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To what extent does upright sessile epifauna affect benthic biodiversity and community composition?

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Abstract Small-scale habitat complexity, including that caused by biological structures, is an important factor in structuring benthic communities and also sometimes in increasing biodiversity. The aim of this study was to determine if hydroid colonies have an effect on the composition of benthic communities in the Irish Sea, and if so, which components of the fauna are affected. Forty-six seabed core samples were taken by divers from two sites off Port Erin, Isle of Man, Irish Sea. Half of these were centred on hydroid colonies, half were not. All taxa retained by a 63-μm sieve from the cores were identified and counted. Community composition and diversity were compared between hydroid and non-hydroid cores using multivariate and univariate methods. Benthic communities were significantly different between the two sample groups. This was almost entirely due to the presence of sessile and mobile epifaunal taxa in the hydroid cores. The tube-building amphipod, *Ericthonius punctatus*, was particularly abundant attached to the hydroid stems. Infauna was not significantly different between the two groups. Upright sessile epifauna may play a particularly important role in the Irish Sea as a settlement substrate for juvenile scallops (*Pecten maximus* and *Aequipecten opercularis*), which are an important fishery resource in this area. The 11-year closure of an area to dredging has not only enhanced scallop stocks but has had the added benefit of enhancing habitat complexity and biodiversity.

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Introduction

Sessile epibiota provide a resource for a range of other animals and plants (Collie et al. 1997; Gili and Hughes 1995). Encrusting animals (e.g., worms, amphipods, bryozoans, hydroids, sponges) use them as substrates on which to settle. This also raises them into the water column, potentially increasing the food supply to filter feeders. Some animals feed on sessile species or other epibiota (e.g., grazers on algae), sometimes forming quite specific associations (e.g., nudibranchs with bryozoans/hydroids), or use them as a place to mate and/or lay eggs (e.g., various molluscs). More mobile animals, including juveniles, use these upright structures to shelter from currents or predators (e.g., Auster et al. 1997, juvenile hake; Jonsson et al. 2001, various crustaceans) or as a base from which to hunt prey (Flynn and Ritz 1999). Sessile epibiota may also stabilise the seabed by binding sediment in roots or stolons, or by forming a baffle to water currents.

All types of sessile epibiota support diverse associated fauna. For example, seagrass beds in tropical and temperate settings support a rich epifauna and infauna and also act as nursery grounds for juveniles of many species (e.g., Heck et al. 1995; Nagelkerken et al. 2001). Examples from other habitats include: the diverse fauna found on serpulid worm tubeheads (Kaiser et al. 1999); epizoites on the hydroid *Nemertesia antennina* (Hughes 1978, 1979); epifauna on the tubes of the worm *Phyllochaetopterus socialis* (Nalesso et al. 1995); tube-building amphipods on tubes of the burrowing anemone *Cerianthus lloydi* (Moore and Cameron 1999); a diverse sponge-associated fauna off the Faroe Islands (Klitgaard 1995); species-rich bryozoan reefs (Cranfield et al. 1999); the diverse epifauna of horse mussel (*Modiolus modiolus*) beds (Jones 1951; Magorrian and Service 1998); epifauna of oyster and polychaete (*Sabellaria spinulosa*) reefs (Reise and Schubert 1987); macroinvertebrate assemblages inside patches of the pinnid bivalve *Atrina zelandica* (Cummings et al. 1998); and epifauna on deep-sea glass sponges (Beaulieu 2001).

Many studies have examined the effect of habitat structure on the survivorship of commercially valuable fish species, particularly salmon and trout in freshwater streams (e.g., Quinn and Peterson 1996; Vehanen et al. 2000) but, more recently, also marine species such as hake (Auster et al. 1997) and cod (Lindholm et al. 1999, 2000). In many cases, the survivorship of juvenile fish is higher in structurally complex habitats, although results vary with different habitats, levels of complexity, and behavioural interactions between species.

Sessile epifauna is an important component of the benthos around the Isle of Man (Irish Sea; Fig. 1). The substrate in many areas is coarse and gravelly, with abundant shell fragments, providing an attachment substrate for many hydroids (e.g., *Halecium* spp., *Hydrallmania falcata*, *Nemertesia* spp., *Sertularella* spp., *Sertularia cupressina*), upright bryozoans (e.g., *Cellaria* spp., *Crisia* spp., *Scrupocellaria* spp.), tunicates (e.g., *Ascidia* spp., *Ascidiella* spp., *Ciona intestinalis*, *Corella parallelogramma*), and octocorals (*Alcyonium digitatum*). Strong tidal currents also provide these filter feeders with a good food source.

This study tests whether upright sessile epifauna (specifically hydroids) increase biodiversity and/or species abundance of both epifauna and infauna. It also discusses the relevance of upright epifauna to commercial scallop dredging (an important Irish Sea industry), as scallop spat has been reported to settle predominantly on hydroids and bryozoans (Brand et al. 1980; Dare and Bannister 1987; Eggleston 1962).

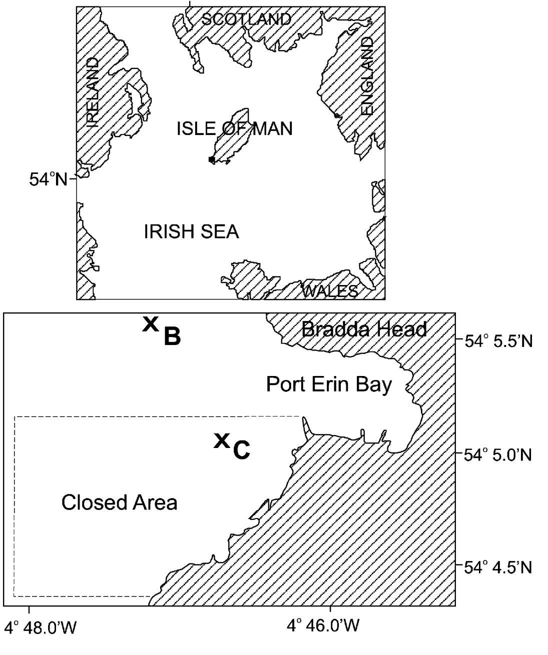

Fig. 1 Positions of the sample area to the south-west of the Isle of Man, and the positions of sites *B* (Bradda) and *C* (closed area) just west of Port Erin Bay

Materials and methods

Location and site selection

Preliminary dives were undertaken to select 100-m^2 areas of seabed with similar densities (approximately 0.2 colonies m^{-2}) of hydroid colonies (regardless of hydroid species). Two sites were chosen, one off Bradda Head (B) and one in the closed area (C; Fig. 1), both at around 25 m water depth. Site B is in an area of high scallop fishing effort, whereas site C previously experienced similarly high effort but has been closed to commercial fishing since 1989 (Bradshaw et al. 2001; Brand et al. 1991). The sediment at both sites consists of muddy sand with stone and shell gravel, although the contribution of the various fractions is slightly different (see below).

Methods

Plastic tubes with an internal diameter of 75 mm, pushed 10 cm into the sediment with the aid of a mallet, were used to take sediment cores of the seabed either with or without colonies of hydroids. The top end was sealed with a rubber bung and the submerged end dug out with a trowel and similarly sealed.

The positions of the cores at each site were chosen haphazardly, within the following limits: large stones, areas covered in sea squirts (*Ascidiella* spp.), and areas recently disturbed by edible crabs (*Cancer pagurus*) were avoided, to reduce variability caused by other factors that may influence faunal composition. Hydroid cores were centred on hydroid clusters of at least 10 cm height. Thirteen hydroid cores and 16 non-hydroid cores were taken at site C; 8 hydroid and 9 non-hydroid cores at site B. All cores were taken between 1 and 10 September 1999.

Within an hour of collection, the cores were extruded into bags and the core tubes rinsed thoroughly to collect all the finer sediment. 500 ml of relaxant (35 ppt $MgCl_2$) were added and left for 10 min, then 500 ml 4% v/v formalin added to preserve the sample. After rinsing the sample over a 63-μm sieve to remove the formalin, all animals were extracted from each core and identified to the lowest possible taxa. The numbers of individuals or colonies of all taxa were counted. Any hydroids were also identified, oven dried, and weighed. The sediment from each core that remained on the 63-μm sieve was dried at 60°C and shaken through a stack of sieves, and the size fractions were weighed to obtain a particle size distribution. The <63-μm fraction was not collected, as analysis of sediment composition in previous studies in the area indicates that this fraction amounts to around half the dry weight of the 63- to 125-μm fraction and would thus make up only 1–4% of these samples. To extract this small amount from the formalin in which it was suspended was considered to be unnecessary for the purposes of this study.

Data analysis

Multivariate clustering methods were used to examine patterns in community structure across all samples (PRIMER software; Plymouth Marine Laboratory). ANOSIM (analysis of similarities) was used to determine whether there was a difference in community composition between sites and/or between hydroid and non-hydroid cores.

Before the faunal communities were examined in more detail, the possible role of sediment characteristics in explaining any of these differences was investigated. A multidimensional scaling (MDS) plot of sites based on the eight sediment fractions was plotted, and BIOENV was used to determine which of these size fractions was most important in structuring the community composition. Graphs of the particle size frequency distributions were also plotted. As a result of the sediment analysis, it was decided to analyse the two sites separately, as sediment characteristics between the two sites were sufficiently different to have an effect on faunal composition.

The species that contributed most to any observed differences in the MDS plots were determined using SIMPER (similarity percentages). Analyses were done on the whole species dataset and on subsets of the fauna, as outlined in the Results section. The total number of species and individuals, species richness, Shannon–Wiener diversity, Pielou's evenness and Simpson's dominance were calculated for each core and differences in those indices between sites and between hydroid and non-hydroid cores were tested using two-way analysis of variance (ANOVA). Univariate indices were also tested for any correlation with hydroid weight.

Results

General trends

The MDS plot of all samples showed a clear difference between communities at sites B and C, and also between hydroid and non-hydroid cores (Fig. 2). A two-way ANOSIM test showed that these effects were both significant. The between-sites comparison gave a global *R* of 0.56, significant at 0.1%; the comparison between hydroid and non-hydroid cores gave a global *R* of 0.45, also significant at 0.1%.

Sediments

The sediments at both sites were bimodally distributed (Fig. 3 top) with a coarse and a fine peak at around 2–4 mm and 0.2 mm, respectively. However, the sediment structure differed slightly between the two sites, with peak frequencies at site B being slightly coarser than at site C. In particular, the site B cores had many more particles in the 0.125–0.5 mm categories. There was no difference between the sediment in the hydroid and non-hydroid cores (Fig. 3 bottom). This result was confirmed by an MDS plot based on clustering by sediment fraction percentages; two-way crossed ANOSIM analyses gave a between-sites global *R* of 0.79 (significant at 0.1%) and a hydroid/non-hydroid global *R* of 0.023 (not significant, $P = 24.7\%$). A BIOENV analysis done on the full species dataset showed that the community composition correlated best with a combination of the 1–2 mm and 0.25–0.5 mm fractions, but the correlation was low at 0.435.

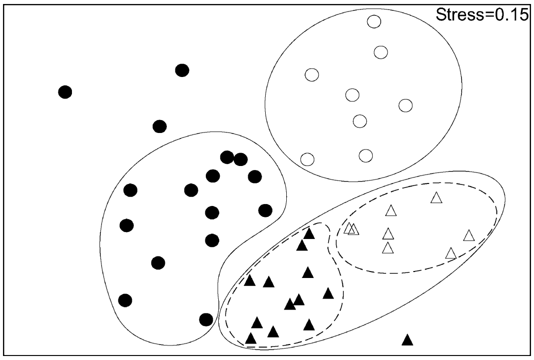

Fig. 2 Multidimensional scaling (MDS) plot of all core samples. Data is fourth-root transformed, standardised, and based on Bray–Curtis similarities. *Circles* samples without hydroids, *triangles* those with hydroids. *White symbols* site B, *black symbols* site C. *Solid lines* 45% similarity, *dashed lines* 49% similarity

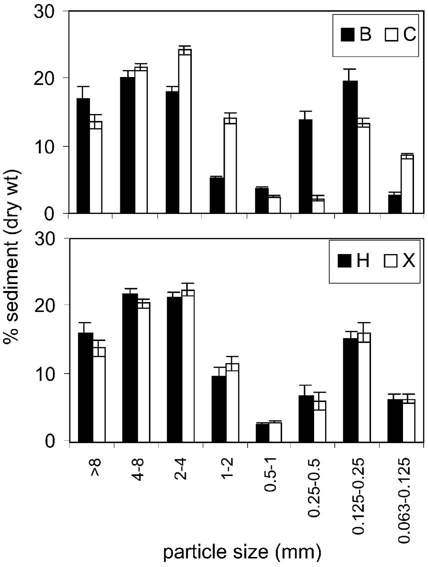

Fig. 3 Sediment particle size distribution: *top* comparing sites B and C, and *bottom* comparing hydroid (*H*) and non-hydroid (*X*) cores

It was concluded that sediment particle size was different between the sites but not between hydroid/non-hydroid cores. A comparison of the communities of the two sites using SIMPER also found there to be distinct differences between the fauna, mainly due to encrusting epifaunal species (mostly bryozoans, but also the encrusting calcareous worm *Pomatoceros triqueter*) being more abundant at site B. It was therefore decided to proceed with the analyses on a site-by-site basis.

Community analysis: effect of hydroids

Cluster analysis shows a clear difference between communities in hydroid and non-hydroid cores at both site B and site C (Fig. 4). SIMPER analysis (on fourth-root-transformed, standardised data) determined the 15 species contributing most to these differences (Table 1) and a one-way ANOSIM test showed this difference to be significant ($P < 0.1\%$) at both sites (site B: global $R = 0.624$; site C: global $R = 0.399$).

The observed difference was due mainly to the greater abundance of epifaunal taxa in the hydroid cores. These taxa fall into three main groups:

1. Taxa that physically attach themselves to the hydroids; especially the amphipod *Ericthonius punctatus*, but also juvenile bivalves (Pectinidae, Mytilidae, and Anomiidae) and the encrusting bryozoans *Electra pilosa* and *Fenestrulina malusii*.
2. Taxa that live amongst the upright structure of the hydroids. The amphipods *Photis longicaudata*,

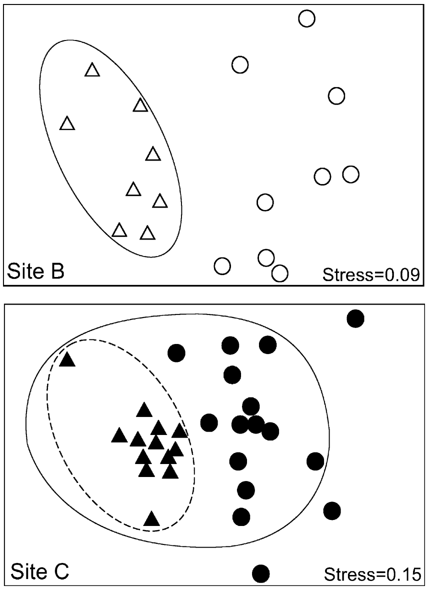

Fig. 4 MDS plots showing the difference in community structure between hydroid (*triangles*) and non-hydroid (*circles*) cores at the two study sites (full dataset, fourth-root transformed and standardised, Bray–Curtis similarities). At site B, all samples are similar at 48%, hydroid samples at 55.5%. At site C, *solid line* indicates 45% similarity, *dashed line* 53% similarity

Stenothoe marina, *Aora gracilis*, and *Gammaropsis maculata*; the caprellids *Pseudoprotella phasma* and *Phtisica marina*; the tanaid *Leptognathia gracilis*; and the worm *Pholoe inornata* are all more common in hydroid cores. At site B, the crinoid *Antedon bifida* also falls into this category. The worms *Autolytus* sp. and *Syllis* sp. might also be included here, or in the following category.

3. Mobile taxa that shelter at the base of the hydroid clump, for example, the squat lobster *Galathea intermedia* and the brittlestars *Ophiura* sp.

The main differences in community composition between hydroid and non-hydroid cores were therefore, unsurprisingly, due to the epifaunal (hydroid-associated) species. A further analysis was run to determine if the other components of the fauna that are not generally considered to associate with hydroids were also being affected in any way by the presence or absence of hydroids but were being masked in the analysis by the more abundant hydroid epifauna. Thus, the species known from the literature to commonly associate with hydroids (either exclusively or non-exclusively) were removed from the dataset and the analysis re-run. MDS plots indicated that there was still quite a clear between-sites difference, so again the analysis was run within site. At both site B and site C, the hydroid and non-hydroid cores no longer clustered separately, suggesting that the presence of hydroids had no effect on the composition of these species (Fig. 5a). One-way ANOSIM indicated that there was no significant difference between hydroid and non-hydroid cores at either site (site B: global $R = 0.104$, $P = 9.6\%$; site C: global $R = 0.079$, $P = 8.1\%$).

Although no significant differences were demonstrated, a SIMPER analysis was run to test if there were any low-level trends apparent. Not surprisingly, this gave mixed and sometimes conflicting results but did show limited evidence for mobile crustaceans (*Liocarcinus depurator*, Hippolytidae, *Eurynome aspera*, *Hyas coarctacus*) being more abundant in hydroid cores, possibly as they gain shelter around the hydroids. However, these results should be treated with caution.

Table 1 The 15 taxa identified by similarity percentages (SIMPER) analysis to contribute most to the difference between hydroid and non-hydroid communities at each of the study sites. At site C, the average dissimilarity is 57.33%; at site B it is 56.90%

Site C						Site B					
Taxa	E/B[a]	H/B/X[b]	Average abundance		Cum %	Taxa	E/B[a]	H/B/X[b]	Average abundance		Cum %
			Non-hyd	Hyd					Non-hyd	Hyd	
Ericthonius punctatus	E	H	0.2	75.9	4.25	*Ericthonius punctatus*	E	H	0.11	47.88	2.75
Autolytus sp.	B	B	0.3	7.3	6.31	*Stenothoe marina*	E	H	0	18.63	4.70
Photis longicaudata	E	X	3.9	3.8	8.05	*Pseudoprotella phasma*	E	H	0	13.13	6.49
Electra pilosa	E	H	0.1	3.9	9.66	*Aora gracilis*	E	H	0.11	6.38	8.22
Capitellidae	B	B	8.6	7.4	11.24	Mytilid juv.	E	H	0	4.38	9.76
Pectinid juv.	E	H	0.3	1.9	12.77	*Antedon bifida*	E	H	0	4.00	11.29
Mytilid juv.	E	H	0.3	2.4	14.26	*Gammaropsis maculata*	E	H	0.22	7.38	12.74
Leptognathia gracilis	E	H	1.3	1.4	15.76	*Phtisica marina*	E	H	0.56	3.75	14.01
Syllis sp.	B	B	0.6	3.1	17.24	Pectinid juv.	E	H	0.33	3.5	15.27
Fenestrulina malusii	E	B	0.3	3.9	18.71	*Galathea intermedia*	E	X	0.56	1.88	16.48
Phtisica marina	E	H	1.3	1.5	20.16	Protodrilidae	B	X	0.44	2.75	17.66
Ophiura sp.	E	X	1.3	1.7	21.58	*Pholoe inornata*	E	B	0.11	1.63	18.83
Anomiidae indet.	E	B	0.0	2.2	22.99	*Aricidea minuta*	B	X	1.22	0.63	19.98
Galathea intermedia	E	X	0.3	2.5	24.39	Nematoda	B	B	0.56	4.63	21.08
Aora gracilis	E	H	0.5	1.9	25.78	*Pododesmus patelliformis*	E	B	2.11	3.50	22.19

[a] This column identifies taxa as 'E' if they are epifaunal and 'B' if they are known to be both epi- and infaunal

[b] This column identifies taxa as 'H' if they are known to associate with hydroids, 'X' if they do not, and 'B' if either mode of life is possible

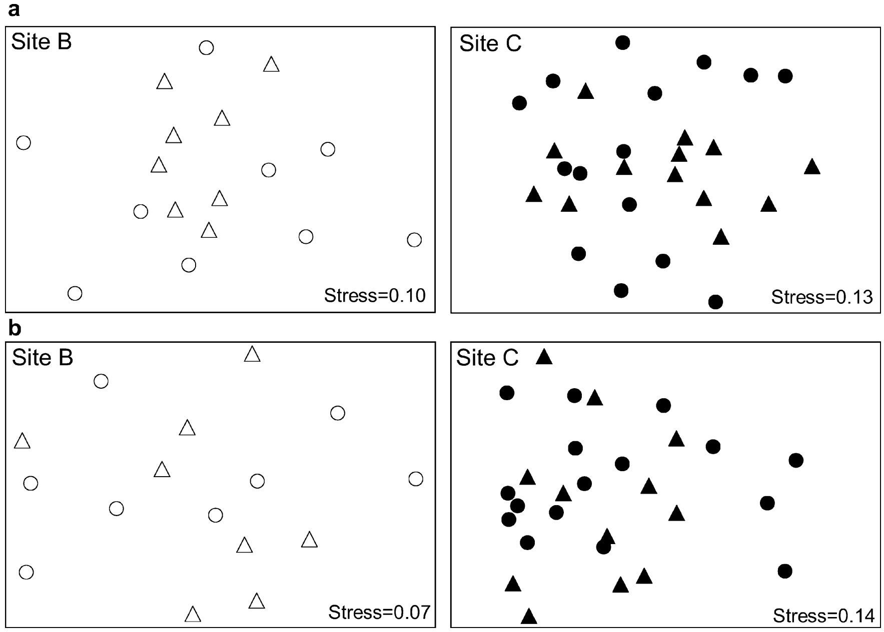

Fig. 5 MDS plots of cluster analyses of **a** data with fauna known to associate with hydroids removed and **b** of infaunal taxa only. In both cases, there is no clear distinction between hydroid (*triangles*) and non-hydroid (*circles*) cores. All plots are based on standardised, fourth-root-transformed data and Bray–Curtis similarities. In **b**, one non-hydroid core from site B and one hydroid core from site C were removed from the plots as they showed 0% similarity with the other samples and thus severely distorted the plots

To investigate whether the presence of hydroids affected the infauna in the sediment beneath them, a separate analysis was run on a dataset of species known from the literature to be *solely* infaunal in habit. Thus, taxa that could be either infaunal or epifaunal were excluded from this analysis. An MDS plot of both sites together showed that even the site difference was minimal at the infauna level and no effect of hydroids was seen (Fig. 5b). A two-way ANOSIM found neither factor to have a significant effect (between-sites global $R=0.051$, $P=13.4\%$; hydroid/non-hydroid global $R=0.001$, $P=44.5\%$). To check the possibility that some species of interest were left out of this analysis, due to being classified as either infaunal or epifaunal, another set of analyses on the dataset 'infaunal' plus 'both' was run. An MDS plot of all samples showed a site difference, so the analyses continued with the two sites treated separately. At both sites, there was no significant difference between the hydroid and non-hydroid cores (one-way ANOSIM site B: global $R=0.04$, $P=26.9\%$; site C: global $R=0.151$, $P=0.8\%$). Despite this, a SIMPER analysis was run to test if there were any low-level trends apparent. There was some evidence that a number of worm taxa that had been categorised as 'both' (*Autolytus* sp., *Syllis* sp., Nematoda, phoronids, Cirratulidae, Capitellidae) were more abundant in the hydroid cores. However, this result should be treated with caution, because of the dual classification of the taxa and the non-significance of the ANOSIM analysis (see Discussion).

Diversity indices were calculated for each core type at each site (Table 2). The fundamental measures of species number (*S*) and total number of individuals (*N*) were chosen, as well as Margalef's species richness (*d*), Shannon–Wiener diversity (*H*′), Pielou's evenness (*J*′), and Simpson's dominance (*D*). These were chosen to give a spread of indices sensitive to various components of the community (number vs abundance of species). Two-way ANOVAs to test the effect of site and presence/absence of hydroids showed a significant effect of both factors in all cases except *D* and *H*′ (Table 3). Within each site, hydroid cores had more species, more individuals, were richer and more even than non-hydroid cores. Shannon–Wiener diversity and Simpson's dominance were not significantly different.

Lastly, to test whether the amount of hydroid present in each hydroid core affected the community composition in any way, the dry weight of hydroid from each core was used as the independent variable in regression

Table 2 Mean (± standard error) of the univariate diversity indices at sites B and C, for benthic communities with and without hydroids. *n* number of samples, *S* species number, *N* number of individuals, *d* Margalef's species richness, *H*′ Shannon–Wiener diversity, *J*′ Pielou's evenness, *D* Simpson's dominance (1–λ′)

	n	*S*	*N*	*d*	*H*′	*J*′	*D*
Site B							
Hydroid	8	61.50 ± 3.06	384.75 ± 27.22	10.20 ± 0.52	3.14 ± 0.08	0.76 ± 0.01	0.10 ± 0.01
Non-hydroid	9	38.00 ± 2.40	143.63 ± 24.06	7.57 ± 0.25	3.00 ± 0.05	0.83 ± 0.03	0.09 ± 0.01
Site C							
Hydroid	13	47.38 ± 2.02	366.00 ± 39.11	7.97 ± 0.29	2.55 ± 0.10	0.66 ± 0.03	0.18 ± 0.02
Non-hydroid	16	26.75 ± 1.33	94.63 ± 11.81	5.81 ± 0.26	2.62 ± 0.08	0.80 ± 0.02	0.13 ± 0.01

Table 3 Summary of two-way ANOVA results comparing the effect of site and presence of hydroids on the various univariate diversity indices. Abbreviations are the same as for Table 2. *df*: site = 1, presence/absence (P/A) hydroids = 1, interaction = 1, residual = 42, total = 43 for each analysis

	F	*P*
S		
Site	36.46	< 0.001
P/A hydroids	102.46	< 0.001
Site×Hydroid	2.61	0.114
N[a]		
Site	4.66	0.04
P/A hydroids	78.32	< 0.001
Site×Hydroid	0.12	0.732
d		
Site	34.96	< 0.001
P/A hydroids	51.18	< 0.001
Site×Hydroid	1.68	0.202
H′		
Site	24.83	< 0.001
P/A hydroids	0.41	0.525
Site×Hydroid	0.69	0.41
J′		
Site	5.38	0.025
P/A hydroids	14.86	< 0.001
Site×Hydroid	0.49	0.487
D		
Site	11.59	0.001
P/A hydroids	2.20	0.146
Site×Hydroid	0.62	0.437

[a] *N* was square-root transformed to normalise the data prior to the ANOVA test

analyses against each of the univariate measures. No significant results were obtained. Hydroid weight was also used as a variable in a multivariate BIOENV test on hydroid core data only (other variables were sediment parameters) but was never selected as a factor influencing community composition. A more ecologically relevant measure of hydroid cluster size would probably have been volume or surface area.

Unfortunately, it was not possible to test whether the species of hydroid affected the associated fauna in any way. Due to faulty sample jar lids, many of the samples had begun to dry out from the top, so that while the specimens in the base of the jars were still preserved, many hydroid clusters were completely desiccated. Only the more robust species could be identified, particularly *Nemertesia* spp., but also *Sertularia cupressina* or *Sertularella* spp. From diver observations, most hydroid clusters in this area comprise a mixture of species, and this also seemed to be the case in the samples where identification was possible.

Discussion and conclusions

Hydroid colonies in this area of the Irish Sea influence benthic community composition and increase both the diversity and abundance of benthic fauna (Fig. 2, Table 2). This agrees with many other habitat complexity studies carried out in a range of habitats and scales. For example, Platell and Potter (1996) found greater species richness, diversity, density, and biomass of benthic invertebrates in areas of an estuary colonised by the macrophyte *Ruppia megacarpa*; coral reef seagrass meadows supported a denser and richer macroinvertebrate assemblage than unvegetated areas (Ansari et al. 1991); and Kaiser et al. (1999) found that serpulid tubeheads increased benthic biodiversity.

The results obtained in this work are mainly due to the larger numbers of taxa that directly utilise the hydroid structure. These taxa use the structure in a variety of ways and are represented by a wide range of trophic groups. The tube-dwelling amphipod, *Ericthonius punctatus*, various juvenile bivalves (Mytilidae, Pectinidae, Anomiidae), and encrusting bryozoans (e.g., *Electra pilosa* and *Fenestrulina malusii*) physically attach themselves (or their dwelling tubes) to the hydroid stems. These taxa are suspension feeders, which are probably utilising the hydroids simply as a physical support to raise themselves above the seabed where currents may be more favourable and where they will be less exposed to adverse sedimentation. Other taxa are found unattached amongst the hydroid clumps. These species may be using the hydroid as a shelter from predators or water currents, as a place in which to actively hunt (e.g., the carnivorous worms *Pholoe inornata* and some Syllidae), or as a food source. This latter category is dominated by taxa that are generalist feeders, either being opportunistic predators or eating encrusting flora and fauna on the hydroid, detritus that settles out from the water column, and waste material from other species in the community. Examples include caprellids (*Phtisica marina* and *Pseudoprotella phasma*), the tanaid *Leptognathis gracilis*, and the amphipod *Stenothoe marina*. Some worm taxa (Protodrilidae, *Aricidea minuta*, Syllidae, Nematoda) are also more abundant in the hydroid cores. These often live interstitially in the sediment but in this case may gain shelter in the basal attachment of the hydroid. Species of the hydroid *Nemertesia* have especially dense fibrous hydrorhiza that are often full of tiny fauna.

Which aspect of the hydroid clusters (physical complexity or biological properties) most influences the faunal composition was not tested in this study. However, as in many other studies, the answer is likely to be both. This question has been tested experimentally (particularly in seagrass habitats) by comparing naturally complex, artificially complex, and un-complex habitats (e.g., Bologna and Heck 1999; Lee et al. 2001; Martin-Smith 1993). Another approach has been to compare areas with different degrees (or presence vs absence) of natural structural complexity (e.g., Cummings et al. 1998; Lindholm et al. 1999; Ragnarsson and Raffaelli 1999). Many mobile species have been shown experimentally to favour complex habitats, particularly those formed by upright biota (e.g., Bostroem and Mattila 1999, isopods in seagrass; Corona et al. 2000, amphipods in seagrass; Gonzalez and Downing 1999, amphipods on zebra mussels; Hall and Bell 1988, various small epifauna on seagrass epiphytes). This may be due to many predators being less efficient at catching prey in a structurally complex environment (Corona et al. 2000; Lee and Kneib 1994) and/or due to the higher food availability (Auster et al. 1997; Bostroem and Mattila 1999). However, results vary widely depending on the type of habitat, the type and density of the complexity, the spatial and/or temporal scale studied, and behavioural interactions between the different taxa in the community, particularly predator–prey relationships.

There was no absolute evidence from this study that the hydroid colonies influenced the composition of the infauna living below them; taxa considered as solely infaunal from hydroid and non-hydroid cores were indistinguishable using either multivariate or univariate measures. Infauna were generally sparse and species poor, comprising mainly the worms *Glycera* spp. and sipunculids, and the bivalves *Mysella bidentata* and *Thracia* spp. However, when taxa deemed to be either infaunal or epifaunal were considered, there was limited evidence that a number of worm taxa that had been categorised as 'both' (i.e., could show either mode of life) were more abundant in the hydroid cores. However, interpretation of this is very difficult, as it could mean that these taxa are either epifaunal and are utilising the hydroid structure, or that they are infaunal species whose numbers are increased by the presence of hydroids. Care should also be taken in interpreting these data as the difference between hydroid and non-hydroid cores was insignificant. It might be expected that the presence of hydroids, especially those like *Nemertesia* spp. with dense hydrorhiza, would help to stabilise the sediment below and around them, and possibly to enrich the immediate area with nutrients, thus affecting the infauna. However, there is only very limited support for this in this study. Other authors have had mixed results from infaunal studies of this type. Woodin (1978) found that the tubes of the polychaete *Diopatra cuprea* (and artificial tubes) increased the abundance and species richness of infauna in a mobile sand environment. Everett (1994) found higher infaunal densities in plots with macroalgae compared with unvegetated plots in one experiment, but not in a second, and Lee et al. (2001) found no difference in infauna richness in a seagrass versus no seagrass comparison but found a higher infaunal abundance in the seagrass bed.

Sessile epibiota is increasingly being recognised as an important component of the benthos, especially for juvenile animals. For example, Dungeness crab (*Cancer magister*) post-settlement survival is greater in more complex habitats (Fernandez et al. 1994; McMillan et al. 1995) and survival of *Crangon crangon* and *Carcinus maenas* increased in experimental complex habitats (Isaksson et al. 1994). Experimental studies have demonstrated that commercially important juvenile fish often favour structurally complex habitats and their survivorship is often higher in such areas (e.g., Auster et al. 1997, silver hake, *Merluccius bilinearis*; Lindholm et al. 1999, cod, *Gadus morhua*; Quinn and Peterson 1996, coho salmon, *Oncorhynchus kisutch*). Other studies have compared areas of high and low epibiotic complexity and demonstrated higher numbers of fish in complex habitats (e.g., Grigg 1994, reef fishes; Kaiser et al. 2000, a variety of temperate marine species; Turner et al. 1999, a variety of marine fish in New Zealand and Australian waters). The importance of benthic habitats is now being taken into account in recent conservation and fisheries legislation in the United States, where areas of 'essential fish habitat' must now be identified and protected.

Upright sessile epifauna may play a particularly important role in the Irish Sea as a settlement substrate for juvenile scallops (*Pecten maximus* and *Aequipecten opercularis*), which form an important fishery in this area. In this study, pectinid spat were present in significantly higher numbers in hydroid cores than in non-hydroid cores (at both sites). Overall, 8.4 times as many pectinid spat were found in hydroid cores as in non-hydroid cores.

The establishment of a dense epifaunal community depends on the habitat not being subject to excessive disturbance. Scallop dredging (for both *P. maximus* and *A. opercularis*) is the most important fishery on the Isle of Man (Brand et al. 1991). That dredging and other types of bottom fishing reduce habitat complexity by impacting sessile epifauna species, and by extension their associated organisms, is now well documented (e.g., Auster 1998; Bradshaw et al. 2000, 2001; Collie et al. 1997; Dayton et al. 1995; Jennings and Kaiser 1998; Kaiser et al. 2000; Reise and Schubert 1987; Turner et al. 1999; Watling and Norse 1998). Mechanisms for this damage are direct contact, overturning of stones to which the epifauna are attached, mixing of epifauna down into the sediment, and smothering by suspended sediment. The implications of this disturbance are that dredging could decrease biodiversity and/or species abundance (including commercial species) by removing upright epifauna or, at the very least, changing the benthic community composition.

This study was not designed to investigate possible fishing impacts, although samples were taken from a fished and a non-fished area. This study shows the effect of individual hydroid clusters on species composition, and at that spatial scale, hydroids play the same role regardless of the level of fishing. Any potential difference would be revealed at a larger spatial scale, as hydroids (and other upright epifauna) are generally less abundant in fished areas of the Irish Sea (Bradshaw et al. 2000, 2001). At these two study sites, diver surveys over a larger area (1–2 km^2) have shown the average density of hydroids to be approximately 50 per 100 m^2 in the closed area and 30 per 100 m^2 off Bradda Head (based on estimates from 54 band transect surveys during the summers of 1998–2000). Over this wider area, overall species diversity and abundance of epifauna-associated fauna will therefore be substantially lower in fished areas.

It is interesting that even in the heavily fished area, hydroid colonies are still present, albeit at lower densities than in the closed area. This may largely be because the Isle of Man scallop fishery is closed during the summer (1 June–31 October), so at the time the samples were taken for this study, the seabed had been undredged for at least 3.5 months. This summer period is also the peak growing/breeding season for many marine species. Given that hydroids are evidently an important settlement substrate for scallop spat, seasonal closure must be very important in allowing the spat to settle and grow undisturbed during the early stages of their lives. In the closed area, spat will have a greater density of hydroids on which to settle, and will be able to grow undisturbed for the whole of their lives. This is undoubtedly one reason why, 11 years after the closure of this area, scallops in the closed area are found in greater densities and are on average larger than their counterparts off Bradda Head (Bradshaw et al. 2001). Other authors have also recognised the importance of closed areas in increasing structural complexity, and thus biodiversity and numbers or biomass of commercial species (Grigg 1994; Kaiser et al. 2000; Lindholm et al. 2000; Watling and Norse 1998). The incorporation of closed areas into future conservation and fisheries legislation would seem to be an obvious multipurpose tool for enhancing benthic communities.

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