Assemblage composition in key habitats of Marine Protected Areas

Seasearch data report to Natural England

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Further information

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 condition assessments have been partially completed for habitat features in a few SACs, and more are planned. The Sentinel MPA monitoring approach will collect long-term data sets and evidence on habitats within MPAs and the wider marine environment. 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 and historical conditions in MPAs.

This is a report to Natural England (NE) about the use and value of records for species and habitats in English MPAs, collected since 2009 (11 years), that are held and curated by the Seasearch programme. The overarching intentions are to demonstrate whether novel approaches using citizen science data can be developed to support formal condition assessment and to expand our knowledge and understanding of marine benthic diversity in MPAs.

The remit of this report is five-fold.

1. Assess whether Seasearch data are amenable to analyses comparing assemblages of benthic species in major habitats of MPAs.
2. Develop a protocol for formatting data such that it can be used in future analyses.
3. Test hypotheses about diversity of assemblages of benthic species.
4. Provide information that can act as a ‘baseline’ against which to assess future change.
5. Provide focus and guidance for future sampling and condition assessment.

Within these, the main focus is on the diversity and composition of benthic assemblages on infralittoral or circalittoral reefs in a small selection of MPAs. A secondary focus is to assess availability of data for seagrass habitat.

In Plymouth Sound and Estuaries SAC, Seasearch data from the last six years were compared with condition assessment data from Natural England to learn how these two methods differ in what they can tell us about benthic diversity.

For seven MPAs on the south and east coasts of England, temporal analyses were used to assess change in benthic assemblages. Seasearch data starting from (and including) 2009, were divided into two blocks (2009-13, 2014-19) of five and six years, respectively, and comparisons made between these.

To maximise the likelihood of reliable outputs, a protocol of data filters and treatments was developed. This should be applied to all Seasearch data prior to its use in similar analyses in the future. A range of indices were used to quantify diversity and to make quantitative comparisons about the compositions of assemblages of organisms that live on the seabed.

Seasearch provided a greater volume of data for analysis than did condition monitoring. In circalittoral reefs, the two organisations accrued new taxa at similar rates, but in infralittoral reefs, species accumulation was much faster by Seasearch surveys than by condition monitoring.

As a consequence of greater survey effort, Seasearch found more taxa in total in each habitat than did condition monitoring. Seasearch also found significantly more taxa on average in infralittoral habitat, but not in circalittoral habitat. For each habitat, multivariate analyses showed that the composition of assemblages recorded differed among samples collected by condition monitoring or Seasearch. The latter included large or mobile taxa that were absent from samples collected by condition monitoring.

Of the seven MPAs assessed for change through time, most showed little change in diversity, but there were differences in composition. The main exception was the Berwickshire and North Northumberland Coast SAC, where there was a significant increase in the mean number of taxa recorded from each habitat. Reasons for this increase are not clear. No changes were found in the composition of assemblages from circalittoral rock, but there were significant changes in infralittoral rock. The former somewhat counter-intuitive, lack of pattern in composition can be explained by the multivariate analyses of composition being done on the 50 most important taxa which changed little, and the increase in diversity being driven by recording a greater number of rare or infrequently occurring taxa. There were insufficient data to make any comparisons for the Essex Estuaries SAC. There were also very few data for seagrass habitat in any MPA.

A scoring system was developed, based on sample size and consistency of results from permuted tests of equal sample size, that allowed different confidence ratings to be allocated to comparisons of diversity indices between the two periods of time. This may prove to be a useful approach when judging the outcomes of comparisons of datasets with differing sample effort.

The different methods employed by Seasearch and condition monitoring provide different information about benthic diversity and cannot be treated as analogues, but actually give information on different aspects of diversity. Combining different methods and analyses may give the most complete and informative picture of diversity. Where conservation agencies are legally obliged to survey features of conservation interest, but where data are challenging to collect, records collected by trained volunteer divers and curated by Seasearch may be able to go some way to filling gaps.

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Contents

Introduction

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 MCS and comprising representatives from the UK statutory conservation bodies (CCW, EHS(NI), JNCC, NE, SNH), 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). Volunteer divers and snorkellers can participate in training courses and many dive surveys organized during the season. At present we do not organise snorkel surveys. For more information visit the Seasearch website. 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;

- 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. These 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.

Marine Conservation Society

The Marine Conservation Society (MCS) 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 annual Good Beach Guide, as well as promoting public participation in volunteer projects and surveys such as Adopt-a-Beach, Seasearch and Basking Shark Watch.

Background

This is a report to Natural England (NE) about the use and value of records for species and habitats in English MPAs, collected since 2009 (11 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 species and habitats in designated MPAs. Legislation for Special Areas of Conservation (SAC) requires reports every six years to the Secretary of State (Williams, 2006), on the conservation status of habitats and species listed under the Habitats Regulations. The Marine and Coastal Access Act (2009) also requires assessment of conservation objectives for marine conservation zones (MCZ). To provide appropriate guidance on management within protected sites, current knowledge about the condition of features is crucial. These obligations require data that can provide robust results and information on the condition of features within MPAs. A condition assessment is a judgement about a conservation feature against a set of six reportable categories (Favourable; Unfavourable recovering; Unfavourable no change; Unfavourable declining; Partially destroyed; Destroyed), based on collation of data and evidence from a range of sources. 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.

Marine Condition Assessment methodology is, as yet, applied only to ‘marine habitat features’ listed in Annex I of the EC Habitats Directive, and there is recognition that current efforts need to be improved (Kröger and Johnston, 2016). This is particularly important if we are to meet requirements of legislation adopted from the EU Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC), where monitoring is necessary to assess whether or not Good Environmental Status (GES) has been achieved (Danovaro *et al.*, 2016; Kröger and Johnston, 2016). One important aspect of monitoring habitats in protected areas requires establishment of current status and any changes in composition of assemblages of species in these habitats. Such condition assessments have been partially completed for habitat features in a few SACs, and more are planned in the future (T Russell, pers. comm.; Natural England 2020).

Marine monitoring in MPAs can be complex and difficult; benthic habitats are hugely diverse, long term data trends can be absent, or methods are insufficient to describe habitat condition or identify pressure indicators. Several of the statutory conservation agencies (Natural England, NatureScot, JNCC) have adopted a Sentinel MPA monitoring approach to collect long-term data sets and evidence on habitats within MPAs and the wider marine environment. The Sentinel MPA monitoring approach consists of a subset of sub-feature locations within MPAs, which are chosen to be representative of the sub-feature as a whole. Sentinel MPAs were selected by assigning habitats a ‘Monitoring Efficiency Score’; a categorisation based on expert judgement regarding how likely monitoring the habitat is to deliver meaningful results taking account of factors such as inherent natural variability, exposure, and practical ability to monitor. To ascertain if the Sentinel MPAs are representative of the wider MPA network, additional monitoring will target sub-features of MPAs not in the core Sentinel MPA programme. Sentinel MPA monitoring is underway for infralittoral and circalittoral reef habitats within Plymouth Sound and Estuaries SAC, and additional sentinel sites planned in future.

Obligations for ongoing monitoring are considerable and the COVID-19 pandemic in 2020-21 has made this even more challenging. Natural England seeks alternative sources of information to understand current and historical conditions in MPAs.

This report describes a study that demonstrates proof of concept for the use of citizen science data to support formal condition assessment and develops novel approaches which will expand our knowledge and understanding of marine benthic diversity in MPAs. The citizen science records in the Seasearch database provide one possible alternative or supplement to standard condition assessment or sentinel monitoring. The broad aims of this study are, therefore, first to establish whether data collected via the standard Seasearch protocols have appropriate resolution, adequate detail and can be formatted such that they can justifiably be used in standard analyses of biodiversity. If the data appear appropriate, then they will be used to describe biodiversity and composition of assemblages of benthic species in major habitats of selected MPAs. Such analyses will provide information about the present condition (or a baseline), which can then be used for comparison with other site and as a benchmark against which to compare future change or the effects of management. The results can also provide direction for future monitoring efforts.

The methods used by Seasearch and NE are carefully considered, refined through time and appropriate, but designed for different purposes. The NE condition assessment and sentinel monitoring programmes are completed by professional scientific divers under the Diving at Work Regulations (1997) to answer specific questions. Data within Seasearch are opportunistic and *ad hoc*, collected from amateur (but often very experienced) citizen scientists, but not specifically to monitor composition of assemblages (and how they change) in MPAs. As a consequence, the methodology is not necessarily optimal for the present task. *A priori* provision of clear scope alongside explicit and specific hypothesis to be tested will help establish which parts of the Seasearch dataset are required and whether they can be formatted correctly. Sampling intensity is also likely to differ between methods, which can be a confounding factor.

Selection of Habitats

Given the diversity of marine habitats and species therein, there is little value in considering diversity at the scale of all habitats within whole MPAs. Of the habitats listed in Annex 1, the Seasearch database holds more data for reefs than other habitats, so the primary focus therefore will be on composition of assemblages on reefs in a small selection of MPAs. Seasearch data within the structure of the Marine Recorder database does not easily lend itself to isolating sedimentary habitat in Annex I (e.g. sandbanks which are slightly covered by sea water all the time), but seagrass habitats, which are also of conservation interest, can be readily identified for. Thus, a secondary focus will be on composition of benthic assemblages in seagrass beds in the same MPAs.

Reefs are widely distributed in inshore and offshore waters around the UK (McLeod *et al.*, 2008). The definition of ‘reef’ used here, is where assemblages of flora and/or fauna develop on rock or stable boulders or cobbles. The European Nature Information System (EUNIS, EEA, 2019), which is equivalent to the UK marine habitat classification (Connor *et al.*, 2004), is used to provide a framework for habitats referred to in this study. Reef-dwelling assemblages vary with depth (and therefore light), geology, wave action, tidal flow, water quality, and topography. As light diminishes, seaweeds can no longer grow and are replaced by animal-dominated assemblages (Connor *et al.*, 2004). Shallow, infralittoral reefs are dominated by algae such as kelp forests or meadows of foliose algae, ranging from the low water mark down to depths at which light at the seabed is attenuated to 1% of that at the surface and is no longer able to support algae-dominated assemblages (Cochrane *et al.*, 2010; McBreen *et al.*, 2011). Deeper reefs beyond the influence of sunlight are dominated by animals like sponges, corals and seasquirts (McLeod *et al.*, 2008). Where availability of light is restricted, as in turbid waters, the circalittoral zone can begin quite close to the surface and extends down to the limits of wave influence (typically 50-70m depth; Cochrane *et al.*, 2010; McBreen *et al.*, 2011). Thus, availability of light provides an obvious and fundamental division in the marine habitat classification and these algae-dominated or animal-dominated habitats are sensible treated separately in analyses and discussion presented here.

Assemblages are also strongly influenced by wave action (Connor *et al.*, 2004), giving further sub-divisions in the habitat classification. In the interests of manageability and maintaining an adequate sample size within a somewhat *ad hoc* sampling process, these are not considered here. Thus, infralittoral rock includes those habitats that fall into the Level 3 habitat classifications: A3.1 high energy infralittoral rock, A3.2 moderate energy infralittoral rock, A3.3 low energy infralittoral rock; A3.4 Features of infralittoral rock; in addition to the constituent biotopes at Levels 4 and 5. Circalittoral rock includes: A4.1 high energy circalittoral rock; A4.2 moderate energy circalittoral rock; A4.3 low energy circalittoral rock; A4.4 Features of circalittoral rock; in addition to the constituent biotopes at Levels 4 and 5. Sublittoral seagrass habitats are those that fall into the Level 4 habitat classification: A5.53 Sublittoral seagrass beds and constituent biotopes at Level 5.

Selection of MPAs

Seven inshore MPAs were selected from the large range available. Essex Estuaries SAC, Berwickshire and North Northumberland Coast SAC and Isles of Scilly Complex SAC were chosen because these were intended for partial condition assessments in 2020, and none yet have any existing condition assessment for habitats. The Solent Maritime SAC and the Fal and Helford SAC were selected to provide information to support the LIFE Recreation ReMEDIES project (LIFE, 2020). Plymouth Sound and Estuaries SAC was selected to allow comparison with the Natural England sentinel marine monitoring programme. The Manacles MCZ is included because it is known to be diverse (>600 taxa recorded by Seasearch), contains several sensitive features, and has been well surveyed. Overall, this gives

MPAs along the full southern extent (and one in the far North-East) of England. This selection covers a range of biogeographic areas with different associated flora and fauna which will contribute to differences in composition of assemblages. In addition, data from The Manacles MCZ or Isles of Scilly Complex SAC may provide a benchmark against which diversity in other MPAs with similar conditions in the Southwest can be compared. They could provide an indication of levels of diversity that might be achieved elsewhere if damaging anthropogenic activities were prevented.

The MPAs in the south span three sectors of the UK regional seas (Western English Channel, Eastern English Channel and Southern North Sea), boundaries between which represent change in physiographic character, presence of distributional barriers or locations of known biogeographical separation (Hiscock, 1996). These different sectors would, by definition, be expected to support assemblages of different diversity and composition. Biodiversity, in terms of species richness, biotope richness and taxonomic distinctness can be interpreted to identify hotspots (Hiscock and Breckels, 2007). The south-west of England is recognized as having greater biodiversity than expected, whereas the Essex estuaries on the east coast have less diversity than expected (Hiscock and Breckels, 2007). The western Channel tends to have a wide range of species (i.e. large taxonomic distinctness) and in the south-west, Falmouth and Helford SAC and Plymouth Sound and Estuaries SAC were noted as having many (>800) species. These analyses were done combining all physiographic features but does give an overall impression of where hotspots in biodiversity occur. Different indices used to identify diversity hotspots are not always synonymous (Hiscock and Breckels, 2007) emphasising the importance of using multiple criteria (Orme *et al.*, 2005).

The range of physical habitat also varies along the South coast. Broad-scale seabed habitats (e.g. EUSeaMap; Populus *et al.*, 2017) indicate greater diversity of near-shore habitats in the southwest (a mix of hard and soft substrata) than around the Essex estuaries (mainly sediment). There is long-standing recognition of the positive relationship between diversity and habitat complexity (McCoy and Bell, 1991; Tews *et al.*, 2004). Spatial distribution of suspended particulate matter (and therefore turbidity), which can limit many species (Giberto *et al.*, 2004; Magris and Ban, 2019) is also much greater off the Essex coast than in more oceanic waters off the south-west (DEFRA, 2020). Greater proximity to species in warmer, more-southerly areas and a tendency for polewards 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 strong expectations for differences in diversity among MPAs, but these are not considered here. Rather, the focus is on comparisons within MPAs of different methods or of changes through time.

Figure 1. Locations of MPAs considered in this report: a) Plymouth Sound and Estuaries SAC, Isles of Scilly Complex SAC, The Manacles MCZ and Fal and Helford SAC; b) Solent Maritime SAC and Essex Estuaries SAC; and c) Berwickshire and North Northumberland Coast SAC. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the Open Government Licence 3.0. Map Projection is EPSG:4326 - WGS84.

Temporal change

Benthic assemblages may change through time for a variety of reasons, although mostly as a consequence of human activity. Mobile towed fishing gear causes the greatest disturbance to the seabed (Kaiser *et al.*, 2010; IPBES, 2019) directly removing the target species, but also removes taxa that protrude from the seabed, changes the structural complexity of the habitat and alters trophic linkages by changing the balance between predators and prey. Such changes can alter demographics, function and life-histories of the organisms affected (Tillin *et al.*, 2006), thereby altering the ecosystem goods and services available. Climate change is an ever-increasing threat which is demonstrably altering distributions of organisms and altering interactions within assemblages of organisms (Montoya and Raffaelli, 2010), although such changes are often neither predictable or consistent (Vandvik *et al.*, 2021). Invasive non-native species, introduced by human agency can also drive change in native assemblages (Cottier-Cook *et al.*, 2017). Other human activities such as aggregate extraction, offshore developments such as by the oil and gas or renewable energy industry have their own effects (ICES, 2001; Shields *et al.*, 2011; Dannheim *et al.*, 2020). Extreme events, such as storms, can also influence composition of assemblages and the trajectory of their subsequent recovery (Underwood, 1999). Protection of marine habitats through designation of MPAs has the potential to allow benthic habitats to recover from disturbance, but very little of the area of MPAs in the UK are actually protected from fishing (Dunkley and Solandt, 2021).

So, changes to benthic assemblages in MPAs may change through time for multiple reasons, often acting simultaneously, cumulatively and synergistically. Demonstration of change is, however, not the same at attributing change to any of these mechanisms or processes.

Timeframe

Seasearch holds data from as early as 1977, but the vast bulk has been collected since the early 2000s, when a clear and consistent protocol was introduced. Assemblages can change through time, for a variety of reasons. Thus, it makes little sense to include ‘old’ records when trying to establish present-day conditions or make current comparisons. For methodological comparisons (Seasearch vs NE), data from the last six years were used. For temporal analyses, data starting from (and including) 2009, were divided into two blocks (2009-13, 2014-19) of five and six years, respectively, and comparisons made between these.

Diversity measures

Although the number of taxa (taxon richness) is widely used in the literature to describe biodiversity, it does not give the full picture (Purvis and Hector, 2000). The term ‘biodiversity’ can be represented by a large range of metrics (e.g. Magurran, 2004; Bowden and Hewitt, 2012). To measure biodiversity over different spatial scales, Whittaker (1972) described three terms. Alpha (α) diversity refers to the diversity within a particular area, assemblage, habitat or ecosystem and is typically expressed as the number of taxa (taxon richness) or as some univariate index of diversity (e.g. Shannon or Simpson diversity). Such indices incorporate aspects of richness, relative abundance of taxa and evenness (or equitability) with which the abundances of taxa are distributed. Thus two different types of measure (values for diversity index and evenness) can each be compared between units.

Beta (β)-diversity is used to examine dissimilarities in the composition of assemblages between units of interest. If species are either only lost or gained between units, then the assemblage with fewer species is a subset of the larger (i.e. it is nested in the larger assemblage; Whittaker and Fernández-Palacios, 2007). If species can be lost and gained between assemblages, this is referred to as ‘species turnover’ (Leprieur *et al.*, 2011; Villéger, Grenouillet and Brosse, 2013). β-diversity can be decomposed into two components i) nestedness and ii) turnover (Baselga, 2010). Nestedness of assemblages can occur where environmental conditions change continuously and gradually among units (Sheldon, 1968), and patterns of the turnover are observed with abrupt changes in the environment (e.g. across biogeographical breaks (McGarvey and Hughes, 2008). Partitioning of β-diversity into these components may provide insight to potential causes of spatial variability in benthic assemblages (Soininen, Heino and Wang, 2018). Multivariate statistical methods, such as those found in software packages like PRIMER, are effective for calculating and analysing α- and β-diversity (e.g. Leduc *et al.*, 2012).

Scope, remit and hypotheses

The scope of the work includes the spatial and temporal extents described above. The remit of this report is five-fold.

1) Assess whether Seasearch data are amenable to analyses comparing assemblages of benthic species in major habitats of MPAs.
2) Develop a protocol for formatting data such that it can be used in future analyses.
3) Test hypotheses about diversity of assemblages of benthic species.

4) Provide information that can act as a ‘baseline’ against which to assess future change.
5) Provide focus and guidance for future sampling and condition assessment.

Assuming that data are suitable and adequate, the following questions, hypotheses and predictions, framed around the constructs of α- and β-diversity in major habitats (circalittoral rock, infralittoral rock, seagrass) might reasonably be made.

Two hypotheses about the potential confounding effects of differing sample effort cannot be easily answered using quantitative analysis, but useful understanding can be gained by gained by examination of data.

1) For each major habitat in the Plymouth Sound and Estuaries SAC, is there a difference in the rate of taxon accumulation since 2014 between samples from NE or Seasearch?

Predictions: Accumulation rates between the two organisations will be similar.

2) Do outcomes differ when using datasets with unequal sampling effort or with datasets that have been artificially balanced?

Predictions: Outcomes from the two approaches will be similar.

The remaining six hypotheses will all be answered using inferential statistics.

3) Survey effort – On any survey event, does the number of taxa recorded in a habitat increase with the duration of that survey event?

Predictions: There will be a positive association between taxon richness and duration of survey events.

4) α-diversity – For each major habitat, is there a difference in taxon richness between the Natural England sentinel monitoring data and Seasearch surveyor data from Plymouth Sound and Estuaries SAC in 2014-19?

Predictions: Taxon richness will be similar for the two methods of data collection.

5) α-diversity - For each major habitat in Plymouth Sound and Estuaries SAC, is there a difference in taxon richness, Shannon diversity, Simpson diversity and evenness (for all taxa) between samples from Seasearch or NE sentinel monitoring?

Predictions:

   a. Measures of α-diversity will not differ between the two sets of samples.

6) β-diversity - For each major habitat in Plymouth Sound and Estuaries SAC, is there a difference in composition of assemblages between samples from Seasearch or NE sentinel monitoring?

Predictions:

   a. Measures of β-diversity will not differ between the two sets of samples.

7) α-diversity - For Seasearch data from each major habitat in each MPA, is there a difference in taxon richness, Shannon diversity, Simpson diversity and evenness (for all taxa) between the two time-periods?

Predictions:

   a. Because of different dates of designation, presence of different features, threats, management and byelaws, no consistent patterns of change through time are expected. Patterns of change in individual MPAs may be relatable to local conditions.

8) β-diversity – For each major habitat, does taxonomic composition differ between the two time-periods for each MPA?

Predictions:

   a. Because of different dates of designation, presence of different features, threats, management and byelaws, no consistent patterns of change in taxonomic composition through time are expected. Patterns of change in individual MPAs may be relatable to local conditions.

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.

Methods

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 are were developed from those used in the Marine Nature Conservation Review (Hiscock, 1996; Irving and Wood, 2007; MCS/Seasearch, 2007). Briefly, volunteer divers in Seasearch spend time during a dive 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.

The sampling protocol used by Natural England for sentinel monitoring differs from that used by Seasearch. The NE protocol is much more structured, using a specific number of transects and quadrats ($0.25m^2$) in specific pre-determined places and biotopes. Full details of these methods are available in Northen & Doggett (2019).

Data treatment protocol

In this study, there is a clear need to link species records unambiguously with major habitats which is not always possible with observer-level records, so only surveyor-level records are used. To link species with three major habitats (circalittoral rock, infralittoral rock and seagrass) and to maximise the likelihood of reliable outputs, a protocol of data filters and treatments was developed (Table 1).

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

Exclude survey events that are:		
1.	Not in the time-frame of interest	By filtering on EventDate
2.	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 3.4.15) and 1) clipping these records to polygons of areas of interest (i.e. MPAs, freely available from JNCC or NE), 2) adding a field for MPA name to each record, then 3) exporting attribute tables to .csv.
3.	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.
4.	From December, January and February	Seasonal variations in occurrence or abundance of species can introduce ‘noise’ into the dataset, which can obscure or magnify patterns. Ideally these would be minimised *a priori* by intentionally sampling only within the same ‘season’. In the present case, where datasets exist already, records were filtered to exclude those from outside the main period of survey activity (March-November inclusive). This retained the vast bulk of the records, but eliminated those that may be unusual due to being collected over winter.
Exclude samples that:		
5.	Have no biotope determination	To ensure that species records could be linked with an underlying habitat
6.	Have fewer than five taxa	Whilst some habitats are expected to have few taxa, CR and IR 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.

Exclude taxa that		
7.	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.
8.	Do not have a SACFOR score	Analyses of β-diversity (e.g. Shannon diversity index) require a measure of relative abundance for each taxon.
9.	Uncertain = TRUE	To minimise uncertainty about whether a taxon is actually present in a sample
10.	Dead = TRUE	To minimise uncertainty about whether a taxon is actually present in a sample
Transform SACFOR data		
11.	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).	
Allocate taxa to habitats		
12.	Where possible, each sample was allocated to being from circalittoral rock, infralittoral rock or seagrass. Samples from other habitats (e.g. littoral, sublittoral sediment, etc.) were discarded. Multiple biotopes may be scored against a single sample and the taxa therein, so it is not always immediately apparent how to allocate any given taxon record to a habitat. Allocation of habitats to taxa within a sample was the most complex and least intuitive part of the data preparation. Rules applied are sensible, but somewhat arbitrary.	

	a) If ≥66% of biotopes allocated to a sample belonged within the same Level 2 category of in the EUNIS marine habitat classification (EEA, 2019) (e.g. if 2 of 3 biotope determinations were in MC1 [or CR within the JNCC classification]), then the sample was classed as being in circalittoral rock (CR). b) For samples where the above could not allocate a habitat, then the free-text fields of ‘Habitat’ and ‘Description’ were searched for combinations of keywords. Samples with fields that contained the words circa* plus any of *rock, wall, boulder* were designated as CR. Samples with field that contained any of the words infra*, Lamin*, kelp or weed, plus any of *rock, vertical, boulder*, reef, granite, park, forest were designated as IR (MB1). Samples with fields that contained any of the words grass, zostera, z*marina were designated as SG (MB522 or SS.SMp.SSgr) Samples for which CR, IR or SG could not be designated were then discarded.
Standardise taxon names	
13.	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 in two ways: a) 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. b) When, within any Genus, there existed some records determined to species and some determined only to Genus, but the Genus is polyspecific, all entries were standardised into a higher, unifying identifier (i.e. all were determined only to Genus). For example, records for (i) *Patella vulgata* (ii) *Patella* sp., and (iii) *Patella*, were standardised as ‘*Patella*’.
Eliminate duplicates	
14.	Stage 13 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 *Crisia* and *Crisia eburnea*, it would now contain two entries for *Crisia*, 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.

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). Counts of numbers of taxa give a digestible impression of diversity, provided, when making comparisons, that sample-sizes are equivalent (Magurran, 1996). 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). For comparisons of taxon richness, effort within Seasearch surveys is considered in three ways:

1. The cumulative total of unique taxa recorded will increase with additional survey effort until reaching an asymptote, which represents the total pool of taxa available (hypothesis 1). Different methods are likely to accumulate species at different rates and may reach different asymptotes. Using the specaccum function with 1000 iterations and random selection method (vegan package; Oksanen *et al.*, 2019), mean species accumulation curves with confidence bounds (derived from s.d. of the means) were plotted for each habitat in the Plymouth Sound and Estuaries SAC and used to compare data from NE or Seasearch.
2. Areas with more samples are also likely to feature more species than those areas with fewer samples (hypothesis 2). Differences in intensity of sampling could be for several reasons (e.g. different local density of divers, more or less active dive clubs, different benthic features of interest to citizen scientists). Thus, number of taxa per sample was used for comparisons of α-diversity among MPAs. When comparing groups, initial analyses for difference in richness used the actual sample-sizes, whether unbalanced or not. These were followed by repeated analyses using equal sample-sizes (where 10,000 random subsets equal in size to the smaller sample were picked from the larger sample). This allows a frequency distribution of possible results from samples of equal size. The 95% confidence intervals for the test statistic were compared to the critical value ($\alpha = 0.05$) for a test with appropriate degrees of freedom.
3. The longer a dive, the more species are likely to be recorded (hypothesis 3). This is not completely straight forward for Seasearch surveys which can collect records from more than one habitat, i.e. include >1 sample. Durations of dives are recorded, but not broken down to the level of samples. Thus, taxon richness for a sample cannot be compared with the duration of that sample. To minimise the effect of this mis-match, when investigating

implications of varying survey effort, the dive-duration was correlated against the number of taxa per survey event (dive) rather than number of taxa per sample. If there were no significant correlation, then data for further analyses on taxon richness would use number of taxa. If there was a significant positive correlation, then data to be used would be number of taxa per unit time.

Other forms of bias in survey effort include number of years when Seasearch surveys were done in an area, but this was not considered here.

Statistical analysis

α-diversity

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 α-diversity, indices (taxon richness, Shannon diversity, Simpson diversity and Pielou's evenness) were calculated using the DIVERSE routine in PRIMER (v. 7.0.17) and exported to .csv.

Methods used by the two organisations collected data on abundance in rather different ways and at different spatial scales: densities or percentage covers in 50 x 50 cm ($0.25m^2$) quadrats (NE) versus semi-quantitative estimates of cover or counts in the full extent of the habitat surveyed using the SACFOR scale (Seasearch). These were not comparable. Thus, it was not possible to calculate diversity indices that include a component of relative abundance. Consequently, taxon records were treated as presence/absence data, allowing only comparison of taxon richness. Comparisons of time periods used only Seasearch data with SACFOR scores. Here it was possible to calculate all four diversity indices.

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 Welch's *t*-test was used in all cases. This parametric test is able to handle samples of uneven variance and, when used with large sample sizes, is also robust with data that deviate from normality (Underwood, 1997).

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, a sub-set equal in size to the smaller set of samples was randomly selected from the larger set (without replacement) and then compared to the smaller set, again using Welch's *t*-test. This was iterated 10,000 times to provide a frequency distribution of test-statistics for each comparison.

β-diversity: multivariate analysis of assemblage composition

Data were either already converted to presence/absence (the most extreme transformation) or were converted SACFOR scores (Strong and Johnson, 2020; Table 1). The conversions applied to the SACFOR scores for species' abundances has 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 (between methods or between time periods) were tested using the PERMANOVA routine (Anderson, 2001, 2017), again with Bray-Curtis similarities.

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. Inclusion of species with few occurrences and small abundances does however reduce the percent dissimilarity between groups contributed by each taxon. Where there are many species, many of which occur seldomly, it is harder to represent accurately the multivariate differences in a 2- (or 3-) dimensional ordination (i.e. the nMDS stress is larger). Where stress exceeds 0.2, the ordination no longer effectively summarizes the observed distances among the samples (Clarke, 1993; Legendre and Legendre, 2012).

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.

Effects of methods on assemblages recorded were tested first using the full set of species (avoiding arbitrary decisions about elimination of less common taxa) and then again using the 50 most important species 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 species 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).

Results

Seasearch data and NE sentinel monitoring

Sampling effort and taxon richness

There was 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) (Figure 2). As a consequence, no correction for survey effort per dive on number of taxa recorded was applied in any of the following analyses. Although it would be better to correlate number of taxa against the number of minutes spent for each sample, those data were not available. In addition, a survey-event is not always tidily partitioned among habitats, either because of topography of the site or ambient conditions on the day.

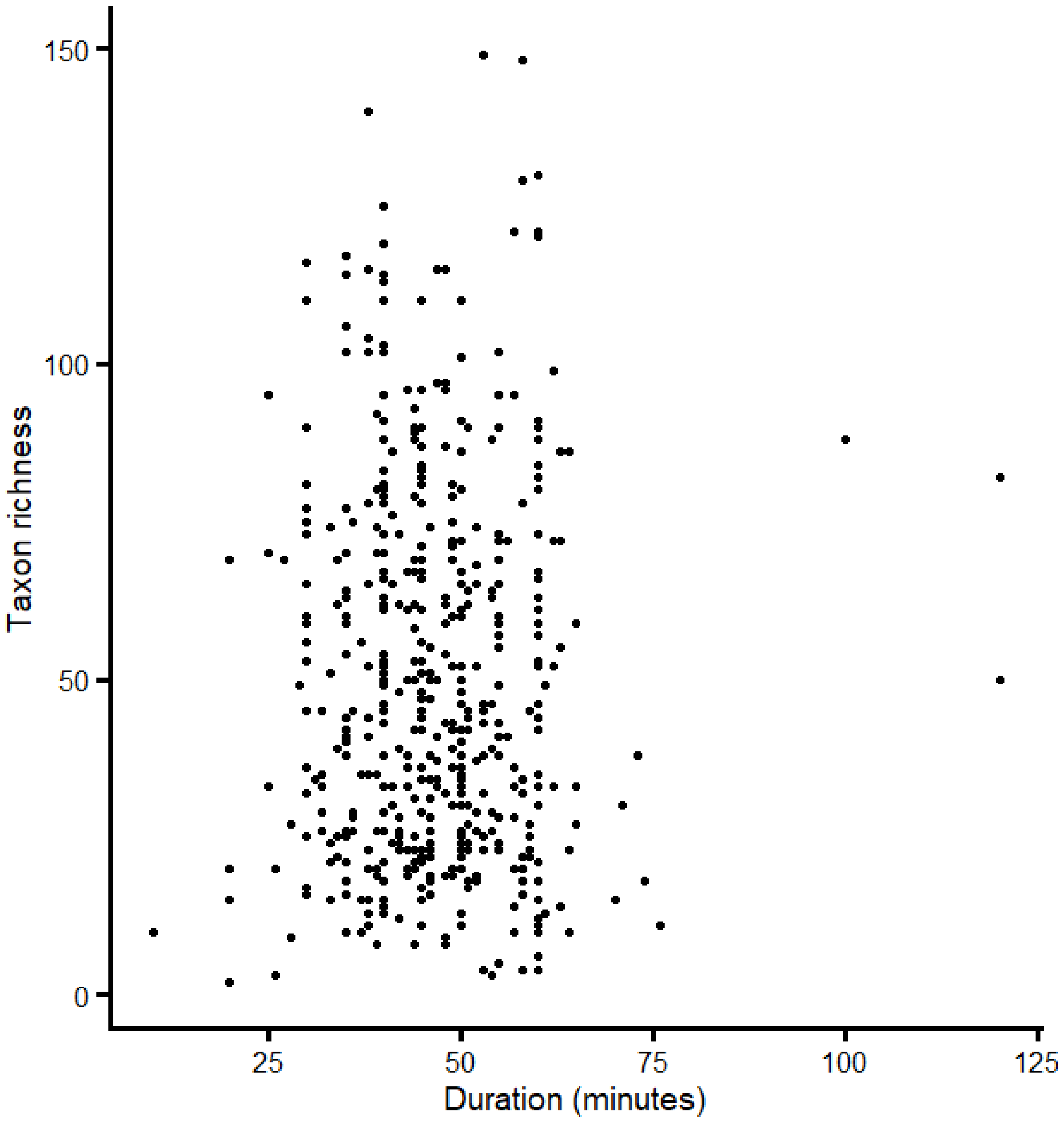

Figure 2. There was no association between number of taxa recorded per survey event (dive) and the duration of dive (minutes); Spearman rank correlation coefficient r_s = -0.03, n = 496, p > 0.76 (1-tailed test).

Taxa accumulation

For circalittoral rock, rates of accumulation of taxa in Seasearch and in NE records increased at similar rates, with considerable overlap of confidence limits (Figure 3a). For infralittoral rock, rates of accumulation were faster and extended further in Seasearch samples than in NE samples (Figure 3b). In each case, there were considerably more Seasearch than NE samples.

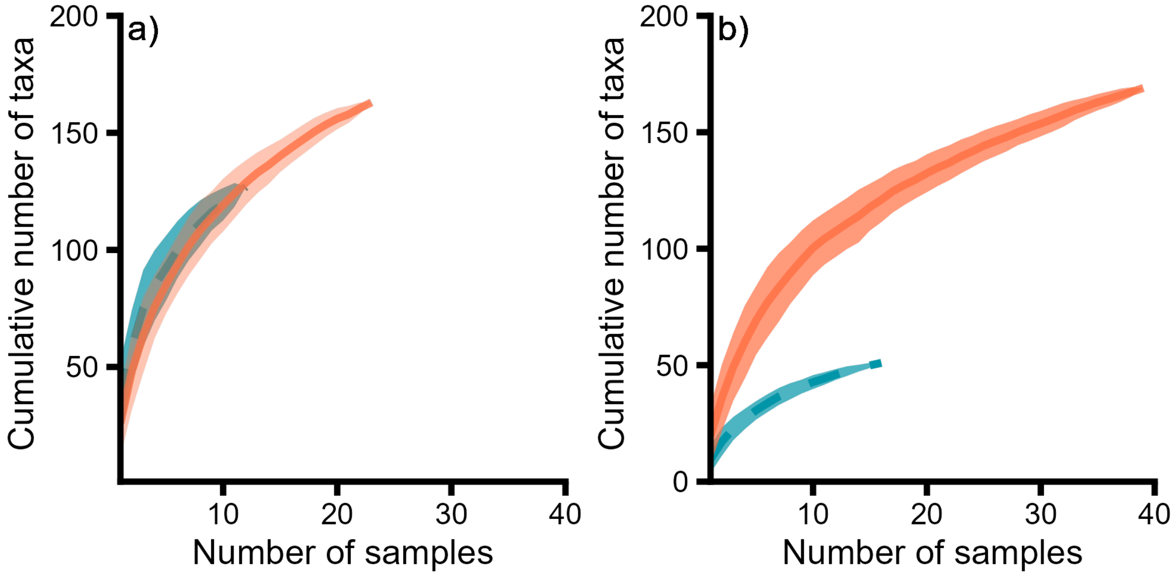

Figure 3. Mean (± s.d.) rates of taxon accumulation in samples from NE (teal, dashed line) or Seasearch (orange, solid line) on a) circalittoral or b) infralittoral rock.

Circalittoral rock – taxon richness (α-diversity)

Circalittoral samples were collected by NE only in 2019, where each sample contained multiple replicate quadrats. This differed from Seasearch records that did not include replicates. This allowed for two different analyses. When replicate quadrats from the NE sampling protocol were compared against Seasearch samples, frequency distributions of data on taxon-richness were not normally distributed (Shapiro-Wilk; W = 0.84, p <0.001), nor were variances of data from the two sources homogeneous (Bartlett; K^2 = 44.9, p <0.001). Significantly fewer taxa (S) were recorded in NE replicate quadrats from sentinel monitoring than in samples recorded by Seasearch surveyors in Plymouth Sound and Estuaries SAC (Welch's *t*-test t = -4.04, d.f. = 27.48, p < 0.001; Figure 4a). When NE samples were compared to Seasearch samples, frequency distribution of taxon richness was normal (Shapiro-Wilk; W = 0.97, p > 0.3) and variances were homogeneous (Bartlett; K^2 = 0.003, p > 0.95). There was no significant difference in mean number of taxa recorded per sample between NE and Seasearch (Welch's *t*-test; *t* = 1.35, d.f. = 21.22, p > 0.1; Figure 4b).

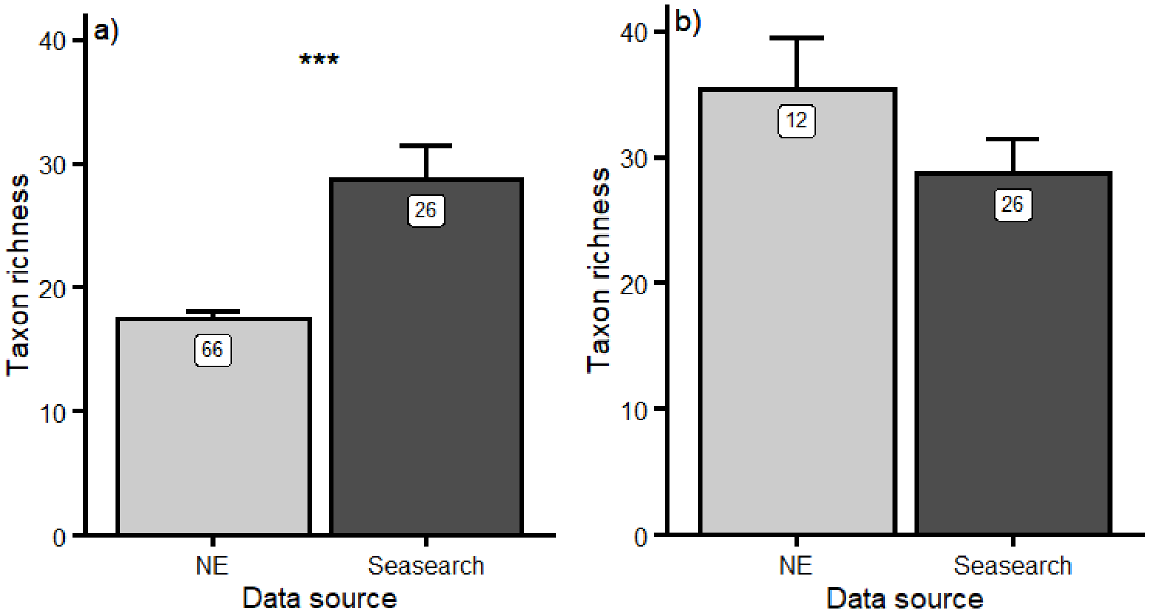

Figure 4. Mean taxonomic richness recorded by divers from Natural England (light grey bars) or Seasearch (dark grey bars) where a) NE replicates are treated the same as Seasearch samples and b) where NE samples are treated the same as Seasearch samples. Labels at the top of columns indicate sample size. ***: $p<0.001$.

Taxon richness of Seasearch samples was much more similar to NE samples than to the smaller, shorter NE replicates. All further analyses for circalittoral rock use NE sample-level rather than replicate-level data. This reduces the sample-size for NE records, but does allow fairer comparisons in terms of area covered and time spent on survey.

Subsequent analysis of β-diversity (Section 4.1.4) suggested differences in composition between the inner and outer Sound, so, although not originally planned, species richness was also compared between source of data and the two areas of the Sound.

Two-way analysis of variance (ANOVA); Data-source: fixed, NE or Seasearch; Position in Sound: fixed, inner or outer; Table 2) showed no significant interaction, and numbers of taxa (S) did not differ between NE samples and Seasearch samples (Figure 4b) nor between samples from the inner or outer Sound (Figure 5).

Table 2. Two-way analysis of variance on taxon richness for samples of assemblages on circalittoral rock collected by two organisations (Data-source; fixed, NE vs Seasearch) from two different areas (Position in Sound; fixed, Inner vs Outer). Samples sizes differ; see labels in Figure 5 & Figure 10. Mean taxonomic richness in samples from infralittoral rock recorded by divers from a) Natural England (light grey bar) or Seasearch (dark grey bar) and b) the inner Sound (black bar) or outer Sound (white bar). Labels at the top of columns indicate sample size. *: p<0.05; **: p<0.01. . Where cells are blank on the bottom row, this is intentional because the analysis produces no values for the Residual analysis term.

Analysis term	d.f.	MS	*F*	*p*
Data-source	1	363	1.87	0.180
Position in Sound	1	3226	1.68	0.203
Data-source * Position in Sound	1	139	0.72	0.402
Residual	34	6584		

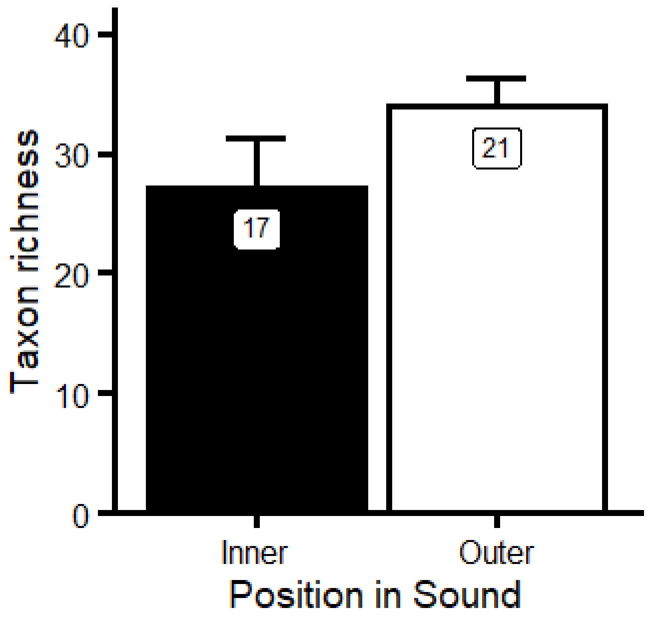

Figure 5. Mean taxonomic richness in samples from circalittoral rock recorded by divers from the inner Sound (black bar) or outer Sound (white bar). These data are for Seasearch and NE records combined. Labels at the top of columns indicate sample size.

Circalittoral rock – composition of assemblages (β-diversity)

Multivariate analyses including all species

nMDS plots created using Bray-Curtis dissimilarity index on presence-absence data show separation in multivariate space of compositions of assemblages on circalittoral rock in Plymouth Sound and Estuaries SAC between the two organisations collecting these data (Figure 6).

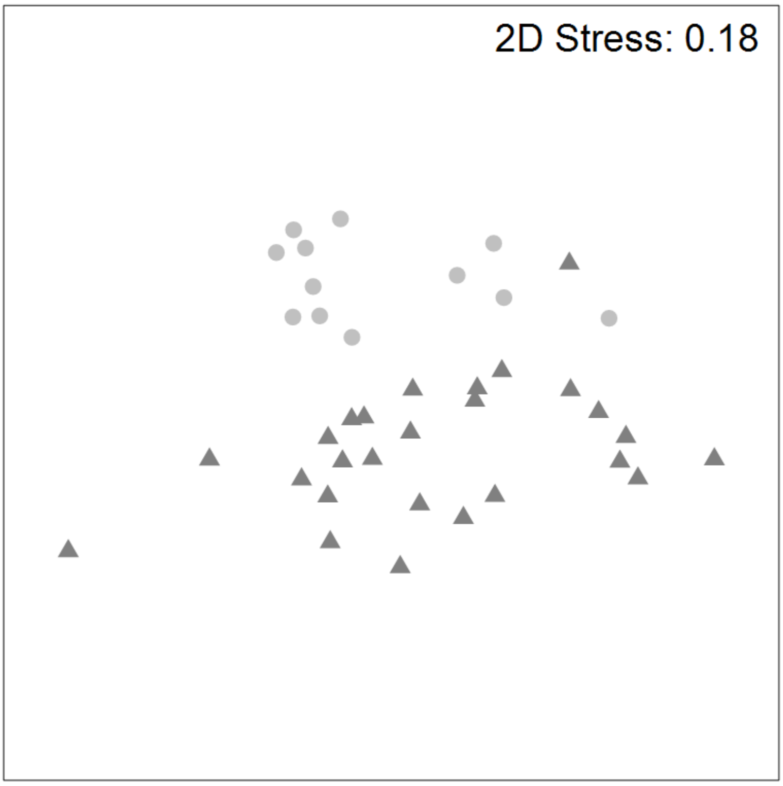

Figure 6. Non-metric multidimensional scaling plots showing separation in multivariate space of composition of assemblages of benthic species from circalittoral rock from samples collected by Natural England (light grey circles) or Seasearch (dark grey triangles). Data included all species recorded. Data were transformed to Presence/Absence (because methods to quantify abundance differed between the organisations). The similarity matrix was calculated using Bray-Curtis dissimilarity index.

Multivariate analysis showed that the composition of assemblages recorded differed between samples collected by NE or Seasearch (Table 3a). There was, however, some indication that data from each organisation fell into two further groups (Figure 6; roughly along the horizontal-axis). Examination of the different locations of the points indicated that these nominal groups were in different areas of Plymouth Sound (Figure 7) prompting additional analysis. When inner or outer Sound (i.e. positioned inside or outside the breakwater) was added as a second factor, this separation was clear (Figure 8). Multivariate dispersion (the spread of samples in multivariate space) was significantly greater in Seasearch than in NE samples (PERMDISP: $F_{1,36} = 11.2$, $p < 0.01$,Figure 6)

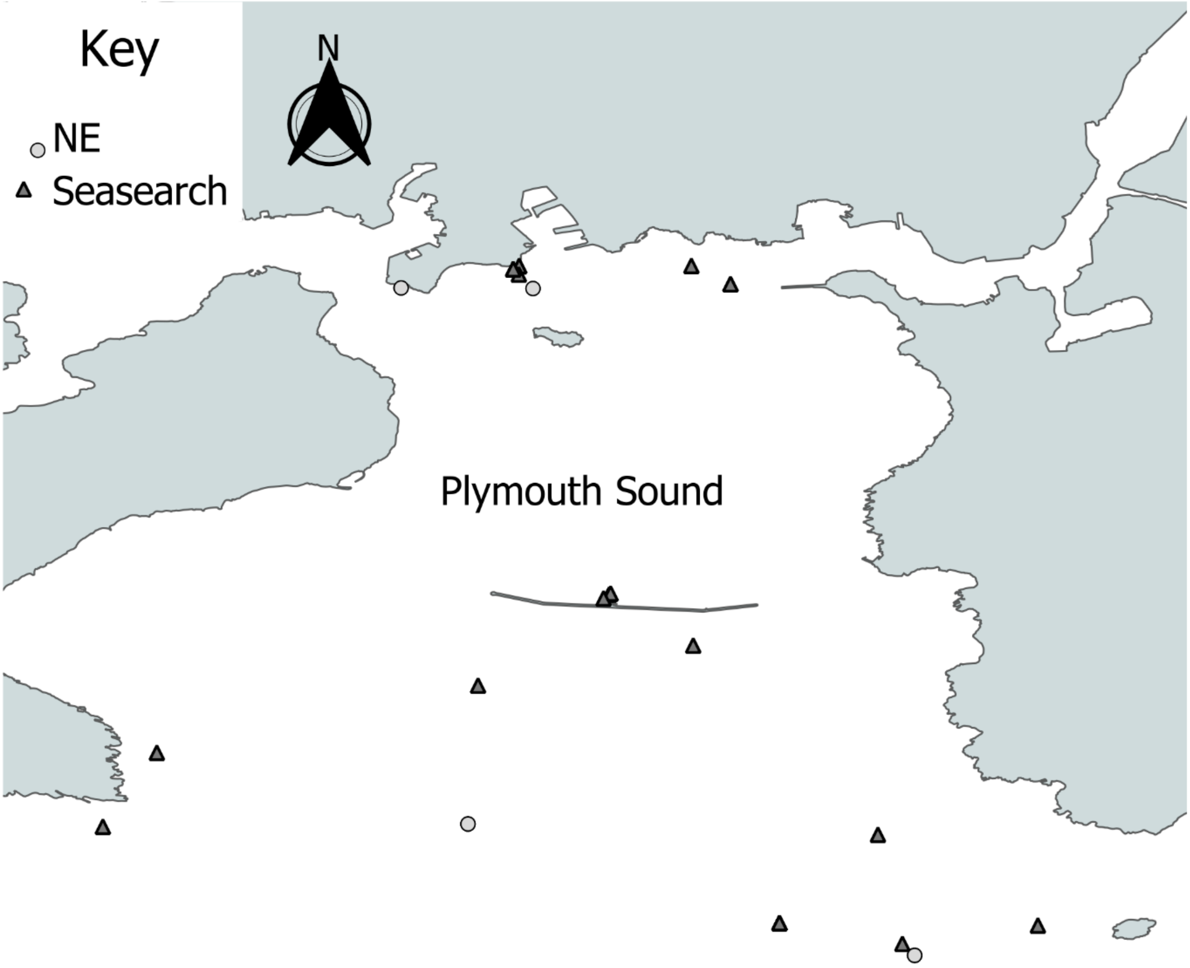

Figure 7. Positions of samples of circalittoral rock in Plymouth Sound, collected by Natural England (light grey circles) or Seasearch (dark grey triangles) between 2014-19. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Map Projection is EPSG:4326 - WGS84.

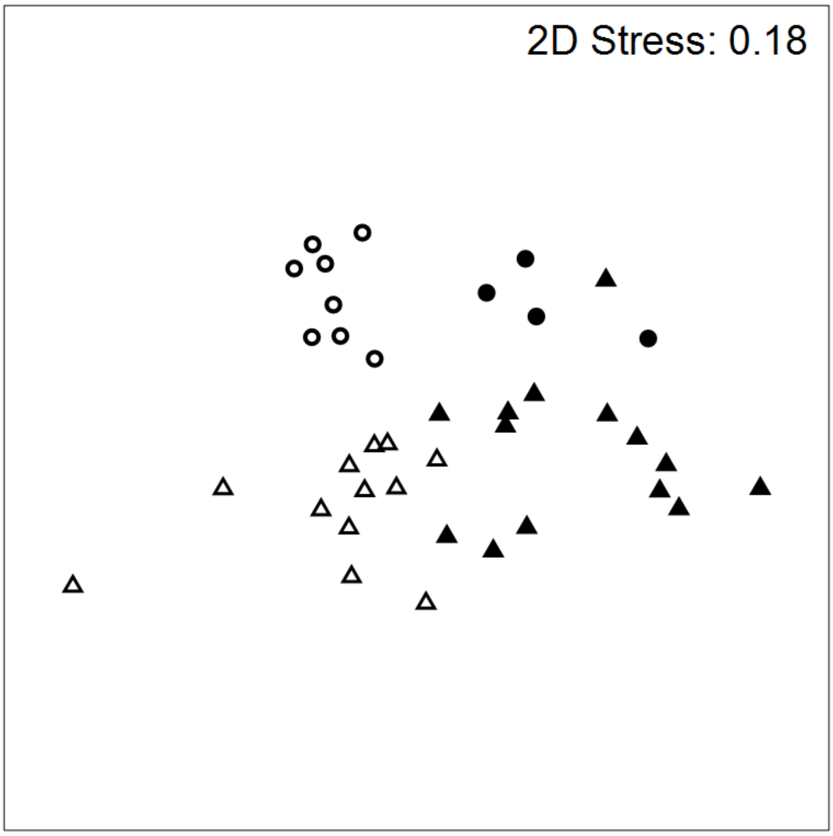

Figure 8. nMDS plot for compositions of assemblages of benthic taxa on circalittoral rock in Plymouth Sound and Estuaries SAC in the period 2014-19. Data were collected by Seasearch (triangles) or Natural England (circles) from sites in either the inner (black symbols) or outer (white symbols) Sound. Data included all species recorded. Data were transformed to Presence/Absence (because methods to quantify abundance differed between the organisations). The similarity matrix was calculated using Bray-Curtis dissimilarity index.

Multivariate analysis indicated that for each of the inner or outer Sound, composition of assemblages recorded by Seasearch or NE differed and this difference was dependent on the position in the Sound (i.e. there was a significant interaction; Table 3b). Pairwise comparisons showed that all combinations were significantly different to each other (Table 3c).

Table 3. Multivariate analyses (PERMANOVA; Anderson 2001) for differences among samples of assemblage composition on circalittoral rock a) collected by two organisations (Data-source; fixed, NE vs Seasearch); b) collected by the same two organisations and further divided into different places (Position in Sound; fixed, Inner vs Outer); and c) pairwise comparisons for the interaction between Data-source and Position in Sound. Probabilities were obtained by permutation of the raw data. Significant effects referred to in the text are in bold. Where cells are blank, this is intentional because the analyses produce no values for these analysis terms.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
a)					
Data-source	1	16541	6.39	**0.001**	998
Residual	36	2589			
b)					
Data-source	1	13621	6.70	0.001	999
Position in Sound	1	16843	8.29	0.001	998
Data-source * Position in Sound	1	5526	2.72	**0.01**	998
Residual	34	2031			
c) pairwise comparisons					
NE (Inner vs Outer)				**0.003**	
Seasearch (Inner vs Outer)				**0.001**	

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
Inner (NE vs Seasearch)				**0.005**	
Outer (Inner vs Seasearch)				**0.001**	

Multivariate analyses including 50 most 'important' species

Samples from circalittoral rock in Plymouth Sound included 269 different taxa, which varied from a single occurrence to being recorded in 25 of the 38 samples. Many of the 269 occurred only in one or two samples. Occurrences of rare species in small numbers are given little weight in effective biological measures such as Bray-Curtis (Clarke, 1993; Clarke and Warwick, 2001; Legendre and Legendre, 2012). 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 here. Analyses of only the 50 most 'important' species for circalittoral rock (where 'importance' is determined as those species that contribute more than a particular % abundance for every sample) again showed a significant interaction between the organisations collecting the data and the position in Plymouth Sound (Table 4a). Pairwise comparisons showed that all combinations were significantly different to each other (Table 4b). Multivariate dispersion was no longer significantly different between Seasearch or NE samples (PERMDISP: $F_{1,36} = 3.8$, $p = 0.09$).

Table 4. Multivariate analyses (PERMANOVA; Anderson 2001) for differences among samples of assemblage composition on circalittoral rock, considering only the 50 'most important' species a) collected by two organisations (Data-source, fixed, NE or Seasearch) and from different places (Position in Sound; fixed, Inner vs Outer); and b) pairwise comparisons for the interaction between Data-source and Position in Sound. Probabilities obtained by permutation of the raw data. Significant effects referred to in the text are in bold. Where cells are blank, this is intentional because the analyses produce no values for these analysis terms.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
a)					
Data-source	1	8006	5.61	0.001	999
Position in Sound	1	16877	11.83	0.001	998
Data-source * Position in Sound	1	3859	2.70	**0.018**	999
Residual	34	1426			
b) pairwise comparisons					
NE (Inner vs Outer)				**0.001**	
Seasearch (Inner vs Outer)				**0.001**	
Inner (NE vs Seasearch)				**0.035**	
Outer (NE vs Seasearch)				**0.001**	

Taxa contributions to dissimilarities

SIMPER analysis showed that several taxa each contributed small percentages (<6%) to the dissimilarity between NE and Seasearch (Appendix 10.2a). This indicated that differences were truly multivariate and not influenced by a tendency for one organisation to record one (or a few) taxa that is missed by the other. Similarly, multiple taxa each contributed small percentages (<4%) to the dissimilarity between inner and outer Sound (Appendix 10.2b).

Differences in patterns of occurrence for particular taxa can be visualised in shade plots (Figure 9). For instance, on circalittoral rock Seasearch records regularly show mobile crustacean or fish taxa, or others like *Holothuria forskali* and *Eunicella verrucosa*, but these are seldom or never seen in NE records.

Figure 9. Shade plot showing the presence of different taxa in samples of circalittoral rock by Natural England (white circles) or Seasearch (white diamonds).

Infralittoral rock – taxon richness (α-diversity)

Infralittoral samples were collected by NE only in 2016; these did not include replicates and so were directly comparable with Seasearch samples. When samples from the NE sampling protocol were compared against Seasearch samples, frequency distributions of data on taxon-richness were not normally distributed (Shapiro-Wilk; W = 0.87, p <0.001), nor were variances of data from the two sources homogeneous (Bartlett; K^2 = 17.6, p <0.001). Two-way analysis of variance (ANOVA) on ranked data (i.e. approximation of a non-parametric test; Data-source: fixed, NE or Seasearch; Position in Sound: fixed, inner or outer; Table 5) showed no significant interaction. There were significantly fewer taxa (S) recorded in NE samples than in Seasearch samples (Figure 10a) and also significantly fewer taxa recorded in samples from the inner than in the outer Sound (Figure 10b).

Table 5. Two-way analysis of variance of ranked data on taxon richness for samples of assemblages on infralittoral rock collected by two organisations (Data-source; fixed, NE vs Seasearch) from two different areas (Position in Sound; fixed, Inner vs Outer). Significant effects referred to in the text are in bold. Samples sizes differ; see labels in Figure 10. Where cells are blank, this is intentional because the analysis produces no values for this analysis term.

Analysis term	d.f.	Mean Square	*F*	*p*
Data-source	1	845.6	4.58	**0.038**
Position in Sound	1	1392.9	7.54	**0.009**
Data-source * Position in Sound	1	91.4	0.50	0.485
Residual	47	184.8		

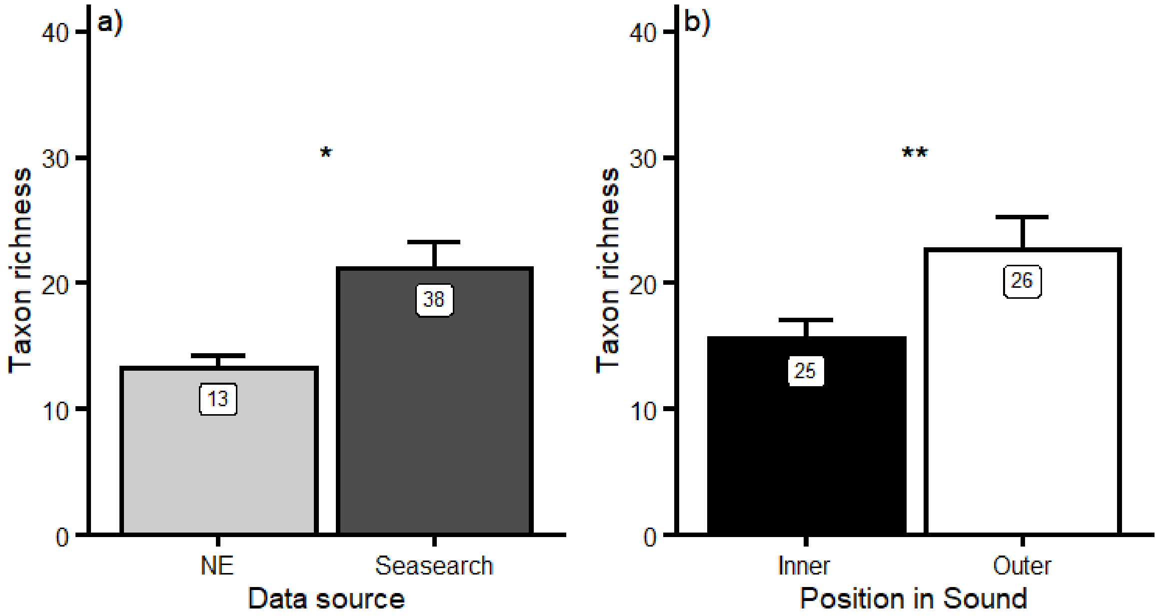

Figure 10. Mean taxonomic richness in samples from infralittoral rock recorded by divers from a) Natural England (light grey bar) or Seasearch (dark grey bar) and b) the inner Sound (black bar) or outer Sound (white bar). Labels at the top of columns indicate sample size. *: $p<0.05$; **: $p<0.01$.

Infralittoral rock – composition of assemblages (β-diversity)

Multivariate analyses including all species

Composition of assemblages on circalittoral rock differed between the inner and outer Sound, so the same experimental design was applied to infralittoral samples. nMDS plots created using Bray-Curtis dissimilarity index on presence-absence data show separation in multivariate space of compositions of assemblages on infralittoral rock in Plymouth Sound and Estuaries SAC (Figure 11). Positions of these samples were divided between the inner and outer Sound (inside or outside the breakwater; Figure 12).

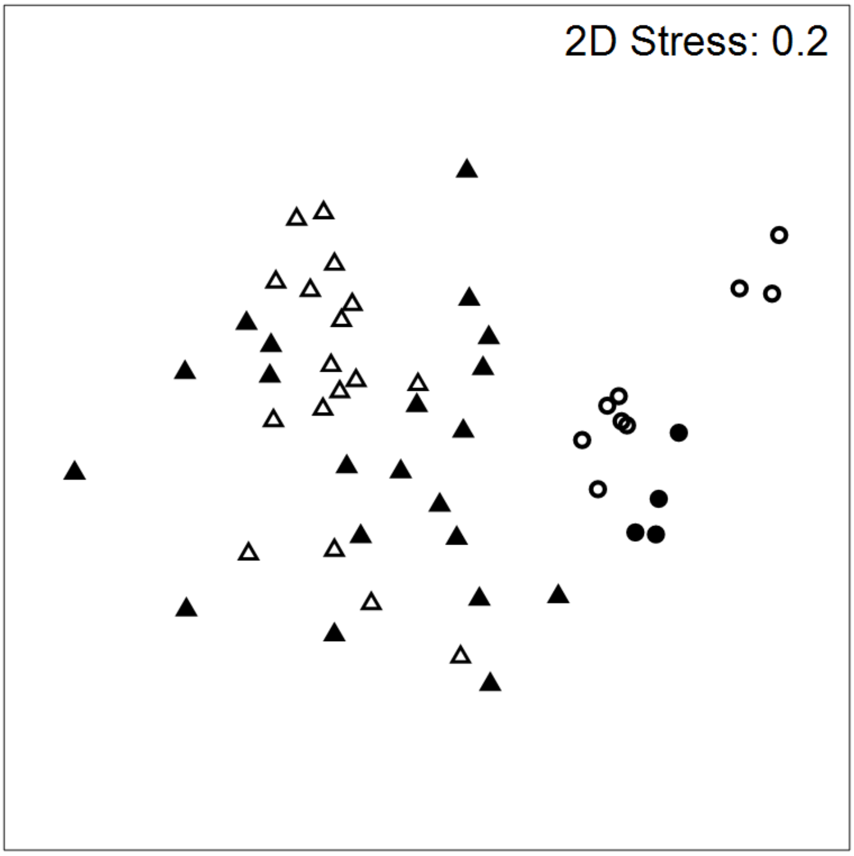

Figure 11. nMDS plot for compositions of assemblages of benthic taxa on infralittoral rock in Plymouth Sound and Estuaries SAC in the period 2014-19. Data were collected by Seasearch (triangles) or Natural England (circles) from sites in either the inner (black symbols) or outer (white symbols) harbour. Data included all species recorded. Data were transformed to Presence/Absence (because methods to quantify abundance differed between the organisations). The similarity matrix was calculated using Bray-Curtis dissimilarity index.

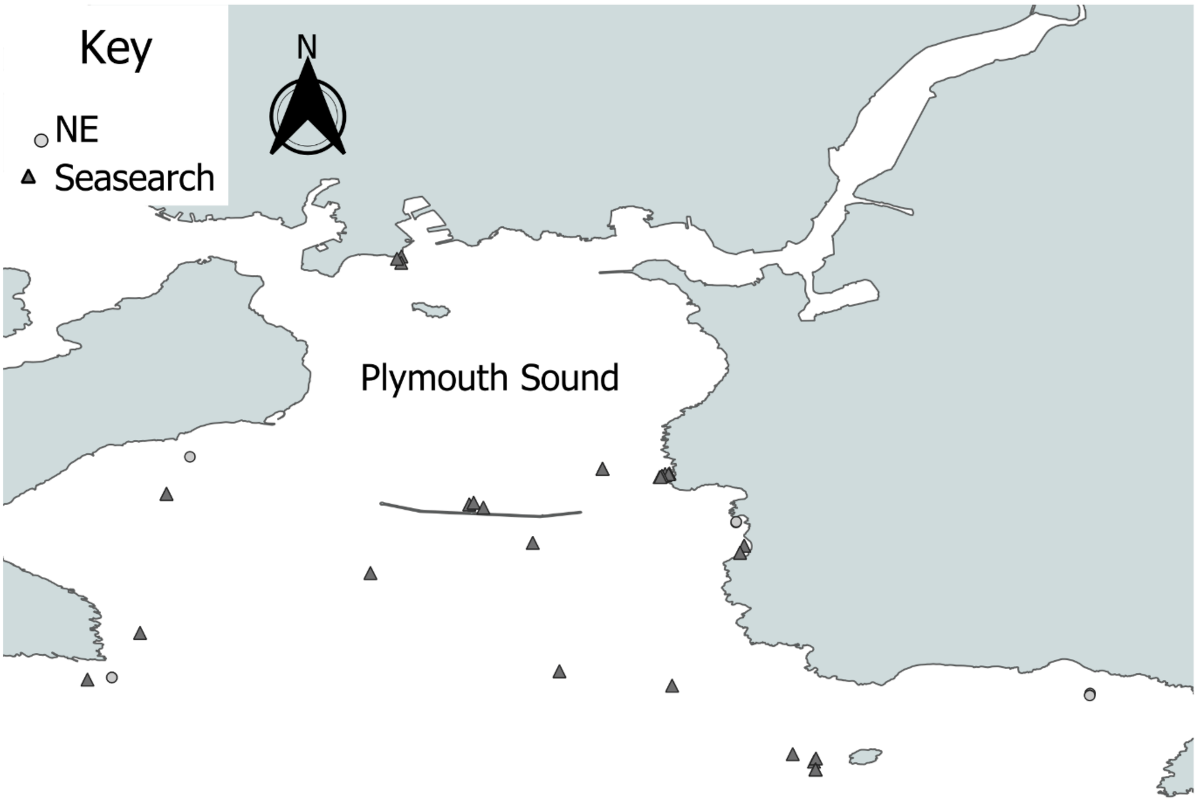

Figure 12. Positions of samples of infralittoral rock in Plymouth Sound, collected by Natural England (light grey circles) or Seasearch (dark grey triangles) between 2014-19. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Map Projection is EPSG:4326 - WGS84.

Multivariate analysis indicated that for each of the inner or outer Sound, composition of assemblages recorded by Seasearch or NE differed and this difference was dependent on the position in the Sound (i.e. there was a significant interaction; Table 6a). Pairwise comparisons showed that all combinations were significantly different to each other (Table 6b). Multivariate dispersion was significantly greater for Seasearch samples than for NE samples (PERMDISP: $F_{1,49} = 18.5$, $p < 0.01$, Figure 11).

Table 6. Multivariate analyses (PERMANOVA; Anderson 2001) for differences among samples of assemblage composition (including all species recorded) on infralittoral rock a) collected by two organisations (Data-source; fixed, NE vs Seasearch) from two different areas (Position in Sound; fixed, Inner vs Outer); and b) pairwise comparisons for the interaction between Data-source and Position in Sound. Probabilities were obtained by permutation of the raw data. Significant effects referred to in the text are in bold. Where cells are blank, this is intentional because the analyses produce no values for these analysis terms.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
a) main test					
Data-source	1	29056	10.83	0.001	997
Position in Sound	1	6923	2.58	0.006	998
Data-source * Position in Sound	1	4799	1.79	**0.047**	999
Residual	47	2683			
b) pairwise comparisons					
NE (Inner vs Outer)				**0.048**	
Seasearch (Inner vs Outer)				**0.001**	
Inner (NE vs Seasearch)				**0.001**	
Outer (NE vs Seasearch)				**0.001**	

Multivariate analyses including 50 most ‘important’ species

Samples from infralittoral rock in Plymouth Sound included 197 different taxa, which varied from a single occurrence to being recorded in 33 of the 57 samples. Many of the 197 occurred only in one or two samples. Analyses of only the 50 most ‘important’ taxa for infralittoral rock showed that the marginally significant interaction from the analysis of all taxa (Table 6) had disappeared, but that there were significant differences in composition of assemblages both between the two organisations and the different positions in the sound (Table 7). Multivariate dispersion remained significantly greater in Seasearch than in NE samples (PERMDISP: $F_{1,49} = 9.6$, $p < 0.05$).

Table 7. Multivariate analyses (PERMANOVA; Anderson 2001) for differences among samples of assemblage composition on infralittoral rock considering only the 50 'most important' species collected by two organisations (Data-source, fixed, NE or Seasearch) and from different places (Position in Sound; fixed, Inner vs Outer). Probabilities obtained by permutation of the raw data. Significant effects referred to in the text are in bold. Where cells are blank in the bottom row, this is intentional because the analysis produces no values for this analysis term.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
Data-source	1	29542	13.82	**0.001**	999
Position in Sound	1	6680	3.12	**0.006**	998
Data-source * Position in Sound	1	2736	1.28	0.226	998
Residual	47	1456			

Taxa contributions to dissimilarities

As with circalittoral rock, several taxa again each contributed a small percentage (<5%) to the dissimilarity between NE and Seasearch (Appendix 10.3a). The taxon contributing most to differences between the two organisations was *Mastocarpus stellatus* (4.9%) followed by *Patella pellucida,* and assorted members of *Patella*. Similarly, multiple taxa each contributed small percentages (<5%) to the dissimilarity between inner and outer Sound (Appendix 10.3b). The top five taxa (*Electra, Cliona, Anemonia viridis, Marthasterias glacialis* and *Labrus bergylta*), were all more abundant in the outer than in the inner Sound.

Differences in patterns of occurrence for particular taxa can be visualised in shade plots (Figure 13). For instance, on infralittoral rock, Seasearch records regularly show mobile crustacean or fish taxa, or others like *Marthasterias glacialis* and *Anemonia viridis*, but these are seldom or never seen in NE records. Conversely, NE samples show records of *Patella*, *Patella pellucida*, *Littorina*, *Crassostrea* (now *Magellana*) *gigas*, *Phorcus lineatus* and *Mastocarpus stellatus* which do not feature in Seasearch samples.

Seagrass – taxon richness

No samples were collected from seagrass by NE and only three samples were collected by Seasearch in the period 2014-19, so comparisons were not possible. This is partly due to a lack of sampling effort and partly due to some sites of interest (e.g. Berwickshire and North Northumberland Coast SAC) having only intertidal seagrass which would not be sampled by the NE survey methods.

Figure 13. Shade plot showing the presence of different taxa in samples of infralittoral rock by Natural England (circles) or Seasearch (diamonds).

Assemblages through time: α-diversity (Seasearch data only)

Mean (± s.e.) values for each diversity index, in each time period and from each MPA (Table 8) and patterns for differences in taxon richness (Figure 14 & Figure 15) are presented. Most variables were not normally distributed or had heterogeneous variances between the two time-periods, so Welch's 2-sample *t*-tests (which assume heterogeneous variance) were applied for all comparisons (Table 9 & Table 10). Diversity indices were not expected to be distributed normally, but parametric tests with large sample-sizes are considered robust to departures from normality (Underwood, 1997). For each MPA, sample-sizes in the two time periods often differed considerably (e.g. Figure 14, Figure 15). Permuted *t*-tests of equal sample-size gave an indication of whether observed patterns were likely due to differences through time or to differing sample size. Where the mean value of the permuted *t* was the same side of the critical value as the original test, this provided moderate evidence that observed patterns were due to real differences or similarities between groups rather than because of sample effort. Where 95% confidence intervals for the permuted *t* were all either side of the critical value for that test, thus providing strong evidence that the pattern observed in the original test was real and was not a function of survey effort. Where the mean value of the permuted *t* was the other side of the critical value than the original test and/or the 95% confidence interval for *t* overlapped the critical value for the test, it was not entirely clear whether any pattern was due to real differences or to survey effort. For each MPA, positions of samples in the two time-periods are shown (Figure 16 to Figure 22).

In no instances were there enough data to make comparisons of diversity indices between time-periods for seagrass habitat.

Plymouth Sound and Estuaries SAC

There were no significant differences between the two time-periods for any diversity indices from either circalittoral or infralittoral rock, and for each comparison, the mean permuted value for *t*, gave the same answer (Table 9 & Table 10). In no case did the range of permuted *t* overlap the critical value (i.e. fewer than 5% of the permuted tests with equal sample size indicated significant differences).

Isles of Scilly Complex SAC

For circalittoral and infralittoral rock, Simpson diversity was significantly greater in 2014-19 than in 2009-13 (Table 9b & Table 10b), although differences were very small (Table 8b). The mean permuted *t* was significant for circalittoral, but not infralittoral rock and in each case the 95% CI for *t* overlapped the critical value. For infralittoral rock, Pielou's evenness was significantly greater in 2014-19 than in 2009-13 and the mean permuted t was significant, but the range of permuted *t* overlapped the critical value (Table 10b). There were no differences for the other comparisons.

The Manacles MCZ

For circalittoral rock, taxon richness was significantly greater in 2014-19 than in 2009-13, but the mean permuted *t* was not and the 95% CI for *t* overlapped the critical value (Table 9c). There were no differences for the other comparisons.

Fal and Helford SAC

For circalittoral rock, evenness was significantly greater in 2009-13 than in 2014-19. The mean permuted *t* was also significant, but the 95% CI for *t* overlapped the critical value (Table 9d). There were no differences for the other comparisons.

Solent Maritime SAC

For circalittoral rock, no diversity indices differed significantly between 2009-13 and 2014-19 (Table 9e). For infralittoral rock, there were not enough samples (i.e. <5 / time-period) to make a test.

Essex Estuaries SAC

In neither habitat, were there enough samples (i.e. <5 / time-period) to make a test).

Berwickshire and North Northumberland Coast SAC

For circalittoral and infralittoral rock, taxon richness, Shannon diversity and Simpson diversity were significantly greater in 2014-19 than in 2009-13 (Figure 14f, Figure 15g, Table 8g, Table 9f & Table 10e). In each case, the mean permuted *t* was also significant. For taxon richness and Shannon diversity on infralittoral rock, all 95% CI values for *t* were also significant. In all other cases, the 95% CI for *t* overlapped the critical value. For circalittoral, but not infralittoral rock, Pielou's evenness was significantly greater in the earlier than in the later period. The mean permuted *t* was also significant, but the 95% CI for *t* overlapped the critical value.

Table 8. Sample sizes (n) and mean (s.e.) values for four diversity indices from circalittoral or infralittoral rock in seven MPAs in time-periods of 2009-13 or 2014-19; a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC, f) Essex Estuaries SAC, and g) Berwickshire and North Northumberland Coast SAC. Means that are significantly different are shown in bold (see Table 9 & Table 10). There were no data for circalittoral rock in Essex.

	Habitat:	Circalittoral rock		Infralittoral rock	
MPA	Time-period:	2009-13	2014-19	2009-13	2014-19
a) Plymouth	n	34	27	23	38
	S	26.1 (1.82)	27.9 (2.79)	20.8 (1.99)	21.2 (2.02)
	Shannon	2.97 (0.07)	2.92 (0.13)	2.77 (0.11)	2.72 (0.1)
	Simpson	0.96 (0.003)	0.95 (0.1)	0.96 (0.008)	0.96 (0.006)
	Evenness	0.934 (0.004)	0.917 (0.01)	0.94 (0.009)	0.94 (0.006)
b) Scilly	n	184	101	120	45
	S	31.1 (1.1)	33.1 (1.36)	22.8 (1.14)	22.4 (1.59)
	Shannon	3.09 (0.041)	3.19 (0.047)	2.8 (0.051)	2.84 (0.08)
	Simpson	**0.96 (0.002)**	**0.97 (0.002)**	**0.96 (0.003)**	**0.97 (0.004)**
	Evenness	0.93 (0.002)	0.94 (0.002)	**0.94 (0.003)**	**0.95 (0.004)**
c) Manacles	n	19	46	13	29
	S	22.2 (2.23)	27.8 (1.49)	19.7 (2.46)	21.5 (2.3)
	Shannon	2.8 (0.111)	3.05 (0.063)	2.7 (0.15)	2.69 (0.12)
	Simpson	0.96 (0.005)	0.97 (0.003)	0.96 (0.007)	0.95 (0.008)
	Evenness	0.93 (0.006)	0.94 (0.004)	0.94 (0.008)	0.93 (0.01)
d) Fal	n	11	23	25	14

	S	20.7 (2.77)	22.9 (1.77)	24.5 (2.37)	22.9 (2.91)
	Shannon	2.75 (0.149)	2.83 (0.084)	2.88 (0.105)	2.79 (0.154)
	Simpson	0.96 (0.009)	0.96 (0.004)	0.97 (0.004)	0.95 (0.011)
	Evenness	**0.94 (0.005)**	**0.92 (0.008)**	0.94 (0.007)	0.93 (0.014)
e) Solent	n	13	6	2	3
	S	18.3 (2.43)	17.5 (3.32)	17.5 (1.5)	18.3 (8.25)
	Shannon	2.57 (0.18)	2.53 (0.197)	2.67 (0.107)	2.48 (0.519)
	Simpson	0.94 (0.017)	0.94 (0.014)	0.96 (0.014)	0.91 (0.066)
	Evenness	0.918 (0.019)	0.903 (0.017)	0.93 (0.01)	0.92 (0.039)
f) Essex	n	No data	No data	2	3
	S	No data	No data	28.5 (3.5)	27.6 (3.47)
	Shannon	No data	No data	3.17 (0.122)	3.1 (0.12)
	Simpson	No data	No data	0.97 (0.004)	0.97 (0.005)
	Evenness	No data	No data	0.95 (0.002)	0.95 (0.006)
g) Berwickshire	n	75	37	47	29
	S	**16.9 (0.956)**	**22.1 (1.44)**	**19 (1.18)**	**30.2 (2.34)**
	Shannon	**2.54 (0.056)**	**2.79 (0.062)**	**2.68 (0.068)**	**3.1 (0.09)**
	Simpson	**0.94 (0.004)**	**0.95 (0.004)**	**0.95 (0.004)**	**0.96 (0.005)**
	Evenness	**0.93 (0.004)**	**0.92 (0.005)**	0.95 (0.003)	0.94 (0.005)

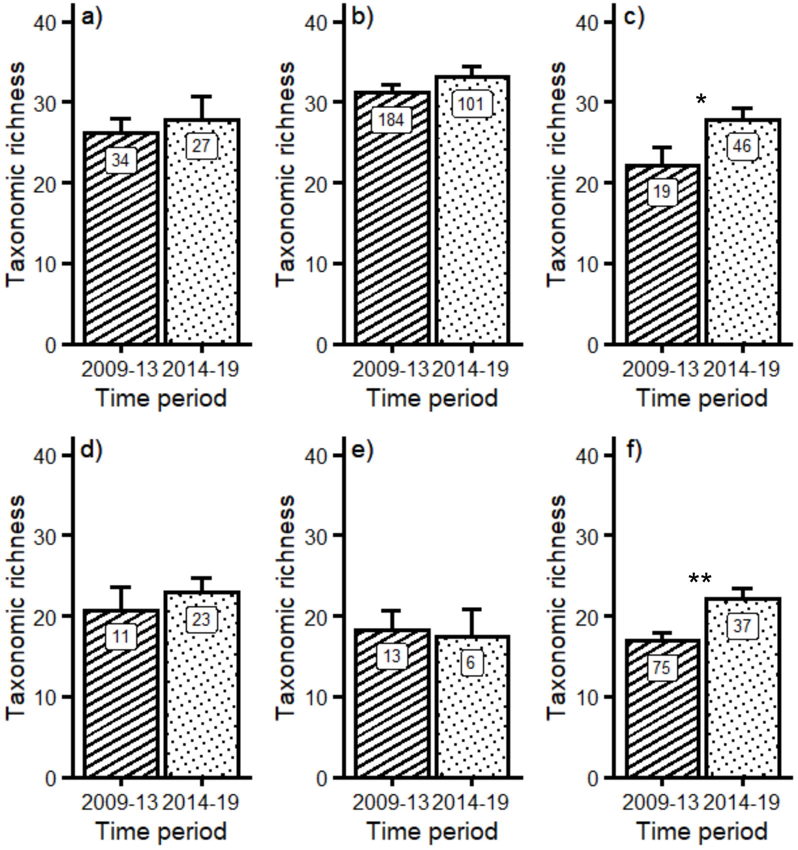

Figure 14. Mean (+s.e.) taxon richness in samples of benthic assemblages on circalittoral rock for two periods of time: 5 y from 2009-13 (diagonal stripes) and 6 y from 2014-19 (dots) in a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC and f) Berwickshire and North Northumberland Coast SAC. There were not enough records to show comparisons for Essex Estuaries SAC. Labels on bars show the number of samples. *, $p < 0.05$; **, $p < 0.01$

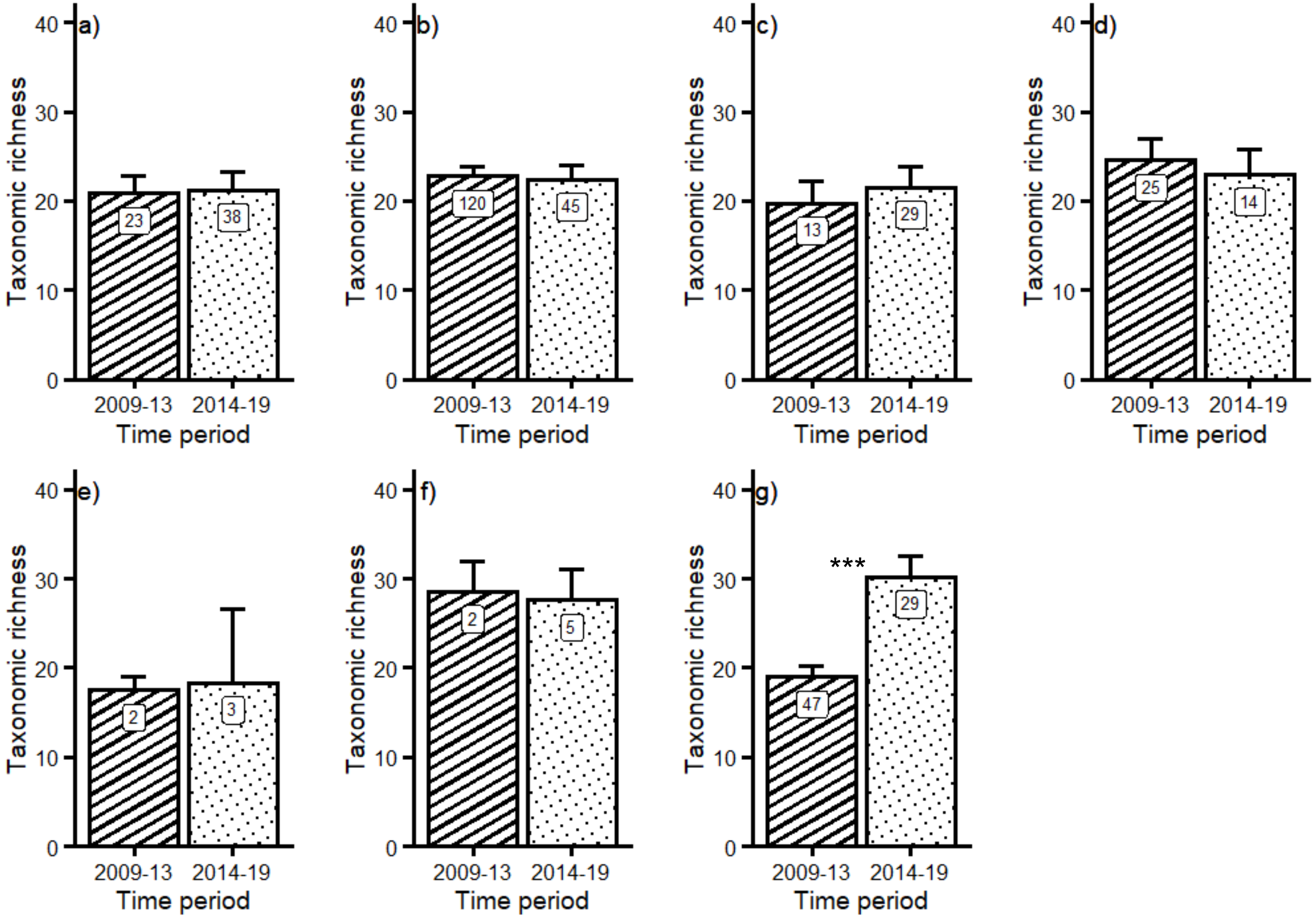

Figure 15. Mean (+s.e.) taxon richness in samples of benthic assemblages on infralittoral rock for two periods of time: 2009-13 (diagonal stripes) and 2014-19 (dots) in a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC, f) Essex Estuaries SAC and g) Berwickshire and North Northumberland Coast SAC. Labels on bars show the number of samples. ***, $p < 0.001$.

Table 9. Welch's t-tests of data on taxon richness (S), Shannon diversity, Simpson diversity and Pielou's evenness for samples of assemblages on circalittoral rock collected in two periods of time (Time-period; 2009-13 vs 2014-19) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC, and f) Berwickshire and North Northumberland Coast SAC. There were not enough data to make comparisons for Essex Estuaries SAC, so these are excluded from the table. For each MPA, the first row shows the test on the original data, typically with unbalanced samples (see labels in Figure 14). The second row shows mean test output from 10,000 iterations of tests with equal sample sizes, where samples were selected randomly from the larger group such that they matched the size of the smaller group. Mean values of *t* from the permuted tests of equal sample size marked with * indicate where they are the same side of the critical value as the original test. The third row shows the range of test outputs within which 95% of 10,000 tests occur. Cells marked with + indicate where the entirety of this range is on either side of the critical value. Significant effects referred to in the text are in bold.

Location	n	d.f.	*t* (richness)	*p* (richness)	*t* (Shannon)	*p* (Shannon)	*t* (Simpson)	*p* (Simpson)	*t* (Evenness)	*p* (Evenness)
a) Plymouth	34, 27	1	-0.521	0.604	0.324	0.747	0.954	0.347	1.484	0.147
Mean permuted *t*	27	1	-0.506*	0.616*	0.317*	0.754*	0.943*	0.354*	1.456*	0.157*
95% c.i. for permuted *t*	27	1	$-1.080 < t < 0.069^+$	$p > 0.29^+$	$-0.170 < t < 0.803^+$	$p > 0.428^+$	$0.625 < t < 1.261^+$	$p > 0.218^+$	$1.089 < t < 1.823^+$	$p > 0.080^+$
b) Scilly	184, 101	1	-1.129	0.260	-1.611	0.108	**-2.857**	**0.005**	-0.826	0.410
Mean permuted *t*	101	1	-0.985*	0.327*	-1.379*	0.171*	**-2.330***	**0.022***	-0.684*	0.496*
95% c.i. for permuted *t*	101	1	$-1.997 < t < 0.028$	$0.049 < p < 0.978$	$-2.375 < t < -0.383$	$0.019 < p < 0.703$	$-3.140 < t < -1.509$	$0.002 < p < 0.134$	$-1.645 < t < 0.276^+$	$p > 0.103^+$
c) Manacles	19, 46	1	**-2.116**	**0.042**	-1.906	0.066	-1.703	0.100	-0.756	0.456

Mean permuted *t*	19	1	1.767	0.093	1.677*	0.110*	1.602*	0.126*	0.674*	0.508*
95% c.i. for permuted *t*	19	1	0.578 < *t* < 2.955	0.008 < *p* < 0.570	0.391 < *t* < 2.963	0.008 < *p* < 0.700	0.137 < *t* < 3.067	0.006 < *p* < 0.892	-0.464 < *t* < 1.813^{+}	*p* > 0.087^{+}
d) Fal	11, 23	1	-0.653	0.522	-0.441	0.665	-0.179	0.860	**2.046**	**0.049**
Mean permuted *t*	11	1	0.562*	0.585*	0.401*	0.696*	0.173*	0.491*	-1.520	0.157
95% c.i. for permuted *t*	11	1	-0.519 < *t* < 1.644^{+}	*p* > 0.131^{+}	-0.650 < *t* < 1.453^{+}	*p* > 0.177^{+}	-0.738 < *t* < 1.085^{+}	*p* > 0.303^{+}	-2.937 < *t* < -0.104	0.014 < *p* < 0.920
e) Solent	16, 6	1	0.196	0.848	0.162	0.874	-0.033	0.974	0.567	0.579
Mean permuted *t*	6	1	0.169*	0.871*	0.196*	0.851*	0.155*	0.882*	0.704*	0.508*
95% c.i. for permuted *t*	6	1	-1.305 < *t* < 1.643^{+}	*p* > 0.161^{+}	-1.531 < *t* < 1.922^{+}	*p* > 0.113^{+}	-1.866 < *t* < 2.178^{+}	*p* > 0.072^{+}	-1.601 < *t* < 3.009	0.024 < *p* < 0.160
f) Berwickshire	75, 37	1	**-3.000**	**0.004**	**-3.000**	**0.003**	**-2.543**	**0.012**	**2.393**	**0.019**
Mean permuted *t*	37	1	**-2.640***	**0.012***	**-2.488***	**0.017***	**-2.033***	**0.049***	**2.047***	**0.048***
95% c.i. for permuted *t*	37	1	-3.810 < *t* < -1.469	0.001 < *p* < *0.150*	-3.661 < *t* < 1.315	0.001 < *p* < *0.197*	-3.062 < *t* < -1.004	0.004 < *p* < *0.322*	0.624 < *t* < 3.470	0.001 < *p* < 0.537

Table 10. Welch's t-tests of data on taxon richness (S), Shannon diversity, Simpson diversity and Pielou's evenness for samples of assemblages on infralittoral rock collected in two periods of time (Time-period; 2009-13 vs 2014-19) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Berwickshire and North Northumberland Coast SAC. There were not enough data to make comparisons for Solent Maritime SAC or Essex Estuaries SAC, so these are excluded from the table. For each MPA, the first row shows the test on the original data, typically with unbalanced samples (see labels in Figure 15). The second row shows mean test output from 10,000 iterations of tests with equal sample sizes, where samples were selected randomly from the larger group such they matched the size of the smaller group. Mean values of *t* from the permuted tests of equal sample size marked with * indicate where they are the same side of the critical value as the original test. The third row shows the range of test outputs within which 95% of 10,000 tests occur. Cells marked with + indicate where the entirety of this range is on either side of the critical value. Significant effects referred to in the text are in bold.

Location	n	d.f.	*t* (richness)	*p* (richness)	*t* (Shannon)	*p* (Shannon)	*t* (Simpson)	*p* (Simpson)	*t* (Evenness)	*p* (Evenness)
a) Plymouth	23,38	1	-0.136	0.893	0.351	0.727	0.120	0.905	0.088	0.931
Mean permuted *t*	23	1	0.090*	0.929*	-0.305*	0.763*	-0.081*	0.936*	-0.056*	0.956*
95% c.i. for permuted *t*	23	1	$-0.975 < t < 1.169^{+}$	$p > 0.254^{+}$	$-1.320 < t < 0.711^{+}$	$p > 0.200^{+}$	$-1.014 < t < 0.852^{+}$	$p > 0.322^{+}$	$-0.899 < t < 0.787^{+}$	$p > 0.378^{+}$
b) Scilly	120,45	1	0.203	0.840	-0.430	0.668	-2.013	**0.048**	**-2.515**	**0.014**
Mean permuted *t*	45	1	0.128*	0.899*	-0.351*	0.727*	-1.663	0.100	**-2.039***	**0.047***
95% c.i. for permuted *t*	45	1	$-1.069 < t < 1.325^{+}$	$p > 0.192^{+}$	$-1.489 < t < 0.787^{+}$	$p > 0.144^{+}$	$-2.639 < t < -0.686$	$0.011 < p < 0.496$	$-3.107 < t < -0.970$	$0.003 < p < 0.337$

c) Manacles	13,29	1	-0.542	0.592	0.048	0.962	0.488	0.628	0.682	0.500
Mean permuted *t*	13	1	0.416*	0.684*	-0.012*	0.990*	-0.262*	0.797*	-0.384*	0.707*
95% c.i. for permuted *t*	13	1	$-0.928 < t < 1.760^{+}$	$p > 0.104^{+}$	$-1.301 < t < 1.277^{+}$	$p > 0.218^{+}$	$-1.680 < t < 1.156^{+}$	$p > 0.119^{+}$	$-1.805 < t < 1.036^{+}$	$p > 0.096^{+}$
d) Fal	25,14	1	0.424	0.675	0.471	0.642	1.316	0.205	0.418	0.681
Mean permuted *t*	14	1	0.362*	0.723*	0.443*	0.664*	1.258*	0.229*	0.405*	0.692*
95% c.i. for permuted *t*	14	1	$-0.702 < t < 1.427^{+}$	$p > 0.177^{+}$	$-0.561 < t < 1.447^{+}$	$p > 0.172^{+}$	$0.562 < t < 1.953^{+}$	$p > 0.073^{+}$	$-0.389 < t < 1.199^{+}$	$0.252 < p^{+}$
e) Berwickshire	47,29	1	**-4.292**	**<0.001**	**-3.712**	**<0.001**	**-2.776**	**0.007**	1.565	0.124
Mean permuted *t*	29	1	**-4.051***	**<0.001***	**-3.352***	**0.002***	**-2.464***	**0.019***	1.62*	0.116*
95% c.i. for permuted *t*	29	1	$\mathbf{-4.824 < t < -3.277^{+}}$	$\mathbf{p < 0.003^{+}}$	$\mathbf{-4.172 < t < -2.533^{+}}$	$\mathbf{p < 0.017^{+}}$	$-3.224 < t < -1.704$	$0.003 < p < 0.10$	$0.592 < t < 2.331$	$0.027 < p < 0.558$

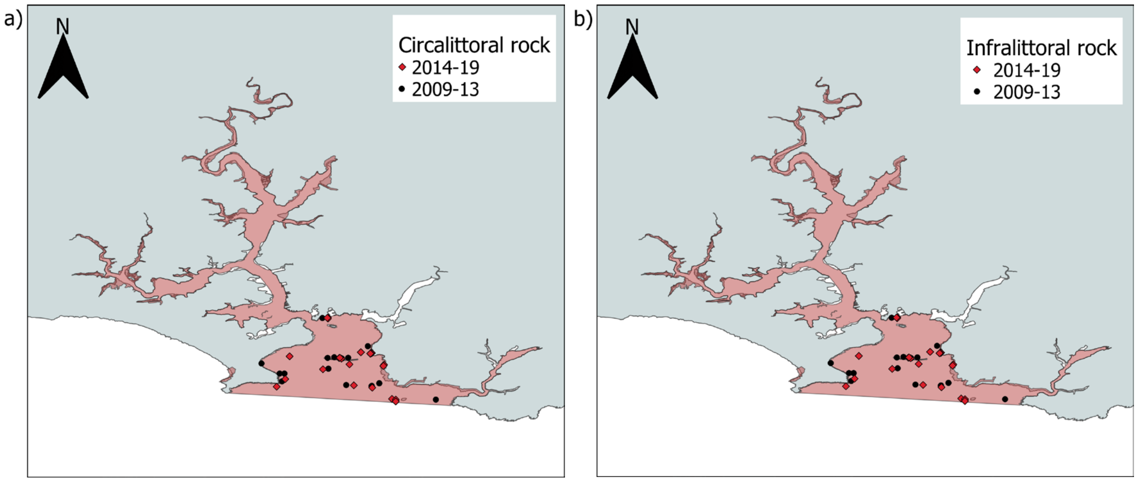

Figure 16. Positions of Seasearch surveys in the Plymouth Sound and Estuaries SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

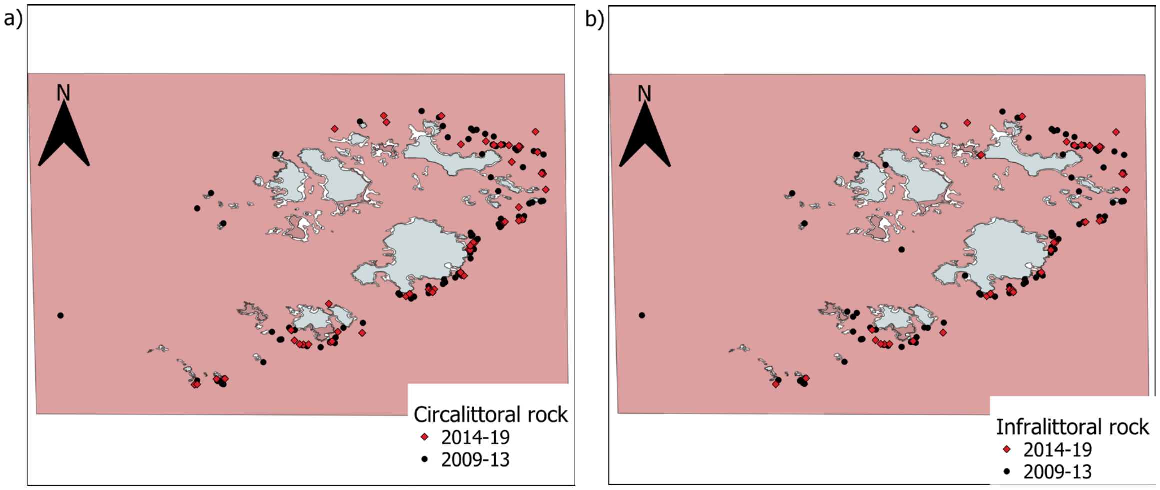

Figure 17. Positions of Seasearch surveys in the Isles of Scilly Complex SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

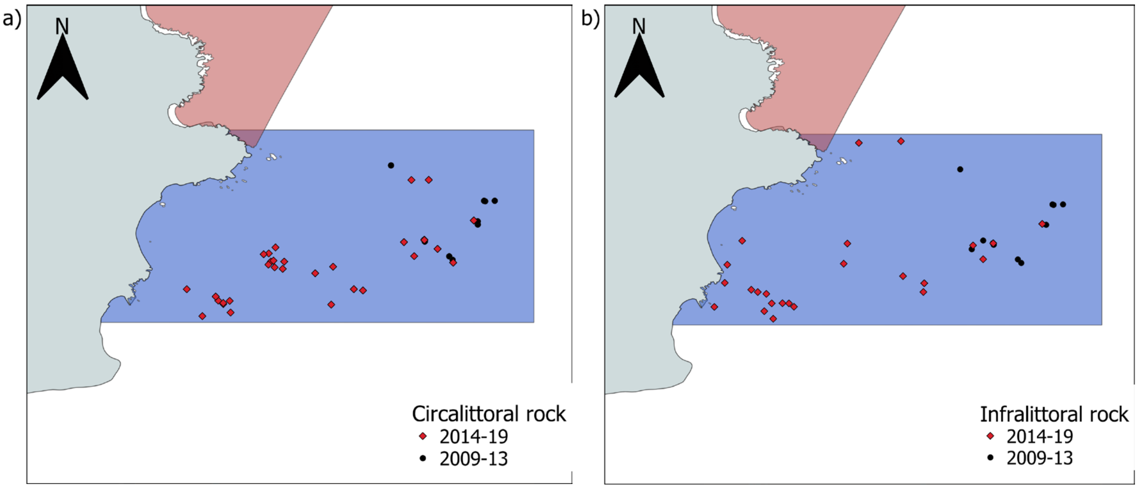

Figure 18. Positions of Seasearch surveys in The Manacles MCZ during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

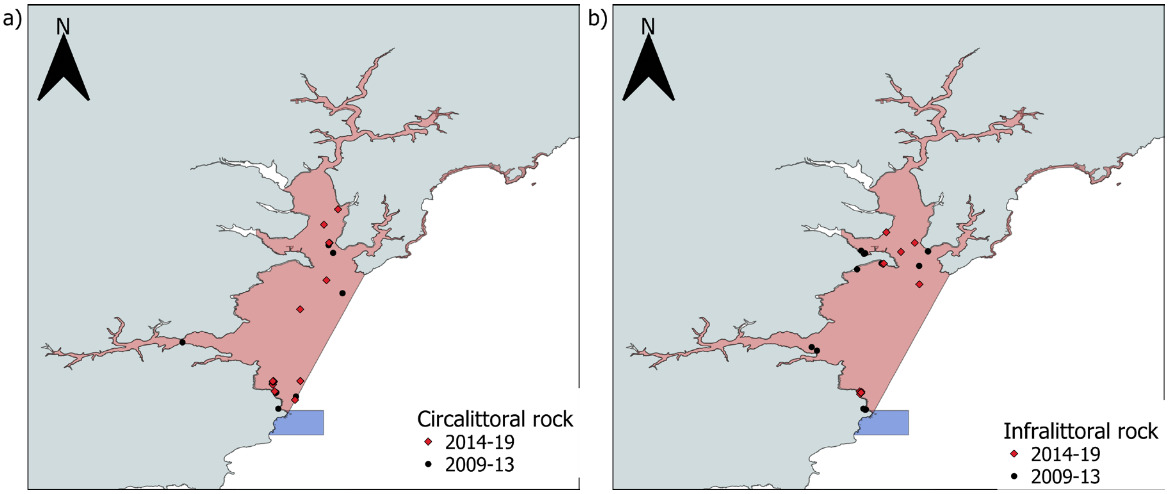

Figure 19. Positions of Seasearch surveys in the Fal and Helford SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

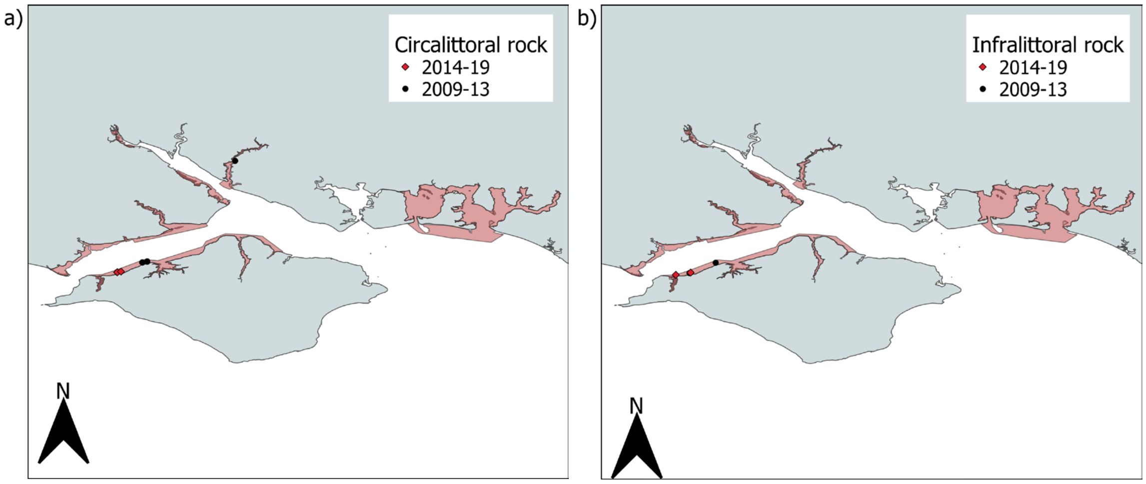

Figure 20. Positions of Seasearch surveys in Solent Maritime SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

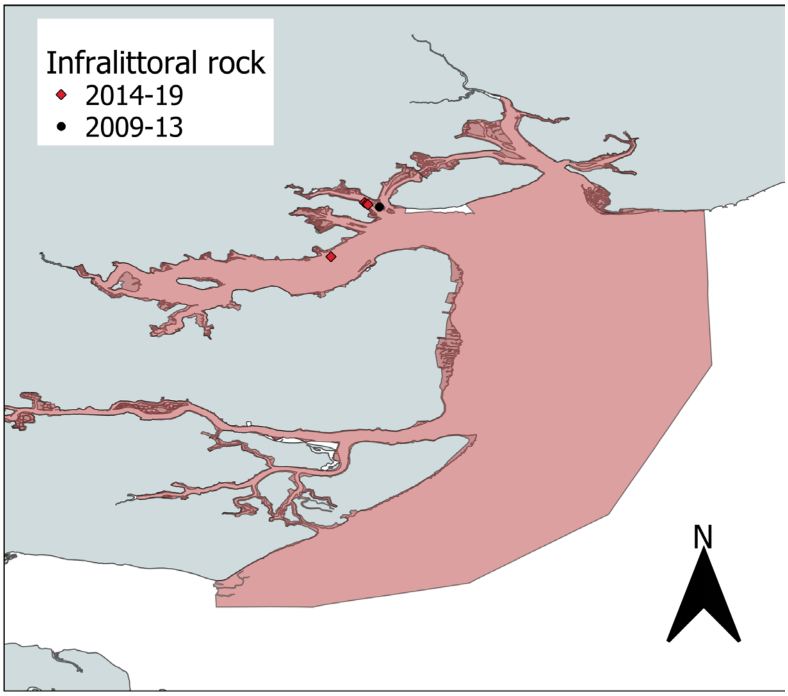

Figure 21. Positions of Seasearch surveys in Essex Estuaries SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for infralittoral rock. There were no records for circalittoral rock. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

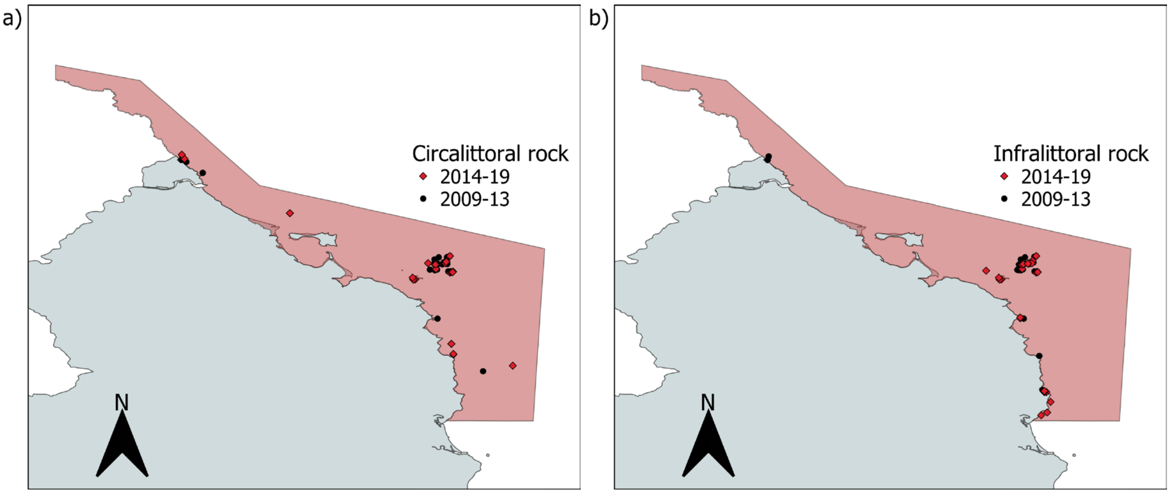

Figure 22. Positions of Seasearch surveys in Berwickshire and North Northumberland Coast SAC during the two time periods 2009-13 (black dots) and 2014-19 (red diamonds) for a) circalittoral rock and b) infralittoral rock. Only 'English' records are shown for this SAC, which includes some area in Scottish waters. © Crown copyright and database rights [2022] Ordnance Survey (100025252). Designated areas: © Natural England, 8 October 2019. These boundaries are licensed under the [Open Government Licence 3.0](). Map Projection is EPSG:4326 - WGS84.

Assemblages through time: β-diversity (Seasearch data only)

Circalittoral rock

There were significant differences in compositions of assemblages (50 most important taxa) on circalittoral rock between the two periods of time for five of the seven MPAs considered (Table 11). In two of these cases (Plymouth, Solent), the significance was marginal. The Berwickshire and North Northumberland Coast SAC was the only case without differences, although p was only marginally >0.05. This was in contrast with the strong patterns in α-diversity in this MPA. Insufficient samples had been collected in the Essex Estuaries SAC to make any comparisons. Differences were not always visually obvious in ordination plots (Figure 23). The ordination plots show distances among centroids, where each centroid is described by the mean abundances for each taxon in each year for that time-period. Plotting averages like this reduces the number of points and thereby reduces the stress value for the ordination nMDS whilst maintaining the ability to illustrate coarse differences among groups (Clarke and Warwick, 2001). In no MPA were there differences in multivariate dispersion of samples from circalittoral rock between the two time periods (PERMDISP: $p > 0.05$).

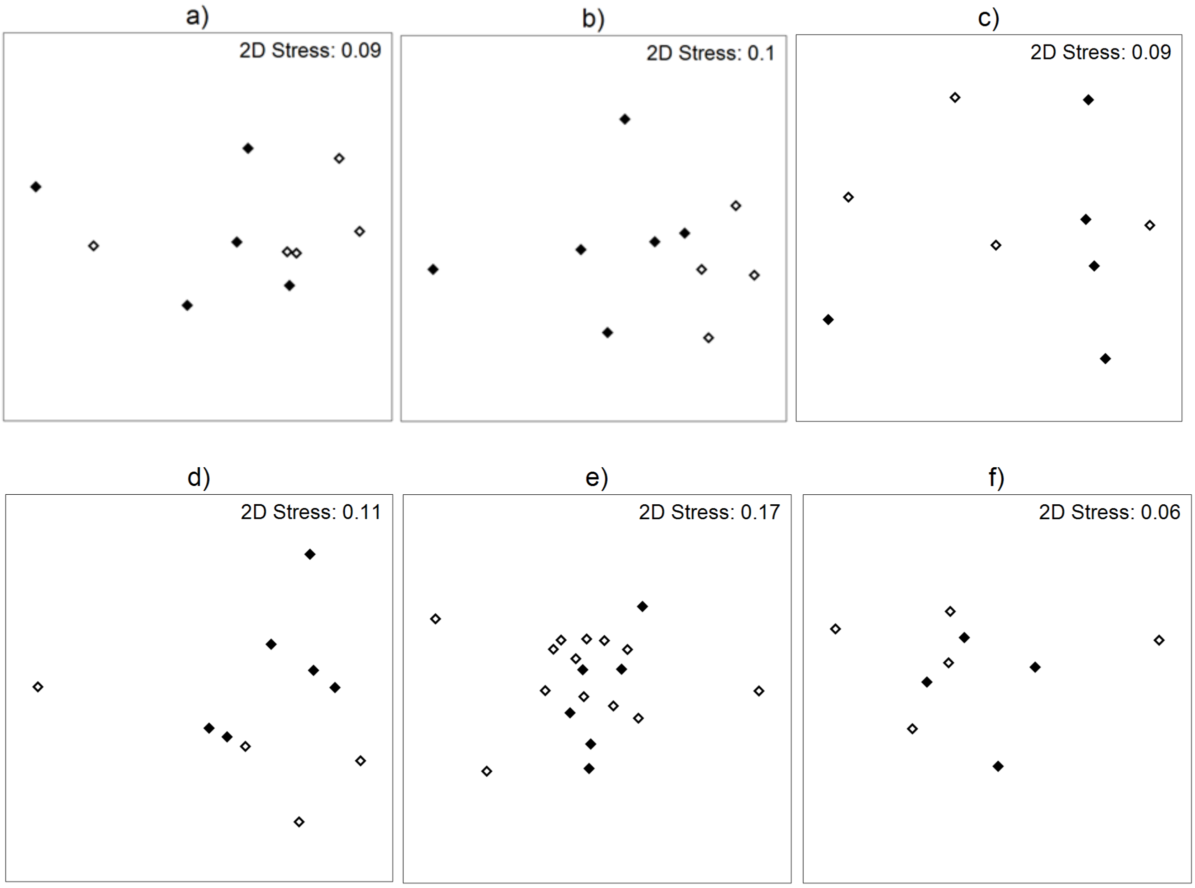

Figure 23. nMDS ordination plots for identities and relative abundances from samples of assemblages on circalittoral rock collected in two periods of time: 2009-13 (white diamonds) or 2014-19 (black diamonds) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC, and f) Berwickshire and North Northumberland Coast SAC. There were not enough data to make comparisons for Essex Estuaries SAC. Plots a-d) and f) are shown as centroids (where abundances for each taxon are averaged for each year in each time period).

Table 11. Multivariate analyses (PERMANOVA) of identities and relative abundances of taxa in assemblages on circalittoral rock collected in two periods of time (Time-period; fixed, 2009-13 vs 2014-19) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Solent Maritime SAC, and f) Berwickshire and North Northumberland Coast SAC. Insufficient data were available to make comparisons for Essex Estuaries SAC. Significant values in bold are referred to in the text. Where cells are blank, this is intentional because the analyses produce no values for these analysis terms.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
a) Plymouth					
Time-period	1	5256	1.80	**0.045**	998
Residual	58	2927			
b) Scilly					
Time-period	1	14043	6.12	**0.001**	999
Residual	283	2293			
c) Manacles					
Time-period	1	4406	2.12	**0.008**	998
Residual	63	2083			
d) Falmouth					
Time-period	1	5696	1.99	**0.017**	997
Residual	32	2856			
e) Solent					
Time-period	1	4454	1.67	**0.049**	978

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
Residual	17	2673			
f) Berwickshire					
Time-period	1	3005	1.65	0.062	997
Residual	110	1819			

Taxa contributions to dissimilarities between times

Where significant multivariate differences exist in composition of assemblages between time-periods, SIMPER analyses can reveal which taxa contribute most to those differences (Clarke, 1993). Taxa contributing to dissimilarities between the two time periods are listed for each MPA (Table 12 to Table 16). For the four MPAs in the south-west, the Devonshire cup coral (*Caryophyllia smithii*) was in the top two of the taxa contributing most to dissimilarities between time-periods. In some cases, the number of records was greater in the more recent period (Plymouth, Manacles) and in other cases it was recorded more in the earlier period (Scilly, Fal). In three MPAs, the edible urchin (*Echinus esculentus*), was found less in the more recent period than in the earlier period. Only in the Fal and Helford SAC was this taxon found more in 2014-19 than in 2009-13.

Table 12. Dissimilarity contributions from 50 'most important' taxa in samples from circalittoral rock in Plymouth Sound and Estuaries SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Antedon bifida	1.73	0.50	3.85	0.76	5.04	5.04
Caryophyllia smithii	2.31	2.24	3.70	1.14	4.85	9.89
Sycon ciliatum	0.58	1.35	3.06	0.82	4.01	13.90
Spirobranchus	1.00	1.06	2.92	0.83	3.83	17.73

Species	**Av.Abund 2014-19**	**Av.Abund 2009-13**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ctenolabrus rupestris	1.35	1.32	2.85	1.11	3.73	21.46
Dendrodoa grossularia	0.38	1.24	2.81	0.64	3.68	25.14
Amphilectus fucorum	0.96	1.06	2.78	0.96	3.64	28.78
Necora puber	0.77	1.27	2.35	1.08	3.08	31.86
Raspailia ramosa	0.69	1.03	2.18	1.01	2.85	34.71
Actinothoe sphyrodeta	0.88	0.47	2.12	0.69	2.78	37.49
Calliostoma	0.88	0.59	2.09	0.84	2.74	40.23
Marthasterias glacialis	0.74	0.95	2.07	1.04	2.72	42.95
Echinus esculentus	0.54	0.77	2.02	0.78	2.64	45.60
Bispira volutacornis	0.50	1.00	1.99	1.05	2.61	48.20
Salmacina	1.00	0.26	1.93	0.58	2.52	50.73
Suberites	0.71	0.62	1.79	0.93	2.34	53.07
Eunicella verrucosa	0.58	0.53	1.77	0.69	2.32	55.39
Spirorbis	0.15	0.88	1.72	0.47	2.26	57.65
Urticina felina	0.73	0.12	1.61	0.52	2.11	59.75
Diaphorodoris luteocincta	0.35	0.53	1.60	0.50	2.09	61.85
Polycarpa	0.54	0.41	1.53	0.50	2.01	63.85
Anemonia viridis	0.50	0.41	1.53	0.65	2.00	65.86
Trivia	0.38	0.47	1.52	0.52	1.99	67.85

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Holothuria forskali	0.47	0.45	1.44	0.79	1.88	69.73
Asterias rubens	0.27	0.62	1.43	0.76	1.88	71.61

Table 13. Dissimilarity contributions from 50 'most important' taxa in samples from circalittoral rock in the Isles of Scilly Complex SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Caryophyllia smithii	2.77	3.39	4.21	1.05	6.22	6.22
Sagartia	1.19	0.91	2.79	0.93	4.13	10.35
Antedon bifida	0.90	1.17	2.67	0.95	3.95	14.30
Isozoanthus sulcatus	0.94	0.99	2.63	0.76	3.89	18.20
Echinus esculentus	1.14	1.41	2.52	1.12	3.73	21.92
Metridium senile	0.96	0.67	2.47	0.82	3.65	25.57
Sycon ciliatum	1.02	0.72	2.42	0.85	3.58	29.16
Suberites	0.89	1.05	2.41	0.98	3.57	32.73
Axinella	1.15	1.04	2.29	1.13	3.40	36.13
Diaphorodoris luteocincta	0.28	1.06	2.16	0.65	3.20	39.32
Parazoanthus axinellae	0.80	0.60	2.13	0.72	3.15	42.47
Calliostoma	0.66	0.72	1.95	0.79	2.89	45.36

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Raspailia ramosa	0.94	0.48	1.89	0.91	2.79	48.15
Polymastia	0.81	0.77	1.79	1.13	2.65	50.80
Trivia	0.36	0.80	1.78	0.63	2.64	53.44
Homaxinella subdola	0.74	0.50	1.69	0.86	2.50	55.94
Pentapora foliacea	0.73	0.69	1.69	1.00	2.50	58.45
Corynactis viridis	1.47	1.29	1.67	1.00	2.47	60.92
Holothuria forskali	0.67	0.78	1.66	1.03	2.46	63.38
Doto	0.66	0.37	1.59	0.55	2.35	65.73
Spirobranchus	0.47	0.41	1.52	0.55	2.25	67.97
Flabellina	0.27	0.69	1.51	0.69	2.23	70.20

Table 14. Dissimilarity contributions from 50 'most important' taxa in samples from circalittoral rock in The Manacles MCZ between 2009-13 and 2014-19

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Caryophyllia smithii	3.32	2.21	4.00	1.17	6.24	6.24
Ctenolabrus rupestris	1.33	1.05	2.77	1.06	4.32	10.56
Echinus esculentus	1.59	1.63	2.73	1.11	4.26	14.82
Eunicella verrucosa	1.44	1.37	2.69	1.12	4.19	19.00
Tritonia	1.30	0.84	2.68	0.98	4.17	23.18

Species	**Av.Abund 2014-19**	**Av.Abund 2009-13**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Labrus mixtus	0.96	0.95	2.21	1.05	3.45	26.63
Calliostoma	0.43	1.11	2.21	0.84	3.44	30.07
Asterias rubens	0.40	1.11	2.13	1.06	3.31	33.38
Antedon bifida	0.52	0.79	2.02	0.70	3.15	36.54
Henricia	1.09	0.42	1.99	0.99	3.09	39.63
Corynactis viridis	0.96	1.66	1.98	1.30	3.08	42.71
Sagartia	0.35	0.90	1.97	0.74	3.07	45.78
Marthasterias glacialis	0.92	0.95	1.90	1.02	2.97	48.74
Sycon ciliatum	0.54	0.68	1.77	0.66	2.76	51.51
Centrolabrus exoletus	0.63	0.58	1.71	0.75	2.66	54.17
Pentapora foliacea	0.77	0.43	1.63	0.88	2.55	56.72
Dictyopteris polypodioides	0.70	0.60	1.56	1.04	2.44	59.15
Holothuria forskali	0.59	0.54	1.51	0.88	2.36	61.51
Labrus bergylta	0.51	0.64	1.51	0.92	2.35	63.87
Simnia	0.76	0.16	1.49	0.58	2.32	66.19
Luidia ciliaris	0.38	0.64	1.40	0.88	2.18	68.37
Nemertesia	0.90	1.21	1.28	1.08	2.00	70.37

Table 15. Dissimilarity contributions from 50 'most important' taxa in samples from circalittoral rock in the Fal and Helford SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Caryophyllia smithii	2.48	2.64	6.02	1.28	7.86	7.86
Ascidiella	1.78	0.18	4.36	0.83	5.70	13.55
Echinus esculentus	1.87	1.45	3.80	1.15	4.96	18.51
Sycon ciliatum	0.09	1.36	3.07	0.85	4.01	22.52
Ctenolabrus rupestris	1.09	0.55	2.88	0.98	3.75	26.28
Eunicella verrucosa	1.04	0.55	2.76	1.03	3.60	29.88
Suberites	0.52	0.91	2.72	1.00	3.55	33.43
Marthasterias glacialis	1.09	0.74	2.67	1.11	3.49	36.92
Tritonia	0.78	0.55	2.52	0.69	3.28	40.21
Trisopterus luscus	0.87	0.00	2.18	0.70	2.85	43.06
Simnia	0.30	0.82	2.07	0.71	2.71	45.76
Aslia lefevrei	0.57	0.45	2.00	0.67	2.61	48.37
Corynactis viridis	0.50	0.68	1.99	1.00	2.60	50.97
Nemertesia	0.57	0.81	1.88	1.17	2.45	53.42
Hemimycale columella	0.70	0.66	1.86	1.14	2.42	55.84
Sagartia	0.78	0.00	1.80	0.52	2.35	58.19
Aiptasia mutabilis	0.65	0.00	1.78	0.48	2.32	60.51
Thorogobius ephippiatus	0.65	0.00	1.77	0.58	2.31	62.82

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Holothuria forskali	0.61	0.27	1.75	0.72	2.28	65.10
Calliostoma	0.35	0.18	1.43	0.52	1.86	66.97
Amphilectus fucorum	0.30	0.36	1.41	0.61	1.85	68.81
Ascidia	0.39	0.27	1.40	0.60	1.82	70.64

Table 16. Dissimilarity contributions from 50 'most important' taxa in samples from circalittoral rock in the Solent Maritime SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Ampelisca	1.83	0.62	4.60	0.76	6.26	6.26
Salmacina	2.00	0.62	4.50	0.97	6.12	12.38
Serpulidae	1.75	0.31	4.46	0.83	6.07	18.45
Molgula	0.33	2.00	3.82	1.28	5.20	23.65
Calliostoma	2.00	1.85	2.93	1.04	3.98	27.64
Spirobranchus	1.17	1.15	2.77	1.01	3.77	31.40
Crepidula fornicata	1.33	0.85	2.74	1.11	3.73	35.13
Actinothoe sphyrodeta	1.17	0.69	2.65	1.00	3.61	38.74
Steromphala	0.33	1.23	2.49	1.02	3.38	42.12
Caprella	0.00	1.08	2.29	0.64	3.11	45.23
Necora puber	1.00	0.62	2.22	0.99	3.02	48.25

Species	**Av.Abund 2014-19**	**Av.Abund 2009-13**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ostrea edulis	1.00	0.31	2.19	1.03	2.98	51.23
Pagurus	0.33	0.92	1.93	1.04	2.62	53.86
Dysidea fragilis	0.67	0.93	1.93	1.08	2.62	56.48
Dendrodoa grossularia	0.33	0.77	1.89	0.69	2.57	59.05
Pomatoschistus	0.83	0.39	1.85	1.00	2.52	61.56
Inachus	0.17	0.85	1.81	0.92	2.46	64.03
Kirchenpaueria	0.96	0.28	1.72	1.43	2.34	66.36
Gobius niger	0.50	0.62	1.70	0.90	2.32	68.68
Anemonia viridis	0.33	0.69	1.67	0.83	2.28	70.96

Infralittoral rock

There were significant differences in compositions of assemblages on infralittoral rock between the two periods of time for three of the seven MPAs considered (Table 17). There was no change through time for infralittoral rock in The Manacles MCZ and the Fal and Helford SAC. Analyses for Solent Maritime SAC and Essex Estuaries were not possible due to the very small sample sizes (<5 per time-period). Differences were not always visually obvious in ordination plots (Figure 24). nMDS ordination plots represent differences between the two time-periods and, as above, are plotted either as distances between individual samples or (where stress is large due to the presence of many samples) as centroids. Patterns in homogeneity of multivariate dispersion were apparent only in Isles of Scilly Complex SAC, where variability was significantly greater in the earlier period than in the later period (PERMDISP: $F_{1,160} = 21.2$, $p < 0.001$; Figure 24b). There were no differences in dispersion between the two time periods for the other MPAs.

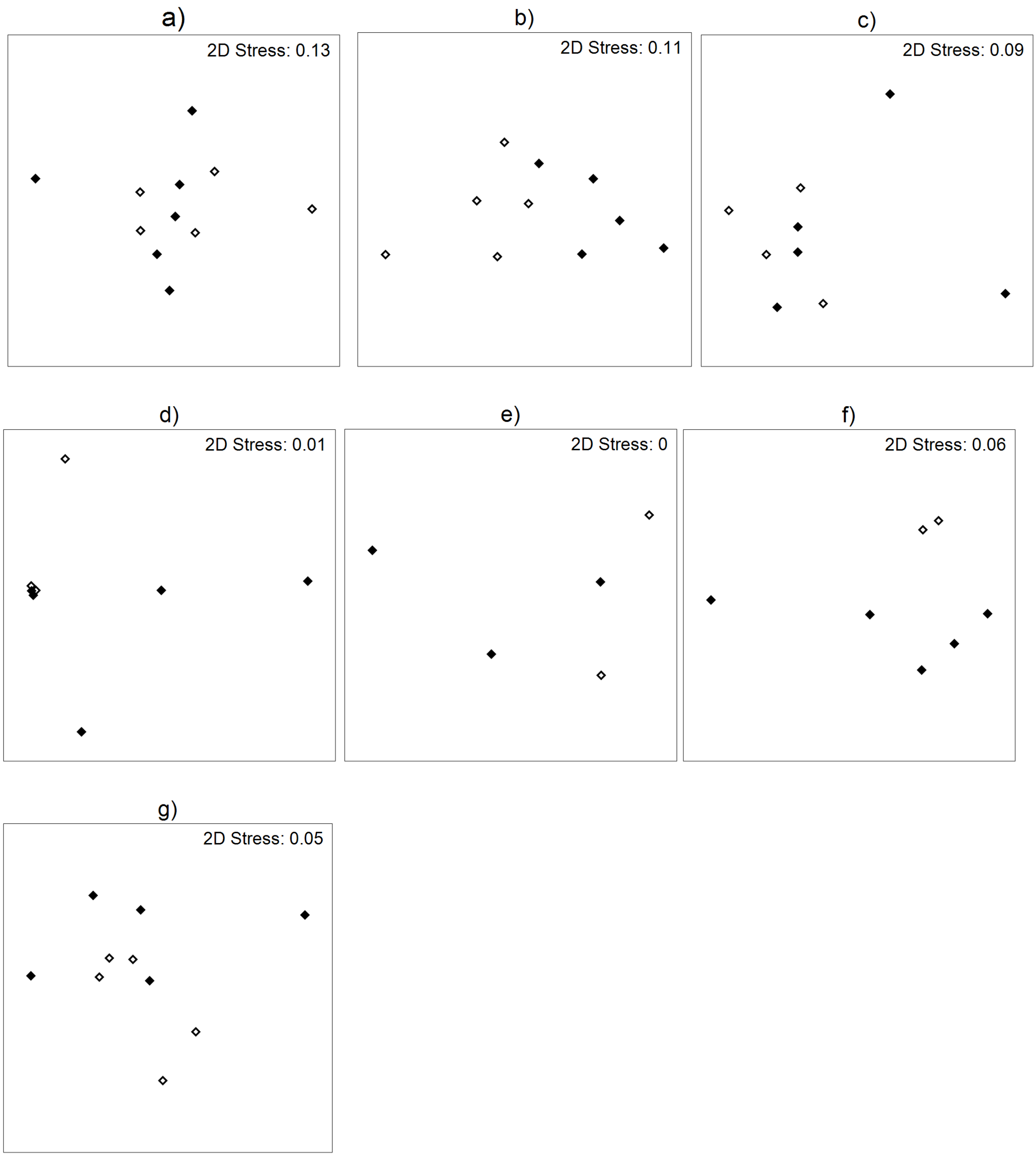

Figure 24. nMDS ordination plots for identities and relative abundances of taxa from samples of assemblages on infralittoral rock collected in two periods of time: 2009-13 (white diamonds) or 2014-19 (black diamonds) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, e) Essex Estuaries SAC, f) Solent Maritime SAC, and g) Berwickshire and North Northumberland Coast SAC. Plots a-d) and g) are shown as centroids (where abundances for each taxon are averaged for each year in each time period).

Table 17. Multivariate analyses (PERMANOVA) of data on identities and relative abundances for samples of assemblages on infralittoral rock collected in two periods of time (Time-period; fixed, 2009-13 vs 2014-19) for a) Plymouth Sound and Estuaries SAC, b) Isles of Scilly Complex SAC, c) The Manacles MCZ, d) Fal and Helford SAC, and e) Berwickshire and North Northumberland Coast SAC. There were inadequate numbers of samples (<5 per time-period) to make comparisons for Solent Maritime or Essex Estuaries SAC. Bold values are significant results referred to in the text. Where cells are blank, this is intentional because the analyses produce no values for these analysis terms.

Analysis term	d.f.	Mean Square	Pseudo-*F*	*p*	Unique permutations
a) Plymouth					
Time-period	1	5430	1.82	**0.04**	999
Residual	72	3484			
b) Scilly					
Time-period	1	17523	6.93	**0.001**	999
Residual	160	2529			
c) Manacles					
Time-period	1	3980	1.57	0.118	997
Residual	40	2542			
d) Falmouth					
Time-period	1	4387	1.44	0.126	997
Residual	37	3056			
e) Berwickshire					
Time-period	1	8053	3.86	**0.001**	998

Residual	74	2084			

Taxa contributions to dissimilarities between times

For the three MPAs where significant multivariate differences existed in composition of assemblages between time-periods from infralittoral rock, SIMPER analyses (Clarke, 1993) revealed which taxa contributed most to those differences (Table 18 to Table 20. No species stood out as contributing unusually large percentages of the distances between times. For the two MPAs in the south-west where assemblages differed between times (Plymouth, Scilly), *Caryophyllia smithii* was again the taxon that contributed most to dissimilarities. In each case the number of records was less in the more recent than in the earlier period. In these two MPAs, directions of change in abundance for this species were not consistent with those on circalittoral rock. Other taxa contributing more to dissimilarities included again, *Echinus esculentus*; in two MPAs (Scilly, Berwickshire), this was more abundant in the earlier period than in the later period.

Table 18. Dissimilarity contributions from 50 'most important' taxa in samples from infralittoral rock in Plymouth Sound and Estuaries SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Caryophyllia smithii	0.49	1.43	5.59	0.78	6.73	6.73
Gobiusculus flavescens	0.57	1.13	4.80	0.70	5.77	12.50
Asterina gibbosa	0.92	0.74	3.90	0.79	4.69	17.19
Laminaria	0.75	1.27	3.86	1.03	4.65	21.84
Anemonia viridis	0.77	0.87	3.84	0.91	4.61	26.45
Steromphala	0.46	0.91	3.44	0.66	4.14	30.59
Membranipora membranacea	0.40	0.93	3.14	1.02	3.78	34.36

Species	**Av.Abund 2014-19**	**Av.Abund 2009-13**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sycon ciliatum	0.29	0.78	2.96	0.61	3.57	37.93
Marthasterias glacialis	0.57	0.65	2.69	0.94	3.24	41.17
Electra	0.54	0.51	2.59	0.85	3.11	44.28
Necora puber	0.45	0.52	2.42	0.71	2.91	47.19
Centrolabrus exoletus	0.22	0.65	2.34	0.59	2.82	50.01
Symphodus melops	0.33	0.57	2.32	0.63	2.79	52.80
Obelia	0.30	0.66	2.31	0.90	2.78	55.58
Saccharina latissima	0.32	0.51	2.22	0.73	2.66	58.24
Labrus bergylta	0.43	0.40	2.10	0.63	2.53	60.77
Saccorhiza polyschides	0.23	0.48	2.07	0.74	2.49	63.26
Trivia	0.12	0.57	1.98	0.44	2.38	65.65
Bispira volutacornis	0.43	0.35	1.93	0.69	2.33	67.97
Dilsea carnosa	0.39	0.42	1.86	0.89	2.23	70.21

Table 19. Dissimilarity contributions from 50 'most important' taxa in samples from infralittoral rock in Isles of Scilly Complex SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Caryophyllia smithii	0.73	1.53	4.27	0.87	6.02	6.02
Echinus esculentus	1.09	1.69	3.81	1.09	5.37	11.38
Actinothoe sphyrodeta	0.77	1.13	3.53	0.77	4.98	16.36
Sagartia	0.98	0.76	3.07	0.95	4.33	20.69
Dictyopteris polypodioides	1.41	0.62	2.96	1.22	4.17	24.86
Dictyota dichotoma	1.34	0.66	2.79	1.16	3.94	28.80
Sycon ciliatum	0.41	0.76	2.49	0.66	3.52	32.32
Membranipora membranacea	0.85	0.77	2.40	1.04	3.39	35.71
Amphilectus fucorum	0.34	0.80	2.38	0.65	3.35	39.06
Corynactis viridis	0.88	0.83	2.32	1.08	3.27	42.33
***Metridium dianthus* (*was senile*)**	0.55	0.38	2.01	0.68	2.84	45.16
Laminaria	1.50	1.43	1.82	0.91	2.57	47.73
Delesseria sanguinea	0.75	0.44	1.78	1.12	2.52	50.25
Trivia	0.20	0.61	1.72	0.52	2.43	52.68
Electra	0.64	0.11	1.70	0.80	2.40	55.09
Halidrys siliquosa	0.51	0.35	1.67	0.86	2.35	57.44
Obelia	0.50	0.31	1.65	0.90	2.32	59.76

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Pollachius pollachius	0.41	0.34	1.63	0.69	2.30	62.06
Calliostoma	0.30	0.47	1.60	0.59	2.26	64.32
Gobiusculus flavescens	0.36	0.42	1.59	0.55	2.25	66.56
Patella pellucida	0.16	0.58	1.59	0.43	2.25	68.81
Labrus bergylta	0.46	0.39	1.58	0.82	2.23	71.04

Table 20. Dissimilarity contributions from 50 'most important' taxa in samples from infralittoral rock in Berwickshire and North Northumberland Coast SAC between 2009-13 and 2014-19.

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Patella pellucida	2.76	2.32	4.53	1.08	6.88	6.88
Spirobranchus	2.31	2.79	4.00	1.13	6.07	12.96
Steromphala	2.45	1.55	3.88	1.18	5.89	18.84
Echinus esculentus	1.69	2.28	3.73	1.22	5.66	24.51
Paguridae	1.52	0.11	2.73	0.99	4.15	28.66
Rissoa	1.41	0.09	2.72	0.56	4.13	32.79
Lacuna	0.62	1.00	2.53	0.62	3.84	36.63
Limacia clavigera	0.93	0.96	2.42	0.86	3.68	40.31
Calliostoma	0.62	1.09	2.32	0.82	3.52	43.83

Species	Av.Abund 2014-19	Av.Abund 2009-13	Av.Sim	Sim/SD	Contrib%	Cum.%
Gobiusculus flavescens	0.93	0.64	2.15	0.83	3.26	47.09
Henricia	1.17	1.23	2.12	1.16	3.22	50.31
Necora puber	0.76	1.02	1.97	1.13	3.00	53.31
Trivia	0.55	0.79	1.86	0.67	2.83	56.14
Polycera	0.93	0.38	1.84	0.81	2.80	58.94
Urticina felina	0.86	0.53	1.77	0.89	2.69	61.63
Spirorbis	0.45	0.64	1.74	0.52	2.65	64.28
Membranipora membranacea	0.81	1.00	1.73	1.10	2.63	66.91
Pagurus	0.48	0.68	1.66	0.70	2.53	69.43

β-diversity on seagrass

There were not enough samples to make any formal comparisons between time periods. This was either because there were records from only one of the periods (e.g. Berwickshire and North Northumberland Coast SAC which had 5 samples in the most recent period, but none from the earlier, or each period had only very small numbers of samples (e.g. Fal and Helford SAC, Plymouth Sound and Estuaries SAC). At least 4 samples are required to make an ordination and multivariate analyses were made only if there were ≥5 samples in each period.

Confidence

Extensive and careful data filtering was applied to ensure that only the most appropriate and best-quality data available were used in analyses (Table 1). Amount of data is an additional factor that influences confidence in the reliability of the results from statistical tests. Tests were not done where sample sizes were below a particular threshold (i.e. no tests were done where sample-sizes were ≤5).

To give some indication of confidence in the outputs, a simple scoring system has been developed. Comparisons of single variables with > 5 samples were further categorised and given a score according to i) sample size, output of permuted tests using equal sample-sizes using ii) mean permuted test statistic and iii) 95% confidence interval of test statistic (Table 21). Scores from these three components were multiplied to give an overall measure of confidence. These overall ratings were categorised as giving low (1-5), medium (6-10) or high (>10) confidence. This process was applied to all tests for differences in diversity indices between the two time-periods for each habitat in each MPA.

Table 21. Scoring system used for univariate comparisons. Values from each of the three components are multiplied to give an overall confidence rating. Where cells are marked as NA, this is because different metrics have different ranges of scores, giving columns of different length.

Sample size (n)	Score	Mean permuted *t*	Score	95% CI for permuted *t*	Score
6-10	1	Different side of critical value as original test	1	All < critical value	3
11-20	2	Same side of critical value as original test	2	Overlap critical value	1
21-50	3	NA	NA	All > critical value	3
>50	4	NA	NA	NA	NA

Table 22. Outcomes, confidence scores and overall confidence rating for Welch's t-tests comparing Seasearch samples from circalittoral rock in seven MPAs during two periods of time (2009-13 vs 2014-19). Final scores were derived as the product of the three scores and rated as low (1-5; light blue), medium (6-10; mid-blue) or high (>10 dark blue). Lack of data prevented scores being calculated for Essex Estuaries SAC so this was excluded from the table.

Habitat	Site	Diversity index	Outcome	Sample-size score	Mean *t* score	95% CI *t* score	Final score	Confidence rating
Circalittoral rock	Plymouth	Richness	09-13 = 14-19	3	2	3	18	High
		Shannon	09-13 = 14-19	3	2	3	18	High
		Simpson	09-13 = 14-19	3	2	3	18	High
		Evenness	09-13 = 14-19	3	2	3	18	High
	Scilly	Richness	09-13 = 14-19	4	2	1	8	Medium
		Shannon	09-13 = 14-19	4	2	1	8	Medium
		Simpson	09-13 < 14-19	4	2	1	8	Medium
		Evenness	09-13 = 14-19	4	2	3	8	Medium
	Manacles	Richness	09-13 < 14-19	2	1	1	2	Low
		Shannon	09-13 = 14-19	2	2	1	4	Low

Habitat	Site	Diversity index	Outcome	Sample-size score	Mean *t* score	95% CI *t* score	Final score	Confidence rating
		Simpson	09-13 = 14-19	2	2	1	4	Low
		Evenness	09-13 = 14-19	2	2	3	12	High
	Fal & Helford	Richness	09-13 = 14-19	2	2	3	12	High
		Shannon	09-13 = 14-19	2	2	3	12	High
		Simpson	09-13 = 14-19	2	2	3	12	High
		Evenness	09-13 > 14-19	2	2	1	4	Low
	Solent	Richness	09-13 = 14-19	1	2	3	6	Medium
		Shannon	09-13 = 14-19	1	2	3	6	Medium
		Simpson	09-13 = 14-19	1	2	3	6	Medium
		Evenness	09-13 = 14-19	1	2	1	2	Low
	Berwickshire	Richness	09-13 < 14-19	3	2	1	6	Medium
		Shannon	09-13 < 14-19	3	2	1	6	Medium
		Simpson	09-13 < 14-19	3	2	1	6	Medium

Habitat	**Site**	**Diversity index**	**Outcome**	**Sample-size score**	**Mean *t* score**	**95% CI *t* score**	**Final score**	**Confidence rating**
		Evenness	09-13 > 14-19	3	2	1	6	Medium

Table 23. Outcomes, confidence scores and overall confidence rating for Welch’s t-tests comparing Seasearch samples from infralittoral rock in seven MPAs during two periods of time (2009-13 vs 2014-19). Final scores were derived as the product of the three scores and rated as low (1-5), medium (6-10) or high (>10). Lack of data prevented scores being calculated for Solent Maritime SAC and Essex Estuaries SAC so these were excluded from the table.

Habitat	Site	Diversity index	Outcome	Sample-size score	Mean *t* score	95% CI *t* score	Final score	Confidence rating
Circalittoral rock	Plymouth	Richness	09-13 = 14-19	3	2	3	18	High
		Shannon	09-13 = 14-19	3	2	3	18	High
		Simpson	09-13 < 14-19	3	1	1	3	Low
		Evenness	09-13 = 14-19	3	2	1	6	Medium
	Scilly	Richness	09-13 = 14-19	3	2	3	18	High
		Shannon	09-13 = 14-19	3	2	3	18	High
		Simpson	09-13 < 14-19	3	1	1	3	Low
		Evenness	09-13 < 14-19	3	2	1	6	Medium
	Manacles	Richness	09-13 = 14-19	2	2	3	12	High
		Shannon	09-13 = 14-19	2	2	3	12	High

Habitat	Site	Diversity index	Outcome	Sample-size score	Mean *t* score	95% CI *t* score	Final score	Confidence rating
		Simpson	09-13 = 14-19	2	2	3	12	High
		Evenness	09-13 = 14-19	2	2	3	12	High
	Fal & Helford	Richness	09-13 = 14-19	2	2	3	12	High
		Shannon	09-13 = 14-19	2	2	3	12	High
		Simpson	09-13 = 14-19	2	2	3	12	High
		Evenness	09-13 = 14-19	2	2	3	12	High
	Berwickshire	Richness	09-13 < 14-19	3	2	3	18	High
		Shannon	09-13 < 14-19	3	2	3	18	High
		Simpson	09-13 < 14-19	3	2	1	6	Medium
		Evenness	09-13 = 14-19	3	2	1	6	Medium

Discussion

After appropriate 'cleaning' and processing, citizen science records from the Seasearch programme were used to compare diversities of benthic assemblages on circalittoral or infralittoral rock i) against comparable data from Natural England and ii) between two different periods of time (2009-13 vs 2014-19) for seven MPAs around the English coast.

Suitability of Seasearch data

Any old numbers can be plugged into an analysis, but that does not mean that the numbers meet the intentions or requirements of the analyses. Where objectives of a data-collection programme are not very specific, it can sometimes be difficult to demonstrate effective delivery of those objectives (de Jonge, Elliott and Brauer, 2006; Lindenmayer and Likens, 2010; Magurran *et al.*, 2010). This is because provision of only high-level description about intentions for data collection do not facilitate technical aspects of analyses, such as the intended effect size to be detected and therefore the power to detect this difference. It is also not always certain about whether data collected are appropriate for other, *post hoc* objectives (as here, when making formal analyses with Seasearch citizen science data). It is valuable, therefore, to consider whether limitations are conferred by the structure and methodology of different data sets and whether this might influence interpretations and conclusions. This is particularly true when data are combined from multiple sources (e.g. when comparing data from Seasearch and NE), each with their own high-level intentions. A lack of consistency in sampling design and methods among different organisations or programmes can hinder analyses that extend beyond the intended scope of each programme (Kröger and Johnston, 2016).

Despite the unstructured nature, and somewhat diffuse aims of Seasearch, I would argue that due to:

i) the volume of data (many thousands of records),
ii) the broad coverage (most of the British coastline),
iii) the frequency of collection (some records for most places in most years),
iv) the resolution and detail (similar taxonomic level to NE condition assessment data)
v) measures of diversity (equal to or greater than estimates from NE data)

these citizen science data are suitable for application to formal statistical analyses that are useful when asking questions about benthic assemblages at the scale of whole MPAs.

Data processing

Comparisons of abundance

There are some concerns that SACFOR scores are not suitable for monitoring data (Eleftheriou and McIntyre, 2005), but Strong & Johnson (2020) suggest that SACFOR data for multiple taxa, in well replicated surveys from large areas of marine habitat, can be useful when other quantitative data are lacking. Whilst use of semi-quantitative assessment of abundance against pre-defined categories (e.g. SACFOR) is recognised as being quick and accurate (Hawkins and Jones, 1992), appropriate for roving surveys and apt for detection of rare taxa (Strong and Johnson, 2020), it is likely that estimates of abundance within a quadrat are more accurate and also more consistent among surveyors. Differences in methodology used by the two organisations meant that estimates of abundance were not included here in comparisons of data from NE or Seasearch. It would not be meaningful to convert Seasearch SACFOR scores into counts or percent covers, but it is theoretically possible to convert the counts and percent covers from NE records into SACFOR scores and then apply Strong & Johnson’s (2020) transformation, thereby making abundance scores comparable between the two organisations. This was not attempted here but could be considered in future analyses.

Taxonomic standardisation and SACFOR conversion

To avoid artificial inflation of the number of taxa recorded, it is important the taxa are handled at a consistent resolution, whilst maintaining taxonomic accuracy. The taxonomic standardisation designed and implemented here (Section 3.2) should be applied prior to any future analyses of diversity in Seasearch records. This reduces the number of records available for analysis, but any loss in power is likely to be outweighed by reductions in noise. Where analyses included measures of relative abundance (i.e. all except comparisons between NE and Seasearch), transformations of the SACFOR scores were important to make sure that abundances for organisms with different growth-forms and sizes were scored on a common scale (Strong and Johnson, 2020). If SACFOR scores from Seasearch data are to be used in future analyses of β-diversity or assemblage composition, my recommendation is that the data treatment protocol described above (Section 3.2) be implemented beforehand. This transformation improves only comparability and makes no alterations to accuracy or precision (Strong and Johnson, 2020). Thus, the usual health warnings apply about over-analysis and interpretation of imprecise ecological data. As was done in the present study, it may be of value to apply similar data processing protocols to other datasets (e.g. sentinel monitoring data by NE), to ensure comparability and to maximise the chances of detecting patterns where they exist.

Choice of diversity indices

Use of multiple diversity indices is generally considered to improve the output from analysis of a dataset. The most basic metric for diversity, taxon richness, is all that can be compared where there are either no scores for abundance or where scores are not comparable. The Shannon index, sensitive to richness, detects the effects of new arrivals or loss of rare taxa on diversity scores and is useful where this is the focus of the analysis. By contrast, the Simpson index responds little to the addition of rare taxa and gives more weight to common taxa and their evenness, assessing how the core set of common taxa changes. Pielou’s evenness assesses the relative numerical distribution of the common taxa and can be informative where the proportions of commonly occurring taxa are changing through time. Condition assessment for habitat features may well benefit from each approach. Data collected to support condition assessment should include, where possible, measures of abundance, ideally in a format that in comparable with complementary datasets.

How many taxa to include?

The total list of species recorded from each habitat in each MPA was quite large (always >100, often >200 and in a few cases >300), and many of these were recorded infrequently and with small abundances. Inclusion of numerous, seldom-recorded taxa is important for calculation of univariate measures of diversity, having obvious effects on taxon richness and Shannon diversity. The value of their inclusion in multivariate analyses is less clear-cut. Multivariate analyses of Seasearch and NE data using either all recorded taxa or only the 50 ‘most important’ taxa gave very similar patterns of difference (Table 3 & Table 4). Using the subset of 50 species (the approach subsequently adopted throughout this report) has perhaps two advantages. 1) The most ‘important’ species (i.e. those included in the top 50) will be those most often detected in quadrat-based sampling and by Seasearch surveys, potentially reducing influence on composition caused by the different sampling protocols. 2) Including fewer taxa in the similarity matrix means that the percent contribution by each species to overall dissimilarity measures will be larger, arguably giving a better feel for which taxa are contributing more to observed patterns of difference.

Seasearch and Natural England

In Plymouth Sound and Estuaries SAC, Seasearch records were compared with condition assessment / sentinel monitoring data from Natural England.

For circalittoral rock, there was no difference in rates of species accumulation with sample effort (Figure 3a) nor any difference in taxon richness of benthic samples

(Figure 4b). There were no differences in taxon richness between different locations in the SAC (Figure 5). Compositions of assemblages differed significantly between the two organisations and between the inner and outer Sound (Figure 8, Table 3, Table 4). For infralittoral rock, rates of species accumulation with sampling effort and the total number of taxa recorded by Seasearch were markedly greater than records from NE (Figure 3b). Mean taxon richness (Figure 10a), was significantly greater in Seasearch records than in those from Natural England (Table 5). There were also significantly greater numbers of taxa in the outer than in the inner Sound (Figure 10b). Compositions of assemblages differed between the two organisations and between the inner and outer Sound (Figure 11, Table 6, Table 7).

Differences caused by methods?

Seasearch surveys and NE condition assessment surveys were done in different ways, so it is perhaps no surprise that differences were often evident in the diversity of samples collected. The greater total number of taxa recorded in each habitat by Seasearch is a direct reflection of the larger amount of survey effort (Figure 3). Samples closer together in space are often considered to be more similar to each other than those farther apart (e.g. Carlile *et al.*, 1989; Palmer, 1992; Underwood and Chapman, 1996), although in the intertidal and marine environments small-scale variability in distribution of organisms is well-recognised (Kennelly, 1987; Chapman, 1994a, 1994b). NE condition assessment uses a concentrated survey of replicated, small quadrats placed only on level substrata within relatively small areas of a specific, predetermined habitat (Northen and Doggett, 2019), and so seems likely to encounter fewer taxa than one that moves across the habitat, even if the total sampling time is similar. This can explain the greater mean number of taxa per sample (Figure 10) and the steeper rate of species accumulation (Figure 3) in Seasearch records of infralittoral rock but does not explain the lack of difference for circalittoral rock. The large number of taxa in the SIMPER analyses, each making small contributions to the overall dissimilarity does indicate that differences in composition were truly multivariate and not influenced by a tendency for one organisation to record (or mis-identify) one or two taxa that are missed by the other. Methodological differences may, however, explain some of the differences in composition. Focussing down in a restricted area (NE) is less likely to allow observation of larger, more mobile taxa than is a more exploratory survey method (Seasearch). This is consistent with shade plots for circalittoral rock showing the presence of fish, echinoderms, sea fans and mobile Crustacea, in Seasearch records, but not in those from NE (Figure 9, Figure 13). In infralittoral samples, NE records included some molluscan taxa missing from Seasearch records, which may be more likely to be observed during a rigorous search of a small area than during the Seasearch method. Some taxa may be encountered so frequently by Seasearch surveys (e.g. *Patella*), that they are not considered of interest and so not recorded.

Alternative explanations

Alternative or additional explanations for observed differences include:

i) Different sampling windows. Seasearch records come from over multiple years, whereas for each habitat data were collected by NE in only a single year. Differences observed may reflect annual variation in assemblages.

ii) Different sampling locations. NE and Seasearch often sampled in different locations with the SAC (Figure 7, Figure 12) and hence may have been sampling fundamentally different assemblages.

iii) Different sub-habitats. The coarse classification of habitat will add large amounts of noise to the data. For instance, the EUNIS level 2 classification of circalittoral rock contains numerous sub-levels, each with its own characteristic assemblage of species. If samples from different organisations happened to be from different sub-levels (quite likely when sample effort by at least one group is small) then this can create apparent differences within the parent habitat. The sentinel monitoring approach uses a subset of locations with a sub-feature, which are selected to be representative of the sub-feature as a whole within an MPA. If selected locations are not actually representative, then would not be surprising for those data to appear different from a broader sampling of that sub-feature. This explanation could be particularly pertinent for infralittoral reef, where condition assessment data are depauperate in comparison with those from Seasearch.

Whilst doing analyses at such a coarse level is clearly problematic, it is at this level for which data and monitoring are required by legislation. Analysing records from more finely resolved habitats would also reduce the amount of data (and hence power) available.

The habitat-specific differences in richness and the consistent marked differences in composition recorded by NE and Seasearch and between the inner and outer Sound certainly indicate that the benthic diversity observed depends heavily on where and how it is sampled. Each Seasearch dive probably covers a greater area of seabed, but arguably less thoroughly, than does a NE dive. Total sampling effort (i.e. number of samples) by Seasearch is also considerably greater than by NE (see labels on bar plots of taxon richness). Coverage of each habitat and the range of taxa present is consequently greater by Seasearch than by NE and could be considered to give a better overall impression of benthic diversity. The less-structured, *ad hoc* nature of Seasearch recording may, however, preclude some analyses that require replication and a more formal experimental design. Structured surveys by Natural England give greater detail limited about extents of specific, targeted biotopes in known locations, but are likely to miss large, mobile taxa or those that occur on steeply sloping substrata.

Assemblages through time

α-diversity

Aside from in the Berwickshire and North Northumberland Coast SAC, there was little evidence of consistent differences in diversity of assemblages from either habitat between 2009-13 and 2014-19. With the exception of Pielou's evenness, diversity recorded in this MPA was consistently greater in 2014-19 than in 2009-13 (Table 8g). In contrast with this pattern, greater evenness (i.e. greater diversity reflected through more equable numeric distribution of taxa) was observed in the earlier than in the later period, although this difference was significant only for circalittoral rock. Although significant, differences in Simpson diversity and evenness were very small. Estimates of evenness were also very large, (in all cases close to the maximum of 1, Table 8) with very small variance, which may cast some suspicion on suitability of transformed SACFOR data for this index.

Recording of benthic taxa might be expected to improve through time (e.g. through having a larger pool of trained surveyors, with surveyors building experience, availability of better identification guides and increasing availability of underwater cameras), potentially revealing increases in recorded diversity that are not a function of actual change in benthic assemblages. If this was the case, we would expect to see similar patterns in each MPA. This did not happen. Thus, the greater diversity observed in Berwickshire and North Northumberland Coast SAC during 2014-19 than in 2009-13, must be better explained by either a consequence of different sampling effort between these periods, a change in locations or sub-habitats (and hence assemblages) surveyed between the two periods, an actual change in benthic diversity, or some, as yet unconsidered mechanism. The presence of varying patterns of temporal differences in different MPAs indicates that Seasearch data are (at least with the survey effort applied) able to detect effect-sizes actually present. Other MPAs with greater (e.g. Scilly Isles) or lesser (e.g. Plymouth, Fal and Helford) survey effort showed no differences, giving credence to observed patterns being real, although the power of the analyses to detect differences of a particular size is not yet known.

Examination of the distributions of records in the English portion of the Berwickshire and North Northumberland Coast SAC (Figure 22) shows that, for each habitat, there was little difference in the coarse distribution of samples between the two periods of time (i.e. clustered around the Farne islands and Alnmouth). Although not attempted here, it is theoretically possible to extract from the full Seasearch records, some information about the sub-habitats sampled. This could indicate whether sub-habitats sampled differed between the time-periods, potentially explaining the observed ‘increase’ in α-diversity. Further exploration of mechanisms to explain the consistent observed increases in diversity for the Berwickshire and North Northumberland Coast SAC would be entirely speculative and are not attempted here but may provide a focus for future survey effort.

Statistical power

The ability (power) of a programme of data collection to detect change or differences depend on the number of samples collected, the natural variability of the system being surveyed and the effect size i.e. the magnitude of the change or difference occurring (Wilding *et al.*, 2015). Statistical power is the probability that data from surveys will detect a real, statistically-significant difference between groups despite natural variability. In systems with small variability, only small amounts of sampling are necessary to detect large differences or changes, while the reverse is true when variability is great. Reliable detection of effects in variable systems can be challenging (Di Stefano, 2001), because statistical power is small.

Where power analyses are done prior to the study, the sampling effort required can be calculated in order to find a stated effect-size given a known level of natural variability. Required sampling effort can then be costed relative to funds available and the scope of the work or accepted effect-size adjusted accordingly. As is more likely with wider, citizen science programmes (like Seasearch) or where data are combined from different programmes for reasons other than the original intentions, such details are not known *a priori*. If subsequent analyses show significant differences, interpretation can be straight-forward, but where no differences are found, it is not clear whether there are truly no differences or whether the analysis simply did not have the power to detect the real effect-size present.

Whilst the concept of effect-size is relatively straightforward for univariate measures (e.g. α-diversity indices), the choice of effect-size to be detected (decided *a priori*) may not be. It may be influenced by choice of variable, the type of change to be measured and potentially legislation that requires change of a particular magnitude. It may also be difficult to find reasons to justify the choice of magnitude. It is more complex to understand what is meant by effect size for multivariate comparisons. At present, there is a lack of well-established guidance for how to decide on an appropriate magnitude of change or difference in studies on marine biodiversity (Kröger and Johnston, 2016).

Sample size and confidence

Differences in sample size in data from the two periods of time raised questions about the validity of outputs from Welch's t-tests (i.e. patterns may be a function of sample effort rather than reality). Permuted tests of equal sample-size showed that in most cases (blue text Table 9 & Table 10), the mean permuted value of *t* gave the same answer (i.e. was the same side of the critical value for significance) as the value of *t* from the original test with unequal sample sizes. This provides some confidence for the notion that observed patterns are likely to reflect reality than be the consequence of different survey effort. In some cases (red text Table 9 & Table 10), 95% of the permuted values of *t* were the same side of the critical value as the original test, providing very strong evidence that patterns were real and not an artefact of sample size. Where the distribution of permuted *t* overlapped the critical value (i.e. in some instances the result was significant and in others not), there remained some question about whether unbalanced sample-sizes contributed to patterns observed.

The scoring system developed, which combined sample-size and the outcomes of the permuted tests with equal sample-size, was used to give some assessment of confidence in the patterns observed. Incidences of test outputs with a 'low' confidence rating were few (Table 22 & Table 23). Having equal sample-sizes should remain an aspiration for analyses of benthic diversity. Where this is not the case, the tendency observed here, for differing sample-size to not affect the outcome of tests gives reason to make the most of all existing data and do analyses, even when sample-sizes differ.

Confidence ratings were not influenced only by the overall number of samples. For example, there were instances of high confidence with relatively small sample-sizes (e.g. 11, Fal & Helford, circalittoral, Shannon) and instances of low confidence with quite large samples (e.g. 23, Plymouth, infralittoral, Simpson).

Using a larger minimal sample-size in future analyses would make it less likely that comparisons could be made with existing data (i.e. minimal requirements not met), but would tend to elicit greater confidence ratings if a larger minimal sample-size was used. This would make it more difficult to justify comparisons between different sources of data, where one has a relatively small amount of survey effort. In the absence of clear guidance about effect sizes for biodiversity studies, approaches using confidence ratings like this could be used in order to decide on an appropriate level of sampling effort for condition assessments or other monitoring objectives.

β-diversity

Differences in composition of assemblages were somewhat more apparent in circalittoral habitat (five of seven MPAs) than in infralittoral habitat (three of seven), although this was partly determined by different numbers of MPAs with insufficient data for analysis (Table 11 & Table 17).

Of interest, given consistent increases in α-diversity in the Berwickshire and North Northumberland Coast SAC, was the absence of any difference in assemblage composition in circalittoral habitat in this MPA. This suggests that observed increases in taxon richness and other diversity indices were likely caused by more rare, infrequently recorded taxa, that were excluded from the multivariate analyses of the 50 ‘most important’ taxa. This re-emphasises the value of doing multiple analyses with different indices to build a complete picture of diversity.

In each case where significant differences were detected, the species contributing to the dissimilarity among times were several (not just one or two taxa differing strongly between times; Table 12 to Table 16 and Table 18 to Table 20). The taxa driving the dissimilarities differed with MPA, although there were some commonalities among MPAs in the south-west. The lack of consistent pattern in contribution of taxa (e.g. *C. smithii*) to dissimilarities between time-periods suggests either regional variation in environmental conditions or disturbances rather than the same process acting throughout the south-west. There was little or no overlap in species contributing to dissimilarities between the Solent Maritime SAC and the MPAs in the south-west. This is perhaps not surprising due to the Solent MPA being in a different biogeographic region with rather different environmental conditions.

Of the MPAs selected because of the need for information to support condition assessment (Isles of Scilly Complex SAC, Berwickshire and North Northumberland Coast SAC and Essex Estuaries SAC), extensive Seasearch surveys over the last 11 years for the first two, can provide great detail about diversity that would otherwise not be available. Very few data have been collected for the Essex Estuaries SAC and there must be a strong case to develop and implement plans to rectify this deficit.

The Solent Maritime SAC and the Fal and Helford SAC were selected to provide information to support the LIFE Recreation ReMEDIES project, which focuses on distribution and restoration of seagrass beds and maerl habitats on the south coast. The work presented here indicate that in neither MPA has there been enough sampling effort in seagrass habitat to be able to make meaningful analyses of diversity. Maerl habitats were outside the scope of this report. The small amount of data should act as stimulus for additional sampling and at the least, provide some signposts to where might benefit most from survey effort.

Although not formally tested, amounts of diversity (in terms of taxon richness) in the MPAs selected, conformed partly with expectations, at least for circalittoral habitat (Figure 14). The greatest richness was recorded in the Isles of Scilly Complex SAC (possibly a consequence of enormous sampling effort) and all the south-western MPAs had greater richness than those further east. Diversity in the Isles of Scilly Complex SAC may provide a standard against which other MPAs can aim, showing the levels of richness that might be attained with more effective management and protection. For infralittoral rock, this pattern did not hold. The MPA with the greatest infralittoral richness was Essex Estuaries SAC (Figure 15f), but with only very small survey effort (only 7 samples from the entire 11 years). Much more data would be required before anything more concrete could be concluded in relation to patterns of diversity hotspots set out by Hiscock & Breckels (2007).

Future work

The Seasearch dataset could be used in the future to test hypotheses about presence or abundance of individual taxa or of diversity indices (α-diversity) or about composition of assemblages (β-diversity). This could be additional comparisons with data from other providers (e.g. conservation agencies, Wildlife Trusts, etc.) or using different components of the Seasearch dataset.

Some specific tasks might be to:

1) Assess whether observed differences in diversity (e.g. for Berwickshire and North Northumberland Coast SAC between 2009-13 and 2014-19 for circalittoral or infralittoral rock) were associated with differences in the actual sub-habitats sampled. It would also be possible to do the same when comparing records from Seasearch or NE.
2) Calculate SACFOR scores for NE data, such that measures of taxon abundance are comparable to Seasearch records.
3) Use outputs of SIMPER analysis to identify those species that contribute most to dissimilarity between time-periods. Apply Bayesian occupancy models to data for these species to investigate trends in population size through time. Taxa of particular interest might be *Caryophyllia smithii* and *Echinus esculentus*.
4) Explore potential reasons for the increases in benthic diversity observed in the Berwickshire and North Northumberland Coast SAC.

5) Include analyses of functional diversity based on species traits (Schleuter *et al.*, 2010). Observational studies on taxonomic diversity can reveal differences and changes in structure of assemblages, but they can not be used to infer causal relationships between those assemblages and environmental features (Menezes, Baird and Soares, 2010). Greater knowledge about differences or changes in how assemblages function can inform us more about their responses to changes in the environment.

Conclusions

The UK biodiversity monitoring strategy (Kröger and Johnston, 2016) recognises the challenges posed by the diversity of data providers. Studies such as this, handling data from different providers, clearly make progress in the direction of an integrated marine biodiversity monitoring scheme.

An objective of NE sentinel monitoring is to provide the context to distinguish directional trends from short-scale variability in space and time by representing variability across space at any one time and documenting changes over time. One aim of the present study was to assess whether citizen science records from Seasearch might contribute to this. Confidence ratings and the detection of different patterns of change in benthic diversity through time for selected MPAs suggest that analyses of Seasearch data for this purpose can provide understanding of changes in circa- or infra-littoral benthic diversity. In the absence of other data, Seasearch records should be used to provide useful information about differences in benthic assemblages among locations or about changes through time.

Data about diversity of benthic assemblages on circalittoral or infralittoral rock in the Plymouth Sound and Estuaries SAC often differed depending on whether it had been collected by Seasearch or by Natural England. Reasons for these differences within a habitat, were probably a combination of effects, such as collecting data with a different method, over different time-frames, in different places and potentially in different sub-habitats. These confounding effects make it difficult to be sure whether either organisation collects data that best represents the status of the conservation feature ‘rocky reefs’. Differences (for uni- or multivariate analyses) between methods tended to be more obvious than for most comparisons between period of time. It is clear that Seasearch data are not analogous to those from condition assessment surveys and that the two methods are representing different facets of benthic diversity.

The NE methodology using replicated quadrats and structured experimental design can give detailed information about the common, sessile or sedentary taxa at a small number of sites (and probably sub-habitats). Seasearch records (being recorded by more exploratory surveys, with greater temporal and spatial extent) consistently gave larger values for species accumulation curves, and total number of taxa recorded, and tended to show assemblages including mobile and rare taxa. Where different recording strategies have a tendency to detect different taxa, choice of strategy will be influenced by any or all of the following: ease of execution, cost, volume of data generated, the goods and services provided by the taxa recorded, inclusion of designated features or the presence of taxa that act as indicators. Depending on need, the optimal solution for gaining the most complete description of diversity in features of conservation importance may well be to combine multiple methods when surveying and multiple indices when analysing data.

With the exception of the Berwickshire and North Northumberland Coast SAC, in the MPAs studied, there was little evidence for change in diversity indices between 2009-13 and 2014-19. In contrast, in most cases, multivariate analyses showed significant differences in composition of assemblages between the two time periods. The taxa driving these differences were numerous (i.e. truly multivariate), and varied among MPAs, but with some common elements among the MPAs in the south-west. Use of a confidence metric, such as that implemented here, may prove useful in judging the outcomes of comparisons of datasets with differing sample effort.

Very little data exist on seagrass habitats in the MPAs selected. Future surveys, in conjunction with research projects such as ReMEDIES, should be planned to ensure that this deficiency is resolved.

Where conservation agencies are legally obliged to survey features of conservation interest, but where data are challenging to collect (due to limited personnel, finances, time, etc.), records collected by trained volunteer divers and curated by Seasearch may be able to go some way to filling gaps. Condition assessments by conservation agencies are required only every six years (Williams, 2006). Considerable change may occur during the interval and having other mechanisms, such as Seasearch surveys, may be valuable in allowing early detection of any change.

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Appendix 1. Seasearch quality control.

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))

Appendix 2: Contributions to % dissimilarity from Circalittoral rock

Table 24. Dissimilarity contributions of taxa between samples collected by Seasearch or NE (irrespective of position in the Sound).

Species	Av.Abund NE	Av.Abund Seasearch	Av.Sim	Sim/SD	Contrib%	Cum.%
Spirobranchus	0.83	0.31	3.16	1.43	5.22	5.22
Aglaophenia	0.67	0.19	2.64	1.16	4.36	9.59
Holothuria forskali	0.00	0.42	2.33	1.08	3.86	13.44
Bugula	1.00	0.42	2.31	0.98	3.82	17.26
Alcyonium digitatum	0.50	0.69	2.31	1.03	3.81	21.08
Halecium	0.50	0.50	2.28	1.05	3.76	24.84
Necora puber	0.00	0.54	2.27	1.03	3.75	28.59
Drachiella	0.50	0.23	2.19	0.96	3.61	32.20
Cliona	0.42	0.69	2.14	0.97	3.54	35.74
Cellaria	0.42	0.23	2.03	0.98	3.36	39.10
Clavelina lepadiformis	0.33	0.50	2.03	0.95	3.35	42.44
Nemertesia	0.67	0.73	1.90	0.82	3.13	45.58
Morchellium argus	0.42	0.27	1.73	0.81	2.86	48.43
Halichondria	0.33	0.23	1.73	0.86	2.86	51.29
Diplosoma	0.50	0.19	1.58	0.70	2.61	53.90
Sertularella	0.33	0.23	1.54	0.77	2.54	56.44

Species	**Av.Abund NE**	**Av.Abund Seasearch**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Labrus mixtus	0.00	0.23	1.51	0.65	2.49	58.93
Crisia	0.00	0.27	1.44	0.71	2.38	61.31
Eunicella verrucosa	0.00	0.35	1.36	0.70	2.25	63.56
Caryophyllia smithii	0.58	0.69	1.26	0.62	2.08	65.65
Cancer pagurus	0.00	0.31	1.23	0.67	2.03	67.68
Aslia lefevrei	0.00	0.27	1.21	0.67	1.99	69.67
Marthasterias glacialis	0.58	0.69	1.20	0.62	1.97	71.64

Table 25. Dissimilarity contributions of taxa between samples collected from the inner or outer sound (irrespective of organisation).

Species	Av.Abund Outer	Av.Abund Inner	Av. Diss	Diss/SD	Contrib%	Cum.%
Amphilectus fucorum	0.15	0.83	2.75	1.38	3.97	3.97
Antedon bifida	0.00	0.67	2.57	1.33	3.72	7.70
Calliostoma	0.05	0.67	2.37	1.23	3.43	11.13
Holothuria forskali	0.50	0.06	2.31	1.32	3.35	14.48
Marthasterias glacialis	0.90	0.39	2.29	1.06	3.31	17.78
Raspailia ramosa	0.05	0.61	2.26	1.13	3.26	21.05
Suberites	0.05	0.61	2.23	1.17	3.23	24.28
Caryophyllia smithii	0.90	0.39	2.21	1.06	3.20	27.48
Halecium	0.45	0.56	2.10	1.05	3.04	30.52
Cliona	0.45	0.78	2.02	0.94	2.92	33.44
Clavelina lepadiformis	0.55	0.33	1.96	1.02	2.83	36.27
Alcyonium digitatum	0.60	0.67	1.88	0.90	2.73	38.99
Halichondria	0.15	0.39	1.85	0.88	2.68	41.67
Morchellium argus	0.50	0.11	1.80	0.96	2.60	44.27
Nemertesia	0.60	0.83	1.78	0.86	2.57	46.85
Diplosoma	0.55	0.00	1.76	0.89	2.54	49.39
Spirobranchus	0.50	0.44	1.63	0.88	2.36	51.75

Species	Av.Abund Outer	Av.Abund Inner	Av. Diss	Diss/SD	Contrib%	Cum.%
Bugula	0.75	0.44	1.63	0.87	2.35	54.11
Labrus mixtus	0.30	0.00	1.61	0.80	2.32	56.43
Necora puber	0.35	0.39	1.57	0.81	2.27	58.70
Cellaria	0.30	0.28	1.53	0.81	2.21	60.91
Urticina felina	0.05	0.39	1.51	0.77	2.18	63.09
Crisia	0.30	0.06	1.48	0.82	2.14	65.23
Drachiella	0.35	0.28	1.44	0.76	2.09	67.32
Sycon ciliatum	0.10	0.39	1.40	0.79	2.03	69.34
Eunicella verrucosa	0.20	0.28	1.40	0.75	2.02	71.37

Appendix 3: Contributions to % dissimilarity from Infralittoral rock

Table 26. Dissimilarity contributions of taxa between samples from infralittoral rock collected by Seasearch or NE (irrespective of position in the Sound).

Species	Av.Abund NE	Av.Abund Seasearch	Av.Sim	Sim/SD	Contrib%	Cum.%
Mastocarpus stellatus	0.77	0.00	4.07	1.61	4.91	4.91
Patella pellucida	0.69	0.00	3.97	1.40	4.79	9.70
Patella	0.69	0.00	3.83	1.41	4.62	14.32
Delesseria sanguinea	0.00	0.63	3.50	1.30	4.23	18.55
Himanthalia elongata	0.69	0.21	3.40	1.13	4.11	22.66
Corallina	0.62	0.24	3.38	1.11	4.08	26.74
Marthasterias glacialis	0.00	0.50	3.16	1.15	3.82	30.56
Labrus bergylta	0.00	0.53	3.08	1.09	3.72	34.28
Steromphala	0.54	0.18	2.99	1.07	3.62	37.90
Anemonia viridis	0.00	0.45	2.74	1.04	3.31	41.21
Cliona	0.00	0.42	2.71	1.01	3.27	44.48
Dilsea carnosa	0.08	0.50	2.62	0.94	3.16	47.65
Laminaria	0.77	0.61	2.53	0.85	3.06	50.71
Spirobranchus	0.38	0.24	2.41	0.83	2.91	53.62
Botryllus schlosseri	0.38	0.08	2.28	0.82	2.76	56.37

Species	Av.Abund NE	Av.Abund Seasearch	Av.Sim	Sim/SD	Contrib%	Cum.%
Membranipora membranacea	0.23	0.37	2.22	0.81	2.68	59.06
Electra	0.46	0.45	2.18	0.77	2.64	61.69
Ulva	0.38	0.21	2.12	0.74	2.57	64.26
Obelia	0.08	0.37	1.95	0.76	2.36	66.61
Gobiusculus flavescens	0.00	0.29	1.89	0.71	2.28	68.90
Cancer pagurus	0.00	0.34	1.85	0.70	2.23	71.13

Table 27. Dissimilarity contributions of taxa between samples from infralittoral rock collected from the inner or outer Sound (irrespective of the organisation doing the collecting).

Species	Av.Abund Outer	Av.Abund Inner	Av.Sim	Sim/SD	Contrib%	Cum.%
Electra	0.65	0.24	3.00	1.09	4.30	4.30
Cliona	0.46	0.16	2.81	1.09	4.02	8.32
Anemonia viridis	0.46	0.20	2.80	1.06	4.01	12.33
Marthasterias glacialis	0.50	0.24	2.79	1.06	4.00	16.33
Labrus bergylta	0.42	0.36	2.50	0.90	3.57	19.90
Laminaria	0.62	0.68	2.49	0.88	3.57	23.47
Corallina	0.50	0.16	2.47	0.89	3.54	27.01
Dilsea carnosa	0.35	0.44	2.40	0.89	3.43	30.44
Membranipora membranacea	0.42	0.24	2.36	0.91	3.38	33.83
Saccharina latissima	0.04	0.44	2.36	0.89	3.38	37.20
Delesseria sanguinea	0.46	0.48	2.30	0.83	3.30	40.50
Gobiusculus flavescens	0.31	0.12	2.26	0.83	3.23	43.73
Obelia	0.27	0.32	2.11	0.84	3.03	46.76
Bispira volutacornis	0.31	0.16	2.09	0.84	3.00	49.76
Ulva	0.12	0.40	2.06	0.75	2.95	52.70

Species	Av.Abund Outer	Av.Abund Inner	Av.Sim	Sim/SD	Contrib%	Cum.%
Cancer pagurus	0.23	0.28	2.06	0.80	2.94	55.65
Spirobranchus	0.35	0.20	1.98	0.75	2.84	58.49
Heterosiphonia plumosa	0.23	0.20	1.95	0.75	2.79	61.28
Himanthalia elongata	0.23	0.44	1.88	0.71	2.69	63.97
Saccorhiza polyschides	0.19	0.20	1.83	0.71	2.63	66.60
Steromphala	0.27	0.28	1.65	0.68	2.37	68.97
Calliostoma	0.08	0.24	1.54	0.61	2.20	71.17

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