



ORIGINAL ARTICLE

Spatial and temporal patterns of bryozoan distribution and diversity in the Scottish sea regions

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Abstract

Diversity and distribution patterns of sessile benthic fauna over space and time are often incompletely known. Understanding the factors that govern these patterns is important for informing marine spatial planning, and monitoring the impacts of climate change and habitat alteration in the marine environment. Historical and contemporary records of bryozoans from Scotland were mapped to produce a GIS distribution layer and were assessed in conjunction with JNCC GIS benthic habitat layers. Bryozoans have predominantly been recorded from the west coast, Orkney, Shetland and Western Isle archipelagos. The greatest number of bryozoan species occurred in high energy, rocky environments; few species have been identified from the continental slope, which also has the least number of records. The biodiversity, as measured by the average taxonomic distinctness and variation in taxonomic distinctness, was assessed for sampling sites and sub-regions within Scotland. High values were concentrated around the Orkney Isles and Southwest Scotland. This is the first known attempt at a comprehensive analysis of changes in Northern European bryozoan diversity and distribution from the 1700s through to the present day, but overall temporal patterns remain uncertain due to differences in the availability of records through time. This study provides an example of the application of methods that may be used to assess benthic diversity to identify potential sites for marine conservation or marine protected areas. As benthic data layers improve, and sampling is extended to unstudied areas, greater insight into the relationship between the physical environment and diversity and distribution patterns of benthic fauna will be gained. This study serves as a baseline for long-term monitoring of biodiversity changes in this poorly studied Phylum.

Introduction

Understanding the factors governing the distribution and spatial patterns of biodiversity of benthic organisms is vital for assessing and mitigating against anthropogenic impacts to the ocean. The lack of local faunistic inventories and limited information on historical biodiversity often prevents rigorous assessments of spatial and temporal changes. Inconsistencies in sampling effort and quantification of abundance make comparisons between geographic regions and time periods difficult.

Bryozoans are sessile colonial invertebrates that inhabit all of the world's oceans and are abundant on rocky shores. They play a significant role in marine ecosystems through contributions to temperate and tropical carbonate sediments (Maxwell 1968; Nelson *et al.* 1988); provision of food sources for other marine species (Lidgard 2008); and provision of three-dimensional structures, attachment surfaces and nursery grounds for other marine species, including some of commercial importance (Bradstock & Gordon 1983). More recently, bryozoans have been recognised as a valuable source of bioactive

compounds (Narkowicz *et al.* 2002; Lopanik *et al.* 2004; Sharp *et al.* 2007).

Previous studies of diversity and distribution

The diversity and distribution of bryozoans have been assessed previously in New Zealand (Rowden *et al.* 2004), Australia (Gordon 1999), the North Atlantic (Clarke & Lidgard 2000), the Southwest Atlantic (López Gappa 2000) and areas of the British Isles (Eggleson 1972; Grant & Hayward 1985). Factors influencing the distribution and diversity have been shown to include: substrate availability (Eggleson 1972), habitat heterogeneity (Clarke & Lidgard 2000), hydrodynamic factors such as current strength and tidal streams (Eggleson 1972), temperature (Ryland 1963) and depth (Grant & Hayward 1985). In addition to these patterns, it has been suggested that the distribution and diversity of bryozoans may reflect that of other benthic marine species (Schopf 1969; López Gappa 2000) and hence bryozoans may serve as a useful indicator taxon for selecting areas to protect marine biodiversity (Rowden *et al.* 2004).

Most previous work on bryozoan diversity has considered either species richness or evenness, or a combination of these (Clarke & Lidgard 2000; López Gappa 2000). As indices of biodiversity, both measures may disregard many aspects such as the diversity of ecosystem functions provided by the biological community (functional diversity) (Hooper *et al.* 2002) and the taxonomic spread of individuals contributing to the assemblage. Species richness, furthermore, may not respond to environmental degradation monotonically, and may in fact increase under moderate levels of disturbance (Wilkinson 1999). These indices are heavily biased by sampling effort and any variation in the methods used to estimate the abundance of colonial species. The use of these methods frequently results in exclusion of historical species lists due to a poor or unknown sampling effort, yet such lists may serve as a vital source of data on past faunal conditions and can greatly assist in the assessment of biodiversity (Ponder 1999).

There has been an increasing move towards assessing biodiversity using information on the relatedness of species (Clarke & Warwick 1998). Two indices that reflect the phylogenetic relationships are the average taxonomic distinctness of species (AvTD) (Warwick & Clarke 1995) and the variation in taxonomic distinctness (VarTD) (Clarke & Warwick 2001). These indices overcome many of the problems associated with species richness and evenness, and Clarke & Warwick (2001) claim that they provide a robust measure of biodiversity, with low values reflecting degraded environments and high values in pristine environments. They can be used in conjunction with

presence/absence data and allow for the inclusion of historical species lists in biodiversity assessments. Both indices were used in the present study to evaluate the diversity of bryozoans from Scottish sea regions.

Objectives

The aim of this study was to assess the distribution and diversity of bryozoans in Scotland in relation to spatial and temporal patterns.

This study has the following objectives:

- 1 To study the distribution of Bryozoa in Scotland and investigate the relationship(s) between the distribution and the physical characteristics of the area.
- 2 To establish the average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD) as indices of bryozoan biodiversity in Scotland and Scottish sub-regions.
- 3 To investigate temporal patterns in bryozoan diversity in Scotland.

The wider implications of this study include contributing to the assessment of the current state of UK seas as required by the EU Marine Strategy Framework Directive, and providing baseline data on Scottish bryozoans, against which changes can be monitored. In the long-term, such data may be used to inform marine spatial planning and the conservation of the Scottish marine environment as required by the Marine (Scotland) Act 2010. This study will form the basis of a much wider project on bryozoan diversity in Britain and Ireland.

Study Area

Scottish bryozoans were defined as occurring from 54°38' 2" N to 60°51'38" N and from 0°46'50" W to 13°40' 13" W.

Sources

Historical records were obtained from the Bryozoa collection at the Natural History Museum, London. The collection includes records from the dredging surveys commissioned by the British Association for the Advancement of Science throughout the 1860s; records from the expedition of HMS *Porcupine*, which visited Shetland in the summer of 1869; the collections of Rev. A. Norman; and the collections of George Barlee, among other historical Scottish records. Contemporary records were sourced primarily from the reports of the Marine Nature Conservation Review (MNCR), which sampled the marine fauna of the UK between 1987 and 1998 (Hiscock 1996). Additional records were sourced from selected literature, a field survey conducted in Orkney

between 26 and 30 June 2010 and the National Biodiversity Network gateway (which includes data collected by the Joint Nature Conservancy Council (JNCC); Scottish Natural Heritage (SNH); MarLin; Seasearch and private contract surveys) (Table 1). Records from North Liverpool Bay were included due to their proximity to the Scottish border.

Records for which the location was uncertain or not provided, and/or the species seemed likely to be wrong, based on its generally accepted distribution (e.g. tropical or Antarctic), were not used. Other records that had only been documented in Scotland by one source, with an unknown or non-expert identifier, were also excluded from all analyses. Incomplete records (no information on the date of collection or not identified to species level) or those based on unpublished data where the methods and identifier were unknown, were included in the distribution analysis but excluded from the diversity analysis.

Material and Methods

Data on location, date of collection, and depth were extracted from the records. All records were adjusted to modern taxonomic usage, using the *Synopses of the British Fauna* (Hayward 1985; Hayward & Ryland 1985, 1998, 1999), the World Register of Marine Species (WoRMS) and through personal communication with M. Spencer Jones (curator of Bryozoa at the NHM). Depth data were converted to metres below chart datum, and the average depth taken for sites sampled at a range of depths. Intertidal records were assigned a depth of 0 m, as most bryozoan species are found in the mid- to lower intertidal (excluding rock pools). This approach is consistent with other assessments of bryozoan diversity (e.g. Rowden *et al.* 2004). Sampling methods for the data vary, and include collections made by hand in the intertidal and via SCUBA diving, dredges, grabs and trawls in the subtidal.

Table 1. Sources of Scottish bryozoan records.

Source	References
MNCR	Bennett (1989); Connor (1989, 1990, 1991); Covey (1990); Davies (1989a,b,c, 1990, 1991); Hiscock & Covey (1991); Holt & Davies (1991); Howson (1989a,b, 1990, 1991)
NBN gateway	www.nbn.org.uk
Literature	Chumley (1918); De Kluijver (1993); Souto <i>et al.</i> (2007)
Synopses	Hayward (1985); Hayward & Ryland (1985, 1998, 1999)
Museum Collections	Natural History Museum, London

Distribution analysis

Records were mapped with ARCMAP version 9.2 to produce a GIS bryozoan distribution layer for Scottish sea regions. Species presence was examined in conjunction with other GIS layers on substrate, energy and biozone; these were obtained from the predictive MESH-EUNIS model of the Mapping the European Seabed Habitats (MESH) project. For a full explanation of the MESH-EUNIS layers, see Coltman *et al.* (2008).

Biodiversity analysis

Two indices of biodiversity (AvTD and VarTD) were calculated for all sampling sites with 10 or more bryozoan species. Average taxonomic distinctness is a measure of the average path length between every pair of species in a sample, traced through a taxonomic tree (Clarke & Warwick 1998). It represents the degree to which the species in a sample are taxonomically related. The AvTD index of biodiversity assumes that there is an increase in taxonomic distinctness with increasing environmental stability, and that in perturbed situations, communities are held in an early successional stage with an assemblage of closely related species (Warwick & Clarke 1995). Variation in taxonomic distinctness is a measure of the degree to which taxa are evenly or unevenly spread across the full taxonomic tree (Clarke & Warwick 2001). The index represents the variance of the path lengths connecting every pair of species in a sample.

The main advantage of using these indices is that they are not, on average, dependent on sampling effort, unlike many other commonly used measures of biodiversity (Clarke & Warwick 1998). This independence allows for comparison across studies with differing and uncontrollable degrees of sampling effort, as is the case with the current dataset. In particular, the sampling effort for the historical data is uncertain and many records represent diffusely collected, single specimens. However, a small bias is manifested at very low species numbers (Clarke & Warwick 1998, 2001); therefore, only sites with 10 or more species were included in the analyses. This led to the exclusion of many of the historical bryozoan records. To overcome this problem and utilise all available data, records were also classified into one of 12 sub-regions, primarily defined according to the MNCR coastal sectors with additional regions defined at Rockall, St. Kilda and an east coast offshore region (Fig. 1). The AvTD and VarTD were then calculated for each Scottish sub-region.

The relative importance of local (ecological) and regional (evolutionary) factors in determining the biodiversity of bryozoans at any one location was assessed. If

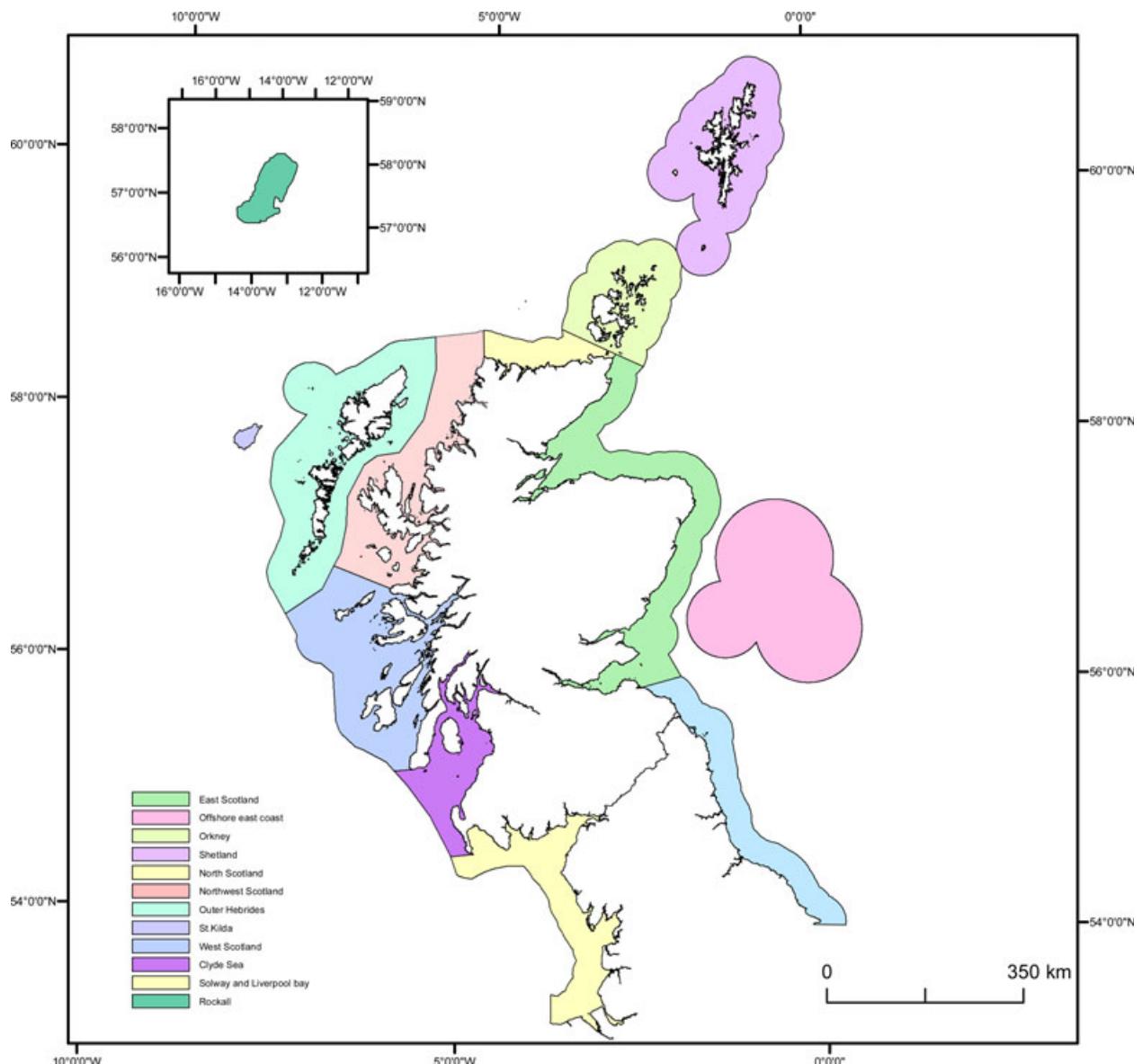


Fig. 1. Scottish sub-regions used for biodiversity and distribution analysis of bryozoans. Regions are based on the MNCR coastal sectors with additional regions defined at Rockall, St. Kilda and an east coast offshore region.

evolutionary mechanisms are responsible for the biodiversity in an area, it would be expected that the species assemblage at that location is merely a random selection of species from the regional species pool (Clarke & Warwick 1998). The observed AvTD and VarTD for Scottish sites were plotted as points on a probability funnel, which shows the mean (expected) AvTD/VarTD and 95% probability intervals. The expected mean and probability intervals were calculated from 1000 random selections of n species (where n = the number of species present at the sample site) from the regional species pool. Where the observed values fall outside of the 95%

confidence funnel, the biodiversity represents a significant departure from the null distribution and suggests that local, ecological factors are modifying the expected biodiversity.

The taxonomic categories used to calculate AvTD and VarTD were: species, genus, family, suborder, order and class. The weightings of path lengths between hierarchical taxonomic levels were standardised, such that two species connected at the highest possible level were assigned a path of 100, with all steps between each level having equal weighting (Clarke & Warwick 1998). The tree for which the AvTD and VarTD are based should represent

the assumed regional species pool, from which bryozoans in Scottish sea regions are theoretically drawn. Deciding what constitutes a regional species pool can be problematic and is a drawback of the taxonomic distinctness method. It may be reasonably assumed that the species for Scotland would consist of Bryozoa present in the two biogeographic regions in which Scotland lies, the North Sea and the Celtic Sea (Spalding *et al.* 2007); however, a complete species list for these two areas was not readily available. To address this issue, a list of British bryozoans, compiled from *Synopses of British Fauna* (Hayward 1985) and from Hayward & Ryland (1985, 1998, 1999), and a list of Bryozoa from the Southern Irish Sea (Robinson *et al.* 2009) were defined as the regional species pool. This tree includes the majority of species expected from the North and Celtic Seas.

Records were grouped into five time periods (1792–1849, 1850–1950, 1950–75, 1975–2000, and 2000–2010). The AvTD and VarTD of each time period were calculated to investigate temporal patterns in bryozoan diversity.

Results

From a total of 17,371 records extracted from the various sources, 214 species of Bryozoa were identified from 3139 localities in Scottish sea regions. The species represented 121 genera belonging to 59 families across all the extant orders. The most commonly occurring species in Scotland is *Membranipora membranacea*, which has been recorded at 1266 locations. The earliest Scottish specimens were collected by Robert Brown in 1792, *Carbasea carbarea* from Leith (NHMUK 2011.1.28.1) and *Bugula plumosa* from Newhaven (NHMUK 2011.1.28.2) (Fig. 2).

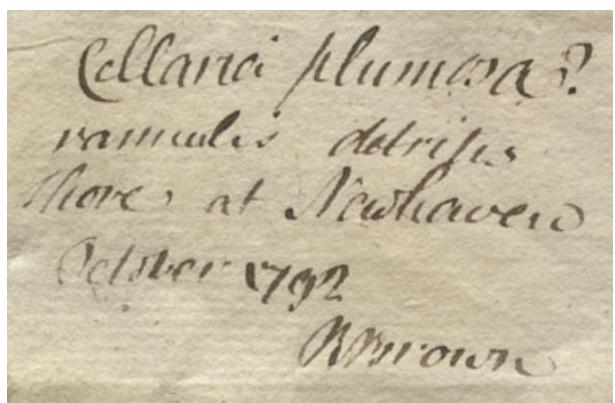


Fig. 2. A museum label identifying one of the earliest bryozoan specimens from Scotland 'Cellaria plumosa? ramulis detritus Shore at Newhaven October 1792 R Brown'.

Bryozoan distribution

Bryozoans have been recorded from all Scottish coasts and archipelagos (Fig. 3). The majority of records are from the west coast and in the Shetland, Orkney and Western Isles archipelagos, with notable gaps on the eastern and northern coasts. There are comparatively few bryozoan records from offshore areas. Figure 4 illustrates the distribution and intensity of sampling from the Marine Nature Conservation Review (from which the majority of bryozoan records were sourced). Sites are distributed throughout the entire Scottish sea region, but again there is an emphasis on the west coast, with fewer samples on the east and north coasts. The distribution of bryozoans in Scottish sea regions is mapped with GIS layers for biological zones (Fig. 5), energy levels (Fig. 6) and substrate types (Fig. 7). The majority of bryozoans have been recorded from the infralittoral to the deep circalittoral, with a few records from the slope close to Rockall (Table 2).

Spatial patterns of bryozoan diversity

A regression of AvTD against VarTD for all sites with 10 or more species indicates a significant positive linear correlation between the two indices ($y = 10.17x - 367.77$, $r^2 = 0.4347$, $P < 0.001$). The 95% probability ellipses for all sites with 10 or more species show broadly the same pattern for the VarTD (Fig. 8) and the AvTD (Fig. 9). In view of this correlation, it is only necessary to consider the AvTD biodiversity index from this point forward.

Figure 10 illustrates the measures of AvTD for sites with 10 or more species within the Scottish sea region. Values vary across the region from 45.08 in Loch Sween, West Scotland, to 70.51 in Sgeir Dhonncha, West Scotland. High values are particularly concentrated in Orkney and the southwest, whereas low values tend to occur in Shetland and between the Outer Hebrides and the mainland. Biodiversity appears independent of water depth, with intertidal sites and sites deeper than 100 m showing similar values of AvTD (Fig. 11).

Figure 12 shows the AvTD for each of the Scottish sub-regions, based on the combined bryozoans for each area. The AvTD for Scottish sub-regions varies over a narrow range. The highest value, 67.97, occurs in Rockall, followed by the Outer Hebrides, West Scotland and the Clyde Sea. North Scotland, Shetland and St. Kilda have the lowest values at 60.36, 60.80 and 60.80, respectively.

The results of the analysis to test whether the AvTD at any one site within Scotland is statistically different from the regional mean are displayed in Fig. 9. The majority of sites have a bryozoan composition representative of the region as a whole; however, a number of

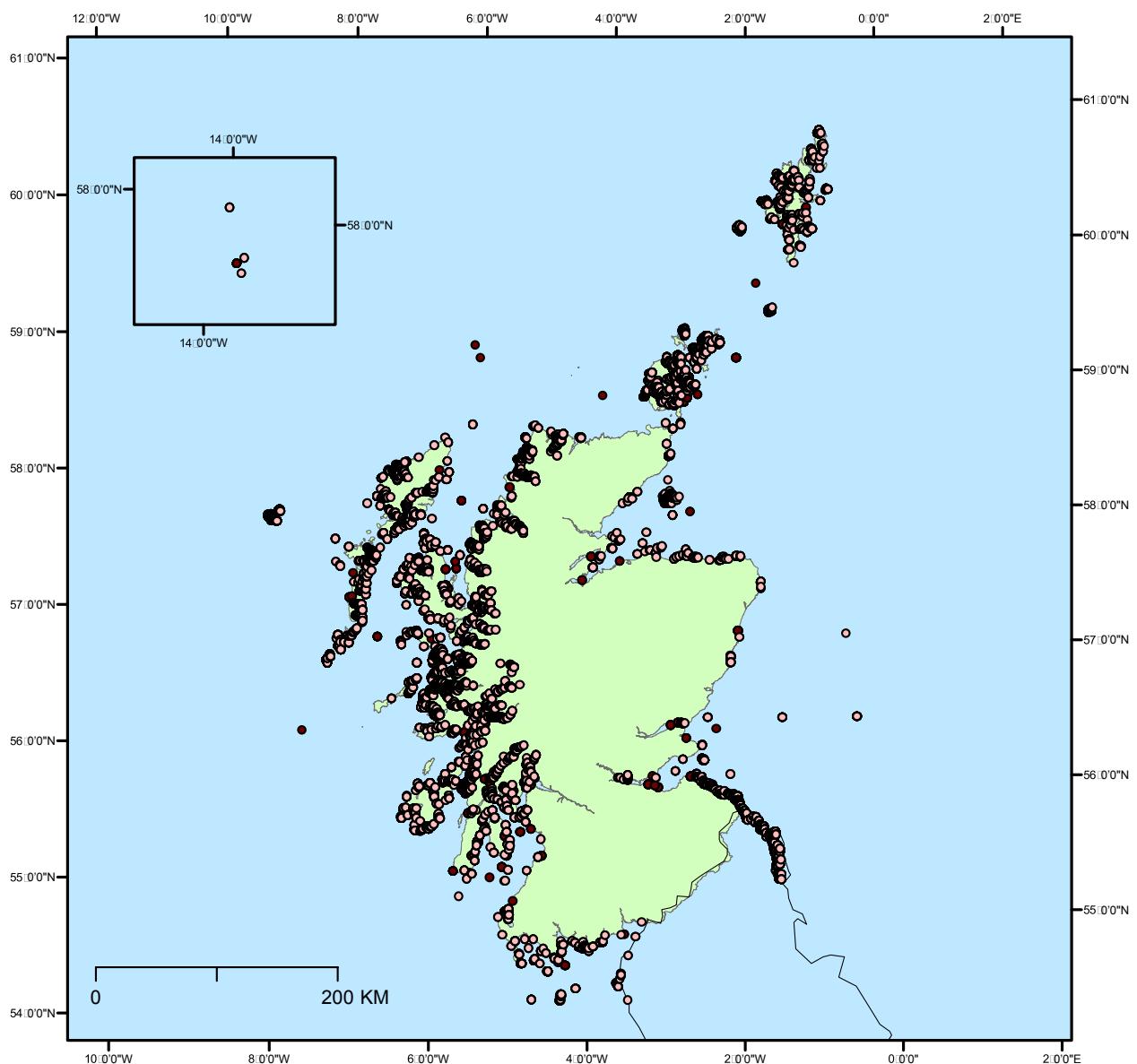


Fig. 3. Locations from which bryozoans have been recorded in Scotland. Records cover the timeframe 1792–2010 and were sourced from the NHM, the MNCR, the NBN gateway, selected literature and a field survey. Lighter circles represent precise records, whereas darker circles are an approximate location. Inset showing Rockall.

sites show a significant departure from the hypothetical mean AvTD in both a negative (nine sites) and positive (eight sites) direction. Figure 10 shows the location of these sites. Six of the eight sites with a significantly higher AvTD are located in Orkney. The other two sites are within the West Scotland sub-region. Two of the nine sites with values of AvTD less than the theoretical mean are also present in the West Scotland sub-region. Four sites with lower AvTD than expected are located in Shetland, with the remaining sites in the Clyde Sea and East Scotland.

Temporal patterns in bryozoan diversity

Table 3 shows the AvTD for bryozoans in Scotland from 1792 to 2010. AvTD peaks between 1792 and 1849 with a second peak between 1975 and 2000. AvTD is lowest in the present time period (2000–2010).

Discussion

The aim of this study was to assess the distribution and biodiversity of bryozoans in Scotland, using a combination

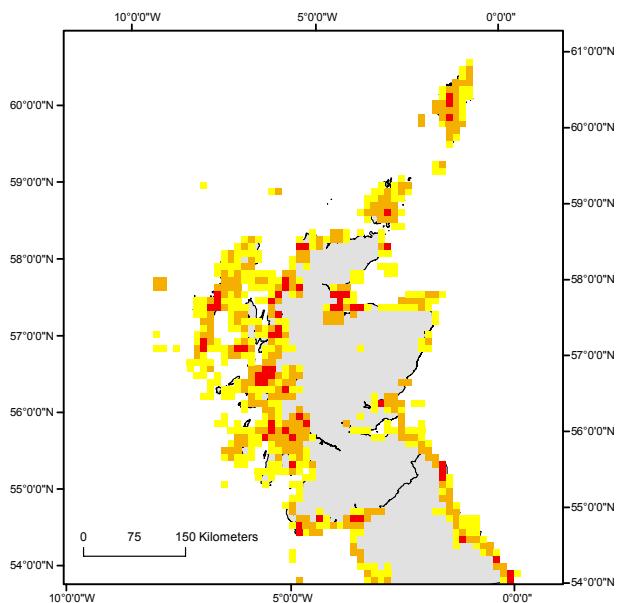


Fig. 4. Sampling sites of the Marine Nature Conservation Review. Colour represents the intensity of sampling: red = 43–489 samples per 10 km^2 ; orange = 8–42 samplers per 10 km^2 ; yellow = 1–8 samples per 10 km^2 . Taken from the NBN gateway website.

of mapping techniques and biodiversity indices. The results provide baseline data on Scottish bryozoans and highlight the regions and habitats that remain poorly studied.

Ecological insight into the distribution and diversity of bryozoans is somewhat confounded by variations in data quality and availability. The MESH-EUNIS data layers have a fairly coarse resolution because of underlying limitations in seabed substratum data from the British Geological Survey. Resolution is lowest in coastal areas (0–3 m) and on rocky substrates, both of which contain a high proportion of the bryozoan records. Moreover, the layers are based on a predictive model and therefore may not accurately represent the benthic habitat of all areas. This, along with the fact that the location of many bryozoan records is only approximate, and that the benthic habitat varies over a relatively small spatial scale, means that the species numbers in each marine zone may not be fully representative of the true distribution of bryozoans in Scotland. It may well be expected that given the modest sampling effort, bryozoan diversity is underestimated in almost all locations.

The inclusion of museum specimens in the present dataset provides information on the historical state of diversity. Museum data has the advantage of being able to confirm species identifications. The date of museum specimens, however, can be misleading, reflecting the date when the specimen was registered, rather than collected. Furthermore, changes in taxonomic usage and place names, and imprecisely defined locations or sampling

methods can restrict comparisons of present day and historical data. Alternatively, present-day survey data will tend to provide accurate information on the location, date and depth of sampling; however, specimens are rarely retained, preventing the identification being checked at a later date.

Comparison of diversity (as measured by AvTD/VarTD) with other studies, and therefore ecological interpretation of the results, is limited, as few studies have considered the relationship of AvTD/VarTD to physical characteristics of the environment (e.g. Ellingsen *et al.* 2005). Fewer still have considered the average taxonomic distinctness of bryozoans (e.g. Rowden *et al.* 2004). Some insight may be gained by considering factors that influence species number, but it is unclear whether species richness and AvTD/VarTD are governed by similar environmental parameters. Preliminary work shows that species richness and taxonomic distinctness relate to different environmental gradients (Ellingsen *et al.* 2005; Heino *et al.* 2005). Assemblages with lower species richness do not necessarily have a lower AvTD than those of many other species, e.g. when there is a limited number of species, but the species represent a broad phylogenetic range.

Despite these problems, the results give an indication of the broad-scale patterns in bryozoan occurrence and enable the identification of localities and habitats that represent future sampling priorities in Scotland.

Bryozoan distribution

The location of bryozoan records largely mirrors the MNCR sampling sites, suggesting that the observed distribution reflects a greater sampling intensity on the west coast and the archipelagos of Shetland, Orkney and the Western Isles. Few species have been recorded from offshore areas, and again this is likely to reflect a bias towards sampling coastal areas, which are both easier and cheaper to access.

Patterns of offshore *versus* near-shore species richness remain ambiguous, with several studies finding fewer species in offshore shallow benthic areas compared with near-shore areas (e.g. Barnes 2000), and others finding the reverse of this pattern (Schopf 1969). Offshore seamounts in the north of Scotland may be expected to support bryozoan species, as they provide suitable substrate and are generally associated with high primary productivity and current speeds (Rogers, 1994). There are so few records of offshore bryozoans in the present study that no conclusions can be drawn regarding offshore *versus* coastal patterns.

Limited surveys have been conducted in areas of the eastern and northern coasts where bryozoans appear to be absent. Potentially, therefore, the distribution of

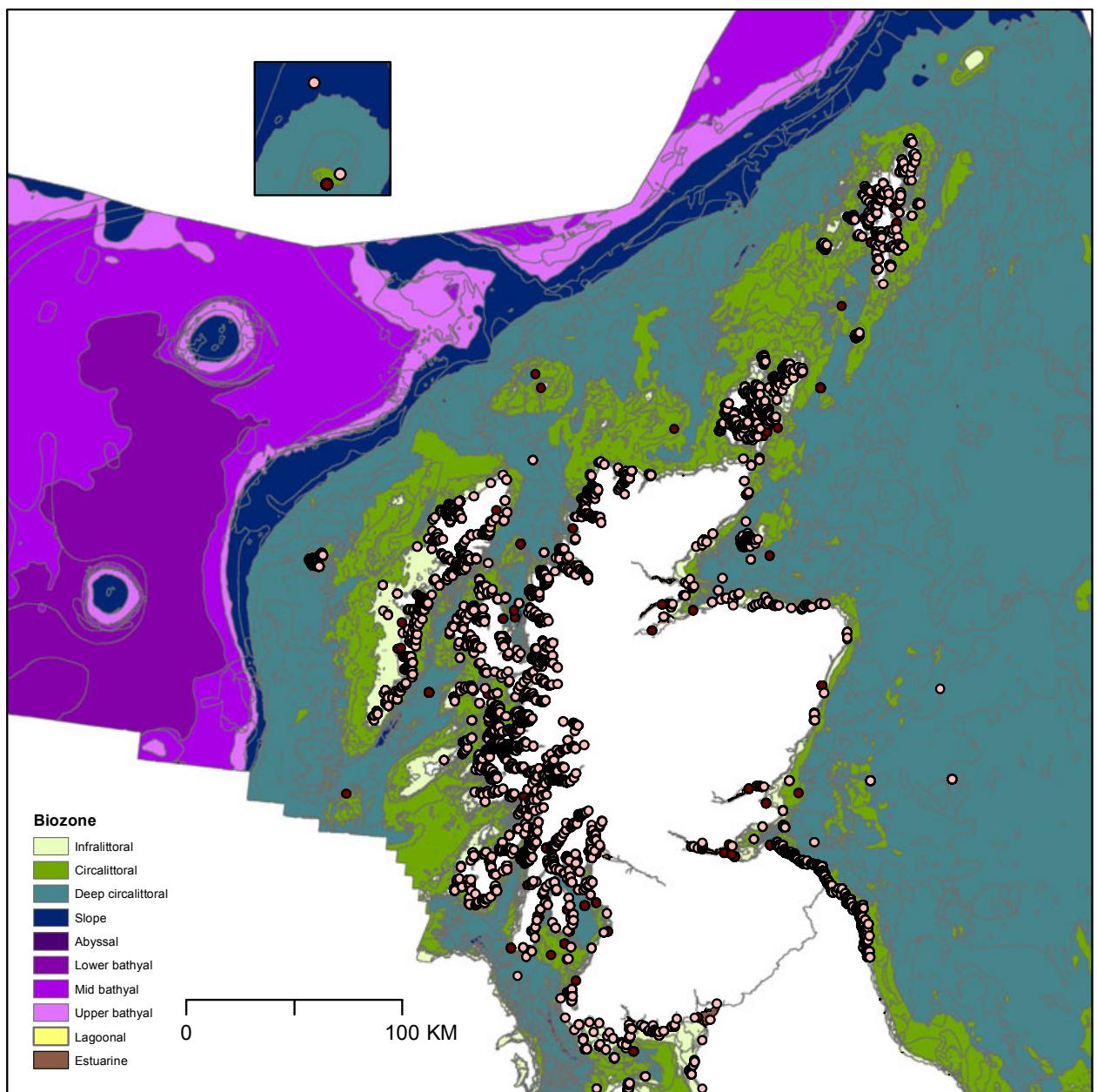


Fig. 5. Distribution of bryozoans in Scotland and the predicted MESH-EUNIS biozones of the Scottish region. Lighter circles represent precise records, whereas darker circles are an approximate location. Inset showing Rockall.

bryozoans reflects underlying differences in the marine environment. Norman (1869) notes that within the British Isles, bryozoan species that are typical of the Mediterranean region can colonise higher latitudes on the west coast than on the east coast. He attributes this to the influence of the Gulf Stream on the west coast, which results in higher temperatures and a more stable temperature regime on the western coast of Scotland (Bennett & Covey 1998a). Temperature has previously been suggested as an important factor in determining the bryozoan

assemblages in the English Channel (Hayward & Ryland 1978), Norway (Ryland 1963) and Hawaii (Soule *et al.* 1988). Many bryozoan species have a narrow temperature tolerance, and variation in temperature impacts growth rates and tolerance to salinity (Dick *et al.* 2006). In addition to temperature differences, water in the east of Scotland can become highly stratified in the summer, with a lack of vertical mixing (Dyer *et al.* 1983). This results in a restricted supply of nutrients to the photic zone, and low primary productivity (McIntyre 1961). It may therefore be

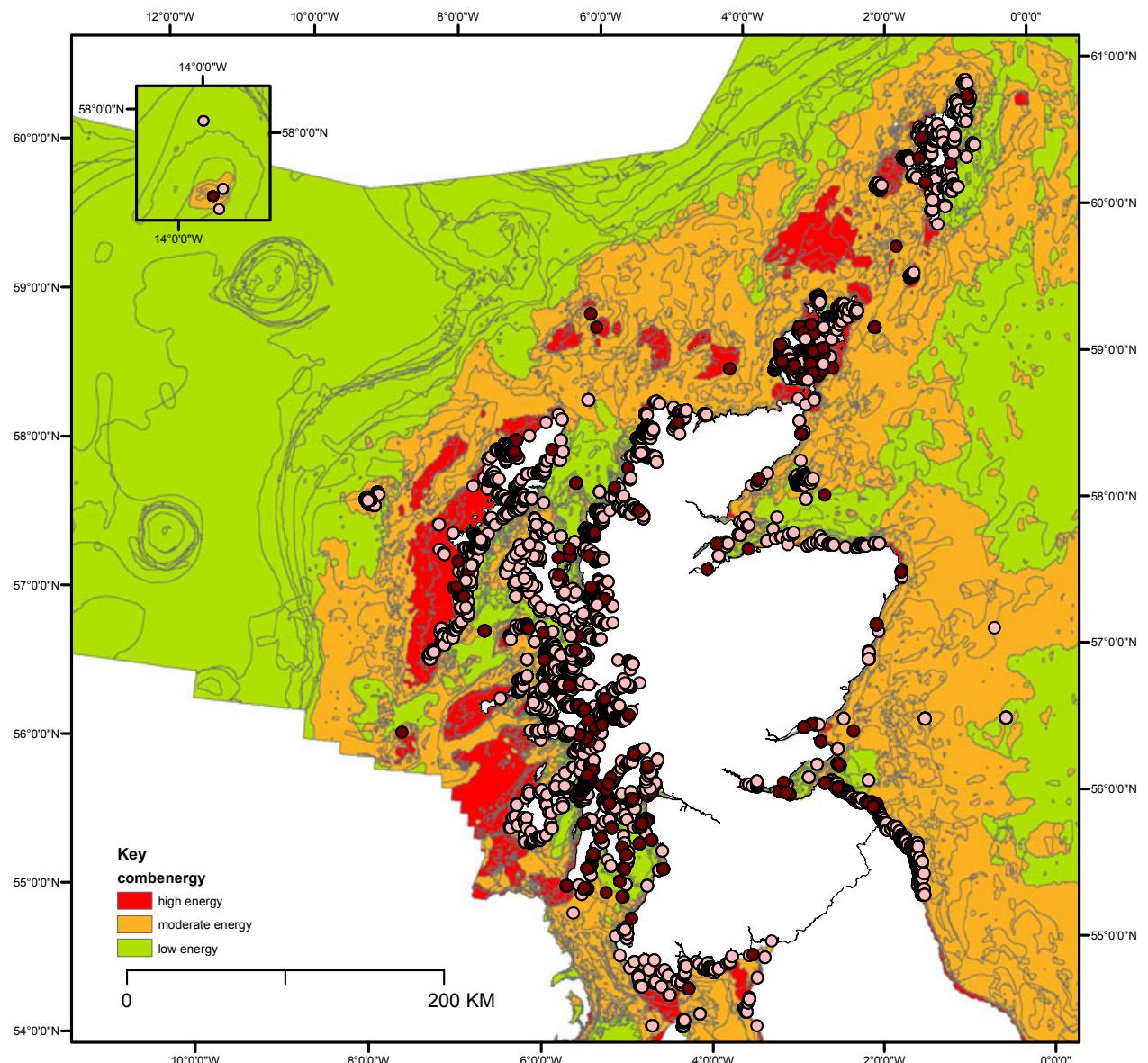


Fig. 6. Distribution of bryozoans in Scotland and predicted MESH-EUNIS energy levels within the Scottish region. Red = high energy; orange = intermediate energy; green = low energy. Lighter circles represent precise records, whereas darker circles are an approximate location. Inset showing Rockall.

expected that little organic material reaches the seabed. In contrast, strong winds on the west coast generally prevent stratification in the summer (Lee 1981) and hence there is a greater availability of phytoplankton to bryozoans. The availability of phytoplankton as a food source is thought to be important in determining bryozoan distribution (Best & Thorpe 1983, 1986; Pratt 2008) and may, in part, be responsible for differences between the west and east coast. Alternatively, differences between the two coasts may not be ecological, but instead represent evolutionary

trends, with Lusitanian species having had insufficient time to colonise the east coast.

The number of species present in the different MESH-EUNIS marine zones gives a further indication of the potential factors influencing bryozoan distribution in Scotland. Bryozoans are typically expected to inhabit intermediate energy zones where there is some degree of shelter (Ryland 2005). Currents and wave exposure will influence bryozoans through impacts on food supply, attachment ability and substrate-mediated effects

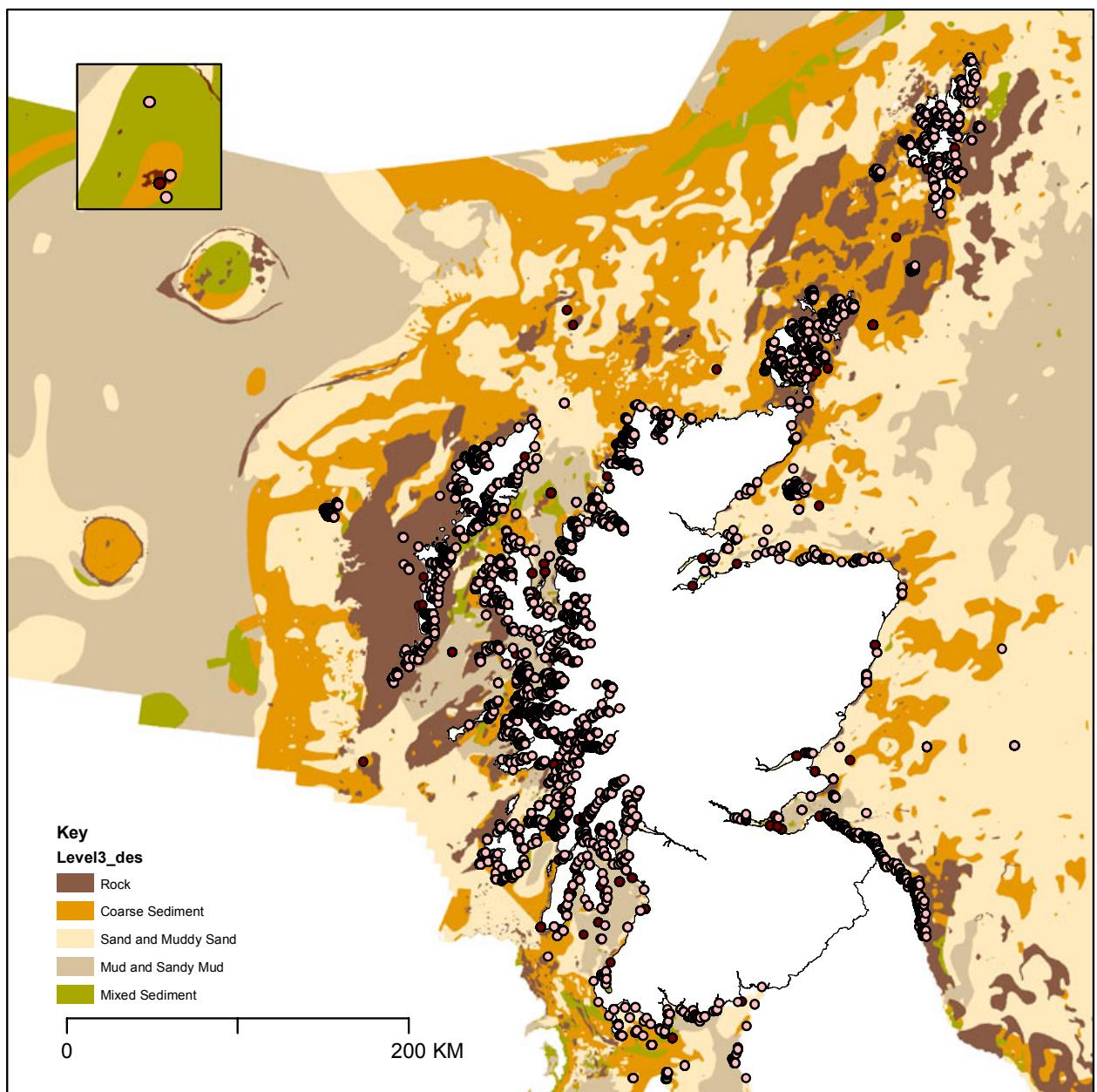


Fig. 7. Distribution of bryozoans in Scotland and predicted MESH-EUNIS substrate type within the Scottish region. Lighter circles represent precise records, whereas darker circles are an approximate location. Inset showing Rockall.

(Cabilioch 1968; Dick *et al.* 2006). The greatest number of bryozoan species in Scotland are from high-energy, rather than intermediate energy, environments, and the greatest biodiversity (AvTD) is within low-energy environments. The three energy zones have similar numbers of bryozoan records, such that sampling should have less of an influence on the number of species. However, the energy layer of the MESH-EUNIS model is constructed only from information on tidal currents and excludes any measure of wave exposure. High energy, therefore, represents areas

of strong or very strong tidal currents with unknown exposure. If wave action were to be incorporated, our understanding of the distribution and diversity of bryozoans across the different energy zones might differ.

Currents will also affect the distribution of bryozoans through their influence on substrate availability and heterogeneity. For all marine species, environmental heterogeneity is one of the strongest correlates of species number (Huston 1994), and peaks in bryozoan species number have been found previously to correspond to

Table 2. Average taxonomic distinctness (AvTD), number of bryozoan species (S) and number of records (R) in different MESH-EUNIS zones in Scotland.

Zone	AvTD	S	R
Biozone			
Infralittoral	62.60	191	13,240
Circalittoral	63.11	98	1179
Deep circalittoral	65.90	74	382
Estuarine	61.82	27	70
Lagoon	65.19	11	34
Slope	–	3	4
Energy zone			
Low energy	64.19	139	4650
Intermediate energy	63.83	122	5130
High energy	62.44	173	5135
Substrate type			
Rock	61.98	193	12,076
Coarse sediment	64.05	76	1259
Mixed Sediment	63.77	89	619

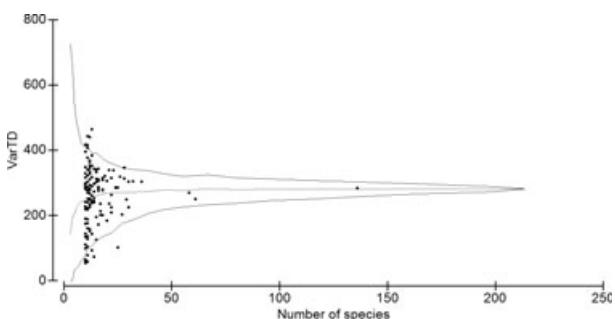


Fig. 8. Departure from the theoretical mean VarTD and 95% confidence funnel of sites in Scotland where >9 species of Bryozoa have been recorded.

increased substratum heterogeneity (Hayward & Ryland 1978; Clarke & Lidgard 2000). Rock, as defined by the MESH-EUNIS model, includes a range of substrates available for bryozoans to colonise, such as rocks and biogenic reefs. Kelp and other species that may be colonised epizooically by Bryozoa will also be available on rocky substrata. In contrast to the results presented here, the greatest number of boreal species has generally been encountered on coarse sediments (Egginton 1972; Kuklinski *et al.* 2005); however, biodiversity (AvTD, rather than species number) of bryozoans in Scotland was found to be highest on coarse sediments. This further emphasises the need for greater sampling of coarse and mixed sediments in Scotland. The lack of available substratum may be a determining factor influencing low species number on the north coast of Scotland. North of the mainland, there are large areas of sediment and only one sea loch

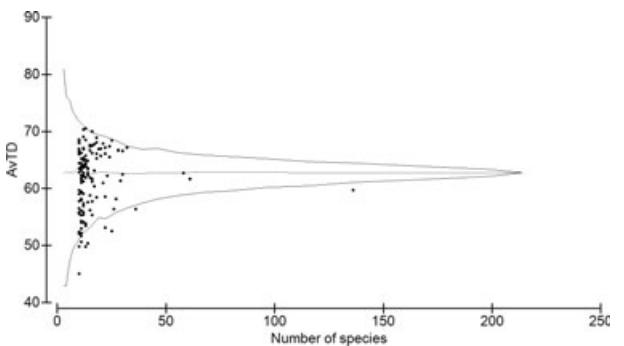


Fig. 9. Departure from the theoretical mean AvTD and 95% confidence funnel of sites in Scotland where >9 species of Bryozoa have been recorded.

(Bennett & Covey 1998b), therefore much of the area is likely to be unsuitable for bryozoan colonisation.

Both the availability and heterogeneity of substratum, and current strength will vary with depth. The MESH-EUNIS biozones GIS layer indicates the depth at which Bryozoa have been recorded. The greatest numbers of species have been recorded from the infralittoral zone; however, this category has more than 10 times the number of records as any other zone. The diversity measured by AvTD is highest in the deep circalittoral.

Overall, it is likely that a variety of physical factors contribute to the observed patterns of bryozoan distribution in Scotland and between different marine habitats. It is necessary to ensure that sufficient sampling has been undertaken to eliminate sampling bias as an explanatory factor for bryozoan occurrence. Gaining a better idea of substrate, temperature and exposure differences between sub-regions and offshore and coastal areas will allow for further explanation of the observed patterns. As seabed maps improve in the future, it will be possible to establish the patterns in bryozoan distribution with greater confidence.

Spatial patterns in bryozoan diversity

The average taxonomic distinctness was calculated for all sites with 10 or more species and from Scottish sub-regions as an index of biodiversity. Depth alone appeared to have little influence on bryozoan diversity. However, the range in diversity values was less variable in deeper waters, which may be due to the lower number of records. Substrate, currents, temperature and food availability vary with depth, and these are factors that are known to influence bryozoan assemblages (Egginton 1972; Hayward & Ryland 1978; Hughes 2001; Kuklinski *et al.* 2005). The AvTD of bryozoans in New Zealand was found to vary with depth, peaking between 10 and 40 m in areas consistent with high habitat heterogeneity

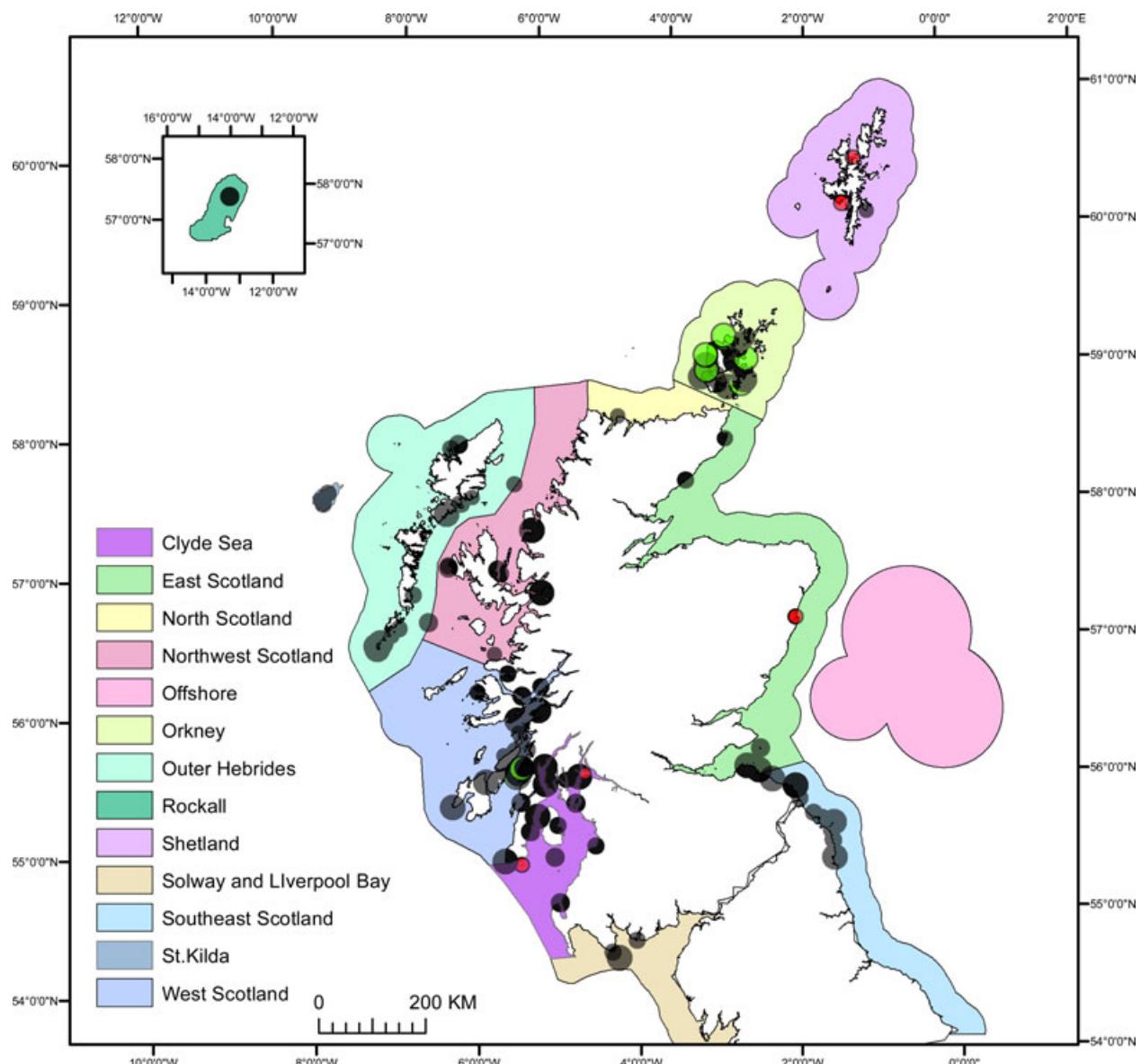


Fig. 10. Distribution of sites with >9 species of Bryozoa recorded in Scotland and associated AvTD values. Circle size is proportional to AvTD. Red circles represent values of AvTD that are significantly lower than the regional mean, and green circles represent those values that are higher than the regional mean.

(Rowden *et al.* 2004). Similarly, Ellingsen *et al.* (2005) concluded that the relationship between AvTD and depth for soft-sediment macrobenthos in the Norwegian continental shelf was due to depth-related differences in the abundance and variation of habitat types. Although it is generally expected that habitat heterogeneity will vary with depth due to reduced light and wave scour, this is not necessarily the case in Scotland. In addition, the diversity within the MESH-EUNIS biozones suggests that habitat heterogeneity is influential for bryozoan diversity. Diversity peaks in the deep circalittoral zone (Table 2), which is defined as starting at the maximum depth that

the seabed is influenced by waves, and extending to 200 m (Coltman *et al.* 2008). This zone will tend to be diverse with a variety of substrates including gravel, shingle, cobbles and shells, typically with a low silt content and reduced wave scour (Connor *et al.* 2004). It is also possible that the lack of a relationship between diversity and depth is the result of the limited depth data available for sampling sites and lack of sampling from deeper water locations.

Bryozoan biodiversity varied across Scotland, with a concentration of high values in Orkney and West Scotland. Both of these regions contain sites in which the

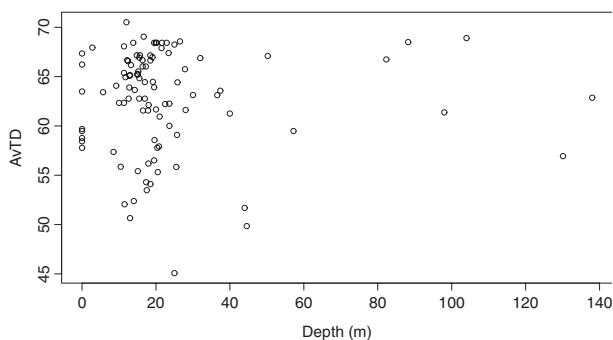


Fig. 11. AvTD in relation to depth for sites with >9 species of Bryozoa in Scotland.

bryozoan fauna has an AvTD significantly higher than the expected regional mean. Lower biodiversity values were widely spread across the region, from Shetland to the Clyde Sea, and were significantly lower than the expected regional mean in Shetland and West Scotland. The concentration of sites with a high diversity in Orkney may reflect the variety of habitats present in this area. As discussed above, habitat heterogeneity is a major factor influencing diversity. Additionally, the stable temperature regime and the availability of sheltered areas with strong tidal currents in Orkney (Bennett & Covey 1998a) are likely to contribute to the high diversity of the area. Hiscock & Breckel (2007) found that the AvTD for benthic assemblages, including species of Bryozoa, was highest in Scottish sea loch environments, followed by island habitats, and similarly attributed this to the variety of habitats that these environments provide. Orkney is made up of 70 islands and has many sea lochs; this is likely to contribute to the higher than expected values of AvTD found for bryozoans in Orkney. Likewise, the West Scotland sub-region has many of these habitat types.

At a regional scale, values of biodiversity of the MNCR sub-regions did not show much variation. The greatest diversity was in the Rockall sub-region, followed by the Clyde Sea and the Outer Hebrides. The lowest values were in North Scotland, which has only one sealoch, and Shetland. Regional patterns for bryozoans were similar to those described by Hiscock & Breckel (2007) for benthic assemblages, who found the highest AvTD at sites within the Northwest Scotland, West Scotland and the Outer Hebrides MNCR regions.

Neither the diversity of individual sites nor the diversity of sub-regions shows any cline with latitude. Latitudinal patterns have generally only been considered in terms of species richness and little work has been done on the relationship between average taxonomic distinctness and latitude. Furthermore, poleward clines in species richness appear to be taxon-specific. For example, Ellingsen *et al.* (2005) found that the AvTD of annelids, crustacean and

molluscs (combined) decreased with latitude on the Norwegian continental shelf, yet if annelids alone were considered, AvTD increased with latitude. Any interpretation of species gradients is confounded by similar latitudinal gradients in the physical characteristics of the environment (Narayanaswamy *et al.* 2010). A more detailed study of bryozoans, possibly over a greater latitudinal range, would be necessary to decipher any relationship.

Spatial scale

The role of spatial scale has long been recognised as important when assessing biodiversity, and is a limiting factor when comparing sites of different size. Different processes operate at different spatial scales and the size of an area will influence the degree of environmental heterogeneity for which biodiversity is assessed (Huston 1994). The problem of spatial scale is highlighted in the present study. Individual sites with 10 or more species show the highest biodiversity within Orkney, but when data are combined on a regional scale, Orkney as a whole has one of the lowest diversities of the Scottish sub-regions. Deciding on an appropriate scale to assess diversity for conservation purposes is problematic and is often determined by the spatial scale for which data are available. Frequently, species-area curves are used to examine the effect of spatial scale on species richness and can be used to work out the minimum sample area needed to capture species diversity adequately. There has been little consideration of the impact of area on AvTD but it is likely that larger areas will cover a greater variety of habitats and hence support a greater taxonomic range of species.

Temporal patterns in bryozoan diversity

Temporal patterns in the diversity of bryozoans were assessed by calculating the AvTD for each time period. AvTD varied over time, peaking between 1792 and 1849, and then again between 1975 and 2000 (Table 3). AvTD was lowest in the present time period (2000–2010). The greatest diversity (AvTD) was associated with the fewest number of species and records. It is likely that during this early time period, a few conspicuous intertidal bryozoans would have been collected. In the intertidal zone the key members of the bryozoan community most likely to be encountered will represent a very broad phylogenetic range. An example of a typical sample could be the Ctenostome *Flustrellidra hispida*, the Cheilostome *Electra pilosa* and the Cyclostome *Crisia denticulata*. This would give a species richness of 3, which is low; however, the AvTD for this would be high due to each species belonging to a different Order. From 1850 to 1949, sampling effort increased due to the activities of the British

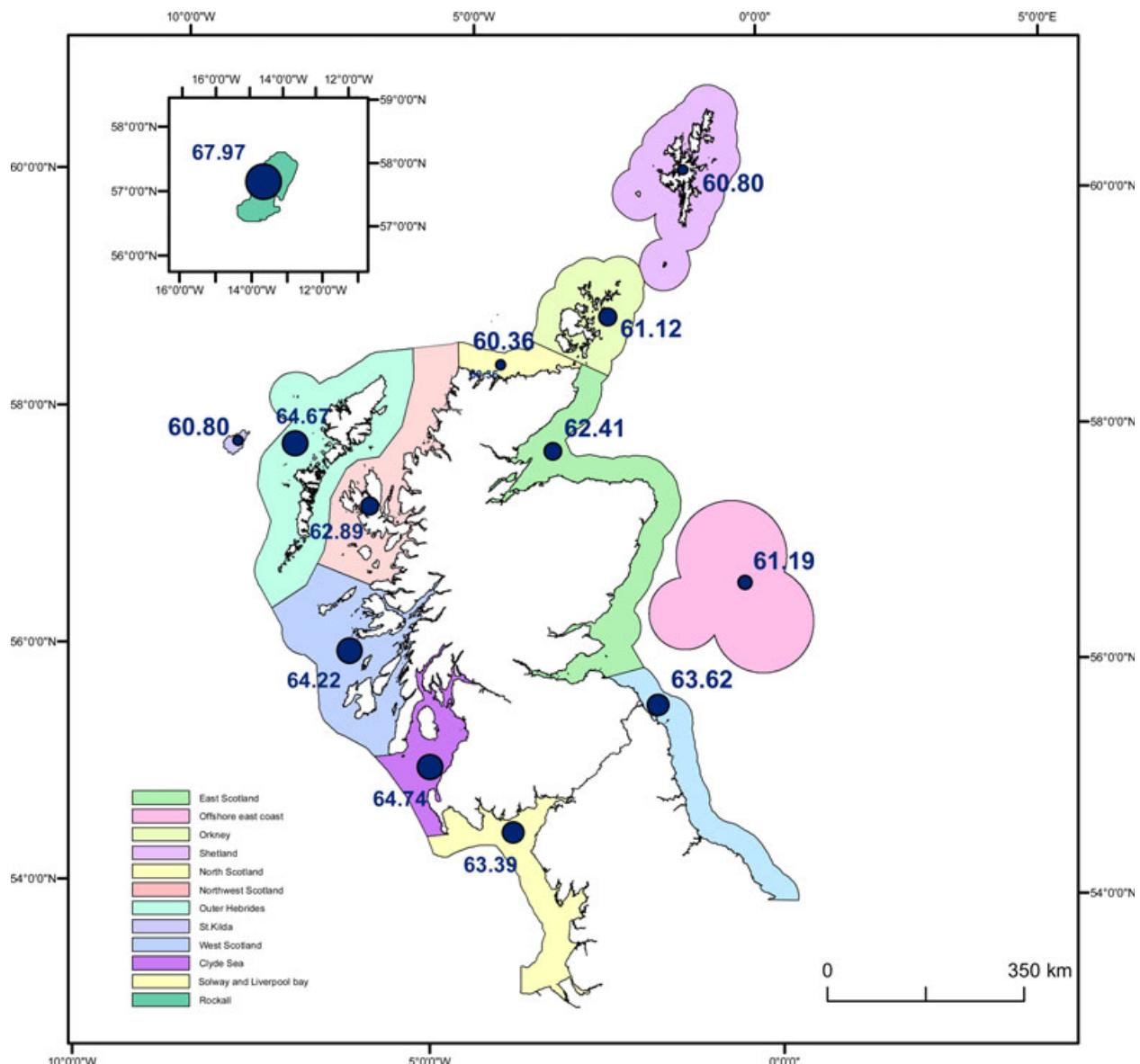


Fig. 12. Biodiversity (as measured by AvTD) of Scottish sub-regions. Circle size is proportional to AvTD value.

Dredging Association. More species would have been collected, increasing the species richness and number of records. Additional species will of necessity belong to one of the three Orders sampled from the intertidal example in the previous time period. It follows then that large increases in the AvTD would not be expected.

With the current data it is not possible to separate genuine temporal changes in Scottish bryozoan diversity from the effects of an uneven spread of records across the time periods and changes in methods of collecting and identifying specimens. Additionally, the geographical range of records in each time period is not equal. This means that the biodiversity for one time period may not

be comparable with that of another time period. Data were insufficient to calculate the AvTD for each time period in each of the Scottish sub-regions, which would have helped to overcome this problem. A more thorough search of historical records, including other museum collections, may yield more data and enable a more robust assessment of diversity through time, in the future.

Implications and recommendations

The data presented here provide baseline information on the distribution and diversity of bryozoans in Scotland,

Table 3. Average taxonomic distinctness (AvTD), number of bryozoan species (S) and number of records (R) in different time periods.

Time period	AvTD	S	R
1792–1849	64.01	40	59
1850–1949	61.17	157	695
1950–1975	61.75	52	74
1975–2000	63.75	142	19,012
2000–2010	59.46	65	2352

which is a vital prerequisite for conservation and environmental monitoring. The identification of sites with a high biodiversity may be used to identify priority sites for protection and conservation.

However, it is important not just to value sites of high diversity. Sites with a low AvTD may represent a small number of closely related species, but those species may be ecologically rare. For example, few species are present in tide-swept faunal communities, yet the species that are able to tolerate such conditions, such as *Alcyonium diaphanum* and *Flustra foliacea*, may be considered to be valuable. Benedetti-Cecchi (2004) noted that the identity of the species in an assemblage, rather than a diversity index, may be needed to make inferences on ecosystem function. The distribution of bryozoans must, therefore, also be considered in terms of individual species, rather than just the broad-scale patterns.

Taxonomic distinctness, like other indices, does not capture all aspects of diversity. Most notably, AvTD measures based on presence-absence data do not account for the abundance of species within an assemblage. Not only were abundance data not available for many of the bryozoan records, but the quantification of abundance for modular or colonial animals is problematic and varies across studies (McKinney & Jackson 1989). It is, therefore, likely that policy decisions based on biodiversity assessments will need to make use of a variety of diversity measures, including taxonomic distinctness and species richness, to capture fully all aspects of diversity.

The sensitivity of AvTD, and its application in environmental monitoring, still remains uncertain. Salas *et al.* (2006) found that only total, not average, taxonomic distinctness was satisfactory in determining disturbed situations, and AvTD was less sensitive than other commonly used diversity measures. Furthermore, Heino *et al.* (2005) found that the AvTD varies along natural gradients, thereby reducing its ability to discriminate between the effects of human disturbance and natural variability.

The availability of regional species pool data is a basic requisite for the application of AvTD to biodiversity assessment but it cannot be certain that the regional species pool, here assumed to be bryozoans of the Celtic and North Sea, is truly representative. Comparisons of Scot-

tish fauna to that of other regions are therefore limited. Moreover, a fully resolved phylogenetic framework is not available for bryozoans, and relatedness is based on the somewhat arbitrary Linnaean classification system (Warwick & Clarke 1995). For bryozoans, as with most phyla, certain groups have received more taxonomic attention than others. In particular, the taxonomy of cyclostomes remains unclear (Waeschbach *et al.* 2009). This results in a truncation of the hierarchy towards the more studied groups. Weighting taxonomic ranks on a linear scale is also somewhat arbitrary, and it must be remembered that the AvTD is an index that provides only a relative measure of biodiversity, for use in comparing areas, rather than providing an absolute measure.

Despite these problems, AvTD is one of only a few indices that make historic, diffusely collected species lists amenable to valid biodiversity analysis. As the historic dataset for Scottish bryozoans represents a significant proportion of the total dataset (~2300 records), and a common aim of biodiversity assessment is to understand temporal changes, it is important that these historical data are included in analysis and not simply ignored because of the limitations of sampling effort. While limitations in taxonomy may limit comparisons between Scotland and other regions, and between Bryozoa and other Phyla, comparisons between sites within Scotland should give a reasonably accurate indication of spatial differences in diversity within Scotland.

The present analysis highlights the need to maintain meticulous records and transparency across institutions. Recent EU and UK legislation aim to make data collection consistent and improve accessibility. In particular, the EU Inspire Directive (2007) focuses on maintaining spatial data and improving transparency across agencies.

Conclusion

In this study we describe how the distribution and diversity of bryozoans varies across Scotland. Sampling effort is largely responsible for the spatial patterns described here; however, indirect evidence from broad-scale habitat data suggests that the patterns may also be determined by a number of ecological factors. Depth, unexpectedly, appears to have little influence on bryozoan diversity. Habitat heterogeneity and substrate availability are likely, in part, to be important factors in determining bryozoan assemblages. To develop more robust explanations for the observed patterns, rather than pure descriptions, it will be necessary to increase sampling effort to those regions (e.g. the north coast) and habitats (e.g. the deep circalitoral) that have been neglected previously. The interpretation of temporal patterns is confounded by the availability of historical data, and a more thorough search

of museum specimens and historical records will be necessary to further investigate temporal changes in bryozoan occurrence. Understanding the factors that influence AvTD has so far been limited by the lack of studies that have used AvTD to assess benthic fauna. Furthermore, there are several caveats when applying AvTD to biodiversity assessments, and it is likely that it will need to be combined with other measures of diversity to provide holistic information on which to base policy decisions.

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