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Local variation in the distribution of benthic megafauna species associated with cold-water coral reefs on the Norwegian margin

Autun Purser [a,*], Covadonga Orejas [b,c], Andrea Gori [c], Ruiju Tong [a],
Vikram Unnithan [a], Laurenz Thomsen [a]

[a] Jacobs University, Campus Ring 1, 28759 Bremen, Germany
[b] Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Baleares, Moll de Ponent s/n, 07015 Palma de Mallorca, Illes Balears, Spain
[c] Institut de Ciències del Mar (CSIC), Pg Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

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ABSTRACT

The spatial variability in the mix of species making up Cold-water coral reef communities is not well known. In this study abundances of a selection of megafauna (Lophelia pertusa, Madrepora oculata, Paragorgia arborea, Primnoa resedaeformis, Mycale lingua, Geodia baretti, Acesta excavata and fish) were quantified throughout 9 manned submersible video transects from 3 reef complexes (Røst Reef, Sotbakken Reef and Traena Reef) on the Norwegian margin. Substrate type (coral structure, rubble, exposed hardground or soft sediment) was also recorded. Variations in the densities of these fauna (with respect to both reef complex and substrate type) were investigated, with spatial covariance between species assessed.

For the majority of fauna investigated, densities varied by both reef and substrate. Spatial covariance indicated that some species may be utilising similar habitat niches, but that minor environmental differences may favour colonisation by one or other at a particular reef. Fish densities were generally higher in regions with biogenic substrate (coral structure and coral rubble substrates) than in areas of soft or hardground substrate. Further, fish were more abundant at the northerly Sotbakken Reef at time of study than elsewhere. Community structure varied by reef, and therefore management plans aimed at maintaining the biodiversity of reef ecosystems on the Norwegian margin should take this lack of homogeneity into account.

1. Introduction

Cold-water coral (CWC) reefs are recognised as biodiverse ecosystems throughout the oceans of the world (e.g., Roberts et al., 2006; Duineveld et al., 2007; Henry and Roberts, 2007; Reveillaud et al., 2008; Clark et al., 2010; Henry et al., 2010; Lessard-Pilon et al., 2010; D'Onghia et al., 2010; Mastrototaro et al., 2010). In European seas, these reefs are often located at depths associated with the edge of the continental shelf or deeper, commonly in regions with a hard substrate and high volumes of particulate organic matter regularly delivered to the benthic community. Elevated flow velocities close to the seabed, such as may be found at sills (Lavaleye et al., 2009; Rüggeberg et al., 2011; Wagner et al., 2011), seamounts or mound structures (De Mol et al., 2002; Kenyon et al., 2003; Duineveld et al., 2004; Dorschel et al., 2005; White, 2007; Frank et al., 2009; Rowden et al., 2010; Tracey et al., 2011), within canyons (Taviani et al., 2005; Orejas et al., 2009;

Huvenne et al., 2011) or the edge of the continental shelf (Freiwald et al., 2002; Fosså et al., 2005; Wheeler et al., 2007) increase the suspended food flux locally, and may supply a suitable quantity for coral reef development (Duineveld et al., 2004; Davies et al., 2008; Wagner et al., 2011). Periodic downwellings from surface waters of fresh, labile material is an alternative primary food supply mechanism at some reefs (Davies et al., 2009, Duineveld et al., 2012).

Lophelia pertusa (Linnaeus, 1758) is the most common reef building scleractinian coral within the majority of European reef ecosystems (Roberts et al. 2009). With growth, coral polyps secrete an aragonite skeletal cup of ~ 1 cm diameter, either directly onto the underlying substrate, on top of the dead skeletal remains of previous generations or as a bud from a living parent polyp. Despite a moderate longitudinal growth rate (~ 1 cm yr^{-1} appears to be a roughly average across European reefs (Mikkelsen et al., 1982; Rogers, 1999; Orejas et al., 2008, 2011; Roberts et al., 2009)), sizable reef frameworks can develop. Geological investigations have indicated that the development of the majority of current North European extant reefs likely commenced shortly after the retreat of ice at the end of the last ice age, $\sim 10,000$ years b. p. (Freiwald et al., 1999). From this date, reef complexes on the Norwegian margin have grown to form structures of varying size,

* Corresponding author. Tel.: +49 421 200 5865.
E-mail addresses: a.purser@jacobs-university.de,
autunpurser@gmail.com (A. Purser).

from those consisting of collections of small coral thickets a few meters in diameter, to large structures many km in length and with heights above the substrate measured in tens of metres (Freiwald et al., 2002). These complex structures greatly increase habitat heterogeneity on the seabed (Reed et al., 1982; Henry and Roberts, 2007; Cordes et al., 2008; Roberts et al., 2009; Buhl-Mortensen et al., 2010). The aragonite skeleton laid down by scleractinian growth provides a hard substrate suitable for settlement by a variety of sessile organisms (Mortensen et al., 1995; Henry, 2001; López Correa et al., 2005; Metaxas and Davis, 2005; Roberts et al., 2006; Orejas et al., 2008; Purser et al., 2009). This skeletal structure also interacts with and impacts on local hydrodynamic flow (White, 2007) providing refuges for fish (Husebø et al., 2002; Auster, 2005; Costello et al., 2005; Edinger et al., 2007; Clark and Tittensor, 2010; Söffker et al., 2011; Baker et al., 2012) and other mobile invertebrate fauna (Reed et al., 1982; Henry and Roberts, 2007; O'Hara et al., 2008; Clark and Rowden, 2009; Lessard-Pilon et al., 2010; Buhl-Mortensen et al., 2010).

The extensive acoustic mapping of the continental margins and subsequent Remote Operated Vehicle (ROV), submersible or drop-cam investigations carried out in the last decade has increased our knowledge on the distribution of CWC ecosystems on the European margins (Fosså et al., 2005; Davies et al., 2008; Dolan et al., 2008; Guinan et al., 2009; Orejas et al., 2009; Roberts et al., 2009; Schmiing et al. 2009; Fosså and Skjoldal, 2010; Vertino et al., 2010; Huvenne et al., 2011; Tong et al., 2012). Surveys of fauna within these ecosystems have however varied in overall aim, approach and methodology. Grab sampling and trawling have confirmed the presence of a high number of species at many reefs (Mortensen et al., 1995; Rogers, 1999; Roberts et al., 2006; Henry and Roberts, 2007; Cordes et al., 2008). Video transect data analysis has shown that at the majority of reefs distinct habitat zones are present, differentiated by substrate type (Jonsson et al., 2004; Buhl-Mortensen et al., 2010, Tong et al. 2012). These zones can be summarised as: (1) regions of high density, live scleractinian growth (the 'live reef zone'), (2) dead skeletal regions (the 'dead coral zone') and (3) a surrounding area made up of many broken coral fragments and occasional patches of living polyps (the 'rubble zone') (Buhl-Mortensen et al., 2010). The percentage of reef ecosystem made up of each of these habitat types differs between reefs, likely in response to differences in hydrodynamic regime, food supply or substrate availability (Kenyon et al., 2003; Wheeler et al., 2007; Wagner et al., 2011). Anthropogenic impact has also had an influence on shaping the physical form of many European reefs (Fosså and Skjoldal, 2010).

To date few studies have investigated how densities of species associated with CWC reefs may vary across and between reef habitat zones at individual reefs, or between different reef complexes. Where published, species occurrence data often reports abundances from reefs as a whole (Jensen and Frederiksen, 1992; Henry and Roberts, 2007), with a lesser number of studies attempting to assess beta diversity variation across individual reefs, reef complexes or the surrounding ecosystems (Jonsson et al., 2004; Raes and Vanreusel, 2006; Henry and Roberts, 2007; Rossi et al., 2008; Henry et al., 2010). The role of terrain morphology in influencing gorgonian coral distributions across several reefs was recently investigated on the Norwegian margin (Tong et al., 2012). In Orejas et al. (2009) small scale spatial distribution patterns of a selection of CWC species within a Western Mediterranean canyon system were investigated by using spatial pattern analyses developed for use in terrestrial environments. In this study we used a similar methodology to investigate small scale spatial distribution of a selection of benthic megafaunal species associated with CWC reefs on the Norwegian margin. This area of the continental shelf is rich in CWC ecosystems, as well as being an area of significant human

utilisation, with an active fishery and offshore oil and gas exploration and production ongoing (Fosså and Skjoldal, 2010).

The main aims of our investigation were: (1) to try and determine whether or not the distribution of associated benthic megafauna species varied by reef, substrate type, or with variation in the densities of other megafauna species and (2) to try and determine whether or not the occurrence and the abundance of fish varied with reef, substrate type, or the densities of the investigated seafloor species.

2. Materials and methods

2.1. Survey sites

Three Norwegian reef complexes, Røst Reef, Traena Reef and Sotbakken Reef (Table 1, Fig. 1), were investigated with the 'RV Polarstern' during cruise ARKXXII/1a, June 2007 (Klages and Thiede, 2011). All three reefs are exposed primarily to the Norwegian North Atlantic Current, flowing SW–NE parallel to the Norwegian coast (Dullo et al., 2008).

The Røst Reef complex is one of the most spatially extensive in Norwegian waters (Thorsnes et al., 2004; Dullo et al., 2008; Wehrmann et al., 2009), and has been protected from bottom trawling since 2003 (Fosså et al., 2005; Hall-Spencer et al., 2008). The complex is formed from a number of healthy coral banks located on the crests of ridges running parallel to the edge of the continental margin, formed by the Traenadjupet landslide during the Cenozoic (Damuth, 1978). Between each coral bank there are depressed regions of coral rubble and less vigorously growing coral thickets (Wehrmann et al., 2009).

The Traena Reef complex contains a number of elongated coral structures, each up to ~150 m in length, growing into the prevailing current direction on the continental shelf. Previous investigation has shown these coral structures to consist of a live coral 'head' or upstream section, downstream of which is a more degraded region of coral structure where sparse living coral growth can be found, trailed and surrounded by an area of coral rubble (Fosså et al., 2005; Buhl-Mortensen et al., 2010; Tong et al., 2012).

The Sotbakken Reef has not been visited often by the research community. Mapping and preliminary oceanographic data from the reef are presented in the G.O. Sars cruise 2005108 and Polarstern FS70 cruise reports (Fosså, 2005; Klages and Thiede, 2011). A recent paper (Tong et al., 2012) relates gorgonian distribution at the reef to physical terrain variables such as seabed slope and orientation, though no other fauna are investigated. At 70°45′N the reef is close to the northerly limit of (documented) L. pertusa occurrence (Fosså et al., 2000).

2.2. Video sampling

The manned submersible JAGO (IFM-Geomar) was used to collect high definition (HD) quality video data with imbedded universal time code (UTC) throughout dives at each reef (Table 1, Fig. 1). The submarine dives were planned to cross cut reef structures, either by travelling from the deepest depths of reef structure occurrence to the shallowest (Røst Reef and Sotbakken Reef) or by passing along the length of the cigar-like reef structures (Traena Reef). Submarine positioning was maintained throughout the dives via a LinkQuest TrackLink 1500 HA USBL positioning system. A pair of parallel laser pointers (positioned 50 cm apart) were used to provide image scale. The camera provided a view of roughly 10 m^2 of seabed, given a submarine altitude of ~1 m above seafloor. The videos were replayed using the Adobe CS4 Premiere Pro software package and the passage of

Table 1
Sampling location, dive designation, date, time, position (start and end), depth, temperature and total usable length of each transect analysed.

| Transect	JAGO Dive code	Date	Start time (GMT)	Transect co-ordinates		Depth range (m)	Average temp (°C)	Usable footage (m)
				From	To			
Rost 1	991 6/14-4	9/6/2007	11:36	67°29.93N, 09°24.41E	67°29.99N, 09°24.34E	282–291	7.4	331
Rost 2	993 8/16-1	10/6/2007	09:19	67°30.86N, 09°26.57E	67°30.70N, 09°26.48E	306–353	7.3	350
Rost 3	998 13/29-1	15/6/2007	09:36	67°33.06N, 09°32.73E	67°33.02N, 09°32.96E	283–330	7.3	340
Rost 4	999 14/31-1	15/6/2007	17:11	67°31.34N, 09°28.02E	67°31.31N, 09°28.23E	358–388	7.3	247
Sotbakken 1	1002 17/40-4	18/6/2007	12:48	70°45.30N, 18°39.72E	70°45.38N, 18°39.95E	247–269	6.5	452
Sotbakken 2	1003 18/41-2	19/6/2007	09:26	70°45.14N, 18°40.70E	70°45.36N, 18°39.76E	246–280	6.5	568
Sotbakken 3	1004 19/42-1	19/6/2007	17:26	70°45.79N, 18°41.60E	70°45.98N, 18°41.53E	256–284	6.5	345
Traena 1	995 10/24-2	13/6/2007	16:55	66°58.09N, 11°08.49E	66°58.13N, 11°07.29E	297–319	7.3	227
Traena 2	996 11/26-1	14/6/2007	10:08	66°58.19N, 11°07.20E	66°58.18N, 11°07.23E	305–314	7.3	368
TOTAL								3228
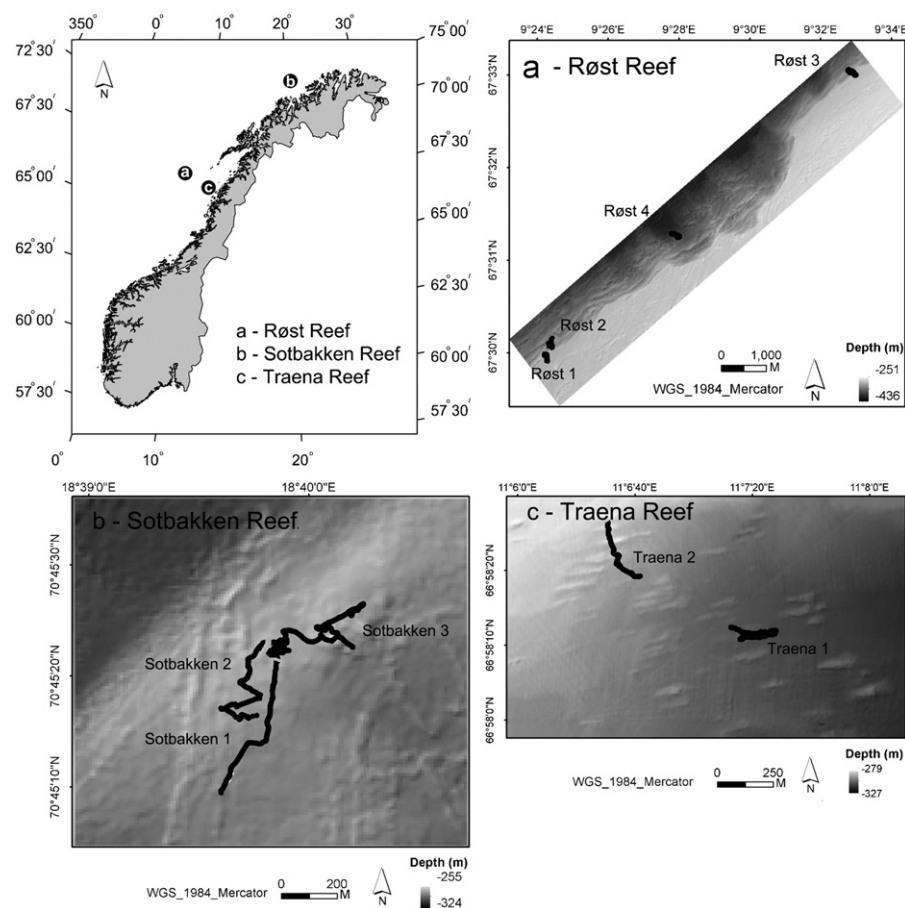
Fig. 1. Map of the Norwegian margin. Locations of investigated reefs marked. Inset figures (a)–(c) represent bathymetric maps of Røst Reef, Sotbakken Reef and Traena Reef, respectively, with dive tracks marked. Across each reef, the dive survey transects are clearly marked and numbered.

each substrate type or fauna individual (see Sections 2.3 and 2.4) through a 1.5 m wide swathe of seabed (this swathe formed from the horizontal line between laser points, plus comparable length continuations of this line to the left and right of the laser points) were recorded. The submarine position data collected by the LinkQuest system was then used in combination with the video time-codes to assign a linear distance from start of each transect for each of these recorded observations. The observations were then divided into 1×1.5 m^2 quadrats for the full length of each video transect; Quadrats were defined considering the transect distance travelled as determined from the LinkQuest position as the 1 m quadrat axis, the 1.5 m axis divided from the swathe between and to either side of the lazer points. The densities of

each species of interest within each quadrat were computed. Wherever image quality was low due to excess turbidity/unsuitable viewing angle etc. a gap was recorded in the transect data.

2.3. Substrate categories

Substrate passing through the 1.5 m swathe throughout each dive transect was placed into one of four categories: (1) soft sediment (2) hardground compacted sediment (3) coral rubble (4) coral structure (comprising both living and dead coral framework) (Fig. 2). In situations where two substrate types were present within the 1.5 m swathe, the dominant (> 50%) coverage category was assigned. These substrate categories were selected

to allow fauna density comparisons to be made between regions of biogenic substrate (coral structure and coral rubble categories) and those not originating from CWC reef development (hard-ground compacted sediment and soft sediment categories). Though further categories could possibly have been derived from the video data (such as 'coral wall', 'soft sediment with pebbles' etc.), we concluded that to do so would have made analysis more cumbersome and the areas of seafloor covered by each category more unequal. Further categories would have reduced the number of transect sections suitable for Morisita's index of patchiness analysis (see Section 2.5.1).

2.4. Investigated species

A selection of megafauna species were recorded throughout the video transects. Additionally, any sightings of fish, regardless of species, were recorded (hereafter, the investigated species and fish will be referred to as the 'fauna categories') (Fig. 3). Observations of lost fishing equipment or litter were also logged. The selection of species to be investigated was based primarily on ease of identification from the video data collected, with larger reef species preferentially selected. Samples of the sessile investigated species (fish were not sampled) were collected directly by the JAGO submersible during dive transects, to ground truth the video observations. Despite this groundtruthing, there may have been a degree of misidentification of the more difficult fauna from the video data, particularly of the two sponge species, *Geodia baretti* and *Mycale lingua*.

L. pertusa (Linnaeus, 1758), the most widespread and significant habitat building scleractinian coral in European waters (Wilson, 1979; Mortensen et al., 1995; Roberts et al., 2009), was recorded by live coral coverage % throughout each transect. Five grades of coverage were used: 0%, 1–25%, 25–50%, 50–75% and
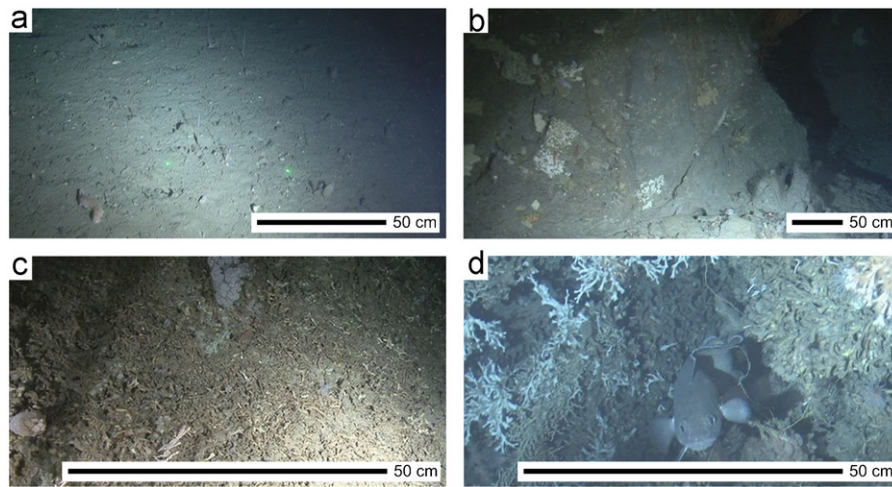

Fig. 2. Substrate categories used in this study. (a) Soft sediment. (b) Hardground. (c) Coral rubble. (d) Coral framework (with fish). Scale bar represent 50 cm.
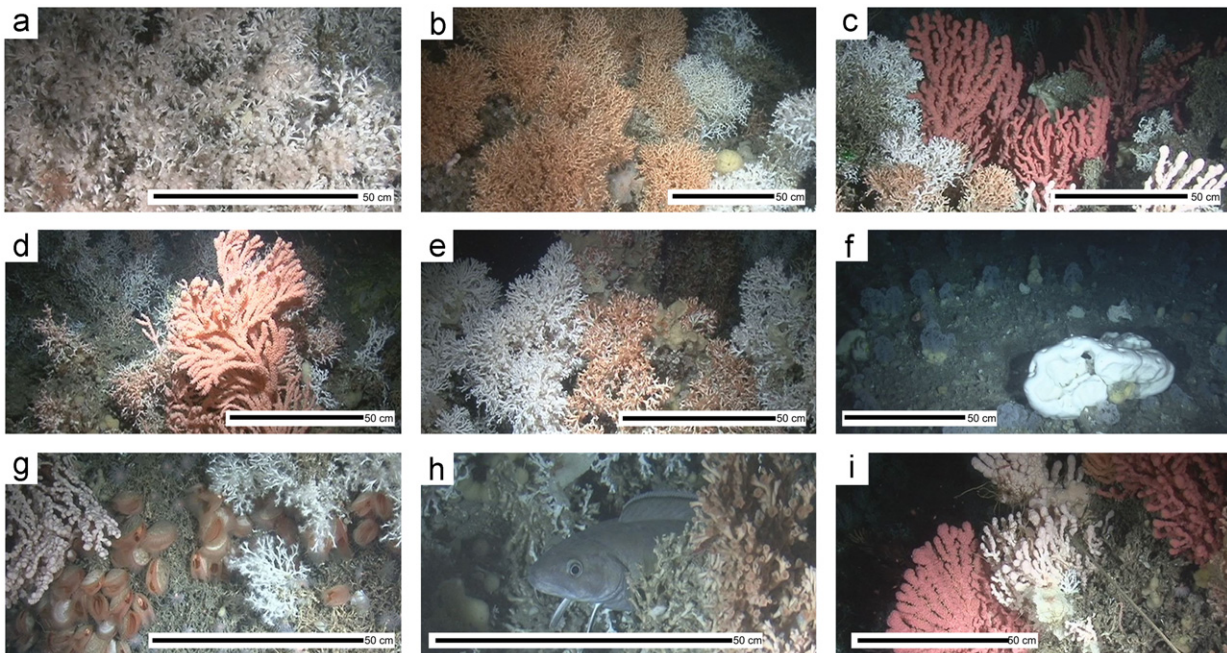

Fig. 3. Species investigated across the reefs. (a) *L. pertusa*, (b) *M. oculata*, (c) *P. arborea*, (d) *P. resedaeformis*, (e) *Mycale lingua* within *L. pertusa* framework, (f) *G. baretti*, (g) *A. excavata*, (h) Fish with coral framework and (i) Rope trapped within coral framework and *P. arborea* colonies. Scale bar represent 50 cm.

75–100%, with each 1 m section of transect being assigned one of these grades.

Madrepora oculata, Linnaeus, 1758, a scleractinian coral with a widely reported distribution on the Norwegian margin (Fosså et al., 2002; Freiwald and Wilson, 1998; Fosså et al., 2005; Reitner, 2005) and elsewhere (Orejas et al., 2009; Roberts et al., 2009; Vertino et al., 2010). The species forms a less expansive and less resilient framework structure than *L. pertusa* (Zibrowius, 1984). In this study this species was recorded by patch occurrence (patches m^{-2}), as the observed patches were not extensive enough to warrant seabed % coverage estimates, as recorded for *L. pertusa*.

Paragorgia arborea (Linnaeus, 1758) is one of the gorgonian corals most frequently found in CWC ecosystems, often positioned prominently on the top of ridges or boulders, with colonies curving into the prevailing current (Mortensen et al., 1995; Risk et al., 2002; Mortensen and Buhl-Mortensen, 2005). Colonies can measure several meters in height (Mortensen and Buhl-Mortensen, 2005) providing habitat niches for a selection of invertebrates (Buhl-Mortensen and Mortensen, 2004) and fish (Krieger, 1993). Throughout each transect, *P. arborea* were recorded by colony occurrence (col. m^{-2}). Colony size was logged as either >50 cm or <50 cm height, with the size estimation based on the fixed 50 cm laser spacing distance. The aim of gauging *P. arborea* colony size was to investigate whether or not any observed differences in the sizes of this prominent organism corresponded to differing levels of fishing activity (as indicated by the presence of lost fishing equipment or historical fishery records).

Primnoa resedaeformis (Gunnerus, 1763) is another gorgonian coral commonly found on the Norwegian margin (Mortensen et al., 1995). This species tends to form less sizable colonies than *P. arborea* (Watanabe et al., 2009), but with a greater number of branches and a higher polyp density on those branches (Mortensen and Buhl-Mortensen, 2005). *P. resedaeformis* colonies have often been reported in close proximity to *P. arborea* (Andrews et al., 2002). *P. resedaeformis* colonies also provide habitat niches for a host of invertebrates (Buhl-Mortensen and Mortensen, 2004; Metaxas and Davis, 2005), hydroids (Henry, 2001), and fish (Krieger and Wing, 2002). This species was recorded throughout each transect by colony occurrence (col. m^{-2}).

M. lingua (Bowerbank, 1866) is one of the few sponge species which can successfully colonise areas of reef where the density of living *L. pertusa* is high (Armstrong et al., 2009; Purser et al., 2009). As a non-selective grazer of small (<10 μm) plankton (Pile et al., 1996) *M. lingua* may well benefit from the additional food flux associated with the increased flow velocities found above *L. pertusa* structure. The species was recorded throughout each transect by individual sponge occurrence (ind. m^{-2}), though it is to be noted that differentiation of individuals can be difficult in areas of high sponge density.

G. baretti Bowerbank, 1858 is a common sponge species found across the Norwegian margin, often in abundance in the general vicinity of CWC ecosystems (Klitgaard and Tendal, 2004). Usually grey in colour, the sponge can form large, distinct barrel like forms with growth, providing habitat niches for other species. The sponge has been of interest to the pharmaceutical industry since the 1980s, potentially rendering its distribution to be of commercial significance (Lidgren and Bohlin, 1988; Sjögren et al., 2004). The species was recorded throughout each transect by individual occurrence (ind. m^{-2}).

Acesta excavata (Fabricius, 1779) is the largest (>10 cm shell diameter) of the bivalves commonly found in CWC habitats on the Norwegian margin (Hovland, 2005; López Correa et al., 2005), in fjord settings (Gilmour, 1990), or on rock outcrops (Gagnon and Haedrich, 2003). Although widely reported, variation in population density between and across reefs has not been described in detail to date. This bivalve is often situated on the edges of

vertical structures within reefs, or on the edges of reef crests within live *L. pertusa* structure. The species was recorded as individuals occurrence (ind. m^{-2}) throughout each transect.

Fish were not recorded to species level, with all fish observations summed together into one fauna category for analysis. To quantify fish distribution across the reefs a different logging strategy was used than with the sessile fauna. Each fish coming into the field of view of the camera was recorded on first observation, regardless of whether it actually passed within the 1.5 m transect swathe. The field of view of the JAGO submarine was assumed to cover 10 m^2 of seabed (see 2.2), and fish densities were based on this area estimation (ind. m^{-2}). Fish densities have historically been assessed from survey trawls conducted over large areas (Gordon, 2001) whereas in this study the aim was to assess distributions at a smaller spatial scale and to see if observations of fish densities correlated with particular substrates, reef, or densities of the investigated benthic species.

Anthropogenic material was recorded (items m^{-2}) with all pieces of rubbish or lost fishing equipment observed in the dive transect videos passing through the 1.5 m transect swathe being logged.

2.5. Statistics

2.5.1. Sessile species and fish density variation

Mean densities of each fauna category observed on or above each of the substrate categories was determined for each transect. Morisita's index of patchiness (Morisita, 1959) was used to assess whether individuals or colonies of the investigated species tended to be distributed randomly along the dive transects, or were clustered in distribution. This index has been increasingly used in tropical reef environments for distribution analysis (Hattori and Kobayashi, 2009; Lazar et al., 2011) The index is the scaled probability that two individuals (or colonies for the colonial organisms) present on a survey transect will be present in the same transect quadrat. Scores below 1 indicate a random distribution, with scores above 1 indicating a progressively greater degree of clustering with score increase. Given the lack of homogeneity within the dive transects, only sections of transect data where substrate category was uniform for >20 m was used in computing this index score. Following analysis of all dive data from a particular reef, the average Morisita's index score for each fauna category found on each substrate type was determined for each reef. The PASSaGE 2.0 software package (Rosenberg and Anderson, 2011) was used to compute the Morisita's index of patchiness scores.

2.5.2. Spatial covariance between fauna categories

From the observations of each fauna category logged from each dive transect video, density plots were produced for each transect with the PASSaGE 2.0 software package as in previous studies on Mediterranean CWC and gorgonian species (Orejas et al., 2009; Gori et al., 2011a, 2011b). Spatial covariance's between *L. pertusa* coverage and densities of the other fauna categories, as well as for each paired combination of the other fauna categories across each transect were analyzed with a Three-Term Local Quadrat Covariance (3TLQC) analysis, using the PASSaGE 2.0 software package. In the 3TLQC the variance as a function of block size for fauna category A (Var A), fauna category B (Var B), and their combined number (Var A+B) (Cov=Var A+B−Var A−Var B) is examined (Dale, 1999). To test the null hypothesis of an independent distribution of one fauna category with respect to the other along each transect, randomized transects were generated for comparison by randomly permuting the "labels" (fauna category A or B) of all the observed colonies/organisms along each transect. For statistical significance

(95% confidence interval) the values at the limit of 2.5% tails of 999 of these randomizations was used. In the produced plots of covariance as a function of block size, positions of a significantly positive deviated sample statistic from the bounds of the confidence interval (peaks) indicates the scale of any positive association (attraction) between fauna categories, whereas significant negative deviations (valleys) indicate the scale of any negative association (repulsion) (Dale, 1999).

2.5.3. Paragorgia arborea size variation

One-way ANOVA tests were carried out to see whether there was a significant difference in P. arborea colony size between reef sites. All data was tested against a significance level of 0.05. Post-hoc testing to determine between which reef and significant differences were logged was carried out using a LSD test. Statistical analyses were carried out using the SPSS v. 17.0 software package.

3. Results

3.1. Species and fauna categories density variations

3.1.1. Lophelia pertusa

Seabed coverage by live L. pertusa was higher across structure substrate on transects made at Røst Reef and Sotbakken Reef than at Traena Reef (Fig. 4). At Røst Reef and Sotbakken Reef, live coral percentage coverage varied from 0% to > 75% throughout each section of structure substrate surveyed (Figs. 5 and 6). At Traena Reef, areas of dense living coral (> 75% coverage) were less than ~10 m in transect length, located at one end of each area of structural substrate surveyed (Fig. 7), i.e., covering the upstream tips of the cigar-like reef structures (Fosså et al., 2005; Buhl-Mortensen et al., 2010).

3.1.2. Madrepora oculata

M. oculata was only observed at Røst Reef, and predominantly as patches < 50 cm diameter (data not shown). The highest density of patches observed was 0.061 patches m^{-2} on rubble during Røst Reef transect 2 (Table 2). Occasional the species was observed on hardground, soft sediment (attached to pebbles) during Røst Reef transects. Given the insufficiency of observations of this species, the data was not investigated statistically.

3.1.3. Paragorgia arborea

Highest densities of P. arborea were observed at Røst Reef (Table 2). Morisita's Index, (Table 3) indicated a tendency for a clustered distribution of P. arborea colonies across the various substrate categories.

3.1.4. Primnoa resedaeformis

P. resedaeformis was observed at all reefs surveyed in this study (Table 2). The highest densities recorded were at Røst Reef (0.35 col. m^{-2}, structure substrate, Røst Transect 4). Densities were higher in association with coral structure and hardground substrates than in areas of soft sediment. Morisita's index (Table 3) showed a generally clustered distribution of colonies throughout each substrate, with particularly tight clustering indicated by the index score > 10 for colony densities recorded in association with hardground and structure at Røst Reef, and with coral structure at Sotbakken Reef.

3.1.5. Mycale lingua

Densities of M. lingua were similar at Røst Reef and Sotbakken Reef, with a lower density apparent at Traena Reef (Table 2). Densities were lower in regions of soft substrate than in areas of coral structure.

A clustered distribution of M. lingua was recorded on structure substrates at all reefs (Morisita's index > 9 at all reefs, Table 3), particularly at Røst Reef (Morisita's index=68.94, SD=218.26). The high standard deviation in the Morisita's index scores indicates that in some locations clustering was very much greater than in others.

3.1.6. Geodia baretti

The highest density of G. baretti (0.37 individuals. m^{-2}) was recorded on the hardground outcrops during Røst Reef transect 3, 0.123 ind. m^{-2} (SD=0.21), (Table 2). Densities did not differ greatly by reef. The Morisita's index scores for all reefs indicated quite a random distribution (Table 3), although there was some significant clustering in some of the soft sediment areas of Sotbakken Reef (Morisita's index=17.12, SD=32.46).

3.1.7. Acesta excavata

Much higher numbers of A. excavata were observed at Sotbakken Reef and Røst Reef that at Traena Reef (Table 2), with shells being observed exclusively in coral structure habitat category areas. A clustered distribution was indicated for this species (Morisita's index of 3.44 (SD=1.34) (Table 3) with the high number of shell observations (Table 2, Fig. 6) and low standard deviation across transects indicating a reasonably uniform pattern of clustering across the structure substrate.

3.1.8. Fish

The highest fish density recorded was associated with structure substrate during Sotbakken Reef transect 1 (0.025 ind. m^{-2}). A generally random distribution of fish across the various reefs and substrates was indicated (Table 3), although some clustering was indicated in association with rubble substrates at Sotbakken Reef (Morisita's index=14.68, SD=20.05) and Traena Reef (Morisita's index=31.33, SD=38.85).

3.1.9. Anthropogenic material

There were few clear signs of anthropogenic impact at any of the reefs visited. On 4 of the 9 transects occasional ropes were recorded on the seabed, with the most (5 occurrences) being recorded snagged within structural substrate during Traena Reef transect 1 (Table 2).

3.2. Spatial covariance between species and fauna categories

Given the range of species and fauna categories investigated in this study, the assessment of spatial covariance is complex, and presented in full in Table 4. Key results include:

1) Generally positive associations were indicated between L. pertusa and both P. arborea and P. resedaeformis across all the studied reefs.
2) L. pertusa and M. lingua were positively associated on a ~10 m scale at Røst Reef, but not at the other surveyed reefs.
3) A negative covariance between L. pertusa and G. baretti.
4) A generally positive covariance between P. arborea and P. resedaeformis on a local (~5–20 m) scale.
5) Both gorgonian species, P. arborea and P. resedaeformis, were positively associated with A. excavata bivalves on a scale of ~10 m.
6) Aside from a generally negative covariance with G. baretti, fish showed no clear spatial covariance trends with other investigated fauna.

3.3. Paragorgia arborea size variation

P. arborea colony size varied significantly with reef (ANOVA, F=6.687, p < 0.01), with a Bonferroni multiple comparison indicating
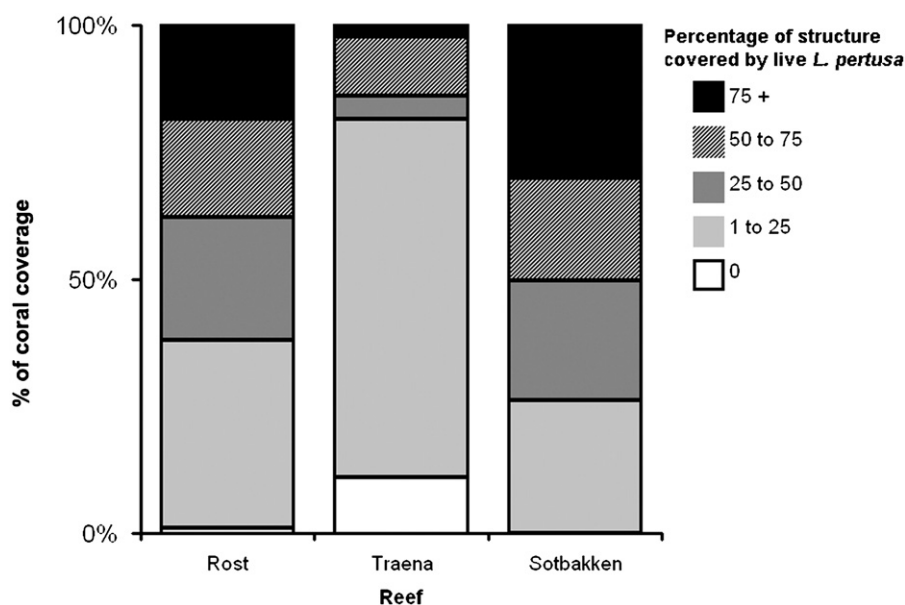
Fig. 4. *L. pertusa* live colony coverage of structure substrate at each reef. Coverage estimates are based on % coverage of each transect quadrat covered by *L. pertusa*.

that this difference was significant between Røst Reef and Sotbakken Reef and Røst Reef and Traena Reef (Fig. 8). ~80% of colonies recorded at Røst Reef were < 50 cm in height, whereas at Sotbakken Reef and Traena Reef, ~40% of colonies were < 50 cm in height.

3.4. Anthropogenic material

Clear evidence of anthropogenic impact on the reefs was limited to rare recordings of lost ropes, scattered across the surveyed reefs, lodged amongst coral structure (and occasionally rubble areas) of Røst Reef and Traena Reef (Table 2). The transects in this study were planned to cover as wide a range of reef habitats as possible, and did not focus on the edges of reef regions, with these regions commonly being those most often damaged by fishing activity (T. Lundälv, pers. comm.).

4. Discussion

The Røst Reef and Sotbakken Reef, both situated closer to the edge of the continental slope than the Traena Reef, may benefit from enhanced nutrient supplies resulting from slope related Ekman transport (Thiem et al., 2006), general cross-slope transport of organic rich particles which accumulated on the productive shelf seas (Thomsen, 1998) and tidal resuspension of material previously deposited on the slope (Kiriakoulakis et al., 2007). The flow regime in the bottom waters at Traena Reef has been reported to be unidirectional (Fosså et al., 2005; Klages and Thiede, 2011) whereas flow direction at the reefs on the edge of the continental slope is more variable in direction (Klages and Thiede, 2011). Sotbakken Reef was observed to be a well-developed reef (Tong et al., 2012), with spatially extensive regions of high density living *L. pertusa*.

4.1. Fauna distribution

The densities of the investigated species were generally higher at Røst Reef than at either Traena Reef or Sotbakken Reef.

4.1.1. Paragorgia arborea

The percentage of *P. arborea* colonies > 50 cm in height varied significantly with reef, with roughly twice the percentage of large colonies observed at Sotbakken Reef and Traena Reef than at Røst Reef. Occasional colonies at Sotbakken Reef appeared to be in excess of 2 m height (data not shown), approaching the reported species maximum in Norwegian waters (Broch, 1912 cited in Mortensen and Buhl-Mortensen, 2005). The temperature difference between the northerly and southerly developed reefs (Røst Reef and Sotbakken Reef) is unlikely the cause of the colony size difference, as (at time of study) the temperatures measured at both sites was comfortably within the range reported for the species (Leverette and Metaxas, 2005; Bryan and Metaxas, 2007). Differences in substrate can account for variation in maximum colony height (Mortensen and Buhl-Mortensen, 2005; Watanabe et al., 2009), although this is unlikely the cause here, given the comparable substrates available at each of these locations. *P. arborea* are often reported in areas with strong currents and less turbulent waters (Wainwright and Dillon, 1969; Warner, 1977), and possibly such favourable environmental conditions are more prevalent at Sotbakken Reef and Traena Reef than at Røst Reef. Tong et al. (2012) show that topographical features can have an influence on the distribution of the species, though in their study no attempt was made to determine whether the sizes of colonies also changed with particular terrain variables, such as slope, aspect or rugosity. A further possible explanation for this difference in colony heights could be that colonies at Røst Reef are younger than those at Sotbakken Reef. This could be the case if fishery activity in the vicinity of the Røst Reef has been higher during the last decades (Fosså and Skjoldal, 2010). Both trawl and long-line fishing are capable of readily dislodging *P. arborea* colonies from the seabed (Mortensen et al., 2005; Sherwood and Edinger, 2009). Although little direct evidence of fishing activity was observed during the survey dives in this study, reports of fishery activity in the literature and official reports for the Norwegian margin are summarised in Fosså et al. (2002). Therein they divide the Norwegian waters into 4 zones and tabulate the numbers of damaged and intact reefs reported from these zones by fishermen, industry and fishery surveys. The Røst Reef and Traena Reef are both located in their 'Zone 2', whereas Sotbakken Reef falls into 'Zone 1'. According to the combined data presented on known health status of reefs in each of these zones, 40% of those in Zone 1 were damaged by fishery activity, whereas ~60% of those in
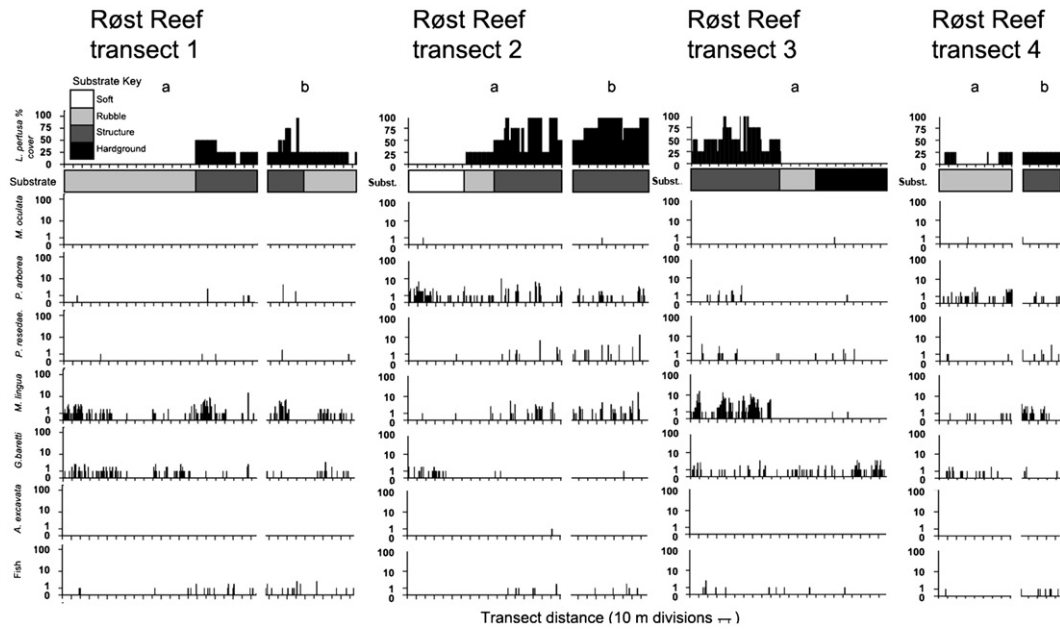
Fig. 5. Røst Reef species density plot for each analysed transect. Densities given as % coverage for *L. pertusa* and individuals m^{-2} or colonies m^{-2} for the other species. Letters represent the transect sections with usable video footage. Each division for the transect distance (*x* axis) correspond to 10 m.

Fig. 6. Sotbakken Reef species density plot for each analysed transect. Densities given as % coverage for *L. pertusa* and individuals m^{-2} or colonies m^{-2} for the other species. Letters represent the transect sections with usable video footage. Each division for the transect distance (*x* axis) correspond to 10 m.
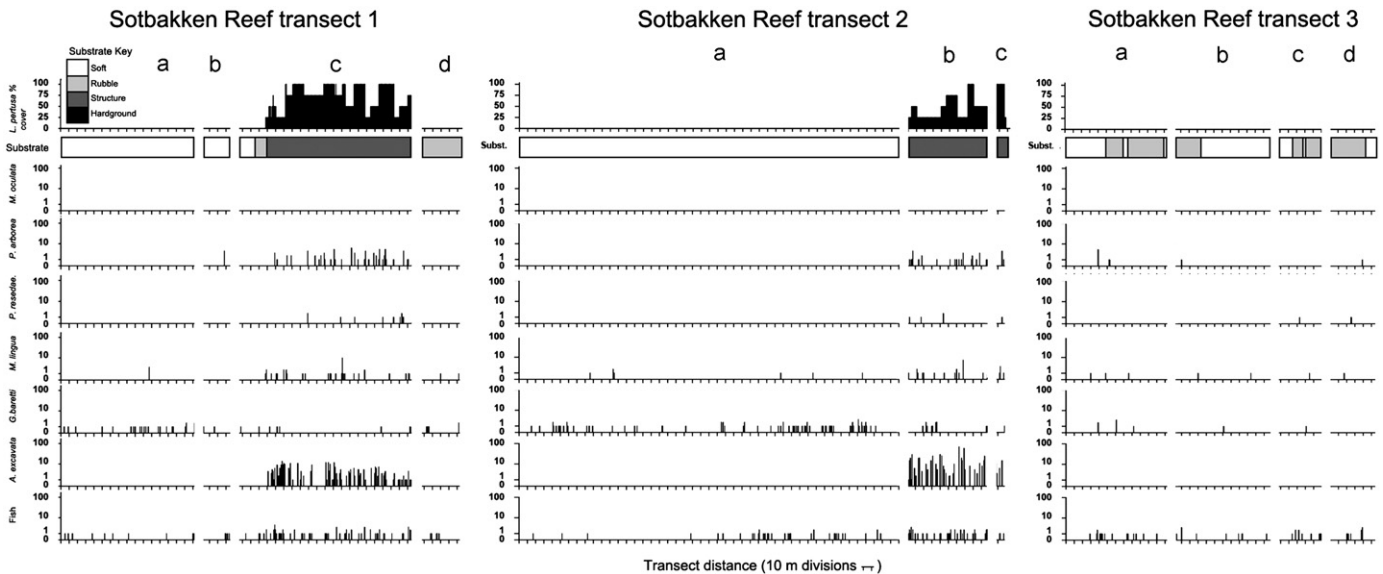
Zone 2 were damaged. This is indicative of historically higher fishery activity in the vicinity of the southerly Røst Reef and Traena Reef than the more northerly Sotbakken Reef. The fish abundances recorded in the current study, though only a snapshot and not a representative or exhaustive data set, were higher at the Røst Reef than at the Traena Reef. Should this observation reflect the general condition, it is likely fishing effort prior to the fishery closure would have been higher in the vicinity of Røst Reef than Traena Reef. This greater activity could have resulted in a greater percentage removal of the more sizable colonies at Røst Reef than at Traena Reef. The positive covariance in *A. excavata* and *P. arborea* distributions (observed across all transects were both species were present) indicates that they may both utilise similar habitat or food sources.

4.1.2. Primnoa resedaeformis

The growth morphology and diet of *P. resedaeformis* differs from that of *P. arborea* (Wainwright and Dillon, 1969; Warner, 1977). Colonies were commonly observed within all transects to be draped over substrate, attached within grooves in reef structure or attached to the sides of structure blocks (Tong et al. 2012). Densities of *P. resedaeformis* were generally lower at Sotbakken Reef than at the more southerly reefs however. There are indications that under low temperature conditions, calcite growth is favoured over gorgonin in *P. resedaeformis*, which may have significance for the reduced colonisation success of this gorgonian within these slightly colder waters when compared with the slightly warmer waters found at Traena Reef and Røst Reef (Sherwood et al., 2005). However, other factors have been documented, which seem to strongly influence
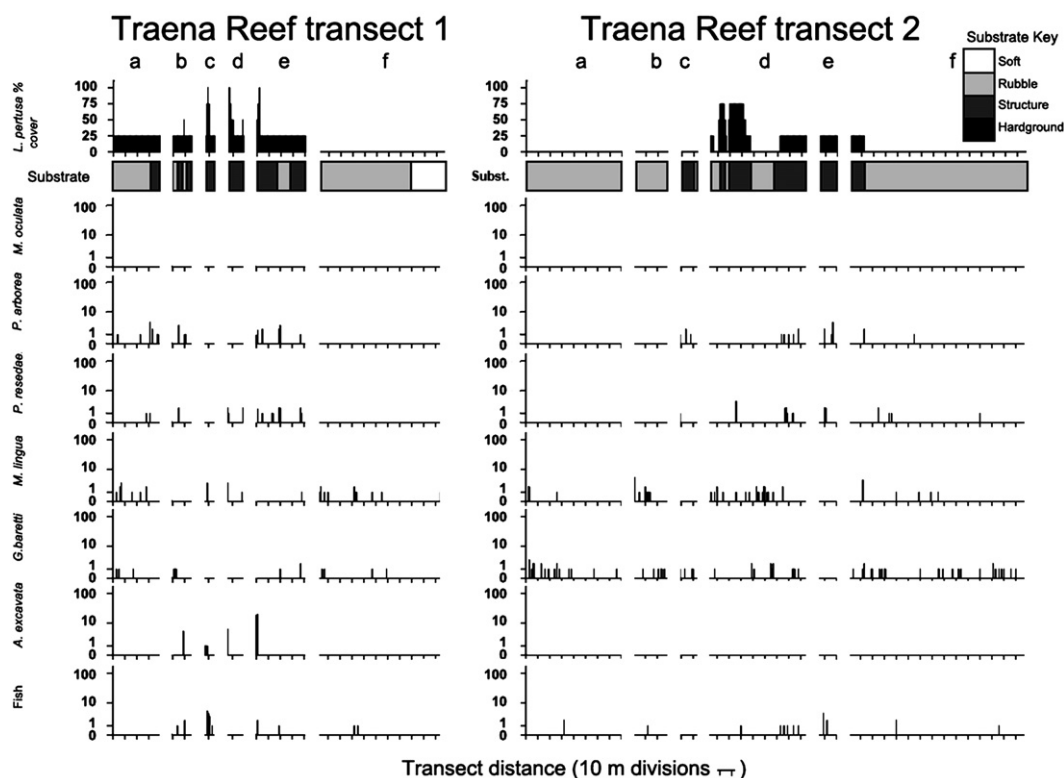
Fig. 7. Traena Reef species density plot for the analysed transects. Densities given as % coverage for *L*. pertusa and individuals m^{-2} or colonies m^{-2} for the other species. Letters represent the transect sections with usable video footage. Each division for the transect distance (x axis) corresponds to 10m.

the occurrence and distribution of this species (as well as that of *P. arborea*): bathymetric position index (BPI), slope, substrate rugosity and curvature (Tong et al. 2012).

4.1.3. Mycale lingua

The positive covariance between *M. lingua* and *L. pertusa* at Røst Reef and Sotbakken Reef but not at Traena Reef could indicate that although at Traena Reef much of the fresher material reaching the reef is collected by live *L. pertusa* and other species found in their highest densities at the upstream tip of each elongated reef structure. Food of sufficient quality and quantity for *M. lingua* growth passes downstream to the other reef regions. Such material could be the finer sized suspended material, *M. lingua* can use fine zooplankton as a food source (< 10 μm) (Pile et al., 1996), possibly too fine for efficient collection by species such as *L. pertusa,* dominant at the reef head.

4.1.4. Geodia baretti

G. baretti individuals generally had a random distribution across the various substrates (except for the clustering observed on soft sediments at Sotbakken Reef), with no sizable differences in density observed by reef or substrate, although a negative covariance with living *L. pertusa* was indicated. This possibly slow growing sponge species (Hoffmann et al., 2003) requires a hard substrate for attachment (individuals observed in soft sediment regions presumably attached to rocks or something solid such as shells or coral rubble within the sediment), but may not be able to compete with *L. pertusa* in speed of growth in regions suitable for coral colonisation.

4.1.5. Acesta excavata

One of the most striking differences between the reefs investigated was the near total absence of *A. excavata* from Røst Reef, despite the species being present in abundance at both Traena Reef and Sotbakken Reef. Highest abundances of *A. excavata* were most often recorded on the sides of coral structure blocks, on overhangs within the structure substrate or in grooves within and between coral colony blocks at these reefs (data not known), a tendency which has been observed at other CWC sites (López Correa et al., 2005; Huvenne et al., 2011). *A. excavata* are hypothesised to be adapted for regions with low, steady temperature and/or low or refractory food availability (Järnegren and Altin, 2006). Given the comparable temperatures observed at Røst Reef and Traena Reef during this study it is unlikely that any variation in temperature at other times of the year at these two neighbouring reefs could account for the high abundance of *A. excavata* at one and near absence from the other. Occurrence of *A. excavata* individuals at Traena Reef correlated closely with the peaks in *L. pertusa* coverage density (Fig. 7). This indicates that only the head sections of the Traena Reef elongated reef structures were suitable for successful colonisation and growth by the species. Potentially, colonisation of such upstream positions on the reef structure allows individuals to filter large volumes of suspended material from the unidirectional flow, acquiring a sufficient flux of (possibly low quality, refractory) food to flourish in such locations, and to outperform other species which may require a more labile carbon source. Alternatively, the colonisation of the upstream regions of the elongated reef structures at Traena Reef could give individuals the opportunity to filter any episodic fresh food deliveries (as may result from algal blooms, storm mixing etc.) before organisms situated further downstream the elongated structures get a chance at it. Both of these feeding strategies (utilisation of low quality food or utilisation of periodic high

Table 2

Densities (ind. m^{-2} or col. m^{-2}) of each investigated fauna category observed in association with each substrate category in each transect. Densities of pieces of lost fishing equipment observed are recorded as items m^{-2}. (n=number of counted individuals in each transect for each substrate). *L. pertusa* is not included in this table as for this species % coverage was calculated throughout each dive transect.

Transect	Length (m)	Substrate	Length (m)	Length (%)	*M. Oculata*		*P. arborea*		*P. resedaeformis*		*M. lingua*		*Geodi baretti*		*Acesta excavate*		Fish		Anthropogenic	
					n	patches m^{-2}	n	colonies m^{-2}	n	colonies m^{-2}	n	ind. m^{-2}	n	ind. m^{-2}	n	ind. m^{-2}	n	ind. m^{-2}	n	items m^{-2}
Rost 1	331																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Rubble	204	62	0	0	1	0.003	2	0.007	106	0.346	90	0.294	0	0	12	0.004	0	0
		Soft	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Structure	127	38	0	0	20	0.105	6	0.031	147	0.772	12	0.063	0	0	33	0.017	0	0
Rost 2	350																			
		Hardground	15	4	0	0	5	0.222	6	0.267	0	0	0	0	0	0	0	0	0	0
		Rubble	66	19	6	0.061	26	0.263	11	0.111	14	0.141	7	0.071	0	0	0	0	0	0
		Soft	62	18	1	0.011	0	0	1	0.011	2	0.022	22	0.237	0	0	0	0	1	0.011
		Structure	207	59	1	0.003	111	0.357	78	0.251	130	0.419	4	0.013	1	0.003	15	0.005	0	0
Rost 3	340																			
		Hardground	99	29	1	0.007	4	0.027	20	0.135	6	0.040	55	0.370	0	0	2	0.001	0	0
		Rubble	79	23	0	0	4	0.034	10	0.084	9	0.076	22	0.186	0	0	2	0.002	0	0
		Soft	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Structure	162	48	0	0	18	0.074	33	0.136	545	2.245	44	0.181	1	0.004	12	0.005	1	0.004
Rost 4	247																			
		Hardground	25	10	0	0	4	0.107	6	0.160	0	0	0	0	0	0	0	0	0	0
		Rubble	137	55	1	0.005	83	0.404	20	0.097	17	0.083	29	0.141	0	0	10	0.005	0	0
		Soft	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Structure	83	34	1	0.008	31	0.249	44	0.353	65	0.522	12	0.096	0	0	10	0.008	0	0
Sotbak. 1	452																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Rubble	62	14	0	0	0	0	0	0	2	0.022	7	0.075	0	0	11	0.012	0	0
		Soft	213	47	0	0	4	0.013	0	0	3	0.009	26	0.081	0	0	15	0.005	0	0
		Structure	177	39	0	0	72	0.271	11	0.041	38	0.143	5	0.019	333	1.254	65	0.025	0	0
Sotbak. 2	568																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Rubble	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Soft	459	81	0	0	0	0	0	0	7	0.007	76	0.074	0	0	35	0.003	0	0
		Structure	109	19	0	0	29	0.118	5	0.020	25	0.102	14	0.057	566	2.307	42	0.017	0	0
Sotbak. 3	345																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
		Rubble	170	49	0	0	4	0.016	3	0.012	4	0.016	5	0.020	0	0	79	0.031	0	0
		Soft	175	51	0	0	5	0.019	0	0	3	0.011	3	0.011	0	0	16	0.006	0	0
		Structure	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Traena 1	227																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Rubble	118	52	0	0	9	0.051	5	0.028	21	0.119	10	0.056	5	0.028	3	0.002	1	0.006
		Soft	31	14	0	0	0	0	0	0	1	0.022	0	0	0	0	0	0	0	0
		Structure	78	34	0	0	20	0.171	16	0.137	8	0.068	3	0.026	48	0.410	18	0.015	5	0.043
Traena 2	368																			
		Hardground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Rubble	273	74	0	0	6	0.015	2	0.005	36	0.088	57	0.139	0	0	6	0.002	0	0
		Soft	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Structure	95	26	0	0	17	0.119	16	0.112	11	0.077	12	0.084	0	0	12	0.008	1	0.007

Table 3
Morisita's index scores for each species and substrate type at each reef. All transect areas of >20 m uniform substrate were analysed. (** indicates insufficient transect sections covering a sufficient substrate length to determine SD).

Reef	Substrate	Number of video segments	Length analysed (m)	M. oculata			P. arborea			P. resedaeformis			M. lingua			G. baretti			A. excavata			Fish		
				n	Index	(SD)	n	Index	(SD)	n	Index	(SD)	n	Index	(SD)	n	Index	(SD)	n	Index	(SD)	n	Index	(SD)
Rost	Hardground	2	79	1	0.00	**	1	0.00	**	6	10.53	**	2	0.00	**	53	2.00	**	-	-	-	1	0.00	**
Rost	Rubble	6	355	1	0.00	**	13	5.05	9.23	6	0.00	0.00	110	3.94	6.81	102	3.20	3.78	-	-	-	14	1.69	3.77
Rost	Soft	1	62	1	0.00	**	-	-	-	-	-	-	2	0.00	**	22	0.00	**	-	-	-	56	2.26	2.53
Rost	Structure	8	403	2	0.00	0.00	131	11.84	16.35	91	11.12	12.38	528	68.94	218.26	51	0.74	1.38	1	0.00	**	-	-	-
Sotb.	Hardground	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sotb.	Rubble	3	133	-	-	-	1	0.00	0.00	2	0.00	0.00	4	0.00	0.00	7	1.60	2.26	-	-	-	72	14.68	20.05
Sotb.	Soft	4	708	-	-	-	5	48.00	0.00	-	-	-	13	45.97	12.62	101	17.12	32.46	844	3.44	1.34	57	0.91	1.16
Sotb.	Structure	6	269	-	-	-	102	5.06	1.39	15	13.87	18.28	58	4.99	5.30	14	0.25	0.56	-	-	-	103	2.07	0.72
Traena	Hardground	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Traena	Rubble	5	347	-	-	-	10	20.24	23.05	6	6.80	9.62	41	5.44	6.16	56	0.79	1.28	-	-	-	8	31.33	38.85
Traena.	Soft	1	30	-	-	-	6	8.00	0.00	-	-	-	1	0.00	**	-	-	-	-	-	-	-	-	-
Traena	Structure	1	28	-	-	-	6	1.87	**	7	2.67	**	3	9.33	**	6	1.86	**	-	-	-	5	0.00	**

quality food inputs) have been observed by *L. pertusa* in other locations (Davies et al., 2009; Mienis et al., 2009; Van Oevelen et al., 2009; Wagner et al., 2011) and under different nutrient availability regimes (Kiriakoulakis et al., 2005), possibly explaining the high densities of the scleractinian coral only at the upstream tips of these reef structures. Given the co-occurrence of the highest densities of *A. excavata* with high densities of *L. pertusa*, the two species could be using the same feeding strategies at Traena Reef, or possibly be the most successful two investigated species in collecting food in the high flow, unidirectional current conditions reported for the location, but feeding on different sized material (*L. pertusa* on the larger, *A. excavata* on the smaller suspended material fractions). The pattern of *A. excavata* distribution at Sotbakken Reef is however very different. The near absence of *A. excavata* from Røst Reef may indicate that at that location, the exposed structure substrate is swiftly overgrown by young *L. pertusa* coral polyps, which are possibly able to grow at a swifter rate than *A. excavata,* given a hypothesised fresher nutrient supply being available at that reef. At the northerly Sotbakken Reef temperatures recorded during the survey dives were 1° C lower than those recorded at the other two reefs. Järnegren and Altin (2006) showed that *A. excavata* is capable of filtering a large volume of water whilst maintaining a low respiration rate at low temperatures. Metabolism in *L. pertusa* is highly temperature dependant (Dodds et al., 2007; Brooke et al., in press), Potentially, the ability of *A. excavata* to function well under low temperatures allows them to colonise dead coral structure more preferentially than *L. pertusa* in northerly Norwegian reefs exposed to generally colder waters. *A. excavata* has also been observed in high abundance in association with smaller, less developed *L. pertusa* structures at the Mid-Atlantic Ridge (Mortensen et al., 2008), again indicating that this species may only be able to establish itself amongst living *L. pertusa* coral structure when conditions are not optimal for rapid *L. pertusa* colony development.

4.1.6. Fish

The importance of CWC reefs as fish habitats has been a subject of discussion throughout the last ten years (Auster, 2005; Fosså and Skjoldal, 2010; Murillo et al., 2011). Husebø et al. (2002) investigated the abundance of individual fish species across various reef substrate types. In this study we made no attempt to differentiate fish by species. We observed a greater density of total fish numbers above and within the structure substrate category than above outcroppings of hardground, rubble or soft sediments. A higher density of fish was present at both the Røst Reef and Sotbakken Reef than at Traena Reef (average fish densities recorded across all substrate categories combined). This observation, given the more extensive and complex Røst Reef and Sotbakken Reef structures, supports the argument that fish are present in generally higher densities at developed reef sites (D'Onghia et al., 2012), and that these densities are not exclusively found in association with the areas of coral structure substrate but throughout the environment surrounding such structures as well. The higher fish numbers recorded in this study across these reefs could be the result of generally higher food availability in the waters surrounding the reefs, as a result of increased turbulence or physical drawdown processes (Wagner et al., 2011). Also attractive to fish may be the elevated local concentrations of zooplankton often observed at reefs (Mortensen, 2001; Kiriakoulakis et al., 2004). Additionally, both zooplankton and phytoplankton may be aggregated with suspended coral mucus, commonly found in suspension within and downstream of the reef environment (Wild et al., 2008; Wagner et al., 2011). Also of use to fish may be the high physical habitat complexity offered by these two shelf edge reefs (a typically

Table 4
Summary of the 3 term local quadrat covariance (3TLQC) species association results for the 9 transects. The scale of any positive or negative associations between distributions of each pair of species is indicated with a plus or minus. No significant correlation is indicated with (0). Where insufficient numbers of individuals were present for 3TLQC analysis to be conducted, a gap has been left in the table. *M. oculata* has been not included in the table as the low density of colonies observed across all reefs rendered 3TLQC analysis impossible.

Species Compared	Reef transect								
	Rost 1	Rost 2	Rost 3	Rost 4	Sotb 1	Sotb 2	Sotb 3	Traena 1	Traena 2
L. pertusa/P. arborea	(+) 12–58	(+) 6–22 (+) 38–120	(−) 5–12 (+) 19–37 (+) 90–104	(+) 5–10 (+) 23–72	(+) 42–142	(+) 77–200		(+) 7–14 (+) 42–54 (62–80)	(−) 29–75 (+) 84–135
L. pertusa/P. resedaeformis	(+) 10–69	(+) 59–99	(+) 27–60 (−) 73–109	(+) 30–75	(+) 25–52 (+) 114–137	(+) 80–200		(+) 13–88	(+) 9–33 (+) 59–135
L. pertusa/M. lingua	(+) 10–102	(+) 30–107	(+) 8–109	(+) 18–44 (−) 53–78	(+) 60–137	(−) 5–20 (+) 65–200		(−) 38–78	(−) 12–33 (+) 62–135
L. pertusa/G. baretti	(−) 20–56 (−) 86–102	(−) 30–120	(−) 26–42 (−) 89–109	(+) 5–10 (−) 35–58	(−) 80–145	(−) 75–200		(−) 50–70	(−) 18–57 (−) 116–135
L. pertusa/A. excavata					(+) 35–160	(−) 5–18 (+) 50–200		(+) 3–15 (−) 20–37 (+) 47–84	
L. pertusa/Fish	(−) 11–20 (+) 24–102	(+) 30–120	(+) 34–60 (−) 70–102	(0)	(+) 65–145	(+) 14–30 (+) 65–125 (−) 138–162		(+) 3–10 (+) 19–37 (−) 65–88	(−) 42–52 (+) 83–135
P. arborea/P. resedaeformis	(+) 4–19 (+) 32–53	(+) 5–17	(−) 63–77	(+) 32–86	(−) 18–36			(+) 7–10	(+) 11–20 (+) 58–133
P. arborea/M. lingua	(+) 5–57	(+) 6–20	(−) 7–13 (+) 18–30 (−) 46–90	(−) 17–28 (−) 47–86	(−) 8–13 (+) 67–123	(+) 20–30 (+) 157–200	(−) 6–11	(−) 24–56	(−) 17–72 (+) 98–133
P. arborea/G. baretti	(0)	(0)	(−) 12–35 (+) 78–85		(0)	(−) 85–168	(0)	(0)	(−) 127–133
P. arborea/A. excavate					(+) 85–122	(+) 85–200	(+) 7–13		
P. arborea/Fish	(0)	(+) 58–102	(0)	(−) 69–86	(0)	(+) 12–35	(+) 11–25	(−) 33–60	(+) 10–18 (+) 34–133
P. resedaeformis/M. lingua	(+) 10–63	(+) 2–18	(+) 23–74	(+) 9–18 (−) 36–86	(−) 44–54			(0)	(−) 13–34 (+) 90–133
P. resedaeformis/G. baretti	(−) 31–44	(0)	(0)	(−) 2–4 (+) 7–67	(0)			(0)	(−) 125–133
P. resedaeformis/A. excavate					(−) 20–38 (−) 120–155			(+) 6–10 (−) 15–21	
P. resedaeformis/Fish	(+) 36–52	(0)	(0)	(0)	(−) 118–145			(−) 33–88	(+) 5–133
M. lingua/G. baretti	(+) 7–15 (−) 22–50 (−) 77–111	(0) (0)	(−) 23–51 (−) 64–122	(−) 76–86	(−) 98–121	(0)	(0)	(0)	(+) 29–43 (−) 126–133
M. lingua/A. excavata					(+) 20–135	(+) 6–30 (+) 87–200		(−) 27–74	
M. lingua/Fish	(−) 12–22	(0)	(−) 10–18 (+) 30–63	(+) 4–10 (−) 18–26 (+) 71–86	(−) 2–8 (+) 24–55 (+) 87–127	(+) 20–32	(0)	(0)	(−) 24–53 (+) 99–133
G. baretti/A. excavata					(+) 27–67 (−) 85–160	(−) 87–172		(−) 33–67	
G. baretti/Fish	(−) 29–43	(0)	(−) 6–18	(0)	(−) 90–157	(−) 15–45	(0)	(−) 18–26 (−) 49–65	(−) 22–36 (−) 127–133
A. excavata/Fish					(+) 15–160	(+) 80–112		(−) 30–45 (−) 72–85	

observed utilisation of structure by *Brosme brosme* is given in Fig. 3h).

5. Conclusions

Differences in abundance of many of the fauna investigated were apparent between reefs, as were trends in species covariance observed at each reef. Although only a small selection of the numerous reef species thus far reported from European CWC reefs (Hovland, 2008; Henry et al., 2010; Mastrototaro et al., 2010) were included in this study, it is quite possible that other species may vary in abundance between reefs to a similar degree. Certainly the abundances of fauna closely associated with the investigated species, such as the arthropod communities supported by the gorgonians (Buhl-Mortensen and Mortensen, 2004) or the polychaete *Eunice norvegica,* often symbiotic with *L. pertusa*

(Roberts, 2005) will vary in abundance with the change in density of their associated fauna species.

Fish abundances observed during the survey transects varied with respect to both substrate type and reef, but were generally higher in areas of substrate of biogenic origin (coral rubble and coral structure substrate categories) than those unrelated to reef presence/absence (hardground and soft sediment categories).

From this study, it is clear that community structure varies significantly between CWC reefs on the Norwegian margin. Management plans for such areas should therefore not be based on the assumption that all areas of the seabed labelled as 'Cold-water coral ecosystem' are comparable and interchangeable in morphology, species composition or population density. Reefs with broadly similar live *L. pertusa* coverage (such as at Røst Reef and Sotbakken Reef in this study) can clearly have quite different associate fauna populations.
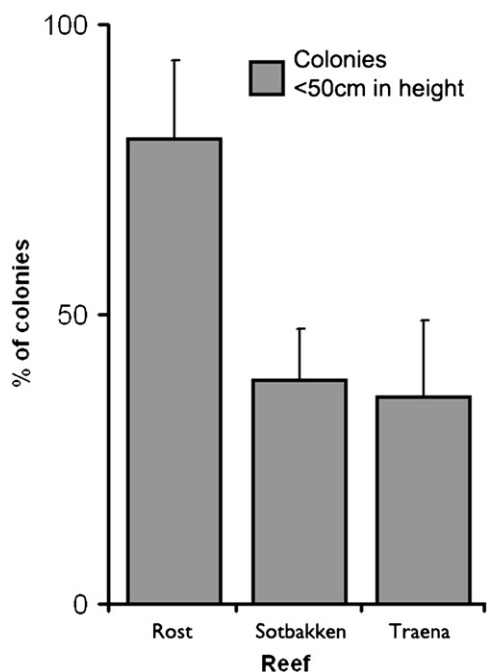
Fig. 8. *P. arborea* colony sizes (< 50 cm or > 50 cm height categories) observed at each reef. Error bars represent 1 SD.

Acknowledgements

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