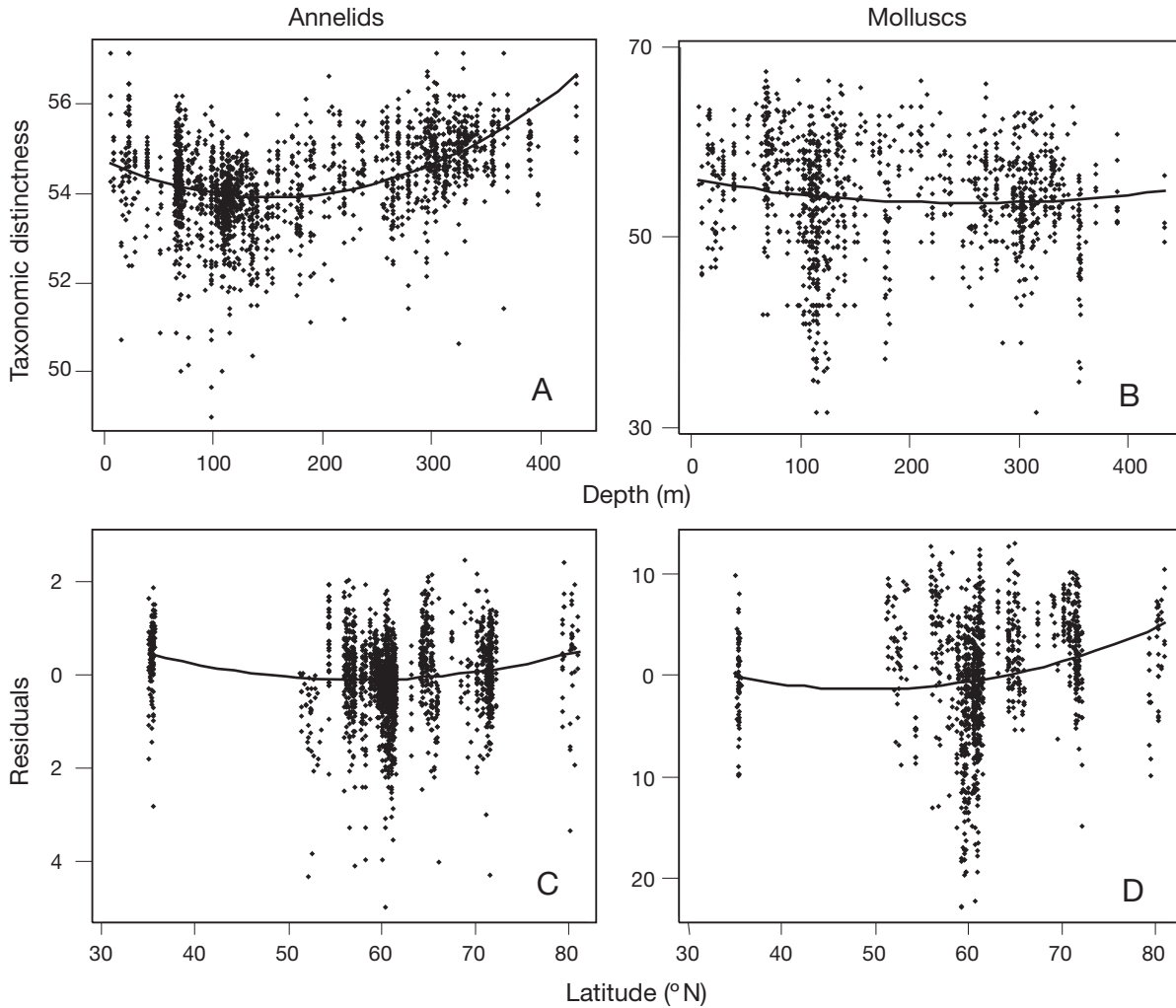


Fig. 7. (A,B) Average taxonomic distinctness against depth and (C,D) residuals from this relationship plotted against latitude for (A,C) annelids and (B,D) mollusks. Fitted lines from polynomial regressions

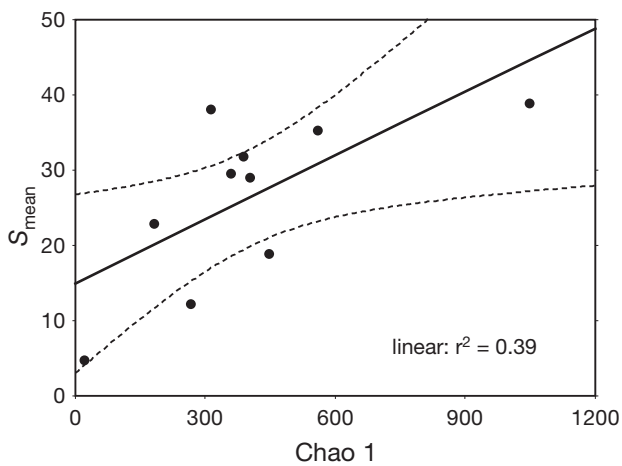


Fig. 8. Regional diversity (Chao1) against the mean species richness (S_{mean}) per dataset. Dashed lines: 95% confidence intervals

plying communities along the Norwegian continental shelf or the French Mediterranean coast. It is not clear whether investigations of continental-scale patterns encompassing multiple regional species pools should be expected to find trends or mechanisms from the smaller scale to be relevant. There is no environmental gradient consistent with latitude over this geographical range, and no *a priori* reason to suspect that factors responsible for determining biodiversity in one region would be applicable over the entire European continental shelf. Perhaps testing the latitudinal species-diversity gradient paradigm should then be left to empirical (e.g. the present study) and meta-analytical studies (e.g. Willig et al. 2003, Hillebrand 2004) that 'sample' over a domain spanning multiple regional species pools. Identifying patterns for entire communities or for major taxonomic groups at this scale may be the best first step in determining mechanisms responsible for generating and maintaining biodiversity.

Patterns observed for the entire community were also seen in the 3 dominant taxonomic groups (mollusks, annelids, and crustaceans), although mollusk diversity exhibited a positive trend with increasing latitude with a higher r^2 of around 0.2 (Fig. 5, Table 4). It has been proposed that calcification is energetically costly at low temperatures, possibly resulting in lower diversity of mollusks and foraminiferans toward the poles (Clarke 1992). We see no evidence to support this idea in our data, and in fact see an opposite pattern. The similarity of responses among the different groups is somewhat surprising following the recent suggestion that diversity of different functional groups may vary differently across latitudinal gradients (Roy et al. 2000, Valentine et al. 2002, Ellingsen et al. 2005). It is possible that characteristic responses of different subsets of the community were masked by treating each group without regard to functionality of component taxa. Each taxon could be further dissected in effort to identify which components contributed to the diversity at different latitudes (e.g. Roy et al. 2000).

Two additional spatial patterns in biodiversity were observed: (1) The well-known low diversity of the Baltic Sea was confirmed (Fig. 3). While low salinity excludes some taxa and thus affects species diversity, Bonsdorff (2006) suggested that low diversity in the Baltic in general is not due to an inherent property of the Baltic environment (low salinity, reduced water exchange, etc.), but instead to its ecological youth. Only 8000 yr ago it was completely glaciated and it is being recolonized slowly (see discussion in Bonsdorff 2006). More than 40% of the individuals included in the present analyses were sampled during intensive studies of the Baltic, but removing them from the analysis resulted in virtually identical results (Table 3, Fig. 4). This suggests that these data did not bias our results, and that the patterns we observed are robust to exclusion of even such a large subset of the data. (2) We see a higher point diversity (grab-level) at stations north of about 50° N than in datasets from more temperate areas (Fig. 3). Much of this, however, be due to the depth covariate, as the trend toward increasing diversity at high latitudes is less clear when this is taken into account (Fig. 4). Increased sampling across a wider depth range at these high-latitude areas would help clarify this.

Whereas the present study does not test specific hypotheses regarding mechanisms responsible for generation or maintenance of diversity, the patterns observed may aid in validation or refutation of some of the prevailing ideas. As mentioned in the Introduction, a major hypothesis explaining observed declines in diversity with latitudes north of the equator, and an absence of this decline toward the Antarctic continent, suggests that recent glaciation in the Arctic has led to a younger fauna that relies on recolonization from the

south, and limited speciation in recent millennia, compared to the extensive and geologically old Southern Ocean (e.g. Gray 2001). We see little evidence for a strong cline from 36 to 81°N, and the taxonomic distinctness data suggest equally diverse clades in the highest-latitude fauna, which is presumably geologically younger. Ecological mechanisms, from primary productivity and hydrographical events to sediment grain-size patchiness, have been invoked for explaining local and regional differences in diversity (e.g. Roy et al. 1998, Deubel 2000, Levin et al. 2001, MacPherson 2002). We do not have accompanying data on these parameters for our sampling stations, but these may be fruitful areas of future research into causes of diversity patterns. Finally, diversity can vary within an area — or at the same location — over decadal time scales. Climate variability affects benthic community structure, including biodiversity parameters (e.g. Kröncke et al. 1998, Beuchel et al. 2006), largely through the effect of temperature. Regional temperature changes can then affect both physical (e.g. stratification) and biological (e.g. primary production) parameters impacting reproduction, recruitment, and persistence in the system. These findings also suggest potential mechanisms acting on regional scales.

While a unimodal depth–diversity relationship with a peak in diversity between 2000 and 3000 m is well supported in the deep-sea literature (reviewed in Rex 1981, Levin et al. 2001), 2 recent studies conducted along depth transects in the North Atlantic and Arctic have failed to identify such a trend (Włodarska-Kowalczyk et al. 2004, Renaud et al. 2006). In the present study, we found that water depth explained over 20% (and up to 40%) of the variability in community diversity measures, and had contrasting effects for different components of the community. We also found a unimodal response with peak diversity (S and $E[S_{50}]$) and reduced average taxonomic distinctness (Δ^+) from quadratic fits between 200 and 250 m depth. It is unclear what could explain such a pattern across the narrow depth range of the continental shelf. Explanations for observed variability of diversity with water depth range from disturbance frequency and food supply (Levin et al. 2001), to sediment properties (Etter & Grassle 1992), to an artifact of constrained species range boundaries (mid-domain effect, Colwell et al. 2004). Additionally, site-specific factors may play a role, since the only deep shelf stations are at the northern end of the latitudinal range. The contrast between S and Δ^+ indicates that there are more species in the middle of the range, but they are more closely related to each other, lending some weight to the possibility of either the mid-domain artifact interpretation, or some local ‘hot spot’ of biological diversity. We have no evidence to support or discount any of these possibilities.

MacroBen database: strengths and caveats

It is only through the vision of contributors to and managers of MarBEF's MacroBen database that this analysis is possible. The sampling density, geographical range, and habitat distribution of the data allow in-depth studies of many questions regarding biodiversity in European waters. Subsets of the database can be analyzed to test for sensitivity to specific components (e.g. Table 3), or for methodological biases. Specific actions taken to achieve such a database are described in more detail in Vanden Berghe et al. (2009).

Despite all these efforts, the database is not perfect. Any dataset is biased in what it includes and what it excludes. Confining our study to the European continental shelf excludes the apparently more diverse western Atlantic basin (MacPherson 2002). Component datasets, many of which have been the subject of site-specific biodiversity publications, represent non-random and non-regular sampling. Another issue arising in the present study is that not all latitudinal zones were sampled across their entire depth range (Table 2), and samples were not available from all latitudes. This likely resulted in under-sampling of diversity from deeper areas at the south and shallower areas further north. Although we were able to control for some of this bias statistically (e.g. Fig. 4), it is not possible to completely factor out the potential biological significance of a water-depth covariate from sections of the latitudinal range where, for example, water depths >100 m were not sampled. Additionally, sediment parameters may vary among sites, even if water depth is controlled for. These issues will have to be addressed further when more datasets are added to the European benthic database.

A second potential problem is the effect of unequal sampling density across the gradient range. We show that the number of species identified per degree of latitude is influenced by the area and number of individuals sampled per degree. Residual analysis and multiple linear regression, however, indicated no trend in γ -diversity with latitude after correction for sampling effort (Fig. 1B,D, and 'Results'). This is in agreement with our results for α -diversity (Figs. 2 & 4, Table 3), suggesting that sampling-effort differences did not bias our results. Furthermore, Δ^+ is relatively sample-size independent (Warwick & Clarke 2001), and similar patterns were apparent in analyses of this measure. Most studies evaluating the presence of a latitudinal gradient in diversity use point or station (α) diversity measures to address regional diversity questions (e.g. Gray 2002). Our results show that mean α (point) diversity for each dataset was positively correlated with regional diversity estimates for that dataset (Fig. 8). While we do not necessarily imply a causal relation-

ship, it does show that α -diversity patterns may be suitable for investigating regional-scale patterns.

Biodiversity research: future directions and needs

The present study highlights the importance of using large databases to answer questions across regional spatial scales. Such databases have been lacking, but this is being addressed through international cooperation coordinated by organizations such as MarBEF and the Census of Marine Life (CoML). These efforts must be continued in order to address similar questions, whether they be investigating trends in different habitats, on temporal scales, or in other regions of the world's oceans.

Progress in macroecology has been rapid in recent years (e.g. Brown 1995, Blackburn & Gaston 2003), and focus has shifted from identifying patterns in regional diversity to determining the processes underlying the patterns (Gaston & Blackburn 2000). Willig et al. (2003) showed that we are still far from distinguishing among the many proposed mechanisms that may be responsible for geographical patterns in diversity. However, a fundamental prerequisite to any such mechanistic analysis is to document the patterns in a robust fashion. The present study provides such an input into future studies of diversity gradients in the European soft-sediment marine benthic fauna. Importantly, our results mean that any mechanism predicting strong latitudinal gradients in diversity in these taxa may not be valid.

Studies conducted over long periods of time and at large spatial scales would be invaluable in aiding the transition from describing pattern to elucidating process. One promising avenue would be to expand the recolonization study underway in the Baltic Sea by Bonsdorff (2006) and follow the system as it develops, with carefully designed studies and targeted research questions. Such studies, combined into databases such as those analyzed here, will help to instill a more data-driven, hypothesis-led approach to marine biodiversity studies. The need for such studies gains urgency as the effects of human activities on natural systems become apparent at ever-larger spatial scales (Chapin et al. 2000).

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Distribution patterns of macrofaunal species diversity in subtidal soft sediments: biodiversity–productivity relationships from the MacroBen database

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ABSTRACT: We analyzed patterns of species diversity in a compiled data set covering the European coast (from Norway to Crete) that was made available in the framework of the MarBEF European Network of Excellence. The focus was on the distribution patterns of species diversity over large areas across Europe. The objectives of our analysis were two-fold. First, we attempted to separate the effects of species–area relationships from that of species accumulation. Second, we explored the relationship between species diversity and productivity, and compared this to the proposed explaining factors (depth, survey area and latitude). The following conclusions are drawn. (1) Within a given habitat (subtidal soft sediment), the distribution of marine macrofaunal species richness in different areas between 3 and 200 m in average depth throughout Europe is shown to follow general rules derived from observations and experiments mostly based on terrestrial communities; (2) soft-bottom macrofauna accumulate in the subtidal environment (up to 200 m) following the Arrhenius plot model at a rate (≈ 0.5) corresponding to about a 3-fold increase in the number of species when the sampling area increases by 1 order of magnitude; (3) the distribution of the intrinsic species richness (point species richness) between the selected data sets (subtidal soft sediment) is significantly correlated with the levels of organic flux reaching the sea bottom; and (4) the close relationship between depth and the fraction of surface primary production that reaches the sea bottom is proposed as an explanation for the previously described increase of species richness with depth.

KEY WORDS: Species–area relationship · Species accumulation curve · Macrobenthos · Species richness · Productivity

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INTRODUCTION

International agreements (e.g. EU Marine Strategy) require signatory nations to make inventories of biodiversity, monitor changes and mitigate negative effects of human activities on biodiversity. Logistics, however, often prevent the direct census of species at large spatial scales. On the other hand, the observed species richness could seriously underestimate the actual species richness due to undersampling of rare species (Gray et al. 2005). This is particularly true for soft-bottom macrofauna (sediment-dwelling metazoans retained by a 1 mm sieve), where individual sampling areas of at most 1 m² are used

to describe species richness for areas that are usually about 6 orders of magnitude larger (km²). Therefore, an accurate description of biodiversity and changes therein requires a proper understanding of the spatial patterns and driving factors of species diversity.

Historical and present views on marine biodiversity have recently been depicted by Gray (1997, 2000, 2001, 2002). These studies emphasize the main drivers of species diversity patterns. In addition, they define different scales of observation at which biodiversity might be considered, along with biological organization scaling from genes to ecosystems and through spatial scales from habitats to landscapes and biogeographical provinces.

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Based on the work published by Sanders (1968), 2 main paradigms in benthic macrofaunal species diversity patterns have been identified: (1) a positive cline from the poles to the tropics and (2) an increase with depth from shallow waters to a maximum just seaward of the continental rise followed by a decrease thereafter (Levinton 1995). Gray (2001) reviewed these patterns and acknowledged a cline in increasing species richness from the Arctic to the tropics and the surprisingly high species richness in deep-sea areas. The high diversity in the deep sea might be explained, following Gray et al. (1997), at least partly by the vast area surveyed by oceanographers in this kind of environment in comparison to coastal areas. Besides the latitudinal cline, 2 key factors may explain patterns of marine macrofaunal species diversity: habitat heterogeneity and surveyed area (Gray 2001). Furthermore, Gray (2002) identified the available food resources as a limiting factor for the maximum range of species. As a consequence, where point species richness (at the scale of sampling stations) is concerned for similar habitats (e.g. soft bottom in the present study), latitude, depth, surveyed area and productivity could then be expected to be responsible for the observed patterns.

It is generally known that species diversity in natural systems can strongly depend on productivity as predicted with the energy hypothesis by Wright (1983), who interprets the difference in species–area relationships between the polar regions, with low (solar) energy input, and the tropics. Marine sediments, with the exception of very shallow and intertidal sites where primary production by microphytobenthos can be important, receive most their energy input from the pelagic system and this input is strongly depth-dependent (Andersson et al. 2004). The decreased food input as a function of depth was furthermore proposed by Rex & Etter (1998) as an explanation for the decrease in gastropod species richness from coast to abyss in the North Atlantic.

Mostly unimodal (i.e. humped) relationships between species richness and measures of ecosystem productivity have been described (Rex 1981, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, Hall et al. 2000). The diversity–productivity (D–P) hypothesis states that there is a corresponding increase in species richness as productivity increases, until a point where additional productivity results in lower species richness (Connell & Orias 1964). This hypothesis is in opposition, however, to a number of model predictions of a monotonic D–P relationship, a fact which is interpreted by Rosenzweig (1992, 1995) and Leibold (1999) as a difference in spatiotemporal scale: monotonic curves represent a transient response to (mostly experimental) increases in resources whereas unimodal patterns are established in the longer term under quasi-steady state conditions.

The part of the unimodal curve where species richness decreases for increasing productivity corresponds to the so called paradox of enrichment (Rosenzweig 1971) that describes an inverse relationship between productivity and diversity.

For benthic systems, Levin et al. (2001) provided an extensive overview of the possible influence of productivity on diversity in the deep sea. They show that diverse relationships (increasing, decreasing and humped) are found, but also point out that these are not necessarily contradictory. In general, ascending relations between productivity and diversity are described from very oligotrophic areas, whereas the reverse is true in more eutrophic areas and humped curves are described for broader ranges of productivity (Levin et al. 2001).

Leibold (1999) compared the patterns of 4 well-developed models predicting unimodal D–P relationships (paradox of enrichment, resource heterogeneity hypothesis, resource-ratio hypothesis and the keystone predation hypothesis) with those observed in fishless ponds in Michigan, USA, between the nutrient levels and the density, diversity and composition of plants (phytoplankton) and herbivores (zooplankton). The observed changes in the patterns of distribution of planktonic organisms were consistent with the keystone predation hypothesis, where species richness results from the balance between resource competition and differential grazing pressure by shared predators. At low productivity levels, and when predators are rare, the community is dominated by a few efficient exploiters (mostly vulnerable for predation) who might coexist with poorer resource exploiters (mostly predation resistant) when productivity increases. This agrees with the findings of Gross & Cardinale (2007) from metacommunity models where humped D–P curves were observed in communities that are structured by resource competition because species are able to coexist only via niche partitioning at intermediate levels of resource supply. Experimental nutrient enrichment experiments by Hall et al. (2000) also suggested the unimodal form of the D–P relationship by macrofauna, which contradicts the resource heterogeneity hypothesis as a monotonic increase of algal diversity with the nutrient enrichment.

The species–area hypothesis is one of the general principles in ecology that describes an increase in the number of species found with surveyed area (Rosenzweig 1995). As pertinently noticed by Gray (2001), the species–area relationship should not be confused with the species accumulation curve that describes how the number of species increases with the area and/or number of samples taken in a given environment. Rosenzweig (1995) explained the increasing number of species with area as due to the space and/or niche requirements, with generally higher habitat diversity

and higher numbers of individuals in large than small areas. In contrast with the terrestrial environment, few marine data have been used to test this hypothesis. This hypothesis is particularly difficult to test using data sets on benthic macrofauna, since all data have been collected in point samples of small area, not by area-covering surveys. These point samples may be spread uniformly or randomly over the surveyed area. When looking at total number of species sampled when accumulating 1, 2 ... n samples within a data set, inevitably the total surveyed area (i.e. the domain in which the samples have been taken) increases concomitantly with the total area sampled (i.e. the summed area of all box or grab cores taken). Tearing apart the 2 aspects is not a trivial task and requires insight into the spatial organization of species diversity.

In the present study we analyzed patterns of species diversity in a compiled data set covering the European coast. The issues investigated by our analysis were: (1) the respective effects of species–area relationships and of species accumulation on the assessment of species diversity, and (2) the shape of the relationship between species diversity and productivity follows the unimodal pattern. We also explored the environmental factors (depth, survey area and latitude) which may affect the aforementioned D–P relationship.

MATERIALS AND METHODS

Macrofaunal diversity data set. We used the MacroBen database, developed within the MarBEF Network of Excellence (Vanden Berghe et al. 2009, this Theme Section). Depth values are available for 385 150 distribution records (86%) which are distributed over a geographical area between 30–80° N in latitude and 30° E to 30° W in longitude. Nevertheless, the samples are not evenly distributed over the zone covered by the data as a result of highly variable sampling intensities (Fig. 1).

The sampling points are identified by their geographical location together with the date and the data set they belong to. A data set represents here a group of records that was delivered by a data provider to the MarBEF project. The sampling and analytical procedures within a given dataset are generally homogeneous.

In order to standardize the data extracted from the database (Microsoft Visual Basic for Applications), routines have been made available by the Flanders Marine Institute (VLIZ) that control the extraction of the data according to criteria about the data sets to be used, required level of taxonomic identification, spatial-temporal lumping and a cut-off for rare species when required. Other routines allow standard operations such as export data, preliminary analysis, calculation of indices and calculation of grid cells.

An effort to limit the data heterogeneity was attempted through preliminary filtering by selecting for each data set the years where at least 20 sampling stations were visited. A total of 78 distinct combinations of dataset \times year complying with this criterion were selected, and 25 distinct geographical groups with no more than 1 data set per group were thus identified. A final selection was made of the data sets with taxonomic identifications to the species level with the sub-select routine that is provided along with the database. This selection retained data sets representing 15 geographical groups (A to O) with a total of 93 860 distribution records, 5888 sampling records and 2584 species. Each record contains the species name, number of counted individuals and corresponding sampling surface.

Data processing. Two different approaches were used to establish species accumulation curves (i.e. curves representing how the total number of species sampled increases with total area of the samples). In the gridded approach, species were accumulated in samples that are geographically as close to each other as possible. The total area surveyed by a group of n samples thus increases with increasing sample number. In the randomization approach, the total area surveyed is always equal to the maximum area (total span of the data set), and samples are accumulated by random selection from the total set. We consider these approaches as the extremes in establishing species accumulation curves.

For the gridded approach, we subdivided the total area sampled by a dataset into a grid, so that, on average, every grid cell contained 1 sample. Subsequently, coarser grids were constructed from the basic grid by lumping neighbouring cells. Thus, the final set of grids was designed such that grid cells respectively contained, on average, 1, 2, 4, 8 ... 1024 sampling points. For each of these grids, the average number of species found per cell was plotted against the corresponding average sampling surface per cell.

For the randomization approach, we accumulated (without replacement) 1, 2, 4, 8 ... 1024 randomly chosen samples from the total data set without consideration of their geographical position, and repeated this procedure 1000 times. The average number of species found in the 1000 draws of 1, 2, 4, 8 ... 1024 samples was plotted against the average sampling surface.

Both approaches were compared with respect to the parameters of the species accumulation curves fitted to the data. For this comparison, the Arrhenius (log–log) plot model was selected (see 'Discussion'):

$$\log(S) = z \log(A) + \log(c) \quad (1)$$

where S is the average number of species observed at a given average sampling surface area A , z is the rate

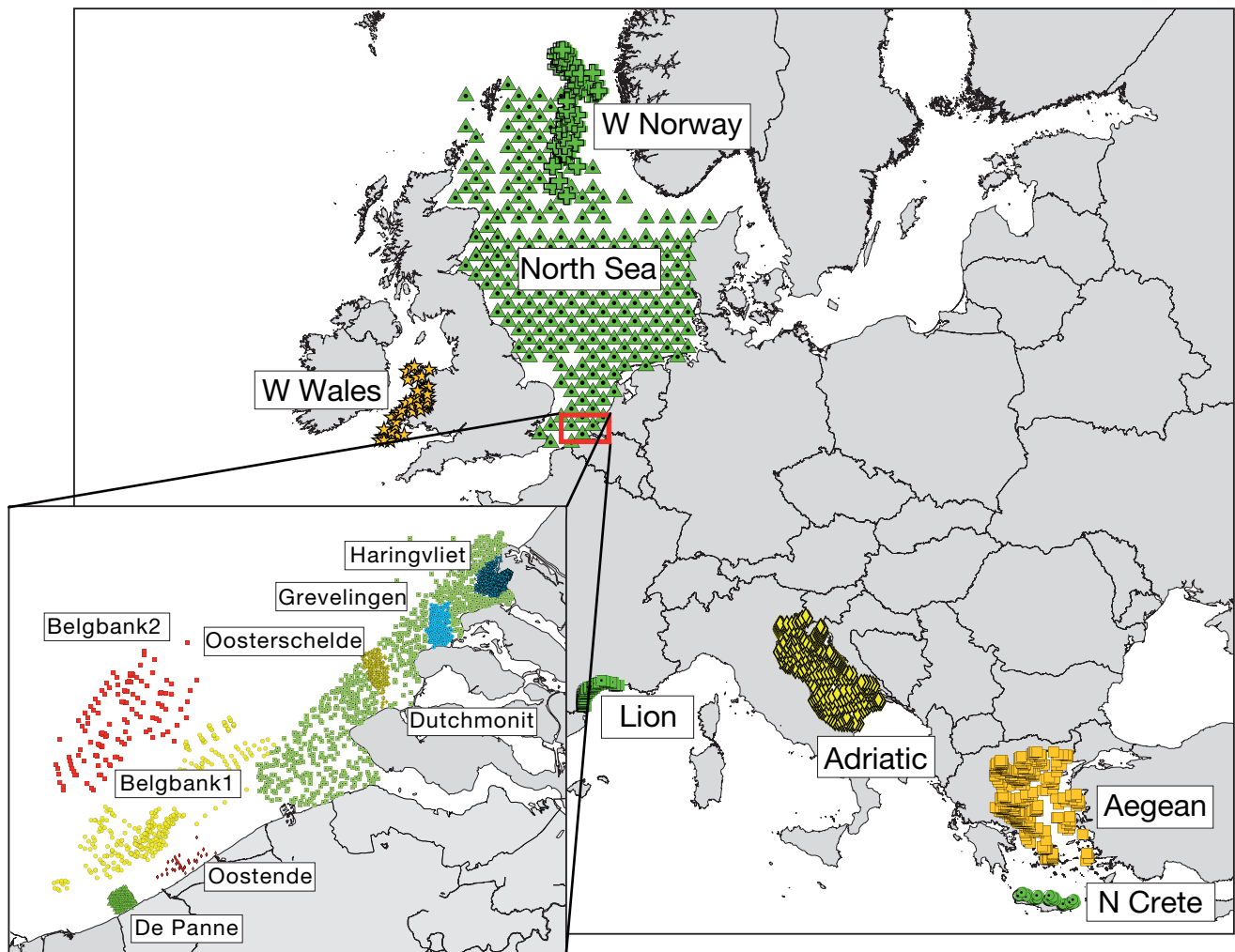


Fig. 1. Geographic groups selected for the present study ($n = 15$)

of increase of species richness with increasing sampling area and c is the species richness for the elemental unit of area (Rosenzweig 1995). According to Gray's (2000) terminology on scales of diversity, and depending upon the extent of the surveyed area, S represents SR_S , the sample species richness, or the species richness of a number of sampling units from a site of defined area. Following the same terminology, c can be interpreted as SR_R , the point species richness, and z as a measure of the β diversity as defined by MacArthur & Wilson (1967).

Additional environmental data. Besides depth, which is available for most individual records in the data set, and the surveyed surface that was estimated with elementary GIS techniques, data on net primary production ($gC\ m^{-2}\ mo^{-1}$) at the scale of the geographic groups were downloaded from the Environmental Marine Information System (EMIS) website (<http://emis.jrc.ec.europa.eu>). These data are derived from satellite remote sensing of ocean color for the years 2000 to 2004 and the primary

production calculation itself is based on the formulation obtained through dimensional analysis by Platt & Sathyendranath (1993). The assignment of the photosynthetic parameters P_{max}^B and E_k is achieved by the combined use of a temperature-dependent relationship for the maximum growth rate (Eppley 1972) and the use of variable formulation to retrieve the carbon:chlorophyll ratio following the empirical relationship of Cloern et al. (1995). In order to account for the diminution of the downwards flux of primary production as a function of depth, the estimates of primary production obtained from EMIS were corrected with a semi-empirical model for the depth dependence of remineralization rate as proposed by Andersson et al. (2004):

$$F_z = F_0[(1 - p)e^{-b_1z} + pe^{-b_2z}]$$

with F_z the flux of remineralization at depth z , F_0 the flux at the surface and fitted parameters p (0.17), b_1 (0.018) and b_2 (0.00046). Metadata information is provided in Table 1.

Table 1. Main characteristics of the 15 data sets selected for the present study. Average primary production is expressed as $g\ C\ m^{-2}\ mo^{-1}$, after correction for the downwards decrease of flux following Andersson et al. (2004). I: Italy; GR: Greece; B: Belgium; NL: Netherlands; F: France; GB: Great Britain; N: Norway

Data set (country)	Code	Latitude min, max	Longitude min, max	Surveyed area (km ²)	Sampling surface (m ²)	No. species	No. stations	Average depth (m)	Average primary production	Source
Adriatic (I)	A	41.95°N, 45.69°N	12.31°E, 17.19°E	67539	37.9	265	379	45	5.7	www.medobis.org/
Aegean (GR)	B	36.88°N, 40.95°N	22.57°E, 27.01°E	38328	34.4	1033	344	200	0.9	Koukouras et al. (2001, 2007)
Belgbank1 (B)	C	51.15°N, 51.57°N	02.31°E, 03.15°E	481	340.03	201	383	20	17.5	Degraer et al. (2008)
Belgbank2 (B)	D	51.40°N, 51.75°N	02.32°E, 02.86°E	449	65.23	115	136	20	17.5	Van Hoey et al. (2004)
De Panne (B)	E	51.10°N, 51.16°N	02.52°E, 02.63°E	31	257.62	157	329	20	17.5	See 'Acknowledgements'
Dutchmonit (NL)	F	51.36°N, 52.01°N	03.09°E, 04.06°E	992	258.31	198	909	11	16.1	See 'Acknowledgements'
Lion (F)	G	42.56°N, 43.49°N	03.05°E, 04.75°E	1766	27.6	367	92	28	10.5	Labrunne et al. (2007)
Grevelingen (NL)	H	51.74°N, 51.85°N	03.73°E, 03.83°E	53	217.05	119	227	6	17.5	See 'Acknowledgements'
Haringvliet (NL)	I	51.86°N, 51.96°N	03.92°E, 04.06°E	53.5	386.35	148	2196	3	18.3	See 'Acknowledgements'
Oosterschelde (NL)	J	51.60°N, 51.74°N	03.49°E, 03.59°E	47.7	83.69	111	208	11	16.2	See 'Acknowledgements'
N Crete (GR)	K	35.14°N, 35.65°N	23.67°E, 26.15°E	1589	8.3	407	83	98	2.2	Karakassis & Eleftheriou (1997)
North Sea (GB)	L	51.25°N, 60.75°N	03.00°E, 09.00°E	392588	27.9	575	279	62	3.3	Kunitzer et al. (1992)
Oostende (B)	M	51.19°N, 51.28°N	02.71°E, 02.93°E	23	45.51	104	63	20	17.5	Degraer et al. (2008), Van Hoey et al. (2004)
W Norway (N)	N	58.00°N, 61.53°N	01.67°E, 03.84°E	10934	83.4	782	197	156	1.7	See 'Acknowledgements'
W Wales (GB)	O	51.27°N, 53.44°N	06.51°W, 04.15°W	9544	5	522	50	67	5.1	Mackie et al. (1995)

RESULTS

Species accumulation curve: gridded approach

Fig. 2 shows, for each of the 15 data sets, the number of species observed within the grid cells of the gridded approach versus the average area sampled (m² per grid cell). The Arrhenius plot model (Eq. 1) fits very well to the data with average *c*-values of 1.56 ± 0.25 and average *z*-values of 0.51 ± 0.05 for an average $r^2 = 0.99$ (Table 2). Due to interdependence between the observed numbers of species at the different scales, we refrained from providing significance levels to the regressions and formal intergroup comparisons.

The values of the species accumulation curve intercept (*c*) show a clear geographical dependency (Fig. 3). The 8 data sets from the Dutch and Belgian shallow waters are characterized by low *c*-values with an average of 14.3 ± 0.9 as expressed in number of species (after log inverse transformation of the intercept values). The remaining 7 data sets (Mediterranean, North Sea and North Atlantic) show considerably higher *c*-values with an average of 102.8 ± 1.4 species.

The slopes of the species accumulation curves show much less variability. In contrast to the intercepts, the slopes of the species accumulation curves showed almost no variability. When the value of the intercepts (no. of species m⁻²) for each accumulation curve was subtracted from the number of species values, all the curves overlapped (see Fig. 4). The intercept-corrected numbers of species (log) show a strong relation with the log of the sampled area (Fig. 4, $r^2 = 0.94$). The value

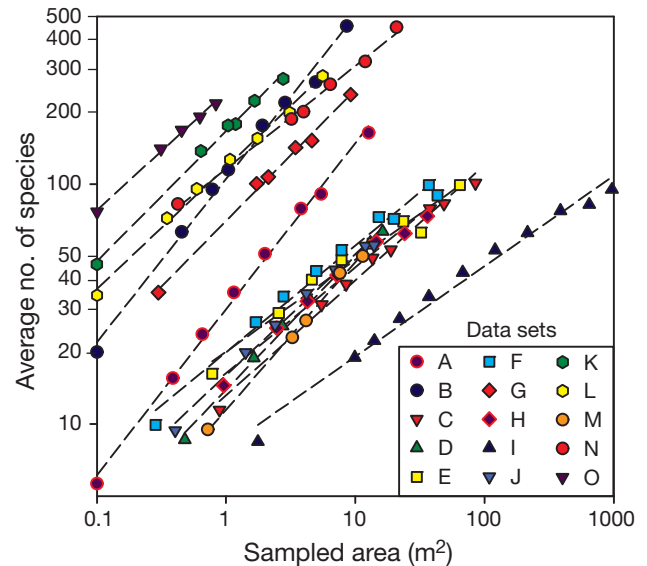


Fig. 2. Species accumulation curves (Eq. 1) fitted for each data set between the average number of species and corresponding average sampling areas at the different spatial scales (gridded approach). Data set codes are listed in Table 1

Table 2. Parameter values of the species accumulation curves (Eq. 1) fitted for each geographical group following the gridded approach. *z*: rate of increase of species richness with increasing sampling area; *c*: species richness for the elemental unit of area. The number of observations (*N*) and the corresponding *R*² are also indicated

Data set	Code	<i>c</i>	<i>z</i>	<i>N</i>	<i>R</i> ²
Adriatic	A	1.478	0.692	8	0.996
Aegean	B	2.021	0.681	8	0.992
Belgbank1	C	1.119	0.480	8	0.990
Belgbank2	D	1.141	0.560	7	0.994
De Panne	E	1.300	0.383	8	0.961
Dutchmonit	F	1.299	0.444	9	0.982
Lion	G	1.846	0.548	6	0.994
Grevelingen	H	1.211	0.441	7	0.979
Haringvliet	I	0.904	0.377	11	0.984
Oosterschelde	J	1.203	0.505	7	0.990
North Crete	K	2.220	0.543	6	0.995
North Sea	L	2.071	0.509	7	0.995
Oostende	M	1.058	0.617	5	0.995
W Norway	N	2.064	0.429	6	0.994
W Wales	O	2.384	0.493	5	0.996

for the *z*-parameter calculated for the whole data set after the intercept correction is estimated as 0.44, corresponding with a 3-fold increase of the number of species when the sampling surface increases by 1 order of magnitude ($S \approx A^{0.44}$). The homogeneity of slopes among the different geographic groups reflects the similar increase in species richness as function of the sampling area in the different datasets.

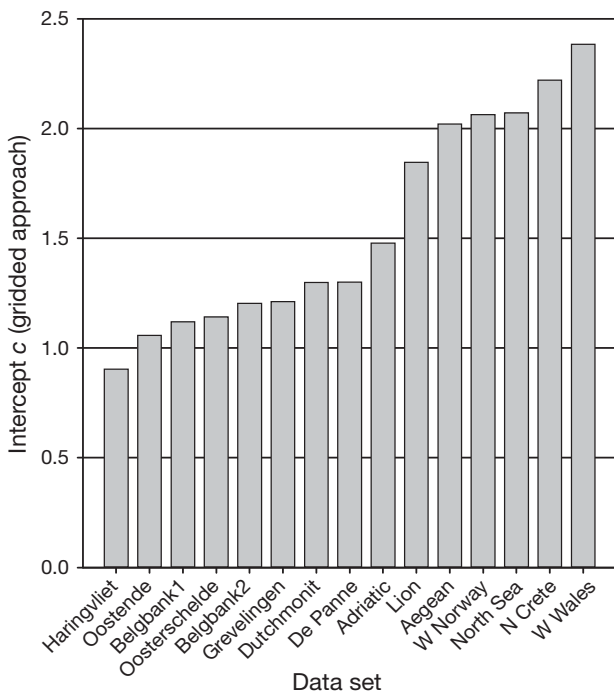


Fig. 3. Intercepts (*c*, log [no. of species *m*⁻²]) of the species accumulation curves (See Fig. 1) fitted for each geographical group and sorted by increasing values

Species accumulation curves: randomization approach

The species accumulation curves obtained by randomly assembled samples from the entire dataset (Fig. 5) show distinctive curvilinearity. In particular, the groups assembled from only a few original samples have fewer species than would be expected on the basis of extrapolation from the larger assembled groups.

The values of the slope, however, did not vary much among the data sets (0.41 ± 0.05) and showed a very strong relationship (Fig. 6) with the slopes obtained with the gridded approach ($z_{rand} = 1.01 \times z_{avg} - 0.11$, $r^2 = 0.92$). The intercepts obtained with the randomization approach were also very closely related to the values obtained with the gridded approach ($c_{rand} = 2.61 \times c_{grid}^{0.88}$, $r^2 = 0.95$)

Relating species richness to the environment

A corollary of the homogeneity of slopes of the species accumulation curves among the selected data sets is that most of the variation in the number of species observed in the database is accounted for by the intercept of this relation. The value taken by the intercept can therefore be considered as a measure of intrinsic species richness of the fauna sampled in the different data sets. The distribution of these values was com-

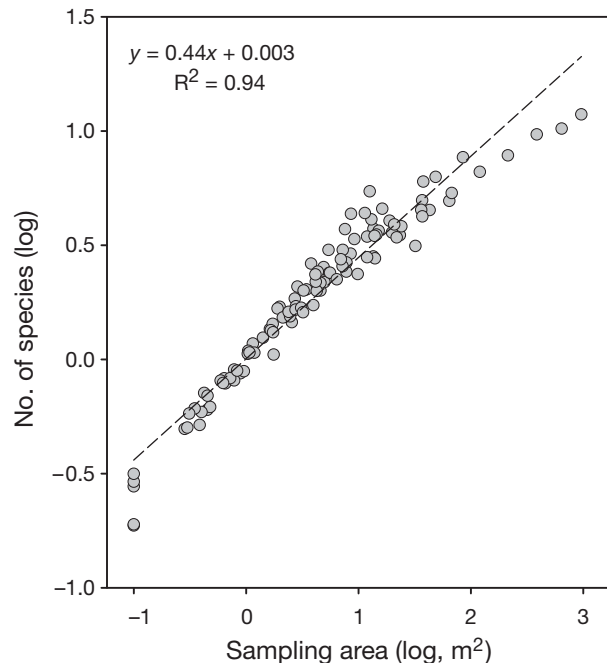


Fig. 4. Pooled regression of the average number of species (log) corrected for the intercepts of the species accumulation curves (see Fig. 1) as function of the average sampling areas (log) at the different spatial scales (gridded approach)

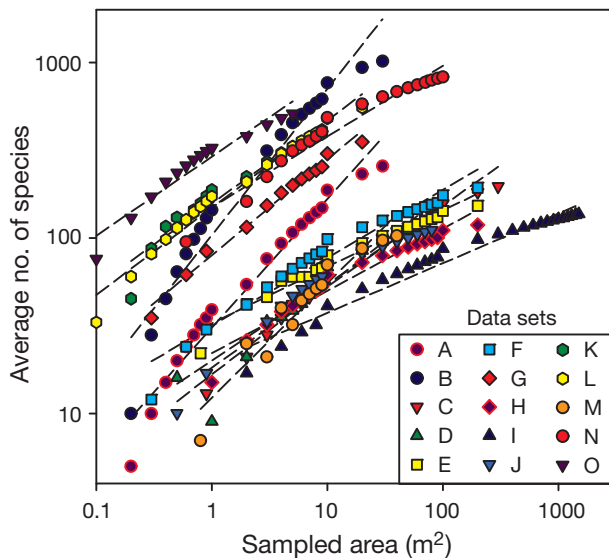


Fig. 5. Species accumulation curves (Eq. 1) fitted for each dataset between the average number of species and the average sampling areas obtained by randomized accumulation of the individual grid cells over the whole surveyed area (randomization approach)

pared with that of the factors retained in the prevailing hypotheses for the determination of species richness: surveyed area, latitude, depth and productivity. Whereas no relationship was found between the intercepts calculated for the 15 geographic groups and their average latitude ($r^2 = 0.07$), significant relationships ($r^2 > 0.50$) were found with the surveyed area, depth and productivity (Fig. 7A–C). However, these 3 explaining factors show strong interrelationships (Fig. 7D) as small (area) monitoring surveys are generally designed in shallow, productive, coastal waters whereas extended surveys are mostly preferred in deep, oligotrophic, offshore areas. Among the 3 explaining factors that were tested here, the highest coefficient of determination was found for productivity ($r^2 = 0.83$).

DISCUSSION

Species–area relationship versus species accumulation

In the gridded approach, where species were accumulated in samples collected over increasing surface area (grids containing on average 1, 2, 4 ... 1024 sampling locations), the species accumulation curve accounts for the numbers of species found in increasingly larger areas. As a result of the linear increase of the sampling surface with the surface of the grid cells, the accumulation curve between the number of species and the sampling surface is homologous to a species–

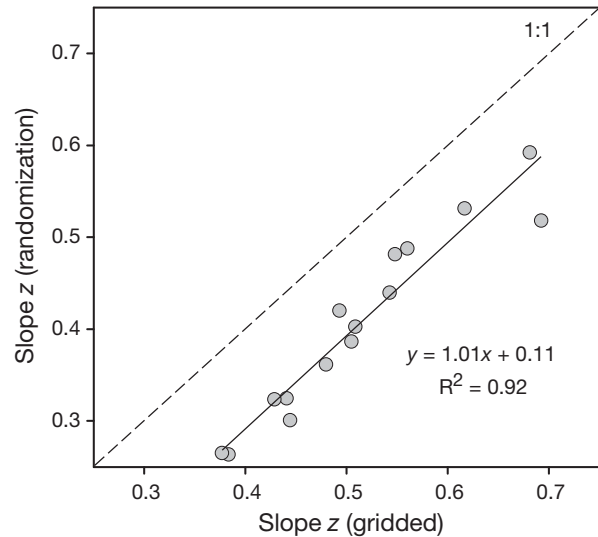


Fig. 6. Relationship between the slopes (z) of the species accumulation curves obtained with the 2 methods: randomization vs. the gridded approach

area relationship. In the randomization approach, where samples were randomly selected over the whole survey area, the numbers of species found at increasing sampling surface area typically represent a species accumulation curve.

Ugland et al. (2003) warned against the confusion between species accumulation curves and species–area relationships, as the former measures the rate of accumulation of different species as the area sampled is increased and the latter describes how the number of species varies with the size of the surveyed area (Gray et al. 2004a,b). Furthermore, the data analysis by Ugland et al. (2003) showed intrinsic differences in the formulation of both relationships as the species accumulation follows a semi-log increase, whereas the species–area relationship is log–log.

We have applied both models (log–log and semi-log) to our data in order to compare their suitability for describing both the grid and random approaches. The quality of fit in all cases is quite high, with average r^2 values all > 0.93 . However, both models showed systematic error patterns respective to the true data, with concave and convex distribution of the residuals against the sampling area when fitting with the semi-log and the log–log functions, respectively.

As expected, the semi-log function produces a better fit than the log–log function in the randomization approach, with average r^2 values reaching 0.99 and 0.96, respectively. Conversely, the fit was lower with the semi-log ($r^2 = 0.93$) than with the log–log function ($r^2 = 0.99$) in the gridded approach. Given both models showed conceptual discrepancies with the true data as evidenced from the systematic error patterns,

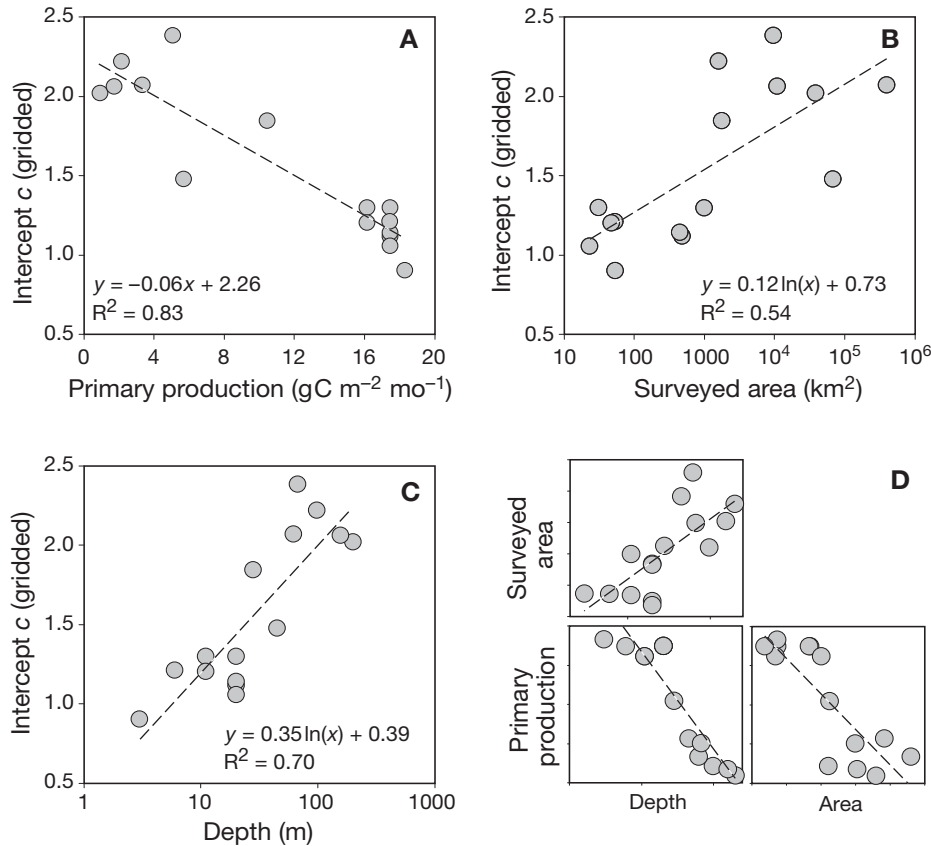


Fig. 7. Intercept (c) of the species accumulation curves (gridded approach, see Fig. 1) as a function of the average values of (A) primary production, (B) surveyed area and (C) depth, and (D) relationships between these explaining factors

there is no clear argument to choose one model over another in our comparison between the different approaches. As a single model has to be employed to allow direct comparisons between the parameters fitted with our 2 approaches, the log–log model was chosen given it produced a slightly better fit than the semi-log model.

The comparison between the 2 approaches shows that the randomization method includes the total geographic variation in habitats into the estimates of number of species for groups with a certain sampling surface. This inclusion is incomplete in the smallest groups, but reasonably consistent from approximately 10 samples and above (Fig. 5). In the gridded approach, more heterogeneity in habitat is added as the sampled surface increases, since this corresponds to larger and larger grid cells. Consequently, the slopes of the Arrhenius plots in the gridded approach are systematically higher than those in the randomization approach. Intercepts in the randomization approach are also estimated as higher values than in the gridded approach, because the randomization procedure projects some of the large-scale geographical variation down to the smallest scale.

Despite these differences, however, the estimates of the intercepts in both methods are very highly correlated to one another. The intercepts represent number

of species expected at the unit sample area, and can be considered as an adequate biodiversity indicator of the fauna sampled. The correlation between these intercepts and environmental values that can serve as an explanatory factor for biodiversity is warranted, since the result appears to be relatively independent of the method used to estimate the intercepts.

Species richness and the environment

Exploring causality in the observed patterns remains a risky task since the associated environmental variables are closely interrelated (Fig. 7). In addition, the present study does not consider the many other factors which likely control the species richness, such as habitat boundaries (Gray 2000), rarity vs. dominance (Gray et al. 2005), historical constraints (Gray 2001) and, at a smaller scale, the influence of the physical variables such as temperature, salinity and hydrodynamics. Nevertheless, the spatiotemporal scales at which the variables (biotic and abiotic) are considered in the present study are larger than the range of action of the previously mentioned control factors, the effects of which are leveled off at the present observation scale.

Therefore, further reflection on the present observations and additional data analysis might help at

improving our insight into the processes controlling marine benthic macrofaunal biodiversity.

Depth

Among the 3 factors found to be associated with diversity levels (depth, area and productivity), depth is the most controversially linked to biodiversity. Sanders (1968) attempted to explain the increase in diversity with depth from coastal areas to 2000 m (his deepest observations) with his stability-time hypothesis. This hypothesis states that the species richness of shallow areas is physically controlled, whereas it becomes biologically accommodated in the deep sea. The mechanism suggested is that competitive interactions over evolutionary time in the stable environment of the deep sea have led to a large number of specialized species within narrow niches. Peters (1976) pointed at the tautological nature of this hypothesis, as complex competitive interactions can be considered as both the cause and the result of the presence of a large number of specialized species. Furthermore, it is worth observing that the data set studied by Sanders (1968) only contains 37 samples, only 4 of which are from the deep sea, a singularly small number when compared with the general scope of the hypothesis (Abele & Walters 1979). Abele & Walters (1979) (re)evaluated the data used by Sanders (1968) and showed clear flaws in the data, such as heterogeneous sampling techniques, arbitrary taxonomic (polychaete–bivalve fraction) selection of data and heterogeneous habitat origin of samples. Finally, Gray (2001) (re)examined the depth (stability-time) hypothesis, showed that it was falsified in most available data sets and concluded that no clear trend in increasing species was observed from coasts to the deep sea. Abele & Walters (1979) also showed that the observed coast–deep sea gradient in (polychaete) species richness could be satisfactorily associated (99%) with the species–area relationship, as larger domains were generally surveyed in the deep sea than in coastal areas. The data from the present study show the same pattern, with a strong relationship between average depth and the surveyed area of the data sets, a finding which might be indicative of a coincidental relationship between depth and species richness.

Surveyed area

Gray (2001) verified the validity of the species–area curve (Arrhenius curve) on a data set from the benthos of the Norwegian continental shelf, and concluded that such a general rule that has been mostly observed in

terrestrial systems was also due to apply to the marine environment. However, total survey area as an explanatory variable is unsatisfactory from an ecological point of view, as it basically depends on the configuration of the sampling designs which are characterized by larger areas covered in deep waters than in coastal areas.

Our different approaches to the species accumulation curves only partly compensate for this artefact. The gridding method uses smaller geographic grid cells in the data sets with smaller total area surveyed. Therefore, samples that are found together in a grid of sufficient size to harbour, say, 4 samples, are geographically closer together in the data sets with a small total area surveyed than in the data sets with a larger area. Thus, if geographical distance was the major factor determining the similarity between a pair of samples, it would be possible that this spatial autocorrelation interferes with our analysis. There are 2 reasons why this seems unlikely. The first is that total area surveyed correlates with the intercepts of the species accumulation curves (in the gridded approach) and not with the slopes. If the increase of the intersample distance controlled the number of species found in a grid, the number of species should grow faster with grid size in the data sets with a large surveyed area. Consequently, the size of the total area would correlate with the slopes and not with the intercepts, as in the present case. The second reason is that the slopes determined in the 2 methods are highly correlated. The randomization approach always samples from the entire geographical range. Except for the lowermost samples, where this sampling is incomplete, one would not expect that enlargement of the geographical range sampled has a strong influence on the slopes in the randomization approach. Consequently, since the slopes in the gridded approach are correlated to those from the randomization approach, it seems unlikely that the former are dominated by the range extension effect. Finally, we note that the intercepts between both approaches are highly correlated. Intercepts of the randomization approach are expected to reflect effects of the geographical range surveyed, since this method extrapolates the variability in habitats down to the lowest scale. In accordance with this hypothesis, we do find larger intercepts in this approach. Again, however, the effect does not override the influence of differences in point species richness that appear to be present in the data sets. We therefore conclude that the differences in intercepts primarily reflect real differences in point species richness, and that the correlation between these intercepts and total area surveyed is a coincidental consequence of the configuration of the sampling designs that are characterized by larger areas covered in deep waters than in coastal areas.

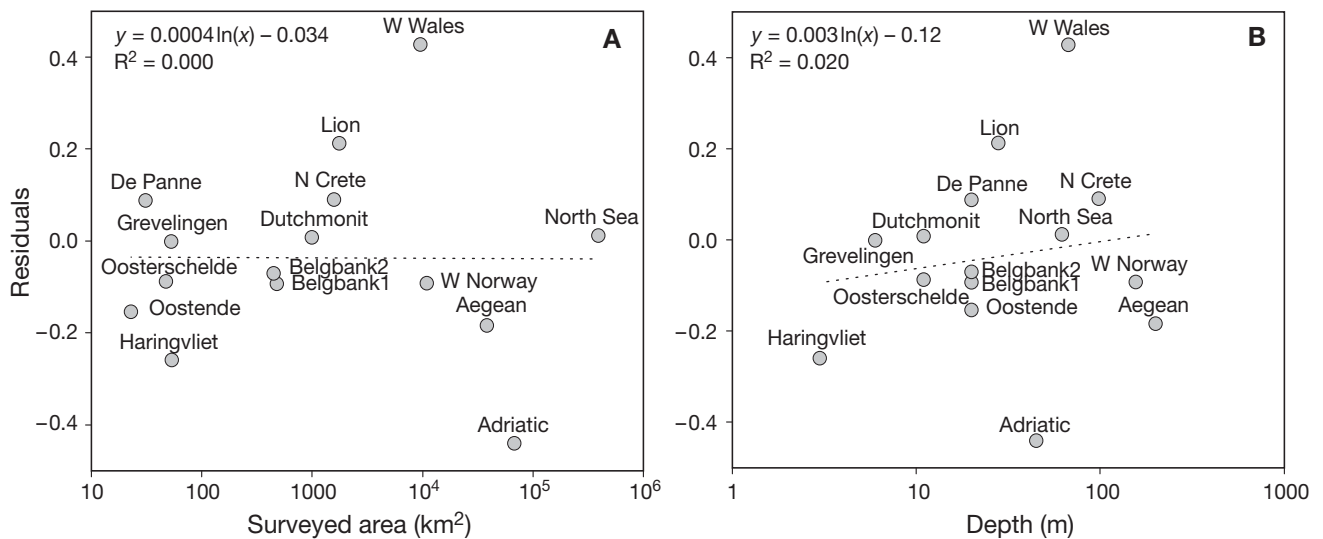


Fig. 8. Residuals from the regression of the species accumulation curve intercepts (c) on primary production (see Fig. 7A) as a function of (A) surveyed area and (B) depth

Productivity

Both data sets used to investigate the D–P relationship (macrofauna and productivity) are characterized by their high level of spatiotemporal integration (average values over whole study areas). This inaccuracy is advantageously compensated by the robustness of the averaged data where local heterogeneities due, for example, to advective transports, might have blurred the signals when considered at the scale of the individual samples. The present data showed a strong negative relationship between the intercept of the species richness (point species richness) and the fraction of primary productivity reaching the bottom. This relation might correspond with the decreasing part of the unimodal D–P curve. Smith (2007) compiled a large number of studies confirming the prevalence of hump-shaped distributions of species richness against system productivity. In cases where monotonic (negative/positive) trends were found, it was suggested that a wider range (often ≥ 2 orders of magnitude) of productivities would have been necessary to reveal the entirety of a humped D–P curve. This might be the case in the present study, where no data were available from regions with average productivity levels lower than about $1 \text{ g C m}^{-2} \text{ mo}^{-1}$. It is indeed likely that an increase in species diversity with increasing resource supply should be observed in very unproductive conditions due to minimum resource requirements. After all, one can be sure that the origin lies on the curve: no animal could survive when resources are nil. If such a situation occurred within the present data set, the resolution used for both the benthos and the production data (average over study areas) would not have allowed us to isolate it.

Levin et al. (2001) describe a deep-sea data set where diversity of nematodes increases with organic flux. The range of flux is 2 orders of magnitude lower than the range described in the present study. Thus, it is very likely that this increasing trend of diversity with productivity can present the ascending part of what is, essentially, a humped curve.

Residual analysis of the relationship with productivity is an interesting way to study the importance of the other factors, depth and surveyed area. As stressed in Fig. 8, the residuals of this regression show no relationship at all with surveyed area or depth. Conversely, a significant relationship was found between the residuals of intercepts on depth or surveyed area and productivity.

When the intercepts of the species–area relationship are plotted against the values of primary production measured at sea surface, the regression coefficient equals 0.68, compared with the value of 0.83 that is obtained when primary production is corrected for the depth dependence of organic flux to the sediment. After the correction for depth, the average ratio between the levels of carbon enrichment and the surface levels of primary production was about 80% in the 8 data sets from the Dutch and Belgian shallow waters, whereas it was about one-third in the remaining 7 data sets (Mediterranean, North Sea and North Atlantic). The present data suggests that the strong control of the bottom enrichment by depth might account for the effect of depth on species richness.

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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

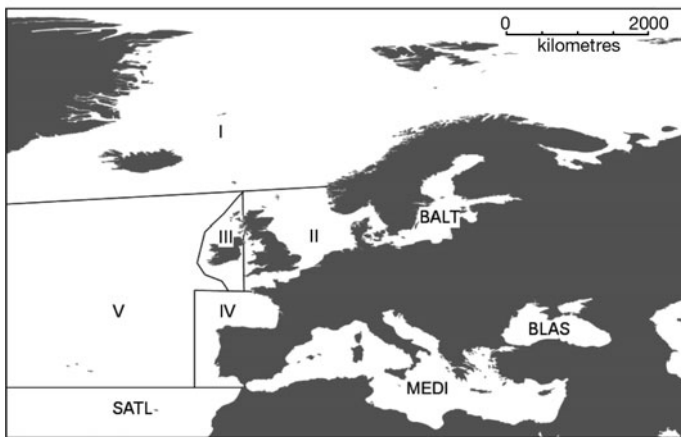


Fig. 1. European marine provinces defined by the Oslo-Paris Commission (OSPAR) and modified for the purposes of the present study. I: Arctic waters, II: Greater North Sea, III: Celtic Seas, IV: Bay of Biscay and Iberian Coast, V: Wider Atlantic, SATL: South European Atlantic, BALT: Baltic Sea, MEDI: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

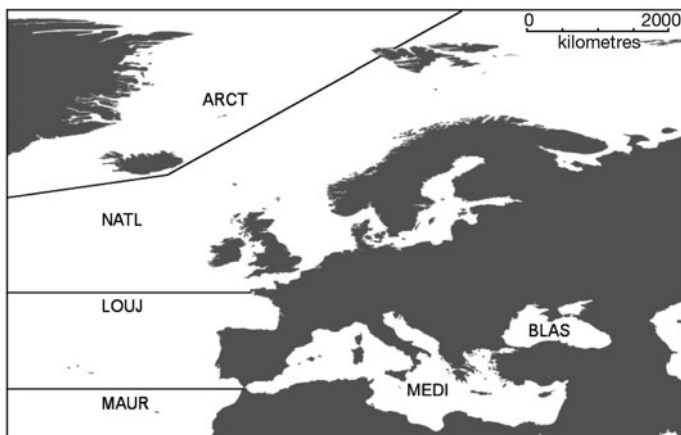


Fig. 2. European marine provinces defined by Fredj (1974) and modified for the purposes of the present study. ARCT: Arctic province, NATL: North Atlantic, LOUJ: Lousitanian, MAUR: Mauretania; remaining provinces as in Fig. 1

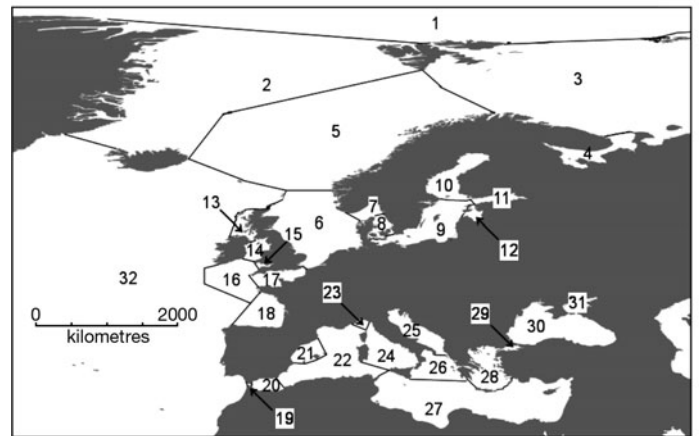


Fig. 3. European marine provinces defined by the International Hydrographic Organization (IHO). 1: Arctic Ocean, 2: Greenland Sea, 3: Barents Sea, 4: White Sea, 5: Norwegian Sea, 6: North Sea, 7: Skagerrak, 8: Kattegat, 9: Baltic Sea, 10: Gulf of Bothnia, 11: Gulf of Finland, 12: Gulf of Riga, 13: Inner 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

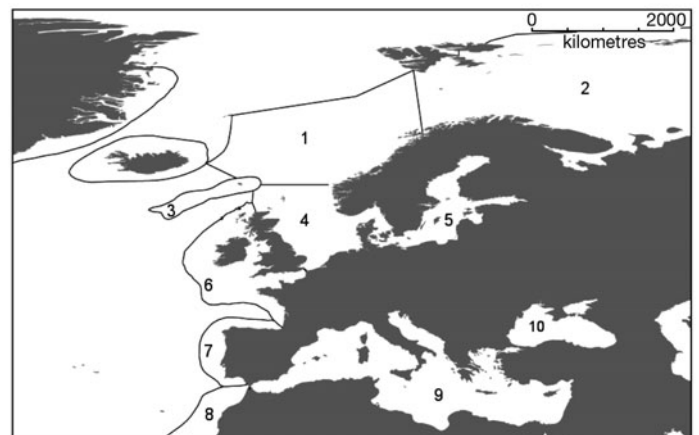


Fig. 4. European marine provinces defined in the Large Marine Ecosystems concept. 1: Norwegian Sea, 2: Barents Sea, 3: Faroe Plateau, 4: North Sea, 5: Baltic Sea, 6: Celtic-Biscay Shelf, 7: Iberian coastal, 8: Canary current, 9: Mediterranean Sea, 10: Black Sea

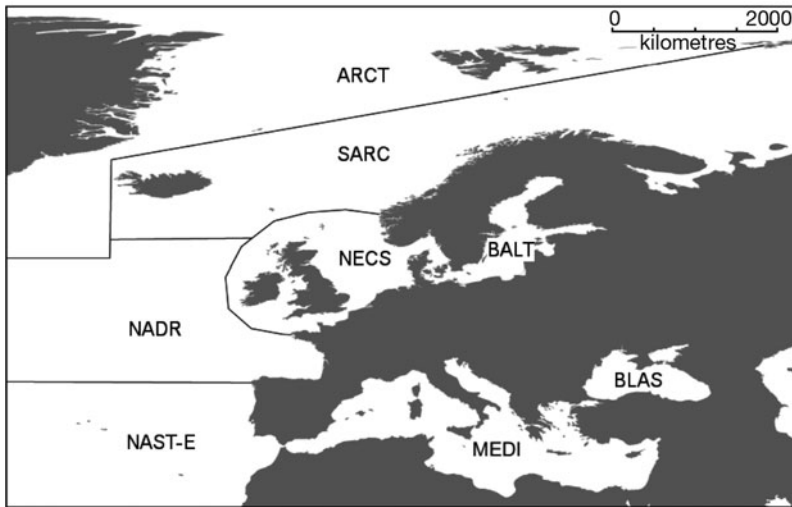


Fig. 5. European marine provinces defined by Longhurst (1998) and modified for the purposes of the present study. ARCT: Arctic, SARC: Subarctic, NECS: North-east Atlantic Shelf, NADR: North Atlantic Drift, NAST-E: North Atlantic Sub-tropical Gyre, East, MEDI: Mediterranean, BLAS: Black Sea, BALT: Baltic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

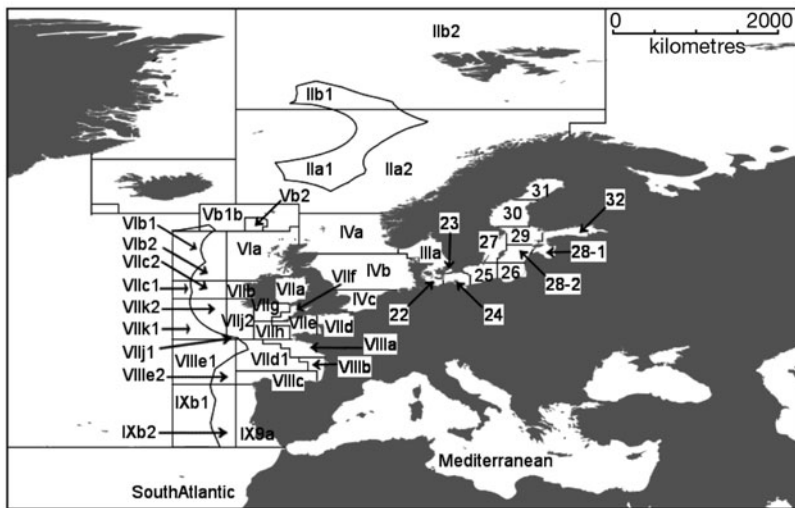


Fig. 6. Rectangles defined by the International Council for the Exploration of the Sea (ICES) for the European seas

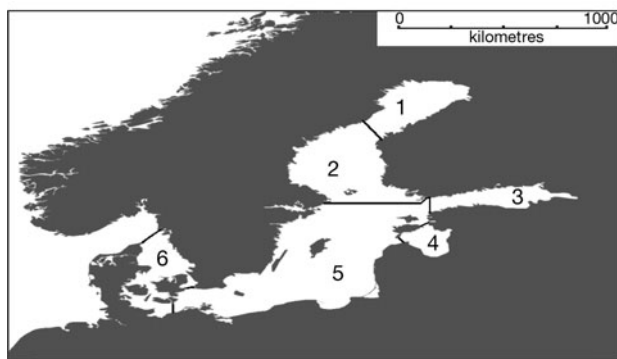


Fig. 7. Baltic Sea marine sectors defined by the Helsinki Commission (HELCOM). 1: Bothnian Bay, 2: Bothnian Sea, 3: Gulf of Finland, 4: Gulf of Riga, 5: Baltic Proper, 6: Kattegat Sound

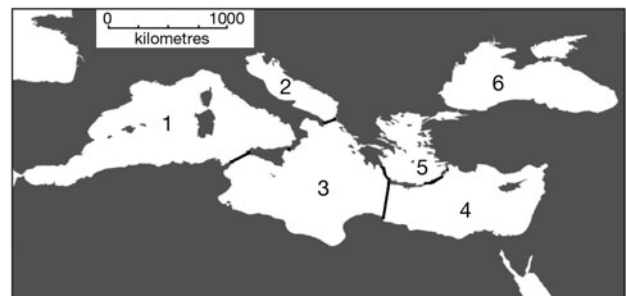


Fig. 8. Mediterranean and Black Seas marine sectors defined by Por (1989). 1: Western Mediterranean, 2: Adriatic Sea, 3: Central Basin, 4: Levantine Basin, 5: Aegean Sea, 6: Black Sea

(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

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

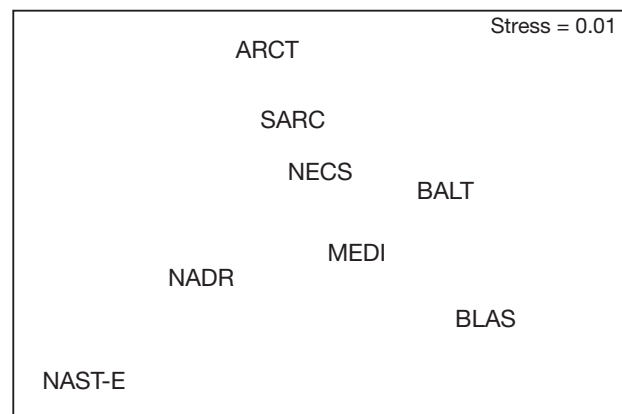


Fig. 10. Non-metric multidimensional scaling (NMDS) ordination plot resulting from the resemblance matrix of the provinces defined by Longhurst (1998), based on the Jaccard coefficient calculated from the soft-bottom macrobenthic inventories (the plot from polychaete inventories, not shown, is identical).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

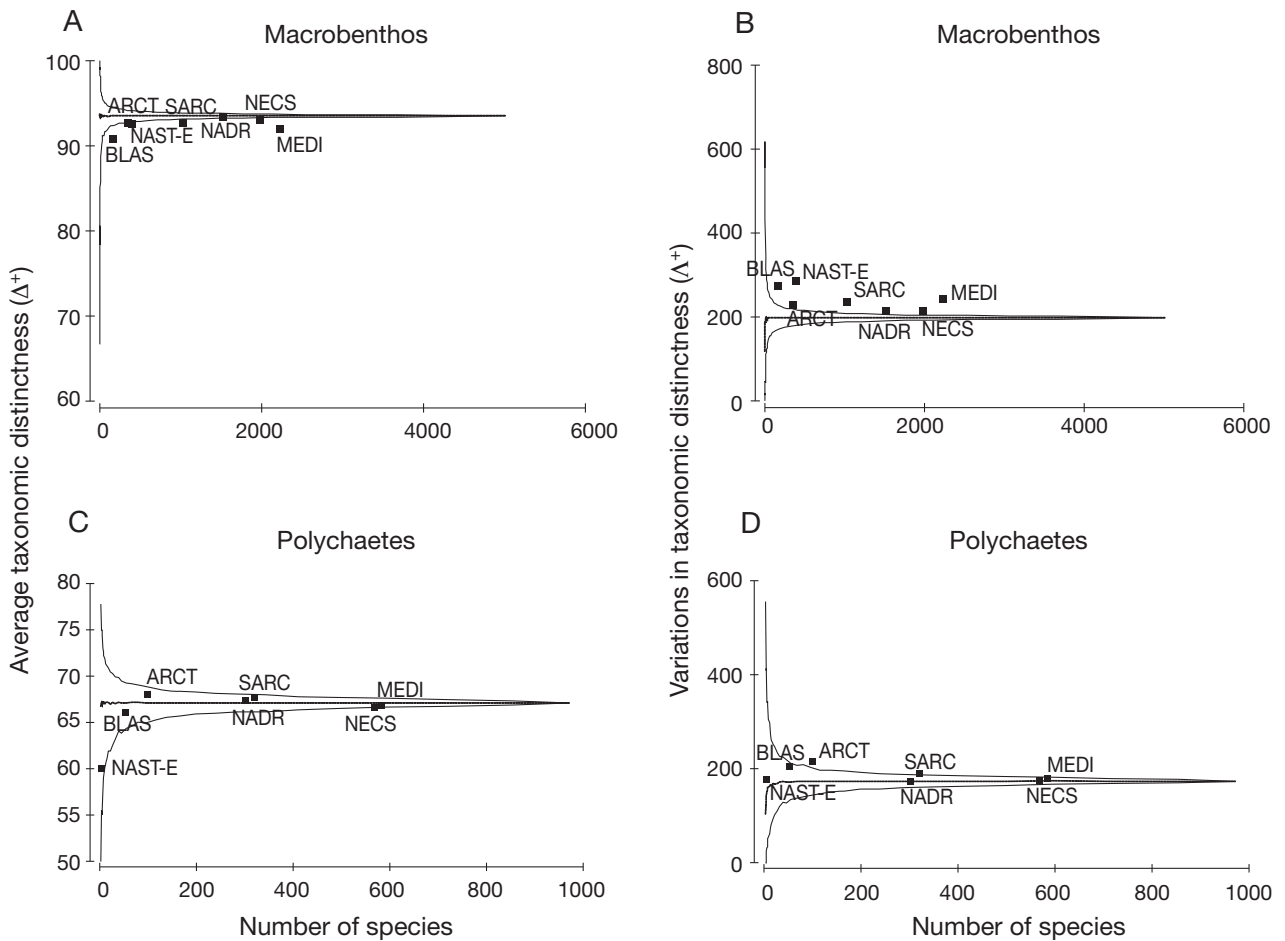


Fig. 11. 95% probability funnel for taxonomic distinctness (Δ^+ , Λ^+) for (A, B) macrobenthos and (C, D) polychaetes, as calculated for Longhurst (1998) provinces. Expected average indicated by the straight line in the middle of the funnel. Abbreviations as in Fig. 5

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).

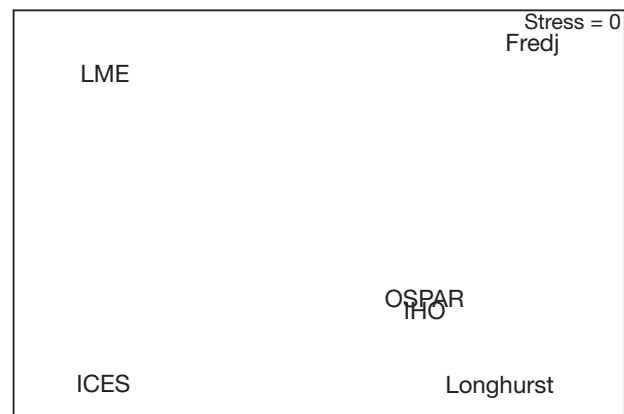


Fig. 12. Third-stage ordinations of ranked inter-matrix correlations between the systems of division of the European Seas, based on their polychaete inventories and the classification of the species to higher categories

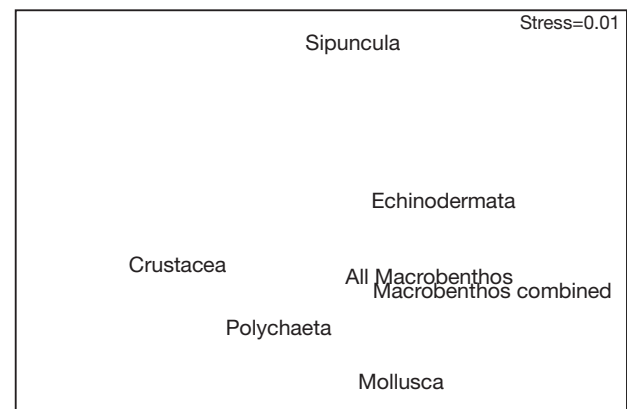


Fig. 13. Third-stage ordinations of ranked inter-matrix correlations between the benthic groups used in the analyses, based on their inventories and the classification of the species to higher categories, for Longhurst's (1998) system

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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Assessing evidence for random assembly of marine benthic communities from regional species pools

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ABSTRACT: Local species diversity may be determined by processes operating locally, such as disturbance, predation and competition, or by regional processes, such as environmental structuring or history. Classical theory focusing on competition predicts that the species combining to form communities will be less similar to each other than they would be if they were assembled at random from a regional species pool. Theory focusing on environmental structuring predicts that species will be more similar to each other than expected by chance. A randomisation test that determines the extent to which local species lists represent random selections from a regional list, based on the average relatedness between species, was applied to data held in the MacroBen database. Little or no evidence was found for species lists of whole faunas at any scale being random subsets of species lists at larger scales. Species tend to be more closely related to each other than would be expected if they were assembled at random. Thus marine soft-sediment macrofauna are not locally assembled at random from regional species pools and it is likely that regional processes determine the assembly of communities. Focusing on the most abundant class within the macrofauna, a different pattern emerges, in that there is a much stronger tendency for local polychaete composition to be a random subset from regional pools at all scales. Thus it is not possible to determine whether local polychaete diversity is independent of both local and regional processes, or determined by a combination of both acting antagonistically.

KEY WORDS: Benthos · Soft sediment · Community assembly · Local–regional relationships · Species pools · Taxonomic distinctness

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INTRODUCTION

The idea that species occurring in a particular place at a particular time are not simply a random collection is not new (Raunkjær 1934, Williams 1947) and there have been a number of attempts to model the way in which actual communities come to be (Diamond 1975, Tofts & Silvertown 2000). In essence, studies focus on the relationship between local (however defined) species composition and species pools reflecting species which could occur in the local assemblage (regional pools). Assembly is considered to be a fundamental

process underpinning the construction and evolution of biological systems (Drake 1990), and there are 2 views of how non-randomness in species composition arises and how it relates to the set of potential colonists. Many ecological studies focus on interactions between organisms, generally concluding that competition is of primary importance in determining species composition and that competition is greatest between those species that are most similar (e.g. Johansson & Keddy 1991, Wilson & Watkins 1994, Wilson & Gitay 1995), so communities are most stable when coexisting species are dissimilar and traits are overdispersed with

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respect to an appropriate null model. An alternative viewpoint (e.g. Schimper 1903, Tofts & Silvertown 2000) is that, given a set of environmental conditions, only species possessing certain subsets of attributes will be able to establish themselves in a community, leading to an assemblage in which traits are under-dispersed with respect to a null model.

Issues concerning assembly rules, and the appropriateness of null models, have been the subject of vigorous debate amongst ecologists for decades (Weiher & Keddy 1999). Although it is possible to construct hypotheses concerning the randomness or otherwise of local community assembly from regional species pools, in practice it is far from straightforward to construct sensible statistical tests to examine such hypotheses. Several studies have correlated local species richness with regional species richness across different communities (e.g. Cornell 1985a,b, Ricklefs 1987, Caswell & Cohen 1993), interpreting non-linearities in the relationship between local and regional species numbers as evidence of 'saturation' (Srivastava 1999, Loreau 2000). Another approach has been to model assembly explicitly using, for example, patch-occupancy models (Caswell & Cohen 1991, 1993, Huguency et al. 2007). A problem with such approaches is that they tend to exclude details of the relationships between species, or at best to examine them rather superficially, focusing on numerical distributions rather than taxonomic or ecological similarities or differences between organisms.

One approach to investigating community assembly has been to examine variation in taxonomic ratios, such as the ratio between numbers of species and numbers of genera (Elton 1946, Williams 1947). This implies that the relatedness of species in assemblages may provide useful insights into community assembly. Measures based on the taxonomic (Warwick & Clarke 2001) or functional (Sommerfield et al. 2008) relatedness of species provide an alternative view of biodiversity to that based on numbers alone. Clarke & Warwick (1998) demonstrated that average taxonomic distinctness (Δ^+), the mean path-length between species in a list through a taxonomic tree, has useful statistical properties. If all species in a regional list are equally likely to appear in a local assemblage, the measure is sample-size independent, and Clarke & Warwick (1998) present a randomisation test that specifically addresses the question of whether 1 species list represents a random subset of species from another. Such a test provides the opportunity to address relationships between local and regional species lists explicitly. In addition to the general ecological interest in assembly rules, there is also a practical aspect to understanding relationships between local and regional species pools. Indices of relatedness, and their associated randomisation tests,

have been proposed as measures of stress in communities (Warwick & Clarke 1995, 1998, 2001); species in stressed assemblages tend to be more closely related to each other than expected. For indices of relatedness and their associated randomisation tests to be generally applicable, we need to know what the appropriate regional pool may be against which to test a local species list.

In the present study we apply Clarke & Warwick's (1998) test to species occurrences in a large number of samples of macrobenthic infauna from across the European continental shelf to address 2 main issues: (1) Is there evidence that species within assemblages are assembled at random from regional species pools at larger spatial scales? (2) If so, are there appropriate scales for defining local and regional species pools? It is arguable whether studies of relatedness within assemblages should be restricted to taxonomically coherent groups (Clarke & Warwick 2001, Ellingsen et al. 2005). To assess this, analyses were conducted using occurrence data for all macro-infauna, and then repeated using only occurrence data for the most abundant class, the polychaetes.

DATA AND METHODS

Data. The MacroBen database contains nearly 0.5 million distribution records of 7203 taxa at 22 897 stations; a full description is given in Vanden Berghe et al. (2009, this Theme Section). A major effort was made to harmonise the taxonomy across the different datasets within the database: all names were matched, both for spelling and synonymy, with the European Register of Marine Species (ERMS; www.marbef.org/data/erms.php). Raw data were retained whenever possible to allow maximum flexibility during analyses. Most data providers also furnished geographical and physical data. To work with the most inclusive, yet most comparable, dataset possible, we performed initial filtering on the database. Datasets for which subtidal soft-sediment samples were collected with 0.1 m² grabs, sieved on 0.5 or 1 mm meshes and abundances recorded to the species level were selected. For taxonomic consistency, only datasets collected after 1980 were included, and to avoid confounding, samples known to be affected by natural or anthropogenic stressors were excluded. Where possible, datasets with repeated observations (e.g. multiple grabs from each station) were chosen to allow tests at the lower levels (e.g. individual grabs against stations). The main focus of the present study was adult macro-infauna, so taxa identified as juveniles or colonial animals (e.g. Bryozoa, Hydrozoa, Porifera) were excluded, as were samples containing <5 species, as relatedness measures

based on very few species are too variable to be of use. The resulting database, on which the present study is based, contained information on the distributions of 2477 species, comprising 63 281 occurrences distributed among 1238 samples derived from 31 original datasets from continental shelf locations distributed from the Arctic to the Black Sea (Table 1).

Local and regional species lists. There is no universally agreed or sensible definition of what constitutes a location or a region for the purposes of comparing local and regional diversity, or determining how local diversity reflects regional patterns. All that matters for the definition is that the regional list is larger than the local list. We took a hierarchical approach to examining local/regional relationships. Within the database we defined a number of hierarchical groupings of samples, reflecting how an investigator might choose to

define species lists for the purposes of conducting tests: individual samples (grabs) within stations, stations within surveys, surveys within regions and regions within the complete database. Tests were conducted for all pairs of levels, except samples against the regional lists and the European list (being the complete list of species from all of the samples in the database), as the computational demands of such tests would have been very large. Thus species lists from individual grabs were tested against the combined species list from the station at which they were collected. Lists from each sample and combined lists from each station were tested against the combined list from the survey at which they were collected. Lists from each station and each survey were tested against combined lists from areas within regions, defined using a range of schemes, within which they were collected.

Lists from stations, surveys, and regions (areas within regional schemes) were tested against the European list, the combined list from all soft-sediment samples in the database.

Several regional schemes were used to divide European waters into areas, reflecting different ways in which an investigator might attempt to construct 'regional' lists for the purposes of tests of relatedness. These were: the scheme proposed by Fredj (1974); areas defined by the International Council for the Exploration of the Seas (ICES; www.ices.dk/aboutus/icesareas.asp); regional seas proposed by the International Hydrographic Organization (IHO 1953); large marine ecosystems (LMEs; www.lme.noaa.gov/Portal/) reviewed by Sherman (1994); regions defined by the Oslo-Paris Commission (OSPAR) for the Quality Status Report process; and biogeochemical provinces described by Longhurst (1998). A more detailed description of these classifications (and their relative merits) can be found in Arvanitidis et al. (2009, this Theme Section).

Statistical analysis. The complete set of analyses was conducted using all macrofaunal species in samples (with the exception of those excluded using the criteria outlined in 'Data'), and again using only species within the most abundant class, namely the polychaetes.

Average taxonomic distinctness (Δ^+), a measure of the average degree to which species in an assemblage are related to each other, is defined as:

Table 1. Summary of sources of data used. For details see Vanden Berghe et al. (2009, this Theme Section). Shown are numbers of samples and stations used following data filtering, and proportion of the total provided by those surveys contributing $\geq 1\%$. Parentheses: fewer samples or stations used for analyses of polychaete data following data filtering

Survey	Code	Samples		Stations	
		No.	%	No.	%
Arctic Ocean and Barents Sea	ar			22	2
Franz Josef Land	o8	45	2	9	1
Kongsfjord, Spitzbergen	ko			6	
Hornsund, Spitzbergen	hs			34	3
Northern Barents Sea	o2	44	2	10	1
Pechora Sea	o7	71 (66)	3	15 (14)	1
Finmark	o6	275	11	53	4
Norwegian and Barents Seas	o4	1146 (1091)	45	183 (129)	15
North and Norwegian Seas	o3	269 (262)	10	30 (26)	2
Bay of Puck	pu			29	2
Gulf of Gdansk	gd			13	1
Kiel Bay N3	n3	321	12	1	
Kiel Bay intercalibration	70	70	3	1	
North Sea benthos survey	ns			231	19
BIOMÔR ^a	o5			51	4
Blanes Bay	bl			2	
Redit	gr			92	7
LBMRev	lm			28	2
Cesenatico	oc			1	
Cretan shelf	ka			199	16
Crete (Mop)	do			56	5
Mytilini	M2	71 (70)	3	9	1
Saronikos	M3	76 (74)	3	6 (5)	
Kalamitsi	M6			22	2
Kerkyra	M7			12	1
Kyklades	M8	55	2	14	1
Gialova	M0	134 (116)	5	7 (6)	1
Megfeod	M1			24	2
Strel Bay	M4			18	1
Jalta	M5			26	2
Laspi Bay	M9			33	3

^aData from Mackie et al. (1995)

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

where s is the number of species present, the double summation is over $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$, and ω_{ij} is the 'distinctness weight' given to the path length linking species i and j in a hierarchical classification (Clarke & Warwick 1998). As advocated by Clarke & Warwick (1998), values of Δ^+ were based on equal step-lengths between taxonomic levels. For macrofauna, the taxonomic levels used in the present study were species, genus, family, order, class and phylum, according to the classification contained within the ERMS. Thus the step-length between adjacent taxonomic levels was 16.67, e.g. for different species in the same genus $\omega = 16.67$, for species in different genera, but the same family $\omega = 33.33$, for species in different families, but the same order $\omega = 50$, etc., and $\omega = 100$ for species connected at the highest (taxonomically coarsest) level. For polychaetes the levels were species, genus, order and class, and step-lengths ($\omega = 25$) were adjusted accordingly.

Values of Δ^+ calculated for 'local' species lists were compared with the expected range of values from 'regional' lists using the routine TAXDTEST in the PRIMER software (Clarke & Gorley 2006). Subsets of m species, where m is the number of species in the local list, were drawn at random from the regional list and Δ^+ calculated. The value of Δ^+ was calculated from the local species list was compared with the distribution of Δ^+ values from a large number (1000 in the present study) of random draws from the regional list. If the observed Δ^+ fell outside the central 95% of the simulated Δ^+ values, it was considered to have departed significantly from expectation: a 2-sided test was appropriate since departure may theoretically be in the direction of enhanced as well as reduced distinctness. The result of each of the >1000 tests was treated as an independent observation for the purpose of calculating confidence intervals about the mean number of tests falling within 95% probability intervals for tests at each level. It could be argued that a series of tests for samples from a particular dataset against a single species list are not strictly independent, but we took the view that any apparent decrease in variability between observations introduced by such a lack of independence would be counterbalanced by the range of surveys included at each level.

RESULTS

Fig. 1 is a highly condensed summary of results from tests at all spatial levels. If species are behaving as if assembled at random from the regional species pool, then on average 95% of tests should fall within the

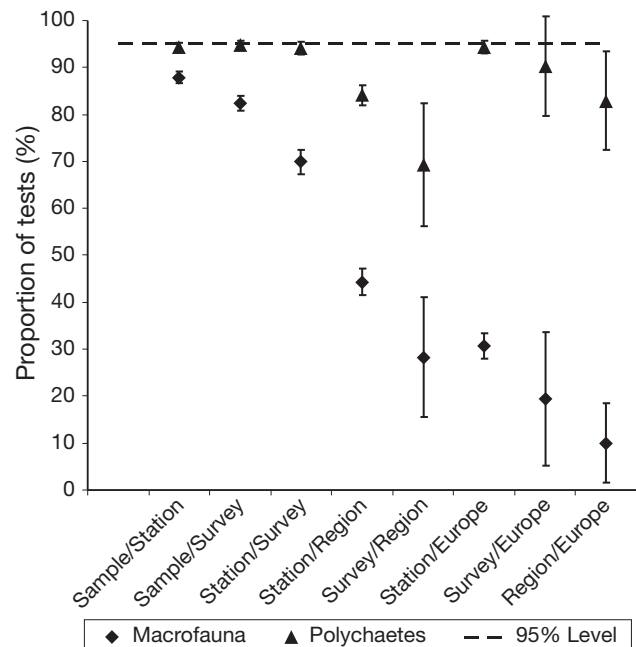


Fig. 1. Summary of randomisation tests at all spatial levels. Values on the y-axis are the average percentage of species lists ($\pm 95\%$ CI) for which average taxonomic distinctness (Δ^+), calculated from combined lists at the level of the first category (= 'local' lists) on the x-axis label, falls within the 95% probability levels of Δ^+ calculated from the appropriate combined lists at the level of the second category (= 'regional' lists). Values were averaged across all datasets for each pair of levels. Values were re-averaged across regional schemes for comparisons involving regions. All tests were repeated for macrofauna and for polychaetes. The 95% line indicates a level at which it might be reasonable to assume that the hypothesis of assembly at random cannot be rejected

95% probability limits for those tests. Thus the confidence intervals for the mean number of tests falling within those 95% limits should also encompass the 95% line in Fig. 1. For macrofauna the pattern is very clear. For no pair of scales (local and regional) does the local species list represent a random subset of the regional list, since in all cases the percentage of local samples falling within 95% probability limits for Δ^+ derived from the regional list is <95%. Although not illustrated here, the general tendency is for species to be more closely related to each other (samples falling below the lower 95% limit). As the areas from which both local and regional species lists are derived increase, so the tendency for Δ^+ values to fall below expectation (i.e. rejecting the hypothesis of random assembly) also increases (Fig. 1). Similarly, as the mismatch in spatial scale between localities and regions increases, the hypothesis of assembly at random from the regional pool appears less likely to be true.

Confining the analyses to tests of random assembly within the polychaetes (Fig. 1) produces a very differ-

ent pattern. While a rigid adherence to the idea that a value of 95% must be achieved in order to reject the null hypothesis (assembly is not random) would allow the conclusion that there is no evidence that the null hypothesis is falsified, it is very clear that values in many cases approach this value and the confidence intervals about the mean include the 95% value. Thus a hypothesis of random assembly of local communities from regional pools is plausible at the scales of samples versus stations and surveys, stations versus surveys, or even stations and surveys versus the whole European fauna collected in all of the surveys (Fig. 1). All values are very much higher than for macrofauna and the clear relationships between area, differences in scale and the likelihood of the null hypothesis being false, which were evident for the macrofauna, are less apparent for analyses based on polychaetes alone. Of all the different groupings of samples it is those associated with the regional schemes that show evidence for non-random assembly.

DISCUSSION

The recognition that the numbers of species in local communities are not governed solely by processes operating at local scales and that regional biogeographical processes are also important (Ricklefs 1987, Ricklefs & Schluter 1993) represented a paradigm shift in community ecology (Loreau 2000). Most studies examining relationships between local and regional species numbers (e.g. Cornell & Lawton 1992, Srivastava 1999) have found evidence for local richness increasing with regional richness, as if local communities are obtained by proportional sampling from the regional pool (Loreau 2000). Prior to this, questions concerning the degree to which species within communities are assembled at random, or if not, then how, and how one can tell, had been the subject of vigorous debate (Connor & Simberloff 1979, Diamond & Gilpin 1982, Gilpin & Diamond 1982) which is by no means resolved to this day (Weiher & Keddy 1999). More recent developments, such as the unified neutral theory of biodiversity and biogeography (Hubbell 2001), have led to a reexamination and reevaluation of many of the issues involved (Bell et al. 2006, Holyoak & Loreau 2006, Hubbell 2006, McGill et al. 2006), still with conflicting results and interpretations.

Coupled with this, and relevant to the present work, are developments in the incorporation of phylogenetic information into community ecology (e.g. Webb et al. 2002, Helmus et al. 2007), often using measures that are simple mathematical transformations of Clarke & Warwick's taxonomic diversity and taxonomic distinctness (Warwick & Clarke 1995, Clarke & Warwick

1998), which in turn are closely related to Rao's quadratic entropy (Rao 1982). Species which are closely related might have similar tolerances to environmental stressors, and would thus be expected to occur within the same communities (Webb 2000) or, conversely, closely related species may have similar resource requirements, leading to inter-specific competition and exclusion from communities (Elton 1946). The emphasis here is on relatedness, which may be reflected in taxonomic similarity, rather than on traits, the assumption being that closely related species will tend to share many traits. While this distinction is important, the resulting hypotheses, that inter-specific interactions will tend to decrease relatedness while environmental or evolutionary factors will tend to lead to communities which are more closely related, are exactly analogous to those outlined in our 'Introduction'.

Against a background of shifting evidence and opinion, alternative methods, and continuing debate about the extent to which local communities are assembled at random from regional species pools, a fundamental issue has to be remembered. 'Local' and 'regional' are relative terms. Loreau (2000) showed that the form of local-regional richness curves is determined by the way total diversity is partitioned between its α and β components, which itself is a matter of scale. Although a few studies exist which have combined 'phylogenetic' relatedness approaches with scale issues (e.g. Kembel & Hubbell 2006, Swenson et al. 2006), none has approached this study in terms of variation in spatial scales.

We show that species within marine macrobenthic communities tend to be more closely related to each other than would be expected if species behave as though assembled at random from regional species pools. This non-randomness increases as the difference in scale between what is considered 'local' and the scale at which the regional pool is defined increases. This may be taken as evidence that at the scales of observation, environmental and evolutionary factors are important determinants of community composition, and inter-specific interactions are not. In marine benthic systems this makes sense. Species in marine systems have evolved to exploit regularities in the physical dynamics of the environment as part of their reproductive processes, and often use diffusive dispersal to counteract the longer-term consequences of variability in the physical environment (Steele 1991). Thus marine systems are relatively dynamic and open, compared to terrestrial systems, and species, even those which are rarely captured, tend to be widely distributed. Conditions where one species may outcompete and exclude closely related species in a marine benthic community at anything other than short time scales and small spatial scales are difficult to

imagine, and community structure can be expected to vary with environmental conditions and to be determined by processes operating over large scales of space and time. A similar conclusion was drawn by Bellwood & Hughes (2001), in a study of fish and coral communities in the Indian and Pacific Oceans.

The pattern within analyses confined to the polychaetes suggests that random assembly is a plausible hypothesis within surveys for this group, and that for groups of samples (stations), polychaete species are a random subset from the European list. Following the reasoning outlined above, it would appear that heterogeneity in environmental conditions and history are less important for polychaete assemblages, and that we cannot distinguish between their effects and the effects of inter-specific interactions. In other words, it is not possible to determine whether local polychaete diversity is independent of both local and regional processes, or determined by a combination of both acting antagonistically. Why, then, do we observe a different pattern when confining our analyses to the polychaetes? It may be something to do with the ecology of polychaetes or their taxonomy. Typical polychaete assemblages are taxonomically and trophically diverse (Fauchald & Jumars 1979, Olsford & Somerfield 2000). The taxon has received a recent phylogenetic review (Rouse & Pleijel 2001) and, as they are a key component of macrofaunal assemblages, taxonomic expertise is widespread in Europe — factors which may imply a greater homogeneity in approaches among the different datasets combined in our analysis.

On the other hand, it may tell us something about the analytical method. Potential problems with the use of a taxonomic, as opposed to a phylogenetic, classification are discussed by Ellingsen et al. (2005). Leaving that aside, it is to be expected that relatedness measures are heavily influenced by the largest differences between species, namely the distances between species in different taxa at the higher levels in the classification. Although Clarke & Warwick (1999) and Rogers et al. (1999) showed strong insensitivity of Δ^+ to major variations in the branch step-lengths between taxonomic ranks, it is likely that analyses of assemblages with a great deal of structure at higher taxonomic levels will reflect heterogeneity in the balance of species within those higher taxonomic levels. Clarke & Warwick (1999) pointed out that measures such as Δ^+ are not constrained to hierarchies with fixed points of genus, family, order, etc., but carry over naturally and forcefully to continuous phylogenies in which the branch lengths are fully determined, for example by genetic distances (e.g. Nei 1996), so this is not an artifact introduced by the use of a taxonomic classification.

The fact that we observed different relationships between scale and randomness when looking at as-

semblages of mixed phyla as compared to assemblages of polychaetes (which do, after all, contribute a large proportion of species in macrofaunal assemblages) suggests that a useful way forward might be to examine in more detail the way in which species are distributed among higher taxonomic levels, and contribute to measures of relatedness in mixed assemblages. There is a lot of evidence for structural redundancy in marine macrobenthic assemblages, and it is likely that closely related species may be interchangeable in communities (Warwick 1993, Olsford et al. 1997, 1998), whereas large-scale heterogeneity may influence the distribution of phyla, and species within phyla, in ways that differ. The vast majority of studies considering community assembly and species distributions have focused on species (or populations) as the units of interest. It is possible that analyses focusing on the presence of groups of species, taxonomically or functionally related, may provide insights into the processes structuring communities.

In the meantime, what recommendations can be made for those wishing to examine the idea that assemblages under stress consist of subsets of species which are more closely related to one another than would be expected under a null expectation that all species are equally likely to occur? What are the appropriate scales at which to define 'local' and 'regional' species lists, in order that such tests may be valid? It would appear from the results of the present study that such tests should be based on taxonomically coherent subsets of species. It is worth noting that much of the development work on the testing structure (e.g. Clarke & Warwick 1998) was based on nematode assemblages. Certainly for the polychaetes it appears that, as long as one avoids lists based on the various regional schemes, any combination of 'local' and 'regional' lists may be appropriate. For tests based on whole macrofaunal assemblages, it would appear that a null hypothesis of random assembly with equal probabilities of occurrence is not generally appropriate.

Finally, it must be remembered that the null hypothesis examined here, that species in local assemblages are random subsets of the species in the appropriate regional pool, implies that all species in the regional pool have an equal probability of appearing in any subset. There are a range of other, perhaps more sensible, alternative hypotheses which should be examined (Gotelli 2000, Helmus et al. 2007). For example, most species in assemblages are rare (Gray et al. 2005), and a few are abundant and widely distributed. The simulation of random draws from the regional pool can be constrained to match the probabilities of occurrence of each species, defined by their frequency of occurrence in a large number of samples (Somerfield et al. 2008). Thus certain species will be picked more often

in the random subsets, because they are observed to be present more often in real samples. The hypothesis, therefore, is that species in assemblages are random subsets of a regional pool but their probability of occurrence is determined by processes affecting species abundance distributions, operating independently. This would also fit neatly with the idea that most species patterns observed in nature may be derived from a simple model in which distributions are determined by abundances of species at the largest measured scale (Harte et al. 2005).

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Macroecology of the European soft sediment benthos: insights from the MacroBen database

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ABSTRACT: Macroecology provides a novel conceptual framework for analysis of the distribution and abundance of organisms at very large scales. Its rapid development in recent years has been driven primarily by studies of terrestrial taxa; the vast potential of marine systems to contribute to the macroecological research effort remains largely untapped. International collaborative efforts such as MarBEF have provided fresh impetus to the collation of regional databases of species occurrences, such as the newly available MacroBen database of the European soft sediment benthic fauna. Here, we provide a first macroecological summary of this unique database. We show that in common with almost all previously analysed assemblages, the frequency distribution of regional site occupancies across species in the MacroBen database is strongly right-skewed. More unusually, this right skew remains under logarithmic transformation. There is little evidence for any major differences between higher taxa in this frequency distribution (based on the 8 animal classes for which we have sufficient data). Indeed, considerable variation in occupancy persisted across the taxonomic hierarchy, such that most variation occurred between species within genera. There was a weak positive relationship between local population density and regional occupancy across species, but this abundance–occupancy relationship varied considerably between higher taxa and between geographical areas. Our results highlight the potential of databases such as MacroBen to consolidate macroecological generalities and to test emerging theory.

KEY WORDS: Marine macroecology · Macrobenthic · Europe · Large marine ecosystems · Species–range size distributions · Phylogeny · Abundance–occupancy relationships

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INTRODUCTION

Macroecology draws on insights from fields including ecology, biogeography, palaeontology, macroevolution and applied statistics to understand how large-scale processes affect the organisation of ecological systems at multiple scales (Brown 1995, Gaston & Blackburn 2000, Blackburn & Gaston 2006). It has defined novel and important concepts and methodological techniques to describe the form and structure of large-scale ecological patterns and has developed in a relatively short time into a thriving and productive discipline (Gaston &

Blackburn 2000, Blackburn & Gaston 2003). The importance of a macroecological approach becomes still more apparent with the realisation that human impacts on ecological systems are detectable at the same very large scales that interest macroecologists (Chapin et al. 2000, Kerr et al. 2007), and that many of the most pressing issues in applied ecology involve very general questions relating to habitat modification, invasive species, over-exploitation, pollution and climate change (Sutherland et al. 2006). In a marine context, considerable large-scale changes in ecosystems have already occurred without rigorous documentation (Jackson

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2001), which brings into sharp relief the need to understand large-scale patterns of biodiversity that we may better predict the consequences of current and future human-induced global change.

A guiding principle of the macroecological approach is the search for generality — to what extent are large-scale patterns in the abundance and distribution of organisms consistent across taxa and environments? Certain macroecological patterns and relationships appear to be very general. For instance, across a taxonomically constrained group of species, the frequency distribution of range sizes measured at regional to global scales will typically display a characteristic right skew: most species are rare, but a few are extremely widely distributed (Gaston 2003). Similar generalities are observed in relationships between geographic distribution and local population density (Gaston et al. 2000, Blackburn et al. 2006). This so-called abundance–occupancy relationship is typically positive such that locally abundant species tend to be geographically widespread (Gaston et al. 2000, Blackburn et al. 2006), and is important as it provides a link between local and regional population processes (Freckleton et al. 2005, 2006).

An important caveat to the inferred generality of such patterns, however, is that macroecology has developed as an overwhelmingly terrestrial discipline (Raffaelli et al. 2005, Clarke et al. 2007), whereas the sea is home to most of life's higher-taxon diversity (May 1994). Only a minority of studies making explicit reference to 'macroecology' have had a primarily marine focus (Raffaelli et al. 2005), and just 18 of the 279 abundance–occupancy relationships reviewed by Blackburn et al. (2006) derived from marine or intertidal systems. This paucity of marine macroecological studies can be partially explained by the particular practical, logistical and financial challenges posed by working in the marine environment that make the kinds of datasets relied upon by terrestrial macroecologists (often compiled largely through the efforts of committed volunteer naturalists) difficult to obtain for marine taxa. In addition, it can prove difficult to define variables crucial to macroecological analyses such as 'range size' and 'population size', particularly for highly mobile pelagic taxa or for regions with (often highly) incomplete sampling. Despite these difficulties, there exist several excellent macroecological studies of the marine environment (e.g. Li 2002, Foggo et al. 2003, Macpherson 2003, Fisher & Frank 2004, Irigoien et al. 2004, Jennings & Blanchard 2004, Hsieh et al. 2006). In the main, these have tended to support general conclusions reached by terrestrial macroecologists on the basic form of the principal patterns. For instance, species–range size distributions display a similar characteristic right skew for both marine and terrestrial taxa (Gaston 2003), and similar patterns are

also seen for species–abundance distributions; Gray et al. (2006) show that these are of similar form in a variety of marine and terrestrial taxa under similar sampling regimes. Importantly, macroecological relationships such as the abundance–occupancy relationship are also observed in the sea (e.g. Foggo et al. 2003, Fisher & Frank 2004, Blackburn et al. 2006), indicating that similar processes may act on communities in both environments. Efforts to increase communication between marine and terrestrial ecological research communities (e.g. Stergiou & Browman 2005) are stimulating progress in marine macroecology, and this trend will only increase as national and international organisations consolidate the data collected by individual research organisations into regional databases that provide a broader-scale overview of the distribution of marine diversity. The Marine Biodiversity and Ecosystem Functioning EU Network of Excellence (MarBEF, www.marbef.org) has been established specifically to investigate patterns of marine biodiversity, with an emphasis on the analysis of large-scale patterns and processes that would not be tractable without such international cooperation.

It is important to realise that macroecology is about more than simply describing patterns (Blackburn & Gaston 2006), and recent efforts have shifted towards seeking a mechanistic understanding of the processes that drive these patterns. For instance, population models that view interspecific macroecological patterns as the result of intraspecific dynamics have provided a powerful approach for generating mechanistic hypotheses (He & Gaston 2003, Freckleton et al. 2005, 2006), and make testable predictions about the roles of ecological and life history parameters in shaping macroecological patterns and relationships. Testing these predictions in terrestrial systems has been limited by the fact that parameters thought to be important in determining the form of macroecological patterns, such as colonisation ability, often do not vary substantially within the highly mobile taxa (such as birds) typically studied (Freckleton et al. 2005). Indeed most macroecological datasets tend to be somewhat taxonomically restricted, and thus encompass only limited functional diversity. This underlines the vast potential of macroecological studies of marine systems to aid in a more general understanding of macroecological process. The same sampling regime within a single marine habitat type will typically capture significant taxonomic diversity, recording species that differ markedly in characteristics (e.g. larval dispersal potential) hypothesised to be important in determining large-scale patterns of distribution and abundance (Foggo et al. 2007). Similarly, samples will often traverse steep environmental gradients (e.g. depth, salinity, fishing intensity). Because experimental manipula-

tions at macroecological scales are largely precluded, testing macroecological hypotheses across taxa and along environmental gradients may provide the most powerful test of their generality; this principle is taken to its extreme by testing in marine systems hypotheses generated from studies of terrestrial taxa (Steele 1991).

A necessary prerequisite to exploiting this vast potential of marine databases for testing emerging macroecological theory is a rigorous description of the observed patterns. Here, we analyse the MacroBen database to provide the first such summary for the soft-sediment macrobenthos throughout European coastal waters. We start by defining a simple measure of regional distribution based on presence/absence across a 100 km grid, and consider the frequency distributions of occupancy across 2292 species. We then use the exceptional taxonomic coverage of the MacroBen database to compare occupancy patterns among higher taxa. Specifically, we compare occupancies between 8 classes of animals for which we have distribution records for sufficient species, and provide the first analysis with this taxonomic scope of the way that variance in range size is partitioned across the taxonomic hierarchy. Finally, we introduce measures of population density allowing us to quantify abundance–occupancy relationships across and within classes, accounting for differences in mean density between geographic areas.

DATA AND METHODS

The MacroBen database. Producing comprehensive regional-scale databases through the integration of smaller-scale datasets has been a core objective of the MarBEF network. The MacroBen database is the first such regional database, comprising distribution records for soft sediment benthic taxa throughout European coastal waters compiled from many sources and published accounts including Karakassis & Eleftheriou (1997) and Mackie et al. (1995). The systematic nomenclature of the database has been checked for both orthography and synonymy against the European Register of Marine Species (ERMS, www.marbef.org/data/erms.php). Raw data were retained whenever possible to allow maximum flexibility during analyses, and geographical and physical data were available for large numbers of records. The final database contains 465 354 distribution records, from 7203 valid taxa and 22 897 sampling stations, collated from 44 individual data sets. It is presented as an MS Access file, and is described in full in Vanden Berghe et al. (2009, this Theme Section).

The MacroBen database includes tools to extract data and to calculate basic statistics and diversity coefficients. We applied the following filtering rules: only taxa identified to the species level were considered,

and samples were required to contain quantitative data on species numbers so that analyses using abundance data could proceed on the same set of species as analyses of occupancy patterns. Taxa not considered to be part of the macrobenthos were excluded, as were immature individuals. Only records collected since 1990 were retained, to reduce the influence of temporal trends in species distributions. All records were required to contain information on the area sampled, to allow estimates of population density (ind. m⁻²) to be calculated for each species. All included datasets sampled using Van Veen grabs or hand-operated Van Veen grabs, generally with a sampling area of 0.1 m² (range 0.04 to 1 m², including pooled samples, and the mesh size used to sort samples was always 1 mm. Other potentially confounding factors remain in the dataset, either because their variation over large scales is seen as important in structuring macroecological relationships (e.g. spatial variability in habitat type) or because we had insufficient information to control for them (e.g. variability in the seasonality of sample collection). Our filtering rules resulted in a database containing 211 518 records, representing 2292 species from 15 024 sampling stations distributed between 6.5° W and 58.9° E and between 35.3° N and 81.5° N.

Measures of occupancy and population density. Site occupancy ('area of occupancy' in the terminology of Gaston 2003) is regularly used in macroecology as a measure of the extent of the distribution of a species. The simplest measure of site occupancy in our dataset would be the number (or proportion) of sampling stations at which a species was recorded. However, sampling effort was highly heterogeneous across space. To address this issue, we superimposed a 100 × 100 km grid onto the entire sampling area, projected using the Lambert Azimuthal Equal Area projection. Each individual spatially-referenced record could then be assigned to a single 100 × 100 km grid square, and occupancy was measured as the proportion of the total number of grid squares covered by the sampling area ($n = 99$) in which a given species was recorded. There are problems with this approach, particularly as some grid squares have been more heavily sampled than others. Thus, while presences can be interpreted with confidence, absences cannot; it is likely that most species occupy more squares than those in which they have been recorded. However, we assumed that the recorded occupancy of a species will be roughly in proportion to its actual occupancy. Thus, our occupancy estimates should give a reasonable approximation of the relative commonness or rarity of a species. The scale of grid chosen was also made primarily on pragmatic grounds, with 100 × 100 km resolution providing a good compromise between fine resolution and reasonable sampling effort. Fortunately, macroecological patterns

have proven to be remarkably robust to different scales of occupancy measure (Blackburn et al. 2004).

Population densities were calculated at the sampling station level, i.e. the total number of individuals of a species recorded across all replicate samples at a station was divided by the total area sampled. The mean density of a given species is taken as the geometric mean of its density estimates across all samples in which it was recorded (i.e. excluding zero densities).

A common feature of marine datasets is the presence of singletons, that is species recorded in the dataset as a single individual. Although they frequently form an important component of benthic samples, it has been argued that such very rare species may not play a significant role within communities, and that most are likely to be vagrants or transients that have immigrated from outside the sampling area (Gray et al. 2006). To quantify the effect of such species, we defined 2 kinds of singleton: (1) species represented by only a single individual across all replicates and sampling stations, and (2) species with a maximum abundance of 1 in any single sample. Whilst we recognise that sampling effects may create some 'artefactual' singletons (e.g. some large-bodied organisms may be inefficiently sampled, yet have important ecological interactions), using this compilation of multiple datasets means that the probability of erroneously excluding such rare or poorly-sampled important species is minimised.

Statistical analyses. The shape of the untransformed and \log_{10} -transformed frequency distributions of occupancies were quantified by their skewness, using the unbiased estimator of skewness (g_1) and its standard error given by Sokal & Rohlf (1995), which can be tested against a null expectation of 0 using the t distribution with $df = \infty$ (Sokal & Rohlf 1995). We performed this analysis for occupancies of all species, and for all non-singleton species (using the definitions of singletons described above).

Taxonomic patterns in occupancy were examined by first identifying those classes that contained at least 20 species (Table 1). These 8 classes, although representing just 24% of the classes present in the total database, together contained 93% of all recorded species and 97% of all distribution records. The variance in occupancy within this reduced dataset was partitioned between the levels of taxonomic hierarchy, i.e. class, order, family and genus, using a fully nested model, with variance components estimated using restricted maximum likelihood (REML). This procedure essentially partitions variance in occupancy into between and within group components at each subsequent taxonomic level. A high value for order, for example, would indicate that a large proportion of total variation in occupancy occurs between orders, with little variation within orders (i.e. species within an or-

Table 1. Number of species in each class in the complete dataset. The 8 classes shown in bold, with at least 20 species recorded in each, were used in analyses of individual classes

Phylum	Class	No. of species
Annelida	Polychaeta	724
Arthropoda	Malacostraca	656
Mollusca	Bivalvia	290
Mollusca	Gastropoda	240
Bryozoa	Gymnolaemata	128
Echinodermata	Stelleroidea	50
Echinodermata	Holothuroidea	28
Chordata	Asciacea	27
Cnidaria	Hexacorallia	19
Echinodermata	Echinoidea	17
Arthropoda	Pycnogonida	15
Bryozoa	Stenolaemata	14
Sipuncula	Sipunculidea	11
Mollusca	Aplacophora	10
Mollusca	Polyplacophora	9
Annelida	Clitellata	8
Cnidaria	Octocorallia	8
	Others (n = 14)	38
	Total	2292

der tend to be similar in terms of their occupancy). The residual variation from the model represents variation occurring between species within genera; a high value would indicate that even very closely related species (congeners) can differ substantially in their occupancies. This analysis is equivalent to the nested ANOVAs used for similar purposes elsewhere (e.g. Gaston 1998, Webb et al. 2001, Qian & Ricklefs 2004), although the REML estimation is more robust with unbalanced designs (Rao & Heckler 1997). Results need to be interpreted with caution, however, due to the influence of a large number of monotypic higher taxa: 19 of 69 orders (28%), 138 of 365 families (38%) and 584 of 1003 genera (58%) in the dataset were monotypic. Clearly, no variation is possible within a monotypic higher taxon, and such taxa will tend to inflate the proportion of variance explained at higher taxonomic levels. Our estimate of residual variation (i.e. the degree to which occupancy varies among congeneric species) is therefore bound to be an underestimate.

We estimated abundance–occupancy relationships using the Pearson product moment correlation between $\log_{10}(\text{occupancy})$ and $\log_{10}(\text{mean density})$. Although such relationships are frequently non-linear, the correlation coefficient provides a good approximation of their general form and strength (Webb et al. 2007). We first considered the relationship across all species in the dataset. We next examined the structure of this relationship by considering separately each of the 8 classes described above. In an attempt to control for differences in species composition and/or mean density across regions, we also estimated abundance–

occupancy relationships separately for each of the large marine ecosystems (LMEs, Sherman 1991) covered by our dataset. This involved calculating a separate occupancy and density value for each species in each LME. We excluded the Black Sea LME from this analysis, as all samples fell within a single 100 km square, meaning that there was no variance in occupancy within this LME. Finally, we combined the taxonomic and geographic stratification to estimate an abundance–occupancy relationship separately for each class within each LME.

All data manipulations and statistical analyses were executed with R 2.2.1 (R Development Core Team 2005, available at: www.R-project.org). The variance components analyses made use of the *nlme* package described in Pinheiro & Bates (2002).

RESULTS

Occupancy

The frequency distribution of occupancy was highly significantly right-skewed (skewness \pm SE = 2.99 ± 0.051 , $t = 58.5$, $p < 0.00001$; Fig. 1A). Substantial right-skew remained after log-transformation (skewness = 0.48 ± 0.051 , $t = 9.32$, $p < 0.00001$; Fig. 1B). The vast majority of species, therefore, had extremely restricted recorded distributions; 680 species (30% of all species) occurred in only a single 100 km square. In contrast, the

most widespread species (the polychaete *Heteromastus filiformis*) has been recorded in 73% of the sampled 100 km squares. The skew of the distributions does not result simply from the inclusion of ‘accidental’ species, at least if these were identified according to our definitions of singletons; significant right skew remained in untransformed and transformed distributions after the exclusion of both types of singleton (Fig. 1; excluding singletons with total count = 1, skewness of untransformed and log-transformed occupancy = 2.85 ± 0.054 and 0.35 ± 0.054 ; excluding singletons with maximum count = 1, skewness = 2.67 ± 0.058 and 0.22 ± 0.058 ; $t > 3.7$ and $p < 0.0001$ in all cases). Note that although ‘true’ singletons (those recorded as only a single individual across the entire dataset, $n = 248$ species) necessarily occur in only 1 square, species with a total abundance >1 but a maximum recorded abundance of 1 can be rather widespread (proportional occupancy ranged from 0.01 to 0.18; $n = 253$ species). We therefore consider these latter species to be integral, if under-sampled, components of the communities, and in subsequent analyses ‘singleton’ refers only to the former kind (only a single individual recorded).

Occupancy remained very variable, and highly skewed (skewness > 1.3 , $p < 0.0001$) within each of the 8 classes that contained at least 20 species. After log transformation, all 8 distributions remained right-skewed (skewness ranged from 0.10 to 0.98), significantly so in the Ascidiacea, Gastropoda, Gymnolae-mata and Malacostraca (Fig. 2A). The minimum

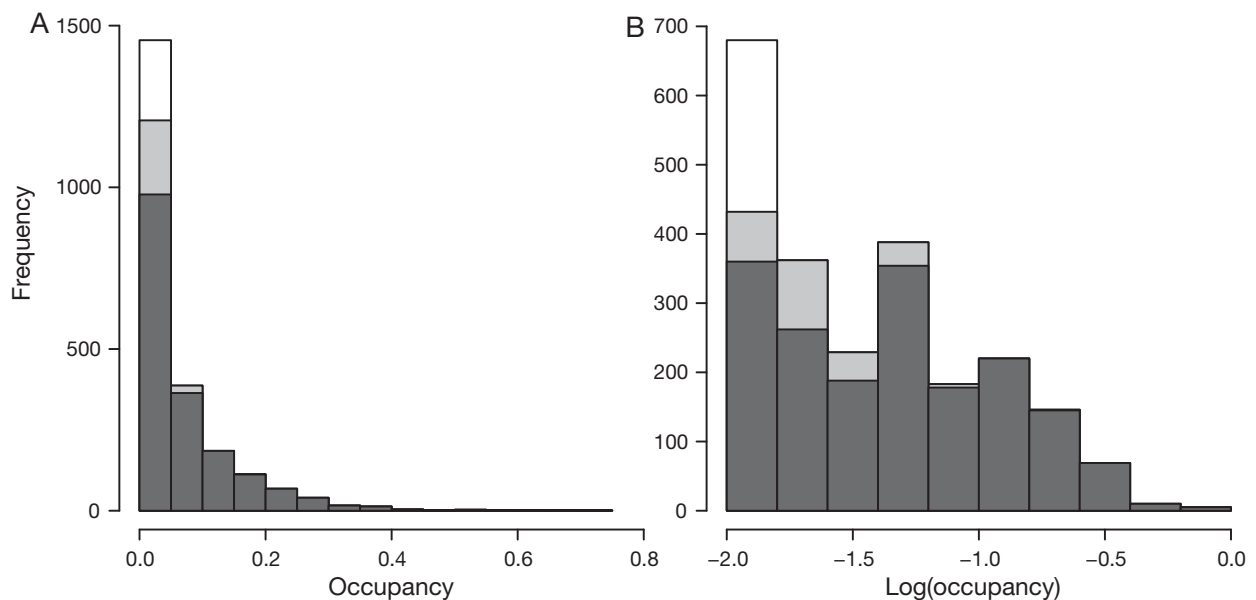


Fig. 1. Frequency distribution of occupancies (proportion of sampled 100 km squares in which a species was recorded) of European soft-sediment macrobenthic species. (A) occupancy untransformed; (B) occupancy \log_{10} -transformed. In both cases, the total heights of bars represent the distributions for all 2292 species in the database; unshaded portions of the bars represent singletons, based on a total recorded count across all samples of 1 individual ($n = 248$); and light-shaded portions of the bars represent singletons that had a total abundance >1 , but a maximum count in any one sample of 1 ($n = 253$)

observed occupancy was 0.01 (a single 100 km square) in all 8 classes. Polychaeta was the only class in which occupancies >0.35 occurred (in the total dataset, but not included in this class-level analysis, the sipunculid *Phascolion strombi* was the most widespread non-polychaete with an occupancy of 0.42). Maximum occupancies in 5 of the remaining 7 classes varied only between 0.26 and 0.35, with somewhat lower maximum occupancies in Class Ascidiacea (0.12) and Class Gymnolaemata (0.18). Overall, these results suggest that there was considerable variation in geographic distribution within classes. The taxonomically nested model shows that this variation persisted across the taxonomic hierarchy, such that the majority (73.3%) of variance in occupancy occurred between species within genera (Fig. 2B), despite the confounding issues surrounding the inclusion of monotypic higher taxa discussed in 'Data and methods'. Note that the proportion of variance explained at each taxonomic level was barely altered when singletons were excluded, and when monotypic genera were excluded (residual ['species within genera'] variation = 74.7 and 71.4%, respectively).

Abundance–occupancy relationships

Estimated population densities across the 2292 species in the total dataset spanned 6 orders of magnitude. The gastropods *Lacuna pallidula* and *Trophonopsis truncatus* and the polychaete *Orbinia norvegica* occurred at densities of just a single individual in 93 m², while the bivalve *Chamelea gallina* occurred at a geometric mean density of >1600 ind. m⁻² across the 38 sampling stations at which it was recorded.

Although the correlation between mean population density and the proportion of 100 km squares occupied (across all species) was significantly positive (both variables log₁₀-transformed, $r = 0.22$, $df = 2290$, $p < 0.00001$), the overriding impression obtained from Fig. 3 is of a relationship characterised by enormous variation. This impression is strengthened if singletons (which by definition have very low densities and can occupy only a single square) are excluded (r is reduced to 0.11 for the remaining 2044 species). In contrast to positive abundance–occupancy relationships observed in other systems, the pattern here was far from linear; low occupancies were observed across the range of densities, but high occupancies only occurred at intermediate to high densities.

One potential reason for the large amount of scatter in this cross-species relationship is that it is confounded by differences between higher taxa. As shown above, occupancy is not strongly constrained by taxonomy (closely related species can differ markedly in occupancy), but it is possible that different classes will

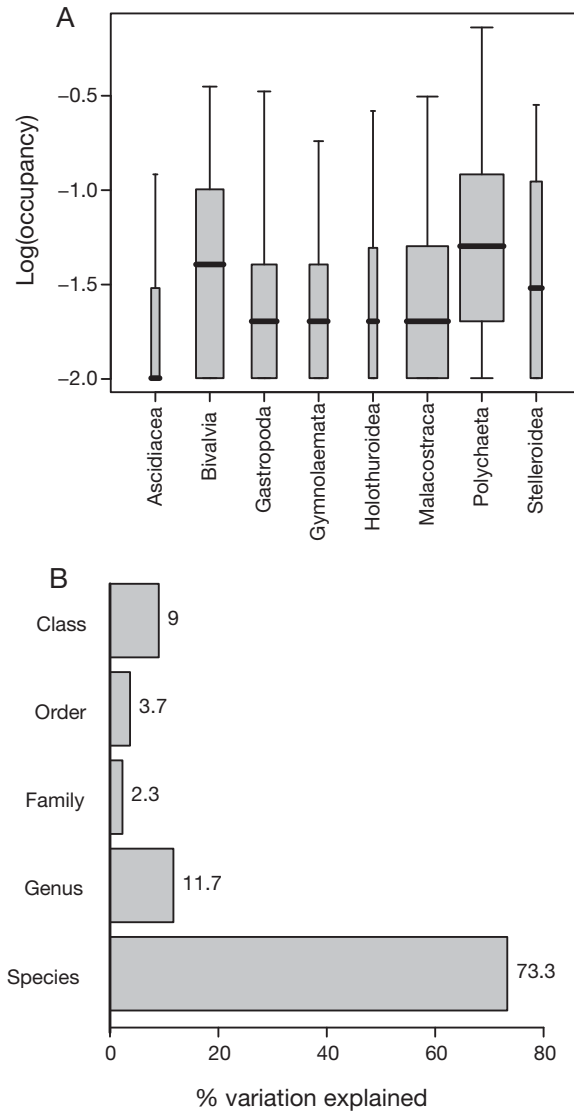


Fig. 2. (A) Box and whisker plots showing the distribution of log₁₀-transformed occupancies within each of 8 classes in the database that contained >20 recorded species. The horizontal lines show the median occupancy for each class, boxes show the interquartile range, and whiskers extend to the data extremes. The width of each box is proportional to the number of species in that class. (B) Percentage of variation in log₁₀-transformed occupancy explained at taxonomic levels from class to genus; unexplained (residual) variation is labelled 'Species', as it represents variation between species within genera. Variance components were estimated using restricted maximum likelihood, and the analysis included the 2143 species that occurred within the 8 classes illustrated in (A)

differ in the typical density achieved at a given level of occupancy (as predicted by population models for taxa with different population structures and life histories; Freckleton et al. 2005, 2006), thus introducing scatter into the cross-species relationship. In fact, mean population density varied by orders of magnitude between species within each class (Table 2), and in all classes

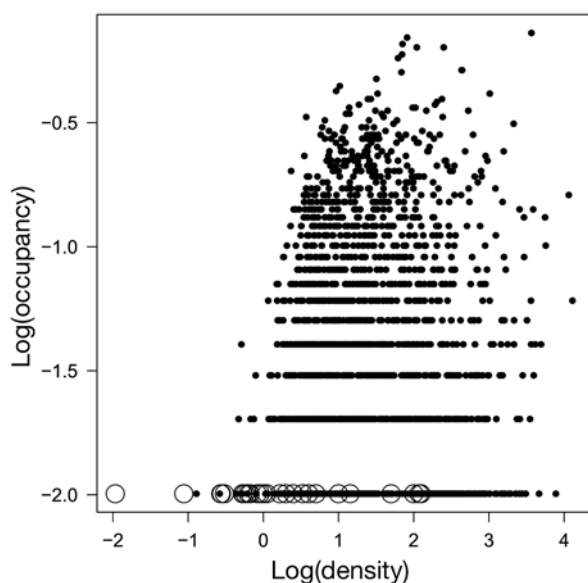


Fig. 3. Abundance–occupancy relationship for 2292 species in the database. The occupancy of a species is the proportion of 100 km squares in which it occurred; its density is the mean population density (ind. m⁻²) in samples in which it was recorded. O: singletons (species recorded as only a single individual across all samples; n = 248). Note that singletons can differ in density due to differences in the area sampled at different sampling stations

abundance–occupancy relationships were weak, with a maximum correlation of 0.28 in the Stelleroidea (Table 2). Although the within-class relationships were generally positive (in 5 of 8 classes, mean correlation [weighted by the square root of the number of species within each class] = 0.03), they typically retained the roughly triangular shape of the relationship across classes, with wide variation in occupancy across all except the lowest observed densities. Indeed, when singletons were removed, only 3 of 8 relationships remain positive, the strongest correlations were negative (Table 2), and the weighted mean correlation was negative (−0.09).

Another potential reason for the generally weak abundance–occupancy relationships concerns differences between LMEs in the typical densities attained by benthic species, which may be influenced by differences in, for example, productivity, habitat heterogeneity, ocean circulation, frequency or intensity of disturbance, and broad-scale heterogeneity in sampling effort. We therefore estimated separately for each LME the abundance–occupancy relationships across species. Here, oc-

cupancy was the proportion of 100 km squares within an LME occupied by a species, and density was its mean population density within those occupied squares. Again, mean density varied considerably between species within each LME (Table 3). Abundance–occupancy relationships were positive in all LMEs except the North Sea (Table 3), with a maximum correlation of 0.52 in the Baltic Sea and a weighted mean value of 0.21. Excluding singletons weakened all relationships (although that in the North Sea became more negative), and reduced the weighted mean correlation to 0.07, but it did not result in any changes of sign (Table 3). Again, however, all relationships contained more scatter than is frequently seen in other systems (e.g. Blackburn et al. 2006).

Finally, we investigated the interaction between taxonomy and geography by estimating abundance–occupancy relationships separately for each class in each LME. We only estimated relationships for classes with at least 8 species in any given LME. The majority of relationships (29 of 35) were positive, with a weighted mean correlation of 0.18, a pattern that held when singletons were removed (21 of 34 positive, weighted mean correlation = 0.04). The interaction between taxonomy and geography appears complex, however, as the rank order of classes in terms of their abundance–occupancy correlation differed between LMEs (Fig. 4). This suggests that the link between local and regional population processes in the marine benthos is influenced by both biotic and abiotic factors.

DISCUSSION

This first analysis of the macroecology of the European marine macrobenthic fauna has upheld several generalities familiar to macroecologists working in other systems. Thus, the frequency distribution of spe-

Table 2. Pearson product moment correlation coefficients for the relationship between log(population density) and log(occupancy) separately for each of 8 classes with >20 species, both including and excluding singletons. Also shown are the numbers of species in each class (number excluding singletons), and the range across species within each class in geometric mean population density

Class	No. of species	Abundance–occupancy correlation		Range in geometric mean density (ind. m ⁻²)
		All species	Excluding singletons	
Polychaeta	724 (675)	0.13	0.02	0.01–1635
Malacostraca	656 (580)	−0.08	−0.19	0.10–1433
Bivalvia	290 (276)	−0.02	−0.08	0.53–1673
Gastropoda	240 (196)	−0.17	−0.36	0.01–873
Gymnolaemata	128 (102)	0.14	−0.13	0.28–1235
Stelleroidea	50 (43)	0.28	0.18	0.76–1151
Holothuroidea	28 (23)	0.22	0.31	0.78–21
Ascidacea	27 (21)	0.05	−0.15	0.85–617

Table 3. Pearson product moment correlation coefficients for the relationship between log(population density) and log(occupancy) separately for each of the 6 large marine ecosystems (LMEs) for which relationships could be estimated. Correlations were performed both including and excluding singletons. Also shown are the number of species recorded in each LME (number excluding singletons), and the range across species within each LME in geometric mean population density

LME	No. of species	Abundance–occupancy correlation		Range in geometric mean density (ind. m ⁻²)
		All species	Excluding singletons	
Mediterranean Sea	947 (839)	0.24	0.15	0.09–860
Celtic-Biscay Shelf	494 (411)	0.22	0.09	3.13–3100
North Sea	1096 (954)	–0.08	–0.22	0.63–1660
Baltic Sea	222 (195)	0.52	0.41	0.01–1149
Norwegian Sea	492 (398)	0.26	0.13	0.91–73
Barents Sea	873 (728)	0.28	0.09	1.00–1187

cies occupancies displayed the strong right-skew typical of regional studies in a broad range of taxa in both terrestrial and aquatic systems using various measures of geographic distribution (e.g. Gaston 2003, Macpherson 2003, Clarke et al. 2007). Most species in the MacroBen database were narrowly distributed (or at least, have been recorded in only a few locations), whereas some were much more widely distributed. Importantly, even the most widely distributed species (the polychaete *Heteromastus filiformis*) did not reach full occupancy, suggesting that this analysis is truly large-scale and captures a range of environmental conditions broader than that which can be occupied by most individual species. At smaller scales, species–range size distributions can tend to bimodality, as several widespread species occur in all sampled locations (e.g. Storch & Sizing 2002).

Whilst the untransformed frequency distributions of occupancies for European benthic taxa conformed to macroecological expectation, the fact that they retained right-skew under a logarithmic transformation is more unusual. Typically, species–range size distributions acquire a moderate left (negative) skew after such a transformation (Gaston 2003, Macpherson 2003). A potential explanation for this difference is that our occupancy measures were at a finer scale (i.e. 100 km squares occupied, as opposed to degrees of latitude spanned), and thus use more comprehensive distributional information than previous regional-scale marine analyses (e.g. Macpherson 2003). At the same time, the fauna in question (European macrobenthic taxa) is considerably richer and has been less exhaustively sampled than many of the faunas considered in terrestrial macroecological analyses (e.g. birds and mammals). The expectation would be that with continued sampling, the right-skew of the distribution would decrease as currently 'rare' species were recorded at more locations (as

happened, for example, when we excluded singletons), although given that additional sampling would likely also uncover further singletons, the amount of extra sampling required may prove to be very large. We would expect that a regional collation of incompletely sampled, species-rich terrestrial datasets, for instance tropical forest invertebrates, would display patterns similar to those observed in the MacroBen database (see Gray et al. 2006 for a discussion of the influence of sampling regime in marine and terrestrial systems on a related macroecological pattern, the species–abundance distribution).

Patterns of regional occupancy in European macrobenthic taxa do not show strong taxonomic patterns; in all of the 8 classes we analysed, occupancy was extremely variable (Fig. 2A). Importantly, this variation persisted down the taxonomic hierarchy, with nearly 75% of interspecific variation in occupancy occurring between species within genera (Fig. 2B). Such patterns are typical of diverse assemblages for which such an analysis has been attempted (e.g. Gaston 1998, Webb et al. 2001, Qian & Ricklefs 2004) and add further evidence that geographic distribution is not highly constrained by phylogeny (Webb & Gaston 2003, 2005, but see Hunt et al. 2005 for a counter-argument).

Across all species in the MacroBen database, there was a positive relationship between local abundance (mean population density at occupied sites) and regional occupancy. Such positive abundance–occupancy relationships are among the most pervasive macroecological patterns (Gaston et al. 2000, Blackburn et al. 2006). However, the relationship documented here was weak ($r = 0.22$), and strongly influenced by the 'singleton effect', i.e. species recorded as single individuals in single samples, which necessarily have very low densities and occupancies. Across much of the observed range of population densities, there was substantial variation in regional occupancy (Fig. 3). Further investigation is required to explore more thoroughly the sources of such variation. For instance, Webb et al. (2007) have shown the utility of linking intra- and interspecific processes; considering the spatial distribution of individuals within species is certainly likely to result in a better understanding of the interspecific abundance–occupancy relationship (Freckleton et al. 2006, Webb et al. 2007), especially if combined with emerging statistical sampling theories of species abundances (e.g. Green & Plotkin 2007). What is clear, however, is that there exists substantial

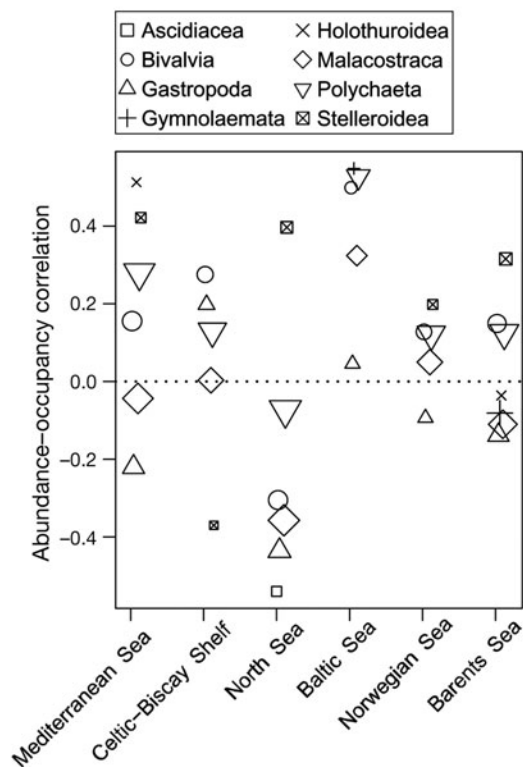


Fig. 4. Summary of abundance–occupancy relationships for each class within each large marine ecosystem (LME). Each point represents the correlation between $\log_{10}(\text{occupancy})$ and $\log_{10}(\text{density})$ for a given class within a particular LME. Occupancy here is the proportion of 100 km squares occurring within an LME in which a species was recorded, and density is the mean density (ind. m^{-2}) attained by a species in samples in which it occurred within that LME. Symbols within an LME are offset slightly horizontally for clarity, and the size of a symbol is proportional to the logarithm of the number of species recorded for a given class in a given LME. The dashed horizontal line is at a correlation of 0

variation in the form and strength of abundance–occupancy relationships between geographic areas (LMEs) and higher taxa (classes); in addition, the same class can have different relationships in different areas (Fig. 4). This suggests that features of both the environment (e.g. disturbance regime) and the life histories of constituent species (e.g. larval dispersal mode) are likely to influence the form of abundance–occupancy relationships, exactly as predicted by recent population models (Freckleton et al. 2005, 2006). Given that human activity can disrupt macroecological relationships (Fisher & Frank 2004, Webb et al. 2007), it would be valuable to include measures of anthropogenic activity as covariates in future analyses; the efforts of Halpern et al. (2008) to map human impacts on marine systems would prove extremely useful here. In general, the considerable variation in abundance–occupancy relationships within the MacroBen database, combined with its wide geographic scope and the vast diversity of life

forms recorded in the database, will make it an invaluable resource for further testing of this emerging area of macroecological theory.

CONCLUSIONS

Macroecology provides a novel conceptual framework in which to analyse large-scale patterns in diversity. It has developed largely as a terrestrial subject, but the potential of marine systems to contribute to the macroecological research effort is enormous. Here, we have provided a first macroecological summary of the MacroBen database. We have shown that the European macrobenthic fauna conformed to general macroecological norms, but that considerable variation remains around certain general trends (e.g. positive interspecific abundance–occupancy relationships). The exploration of this variation, combined with the geographic and taxonomic breadth of the MacroBen database, will provide a unique opportunity to test emerging macroecological theory. Such databases will also provide one of the only means of testing hypotheses regarding the likely human impact upon macroecological patterns and relationships, and thus will provide important information on the magnitude of human effects upon marine and terrestrial ecosystems (Fisher & Frank 2004, Gaston 2004, Jennings & Blanchard 2004, Webb et al. 2007). This further illustrates the benefits to be derived from international cooperative scientific programmes such as MarBEF.

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Comparison of the performances of two biotic indices based on the MacroBen database

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ABSTRACT: The pan-European MacroBen database was used to compare the AZTI Marine Biotic Index (AMBI) and the Benthic Quality Index (BQI_{ES}), 2 biotic indices which rely on 2 distinct assessments of species sensitivity/tolerance (i.e. AMBI EG and BQI E[S₅₀]_{0.05}) and which up to now have only been compared on restricted data sets. A total of 12 409 stations were selected from the database. This subset (indicator database) was later divided into 4 marine and 1 estuarine subareas. We computed E(S₅₀)_{0.05} in 643 taxa, which accounted for 91.8% of the total abundances in the whole marine indicator database. AMBI EG and E(S₅₀)_{0.05} correlated poorly. Marked heterogeneities in E(S₅₀)_{0.05} between the marine and estuarine North Sea and between the 4 marine subareas suggest that sensitivity/tolerance levels vary among geographical areas. High values of AMBI were always associated with low values of BQI_{ES}, which underlines the coherence of these 2 indices in identifying stations with a bad ecological status (ES). Conversely, low values of AMBI were sometimes associated with low values of BQI_{ES} resulting in the attribution of a good ES by AMBI and a bad ES by BQI_{ES}. This was caused by the dominance of species classified as sensitive by AMBI and tolerant by BQI_{ES}. Some of these species are known to be sensitive to natural disturbance, which highlights the tendency of BQI_{ES} to automatically classify dominant species as tolerant. Both indices thus present weaknesses in their way of assessing sensitivity/tolerance levels (i.e. existence of a single sensitivity/tolerance list for AMBI and the tight relationship between dominance and tolerance for BQI_{ES}). Future studies should focus on the (1) clarification of the sensitivity/tolerance levels of the species identified as problematic, and (2) assessment of the relationships between AMBI EG and E(S₅₀)_{0.05} within and between combinations of geographical areas and habitats.

KEY WORDS: AZTI Marine Biotic Index · Benthic Quality Index · Macrozoobenthos · Water framework directive

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INTRODUCTION

The European Water Framework Directive (WFD) establishes a basis for the protection of ground, continental, transitional and coastal waters. It aims at achieving a good ecological status (ES) for all European water bodies by 2015. The first step consists of assessing the current ES of these water bodies, which

is based on a large variety of hydromorphological, physicochemical and biological parameters. In order to unravel natural and man-induced changes, ES values are derived from ecological quality ratios (EQR), which correspond to the ratio of the value of the considered parameter at each sampled station divided by the value of the same parameter at a reference (i.e. non-impacted) station (Wallin et al. 2003).

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Macrozoobenthos is one of the biological compartments considered by the WFD (Borja et al. 2004a, Borja 2005) and a large variety of biotic indices use its composition to infer ES (Grall & Glémarec 1997, Borja et al. 2000, Gomez Gesteira & Dauvin 2000, Rosenberg et al. 2004). In spite of their diversity, most of these indices are based on the same paradigm: disturbances are generating secondary successions during which tolerant species are at first dominant and then progressively replaced by sensitive species (Pearson & Rosenberg 1978). There is, thus, more need for testing and unifying the existing benthic biotic indices than for producing new ones (Diaz et al. 2004). Two of the main indices introduced in view of the implementation of the WFD are (1) the AZTI Marine Biotic Index (AMBI; Borja et al. 2000), and (2) the Benthic Quality Index (BQI; Rosenberg et al. 2004). Although these 2 indices rely on the same concept, they differ in (1) their ways of assessing species sensitivity/tolerance levels, (2) the consideration of species richness, and (3) the procedures used to convert computed indices of ES.

In AMBI, sensitivity/tolerance levels are assessed based on the compilation of expert knowledge and its translation into ecological groups (AMBI EG). This results in a single sensitivity/tolerance per species that is used for all data sets irrespective of geographic location (Borja et al. 2000, Borja et al. 2003, Salas et al. 2004, Muxika et al. 2005). Conversely, for BQI, Rosenberg et al. (2004) assume that species sensitivity/tolerance levels vary according to geographical location. The assessment of sensitivity/tolerance within BQI is based on the concept of $E(S_{50})_{0.05}$ (see 'Data and methods' for definition) (Rosenberg et al. 2004). The availability of $E(S_{50})_{0.05}$ constitutes a severe limitation to the computation of BQI, which is either restricted to large data sets (Rosenberg et al. 2004, Labruno et al. 2006, Dauvin et al. 2007, Zettler et al. 2007) or to areas where a list of $E(S_{50})_{0.05}$ is available (Reiss & Kröncke 2005).

The computation of AMBI is based on the sole sensitivity/tolerance concept (Borja et al. 2000), which makes it largely sampling effort-independent (Fleischer et al. 2007, Muxika et al. 2007b). Conversely, BQI also takes into account species richness (S) through a $\log(S + 1)$ term (Rosenberg et al. 2004), which makes it sampling effort-dependent when computed on lumped data (Fleischer et al. 2007) and/or on individual samples collected with different gears. This constitutes another restriction to its use since large databases are (1) often constituted of several surveys with different sampling strategies (see Table 1 for the present study), and (2) often comprised of a significant proportion of lumped data (i.e. 96.3% of all stations during the present study). Fleischer et al. (2007) proposed to overcome this difficulty by replacing $\log(S + 1)$ by $\log(E[S_{50}] + 1)$ and proved that the so-modified BQI (i.e. BQI_{ES}) is indepen-

dent of sampling effort and correlates tightly with BQI.

AMBI uses a single scale to infer ES (Borja et al. 2004a), whereas BQI assumes that for each habitat the station with the highest BQI constitutes a valid reference for the computation of EQR. The stations with an EQR higher than 0.6 are then considered to at least be in a good ES (Rosenberg et al. 2004).

Multivariate AMBI (M-AMBI) was recently introduced as a refinement of AMBI (Borja et al. 2004b, Borja et al. 2007, Muxika et al. 2007a). Its computation involves a factorial correspondence analysis (FCA) based on AMBI, species richness and the Shannon-Wiener diversity index, H' . FCAs are carried out for each habitat and 2 bad and good reference stations are included. The coordinates of the projection of the stations along the axis linking the bad and good reference stations in the first plane of the FCA constitute EQR, which are transformed into ES using an appropriate conversion scale (Wallin et al. 2003). M-AMBI is much more similar to BQI than AMBI since it accounts for species richness and uses several scales to infer ES. BQI and M-AMBI, however, still largely differ in their assessments of species sensitivity/tolerance.

Both AMBI and BQI were initially proposed and tested based on individual data sets (Borja et al. 2000, Rosenberg et al. 2004). AMBI has, since then, been tested on a large variety of other (but still mostly individual) data sets (Borja et al. 2000, 2003, Salas et al. 2004, Marin-Guirao et al. 2005, Muniz et al. 2005, Muxika et al. 2005, Bigot et al. 2008, Blanchet et al. 2008), BQI has been tested on a much smaller number of datasets due to the difficulty in computing $E(S_{50})_{0.05}$. AMBI and BQI have recently been compared in the North Sea (Reiss & Kröncke 2005), the Gulf of Lions (Labruno et al. 2006), the Seine estuary (Dauvin et al. 2007) and the Baltic Sea (Zettler et al. 2007). All comparisons have shown major discrepancies but have largely ignored their potential causes. The adequacy of the use of a single sensitivity/tolerance list by AMBI as opposed to BQI is, for example, yet to be tested partly due to the lack of any comprehensive database at the pan-European level. The Network of Excellence Marine Biodiversity and Ecosystem Functioning (MarBEF) has recently filled this gap for soft-bottom macrozoobenthos by creating the MacroBen database. The aim of the present study is to use this new tool to (1) promote the use of BQI_{ES} by providing lists of $E(S_{50})_{0.05}$ both at the pan-European level and within distinct geographic subareas, (2) compare AMBI EG and $E(S_{50})_{0.05}$, (3) assess the validity of the use of a single list of sensitivity/tolerance levels by comparing $E(S_{50})_{0.05}$ between subareas, (4) assess the relationships between AMBI and BQI_{ES} and (5) compare the ES assessments derived from AMBI and BQI_{ES} .

DATA AND METHODS

MacroBen database. The main characteristics of MacroBen are described in Vanden Berghe et al. (2009, this Theme Section) and will not be repeated here. The filtering procedure used during the present study consisted of selecting (1) quantitative data, (2) adult animal taxa, (3) organisms identified to the species level, (4) non-colonial organisms and (5) samples collected after 1980. Baltic Sea samples were excluded because an extensive comparison between AMBI and BQI has recently been carried out in this area (Zettler et al. 2007), and Black Sea samples were excluded because they were too few. The data set was further reduced by considering only the most recent sampling date for each station. This reduced indicator database was com-

posed of 29 individual data sets and contained a total of 12 409 stations (Fig. 1, Table 1). It was later divided into 4 subareas based on the Large Marine Ecosystem classification (www.edc.uri.edu/lme/intro.htm), namely: (1) the Celtic-Biscay Shelf (115 stations), (2) the Mediterranean (426 stations), (3) the North Sea (11 664 stations), and (4) the Norwegian and Barents Seas (204 stations). Because of the importance of the ni data set (10 251 stations), North Sea data were divided in an estuarine (i.e. ni) and a marine (1413 stations) data set. The ranges of $E(S_{50})$ (see 'Data and methods—Computation of AMBI and BQI_{ES}' for definitions) in each marine subarea were: 1.95 to 33.53, 2.86 to 34.61, 1.35 to 39.59 and 1.00 to 33.19 in the Celtic-Biscay Shelf, the Norwegian and Barents Seas, the Mediterranean and the marine North Sea, respectively.

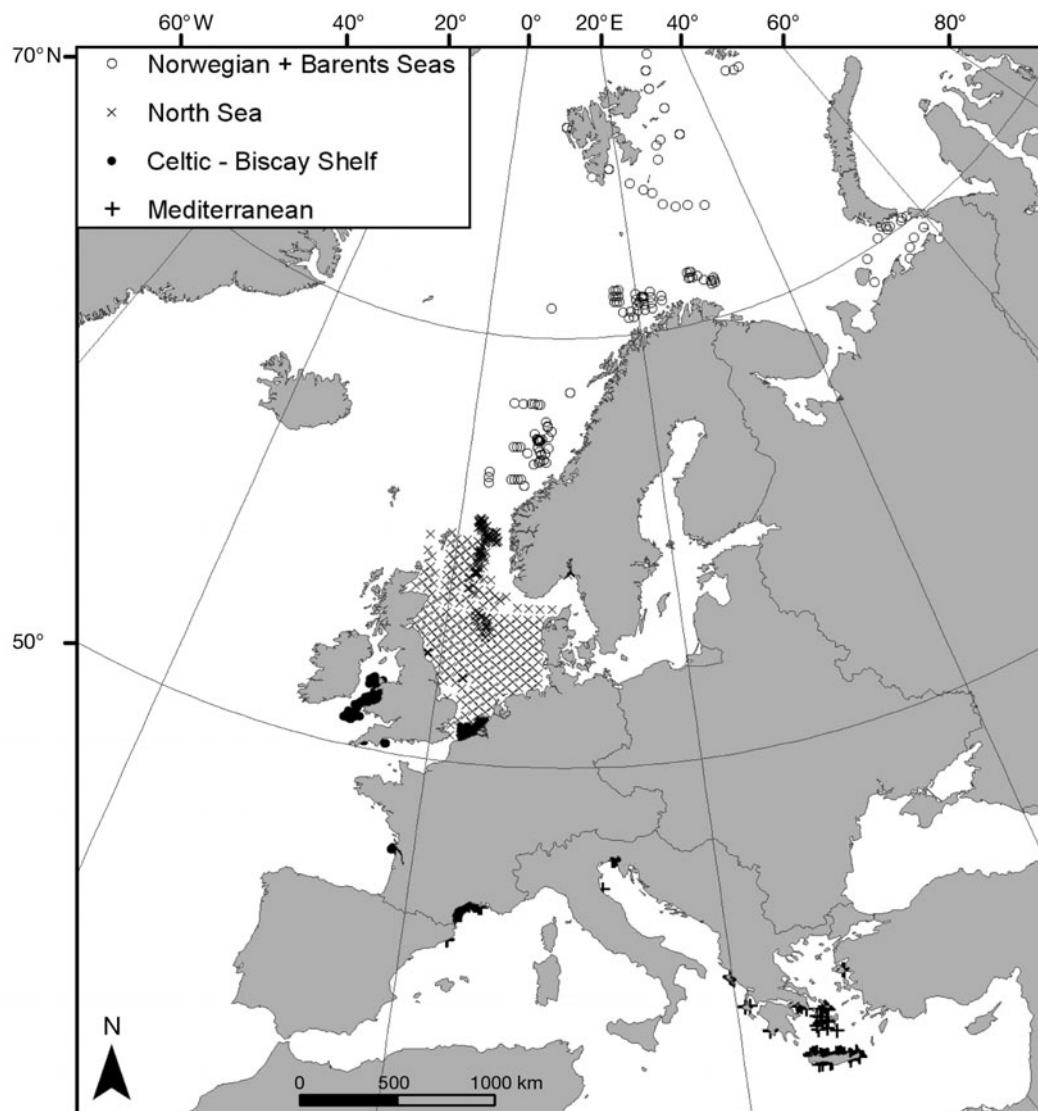


Fig. 1. Location of the stations in the indicator database delimiting of the 4 geographical marine subareas considered during the present study

Table 1. Composition of the indicator data set with information regarding the location and the number of stations in the 4 subareas and in each individual data set. Depth range, sampling gear, sample replication and total sampled area is also provided for each individual data set

Data set and subarea	Location	Depth range (m)	No. stations	Sample gear	No. replicates	Total sampled area (m ²)
Norwegian and Barents Seas						
ar	Svalbard	75–335	22	Box corer	1	0.1
hs	Hornsund	25–203	34	Van Veen grab	1	0.1
ko	Kongsfjorden/Spitsbergen	5–30	6	Box corer	1	–
o2	Northern Barents Sea	–	10	Van Veen grab	4–5	0.4–0.5
o4 _{NB}	Norwegian Sea	71–1520	55	Van Veen grab	1–5	0.1–0.5
o6	Finmark	160–374	53	Van Veen grab	5	0.5
o7	Pechoran Sea	7–207	15	Van Veen grab	3–5	0.3–0.5
o8	Franz Josef Land	52–312	9	Van Veen grab	5	0.5
North Sea						
ni	Dutch Delta area	0–57	10251	–	1	–
np _{NS}	North Sea	35–70	20	–	1	0.1
ns	Belgian part of the North Sea	0–150	231	Van Veen grab	–	–
o3	Staffjord, Oseberg, Ekosfisk	65–91	30	Van Veen grab	1–5	0.1–0.5
o4 _{NS}	Norwegian coast	71–1520	128	Van Veen grab	–	–
of	Oslo Fjord	19–356	57	Van Veen grab	1	0.1
ug	North Sea	0–40	947	–	3	0.09–0.27
Celtic-Biscay Shelf						
np _{CS}	English Channel, Irish Sea	50–96	20	–	1	0.1
o5	Southern Irish Sea	7–130	51	Van Veen grab	1	–
pl	Plymouth Sound	15	44	SCUBA diving	1	0.008
Mediterranean						
bl	Bay of Blanes	–	2	Van Veen grab	5	0.3
do	Continental Cretan Shelf	10–60	56	Smith McIntyre grab	1	0.1
gr	Gulf of Lions	10–50	92	Van Veen grab	2–4	0.2–0.4
ka	Cretan Shelf	10–190	199	–	–	0.1
lm	Gulf of Trieste, Adriatic	4–25	28	Van Veen grab	1	–
M0	Gialova Lagoon, Ionian Sea	–	7	Van Veen grab	5	0.25
M2	Gulf of Geras, Aegean Sea	–	9	Ponar grab	1	0.045
M3	Saronikos Gulf	–	6	Ponar grab	2–5	0.1–0.25
M7	Kerkyra, Ionian Sea	–	12	Van Veen grab	1	0.2
M8	Kyklades, Aegean Sea	–	14	Smith McIntyre grab	3–5	0.3–0.5
oc	Northern Adriatic	12	1	Van Veen grab	1	0.06

Computation of AMBI and BQI_{ES}. AMBI was computed as:

$$\text{AMBI} = [(0 \times \% \text{GI}) + (1.5 \times \% \text{GII}) + (3 \times \% \text{GIII}) + (4.5 \times \% \text{GIV}) + (6 \times \% \text{GV})] / 100 \quad (1)$$

where %GI is the relative abundance of disturbance-sensitive species, %GII is the relative abundance of disturbance-indifferent species, %GIII is the relative abundance of disturbance-tolerant species, %GIV is the relative abundance of second-order opportunistic species and %GV is the relative abundance of first-order opportunistic species (Borja et al. 2000). AMBI was computed as recommended by Borja & Muxika (2005) using a specific function implemented in MacroBen and based on the species reference list available at www.azti.es in July 2006. We used a single fixed scale to infer ES from AMBI (Borja et al. 2004a).

E(S₅₀)_{0.05} is defined as the E(S₅₀) (Hurlbert 1971) corresponding to the 5 lowest percentiles of the total

abundance of the considered species within the studied area (Rosenberg et al. 2004). E(S₅₀)_{0.05} values were computed for the whole marine indicator data set and each subarea.

BQI_{ES} was then computed as:

$$\text{BQI}_{\text{ES}} = \left\{ \sum_{i=1}^s \left[\frac{A_i}{A_{\text{Tot}}} \times E(S_{50})_{0.05i} \right] \right\} \times \log_{10} [E(S_{50}) + 1] \quad (2)$$

where A_i is the abundance of the *i*th species at the considered station, E(S₅₀)_{0.05i} is the E(S₅₀)_{0.05} of species *i* in the considered subarea, A_{Tot} is the total abundance of the individuals belonging to the species for which E(S₅₀)_{0.05} can be computed and E(S₅₀) is the expected number of species in a sample of 50 individuals taken at the considered station (Fleischer et al. 2007). E(S₅₀)_{0.05} and BQI_{ES} were computed on lumped data using a specific function implemented in MacroBen. E(S₅₀)_{0.05} values were not computed for species present at less than 20 stations. We used several conversion

scales to infer ES from BQI_{ES} . Homogeneous habitats were defined based on multi-dimensional scaling and cluster analyses of macrozoobenthos composition carried out on the whole subarea data set (Celtic-Biscay Shelf and Norwegian and Barents Seas) or on each major individual data set (i.e. ka, gr and do, see Table 1) in the Mediterranean and the North Sea. The highest value of BQI_{ES} in each homogeneous habitat was used to compute an EQR. Each scale was then obtained by dividing these maximal values into 5 equal classes (Rosenberg et al. 2004).

RESULTS

Computation of $E(S_{50})_{0.05}$ between subareas and with AMBI EG

We computed the $E(S_{50})_{0.05}$ of 76 species in the Celtic-Biscay Shelf, 246 in the Mediterranean, 165 in the Norwegian and Barents Seas, 337 in the marine North Sea and 158 in the estuarine North Sea. The corresponding lists are available at: www.marbef.org/documents/data/theme1/es50_005.xls. The proportions of species and/or individuals — which are attributed sensitivity/tolerance levels, essential for a sound assessment of ES using either AMBI and BQI_{ES} — with an $E(S_{50})_{0.05}$ were between 16.0 (Celtic-Biscay Shelf) and 54.7% (estuarine North Sea), much lower than for AMBI EG (91.8 and 92.4%, respectively) (Fig. 2A). Differences between the 2 indices were lower when considering the number of individuals. The proportions of individuals with an $E(S_{50})_{0.05}$ were between 69.9% (Norwegian and Barents Seas) and 99.8% (estuarine North Sea), which were still lower than for AMBI EG (88.7 and 99.9%, respectively) (Fig. 2B). When considering the marine indicator data set as a whole, 643 species (46.7%) corresponding to 91.8% of individuals were attributed an $E(S_{50})_{0.05}$ (versus 97.1% of individuals for AMBI EG).

Dipolydora quadrilobata, *Microdeutopus gryllotalpa*, *Boccardiella ligERICA*, *Streblospio shrubsolii*, *Spio armata*, *Corophium volutator* and *Hydrobia ulvae* were the most dominant (rank < 97) species in the marine indicator data set lacking an $E(S_{50})_{0.05}$ (Table 2). *Dacrydium vitreum*, *Potamides conicus*, *Eudorellopsis deformis*, *Micronephthys maryae* and *Crenella decussata* were the most dominant (rank < 141) species in the marine indicator data set lacking an AMBI EG (Table 2).

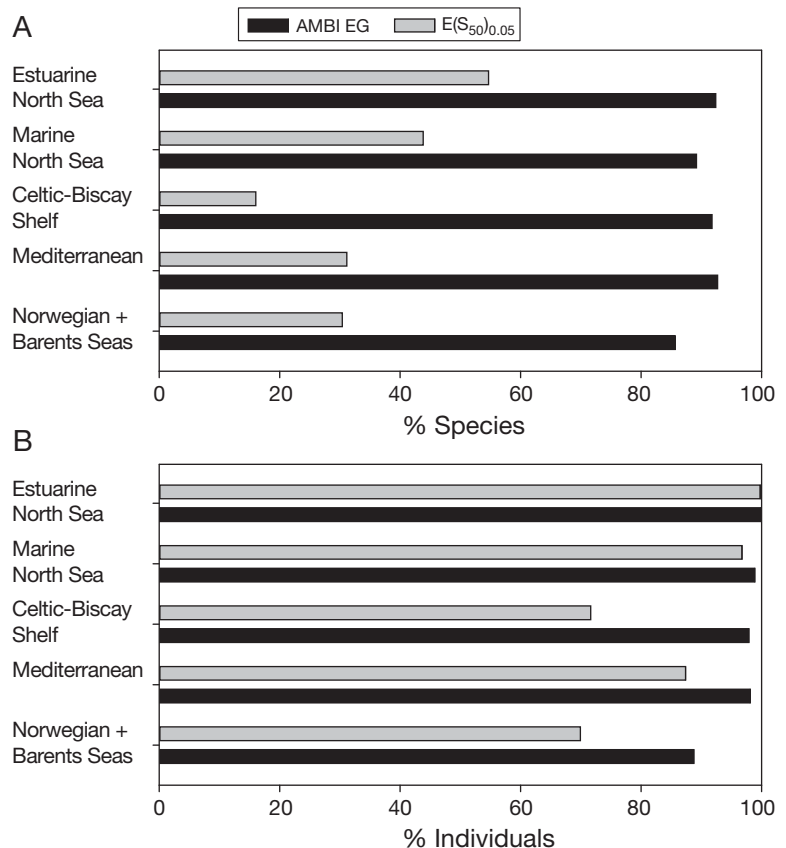


Fig. 2. Proportions of the number of (A) species and (B) individuals with an AMBI EG or an $E(S_{50})_{0.05}$ value in the different subareas

Table 2. Most dominant (ranks based on decreasing abundances) species in the whole marine indicator data set which are still lacking an $E(S_{50})_{0.05}$ and/or an AMBI EG value

Species	Rank	$E(S_{50})_{0.05}$	AMBI EG
<i>Dipolydora quadrilobata</i>	16	–	IV
<i>Microdeutopus gryllotalpa</i>	33	–	III
<i>Boccardiella ligERICA</i>	39	–	III
<i>Streblospio shrubsolii</i>	43	–	III
<i>Spio armata</i>	56	–	III
<i>Dacrydium vitreum</i>	67	9.82	–
<i>Corophium volutator</i>	91	–	III
<i>Hydrobia ulvae</i>	96	–	III
<i>Langerhansia heterochaeta</i>	102	–	II
<i>Potamides conicus</i>	122	–	–
<i>Eudorellopsis deformis</i>	127	12.27	–
<i>Micronephthys maryae</i>	139	13.25	–
<i>Crenella decussata</i>	140	–	–
<i>Aricidea fragilis mediterranea</i>	163	–	I
<i>Microphthalmus similis</i>	167	–	II
<i>Malacoceros fuliginosus</i>	169	–	V
<i>Ophelina abranchiata</i>	173	17.88	–
<i>Pectinaria belgica</i>	179	–	I
<i>Dendrodoa grossularia</i>	180	–	I
<i>Axinopsida orbiculata</i>	184	–	–
<i>Octobranchus floriceps</i>	195	23.43	–

$E(S_{50})_{0.05}$ values were between 1.00 and 10.48, 1.96 and 24.14, 5.64 and 25.77, 1.35 and 28.36, and 2.86 and 27.85 in the estuarine North Sea, marine North Sea, Celtic-Biscay Shelf, Mediterranean and Norwegian and Barents Seas, respectively. When considering the whole marine indicator data set, there was a significant

negative correlation between AMBI EG and $E(S_{50})_{0.05}$ (Fig. 3, Table 3), even though the explicative power of the corresponding linear regression model was low. There were significant (but still weak) negative correlations between these 2 parameters in the marine and estuarine North Sea and in the Norwegian and Barents

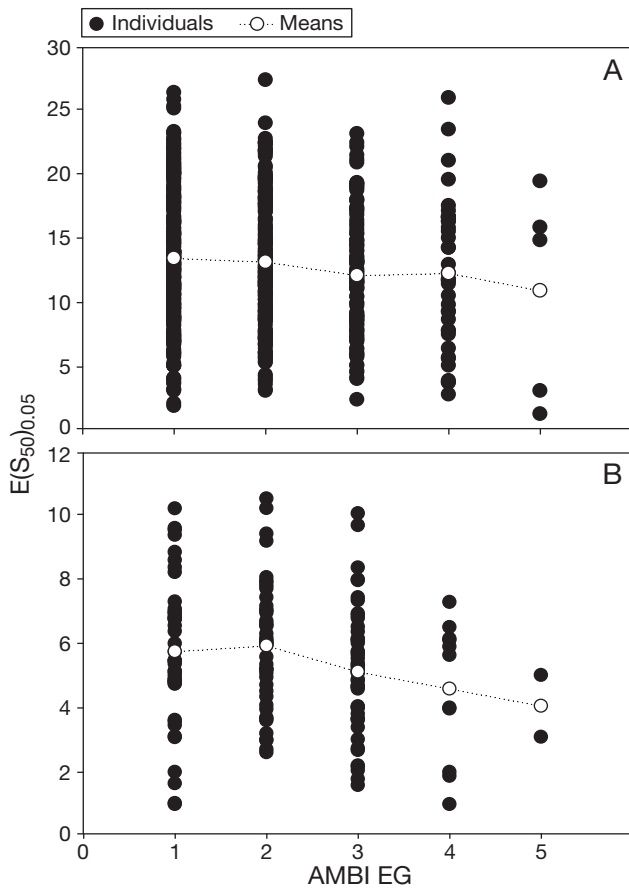


Fig. 3. Relationship between AMBI EG and $E(S_{50})_{0.05}$ in the (A) whole marine indicator data set and (B) estuarine North Sea. Closed symbols refer to individual stations and open symbols to the mean value of $E(S_{50})_{0.05}$ for each AMBI EG

Table 3. Main characteristics of the simple linear regression models linking AMBI EG and $E(S_{50})_{0.05}$ in the whole marine data set and within each subarea. Significant ($p < 0.05$) negative correlations are in bold

Subarea	N	r	p	Intercept	Slope
Marine indicator data set	669	-0.150	<0.0001	14.86	-1.32
Celtic-Biscay Shelf	75	0.022	0.848	-	-
Mediterranean	240	0.037	0.572	-	-
Marine North Sea	95	-0.324	0.001	17.82	-1.64
Norwegian and Barents Seas	143	-0.217	0.009	19.75	-1.38
Estuarine North Sea	152	-0.185	0.023	6.350	-0.385

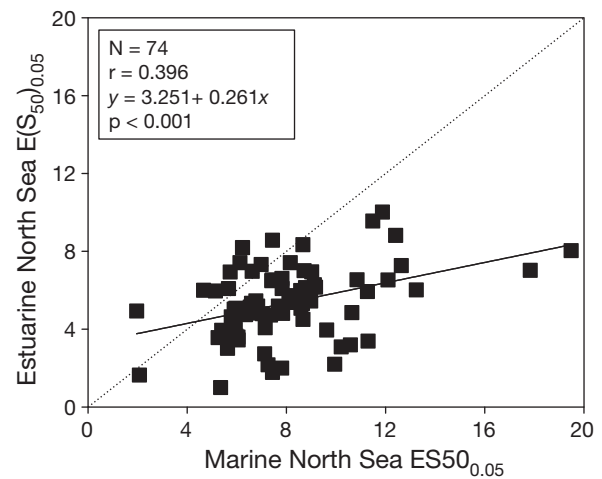


Fig. 4. Relationship between $E(S_{50})_{0.05}$ in the marine and estuarine North Sea. Solid line: linear regression; dotted line: $y = x$

Table 4. $E(S_{50})_{0.05}$ of the 11 species for which they could be computed in all 4 marine subareas. VC: variation coefficient computed for the 4 marine subareas

Species	Celtic-Biscay Shelf	Mediterranean	Marine North Sea	Norwegian and Barents Seas	Marine indicator data set	VC (%)
<i>Heteromastus filiformis</i>	5.64	2.56	7.81	16.81	16.81	74.6
<i>Goniada maculata</i>	9.21	18.98	11.16	22.34	22.34	40.5
<i>Scoloplos armiger</i>	9.34	18.51	7.26	11.24	11.24	42.2
<i>Myriochele oculata</i>	11.90	7.16	6.95	13.99	13.99	35.1
<i>Owenia fusiformis</i>	10.36	6.18	13.24	9.82	9.82	29.3
<i>Aricidea catherinae</i>	17.49	18.56	17.10	15.71	15.71	6.8
<i>Paradoneis lyra</i>	17.54	18.93	18.28	19.43	19.43	4.4
<i>Scalibregma inflatum</i>	9.34	21.78	11.88	9.94	9.94	43.8
<i>Prionospio cirrifera</i>	17.99	10.55	13.28	12.01	12.01	23.9
<i>Spiophanes kroyeri</i>	17.50	18.13	12.06	16.09	16.09	17.1
<i>Terebellides stroemii</i>	16.73	19.46	17.81	9.82	9.82	26.6

Seas (Table 3). This correlation was not significant in the Mediterranean or in the Celtic-Biscay Shelf, where AMBI was initially developed.

There was a weak but significant positive correlation between $E(S_{50})_{0.05}$ in the marine and estuarine North Sea (Fig. 4). However, $E(S_{50})_{0.05}$ tended to be lower in the estuarine than in marine North Sea (Wilcoxon signed-rank test, $p < 0.001$). There were only 11 species for which we were able to compute $E(S_{50})_{0.05}$ in all

4 marine subareas (Table 4). Overall there were marked changes in $E(S_{50})_{0.05}$ between subareas as indicated by variation coefficients between 4.4% (*Paradoxeis lyra*) and 74.6% (*Heteromastus filiformis*). When comparing the $E(S_{50})_{0.05}$ of species occurring in any combination of 2 subareas, we found significant positive correlations between the marine North Sea and both the Celtic-Biscay Shelf and the Norwegian and Barents Seas (Fig. 5). Here again, the explicative pow-

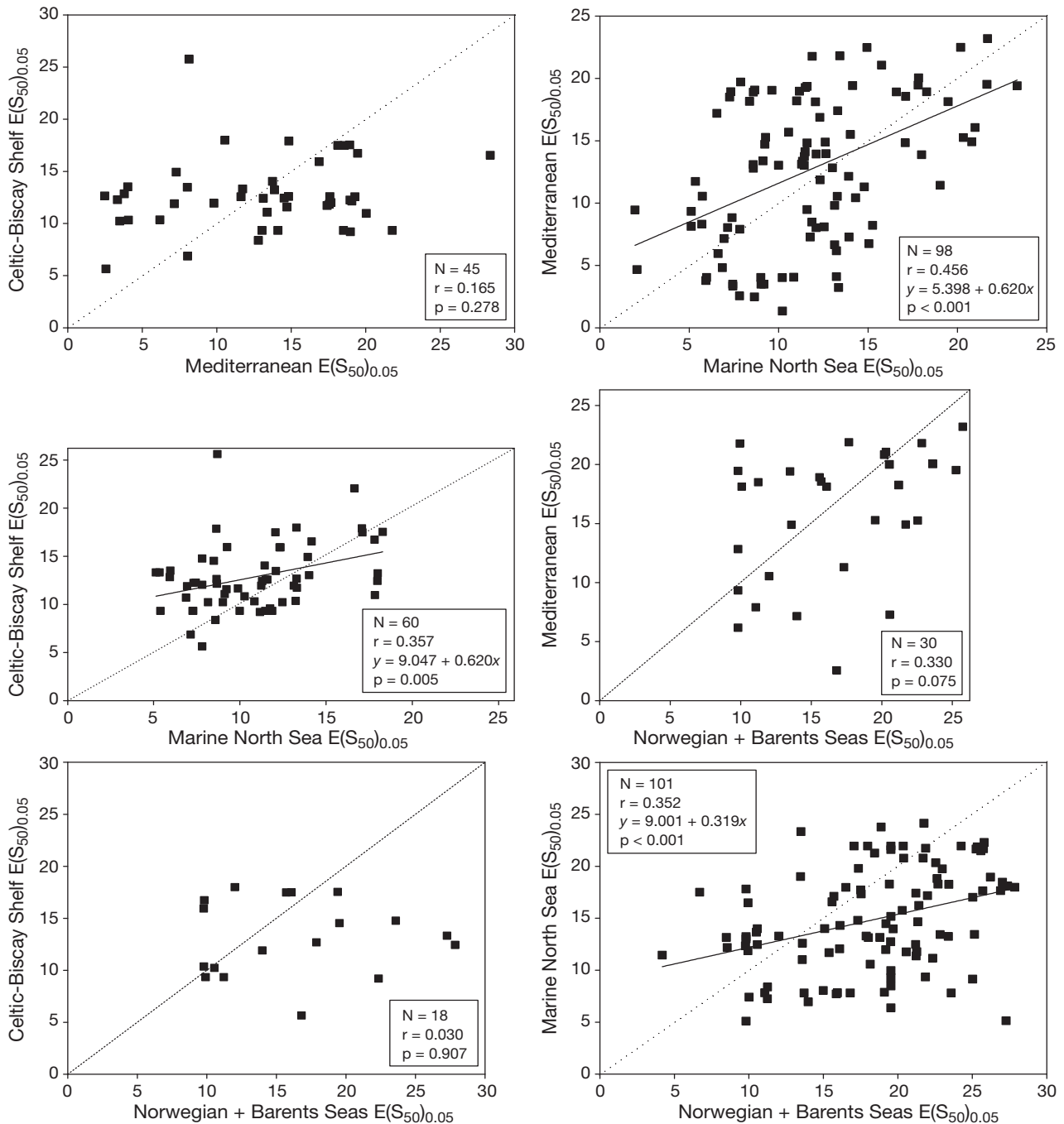


Fig. 5. Relationships between $E(S_{50})_{0.05}$ in the 4 marine subareas. Solid line: linear regression, dotted line: $y = x$

Table 5. Significance of the Wilcoxon signed-rank tests used to compare the $E(S_{50})_{0.05}$ computed within different marine subareas. N: number of species for which $E(S_{50})_{0.05}$ could be computed in the 2 considered subareas. Significant ($p < 0.05$) differences are in bold

	Celtic-Biscay Shelf		Mediterranean		Marine North Sea	
	p	N	p	N	p	N
Celtic-Biscay Shelf	–					
Mediterranean	0.505	45	–			
Marine North Sea	<0.001	60	0.184	98	–	
Norwegian and Barents Seas	0.099	18	0.508	30	<0.001	101

Table 6. Main characteristics of the simple linear regression models linking AMBI and BQI_{ES} in the different subareas and individual data sets. Significant ($p < 0.05$) negative correlations are in bold

Data set	N	r	p	Intercept	Slope
Norwegian and Barents Seas	204		<0.001	31.267	–5.991
ar	22	–0.308	0.164	–	–
hs	31	–0.911	<0.001	9.557	–1.397
ko	6	–0.667	0.148	–	–
o2	10	–0.366	0.298	–	–
o4 _{NB}	57	–0.745	<0.001	40.930	–8.476
o6	54	0.220	0.110	–	–
o7	15	–0.083	0.769	–	–
o8	9	0.355	0.349	–	–
Marine North Sea	850	0.013	0.715	–	–
np _{NS}	14	–0.530	0.051	–	–
ns	224	0.315	<0.001	10.606	1.812
o3	30	–0.913	<0.001	29.347	–7.603
o4 _{NS}	128	–0.416	<0.001	28.632	–6.140
of	57	–0.800	<0.001	20.181	–3.141
ug	357	0.261	<0.001	4.343	0.506
Estuarine North Sea	3889	–0.040	0.017	4.120	–0.051
Celtic-Biscay Shelf	115	–0.602	<0.001	20.402	–2.489
np _{CS}	20	–0.276	0.239	–	–
o5	51	–0.212	0.136	–	–
pl	44	–0.160	0.299	–	–
Mediterranean	394	–0.250	<0.001	19.620	–1.803
bl	2	–	–	–	–
do	49	0.291	0.042	17.437	4.196
gr	47	0.720	<0.001	4.097	6.391
ka	190	–0.587	<0.001	25.389	–3.893
lm	28	–0.480	0.010	22.373	–3.665
M0	7	0.254	0.582	–	–
M2	9	–0.727	0.026	31.935	–4.807
M3	6	–0.989	<0.001	38.864	–7.583
M7	4	–0.371	0.629	–	–
M8	8	0.395	0.333	–	–
oc	1	–	12	–	–

ers of corresponding simple linear regression models always remained low, and these models differed clearly from the $y = x$ equation. $E(S_{50})_{0.05}$ tended to be lower in the marine North Sea than in the Celtic-Biscay Shelf and the Norwegian and Barents Seas (see Table 5 for the significance of corresponding Wilcoxon signed-rank tests).

Comparisons between AMBI and BQI_{ES}

AMBI and BQI_{ES} correlated negatively in all 4 marine subareas and in the estuarine North Sea (Table 6, Figs. 6–10). However, in most cases these correlations were weak and found in only a few individual data sets.

The Celtic-Biscay Shelf was the only subarea where the use of a simple linear regression model seemed appropriate to account for the general negative relationship between AMBI and BQI_{ES} (Fig. 6, Table 6). However, there was no significant negative correlation between AMBI and BQI_{ES} in any individual data set within this subarea (Table 6).

A simple linear regression model did not seem appropriate to account for the relationship between AMBI and BQI_{ES} in the Norwegian and Barents Seas (Fig. 7). AMBI and BQI_{ES} correlated negatively in only 2 individual data sets (i.e. hs and o4_{NB}, Table 6), and the slopes and the intercepts of the corresponding linear regression models differed significantly (ANCOVA, $p < 0.001$ in both cases). Moreover, low values of AMBI sometimes also corresponded to low values of BQI_{ES} (stations in the shaded area in Fig. 7).

Negative correlations between AMBI and BQI_{ES} were found in only 4 Mediterranean individual data sets (i.e. ka, lm, M2 and M3) (Fig. 8, Table 6). The

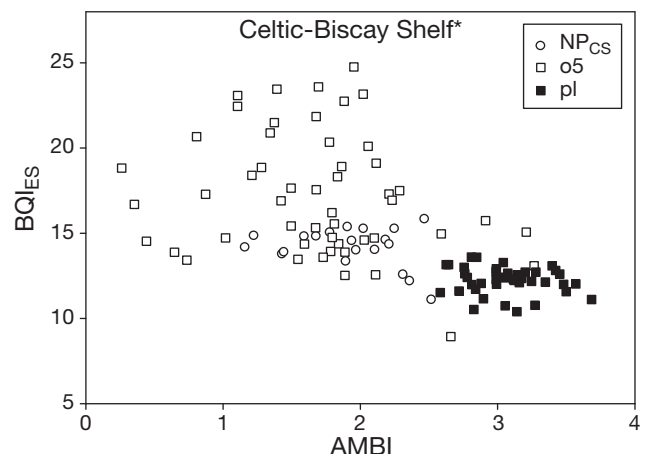


Fig. 6. Relationships between AMBI and BQI_{ES} in the Celtic-Biscay Shelf. Symbols refer to individual data sets (see Table 1). *Significant negative correlation (for the subarea or the individual data sets) between AMBI and BQI_{ES}

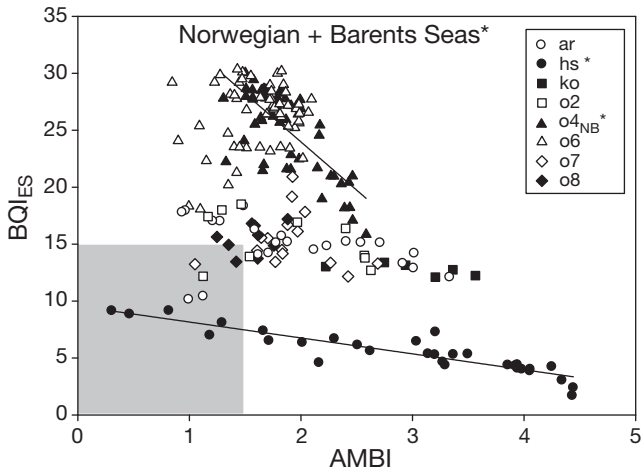


Fig. 7. Relationships between AMBI and BQIES in the Norwegian and Barents Seas. Symbols refer to individual data sets (see Table 1). *Significant ($p < 0.05$) negative correlation (for the subarea or the individual data sets) between AMBI and BQIES. Shaded rectangle in the bottom left delimits stations with a low AMBI (<1.5) and BQIES (<15) (see 'Results-Comparisons between AMBI and BQIES' for details)

slopes of corresponding linear regression models did not differ significantly (ANCOVA, $p = 0.473$), whereas intercepts did ($p = 0.027$). Both ka and gr contained stations characterized by low values of AMBI and BQIES (shaded area in Fig. 8, all data), which weakens the use of simple linear regression models to infer the relationships between the 2 indices for the whole Mediterranean.

In the marine North Sea (Fig. 9), high values of AMBI were also always associated with low values of BQIES. Conversely, very low values of AMBI tended to be associated with very low values of BQIES (shaded area in Fig. 9, marine North Sea). Intermediate values of AMBI were associated with a very large range (i.e. from very high to very low) of BQIES values. The analysis of individual data sets showed the occurrence of significant negative relationships between AMBI and BQIES in o3 (Fig. 9), o4_{NS} (data not shown) and 'of' (Fig. 9). The slopes and the intercepts of corresponding linear regression models differed significantly (ANCOVA, $p < 0.001$ and $p = 0.007$, respectively). Con-

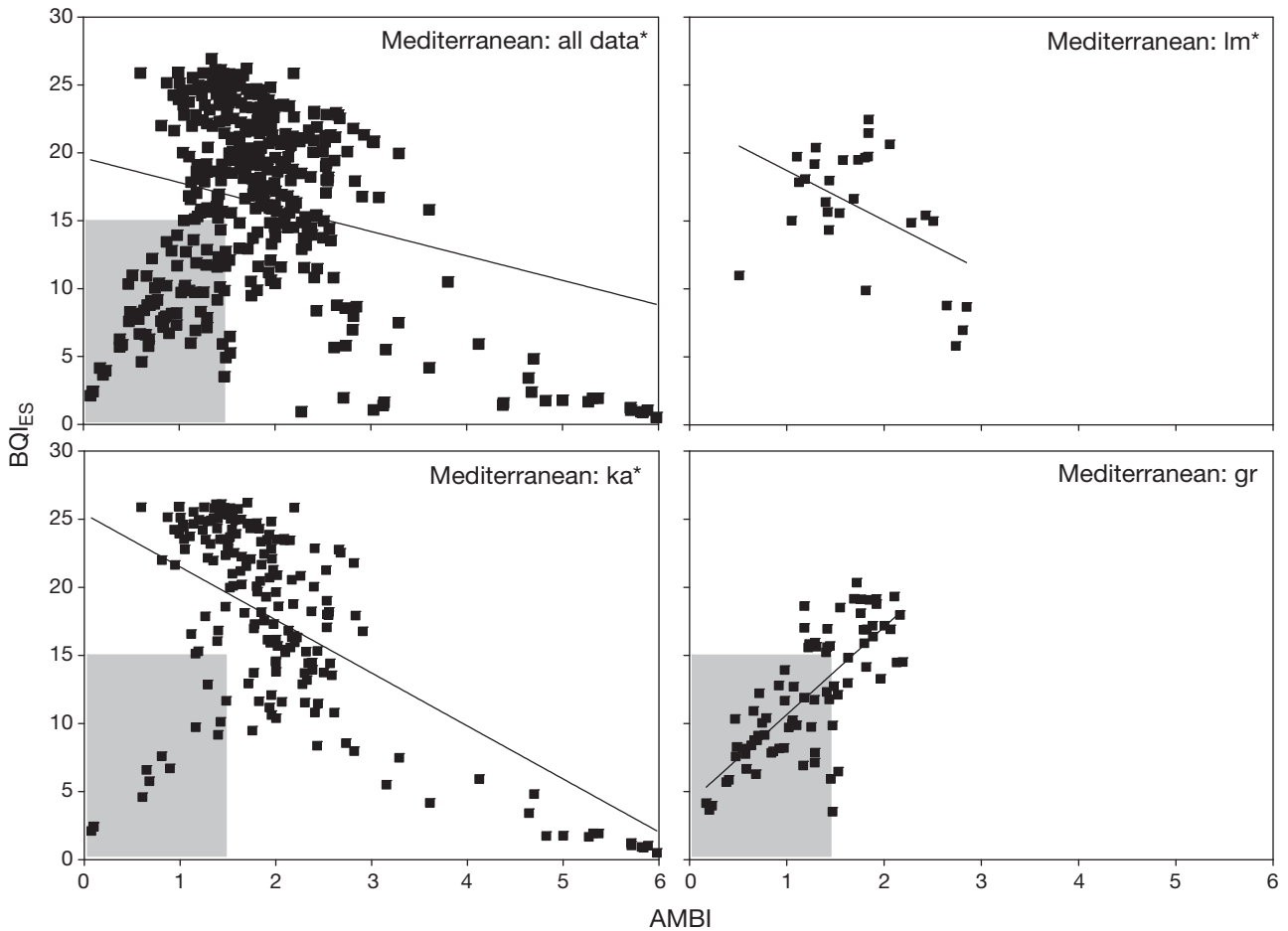


Fig. 8. Relationships between AMBI and BQIES in the Mediterranean. Data are provided for the whole Mediterranean and 3 individual data sets (see Table 1). *Significant ($p < 0.05$) negative correlation (for the subarea or the individual data sets) between AMBI and BQIES. Shaded rectangles in the bottom left of the Mediterranean, ka and gr graphs delimit stations with a low AMBI (<1.5) and BQIES (<15) (see 'Results-Comparisons between AMBI and BQIES' for details)

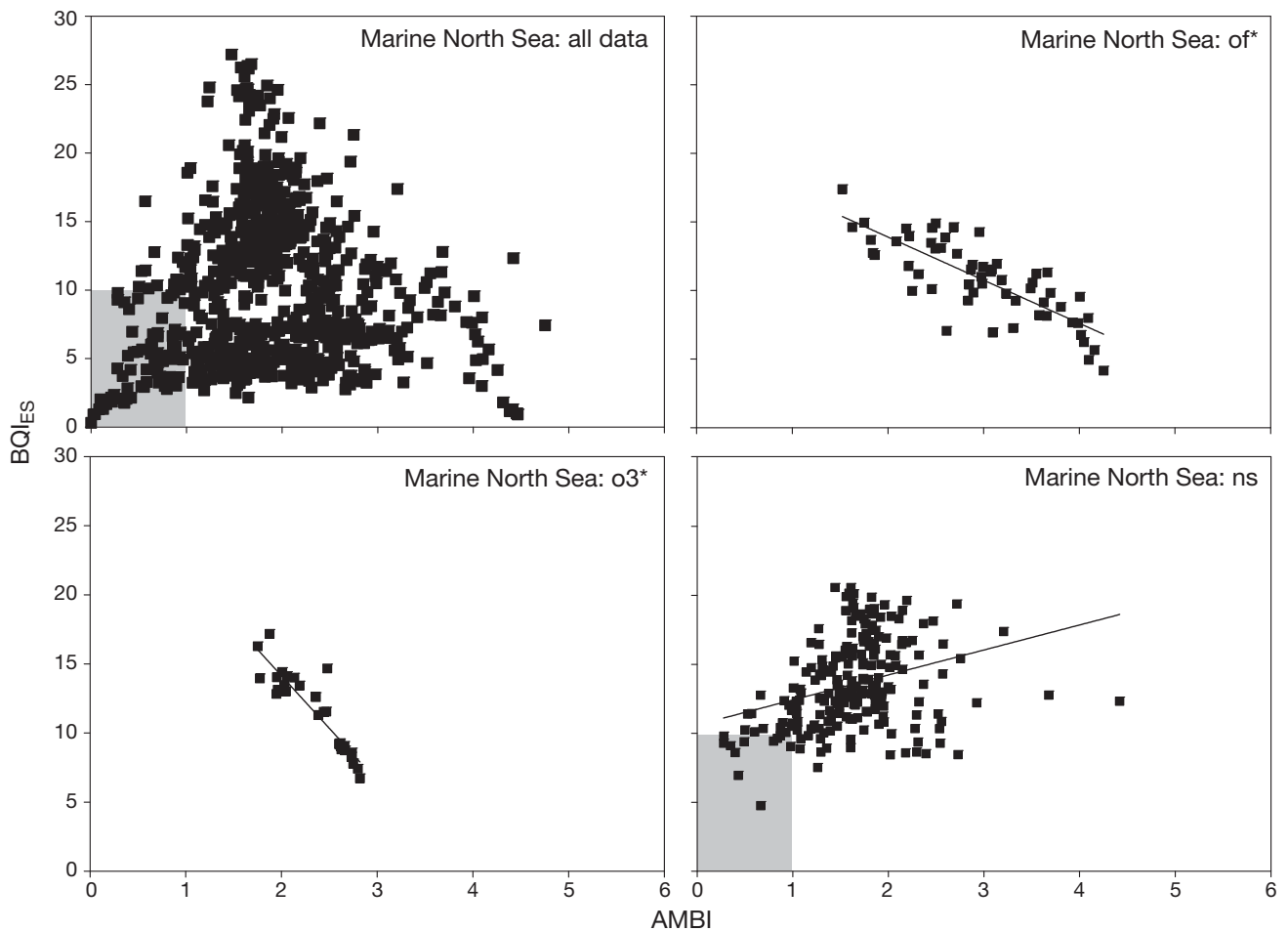


Fig. 9. Relationships between AMBI and BQ_{ES} in the marine North Sea. Data are provided for the whole marine North Sea and 3 individual data sets (see Table 1). *Significant ($p < 0.05$) negative correlation (for the subarea or the individual data sets) between AMBI and BQ_{ES} . Shaded rectangles in the bottom left of the marine North Sea and ns graphs delimit stations with a low AMBI (< 1) and BQ_{ES} (< 10) (see 'Results-Comparisons between AMBI and BQ_{ES} ' for details)

versely, AMBI and BQ_{ES} correlated positively in ns (Fig. 9) and ug (data not shown). The relationship between AMBI and BQ_{ES} in the estuarine North Sea (Fig. 10) was very similar to that observed in the marine North Sea.

The $E(S_{50})_{0.05}$ and the AMBI EG of the most dominant species for each station characterized by low AMBI and BQ_{ES} (shaded areas in Figs. 7–9) are listed in Table 7. In most cases $E(S_{50})_{0.05}$ were lower than expected from the AMBI EG values. This mismatch was especially clear for the most dominant species in the Norwegian and Barents Seas (*Maldane sarsi*), the Mediterranean (*Ditrupa arietina*, *M. glebifex*, *Turritella communis* and *Owenia fusiformis*) and the marine North Sea (*Magelona mirabilis*, *Modiolus modiolus* and *Spisula subtruncata*). Moreover, these species tended to be more dominant at the stations characterized by low AMBI and BQ_{ES} than in the whole subareas.

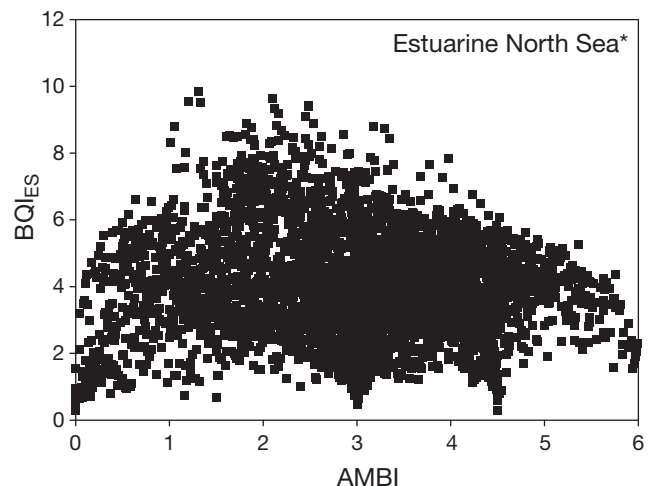


Fig. 10. Relationships between AMBI and BQ_{ES} in the estuarine North Sea. *Significant ($p < 0.05$) negative correlation (for the subarea or the individual data sets) between AMBI and BQ_{ES}

Table 7. Comparison of the $E(S_{50})_{0.05}$ and the AMBI EG of the most dominant species at each of the stations characterized by low AMBI and BQI_{ES} (shaded areas in Figs. 7–9). Species in **bold** are those for which (1) there is a clear mismatch between $E(S_{50})_{0.05}$ and AMBI EG, and (2) dominance is higher in the corresponding shaded area. The ranges of $E(S_{50})_{0.05}$ in each subarea are given for comparison

Species	AMBI EG	$E(S_{50})_{0.05}$	Mean dominance in shaded area (%)	Mean dominance in whole subarea (%)
Norwegian and Barents Seas				
<i>Maldane sarsi</i>	I	8.5	29.7	9.7
<i>Dacrydium vitreum</i>		9.8	26.2	4.4
<i>Lumbrineris mixochaeta</i>	II	5.6	25.4	16.1
<i>Lumbriclymene minor</i>	III	13.5	13.9	1.8
<i>Ophiura robusta</i>	II	11.5	9.5	4.2
<i>Chone duneri</i>	II	9.8	7.8	2.9
Range		2.9–28.3		
Mediterranean				
<i>Ditrupa arietina</i>	I	3.2	37.8	17.0
<i>Maldane glebifex</i>	I	9.1	23.4	5.6
<i>Turritella communis</i>	II	4.4	16.4	8.9
<i>Owenia fusiformis</i>	II	6.2	13.9	8.0
<i>Nucula nucleus</i>	I	12.1	12.0	3.0
<i>Paradoneis armata</i>	III	11.6	8.7	4.3
<i>Spisula subtruncata</i>	I	4.7	8.6	7.6
Range		1.3–28.3		
Marine North Sea				
<i>Magelona mirabilis</i>	I	2.0	51.5	15.1
<i>Modiolus modiolus</i>	I	5.9	18.2	7.2
<i>Urothoe brevicornis</i>	I	6.1	12.2	16.5
<i>Spisula subtruncata</i>	I	2.1	8.9	6.8
Range		1.0–24.1		

Comparison between ES derived from AMBI and BQI_{ES}

The frequency distributions of the ES derived from AMBI and BQI_{ES} in the 4 marine subareas are shown in Fig. 11. In all cases there were clear discrepancies. In the Celtic-Biscay Shelf and in the Mediterranean, both indices resulted in the classification of a large majority of stations as high and good. The main differences between indices were (1) the dominance of stations classified as good by AMBI versus high for BQI_{ES} and (2) the occurrence of a larger proportion of stations classified as moderate, poor and bad by BQI_{ES} than by AMBI. Discrepancies between the indices were much larger in the Norwegian and Barents Seas and in the marine North Sea, where the majority of stations were classified as good by AMBI versus moderate, poor and bad by BQI_{ES} . In the estuarine North Sea, AMBI classified most of the stations as moderate and good versus moderate and poor for BQI_{ES} (Fig. 12). The differences in the proportions of the stations classified as high and good versus moderate, poor and bad were 15.6, 34.8, 29.3, 51.5 and 46.1% in the Celtic-Biscay Shelf, the Norwegian and Barents Seas, the Mediterranean and the marine and estuarine North Sea, respectively.

DISCUSSION

To our knowledge, the largest comparison between EQR derived from macrozoobenthos composition in European waters was based on a database encompassing data from ca. 192 stations located in the Celtic-Biscay Shelf, the North Sea and the Kattegat (Borja et al. 2007). Three of the 4 procedures compared were based on the use of AMBI and the last one was based on the Indicator Species Index (ISI index), which is an equivalent. It was therefore not surprising that EQR computed using these procedures correlated tightly. The present study is the first to be performed at a pan-European scale (12 409 stations, including 2158 marine stations located in the Celtic-Biscay Shelf, the Mediterranean, the North Sea and the Norway and Barents Seas). Moreover, it compares AMBI and BQI_{ES} , 2 indices which show major differences in their way of assessing the sensitivity/tolerance level of individual species, and which have been shown to locally result in different ES assessments (Labruno et al. 2006, Dauvin et al. 2007, Zettler et al. 2007).

Facilitation of the use of BQI_{ES}

One of the major limitations to the spread of the use of BQI_{ES} is the difficulty in deriving $E(S_{50})_{0.05}$, which

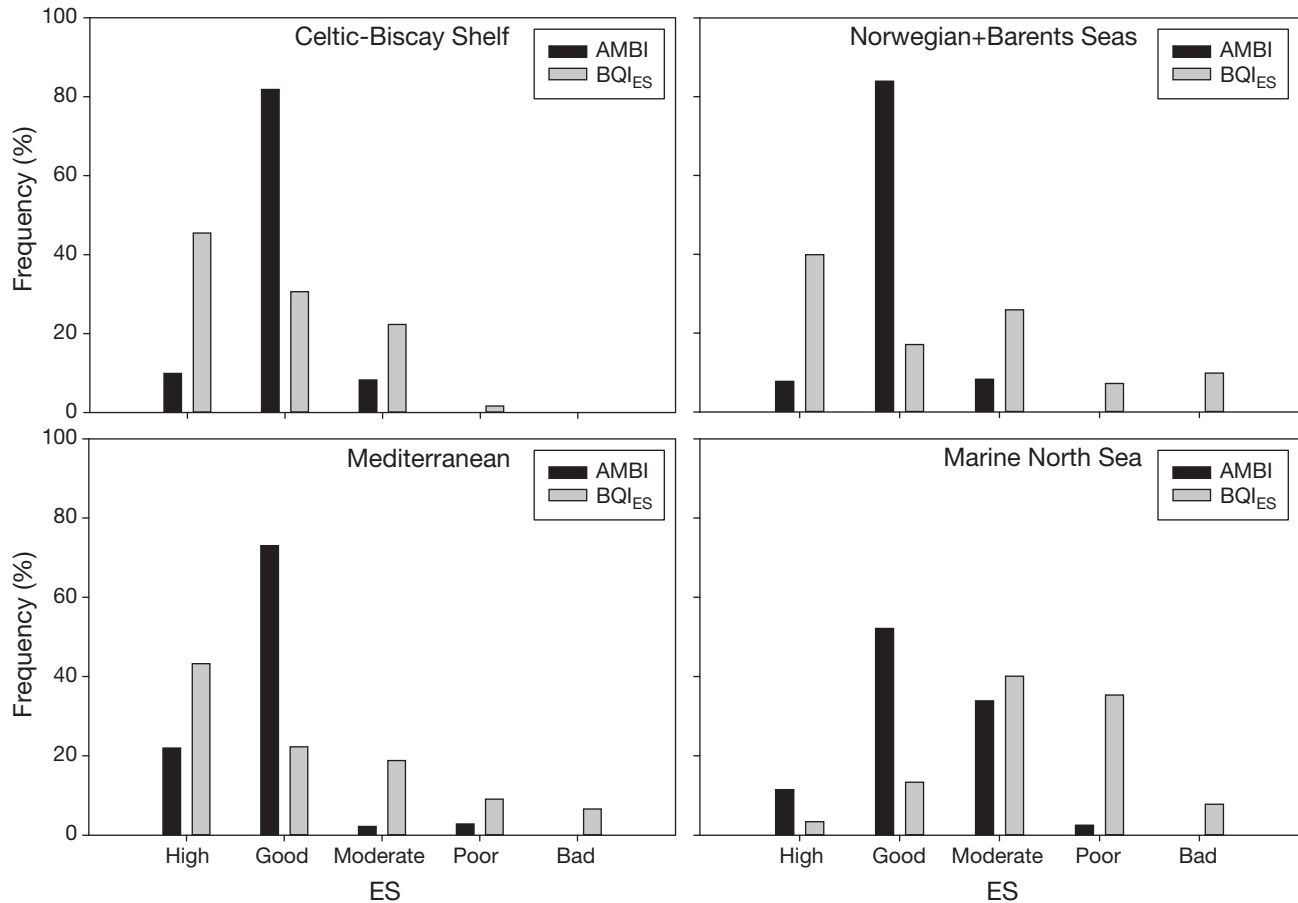


Fig. 11. Frequency distributions of ES derived from AMBI and BQI_{ES} in the 4 marine subareas: the Celtic-Biscay Shelf, the Norwegian and Barents Seas, the Mediterranean and the marine North Sea

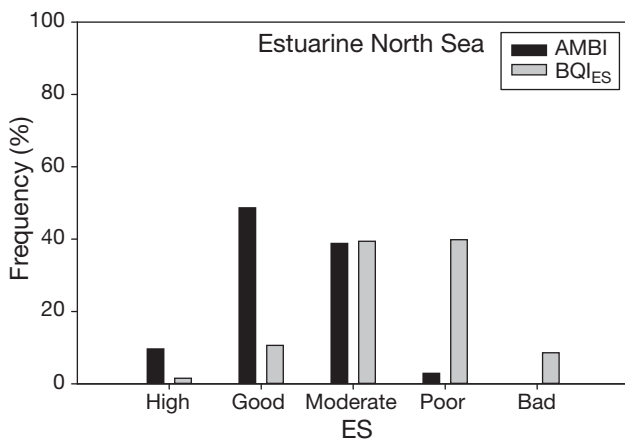


Fig. 12. Frequency distributions of ES derived from AMBI and BQI_{ES} in the estuarine North Sea

requires the species to be present in at least 20 samples (Rosenberg et al. 2004). To our knowledge, $E(S_{50})_{0.05}$ lists have only been compiled for the Swedish West Coast (Rosenberg et al. 2004), the Gulf of Lions (Labruno et al. 2006), the Southern Baltic (Zettler et al. 2007), the Seine estuary (Dauvin et al. 2007) and the

Marennes Oléron and Arcachon Bays (Blanchet et al. 2008). All lists are limited regarding species numbers and are not available online except for Rosenberg et al. (2004). The present study resulted in the computation of $E(S_{50})_{0.05}$ for 643 species in the whole marine indicator data set, 76 species in the Celtic-Biscay Shelf, 246 species in the Mediterranean, 337 species in the marine North Sea and 158 species in the Norwegian and Barents Seas. The proportions of species with an $E(S_{50})_{0.05}$ increased with the number of stations within each subarea, which simply corresponded to the increase of the proportions of species present at more than 20 stations. In spite of the size of our data sets, the proportions of species with an $E(S_{50})_{0.05}$ were always lower than for AMBI EG, which further underlines practical difficulty in computing $E(S_{50})_{0.05}$ and thus BQI_{ES}. AMBI should be interpreted with caution when the proportion of non-assigned taxa is higher than 20% (Borja & Muxika 2005). To our knowledge, no such recommendation is yet available for BQI_{ES}. Due to the strong analogy in the formula used to compute the sensitivity/tolerance terms in both AMBI and BQI_{ES}, this figure can nevertheless also probably be used for

BQI_{ES} . In this sense, it is important to note that although $E(S_{50})_{0.05}$ were available for 91.8% of the individuals in the whole marine indicator data set, these proportions were lower than 80% both in the Norwegian and Barents Seas and in the Celtic-Biscay Shelf.

Our $E(S_{50})_{0.05}$ lists clearly could be improved and we want to stress that other data sets could be aggregated to MacroBen to refine estimates of $E(S_{50})_{0.05}$ in each subarea. This will facilitate the use of BQI_{ES} on small individual data sets and allow further testing of the response of BQI_{ES} to disturbances. In this sense, the present study will contribute to further testing of BQI_{ES} and/or to more specific comparative studies between AMBI and BQI_{ES} . We have also identified a list of the most dominant species in the marine indicator data set which are still either lacking an AMBI EG or an $E(S_{50})_{0.05}$. Effort should now be preferentially focussed on the assessment of their sensitivity/tolerance levels to further improve the use of both indices in European waters.

Comparison between AMBI EG and $E(S_{50})_{0.05}$

One would expect a strong negative correlation between AMBI EG and $E(S_{50})_{0.05}$ in the case of a similar assessment of species sensitivity/tolerance levels using these 2 parameters. We indeed reported negative correlations in the whole marine indicator data set, the Norwegian and Barents Seas, and the marine and estuarine North Sea. However, the explanatory powers of the corresponding linear regression models always remained limited and we found no significant negative correlation in both the Celtic-Biscay Shelf and the Mediterranean. Our overall conclusion is that there is no good agreement between AMBI EG and $E(S_{50})_{0.05}$, and in this sense our results support those already collected in more restricted areas such as the Gulf of Lions (Labruno et al. 2006) or in other subareas such as the Baltic Sea (Zettler et al. 2007).

Assessment of the validity of the use of a single list of sensitivity/tolerance levels

Bustos-Baez & Frid (2003) showed that the response of potential indicator species to organic enrichment differed between locations, and Rosenberg et al. (2004) found that AMBI EG may vary between geographical areas. It was, therefore, interesting to compare $E(S_{50})_{0.05}$ between subareas; the poor agreement probably did not result from differences in anthropogenic pressures. $E(S_{50})_{0.05}$ values are mostly dependent on the $E(S_{50})$ of stations with low species richness. For $E(S_{50})_{0.05}$ to be comparable, it is thus not necessary for

the levels of anthropogenic pressures to be strictly equivalent between subareas, but rather that a wide range from disturbed to undisturbed stations is present in all subareas. Unfortunately, there is no comprehensive information available on the level of disturbance experienced by each station in MacroBen. However, the Pearson & Rosenberg (1978) model states that species richness decreases with disturbance. The large ranges of $E(S_{50})$ recorded within each subarea therefore suggest that both disturbed and undisturbed stations were indeed present in each subarea. This was further confirmed by the large ranges of $E(S_{50})_{0.05}$ found within each marine subarea (see Table 7). Our results thus support those of Labruno et al. (2006) in showing that there are heterogeneities in $E(S_{50})_{0.05}$ computed for different subareas. This does not support the use of a single list of species sensitivity/tolerance levels at the pan-European scale.

Overall, the relationships (1) between AMBI EG and $E(S_{50})_{0.05}$ and (2) of $E(S_{50})_{0.05}$ between subareas were rather noisy. If sensitivity/tolerance levels indeed vary between geographical areas, they also probably vary between habitats within a single geographic area, which may be partly responsible for the noise observed during the present study. Up to now (and the present study is no exception), AMBI EG and even $E(S_{50})_{0.05}$ have never been assessed at the habitat level. Interesting lines for future research would thus consist of comparing $E(S_{50})_{0.05}$ (1) within the same subarea but between habitats and (2) within the same habitat but between subareas. In both cases, this will require the construction of large and comprehensive databases and we suggest that this exercise should first focus on a restricted set of well-studied habitats.

Unravelling the causes of discrepancies between the 2 indices

The negative correlation between AMBI and BQI_{ES} was satisfactory only in the Celtic-Biscay Shelf. Interestingly, there was no significant negative correlation between AMBI EG and $E(S_{50})_{0.05}$ in this subarea, which suggests that the agreement between the values of the 2 indices is not necessarily reliant on the general correlation between their assessments of sensitivity/tolerance levels. In all other subareas, AMBI and BQI_{ES} correlated only poorly. Overall, stations with high AMBI also tended to have low BQI_{ES} . Conversely, some of the stations with low AMBI also featured low BQI_{ES} . The present study shows that this mostly resulted from strong dominance by species classified as sensitive by AMBI but with a low $E(S_{50})_{0.05}$. Labruno et al. (2006) reported a positive correlation between AMBI and BQI in the Gulf of Lions and attributed this result to the

strong dominance of the serpulid polychaete *Ditrupa arietina* (Grémare et al. 1998, Labruno et al. 2007a), which was classified as sensitive by AMBI and had a low $E(S_{50})_{0.05}$. Our results support this interpretation and generalize it to other geographical areas (e.g. the Cretan Shelf) and to other species. The present study provides the first lists of the most dominant species within each marine subarea for which there are important discrepancies between AMBI EG and $E(S_{50})_{0.05}$. All were classified in AMBI EG I or II. However, some of them are known to be influenced by natural sources of disturbance such as sediment instability (*D. arietina*, Grémare et al. 1998 and *Magelona mirabilis*, Rayment 2007) or climatic anomalies (*Maldane glebifex*, Glémarec et al. 1986) and cycles (*D. arietina*, Labruno et al. 2007b). These observations are indicative of the tendency of $E(S_{50})_{0.05}$ to automatically classify dominant species as tolerant and its inability to differentiate between natural and anthropogenic sources of disturbance (Labruno et al. 2006, 2007b). Further autoecological studies are nevertheless clearly needed to better unravel the actual sensitivity/tolerance levels of the species highlighted in Table 7.

Comparison of ES assessments derived from AMBI and BQI_{ES}

Given the discrepancies between AMBI and BQI_{ES} , it was not surprising that the frequency distributions of ES derived from these 2 indices differed in most subareas. In the Norwegian and Barents Seas and both the marine and estuarine North Sea, these discrepancies were also apparent when distinguishing stations with a high or good ES from those with a moderate, poor or bad ES as recommended by the WFD. BQI_{ES} resulted in overall poorer ES than AMBI, which supports preliminary results in the Gulf of Lions (Labruno et al. 2006), the Southern Baltic (Zettler et al. 2007) the Bay of Seine (Dauvin et al. 2007) and to a lesser extent the North Sea (Reiss & Kröncke 2005).

It should be underlined that all the above-mentioned studies plus the present one have used a fixed conversion scale to infer ES from AMBI. One of the characteristics of the recently introduced M-AMBI is that it is using a different conversion scale for each homogeneous habitat as does BQI_{ES} (Borja et al. 2007, Muxika et al. 2007a). In both cases, this requires the existence of valid references (i.e. a single high reference in the case of BQI_{ES} , and both a bad and a high reference in the case of M-AMBI). The computation of M-AMBI was not integrated in the MacroBen tool and we did not use this procedure to infer ES during the present study.

CONCLUSIONS

AMBI and BQI_{ES} both ultimately rely on species sensitivity/tolerance levels, which they respectively assess through AMBI EG and $E(S_{50})_{0.05}$. We identified the most dominant species in marine European waters still lacking an AMBI EG or an $E(S_{50})_{0.05}$. Our results support those of previous studies, obtained at much smaller geographical scales, in showing that AMBI EG and $E(S_{50})_{0.05}$ poorly agree. They suggest that the use of a single sensitivity/tolerance list in different geographical areas (such as in AMBI EG) is not appropriate. Discrepancies between the values of the 2 indices are due to the dominance of species characterized as sensitive by AMBI and tolerant by BQI_{ES} . These species were identified and some of them are known to be influenced by natural disturbance, which highlights the tendency of BQI_{ES} to classify dominant species as tolerant and thus to be inefficient in distinguishing anthropogenic from natural disturbances. AMBI and BQI_{ES} thus both present weaknesses relative to the assessment of sensitivity/tolerance. Both indices have been subject to several recent refinements regarding their computation and their procedures to infer ES, which are now quite comparable. However, all these steps are posterior (and thus dependent on) a sound assessment of species sensitivity/tolerance. Changes in the scales used to convert indices to ES can only partially compensate for changes in sensitivity/tolerance levels among geographical areas and/or habitats. Preferential attention should thus now be paid to this particular issue. Future studies should focus on (1) the clarification of the sensitivity/tolerance levels of the species identified as problematic during the present study, and (2) the assessment of the relationships between AMBI EG and $E(S_{50})_{0.05}$ within and between combinations of geographical areas and habitats.

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