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Quantitative analysis of a deep-water bryozoan collection from the Hebridean continental slope

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Bryozoans were collected from nine stations between 569 and 1278 m depth on the Hebridean continental slope north-west of Lewis. The 21 species recorded from 1544 colonies included three species new to the British fauna. The bryozoan fauna, growing on pebbles, cobbles and small boulders, was dominated by species with encrusting, spot or ribbon-like colony morphologies. The few erect species were rare. Colony density on available rock substrata declined from 569 to 855 m, but was high at 1278 m, where the nodular species *Turbicellepora boreale* occurred on pebbles as small as 1 cm diameter. Cyclostomates made up $>90\%$ of the colonies in the shallowest sample and were present in lower numbers to 855 m. None were recorded at 1278 m. In the 569–855 m depth range, diversity and evenness were lowest at 569 m but relatively constant at the other stations. A species accumulation curve suggests that the 20 species recorded is a good estimate of the total fauna in this depth range.

INTRODUCTION

The north-east Atlantic continental shelf edge is a region formerly remote from most human influences, but is now assuming an increased economic importance as the site of an important deep-water trawl fishery (Gordon, 2001) and as a repository of commercially-exploitable oil and gas reserves. Deep-water trawling has already been shown to have a visible impact on the benthic environment in this area (Roberts et al., 2000), and future hydrocarbon extraction also has the potential to affect the deep-water ecosystem. There is consequently a clear need for more information on the structure and functioning of continental slope benthic communities so that potential anthropogenic impacts can be detected and their effects understood (Gage et al., 2000; Bett, 2001; Gage, 2001).

Bryozoans are an abundant and diverse component of the epifauna on many marine hard substrata (McKinney & Jackson, 1989). In the north-east Atlantic, an area with one of the taxonomically best-known bryozoan faunas, the greatest number of species occurs on shell gravels and similar biotopes in relatively shallow offshore waters (Eggleston, 1972; Ward & Thorpe, 1989). However, bryozoans are not confined to shelf seas, but also occur on the continental slope, and at even greater depths where suitable substrata exist (Schopf, 1969; Hayward, 1981). Previous studies of deep-water bryozoans in the north-east Atlantic (Hayward, 1978, 1979; Hayward & Ryland, 1978; Harmelin, 1979; d'Hondt, 1970, 1973a,b, 1974, 1975) and elsewhere (Gordon, 1986, 1989; López Gappa, 2000) have presented systematic descriptions and species lists, with notes on geographic and bathymetric ranges, but there have been no quantitative analyses of community structure. This is partly due to the practical difficulty of remotely sampling hard-substratum epifauna on the continental slope, and partly to the effort required to count bryozoan colonies on the irregularly-shaped rocks and pebbles that comprise the main substrata for attachment in the slope environment.

This paper descibes a bryozoan fauna collected on the upper Hebridean continental slope as part of the environmental assessment of an area licensed for hydrocarbon exploration by the UK government. In addition to providing a list of the species present at the sampled depths, some simple quantitative analyses of the fauna are presented, the first time such measures have been applied to a deep-water bryozoan community.

MATERIALS AND METHODS

Samples were collected between 11 and 18 February 1998 on RRS 'Discovery' cruise 230C from an area in the northern Rockall Trough, approximately 100 km north-west of the Isle of Lewis (Figure 1). The benthic sampling formed part of a pre-drilling environmental assessment of Block 154/1, licensed for hydrocarbon exploration to Enterprise Oil plc. A full account of the survey and its results can be found in Jones et al. (1998). Benthic biological sampling was carried out along a down slope transect from approximately 570–1300 m depth, using gear appropriate to the substratum type at each station. Stations yielding bryozoan specimens are listed in Table 1. Four of the towed gear deployments followed a more or less constant depth contour, but two rock dredge tows ('Discovery' station numbers 13351#1 and 13352#2) covered a depth gradient of 40–70 m. Because their tracks also intersected, these two dredge tows effectively repeat-sampled the same area of seabed between 740 and 810 m.

Rocks, pebbles and shells were washed clean of sediment and preserved dry. In the laboratory, substrata were examined under a binocular microscope and all bryozoan colonies counted and identified to species level. For encrusting species with diffuse, ribbon- or runner-like growth form

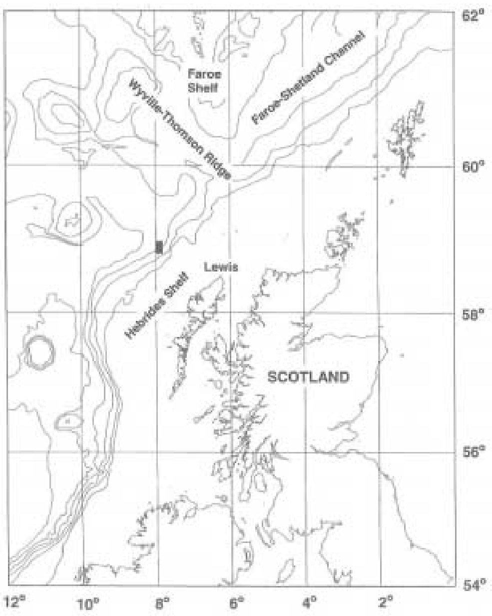

Figure 1. Chart showing the location of the survey area (black rectangle) on the Hebridean continental slope. Depth contours are shown at 200, 500, 1000 and 1500 m.

(Bishop, 1989; McKinney & Jackson, 1989), a colony was defined as a cluster of connected zooids spatially separated from other such groups. Although in such species zooid clusters often result from the fragmentation of a larger original colony (Jackson & Winston, 1981), tracing the pattern of past interconnections was impossible in most cases and was not attempted.

The curvature or irregularity of the individual rock surfaces precluded the measurement of species areal coverage used previously in bryozoan community analysis (Hughes & Jackson, 1992). However, the total area of hard substratum examined in each sample was determined by carefully wrapping each rock or pebble in a single layer of aluminium foil, taking care to trim away overlaps and folds. The total rock surface area was then calculated by comparing the summed weights of the foil wraps (measured to a precision of 0.01 g) with the weight per unit area of a foil square of known dimensions.

Bryozoan community analysis was performed using the BioDiversity Pro software package (©Natural History Museum, London, and Scottish Association for Marine Science). Terminology and methods of analysis broadly follow the recommendations of Gray (2000).

RESULTS

Benthic environment at the sampling stations

Seabed photographs taken at intervals along the depth transect indicated a gradation of substratum type from coarser to finer material with increasing depth (Roberts et al., 2000). This was confirmed by the contents of the recovered samples. At 721 m depth, photographs (Figure 2) showed a high density of pebbles and cobbles approximately 2–10 cm in diameter on a bed of muddy sediment, with occasional small boulders up to 50 cm across. Epifauna visible on the stones included sponges, brachiopods, anemones and encrusting bryozoans. No bottom photographs were taken higher up the slope but the dredged material from 569 and 665 m indicated a similar stone-rich substratum. Photographs from 885 to 918 m showed a mixture of sand and mud with scattered small, rounded stones and occasional boulders. The overall density of stones was generally lower than at 721 m. At 1088–1108 m (a depth interval from which no bryozoans were collected) the substratum consisted of a strongly rippled muddy sediment lacking visible stones but showing some evidence of bioturbation. At 1295–1316 m, photographs showed a heavily bioturbated fine mud bottom with no current-induced bedforms. Stones were not visible on the photographs, but an Agassiz trawl taken at 1278 m did recover a small number of tiny pebbles (mostly 1–2 cm diameter) with attached bryozoans.

Table 1. *List of stations from which bryozoan specimens were collected. Data for towed gear (RD, AT) represent calculated positions on the sea-floor at the start and end of each tow.*

				Position	
'Discovery' station no.	Gear	Depth (m)		N	W
13364#1	RD	569	Start	58°50.41′	07°44.39′
			End	58°50.14′	07°45.46′
13363#1	RD	665	Start	58°50.10′	07°48.50′
			End	58°49.70′	07°49.70′
13350#2	NBC	717		58°0.53′	07°50.36′
13351#1	RD	740–810	Start	58°49.43′	07°53.06′
			End	58°50.46′	07°51.55′
13352#1	RD	760–800	Start	58°49.61′	07°53.35′
			End	58°50.62′	07°50.01′
13365#2	RD	855	Start	58°51.54′	07°49.43′
			End	58°51.40′	07°49.83′
13362#1	UBC	870		58°52.41′	07°48.23′
13349#4	NBC	917		58°51.45′	07°52.15′
13347#5	AT	1278	Start	58°59.16′	07°56.66′
			End	58°57.73′	07°59.65′

RD, Rock dredge; NBC, NIOZ boxcorer; UBC, USNEL boxcorer; AT, Agassiz trawl.

Figure 2. Oblique-view photograph of the seabed at 721 m in the survey area on the Hebridean continental slope (position 58°50.15′N 07°50.05′W). The bed is composed of many small (2–10 cm) stones lying on a muddy sediment. Epifauna are visible on many of the stones. The large cobble to left of centre carries two contracted sea anemones. Whitish lines and patches on other stones are serpulid polychaete tubes and encrusting bryozoans. The field of view is 1.3 m wide at the lower edge of the frame and approximately 2.5 m from front to back.

The recovered material examined for bryozoans consisted of pebbles, cobbles and fragments of clinker, mostly in the 1–10 cm diameter size range. Some small boulders up to 30 cm maximum diameter and a few empty gastropod shells were also included. Cumulative rock substratum area examined ranged from 516 to 10,640 cm^2 per sample (Table 2). The boxcore samples taken at 870 and 917 m contained only 2–3 small pebbles each. These samples extended the observed depth range of a few bryozoan species but did not provide enough material for quantitative analysis.

Total bryozoan abundance

A total of 1544 bryozoan colonies was recorded, with wide variation in number between samples (Table 2). Colony density converted to a common standard of 100 cm^2 rock area (Table 3) indicated a trend of declining abundance from 569 to 855 m depth. However, the highest density was recorded at 1278 m, where, despite their small size, a high proportion of the available hard substrata carried bryozoan colonies.

Since those parts of each rock or pebble in contact with the underlying sediment will be unavailable for bryozoan colonization, the figures for colony density 100 cm^{-2} will underestimate the *in situ* density on 'available' hard substratum. However, the estimates for each station will have the same proportional relationship whatever correction factor is applied, so comparisons between them are still valid. It is also important to note that any estimate of bryozoan density per unit area of rock examined does not equate to the absolute density of colonies per unit area of seabed.

Species identifications and higher-taxon faunal composition

Twenty-one bryozoan species were recorded, the fauna consisting of five cyclostomates, one ctenostomate and 15 cheilostomates (Table 2). Species identifications and family-level taxonomy follow Hayward & Ryland (1985, 1998, 1999). The generally simple skeletal morphologies of cyclostomates create problems in identification (Harmelin, 1979; Hayward & Ryland, 1985), and the specific attributions proposed here should probably be regarded as provisional until the taxonomy of this group is better known.

Two firmly-identified species new to the British bryozoan fauna were recorded: *Alcyonidium candidum*, previously known from the Bergen area of Norway (Ryland, 1963), and *Palmiskenea faroensis*, described by Hayward (1994) from the Faroes. In addition, a calloporid growing as a uniserial chain of five reasonably complete zooids was represented by a single colony in the 740–810 m sample. This specimen may be attributable to the species *Daisyella bathyalis*, recently described from south of Iceland (Rosso & Taylor, in press). Another calloporid, *Doryporellina reticulata*, has only one previous British record (Grischenko et al., 2000).

At 569 m, cyclostomates made up >90% of the colony sample (Table 3). The cyclostomate contribution dropped to 73% at 665 m, and to 31–57% in the depth range 717–855 m. None were recorded at 1278 m, where the small sample of 50 colonies included only the cheilostomates *Turbicellepora boreale* and *Sarsiflustra abyssicola*.

Colony morphologies

The bryozoan fauna was dominated numerically by species with encrusting growth forms. The only erect species were *Bicellarina alderi*, *Palmiskenea faroensis* and the flustrids *Chartella barleei* and *Sarsiflustra abyssicola*. However, the latter three species were represented almost entirely by encrusting basal attachment sheets, with only a few fragments of *Sarsiflustra* indicating the realization of erect arborescent growth. The erect species were all rare (Table 2), although in the case of the delicate *Bicellarina alderi* this scarcity may have been exaggerated by abrasion in the dredge during the collection process. The cyclostomate *Entalophoroecia deflexa* can also form erect branches on some substrata (Hayward & Ryland, 1985), but none were found among the specimens in this study.

Most of the encrusting species had either ramifying, ribbon-like colonies (*Entalophoroecia deflexa*, *Oncousoecia dilatans*) or occurred as small spots or patches (using the terminology of Bishop, 1989), typically measuring 0.25 cm^2 or less. Common species in the spot/patch categories were *Amphiblestrum solidum*, *Ramphonotus minax*, *Escharella octodentata*, *Hemicyclopora polita* and *Celleporina pygmaea*. The cyclostomate *Diplosolen obelia* was the only encrusting species typically forming extensive (>1 cm^2), multiserial sheets. Disciform and multilaminar mound-like colony morphologies were represented by *Plagioecia patina* and *Disporella hispida* respectively. *Turbicellepora boreale* occurred as stout, erect nodules up to 1 cm tall, with the addition of one unilaminar ribbon-like colony growing on an empty gastropod shell.

Quantitative analysis of bryozoan fauna in 569–855 m depth range

The six samples in the 569–855 m depth range included sufficient material for a simple quantitative analysis of

Table 2. *List of bryozoan species collected and their relative abundance in relation to water depth. Figures represent the percentage contribution of a species to the total number of colonies recorded in each sample. Total numbers of colonies, species and rock area examined per sample are given at the foot of the table.*

'Discovery' station number Depth (m)	13364#1 569	13363#1 665	13350#2 717	13351#1 740–810	13352#2 760–800	13365#2 855	13362#1 870	13349#4 917	13347#5 1278
CLASS STENOLAEMATA									
Order Cyclostomata									
Diastoporidae									
Diplosolen obelia (Johnston)	45.9	25.4	0.9	1.0	7.0	1.3			
Entalophoroecia deflexa (Couch)	18.3	7.4	6.3	7.8	7.6	9.0			
Plagioecia patina (Lamarck)	0.7	1.8	7.1	3.9	4.9	23.1			
Oncousoeciidae									
Oncousoecia dilatans (Johnston)	25.3	23.6	17.9	4.9	19.3	9.0			
Lichenoporidae									
Disporella hispida (Fleming)	0.3	14.8	5.4	13.6	24.5	9.0			
CLASS GYMNOLAEMATA									
Order Ctenostomata									
Alcyonidiidae									
Alcyonidium candidum Ryland					1.2				
Order Cheilostomata									
Electridae									
Pyripora catenularia (Fleming)	0.7								
Calloporidae									
Amphiblestrum solidum (Packard)	1.3	4.4	6.3	9.7	7.3	3.9		33.3	
Doryporellina reticulata (Ryland)	0.3	0.2	2.7	1.0	0.6				
cf. *Daisyella bathyalis* Rosso & Taylor				1.0					
Ramphonotus minax (Busk)	0.3	0.4	5.4	3.9	3.1			66.7	
Chaperiidae									
Larnacicus corniger (Busk)		0.2	0.9						
Flustridae									
Chartella barleei (Busk)				1.0					
Sarsiflustra abyssicola (G.O. Sars)				1.0	0.6	1.3			2.0
Bugulidae									
Bicellarina alderi (Busk)	1.0	0.2	1.8	1.0	1.2				
Bryocryptellidae									
Palmiskenea faroensis Hayward					0.3	5.1			
Escharellidae									
Escharella octodentata (Hincks)	1.7	6.0	4.5	17.5	4.0	9.0	50.0		
Hemicyclopora polita (Norman)	1.3	7.6	21.4	8.7	11.6	26.9			
Schizoporellidae									
Escharina johnstoni (Quelch)	1.3	4.8							
Celleporidae									
Celleporina pygmaea (Norman)	1.7	3.5	18.8	24.3	6.7	2.6	50.0		
Turbicellepora boreale Hayward & Hansen									98.0
Total number of colonies	301	568	112	103	327	78	2	3	50
Total number of species	14	14	14	15	15	11	2	2	2
Total rock area examined (cm^2)	3646	10 490	3093	3062	5917	3361	NM	NM	516

NM, not measured (only a few tiny pebbles were collected at these depths).

community structure. Twenty species were recorded, with 11–17 in each boxcore or dredge. The species accumulation curve generated by randomly-pooling different combinations of samples clearly approaches an asymptote at N=6 samples (Figure 3A), suggesting that the total number of bryozoan species present in this depth range is 20 or only slightly greater. This conclusion is supported by the plot of 'uniques' (species which occur only once in each set of pooled samples), which reaches zero at N=6 pooled samples (Figure 3B), indicating that all species present have been encountered. Of the 20 species recorded from 569 to 855 m, 11 occurred across the whole of this depth range (*Ramphonotus minax* and *Doryporellina reticulata* were not recorded at 855 m but both reappeared at 917 m, indicating continuity of distribution).

The heterogeneity diversity measure Exp (H′) (Gray, 2000), where H′ is the Shannon–Wiener index (log base 2), was highest in the three samples between 717 and 810 m, slightly lower immediately above and below this range, and much lower at 569 m (Table 4). Lowest diversity at 569 m was confirmed by values of the Berger–Parker index (the proportion of individuals in the most

Table 3. *Absolute abundance of bryozoan colonies and higher-taxon community composition in relation to sample depth. The samples from 870 and 917 m, which consisted of only 2–3 colonies each, have been omitted. Note that two samples (marked with asterisks) represent overlapping depth ranges.*

Sample depth (m)	Colonies 100 cm^{-2} rock area	% Cyclostomate colonies in sample
569	8.3	90.4
665	5.4	72.9
717	3.6	37.5
740–810*	3.4	31.1
760–800*	5.5	57.2
855	2.3	51.3
1278	9.7	0

abundant species). In this sample, the cyclostomate *Diplosolen obelia* accounted for 46% of colonies. There was little difference in evenness among the other five samples, in which the most abundant species accounted for 21–27% of the total.

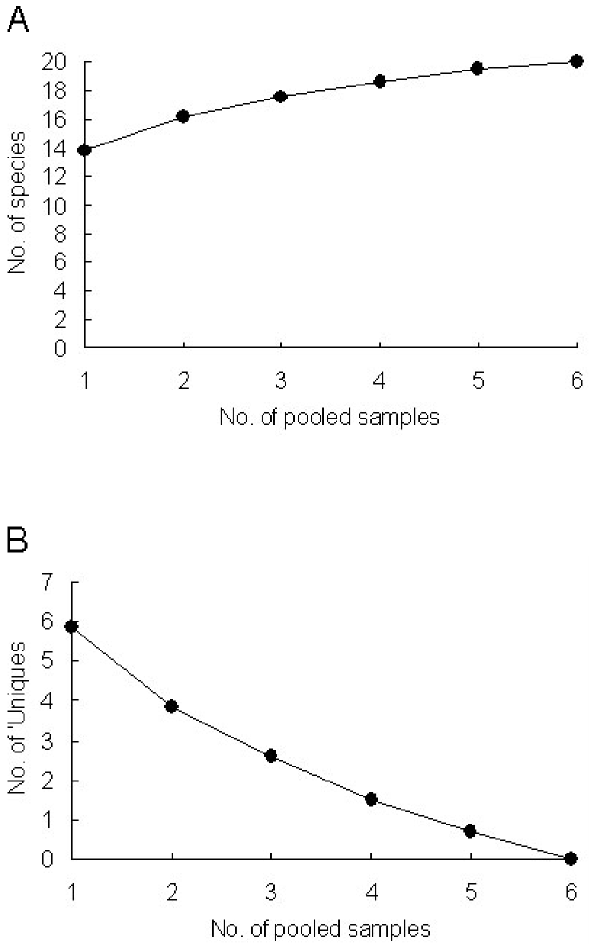

Figure 3. (A) Species accumulation curve for the six stations sampled between 569 and 855 m depth. The total sample consisted of 1489 colonies representing 20 species. Samples were pooled in random order; (B) plot of the number of 'Uniques' (species represented by a single colony) against number of randomly-pooled samples for the 569–855 m dataset.

Table 4. *Heterogeneity diversity indices for the six bryozoan samples from the 569–855 m depth range. H′ is the Shannon–Wiener index (log base 2). Samples marked with asterisks represent overlapping depth ranges.*

Sample depth (m)	Exp (H′)	Berger–Parker
569	8.63	0.46
665	19.32	0.25
717	25.10	0.21
740–810*	24.85	0.24
760–800*	25.28	0.25
855	18.99	0.27

Among the common bryozoan species (defined as those making up >10% of the colony total in any sample), *Diplosolen obelia* and *Entalophoroecia deflexa* peaked in relative abundance at the shallow end of the 569–855 m range (Table 2), whereas *Plagioecia patina* was most common in the deepest sample. *Disporella hispida, Escharella octodentata* and *Celleporina pygmaea* made their greatest percentage contribution in the 740–810 m range. *Oncousoecia dilatans* and *Hemicyclopora polita* showed no marked trends in relative abundance over this depth range.

DISCUSSION

Comparison with other bryozoan faunas of the north-east Atlantic continental slope

The species list presented here is in accord with the known composition of offshore bryozoan communities in the boreal north-east Atlantic. All of the species have geographical ranges that are known to encompass the survey area or could be expected to do so. Minor range extensions are noted for *Alcyonidium* candidum, *Palmiskenea faroensis* and cf. *Daisyella bathyalis*. The low intensity of sampling for hard-substratum epifauna along the shelf edge means that the bathymetric ranges of offshore bryozoans are mostly ill-defined, but none of the species recorded here are unexpected in an upper-slope setting (Hayward & Ryland, 1985, 1998, 1999).

Given the scarcity of quantitative information on the structure of deep-water bryozoan communities, there are few direct comparisons to be made with the patterns described here. The abundance of cyclostomate bryozoans (which were numerically dominant in the 569 and 665 m samples) does not appear to have been noted before on the north-east Atlantic continental slope. None were found in samples from the slope near Brittany (Hayward, 1978), and only unidentifiable abraded specimens from deep stations off Spain and Portugal (Hayward, 1979). Cyclostomates are present in deep-water samples from the Biscay area (Hayward & Ryland, 1978) and their systematics have been reviewed by Harmelin (1979), but these authors made no comment on their abundance relative to cheilostomates. Fernandez Pulpeiro et al. (1988) counted bryozoan colonies on fragments of the coral *Lophelia pertusa* from four stations (depths 198–274 m) in the Norwegian Sea. Although community structure was not analysed, their data show that cyclostomates made up 44–75% of the colony totals, figures very similar to those presented here. At present there are too few data to determine whether cyclostomates are genuinely more abundant in high-latitude deep-water bryozoan communities or if this is merely a sampling artefact.

The inference that the 20 species recorded in the 569–855 m depth interval represent all (or nearly all) of those present is also difficult to place in context owing to the scarcity of data from comparable habitats. The continental slope off northern Spain yielded 21 bryozoan species from a closely-grouped set of stations covering a depth range of 570–910 m (Hayward, 1979). The depths and species count are virtually the same as on the Hebridean slope but the amount of material examined was not stated. *Ramphonotus minax* and *Hemicyclopora polita* were the only species found in both collections. Jensen & Frederiksen (1992) listed 45 bryozoan species on *Lophelia* rubble from the Faroe shelf (252–260 m), of which 12 are shared with the Hebridean collection. Although substratum area and bryozoan colony numbers were not recorded, species number is clearly much higher than the estimate of 20 for the 569–855 m zone on the Hebridean slope.

Environmental determinants of community structure

It has been suggested that the availability of hard substratum limits the abundance and diversity of bryozoans beyond the continental shelf edge (Hayward, 1978). On the stonier upper slope habitats sampled in this study the abundance of ice-rafted dropstones means that there is no shortage of hard substratum for larval settlement. However, the small average size of the individual rocks severely limits the space available for subsequent growth and probably accounts for the prevalence of spot colony form among the species found here. Competition for space is an important structuring factor in many shallow-water bryozoan communities where colony densities are high (Jackson, 1979; López Gappa, 1989) but at the low densities recorded here it is unlikely to be significant. Only where the seabed is composed mainly of fine sediments (at depths below about 1000 m in this area) will space for both settlement and growth become limiting. The 1278 m sample shows that bryozoans are able to colonize pebbles as small as 1–2 cm diameter on a predominantly muddy bottom. It is probably significant that the only two species recorded at this depth (*Turbicellepora boreale* and *Sarsiflustra abyssicola*) are both capable of erect growth and are thus able to take maximum advantage of the extremely limited hard substratum available for larval settlement.

Oschmann (1990) noted the low spatial coverage of epifauna on dropstones from the Norwegian Sea and proposed seasonal food scarcity as a factor limiting community development. Shallow-water bryozoans feed mainly on photosynthetic flagellates and other microalgae (Winston, 1977; McKinney, 1990), but deep-sea species must presumably rely on some combination of heterotrophic protists, non-living particulate detritus and (possibly) dissolved organic matter. In the survey area, epifauna at the 569–917 m stations will be exposed to the northward-flowing Hebridean slope current (Huthnance, 1986; Howe & Humphery, 1995). Near-bed velocities up to 45 cm s^{-1} were measured near the shallowest station in this survey, and bottom currents elsewhere were also strong (Jones et al., 1998). This water movement will be important in maintaining a supply of resuspended detritus that can be exploited by suspension-feeders. However, too little is known about the trophic ecology of deep-water suspension-feeders to say if either the absolute quantity of food available, or seasonal variations in its supply, act as a limiting factor on populations.

Use of hard substratum epifauna in environmental assessment on the continental slope

The difficulty of obtaining replicate quantitative samples on deep hard substrata is one reason why there is as yet no baseline against which potential anthropogenic impacts on these habitats can be detected. In the present survey, linear scars produced by trawling were observed on 2–12% of seabed photographs taken at stations in the 900–1300 m depth range, but were not seen at 700 m (Roberts et al., 2000). The deepest bryozoan communities described here may therefore have already been subjected to anthropogenic disturbance, but the extent to which this may have contributed to the observed depth-related patterns is unknown.

The novel contribution of this paper to our understanding of continental slope bryozoan communities is the quantification of total abundance in relation to rock substratum area and the construction of a species accumulation curve for the 569–855 m depth interval. Although bryozoan colonies are not strictly equivalent to the unitary organisms counted in most analyses of marine benthic diversity, the approach taken here shows that quantitative information on community structure can be obtained if the effort is made to count colonies and relate numbers to a standardized unit of available substratum area. It is important that future studies should aim to move beyond the compilation of species lists and generate numbers as well as names wherever possible.

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