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**Meeting the MPA network design principles of representativity and adequacy:
Developing species-area curves for habitats**

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Summary

- Defra have tasked the Joint Nature Conservation Committee (JNCC) and Natural England with providing detailed scientific advice on the design of the marine protected area (MPA) network and site selection in English inshore waters and offshore waters adjacent to England, Wales and Northern Ireland. This will be provided as Ecological Network Guidance that includes practical scientific advice and technical information.
- To meet the network design principle of representativity JNCC and Natural England have chosen to use broad-scale habitats, also known as EUNIS level 3 habitat types, and the habitats of conservation importance (rare, threatened or declining in UK waters) to represent the range of biodiversity in UK waters.
- To meet the network design principle of adequacy JNCC and Natural England believe habitat-specific conservation targets are required.
- The methodologies that can be used to develop habitat-specific targets are outlined in a report commissioned by JNCC (Rondinini 2009). The report recommended that with the type and amount of data available, species-area curves are the most robust amongst the available methods to set conservation targets for individual habitat types in the developing the MPA network.
- Species-area curves are functions that relate the number of species found in a habitat type with the area of the habitat type.
- The objectives of the present work are as follows: (1) to assess for which habitat types it is possible to fit species-area curves either directly or indirectly; and (2) where data allow, fit habitat-specific species-area curves to aid the development of habitat-specific conservation targets.
- For 14 EUNIS Level 3 habitat types there are enough species samples to estimate species-area curves. However, due to scarce data it was necessary to pool the habitat types within A2: Intertidal sediments and within A6: Deep-sea habitats into their respective Level 2 habitat types, allowing for estimation of species-area curves at EUNIS Level 2 habitat types.
- For six out of 19 habitats of conservation importance there are enough species samples to estimate species-area curves.
- The key results are presented in Tables 7 and 9 on pages 17 and 18 respectively, which show the expected number of species to be represented in a given percentage of each habitat type.
- One of the most efficient ways to address adequacy would be to select the sites to be protected in each habitat type through a site-selection software (e.g. MARXAN).
- The estimates presented here represent the best available data on the benthic diversity of marine habitat types in the UK. Yet, due to limitations and uncertainties in the method and data, any conservation targets that are developed based on these results should be considered as underestimates of the true conservation targets required. This should not deter decision makers from using them. On the contrary, they should be used as a starting point for setting targets that will likely need to be increased in the future. Therefore, periodical revision of these targets as biodiversity data accumulate is advised.

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1 Introduction

The Joint Nature Conservation Committee (JNCC) is working with the UK Government to support the development of an ecologically coherent network of Marine Protected Areas (MPAs).

The UK Government is committed to creating a UK-wide and well-managed ecologically coherent network of MPAs as a key element of its wider work to recover and conserve the richness of our marine environment and wildlife. The seven network design principles which will underpin this network are: representativity, replication, viability, adequacy, connectivity, protection, and best available evidence (Defra 2010). Definitions of these principles are given below:

- **Representativity** - the MPA network should represent the range of marine habitats and species through protecting all major habitat types and associated biological communities present in our marine area.
- **Replication** - all major habitats should be replicated and distributed throughout the network. The amount of replication will depend on the extent and distribution of features within seas.
- **Viability** - the MPA network should incorporate self-sustaining, geographically dispersed component sites of sufficient size to ensure species and habitats persistence through natural cycles of variation.
- **Adequacy** - the MPA network should be of adequate size to deliver its ecological objectives and ensure the ecological viability and integrity of populations, species and communities (the proportion of each feature included within the MPA network should be sufficient to enable its long-term protection and/or recovery).
- **Connectivity** - the MPA network should seek to maximise and enhance the linkages among individual MPAs using the best current science. For certain species this will mean that sites should be distributed in a manner to ensure protection at different stages in their life cycles.
- **Protection** - the MPA network is likely to include a range of protection levels. Ranging from highly protected sites or parts of sites where no extractive, depositional or other damaging activities are allowed, to areas with only minimal restrictions on activities that are needed to protect the features.
- **Best available evidence** - Network design should be based on the best information currently available. Lack of full scientific certainty should not be a reason for postponing proportionate decisions on site selection.

Defra have tasked JNCC and Natural England with interpreting these network design principles and providing detailed scientific advice on the design of the MPA network and identification of Marine Conservation Zones (MCZs) in English inshore waters and offshore waters adjacent to England, Wales and Northern Ireland. This will be provided as Ecological Network Guidance (Natural England and JNCC 2010) that includes practical scientific advice and technical information.

JNCC and Natural England have provided advice that network design principle of representativity can be met by grouping species and habitats into broad-scale habitats and protecting examples of them across the MPA network. The MPA network should also protect those features of conservation importance that are known to be rare, threatened, or declining, in our waters. In the UK the marine environment has been characterised through mapping the distribution of broad-scale habitats at EUNIS Level 3¹. EUNIS Level 3 habitat

¹ EUNIS habitat classification has been developed by the European Topic Centre on Biological Diversity (EEA n.d.).

types are largely classified according to physical characteristics (e.g. depth, substratum and energy levels), but for some, specific biological characteristics are described (e.g. coastal saltmarshes and saline reedbeds). Additionally, habitats of conservation importance (rare, threatened or declining in UK waters) have been listed and mapped (for further details see Appendix 1). These two types of habitat features have been chosen by JNCC and Natural England as the key building blocks for developing the MPA network, and to meet the network design principle of representativity.

The network design principle of adequacy refers to both the overall size of an MPA network and the proportion of each feature protected. To be considered adequate, the MPA network must be of sufficient size and include a large enough proportion of features, in order to deliver the network's ecological objectives and enable the feature's long-term protection and recovery (where necessary). Adequacy should be based on the biological needs of individual species, communities, and ecosystems so they are scientifically credible and robust (Rondinini 2009). Both best practice and research recommend that the amount of each feature to be protected in an MPA network should be described numerically (Rondinini 2009). JNCC and Natural England believe that in order to meet the network design principle of adequacy habitat-specific conservation targets are required.

The methodologies that can be used to develop habitat-specific targets are outlined in a JNCC commissioned research report (Rondinini 2009; Rondinini and Chiozza 2010). In particular, where data allow, the report recommends that conservation targets for species representation in habitat types should be derived from species-area curves, which relate the number of species found in a habitat type with the area of the habitat type. The recommendations from Rondinini 2009 are outlined below:

1. where sampling data (i.e. records of species collected at known coordinates) are sufficient, habitat-specific species-area curves can be directly estimated for each broad-scale habitat type and for each habitat type of conservation importance;
2. where sampling data are insufficient, environmental heterogeneity of habitats can be used to estimate the rate of species accumulation by modelling its relationship with environmental heterogeneity. This model can be fitted for the habitat types with sufficient sampling data, and extrapolated for the remaining habitats;
3. if the modelling approach has low confidence it may be reasonable to assume that species composition and turnover are comparable between similar habitats; and
4. for some habitat types it may not be possible to fit species-area curves, in which case heuristic rules will need to be developed.

The current research report has the following aims to address the first recommendation from Rondinini 2009. Specifically the objectives of this current research are:

1. To assess for which habitat types (EUNIS and habitats of conservation importance) it is possible to fit species-area curves either directly or indirectly; and
2. Where data allow it, fit habitat-specific species-area curves to aid the development of habitat-specific conservation targets.

2 Methods

2.1 The theory: setting habitat-specific conservation targets through the species-area relationship

A well-established relationship exists between habitat area and the number of species that an area can support (species-area relationship) (MacArthur & Wilson 1967):

$$(1) \quad S = cA^z$$

where S is the number of species, A is the area, c a constant, and z a parameter that describes the rate at which species are encountered in an area. If S and A are replaced with proportion of species and proportion of area (S' and A') there is no need to estimate the constant c :

$$(2) \quad S' = A'^z$$

Using the equation above it is possible to predict the number of species observed if a given percentage of a habitat type is sampled, provided that the z -value for the habitat type is known. Here S' denotes the proportion of species expected to be found and A' denotes the proportionate area of the habitat type.

The argument above can be applied to habitat protection as well. Loss of habitat tends, over time, to result in the loss of species within an approximate range (Neely *et al* 2001). On this basis, the approximate number of species that are expected to be retained in a given proportion of the original habitat can be inferred (Figure 1).

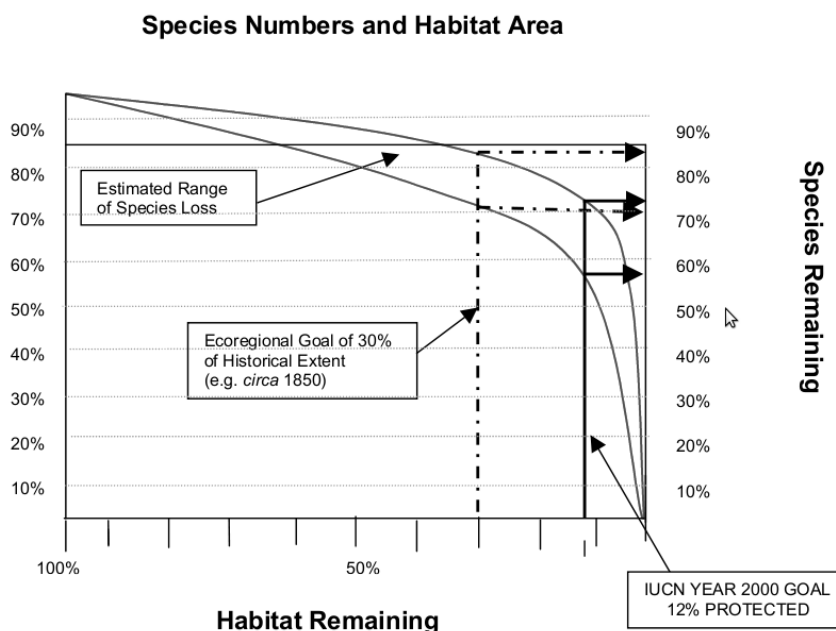


Figure 1. Proportion of species retained as a function of the proportion of original habitat that is conserved (from Neely *et al* 2001).

The two hypothetical curves in Figure 1 represent different estimates of the rate of loss of species. For example, based on these two curves in the figures the IUCN target of

protecting 12% of a habitat type would result in the representation of 57-72% of the species that it contains.

The equations above can be reordered to formulate conservation targets for habitat types, to determine the proportion of area required to represent a given percentage of species:

$$(3) \quad \text{Log } A' = \text{Log } S'/z$$

Because species accumulate at different rates in different habitat types, conserving the same proportion of species in different habitat types requires the protection of different proportions of each habitat type. The method for setting habitat-specific targets involves estimating the area of a habitat type that is required to represent a given proportion of the species occurring in the habitat type (Desmet & Cowling 2004). From the log transformation of the power model, the slope of the curve (hence, the z value) can be determined using the formula for calculating the slope of a straight line:

$$(4) \quad z = (y_2 - y_1)/(x_2 - x_1)$$

Here z is the slope of the straight line, $y_2 = \log$ (total number of species in a habitat type); $y_1 = \log$ (average number of species per survey sample); $x_2 = \log$ (total area of habitat type); and, $x_1 = \log$ (average area of samples). When using species inventory data, three of these variables are known (x_1 , x_2 and y_1), and one (y_2) can be estimated. The estimation of the total number of species that occur in a habitat type is obtained by adding, to the richness of species sampled in a habitat type, the number of species not detected estimated through one of several published formulas (e.g. Chao, Jackknife, Bootstrap). These formulas estimate the number of non-detected species based on the proportion of species that have been recorded only at few sites (Colwell & Coddington 1994, Gotelli & Colwell 2001).

The equations above and their application to real data imply a number of assumptions. These include: homogeneity of habitat types over large areas; migration of individuals between patches of the same the habitat type (connectivity); independence from surrounding habitat types (no edge effect); ecologically meaningful definition of habitat types; accuracy of habitat maps; and adequate, non-biased sampling of species within habitat types.

2.2 Applying the species-area relationship to marine habitat types in the UK

By using equation 4 above the habitat-specific values of z can be estimated with the following four variables:

- y_2 , the log total number of species in a habitat type. This is estimated (after assigning species records to habitat types) using a species estimator based on the abundance of species detected across all samples;
- y_1 , the log mean number of species detected in each sample. This is calculated after assigning species records to habitat types;
- x_2 , the log total area of each habitat type. This is calculated from the habitat maps;
- x_1 , the log mean area of a sampling site, which can be difficult to accurately derive from the available data and depends on the type of sampling used. For much of the data used in this study this information is not known precisely, and as such a range of values was used to estimate the sensitivity of the analysis to this parameter. It

should be noted that the value of z is related to the logarithm of this parameter, and therefore it is anticipated that it should be relatively insensitive (see also Desmet & Cowling 2004).

2.2.1 Data sources and summary statistics

The estimation of y_2 and the computation of x_1 and x_2 required both maps of the habitat types; including intertidal and subtidal EUNIS level 3 habitat maps, and 19 maps of habitats of conservation importance (HCI); and the databases of sites sampled with the associated species list. The full list of datasets used is reported in Appendix 2, along with details of how the habitat maps were derived.

Data were loaded in a POSTGRESQL/POSTGIS database. All habitat maps were analysed separately, rather than merging them together. This is because many of the maps overlap due to the different methodologies used to create them. For example, the intertidal and subtidal EUNIS Level 3 habitat maps overlap each other, and as a consequence, some sampled sites can be classified at the same time with two different EUNIS level 3 codes. This is a consequence of the intertidal habitat maps being developed directly from detailed phase 1 intertidal surveys, whilst the subtidal habitat maps were generated through a coarser modelling approach (see Appendix 1 for further details).

Before calculating the log total area of each habitat type (x_2), the habitat maps were projected to a Lambert Azimuthal Equal Area (EPSG code: 3035) to ensure a correct computation of the areas.

The species records were intersected with the intertidal and subtidal EUNIS Level 3 habitat maps; and the HCI maps. This was done to calculate the area of each habitat type (x_2), the number of sampling sites within each habitat type, and the number of species recorded within each habitat type. The mean number of species per sample observed in each habitat type (y_1) was calculated, and the data exported to the statistical programme R (R Development Core Team 2009) for the estimation of y_2 and the subsequent analyses.

2.2.2 Assessment of data availability for the development of species-area curves

Estimates of the total number of species based on few sampling sites and few species are very likely to be smaller than the real (unknown) value. To avoid substantial underestimations of this parameter, an analysis was undertaken (following Desmet & Cowling 2004) to assess whether the sample size of species records was sufficient for a stable estimate. For each habitat type, the total number of species was estimated using 100 random sub-samples of increasing size taken from the full sample (e.g. for habitat type A1.1, with 302 samples, 100 sub-samples of size 10, 100 sub-samples of size 11, 100 sub-samples of size 12, ... 100 sub-samples of size 301). If, for sub-samples smaller than 80% the size of the full sample, the standard deviation of the estimates stabilised to within $\pm 5\%$ of the mean, then the estimate of the total number of species based on the full sample was considered stable. The rationale for using the 80% threshold is that the standard deviation of estimates based on sub-samples that are very close in size to the full sample are always small, because the number of different random sub-samples is small.

2.2.3 Development of habitat-specific species-area curves

Four estimators for calculating expected total species number per habitat type have been used, including Chao, two types of Jackknife, and Bootstrap. This was done to obtain a range of possible values of z . All these estimators have been used frequently in peer-

reviewed literature and more details on their formulas can be found in Appendix 3. Habitat-specific values of z have then been computed using eq. 4 (page 4). The habitat-specific species-area curves have been individually described using eq. 2 (page 3), and have been used to estimate the percentage of species that are expected to be represented by any given percentage of habitat protected. The percentage of habitat type required to represent a given percentage of species occurring in that habitat type has been provided at 10 equal intervals between 10 and 100%.

2.3 Quality control procedures

In order to avoid those risks that may lower the quality of the work at various stages and leading to an incorrect recommendation, the actions detailed in Table 1 were undertaken.

Table 1. Procedures applied for quality control during the analysis process.

Risks	Action
Incorrect interpretation of data (maps and species data)	Check data cartography and database structure with JNCC staff
Human errors in data preparation and analysis	Double check all steps of data preparation; use scripts that allow checking and reduce chance of human error Use scripts as they allow easy checking
Wrong estimation of the total number of species per habitat type	Use a range of estimators and provide range of possible values
Incorrect grouping of habitat types into broad habitat classes	Check appropriateness of grouping with JNCC staff
Unclear report	Get feedback on draft report

Drafts of this research report were also reviewed by staff from JNCC and Natural England, external independent specialists and the Chief Scientists of the Department for Environment, Food and Rural affairs (Defra), JNCC and Natural England. The final report has taken on board comments received from the reviewers.

3 Results and discussion

3.1 Summary statistics

The species databases contained 1,679,990 species records collected across 28,687 samples. Of these species records, 1,153,758 fall within the subtidal EUNIS Level 3 habitat map, 53,556 fall within the map of intertidal habitat types, and 291,478 fall within at least one HCI map. The descriptive statistics for each EUNIS level 3 habitat type are reported in Table 2, those for HCI are reported in Table 3.

Table 2. Descriptive statistics for species and samples within EUNIS Level 3 habitat types.

EUNIS L. 3	Name	Area (km ²)	Number of sampling sites	Number of species collected	Mean number of species per site
A1.1	High energy intertidal rock	21.7	302	1,394	32.997
A1.2	Moderate energy intertidal rock	9.8	141	1,085	31.674
A1.3	Low energy intertidal rock	14.3	200	981	23.645
A2	Intertidal sediment	496.0	1373	1,908	13.080
A2.1	Intertidal coarse sediment	10.1	88	282	5.761
A2.2	Intertidal sand and muddy sand	351.3	778	1,505	12.607
A2.3	Intertidal mud	49.7	222	552	11.293
A2.4	Intertidal mixed sediments	4.2	59	787	36.119
A2.5	Coastal saltmarshes and saline reedbeds	61.6	62	409	12.113
A2.6	Intertidal sediments dominated by aquatic angiosperms	3.9	26	76	10.923
A2.7	Intertidal biogenic reefs	13.7	133	396	13.421
A3.1	High energy infralittoral rock ²	256.4	257	1,250	37.953
A3.2	Moderate energy infralittoral rock	344.6	396	1,364	31.831
A3.3	Low energy infralittoral rock	4,294.1	1714	2,636	39.806
A4.1	High energy circalittoral rock ³	1,161.9	106	632	24.642
A4.2	Moderate energy circalittoral rock	957.9	125	1,012	31.944
A4.3	Low energy circalittoral rock	13,456.5	710	1,662	21.254
A5.1	Subtidal coarse sediment	163,289.1	8532	4,584	29.562
A5.2	Subtidal sand	265,364.5	9065	4,774	30.289
A5.3	Subtidal mud	51,947.2	2064	3,076	35.164
A5.4	Subtidal mixed sediments	17,411.0	1922	3,115	34.013
A6	Deep-sea bed	181,545.2	108	1,145	85.769
A6.1	Deep-sea rock and artificial hard substrata	7.3	0	-	-
A6.2	Deep-sea mixed substrata	33,375.4	60	775	114.700
A6.3	Deep-sea sand	21,448.1	2	292	158.000
A6.5	Deep-sea mud	115,356.9	29	256	35.241
A6.X	Deep-sea coarse sediment	11,357.5	17	317	61.353

Two separate maps exist for three HCI (mud habitats in deep sea, sheltered muddy gravels, subtidal sand and gravels). In all three cases the area of the habitat type estimated through the maps derived from British Geological Survey (BGS) data⁴ is one order of magnitude

² Infralittoral rock includes habitats of bedrock, boulders and cobbles which occur in the shallow subtidal zone and typically support seaweed communities. The upper limit is marked by the top of the kelp zone whilst the lower limit is marked by the lower limit of kelp growth or the lower limit of dense seaweed growth.

³ Circalittoral rock is characterised by animal dominated communities (a departure from the algae dominated communities in the infralittoral zone). The depth at which the circalittoral zone begins is directly dependent on the intensity of light reaching the seabed; in highly turbid conditions, the circalittoral zone may begin just below water level.

⁴ Maps were derived from BGS sediment distribution maps (digSBS250).

larger than through the other corresponding map (Table 3). These differences are a result of differences in the methodologies of how the maps were derived. The maps derived from the BGS data only consider modelled physical gradients in delineating habitat extent, whilst the corresponding maps were derived from direct marine survey data (i.e. acoustic data plus ground-truthing). Direct marine survey data only covers a proportion of the UK seabed, and as such may produce serious underestimates in any z values derived as the total area of the habitat type is one of the four pieces of information used to calculate estimated z values. The fact that there is no agreement between pairs of maps of the same HCI results in very different estimates of the z value for the same HCI. In addition, the mean number of species per site (another piece of information used to compute z values) also varies widely for these three habitat types (Table 3). Therefore, the z values for these HCI (and possibly for other HCI if they share the same uncertainties) may not be reliable. In this situation, the precautionary principle suggests the use of the most conservative result (i.e. the highest among the z estimates).

Table 3. Descriptive statistics for species and samples within habitats of conservation importance (HCI).

HCI	Area (km ²)	Number of sampling sites	Number of species collected	Mean number of species per site
Blue mussel beds	91.60	106	465	36.783
Coastal saltmarsh	296.80	179	393	17.726
Estuarine rocky habitats	12.00	73	583	34.055
Fragile sponge & anthozoan communities on subtidal rocky habitats	0.50	12	27	4.250
Intertidal boulder communities	0.50	18	247	43.611
Intertidal mudflats	906.00	1,088	1,371	19.474
Littoral chalk communities	0.30	10	352	56.500
Mud habitats in deep water	4,343.00	328	1,499	31.421
Mud habitats in deep water (BGS)	10,023.90	79	204	21.911
<i>Sabellaria alveolata</i> reefs	4.80	62	687	101.452
<i>Sabellaria spinuolsa</i> reefs	672.00	252	970	44.159
Saline lagoons	54.70	313	862	19.780
Seagrass beds	158.70	0	-	-
Seamounts	7,175.00	13	139	28.231
Sheltered muddy gravels	20.30	1,413	1,936	25.258
Sheltered muddy gravels (BGS)	706.50	4,917	3,915	35.470
Subtidal chalk	3,040.20	124	860	35.435
Subtidal sands and gravels	36,770.60	243	1,395	36.333
Subtidal sands and gravels (BGS)*	379,603.10	NA	NA	NA

*Note the analysis for subtidal sands and gravels derived from BGS data has not been completed due to the large and complex nature of the dataset.

3.2 Assessment of data availability for the computation of z values

For all A1, A3, A4 and A5 EUNIS Level 3 habitats there are enough species samples to calculate a stable (within $\pm 5\%$ SD) estimate of the total number of species (Table S1, Appendix 4). However, among A2 EUNIS Level 3 habitat types, which have a low number of samples, no stable estimate is reached. Among A6 habitat types, only for A6.2 is the number of samples sufficient to calculate a stable estimate (Table S1, Appendix 4). For this reason it was decided to pool all A2 habitat types, and all A6 habitat types, to increase the number of samples. While this allowed achievement of a stable estimate for the pooled A2 habitat types, it was not sufficient for A6 habitat types pooled (Table S1, Appendix 4). Nonetheless, because no other information is available for A6 habitat types, it was decided to retain the estimated total number of species for A6 habitats and use it to develop a species-area curve for this habitat type. Because the total number of species for A6 is certainly underestimated, the resulting target will be also underestimated and this should be clearly communicated. It should be noted that for habitat type A6.2 the estimate of the total number of species is stable. Therefore, for A6.2 this estimate, not the general estimate for A6, should be used.

For six out of the 19 maps of HCI (blue mussel beds; mud habitats in deep water; *Sabellaria alveolata* reefs; sheltered muddy gravels; sheltered muddy gravels - BGS; subtidal sands and gravels) there is a sufficient number of samples for the estimation of z values (Table S2, Appendix 4). For all other HCI no stable estimate of the total number of species is possible (Table S2, Appendix 4), and species-area curves were not developed.

In the present analysis the four estimators used for calculating total species number reached stability of the estimate at very different numbers, with the Bootstrap estimator reaching stability with a smaller number of samples (and therefore for a greater number of habitat types) (Tables S1 and S2, Appendix 4). For this reason the Bootstrap estimator is used as the preferred estimator in this report, although z values have been calculated for all four estimators to provide a range of values.

3.3 Computation of habitat-specific z values

The four estimators were used to produce different estimates of the total number of species in each EUNIS habitat type and HCI (Tables S3 and S4, Appendix 4). The Bootstrap estimator usually produces the lowest estimate of total number of species. This pattern has also been observed in peer-reviewed literature (Chiarucci *et al* 2003). Therefore, if using the Bootstrap estimator for total species number the subsequent estimates of the amount of each habitat type needed to represent any given number of species should be considered as a minimum estimate.

The habitat-specific z values were computed based on the estimated total number of species per habitat type for each estimator (y_2), the mean number of species per sampling site (y_1), the total area of each habitat type (x_2), and on four different estimates of the area (x_1) of each sample (0.5 m², 1 m², 10 m², 25 m²). Results for the Bootstrap estimator are reported in Table 4 (EUNIS Level 3 habitat types) and Table 5 (HCI). Results for the other three estimators are very similar to those obtained using the Bootstrap estimator. They are reported in Tables S5-S7, Appendix 4 (EUNIS Level3 habitat types) and Tables S8-S10, Appendix 4 (HCI).

Table 4. Estimated z value for each EUNIS Level 3 habitat type based on the Bootstrap estimator of the total number of species and on four estimates of the size of the average area of sample sites (x_1).

EUNIS Level 3 habitat type		z value for different values of x_1			
Code	Name	0.5 m ²	1 m ²	10 m ²	25 m ²
A1.1	High energy intertidal rock	0.21	0.23	0.32	0.34
A1.2	Moderate energy intertidal rock	0.21	0.23	0.32	0.35
A1.3	Low energy intertidal rock	0.22	0.24	0.33	0.36
A2	Intertidal sediment	0.24	0.26	0.33	0.35
A3.1	High energy infralittoral rock	0.18	0.19	0.25	0.26
A3.2	Moderate energy infralittoral rock	0.19	0.20	0.26	0.28
A3.3	Low energy infralittoral rock	0.18	0.19	0.24	0.26
A4.1	High energy circalittoral rock	0.15	0.16	0.21	0.22
A4.2	Moderate energy circalittoral rock	0.16	0.18	0.23	0.24
A4.3	Low energy circalittoral rock	0.18	0.19	0.24	0.25
A5.1	Subtidal coarse sediment	0.19	0.20	0.24	0.25
A5.2	Subtidal sand	0.18	0.19	0.22	0.23
A5.3	Subtidal mud	0.17	0.18	0.23	0.24
A5.4	Subtidal mixed sediments	0.18	0.20	0.24	0.26
A6	Deep-sea bed	0.10	0.11	0.13	0.13
A6.2	Deep-sea mixed substrata	0.08	0.08	0.10	0.11

Table 5. Estimated z value for each HCI based on the Bootstrap estimator of the total number of species and on four estimates of the size of the average area of sample sites.

Habitats of conservation importance	z value for different values of x_1			
	0.5 m ²	1 m ²	10 m ²	25 m ²
Blue mussel beds	0.14	0.15	0.2	0.21
Mud habitats in deep water	0.17	0.18	0.23	0.24
<i>Sabellaria alveolata</i> reefs	0.12	0.13	0.19	0.21
Sheltered muddy gravels	0.24	0.26	0.36	0.39
Sheltered muddy gravels (BGS)	0.22	0.24	0.3	0.32
Subtidal sands and gravels	0.15	0.16	0.19	0.2

3.4 Habitat-specific targets based on species-area curves: proportion of species represented

Theoretical species-area curves for EUNIS Level 3 habitat types (Figures 2-7) and HCI (Figures 8) were developed on the basis of the habitat-specific z values reported in Table 4 and Table 5 respectively and assuming an average area of sample sites of 1 m². Only curves based on the Bootstrap estimator have been drawn because the other estimators produced very similar results. These curves represent the expected proportion of species that is represented (i.e. included one or more times) in any given proportion of each habitat type. The shapes of the curves depend on the values of z, which in turn depend on what percentage of the species of each habitat type is included in an average sample. This is influenced by the proportion of rare species in a habitat type, the intensity of sampling, and the likelihood that species are not detected, thus increasing their perceived rarity. For example, the average samples of EUNIS habitat type A1.1 are more different among each other, are less representative of the overall habitat type, and contain more rare species than average samples in EUNIS habitat type A6.2. As a result, 20% of habitat type A1.1 is

expected to represent ca. 60% of its species (Figure 2), while 20% of habitat type A6.2 is expected to contain ca. 80% of its species (Figure 7).

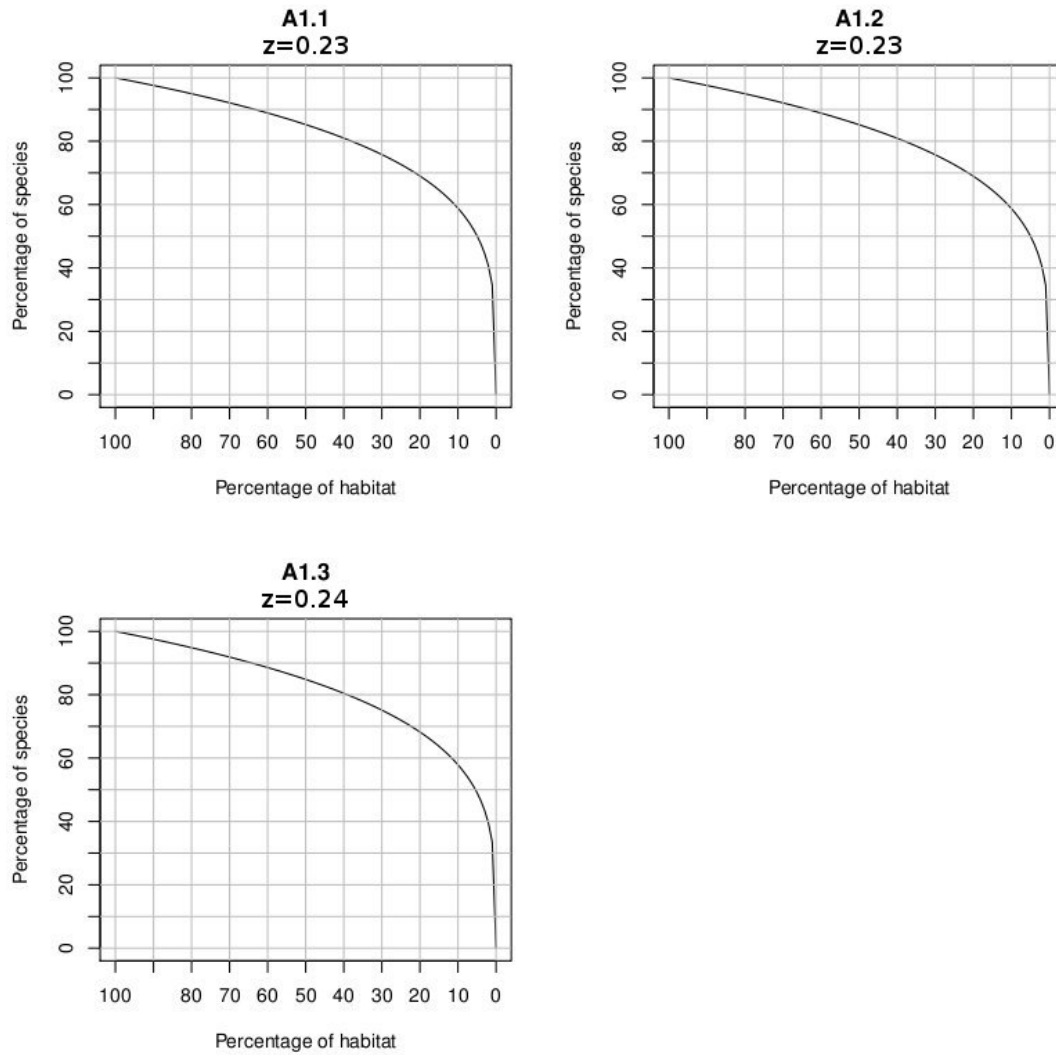


Figure 2. Percentage of species represented in decreasing percentage of EUNIS A1 (intertidal rock) habitat types.

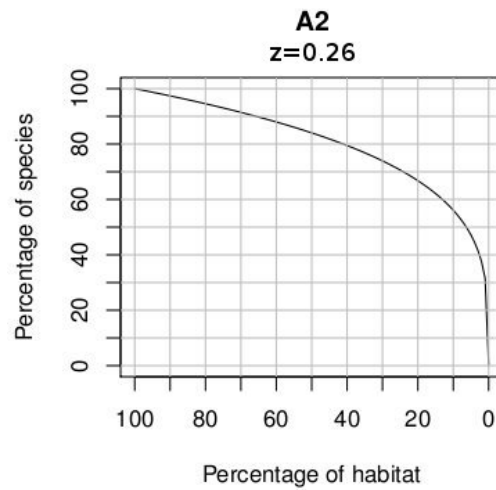


Figure 3. Percentage of species represented in decreasing percentage of EUNIS A2 (intertidal sediment) habitat types.

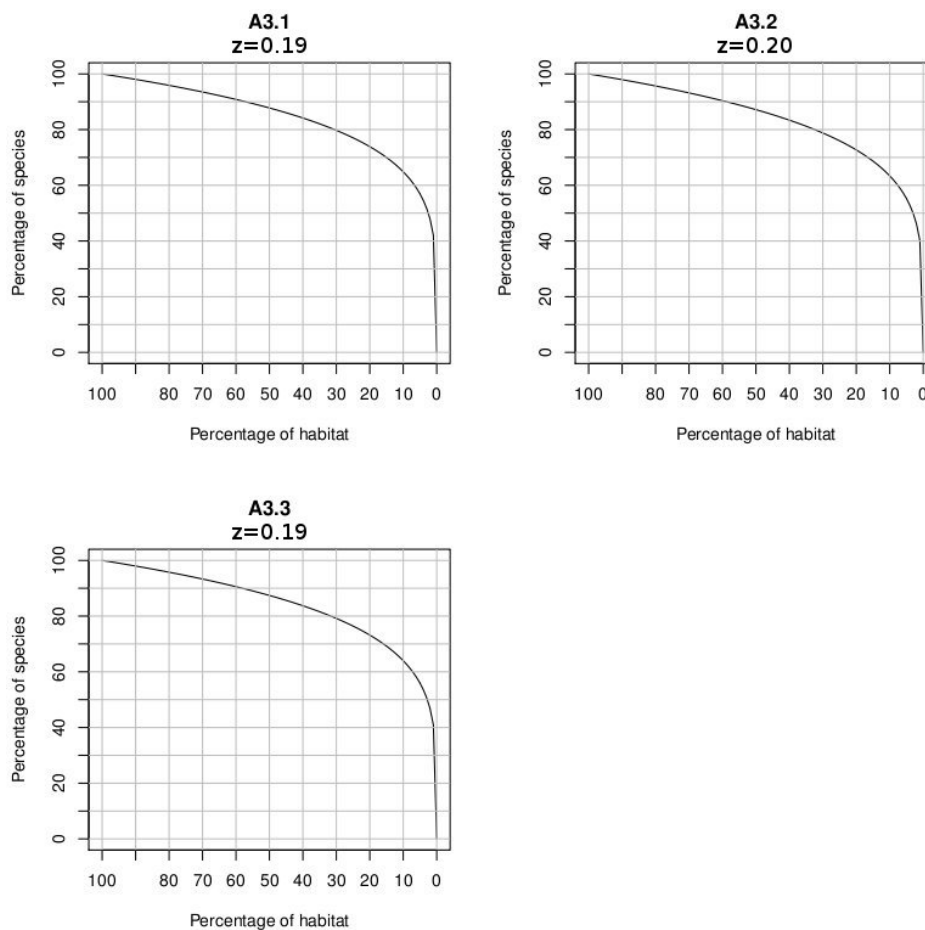


Figure 4. Percentage of species represented in decreasing percentage of EUNIS A3 (infralittoral rock) habitat types.

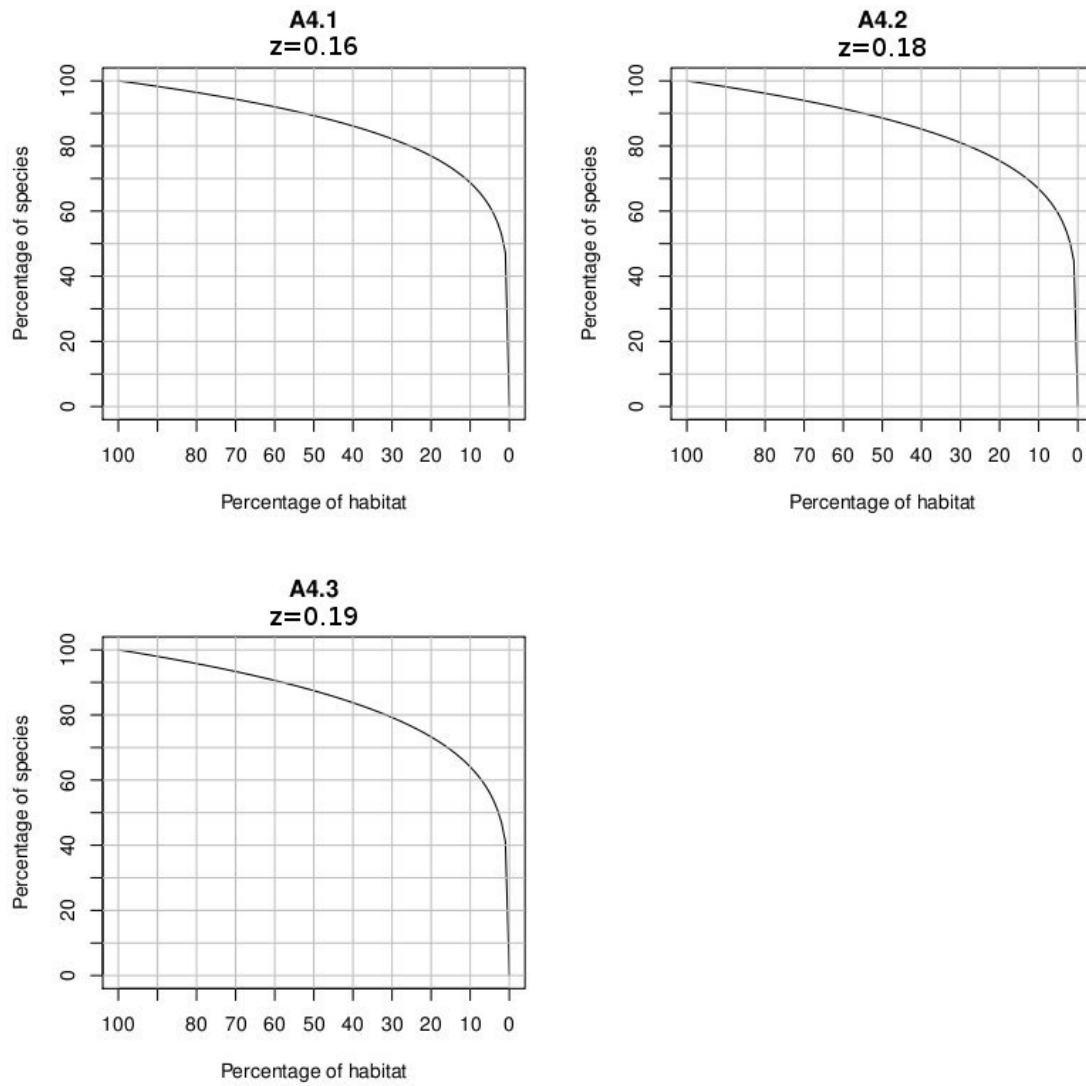


Figure 5. Percentage of species represented in decreasing percentage of EUNIS A4 (circalittoral rock) habitat types.

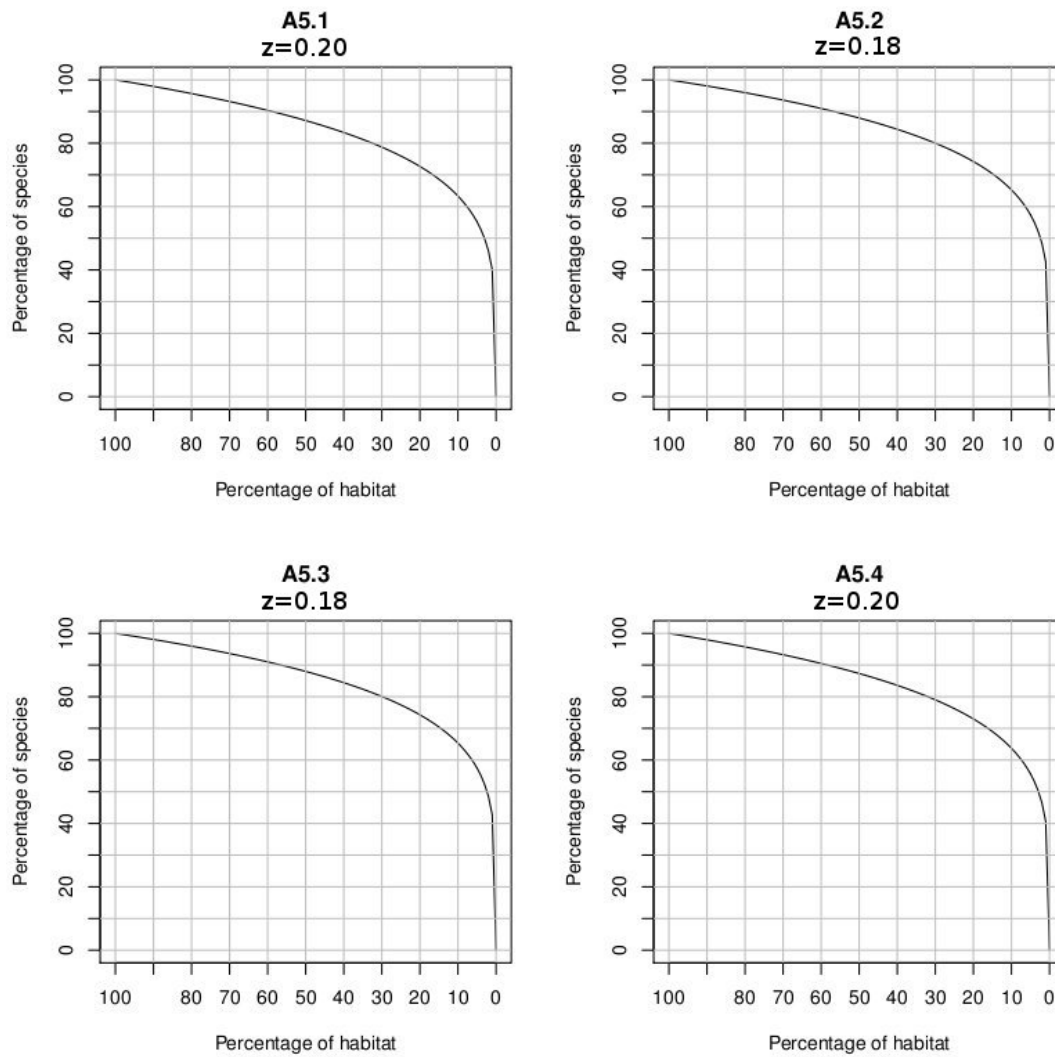


Figure 6. Percentage of species represented in decreasing percentage of EUNIS A5 (subtidal sediment) habitat types.

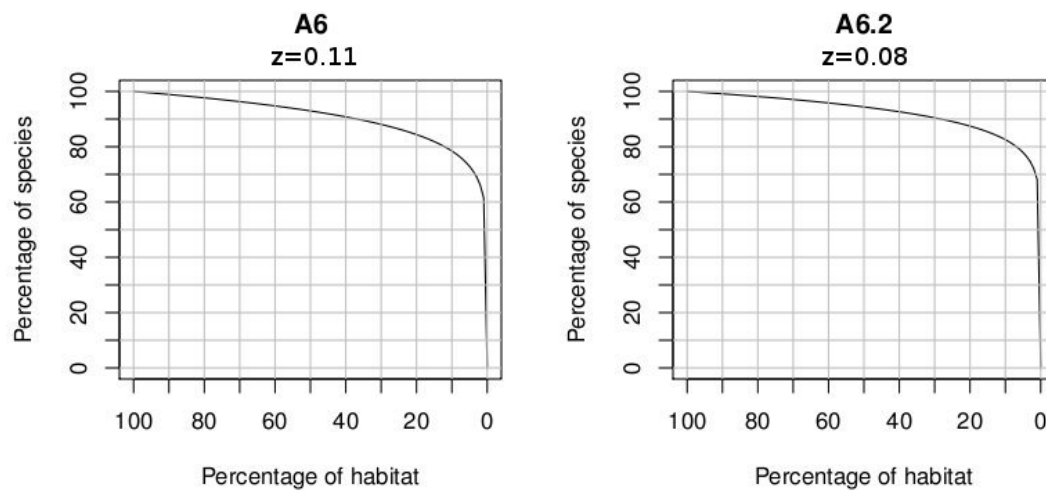


Figure 7. Percentage of species represented in decreasing percentage of EUNIS A6 (deep sea bed) habitat types.

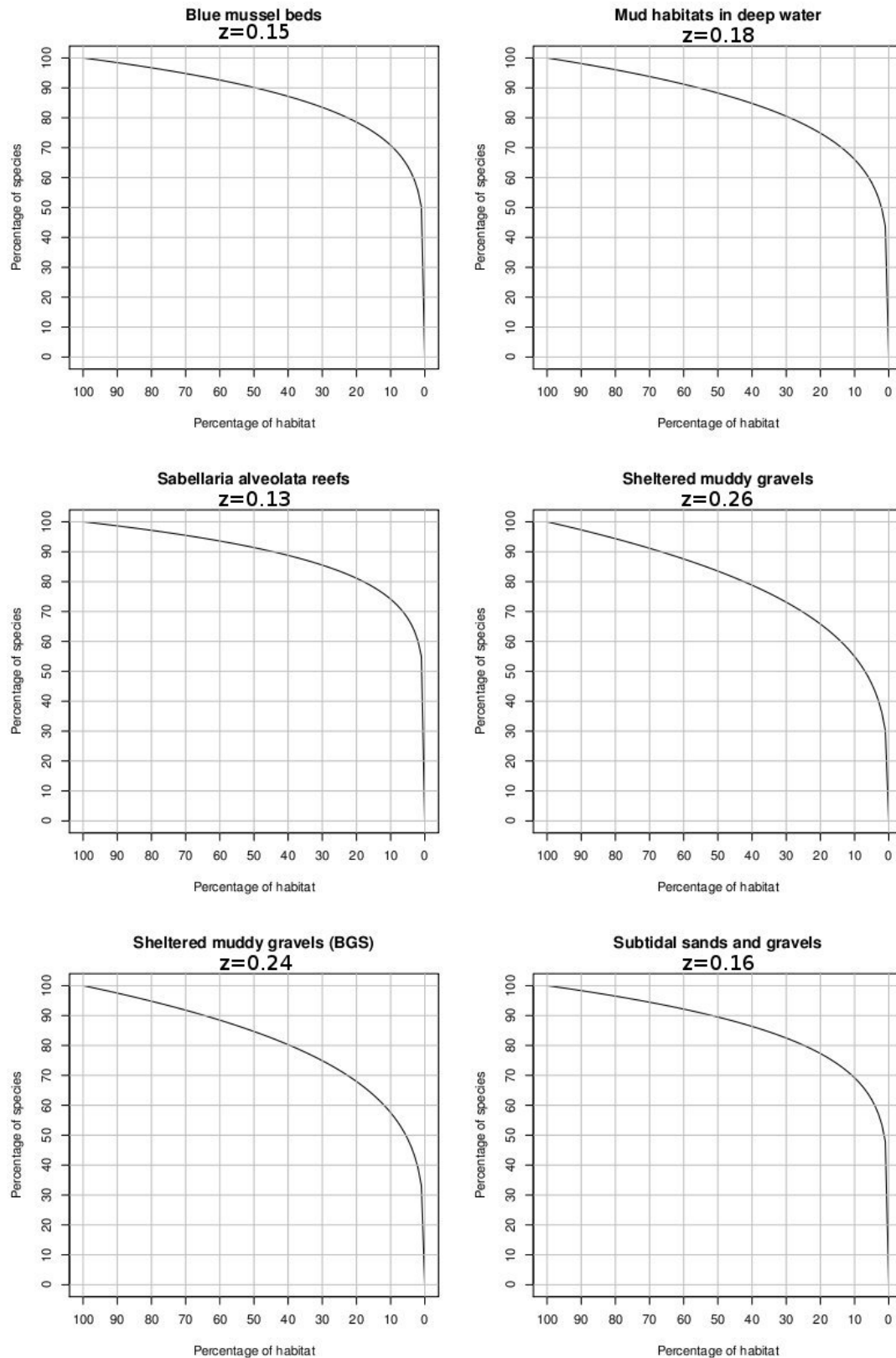


Figure 8. Percentage of species represented in decreasing percentage of habitats of conservation importance.

The expected percentages of species represented in increasing percentages of each habitat type are reported in Table 6 (EUNIS habitat types) and Table 8 (HCI). The percentage of each habitat type necessary to represent increasing percentages of species is reported in Tables 7 and 9 for EUNIS habitat types and HCI respectively. To calculate the exact expected percentage of species in any given percentage of a habitat type other than those shown in Tables 6-9, eq. 3 (page 4) with z values from Tables 4 and 5, should be used.

Table 6. Expected percentages of species represented in increasing percentages of each EUNIS Level 3 habitat type. Values calculated with the Bootstrap estimator of the total number of species and an estimated area of the sampling sites equal to 1 m².

EUNIS Level 3 habitat type	Percentage of species	Percentage of total EUNIS Level 3 habitat type area (10% incremental steps)								
		10%	20%	30%	40%	50%	60%	70%	80%	90%
A1.1		58.8	69.0	75.8	81.0	85.2	88.9	92.1	95.0	97.6
A1.2		58.7	68.9	75.7	80.9	85.2	88.9	92.1	95.0	97.6
A1.3		57.9	68.2	75.1	80.4	84.8	88.6	91.9	94.8	97.5
A2		55.5	66.2	73.5	79.1	83.7	87.7	91.3	94.4	97.3
A3.1		64.8	73.9	79.7	84.2	87.8	90.8	93.5	95.9	98.0
A3.2		63.4	72.7	78.8	83.4	87.2	90.4	93.2	95.7	97.9
A3.3		64.0	73.2	79.2	83.7	87.4	90.6	93.3	95.8	98.0
A4.1		68.7	76.9	82.2	86.1	89.3	92.0	94.4	96.4	98.3
A4.2		66.8	75.4	81.0	85.2	88.6	91.4	93.9	96.2	98.2
A4.3		64.1	73.3	79.2	83.8	87.5	90.6	93.3	95.8	98.0
A5.1		63.3	72.7	78.8	83.4	87.2	90.4	93.2	95.7	97.9
A5.2		65.3	74.2	80.0	84.4	87.9	91.0	93.6	95.9	98.1
A5.3		65.4	74.3	80.1	84.4	88.0	91.0	93.6	96.0	98.1
A5.4		63.7	73.0	79.0	83.6	87.3	90.5	93.3	95.7	98.0
A6		78.4	84.4	88.1	90.8	93.0	94.8	96.3	97.7	98.9
A6.2		82.5	87.5	90.5	92.7	94.4	95.8	97.1	98.2	99.1

Table 7. Estimated percentages of area necessary to represent increasing percentages of species in each EUNIS Level 3 habitat type. Values calculated with the Bootstrap estimator of the total number of species and an estimated area of the sampling sites equal to 1 m².

EUNIS Level 3 habitat type	Percentage of total EUNIS Level 3 habitat type area	Percentage of species (10% incremental steps)								
		10%	20%	30%	40%	50%	60%	70%	80%	90%
A1.1		0.005	0.092	0.536	1.870	4.929	10.879	21.247	37.945	63.283
A1.2		0.005	0.095	0.547	1.900	4.988	10.975	21.379	38.092	63.399
A1.3		0.006	0.114	0.629	2.111	5.401	11.638	22.272	39.079	64.170
A2		0.012	0.186	0.907	2.789	6.669	13.594	24.825	41.824	66.260
A3.1		0.000	0.019	0.166	0.767	2.510	6.617	15.016	30.537	57.116
A3.2		0.001	0.030	0.229	0.980	3.022	7.587	16.520	32.417	58.750
A3.3		0.001	0.025	0.202	0.888	2.807	7.184	15.903	31.654	58.092
A4.1		0.000	0.005	0.062	0.361	1.420	4.349	11.201	25.421	52.379
A4.2		0.000	0.010	0.103	0.534	1.909	5.407	13.041	27.958	54.785
A4.3		0.001	0.024	0.197	0.873	2.770	7.115	15.796	31.521	57.977
A5.1		0.001	0.030	0.231	0.986	3.037	7.615	16.563	32.470	58.795
A5.2		0.000	0.017	0.151	0.712	2.374	6.349	14.589	29.992	56.632
A5.3		0.000	0.016	0.148	0.701	2.346	6.294	14.500	29.877	56.530
A5.4		0.001	0.027	0.213	0.925	2.894	7.348	16.155	31.967	58.363
A6		0.000	0.000	0.001	0.017	0.140	0.787	3.396	12.049	36.818
A6.2		0.000	0.000	0.000	0.002	0.024	0.217	1.382	6.864	28.227

Table 8. Expected percentages of species represented in increasing percentages of each HCI. Values calculated with the Bootstrap estimator of the total number of species and an estimated area of the sampling sites equal to 1 m².

Habitat of conservation importance	Percentage of species	Percentage of total habitat of conservation importance area (10% incremental steps)								
		10%	20%	30%	40%	50%	60%	70%	80%	90%
Blue mussel beds		70.8	78.6	83.5	87.2	90.1	92.6	94.8	96.7	98.4
Mud habitats in deep water		66.1	74.8	80.5	84.8	88.3	91.2	93.8	96.1	98.1
<i>Sabellaria alveolata</i> reefs		74.1	81.1	85.5	88.8	91.4	93.6	95.5	97.1	98.6
Sheltered muddy gravels		55	65.8	73.1	78.8	83.5	87.6	91.1	94.4	97.3
Sheltered muddy gravels (BGS)		57.5	68.0	74.9	80.3	84.7	88.5	91.8	94.8	97.5
Subtidal sands and gravels		69.2	77.3	82.5	86.4	89.5	92.2	94.5	96.5	98.3

Table 9. Expected percentages of area necessary to represent increasing percentages of species in each HCI. Values calculated with the Bootstrap estimator of the total number of species and an estimated area of the sampling sites equal to 1m².

Habitat of conservation importance	Percentage of total habitat of conservation importance area	Percentage of species (10% incremental steps)								
		10%	20%	30%	40%	50%	60%	70%	80%	90%
Blue mussel beds		0	0.002	0.033	0.222	0.984	3.319	9.275	22.591	49.539
Mud habitats in deep water		0	0.013	0.124	0.615	2.126	5.855	13.786	28.947	55.692
<i>Sabellaria alveolata</i> reefs		0	0	0.010	0.087	0.483	1.965	6.433	17.970	44.465
Sheltered muddy gravels		0.014	0.205	0.975	2.948	6.953	14.020	25.364	42.391	66.682
Sheltered muddy gravels (BGS)		0.007	0.122	0.663	2.197	5.568	11.902	22.624	39.465	64.468
Subtidal sands and gravels		0	0.004	0.054	0.326	1314.00	4106.00	10.761	24.792	51.763

The only study that is directly comparable with the finding of this report was the development of targets for each vegetation type listed in the national vegetation classification system for the South Africa's first National Spatial Biodiversity Assessment (NSBA). Available phytosociological survey data were used to estimate the z-value for the species-area relationship. Within this assessment the planning team in consultation with the reference group decided that the goal for statutory reserves should be to represent at least 75% of species that occur in a vegetation type within at least one or more statutory reserves. This goal translates into conservation targets ranging between 16% and 36% of the total extent of vegetation types (Rouget *et al* 2004), which is in line with the results of the present report which show that between 11% and 33% of HCI and between 20% and 32% of EUNIS Level 3 habitat types are necessary to represent 75% of the species. The only exception is represented by EUNIS A6 habitat types, for which the percentage of area required to represent 75% of the species is as low as 7%. This measure has been evaluated as unstable and as such it is strongly recommended that the result should be treated with caution. It is likely that the instability is a result of a low sampling effort in deep-sea habitat types. The low values for the HCIs are also likely to be a result of limited knowledge about their true distribution. The known distribution of HCIs is likely to be a fraction of their historical distribution. If conservation targets for adequacy were applied only to the known extent of HCI they will be misleading, failing to provide adequate protection for these features and create a false sense of security that sufficient action has been taken.

For all species in all habitat types, the percentage of sites where each species is present is very low (ca. 1.5% for the most common species). This is very likely an effect of the overall low sampling effort (relatively few and small sites have been sampled for each habitat type). This is an indication that any habitat-specific conservation target based on these data should be considered an underestimation. More generally, even with improved data, addressing adequacy only at the level of habitat type would not be sufficient. Adequacy can be defined as the ability of selected areas to ensure species persistence (Rondinini *et al* 2006), or in other words to ensure the long-term viability of the population of each species. Population viability is an inherently species-specific property, as it depends on population and spatial parameters of the species (including habitat-specific natality and mortality rates, the minimum size of a habitat patch to contain a viable (sub) population, the dispersal ability of species among habitat patches). The distribution of species usually spans over more than one habitat type. Species do prefer some habitat types over others and as a result are often more common in their preferred habitat and uncommon in their marginal habitat. If adequacy were addressed only at the level of habitat types, species that are rare in a marginal habitat type would drive the target in that habitat type, while in reality they occur there only occasionally. It is recommended that other properties of network design are considered if applying conservation targets related to adequacy, including the distribution of species, connectivity, viability, and replication.

A second reason why adequacy should also be addressed at the species level as well as the habitat level is explained by the following reasoning. Species occur in certain percentage of a habitat type (somewhere between 0% and 100%). Let us consider a hypothetical species that occurs in 40% of a hypothetical habitat type whose area is 100 km². If the conservation target for the habitat type were set to, for example, protecting 20% of its area, and this area is selected randomly with respect to species distributions, the species would be present in 40% of the protected area, and the amount of habitat that it occupies would be 40% * 20% * 100 km² = 8 km². By selecting more habitat at random, doubling the area occupied by the species would require doubling the size of the protected area.

In reality, species could be protected more efficiently by targeting for protection the portions of the habitat types where they are known or expected to occur. This would require a knowledge, at least approximate, of the distribution of the species within the habitat type, to be analysed using a reserve selection algorithm (e.g. the simulated annealing implemented in the software MARXAN [Ball and Possingham 2000]) that could identify the sites, within the habitat type. MARXAN uses a simulated annealing algorithm to minimise the total cost of the reserve system, while achieving a set of conservation goals (typically that a certain percentage of each geographical/biological feature is represented by the reserve system). This would require a good knowledge of the distribution of taxa selected as surrogates of the overall biodiversity. Currently, the paucity of data on benthic species distributions limits the applicability of the method. Yet, at least for the species that have been sampled more intensively, the use of MARXAN would help to further address more satisfactorily the issue of adequacy alongside habitat conservation targets.

3.4.1 Strengths and limitations of this analysis

With the type and amount of data available, species-area curves are the most robust amongst the available methods to set conservation targets for individual marine habitat types in the UK. The main advantages of this method are the repeatability of the analysis, due to the use of quantitative data, and the reliance on a well established piece of ecological theory (Rondinini & Chiozza 2010). The South African National Biodiversity Institute (SANBI) has used this methodology to set targets for each vegetation type listed in the national vegetation classification system for the South Africa's first National Spatial Biodiversity Assessment (NSBA) (Reyers *et al* 2007). The use of this method for setting

targets for MPAs in Europe and the UK has recently been advocated by Smith *et al* (2009). These authors outlined potential solutions to issues related to systematic conservation planning that further enhance the scientific defensibility of this type of planning approach.

The variability around z values with respect to the four different estimators of the total number of species is expected and does not influence significantly the results. Therefore, the z values calculated here are robust in this respect. The Bootstrap estimator requires fewer samples to achieve a stable estimate of the total number of species and therefore has been chosen for the analyses presented in this report. As the Bootstrap estimator always produces the lowest among the four possible z estimates, the resulting targets should always be considered minimum estimates. Averaging the four estimators would change the z values only slightly, with the disadvantage that in some cases stable and unstable estimates would be averaged.

The sensitivity analysis showed that a potentially large source of variability is given by the average size of the sample sites. Although the calculation of z is robust to this uncertainty too, a variation of two orders of magnitude of this value (from 0.5 m² to 25 m²) produces a significant variability in the z values. This variability should be reduced by trying to better define the range of potential variability of the size of sampling sites, by estimating the area sampled with each sampling methodology and the most frequent method used in each habitat type. An additional potential source of uncertainty is the estimate of the total area of each habitat type. If this parameter is underestimated, the total number of species in that habitat type is as well underestimated and the amount of habitat that needs to be protected is underestimated. This is likely to be the case for all the habitats of conservation importance analysed here as not one habitat of conservation importance is mapped across its full extent.

The use of species-area curves for setting conservation targets for habitat types also presents limitations and caveats that should be known while interpreting the results. Most importantly, targets based on species-area curves are aimed only at species representation, and ecological processes are not considered. Conservation targets that consider both species and processes would certainly be larger (Desmet and Cowling 2004). Targets based on species-area curves do implicitly assume that protected sites are connected. Without connectivity and migration of individuals among sites, some of the species represented would go extinct, thus the amount of species represented would decline over time. Also, z values say nothing about where species are located in the landscape, and only if species are distributed randomly in a habitat type, then reserving any given proportion of habitat type should capture roughly the predicted proportion of species targeted (Desmet and Cowling 2004). Another intrinsic problem of targets set using species-area curves is that they ignore complementarity between habitats. Many species occur across a range of different habitats, and this is not taken into account by the species-area curve method, which treats all habitat types independently. Therefore, targeting habitat types to represent a given proportion of species may result in the over-protection of common species and under-protection of rare species, in particular of rare species restricted to one habitat type. For this reason, targets on habitat types should be regarded as coarse-filter targets on overall biodiversity (of which species richness is only one and incomplete indicator), and should be complemented by species-level targets. Many of the above limitations could be overcome by using multiple different datasets within a reserve selection software (e.g. MARXAN).

In addition to the inherent limitations of the method, its application is prone to further uncertainty due to limitations in the data used. Although the data set used here is very large (more than 1.2 million records from almost 30 000 sites), it only represents a small proportion of marine biodiversity in the UK. Moreover, when the species-area curve relationship is applied to habitats that are poorly sampled it will underestimate the z values. As offshore marine habitats are poorly sampled compared to inshore marine habitats there is

a risk of entrenching the bias that already exists in our knowledge regarding these different habitats. Offshore marine habitats are likely to be far more diverse than we currently recognise. This is reflected in the results for the deep-sea habitat types (A6) which failed to reach a stable estimate of total number of species. In addition, the method adopted here for assessing whether species data were sufficient to obtain a stable estimate of the total species numbers for each habitat types, developed by Desmet & Cowling (2004) does not guarantee that the estimated species number would not increase with more data. Indeed, other applications of the species-area curves indicate that as targets are refined with better data they tend to increase rather than decrease (Rouget *et al* 2004). On the other hand, the true number of species in each habitat type is impossible to know as it would require a complete biodiversity inventory.

The estimates presented here represent the best available data on the benthic diversity of marine habitat types in the UK. Yet, due to the limitations and uncertainties outlined above, any conservation targets developed based on these results should be considered as underestimates of the true conservation targets required. This should not deter decision makers from using them. On the contrary, they should be used as a starting point for setting targets that will likely need to be increased in the future. Moreover, following the precautionary approach, where there is uncertainty and known underestimation higher conservation targets should be set than those simply derived from this current analysis. Therefore, a periodical revision of these targets as biodiversity data accumulate is advised.

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Appendix 1. Habitat types

EUNIS Level 3 habitat types

In total there are 56 marine EUNIS Level 3 habitat types. Thirty three EUNIS Level 3 habitat types have been excluded from the current research including:

- Four ice-associated marine habitats as they do not occur in UK waters;
- Six Baltic habitat types as they do not occur in UK waters;
- Ten pelagic water column features as the species-area curve analysis is not suited to these mobile habitats; and
- Five feature habitat types (features of intertidal rock, intertidal sediment, infralittoral rock, circalittoral rock and subtidal sediments) as they are not considered to be broad-scale habitat types.

Descriptions of the EUNIS Level 3 habitat types are provided below, along with information as to whether appropriate spatial data were available for the species-area curve analysis.

EUNIS habitat code	EUNIS habitat name	EUNIS habitat description	Appropriate spatial data available?
A1.1	High energy littoral rock	Extremely exposed to moderately exposed or tide-swept bedrock and boulder shores. Extremely exposed shores dominated by mussels and barnacles, occasionally with robust fucoids or turfs of red seaweed. Tide-swept shores support communities of fucoids, sponges and ascidians on the mid to lower shore.	Yes
A1.2	Moderate energy littoral rock	Moderately exposed shores (bedrock, boulders and cobbles) characterised by mosaics of barnacles and fucoids on the mid and upper shore; with fucoids and red seaweed mosaics on the lower shore. Other shores support communities of mussels and fucoids in the mid to lower shore.	Yes
A1.3	Low energy littoral rock	Sheltered to extremely sheltered rocky shores with very weak to weak tidal streams are typically characterised by a dense cover of fucoid seaweeds which form distinct zones (the wrack <i>Pelvetia canaliculata</i> on the upper shore through to the wrack <i>Fucus serratus</i> on the lower shore).	Yes
A2.1	Littoral coarse sediment	Littoral coarse sediments include shores of mobile pebbles, cobbles and gravel, sometimes with varying amounts of coarse sand. The sediment is highly mobile and subject to high degrees of drying between tides.	Yes

EUNIS habitat code	EUNIS habitat name	EUNIS habitat description	Appropriate spatial data available?
A2.2	Littoral sand and muddy sand	Shores comprising clean sands (coarse, medium or fine-grained) and muddy sands with up to 25% silt and clay fraction. Shells and stones may occasionally be present on the surface. The sand may be duned or rippled as a result of wave action or tidal currents.	Yes
A2.3	Littoral mud	Shores of fine particulate sediment, mostly in the silt and clay fraction (particle size less than 0.063 mm in diameter), though sandy mud may contain up to 40% sand (mostly very fine and fine sand). Littoral mud typically forms extensive mudflats, though dry compacted mud can form steep and even vertical structures, particularly at the top of the shore adjacent to saltmarshes.	Yes
A2.4	Littoral mixed sediments	Shores of mixed sediments ranging from muds with gravel and sand components to mixed sediments with pebbles, gravels, sands and mud in more even proportions.	Yes
A2.5	Coastal saltmarshes and saline reedbeds	Angiosperm-dominated stands of vegetation, occurring on the extreme upper shore of sheltered coasts and periodically covered by spring high tides.	Yes
A2.6	Littoral sediments dominated by aquatic angiosperms	Mid and upper shore wave-sheltered muddy fine sand or sandy mud with the narrow-leaved eel grass <i>Zostera noltii</i> at an abundance of frequent or above.	Yes
A2.7	Littoral biogenic reefs	The Littoral Biogenic Reefs habitat complex contains two biotope complexes (littoral Sabellaria reefs, and mixed sediment shores with mussels), encompassing the littoral biotope dominated by the honeycomb worm <i>Sabellaria alveolata</i> , and littoral <i>Mytilus edulis</i> -dominated communities. <i>S. alveolata</i> can form honeycomb reefs on mid to lower shore on exposed coasts, where there is a plentiful supply of sediment. The underlying substratum may consist primarily of rock or stable cobbles and boulders, or of cobbles and boulders on sand.	Yes
A3.1	High energy infralittoral rock	Rocky habitats in the infralittoral zone subject to exposed to extremely exposed wave action or strong tidal streams. Typically the rock supports a community of kelp <i>Laminaria hyperborea</i> with foliose seaweeds and animals, the latter tending to become more prominent in areas of strongest water movement.	Yes

EUNIS habitat code	EUNIS habitat name	EUNIS habitat description	Appropriate spatial data available?
A3.2	Moderate energy infralittoral rock	This habitat complex occurs on predominantly moderately wave-exposed bedrock and boulders, subject to moderately strong to weak tidal streams. On the bedrock and stable boulders there is typically a narrow band of kelp <i>Laminaria digitata</i> in the sublittoral fringe which lies above a <i>Laminaria hyperborea</i> forest and park. Associated with the kelp are communities of seaweeds, predominantly reds and including a greater variety of more delicate filamentous types than found on more exposed coasts (KFaR).	Yes
A3.3	Low energy infralittoral rock	Infralittoral rock in wave and tide-sheltered conditions, supporting silty communities with <i>Laminaria hyperborea</i> and/or <i>Laminaria saccharina</i> .	Yes
A4.1	High energy circalittoral rock	This habitat complex occurs on extremely wave-exposed to exposed circalittoral bedrock and boulders subject to tidal streams ranging from strong to very strong. Typically found in tidal straits and narrows.	Yes
A4.2	Moderate energy circalittoral rock	This habitat complex mainly occurs on exposed to moderately wave-exposed circalittoral bedrock and boulders, subject to moderately strong and weak tidal streams.	Yes
A4.3	Low energy circalittoral rock	This habitat complex occurs on wave-sheltered circalittoral bedrock and boulders subject to mainly weak/very weak tidal streams. The biotopes identified within this habitat complex are often dominated by encrusting red algae, brachiopods and ascidians.	Yes
A5.1	Sublittoral coarse sediment	Coarse sediments including coarse sand, gravel, pebbles, shingle and cobbles which are often unstable due to tidal currents and/or wave action. These habitats are generally found on the open coast or in tide-swept channels of marine inlets.	Yes
A5.2	Sublittoral sand	Clean medium to fine sands or non-cohesive slightly muddy sands on open coasts, offshore or in estuaries and marine inlets.	Yes
A5.3	Sublittoral mud	Sublittoral mud and cohesive sandy mud extending from the extreme lower shore to offshore, circalittoral habitats. This biotope is predominantly found in sheltered harbours, sealochs, bays, marine inlets and estuaries and stable deeper/offshore areas where the reduced influence of wave action and/or tidal streams allow fine sediments to settle.	Yes

EUNIS habitat code	EUNIS habitat name	EUNIS habitat description	Appropriate spatial data available?
A5.4	Sublittoral mixed sediments	Sublittoral mixed (heterogeneous) sediments found from the extreme low water mark to deep offshore circalittoral habitats. These habitats incorporate a range of sediments including heterogeneous muddy gravelly sands and also mosaics of cobbles and pebbles embedded in or lying upon sand, gravel or mud.	Yes
A5.5	Sublittoral macrophyte-dominated sediment	This complex includes maerl beds, seaweed dominated mixed sediments (including kelps such as <i>Laminaria saccharina</i> and filamentous/foliose red and green algae), seagrass beds, and lagoonal angiosperm communities	Yes
A5.6	Sublittoral biogenic reefs	Sublittoral biogenic reef communities. This complex includes polychaete reefs, bivalve reefs (e.g. mussel beds) and cold water coral reefs. These communities develop in a range of habitats from exposed open coasts to estuaries, marine inlets and deeper offshore habitats and may be found in a variety of sediment types and salinity regimes.	Yes
A6.1	Deep-sea rock and artificial hard substrata	Deep-sea benthic habitats with substrates predominantly of bedrock, immobile boulders or artificial hard substrates.	Yes
A6.2	Deep-sea mixed substrata	Deep-sea benthic habitats with substrates predominantly of mixed particle size or gravel. Includes habitats with mobile substrates of biogenic origin but no longer living, and of allochthonous material such as macrophyte debris. Deep-sea habitats with living biogenic substrates are included in A6.6.	Yes
A6.3	Deep-sea sand	Deep-sea benthic habitats with substrates predominantly of sand.	Yes
A6.4	Deep-sea muddy sand	Deep-sea benthic habitats with substrates predominantly of muddy sand.	No
A6.5	Deep-sea mud	Bathyal and abyssal benthic habitats with substrates predominantly of yellowish or blue-grey mud, relatively consistent, whose population is extremely sparse. This biocoenosis is characterised by constant homothermy and an almost total absence of light.	Yes
A6.6	Deep-sea bioherms	A bioherm is a mound, dome, or reef-like mass of rock that is composed almost exclusively of the remains of sedentary marine organisms and is embedded in rock of different physical character.	No

EUNIS habitat code	EUNIS habitat name	EUNIS habitat description	Appropriate spatial data available?
A6.7	Raised features of the deep-sea bed	Habitats on the deep-sea bed with significant elevation (typically >200m) in relation to their surroundings.	No
A6.8	Deep-sea trenches and canyons, channels, slope failures and slumps on the continental slope	Habitats on the deep-sea bed significantly below the deep-sea bed, including deep ocean trenches.	No
A6.9	Vents, seeps, hypoxic and anoxic habitats of the deep sea	Deep-sea habitats characterised by chemical conditions.	No
A6.X	Deep-sea coarse sediment	Deep-sea benthic habitats with substrates predominantly of coarse sediment.	Yes

Habitats of conservation importance (HCI)

Habitats of conservation importance were identified from the Initial OSPAR List of Threatened and/or Declining Species and Habitats and the UK List of Priority Species and Habitats (UK BAP). The habitats on these lists overlap to some extent as identified in Table 2 which also identifies those habitats where appropriate spatial data were available for the species-area curve analysis.

HCI	UK BAP	OSPAR	Spatial data available?
Blue Mussel beds (including intertidal beds on mixed and sandy sediments) ⁵	Yes	Yes	Yes
Carbonate mounds	Yes	Yes	
Coastal saltmarsh	Yes		Yes
Cold-water coral reefs	Yes	Yes	
Coral Gardens		Yes	
<i>Cymodocea</i> meadows	Yes		
Deep-sea sponge aggregations	Yes	Yes	
Estuarine rocky habitats	Yes		Yes
File shell beds	Yes		
Fragile sponge & anthozoan communities on subtidal rocky habitats	Yes		Yes
Intertidal underboulder communities	Yes		Yes
Intertidal mudflats	Yes	Yes	Yes
Littoral chalk communities	Yes	Yes	Yes
Maerl beds	Yes	Yes	
Horse mussel (<i>Modiolus modiolus</i>) beds	Yes	Yes	
Mud habitats in deep water	Yes		Yes
Sea-pen and burrowing megafauna communities		Yes	

⁵ The UK BAP habitat 'Blue mussel beds' has a wider definition than the OSPAR habitat 'Intertidal mytilus edulis beds on mixed and sandy sediments', which is restricted only to blue mussel beds on intertidal mixed and sandy sediments.

HCI	UK BAP	OSPAR	Spatial data available?
Oceanic ridges with hydrothermal vents/fields	Yes		
<i>Ostrea edulis</i> beds		Yes	
<i>Peat and clay exposures</i>	Yes		
<i>Sabellaria alveolata</i> reefs	Yes		Yes
<i>Sabellaria spinulosa</i> reefs	Yes	Yes	Yes
Saline lagoons	Yes		Yes
Seagrass beds	Yes	Yes	Yes
Seamounts	Yes	Yes	Yes
Serpulid reef		Yes	
Sheltered muddy gravels	Yes		Yes
Subtidal chalk	Yes		Yes
Subtidal sands and gravels	Yes		Yes
Tide-swept channels	Yes		

Appendix 2. Data sources

Dataset/ Derived Data Layer	General Description of Data layer	Specific Data layer Details	Data owner	Further information and availability
MESH EUNIS model (subtidal habitats)	The MESH EUNIS Model map layer is a predictive map based on combining physical data layers. The aim of this work was to use 'habitat envelopes' to predict/model the distribution of broad-scale EUNIS marine habitat types, across the MESH area. Through the development of the EUNIS marine habitat classification, key physical and environmental variables have been identified which are known to drive the distribution of biological communities, and thus EUNIS habitat types in our seas. Each habitat type within EUNIS is defined by its unique combination of environment variables (referred to as the habitat envelope) together with its associated biological community.	Environmental variables are used to define EUNIS habitat types; the upper part of the classification hierarchy (EUNIS levels 1, 2 & 3) is divided based on environmental variables (commonly referred to as the top-down approach). At EUNIS level 3 the classification is split using seabed characteristics in the following three groupings: (1) Seabed substrate (e.g. mud, sand, rock) (2) Biological zone (e.g. infralittoral, circalittoral) (3) Energy - Wave action (e.g. extremely exposed, sheltered) - Tidal currents (e.g. >6 kn, 3-6 kn) As part of the development of the EUNIS classification each habitat type has been defined by its unique combination of environment variables, referred to as the habitat envelope, together with its associated biological community for EUNIS levels 4 and below. The aim of the current study was to use these habitat envelopes to predict the distribution of EUNIS Level 3 types across the study area, using the available environmental variables.	JNCC	See details in MESH EUNIS model report available from: http://www.searchmesh.net/pdf/MESH%20EUNIS%20model.pdf Available to download from: http://www.searchmesh.net/default.aspx?page=1953
EUNIS intertidal map (Phase I Intertidal survey for Wales)	Intertidal Phase 1 survey data: Biotope maps, survey reports, site data & scientific assessment packages for site notification		CCW	Available from CCW on request.

Dataset/ Derived Data Layer	General Description of Data layer	Specific Data layer Details	Data owner	Further information and availability
UKOOA database	Database of offshore benthic environmental surveys in the UK sector of the North Sea containing detailed biological, chemical and locational data.	This database holds benthic species location information for the north sea, a version of this database is available in Marine Recorder snapshot format from JNCC. This database was commissioned by the Oil & Gas UK to provide a comprehensive review of seabed environmental surveys carried out by, or on behalf of the UK North Sea offshore operators.	UKOOA	http://www.ukooa.co.uk/issues/ukbenthos/ Available from: http://www.ukooa.co.uk/issues/ukbenthos/ and from JNCC on request in Marine Recorder format."
Marine Recorder	The Marine Recorder application is used to store marine benthic biological data, both species and biotope records. It is the main database used by the conservation agencies (CCW, EHS, SNH, Natural England (formally English Nature)) to hold marine monitoring habitat data for Special Areas of Conservation (SACs).	The Marine Recorder snapshot database holds > 4 million benthic species records and > 4000 benthic biotope records across the full range of marine biodiversity in our seas.	JNCC	See http://esdm.co.uk/MarineRecorder/index.html and http://www.jncc.gov.uk/page-1599 Marine Recorder database available from JNCC on request. Please note that this database is updated every 6 months.
Habitats of conservation importance	Distribution maps for the habitats of conservation importance derived from the Initial OSPAR List of Threatened and/or Declining Species and Habitats and the UK List of Priority Species and Habitats (UK BAP). Points and polygon records for the 31 habitats of conservation importance in the UK marine area.	Habitats included in this work are: Blue mussel beds Coastal saltmarsh Estuarine rocky habitats Fragile sponge & anthozoan communities on subtidal rocky habitats Intertidal boulder communities Intertidal mudflats Littoral chalk communities Mud habitats in deep water Sabellaria alveolata reefs Sabellaria spinulosa reefs Saline lagoons Seagrass beds Seamounts Sheltered muddy gravels Subtidal chalk Subtidal sands and gravels	Defra	Delivered as part of the MB102 contract. For further details on the contract please see: http://randd.defra.gov.uk/Document.aspx?Document=MB0102_8061_IR.pdf For detailed information on this particular dataset please contact JNCC.

Appendix 3. Methods for estimating the total number of species

The function *specpool* in the package *vegan* (Oksanen *et al* 2009) for R was used to estimate the total number of species per habitat type (y_2). The function estimates the extrapolated species richness in a species pool, or the number of unobserved species. It is based on incidences in sample sites and uses the following four alternative equations :

Chao:
$$S_T = S_o + a_1^2 / (2 * a_2)$$

First order Jackknife (Jackknife 1):
$$S_T = S_o + a_1 * (n-1) / n$$

Second order Jackknife (Jackknife 2):
$$S_T = S_o + a_1 * (2 * n - 3) / n - a_2 * (n-2)^2 / (n * (n-1))$$

Bootstrap:
$$S_T = S_o + \text{Sum}(1 - p_i)^n$$

where S_T is the extrapolated richness in a pool, S_o is the observed number of species in the collection, a_1 and a_2 are the number of species occurring only in one or only in two sites in the collection, p_i is the frequency of species i , and n is the number of sites in the collection.

The estimation of the total number of species with increasingly large random sub-samples was made using the function *poolaccum*, which estimates extrapolated richness indices of *specpool* for random ordering of sampling units.

Appendix 4. Further results

Table S1. Minimum number of sampling sites needed for a stable estimate of the number of species for each EUNIS habitat type, based on four estimators of total species number. Habitat types with insufficient samples to reach a stable estimate are in italics⁶.

EUNIS Level 3 habitat type	Number of sampling sites	Minimum number of sites for a stable estimate				Stable
		Chao	Jackknife 1	Jackknife 2	Bootstrap	
High energy intertidal rock	302	202	157	164	156	yes
Moderate energy intertidal rock	141	130	119	127	112	yes
Low energy intertidal rock	200	167	161	161	161	yes
Intertidal sediment	1542	1004	950	985	924	yes
Intertidal coarse sediment	88	84	83	83	83	<i>no</i>
Intertidal sand and muddy sand	778	667	663	666	663	<i>no</i>
Intertidal mud	222	200	200	199	200	<i>no</i>
Intertidal mixed sediments	59	49	48	47	48	<i>no</i>
Coastal saltmarshes and saline reedbeds	62	59	59	59	59	<i>no</i>
Intertidal sediments dominated by aquatic angiosperms	26	23	21	22	19	<i>no</i>
Intertidal biogenic reefs	133	123	109	112	110	<i>no</i>
High energy infralittoral rock	257	196	139	163	115	yes
Moderate energy infralittoral rock	396	234	149	178	134	yes
Low energy infralittoral rock	1714	272	188	216	182	yes
High energy circalittoral rock	106	93	73	74	74	yes
Moderate energy circalittoral rock	125	99	86	93	91	yes
Low energy circalittoral rock	710	611	596	605	571	yes
Subtidal coarse sediment	8532	549	356	493	327	yes
Subtidal sand	9065	663	281	389	276	yes
Subtidal mud	2064	616	336	464	316	yes

⁶ The method for defining the cut-off is detailed in the paragraph on Assessment of data availability for the development of species-area curves, page 6.

EUNIS Level 3 habitat type	Number of sampling sites	Minimum number of sites for a stable estimate				Stable
		Chao	Jackknife 1	Jackknife 2	Bootstrap	
Subtidal mixed sediments	1922	722	333	464	307	yes
Deep-sea bed	108	104	99	100	96	no
Deep-sea rock and artificial hard substrata	0	-	-	-	-	no
Deep-sea mixed substrata	60	23	13	16	13	yes
Deep-sea sand	2	-	-	-	-	no
Deep-sea mud	29	25	24	25	23	no
Deep-sea coarse sediment	17	14	10	11	10	no

Table S2. Minimum number of sampling sites needed for a stable estimate of the number of species for each HCI, based on four estimators of total species number. Habitat types with insufficient samples to reach a stable estimate are in italics.

Habitats of conservation importance	Number of sampling sites	Minimum number of sites for a stable estimate				Stable
		Chao	Jackknife 1	Jackknife 2	Bootstrap	
Blue mussel beds	106	95	72	76	71	yes
<i>Coastal saltmarsh</i>	179	171	164	165	161	<i>no</i>
<i>Estuarine rocky communities</i>	73	69	64	65	64	<i>no</i>
<i>Fragile sponge & anthozoan communities on subtidal rocky habitats</i>	12	9	9	9	9	<i>no</i>
<i>Intertidal boulder communities</i>	18	15	15	15	15	<i>no</i>
<i>Intertidal mudflats</i>	1088	983	945	957	935	<i>no</i>
<i>Littoral chalk communities</i>	10	7	7	7	7	<i>no</i>
Mud habitats in deep water	328	265	245	249	246	yes
<i>Mud habitats in deep water (BGS)</i>	79	76	70	70	70	<i>no</i>
<i>Sabellaria alveolata</i> reefs	62	54	32	45	26	yes
<i>Sabellaria spinuolsa</i> reefs	252	221	214	215	211	<i>no</i>
<i>Saline lagoons</i>	313	277	260	260	260	<i>no</i>
<i>Seagrass beds</i>	0	-	-	-	-	<i>no</i>
<i>Seamounts</i>	13	10	9	10	9	<i>no</i>
Sheltered muddy gravels	1413	318	228	250	228	yes
Sheltered muddy gravels (BGS)	4917	846	389	564	311	yes
<i>Subtidal chalk</i>	124	108	105	105	105	<i>no</i>
Subtidal sands and gravels	243	149	113	129	116	yes
Subtidal sands and gravels (BGS)*						

*Note the analysis for subtidal sands and gravels derived from BGS data has not been completed due to the large and complex nature of the dataset.

Table S3. Estimated total number of species in each EUNIS habitat type based on four different estimators. Unstable estimates, for habitats without sufficient samples, are in italics. S.E.: standard error. No formula was available to calculate the S.E. For the Jackknife 2 estimator.

EUNIS	Number of species collected	Chao	S.E. Chao	Jack. 1	S.E. Jack. 1	Jack. 2	Boot.	S.E. Boot.
A1.1	1394	2024.66	76.19	1893.34	71.92	2194.00	1614.63	43.90
A1.2	1085	1920.56	100.90	1614.22	119.65	1973.27	1309.66	67.87
A1.3	981	1642.42	82.91	1455.62	107.70	1758.42	1183.84	62.40
A2	1908	2600.48	72.15	2558.52	124.76	2903.24	2200.62	81.35
A2.1	282	764.23	101.40	485.66	76.73	644.47	363.88	40.20
A2.2	1505	2134.94	68.63	2099.24	152.89	2412.79	1770.94	95.96
A2.3	552	893.96	55.31	828.75	84.12	992.77	671.80	50.16
A2.4	787	1287.63	67.75	1179.24	130.05	1413.75	957.26	75.02
A2.5	409	3316.03	724.28	744.50	264.93	1055.46	536.81	130.11
A2.6	76	144.06	33.35	109.65	10.90	133.99	90.05	5.65
A2.7	396	657.59	51.90	584.57	46.07	704.27	476.67	26.86
A3.1	1250	1820.63	72.11	1705.22	69.43	1977.80	1448.99	39.22
A3.2	1364	1921.07	70.49	1816.85	58.14	2084.96	1563.10	35.85
A3.3	2636	3381.39	76.06	3317.60	44.84	3687.35	2941.63	28.92
A4.1	632	851.41	37.52	866.76	50.27	974.90	739.00	34.50
A4.2	1012	1450.06	57.70	1416.74	79.68	1632.76	1193.77	56.96
A4.3	1662	2410.88	82.00	2268.15	170.17	2628.47	1928.18	100.01
A5.1	4584	5329.06	69.33	5383.91	44.75	5753.87	4955.45	30.83
A5.2	4774	5565.06	74.00	5571.91	46.07	5966.87	5141.27	29.96
A5.3	3076	3707.99	68.02	3682.71	64.76	3997.54	3352.59	40.99
A5.4	3115	3720.09	61.16	3789.65	56.00	4087.53	3430.58	45.04
A6	1145	1693.51	74.15	1548.23	187.37	1800.87	1319.91	98.56
A6.1	-	-	-	-	-	-	-	-
A6.2	775	969.01	36.74	966.75	30.88	1062.12	863.24	17.45
A6.3	292	1788.33	358.06	426.00	183.75	426.00	359.00	111.48
A6.5	256	393.81	36.55	357.38	41.03	419.23	300.44	21.18
A6.X	317	447.01	30.30	438.41	39.06	499.29	372.17	24.04

Table S4. Estimated total number of species in each HCI based on four different estimators. Unstable estimates, for habitats without sufficient samples, are in italics. S.E.: standard error. No formula was available to calculate the S.E. For the Jackknife 2 estimator.

HCI	No of species collected	Chao	S.E. Chao	Jack. 1	S.E. Jack. 1	Jack. 2	Boot.	S.E. Boot.
Blue mussel beds	466.00	758.32	55.59	672.04	44.33	804.20	555.00	26.26
<i>Coastal saltmarsh</i>	394.00	752.89	68.74	608.79	66.30	758.47	483.46	37.24
<i>Estuarine rocky communities</i>	584.00	1324.28	113.74	942.03	98.08	1209.72	730.55	50.60
<i>Fragile sponge & anthozoan communities on subtidal rocky habitats</i>	28.00	34.00	4.58	39.00	5.98	39.91	33.58	4.49
<i>Intertidal boulder communities</i>	248.00	1168.11	257.99	419.89	94.22	566.61	315.69	45.72
<i>Intertidal mudflats</i>	1372.00	2049.58	74.16	1968.45	176.04	2302.08	1633.10	104.70
<i>Littoral chalk communities</i>	353.00	841.00	91.08	572.60	93.15	724.42	445.67	43.36
Mud habitats in deep water	1500.00	2058.03	62.76	2052.31	131.87	2330.45	1750.52	85.93
<i>Mud habitats in deep water (BGS)</i>	205.00	352.35	39.92	306.70	33.28	372.45	248.10	20.32
<i>Sabellaria alveolata reefs</i>	688.00	1056.17	66.95	919.21	47.87	1075.24	786.65	24.70
<i>Sabellaria spinuolsa reefs</i>	971.00	1547.14	80.59	1359.45	105.57	1615.93	1137.38	59.90
<i>Saline lagoons</i>	863.00	1407.91	73.15	1272.69	98.32	1527.54	1040.38	61.52
<i>Seagrass beds</i>	0	-	-	-	-	-	-	-
<i>Seamounts</i>	140.00	164.51	9.35	184.31	16.92	188.47	162.84	12.99
Sheltered muddy gravels	1937.00	2415.39	56.95	2428.65	42.15	2667.49	2163.19	28.32
Sheltered muddy gravels (BGS)	3916.00	4770.40	78.31	4751.83	77.45	5178.74	4296.56	48.24
<i>Subtidal chalk</i>	861.00	1434.49	76.10	1280.59	129.54	1544.53	1041.37	75.56
Subtidal sands and gravels	1396.00	1866.00	57.29	1865.06	66.37	2099.09	1610.01	45.45
Subtidal sands and gravels (BGS)*								

*Note the analysis for subtidal sands and gravels derived from BGS data has not been completed due to the large and complex nature of the dataset.

Table S5. Estimated z value for each EUNIS habitat type based on the Chao estimator of the total number of species and on four estimates of the size of the average area of sample sites.

EUNIS L.3	Name	z (0.5 m²)	z (1 m²)	z (10 m²)	z (25 m²)
A1.1	High energy intertidal rock	0.23	0.24	0.33	0.36
A1.2	Moderate energy intertidal rock	0.23	0.25	0.36	0.39
A1.3	Low energy intertidal rock	0.24	0.26	0.36	0.39
A2	Intertidal sediments	0.25	0.26	0.34	0.36
A3.1	High energy infralittoral rock	0.19	0.20	0.26	0.28
A3.2	Moderate energy infralittoral rock	0.19	0.21	0.27	0.29
A3.3	Low energy infralittoral rock	0.19	0.20	0.25	0.27
A4.1	High energy circalittoral rock	0.16	0.17	0.22	0.23
A4.2	Moderate energy circalittoral rock	0.17	0.18	0.24	0.25
A4.3	Low energy circalittoral rock	0.19	0.20	0.25	0.27
A5.1	Subtidal coarse sediment	0.19	0.20	0.24	0.26
A5.2	Subtidal sand	0.18	0.19	0.23	0.24
A5.3	Subtidal mud	0.18	0.19	0.23	0.24
A5.4	Subtidal mixed sediments	0.19	0.20	0.25	0.26
A6	Deep-sea bed	0.11	0.12	0.14	0.15
A6.2	Deep-sea mixed substrata	0.08	0.09	0.11	0.11

Table S6. Estimated z value for each EUNIS habitat type based on the Jackknife 1 estimator of the total number of species and on four estimates of the size of the average area of sample sites.

EUNIS L.3	Name	z (0.5 m²)	z (1 m²)	z (10 m²)	z (25 m²)
A1.1	High energy intertidal rock	0.22	0.24	0.33	0.36
A1.2	Moderate energy intertidal rock	0.22	0.24	0.34	0.37
A1.3	Low energy intertidal rock	0.23	0.25	0.35	0.38
A2	Intertidal sediments	0.25	0.26	0.34	0.35
A3.1	High energy infralittoral rock	0.18	0.20	0.26	0.27
A3.2	Moderate energy infralittoral rock	0.19	0.21	0.27	0.29
A3.3	Low energy infralittoral rock	0.19	0.20	0.25	0.27
A4.1	High energy circalittoral rock	0.16	0.17	0.22	0.23
A4.2	Moderate energy circalittoral rock	0.17	0.18	0.24	0.25
A4.3	Low energy circalittoral rock	0.19	0.20	0.25	0.26
A5.1	Subtidal coarse sediment	0.19	0.20	0.25	0.26
A5.2	Subtidal sand	0.18	0.19	0.23	0.24
A5.3	Subtidal mud	0.18	0.19	0.23	0.24
A5.4	Subtidal mixed sediments	0.19	0.20	0.25	0.26
A6	Deep-sea bed	0.11	0.11	0.14	0.14
A6.2	Deep-sea mixed substrata	0.08	0.09	0.11	0.11

Table S7. Estimated z value for each EUNIS habitat type based on the Jackknife 2 estimator of the total number of species and on four estimates of the size of the average area of sample sites.

EUNIS L.3	Name	z (0.5 m ²)	z (1 m ²)	z (10 m ²)	z (25 m ²)
A1.1	High energy intertidal rock	0.23	0.25	0.34	0.37
A1.2	Moderate energy intertidal rock	0.24	0.26	0.36	0.39
A1.3	Low energy intertidal rock	0.24	0.26	0.36	0.39
A2	Intertidal sediments	0.25	0.27	0.35	0.37
A3.1	High energy infralittoral rock	0.19	0.20	0.27	0.29
A3.2	Moderate energy infralittoral rock	0.20	0.21	0.28	0.30
A3.3	Low energy infralittoral rock	0.19	0.20	0.26	0.27
A4.1	High energy circalittoral rock	0.17	0.18	0.23	0.24
A4.2	Moderate energy circalittoral rock	0.18	0.19	0.24	0.26
A4.3	Low energy circalittoral rock	0.19	0.21	0.26	0.27
A5.1	Subtidal coarse sediment	0.19	0.20	0.25	0.26
A5.2	Subtidal sand	0.18	0.19	0.23	0.24
A5.3	Subtidal mud	0.18	0.19	0.24	0.25
A5.4	Subtidal mixed sediments	0.19	0.20	0.25	0.27
A6	Deep-sea bed	0.11	0.12	0.14	0.15
A6.2	Deep-sea mixed substrata	0.09	0.09	0.11	0.12

Table S8. Estimated z value for each HCI based on the Chao estimator of the total number of species and on four estimates of the size of the average area of sample sites.

HCI	z (0.5 m ²)	z (1 m ²)	z (10 m ²)	z (25 m ²)
Blue mussel beds	0.15	0.17	0.22	0.24
Mud habitats in deep water	0.18	0.19	0.24	0.25
<i>Sabellaria alveolata</i> reefs	0.14	0.15	0.22	0.24
Sheltered muddy gravels	0.25	0.27	0.37	0.40
Sheltered muddy gravels (BGS)	0.23	0.24	0.31	0.33
Subtidal sands and gravels	0.15	0.16	0.20	0.21

Table S9. Estimated z value for each HCI based on the Jackknife 1 estimator of the total number of species and on four estimates of the size of the average area of sample sites.

HCI	z (0.5 m ²)	z (1 m ²)	z (10 m ²)	z (25 m ²)
Blue mussel beds	0.15	0.16	0.21	0.23
Mud habitats in deep water	0.18	0.19	0.24	0.25
<i>Sabellaria alveolata</i> reefs	0.13	0.14	0.20	0.22
Sheltered muddy gravels	0.25	0.27	0.37	0.40
Sheltered muddy gravels (BGS)	0.23	0.24	0.31	0.33
Subtidal sands and gravels	0.15	0.16	0.20	0.21

Table S10. Estimated z value for each HCI based on the Jackknife 2 estimator of the total number of species and on four estimates of the size of the average area of sample sites.

HCI	z (0.5 m²)	z (1 m²)	z (10 m²)	Z (25 m²)
Blue mussel beds	0.16	0.17	0.22	0.24
Mud habitats in deep water	0.18	0.19	0.24	0.26
<i>Sabellaria alveolata</i> reefs	0.14	0.15	0.22	0.24
Sheltered muddy gravels	0.26	0.28	0.38	0.41
Sheltered muddy gravels (BGS)	0.23	0.24	0.32	0.34
Subtidal sands and gravels	0.16	0.17	0.21	0.22