

Assessing functional diversity in marine benthic ecosystems: a comparison of approaches

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ABSTRACT: Two methods traditionally employed to investigate functional diversity in marine benthic ecosystems are relative taxon composition analysis, which interprets changes in the distribution of taxa in terms of the characteristics they exhibit, and trophic group analysis, which investigates differences in feeding mechanisms between assemblages. An alternative approach, biological traits analysis, considers a range of biological traits expressed by organisms to assess how functioning varies between assemblages. This study compares biological traits analysis to the relative taxon composition and trophic group approaches. Biological trait scores were assigned to a range of epibenthic invertebrate taxa from the southern North Sea and eastern English Channel and differences in the relative proportions of these traits were investigated using multivariate methods. The traits important in differentiating stations were attachment, flexibility, body form, mobility, feeding method and life habit. Such assemblages were spatially heterogeneous and there was no obvious distinction between different geographical sectors. This contrasted with the results of the relative taxon composition approach, which showed broad patterns in assemblage distribution in the eastern English Channel and southern North Sea. The biological traits approach provided information on a larger variety of ecological functions than the other techniques and revealed very different relationships between assemblages. It highlighted a greater diversity of assemblage types and was resistant to large-scale biogeographic variation. Therefore, it is potentially more useful than the traditional approaches for assessing ecosystem functioning on both large and small scales in benthic environments.

KEY WORDS: Ecosystem functioning · Biological traits · Relative taxon composition · Trophic groups · Megabenthos

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INTRODUCTION

Functional diversity relates to the number, type and distribution of functions performed by organisms within an ecosystem (Diaz & Cabido 2001). It incorporates interactions between organisms and their environment into a concept that can portray ecosystem-level structure in marine environments. In marine benthic ecosystems, functional diversity has traditionally been addressed by describing the taxonomic composition of assemblages. Typically, a pattern in taxonomic composition is revealed that is subsequently

interpreted in the light of changes in a few ecological characteristics exhibited by the taxa, which are relevant to presumed functional roles.

This approach has been used to investigate the effects of different anthropogenic disturbances on functioning in marine systems. Studies have linked characteristics such as feeding mechanisms, longevity, body size and mobility to changes in species distribution in communities exposed to stressors such as sewage pollution (Poore & Kudenov 1978, Grizzle 1984), anoxia (Beukema et al. 1999) and fishing (Brown & Wilson 1997, Ramsay et al. 1998, Spencer et al. 1998, Hall-Spencer et al. 1999).

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Although the approach detects the responses of individual taxa to environmental stress, it can be difficult to confirm which ecological functions are driving those responses. Organisms that appear to perform similar ecological roles may not always respond to stressors in the same way (Ramsay et al. 1998) because although they share some important attributes, they are likely to differ in other, more subtle ways.

A more targeted approach proposed for the study of functional diversity focuses specifically on feeding mechanisms, which are generally thought to be one of the central processes structuring marine ecosystems (Pearson & Rosenberg 1978, 1987). Trophic group analyses combine taxa into guilds based on their feeding modes and investigate how these feeding guilds are distributed across assemblages. Such analyses have been used to investigate pollution effects (Gaston et al. 1998, Cardell et al. 1999, Mistri et al. 2000, Mirto et al. 2002), habitat modification (Schlosser 1982), fishing impacts, including dredging (Chicharo et al. 2002) and bottom trawling (Garrison & Link 2000), and natural variability in environmental parameters (Roth & Wilson 1998, Desrosiers et al. 2000).

Although this approach provides a stronger link between species and ecosystem functions than the relative taxon composition methods, the reduction of taxa to a small number of groups represents a loss of potentially important ecological information (Charvet et al. 1998). Another problem is that it does not account for interactions other than feeding relationships, and other ecological functions performed by organisms that are important in structuring ecosystems may be overlooked (Mancinelli et al. 1998).

Biological traits analysis takes these approaches further and considers a range of taxon characteristics across the entire assemblage. The approach has received little attention in the marine environment, originating in terrestrial plant (Olf et al. 1994, McIntyre et al. 1995) and freshwater invertebrate (Townsend & Hildrew 1994, Castella & Speight 1996) ecology. Biological traits analysis is based on habitat templet theory, which states that species' characteristics evolve in response to habitat constraints (Southwood 1977). Community structure is governed by habitat variability and the biological traits exhibited by organisms will provide information about how they behave and respond to stress (Lavorel et al. 1997), thereby indicating the state of the environment (Usseglio-Polatera et al. 2000b).

The biological traits approach, which describes the contribution of a suite of ecological characteristics to species' abundance patterns, has a number of advantages over the more traditional functional diversity measures. It is based on sound ecological theory (Townsend & Hildrew 1994) and there are strong links

between functional traits and ecosystem processes (Diaz & Cabido 2001, Coleman & Williams 2002). As biological trait distribution can be directly related to ecosystem structuring mechanisms (Usseglio-Polatera et al. 2000b), reasons for change in communities are highlighted directly and not merely inferred, as with the relative taxon composition approach.

Species replacements generally occur over extensive biogeographic gradients (Gee & Warwick 1996, Engle & Summers 1999, Lancellotti & Vasquez 1999), and generalisations about assemblage structure and function can be difficult when taxon composition varies. Biological traits analysis uses the characteristics shared by many different taxa in a community regardless of species composition, and is a valuable approach for measuring ecosystem structure that is independent of biogeographic location (Doledec et al. 1999, Charvet et al. 2000, Usseglio-Polatera et al. 2000b).

In freshwater systems, the approach has been shown to discriminate the effects of disturbance on biological traits (Charvet et al. 2000). Trait structure appears to show a positive relationship with disturbance regimes, where the magnitude of response increases with the level of disturbance (Townsend et al. 1997). Frid et al. (2000b) briefly investigated the use of biological traits analysis in marine benthic ecosystems, using epibenthic invertebrate data from the southern North Sea and eastern English Channel. They showed that the traits approach had potential for describing functional diversity in marine systems.

In this study we critically compare the biological traits approach with the relative taxon composition and trophic group composition approaches. We focus on determining the extent to which the approaches can (1) identify the main ecological characteristics that distinguish epibenthic invertebrate assemblages from different sites and (2) highlight differences between assemblages within an area. As the biological traits approach incorporates information on a large variety of ecological characteristics, it was predicted *a priori* that it would highlight the ecological functions most important for community structure in the ecosystem to a greater degree than the other 2 approaches. It was also expected to identify more heterogeneity between stations than the other approaches because trait structure should be governed by environmental conditions on a smaller scale than taxonomic composition.

MATERIALS AND METHODS

Data collection. Epibenthic megafauna from 99 subtidal stations in coastal waters (10 to 50 m depth) of the southern North Sea and eastern English Channel

(ICES divisions IVc and VIIId respectively) were sampled from RV 'Corystes' during August 1998. Trawls of 30 min duration, covering around 15 000 m² (Ellis & Rogers 2000), were carried out using a 4 m beam trawl with a 40 mm stretched cod-end, chain mat and flip-up rope (Rogers et al. 1998).

Invertebrate taxa were identified to species where possible and the biomass of each recorded as wet weight (kg h⁻¹). For small samples the whole catch was processed, whilst for larger samples, subsamples of known weight were sorted and the resulting taxa biomass raised to that of the full catch weight.

To focus the investigation on the taxa that contributed most to similarity or variation between stations, the invertebrate dataset was reduced to those taxa found either (1) in the top 90% of biomass at any station or (2) at more than 50% of stations. This incorporated taxa that were dominant in the biomass of any station in addition to those that were distributed widely but not necessarily of high biomass.

Data analysis. The software packages ADE-4 (Thioulouse et al. 1997) and Minitab (Minitab 2000) were used for all analyses. Invertebrate biomass data were log₁₀(x + 1) transformed prior to analysis to prevent dominant taxa from masking responses of lower-biomass organisms (Clarke & Warwick 1994).

Relative taxon composition analysis. Centred (co-variance) principal components analysis (PCA) was used to investigate patterns in the relative biomass of taxa over the stations. PCA is a linear ordination method based on actual differences in biomass between samples. It is calculated on the same basis as the methods used to assess biological trait structure (see below) and

is useful for comparison of the relative taxon composition and trait ordinations.

Trophic group analysis. Each taxon in the study was classified as either deposit feeder, filter/suspension feeder, opportunist/scavenger or predator, based on information retrieved from literature sources and specialist knowledge (Table 1). Biomass values were then summed for each trophic group at each station. This resulted in a station by trophic group table that was assessed in the same way as the taxonomic data, using centred PCA.

Biological traits analysis. Nine biological traits were chosen for the analysis. These reflected life history (individual or colony size, relative adult longevity and reproductive technique), morphology (body flexibility and form) and behaviour (relative adult mobility, degree of attachment, adult life habit and feeding type) characteristics and were chosen for their potential to maximise differences between taxa. The 9 traits were sub-divided into categories, for example feeding type was separated into the categories deposit feeder, filter/suspension feeder, opportunist/scavenger and predator (Table 2).

Individual taxa were then coded for the extent to which they displayed the categories of each trait using a 'fuzzy coding' procedure. Fuzzy coding, as described by Chevenet et al. (1994), allows taxa to exhibit categories of a variable to different degrees. This takes account of variations in trait expression both between life stages and between individuals at each life stage (Castella & Speight 1996, Charvet et al. 2000). The scoring range of 0 to 3 was adopted, with 0 being no affinity to a trait category and 3 being total affinity. For

Table 1. Feeding mechanisms of southern North Sea and eastern English Channel macrobenthic taxa. Where a taxon exhibited more than one feeding method, it was classified by the preferred or most frequently documented method

Deposit feeder	Filter/suspension feeder	Opportunist/scavenger	Predator
<i>Echinocardium cordatum</i>	<i>Acanthocardia</i> spp.	<i>Aphrodita aculeata</i>	<i>Asterias rubens</i>
<i>Spatangus purpureus</i>	<i>Aequipecten opercularis</i>	<i>Buccinum undatum</i>	<i>Crossaster paposus</i>
	<i>Alcyonidium diaphanum</i>	<i>Cancer pagurus</i>	<i>Philine aperta</i>
	<i>Alcyonium digitatum</i>	<i>Inachus</i> spp.	<i>Urtica felina</i>
	Asciacea	<i>Hinia reticulata</i>	
	<i>Crepidula fornicata</i>	<i>Homarus gammarus</i>	
	<i>Chaetopterus variopedatus</i>	<i>Liocarcinus depurator</i>	
	<i>Flustra foliacea</i>	<i>Liocarcinus holsatus</i>	
	Hydroida	<i>Liocarcinus marmoreus</i>	
	<i>Laevicardium crassum</i>	<i>Macropodia</i> spp.	
	<i>Metridium senile</i>	<i>Maja squinado</i>	
	<i>Mytilus edulis</i>	<i>Necora puber</i>	
	<i>Ophiothrix fragilis</i>	<i>Ophiura albida</i>	
	<i>Ostrea edulis</i>	<i>Pagurus bernhardus</i>	
	<i>Pecten maximus</i>	<i>Pagurus prideaux</i>	
	<i>Pentapora foliacea</i>	<i>Psammechinus miliaris</i>	
	Porifera		
	<i>Sabellaria spinulosa</i>		

Table 2. Biological trait variables and categories used to describe functional diversity in the macrobenthic communities of the southern North Sea and eastern English Channel

Trait	No.	Category
Individual/colony size (relative weight)	1	Small
	2	Small–medium
	3	Medium
	4	Medium–large
	5	Large
Adult longevity (yr)	1	<2
	2	2–5
	3	>5
Reproductive technique	1	Asexual (budding)
	2	Sexual (broadcast spawner)
	3	Sexual (egg layer/brooder—planktonic larvae)
	4	Sexual (egg layer/brooder—mini-adults)
Relative adult mobility	1	None
	2	Low
	3	Medium
	4	High
Degree of attachment	1	None
	2	Temporary
	3	Permanent
Adult life habit	1	Sessile
	2	Swim
	3	Crawl
	4	Burrow
	5	Crevice-dweller
Body flexibility (degrees)	1	>45
	2	10–45
	3	<10
Body form	1	Flat
	2	Mound
	3	Erect
Feeding habit	1	Deposit
	2	Filter/suspension
	3	Opportunist/scavenger
	4	Predator

example, *Aphrodita aculeata* (Linnaeus) are mostly scavenging organisms but may also deposit feed, so they were coded 1 (deposit), 0 (filter/suspension), 2 (scavenger), 0 (predator) for the trait variable 'feeding type'. The resulting table of taxa by trait scores is included as Appendix 1. Information on biological traits was obtained from a variety of sources including primary and secondary literature and by consulting relevant experts. Where information on a particular trait could not be obtained for a taxon, it was assigned the average score for that trait, so that it had no influence on the overall results (Chevenet et al. 1994).

The links between the biomass of taxa at each station and the traits they showed were investigated using co-inertia analysis (Doledec & Chessel 1994).

Co-inertia analysis assesses the co-structure between 2 data tables by simultaneously ordinating them, maximising both the variance from the individual tables and the correlation between them (Doledec & Chessel 1994). This produces scores for each station that incorporate both the biomass and trait information (Doledec et al. 1999). These scores can be plotted on ordination maps in the same way as other multivariate techniques, with each point representing the biomass-weighted biological trait composition of each station. The co-inertia procedure was developed for biological traits analysis in freshwater systems. Although this procedure and the other parametric methods employed in the study may have some limitations in their ability to describe marine epibenthic communities, their use allows the results of the study to be compared with those obtained from the larger body of work dedicated to freshwater ecosystems.

Firstly, separate ordinations of the individual data tables were carried out. As before, centred PCA was used to investigate the relative taxon composition of the stations. However, for this analysis the table was transposed so that the taxa were in rows. Fuzzy correspondence analysis was used to assess the taxa by traits table. This is a form of correspondence analysis used when variables are fuzzy coded (Chevenet et al. 1994). Co-inertia analysis was then carried out using both ordinations and the significance of the resulting co-structure examined with a random permutation test (Doledec & Chessel 1994). This test randomly permuted the rows of the co-inertia table and recalculated the inertia statistics 100 times. The observed co-inertia value was then compared to the frequency distribution of the randomly permuted values to assess if it was significantly larger.

Comparison of approaches. The relative taxon composition approach does not directly identify the ecological functions involved in differentiating communities, so these functions were inferred by examining the biological characteristics of taxa shown by the PCA to make a large contribution to differences between stations. For the trophic group and biological trait approaches, important ecological functions were identified directly from the respective ordinations.

In order to investigate how each approach portrayed differences between assemblages within an area, 4 separate measures were devised. Initially, the number of distinct assemblage types present amongst the stations was identified for each approach. Complete-linkage cluster analysis was applied to the station scores from the first 2 axes of each of the 3 separate analyses (Principal Components 1 and 2 for the relative taxon composition and trophic group analyses, and Co-inertia Axes 1 and 2 scores for biological traits analysis) (Reynaud & Thiouliouse 2000). This measure showed

the degree to which each approach could identify different types of benthic assemblage, based on the information included in the analysis.

The other 3 measures compared the ability of each approach to detect spatial relationships between these community types. The study area was split into 4 arbitrary sectors: the southern North Sea, north-eastern English Channel, mid-eastern English Channel and south-eastern English Channel (see Ellis & Rogers 2000). Within each sector, the number of community-types present and the number of stations that differed from the modal community-type were calculated in order to assess how each approach portrayed small-scale assemblage-type diversity. The number of stations within each sector that contained a different assemblage type to their nearest neighbour (using euclidean distance) was then calculated to assess the ability of each approach to differentiate communities from similar geographical locations.

RESULTS

Relative taxon composition analysis

The first 2 principal components accounted for 43% of the variability in the composition of the benthic communities, with 27% on Axis 1 and 16% on Axis 2 (Table 3a). The cluster analysis identified 5 groups of stations on the basis of the principal component scores. When overlaid on the PCA ordination, 2 of these groups separated out from the others along Axis 1 (Fig. 1). Group 3 separated out to the right of the axis and Group 5 towards the left. The organisms most influencing the differences between groups along this axis were *Aster-*

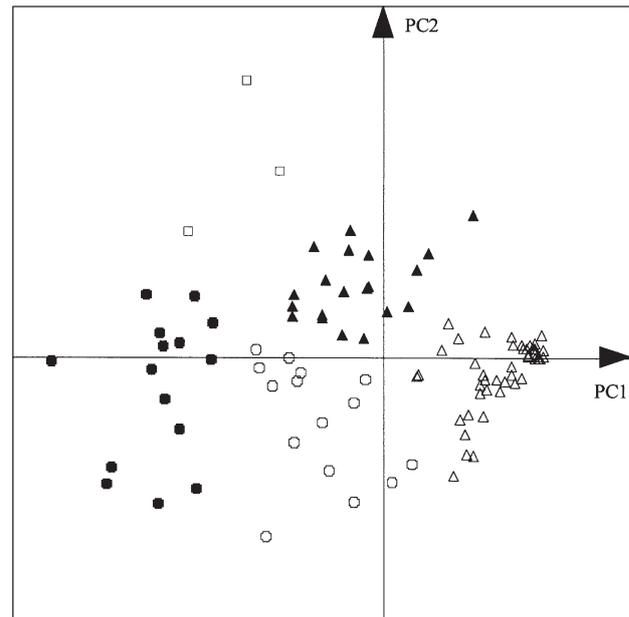


Fig. 1. First plane principal component analysis (PCA) ordination of southern North Sea and eastern English Channel benthic stations, based on the relative taxon composition of macroinvertebrate communities. Stations are marked by groups identified from cluster analysis; \square = Group 1, \blacktriangle = Group 2, \triangle = Group 3, \circ = Group 4, \bullet = Group 5

ias rubens (Linnaeus), *Alcyonium digitatum* (Linnaeus), *Necora puber* (Linnaeus) and *Psammechinus miliaris* (Gmelin) (Table 3). Group 5 had high biomass of all 4 species, whilst stations within Group 3 exhibited relatively low biomass values across taxa.

On the second axis, Groups 1 and 2 separated out from the other stations. Stations within these groups had relatively low biomass of *Alcyonium diaphanum* (Hudson) and higher biomass of *Ophiothrix fragilis* (Abildgaard) and *Aequipecten opercularis* (Linnaeus) (Table 3). Stations within Group 1 were distinguished from those within Group 2 by relatively higher proportions of *O. fragilis*.

Stations in the north-eastern English Channel were quite homogenous in terms of their taxonomic composition (Fig. 2). They differed from other stations in the region in that they shared relatively low biomass of *Asterias rubens*, *Psammechinus miliaris*, *Alcyonium digitatum* and *Necora puber*. However, stations in the southern North Sea were more variable in their composition, and although some were similar to the north-

Table 3. Principal components analysis (PCA) of (a) relative taxon composition and (b) trophic group composition of macrobenthic assemblages from the southern North Sea and eastern English Channel

PCA axes	Eigenvalue	Relative inertia (%)	Cumulative inertia (%)	Major contributing variables
(a) Relative taxon composition analysis				
1	1.1184	26.95	26.95	<i>Asterias rubens</i> <i>Alcyonium digitatum</i> <i>Necora puber</i> <i>Psammechinus miliaris</i>
2	0.6684	16.11	43.06	<i>Alcyonidium diaphanum</i> <i>Ophiothrix fragilis</i> <i>Aequipecten opercularis</i>
(b) Trophic group analysis				
1	1.0678	60.74	60.74	Filter/suspension feeder Predator
2	0.4616	26.26	87.00	Filter/suspension feeder Predator

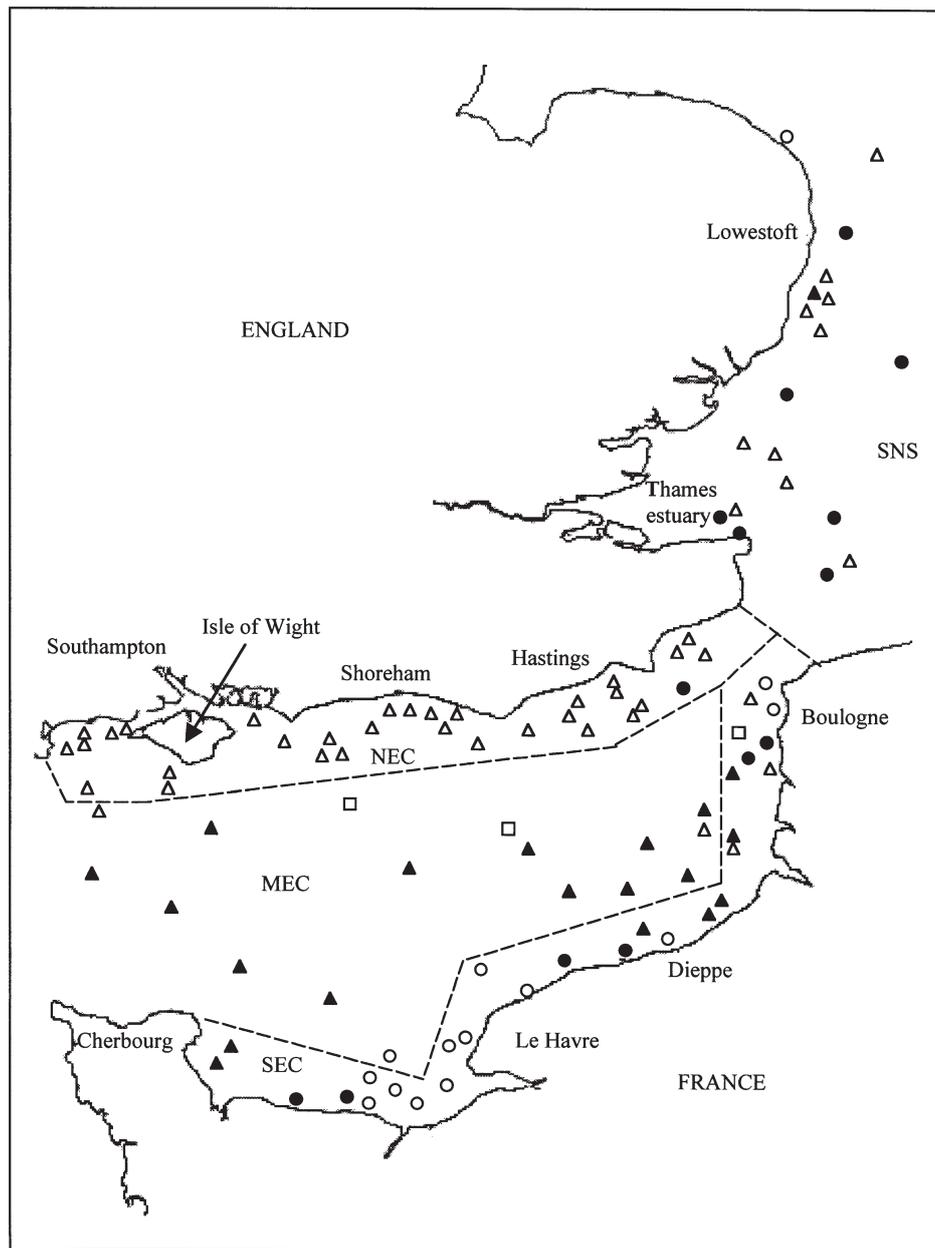


Fig. 2. Assemblage types present in the eastern English Channel and southern North Sea, based on the relative taxon composition of benthic invertebrate communities (assemblage types as shown in Fig. 1; \square = Group 1, \blacktriangle = Group 2, \triangle = Group 3, \circ = Group 4 and \bullet = Group 5). Sectors are as follows: SNS = southern North Sea, NEC = north-eastern English Channel, MEC = mid-eastern English Channel, SEC = south-eastern English Channel (after Ellis & Rogers 2000)

eastern English Channel stations, several were members of other groups.

Macroinvertebrate communities in parts of the south-eastern English Channel were also heterogeneous, with stations around the port of Boulogne consisting of mixed assemblages representing all 5 of the cluster analysis groups. In contrast to the north-eastern English Channel, which was quite distinct in taxon composition from the deeper mid-eastern English

Channel, several of the south-eastern English Channel stations south of Boulogne were quite similar to those located in the mid-eastern Channel region (Group 2, Fig. 2). These shared characteristically high biomasses of *Ophiothrix fragilis* and *Aequipecten opercularis*. One exception to this was a cluster of stations around the Le Havre area (Group 5, Fig. 2), which displayed particularly high biomass of *Asterias rubens*.

Trophic group analysis

PCA of the trophic group composition showed that the first 2 axes accounted for 87% of variability between the stations, with 61% of this variability projected onto Axis 1 and 26% on Axis 2 (Table 3b). Five station groups were identified by the cluster analysis. Groups 3 and 4 separated out to the right of Axis 1, whilst Group 1 was distinguished towards the left (Fig. 3). Group 5 showed some separation from the other groups along the second axis. Filter feeders and predators accounted for most of the variation along each of the first 2 axes (Table 3b), with predator biomass contributing most to projections along Axis 1 and filter feeders to Axis 2.

As with the relative taxon composition analysis, stations around Le Havre grouped apart from the others, including nearby south-eastern English Channel stations (Group 4, Fig. 4). These were characterised by a relatively higher predator biomass than the other stations. Stations around Boulogne were as variable trophically as they were in terms of taxon composition, again including representatives of all of the cluster analysis groups. There was also some continuity between the 2 approaches when stations in the mid-eastern English Channel were examined. Many of the stations in the sector exhibited homogenous trophic group compositions (Group 2, Fig. 4).

Several differences between the approaches were however noted. Stations towards the eastern end of the mid-eastern English Channel formed a distinct group (Group 5, Fig. 4). These stations had been similar in terms of taxon composition to the other mid-eastern English Channel stations, but were now distinguished by a relatively low filter feeder biomass. This was also the case for stations between Boulogne and Dieppe, in the south-eastern English Channel.

Some homogeneity in trophic group composition was noted in the north-eastern English Channel, with stations in Group 1 exhibiting low predator biomass. However, several stations in the sector, particularly around Southampton and the Isle of Wight, showed higher predator biomass than their coastal neighbours (Group 2, Fig. 4). These stations were more similar to the mid-eastern Channel communities in terms of their trophic group composition.

Biological traits analysis

The purpose of the co-inertia analysis was to combine information on taxon distributions over the study area with information on the biological traits that they exhibited. The analysis expressed the taxon composition of each station in terms of the component taxa's

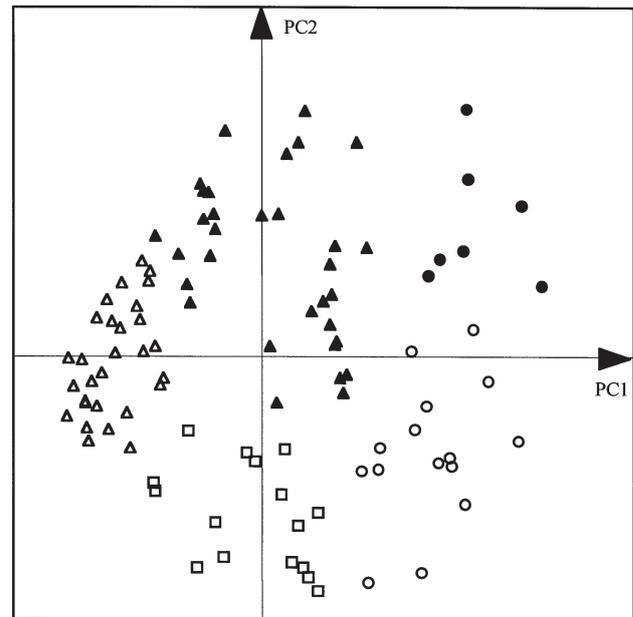


Fig. 3. First plane principal component analysis (PCA) ordination of southern North Sea and eastern English Channel benthic stations, based on the trophic group composition of macroinvertebrate communities. Stations are marked by groups identified from the cluster analysis; Δ = Group 1, \blacktriangle = Group 2, \bullet = Group 3, \circ = Group 4, \square = Group 5

biological traits, producing a table of the biomass-weighted biological trait composition of each station. Analysis of the table showed how stations varied in terms of their trait composition.

Axes 1 and 2 of the co-inertia analysis accounted for 79% of the variability in biological trait composition between the stations, with 59% of inertia projected along Axis 1 and 20% along Axis 2. The random permutation test confirmed that the distribution of biological traits between stations was not random (estimated $p < 0.05$). The cluster analysis identified 5 station groups. Groups 1 and 2 separated from the others along Axis 1 of the ordination and Groups 4 and 5 showed some distinction along the second axis (Fig. 5).

The traits with the greatest influence on variability between groups of stations were identified by plotting the individual co-inertia scores for each trait category (Fig. 6). Traits contributing to the variation along Axis 1 were attachment, flexibility and body form, with Groups 1 and 2 being characterised by permanently attached organisms, highly flexible organisms and those of erect stature (Fig. 6e,g,h). Groups separating along Axis 2 were differentiated by a number of traits: mobility, flexibility, body form, feeding habit and adult life habit. Groups 4 and 5 were characterised by high biomass of very flexible organisms, those that were flat and those of medium mobility (Fig. 6d,g,h). They also had relatively

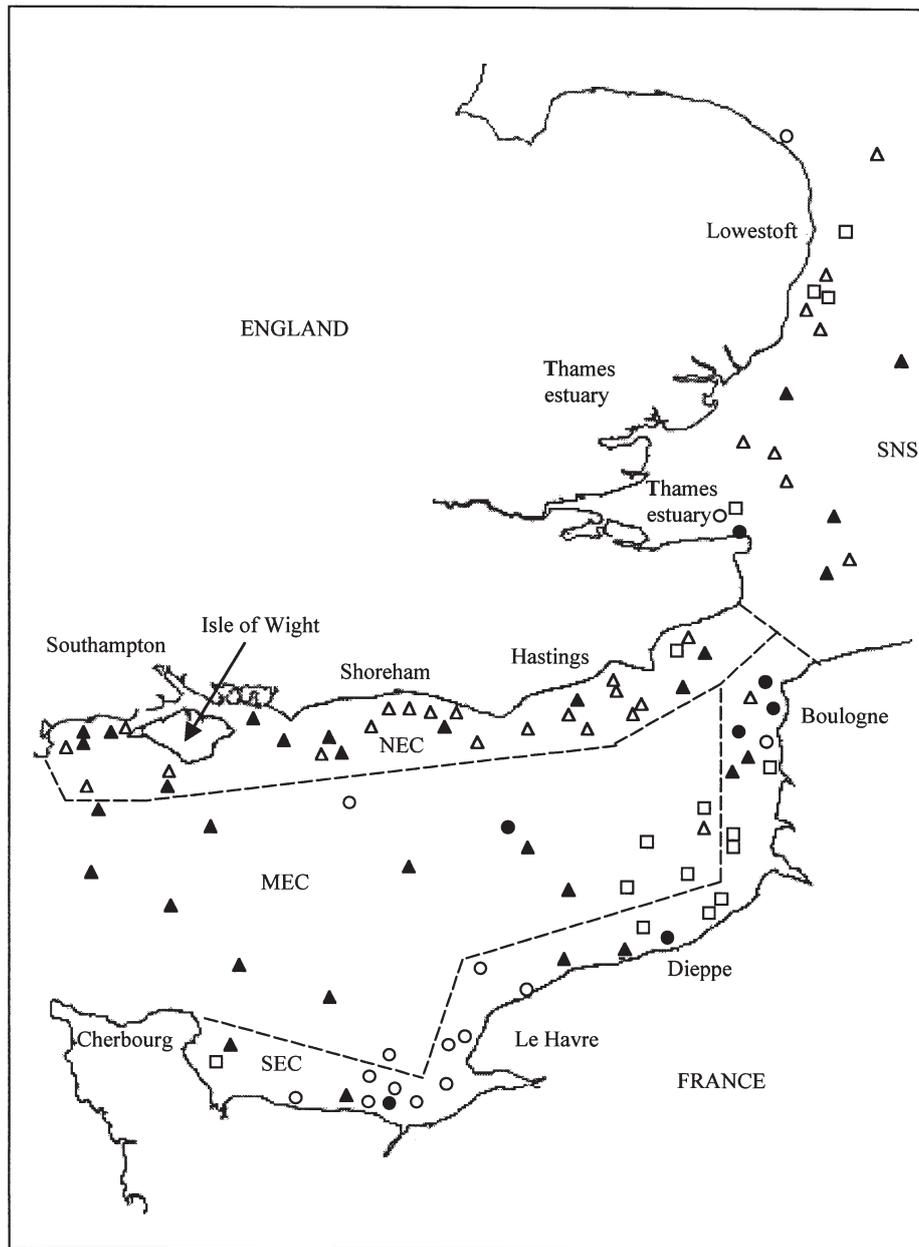


Fig. 4. Assemblage types present in the eastern English Channel and southern North Sea, based on trophic-group composition of benthic invertebrate communities (assemblage types as shown in Fig. 3; Δ = Group 1, \blacktriangle = Group 2, \bullet = Group 3, \circ = Group 4 and \square = Group 5). Sector codes are as follows: SNS = southern North Sea, NEC = north-eastern English Channel, MEC = mid-eastern English Channel, SEC = south-eastern English Channel (after Ellis & Rogers 2000)

higher biomass than other stations of organisms that swam, crawled or dwelled in crevices and those that were predators or opportunists/scavengers (Fig. 6f,i).

Stations grouped together differently when described by their biological trait composition rather than by their taxon or trophic group composition (Fig. 7). The distinct mid-eastern English Channel grouping highlighted by both previous analyses was no longer

evident. Several of these stations were similar in their trait structure to those around Le Havre in the south-eastern Channel (Group 4, Fig. 7). These were dominated by flexible, flat, moderately mobile predators or scavengers that were swimming, crawling or crevice-dwelling.

In the north-eastern English channel, $\frac{2}{3}$ of the stations were similar in their trait composition (Group 3,

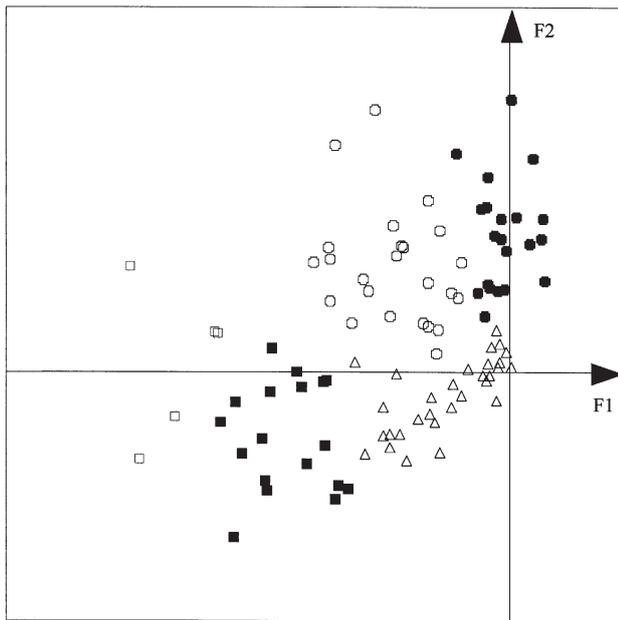


Fig. 5. First plane co-inertia ordination of southern North Sea and eastern English Channel benthic stations, based on biological trait composition of macroinvertebrate communities. Stations are marked by groups identified from the cluster analysis; ■ = Group 1, □ = Group 2, △ = Group 3, ○ = Group 4, ● = Group 5

Fig. 7); however, stations around Hastings exhibited a variety of trait structures. A cluster of stations between Shoreham and Southampton were distinguished from those nearby by a relatively higher biomass of permanently attached, erect, flexible organisms.

In keeping with the spatial arrangement of stations described in the relative taxon composition and trophic groups analyses, areas of heterogeneous trait composition were evident in stations around Boulogne and Lowestoft. However, using the biological traits approach these heterogeneous areas were extended, south towards the Thames estuary in the southern North Sea and southwest to Dieppe in the south-eastern English Channel.

Comparison of approaches

There was little difference between the approaches in their ability to identify assemblage types over the whole region, with each approach identifying 5 different types of assemblage at

a distance of 0.5 (50%). Within each geographic sector, assemblage types were more evenly distributed when defined by biological traits than by relative taxon composition or trophic groups (Fig. 8), but only in the north-eastern English Channel were relatively more community types identified by the biological traits approach than by both of the others (Table 4).

The biological traits approach provided consistently more spatial heterogeneity than the relative taxon composition approach. Within each sector, the number of stations differing from the modal community type increased between the relative taxon composition and biological traits analyses, as did the number of stations differing from their nearest neighbour in the north-eastern, mid-eastern and south-eastern Channel (Table 4).

When the biological traits approach was compared to the trophic group approach, there was an increase in the number of stations differing from their nearest neighbours in the southern North Sea, mid-eastern and south-eastern English Channel (Table 4). The number of stations differing from the modal assemblage type increased between the 2 approaches in the southern North Sea and mid-eastern English Channel. Within the north-eastern English Channel, however, the number of stations differing from their nearest neighbour and from the modal community type both decreased between the trophic group and biological traits analyses.

Table 4. Assemblage type and spatial heterogeneity for stations within each sector of the southern North Sea and eastern English Channel, as described by relative taxon composition, trophic group and biological trait analyses. Each approach identified 5 assemblage types, based on a distance of 50% derived from cluster analysis

	Community types present (%)	Stations differing from nearest neighbour (%)	Stations differing from modal community type (%)
Southern North Sea			
Relative taxon composition	80	73.7	47.4
Trophic group	100	68.4	57.9
Biological traits	100	73.3	68.4
North-eastern English Channel			
Relative taxon composition	40	3.1	3.1
Trophic group	60	50.0	40.6
Biological traits	80	28.1	34.4
Mid-eastern English Channel			
Relative taxon composition	60	53.0	29.4
Trophic group	100	47.1	47.1
Biological traits	60	58.8	52.9
South-eastern English Channel			
Relative taxon composition	100	50.0	56.7
Trophic group	100	60.0	63.3
Biological traits	100	76.7	60.0

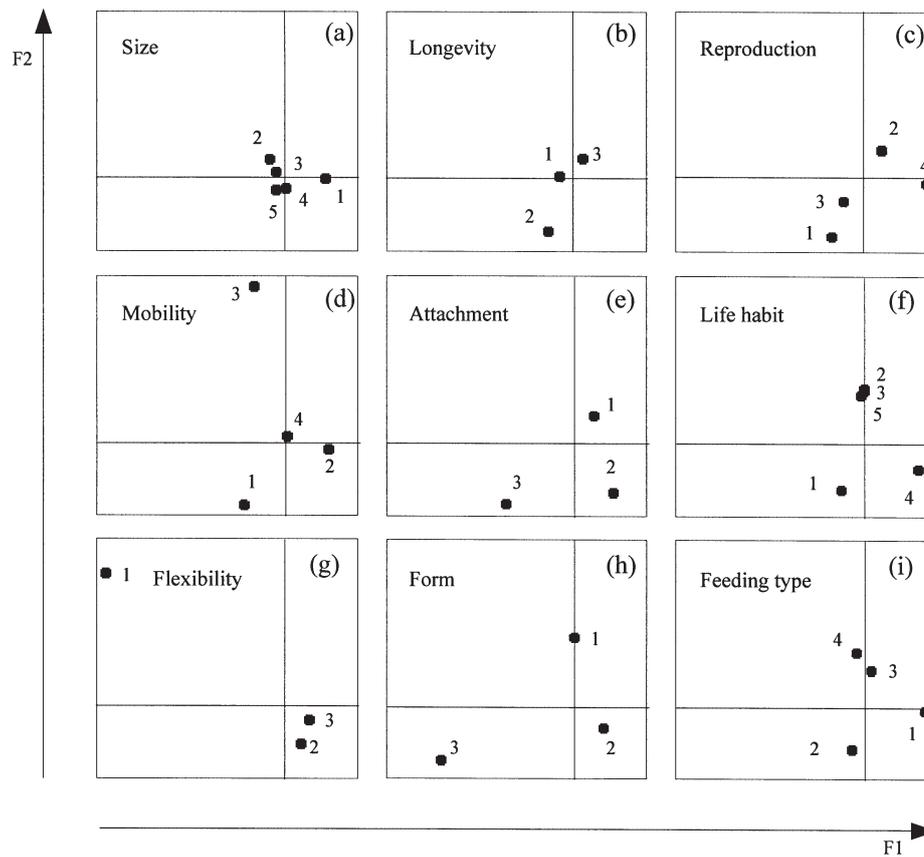


Fig. 6. Ordination of the biological trait categories from the co-inertia analysis. Trait variables are (a) individual/colony size, (b) relative adult longevity, (c) reproductive technique, (d) relative adult mobility, (e) degree of attachment, (f) adult life habit, (g) body flexibility, (h) body form and (i) feeding type. Trait categories are described in Table 2

DISCUSSION

The relative taxon composition approach aims to describe epibenthic functioning by relating changes in composition to characteristics of selected taxa. With its incorporation of information on the biological roles of all component taxa, the biological traits approach would seem to offer several advantages over relative taxon composition analysis in terms of characterising differences in the underlying structure of the epibenthic assemblages of the southern North Sea and eastern English Channel. The first 2 axes of the relative taxon composition PCA accounted for less than 50% of variance in the communities. This suggests that more than half of the variation between stations was explained by subtle differences in taxon distributions. However, around 80% of variance was accounted for in the first 2 axes of the biological traits ordination, indicating that the majority of the variability in trait structure between the communities was governed by distinct changes in a number of ecological functions. The fact that so much more of the variation between

sites was accounted for by consideration of the biological traits than taxon composition suggests that there may be general trends in ecological functioning across benthic communities that are not revealed using taxon identities alone.

Biological traits analysis also highlighted more small-scale heterogeneity than the relative taxon composition analysis, with more stations in general differing from their nearest neighbour and an increase in functional diversity, both in terms of community-type richness and 'evenness' (stations differing from the modal community type).

There was some evidence of a geographical gradient in relative taxon composition within the region, with a high degree of similarity in the north-eastern English Channel and the southern North Sea, but differences between these sectors and the mid-eastern and south-eastern English Channel. Other studies have identified geographical variation in both fish (Rogers et al. 1998) and invertebrate (Holme 1961, 1966, Dyer et al. 1982) taxon composition in the North Sea and English Channel, linked to large-scale processes such as tidal action,

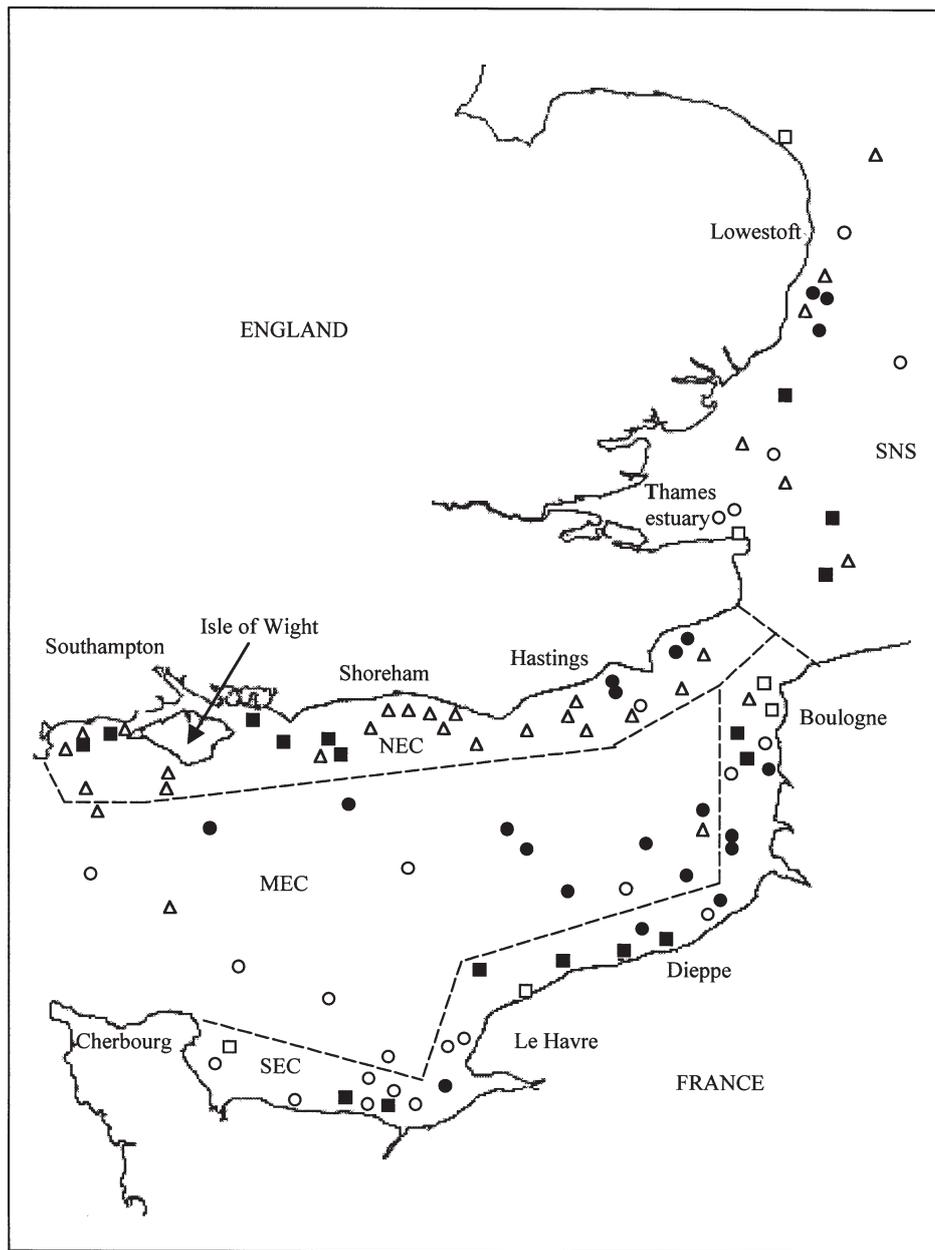


Fig. 7. Assemblage types present in the eastern English Channel and southern North Sea, based on the biological trait structure of benthic invertebrate communities (assemblage types as shown in Fig. 5; ■ = Group 1, □ = Group 2, △ = Group 3, ○ = Group 4 and ● = Group 5). Sector codes are as follows: SNS = southern North Sea, NEC = north-eastern English Channel, MEC = mid-eastern English Channel, SEC = south-eastern English Channel (after Ellis & Rogers 2000)

sand transport, circulation patterns and temperature gradients (Dyer et al. 1983, Sanvicente-Anorve et al. 1996).

The role of smaller-scale factors such as substrate type and seabed morphology in determining differences in taxon composition of communities is not certain. Some authors have identified a relationship (Ford 1923, Brown et al. 2002, Sanvicente-Anorve et al. 2002)

but others argue that it is not universal (Seiderer & Newell 1999, Newell et al. 2001). Recent evidence suggests that species' distributions are influenced by habitat on a small scale; however, the relationship is complex and incorporates multiple factors (Freeman & Rogers in press). The lack of geographical gradients and the increase in local heterogeneity in biological trait structure suggest that ecological functioning is

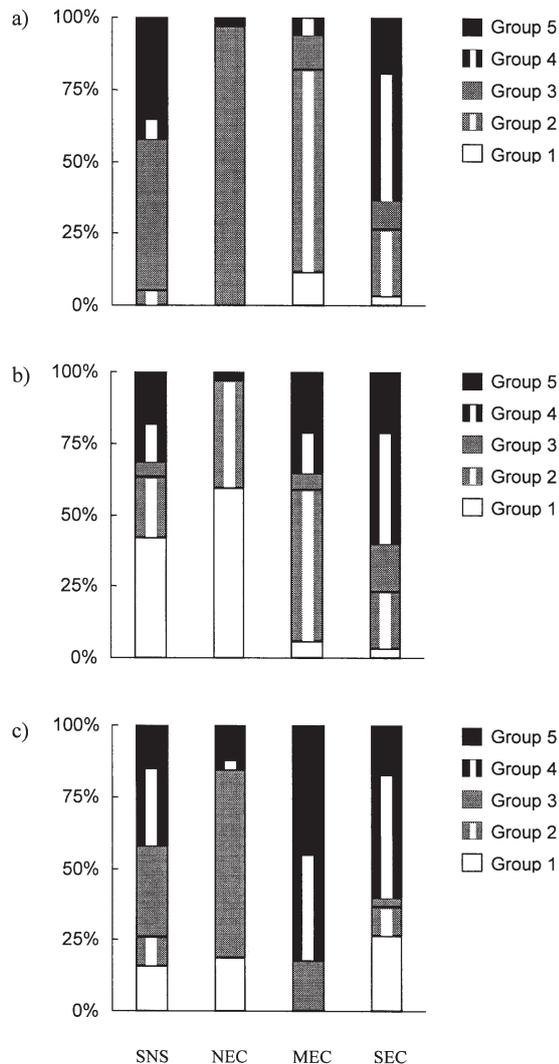


Fig. 8. Distribution of assemblage types in the southern North Sea and eastern English Channel, based on (a) relative taxon composition, (b) trophic group composition and (c) biological trait composition. Sectors are as follows: SNS = southern North Sea, NEC = north-eastern English Channel, MEC = mid-eastern English Channel, SEC = south-eastern English Channel

driven primarily by small, local-scale differences in environmental conditions and that it is robust in the face of large-scale geographical influences. In addition to providing information on the scales of organism-environment relationships, this makes traits analysis potentially useful for investigations of trends in ecosystem functioning on large scales that are not practical using relative taxon composition analysis.

Any analysis of multi-species data sets using advanced statistical techniques will always be prone to 2 confounding factors. Firstly, the mathematical techniques used will always introduce some level of bias and different approaches will bring different distur-

tions to the output. Secondly, ecological effects, whether they are natural (e.g. geographic gradients, salinity clines) or anthropogenic in origin are likely to operate on a continuum and so multivariate analyses must often distinguish gradients rather than discrete changes. The 3 approaches are increasingly explicit in their incorporation of information on functioning. The consistency in the direction of change between the approaches, particularly the dampening of the biogeographic gradient and the increase in functional diversity, leads to the conclusion that the results presented here do have real ecological significance and are not just artefacts of the statistics used.

Freshwater studies have shown that biological trait composition is more stable than taxonomic composition in semi-natural systems (Charvet et al. 2000), but this functional composition is affected by human impacts (Doledec et al. 1999, Charvet et al. 2000). The benthos of the North Sea and English Channel are subject to several types of human disturbance, including fishing (Rijnsdorp et al. 1991, 1998), mineral extraction (Desprez 2000, van Dalfsen et al. 2000, ICES 2001) and pollutants/contaminants (Jones & Franklin 2000), the distribution of which are patchy and localised in nature. Local differences in the severity of these impacts may well have an influence on the biological traits expressed in communities, leading to functional differences between neighbouring assemblages.

It is difficult to say whether the observed differences in trait structure are influenced by human impacts. Resistance/resilience traits that may increase in impacted systems, e.g. mobility and avoidance mechanisms, robustness and opportunistic life history tactics (Frid et al. 2000a, Bradshaw et al. 2002), are not necessarily excluded from stable or unimpacted communities (Townsend et al. 1997). Investigating changes in the relative proportions of biological traits over time may provide the only reliable means to identify impact-driven alterations to ecological functioning.

Some of the traits linked to resistance/resilience were important in differentiating communities. Groups 4 and 5 were distinguished by high biomass of moderately mobile, flexible animals that swam or crawled. However, most of the differences between stations were accounted for by traits associated with structure-forming organisms, i.e. permanent attachment and erect stature. Changes in the proportions of these organisms have been linked to fishing (Auster et al. 1996), but in the present study insufficient information on fishing effort was available to investigate this link. Kaiser et al. (1999) linked the occurrence of sessile, structure-forming fauna to water depth, and stations characterised by permanently attached organisms did appear limited to shallow, coastal areas of the study (Fig. 7).

Feeding interactions have been promoted as the most important factor structuring invertebrate communities (Pearson & Rosenberg 1987), and organisms' feeding mechanisms can dictate their response to impacts such as fishing (Rumohr & Kujawski 2000, Chicharo et al. 2002). In this respect, trophic analysis should be useful in differentiating communities in the region. However, the low range of feeding types encountered in the study, combined with the recent suggestion that trophic interactions are not always altered in impacted systems (Ramsay et al. 1996, 1998, Jennings et al. 2001), casts doubt on the usefulness of the trophic group approach in monitoring human impacts. Traits analysis showed that feeding mechanisms were influential in determining differences between the communities, but they were less important than attachment, body form and mobility.

Body size has also been implicated in community structure in impacted systems (Jennings et al. 1999, Kaiser et al. 2000). It is perhaps surprising that body size does not appear to be an important factor in differentiating these communities (but see Frid et al. 2000a). Usseglio-Polatera et al. (2000a) found that 2 traits connected to species' life cycles (life duration and aquatic stages), which were thought *a priori* to be important in generating differences between groups of benthic invertebrates, were in fact relatively unimportant. It seems that a whole range of biological traits, not just those currently viewed as important, contribute to variation in benthic communities.

In this respect, biological traits analysis is more useful than the relative taxon composition and trophic group approaches. Relative taxon composition can only address functioning indirectly and to a limited extent. A restricted number of characteristics (commonly feeding preferences and body size) are chosen to interpret changes in taxon biomass, the characteristics are only applied post-analysis and only on selected taxa. So although the approach includes a degree of information on ecological characteristics, the method is subjective and only ever allows a superficial insight into the functioning of the system. The trophic group approach incorporates biological characteristics into the initial phase of the analysis, but because they focus only on feeding interactions, they have limited potential to capture functioning in the epibenthic system. The important point about biological traits analysis is that it is an objective measure of functional diversity, directly incorporating into the analysis information on a range of ecological characteristics exhibited by the full complement of taxa.

It is interesting to note that the species replacements do not always lead to changes in ecological functioning. Stations around Le Havre, characterised by high biomass of *Asterias rubens*, differed in relative taxon

composition from those in the mid-channel. However, they were quite similar in terms of their biological trait structure. In this area, other organisms were fulfilling the same functions as *A. rubens*. Ecological functioning persisted even when the species composition had altered. This consistency of functional structure will have consequences for ecosystem monitoring, management and conservation where geographical gradients in taxonomic composition make these difficult on a large scale. The present study addressed only one component of marine benthic ecosystems: the large epifauna. The usefulness of the approach in this respect highlights its potential for providing insights into functioning of other system components, such as infauna (Bremner et al. 2003) and perhaps, in future, of the marine benthic ecosystem as a whole.

Biological traits analysis provides more information on the ecological functions performed by organisms in marine benthic communities than both the relative taxon composition, relative composition and trophic group approaches. Biological trait structure is less affected by the large-scale geographic influences that hamper studies of relative taxon composition and is linked more to small, local-scale environmental conditions. It provides a robust method for studying ecological functions of benthic systems that has the potential to be applied at both local and international scales.

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