

Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras

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The spatial heterogeneity of epifauna on a Modiolus modiolus reef off north-west Wales was investigated using divers. The community associated with these horse mussels was similar to that described previously from Loch Creran and the north basin of Strangford Lough. Some differences in epifauna may be attributable to the less sheltered nature of the site. Modiolus modiolus numbers and the associated epifaunal community were significantly different between ridge and trough sub-habitats. Troughs can be considered 'reduced' ridge communities whereas ridges have high densities of horse mussels and certain sessile taxa were correlated with their abundance. Modiolus modiolus aggregation as a competitive response to the feeding environment, enhanced food availability on ridges and sediment deposition amongst mussel clumps may start to explain the undulating bed-form. Patchiness in community composition and periodic cover by ophuroids has implications when considering the monitoring of the horse mussel community. Stratified, in situ recording of the highly populated ridges could improve the statistical sensitivity of monitoring horse mussel reefs whilst simultaneously focusing on the more sensitive indicators of fishing threats.

Keywords: *Modiolus*, biogenic reef, bioherm, epifauna, Irish Sea, community heterogeneity, monitoring, indicator, SAC, conservation management

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INTRODUCTION

Biogenic *Modiolus modiolus* (L.) reef communities are rich in species (e.g. Thorson, 1971; Holt *et al.*, 1998; Rees *et al.*, 2008) and have a limited distribution in UK coastal waters (see Holt *et al.*, 1998). They are of nature conservation importance partly because of the rich assemblage of organisms associated with them, and they are identified as one of the important reef types in Special Areas of Conservation (1992 EC Habitats and Species Directive: Council Directive 92/43/EEC) and as a priority habitat by the Oslo Paris Commission (OSPAR). Lindenbaum *et al.* (2008) provide evidence that established reefs are long-lived features of 150 years or more. However, some *M. modiolus* beds have been degraded or destroyed by fisheries using mobile gear, particularly scallop dredges and trawls (Service & Magorrian, 1997; Veale *et al.*, 2001; Roberts *et al.*, 2004).

Some *M. modiolus* reefs appear on side-scan sonar images to have an undulating bed-form (see Wildish *et al.*, 1998). This morphology is characteristic of the reef surveyed in our study, which was located in the Irish Sea, north of Pen Llŷn, in north-west Wales (52°56' N 04°38' W; Lindenbaum *et al.*, 2008; Figure 1). Side scan sonar and multibeam images from this

reef area are shown in part I of this series of papers (Lindenbaum *et al.*, 2008), where the extent of the reef, mapped by applying geographical information system methods to geoaoustic data, is shown to be between 349 and 373 ha.

Photographic series from sledge-mounted still-cameras triggered by timers had previously indicated patchiness in epifaunal composition at this site (E.I.S. Rees, personal observation) as did a diving survey (Bunker, 1999). Some of the spatial variation seemed to relate to the sequence of sub-habitats associated with the undulating surface, where a mass of *Alcyonium digitatum* (L.) colonies and other fauna appeared to be attached to the live *M. modiolus*. Variation in community assemblage associated with the physical structure or complexity of mussel matrices have been shown in other species (Suchanek, 1980; Tsuchiya & Nishihara, 1985, 1986; Asmus, 1987; Lintas & Seed, 1994; Stewart *et al.*, 1998) and mussel beds often support diverse macrofaunal communities (e.g. Lintas & Seed, 1994; Gunther, 1996; Seed, 1996; Ragnarsson & Raffaelli, 1999; Thiel & Ullrich, 2002; Tsuchiya, 2002) especially when compared to surrounding assemblages (Valentine & Heck, 1993; Crooks, 1998). The present work aimed to use targeted *in situ* recording by divers to measure the spatial variations in the epifaunal community between the sub-habitats formed by the ridge and trough morphology of the horse mussel reef. Monitoring the horse mussel reef is desirable because of its designated importance in European legislation and

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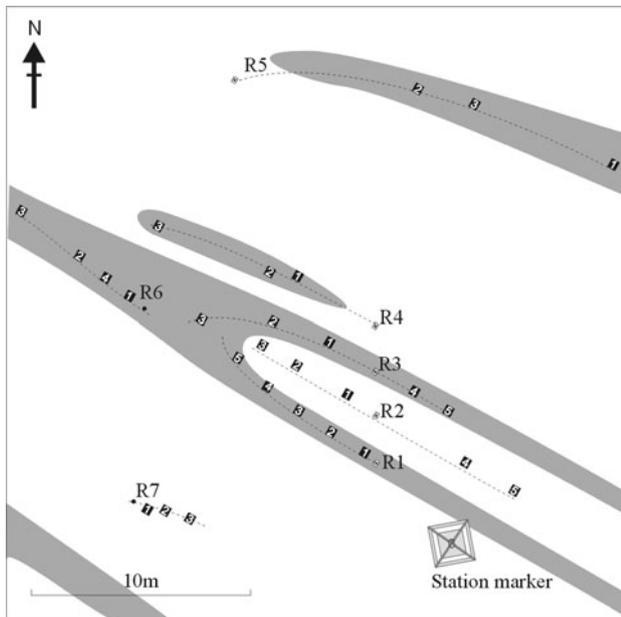


Fig. 1. Schematic scale diagram of epibenthic quadrats at the north Pen Llŷn *Modiolus* reef station in June 1999. Quadrat positions were deployed along transects originating from row markers (R1–R7). Grey areas indicate distinctive ridges.

identifying, accounting for, and removing sources of natural variation is an important precursor to the development of assemblage-based monitoring schemes (e.g. Holland *et al.*, 1987; Underwood, 1997; Krebs, 1999).

MATERIALS AND METHODS

Using the acoustic mapping work of Lindenbaum *et al.* (2008: figure 4), a fixed benthic station marker, re-locatable by an acoustic beacon, was placed on part of the same horse mussel reef. The station was 1.5 km from the north Pen Llŷn coast (Lindenbaum *et al.*, 2008; Figure 1) with a prevailing south-westerly fetch to St Georges Channel and the Irish coast of about 200 km. The depth was 32 m below chart datum and the seawater was fully saline in this area with an average spring tidal run of approximately 2 knots or 100 cm s^{-1} (Hydrographic Office, 1992). Near-benthic seawater temperatures here typically range from 8 to 16°C over a year (W.G. Sanderson & R.H.F. Holt, unpublished data). Ridge and trough sub-habitats around the station were marked by SCUBA divers on 5 June 1999. Quadrats were then deployed at stratified random positions along transect lines on five reef ridges and two troughs (rows 1–7; Figure 1). The quadrats used were 0.5 × 0.5 m and were divided into 25 equal squares with cord to assist *in situ* recording. A team of divers were trained to recognize a list of species based on a previous inventorial survey (Bunker, 1999) and to spread observer variability across the bed-form types each person recorded from the different ridge and trough features.

All multivariate analyses employed the Bray–Curtis similarity coefficient and were carried out using PRIMER v.6 (Clarke & Gorley, 2006). Numerical abundances in the cluster analysis of the quadrat samples were scaled by a square root transformation in order to limit the influence of species exhibiting high numerical dominance. The hierarchy of the dendrogram was determined by group average fusion

and a SIMPROF permutation procedure tested the significance (at 5% level) of the clusters. Analysis of similarities (ANOSIM) was used to examine the effect of the location factor, and the species contributing most to the dissimilarity between ridge and trough samples were examined using SIMPER analysis.

Still photographs from an underwater camera sledge survey of the whole horse mussel reef in July 1994 and video footage from another survey across the reef in July 1999 (E.I.S. Rees, unpublished data) were reviewed to provide context to the present work.

RESULTS

The majority of epifaunal species encountered were readily enumerated *in situ*. However, some species could not be reliably counted because they were small and hidden in the crevices made by the *Modiolus modiolus* clumps. For this reason *Alcyonium digitatum* colonies <15 mm were not counted and records of several abundant species such as the porcelain crab *Pisidia longicornis* (L.), saddle oyster *Pododesmus patelliformis* (L.), slit-limpet *Emarginula fissura* (L.), calcareous tubeworm *Pomatoceros* spp., and the barnacles *Balanus balanus* (L.) and *Verruca stroemia* (Müller) were excluded from subsequent multivariate analyses. Colonies of the hydroids *Abietinaria abietina* (L.) and *Halecium halecinum* (L.) were too aggregated for separate colonies to be counted so the numbers of clumps were recorded.

Divers noted 61 epifaunal taxa on the ridges and 27 in the troughs (Figure 2). All except four of the taxa from troughs were also found on the ridges. Of these, two were single records of motile fauna (*Liocarcinus depurator* (L.) and *Onchidoris bilamellata* (L.)) and the others were incompletely determined taxa (Hydrozoa indet. and ?*Polycarpa* sp.) that could have been species that were recorded on the ridges.

Table 1 shows the estimated numbers m^{-2} of the more abundant taxa that could be counted *in situ*. *Modiolus modiolus* (not including spat) was about 17 times more abundant in the ridge than the trough quadrats. Similar or greater differences applied to the species that preferentially settle on the living mussels, such as *Alcyonium digitatum* and *Chlamys varia* (L.). For species less directly exploiting the mussels for attachment the differences were much less, these included the brittle star *Ophiothrix fragilis* (Abildgaard), the gastropod *Hinia incrassata* (Ström), the hermit crab *Pagurus bernhardus* (L.) and the sea urchin *Psammechinus miliaris* (Gmelin).

Clustering and ANOSIM showed the separation between the ridge and trough quadrats (Figure 3; Table 2). Collectively, trough records accounted for at least 40% of the total dissimilarity. Individual ridges did not seem to show any aggregation. Dissimilarities between rows 4 and 5 and row 7 were not statistically significant (Table 2) but these ridges were reported to be more morphologically variable and had lower levels of replication.

Within the group of quadrats from the ridges there were significant positive correlations between the ranked abundances of *Modiolus modiolus* in each quadrat and the abundances of *Alcyonium digitatum*, and *Chlamys* spp. (Table 3). Porifera and Decapoda were also correlated with mussel abundance, but there was no significant relationship for *Ophiothrix fragilis*, Hydrozoa or Gastropoda.

The brittle star *Ophiothrix fragilis* was common on still images from the July 1994 survey but in video footage from

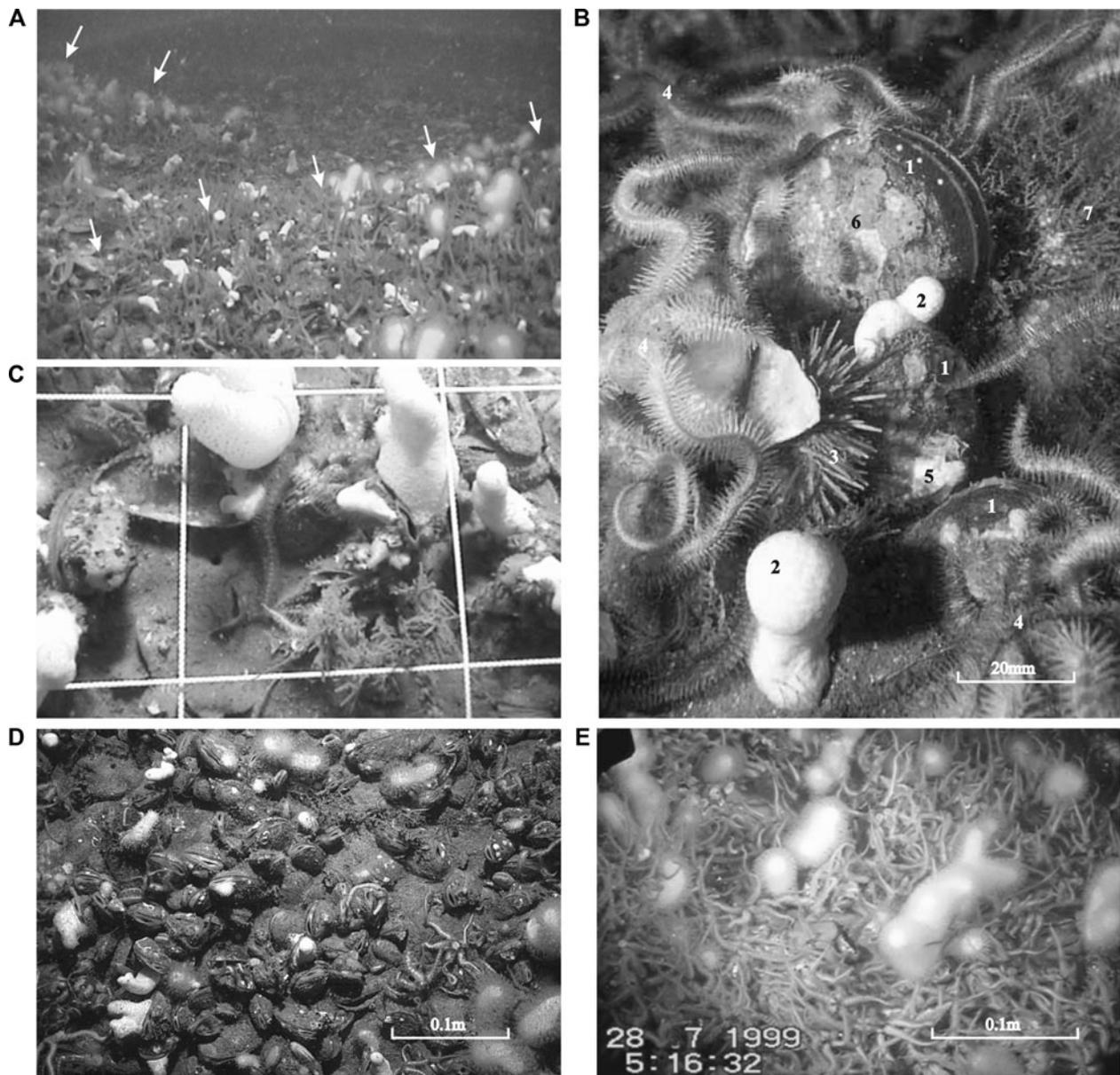


Fig. 2. North Pen Llŷn *Modiolus modiolus* reef. (A) General view of bed-forming ridges (arrows); (B) close-up view of horse mussel ridge community: 1, *Modiolus modiolus*; 2, *Alcyonium digitatum*; 3, *Psamechinus miliaris*; 4, *Ophiothrix fragilis*; 5, *Balanus balanus*; 6, encrusting Bryozoa indet.; 7, *Sertularella* sp.; (C) image from video record of quadrat from row 7. One complete sub-square (10×10 cm) is visible; (D) image from towed camera on sled during July 1994; and (E) image from towed video in approximately the same place and depth (30 m) as D in July 1999. Images from: (A) Paul Kay, Marine Wildlife Photo Agency; (B) B. Sanderson; (C) R. Holt; (D) I. Rees; and (E) University of Wales Bangor/Countryside Council for Wales.

July 1999 it was so abundant that *M. modiolus* were often entirely obscured by them (Figure 2D & E).

DISCUSSION

Our study finds the same three main components of the *Modiolus modiolus* reef as Magorrian (1996) in Strangford Lough: (a) very dense aggregations of living *M. modiolus* and dead shells; (b) an assemblage of free living and sessile epifauna and predators; and (c) a diverse community which shelters in the crevices between the *M. modiolus* shells and the byssus threads, and which flourishes on its sediment. This seems to be a predictable pattern (Holt *et al.*, 1998) and closely corresponds to the overall components of *Mytilus edulis* beds (e.g. Seed & Suchanek, 1992).

Three different *M. modiolus* bed community types were found by Mair *et al.* (2000) in three Scottish sea-lochs. Although there were many similarities in species due to the niches provided by the horse mussels, there were distinctions due to turbidity, depths at which red algae could grow and tidal currents. The Pen Llŷn horse mussel reef community compares well with the tide swept beds described in Loch Creran by Mair *et al.* (2000) and those from the north basin of Strangford Lough described by Erwin *et al.* (1990) and Roberts *et al.* (2004). Connor *et al.* (2004) described this community as '*Modiolus modiolus* beds with *Chlamys varia*, sponges, hydroids and bryozoans on slightly tide-swept very sheltered circalittoral mixed substrata' (i.e. tidal streams < 1 kn or 50 cm s^{-1} to 3 kn or 150 cm s^{-1} and fetch < 20 km). The Pen Llŷn location has tidal streams in the middle of this range but is not 'sheltered' from wave action.

Table 1. Abundances, converted to N/m² of the species contributing most to significant ridge/trough dissimilarity based on 28 quadrats. (ANOSIM significant at 0.1% based on 999 permutations; global R value 0.721.) The contribution and cumulative contribution made by each species to this difference was provided by SIMPER analysis.

Species	Ridge N = 20	Trough N = 8	Contribution (%)	Cumulative (%)
<i>Alcyonium digitatum</i> ² (size >15 mm)	126	9	15	15
<i>Modiolus modiolus</i> (not including spat)	100	6	14	30
<i>Ophiothrix fragilis</i>	95	68	12	42
<i>Chlamys varia</i>	24	0	7	49
<i>Hinia incassate</i>	19	13	4	53
<i>Buccinum undatum</i> ²	11	3	4	57
<i>Pagurus bernhardus</i>	8	7	3	61
<i>Abietinaria abietina</i> (clumps)	7	2	3	64
<i>Asterias rubens</i>	3	0	2	66
<i>Dysidea fragilis</i> ³	3	0	2	68
<i>Psammechinus miliaris</i> ²	7	5	2	70
<i>Calliostoma zizyphinum</i>	3	1	2	71
<i>Phorbas fictitius</i> ³	3	0	2	73
<i>Balanus</i> spp. ¹ (probably under-recorded)	223	4	n.a.	n.a.
<i>Pomatoceros triquetus</i> ¹ (under-recorded)	5	2	n.a.	n.a.

¹Species not included in multivariate analyses; ²species sensitive to scallop dredging (Hill *et al.*, 1997, 1999); ³Poriphera likely to be sensitive to scallop dredging (Veale *et al.*, 2001); n.a., not applicable.

On the Pen Llŷn reef, *Modiolus modiolus* and *Chlamys varia*, bryozoans, hydroids and sponges were nevertheless abundant. As in Loch Creran and Strangford Lough, *Alcyonium digitatum* and *Pisidia longicornis* were also abundant fauna but the open coast Pen Llŷn reef lacked some of the abundant sheltered fauna from Loch Creran and Strangford Lough such as the caprellid *Phtisica marina* (Slabber); the ascidian *Pyura microcosmus* (Savigny) and the holothurians *Thyone fusus* (Müller) and *Thyonidium drummondii* (Thompson) (see Millar, 1970; Picton, 1993).

Despite the significant difference between the trough and ridge community, species composition was markedly similar in our study with most of the dissimilarity between ridges and troughs explained by greater abundance on the ridges rather than species exclusive to either sub-habitat (Table 1). Trough communities are therefore 'reduced' ridge communities, in epifaunal terms, rather than truly different assemblages. This is in keeping with the lower number of *M. modiolus* in the trough areas (Table 1) and the associated reduction in habitat complexity.

Horse mussel numbers are greater on the ridges at this site than in any other comparable UK study (Roberts, 1975; Mair *et al.*, 2000; Roberts *et al.*, 2004), although records by divers underestimate the actual number recorded from samples (see Rees *et al.*, 2008). Dense *M. modiolus* can cause depletion in seston concentrations (Wildish & Kristmanson, 1984, 1985) and food limitation can occur in dense aggregations of intertidal and infaunal bivalves (e.g. Fréchette & Bourget, 1985; Peterson & Black, 1987). Food availability has also been implicated as one of the factors influencing the distribution and

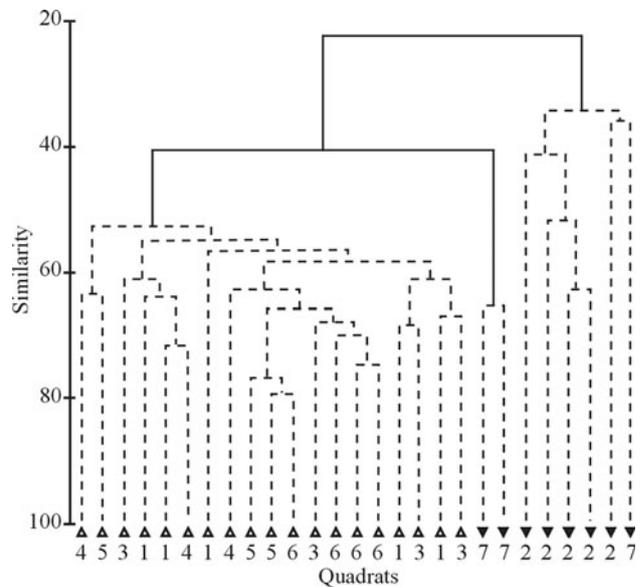


Fig. 3. Cluster diagram based on Bray-Curtis similarity matrix for square root transformed epifaunal records on the horse mussel bed. Codes for records indicate the ridges/troughs from which they are derived (see Figure 1). Hatched lines, non-significantly differing quadrats (SIMPROF $P > 0.05$); open triangles, ridge; filled inverted triangles, trough.

density of *M. modiolus* in the Gulf of Maine (Lesser *et al.*, 1994). Therefore, competition for available suspended food resources in the downstream benthic boundary layer may be partly responsible for the greater aggregation of horse mussels and other suspension feeders on the ridges of the reef where there is a greater chance of escaping near-bed food-depleted water. Elevated position may also increase flow rates over a biogenic reef and therefore enhance food supply further (e.g. Lenihan, 1999). Greater accretion and less winnowing of fine faecal muds also occurs in areas of high mussel density and accumulated sediment and mussel density have been shown to play an important role in structuring mussel patch communities in the intertidal (e.g. Seed & Suchanek, 1992; Crooks, 1998). Overall, the processes of aggregation and deposition may start to explain the undulating bed-form of the Pen Llŷn reef (see Lindenbaum *et al.*, 2007; Figure 2).

The present work shows that, in an epifaunal monitoring campaign, a large degree of the spatial variance in the data could be eliminated if monitoring stations were stratified on ridges in preference to stations throughout the range of sub-habitats present. Removal of sources of variation in space and time are common issues in monitoring (e.g. Holland *et al.*, 1987; Krebs, 1999). This approach would make monitoring horse mussels more sensitive to change (more precise), apparently without having to account for differences in ridges. Additionally, this approach would focus on the richer, more 'biodiverse' fraction of the epifaunal community, which is appropriate because horse mussel reef communities are valued, in part, for being species-rich assemblages.

It is now well established that trawling and dredging can damage seabed communities, emergent epifauna and biogenic reefs (e.g. Watling & Norse, 1998; Auster & Langton, 1999; Cranfield *et al.*, 2003) and scallop dredges and trawls have been documented destroying the structure of *Modiolus modiolus* and *Limaria hians* bivalve reefs in UK waters (Service & Magorrian, 1997; Magorrian & Service, 1998; Hall-Spencer & Moore, 2000). Overall, Auster & Langton

Table 2. R values and significance of pairwise comparisons between rows from analysis of similarities (ANOSIM). Based on 999 permutations: random sample from a large number. Global test has R value of 0.368. Significant at 0.1%. Significantly different pairwise comparisons in bold.

R values: Row	1	2	3	4	5	6
2	0.88	–	–	–	–	–
3	–0.175	0.919	–	–	–	–
4	0.272	0.795	0.056	–	–	–
5	0.241	0.764	0.333	–0.185	–	–
6	0.075	0.831	0.198	0.315	0.074	–
7	0.682	0.621	0.556	0.481	0.444	0.648
Significance:						
2	0.8	–	–	–	–	–
3	84.1	0.8	–	–	–	–
4	14.3	1.8	40	–	–	–
5	10.7	1.8	8.6	90	–	–
6	30.2	0.8	5.7	11.4	31.4	–
7	1.8	3.6	2.9	10	10	2.9

Table 3. Spearman's rank correlation with abundance of *Modiolus modiolus* in quadrats from ridges.

<i>Alcyonium digitatum</i>	0.594	*
Porifera spp.	0.581	*
<i>Chlamys</i> spp.	0.516	*
Decapoda	0.468	*
Hydrozoa	0.171	n.s.
Gastropoda	0.078	n.s.
<i>Ophiothrix fragilis</i>	0.058	n.s.

*, significant; n.s., not significant.

(1999) found that in 22 studies, mobile fishing gear reduced habitat complexity; removed or caused epifauna to be killed; smoothed sedimentary bed-forms and reduced bottom roughness and removed taxa that produce structure. The epifaunal element of the *M. modiolus* community that protrude from the reef are sensitive to queen scallop fisheries (Magorrian & Service, 1998; Roberts *et al.*, 2004). Species such as the dead-man's-fingers *Alcyonium digitatum*; the sea urchin *Psammechinus miliaris* (Gmelin); the whelk *Buccinum undatum* (L.); the spider crabs *Inachus* and *Hyas*; and sponges were all concentrated on the ridges in our study (e.g. Table 1) and have all been found to be damaged by scallop fishing elsewhere (Hill *et al.*, 1997, 1999; Magorrian & Service, 1998; Veale *et al.*, 2001; Roberts *et al.*, 2004). Mobile fishing gear presents one of the greater threats to the Pen Llŷn reef and therefore sensitive erect sessile species, found in greatest numbers on the more complex ridges of the horse mussel reef, are an important indicator of anthropogenic activity within the Special Area of Conservation. The abundant *Ophiothrix fragilis* in the present study and the video images from July 1999 (Table 1; Figure 2) were not seen in the images from the 1994 survey. Mair *et al.* (2000) also showed another ophiuroid, *Ophiopholis aculeata*, to vary considerably between surveys in Loch Creran and, although Holme (1984) related major changes in brittle star beds in the Plymouth area to changes in the predatory starfish *Luidia ciliaris*, there is no apparent mechanism for the variation we observed. However, temporal variability in echinoderm populations could create difficulties in viewing the ridge epifauna in a

monitoring time series with remote camera methods, whereas divers are able to look-around such obstructions (e.g. Munro, 2005).

Overall, this study shows that *in situ* recording, stratified to ridges, could reduce variance associated with monitoring the fauna of the horse mussel reef, improving the statistical sensitivity of a monitoring campaign and simultaneously focusing on the more sensitive threat indicators relevant to management.

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