Environmental and sediment conditions, infaunal benthic communities and biodiversity in the Celtic Sea

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ABSTRACT

While it is recognised that the nature of the sediment is a major driver of benthic macro-infaunal community structure, it is also true that diverse environmental factors determine the distribution and composition of sediments. Among those factors are depth, tidal stress and seasonal stratification of the water column. In the Celtic Sea an area of seabed approximately 20 km wide and 125 km long was selected in which variation in water depth, stratification, primary production and current velocity were minimised, but which contained sediments ranging from fine muds to coarse gravelly sands. 55 stations were sampled across the area using a box-corer. At each station a comprehensive suite of sediment and biogeochemical measurements were made. Macrofauna were identified and weighed. Of the stations sampled, four had been chosen as focal sites for a study of relationships between benthic biogeochemistry and sediment type. Relationships between variation in environmental and sediment variables and macrofaunal community structure were analysed using a range of non-parametric multivariate techniques. Environmental variables were discriminated into situational variables that broadly encapsulate potential drivers of spatial heterogeneity in the benthos such as depth and fishing effort, and *in-situ* variables that were measured at each site concurrently with the sampling of the macrobenthos, such as sediment properties and biogeochemical measurements. Among the former, analyses tended to identify the importance of average shear stress and depth in explaining observed variation in benthic community structure, even though the area had been chosen to minimise variation in those factors. Analyses using *in-situ* measurements of sedimentary conditions at each site identified very fine sand content (correlated with average shear stress) as the most important explanatory variable. Most of the measured biogeochemical variables varied with sediment structure, particularly reflecting differences between finer-grained sediments with higher organic content (generally from deeper areas) and coarser sediments with lower organic content. While clear spatial heterogeneity in sediments and associated biogeochemical variables could be demonstrated, spatial variation in benthic abundance and biomass was less clear. Benthic community structure varied significantly with sediment type, but did not vary closely with the *in-situ* environmental variables measured at the same sites. This may indicate that the samples collected were too small to accurately characterise the benthic assemblage at each site, or that most species inhabiting the area inhabit a range of sediment types, or that processes which are not reflected in sediment or biogeochemical measurements are also important determinants of benthic community structure.

Key Words: Benthos . Celtic Sea . Biogeochemistry . Biodiversity . Infauna . Mapping

HIGHLIGHTS

- 55 stations were sampled in the Celtic Sea using a box corer
- Stations represented a range of environmental and sediment conditions
- Infaunal microbenthic abundance and biomass were determined
- Infaunal communities varied weakly with sediment type
- Variation in communities did not closely match measured environmental variables

1. INTRODUCTION

It is a long-held belief that one of the key determinants of marine benthic infaunal community structure is the composition of the sediment (Holme, 1966; Thorson, 1957). In continental shelf systems, sediments generally range from coarse gravels to fine silts, with most of the seabed consisting mainly of various grades of sand. The composition of sediments found at any particular location represents the end result of a complex interplay between long-term geological processes and shorter term physical (hydrodynamic) processes (Gray & Elliott, 2009). Along the shelf, a gradient in sediment composition is often found from coarse gravels, where tidal and wave energies are high, to fine silty sediments where levels of physical energy are low. These spatial differences in sediment compositions are thought to have concomitant effects on the infaunal species composition (Bolam et al., 2008; Rees et al., 1999; Thorson, 1957). This may reflect adaptation of species to different physicochemical environments in diverse sediment types, but may also reflect the effects of physical processes which not only move sediment particles but also distribute pelagic larvae (Gray, 1974) and the plankton which are the primary source of energy for the benthos (Snelgrove & Butman 1994). The presence and activities of the organisms themselves can modify the structure and biogeochemistry of sediments (Gray, 1974; Pearson & Rosenberg 1978; Queiros et al., 2013; Rhoads, 1974) and the selection of sediment for the settlement of larvae is governed by a combination of (often interrelated) physical, chemical and biological factors, such as the structure and contours of the surface, sediment particle size, the presence of organic and inorganic compounds, biofilms and populations of the same species (Gray, 1974).

In addition to sediment measures such as mean grain size, large-scale (> 1000 km^2) investigations of the benthos in the NE Atlantic (Ellingsen et al., 2005; Renaud et al., 2009) and around the UK (Rees et al. 1999, Bolam et al. 2010, Barrio Froján et al. 2012) have identified latitude, depth, tidal stress and stratification as correlates with large-scale community structure. These large-scale factors are obviously related to those physical factors that determine the sedimentary environment and its food supply. Wave energy, and to some extent tidal stress, decline with depth. Stratified waters tend to be deeper, especially in the North Sea, while shallower waters may remain tidally mixed. Primary production tends to be less in strongly stratified waters where nutrients can become depleted, but is also affected by complex combinations of multiple physical drivers (Holt et al., 2016). Jones (1950) concluded that the distribution of benthic communities was determined by a range of environmental conditions, and that physical factors were more influential in determining community type than biological ones, proposing a benthic community classification system based mainly on temperature, salinity, sediment type and depth. Gray (2002) concluded that environmental factors such as productivity, temperature, and sediment grain-size diversity play dominant roles in determining patterns of regional-scale benthic species richness and patterns in species turnover. The overall picture, therefore, is that the processes identified as correlates of benthic community structure at large scales are also those that play a role in determining the nature of the sediment in which the animals live.

Given the complex inter-relationships between all of the various factors which may influence the structure and diversity of infaunal assemblages, disentangling these factors using *in-situ* observational data and quantifying the relative importance of individual, or subsets, of specific environmental variables is inherently difficult. In this study, we use marine benthic invertebrate community structure data together with environmental and biogeochemical data from 55 sampling stations situated in the southern Celtic Sea to identify which physical and chemical aspects of the sediment environment could best explain the variability seen in benthic fauna across a range of sediment types. The specific survey area was selected to minimise many of the compromising environmental factors that could mask the effects of sediment type, such as water depth, stratification, primary production and current velocity, all of which were comparatively consistent in the study area (Thompson et al., 2017). The sediment in the survey area covered a broad range of sediment types from coarse sand with varying gravel components to soft muds. Within this area, four focal sites were selected for a comprehensive research programme (see Thompson et al., 2017) investigating seasonality in interactions between sediment type, biology and chemistry, results from which are presented in this volume and a previous special issue in the journal Biogeochemistry (volume 135, 2017).

The aims of this paper are to examine relationships between macrofaunal abundance, biomass and diversity and environmental variables which reflect potential drivers of spatial heterogeneity in the benthos at larger scales (here termed situational environmental variables) and the suite of measured variables collected concurrently with the macrofaunal samples (here termed *in-situ* environmental variables) over a large area of Celtic Sea selected to minimise the influence of the situational variables.

2. MATERIALS AND METHODS

2.1 Study area

Stretching to the edge of the European continental shelf, and bordered to the north by Ireland, by England and Wales to the east, and by the western extremity of Brittany to the southeast, the Celtic Sea is a low-gradient shelf sea with an area of about 130,000 km^2 (Haas et al., 2002). Although large tidal ridges are found on the mid and outer shelf, the inner shelf is almost featureless with surface sediments consisting largely of reworked mobile sediments deposited in Pleistocene and early Holocene transgressions, along with biogenic carbonate. These are mostly fine and coarse sands with lesser amounts of gravel and mud. Within this large geographic area, a smaller survey area of approximately 87 x 95 km in the Celtic Sea was identified, with minimal variation in bathymetry (average water depth 95 m below chart datum), hydrodynamic or water column properties, away from shallower coastal regions where bed stresses are higher and variable, and from freshwater inputs which could affect salinity and temperature (Thompson et al., 2017). Although restricted in spatial extent this selected area still encompassed a wide range of sediment types. Within the study area a broad transect (approximately 20 km wide with an area of approximately 2500 km^2), aligned with the major tidal flow and wave directions running from the south-west to the north-east, was defined, within which a spatial survey consisting of 55 individual stations was conducted (Fig. 1).

2.2 Situational variables

Six variables were recorded for each sampling station to encapsulate potential drivers of spatial heterogeneity in the benthos. These were latitude, longitude, water depth, average and maximum bed shear stress from the NEMO framework adapted for use on the 7 km Atlantic Margin Model (AMM7) domain (Plymouth Marine Laboratory, unpublished data), and fishing pressure as effort (h.engine power(kw).yr^{-1}), based on data from 2009-2014 (Cefas, unpublished data).

2.3 Collection, processing and identification of macrofaunal samples

Macrofauna samples were collected from 55 sites (Fig. 1) in March 2015 during cruise DY021 (https://www.bodc.ac.uk/resources/inventories/cruise_inventory/reports/dy021.pdf). Samples were taken with a 0.08 m^2 NIOZ box corer then sieved over a 1 mm mesh and preserved in 10 % buffered formaldehyde. In the laboratory, each sample was washed over a nested sieve stack of 4 mm, 2 mm and 1 mm meshes and elutriated to extract the fauna which was then transferred to 70 % industrial methanol solution (IMS). Organisms were identified to species level using a stereo microscope and abundances recorded. For each sample, the blotted wet weight of each species was measured on an electronic microbalance.

2.4 Collection of *in-situ* environmental data

Physical and chemical data were collected with the macrofauna samples. Although measurements were made in different depth horizons only measurements from the top 5 cm are used here. Oxygen penetration depth (OPD) was measured with a Clark-type oxygen microelectrode (Unisense), equipped with an internal reference and a guard cathode (Revsbech, 1989). Pore-water samples were taken from NIOZ cores at 1 cm sediment-depth intervals. From each sediment slice approximately 10 ml of water was extracted using a vacuum motor, syringe filtered (0.2 µm) and analysed for nutrients using a micro-molar segmented flow auto-analyser. Nutrient data were pooled, and the mean and maximum measurements for the top 5 cm of nitrite (NO_2), nitrate (NO_3), oxidised nitrogen (NO_2+NO_3 = NO_X), phosphate (PO_4), silicate (SiO_4) and ammonium (NH_4) are used in this study. Sub cores were taken from the NIOZ cores using a 5 cm diameter perspex tube for particle size analysis (PSA), organic carbon and nitrogen, porosity, chlorophyll a and phaeopigment measurements. PSA was conducted following the NMBAQC method (Mason, 2011) and graphical methods were used to determine a range of sediment parameters including median, mean, standard deviation, skewness and kurtosis. For organic carbon and nitrogen (OC, ON) measurements the method of Kirsten (1979) was used. Sediment was freeze-dried, ground and analysed using a Carlo Erba EA1108 Elemental analyser.

2.5 Statistical analyses

Abundance, biomass and environmental data (Somerfield et al., 2018) were analysed using a range of univariate, graphical and multivariate approaches (Clarke et al., 2014), primarily using PRIMER v7 (Clarke & Gorley, 2016). Where appropriate, environmental variables (generally those representing concentrations) were log transformed to reduce the effect of outliers, and normalised by subtracting the mean and dividing by the standard deviation. The correlation structure among variables was analysed using a combination of clustering and Type 3 similarity profiles (SIMPROF) analysis (Somerfield & Clarke, 2013), testing the hypothesis that groups of variables identified by the clustering algorithm are coherent (varying in the same way across samples). Resemblances among sites were calculated using Euclidean distance and tested for multivariate structure using clustering and Type 1 SIMPROF (Clarke et al., 2008). Relationships among samples were ordinated using metric multidimensional scaling (Clarke et al., 2014). Biotic (abundance and biomass) data were analysed in their raw form (to focus on patterns in numerical and biomass dominants) and following a fourth-root transformation. Resemblances among samples were calculated using the Bray-Curtis similarity measure, tested for structure using SIMPROF and ordinated using nonmetric MDS. Relationships between biotic similarities and environmental variables were analysed using a non-parametric

Mantel test (RELATE) which tests a hypothsis of 'no relationship' between resemblance matrices (Somerfield & Gage, 2000), the biota-environment matching (BIO-ENV) routine which searches for a subset of predictor variables that most closely matches a target resemblance matrix, where the closest match is defined as the highest rank correlation which is then tested using an appropriate permutation test (Clarke et al., 2008), and analysis of similarities (ANOSIM) tests (Clarke et al., 2014) which test a hypothesis of 'no difference among (predefined) groups of samples (Clarke, 1993). Taxa contributing to differences among groups of samples were examined with similarities percentages (SIMPER) analysis (Clarke, 1993).

Univariate measures of community structure were calculated for each sample. These were species richness (S), total abundance (N), Margalef's d, Pielou's J', Shannon (H'), Simpson ($1-\lambda'$), taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), total biomass (B), biomass diversity (as Pielou's J', Shannon (H'), Simpson ($1-\lambda$)) and the Warwick statistic (W), a measure of the difference in abundance and biomass profiles within each sample (Clarke et al., 2014). N and B were log transformed prior to analysis. Univariate measures were included in correlation analyses with environmental variables. Normalised values were used to construct a Euclidean distance matrix representing variation in multivariate diversity, and this resemblance matrix was subjected to many of the analyses applied to the biotic resemblance matrices described above (e.g. nMDS, RELATE, ANOSIM, BIO-ENV).

3. RESULTS

3.1 Environmental variables

Analysis of the correlations among variables (Fig. 2) with hierarchical agglomerative clustering of Pearson correlations and Type 3 SIMPROF analysis showed that many variables are intercorrelated, many of them significantly so. Group A, longitude and latitude, reflects the overall gradient from north-east to south-west. No other variables group significantly with these positional variables, although those that are closest include fishing pressure (Group E), nitrite (Group M) and kurtosis (Group I). Weakly, but positively, correlated with these variables are depth (Group B) and the C:N ratio of the sediment (Group J) which do not covary significantly with other variables, but are most closely grouped with a group of covarying variables (Group H) which includes organic carbon and nitrogen, porosity, mud content, median and graphical mean particle diameter, and the significantly intercorrelated variables chlorophyll a and phaeopigments (Group K). Average bed-stress and very fine sand content covary significantly (Group C), as do silicate and ammonium (Group O), and these form a group with phosphate which correlates ($\rho > 0.5$) with depth and the other associated variables. The overall picture, therefore, is one of variation in depth and mud-content, with associated measures. Variables that are negatively correlated with those already mentioned include a significantly intercorrelated set of variables (Group G) that includes coarse sand, medium sand, total sand content and skewness. Oxygen penetration depth (Group L) is most closely associated with this group, followed by the covarying nitrate and total oxidised nitrogen (NO_X, Group N), and then by the significantly covarying very coarse sand and gravel content (Group F). A third group of covarying variables (Group D) consists of fine sand, maximum stress, and the inclusive graphical standard deviation of the sediment.

Variables can be discriminated into situational variables that give information about the sites (latitude, longitude, depth, average stress, maximum stress, fishing pressure) and *in-situ* variables that are derived from sampling at the site (the rest). It is notable that between these groups only average shear stress and very fine sand content covary significantly.

Hierarchical agglomerative clustering with Type 1 SIMPROF analysis (9999 permutations, $p < 0.001$) based on those variables that are derived from sites shows that samples fall into 10 groups (Fig. 3), ranging from muddy sediments (Group i) to coarse gravelly sediments (Group j). In between, with significant internal heterogeneity, are sediments which are predominantly sand with variable mud content. For further analysis samples were grouped into fine (groups h and i), medium (groups c – g), coarse (groups a and b) and very coarse (group j) sediment types.

3.2 Relationships with infaunal community structure

3402 individuals belonging to 322 taxa were identified, with an average of 61.9 individuals and 26.3 species in each 0.08 m^2 sample. The average biomass in each sample was 0.8 g.

To examine which variables or groups of variables may be important determinants of benthic community structure a series of analyses were conducted (Table 1) using Bray-Curtis similarity matrices derived from raw and fourth-root transformed abundance and biomass data. These were a non-parametric Mantel test (RELATE) with a Euclidean distance matrix representing differences in sample location (a test of spatial autocorrelation), a full-subset (BIO-ENV) search with a subsequent significance test for the most closely matching subset of situational variables, and another for the most closely matching subset of measured in-situ variables, and finally an analysis of similarities (ANOSIM) test for differences among sediment groups. For the BIO-ENV tests with *in-situ* variables one variable from each correlated group was chosen (Table 3), to act as a proxy for all group members. This is because adding correlated variables does not add information, and the all-subsets search rapidly becomes prohibitive if there are too many variables. All tests were significant (Table 1), the majority highly so ($p<0.001$).

Among the situational (environmental) variables, a combination of average and maximum shear stress and depth most closely matched patterns in raw and transformed abundances and transformed biomass (Table 2). Variation in raw biomass was less closely linked to variation in the situational variables, with longitude replacing maximum shear stress in the best subset. For BIO-ENV analyses linking the *in-situ* variables to biotic resemblance matrices a subset of measured variables were selected (Table 3) to act as proxies for variable groups identified in the Type 3 SIMPROF analysis (Fig. 2). Among the measured variables (Table 3), the subsets of variables best explaining variation in benthic community structure all contained very fine sand content (correlated with average shear stress), median particle diameter (correlated with mud content, mean particle diameter, organic carbon and nitrogen and porosity), skewness (correlated with total, coarse and medium sand content) and kurtosis. For raw and transformed abundance, and transformed biomass, chlorophyll a (correlated with phaeopigments) and phosphate were included, while for raw and transformed abundance the inclusive graphical standard deviation was included. For both abundance and biomass NO_X (correlated with NO_3) was included in the subsets explaining raw values, but replaced by oxygen penetration depth in subsets explaining transformed values. The only other variable included was the C:N ratio, in the subset best explaining variation in raw biomass. The single variable giving the highest rank correlation with inter-sample similarities in each case was median particle diameter.

Nonmetric MDS ordinations of the inter-sample Bray-Curtis similarities calculated from fourth-root transformed abundance (Fig. 3A) and biomass (Fig. 4A) show that both indicate a gradient in community structure related to sediment type. The stress of these ordinations is high (>0.2) so the fine detail should not be interpreted, but the Shepard diagrams (not shown) indicate broad agreement between the plots and the underlying data. While ANOSIM (Table 1) confirms these differences among sediment types, analyses using the same methods and criteria applied to the sedimentary variables (hierarchical agglomerative clustering with Type 1 SIMPROF with 9999 permutations and a significance level of 0.001) shows that while there is significant heterogeneity among groups of samples, these groups do not map onto those identified in the sediment analyses. Overlaying these groupings on the same ordination plots indicate that, in terms of abundance and excepting some outliers, samples fall into one of three groups along a gradient broadly related to sediment type (Fig. 3B), while in terms of biomass most samples fall into one highly variable group, with the rest representing samples from the coarser sediments (Fig. 4B).

Similarities percentages (SIMPER) analysis based on raw abundances identify the numerical dominants (contributing up to 25 % of average within-group similarity) in fine sediments as the polychaetes *Abyssinoe hibernica* and *Mediomastus fragilis*, in medium sediments as the polychaete *Magelona minuta* and juveniles of the ophiuroid *Amphiura*, in coarse sediments as juvenile *Amphiura* alone and in very coarse sediments as juvenile *Amphiura* and the small echinoid *Echinocyamus pusillus*. Analysis of fourth-root transformed abundances adds nemerteans in medium sediments, the polychaete *Ampharete falcata* and the bivalve *Abra nitida* in coarse sedments and swaps the capitellid polychaete *Notomastus* sp. for *E. pusillus* in very coarse sediments. Biomass dominants are *Abyssinoe hibernica* and the capitellid polychaete *Dasybranchus* sp. in fine sediments, the burrowing shrimp *Callianassa subterranea*, *Notomastus* sp. and the polychaete *Nephtys hystricus* in medium sediments, the burrowing anemone *Edwarsia claparedii*, ophiuroid *Amphiura filiformis* and *Notomastus* sp. in coarse sediments and also in very coarse sediments, but contributions are highly varable and within-group similarities are low (< 10), reflecting major contributions from small numbers of large individuals. Analysis of transformed biomass also reflects highly variable contributions. On the transformed scale *Abra nitida* replaces *Dasybranchus* sp. in fine sediments, a completely different group of taxa (Nemertea, juvenile *Amphiura*, *Abra nitida* and the polychaete *Amphictene auricoma*) characterises medium sediments and another characterises coarse sediments (juvenile *Amphiura*, *Abra nitida*, the polychaete *Ampharete falcata*) while in very coarse sediments juvenile *Amphiura* are added as an important contributor. The overall pattern is of variable contributions from a number of taxa, with a great deal of overlap in taxonomic composition between sediment groups.

While the four focal sites (A, H, I, G) chosen to represent the range of sedimentary and biological conditions on the UK shelf fall into different groups defined on the basis of sediment type and chemical measurements (Figure 2), in terms of community structure based on abundance site A, representing fine sediments, and I, one of two sites representing medium sand, group together (Fig. 3). Site H does represent intermediate conditions, and site G groups with the coarser sites. In terms of biomass (Figure 4), however, all sites fall within one group.

3.3 Relationships with diversity

A correlation analysis (using absolute Pearson correlation) showed that none of the univariate measures of community structure was closely correlated with any of the situational or measured variables. To encapsulate variation in diversity among samples a normalised Euclidean distance matrix was created using values of the full range of univariate measures calculated, which was then subject to the same range of tests applied to the Bray-Curtis similarities among samples (Tables 2 and 3). Relationships with diversity were generally weaker and less significant. The subset of situational variables most closely matching variation in diversity included depth and fishing pressure, and the subset of measured variables included median grain size, inclusive graphical standard deviation, skewness, kurtosis, nitrite and NO_X. Notably, the subsets did not include average shear stress or very fine sand content.

4. DISCUSSION

A range of different analyses were used to explore relationships between variation in infaunal community structure (abundance and biomass) and variables reflecting environmental heterogeneity. Each analysis tests a specific hypothesis, and those hypotheses need not be mutually exclusive. Significant RELATE tests with a matrix representing distances among samples indicate that benthic communities are spatially autocorrelated, with a tendency for the assemblage in one sample to be more similar to those in samples collected close by than to those in samples collected further away. This could simply reflect the fact that there is spatial autocorrelation among the driving variables, and as a consequence, among sedimentary measures. BIO-ENV analyses using potential driving variables tended to identify the importance of average stress and depth, while analyses using measurements of conditions at each site identified very fine sand content (correlated with average stress) and those related to sediment type, especially those separating finer sediments from coarser ones. ANOSIM analyses test whether the communities in groups of samples determined by their sediment differ, confirming that they do. These findings reflect the fact that environmental conditions in the sediment are ultimately driven by hydrodynamics of the area, for example high wave and current activity increase homogeneity of grain sizes in the sediment (Gray & Elliott, 2009). Other environmental parameters also reflect, directly or indirectly, the hydrodynamic regime. Particle size and the sorting of the sediment influence the porosity and permeability, which in turn affect oxygen content and sediment chemistry. Thus, the hydrodynamic nature of the region determines the sediment type which is linked to the chemical nature of the site. Given these facts, it is unsurprising that sites chosen as representative of different sediment conditions, but otherwise similar, turn out to have differing hydrodynamic conditions as a result of, sometimes subtle, differences in depth and bed stress.

Among the situational variables which reflect potential drivers of spatial differences in the distribution of infaunal communities are average bed shear stress and depth, despite the area being chosen specifically to minimise such variation. Groups of *in-situ* measured variables were intercorrelated, and few clear patterns were found. The clearest set of relationships show that the main differences among groups of samples result from differences between finer and coarser sediments, or from differences in the chemistry of coarse and fine sediments. The importance to biotic community structure of variation in the very fine sand content of the sediment, and the correlation of this with average bed stress, reflects that fact that particles of about 0.18 mm are the easiest to move (Gray & Elliott, 2009). Coarser particles are more difficult for currents to mobilise, whereas particles finer than 0.18 mm tend to pack into a smooth surface making them difficult to resuspend. Sediments made up largely of fine sand should be the most stable, as they can only occur when current or wave disturbance are minimal (Gray & Elliott, 2009).

Four focal sites were chosen to represent the range of sediments found on the Celtic Sea continental shelf (Thompson et al., 2017). While the sites fall within expected groups of samples defined on the basis of sediment measures, their distinctiveness in terms of biological community structure is less clear. Partially reflecting the weak relationships between infaunal community structure, sediment and chemical measures and community structure (as determined by species' abundances) site A, which represents fine sediments, groups with site I (representing medium sand). In a comparable analysis based on biomass, all four focal sites fall within a single biotically-defined group. Thus, the biota inhabiting different sediments in the study area do not seem to discriminate amongst sites as much as anticipated. Although some species appear to be limited to certain sediment types, such as the small urchin *Echinocyamus pusillus* which only tends to occur in coarse sediments, there is a high degree of taxonomic overlap among samples from different grades of sediment with some taxa, such as *Abra nitida*, frequently occurring in all of them. Analyses suggest that those species which tend to dominate the biomass at each site are highly variable, while the numerical dominants differ, to some extent, between different sediments. Thus, the strength of the relationship between infaunal assemblage structure and sediment composition depends on whether assessments are biomass- or abundance-based.

Communities in sediments with significantly different environmental conditions are similar, and although there is a gradient in community structure from fine to very coarse sediments there is also a great deal of overlap. This could reflect the fact that the single samples taken from each site insufficiently characterise the community present or differences in communities between sites. This observation also supports the notion that other non-sediment related processes operating at a range of spatial and temporal scales determine which species may be found at any location. Of note are the processes that determine larval production, transport, settlement and survival, which were highlighted as being important in the classic reviews of relationships between sediment and biota (e.g. Gray, 1974; Rhoads, 1974; Thorson, 1957). Most of the species inhabiting the sediments in the study area produce pelagic larvae, and larvae produced within the area can potentially reach and settle elsewhere within the area. How individuals arrive, colonise and survive in different sediments is poorly understood. Despite the apparent importance of larval biology to understanding distributions it has not been the focus of research that perhaps it should be. Other factors operate at larger scales, such as those determining regional and biogeographic differences. Barrio-Froján et al. (2012) concluded that relationships between patterns in benthic macrofaunal assemblages and the physical conditions that shape them at broad spatial scales are complex and interconnected, but that similar faunal assemblages occurred wherever the same environmental conditions were present on the UK shelf. They concluded that no single variable can be used to predict richness or diversity, but three together (depth, stratification and kurtosis) could possibly be used to infer relative diversity, and the species contributing to that diversity in different regions. Operating at a relatively large spatial scale, their study grouped samples from large parts of the Celtic Sea together as being similar in terms of species composition. Within a comparatively small part of the Celtic Sea in which stratification is relatively constant, the results from the present study suggest that depth and kurtosis (along with several other measures) are important correlates of faunal community structure. Predicting community structure from environmental information to extrapolate broad-scale patterns from limited sampling (a general problem in sublittoral studies), for “habitat” or “biotope” mapping, predicting functioning or studying changes in response to long-term variations such as climate change, is a common approach (e.g. Dutertre et al., 2013; McBreen et al., 2008; McArthur et al., 2010). However, in addition to potential flaws in the ecological thinking underpinning some such approaches (Warwick & Somerfield, 2015) the present study supports many of the conclusions in the review by McArthur et al. (2010), suggesting that the complexity of inter-relationships among variables, a reliance on samplers which only collect small samples of one component of the benthic community to ground-truth larger-scale remotely-sensed maps, and the lack of information about important processes, mean that the use of environmental information to meaningfully predict benthic community structure remains problematic.

In a review of species richness in marine benthic communities, Gray (2002) concluded that available food resources probably control population densities at a variety of scales and set the maximum range of species richness, but that variability in species richness for a given resource level is determined by spatial and temporal heterogeneity in sediment structure caused by both biological activities and by hydrodynamical and geomorphological factors. As with larval supply, recruitment and survival, genuine information about food supply is lacking among the variables used in this study. It may be inferred that chlorophyll, phaeopigments and organic carbon in the sediments provide some relevant information, but these measured variables probably reflect unconsumed food rather than estimating the amount available. No single univariate measure of diversity correlated closely with the situational or measured variables. That being said, regarding diversity as a multivariate concept there is evidence that it varies with environmental factors in a similar, if weaker, fashion to community structure defined by abundance, that variation being weakly influenced by sediment conditions and the processes that drive variation in them. Of course, the two approaches are not entirely independent, as total abundance and biomass (both log transformed) are included in the multivariate diversity matrix.

Finally, for all the interest in the relationships between macrofaunal community structure and sediment biogeochemistry, there is little evidence that, at the scales of this investigation, the relationships are particularly strong. Most of the measured biogeochemical variables varied with sediment structure, particularly reflecting differences between finer-grained sediments with higher organic content (generally from deeper areas) and coarser sediments with lower organic content. While clear spatial heterogeneity in sediments and associated biogeochemical variables could be demonstrated, spatial variation in benthic abundance and biomass was less clear.

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Table 1. Summary results of tests for relationships between biotic and environmental variables. Resemblance: the biotic Bray-Curtis similarity matrix used for the test derived from raw or fourth-root transformed (*) data, or a normalised Euclidean distance matrix calculated from a range of diversity measures; Lat/Long: RELATE test with positional variables (Spearman's ρ and p); Situational: BIO-ENV with the 6 situational variables (maximum Spearman's ρ and p); In-situ: BIO-ENV with the measured sediment variables (maximum Spearman's ρ and p, see Table 2 for detail); ANOSIM: Global test for differences between sediment groups (Global *R* statistic and p).

Resemblance	Lat/Long	p	Situational	p	*In-situ*	p	ANOSIM	p
Abundance	0.248	<0.001	0.411	<0.001	0.498	<0.001	0.478	<0.001
Abundance*	0.180	<0.001	0.357	<0.001	0.496	<0.001	0.505	<0.001
Biomass	0.125	0.002	0.174	0.032	0.287	0.003	0.250	<0.001
Biomass*	0.173	<0.001	0.303	<0.001	0.453	<0.001	0.479	<0.001
Diversity	0.065	0.022	0.273	0.002	0.254	0.049	0.089	0.068

Table 2. Summary of BIO-ENV analyses with the situational variables. Those variables within the subset best explaining variation in each of the resemblance matrices (Ab: Bray-Curtis, raw abundances; Ab*: Bray-Curtis, fourth-root transformed abundances; Bm: Bray-Curtis, raw biomasses; Bm*: Bray-Curtis, fourth-root transformed biomasses; Div: normalised Euclidean distance, univariate measures of community structure) denoted by x.

Situational variables	Ab	Ab*	Bm	Bm*	Div
Latitude					
Longitude			x		
Depth	x	x	x	x	x
Average shear stress	x	x	x	x	
Maximum shear stress	x	x		x	
Fishing pressure					x

Table 3. Summary of BIO-ENV analyses with the *in-situ* environmental variables. Group: variables grouped together in an analysis of correlations (see Fig. 2); Reduced: variables (R) selected for inclusion in analyses, acting as proxies for other group members. Those variables within the subset best explaining variation in each of the resemblance matrices (Ab: Bray-Curtis, raw abundances; Ab*: Bray-Curtis, fourth-root transformed abundances; Bm: Bray-Curtis, raw biomasses; Bm*: Bray-Curtis, fourth-root transformed biomasses; Div: normalised Euclidean distance, univariate measures of community structure) denoted by x.

In-situ variables	Group	Reduced	Ab	Ab*	Bm	Bm*	Div
Gravel	F						
Very coarse sand	F	R					
Coarse sand	G						
Medium sand	G						
Fine sand	D						
Very fine sand	C	R	x	x	x	x	
Total sand	G						
Mud	H						
Median particle diameter	H	R	x	x	x	x	x
Graphic mean M	H						
Inclusive graphical sd D	D	R	x	x			x
Skewness S	G	R	x	x	x	x	x
Kurtosis K	I	R	x	x	x	x	x
OC	H						
ON	H						
C:N	J	R		x			
Chlorophyll a	K	R	x	x		x	
Phaeopigment	K						
OPD	L	R		x		x	
Porosity	H						
NO_2	M	R					x
NO_X	N	R	x		x		x
NO_3	N						
NH_4	O	R					
SiO_4	O						
PO_4	P	R	x	x		x	

FIGURE LEGENDS

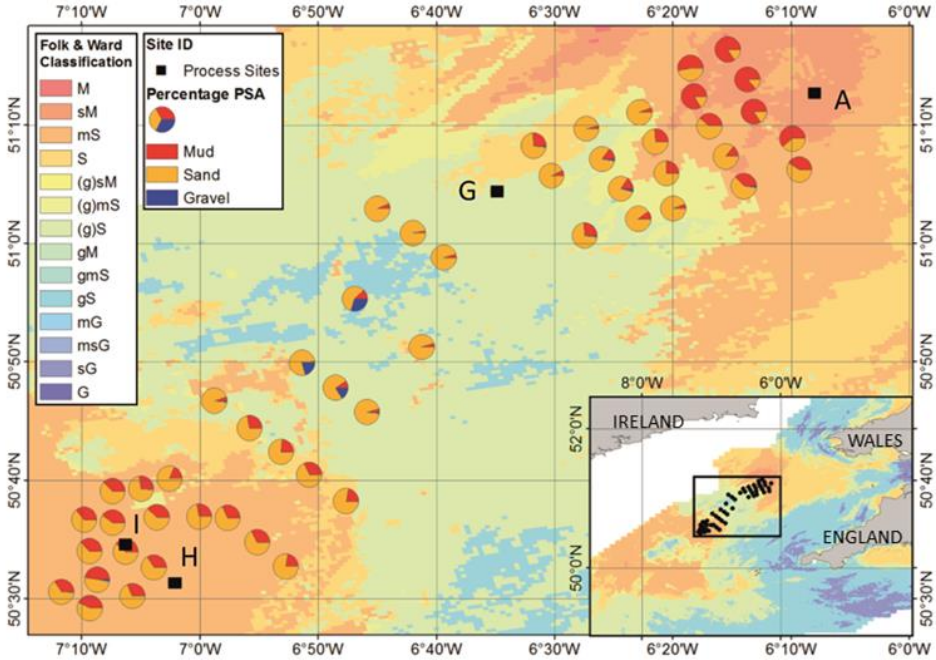
1. Map of sampling locations and broad sediment characteristics, modified from Thompson et al. (2017).

2. Dendrogram from hierarchical agglomerative clustering of variables based on Pearson correlations. Variables grouped using Type 3 SIMPROF ($p<0.001$).

3. Metric MDS (2D stress = 0.09) of sites based on normalised Euclidean distances calculated from sediment measures. Symbols indicate significant groupings from Type 1 SIMPROF analysis. Letters (A, G, H, I) indicate focal stations.

4. Nonmetric MDS of sites (2D stress = 0.24) based on Bray-Curtis similarities calculated from fourth-root transformed abundance data overlain with symbols denoting (A) sediment groups (VCoarse = very course) and (B) results from Type 1 SIMPROF analysis ($p<0.001$). Letters (A, G, H, I) indicate focal stations.

5. Nonmetric MDS of sites (2D stress = 0.25) based on Bray-Curtis similarities calculated from fourth-root transformed biomass data overlain with symbols denoting (A) sediment groups (VCoarse = very course) and (B) results from Type 1 SIMPROF analysis ($p<0.001$). Letters (A, G, H, I) indicate focal stations.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6°20'W
6°10'W
6°0'W
51°10'N
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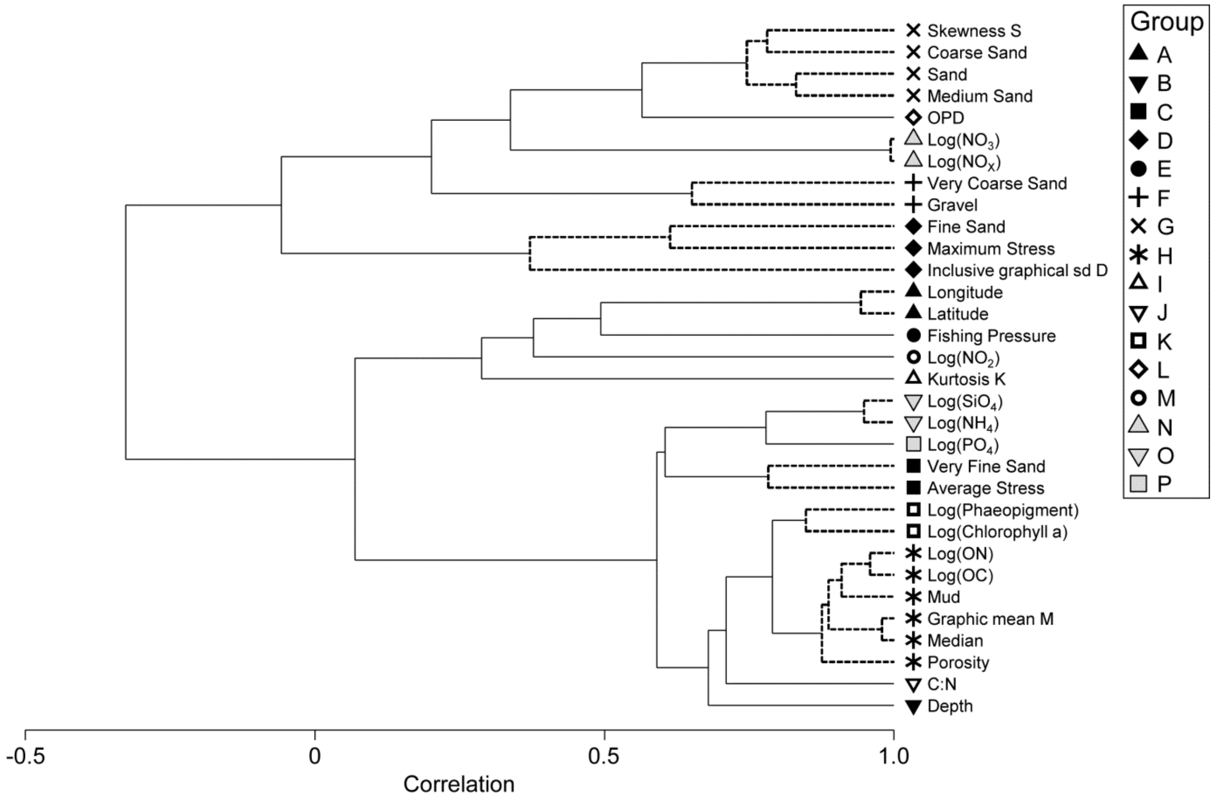
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Log(PO4)
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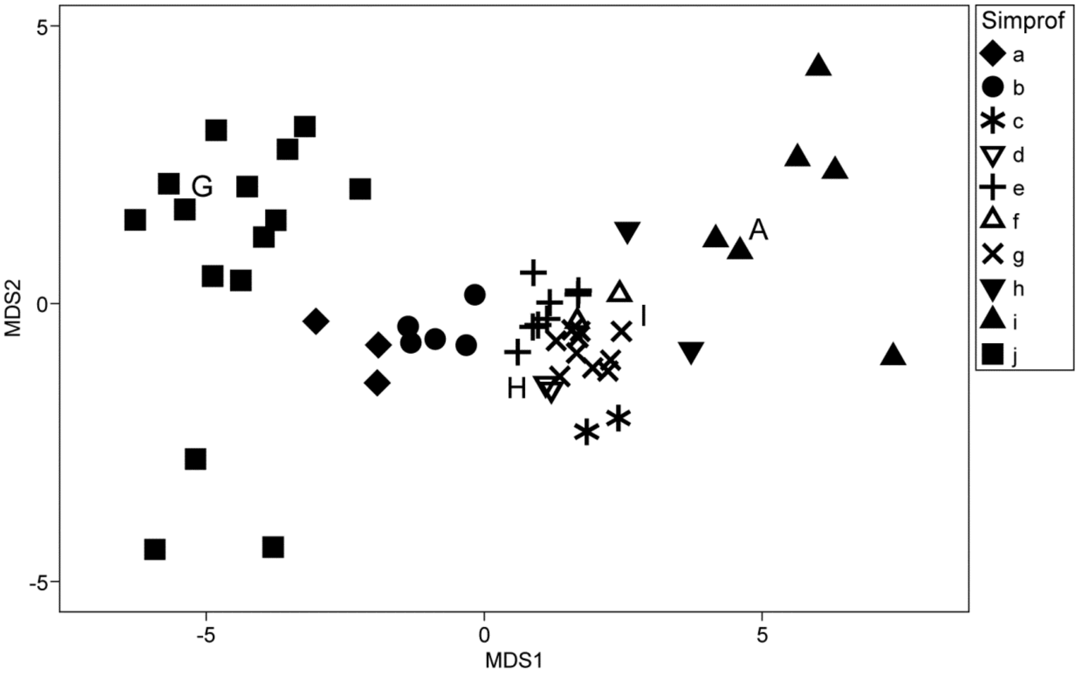
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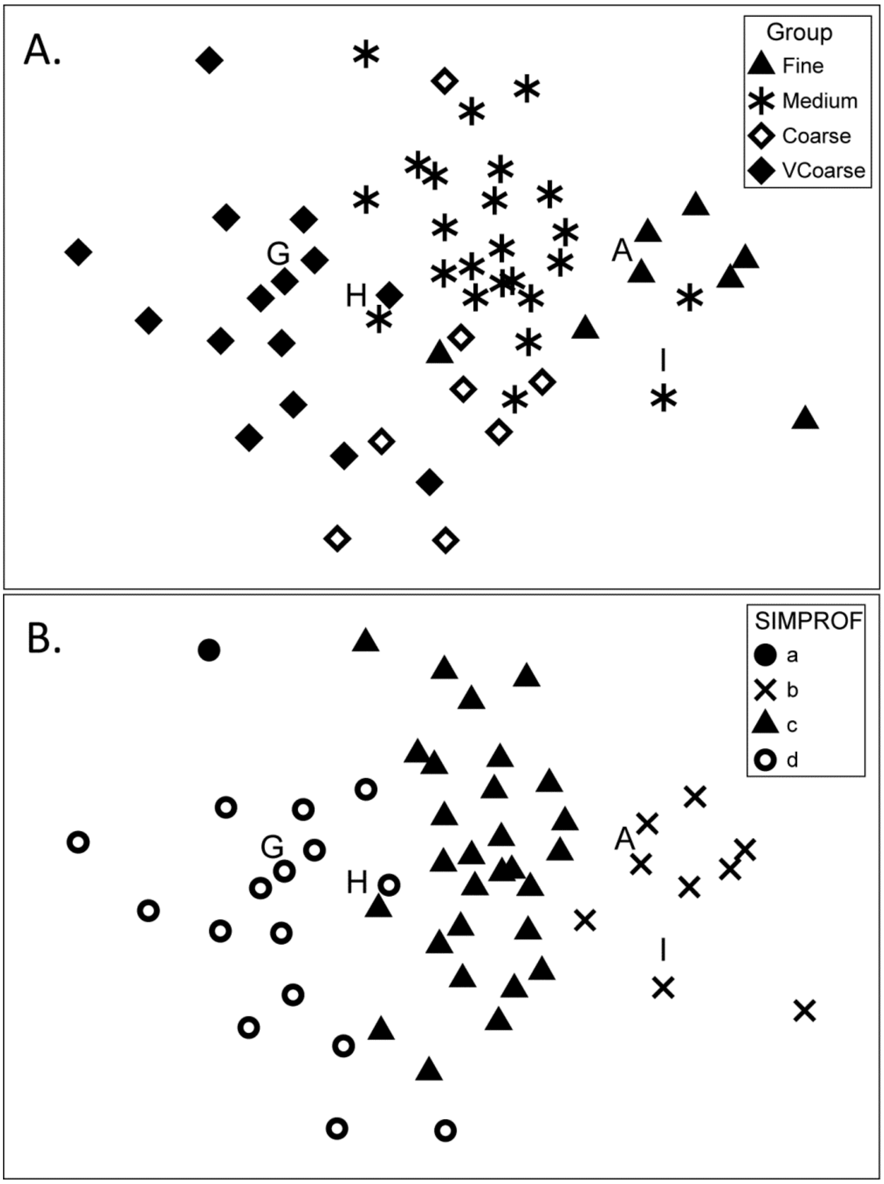
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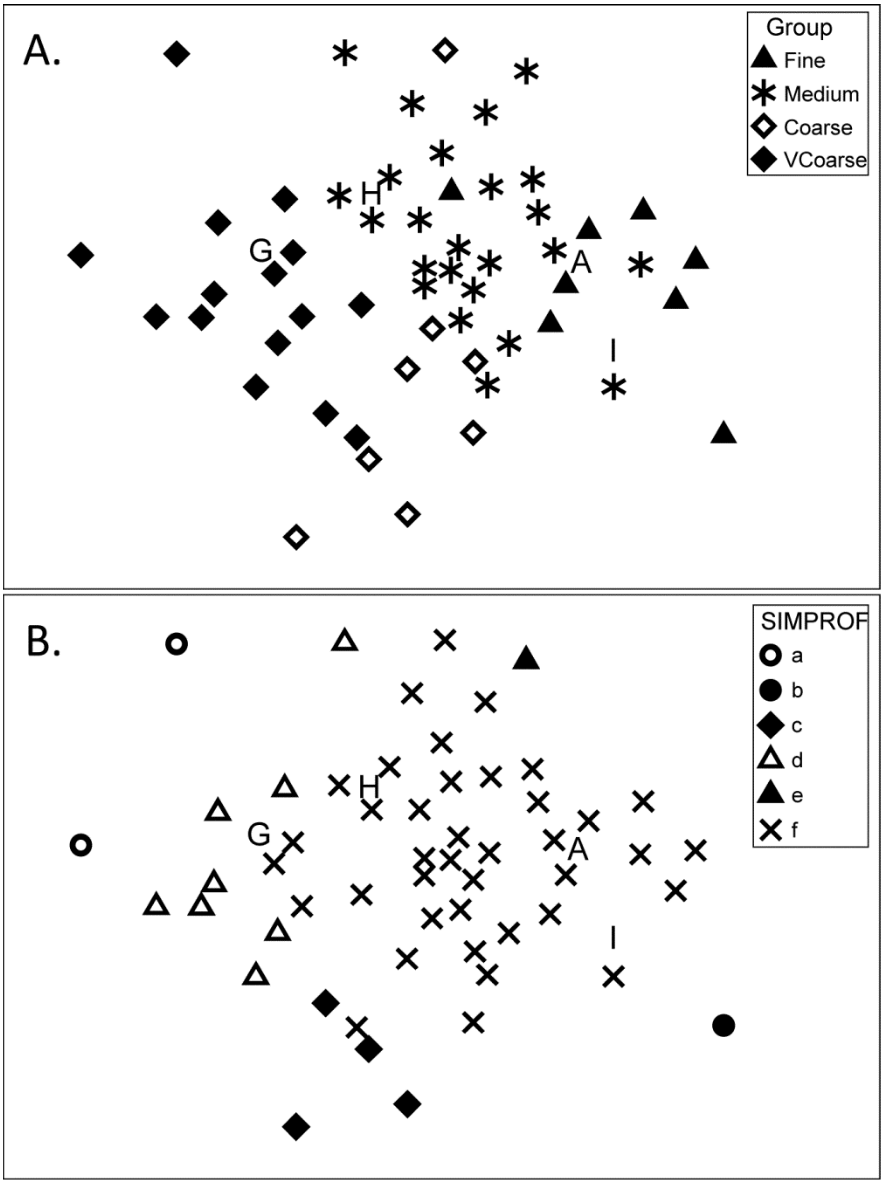
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