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Species diversity and spatial distribution of invertebrates on deep–water *Lophelia* reefs in Norway

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Abstract Diversity and spatial distribution of invertebrates were studied on four inshore and four offshore *Lophelia pertusa*-reefs in Norway using ROV (Remotely Operated Vehicle), dredge, and grab. A total of 361 species was identified. Mollusca, Arthropoda and Bryozoa were the most species rich phyla contributing 48% to the total number of species. The species diversity (H') was highest in samples with a low proportion (1-20%) of live coral, and lowest for samples from the coral rubble zone surrounding the reefs. The number of individuals was highest in samples with a high proportion (> 20%) of live coral. Deposit feeders were most common in the rubble, whereas suspension feeders dominated among live coral. Most higher taxa were represented by more species on the inshore compared to the offshore reefs. This was most evident for Cnidaria, Crustacea, Polychaeta and Tunicata, whereas Foraminifera were more species rich offshore. Our results were compared with those of three earlier studies in the Northeast Atlantic. A total of 769 species have been recorded, but only 21 were common for all four studies. The cumulative number of species with increasing number of investigations indicates that far more species occur on *Lophelia*-reefs than recorded so far. The results from sampling with different gears were compared. To describe the spatial distribution of invertebrates within a *Lophelia*-reef, and to increase the sampling precision, we recommend using a grab equipped with a video camera because it samples the fauna more representatively and damages less coral compared to a dredge.

Keywords Scleractinia, coral, deep-water, cold-water, *Lophelia pertusa*, associated fauna, diversity, ecology

Introduction

Colonial scleractinian corals represent habitats with a high diversity of associated species (e.g., McCloskey 1970; Connell 1978; Reaka-Kudla 1997). This is true not only for the shallow water or zooxanthellate scleractinians, but also deep-water or azooxanthellate corals such as *Lophelia pertusa* (L., 1758) support a significant biodiversity (Dons 1944; Burdon-Jones & Tambs-Lyche 1960; Jensen & Frederiksen 1992; Fosså & Mortensen 1998; Rogers 1999). However, the ecology and dynamics of the community is poorly understood. *Lophelia pertusa* is widely distributed, occurring in the Atlantic, Pacific, and Indian Ocean, and the Mediterranean, mainly at depths between 200 and 1000 m (Zibrowius 1980; Cairns 1982; Rogers 1999). It seems to be most abundant in the Northeast Atlantic Ocean (Zibrowius 1980; Rogers 1999; Fosså et al. 2002). This coral can form reefs alone or together with other deep-water corals (e.g. *Madrepora oculata* L., 1758, *Solenosmilia variabilis* Duncan, 1873, and *Enallopsammia* spp.) (Cairns 1979). Along the Norwegian coast *Madrepora* often occur together with *Lophelia*, but contributes little to the reef-construction (Dons 1944; Mortensen et al. 1995).

Even though there are many similarities between shallow-water and deep-water coral reefs, the trophic structure of the communities shows fundamental differences. The internal cycling of nutrients and the significance of phototrophy in shallow reefs (Froelich 1983) is a great contrast to the food supply to the deep dark reefs consisting of advected particulate organic matter (Duineveld et al. 2004).

The *Lophelia*-reefs are complex habitats constituted by coral colonies up to c. 2 m high and fragments of dead skeleton with variable size and age (Wilson 1979; Mortensen et al. 1995; Hovland & Mortensen 1999). Habitats within the *Lophelia*-reefs can be defined at different spatial scales (Mortensen et al. 1995; Jonsson et al. 2004). Viewed at a large scale a reef typically consists of three vertical zones, or reef habitats: 1) "The live *Lophelia*-zone" (LL) occurs at the top of the reef and consists of mainly living *Lophelia* colonies separated by areas with dead broken skeletons. 2) "The dead *Lophelia*-zone" (DL) is found between the top and the foot of the reef. The bottom here is characterised by large fragments of dead corals, and a high diversity of megafauna. 3) "The *Lophelia* rubble-zone" (LR), has small skeletal fragments mixed with sediments flanking the foot of the reef. The horizontal extent of this zone varies from only a few metres to several tens of metres. The live and the dead zone comprise steep bottoms, and normally have a similar vertical range, whereas the *Lophelia* rubble-zone has a narrower depth range and a lower bottom inclination. At a smaller scale, four sub-habitats can be recognised within the coral colonies: 1) the smooth surface of living corals, 2) the detritus laden surface of dead corals, 3) the cavities inside dead skeleton, and 4) the free space between the coral branches (Mortensen et al. 1995). The composition of

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associated species is clearly different in these sub-habitats but has not been studied specifically so far (Jensen & Frederiksen 1992). More studies on the small-scale distribution of species within *Lophelia*-reefs are needed to understand the habitat requirements of the species, and to learn more about the structure and functioning of the reef community.

The main objective of this investigation is to describe the diversity and distribution of associated invertebrate species living on *Lophelia*-reefs in mid-Norway. Three subgoals of the study are: 1) to compare the faunistic composition of inshore and offshore reefs, 2) to compare results from different sampling gears to determine which method is most effective to sample the fauna and to describe the spatial distribution of species within the reefs, and 3) to compare the results with earlier investigations of *Lophelia* communities in the Northeast Atlantic.

Material and Methods

The study area

Many areas within the study area have seabed with hard substrata suitable as attachment sites for deep-water corals. Moraine deposits dominate the bottom substrata on the mid-Norwegian shelf, but clay is common in the deeper parts (Holtedahl 1993). Gravelly and sandy bottoms are found near the shelf-break and on ridges where the currents are strong and the sedimentation rates low (Holtedahl 1993). Exposed crystalline bedrock is common near the coast and in the fjords, but smaller moraines occur on the sills of the fjords.

Atlantic Water and Coastal Water are the two main water bodies on the Norwegian shelf. The Atlantic Water has a temperature of around 8 °C, and its main flow follows the continental slope northward, with the lower boundary at a depth between 500 and 600 m off mid-Norway (Blindheim 1990). The Norwegian Deep Water occurs below this depth on the continental slope. Closer to the coast Coastal Water covers the heavier Atlantic Water as a wedge thickest near the coast. This water mass has a salinity less than 35, and has large seasonal variations in temperature. Near the coast, the depth of the boundary between these two water masses is commonly around 100 m in the summer, and deeper in the winter (Sætre 1999). The temperature at depths around 200 m on the shelf and in the fjords varies roughly between 6 and 8 °C, and the salinity between 34.5 and 35.2 (Eide 1979). Current direction and velocity are controlled by the Norwegian Atlantic Current and by the semidiurnal tidal current, but ridges, breaks and sounds locally increase the current velocity near the bottom. Eide (1979) measured average velocities near the bottom in the Sula Trough (Fig. 1) from less than 7 cm s^{-1} up to 44 cm s^{-1}.

The studied reefs

The studied *Lophelia*-reefs are situated offshore on the continental shelf, and inshore in two fjords and east of the Island Hitra (Fig.1).

Four offshore reefs (A, B, C and D) within the Sula Reef complex were investigated as part of an environmental study before the laying of the Halten gas-pipeline (Mortensen et al. 1995; Hovland et al. 1997). The reefs are located on the Sula Moraine, deposited between 13 000 and 12 000 yr. BP (Rokoengen 1980). The studied reefs were about 150 m long, and 100 m wide, situated at depths between 240 and 300 m.

The Midfjorden Reef (M) is located inshore on a sill in Midfjorden, one of the entrances to Romsdalsfjorden. It is situated at 190 m depth. The reef is approximately 100 m wide (Fosså et al. 1997).

The Nordleksa Reef (N) is constituted of two adjacent large inshore coral mounds, approximately 300 m long and 100 m wide, occurring at depths between 140 and 175 m outside Trondheimsfjorden (Mortensen et al. 2001).The Rødberg Reef (R) is situated on an inshore rocky outcrop on the northern side in the middle of Trondheimsfjorden at a depth of ~250 m. The location has been sampled several times before (Dons 1944; Strømgren 1971; Mikkelsen et al. 1982), but the size of the reef is not known.

The Selliggrunnen Reef (S) occurs on an inshore sill, the Tautra Ridge, inside Trondheimsfjorden. The reef is situated between 40 and 80 m depth. It is the shallowest occurrence of *Lophelia pertusa* in the world (Mortensen & Fosså 2001).

Sampling of corals

Twenty-four samples were collected from depths between 50 and 295 m during five cruises from 1993 to 2000 (Fig. 1, Table 1). The sampling was performed with ROV (Remotely Operated Vehicle) (8 samples), triangular dredge (6 samples), and a 0.25 m^2 van Veen grab (10 samples).

The ROV was equipped with a manipulator-arm used to handle a scoop for collection of coral fragments. The samples were transported to the surface in an open box with a net (0.5 cm mesh) inside, mounted on the ROV.

The dredge consisted of triangular steel frame (80 cm sides), equipped with a strong nylon net (0.5 cm mesh). It was equipped with a protection sheet of rubber and a buoy attached to the opposite corner to keep it in position.

The van Veen grab has long lever arms allowing the scoops to cut deep into soft bottoms, and to cut coral skeleton. Samples obtained when the grab did not close fully were not included in this investigation. The grab was modified with a video camera and light to improve the precision of the sampling prior to the cruise to the Selliggrunnen Reef in 2000. See Mortensen et al. (2000) for a description of this configuration.

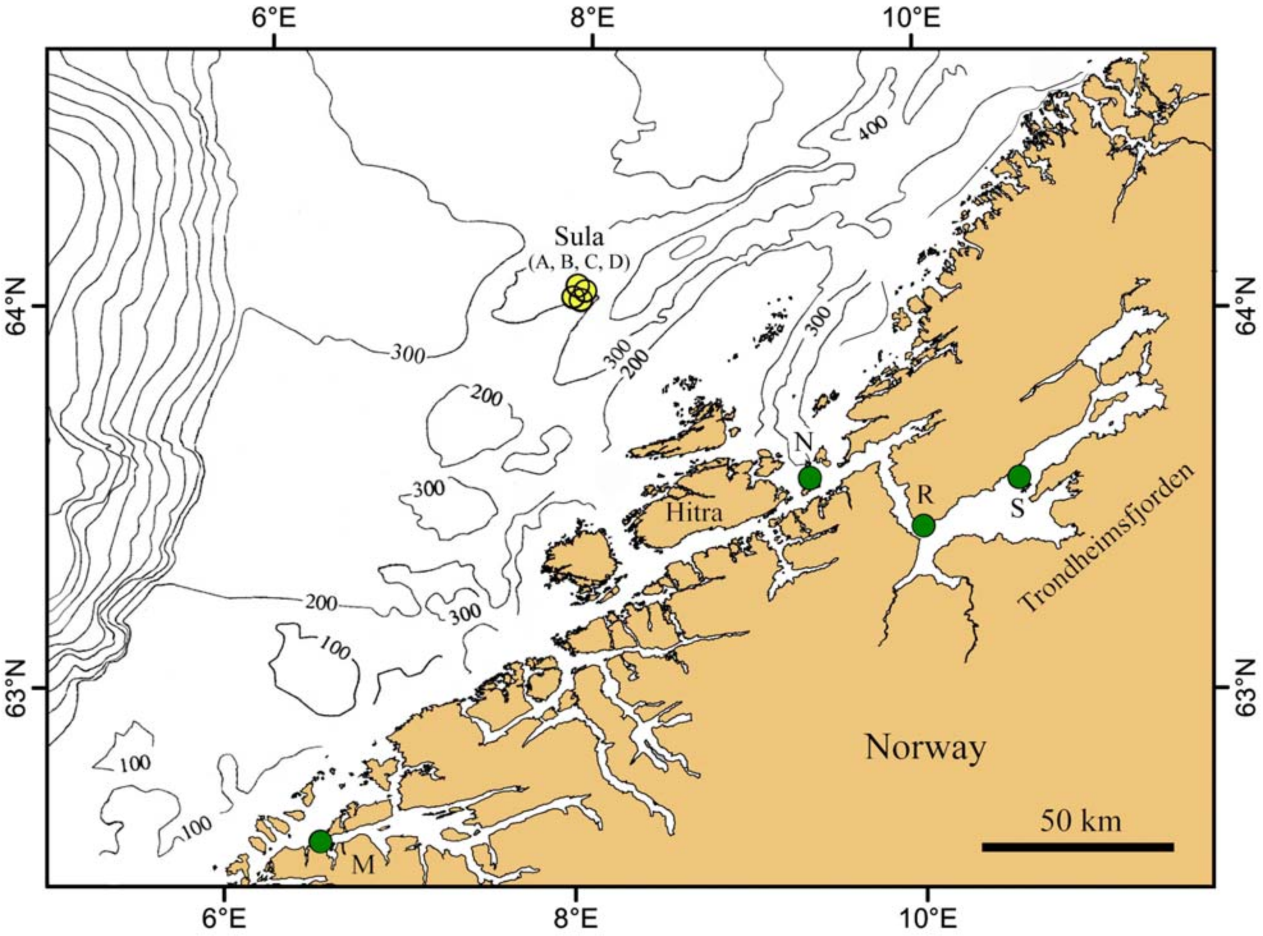

Fig. 1. Map showing the locations of sampled reefs. The bright yellow circles represent offshore reefs, and the dark green circles inshore reefs.

The Sula reefs were sampled in 1993 and 1997. During a cruise with SV *Polar Queen* September 1993, samples were collected with a ROV and a van Veen grab. The ROV samples were collected from selected parts of the reefs, while the grab samples were collected along a transect from the foot to the top of the reef. In 1997 two samples were collected with ROV operated from SV *Seaway Commander*. In 1996 RV *Håkon Mosby* was used to take samples with triangular dredge from the Nordleksa and Rødberg reefs. On a cruise with RV *G.O. Sars* in April 1997 samples were collected from the Midfjord Reef using triangular dredge and van Veen grab.

Table 1. Geographic location of sampled reefs and the number of samples collected with different gear.

Date	Locality	Position		Depth (m)	ROV	Dredge	Grab
14.09.93	Sula Reef (A)	63°55.87' N	07°53.71' E	275	2	0	0
14.09.93	Sula Reef (B)	63°55.91' N	07°53.53' E	280	1	0	0
14-16.09.93	Sula Reef (C)	63°55.80' N	07°53.34' E	275-295	3	0	5
16.09.97	Sula Reef (D)	63°57.50' N	07°58.80' E	280-281	2	0	0
21.02.96	Rødberg (R)	63°27.87' N	10°00.00' E	200-250	0	1	0
22.02.96	Nordleksa (N)	63°36.55' N	09°23.13' E	200	0	2	0
29.03-02.04.97	Midfjord (M)	62°37.60' N	06°29.59' E	150-160	0	3	2
21-22.09.00	Selliggrunnen (S)	63°35.57' N	10°31.10' E	50-51	0	0	3
Sum					8	6	10

Processing of the samples

Samples collected with ROV and grab were fixed in 4% buffered formaldehyde, or frozen without any sieving or sorting onboard. The large samples provided with triangular dredge were subsampled onboard. The three largest colony fragments were frozen "intact", and

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megafauna (sponges, gorgonians, decapods, echinoderms, and larger molluscs) were sorted out and fixed on formaldehyde. The rest of the sample was sieved through 1and 5 mm sieves, and fixed in formaldehyde.

Weight, volume, and percentage of live polyps were estimated for the analysed coral fragments. The volume of the fragments with associated fauna and trapped sediments (sample volume) was measured as the displacement volume in water. Displacement volumes were also measured with a plastic bag surrounding the fragments (total volume). The difference between these two volumes represents the volume of the free space between the branches (free volume). The ratio between weight and volume of a coral fragment gave an estimate of the density of the fragments. Large fragments were divided into sub-samples representing the outer and inner parts, or live or dead coral. The coral fragments were broken into smaller pieces to be able to sort out cryptic organisms.

Analyses of species composition

The samples were classified in four classes according to the amount of *Lophelia* rubble, and amount of live coral: 1) *Lophelia* rubble with 0% live corals, 2) samples containing larger coral fragments with 0% live corals, 3) 1 – 20%, and 4) > 20% live corals. The reason for the low percentage used to separate class 3 and 4 is that there were very few samples containing large proportions of living corals even though the samples were collected from live colonies. Fragments > 200 g were treated as separate subsamples, and classified according to the same four categories as used for whole samples.

Species diversity, composition and abundance were compared between reefs, and between different categories of degree of living coral. Solitary sessile and mobile animals were counted, while encrusting colonies were counted and measured as approximate areas. The species were classified with respect to feeding type (suspension feeders, deposit feeders, predators, omnivores, scavengers and parasites) based on information published by Miskov-Nodland et al. (1999), Jonsson et al. (2004) and ecological remarks in the taxonomic literature used in our study.

Detrended Correspondence Analysis, DCA was applied to group samples and species, based on abundance and composition of species, using the software PC-Ord version 4.14. Only species occurring in more than one sample were included. This criterion left 199 species for the analysis.

Results

General description of the coral samples

The 24 samples contained fragments of coral colonies and smaller amounts of trapped sediments and mollusc shell debris. The weight of coral skeleton in the samples varied between 16g and 74 kg (Table 2). For the dredge samples only a fraction was analysed, and the total weight of analysed coral was 20.85 kg: 2.82 kg live and 18.04 kg dead coral. The triangular dredge provided the largest samples with material collected over distances of up to ca 200 m, but with generally small fragments (< 1 kg). On average the size of grab and ROV samples was approximately the same. However, some grab samples contained larger fragments (up to 6.5 kg) of colonies than obtained with the dredge. The proportion of live coral in the samples varied between 0 and 100% of the skeleton weight, with an average of 13%. Eleven of the 24 samples consisted of only dead coral fragments. Four of these contained only small fragments from the rubble zone, and seven had larger fragments. Seven samples had between 1 and 20% live coral skeleton, while six had more than 20% live skeleton. The displacement volume of fragments wrapped in plastic (total vol.) varied between 40 and 3240 ml. On average 57% of this volume was open space.

Diversity of associated species

A total of 361 taxa were identified (Appendix Table 1). Of these 243 were identified to species level, 48 only to genus and 70 to higher taxa. Solitary species dominated with 266 species, whereas 94 species were colonial. Seventeen taxa were found in more than 50% of the samples. All of these, except two (unidentified errant polychaetes and the polychaete *Eunice norwegica*), were sessile organisms. In general, the number of sessile species was higher than mobile (197 versus 164, respectively). The number of species per sample varied from 11 to 155 (average = 48), and was best correlated with the weight of coral skeleton in samples ($r^2 = 0.53$, $p < 0.005$). Standardised to 100 g coral the number of species was between 2.3 and 103.3 (average = 23.8), and had the highest correlation with the percentage open volume of coral fragments ($r^2 = 0.49$, $p < 0.005$). The number of species was highest in samples with 1-20% live coral (255 species, Table 3), and lowest in samples from the rubble zone (107 species). The same trend was reflected by the diversity index (average H' = 4.8 for LL 1-20% and 3.8 for LR) (Table 3). Samples with more than 20% live skeleton contained only about half the number of species in comparison to samples with no live coral and had only slightly higher species richness than coral rubble (Fig. 2A). Comparison of the species richness of individual coral fragments showed that the diversity was highest for fragments with no live coral (Fig. 2B). On average 29.6 species were found per 100 g coral in fragments of this category. In contrast, fragments with more than 50% live coral had only 9.2 species per 100 g coral on average.

Table 2. Weight and volume of analysed samples. The weight of *L. pertusa* in dredge samples is in parentheses. The information about habitat refers to the sub-habitats as defined in the text (LL = Living *Lophelia*, DL = Dead *Lophelia*, LR = *Lophelia* rubble).

Location	Date	Gear	Depth	Sample no	Habitat	Weight (g) of *L. pertusa*	% live coral	Shell	Sample volume with bag	Sample volume without bag
Sula Reefs										
	14.09.93	ROV	275	A1	LL	276	10	0	320	125
	14.09.93	ROV	275	A2	LL	16	50	0	40	5
	15.09.93	ROV	275	B5	LL	396	25	0	510	175
	15.09.93	ROV	281	C7	DL	1866	0	22	2880	1200
	15.09.93	ROV	275	C8	LL	16	100	0	50	7
	16.09.93	ROV	275	C9	DL	125	0	45	120	59
	14.09.93	Grab	293	C3a	LR	258	0	235	290	140
	14.09.93	Grab	293	C3b	LR	246	0	50	230	100
	14.09.93	Grab	282	C4a	DL	535	0	0	840	300
	14.09.93	Grab	282	C4b	LL	1608	4	396	2380	1017
	14.09.93	Grab	295	C5a	DL	713	0	13	800	382
	19.06.97	ROV	280	D1	DL	622	0	0	790	263
	19.06.97	ROV	281	D2	DL	408	0	5	550	220
Midfjord										
	28.03.97	Dredge	155-160	M1	LL	613 (14120)	17	60	838	317
	28.03.97	Dredge	150-160	M4	LL	756 (74500)	60	1	1000	320
	29.03.97	Dredge	155-165	M8	DL	937 (34000)	0	153	1800	530
	02.04.97	Grab	145-160	M9c	LL	6464	17	243	6500	3751
	04.02.97	Grab	145-160	M9d	LL	1245	5	120	1958	795
Nord-Leksa										
	22.02.96	Dredge	239-144	N1	LL	1980 (17900)	10	180	2910	1250
	22.02.96	Dredge	169-167	N2	LL	250 (6700)	28	3	240	90
Røberg										
	21.02.96	Dredge	265-230	R1	LL	255 (45000)	15	0	73	28
Selliggrunnen										
	22.09.00	Grab	50	S1	LR	468	0	720	630	247
	22.09.00	Grab	50	S2	LL	724	74	0	1455	423
	22.09.00	Grab	51	S3	LR	70	0	1684	70	29
SUM						20847 (192220)	-	3930	27274	11744
AVERAGE						869 (32037)	13	164	1136	491

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Taxonomic composition

Mollusca, Arthropoda (Crustacea) and Bryozoa were the most species rich phyla (68, 55 and 52 species, respectively) contributing 48% to the total number of species. Mollusca were comprised mainly of Bivalvia (40 species) and Prosobranchia (20 species). The most species rich groups of Crustacea were Amphipoda (20 species) and Isopoda (18 species). Bryozoa was represented by 24 species of Ascophpora, of 22 species Cyclostomata, and six species Anascophora. The most abundant phyla were Foraminifera, Annelida, and Mollusca, all occurring with more than 12 individuals per 100 g coral. 166 species occurred in one sample only. These were represented by most phyla except Nematoda and Nemertini, which occurred in 42 and 17% of the samples, respectively, but were not identified to species level.

Table 3. Total weight (g) and volume (ml) of coral skeleton in four categories with respect to the proportion of dead skeleton. The habitat abbreviations are the same as in Table 2. The LL habitat is divided into two categories, one with a low percentage live coral (1 – 20%), and one with high percentage live coral (> 20%). The percentage of live coral is based on skeleton weight. Standard deviation is in parentheses.

Habitat	LR	DL	LL (1-20%)	LL (>20%)
No of samples	4	7	7	6
Weight of coral	1042 (163)	5206 (556)	12263 (2192)	2089 (334)
% live coral	0	0	14.3 (5.4)	55.7 (28.5)
% open volume	57 (3.9)	60 (7.3)	57 (6.9)	73 (10.7)
Ind. and col./100g coral	94.9 (56.4)	65.9 (84.5)	66.2 (86.9)	145.3 (100.0)
Mean diversity (H')	3.8 (0.9)	4.3 (1.0)	4.8 (0.5)	4.0 (0.6)
Species/100g coral	16.6 (10.9)	7.8 (4.7)	12.5 (17.8)	38.0 (39.3)
Tot. no of species	107	186	255	151

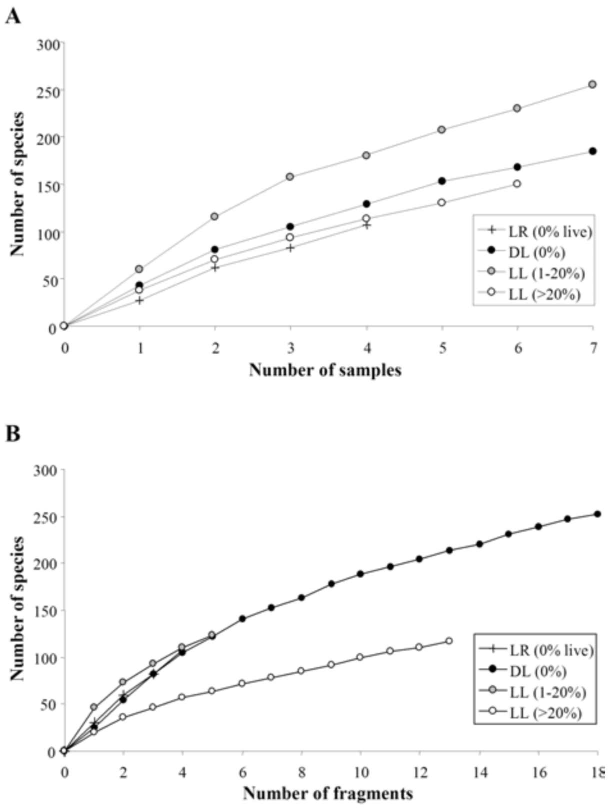

Fig. 2. Cumulative number of species with increasing number of samples (A) and sub-samples (fragments) (B). The samples and fragments are classified according to definitions of sub-habitats as described in the text. The species number is estimated as the average for 30 random combinations of samples or fragments.

Trophic composition

Suspension and deposit feeders were represented with approximately the same number of species with 142 and 146 species, respectively. Forty-four species were predators, while 17 and 12 species were omnivores and scavengers, respectively.

Only three parasitic species (*Hyrrokkin sarcophaga, Eulima bilineata*, and *Vitreolina philippi*) were recorded. Predators were represented by more species on inshore reefs than offshore, contributing 15% to the total number of species on inshore reefs compared to only five percent on the offshore reefs. The opposite was the case for omnivorous species, which contributed eight % to the total number of species on offshore reefs, compared to five percent inshore. There was a clear tendency of increased proportion of suspension feeders from habitat class 1 (LR) to class 3 (LL 1-20% live) (Fig. 3).

The proportion of suspension feeders in samples with more than 20% live coral was comparable to samples of dead coral (class 2). The proportion of suspension feeders decreased from LR to the LL classes (Fig. 3). The samples with 1 -20% live coral contained a slightly lower proportion of suspension feeders than samples with more than 20 percent. The proportion of predators was low for all habitat classes and differed little between the classes.

Distribution patterns

Thirty-four species were recorded from the living parts of the skeleton. Of the sessile animals only two species (*Hyrrokkin sarcophaga* and *Eunice norvegica*) occurred in direct contact with the living tissue.

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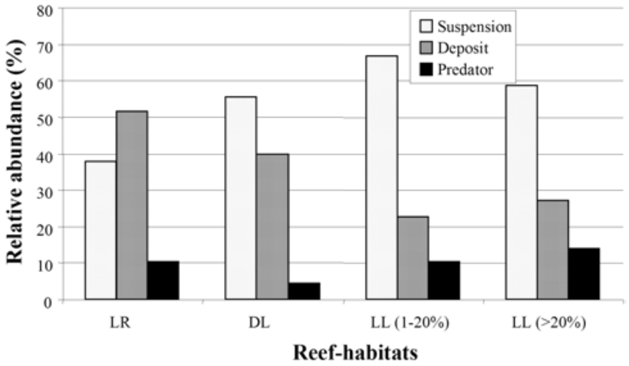

Fig. 3. The composition of individuals and colonies representing the three dominant feeding modes (suspension feeders, deposit feeders and predators) in the four different sub-habitats of the studied *Lophelia*-reefs.

In many cases an upper and lower side could be identified for the coral fragments. In fragments of dead corals the upper side was typically dark with a denser cover of detritus and epifauna compared to the lower side. Erect cyclostomate bryozoans, such as *Hornera lichenoides* were commonly found on skeleton surfaces at protected sites just inside the outer branches of the coral fragments.

Table 4. Differences between offshore and inshore *Lophelia*-reefs. The percentage of live coral is based on skeleton weight. Standard deviation is given in parentheses.

	Offshore reef samples (N =13)	Inshore reef samples (N = 11)
Live and dead (g)	7085	13515
% live	15	21
No of species	218	286
Species/100 g coral	22.2 (29.8)	13.5 (15.3)
Sum of ind. & col.	3483	8145
Ind. & col./100 g coral	83.5 (79.4)	99.2 (98.5)
Mean diversity (H')	4.2 (0.8)	4.4 (0.8)

Faunal composition of pooled samples from reefs and gear types were grouped by DCA with respect to sampling method rather than geographical location (Fig. 4). However, the DCA of the sample data set separated the offshore samples from the inshore along the first axis (Fig. 5).

The difference between offshore and inshore reefs was also expressed by the species richness and diversity (Table 4). The total number of associated species was highest for the coastal reefs with 277 species (77% of the total number of species) compared to 212 from the offshore reefs.

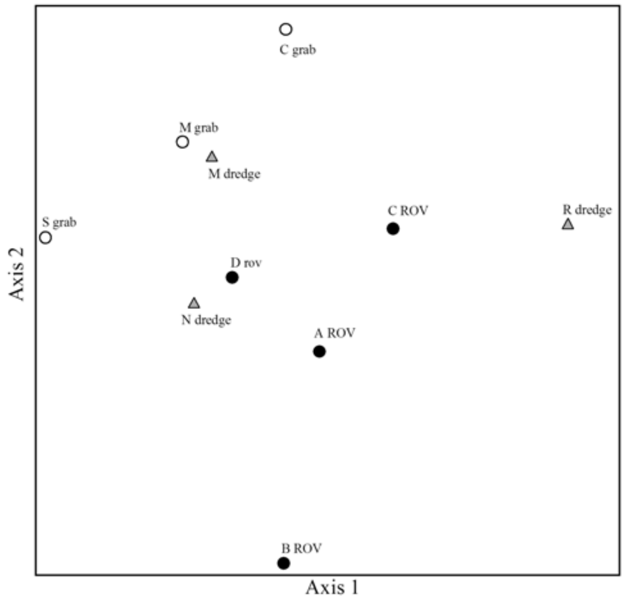

Fig. 4. Plot of the results from Detrended Correspondence Analysis (DCA) of pooled samples for gear types and reefs.

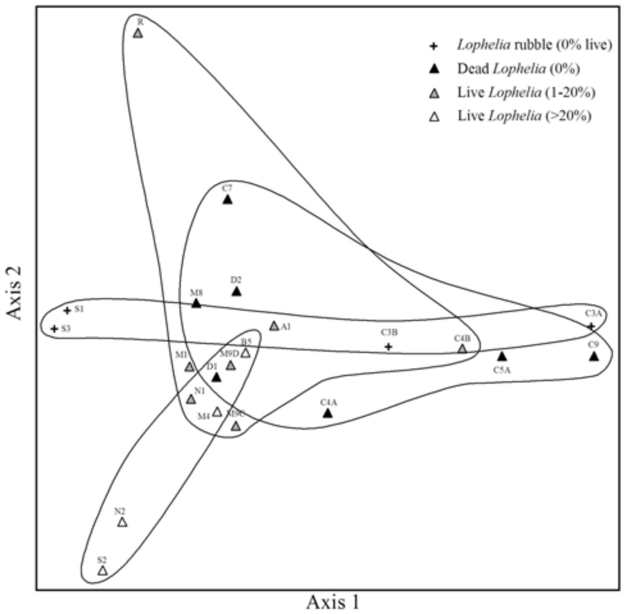

Fig. 5. Plot of the results from Detrended Correspondence Analysis (DCA) of samples. The different sub-habitats are indicated with different symbols, and the symbol labels refer to sample numbers as given in Table 2.

The composition of associated fauna on the offshore reefs differed from that on the coastal reefs. This was especially evident for Cnidaria, Crustacea, Foraminifera, Polychaeta and Tunicata (Fig. 6). Except for Foraminifera, all of these taxa were represented with more species on the coastal reefs than the offshore reefs. Foraminifera were more species rich offshore.

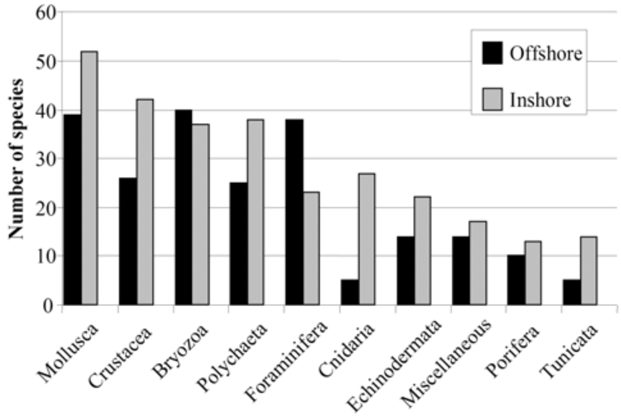

Fig. 6. Number of species in different taxonomic groups compared between offshore and inshore reefs.

The DCA plot of samples indicated a tendency of separation of the samples with respect to reef habitat along the second axis (Fig. 5). Twenty-one species formed a separate group together with samples containing live coral (> 20% live). These species are indicated with an asterix in Appendix Table 1. The proportion of mobile versus sessile species was greatest in the *Lophelia* rubble (Fig. 7).

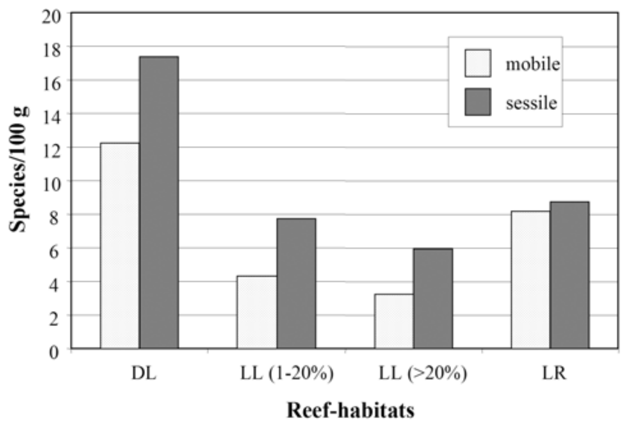

Fig. 7. The composition of mobile and sessile species in the four sub-habitats.

Abundance and frequency of occurrence of associated species

The numbers of individuals and colonies were strongly correlated with the weight of corals in the samples ($r^2 = 0.90$, $p < 0.005$). The total number of individuals and colonies per 100 g coral varied between 10 and 362, with an average of 115. The two most abundant taxa were Foraminifera and Polychaeta with an average abundance of 22.7 and 13.8 individuals per 100 g coral, respectively. *Verruca stroemia* (Cirripedia) and *Delectopecten vitreus* (Bivalvia) were the most abundant species (3.5 and 2.6 individuals per 100 g coral, respectively). In terms of frequency of occurrence the bivalve *Hiatella arctica* and the colonial tunicate *Didemnum albidum* dominated with presence in 71 and 63%, respectively. The abundance was highest for live coral samples > 20% live (145.4 individuals and colonies per 100 g coral), and lowest for samples containing only fragments of dead coral blocks (65.9 individuals and colonies per 100 g coral).

Differences between gears

The number of species per sample was lower for samples collected with ROV (average = 35.6) than for triangular dredge (average = 58.5) and grab (average = 52.1). This was also clearly illustrated by the cumulative number of species for each gear type (Fig. 8A). The samples contained between 28 and 4630 individuals and colonies. Per 100 g coral the number was highest for grab samples (average = 66.4) and lowest for dredge samples (average = 49.6). The ratio of mobile to sessile species was higher for grab samples than both ROV and dredge samples (Fig. 9).

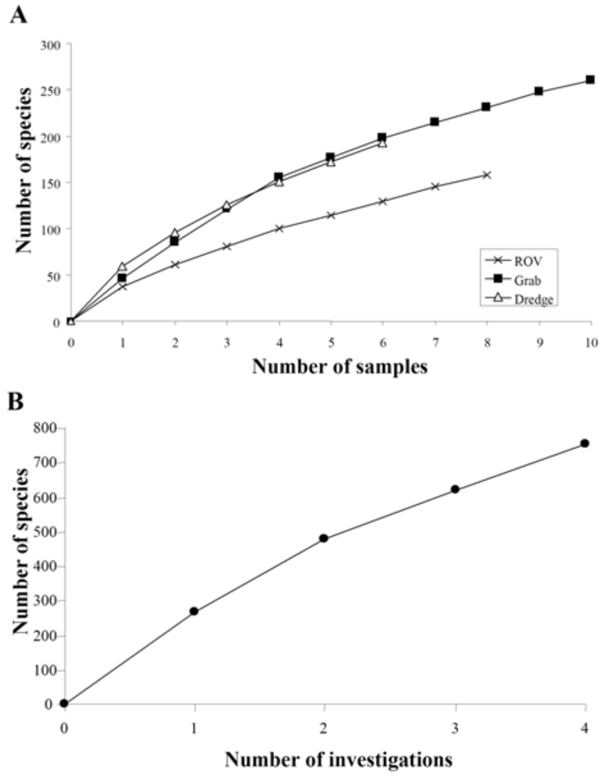

Fig. 8. A) Cumulative number of species with increasing number of samples for the three different gears used in this study. B) Cumulative number of species with increasing number of investigations of the reef fauna. The species number is estimated as the average for 30 random combinations of samples or fragments.

Discussion

Methods

The structural habitat complexity of *Lophelia*-reefs makes it difficult to standardise the sampling. The study material was collected with three types of sampling gear with different sampling characteristics. A dredge gives a poor spatial resolution and does not collect the mobile species representatively. Previous studies of the associated macrofauna on *Lophelia pertusa* based on dredge samples are limited mainly to presence/absence

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data (Dons 1944; Burdon-Jones & Thambs-Lyche 1960; Jensen & Frederiksen 1992). Grabs were not used in the earlier studies because the reefs were difficult to locate precisely without modern navigation tools, and because grabs commonly do not close properly on gravely bottoms. However, in this investigation we demonstrated that the van Veen grab normally cuts skeletal pieces and closes properly as long as the samples do not contain gravel. One source of errors to the composition of associated fauna is loss of specimens on the bottom during sampling and during transport to the surface. Mobile animals may escape during sampling especially when it is slow as in the case of using an ROV manipulator arm. Furthermore, mobile animals may be washed out from an unprotected sample when hauled trough the water column. In this study the samples collected with the grab were best protected from wash-out. This is also evident for the relative composition of mobile versus sessile species for the different gears (Fig. 9).

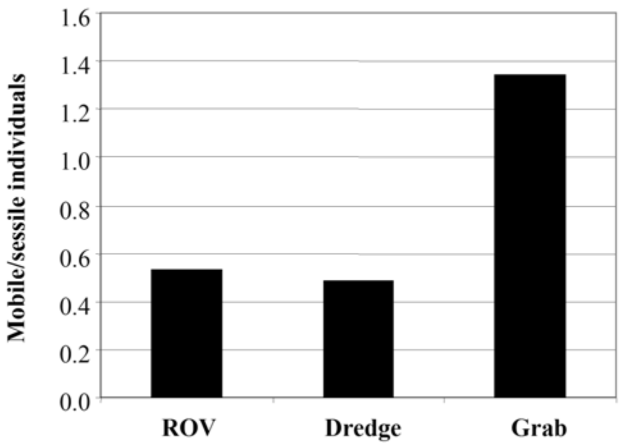

Fig. 9. The ratio of mobile and sessile species in samples collected with different sampling gears, based on number of individuals.

The quantitative composition of the associated fauna of *L. pertusa* is difficult to study because the coral skeleton has a complex architecture. Most mobile species found in coral samples are not attached to the coral skeleton and can therefore not be included in a description of distribution patterns within a sample.

To describe the spatial distribution of invertebrates within a *Lophelia*-reef, and to increase the sampling precision, we recommend using a grab because it samples species effectively and damages fewer corals compared to a dredge. Another advantage with grab sampling is that the amount of coral in samples is less variable than for a dredge. Corals can be targeted more easily if the grab is equipped with a video camera, thus reducing the number of misses, which makes the sampling more efficient.

Diversity and composition of associated species

A diverse fauna is associated with *Lophelia pertusa* (Dons 1944; Burdon-Jones & Tambs-Lyche 1960; Jensen & Frederiksen 1992; Fosså & Mortensen 1998; Rogers 1999). The majority of these species are sessile invertebrates that use the exposed skeleton as an attachment site in an environment suitable for suspension feeding.

The species diversity was highest in samples with small proportions of live coral. In contrast to samples consisting entirely of dead coral these samples comprised both living and dead coral, thus representing greater habitat diversity. On a smaller scale the diversity of the associated macrofauna was higher for fragments of dead coral skeletons than for living coral, also demonstrated by Jensen & Frederiksen (1992). The high species diversity within *Lophelia*-reefs is best explained by the great habitat diversity similar to what has been suggested for warm-water coral reefs (e.g., Connel and Slatyer 1977; Reaka-Kudla 1997).

One factor related to the habitat diversity is the variable ages of the coral skeleton. The presence of substrata of different age allows different stages of succession to be present simultaneously. A mosaic of different sub-habitats facilitate the presence of a large local species pool ready to colonize new space produced by coral skeleton growth or physical disturbance (e.g., breaking of coral colonies and predation). This situation fits with the *intermediate disturbance model of diversity* (Connell 1978), and probably also the *tolerance model for succession* (Connell and Slatyer 1977), since there are very few examples of species facilitating or inhibiting the succession of others. The size and relative composition of the sub-habitats (living and dead skeleton surface, trapped detritus, skeletal cavities and free space) is probably also related to the substratum age. The composition of associated species differed between these sub-habitats inside a coral colony. Specific sampling of the fauna from these sub-habitats would be extremely difficult in the field.

The number of individuals and colonies was highest in samples with a high proportion of live coral, because of a high abundance of a few species. Opportunistic utilisation of newly exposed skeleton close to the living coral may be one way of characterising these occurrences. No species are known to have obligate relationships with *Lophelia pertusa*, and there are few examples of species showing clear adaptations to live in this habitat. Only two species (*Hyrrokkin sarcophaga* and *Eunice norwegica*) were found living in direct contact with the coral's soft tissue. Observations of *Lophelia* and some associated species in aquarium showed that only one (an unidentified hymedesmid sponge) of 12 sessile species lived directly on the coenosarc tissue of *Lophelia* (Mortensen 2001). Other species previously reported living on the skeleton of live *Lophelia*, such as the bivalve *Delectopecten vitreus* (Jensen & Frederiksen 1992) are attached to exposed areas of the skeleton (Mortensen 2001). The absence of sessile invertebrates on the coenosarc may be due to antifouling properties of the tissue or instability of this living substrate. Even though none of the species are found exclusively on the reefs, some are rare in other habitats (i.e. *Munidopsis serricornis* and *Bathyarca pectunculoides*). *Lophelia*-reefs may be important habitats to many benthic invertebrates and may also

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provide larval supply supporting high species diversity in other nearby hard bottom habitats.

The number of species increased with the number of samples and had only a weak tendency of approaching an upper level for all three gear types (Fig. 8A). The number of samples was clearly not sufficient to identify the total number of species that can occur on the reefs off the Norwegian coast.

The results of the present investigation were compared with results published by Dons (1944), Burdon Jones & Tambs-Lyche (1960), and Jensen & Frederiksen (1992) from *Lophelia*-reefs in the Northeast Atlantic. The number of species they reported varies between 173 and 282. Including the present study a total of 796 species have been recorded. Of these, 621 have been documented from reefs along the Norwegian coast. Forty-four of the species reported in any of the three studies from Norway (Dons 1944; Burdon Jones & Tambs-Lyche 1960; present study) are not reported from off the Faroe Islands in the study by Jensen & Frederiksen (1992). Most species (536) have been reported from only one study, whereas only 21 species are common for all (see Appendix Table 1). Mollusca and Annelida (represented only by Polychaeta) are the two most speciose phyla with 141 and 116 species, respectively. After four faunistic investigations of *Lophelia*-reefs the number of species is still increasing significantly and shows only a weak tendency of attaining an asymptote (Fig. 8B. This demonstrates a great variation of the coral community and indicates that the actual number of species occurring on *Lophelia*-reefs in the North-east Atlantic Ocean is much higher than recorded so far. However, it may also reflect different taxonomic focus by the different authors.

The diversity of species associated with *Lophelia* is similar with that of some zooxanthellate scleractinians (Jensen & Frederiksen 1992). One example is *Oculina arbuscula* in Florida where McCloskey (1970) documented 309 species larger than 0.2 mm. However, the species richness of tropical coral reefs in general is much higher than that of *Lophelia*-reefs (Reaka-Kudla 1997). This is best explained by the higher diversity of scleractinians, the presence of numerous seaweed species, and thus, a higher number of food sources on the tropical reefs. On the Great Barrier Reef, 350 species of reef-building corals are recognized (Veron 1986). Probably, the most important difference between deep-water reefs and tropical reefs is the absence of photosynthetic organisms in the deep-water. The zooxanthellae and macroalgae increase the production and habitat diversity of the reefs, which is related to high diversity of associated species (Huston 1994). From coral reefs in the Philippines 3967 species have been recorded (Philippines, Department of Environment and Natural Resources 1997). However, these were largely fish and seaweed species (2773 species), and the number of invertebrates was 1866. Considering the relative high number of reef community studies from the Philippines this number does not appear to be much higher than the number of species recorded on *Lophelia*-reefs in the northeast Atlantic.

In contrast to the numerous examples of highly developed interspecific relationships in shallow water tropical reefs (e.g., Patton 1976, and references therein; Tsuchiya and Yonaha 1992; Martin and Britayev 1998), there are no examples of species found exclusively on *Lophelia*-reefs. Many of the invertebrates occurring on *Lophelia*-reefs in the northeast Atlantic have a wide depth range and have even been recorded in kelp forests (*Laminaria hyperborea*) and littoral seaweed communities (Hayward 1988; Schultze et al. 1990; Mortensen 1992). However, some of the species (i.e. *Acesta excavata*, *Asperarca nodulosa, Eunice norvegica, Harmothoe oculinarum*,and *Hyrrokkin sarcophaga*) are much more common on the reefs than in other habitats (Dons 1944; Burdon Jones & Tambs-Lyche 1960; Jensen & Frederiksen 1992).

The relationship between *Lophelia pertusa* and the polychaete *Eunice norvegica* (L., 1767) is one example of special adaptation of species within deep-water coral communities. *Eunice* commonly occurs together with *Lophelia* and *Madrepora oculata* in the Atlantic Ocean (Dons 1944; Winsnes 1989) but also occurs in other habitats (Kirkegaard 1992). The relation of *E. norvegica* to *Lophelia* has both parasitic and mutualistic elements, and can be regarded as a non-obligate mutualism. The polychaete commonly “steals” food from *Lophelia* but also removes sediment particles from the polyps, which may reduce the risk of being colonised by sessile invertebrates or infected by microbes (Mortensen 2001).

Zonation patterns

Differences in the abundance, diversity and trophic composition of associated species were related to differences between the studied sub-habitats. The lowest species diversity (H’) was found in samples from *Lophelia* rubble, and there was a maximum in species diversity in samples from areas of the reefs where live and dead coral occur mixed. The increasing relative abundance of deposit feeders with distance from reef summit (Fig. 3) (from living *Lophelia* to *Lophelia* rubble) is probably related to increased load of finer sediments and organic particles. This pattern has also been observed by Jonsson et al. (2004). Mortensen et al. (1995) presented results from analyses of video-recorded transects across 10 reefs on the mid-Norwegian shelf. A total of 31 megafaunal taxa, 15 from the *Lophelia* rubble-zone, 24 from dead *Lophelia*-zone and 26 from the living *Lophelia* -zone were observed. They suggest that the diversity pattern is related to habitat type and current patterns. Local differences in current velocities and age of skeleton fragments may result in a mixed effect on biological succession and environmental requirements among the species. Our study agrees with the results of Mortensen et al. (1995) because the mixture of live and dead coral is found within the living zone of the reef. The low number of species in the *Lophelia* rubble zone may be a result of the instability of the substratum and small area of exposed surface. This is also indicated by the higher proportion of mobile species compared to the other sub-habitats studied (Fig. 4). A distinct zonation of species occurs within coral colonies, but unfortunately, time did not allow for more fine-

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scaled studies than presented here. A description of more small-scaled distribution patterns would certainly add significantly to the understanding of the *Lophelia*-reef community.

Conclusions

- The number of species occurring on *Lophelia*-reefs can be expected to be much higher than described so far, because the fauna is incompletely sampled.
- The species composition of the associated fauna has high variation between reefs. Some of the variation is due to the difficulty of standardizing the sampling.
- The associated fauna in samples representing four different reef-habitats were compared: 1) *Lophelia* rubble, 2) dead block, 3) mixed live and dead coral (1-20% live), and 4) live coral (> 20%). The fauna from these sub-habitats can be chararacterised as:
  1) *Lophelia* rubble: lowest species diversity, fauna dominated by mobile deposit feeders
  2) Dead blocks: moderate species diversity with relatively even composition of suspension and deposit feeders
  3) Mixed live and dead coral: highest species diversity, fauna dominated by suspension feeders
  4) Live coral: low species diversity, fauna dominated by suspension feeders
- Inshore reefs seem to have higher species diversity than offshore. This may be explained by higher diversity of habitats near the coast in general, providing a greater variety of larval supply from the intertidal down to great depths.
- To describe the spatial distribution of invertebrates within a *Lophelia*-reef, and to increase the sampling precision, we recommend using a grab equipped with a video camera. A grab samples the fauna more representatively and damages less coral compared to a dredge, which has been the traditional sampling gear until recently.
- The species richness of *Lophelia*-reefs in the Northeast Atlantic seems to be comparable with at least some shallow water coral reefs. However, comparison is difficult because both deep and shallow-water reefs most probably are incompletely sampled.

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Appendix Table 1. The abundance of species (n per 100 g coral) identified in coral samples from the eight *Lophelia*-reefs in mid-Norway. *: species typical for live *L. pertusa* (> 20%) indicated by DCA. +: species occurring in this and four other studies from the northeast Atlantic Ocean (Dons 1944; Burdon-Jones & Tambs-Lyche 1960; Jensen & Frederiksen 1992). Station letters are identified in Table 1 and can be located in Figure 1.

Species	A	B	C	D	M	N	R	S
Foraminifera								
Acervulina inhaerens Schultze, 1854			0.01					
Adercotryma cf. *glomerata* (Brady, 1878*)*			0.33					
Ammodiscus cf. *incertus* (d'Orbigny, 1839)			0.10	1.46	0.51			
Ammodiscus sp.			0.03					
Ammolagena cf. *clavata* (Jones & Parker, 1860)			0.51					
Astrorhiza sp.			0.05					
Bolivina sp.					0.04			
Cibicides lobatulus (Walker & Jones, 1798)			0.18					
Cibicides sp.				0.39	0.03			
Clavulina parisiensis d'Orbigny, 1826			0.03					
Cornuspiroides foliacea (Phillipi, 1824)	0.34		0.31					
Cornospiroides sp.			0.01					
Cristellaria sp.			0.15					
Foraminifera agglutinated sp. 1				1.36	3.70	1.34		
Foraminifera agglutinated sp. 2			0.74	6.50	8.27			
Foraminifera hyalinoecious			0.80	0.78	0.76			
Globobulimina sp.	0.34		0.24					
Globulina sp.					0.04			
Haplophragmoides glomeratum (Brady 1878)					0.01			
Hyrrokkin sarcophaga Cedhagen, 1994			0.88	1.07	1.20			1.58
Islandiella sp.				0.39	0.03			
Lagena striata (d'Orbigny, 1839)			0.01	0.58	0.03			
Lagotia sp.			0.62					
Miliolinidae indet.			0.44	0.29	0.01			
Nonion sp.			0.06	0.10	0.03			
Paramolina coronata (Parker & Jones, 1857)			0.58	5.15	3.04			
Planorbulina cf. *ariminensis* (d'Orbigny, 1826)	0.68		0.28					
Planorbulina sp.	8.22	6.31	1.84	6.21	2.58			0.48
Polymorphina sp.	0.34		0.81	0.97	0.04			
Pyrgo murrhyina (Schwager, 1866)			2.03					
Radicula limosa Christiansen, 1958								0.79
Rhabdammina abyssorum M. Sars, 1868			0.26					
Rosalina anomala Terquem, 1875			0.25	1.36	0.31			
Saccammina sphaerica M. Sars, 1868			0.28					
Textularia agglutinans d'Orbigny, 1839	0.34		2.08		0.04			
Textularia sp.			0.27	4.76	2.22	0.05		
Trifarina angulosa (Williamson, 1858)			0.01	0.19				
Uvigerina mediterranea Hofker, 1932			0.09		0.02			
Uvigerina pygmaea d'Orbigny, 1826			0.06					
Quinqueloculina seminula (L., 1767)			0.85		0.03			
Valvulina conica (Parker & Jones, 1865)			0.03					
Porifera								
Antho dichotoma (Esper, 1794)					0.02			

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Calcarea indet.				2.82	0.45			
Clionidae indet.		0.25	0.12	1.46	0.18		0.78	0.16
Demospongiae indet.	3.08	1.01	0.36	6.21	1.76		5.88	0.79
Dysidea sp.			0.02					
Geodia sp.					0.04			
Hemigellius hartlaubi (Hentschel, 1928)			0.02					
Hymedesmidae indet.				0.78	0.03			
Mycale lingua (Bowerbank, 1866)					0.09			0.16
Phakellia ventilabrum (Johnston, 1842)					0.09			
Phakellia sp.					0.04			
Demospongia (Red thorny)			0.04	0.58	0.15		2.35	
Plocamionida ambigua (Bowerbank, 1866)			0.07	2.72	0.86	0.09	1.37	0.63
Sycon sp.			0.01					
Tentorium semisuberites (Schmidt, 1870)			0.07	0.39	0.11	0.05	0.98	
Aphroceras ensata (Bowerbank, 1858)					0.02			
Hydrozoa								
Abietinaria abietina (L., 1758)				0.10		0.05		
Aeta sp.					0.02			
Campanularidae indet.								1.58
Corynidae indet.								11.09
Eudendrium rameum (Pallas, 1766)								0.79
Filellum serpens (Hassal, 1848)						0.05		
Grammaria abietina (M. Sars, 1851)								0.63
Hydrozoa indet.		0.25	0.03	0.10	0.03	0.19	0.12	
Kirchenpaueria pinnata (L., 1758)					0.05			
Lafoea dumosa (Fleming, 1828)						0.09		1.11
Lovenella producta (G.O. Sars, 1874)								1.58
Laomedea cf. *neglecta* Alder, 1856								0.16
Zygophylax pinnata (G.O. Sars, 1874)								0.79
Obelia dichotoma (L., 1758)								1.27
+ *Sertularella gayi* (Lamouroux, 1821)					0.07			
Sertularella polyzonias (L., 1758)					0.02			
Sertularella tenella (Alder, 1856)					0.01			
Stegopoma plicatile (M. Sars, 1863)								0.32
Actiniaria								
Actiniaria indet.						0.09		
Edwardsiella carnea (Gosse, 1856)					0.05	0.09		
Edwardsiella loveni (Carlgren, 1893)	1.03		0.74		0.31		2.35	
Edwardsiella sp.				1.17	0.08	0.28		
Gersemia rubiformis (Ehrenberg, 1834)							0.39	
* *Protanthea simplex* Carlgren, 1891					0.13			0.32
Gorgonacea								
Anthothela grandiflora (M. Sars, 1856)							0.39	
Paramuricea placomus (L., 1758)					0.02			
Paragorgia arborea (L., 1758)			0.02				0.78	
Nematoda								
Nematoda indet.	1.71		0.13	1.26	1.04	0.14		1.11
Nemertini								
* Nemertini indet.	0.34				0.02	0.79		0.16
Polychaeta								
Acanthicolepsis asperrima (M. Sars, 1851)			0.04					
Alentia gelatinosa (M. Sars, 1835)			0.05					

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Branchiomma bombyx (Dalyell, 1853)			0.05					
Circeis spirillum (L, 1758)				0.10	0.01			
Cirratulidae indet.					0.02			
+ *Eunice norvegica* (L., 1758)	0.68	0.76	0.04	0.78	0.75	0.56	0.39	
Eunice pennata (O.F. Müller, 1776)					0.06			
Cf. *Eunoe nodosa* (Sars, 1861)					0.03			
Euphrosine sp.						0.05		
Eusyllis blomstrandi Malmgren, 1867						0.23		
* *Filograna implexa* Berkeley, 1828			0.04		0.15			0.48
Flabelligeridae indet.					0.11			
Glycera sp.			0.06		0.01			
Harmothoe fragilis Moore, 1910						0.05		
Hesionidae indet.			0.03		0.04			
Hydroides norvegica Gunnerus, 1768	1.37		0.07				0.39	
Lepidonotus squamatus (L., 1758)					0.02			
Lumbrinereidae indet.					0.01			
Maldanidae indet.					0.15			
Melinna cf. *cristata* (M. Sars, 1851)					0.01			
Nereidae indet.			0.01	0.10	0.02			
Cf. *Omphalopomopsis fimbriata* (Delle Chiaje,1828)		0.51						
Opheliidae indet.			0.01					
Pectinaria auricoma (O.F. Müller, 1776)					0.02			
Phyllodocidae indet.	0.68				0.12			
+ *Placostegus tridentatus* (J.C. Fabricius, 1779)			0.17	0.78	0.13			0.32
Platyneris cf. *dumerilii* (Audouin & Milne-Edwards, 1834)			0.01					
Polychaeta indet.	2.40	0.51	0.65	0.19	1.20	1.71		2.38
Polynoidae indet.			0.09		0.44	0.42		
Potamilla neglecta (Sars, 1851)					0.09			
+ *Sabella penicillus* L., 1767			0.01		0.21			
Sabellidae indet.			0.09	0.10	0.05	0.09		
+ *Serpula vermicularis* L., 1767	0.68	0.76	0.50	0.10	0.01		0.39	0.63
Serpulidae indet.	0.68			10.19	0.57	0.37		
Sigallionidae indet.					0.03			
Spionidae indet.					0.07			
Spirorbis tridentatus (Levinsen, 1883)	2.05	1.52	0.20	0.19	0.03			
* Spirorbidae indet.	2.74	2.53	0.12	12.52	0.84	5.00		0.79
Syllidae indet.	1.03		0.03	0.10	0.11			
Terebellidae indet.					0.03			
Terebellomorpha indet.					0.42			
Typosyllis armillaris (O.F. Müller, 1776)					0.03			
Typosyllis hyalina (Grube, 1863)				0.19				
Typosyllis sp.						0.05		
Echiuroidae								
Echiuroidae indet.					0.06			
Sipunculoida								
Golfingidae indet.				0.39	0.03			
Golfingia sp.					0.04			
Ochnesoma steenstrupi Korén & Danielssen, 1875			0.10					

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Phascolosoma sp.					0.01			
Sipunculoida indet.	0.68	0.51	0.02		0.06	0.05		0.16
Polyplacophora								
Lepidochiton alveolus (Lovén, 1846)					0.11			
Leptochitona cinerus (L., 1767)			0.03					
Polyplacophora indet.			0.01	0.19	0.03	0.05		0.32
Prosobranchia								
Alvania cimicoides (Forbes, 1844)			0.07		0.01			
* *Alvania jeffreysi* (Waller, 1864)				0.29	0.15	0.14		0.16
Anachis haliaeeti (Jeffreys, 1867)			0.07					
Anatoma crispata (Fleming, 1828)			0.03		0.06	0.05		
Buccinidae indet.					0.02			
Buccinum undatum L., 1758					0.06			
Colus sp. Juv.						0.19		
Cylichna alba (Brown, 1827)			0.01					
Emarginula crassa J. Sowerby, 1813			0.07	0.19	0.07			
* *Emarginula fissura* (L., 1767)					0.01	0.09		0.16
Epitonum sp.			0.01					
Eulima bilineata Alder, 1848			0.01					
Odostomia cf. *conoidea* (Brocchi, 1814)	0.34							
Polynices pallida (Broderip & Sowerby, 1829)					0.01			
* *Skenea basistriata* (Jeffreys, 1877)			0.01	0.68		0.32		
Skenea sp.						0.23		
Trophon clathratus (L., 1767)			0.01		0.01			
Trophon truncatus (Ström, 1767)			0.03		0.19			
Velutina velutina (Müller, 1776)			0.05					
Vitreolina philippi (de Rayneval & Ponzi, 1854)				0.10				
Opistobranchia								
Doto sp.					0.04			
Iothia fulva (Müller, 1776)					0.01			
* Nudibranchiata indet.						0.05		0.16
Philine sp.					0.01			
Scaphopoda								
Antalis entalis L., 1758					0.04			
Entalina quinquangularis (Forbes, 1843)					0.02			
Caudofoveata								
Falcidens crossotus Salvini-Plawen, 1968					0.02			
Scutopus robustus Salvini-Plawen, 1970					0.08			
Bivalvia								
Abra nitida (Müller, 1776)					0.15			
Abra sp.					0.03			
+ *Acesta excavata* (J.C. Fabricius, 1779)			0.02					
Anomidae indet.	0.34	0.51	0.06	5.53	0.45	0.19		0.95
Arca tetragona Poli, 1795				0.10				
Astarte sulcata (da Costa, 1778)						0.05		
+ *Asperarca nodulosa* (Muller, 1776)			0.01		0.01			
Bathyarca pectunculoides (Scacchi, 1834)	2.74	0.25	0.26	0.19	0.11	0.32	1.18	
+ *Chlamys sulcata* (Müller, 1776)		0.25	0.08	0.10	0.02			
Chlamys sp.			0.01		0.04			
Dacrydium sp.			0.01					
+ *Delectopecten vitreus* (Gmelin, 1791)	0.34	0.25	0.04	0.49	7.11	2.68	0.78	0.95
Heteranomia squamula (L., 1758)	0.34		0.06	5.15	4.80	1.53		
Hiatella arctica (L., 1767)	0.68		0.15	0.58	2.55	0.93	6.27	0.95
Limopsis aurita (Brocchi, 1814)			0.04					

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Limopsis minuta (Philippi, 1836)			0.01					
Modiolus modiolus (L., 1758)					0.05			1.74
Modiolula phaseolina (Philippi, 1844)			0.05	0.19	0.95	0.74	1.96	3.01
Monia squama (Gmelin, 1791)					0.12			
Myrtea spinifera (Montagu, 1803)					0.01			
Mytilidae indet.						0.32		
Nucula sp.			0.03					
Palliolum striatum (Müller, 1776)					0.15			
Palliolum tigerinum (Müller, 1776)					0.01			
Pectiniacea indet.				0.29				
* *Pododesmus patelliformis* (Gmelin, 1791)			0.03					
Protobranchiata indet.			0.01					
Pseudamussium septemradiatum (Müller, 1776)					0.02			
Thyasira equalis (Verill & Bush, 1898)					0.14			
Thyasira ferruginea (Forbes, 1851)			0.18		0.01			
Thyasira flexuosa (Montagu, 1803)					0.17			
Thyasira sarsii (Philippi, 1845)					0.08			
Thyasira cf. *obsoleta* (Verill & Bush, 1898)					0.06			
Thyasira pygmaea Verrill & Bush, 1898			0.04		0.03			
Thyasira sp.			0.01		0.01			
Yoldiella lucida (Lovén, 1846)					0.01			
Yoldiella sp.			0.01					
Pycnogonida								
Nymphon leptocheles G.O. Sars, 1888			0.01			0.05		
Pallenidae indet.				0.10				
Pycnogonida indet.					0.01			
Acarina								
Acarina indet.				1.46				
Copepoda								
Harpacticoida indet.					0.01			
Ostracoda								
Cyprididae indet.				0.10				
Ostracoda indet.				0.10				
Philomedes globosus (Lilljeborg, 1853)					0.01			
Cirripedia								
Scalpellum sp.						0.05		4.28
+ *Verruca stroemia* (O.F. Müller, 1776)					0.77		21.96	
Cumacea								
Eudorella emarginata (Krøyer, 1846)					0.01			
Tanaidacea								
Aspeudes spinosus (M. Sars, 1858)					0.13			
Isopoda								
Aega monophtalma Johnston, 1834					0.01			
Aega ventrosa M. Sars, 1848					0.02			
Anthuridae indet.			0.01					
Desmosomatidae indet.				0.10				
Disconectes furcatum (G.O. Sars, 1870)			0.04					
Echinozone coronata (G.O. Sars, 1870)				0.10	0.05			
Gnathia dentata (G.O. Sars, 1872)	0.34		0.13	0.10	0.15			
Gnathia elongata (Krøyer, 1846)					0.01			
Gnathia maxillaris (Montagu, 1804)					0.06			
* *Gnathia* sp.					0.08			0.16
+ *Janira maculosa* Leach, 1814			0.09	0.10	0.05	0.09		0.16

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Leptanthura tenuis (G.O. Sars, 1872)	0.34							
Munna boecki Krøyer, 1839				0.10	0.10			
Munna kroeyeri Goodsir 1842					0.04			
* *Munna minuta* Hansen, 1910						0.19		0.95
Munna sp.			0.02	0.29	0.01		0.39	
Nannoniscus oblongus G.O. Sars, 1869				0.29				
Isopoda indet.						0.05		
Amphipoda								
Aeginella spinosa Boeck, 1861					0.22	0.28		
Amphilocus manudens Bate, 1862					0.04			
Epimeria tuberculata G.O. Sars, 1893			0.02					
Eriopisa elongata (Bruzelius, 1859)			0.01					
* Gammaridae juv. indet.			0.03		0.03	0.23		9.51
* Gammaridae indet.			0.03		0.13			2.38
Harpinia pectinata G.O. Sars, 1891					0.08			
Jassa pusilla (G.O. Sars, 1894)						0.28		
Leucothoe spinicarpa (Abildgaard, 1789)					0.02	0.05		0.16
Lilljeborgia pallida (Bate, 1857)					0.01			
Lysaniasidae indet.			0.02		0.02			
* *Metopa* sp.					0.04	0.09		
Monoculodes tuberculata Boeck, 1871					0.05			
Orchomene amblyops G.O. Sars, 1890						0.19		
Orchomene crispatus (Goës, 1866)						0.09	1.96	
Phippsiella similis (G.O. Sars, 1891)			0.05					
Proboloidesgregaria (G.O. Sars, 1882)					0.04			
Stegocephalus inflatus Krøyer, 1842			0.02					
Stegocephalidae						0.09		
Stenothoidae indet.				0.19				
Decapoda								
Caridion gordoni (Bate, 1858)			0.02		0.04			
Eualus gaimardii (H. Milne-Edwards, 1837)			0.03					
Galathea dispersa Bate, 1859					0.02			
Lebbeus polaris (Sabine, 1824)			0.05					
Munida sarsi Huus, 1935	0.34		0.03		0.42			
Munidopsis serricornis (Lovén, 1852)						0.46	3.53	
Pagurus bernhardus (L, 1758)					0.02			
Pagurus pubescens Krøyer 1838						0.14		
+ *Pandalus propinquus* G.O. Sars, 1870			0.05		0.01			
Bryozoa								
Amphiblestrum flemingii (Busk, 1854)					0.03			
Amphiblestrum cf. *minax* (Busk, 1860)			0.01		0.02			
Amphiblestrum sp.					0.04			
Anarthropora monodon (Busk, 1860)				0.87				
Annectocyma major (Johnston, 1847)							0.39	
Ascophora indet.				0.39				
Atecata indet.					0.01			
* *Bicellarina alderi* (Busk, 1859)						0.65		
* *Callopora dumerilii* (Audouin, 1826)				0.19				0.32
Celleporina pygmaea (Norman, 1868)	1.71		0.08		0.01			
Porelloides laevis (Fleming, 1828)					0.02			
Crisia denticulata (Lamarck, 1816)			0.01					
Crisia eburnea (L., 1758)				0.19				

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Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Crisidea indet.		0.25	0.05	3.30				0.16
Cyclostomata indet.			0.01	0.10	0.07			
Diastoporidae indet.			0.06	0.19	0.01			
Diplosolen obelia (Johnston, 1838)				5.53	0.31			0.79
Diplosolen sp.			0.01					
Disporella hispida (Fleming, 1828)	1.03	0.25	0.13	9.81	0.34	0.14	1.96	0.63
* *Entalophoroecia deflexa* (Couch, 1842)			0.02	0.10				0.16
Escharella abyssicola (Norman, 1869)				3.01	0.01			
Escharella klugei Hayward, 1979				0.10				
Escharella octodentata (Hincks, 1880)				7.09	0.32			
Escharella ventricosa (Hassall, 1842)				7.09	0.16			
Escharella sp.				1.55			1.96	
Escharina alderi (Busk, 1856)			0.01				0.39	
Filicrisia geniculata (Milne Edwards, 1838)	0.68		0.04					
Hemicyclopora polita (Norman, 1864)	1.71	0.76	0.27	3.88	0.02	0.37		
+ *Hornera lichenoides* (L., 1758)	0.34	0.25	0.02	0.19	0.01		0.12	
Idmidronea atlantica (Forbes. in Johnston 1847)			0.07	2.33	0.03	0.37		
Larnacicus corniger (Busk, 1859)				0.78				
Lichenopora verrucaria (O. Fabricius 1780)			0.04					
Notoplites jeffreysii (Norman, 1868)			0.01					
* *Oncousoecia diastoporides* (Norman, 1869)					0.02	0.05		0.48
Oncousoecia dilatans (Johnston, 1847)				0.39	0.01			
Oncousoecia sp.					0.01			
Plagioecia patina (Lamark, 1816)				0.97	0.09	0.14	0.39	
Porella compressa (J. Sowerby, 1805)					0.02	0.23		
Pyripora catenularia (Fleming, 1828)								0.79
Ramphonotus minax (Busk, 1860)							0.78	
Schizomavella linearis (Hasall, 1841)				0.58				
Schizomavella sp.				0.19	0.01			
Scrupocellaria scrupea Busk, 1852				0.49				
+ *Reteporella beaniana* (King, 1846)	0.34	0.25	0.08	4.66	0.15			
Smittina crystallina (Norman, 1867)					0.04			
Smittoidea reticulata (J. MacGillivray, 1842)				0.10				
Stomatopora sp.				0.78	0.12		1.37	
Tessarodoma boreale (Busk, 1860)				0.19	0.02			
Tubulipora cf. *aperta* (Harmer, 1898)				0.10	0.02			
Tubuliporiidae indet.	0.34	0.51	0.02	10.78	0.81	1.94	2.55	0.32
Turbicellopora smitti (Kluge, 1962)				0.10				
Umbonula cf. *arctica* (Sars, 1851)			0.01					
Brachiopoda								
Crania anomala (O.F. Müller, 1776)			0.14	3.11	0.57	0.37	1.57	
+ *Macadrewia cranium* (O.F. Müller, 1776)	0.34		0.09	0.68	0.06	0.05		
+ *Terebratulina retusa* (L., 1758)	1.71	0.51	0.08	1.65	0.44	0.71		
Brachiopoda indet.						0.05		
Ophiuroidea								
Amphipholis squamata (Delle Chiaje, 1829)			0.03					
Amphiura chiajei Forbes, 1843	0.34		0.01		0.03			
Amphiura sp.						0.05		
Hathrometra sarsi (Düben & Koren, 1846)			0.09	0.10				
+ *Ophiacantha abyssicola* G.O. Sars, 1871			0.30	0.97	0.25	0.42		
Ophiacantha anomala G.O. Sars, 1871			0.42	0.78		0.05		

Appendix Table 1 (continued).

Species	A	B	C	D	M	N	R	S
Ophiacantha bidentata (Retzius, 1805)			0.48	0.29	0.02		0.39	
Ophiacantha spectabilis G.O. Sars, 1871					0.01	0.05		
Ophiactis abyssicola (M. Sars, 1861)			0.07	0.29	0.02	0.05	0.39	
+ *Ophiactis balli* (Thompson, 1840)			0.10		0.01	0.23	0.78	
Ophiactis nidarosensis Mortensen, 1920						0.14		
Ophiomitrella clavigera (Ljungman, 1865)			0.04	0.19				
+ * *Ophiopholis aculeata* (L., 1767)					0.44	0.88		0.16
Ophioscolex glacialis J. Müller & Troschel, 1842						0.09		
Ophioscolex purpureus Düben & Koren, 1846			0.09	0.10		0.09		
+ * *Ophiotrix fragilis* (Abildgaard, 1789)				0.10	0.02	0.28		
Ophiuroidea juv. indet.			0.15		0.20	0.42	0.39	0.32
Asteroidea								
Henricia sanguinolenta (O.F. Müller, 1776)					0.05	0.14		
Ceramaster granularis (O. F. Müller, 1776)						0.05		
Porania pulvillus (O.F. Müller, 1776)					0.04			
Echinoidea								
Echinus acutus Lamarck, 1816					0.01		0.39	
Echinus elegans Düben & Koren, 1846					0.01	0.05		
Echinoidae indet. Juv.			0.01					
Holothuroidea								
Psolus squamatus (Koren, 1844)				0.19	0.04			
Psolus sp.					0.04			
Rhabdopleura normani Allman, 1869			0.07	2.04	0.52	0.56		0.32
Hemicordata indet.						3.93		
Pterobranchia								
Tunicata								
Ascidia conchylega O.F. Müller, 1776					0.01			
Ascidia mentula O.F. Müller, 1776						0.14		
Boltenia echinata (L., 1767)								0.16
Ciona intestinalis (L., 1767)					0.07	0.05		
Cnemidocarpa cf. *rhizopus* (Redikorzev, 1907)					0.01			
Didemnum albidum (Verrill, 1871)	0.68	1.01	0.09	2.33	0.25	0.23		0.16
Didemnidae indet.					0.01			
Leptoclinides faeroeensis Bjerkan, 1905				0.29	0.07		3.53	
Molgula siphonalis M. Sars, 1859			0.01					
Polycarpa pomaria (Savigny, 1816)			0.01		0.02	0.09		
Polyclinidae indet.					0.03			
Pyura tesselata (Forbes, 1848)				0.10	0.18			
* *Styela atlantica* (Van Name, 1912)					0.02			0.16
Styela theeli (Ärnbäck-Christie-Linde, 1921)						0.09		
Ascidia indet.					0.15	0.09		0.32