Taxonomic composition and recording of priority habitat maerl using citizen science data

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Taxonomic composition and recording of priority habitat maerl using citizen science data

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Further information

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Executive summary

Natural England has a statutory obligation to monitor and report on species and habitats in designated MPAs. This is particularly important if the UK is to meet legislation adopted from the EU Marine Strategy Framework Directive and achieve Good Environmental Status. One important aspect of monitoring protected areas requires establishment of current status and any changes in composition of assemblages of species in these habitats. Such monitoring is challenging because benthic habitats are hugely diverse, long term data trends are often lacking, and methods are insufficient to describe habitat condition or identify pressure indicators. Thus, Natural England seeks alternative sources of information to understand current conditions in priority habitats such as maerl beds.

This is a report to Natural England (NE) about the biological records for maerl held in the Seasearch database. The overarching intention is to explore distributions and spatial variability in composition of maerl biotopes. Specific objectives included comparison of diversities and compositions of assemblages of benthic taxa in 1) named maerl biotopes at Levels 4 and 5 in the JNCC marine habitat classification (MHC; Connor *et al.*, 2004) from different areas of Britain and Ireland and 2) named maerl biotopes against other biotopes that contain maerl (Level 4 only) from England. A new system for categorising maerl habitat was applied to all existing English records of maerl in the Seasearch database (Axelsson, 2022). Maps were then created showing distributions of these categories of habitat in relation to known distribution of maerl biotopes from the MHC.

There were no differences in diversity among samples of Level 4 maerl biotope (SS.SMp.Mrl) from different areas of Britain and Ireland, but multivariate analyses of taxonomic composition showed differences between southern and northern areas. Similarly, there were no differences in diversity between different Level 5 maerl biotopes from different areas, but taxonomic composition of Level 5 biotopes in Scotland differed from those further South. Different Level 5 maerl biotopes from England did not differ in composition. Level 4 maerl biotope from England had similar taxonomic composition to samples of infralittoral mixed sediment (SS.SMx.IMx) that contained maerl, but differed significantly from all other Level 4 biotopes with maerl. Patterns observed are likely caused by a combination of actual patterns plus the confounding effects of small sample-sizes and inaccurate determinations of maerl biotopes. The latter is a consequence of the inability of the MHC to capture the diversity of maerl habitats and a lack of clear guidance about how to record maerl habitat.

Distributions of different maerl habitats clearly occur more broadly than the known distributions of MHC maerl biotopes. Maps of a broader range of maerl habitats (including for example, dead maerl, veneers and small patches) will permit

assessment of where and whether ecologically-valuable maerl habitat merits protection over and above existing conservation designations.

Where statutory nature conservation bodies are legally obliged to monitor and conserve priority features of conservation interest, but where data are challenging to collect, records collected by trained volunteers and curated by Seasearch can make valuable contributions to our understanding and responsibilities. Consistency and quality of such records will be much improved if approved national guidance is made available.

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1 INTRODUCTION

1.1 Seasearch

Seasearch is a volunteer underwater survey project for recreational divers and snorkellers to record observations of marine habitats and the life they support. The information gathered is used to increase our knowledge of the marine environment and contribute towards its conservation. In its earliest incarnation, Seasearch coordination came under the remit of a Steering Group led by the Marine Conservation Society (MCS) and comprising representatives from the UK statutory nature conservation bodies (NRW, EHS(NI), JNCC, NE, NatureScot), the Environment Agency, The Wildlife Trusts, the Marine Biological Association, the diver training agencies (BSAC, PADI, SAA, SSAC), Nautical Archaeology Society and independent marine life experts. In recent years, the project has been delivered in partnership by local coordinators under contract to the MCS and, in some areas, employees of the local Wildlife Trust. Overall coordination and financial under-writing of the project has been the responsibility of the Marine Conservation Society. Ongoing financial support comes in part from NatureScot (funding Seasearch activities in Scotland), Natural Resources Wales (ditto in Wales) and Natural England (specific projects within England), as well as various other grants (restricted and unrestricted). Volunteers can participate in training courses and many dive surveys organized during the season. For more information visit www.seasearch.org.uk.

The objectives of the Seasearch programme are to:

- Gather information on seabed habitats and associated wildlife throughout Britain and Ireland, by the participation of recreational SCUBA divers and snorkellers;
- Provide standardized training to enable volunteer divers and snorkellers to participate in Seasearch surveys or undertake their own independent surveys and report back what they find;
- Ensure the quality of the data gathered;
- Make the data available through websites, reports, and publications;
- Raise awareness of the diversity of marine life in Britain and Ireland and its environment through participation of volunteer divers/snorkellers and dissemination of information.

The Seasearch programme has collected, maintains and uses almost 800,000 records of taxa or habitats. This exceeds the MNCR (jointly supplied by JNCC and English Nature/NE) with 593,313 taxon records. Seasearch records are broadly recognised as a robust and reliable source of data and information (e.g. Pikesley *et al.*, 2016), in part due to the careful and ongoing process of quality assurance (Bolton, 2018). Seasearch data have already been used effectively by statutory nature conservation bodies (SNCB) to support designation of marine protected areas (MPA), making use of information about distributions of features of conservation interest.

1.2 Marine Conservation Society

The Marine Conservation Society is the UK Charity dedicated to the protection of the marine environment and its wildlife. Since its formation in 1983, MCS has become a recognized authority on marine and coastal conservation and produces the Good Fish Guide (https://www.mcsuk.org/goodfishguide/) in addition to promoting public participation in volunteer projects and surveys such as Great British Beach Clean, Adopt-a-Beach, Seasearch and Basking Shark Watch.

1.3 Background

This is a report to Natural England (NE) about the distribution of habitats containing maerl and their taxonomic composition in records collected since 2000 (21 years), that are held and curated by Seasearch.

As part of its vision for the marine environment (DEFRA, 2002), the UK Government made a commitment to achieve “clean, healthy, safe, productive and biologically diverse oceans and seas”. To do this, we clearly need to expand our understanding of the marine environment, and this need has been established as one of the six policies of the Governments 25 Year Environment Plan for sustainable farming and fisheries (DEFRA, 2018). The concept that “sound evidence and monitoring underpins effective marine management and policy development” is clearly embedded in the High-Level Marine Objectives of the UK Government (DEFRA, 2009).

The UK has a large marine extent and a great variety of habitats supporting a wealth of biodiversity, for which comprehensive monitoring presents a considerable challenge. Natural England has a statutory obligation to monitor and report on designated species and habitats (conservation features). Designated features include maerl, both as a species and a habitat. To provide appropriate guidance on protection and management of such features, current knowledge about their distribution and

condition is crucial. These obligations require data that can provide robust results and information. To rise to the challenges presented when monitoring marine biodiversity in the present climate and circumstance, there is a need to identify new and innovative ways to collect more data or make more efficient use of existing data, including those from citizen science projects.

1.4 Maerl

Maerl is the common and collective term used for unattached nodules ('rhodoliths') of several free-living, unattached species of coralline red algae (Riosmena-Rodriguez, R. Peña-Freire *et al.*, 2016) including in the UK, *Phymatolithon calcareum*, *Lithothamnion corallioides*, *Lithothamnion glaciale* and *Lithophyllum fasciculatum* (OSPAR, 2008). These are slow-growing species, but over time, with growth and fragmentation, can develop into beds of complex biogenic habitat. Maerl beds are recognised as biogenic habitats that are valuable for multiple reasons. The complex, 3D matrix of such maerl beds can: support a diverse range of organisms often in large densities (Birkett, Maggs and Dring, 1998; Hall-Spencer, 1998; Barbera *et al.*, 2003; Jackson *et al.*, 2004; Axelsson *et al.*, 2008; Peña *et al.*, 2014; Sheehan, Bridger and Attrill, 2015); support rare and endemic species (Hall-Spencer, 1998; Axelsson *et al.*, 2008); function as a nursey for ecologically or commercially important species including scallops, clams, cod, crab and sea urchin (Hall-Spencer *et al.*, 2003; Kamenos, Moore and Hall-Spencer, 2004b, 2004a); and can provide spatial and biochemical benefits that encourage the settlement of a range of taxa (Jackson *et al.*, 2004; Kamenos, Moore and Hall-Spencer, 2004b, 2004a; Roberts, Barker and Mladenov, 2010).

Definitions of what constitutes a maerl biotope are not universally agreed but are typically designated when there is at least 20% seabed cover of maerl (dead or live) with the habitat covering an area at least 25m^2, providing 3D structure and with maerl thalli >1cm in size (Mercer *et al.*, 2018; Axelsson, 2022). These criteria for categorisation as a maerl biotope exclude many of the conditions where maerl occurs, thereby often missing much of the value provided by maerl habitat.

Whilst the Marine Habitat Classification (MHC) includes biotopes (at Levels 5 and 6) that refer to particular species of maerl (see Results for details), it is increasingly recognised that achieving this degree of taxonomic resolution is not possible without microscopic examination of reproductive structures or genetic testing of specimens. Thus, recorded distributions for maerl species (see NBN maps in Axelsson, 2022) and for biotopes including these species may be inaccurate due to errors in historic identification based on morphology only.

There is increasing recognition that the MHC is inadequate to capture the diversity of conditions in which maerl occurs and that this inadequacy hinders full recognition of the distribution of maerl habitat with implications for its designation, protection and

management. Being able to label assemblages and their physical habitat is a useful and convenient approach, but not without problems. For instance, there is large regional variation in physical habitat and the ways in which taxa co-occur; the MHC is not (yet) able to accommodate this variety for maerl, meaning that observed assemblages do not always fit neatly into defined pigeonholes. Obvious examples of this include occurrence of veneers of extensive maerl over rocky substrata which do not match well with maerl biotopes on sedimentary substrata.

Selley (2016) states that “the use of a percentage coverage threshold of live / dead maerl to define maerl beds has no scientific evidence to be justified as an approach”. It is not clear whether this refers to either or both of:

- the use of a minimal threshold of maerl (whether live or dead) to merit classification as a maerl biotope or ‘bed’ (as in the typical criteria described above)
- the use of some ratio in percentage cover of live:dead maerl to merit classification as a maerl biotope or ‘bed’

Whichever was originally intended, observations which might indicate that thresholds in percentage-cover lack utility include:

- A lack of scientific evidence that indicates that the current, arbitrary minimal threshold of 20% is appropriate;
- Diverse assemblages, nursery function and/or rare taxa being supported in habitats where cover of maerl is less than the current minimal threshold of 20%.
- Diverse assemblages, nursery function and/or rare taxa being supported in habitats where there is little or no live maerl;
- Thin veneers of gravel with small amounts of live maerl contributing to extensive covers of dead maerl gravel in adjacent habitat;
- Mobile veneers of maerl-rich sediment changing in position, extent and percentage cover.

Whilst use of a single arbitrary threshold is clearly sub-optimal, there must come a point below which percentage-cover declines where a habitat ceases reasonably to be or function as a maerl ‘bed’ or maerl biotope (e.g. by acting as substratum for larval settlement Roberts, Barker and Mladenov, 2010). Selley (2016) recommends that for management, records of maerl should be considered on a case-by-case

basis, but this does not help with development of guidance about how best to record information about maerl habitat (particularly for citizen scientists), or for how post-survey assessors should determine biotopes from assemblages of species that include maerl.

This lack of clarity results in inconsistent reporting in the Seasearch database such that:

- Some habitats are not determined as maerl biotope, but have very large abundance of maerl.
- Some habitats are determined as maerl biotope, but do not have lots of maerl.
- The Manacles MCZ and Purbeck coast MCZ have maerl as a feature, but although there have been many Seasearch dives there, none have been determined as having maerl biotopes, even when it is abundant.

Other recommendations by Selley (2016) include consideration of areas >5m^2 (rather than >25m^2) for designation where:

- habitat is determined as a maerl biotope;
- maerl is present as Superabundant, Abundant or Frequent[1] (on SACFOR scale) if sourced from a single observation (large abundance suggests an established maerl bed);
- if clusters of maerl records at smaller abundance occur within a relatively small area, expert judgement may be used to assess whether these provide evidence of maerl beds;
- Low density records of live maerl and records which have not been classified to species level (i.e. ‘maerl indet.’ or ‘Melobesioideae’) should also be considered as potential maerl.

[1] Although Selley (2016) refers here to the ‘Frequent’ category, I believe that it should refer instead to ‘Common’ (that being the category adjacent to ‘Abundant’).

The distribution of maerl is dependent on particular environmental conditions and consequently has a patchy distribution around the UK (Figure 1). Maerl habitats vary in the composition of maerl-forming species. In England, *Phymatolithon calcareum* and *Lithothamnion corallioides* occur in the southwest (Figure 2) and although *L. glaciale* is considered a more northern species, it also occurs along the south coast westwards from the Isle of Wight (Birkett, Maggs and Dring, 1998; MCCIP, 2018; NBNAtlas, 2021). The recently described *L. erinaceum* and *P. lusitanicum* occur in northern waters.

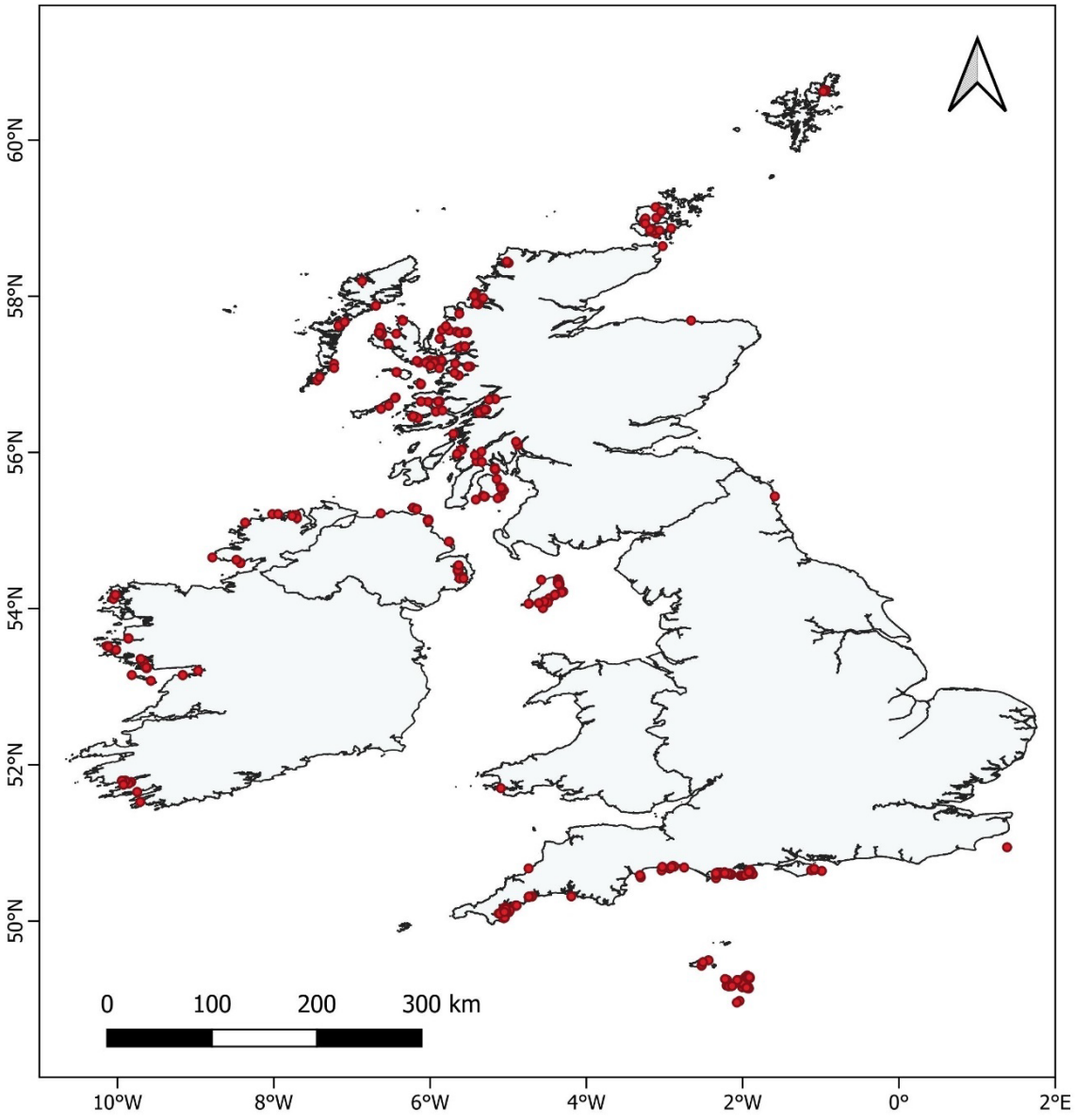


Figure 1. Distribution of maerl records around the UK and Ireland made by Seasearch between 2000-2020.

The largest maerl habitats in England are found in and around the Fal Estuary (NE, 2000). Other noteworthy maerl habitats occur at The Manacles, Helford River, Falmouth Bay, Gerrans Bay and St. Austell Bay. Maerl beds are currently designated within four sites in England:

- Fal and Helford SAC as a sub-feature of the Annex 1 Sandbank Feature;
- The Manacles MCZ, as a habitat feature of conservation importance (HOCI) and as the main constituent of the broad scale habitat 'Sublittoral macrophyte-dominated sediment'. Common Maerl is also a designated species feature of conservation importance (SOCI);
- Purbeck Coast MCZ as a HOCI;
- Bembridge MCZ as a HOCI.

Given the lack of clear definitions and varied, inconsistent methods for recording maerl, it is likely that other areas exist where maerl is present and which would merit protection and/or management. Protection of maerl by the current network of MPAs is by no means complete. In fact, a 'gap' in the network coherence of MPAs in the Eastern Channel has been identified (Carr *et al.*, 2014).

Considering the variation in distribution, underlying substrata, extent, condition and species-composition of maerl habitats in England, there is surely a need for a broader approach (than the MHC) when categorising them. This broader approach (including different percentage covers, the ratio of live:dead nodules and underlying substrata) would be beneficial in terms of understanding the range of habitats present, facilitating more reliable assessments in the field (by citizen volunteers and professional scientists alike), better mapping of distributions of similar habitats, allowing more robust analyses and comparisons among regions with clearer reporting and by allowing differentiation in management for legally protected habitats with varying character.

To address this range of issues, Natural England with assistance from Seasearch are developing a more comprehensive system for categorising maerl habitat (Table 2), that incorporates spatial extent, percentage cover, the live versus dead maerl ratio and the physical structure (3D versus 2D), and other recommendations from Selley (2016). This will be used to inform better designation and protection of maerl as a Species and Habitats of Conservation Importance (Selley, 2016; Axelsson, 2022).

1.5 Seasearch records

The Seasearch database includes many records of maerl, ranging from a generic ‘maerl indet’ through to (questionable) determinations to species level. Some of these have been determined as maerl biotopes, but others have not. Reasons for this probably include:

- Partial (or total) mis-matches between the observed physical habitat and composition of species with those described in the marine habitat classification;
- A lack of clarity about the spatial extent required to be classed as a maerl ‘bed’;
- A lack of clarity about the abundance (SACFOR score (see Table 1) or % seabed cover) that might constitute a ‘bed’ or a maerl biotope;
- A lack of clarity about whether dead maerl or what composition of live and dead maerl might constitute maerl biotope;
- Uncertainty about whether encrusting forms of coralline red algae belong to maerl-forming species (species of maerl also exist as encrusting forms during the sexual stage of their reproductive cycle (Pardo *et al.*, 2019). These provide additional confusion as there are several species of encrusting red calcareous algae that look similar to this sexual stage, but which do not form detached nodules). This issue is particularly acute for ‘hedgehog’ forms of crust.

Some of these records are of habitats that include large densities or extents of maerl, or which do not yet fit into the MHC or which contribute to biodiversity of adjacent habitats either through a trickle of live maerl fragments or dead maerl. These could all be considered for protection over and above habitat that has been determined as maerl biotope, because they probably include either or both of the two species listed in the NERC Act 2006 (as amended 2016) and are of ecological value.

This report describes a study that delves into Seasearch records of maerl, associated taxa and the habitats in which they occur. It follows previous conclusions that the Seasearch dataset can be used effectively to test hypotheses about composition of assemblages (Jackson, 2022).

1.6 Scope, remit and hypotheses

The scope of the work includes the spatial extent of maerl in England (Figure 1). The remit of this report is six-fold.

1. Develop a protocol for formatting Seasearch data such that they can be used in analyses about maerl now and in the future.
2. Analyse diversity and compositions of assemblages in maerl habitat in different areas and among different biotopes. UK waters cover a range of biogeographic areas with different associated flora and fauna. Greater proximity to species in warmer, more-southerly areas and a tendency for poleward shifts in species' distributions may also mean that species richness in the south west is boosted by species at the northerly edge of their range expanding northwards (Encarnacao *et al.*, 2019; Zarco-Perello *et al.*, 2020). Such biogeographic variation in diversity would lead to expectations for differences in composition of assemblages even within the same maerl biotope. It may be possible however, to distinguish different maerl biotopes on the basis of the taxonomic composition of the associated assemblage.
3. Analyse diversity and compositions of assemblages that contain maerl but which are not maerl biotopes (as per MHC) to explore potential overlap with 'actual' maerl biotopes, thereby identifying records that may benefit from redetermination or to indicate areas of seabed that merit re-survey or to be considered for management or protection.
4. Allocate Seasearch records of maerl that are not determined as being within maerl biotope to the extended categories of maerl habitat and map these in relation to geographic areas recognised as being important for maerl (because maerl biotopes were observed there).
5. Provide information that can act as a 'baseline' against which to assess future change.
6. Provide focus and guidance for future sampling and determination of a range of maerl habitats (not only MHC biotopes).

The following questions, hypotheses and predictions, might reasonably be made.

Hypothesis 1: Taxonomic diversity and composition of Level 4 maerl biotope (SS.SMp.Mrl) will differ among the areas in which it occurs (because of biogeographic variation in species' distributions)

Hypothesis 2: Taxonomic diversity and composition will differ among Level 5 maerl biotopes and among areas in which they occur (because of biogeographic variation in species' distributions and differences in the taxa that characterise different biotopes. Alternatively, diversity and composition of samples from maerl biotopes may not differ because of challenges in correct identification of maerl taxa and lack of clarity about what constitutes a maerl bed.)

Hypothesis 3: Taxonomic composition will differ between Level 4 maerl biotopes and other biotope records that include maerl. Logically, clear-cut differences should be apparent, because different taxa are used to characterise different biotopes, but in reality, there may be errors in identification of taxa or biotopes that create similarity between biotopes.

Such analyses and maps will provide information about the distribution, diversity and composition of habitats that contain maerl, which can then be used a baseline against which to compare future change or the effects of management. The results can also provide direction for future monitoring efforts.

1.7 Marine Recorder terminology

Seasearch data are entered to and saved within an Access-based database called Marine Recorder (MR). To allow ready comprehension of the issues being addressed in this report, some relevant terms are defined here.

Observer records – records from an ‘observation form’ collected by divers or snorkellers qualified to observer or surveyor level. All data are linked to a single sample.

Surveyor records – records from a ‘survey form’ collected by divers or snorkellers qualified to surveyor level. Data may be linked to one or more samples.

Survey – collection of dives for a stated location or area over a stated time period (often a year)

Survey-event – falls within a survey and is usually a single dive of a stated duration.

Sample – data from a distinct habitat, within a single survey-event. Multiple samples (habitats) per survey-event may be recorded by Seasearch surveyors using a survey form.

Location – an area of seabed that can contain one or more survey-events.

Position – The latitude and longitude of a single survey event (and/or sample) using the WGS84 coordinate system.

2 METHODS

2.1 Suitability of Seasearch data

For analyses to be robust and interpretable, the data going into them must meet certain conditions. Perhaps most important is the need to ensure that records collected across a period of time are comparable. The Seasearch sampling protocols have remained unchanged since they were introduced in 2003. The methods are consistent, well-established and used by all who are trained to collect data, by Seasearch and partner organisations. Seasearch sampling methods were developed from those used in the Marine Nature Conservation Review (Hiscock, 1996; Irving and Wood, 2007; MCS/Seasearch, 2007). Briefly, volunteers in Seasearch spend time under water recording all the species that they are able to identify along with details of the physical environment. Abundance of each species is scored on the semi-quantitative SACFOR scale. There is, however, more than one protocol and level of training. Those with the entry level of training (Seasearch observers) collect species records in only a single 'sample' (which may include multiple habitats), score abundance on a simplified scale and give only generalised information about the physical conditions at the site. Those with the more advanced level of training (Seasearch surveyors) collect species records for more finely resolved habitats, with more detail about the physical environment, which are then determined (by an analyst, after the dive) as representing one or more biotopes.

2.2 Data treatment protocol

In this study, there is a clear need to link species records unambiguously with specific biotopes which is not always possible with observer-level records, so only surveyor-level records are used. To extract reliably samples that include records of maerl and to maximise the likelihood of reliable outputs, a protocol of data filters and treatments was developed (Table 1).

Seasearch records for maerl taxa that had not been determined as being in a core maerl biotope were allocated to one of the new extended set of categories (Table 2) as follows. Seasearch abundance scoring and descriptions are not (yet) made with these categories in mind, so some arbitrary thresholds of abundance were used and some subjective decisions had to be made (Table 3). In order to best understand the distribution of maerl habitat, this study used all Seasearch records for maerl since 2000, not just those in designated sites.

Table 1. Protocols for data filtering and treatment prior to analysis (applicable only to Seasearch records).

Procedure	Explanation
1. Exclude survey events that are:	
Not in the time-frame of interest	By filtering on EventDate to exclude records prior to 2000
Not in the spatial areas of interest	By importing positions (as Latitude & Longitude using coordinate reference system EPSG:4326, WGS84) and associated fields to the QGIS package (QGIS long-term release 3.16.16) and clipping these records to a polygon of UK territorial area, adding a field for area name to each record, then exporting attribute tables to .csv.
Not done by Seasearch surveyors	This ensures a more advanced level of training and greater experience. The recording of multiple samples per dive (where appropriate) also makes it much easier to attribute species to particular habitats. Some analyses about single species may not need to be so restrictive.
2. Exclude samples that:	
Have no biotope determination	To ensure that species records could be linked with an underlying biotope
Have fewer than five taxa	Whilst some habitats are expected to have few taxa, maerl habitat should include numerous taxa. Samples with very small numbers of taxa suggest incomplete records. They also add very large variance, obscuring patterns in multivariate data.
3. Exclude taxa that:	
Are recorded at greater than Family level	Whilst such records are much better than nothing and may be useful when determining biotopes, they can too broad and vague for analysis of biodiversity. Their inclusion can artificially inflate taxon richness.

Procedure	Explanation
Do not have a SACFOR score	SACFOR provides an assessment of abundance with values of Superabundant (S), Abundant (A), Common (C), Frequent (F), Occasional (O) and Rare (R). Analyses of diversity and composition require a measure of relative abundance for each.
Uncertain = TRUE	To minimise uncertainty about whether a taxon is actually present in a sample
Dead = FALSE	To minimise uncertainty about whether a taxon is actually present in a sample. One exception is for records of dead maerl – these were retained, because they are an important component of maerl biotopes and habitats.
4. Transform SACFOR data	
	Whilst the semi-quantitative SACFOR scale has many advantages (Hawkins and Jones, 1992; Hiscock, 1996; Strong and Johnson, 2020), the data on diversity or composition cannot easily be assessed directly with quantitative statistical methods. This is a consequence of 'count' and 'cover' scores having values over different ranges. Counts go from 0 to >1 $x10^6$ (on a log10 scale), whereas covers range from 0 to ~100 (on a log2 scale). A conversion process developed by Strong & Johnson (2020) merges observations onto a single, aligned scale from 0 – 8. This unified scale allows merging of scores for species of different size or growth form, allows a wide selection of quantitative statistics, and is already log-transformed (appropriate for observations spanning multiple orders of magnitude) ready for multivariate analysis, so that taxa of different sizes and growth forms can be compared in a fair way. The full process is described in detail in Strong & Johnson (2020).
5. Allocate samples with maerl to habitat	

Procedure	Explanation
	Samples that contained a record for maerl (as either *Lithothamnion corallioides, L. glaciale, Phymatolithon calcareum* or 'maerl indet.') were labelled as being from either a maerl biotope or a non-maerl biotope according to the biotope determination. All other taxon records from the same samples were also labelled accordingly. Biotope determinations were standardised such that those determined to Level 5 were also labelled with the parent Level 4 biotope code. Those determined only to Level 4 received no label for Level 5. Analyses of samples with biotopes identified to Level 4 included those identified only to Level 4 (SS.SMp.Mrl) and those identified to the Level 5 sub-biotopes of SS.SMp.Mrl. Analyses of Level 5 biotopes included only samples with biotopes identified to Level 5. Sample sizes were necessarily considerably smaller than those from the Level 4 analyses All other samples were discarded.
6. Standardise taxon names	
	Substantial variation may exist in the taxonomic resolution at which records are made. Many taxa were only recorded to Genus or Family level, which can cause artificial inflation of taxon richness because, for example, a database query would identify *Steromphala*, *Steromphala* sp. and *Steromphala umbilicalis* as three different taxa, when only one may be present in a sample. Taxonomic consistency among samples was improved as follows: When, within any Genus, there existed some records determined to species and some determined only to Genus, but the Genus is monospecific according to Marine Species for the British Isles and Adjacent Seas (MSBIAS), all entries were altered to the full species level.
7. Eliminate duplicates	

Procedure	Explanation
	Stage 12 can create duplicate entries for taxa within a sample. Such duplicates are not logical and cannot be handled correctly by diversity indices or multivariate analyses. For instance, if a sample originally included records of *Pecten* and *Pecten maximus*, it would now contain two entries for *Pecten maximus*, potentially with different scores for abundance. Duplicates were eliminated and the abundance for the single remaining entry was replaced by the mean of the original values.

Table 2. Categories of maerl habitats in England (from Axelsson (2021 draft 1.4)).

Category	Group	Maerl bed habitat	Spatial extent	Structure	% seabed cover	Live/dead (as % seabed cover)*	Substratum
A	1	Dense Maerl 'live & dead'	≥25m^2	3D; raised; ≥10cm depth	≥20%	Some mix of live and dead, with ≥5% live	Maerl
	2	Dense Maerl 'dead'	≥25m^2	3D; raised; ≥10cm depth	≥20%	0% live, ≥20% dead	Maerl
	3	Dense Maerl 'live & dead'	<25m^2	3D; raised; ≥10cm depth	≥20%	Some mix of live and dead, with ≥5% live	Maerl
B	1	Maerl Sediment 'live & dead'	≥25m^2	3D / 2D	≥5% ≤20%	Some mix of live and dead, with ≥5% - live	Gravel, sand, mud, mixed
	2	Maerl Sediment 'dead'	≥25m^2	2D	≥5% ≤20%	0% live, ≥5% - ≤20% dead	Gravel, sand, mud, mixed
	3	Maerl Sediment 'live & dead'	Patchy	2D	≥5% ≤20%	Some mix of live and dead, with ≥5% - live	Gravel, sand, mud, mixed

Category	Group	Maerl bed habitat	Spatial extent	Structure	% seabed cover	Live/dead (as % seabed cover)*	Substratum
C	1	Sparse Maerl 'live & dead'	Sparse	2D	<5% ≥1%	Some mix of live and dead, with ≥1% live	Gravel, sand, mud, mixed, rock
	2	Scattered Maerl 'live & dead'	Scattered	2D	<1%	Some mix of live and dead	Gravel, sand, mud, mixed, rock
D	1	Maerl Veneer 'live & dead', static	≥25m^2	2D	≥20%	Some mix of live and dead, with ≥5% live	Rock
	2	Maerl Veneer 'live & dead', mobile	≥25m^2	2D	≥20%	Some mix of live and dead, with ≥5% live	Rock
	3	Maerl Veneer 'live & dead', static or mobile	Patchy	2D	≥5% ≤20%	Some mix of live and dead, with ≥5% live	Rock
E	1	Potential Maerl	Lacking detail		Lacking detail	Live and/or dead	Any suitable, near horizontal

Category	Group	Maerl bed habitat	Spatial extent	Structure	% seabed cover	Live/dead (as % seabed cover)*	Substratum
		Lithothamnion sp., *Phymatolithon* sp., *Lithophyllum* sp., including encrusting or hedgehog growths.					

Table 3. Thresholds and subjective criteria used to allocate Seasearch records of maerl not in a maerl biotope to the new extended categories of maerl habitat (see Table 2).

Category	Decision criteria
A	Records with a SACFOR score of S or A, plus clear descriptive indication of large extent and depth(e.g. 'beds', 'large waves') and underlying sedimentary substrata were labelled as A1 or A2 according to the proportion of live:dead nodules. Records with S or A with sedimentary substrata, but no indication of extent (or indication of small extent) were scored as A3.
B	Records with a SACFOR score of S or A, plus clear descriptive indication of large extent (e.g. 'plain') and underlying sedimentary substrata were labelled as B1 or B2 according to the proportion of live:dead nodules. Records with C or F with sedimentary substrata and descriptive indication of patchiness were scored as B3.
C	Records with a SACFOR score of O and any type of substrata were labelled as C1 Records with a SACFOR score of R and any type of substrata were labelled as C2
D	Records with underlying bedrock and SACFOR scores of S or A were labelled as D1 or D2 according to apparent mobility of maerl veneer. Records with underlying bedrock and SACFOR scores of C or F were labelled as D3.
E	Records of Genera where some, but not necessarily all, species form maerl (i.e. *Phymatolithon*, *Lithothamnion*, *Lithophyllum*), with suitable substrata (e.g. sand, gravel, bedrock) and no mention of maerl were labelled as E. References to 'hedgehog' growths in the absence of maerl were also labelled as E.
Uncategorised	Records of Genera where some, but not necessarily all, species form maerl (i.e. *Phymatolithon*, *Lithothamnion*, *Lithophyllum*), from unsuitable substrata (e.g. walls, steep rock) were not labelled as any maerl category.

2.3 Survey effort

Avoidance of mechanisms that cause bias (a systematic deviation of an estimate from the true value) is key in the design of robust data collection. Artefacts in the method of data collection used to obtain the estimate (Andrew and Mapstone, 1987), lead to under- or over-estimation of the real value (Walther and Moore, 2005). One obvious source of bias, is the amount of sampling effort; the more you look, the more you find, as shown by species accumulation curves (Gotelli and Colwell, 2001; Ugland, Gray and Ellingsen, 2003). Previous analyses of Seasearch records demonstrated that there is no association between the number of taxa recorded during a survey event (irrespective of the number of samples within that dive) and the duration of a dive (survey event) (Jackson, 2022). As a consequence, no correction for survey effort per dive was applied in any of the following analyses. Another aspect of survey effort concerns the number of survey events within each unit of comparison (the more dives that happen in a particular place (or time, habitat, etc.), the more different species are likely to be recorded. In *ad hoc* survey programmes, sample sizes often differ between groups. Thus, any observed differences may be due to different sampling effort rather than any effect of the factor of interest. This is a potentially serious problem when comparing variables such as taxon richness. Multivariate analyses of assemblage composition can easily handle different sample sizes and, within reason, are much less prone to artefacts arising from differing sample effort. Where sample sizes differ greatly, however, care should be taken in interpretation of patterns.

2.4 Statistical analysis

2.4.1 Diversity indices

The best understanding about diversity is gained when multiple indices are used. Different indices provide different information. For example, the Simpson index is a dominance index because it gives more weight to common or dominant species. The presence of rare taxa with only a few representatives will have little effect on the index value. In contrast, values of the Shannon index are much more strongly affected by the presence of rare taxa.

For hypotheses about differences in diversity, indices (taxon richness, Shannon diversity, and Simpson diversity) were calculated using the DIVERSE routine in PRIMER (v. 7.0.17) and exported to .csv.

Variables were tested for normality of distribution using Shapiro-Wilk tests and for homogeneity of variances with Bartlett tests. Variables with a fixed range of values (e.g. Shannon or Simpson diversity) were not expected to be normal. All

comparisons of diversity indices had only a single factor with >2 groups, so ANOVA or Kruskall-Wallis tests were used depending on the distribution of the data.

In *ad hoc* survey programmes, sample sizes often differ between groups. Thus, any observed differences may be due to different sampling effort rather than any effect of the factor of interest. To help understand the extent of potential confounding by sampling effort, tests were done i) with all groups irrespective of sample size and ii) when groups with small samples (< 10, if present) were removed and remaining groups sub-set by random selection such that they were equal in size to the smallest remaining group. Where significant differences were detected among groups, *post-hoc* pairwise tests (SNK or Dunns test) were used to identify where those differences occurred.

2.4.2 Multivariate analysis of assemblage composition

Data were already as converted SACFOR scores (Strong and Johnson, 2020; Table 1). The conversions applied to the SACFOR scores for species' abundances have a similar effect to transforming data to down-weight the effects of very abundant taxa (Strong and Johnson, 2020) and computation of Bray-Curtis similarities acts to reduce contributions of rare taxa (Capone and Kushlan, 1991). No further transformation was applied to abundance measures.

To visualise any differences in assemblages among MPAs or among blocks of time, Bray-Curtis similarities were ordinated using non-metrical multi-dimensional scaling (nMDS). Multivariate differences in benthic assemblages (among areas or biotopes) were tested using the PERMANOVA routine (Anderson, 2001, 2017) and the ANOSIM routine (Clarke, 1993; Clarke and Warwick, 2001), each with Bray-Curtis similarities. The two routines are similar, but subtly different. ANOSIM tests whether distances between groups are greater than within groups, whereas PERMANOVA tests whether distances differ between groups. PERMANOVA is often more powerful than ANOSIM when detecting differences in assemblage structure (Anderson and Walsh, 2013).

Rare species occurring in small numbers receive little weight in biological measures such as Bray-Curtis (Clarke, 1993; Clarke and Warwick, 2001; Legendre and Legendre, 2012), so the presence of such species is not likely to have a large impact on patterns of multivariate difference. Thus, we would expect that analyses based on a subset of only more frequently occurring taxa would reveal the same patterns as the full dataset. This was the case in previous analyses of Seasearch records, where analyses based on a 'full' set of taxa led to the same conclusions as the same analyses based on only the fifty most important taxa (Jackson, 2022). Where there are many species, many of which occur seldomly, it is also harder to represent

accurately the multivariate differences in a 2- (or 3-) dimensional ordination (i.e. the nMDS stress is larger). Stress values give an indication of how well the ordination plot fits the actual distances among the points in the data (Clarke, 1993; Legendre and Legendre, 2012). Large values of stress (>0.2) indicate a poor fit and the patterns in the plot give a poor representation. Smaller values of stress are obtained when plotting in higher dimensions. Where stress exceeded 0.2 in 2-D, a 3-D plot was used in preference. Large numbers of samples in an ordination plot can obscure visual representation of patters and also increase stress. In such situations, plotting centroids of sets of samples (e.g. per year) reduces the number of points and reduces stress whilst maintaining an impression of underlying patterns in data. When making comparisons with large

Arguably, unusual or rare species are more likely to be missed or not to be recorded (because they are not recognised) or recorded incorrectly or at least recorded at a coarse taxonomic resolution. Thus, inclusion of rare species may just be adding noise to the dataset. Where there are many rare species, this noise may obscure or create patterns of difference in the more common species.

Differences in assemblages among areas and among biotopes were tested using the 50 most important taxa in that dataset (where ‘importance’ is determined as those species that contribute more than a particular % abundance for every sample). Where significant multivariate differences occurred between groups, the SIMPER routine (Clarke, 1993) was used to identify the taxa and their percent contributions to the overall dissimilarity. Multivariate analyses were performed using PRIMER7 v.7.0.17 and PERMANOVA+ v.1.0.1 software (PRIMER-e, Quest Research Ltd., New Zealand).

3 RESULTS

Samples of maerl from around Britain and Ireland included 737 different taxa in 205 samples (Figure 1), of which 360 were in 49 samples from England. Taxon records varied from single occurrences to being recorded in 35 of the 49 samples. Over 200 of the 737 taxa occurred in only one or two samples. The biotopes referred to in this study are listed in Table 4. Other biotopes from the Marine Habitat Classification that mention maerl (e.g. SS.SMx.CMx.MysThyMx, IR.MIR.KT.XKTX, SS.SCS.CCS.Nmix, IR.MIR.KT, LR.HLR.FT.FserTX) were not encountered specifically although may be present as sub-biotopes of those listed in Table 4.

Table 4. List of biotope codes and descriptions observed and referred to in this study. Grey shading indicates core maerl biotopes.

Biotope code	Biotope description
SS.SMp.Mrl	Maerl beds
SS.SMp.Mrl.Lcor	*Lithothamnion corallioides* maerl beds on infralittoral muddy gravel
SS.SMp.Mrl.Lgla	*Lithothamnion glaciale* maerl beds in tide-swept variable salinity infralittoral gravel
SS.SMp.Mrl.Pcal	*Phymatolithon calcareum* maerl beds in infralittoral clean gravel or coarse sand
SS.SCS.ICS	Infralittoral coarse sediment
SS.SMp.KSwSS	Kelp and seaweed communities on sublittoral sediment
SS.SMx.CMx	Circalittoral mixed sediment
SS.SCS.CCS	Circalittoral coarse sediment
SS.SMx.IMx	Infralittoral mixed sediment
SS.SMu.IFiMu	Infralittoral fine mud
SS.SMu.CSaMu	Circalittoral sandy mud
SS.SBR.SMus	Sublittoral mussel beds (on sublittoral sediment)

3.1 Diversity in maerl habitats

3.1.1 Level 4 biotope

Diversity indices

Sample-sizes for maerl biotope (MHC Level 4 SS.SMp.Mrl) varied among the six areas considered (Channel Isles, England, Ireland, Isle of Man, Scotland, Wales), ranging from 2 to 95. There were significant differences among areas for each of the three diversity indices when all areas with varying sample-sizes were analysed (Figure 2, Table 5, shaded cells). *Post-hoc* tests could not resolve the locations of these differences. Repeats of the analyses when small samples (<10) were eliminated and sample-sizes equalised (by random selection to match the smallest remaining sample-size, n = 21) no longer showed differences among areas for any variable (Figure 2, Table 5).

Table 5. Test outputs and summary of patterns for comparisons of taxon richness, Shannon and Simpson diversity indices from samples of maerl biotope (SS.SMp.Mrl) among areas.

Variable	Transformation	Distribution (Shapiro-Wilk test)	Variance (Bartlett test)	No. of areas	Sample-size equalised (Yes/No)	Sample-sizes	Overall differences (ANOVA or Kruskall-Wallis test	*post-hoc* tests (SNK or Dunn's test)	Summary
Taxon richness	Log_{10}	Normal $W = 0.99$, $p > 0.2$	Homogeneous $K^2 = 7.88$, d.f. = 5, $p > 0.1$	6	N	2-95	Significant differences MS = 0.19, $F_{5,186} = 2.95$, $p < 0.05$	$p > 0.05$	For each of taxon richness, Shannon and Simpson indices, differences among areas were present when all sample sizes were considered (shaded cells). *Post-hoc* tests were not able to resolve locations of differences, but these must have been at least between maximal (England) and minimal (Isle of Man) values. Differences among
				4	Y	21	No differences MS = 0.05, $F_{3,80} = 0.68$, $p > 0.5$	NA	
Shannon diversity	None	Normal $W = 0.99$, $p > 0.3$	Homogeneous $K^2 = 7.5$, d.f. = 5, $p > 0.1$	6	N	2-95	Significant differences MS = 1.06, $F_{5,186} = 3.03$, $p < 0.05$	$p > 0.05$	
				4	Y	21	No differences MS = 0.55, $F_{3,80} = 1.22$, $p > 0.3$	NA	
Simpson diversity	None		Non-homogeneous	6	N	2-95	Significant differences	$p > 0.05$	

Variable	Transformation	Distribution (Shapiro-Wilk test)	Variance (Bartlett test)	No. of areas	Sample-size equalised (Yes/No)	Sample-sizes	Overall differences (ANOVA or Kruskall-Wallis test	*post-hoc* tests (SNK or Dunn's test)	Summary
		Non-normal W = 0.78, p < 0.001	K^2 = 29.6, d.f. = 5, p <0.001				χ^2 = 16.84, d.f. = 5, p < 0.01		areas disappeared when sample-sizes were equalised.
				4	Y	21	No differences χ^2 = 4.85, d.f. = 5, p > 0.1	NA	

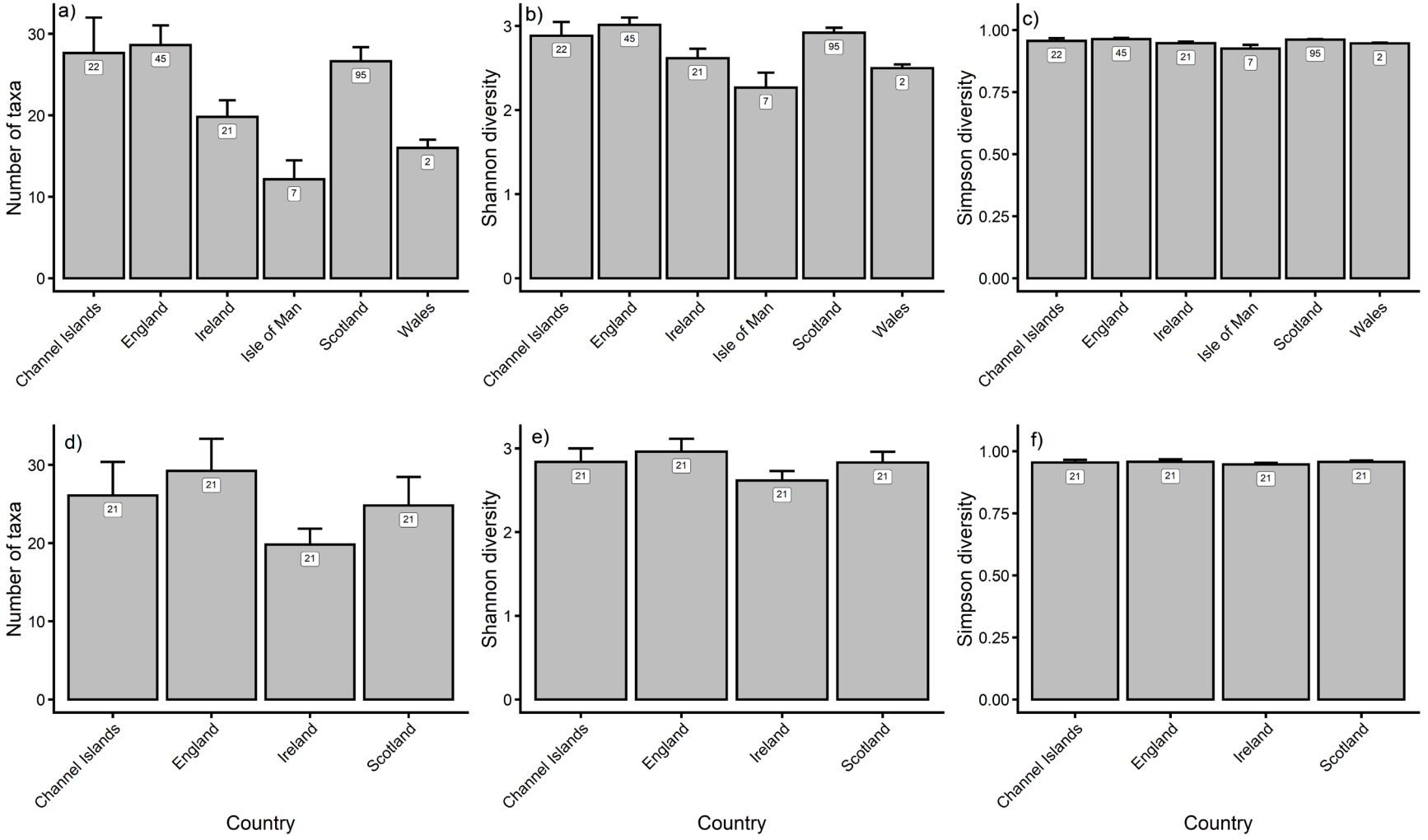


Figure 2. Mean (+s.e.) values for a) number of taxa, b) Shannon diversity and c) Simpson diversity in six areas around Britain and Ireland where the maerl biotope SS.SMp.Mrl was identified. Also for the same variables when small samples (<10) were eliminated and sample-sizes were equalised d-f). White labels indicate the number of samples from each area.

Assemblage composition

Analyses of taxonomic composition of samples of maerl biotope (Level 4) were done using only the 50 most 'important' species (where 'importance' is determined as those species that contribute more than a particular % abundance for every sample). Compositions of assemblages of taxa in the five different sets of samples of SS.SMp.Mrl differed significantly (ANOSIM; $R = 0.19$, $p < 0.01$ or PERMANOVA MS = 14033, Pseudo-$F_{4,162} = 5.02$, $p < 0.01$; Figure 3).

Pairwise comparisons in ANOSIM showed that samples from England were similar to those from the Channel Islands and that those from Scotland, Ireland and Isle of Man were similar to each other (Table 5a). These two groupings differed significantly in taxonomic composition. Pairwise comparisons in PERMANOVA showed that all areas were significantly different to each other (Table 5b). A subset of pairwise comparisons are considered, namely those from England against any other area where assemblages were significantly different. The species contributing most to dissimilarities in assemblages are shown in Table 6. Notable taxa that appear consistently include *Crepidula fornicata* (more abundant in England than elsewhere); *Buccinum undatum* (less abundant in England than in Ireland or Isle of Man); *Echinus esculentus*, *Ophiothrix fragilis* and *Ophiocomina nigra* (less abundant in England than in Scotland or Isle of Man), *Cerianthus lloydii, Cereus pedunculatus, Pecten maximus* and *Aequipecten opercularis* with mixed patterns.

Table 6. Post- hoc pairwise comparisons from a) ANOSIM and b) PERMANOVA. Significant results are in italics ($p < 0.05$); those in bold are referred to in the text.

a)					
Groups	**Statistic**	***p***	**Possible permutations**	**Actual permutations**	**Number >= observed**
England, Channel Isl	0.09	0.052	Very large	999	51
England, Scotland	***0.171***	***0.001***	***Very large***	***999***	***0***
England, Ireland	***0.282***	***0.001***	***Very large***	***999***	***0***
England, Isle of Man	***0.188***	***0.024***	***13983816***	***999***	***23***
Channel Isl, Scotland	*0.319*	*0.001*	*Very large*	*999*	*0*
Channel Isl, Ireland	*0.263*	*0.001*	*Very large*	*999*	*0*
Channel Isl, Isle of Man	*0.37*	*0.002*	*100947*	*999*	*1*
Scotland, Ireland	*0.202*	*0.004*	*Very large*	*999*	*3*
Scotland, Isle of Man	0.003	0.440	666563898	999	445
Ireland, Isle of Man	-0.036	0.590	74613	999	590
b)					
Groups	***t***	***p***	**Unique permutations**		
England, Channel Isl	*1.72*	*0.001*	*998*		
England, Scotland	***2.91***	***0.001***	***999***		
England, Ireland	***1.86***	***0.001***	***998***		
England, Isle of Man	***1.92***	***0.001***	***997***		
Channel Isl, Scotland	*2.96*	*0.001*	*999*		
Channel Isl, Ireland	*1.97*	*0.002*	*999*		
Channel Isl, Isle of Man	*2.03*	*0.001*	*996*		
Scotland, Ireland	*1.73*	*0.002*	*999*		
Scotland, Isle of Man	*1.63*	*0.004*	*998*		
Ireland, Isle of Man	*1.51*	*0.034*	*993*		

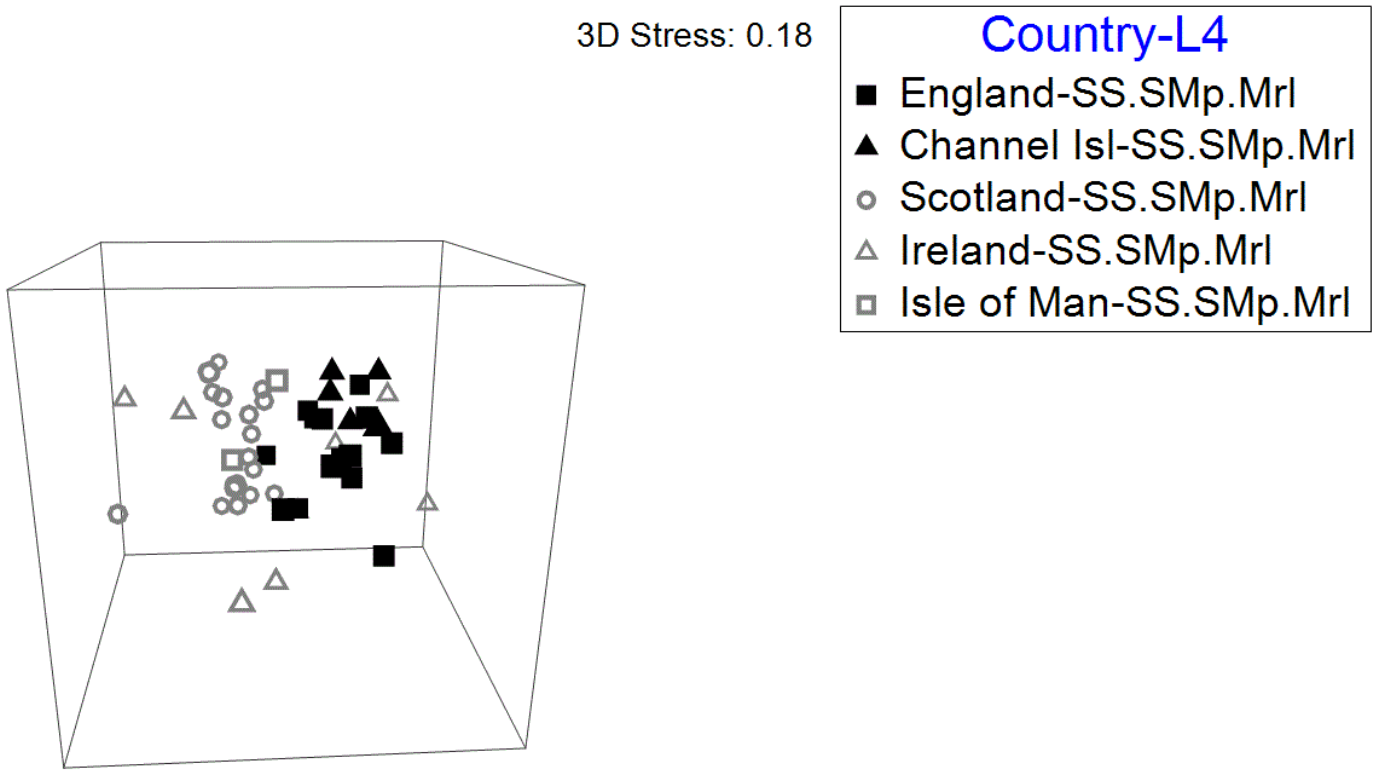


Figure 3. nMDS plot of centroids for the Level 4 biotope SS.SMp.Mrl from five different areas. Composition of assemblages in areas with black symbols differ significantly from areas with grey symbols (ANOSIM pairwise comparisons: Table 5a). Compositions of assemblages in areas with the same colour do not differ.

Table 7. Dissimilarity contributions of taxa between samples from England or from Scotland, Ireland or Isle of Man (i.e. where assemblages were different). NB *Gibbula cineraria* is now called *Steromphala cineraria*.

Taxon	Av.Abund England	Av.Abund Scotland	Av.Sim	Sim/SD	Contrib%	Cum.%
Cerianthus lloydii	0.95	1.81	4.94	1.13	6.31	6.31
Spirobranchus	1.14	1.02	4.38	0.84	5.59	11.89
Pagurus bernhardus	1.26	1.09	4.21	1.00	5.37	17.27
Pecten maximus	1.09	1.17	3.71	1.11	4.73	22.00
Gibbula cineraria	1.00	0.58	3.22	0.71	4.11	26.11
Aequipecten opercularis	0.86	0.73	3.10	0.87	3.96	30.08
Maerl indet	1.42	1.18	3.07	1.15	3.92	33.99
Crepidula fornicata	1.09	0.00	2.92	0.80	3.72	37.72
Marthasterias glacialis	0.80	0.87	2.88	1.04	3.68	41.40
Pomatoschistus	0.84	0.28	2.82	0.69	3.60	45.00
Ophiothrix fragilis	0.21	0.77	2.59	0.54	3.31	48.31
Anemonia viridis	0.93	0.09	2.56	0.88	3.27	51.58
Pomatoschistus pictus	0.42	0.68	2.42	0.69	3.09	54.67
Lanice conchilega	0.61	0.57	2.38	0.81	3.03	57.70
Echinus esculentus	0.05	0.86	2.34	0.82	2.99	60.69
Ophiocomina nigra	0.12	0.74	2.28	0.47	2.91	63.60
Paguridae	0.70	0.09	2.28	0.59	2.91	66.51
Cancer pagurus	0.24	0.67	2.00	0.85	2.55	69.05
Cereus pedunculatus	0.68	0.01	1.98	0.71	2.53	71.58
Taxon	**Av.Abund England**	**Av.Abund Isle of Man**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Buccinum undatum	0.42	2.17	6.40	1.29	8.31	8.31
Echinus esculentus	0.05	1.67	5.07	1.82	6.59	14.90
Pagurus bernhardus	1.26	1.33	4.62	1.10	6.00	20.90
Gibbula cineraria	1.00	1.00	4.22	0.87	5.48	26.38
Aequipecten opercularis	0.86	1.00	3.94	0.87	5.12	31.50
Spirobranchus	1.14	0.50	3.70	0.74	4.80	36.30
Pecten maximus	1.09	1.33	3.64	1.22	4.73	41.03
Lanice conchilega	0.61	1.00	3.52	0.80	4.57	45.60
Cerianthus lloydii	0.95	0.33	3.07	0.85	3.98	49.58
Crepidula fornicata	1.09	0.00	3.04	0.82	3.94	53.52
Paguridae	0.70	0.50	2.90	0.72	3.77	57.29
Calliostoma zizyphinum	0.60	0.50	2.86	0.64	3.71	61.00
Anemonia viridis	0.93	0.00	2.65	0.88	3.43	64.44

Taxon	Av.Abund England	Av.Abund Isle of Man	Av.Sim	Sim/SD	Contrib%	Cum.%
Pomatoschistus	0.84	0.00	2.63	0.62	3.41	67.85
Maerl indet	1.42	1.76	2.47	1.17	3.21	71.06
Taxon	**Av.Abund England**	**Av.Abund Ireland**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ophiothrix fragilis	0.21	1.50	4.77	0.79	5.96	5.96
Ophiocomina nigra	0.12	1.44	4.48	0.73	5.59	11.55
Pagurus bernhardus	1.26	0.81	3.94	0.99	4.92	16.46
Anemonia viridis	0.93	0.75	3.42	0.95	4.26	20.73
Spirobranchus	1.14	0.31	3.34	0.70	4.16	24.89
Pecten maximus	1.09	0.56	3.30	1.05	4.12	29.01
Pomatoschistus pictus	0.42	1.00	3.28	0.79	4.09	33.10
Paguridae	0.70	0.69	3.24	0.78	4.05	37.15
Nassarius reticulatus	0.53	0.81	3.16	0.60	3.94	41.09
Pomatoschistus	0.84	0.38	3.12	0.71	3.89	44.98
Maerl indet	1.42	1.51	3.06	1.10	3.82	48.81
Cerianthus lloydii	0.95	0.44	3.06	0.89	3.82	52.62
Crepidula fornicata	1.09	0.00	2.95	0.82	3.68	56.30
Aequipecten opercularis	0.86	0.50	2.90	0.84	3.62	59.92
Marthasterias glacialis	0.80	0.58	2.85	0.96	3.55	63.47
Gibbula cineraria	1.00	0.25	2.79	0.63	3.48	66.95
Buccinum undatum	0.42	0.63	2.51	0.67	3.13	70.08

3.1.2 Level 5 biotopes

Diversity indices

Sample-sizes for different maerl biotopes (MHC Level 5 SS.SMp.Mrl.Pcal, SS.SMp.Mrl.Lcor, SS.SMp.Mrl.Lgla) varied among the areas (Channel Isles, England, Scotland) where these biotopes occurred, ranging from 2 to 26 (Figure 4). Not all biotopes were present in each area so an orthogonal analysis with two factors (biotope and area) was not possible. Five different combinations of Level 5 biotope and area occurred and these groups were used in the analysis. In this instance, small sample-sizes were not excluded because this would eliminate all data from England (which is the primary focus of this study). In order to avoid discarding a large proportion of available data, sample-sizes were not equalised.

Table 8. Test outputs and summary of patterns for comparisons of taxon richness, Shannon and Simpson diversity indices from samples of maerl biotope for five combinations of Level 5 maerl biotopes and different areas around the UK (see Figure 4).

Variable	Transformation	Distribution (Shapiro-Wilk test)	Variance (Bartlett test)	No. of groups	Sample-size equalised (Yes/No)	Sample-sizes	Overall differences (ANOVA or Kruskall-Wallis test	*post-hoc* tests (SNK or Dunn's test)	Summary
Taxon richness	Log_{10}	Normal $W = 0.98$, $p > 0.7$	Homogeneous $K^2 = 6.96$, d.f. = 4, $p > 0.1$	5	N	2-26	No differences MS = 0.05, $F_{4, 39} = 0.68$, $p > 0.5$	NA	For each of taxon richness, Shannon and Simpson indices, there were no significant differences among the five combinations of Level 5 biotope and sampling area, despite small and variable sample-sizes.
Shannon diversity	None	Normal $W = 0.98$, $p > 0.5$	Homogeneous $K^2 = 6.81$, d.f. = 4, $p > 0.1$	5	N	2-26	No differences MS = 0.02, $F_{4, 39} = 0.06$, $p > 0.9$	NA	
Simpson diversity	None	Non-normal W = 0.90, p < 0.01	Homogeneous $K^2 = 4.79$, d.f. = 4, p >0.3	5	N	2-26	No differences $\chi^2 = 1.73$, d.f. = 4, $p > 0.7$	NA	

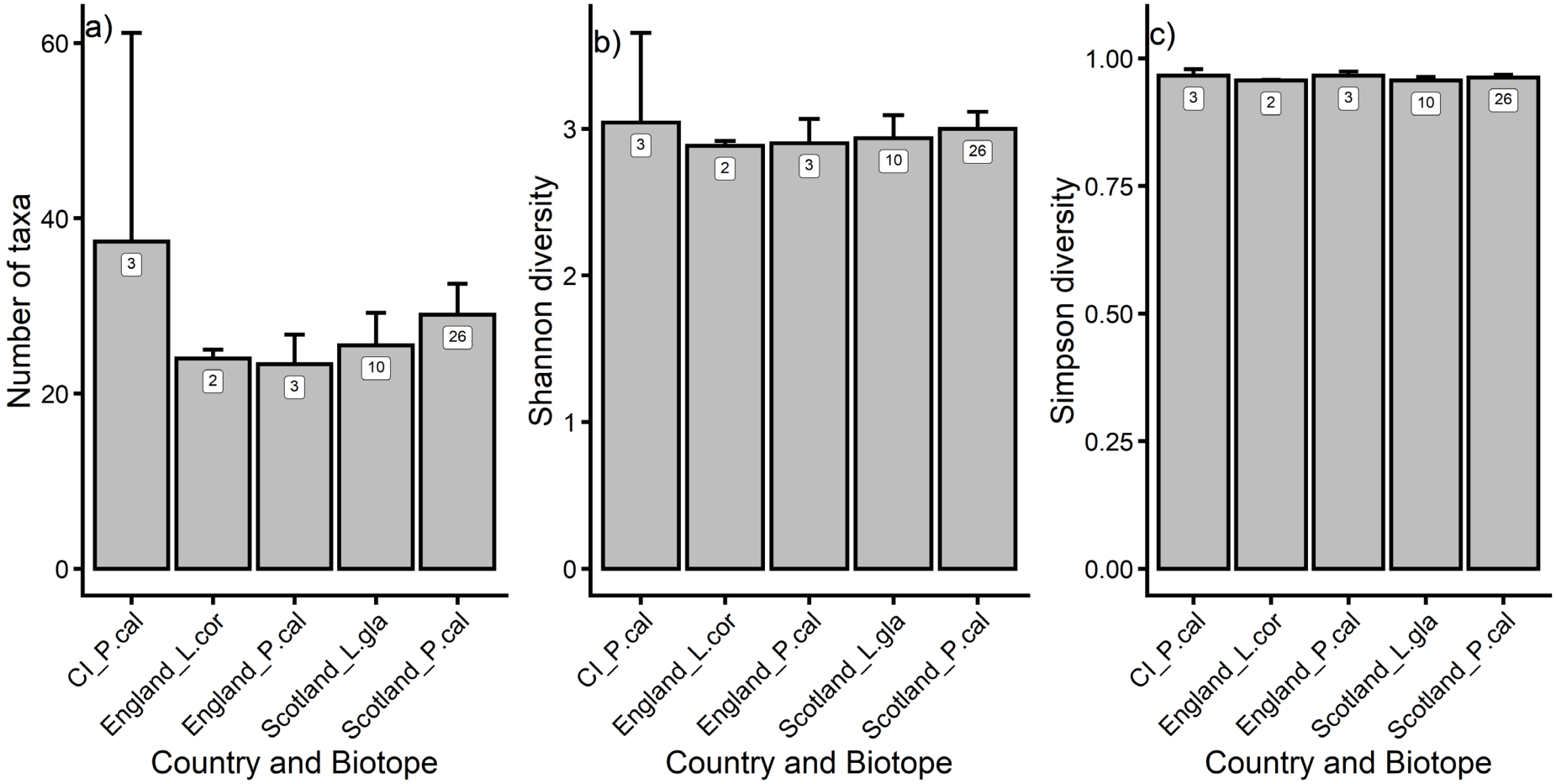


Figure 4. Mean (+s.e.) values for a) number of taxa, b) Shannon diversity and c) Simpson diversity in five areas around the UK where Level 5 maerl biotopes (SS.SMp.Mrl.Pcal, SS.SMp.Mrl.L.cor and SS.SMp.Mrl.Lgla) were identified. White labels indicate the number of samples from each area.

Assemblage composition

Compositions of assemblages of taxa differed significantly among the five different groups of samples (ANOSIM; $R = 0.56$, $p < 0.01$ or PERMANOVA MS = 12268, Pseudo-$F_{4,34} = 5.81$, $p < 0.01$; Figure 5).

Pairwise comparisons in ANOSIM showed only two sets: Scotland.*.Lgla differed from other groups and that all other groups were similar to each other (Table 7a). Pairwise comparisons in PERMANOVA showed that samples fell into three sets that differed significantly: Scotland.*.Lgla and Scotland.*.Pcal were each different to all other groups, whilst England.*.Lcor, England.*.Pcal and ChannelIsles.*.Pcal were similar to each other (Table 7b).

A subset of pairwise comparisons are considered, namely maerl biotopes from England against those from Scotland where assemblages were significantly different. The species contributing most to dissimilarities in assemblages for these pairs are shown in Table 8. Notable taxa that contributed consistently include *Crepidula fornicata* (more abundant in England than in Scotland); *Aequipecten opercularis, Echinus esculentus*, *Ophiothrix fragilis* and *Ophiocomina nigra* (less abundant in England than in Scotland).

Table 9. Post- hoc pairwise comparisons from a) ANOSIM and b) PERMANOVA. Significant results are in italics; those in bold are referred to in the text. Asterisks indicate omitted characters SS.SMp.Mrl.

a)					
Groups	**Statistic**	***p***	**Possible permutations**	**Actual permutations**	**Number >= observed**
Engl*Lcor, Engl*Pcal	0.083	0.600	10	10	6
Engl*Lcor,Channlsl*Pcal	0.500	0.200	10	10	2
Engl*Lcor,Scot*Pcal	0.366	0.063	253	253	16
Engl*Lcor,Scot*Lgla	***1.000***	***0.015***	***66***	***66***	***1***
Engl*Pcal,Channlsl*Pcal	0.444	0.100	10	10	1
Engl*Pcal,Scotl*Pcal	0.133	0.227	2024	999	226
Engl*Pcal,Scotl*Lgla	***1.000***	***0.003***	***286***	***286***	***1***
Channlsl*Pcal,Scot*Pcal	*0.484*	*0.016*	*2024*	*999*	*15*
Channlsl*Pcal,Scot*Lgla	***1.000***	***0.003***	***286***	***286***	***1***
Scot*Pcal,Scot*Lgla	***0.566***	***0.001***	***44352165***	***999***	***0***
b)					
Groups	***t***	***p***	**Unique permutations**		
Engl*Lcor, Engl*Pcal	1.03	0.598	10		
Engl*Lcor,Channlsl*Pcal	1.41	0.179	10		
Engl*Lcor,Scot*Pcal	***1.38***	***0.037***	***244***		
Engl*Lcor,Scot*Lgla	***3.42***	***0.017***	***66***		
Engl*Pcal,Channlsl*Pcal	1.53	0.100	10		
Engl*Pcal,Scotl*Pcal	***1.42***	***0.023***	***811***		
Engl*Pcal,Scotl*Lgla	***4.11***	***0.004***	***277***		
Channlsl*Pcal,Scot*Pcal	***1.84***	***0.002***	***780***		
Channlsl*Pcal,Scot*Lgla	***4.05***	***0.004***	***275***		
Scot*Pcal,Scot*Lgla	***3.51***	***0.001***	***998***		

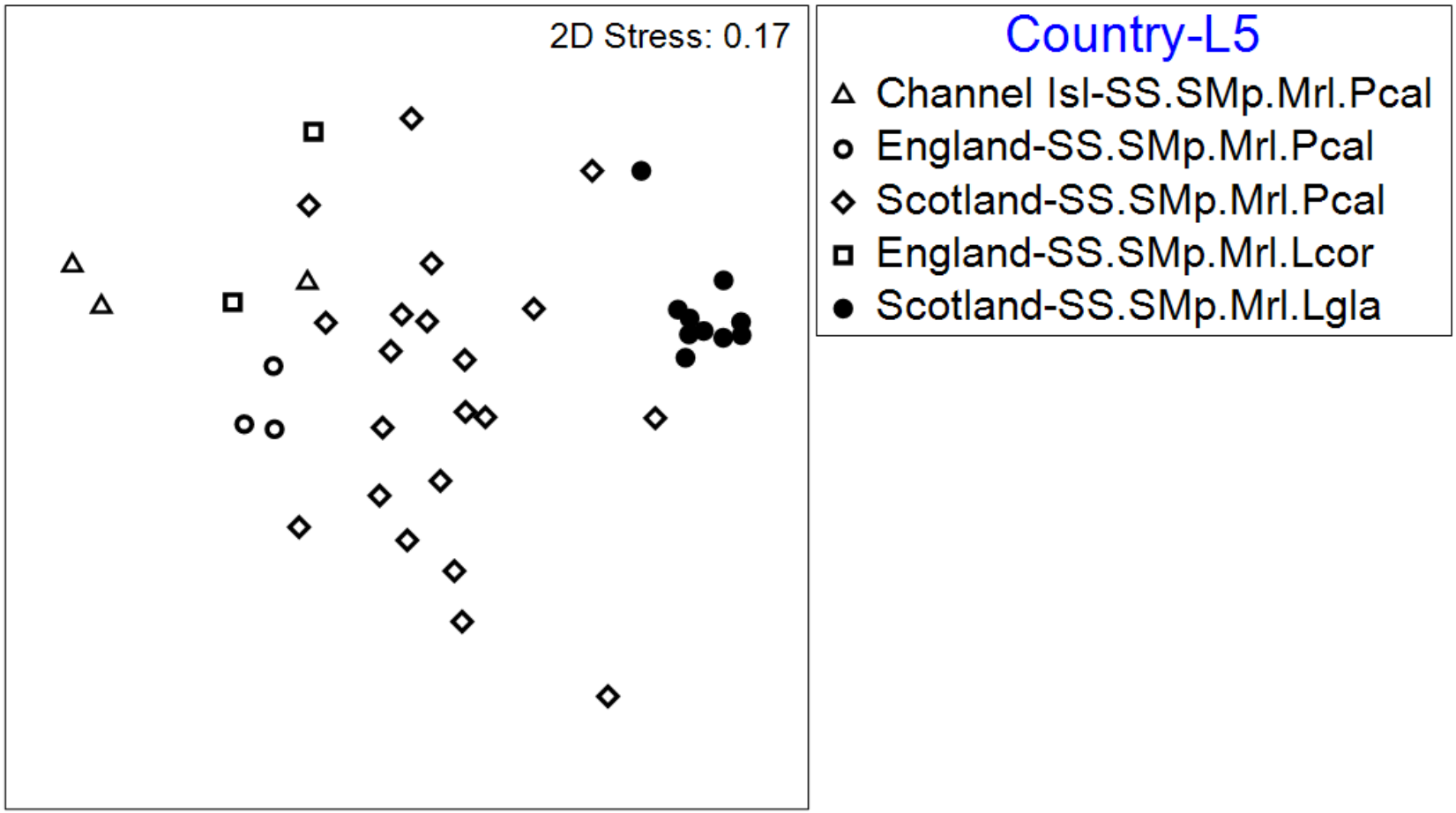


Figure 5. nMDS plot of samples of Level 5 biotopes SS.SMp.Mrl.Pcal, *.Lcor and *.Lgla from England, Scotland or the Channel Islands. Other areas with maerl did not have biotopes determined to this level. Composition of assemblages in areas with black symbols differed significantly from those with white symbols (ANOSIM pairwise comparisons: Table 7a). Compositions of assemblages in areas with the same colour do not differ. NB This is not animated.

Table 10. Dissimilarity contributions of taxa between samples from England or from Scotland, (i.e. where assemblages were different). NB *Gibbula cineraria* is now called *Steromphala cineraria*.

Taxon	Av.Abund England*Pcal	Av.Abund Scotland*Pcal	Av.Sim	Sim/SD	Contrib%	Cum.%
Paguridae	2.00	0.10	5.41	1.30	7.19	7.19
Cerianthus lloydii	1.67	1.91	5.12	1.22	6.81	13.99
Pomatoschistus	2.00	0.38	4.90	1.90	6.50	20.50
Spirobranchus	0.00	1.81	4.59	0.91	6.10	26.60
Gibbula cineraria	1.00	1.05	3.56	0.88	4.74	31.33
Lanice conchilega	1.33	0.43	3.56	1.25	4.74	36.07
Pecten maximus	1.34	1.62	3.48	1.66	4.63	40.69
Pagurus bernhardus	0.00	1.38	3.33	0.77	4.42	45.12
Pomatoschistus pictus	1.00	0.67	3.08	0.87	4.09	49.20
Neopentadactyla mixta	1.00	0.24	2.61	1.18	3.47	52.67
Ensis	0.67	0.57	2.45	0.83	3.25	55.93
Aequipecten opercularis	0.00	1.05	2.18	0.72	2.89	58.82
Echinus esculentus	0.00	0.86	2.13	0.86	2.84	61.66
Gobiusculus flavescens	0.00	0.86	2.12	0.57	2.82	64.47
Phymatolithon calcareum	2.11	1.49	2.05	0.86	2.72	67.19
Saccharina latissima	0.71	0.83	1.95	1.23	2.59	69.78
Crepidula fornicata	0.67	0.00	1.90	0.68	2.52	72.30

Taxon	Av.Abund England*Pcal	Av.Abund Scotland*Lgla	Av.Sim	Sim/SD	Contrib%	Cum.%
Ophiothrix fragilis	0.00	4.40	12.54	9.96	13.05	13.05
Ophiocomina nigra	0.00	4.20	11.65	2.63	12.13	25.18
Phymatolithon calcareum	2.11	0.00	6.03	6.90	6.28	31.45
Paguridae	2.00	0.00	5.89	1.37	6.13	37.59
Pomatoschistus	2.00	0.00	5.70	2.47	5.94	43.52
Ascidiella aspersa	0.00	1.70	4.73	1.37	4.92	48.45
Cerianthus lloydii	1.67	0.00	4.58	0.97	4.76	53.21
Lanice conchilega	1.33	0.00	3.93	1.37	4.09	57.30
Pecten maximus	1.34	0.00	3.89	2.36	4.05	61.36

Taxon	Av.Abund England*Pcal	Av.Abund Scotland*Lgla	Av.Sim	Sim/SD	Contrib%	Cum.%
Aequipecten opercularis	0.00	1.40	3.89	1.08	4.05	65.40
Marthasterias glacialis	0.35	1.51	3.56	1.34	3.70	69.11
Pomatoschistus pictus	1.00	0.40	3.12	0.84	3.25	72.35
Taxon	**Av.Abund England*Lcor**	**Av.Abund Scotland*Pcal**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Pomatoschistus	2.50	0.38	8.03	0.98	9.91	9.91
Gibbula cineraria	2.50	1.05	7.04	1.04	8.68	18.59
Spirobranchus	0.00	1.81	5.11	0.89	6.30	24.90
Pagurus bernhardus	1.50	1.38	5.02	1.00	6.20	31.09
Cerianthus lloydii	1.00	1.91	4.82	1.12	5.94	37.03
Crepidula fornicata	1.50	0.00	4.38	2.82	5.40	42.44
Phymatolithon calcareum	0.00	1.49	4.31	1.54	5.32	47.76
Anemonia viridis	1.50	0.10	4.24	2.53	5.23	52.99
Pecten maximus	1.50	1.62	3.90	1.70	4.81	57.80
Cereus pedunculatus	1.00	0.05	2.77	0.98	3.41	61.22
Aequipecten opercularis	0.00	1.05	2.37	0.71	2.92	64.14
Echinus esculentus	0.00	0.86	2.36	0.85	2.91	67.05
Gobiusculus flavescens	0.00	0.86	2.34	0.56	2.89	69.95
Saccharina latissima	1.06	0.83	2.08	1.46	2.56	72.51
Taxon	**Av.Abund England*Lcor**	**Av.Abund Scotland*Lgla**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ophiothrix fragilis	0.02	4.40	13.97	7.91	14.57	14.57
Ophiocomina nigra	0.00	4.20	13.00	2.57	13.56	28.12
Pomatoschistus	2.50	0.00	8.73	0.96	9.11	37.23
Gibbula cineraria	2.50	0.00	7.35	0.96	7.67	44.90
Pagurus bernhardus	1.50	0.40	5.51	1.02	5.74	50.65
Ascidiella aspersa	0.00	1.70	5.28	1.36	5.51	56.15
Crepidula fornicata	1.50	0.00	4.70	3.50	4.90	61.05
Pecten maximus	1.50	0.00	4.70	3.50	4.90	65.95
Marthasterias glacialis	0.00	1.51	4.56	1.43	4.76	70.71

3.1.3 Maerl biotopes vs other biotopes with maerl

Since there were no significant differences in diversity or composition between the two Level 5 maerl biotopes in England (Table 7), comparisons were then made between samples of Level 4 maerl biotope and Level 4 non-maerl biotopes which included maerl (all from England). Biotopes which had fewer than 3 samples were excluded. Compositions of assemblages of taxa differed significantly among Level 4 maerl biotopes and other Level 4 biotopes in which maerl was present (11 biotopes in total) (ANOSIM; $R = 0.36$, $p = 0.01$ or PERMANOVA MS = 9814, Pseudo-$F_{10,116} = 3.55$, $p = 0.01$; Figure 6). Pairwise comparisons in ANOSIM and in PERMANOVA showed that assemblages in maerl biotope SS.SMp.Mrl were similar to those in SS.SMx.IMx where maerl was present, but were significantly different to all other Level 4 biotopes where maerl was present (Table 9). There were no hypotheses about comparisons among non-maerl biotopes with maerl, so these pairwise comparisons were not considered.

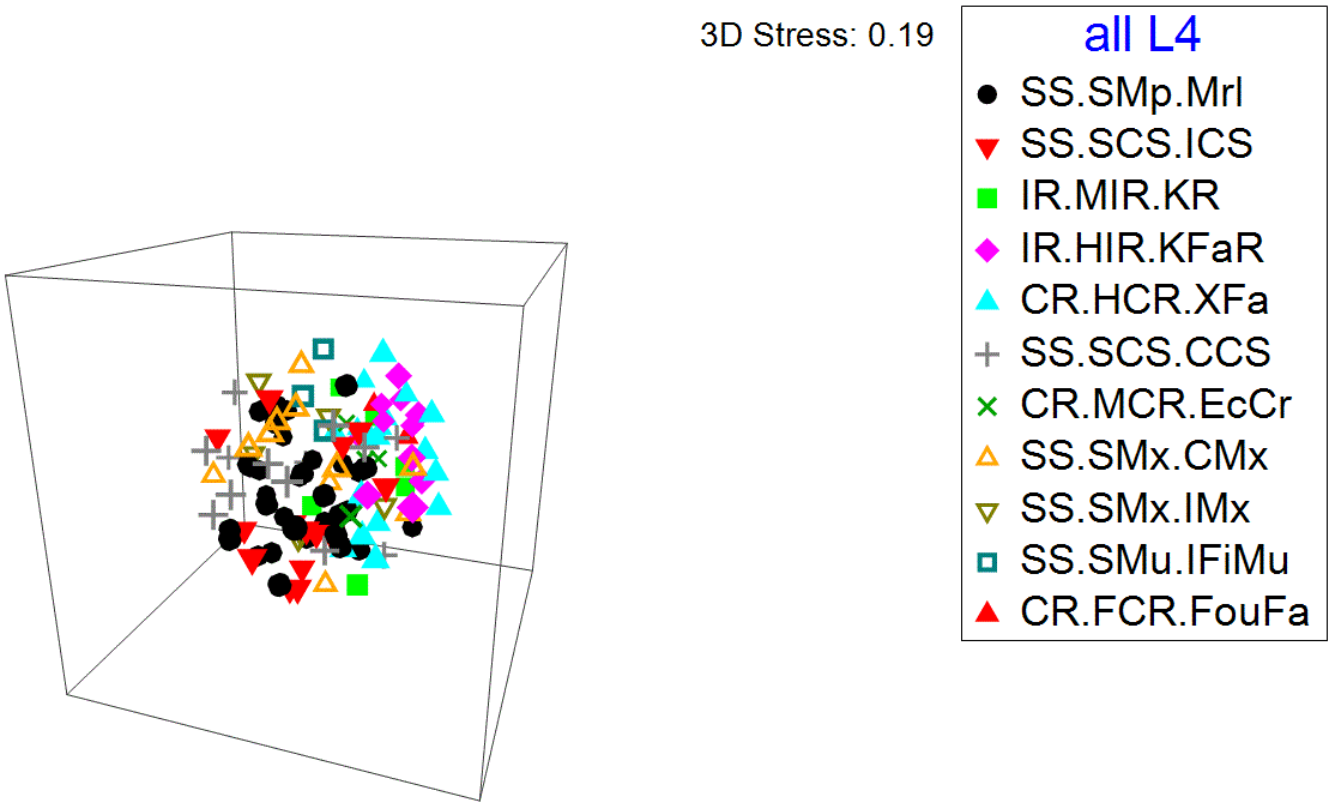


Figure 6. nMDS plot for samples of Level 4 maerl biotopes (black circles) and Level 4 non-maerl biotopes with maerl as a component taxon (coloured symbols).

Table 11. Pairwise comparisons between assemblages from Level 4 maerl biotope from England and ten Level 4 biotopes in which maerl was recorded as a taxon. Significant results are in italics (pairwise test; $p < 0.05$); those in bold are referred to in the text for a) ANOSIM and b) PERMANOVA. Comparisons among non-maerl biotopes are not shown.

a)					
Groups	**Statistic**	***p***	**Possible permutations**	**Actual permutations**	**Number >= observed**
SS.SMp.Mrl, SS.SCS.ICS	*0.111*	*0.024*	*Very large*	*999*	*23*
SS.SMp.Mrl, IR.MIR.KR	*0.632*	*0.001*	*5245786*	*999*	*0*
SS.SMp.Mrl, IR.HIR.KFaR	*0.638*	*0.001*	*Very large*	*999*	*0*
SS.SMp.Mrl, CR.HCR.XFa	*0.517*	*0.001*	*Very large*	*999*	*0*
SS.SMp.Mrl, SS.SCS.CCSI	*0.417*	*0.001*	*Very large*	*999*	*0*
SS.SMp.Mrl, CR.MCR.EcCR	*0.624*	*0.001*	*91390*	*999*	*0*
SS.SMp.Mrl,SS.SMx.CMx	*0.248*	*0.001*	*Very large*	*999*	*0*
SS.SMp.Mrl, SS.SMx.IMx	**0.122**	**0.097**	**5245786**	**999**	**96**
SS.SMp.Mrl, SS.SMu.IFiMu	*0.290*	*0.019*	*9139*	*999*	*18*
SS.SMp.Mrl, CR.FCR.FouFa	*0.858*	*0.001*	*703*	*999*	*1*
b)					
Groups	***t***	***p***	**Unique permutations**		
SS.SMp.Mrl, SS.SCS.ICS	*1.502*	*0.016*	*999*		
SS.SMp.Mrl, IR.MIR.KR	*2.499*	*0.001*	*999*		
SS.SMp.Mrl, IR.HIR.KFaR	*2.831*	*0.001*	*998*		
SS.SMp.Mrl, CR.HCR.XFa	*3.193*	*0.001*	*999*		
SS.SMp.Mrl, SS.SCS.CCSI	*2.068*	*0.001*	*999*		
SS.SMp.Mrl, CR.MCR.EcCR	*2.043*	*0.001*	*992*		
SS.SMp.Mrl,SS.SMx.CMx	*1.612*	*0.005*	*996*		
SS.SMp.Mrl, SS.SMx.IMx	**1.092**	**0.255**	**998**		
SS.SMp.Mrl, SS.SMu.IFiMu	*1.493*	*0.016*	*949*		
SS.SMp.Mrl, CR.FCR.FouFa	*2.033*	*0.002*	*536*		

3.2 Distributions of maerl biotopes and other maerl records

In England, maerl biotopes (SS.SMp.Mrl) are recorded by Seasearch since 2000 only from the South coast (Figure 7a). A small number of these are identified at finer resolution on the MHC. For instance, there are records of SS.SMp.Mrl.Lgla (only from Scotland Figure 7b) and records of SS.SMp.Mrl.Lcor and SS.SMp.Mrl.Pcal + sub-biotopes (Figure 7c, d), although veracity of these determinations is uncertain if made without microscopic or genetic analysis.

Simple maps of dots do not always give a clear impression of the actual numbers and distributions of records (e.g. multiple points may be superimposed). Heatmaps can give a clearer indication of where most records are found. The greatest concentration of records for maerl biotope was very clearly off St. Mawes in the Fal estuary (Figure 8a). Other areas were represented by only very small numbers of records (light patches in the heatmaps; Figure 8).

Figure 7. Locations of Seasearch samples containing maerl biotopes, specifically a) all SS.SMp.Mrl plus all sub-biotopes (red), b) SS.SMp.Mrl.Lgla (pink), c) SS.SMp.Mrl.Lcor (orange) and d) SS.SMp.Mrl.Pcal plus all sub-biotopes (light blue).

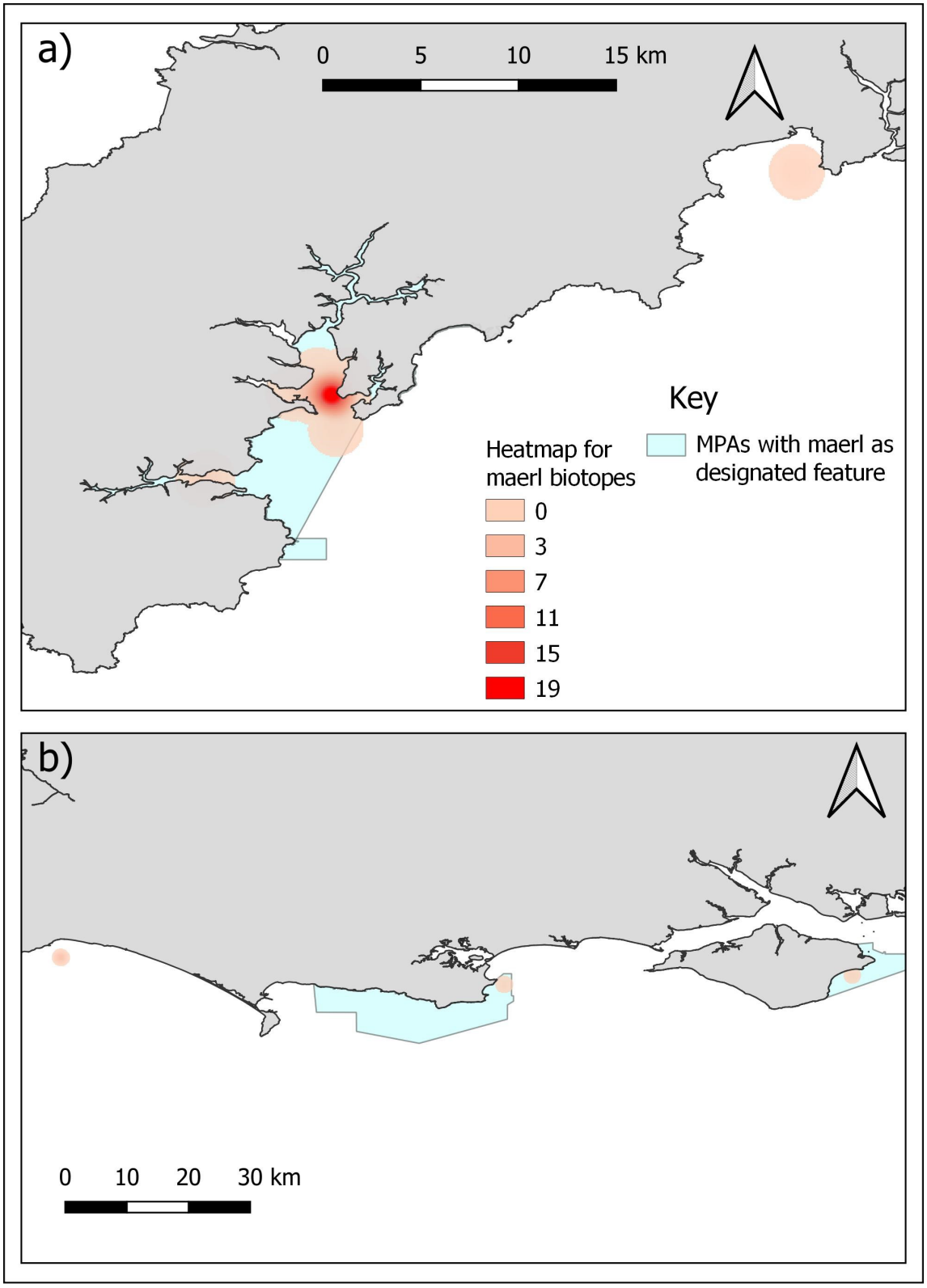


Figure 8. Heatmap for Seasearch samples containing maerl biotopes (SS.SMp.Mrl) for a) South Cornwall and b) Dorset and Hampshire. Heatmap search radius was 0.02° (~2.2 km) with pixel size of 0.001° (~110 m). The colour ramp applies for each map. Note the different scales between the two maps.

Records of maerl that are not within core maerl biotopes (Table 4) give more comprehensive information about the distribution of these taxa. Records of any type of maerl that is not within a maerl biotope show a broader, less patchy distribution along the South coast, extending from the Scilly Isles as far East as Selsey Bill (Figure 9). When broken down into the five new categories of maerl habitat (Axelsson 2021; Table 2) more detailed understanding of the distributions of different types of maerl habitat is gained (Figure 10 a-e). There are two instances of thick, extensive maerl habitat (Category A) outside of maerl biotope recorded by Seasearch within the Purbeck Coast MCZ (Figure 10a black arrow). These match the locations of other known records of maerl beds within this MCZ (DEFRA, 2019).

Instances of extensive 2-D layers of maerl (Category B) are more numerous than for Category A. They occur in Purbeck Coast MCZ, beyond the concentrations of maerl biotope in the Fal and Helford estuaries (Figure 10b white arrows).

Records of scattered or sparse maerl are the most numerous, being found as far East as Selsey, at multiple sites between Studland and Portland, in Lyme Bay, on the east coast of the Lizard, particularly in The Manacles MCZ and the only record from the North coast of Cornwall (Figure 10c grey arrows).

Veneers of maerl are the newest category to be considered. These thin layers of maerl (typically mostly dead with up to 5% live) over bedrock are scarce (or at least have not yet been recognised or recorded as such), being restricted to areas off Studland, in Purbeck Coast MCZ and the South-east of the Isle of Wight (Figure 10d, blue arrows).

Records that are potentially of maerl are scattered across the South-west, with concentrations in the Scilly Isles and to the East of Plymouth Sound (Figure 10e, orange arrows).

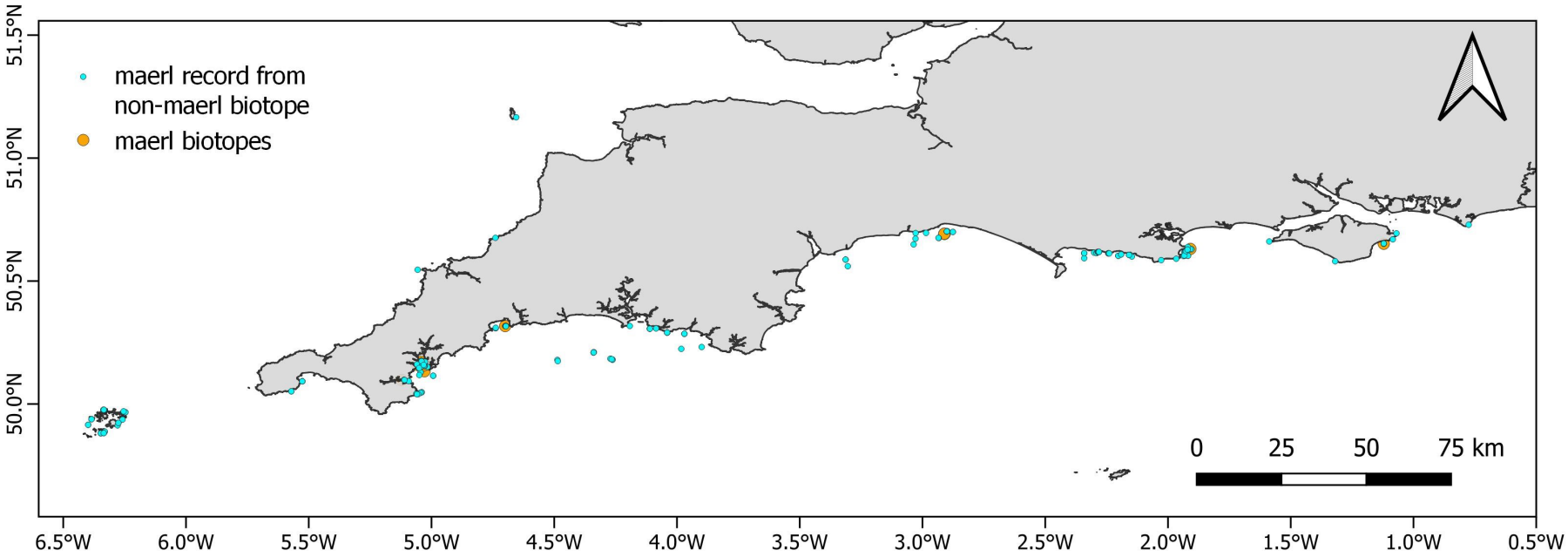
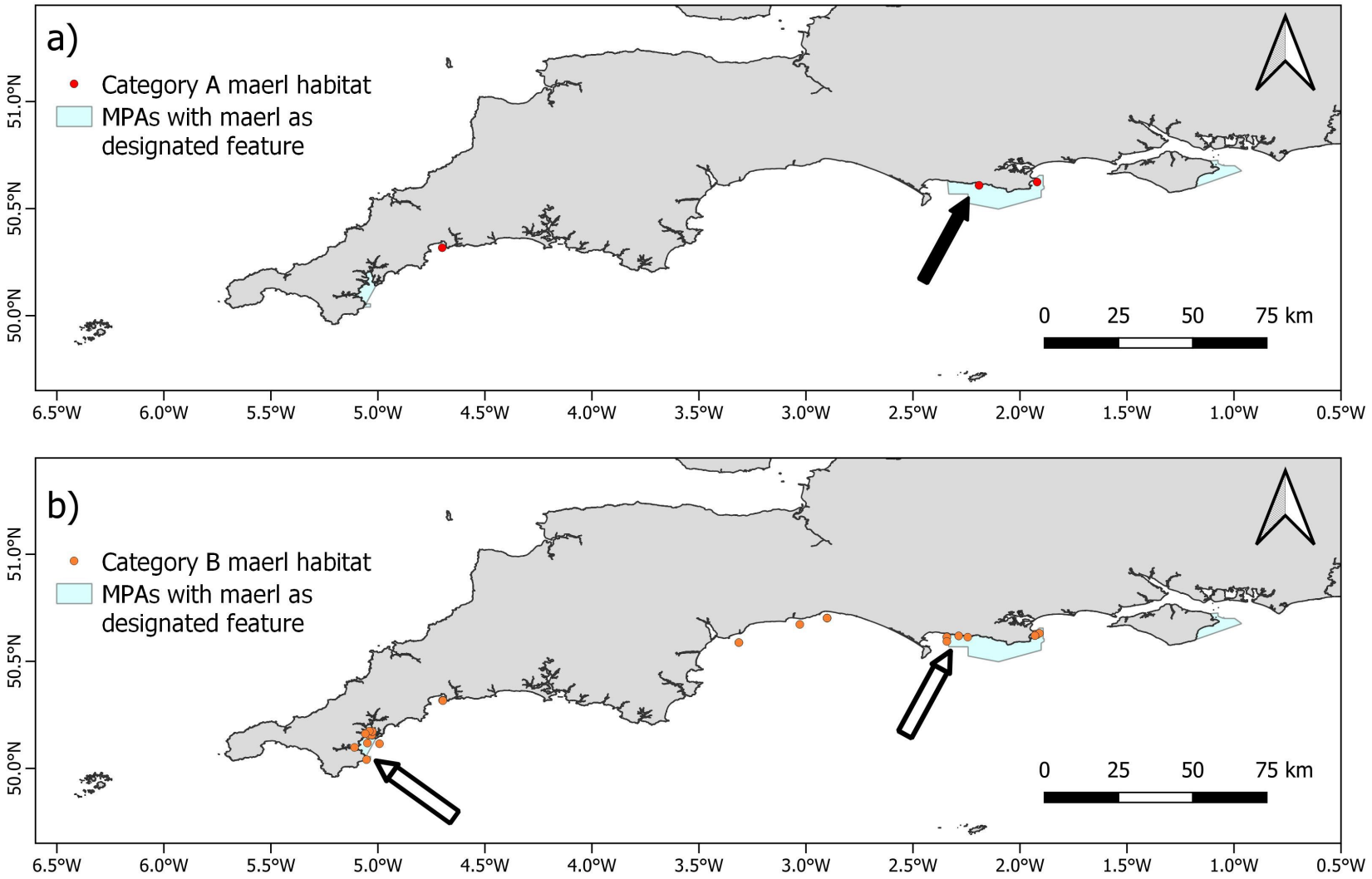
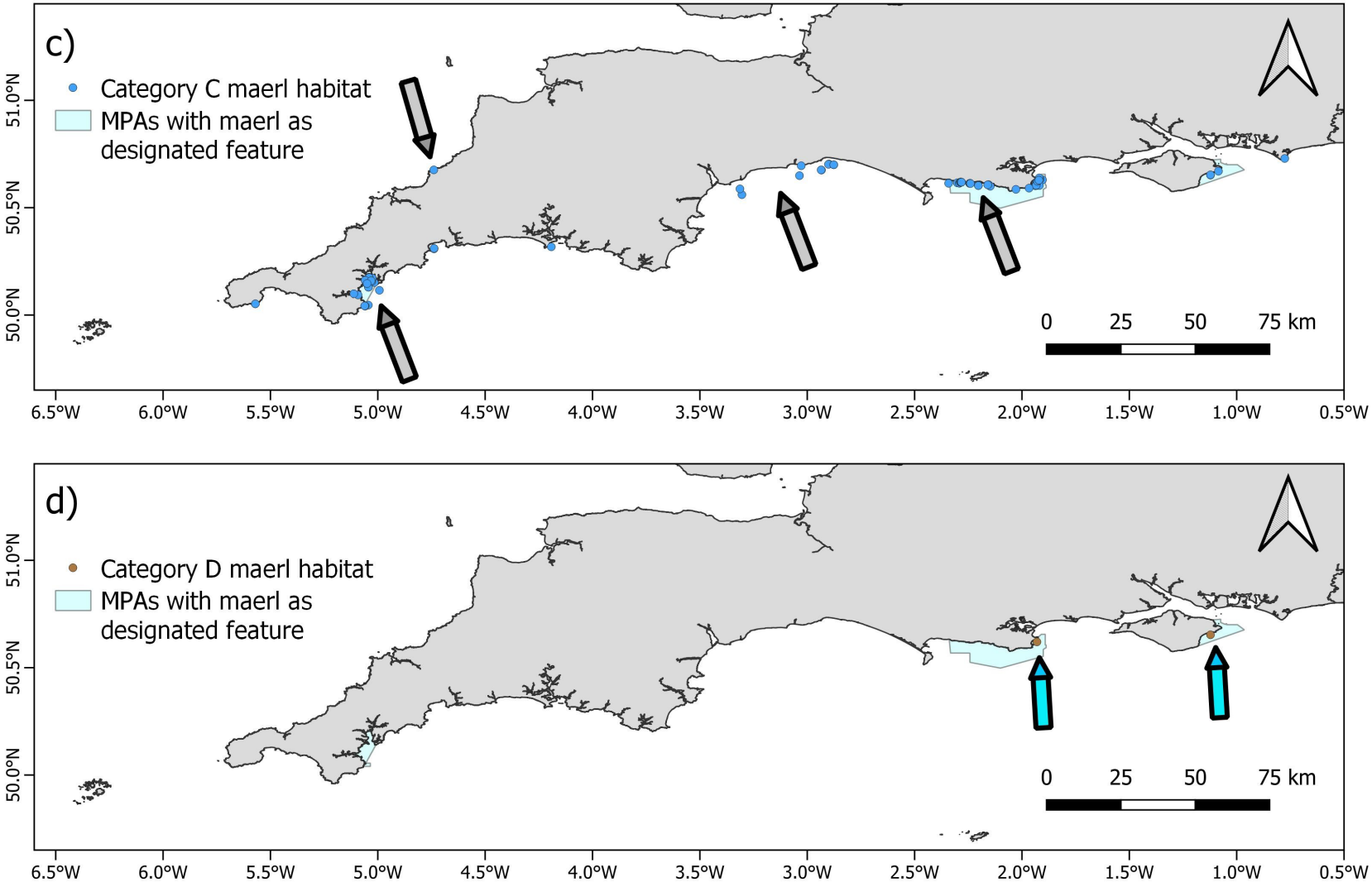


Figure 9. Locations of Seasearch samples in England that contain either records of maerl taxa but which are not in a maerl biotope (blue dots) or which are records of maerl biotopes (SS.SMp.Mrl and any sub-biotopes; large orange dots).


a)
Category A maerl habitat
MPAs with maerl as designated feature
0 25 50 75 km
b)
Category B maerl habitat
MPAs with maerl as designated feature
0 25 50 75 km
51.0°N
50.5°N
50.0°N
6.5°W
6.0°W
5.5°W
5.0°W
4.5°W
4.0°W
3.5°W
3.0°W
2.5°W
2.0°W
1.5°W
1.0°W
0.5°W

Continued…


c)
Category C maerl habitat
MPAs with maerl as designated feature
0 25 50 75 km
d)
Category D maerl habitat
MPAs with maerl as designated feature
0 25 50 75 km
51.0°N
50.5°N
50.0°N
6.5°W
6.0°W
5.5°W
5.0°W
4.5°W
4.0°W
3.5°W
3.0°W
2.5°W
2.0°W
1.5°W
1.0°W
0.5°W

Continued…

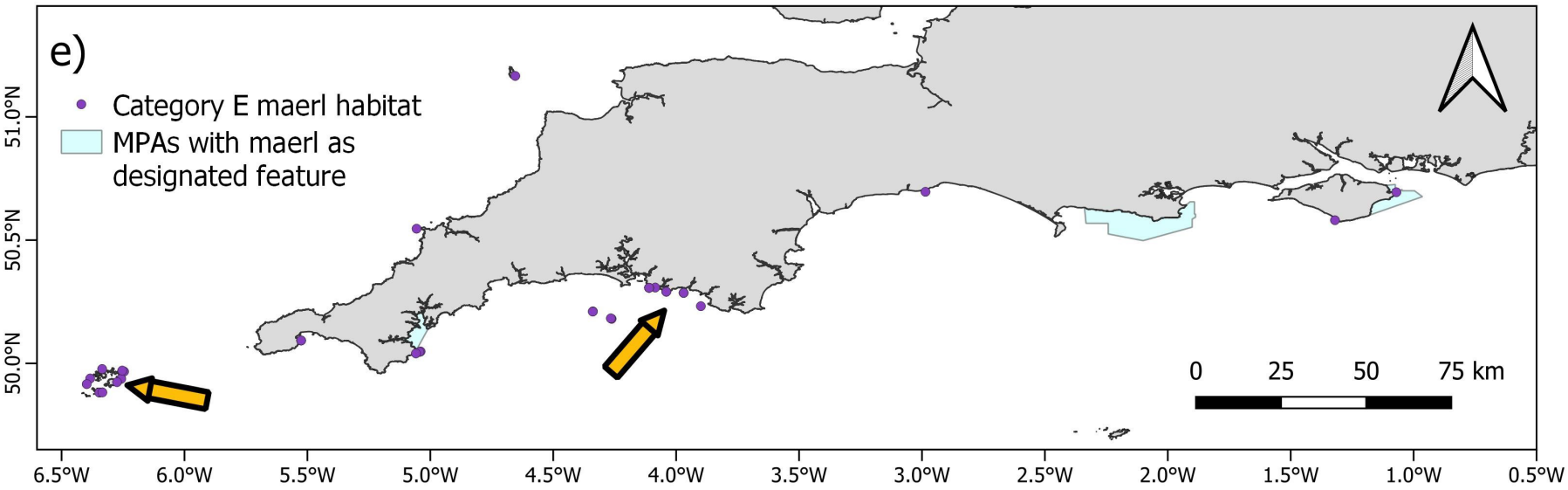


Figure 10. Locations of Seasearch samples in England that contain records of maerl habitat from a) Category A (red); b) Category B (orange); c) Category C (blue); d) Category D (brown); e) Category E (purple) maerl habitat. See Table 2 for details of maerl categories. The arrows indicate areas referred to in the text.

4 DISCUSSION

Data treatments and analyses developed by Jackson (2022) demonstrated that samples in the Seasearch database can be used effectively for testing hypotheses about differences in diversity and taxonomic composition of assemblages. These were applied here to compare taxonomic diversities and compositions of samples from different maerl biotopes and with samples that contained maerl, but which were not recognised as maerl biotopes. A new extended set of categories for maerl habitat (Axelsson, 2022) was applied to all Seasearch records of maerl and maps used to compare with known distributions of maerl biotopes.

4.1 Differences among maerl biotopes

Biotopes are recognised not only by their component taxa, but also by the physical conditions in which they occur. Not all these variables are collected by Seasearch, so it was not possible to discriminate on biological and physical data. This raises the potential during analyses, for biotopes to appear similar on a taxonomic basis, but which in the real world actually look rather different.

There were clear inconsistencies in the determination of maerl biotopes in the Seasearch database. It is likely that this was due to the development of our understanding over the last ten years about the challenges of reliably identifying different species of maerl. This knowledge developed well after collection of maerl records began. Inability to correctly determine the species of maerl involved (and hence the biotope allocated) is likely to lead to homogenisation of samples among different biotopes, leading to difficulties in differentiating samples among biotopes on the basis of taxonomic composition alone.

When small samples were eliminated and sample-sizes equalised, there was no evidence for differences in taxonomic diversity (taxon richness, Shannon or Simpson indices) between samples of Level 4 maerl biotope in four different areas (Section 4.1.1). This was not consistent with the first part of hypothesis 1 (i.e. taxonomic diversity differs among areas). Taxonomic compositions of samples from different five areas did however vary (supporting the second part of hypothesis 1 - taxonomic composition differs among areas), forming at least two groups (depending on analysis selected). These areas could be roughly separated latitudinally (Channel Isles & England vs Isle of Man, Ireland & Scotland). Some of the taxa that caused these differences had known northerly or southerly distributions (e.g. *C. fornicata* is expanding northwards, but as yet has no or very restricted presence in Isle of Man and Scotland). Others have distributions that cover the geographic range of maerl biotopes in the UK and reasons for the relative abundances in maerl habitat from different areas are unclear.

Among the five different combinations of area and Level 5 maerl biotopes, there were no differences in taxonomic diversity (taxon richness, Shannon or Simpson indices), despite some very small samples and considerable variation in sample sizes. This provided no

support for the first part of hypothesis 2 (i.e. taxonomic diversity will differ among combinations of area and Level 5 maerl biotopes). In England at least, few samples had been determined to Level 5, so these small samples were retained in order to allow any comparisons to be made. Aside from the Channel Isles, there was some indication that taxon richness and Shannon diversity increased with sample size (Figure 4; although this was not tested formally). Some interpretation of pattern is provided here, but bear in mind that these analyses are made with very small sample-sizes, which may not be representative of the actual make-up of assemblages of species in maerl habitat. It might be expected that if samples were larger and more equable, the lack of differences would persist. There was evidence that taxonomic composition differed among the five groups, consistent with the second part of hypothesis 2 (i.e. taxonomic composition will differ among combinations of area and Level 5 maerl biotopes). Specifically, SS.SMp.Mrl.Lgla and SS.SMp.Mrl.Pcal from Scotland contained different mixes of taxa to the other three biotopes (England: SS.SMp.Mrl.Lcor, SS.SMp.Mrl.Pcal; Channel Isles: SS.SMp.Mrl.Pcal; Figure 5). So, although there is uncertainty about correct identification of individual species of maerl, differences exist more broadly between maerl biotopes from different parts of the UK. When considering the two Level 5 biotopes from England (SS.SMp.Mrl.Pcal, SS.SMp.Mrl.Lcor), no differences were apparent. This may be because of any or all of i) insufficient power (small sample-sizes) to detect actual differences, ii) incorrect labelling of species of maerl, or iii) an actual lack of differences. Whichever is correct is unclear, but it certainly provides support for the notion that it may not be useful or appropriate in England to determine biotopes to Level 5. In the absence of more accurate identification of the maerl species present, it would be more appropriate for these samples to be determined as the parent biotope at Level 4 (SS.SMp.Mrl).

4.2 Differences between maerl biotopes and non-maerl biotopes with maerl

Given some of the uncertainties inherent in determining maerl biotopes when criteria for determination are vague, it might be expected that

- actual maerl biotope is labelled as something else
- other biotopes may be mislabelled as maerl biotope
- there is considerable overlap between maerl biotope and other Level 4 biotopes such that they are hard to distinguish.

Multivariate comparisons of taxonomic composition of assemblages in Level 4 biotopes showed that SS.SMp.Mrl was similar to SS.SMx.IMx (infralittoral mixed sediment) but significantly different to all other non-maerl biotopes which contained maerl. With a single exception, this is consistent with hypothesis 3 (i.e. taxonomic composition will differ between Level 4 maerl biotopes and other biotopes that include maerl). The observed similarity is not too surprising given that when determining biotopes for infralittoral

sedimentary habitat, SS.SMx.IMx is often used as a ‘catch-all’ if there is insufficient information to progress further into the MHC. One consequence of this similarity, when refining known distributions of maerl biotopes, would be to reconsider whether examples of SS.SMx.IMx with large abundance of maerl should actually be SS.SMp.Mrl and conversely whether instances of SS.SMp.Mrl with small abundance of maerl would be better as SS.SMx.IMx. In addition, biotopes containing maerl, but not determined as a core maerl biotope should be further categorised using the extended set of maerl habitats.

4.3 Categorising and mapping maerl habitat

Once a set of criteria (Table 3) had been decided on, categorisation of all Seasearch maerl records not from a maerl biotope, was quite straightforward. The set of categories for maerl habitat may undergo further development or the criteria used to allocate existing Seasearch records of maerl (which are not determined as maerl biotope) may be altered, after which it may be helpful to re-categorise the records and re-plot their distributions. Until that is necessary, the maps provided here give a much better indication of the true distribution of species that form maerl then either i) a map of maerl biotope records or even ii) a map of all maerl records. Allocation of different categories of maerl habitat (including those that have been given little consideration in the past, e.g. veneers of maerl on bedrock or areas with small extents or percent covers of maerl, but which might have considerable ecological value) allows production of distribution maps with much greater detail of the biogenic habitat provided by maerl taxa. Knowing about the extent, depth, cover, vitality, mobility, substratum, etc. of maerl habitat will likely allow much greater and more realistic interpretation of the type and extent of the ecological functions and ecosystem services provided by the seabed. Knowing the distributions of different maerl habitat, particularly when outside of areas where maerl is a designated feature, will also allow more effective monitoring, management of activities and opportunities for protection.

Transformations of the SACFOR scores, some taxonomic standardisation, thresholds for minimal, equal (where possible) sample-sizes and, for multivariate hypotheses, subsets of the 50 ‘most important’ taxa were applied prior to analysis to make sure that:

- abundances for organisms with different growth-forms and sizes were scored on a common scale (Strong and Johnson, 2020);
- inappropriate inflation of taxonomic richness was avoided;
- any patterns observed were more likely to be caused by the factor of interest rather than by differing sample-size; and
- presence of large numbers of rare taxa did not obscure patterns.

Although, such precautions improve the reliability of analyses and robustness of interpretations, it should be remembered that Seasearch records were not originally collected for the purpose of comparing taxonomic assemblages of maerl habitat and the usual health warnings apply about over-analysis and interpretation of imprecise ecological data.

4.4 Recommendations for recording

From the perspective of Seasearch (and possibly other recorders such as JNCC, NE), **maerl biotopes should not be determined to Level 5**, because reliable identification underwater is not possible, and in the absence of genetic or microscopic evidence, should instead be determined at a coarser level (i.e. Level 4 SS.SMp.Mrl, maerl beds). In addition, in the interests of maximising information on distributions, extent and characteristics of maerl habitat, the extended set of maerl categories should be used to add more detail to free-text fields (in Marine Recorder) for all records that are actual or potential maerl habitat. This categorisation should be standardised as much as possible and done only by a subset of informed, collaborating people e.g. survey coordinators or data enterers, supported by clear guidance from NE. Demonstration of a clear methodology for recording maerl could then be used to encourage SNCBs from other countries to adopt the same model, giving much broader consistency in data collection and quality.

Recording at the level of Genus for taxa such as *Lithothamnion*, *Lithophyllum* and *Phymatolithon* should be avoided because it is not then clear if the record pertains to something that is considered to be maerl or not. If the record is for free-living maerl nodules, these should be recorded as 'maerl indet'. If the record is for crusts of coralline red algae or hedgehog growths, but clearly not free-living maerl, determination should not be made as a Genus that can also form maerl and it may be necessary to record at Order level, with additional detail added to the SpeciesQualifier field. The correct name for Order would depend on the taxonomy being used (e.g. in MSBIAS it would be Corallinales but in AlgaeBase it would be Hapalidiales). Further work is clearly required to clarify the taxonomy of these red algae and how best to record and classify them. There may be options for future projects to collect samples of maerl to contribute to the Darwin Tree of Life genome sequencing project (https://www.darwintreeoflife.org/), thereby improving our understanding of the systematics of these algae.

4.5 Future work

Some specific tasks might be to:

- Use the broader range of maerl categories proposed by Axelsson (2021) as a basis for more effective labelling of ecologically valuable maerl habitats that merit protection and management of damaging anthropogenic activity;

- Apply further refinement of the new categories for maerl habitat e.g. to include records that should definitely not be classed as maerl.
- Re-assess known distributions of maerl based on MHC biotopes, particularly within MPAs
- Consider whether maerl should be included as a designated feature in additional MPAS
- Identify locations that might benefit from additional targeted surveys for maerl habitat by the NE dive team or by Seasearchers (e.g. those records labelled here as category A or B). Such reassessment might prompt recategorization of habitat as maerl biotopes or confirm actual differences from maerl biotopes.

5 CONCLUSIONS

Citizen science data from the Seasearch programme are suitable for application to formal statistical analyses and protocols have been developed such that they can be used in analyses about maerl. The protocols and statistical approach can be used on historic data and on those yet to be collected, provided the same Seasearch methods are used.

Statistical analyses of Level 4 maerl habitat from different areas in the UK revealed that although no differences were apparent in several measures of diversity, taxonomic composition varied broadly on a latitudinal basis, where samples from more southerly areas (Channel Isles and South England) differed from those further north (Ireland, Isle of Man & Scotland). Analyses of Level 5 maerl habitats demonstrated again no differences among measures of diversity, but that taxonomic composition of maerl beds in Scotland (with maerl species of *Lithothamnion glaciale* or *Phymatolithon calcareum*) differed significantly from other maerl beds in England and the Channel Isles. Thus, it is partially possible to distinguish different maerl biotopes on the basis of the taxonomic composition of the associated assemblage, but that some of the differences in composition may be driven more by Latitude than by different types of biotope. Small sample-sizes for several biotopes from different areas indicate that care should be taken not to over-interpret these results. This all serves to re-emphasise the imperfections and limitations of the MHC (Connor *et al.*, 2004) that is presently used to categorise the seabed into biotopes on the basis of taxonomic composition and physical conditions.

Comparisons of taxonomic compositions of samples showed that maerl beds (Level 4, SS.SMp.Mrl) were similar to circalittoral mixed sediments (Level 4, SS.SMx.IMx) but were clearly differentiated from all other Level 4 biotopes containing maerl. Thus, there is some overlap in biotope determinations from samples that contain maerl and there may be benefit in considering whether or not re-assessment of existing samples is appropriate or helpful.

The MHC has few categories for maerl habitat, which are based on (often questionable) taxonomic identification of maerl, the new categories proposed by Axelsson (2022) disregard taxonomy and instead focus more on physical characteristics of maerl habitat. Although assessment of these characteristics has some degree of subjectivity, it can be done without specialist training or advanced taxonomic skills. All existing Seasearch samples that included maerl, but which were not considered maerl biotope were classified using the new, extended set of categories of maerl habitat(Axelsson, 2022). Using these new categories, it is now possible to map the distribution of maerl habitat much more comprehensively and realistically and for this distribution to be divided according to different characteristics of the habitat (extent, depth, percent cover, substratum, vitality, mobility, etc.). The distribution of maerl habitat is clearly greater than indicated by records of MHC categories with maerl in the name.

Having a classification scheme with greater resolution than the MHC and which includes physical traits of relevance to benthic ecology, is likely to be of great value when managing

human activities in and around these legally protected habitats and species. Maps created in this study are unrivalled in their currency, extent and detail. As such, they can act as a ‘current status’ against which to assess future change. They can also provide focus and guidance for future sampling effort, management and conservation.

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7 APPENDICES

Seasearch Quality Control and Assurance Procedures

Seasearch diving and recording is carried out by volunteers. Many of them have a professional background in marine biology and conservation but many do not and are self-taught naturalists. The document sets out the processes which are used to assure the quality of Seasearch data so that they can be used by professionals with confidence.

Seasearch Training Programme

Training is available at three levels to all participants.

Observer Level – this is aimed at volunteers without previous experience of marine recording in British and Irish waters. It comprises a one-day course followed by two survey dives where the individual records are reviewed and discussed with a tutor. The Observer qualification is awarded after completion of a further 3 survey forms.

Surveyor Level – this is aimed at experienced Observers and others with previous relevant experience. The training comprises a two-day course which involves the completion of two Survey Forms (one from video and one from an actual dive). The Surveyor qualification comprises completion of a further 5 Survey forms, two of which are supervised by a Seasearch tutor, and the completion of an ID test.

Specialist level – this is aimed at experienced surveyors to either increase their skills in survey methodologies or individual groups of plants and animals. Courses are workshop style and are led by experts in their field. They are often attended by professional biologists as well as Seasearch surveyors.

In addition to the training process Seasearch produces a series of **ID Guides** aimed at improving in-water ID skills. These comprise:

Seasearch Guide to Marine Life – introductory level containing a selection of widely observed species of plants and animals. (Much expanded and updated second edition published December 2018)

Seasearch Guide to Sea Anemones and Corals of Britain and Ireland – comprehensive guide to all of the anemones and corals found in shallow waters, the only guide of its type. (Two editions)

Seasearch Guide to Seaweeds of Britain and Ireland – again the only guide to be illustrated with in-situ photographs to complement recording by collecting specimens. Equally popular with littoral recorders and divers. (Two editions)

Seasearch Guide to Bryozoans and Hydroids of Britain and Ireland – these are difficult groups to identify but important in biotope terms as they often form significant animal ‘turfs’. This is the only guide to contain *in situ* images as opposed to line drawings alone.

Seasearch Guide to Sea Squirts and Sponges of Britain and Ireland - as with bryozoans and hydroids, these groups can form the dominant animal cover in the right conditions but are often confused. As with the other Seasearch guides, this book concentrates on *in situ* features to allow recording without specimen collection. Most of the sea squirts found the shallow waters around Britain and Ireland, together with the more easily recognised sponges, are included in the guide.

These guides help to ensure high quality records as many of our volunteers use cameras and are able to check their images with those in the guide.

Quality Assurance Process for Recording Forms

Validation and verification of the data follows a three-stage process:

Initial validation can be carried out locally or by the National Coordinator depending on who first receives the forms. It comprises allocating a Seasearch number, checking the completeness of the form, checking the position given and checking the species lists for any unlikely species. If there are queries then these are raised with the recorder and photographs requested to check identifications, especially of unexpected species. Either the recorder or the validator can assign a '?' to a taxon record which is then included in the database as an uncertain record. Supporting verification of an identification, in the form of confirmation by a recognised expert, can be appended to the taxon record within Marine Recorder (*e.g.* "identification confirmed by Bernard Picton" for a rare/unusual nudibranch).

Data Entry into the Marine Recorder database is carried out by a small group of experienced personnel, the majority of whom are professional biologists or extremely experienced recorders. There is a manual and supporting guidance for data entry to ensure consistent standards. The person entering the data can add significant value in the way they describe habitats and they also allocate MNCR Biotopes to the habitats identified in the Survey forms. This is a specialised skill which we do not expect volunteers to have. We have produced two manuals to aid the process and again maintain consistency of approach. At this stage the person entering the data can again refer back to the original recorder to clarify any points.

Merging and final checks are carried out by the National Coordinator, supported by the Seasearch Data Officer. This stage consists of merging all of the separate local datasets into a single UK/Ireland file prior to checking and distribution of the data. Once merged, a 'snapshot' of the data is created which enables checks to be carried out of species (looking for unusual or questionable records), completeness of data and consistency over the dataset as a whole. A map is also created which plots all of the records received and this is also checked for significant positional errors. Any changes required are agreed with the person responsible for entering the data and must be carried out by them to avoid the creation of duplicate datasets. The National Coordinator is responsible for distributing the data to the NBN, JNCC and other users.

Ongoing Data Management

Queries arising from users of the data normally come to the National Coordinator (some through the NBN) but may also arise at a local level. They are discussed and amendments made as appropriate by the holder of the dataset at the local level. Any amendments are incorporated in an, at least, annual update of the whole dataset.

This process we believe makes the Seasearch data reliable and of a professional standard. Whilst many of our volunteer recorders are experts in their own right, that is not always the case and the process ensures that records made by less experienced volunteers are thoroughly checked by experienced people prior to appearing in the dataset.

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Seasearch QA procedures (v2 – updated by CEB November 2017; v3 – ID guide update (CEB Dec.2018))

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