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Sponge diversity and community composition in Irish bathyal coral reefs

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Key words: coldwater, multivariate analysis, North Atlantic, ordination, PCA, Porifera, RDA

Abstract

Sponge diversity and community composition in bathyal cold water coral reefs (CWRs) were examined at 500-900 m depth on the southeastern slopes of Rockall Bank and the northwestern slope of Porcupine Bank, to the west of Ireland in 2004 and 2005 with boxcores. A total of 104 boxcore samples, supplemented with 10 trawl/dredge attempts, were analyzed for the presence and abundance of sponges, using microscopical examination of (sub)samples of collected coral branches, and semi-quantitative macroscopic examination. Approximate minimum size of identified and counted sponge individuals was 1 mm. Literature data were added to the Porcupine Bank results to compensate for a less intensive sampling program in that location. Species richness and abundance were determined at local (sample diversity, pooled-sample diversity, local reef diversity), between-reef (diversity of two reef areas at 15 km distance), and regional scales (diversity of three reef areas over a distance of 200 km). Abiotic and biotic parameters including depth, the presence and cover of live coral, dead coral and sand, local reef, and orientation towards the nearest reef mound summit, were included in a constrained ordination technique (RDA); a Monte Carlo forward selection procedure was used to obtain significant predictors of variation in composition. The results of this analysis were compared with unconstrained ordination (PCA) and cluster analysis. The presence of live coral, depth and the local reefs C1 and C3 proved to be significant predictors of variation in sponge composition. The PCA and cluster analysis confirmed these results. Sample species richness was consistently heterogeneous from zero species and individuals up to 57 species and 90 individuals per (boxcore) sample. Species richness of local reefs determined from pooled samples showed the three localities studied to have similar species richness, namely 105-122 species in each location. Species richness was highest in samples with relatively low live coral cover. As in the RDA, live coral presence and depth appeared to be responsible for most of the variation observed in the cluster results. Cluster analysis of Bray-Curtis dissimilarity values of the pooled samples of all three reef localities using presence / absence data of all available samples indicated that distance appeared to structure the composition of the sponge assemblages of the three reef mound areas, but much less so within and among local reefs. Bathyal reefs of the regions to the west of Ireland were found to have a combined sponge species richness of 191 species, exceeding the richness of individual reef mound areas by c. 38-45%. Sponge presence in CWRs is clearly structured and controlled by biotic and abiotic factors. In particular, live coral presence appears a significant predictor of CWR sponge composition and diversity.

Contents

Introduction

Northwestern European continental slopes and oceanic banks/seamounts contain extensive coral reef formations at depths of 200-1200 m (Freiwald and Roberts, 2005). Reefs are predominantly built by two scleractinian coral species, *Lophelia pertusa* and *Madrepora oculata* (with *Stylaster gemmascens* as an additional structural species). Elsewhere in the world, in similar environments, similar reefs exist consisting of the same or a few other species. The paucity of reef-building species in these coldwater reefs (CWRs) contrasts with high biodiversity and great abundance of suspension feeders, grazers, scavengers and predators (Jensen and Frederiksen, 1992), even rivaling tropical shallow water reef communities in faunal diversity.

The size and frequency of occurrence of these reef communities along the European coasts have previously been reported (*e.g.* Broch, 1922; Dons, 1944), but were largely ignored, until Wilson (1979) 'rediscovered' them. Since then, mapping of CWRs has received unprecedented attention from geologists and biologists. It appears that size and frequency increase from south to north along the continental margins of Europe, with the most extensive reefs reported from areas to the south and west of Ireland (De Mol *et al*., 2002), off northwestern Scotland (Roberts *et al*., 2000), the Far Oer (Bruntse and Tendal, 2001) and along the continental slope of Norway (Broch, 1922; Dons, 1944; Fosså *et al*., 2005). Southwards, along the coasts of France, the Iberian peninsula, and in the Mediterranean coral reefs are apparently only present in smaller formations (*e.g.* Duineveld *et al*., 2004; Alvarez-Perez *et al*., 2005; Taviani *et al*., 2005), but there is ample evidence for the existence of extensive reef formations of Pleistocene and early Holocene age in these areas (De Mol *et al*., 2005). This is consistent with a scenario of Holocene northward extension of previously Mediterranean-Atlantic CWRs, with concurrent extinction and dying off of reefs in the south. Possibly, this scenario is a repetition of similar scenarios in pre-Pleistocene ages, as borings in locations of the northern reefs have yielded reef remnants as old as 10 million years (De Mol *et al*., 2005).

The reefs along the continental slopes of Europe depend on variable abiotic factors, which are currently under study in many different research groups. The precise environmental parameters, however, which make a flourishing reef possible, have not (yet) been identified. Mapping of CWRs has demonstrated the occurrence of island-like reef mounds in the midst of highly sedimented deep sea gullies and plains. (Fosså *et al*., 2005; Foubert *et al*., 2005; Wheeler *et al*., 2005). This island-like distribution of reefs invokes questions about connectivity and interactions of inhabitants of different reefs. It is generally thought that reef faunas - both shallow-water and deepwater reefs - require larval replenishment from proximate reef locations. However, current directions in the Eastern North Atlantic (Bersch, 1995) are a complicated interplay of (1) eastward directed surface currents, (2) northward directed intermediate and bottomwater currents, as well as - in the northern North Atlantic and more to the west - (3) southward directed currents, and (4) strong residual tidal currents (White *et al*., 2005). Also, larval dispersal capabilities of reef organisms may be limited to scales of 10-100 km, even in groups that developed long-distance (teleplanic) larvae, as has been established for shallow-reef fishes (Cowen *et al*., 2006).

The present study focuses on sponges, rather than on an integral community approach (Jensen and Frederiksen, 1992; Mortensen and Fosså, 2006). Often integral community approaches focus on well-known taxa and fail to adequately resolve lesser-known taxa. Mortensen and Fosså's (2006) comprehensive study of the species diversity and spatial distribution of invertebrates in Norwegian CWRs is a case in point; they mention the occurrence of 16 sponge species of which 5 were only identified to higher taxon, whereas a conservative estimate predicts that there may be 5 to 10 times more species in these reefs. Statements about numerical richness and abundance of various invertebrate groups made by these authors cannot be taken as definitive in view of their disregard for the true sponge diversity of Norwegian reefs.

Sponge diversity in tropical shallow-water coral reefs has been the subject of a considerable body of literature (see *e.g.* Hooper and Kennedy, 2002; Hooper *et al*., 2002; Cleary *et al*., 2005; Becking *et al*., 2006; De Voogd *et al*., 2006), in which estimates of local reef and regional diversity are presented, and attempts at explaining this diversity with abiotic and biotic factors are made (*e.g.* Wilkinson and Cheshire, 1989; Wilkinson and Evans, 1989; Schmahl, 1990; De Voogd *et al*., 2006). In contrast, sponge diversity in CWRs has been largely ignored, despite the widely noted extensive presence of sponges in these habitats (*e.g.* Bruntse and Tendal, 2001; Reitner and Hoffmann, 2003; Mortensen and Fosså, 2006). Sponges are thought to be vital components of the reefs as filter feeders capturing organic particles from prevailing currents, harboring microsymbiont communities with a plethora of unknown but likely important functions, and as excavating agents. Studies of sponge diversity and frequency of occurrence in CWRs are limited to two recent papers, van Soest and Lavaleye (2005) on a Rockall Bank CWR recorded 95 species and Longo *et al*., (2005) on a Mediterranean CWR recorded 39 species. A major setback for diversity studies of sponges in deeper water is the relatively complicated taxonomy of sponges, both in the sense of being technically demanding (high magnification microscopic examination is necessary) and the lack of easily accessible identification guides, such as are available for certain shallow-water environments (*e.g.* van Soest *et al*., 2000). This means, that generalist ecologists usually focus on megabenthic, colourful or otherwise characteristic species (*e.g.* Mortensen and Fosså, 2005), ignoring the smaller and cryptic sponges, which often are the most numerous.

In a previous publication, we presented, for the first time, quantitative data on sponge diversity and abundance in extensive CWRs on the southeastern slopes of the mid-oceanic Rockall Bank (van Soest and Lavaleye, 2005). This study revealed high sponge diversity (95 species), low sponge biomass, and an apparent lack of a clear association between coral cover and sponge diversity and abundance. In a follow-up study, presented below, we revisited the Rockall Bank CWR systems, as well as a CWR area on the northwestern Porcupine Bank on the Irish side of the Rockall Trench. In the present study we aim to assess the diversity and community composition of sponges across gradients of coral cover (both dead and alive), depth, local reef, and orientation towards local reef summits. We were in particular interested if the presence of live coral cover affected the composition of sponges. Our biodiversity study is intended to increase the understanding of the diversity of CWR biota along the coasts of Western Europe.

Materials and methods

Sponges were collected during two cruises on board the research vessel ‘Pelagia’, Moundforce 2004 (M2004; Mienis and de Haas, 2004; van Soest and Lavaleye, 2005) and BIOSYS/HERMES 2005 (B2005; Van Duyl

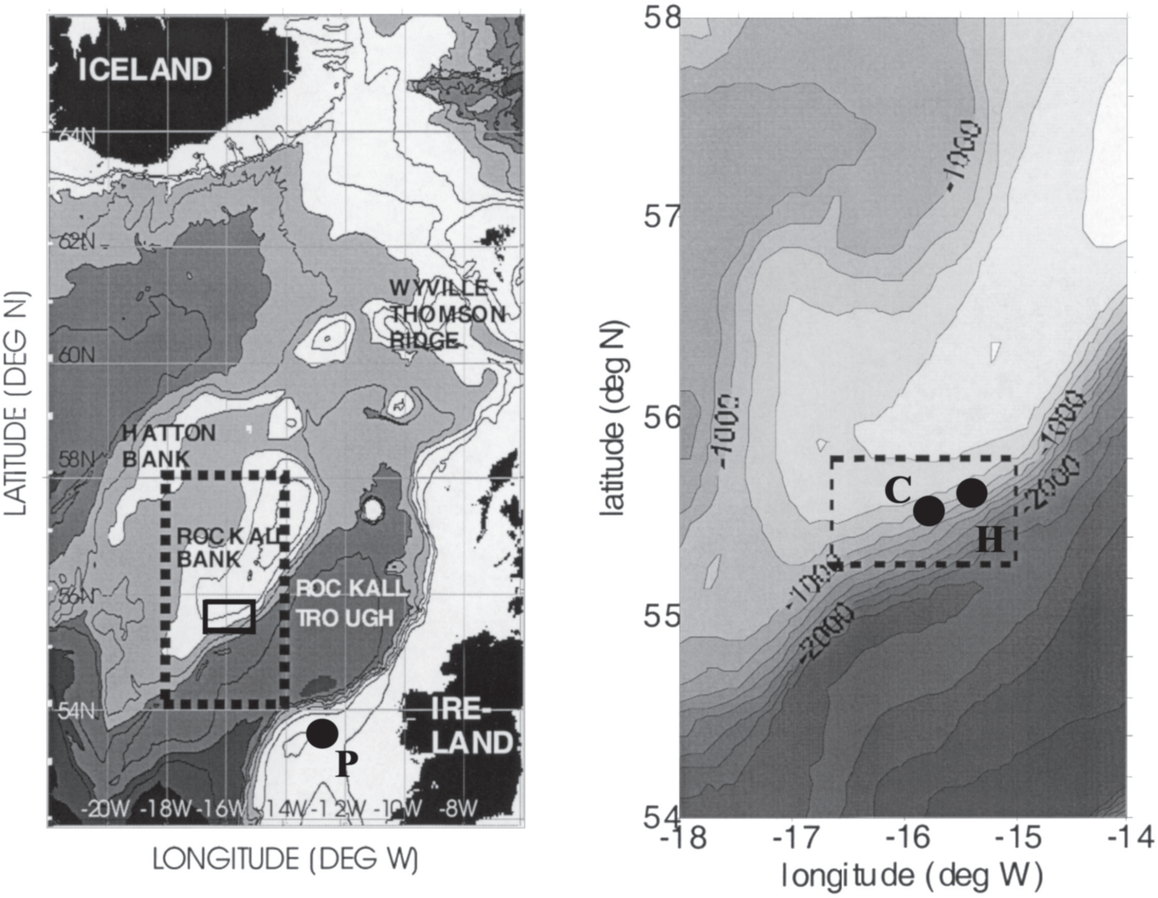


Fig. 1. Maps of study areas. Left: overview of North Atlantic to the west of Ireland with southeastern Rockall Bank (squares) and N Porcupine Bank (P). Right: detail of southeastern Rockall Bank with CLAN (C) and HAAS (H) mound locations.

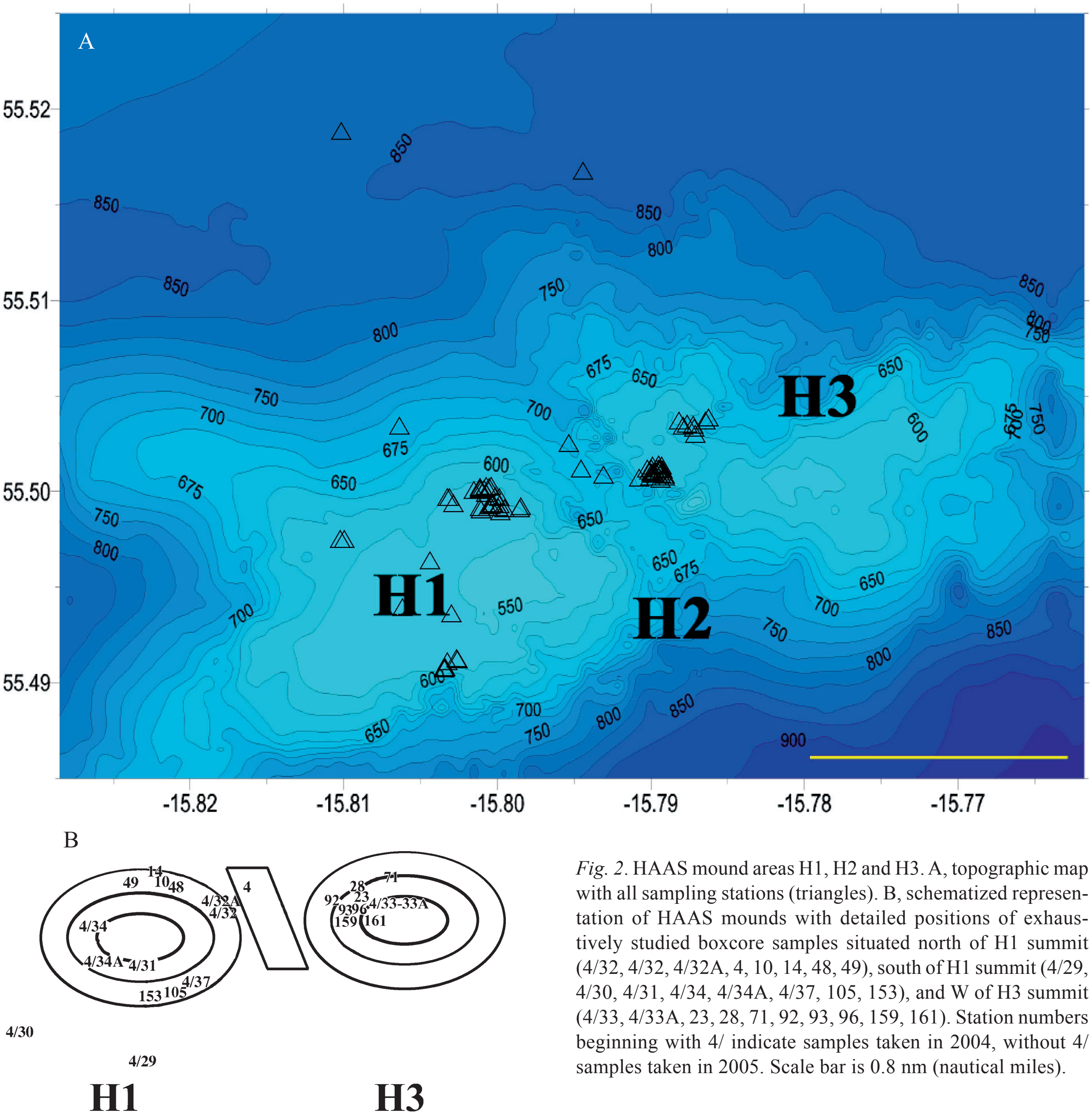
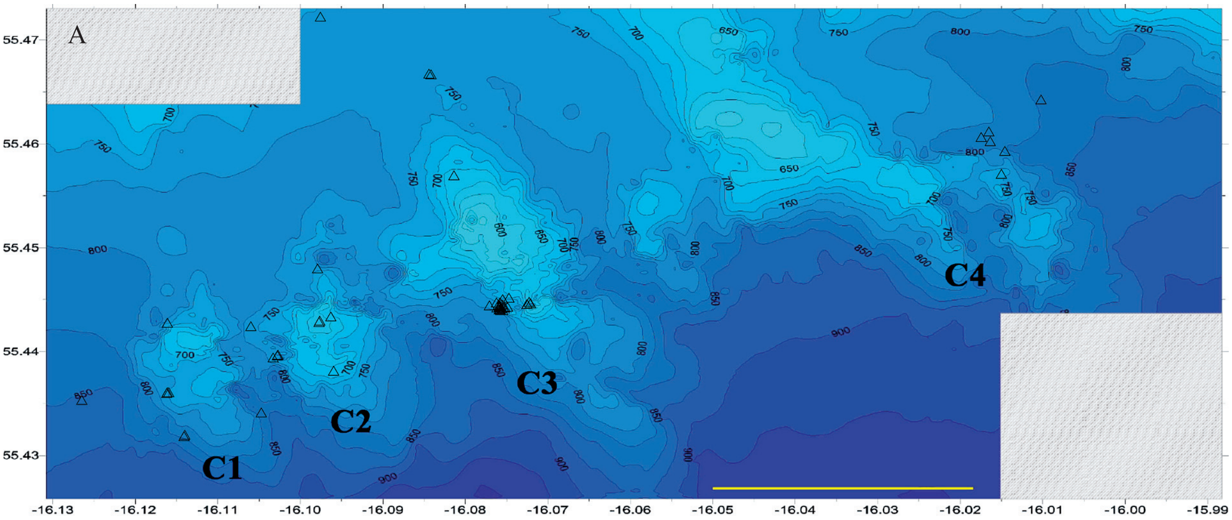


Fig. 2. HAAS mound areas H1, H2 and H3. A, topographic map with all sampling stations (triangles). B, schematized representation of HAAS mounds with detailed positions of exhaustively studied boxcore samples situated north of H1 summit (4/32, 4/32, 4/32A, 4, 10, 14, 48, 49), south of H1 summit (4/29, 4/30, 4/31, 4/34, 4/34A, 4/37, 105, 153), and W of H3 summit (4/33, 4/33A, 23, 28, 71, 92, 93, 96, 159, 161). Station numbers beginning with 4/ indicate samples taken in 2004, without 4/ samples taken in 2005. Scale bar is 0.8 nm (nautical miles).

and Duineveld, 2005), organized by the Royal Netherlands Institute for Sea Research. Sponges were collected during both cruise programs, but mainly during the multidisciplinary research program BIOSYS, which had the study of live corals from CWRs as its main objective.

Study areas (Figs 1-4)

In the southeast Rockall Bank (Fig. 1; Moundforce and BIOSYS/HERMES target areas c. 15 km apart, collectively known as Lochachev Mound area), two sites (i.e., hereafter known as the 'HAAS' and 'CLAN' mounds; 55.4°N 15°W and 55.5°N 16°W respectively) were sampled. Both sites consisted of a complex of reef mounds separated by deeper gullies and plains (Figs 2 and 3). Average depths were 596.7 (range: 562-715 m) for HAAS and 750.5 m (range: 629-826 m) for CLAN mounds. Current directions at these sites were complex and variable over a 24 hour period. Nevertheless, preliminary data indicate that the prevailing current direction at least over the top of the mounds



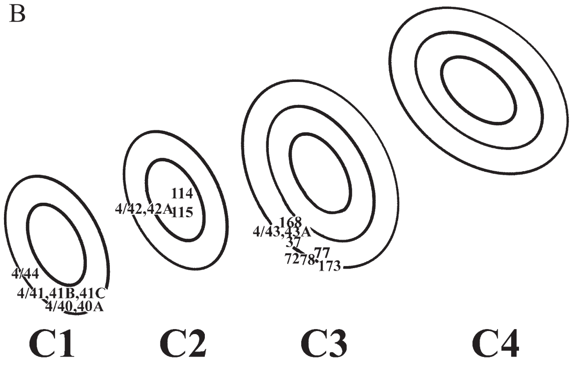


Fig. 3. CLAN mound areas C1, C2, C3, and C4. A. Topographic map with all sampling stations (triangles). B. Schematized representation of CLAN mounds with detailed positions of exhaustively studied boxcore samples situated S of C1 summit (4/40, 4/40A, 4/41, 4/41B, 4/41C, 4/44), W of (near the summit of) C2 (4/42 ,4/42A, 114, 115), and S of the summit of C3 (4/43, 4/43A, 37, 72, 73, 78, 168, 173). Station numbers beginning with 4/ indicate samples taken in 2004, without 4/ samples taken in 2005. Scale bar is 1.5 nm.

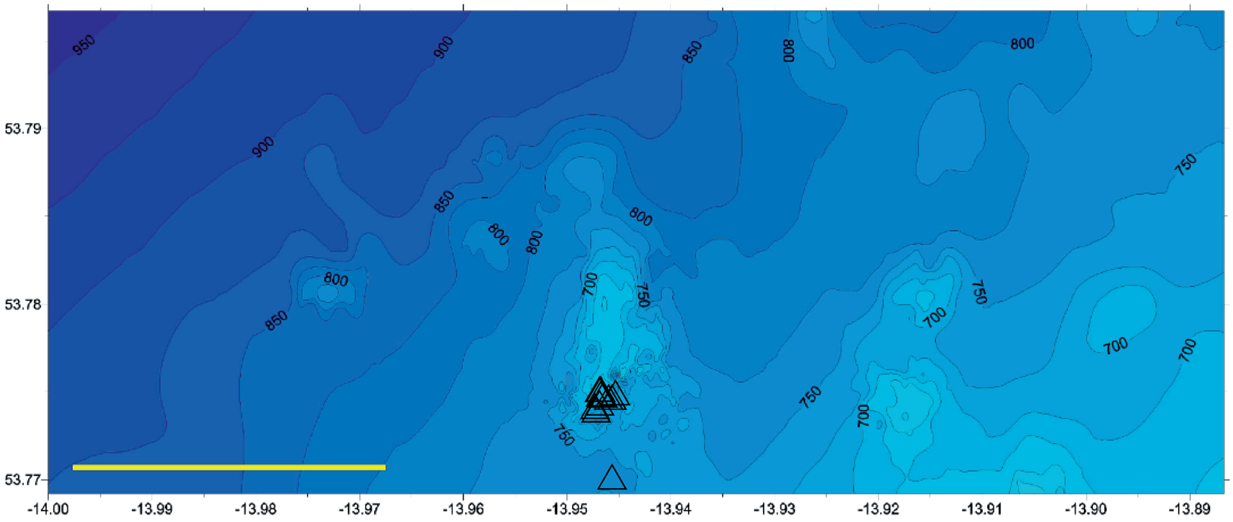


Fig. 4. Topographic map of N Porcupine Bank, showing the position of the stations. Scale bar is 1.0 nm.

Table 1. List of MOUNDFORCE, BIOSYS and HERMES stations taken in and around CWRs west of Ireland during 2004 and 2005 from which sponges were obtained, with data on their geographic position and depth, and (a)biotic content. (BX = Boxcore, DRE = Dredge, DTR = Trawl sample, H = HAAS Mounds, C = CLAN Mounds, Porc = Porcupine Bank, Orientation refers to nearest reef mound summit).

Station Nr	Gear	Date	Deg. N	Deg. W	Depth (m)	Local reef	Orientation	% Live Coral	% Dead Coral	% Sediment	N Species	N Specimens
4/29	BX	sept 7 2004	55.42113	-15.615	1407	H1	S	0	0	100	1	1
4/30	BX	sept 1 2004	55.478	-15.866	917	H1	S	0	88	12	11	25
4/31	BX	sept 1 2004	55.494	-15.804	560	H1	S	0	100	0	25	45
4/32	BX	sept 1 2004	55.499	-15.797	626	H1	N	0	51	49	30	57
4/32A	BX	sept 2 2004	55.499	-15.797	622	H1	N	0	10	90	23	31
4/33	BX	sept 2 2004	55.504	-15.785	679	H3	W	5	95	0	14	18
4/33A	BX	sept 2 2004	55.504	-15.785	673	H3	W	7	93	0	24	44
4/34	BX	sept 2 2004	55.498	-15.808	575	H1	S	0	100	0	9	14
4/34A	BX	sept 2 2004	55.498	-15.808	575	H1	S	0	100	0	8	11
4/37	BX	sept 2 2004	55.496	-15.802	557	H1	S	0	49	51	22	32
4/40	BX	sept 5 2004	55.432	-16.114	824	C1	S	1	44	55	7	11
4/40A	BX	sept 5 2004	55.432	-16.114	827	C1	S	0	30	70	1	1
4/41	BX	sept 5 2004	55.436	-16.116	751	C1	S	1	96	3	13	17
4/41B	BX	sept 5 2004	55.436	-16.116	778	C1	S	35	65	0	15	29
4/41C	BX	sept 5 2004	55.439	-16.116	784	C1	S	14	86	0	6	6
4/42	BX	sept 6 2004	55.440	-16.103	780	C2	W	0	70	30	7	9
4/42A	BX	sept 6 2004	55.440	-16.103	777	C2	W	0	77	23	12	16
4/43	BX	sept 6 2004	55.444	-16.075	773	C3	S	26	74	0	10	20
4/43A	BX	sept 6 2004	55.444	-16.075	765	C3	S	25	75	0	6	8
4/44	BX	sept 6 2004	55.435	-16.126	852	C1	S	0	2	98	1	1
4	BX	jun 25 2005	55.50255	-15.79362	715	H2	N	15	62	23	11	16
8	BX	jun 25 2005	55.50017	-15.7991	584	H3	W	6	15	78	6	13
10	BX	jun 25 2005	55.49978	-15.79815	602	H1	N	9	76	10	16	36
11	BX	jun 25 2005	55.49918	-15.79795	584	H1	N	97	3	0	4	6
12	BX	jun 25 2005	55.49933	-15.79788	587	H1	N	8	41	40	8	16
14	BX	jun 26 2005	55.50015	-15.79887	617	H1	N	11	80	0	16	30
15	BX	jun 26 2005	55.50032	-15.79838	593	H1	N	30	67	0	10	14
16	BX	jun 26 2005	55.50027	-15.7991	584	H1	N	12	72	13	9	18
21	DRE	jun 26 2005	55.50122	-15.79288	672-675	H2	N	n.a.	n.a.	n.a.	6	9
23	BX	jun 27 2005	55.50337	-15.786	667	H3	W	3	91	0	35	84
24	BX	jun 27 2005	55.50353	-15.78663	680	H3	W	0	83	7	9	27
26	BX	jun 27 2005	55.50358	-15.78585	688	H3	W	0	53	46	3	8
28	BX	jun 27 2005	55.5037	-15.67625	614	H3	W	9	62	27	16	26
29	BX	jun 27 2005	55.54538	-15.67607	654	H3	E	10	82	4	4	20
30	BX	jun 27 2005	55.54503	-15.79278	654	H3	E	14	74	7	4	29
31	DRE	jun 27 2005	55.51682	-15.80765	844-857	H2	N	n.a.	n.a.	n.a.	12	19
32	BX	jun 28 2005	55.44443	-16.0759	765	C3	S	17	80	1	4	16
33	BX	jun 28 2005	55.44425	-16.07553	775	C3	S	2	96	0	8	18
34	BX	jun 28 2005	55.4447	-16.0755	767	C3	S	10	86	0	6	34
35	BX	jun 28 2005	55.44438	-16.07572	781	C3	S	26	66	0	8	35
36	BX	jun 28 2005	55.44452	-16.07537	781	C3	S	9	77	4	7	25
37	BX	jun 28 2005	55.44457	-16.07523	757	C3	S	3	89	4	13	21
38	BX	jun 28 2005	55.44397	-16.017	785	C3	S	42	56	0	8	22
40	DRE	jun 28 2005	55.4609	-16.00228	809-863	C4	E	n.a.	n.a.	n.a.	12	39
44	BX	jun 29 2005	55.49942	-15.7983	578	H1	N	23	76	0	9	18
46	BX	jun 29 2005	55.4994	-15.79847	580	H1	N	0	66	28	11	20
47	BX	jun 29 2005	55.4993	-15.79902	577	H1	N	12	78	7	6	23
48	BX	jun 29 2005	55.49905	-15.79907	567	H1	N	6	45	45	33	62
49	BX	jun 29 2005	55.49918	-16.01413	568	H1	N	32	64	0	17	28
51	BX	jun 30 2005	55.45957	-16.0161	826	C4	E	0	3	97	0	0
52	BX	jun 30 2005	55.46148	-16.01592	806	C4	E	0	0.5	100	0	0
54	BX	jun 30 2005	55.4605	-16.10305	816	C4	E	0	0.5	100	1	1
55	BX	jun 30 2005	55.43935	-16.07562	781	C2	W	7	41	52	3	5
57	BX	jun 30 2005	55.44417	-16.07532	772	C3	S	25	75	0	8	12
58	BX	jun 30 2005	55.44423	-16.0756	768	C3	S	40	60	0	13	18

59	BX	jun 30 2005	55.44405	-16.07552	781	C3	S	10	90	0	5	13
60	BX	jun 30 2005	55.44407	-15.79832	780	C3	S	11	83	0	9	37
63	BX	jul 01 2005	55.49932	-15.79762	581	H1	N	15	78	0	14	29
64	BX	jul 01 2005	55.49915	-15.79792	583	H1	N	0	74	25	5	8
65	BX	jul 01 2005	55.49973	-15.80072	600	H1	N	9	62	5	5	16
66	BX	jul 01 2005	55.49942	-15.80112	560	H1	N	13	86	0	7	17
67	BX	jul 01 2005	55.49973	-15.80098	560	H1	N	1	98	0	5	13
68	BX	jul 01 2005	55.4997	-15.78927	562	H1	N	1	92	2	17	42
71	BX	jul 03 2005	55.50073	-16.07562	586	H3	W	1	72	10	15	51
72	BX	jul 04 2005	55.44437	-16.07597	762	C3	S	6	75	18	28	50
73	BX	jul 04 2005	55.44473	-16.0754	757	C3	S	5	87	8	3	7
75	BX	jul 04 2005	55.44445	-16.07447	767	C3	S	8	59	32	6	13
76	BX	jul 04 2005	55.44518	-16.07547	714	C3	S	3	86	8	8	20
77	BX	jul 04 2005	55.44398	-16.07557	777	C3	S	0	83	15	13	22
78	BX	jul 04 2005	55.44405	-16.08965	767	C3	S	13	51	35	28	34
82	DRE	jul 05 2005	55.47007	-16.0973	750-762	C3	N	n.a.	n.a.	n.a.	5	10
83	BX	jul 05 2005	55.46707	-16.08388	768	C3	N	0	0	100	1	1
84	BX	jul 05 2005	55.46703	-16.08413	768	CR	N	0	0	100	0	0
85	BX	jul 05 2005	55.46713	-15.78788	770	CR	N	0	0	100	2	2
88	BX	jul 06 2005	55.50115	-15.78798	586	H3	W	38	61	0	11	15
89	BX	jul 06 2005	55.50123	-15.78795	586	H3	W	11	73	0	8	18
90	BX	jul 06 2005	55.50093	-15.78773	590	H3	W	13	67	0	8	31
91	BX	jul 06 2005	55.50088	-15.7879	590	H3	W	48	50	0	4	7
92	BX	jul 06 2005	55.50103	-15.7877	588	H3	W	8	87	4	32	52
93	BX	jul 06 2005	55.50078	-15.78797	590	H3	W	5	86	0	7	13
96	BX	jul 06 2005	55.50112	-15.78848	577	H3	W	45	52	0	15	26
97	BX	jul 06 2005	55.50135	-15.78812	581	H3	W	0	84	0	6	28
99	BX	jul 07 2005	55.50122	-15.78822	583	H2	N	0	55	17	3	21
100	BX	jul 07 2005	55.50123	-15.78812	573	H2	N	35	63	0	3	9
101	BX	jul 07 2005	55.5014	-15.78805	580	H2	N	14	65	21	5	13
102	BX	jul 07 2005	55.50122	-15.78793	581	H2	N	21	67	12	11	20
103	BX	jul 07 2005	55.50135	-15.8005	588	H2	N	7	81	0	6	34
105	BX	jul 07 2005	55.4913	-15.80088	570	H1	S	100	0	0	6	6
111	DRE	jul 08 2005	55.49365	-15.80088	524	H1	S	n.a.	n.a.	n.a.	22	27
114	BX	jul 09 2005	55.4428	-16.0974	644	C2	W	1	84	11	31	57
115	BX	jul 09 2005	55.44292	-15.80132	644	C2	W	21	77	0	15	24
153	BX	jul 11 2005	55.49072	-15.8011	573	H1	S	13	78	8	29	46
154	BX	jul 11 2005	55.4911	-15.80127	572	H1	S	27	62	10	6	12
156	BX	jul 11 2005	55.4908	-15.7883	573	H1	S	5	83	9	30	54
157	BX	jul 11 2005	55.50103	-15.78857	588	H3	W	7	78	0	8	29
158	BX	jul 11 2005	55.50098	-15.7884	583	H3	W	16	76	0	6	15
159	BX	jul 11 2005	55.50093	-15.78853	586	H3	W	10	37	0	23	46
160	BX	jul 11 2005	55.5012	-15.78842	585	H3	W	4	65	6	11	27
161	BX	jul 11 2005	55.50105	-15.78882	585	H3	W	16	83	0	43	87
162	BX	jul 11 2005	55.5012	-15.78823	581	H3	W	11	85	0	12	16
163	BX	jul 11 2005	55.5008	-15.78862	585	H3	W	16	83	0	15	33
167	BX	jul 12 2005	55.44507	-16.07555	696	C3	S	10	68	7	13	43
168	BX	jul 12 2005	55.44432	-16.07457	691	C3	S	11	78	8	27	55
169	BX	jul 12 2005	55.44428	-16.07518	700	C3	S	21	73	2	11	38
170	BX	jul 12 2005	55.44453	-16.07175	754	C3	S	29	61	6	6	32
172	BX	jul 12 2005	55.4448	-16.07178	650	C3	S	8	63	25	17	26
173	BX	jul 12 2005	55.44463	-13.9464	629	C3	S	3	90	4	57	138
181	BX	jul 14 2005	53.7749	-13.9463	659	n.a	n.a	13	18	69	1	1
182	BX	jul 14 2005	53.77465	-13.94595	770	n.a	n.a	no data	no data	no data	1	1
183	BX	jul 14 2005	53.77487	-13.94533	765	n.a	n.a	0	37	60	18	24
184	BX	jul 14 2005	53.7751	-13.94668	757	n.a	n.a	14	38	46	3	3
185	BX	jul 14 2005	53.77465	-13.94563	657	n.a	n.a	0	49	51	3	3
187	BX	jul 14 2005	53.7748	-13.94673	659	n.a	n.a	0	10	90	1	1
188	BX	jul 14 2005	53.77432	-13.94682	660	n.a	n.a	0	29	71	6	6
189	BX	jul 14 2005	53.77412	-13.94722	683	n.a	n.a	9	47	44	7	7
190	DRE	jul 14 2005	53.77393	-13.94717	683-749	n.a	n.a	n.a	n.a	n.a	6	6
196	BTR	jul 15 2005	53.7451	-13.9472	508-601	n.a	n.a	n.a	n.a	n.a	5	7
209	DRE	jul 16 2005	53.77478	-13.94652	659-747	n.a	n.a	n.a	n.a	n.a	2	4
215	DRE	jul 17 2005	53.77012	-13.94568	745-754	n.a	n.a	n.a	n.a	n.a	16	21
216	BTR	jul 17 2005	53.80523	-13.94568	893-1075	n.a	n.a	n.a	n.a	n.a	0	0

is southeasterly from the shallower parts of Rockall Bank downwards (Van Duyl and Duineveld, 2005). Current strengths near the bottom varied over the investigated areas between 3 and 30 cm s^{-1} (Van Duyl and Duineveld, 2005). Temperature and salinity were also variable over a 24 hour period with an amplitude of 2°C (range: 8-10°C) and 1‰ (34-35.5 ‰). T and S values measured in an individual location, W-HAAS Mound (H1), on July 10 varied between 8 and 9°C and 35.22-35.36 ‰, respectively.

At both sites 10 boxcore samples were taken in 2004 during the exploration of the Moundforce 2004 cruise, and in 2005 50 (HAAS) and 29 (CLAN) boxcore samples were taken during the BIOSYS 2005 cruise. In addition, 4 dredge and 2 trawl samples were taken in the sandy gullies surrounding the reef mounds (4 at HAAS mounds at 508-753 m and 2 at CLAN mounds at 750-863m). All sample locations are shown in Figs. 2 and 3. Samples from 2004 and 2005 were taken at least partially in approximately the same locations. Sample results from 2004 were used to attempt to find optimal live coral localities in 2005 in order to serve the main goals of the BIOSYS program, with limited success, however, since resampling exactly the same locations with the boxcores is extremely difficult.

Based on their positions on individual reef mounds and on their orientation North, West or South of the nearest reef summit, samples were also arranged in informal geographic groups dubbed H1-3 (Fig. 2) and C1-4 (Fig. 3) (see Table 1 for further details). In the case of exhaustively studied samples these groups were reduced to H1 and H3 and C1, C2 and C3 (Figs. 2 and 3); no exhaustively examined samples were available from H2 and C4.

In the northwestern Porcupine Bank (Fig. 4; HERMES target site, known as the Pelagia Mound area, a part of what is known as the Hovland Mound Province), two close-lying reef mounds at approximately 53°N 13°W were sampled by 6 boxcores (at 659-765 m) and 4 trawls/dredges (at 508-747 m). The number of observed species was low (see below), due to insufficient sampling, so additional sponge biodiversity data from the literature were added to our results derived from 37 dredge/trawl samples from nearby reef locations (51-54°N, 10-11°W, Stephens, 1915, 1921). Since these data were collected over a larger area and by methods different from the BIOSYS program, we only included results expressly stated to have come from *Lophelia* beds, and only for the purpose of determining regional diversity.

Boxcores consisted of cylinders that upon impact completely closed off both the under and upper sides, bringing up standard samples of the sediment, the epibenthic fauna and the near bottom ambient seawater. Boxcore samples were usually 50 cm in diameter (surface area approx. 2000 cm^2), but occasionally 30 cm diameter boxcores were used (surface area 700 cm^2). The content of each boxcore was photographed prior to any subsampling in order to record the cover of live and dead coral, other important biota and sand (Van Duyl and Duineveld, 2005: Appendix IIIa). In addition the samples were briefly characterized by dominant faunal components and dead remnants (Van Duyl and Duineveld, 2005: Appendix IIIb). Depth and geographic position were recorded for each sample (Table 1).

In each boxcore sample we identified and counted macroscopically recognizable sponges (see below). Of these sponges, only fragments or representative specimens were retained as voucher specimens. Approximately half the boxcore samples taken in 2005 were exhaustively studied. A subsample of the collected (dead) coral branches consisting of a minimum of 20 coral branches of 10 cm or more in length were taken out, and these were preserved in 96% alcohol for investigation of the microscopical sponges, both on board and in the lab in Amsterdam. All 2004 boxcore samples were similarly exhaustively studied (Van Soest and Lavaleye, 2005), including those with no or only a few coral branches. These exhaustively studied samples were used to relate variation in composition to environmental variables. The remaining samples were included only in the estimates of regional diversity and reef/non-reef diversity.

Boxcore photos were imported into the program ImageJ 1.28 (public domain software by W. Rasmand, National Institute of Health, USA, cf. http://rsb.info.nih.gov/ij/) for image analysis. Coral cover (both dead and live) and bare sediment cover as projection on the boxcore bottom surface were thus obtained (listed in Table 1), and abundance of the macroscopically recognizable sponges was determined.

Other samples were taken with a 3m Beam-trawl with a bottom time of 10 minutes and a 1 m triangular dredge with similar bottom time. Samples were treated the same as the boxcore samples. Trawl and dredge samples were only used for regional scale studies and for reef/non-reef comparisons.

Sponge identification

Species identification followed van Soest and Lavaleye, 2005 (thick sections were dried on microscopical slides and mounted in Canada balsam). Voucher material and preserved branches have been incorporated in the collections of the Zoological Museum of the University of Amsterdam. Sponge species were also classified in one of four trait categories (see van Soest and Lavaleye, 2005): (1) thin small hispid crusts, (2) hollow bladder-like forms, (3) massive, large highly silicified forms, and (4) other forms. All identified sponges are listed in Table 2. A table with species and their abundance per sample site is available upon request as supplementary material.

Analyses

Species richness

Total species richness was assessed (using the program ESTIMATES! (Colwell, 2000) and ECOSIM 6 (Gotelli and Entsminger 2001) using only exhaustively studied samples (boxcores) per study site in order to examine how complete our sampling of the HAAS and

Table 2. List of sponge species, arranged in to systematic order, obtained from CWRs west of Ireland by MOUNDFORCE, BIOSYS and HERMES sample activities. Species are assigned to four growth form categories (crust, bladder, silica and other). Samples are pooled in informal clusters C1-4, H1-3 of proximate locations with similar orientation towards local reefmounds. See also maps of Figs 2-4. 'x' denotes occurrence of species over the clusters. Also, the total number of sponge individuals (N) of each species is given. (C1-4 = CLAN Mounds, H1-3 = HAAS Mounds, Porc = Porcupine Bank).

Species	Growth form	C1	C2	C3	C4	H1	H2	H3	Porc	N
Demospongiae: Homosclerophorida										
Plakortis sp.	silica			x						1
Plakina brachylopha	crust			x		x				2
Plakinastrella trunculifera	crust			x				x		2
Spirophorida										
Tetilla aff. longipilis	bladder					x				2
Astrophorida										
Stelletta tuberosa	silica					x		x		2
Characella pachastrelloides	silica								x	1
Poecillastra compressa	silica			x		x				4
Thenea muricata	silica					x		x		9
Thenea sp.	silica				x			x		2
Vulcanella gracilis	silica			x				x	x	22
Vulcanella ornata	silica	x		x						2
Erylus expletus	silica	x	x	x		x	x	x		38
Geodia barretti	silica		x			x				3
Isops phlegraei	silica						x			1
Hadromerida										
Leptosastra constellata	crust			x					x	6
Paratimea duplex	crust			x				x		2
Atergia corticata	crust		x		x	x		x		19
Polymastia sp.	other				x				x	4
Sphaerotylus capitatus	other							x		1
Tentorium semisuberites	bladder	x	x	x		x		x		13
Protosuberites incrustans	crust		x	x		x		x		9
Pseudosuberites hyalinus	bladder					x				3
Suberites laticeps	silica					x	x	x		9
Timea sp.	crust		x							1
Tethya sp.	bladder					x				4
Alectona millari	other			x		x		x		15
Spiroxya levispira	other			x						3
Chondrosida										
Thymosia sp.	other			x		x				2
Poecilosclerida: Microcionina										
Iophon piceus	other			x		x				3
Clathria (Clathria) anchorata	silica	x	x	x		x	x	x	x	24
Clathria (Microciona) atoxa	crust			x		x		x		8
Clathria (Microciona) basifixa	crust								x	1

Clathria (Microciona) ditoxa	crust	x	x	x		x		x	x	22
Clathria (Microciona) aff.microchela	crust								x	1
Clathria (Clathria) sp.	crust					x				3
Eurypon clavatum	crust			x		x		x		8
Eurypon lacazei	crust					x				2
Eurypon aff. pilosella	crust			x		x		x	x	14
Eurypon viride	crust					x				1
Hymeraphia verticillata	crust	x		x		x		x	x	67
Cyamon spinispinosum	crust		x	x	x	x	x	x		110
Janulum spinispiculum	other			x				x		6
Trachostylea semota	crust		x							1
Rhabderemia intexta	crust			x						1
Myxillina										
Psammoclema finmarchicum	crust	x		x		x			x	17
Histodermella ingolfi	bladder	x		x		x		x	x	16
Forcepia (Forcepia) forcipis	bladder			x					x	2
Forcepia (Leptolabis) luciensis	crust			x		x				2
Lissodendoryx (Ectyodoryx) diversichela	other	x	x	x		x	x	x	x	46
Crella (Yvesia) gracilis	crust							x		2
Crella (Yvesia) hanseni	bladder					x				3
Crella (Yvesia) pyrula	other							x		1
Hymedesmia (Stylopus) acerata	crust							x		1
Hymedesmia (Hymedesmia) baculifera	crust			x		x				4
Hymedesmia (Stylopus) coriacea	crust			x		x				4
Hymedesmia (Hymedesmia) curvichela	crust	x		x		x			x	12
Hymedesmia (Hymedesmia) depressa	crust					x				1
Hymedesmia (Hymedesmia) flaccida	crust			x		x				4
Hymedesmia (Hymedesmia) aff.helgae	crust			x						1
Hymedesmia (Hymedesmia) helgae	crust		x	x		x		x	x	23
Hymedesmia (Hymedesmia) inflata	crust			x						1
Hymedesmia (Hymedesmia) aff. koehleri	crust			x						1
Hymedesmia (Hymedesmia) koehleri	crust			x		x		x	x	15
Hymedesmia (Hymedesmia) longistylus	crust			x						1
Hymedesmia (Hymedesmia) mucronata	crust					x		x		3
Hymedesmia (Hymedesmia) mutabilis	crust							x		1
Hymedesmia (Hymedesmia) planca	crust			x		x				2
Hymedesmia (Hymedesmia) perforata	crust					x		x		2
Hymedesmia (Stylopus) primitiva	crust					x		x		3
Hymedesmia (Hymedesmia) proxima	crust			x		x		x		5
Hymedesmia (Hymedesmia) rugosa	crust			x		x		x		6
Hymedesmia (Hymedesmia) simillima	crust							x	x	2
Hymedesmia (Hymedesmia) similis	crust			x						1
Hymedesmia (Hymedesmia) storea	crust					x				1
Phorbas sp. 18250	bladder		x	x		x		x	x	6
Phorbas demonstrans	bladder			x						1
Phorbas dendyi	other		x	x	x	x		x		11
Phorbas sp. *M2004/32E*	bladder		x	x					x	5
Phorbas neptuni	bladder					x				1
Phorbas sp. with rhaphides	bladder			x						2
Plocamionida ambigua	crust		x	x	x	x	x	x	x	36
Plocamionida spec.	crust							x		1
Iotroata acanthostylifera	crust					x		x		3
Melonanchora elliptica	bladder					x		x		2
Myxilla (Myxilla) fimbriata	bladder		x			x		x		3
Poecilosclerida: Mycalina										
Asbestopluma lycopodium	other					x				1
Asbestopluma pennatula	other			x				x		5
Cladorhiza gelida	other	x	x	x				x		13
Hamacantha (Vomerula) falcula	bladder		x	x		x		x		9

Hamacantha (Hamacantha) johnsoni	bladder		x	x		x		x	x	8
Biemna peracuta	bladder			x		x			x	4
Desmacella aff. inornata	bladder			x		x	x	x	x	22
Desmacella inornata	bladder			x		x				16
Desmacella annexa	crust					x				2
Esperiopsis decora	crust					x				1
Esperiopsis macrosigma	crust								x	1
Sceptrella biannulata	crust			x		x		x		15
Sceptrella normani	crust	x	x	x		x	x	x	x	40
Mycale (Mycale) lingua	silica			x		x		x		4
Mycale (Raphidotheca) marshallhalli	silica					x	x		x	7
Mycale (Aegogropila) tunicata	crust	x		x		x	x	x		23
Mycale (Carmia) fascibula	crust					x				1
Halichondrida										
Axinella flustra	other	x								1
Axinella infundibuliformis	other				x					11
Bubaris subtyla	crust			x						1
Bubaris vermiculata	crust					x				1
Hymerhabdia intermedia	crust			x						1
Alloscleria tenuispinosa	crust			x				x	x	5
Desmoxya pelagiae	crust		x			x		x		6
Heteroxya corticata	crust			x						1
Higginsia thielei	silica		x	x		x	x	x		106
Acanthella erecta	other					x				4
Epipolasis spissa	bladder	x	x	x		x		x		19
Hymeniacidon sp.	other					x		x		14
Spongosorites coralliophaga	silica	x	x	x	x	x	x	x		43
Spongosorites placenta	silica		x	x		x		x		21
Topsentia glabra	bladder	x	x			1				4
Haplosclerida										
Cladocroce parenchyma	other							x		1
Haliclona (Gellius) bioxeata	bladder	x	x	x		x		x	x	39
Haliclona (Gellius) flagellifera	bladder	x	x	x		x		x	x	49
Haliclona (Gellius) foraminosa	bladder	x	x	x		x	x	x		21
Haliclona (Gellius) sp. sigmas	bladder			x						2
Hemigellius pumiceus	silica	x	x	x		x		x		25
Hemigellius sp.	bladder		x	x		x		x	x	19
Aka insidiosa	other			x		x	x	x	x	19
Oceanapia aereum	bladder							x		1
Oceanapia robusta	silica				x			x		4
Dictyoceratida										
Dysidea spec.	other		x			x				1
Pleraplysilla spinifera	crust			x		x			x	3
Spongionella pulchella	bladder			x		x		x		5
Dendroceratida										
Aplysilla wine-red	crust		x			x		x		3
Aplysilla yellow	crust	x	x	x		x	x	x		18
Chelonaplysilla arenosa	crust		x	x		x		x		8
Chelonaplysilla noevus	crust	x		x		x		x		24
Verongida										
Hexadella dedritifera	crust	x	x	x		x	x		x	769
Hexactinellida: Hexasterophora										
Aphrocallistes beatrix	silica	x	x	x	x	x	x	x	x	93
Hertwigia spec.	silica							x		1
Tretodictyum tubulosum	bladder	x	x	x		x		x		26
Leucopsacus scoliodocus	bladder							x		2
Leucopsacus spec.	bladder	x	x	x		x		x		29
Mellonympha velata	silica			x		x	x	x		24
Rossella nodastrella	silica		x			x	x	x		91

Sympagella nux	bladder		x					x		13
Calcarea: Calcinea										
Clathrina ascandroides	bladder			x		x		x	x	19
Clathrina biscayae	bladder	x		x		x		x	x	14
Clathrina ‘red’	bladder		x			x	x	x		7
Clathrina reticulum	bladder		x	x		x	x	x	x	17
Soleneiscus olynthus	bladder	x	x	x		x	x	x		37
Ascaltis lamarcki	bladder					x				1
Levinella thalassae	bladder		x	x		x		x		16
Leuclathrina asconoides	bladder					x		x		7
Leucetta sp.	bladder			x		x	x	x		9
Plectroninia celtica	crust			x				x		3
Calcaronea										
Aphroceras sp.	bladder		x			x	x	x		5
Breitfussia schulzei	other			x		x		x		10
Leucosolenia gegenbauri	bladder		x	x		x	x	x		21
Sycon sp.	bladder		x	x		x		x		12
N specimens										2585

CLAN areas was. In the results we present sample and individual-based rarefaction estimates of cumulative species richness in addition to Chao2 and second order Jackknife nonparametric richness estimators (see Collwell and Coddington, 1994). The Chao2 estimator gave the least biased estimate of true species richness for small numbers of samples in a study of eight species richness estimators (Colwell and Coddington, 1994) and has been previously used to assess marine benthic diversity (Ellingsen, 2002). For estimates of individual-based rarefaction we used 1000 iterations and independent sampling of randomly chosen individuals from the total species pool in each area (HAAS or CLAN).

Ordination and Permanova

Community composition was assessed with Permanova (Anderson and Ter Braak 2003) using PRIMER 6 and PERMANOVA+ β3 (PRIMER-E Ltd), unconstrained ordination, i.e., Principal Components Analysis (PCA), and constrained ordination, i.e, Redundancy Analysis (RDA), using CANOCO for Windows 6.1 (Ter Braak and Smilauer, 1998). Input for the Permanova, PCA and RDA consisted of $\log_{10}(x+1)$ species abundance data that were first ‘transformed’ within the programme TRANSFORMATION (freely available at: http://www.fas.umontreal.ca/biol/casgrain/en/labo/transformations.html). Transformation consisted of modifying the species abundance data such that subsequent analyses, such as PCA and RDA, preserved the chosen distance among objects (transects). The species abundance data were transformed because of the inherent problems of the Euclidean-based distance metric (in standard PCA) and the Chi-square metric (in correspondence analysis, CA) for community data (see Legendre and Gallagher, 2001). In the present case, the Hellinger (Rao, 1995) distance was used, which gave very good results in a comparison of various distance metrics (Legendre and Gallagher, 2001). In particular, the Hellinger distance gave low weights to rare species, was monotonically related to the geographic distance along a model gradient, and reached an asymptote for sites with no species in common. It also produced little ‘horseshoe effect’ or inward folding of sites at opposite ends of the gradient, in ordinations (Legendre and Gallagher, 2001).

Using PERMANOVA we tested for an effect of live coral presence on community composition with a two-way Permanova; the factors were site (HAAS or CLAN) and live coral (present or absent). Live coral presence was included as a fixed factor in the analysis and area was included as a random factor. Constrained gradient analysis using RDA (within CANOCO for Windows v4; Ter Braak 1986; Ter Braak and Smilauer 1998) was used to assess environmental gradients in the species data matrix. RDA arranges sites and species in a multidimensional space whereby the axes are constrained to be linear combinations of environmental variables (Ohmann and Spies 1998). In RDA, the amount of species variation explained by the explanatory variables, or the total variation explained (TVE) is the sum of all constrained eigenvalues divided by the total variation (TV) in the species data. The environmental dataset used in the RDA consisted of the following variables: (1) depth; (2) live coral present (yes: 1 or no: 0); (3) percentage live coral cover,

(4) percentage dead coral cover; (5) percentage sand; (6) reef orientation (North, South or West coded as dummy variables); (7) reef (C1, C2, C3, H1, and H3 coded as dummy variables).

Within CANOCO a forward selection procedure using a Monte Carlo permutation test (999 permutations) and the full model option (Ter Braak and Smilauer 1998) was used to test environmental variables for significance (Ter Braak and Verdonschot 1995). In the results the conditional effects of environmental variables on composition (lambda_A) are presented in addition to P values from the Monte Carlo test. The conditional effects (lambda_A) represent the additional fit or increase in eigenvalue with each consecutively selected environmental variable. Only variables with $P < 0.10$ were included in the final model. The significance of the association between the species and environmental datasets was also assessed using Monte Carlo simulations (999 permutations) of constrained ordination scores against environmental variables. This analysis was performed only with samples from HAAS and CLAN mounds, only at the sample scale, only with exhaustively studied samples and only with samples containing 10 or more individuals.

Cluster analysis

As a complement to the PCA and RDA we performed a cluster analysis with the Bray-Curtis dissimilarity coefficient with subsequent UPGMA classification, using the MVSP package (Kovach, 1999; de Kluijver, 1997). Clusters were formally analyzed for the presence and dominance of species confined to each cluster using the process called 'inverse analysis' (full data matrix and inverse analysis results are available upon request). Obtained clusters were compared informally with cover of live coral, dead coral, sediment, depth and geographic position. This approach has been criticized for its neutral effects: data are clustered, but what the clusters mean is not formally analyzed. Nevertheless, empirical evidence (de Kluijver, 1997) suggests this approach is quite useful for detecting meaningful patterns.

Regional scale diversity was determined by cluster analysis of combined HAAS, CLAN and Porcupine samples, including trawl and dredge samples (the full data matrix is available upon request). Data from Stephens (1915, 1921) were included in the Porcupine data to complement the insufficient sampling effort during BIOSYS/HERMES 2005. Reef/non-reef samples were evaluated only for species contents, due to incomparable sampling devices and number of sampling attempts.

Finally, we used RLQ analysis to relate growth forms (excluding the growth form 'other') to environmental variables (Dolédec *et al*., 1996; Cleary *et al*., in the press). RLQ analysis is an extension of coinertia analysis; 'R' is a table of p environmental variables at m locations, 'L' a contingency table representing the abundance of k species at m locations, and 'Q' a table of k species with n biological traits. With RLQ analysis both traits and environmental variables affected by disturbance, as well as their interrelationships can be assessed (Dolédec *et al*., 1996). A detailed description of the analysis can be found in Dolédec *et al*., (1996), Cleary and Renema 2007 and De Voogd and Cleary 2007.

Results

Coldwater reef sponges from the region W of Ireland

A total of 157 species (Table 2) and 2565 individuals (see supplementary material) were identified during the M2004 and B2005 cruises. Based on an overview comparison of our data with those listed in the World List of Porifera (van Soest *et al*., 2006 at http://www.vliz.be/vmdcdata/porifera/), the composition of the CWR sponge fauna deviates from shallow-water sponge faunas in general by a relative predominance of Myxillina species (especially *Hymedesmia*), Calcineans, hexasterophoran Hexactinellida, and a poor representation of Dictyoceratida, Haplosclerina, and Calcaroneans.

Species richness

Boxcore samples contained between zero and 100 % live coral cover with a similar range in dead coral cover, and bare sand (see Table 1). Sponge species richness varied from zero to 57 species and sponge abundance from zero to 90 individuals (Table 1), demonstrating substantial small-scale spatial heterogeneity.

The full data matrix of species presence and abundance in individual samples is available upon request as supplementary material. Evenness (Pielou's J) values of 41 exhaustively studied boxcores varied from 0.74-1.0 (average 0.914), which confirms and slightly exceeds values obtained by van Soest and Lavaleye (2005).

Pooled samples based on nearby similarly oriented locations taken at individual reef mounds (C1-5, H1-

H3, see figs 2B and 3B and Table 2) yielded similar heterogeneity; average species richness and abundance varied from 11 to 86 species and 26-349 individuals in exhaustively studied sets of 2-8 samples (results not shown).

Of the three reef mound complexes we investigated, there appeared to be some difference between HAAS and CLAN with HAAS somewhat richer based on the number of samples taken and using non-parametric richness estimators (Chao2 and second order Jackknife). With a similar number of samples (18) we found 7 more species in HAAS than CLAN (109 versus 102) (Fig. 5). The Chao2 and Jackknife estimates showed even greater disparity (Chao2: 157.7 versus 142.6 and Jackknife: 170.4 versus 157.8) (Fig. 5). Note, however, that both nonparametric richness estimators showed no evidence of reaching an asymptote so that actual species richness in both areas should be considerably higher than observed species richness. The difference, however, between both areas will probably turn out to be less pronounced as can be seen in the individual-based rarefaction curve for both areas (Fig. 6), which shows very little difference. The value for CLAN (100.4 ± 2.4) is in fact well within the 95% confidence intervals of the value for HAAS (102.8 ± 6.3) at a similar number of individuals (*n* = 500 individuals).

Because Porcupine Bank was clearly understudied we pooled our data with Stephens' (1915, 1921) sponge data obtained from 37 trawl/dredge samples on *Lophelia* banks to the east of our study site (51-54°N 10-11°W). The B2005 Porcupine Bank value (39 species) was obviously the result of insufficient sampling (with only 10 samples taken), but when pooled with Stephens' data, a similar number of species were observed (105 species) as found at both Rockall localities (see Table 3). The aggregate observed species richness of all three investigated reef complexes, including Stephens' data, is 191 species exceeding local reef diversity by 38-45%.

Table 3. Species richness of pooled M2004 and B2005 CLAN and HAAS Rockall Bank samples and pooled B2005 Porcupine Bank samples and Porcupine literature data (Stephens, 1915, 1921), showing aggregate species numbers in the same size range.

	HAAS	CLAN	PORC
M2004	52	88	n.a
B2005	103	106	39
Stephens 1915/21	n.a.	n.a.	92
Aggregate	122	110	105

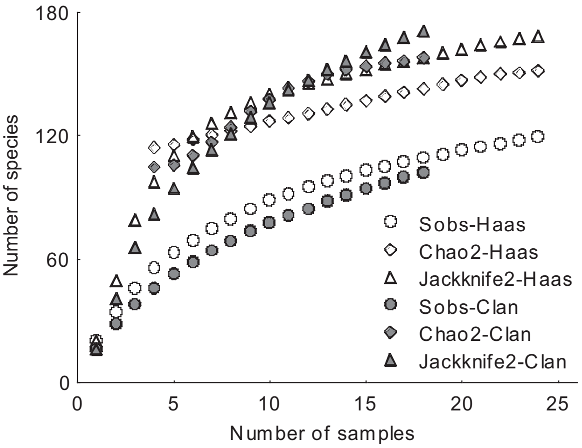


Fig. 5. Observed (Sobs) and estimated species richness of HAAS and CLAN mounds based on the number of samples taken and based on non-parametric richness estimators (Chao2 and second order Jackknife, Jackknife2).

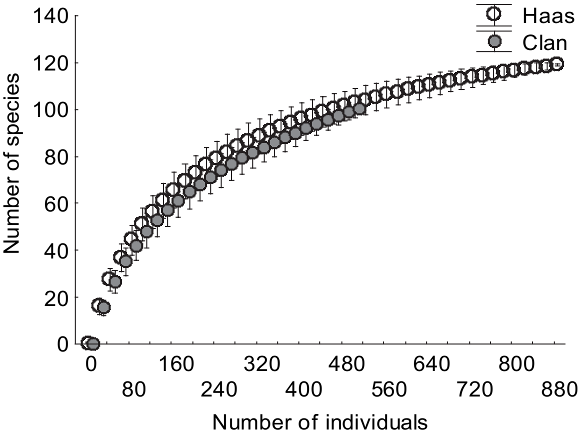


Fig. 6. Individual-based rarefaction curve for species richness of HAAS and CLAN mounds.

Community composition

There was both a significant effect of live coral presence (Pseudo-F = 1.987, P < 0.001) and site (Pseudo-F = 1.437, P = 0.031) on the composition of sponges, although the contribution of live coral presence (components of variation: estimate: 0.099, square root: 0.315) was substantially larger than site (components of variation: estimate: 0.029, square root: 0.169).

In the RDA, the sum of all constrained (canonical) eigenvalues was 0.190 thus explaining 19% of the variation in the dataset (Figs 7 A and B). The species-environment correlations of the first four axes were high (range: 0.872 to 0.917) indicating a strong association between the species matrix and the environmental matrix. A Monte Carlo test showed the first axis and trace (sum of all canonical eigenvalues) to explain a highly significant amount of variation in community composition ($p < 0.001$ for both tests). Significant environmental variables selected with the Monte Carlo forward selection procedure included the presence of live coral ($\text{lambda}_A = 0.08$, $P < 0.001$), depth ($\text{lambda}_A = 0.04$, $P = 0.010$), C1 ($\text{lambda}_A = 0.04$, $P = 0.010$), and C3 ($\text{lambda}_A = 0.03$, $P = 0.071$). Ordinations of the RDA constrained using environmental variables are presented in Figs 7 A and B whereby arrows represent significant environmental variables superimposed onto the ordination; the length of the arrow indicates the correlation between the environmental variable and the ordination axis.

Species strongly associated with live coral cover included *Hexadella dedritifera, Lissodendoryx diversichela* and *Hymeraphia verticillata* (see PCA Axis 1 in Fig. 8A as well as RDA Axis 1 in Fig. 7A) whereas species associated with reefs with no live coral include *Cyamon spinispinosum*, *Desmoxya pelagiae* and *Acanthella erecta*.

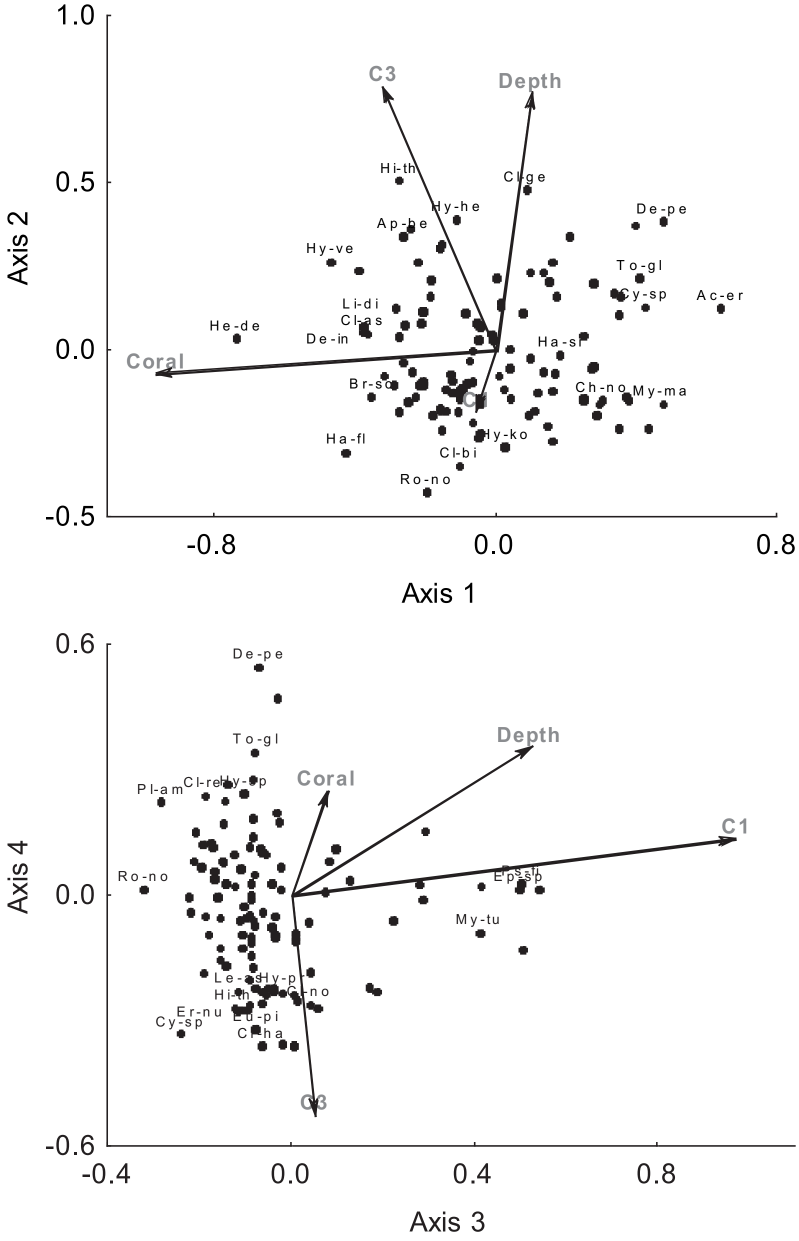


Fig. 7. Ordination based on redundancy analysis showing site scores for the first and second axes. Eigenvalue axis 1: 0.086. Eigenvalue axis 2: 0.044. Arrows represent significant environmental variables superimposed onto the ordination; the length of the arrow indicates the correlation between the environmental variable and the ordination axis. Species codes in (a) represent: Ac-er: *Acanthella erecta*, Ap-be: *Aphrocallistes beatrix*, Ap-ye: *Aplysilla* yellow, Br-sc: *Breitfussia schulzei*, Ch-no: *Chelonaplysilla noevus*, Cl-as: *Clathrina ascandroides*, Cl-bi: *Clathrina biscayae*, Cl-ge: *Cladorhiza gelida*, Cl-re: *Clathrina reticulum*, Cy-sp: *Cyamon spinispinosum*, De-in: *Desmacella* aff. *inornata*, De-pe: *Desmoxya pelagiae*, Ep-sp: *Epipolasis spissa*, Er-nu: *Erylus nummulifer*, Ha-fl: *Haliclona* (*Gellius*) *flagellifera*, Ha-fo: *Haliclona* (*Gellius*) *foraminosa*, Ha-si: *Haliclona* (*Gellius*) sp. *sigmas*, He-de: *Hexadella dedritifera*, Hi-th: *Higginsia thielei*, Hy-he: *Hymedesmia* (*Hymedesmia*) *helgae*, Hy-ko: *Hymedesmia* (*Hymedesmia*) *koehleri*, Hy-mu: *Hymedesmia* (*Hymedesmia*) *mucronata*, Hy-sp: *Hymeniacidon*/*Parasyringella* sp., Hy-ve: *Hymeraphia verticillata*, Le-as: *Leuclathrina asconoides*, Li-di: *Lissodendoryx diversichela*, My-ma: *Mycale* (*Raphidotheca*) *marshallhalli*, My-tu: *Mycale* (*Aegogropila*) *tunicata*, Pl-am: *Plocamionida ambigua*, Ps-fi: *Psammoclema finmarchicum*, Ro-no: *Rossella nodastrella*, Sc-no: *Sceptrella normani*, To-gl: *Topsentia glabra*.

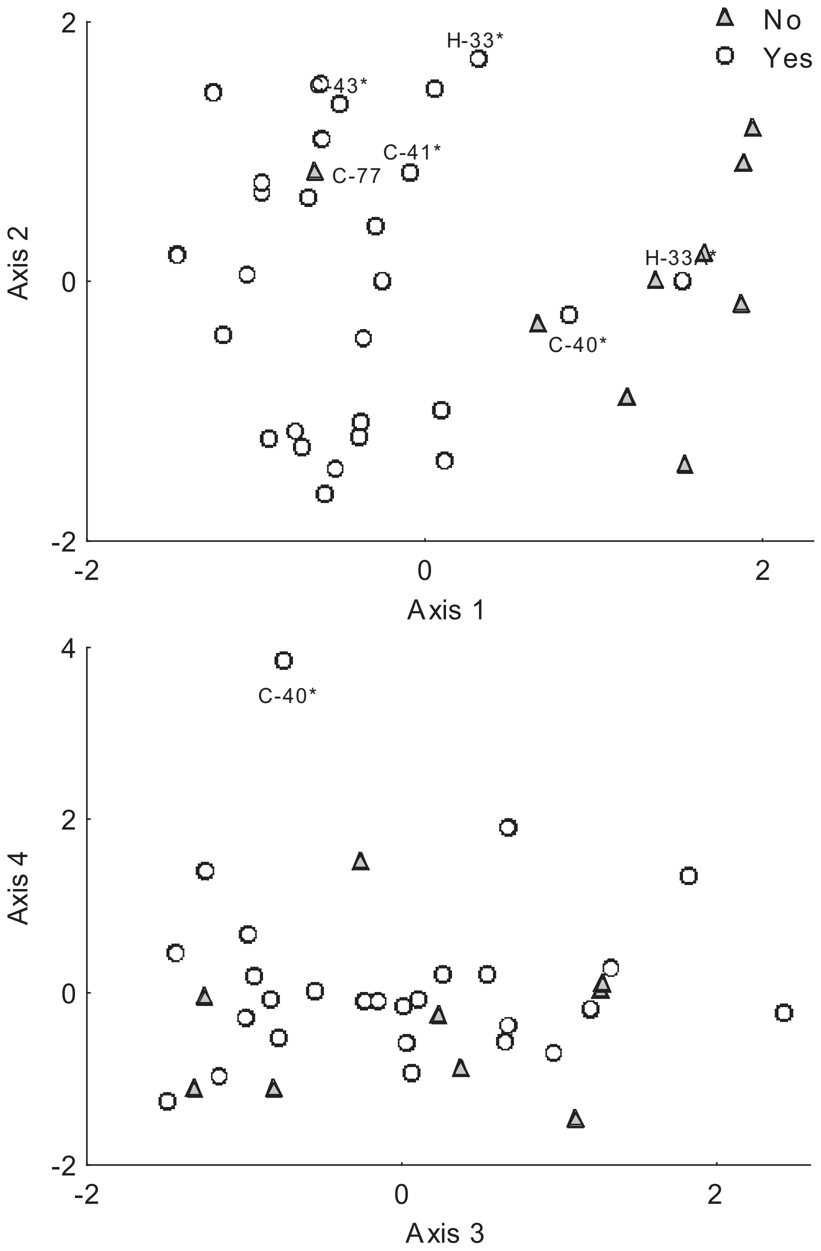
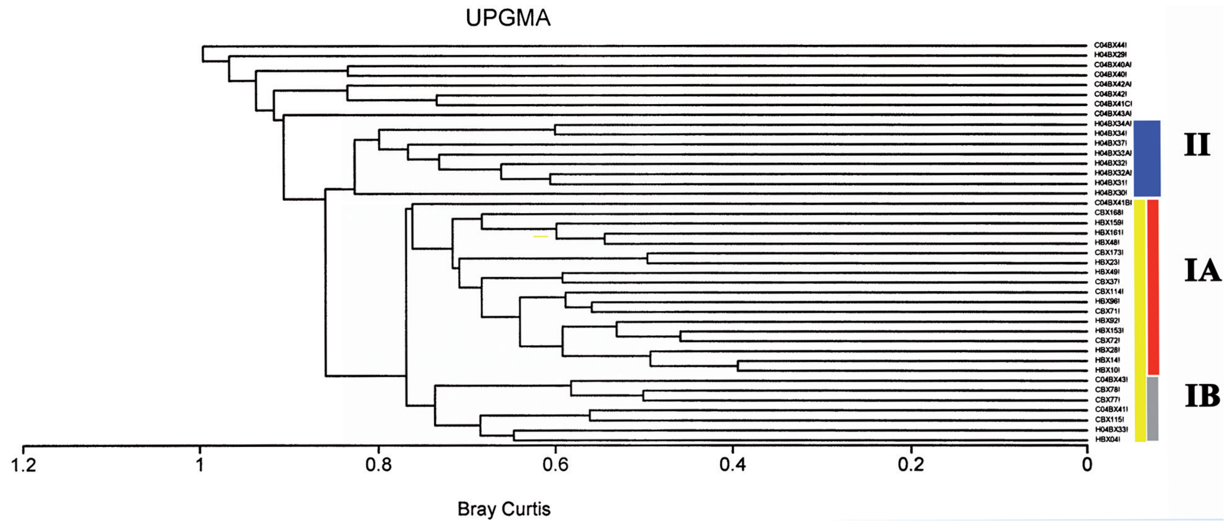


Fig. 8. Principal components ordination of the species abundance matrix showing (A) axes 1 and 2 and (B) axes 3 and 4. Eigenvalue axis 1: 0.116. Eigenvalue axis 2: 0.077. Samples with no live coral (No) and live coral (Yes) are indicated by symbols. Note that most samples with no live coral were sampled in 2004. Interestingly the only sample (C-77) with no live coral sampled in 2005 grouped with the other samples with live coral present. Alternatively samples collected in 2004 with live coral (C-41*, C-43* and H33*) grouped together with the other samples collected in 2005 with live coral.

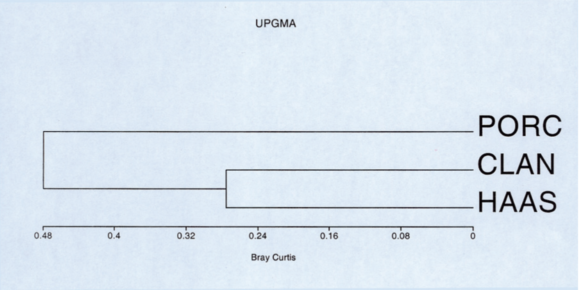
Species associated with shallower samples (axis 2 in Fig. 7B) included *Rossella nodastrella*, *Clathrina biscayae* and *Haliclona* (*Gellius*) *flagellifera* whereas species associated with deeper samples include *Hymedesmia* (*Hymedesmia*) *helgae*, *Cladorhiza gelida* and *Higginsia thielei*.

The significant separation of sites in C1 and C3 when compared to other sites is related to the occurrence of *Cladorhiza gelida*, *Higginsia thielei* and *Hymedesmia (Hymedesmia) helgae* in C3, and *Sceptrella normani* and *Psammoclema finmarchicum* in C1, supported by both the PCA and RDA (Figs. 7B and 8B); note that the orientation towards the nearest reef top is similar for both areas. In addition to local environmental conditions this effect may be related to the year in which samples were taken (C1 was predominantly sampled in 2004, C3 predominantly in 2005). Long-term and detailed studies, however, would be required to ascertain a temporal effect on sponge composition.

Cluster analysis: (Table 4; Fig. 9; supplementary material) yielded in addition to a number of unexplained single sample or two-sample clusters, all from



▲*Fig. 9*. Results of the cluster analysis of Bray-Curtis dissimilarity coefficient values obtained from 41 individual exhaustively studied boxcore samples with subsequent UPGMA classification.



◀ *Fig. 10*. Results of the cluster analysis of Bray-Curtis dissimilarity coefficient values obtained from all available boxcore and trawl/dredge samples - pooled for each of the three locations CLAN-, HAAS-Mound and PORCUPINE (including literature data) - with subsequent UPGMA classification.

2004, two major clusters I and II (Fig. 9) at approx. 0.8 dissimilarity, which appear to a high extent to conform to the presence (I) or absence (II) of live coral in the samples (see Table 4). However, as in the ordination results, the cluster representing zero live coral presence also consisted predominantly of samples from 2004, yielding a mixture of signals of the sample year and live coral presence. A further subdivision of the live coral presence cluster appears to be possible along a depth gradient: deeper, (average: 728 m; range: 644 - 777) (IB), vs shallower (average: 632 m; range: 568 - 778) (IA). The deeper cluster IB has less species per boxcore (average: 14.8; range: 10 - 28) than the shallower IA cluster (average: 25.7; range: 13 - 57) (Table 4; Fig. 9). As in the ordination, the samples from HAAS and CLAN appear to be mixed, therefore, the 15 km distance between both areas does not appear to explain much variation in the observed compositional patterns.

The inverse analysis (de Kluijver, 1987; not shown, but available upon request as supplementary material) identifies many species that support the clusters by only a low frequency of occurrence. Exceptions are *Hexadella dedritifera* and *Hymeraphia verticillata* (characteristic and dominant for cluster I), and *Cyamon spinispinosum*, *Chelonaplysilla noevus* and *Haliclona (Gellius) flagellifera* (characteristic and dominant for clusters I and II combined). No species appear to dominate the subclusters IA and IB.

Regional diversity. - Pooled presence / absence data of each of the three reef areas (boxcore and dredge/trawl samples combined) were subjected to cluster analysis (datamatrix available upon request). The result – HAAS and CLAN locations are less dissimilar than each is to Porcupine Bank (Fig. 10) - indicates that distance may be an important predictor of similarity at larger spatial scales.

Reef / non-reef diversity

Both boxcore and trawl/dredge samples of all three reef complexes were pooled and compared to all samples obtained from sedimented non-reef areas. Since the number of samples from the sedimented gullies and

Table 4. Results of the cluster analysis of Bray-Curtis dissimilarity coefficient values obtained from 41 exhaustively studied boxcore samples with subsequent UPGMA classification (see Fig. 12 for a graphic representation of the results). (Shannon = Shannon's H', Evenness is Pielou's J', provided by the MVSP Package, Kovach, 1999).

Sample	Cluster	Shannon	Evenness	N spp.	depth(m)	%live coral	%dead coral	%sand
HBX04!	IB	3.203	0.926	11	715	15	62	23
H04BX33!	IB	3.684	0.967	14	679	5	95	0
CBX115!	IB	3.689	0.944	15	644	21	77	0
C04BX41!	IB	3.528	0.953	13	751	1	96	3
CBX77!	IB	3.425	0.926	13	777	0	83	15
CBX78!	IB	4.712	0.980	28	767	13	51	35
C04BX43!	IB	2.902	0.873	10	765	25	75	0
HBX10!	IA	2.976	0.744	16	602	9	76	10
HBX14!	IA	3.145	0.786	16	617	11	80	0
HBX28!	IA	3.420	0.855	16	614	9	62	27
CBX72!	IA	4.453	0.917	29	762	6	75	18
HBX153!	IA	4.283	0.891	28	573	13	78	8
HBX92!	IA	4.794	0.959	32	588	8	87	4
CBX71!	IA	3.547	0.908	15	586	1	72	10
HBX96!	IA	3.475	0.889	15	577	45	52	0
CBX114!	IA	4.357	0.880	31	644	1	84	11
CBX37!	IA	3.266	0.883	13	757	3	89	4
HBX49!	IA	3.798	0.929	17	568	32	64	0
HBX23!	IA	3.809	0.743	35	667	3	91	0
CBX173!	IA	4.839	0.830	57	629	3	90	4
HBX48!	IA	4.774	0.938	34	567	6	45	45
HBX161!	IA	5.177	0.954	43	585	16	83	0
HBX159!	IA	4.352	0.962	23	586	10	37	0
CBX168!	IA	4.445	0.935	27	691	11	78	8
C04BX41B!	IA	3.486	0.892	15	778	35	65	0
H04BX30!	II	3.138	0.907	11	917	0	88	12
H04BX31!	II	4.447	0.958	25	560	0	100	0
H04BX32A!	II	4.389	0.970	23	622	0	10	90
H04BX32!	II	4.601	0.938	30	626	0	51	49
H04BX33A!	II	4.374	0.954	24	673	7	93	0
H04BX37!	II	4.304	0.965	22	557	0	49	51
H04BX34!	II	2.835	0.894	9	575	0	100	0
H04BX34A!	II	2.732	0.911	8	575	0	100	0
C04BX43A!	n.a.	2.500	0.967	6	773	26	74	0
C04BX41C!	n.a.	2.585	1.000	6	784	14	86	0
C04BX42!	n.a.	2.725	0.971	7	780	0	70	30
C04BX42A!	n.a.	3.578	0.967	13	777	0	77	23
C04BX40!	n.a.	2.404	0.856	7	824	1	44	55
C04BX40A!	n.a.	0.000	0.000	1	827	0	30	70
H04BX29!	n.a.	0.000	0.000	1	1407	0	0	100
C04BX44!	n.a.	0.000	0.000	1	852	0	2	98

plains was much lower than that of the reef mounds, only a comparison of the species content was considered meaningful. Gullies and plains yielded 44 species, of which 6 were unique to these habitats, the remaining 38 species dwelling on rocks and stones were almost in their entirety also found on the reefs.

Growth forms

There was no significant association between growth forms and environmental variables (Monte Carlo test: P = 0.138). Spcies with different growth forms appeared to occur in similar proportions in each of the habitats and reef mound areas (results not shown, but may be inferred from Table 2).

Discussion

Presence of live coral and occurrence of sponge species

The presence of live corals appears to be an important predictor not only of sponge composition (Fig. 7), but also of diversity. The latter is also evident from a comparison of the species richness of samples with and without live coral present (Fig. 11). The largest number of sponge species were, however, found in the lower live coral cover range, which is in accordance with findings of Mortensen and Fosså (2006) for overall faunal diversity of Norwegian reefs. Certain abundant sponge species, *e.g., Hexadella dedritifera*, appear to be closely associated with the presence of live coral. If this association should be confirmed in future studies, then their interaction is possibly important for the dynamics of the CWRs. As with many sponges, species inhabiting CWRs encrust dead corals, but also share their preferred habitat with live corals, presumably optimal environments for capturing food and oxygen. We have not found specific evidence that they compete with live corals for space in this habitat, but it cannot be excluded that they influence the performance and longevity of live corals along with some other invertebrates. Coral-overgrowth capabilities of certain sponges have been empirically and experimentally (*e.g.* Aerts and van Soest, 1997) demonstrated in shallow-water reefs, and it is quite likely such sponges occur in CWRs as well, with *Hexadella dedritifera* a likely candidate. In the northeast Pacific the sponge, *Desmacella austini* (Lehnert *et al.*, 2005) encrusted dead skeletons of reef-building hexactinellid sponges and occasionally overgrew live individuals of the reef-builder. In another study (Van Soest *et al.*, submitted) we demonstrated that the occurrence of another common species *Rossella nodastrella*, is negatively related to the presence of live coral, possibly a result of competitive exclusion.

Species composition and habitat

In the redundancy analysis, depth and presence of live coral were identified as the most important predictors of spatial variation in sponge composition. Depth was also identified as a structuring factor in the Mediterranean CWR studied by Longo *et al.*, 2005. It is interesting to note that depth appears to be important for both deep-water communities and shallow-water sponge communities (cf. De Voogd *et al.*, 1999, 2006; Alcolado *et al.*, 2004), although the causal relationship in deep-water remains unexplained, whereas the reasons for depth zonation in shallow-water are obvious. Bare sediment devoid of dead or live corals is an obvious negative factor for most sponges. The comparison of species composition between reefs and the surrounding sedimented gullies and plains led to the conclusion that the latter contain an impoverished 'reef' fauna and do not form a separate habitat for sponges. Alternatively, the results could also indicate that the term 'reef' sponges is fictional and that sponges merely prefer the concentrated hard substrate in the form of dead coral branches. They may thus merely profit from the same favorable abiotic circumstances that favor coral growth, i.e. increased food supply. A vital role for sponges in the reef habitat and a more than casual relationship between reefs and sponges still needs to be established.

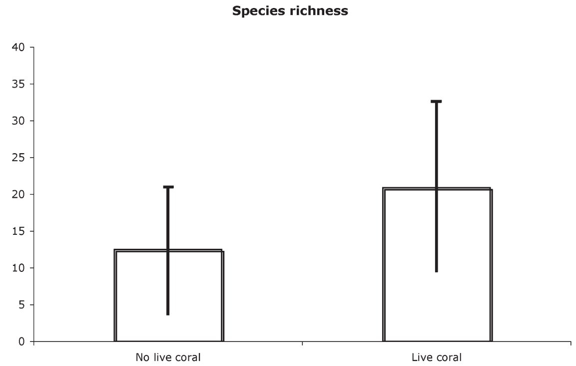


Fig. 11. Average sponge species richness of exhaustively studied boxcore samples without (left column, N=14) and with (right column, N=27) live corals present in the samples. The difference is significant (Mann-Whitney U-test, $p < 0.05$).

Growth forms

The four growth forms distinguished in this study appeared to occur in similar proportions in each of the reef mound areas. They do not seem to represent adaptations to different environmental regimes as was found by Bell and Barnes (2000) for sponges (and for within-species growth forms by Bell *et al.*, (2002) in shallow-water habitats subjected to varying current regimes. Possibly, the deep-water growth forms represent different evolutionary solutions to the deep sea environmental regimes not present in the shallow-water habitats studied by Bell and Barnes (l.c.). An important factor is likely to be the lack of a steady food supply. One can imagine that thin hispid crusts and hollow bladder-like forms both do not need a steady high input of organic matter, and even the large sponge forms with their high inorganic silica content may survive for long periods with little organic food. In any case, most of the sponges in the studied CWRs are elsewhere also known only to occur in the indicated growth forms and do not appear to represent underdeveloped recruits from wide-ranging species.

Species richness of shallow-water reefs and CWRs

De Voogd *et al*. (2006) studied Indonesian shallow-water sponge diversity at all the levels addressed here. Their transect (14-77 species) and total species richness values (151-169 species) appear quite similar to the values obtained from our CWRs (Table 3). Among the factors that were identified by them as important for community composition are depth, live coral cover and distance, all of which also appear to be important in CWRs. There is however a major factor preventing a comparison based on equal conditions, because species forming thin encrustations, by far the most common growth form among CWR sponges (Van Soest and Lavaleye, 2005), were not included in De Voogd *et al*.'s study. Australian coral reef sponge diversity studies (Hooper and Kennedy, 2002) yielded individual reef diversity values of 43-83 sponge species, based on 8 small-scale regional reef-complexes, with overall regional species richness of > 250 species, showing again values in the same range as observed by us. However, as with De Voogd *et al*., (2006), thin encrustations were not included.

Although less species rich than these Indo-Pacific regions (*e.g.* van Soest, 1994), Caribbean reef sponge studies include several in which thin encrustations were included (*e.g.* Kobluk and van Soest, 1989; Meesters *et al*., 1991). Thus, species richness values from these reefs appear more directly comparable to our CWR studies. Species richness values from Caribbean studies, added to inventories of local species including larger growth forms (*e.g.* van Soest, 1981; Lehnert and van Soest, 1998; Alcolado *et al*., 2004), obtain values of 150-250 species for local island reefs (Curaçao, Jamaica, Cuba). CWR sponge diversity at local and regional scale appears to be in the same range as that of shallow-water reef sponge diversity. The present study thus confirms earlier studies (Levin *et al*., 2001) that deep-sea habitats contain a well-structured and dynamic fauna.

Sampling gear

The boxcore used in this study, developed by the NIOZ and employed here as a routine gear for CWR biodiversity research, have a great advantage over other sampling gear because of precisely known sample size combined with the absence of depth restrictions. Living or recently dead coral beds built on a sedimented coral rubble foundation are easily sampled quantitatively, including living material, with a minimum of damage or interference. A distinct disadvantage is that rocky or stony bottoms have to be avoided, so a prior video survey of the bottom is advised (Van Duyl and Duineveld, 2005).

Sample size

Chao2 and Jacknife 2 non-parametric richness estimates indicate that with 18 boxcore samples the observed species richness is still far from the expected richness. Few marine biodiversity studies have yet to demonstrate that asymptotes are reached in rarefaction curves, so we are confident our analysis is credible and state of the art. Our species richness estimates also confirm earlier computations using Kaandorp's (1986) minimal area analysis (Van Soest and Lavaleye, 2005). For future studies using species richness and composition as indicators for connectivity and estimates of reef health, local reefs need more than 18 boxcores to be characterized, which is a considerable effort in a deep-ocean habitat.

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