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Microhabitat and shrimp abundance within a Norwegian cold-water coral ecosystem

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Abstract. Cold-water coral (CWC) reefs are heterogeneous ecosystems comprising numerous microhabitats. A typical European CWC reef provides various biogenic microhabitats (within, on and surrounding colonies of coral species such as *Lophelia pertusa, Paragorgia arborea* and *Primnoa resedaeformis*, or formed by their remains after death). These microhabitats may be surrounded and intermixed with non-biogenic microhabitats (soft sediment, hard ground, gravel/pebbles, steep walls). To date, studies of distribution of sessile fauna across CWC reefs have been more numerous than those investigating mobile fauna distribution.

In this study we quantified shrimp densities associated with key CWC microhabitat categories at the Røst Reef, Norway, by analysing image data collected by towed video sled in June 2007. We also investigated shrimp distribution patterns on the local scale (< 40 cm) and how these may vary with microhabitat.

Shrimp abundances at the Røst Reef were on average an order of magnitude greater in biogenic reef microhabitats than in non-biogenic microhabitats. Greatest shrimp densities were observed in association with live *Paragorgia arborea* microhabitat (43 shrimp m^{-2}, SD $= 35.5$), live *Primnoa resedaeformis* microhabitat (41.6 shrimp m^{-2}, SD $= 26.1$) and live *Lophelia pertusa* microhabitat (24.4 shrimp m^{-2}, SD $= 18.6$). In non-biogenic microhabitat, shrimp densities were < 2 shrimp m^{-2}. CWC reef microhabitats appear to support greater shrimp densities than the surrounding non-biogenic microhabitats at the Røst Reef, at least at the time of survey.

1 Introduction

Cold-water coral (CWC) ecosystems have been subject to much study throughout the last decade (Fosså et al., 2002; Freiwald et al., 2002; Roberts et al., 2006; Reveillaud et al., 2008; White et al., 2012). Commonly identified as local biodiversity hotspots (Weaver et al., 2004; Turley et al., 2007; Levin and Sibuet, 2012), these ecosystems develop over time with the growth of complex biogenic reef structures, formed from the aragonite skeletons of scleractinian coral species. In European waters, *Lophelia pertusa*, Fig. 1(Fosså et al., 2005; Roberts et al., 2009), is commonly the key framework-building species.

Cold-water coral reefs are often associated with elevated seabed features or areas where hydrodynamic conditions assist delivery of large volumes of refractory material, or pulses of labile material to the benthic ecosystem (Duineveld et al., 2004; Kiriakoulakis et al., 2005; Thiem et al., 2006; Kiriakoulakis et al., 2007; Davies et al., 2009; Van Oevelen et al., 2009; Rüggeberg et al., 2010; Wagner et al., 2011; Duineveld et al., 2012). Sizable reef structures can develop with successive generations of coral polyp growth (Mortensen et al., 1995; De Mol., 2002; Dorschel et al., 2005; Wheeler et al., 2007). The aragonite skeleton of the polyps increases habitat complexity both at and above the seafloor (Rogers, 1999). Dead coral polyps provide hard substrate for sessile filter-feeding organisms (López Correa et al., 2004), with the complexity of the reef morphology providing refuge for mobile organisms such as fish (Husebø et al., 2002; Costello et al., 2005; Ross and Quattrini, 2007; Ballion et al., 2012; D'Onghia et al., 2012), shrimp and other crustaceans (Reed et al., 1982; Mortensen et al., 1995; Krieger and Wing., 2002;
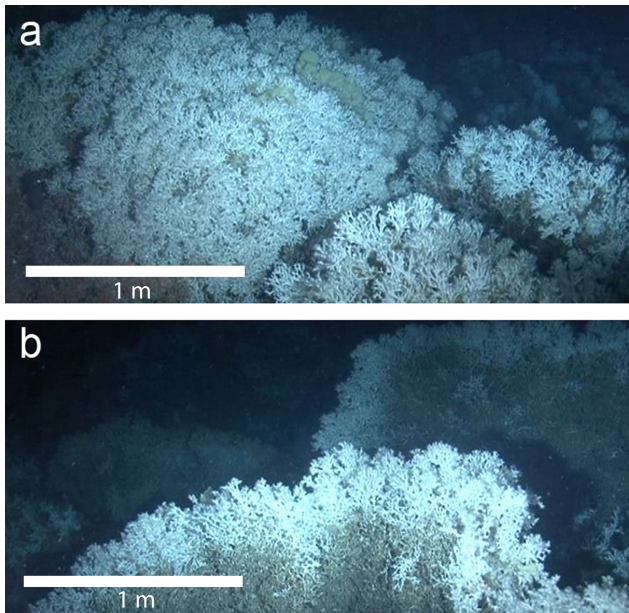
Fig. 1. *Lophelia pertusa* colony at the Røst Reef, Norway. **(a)** typical "cauliflower" growth form at the Røst Reef, with live polyps facing into the prevalent current direction. **(b)** The downstream side of the "cauliflower" reef structure. The upper ~ 25 cm of each cauliflower is made up of living *Lophelia pertusa*; the remainder the dead skeletal structure of previous polyp generations. Image courtesy of IFM-GEOMAR JAGO team.
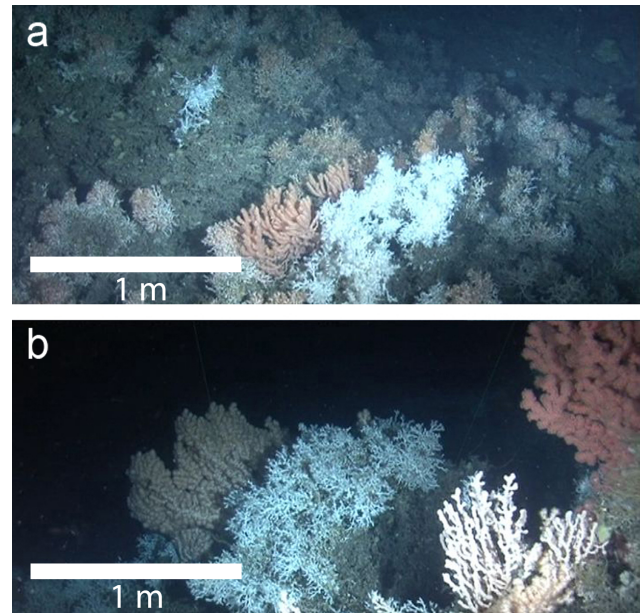

Fig. 2. Typical *Primnoa resedaeformis* and *Paragorgia arborea* colonies at the Røst Reef, Norway. **(a)** *P. resedaeformis*, the orange branching gorgonian in the lower centre of the image. Often located in cracks in the *Lophelia pertusa* structure or on the walls of coral blocks. **(b)** Three colonies of *P. arborea*. A large salmon-coloured colony in the middle distance, a pink colony on the top right and a salmon-coloured colony on the bottom right. The bottom-right colony has its polyps retracted.

Roberts et al., 2008; Le Guilloux et al., 2010; D'Onghia et al., 2012). Local hydrodynamic flow may be influenced by coral structure, enhancing or reducing local depositional rates across a reef, or entrapping suspended material in turbidity loops above the reef structure (Mortensen et al., 1995, 2001; White, 2007; Wagner et al., 2011). Sediments dropping from suspension within and surrounding coral provide further microhabitats for meiofauna (Raes and Vanreusel, 2006; Bongiorni et al., 2010).

In addition to scleractinians, gorgonian corals are found within many European CWC ecosystems. Common species include *Primnoa resedaeformis* and *Paragorgia arborea* (Mortensen et al., 1995; Herrera et al., 2012; Tong et al., 2012a). Growth morphologies of these species differ, with *Primnoa resedaeformis* colonies often comprising a number of branches draped across or close to the underlying substrate, whereas *Paragorgia arborea* colonies stand more erect, often facing fan-like into the direction of prevalent flow (Mortensen and Buhl-Mortensen, 2005) (Fig. 2).

Methodologies for quantitatively assessing CWC reef biodiversity have improved over time. Early studies using dredge sampling (Jensen and Frederiksen, 1992) gave way to campaigns employing Van Veen, box core or video grab sampling techniques (Mortensen et al., 2000; Mortensen and Fosså, 2006; Henry and Roberts, 2007; Henry et al., 2010). Although adept at collecting data on sessile species' abun-

dances, mobile fauna are often missed or under-sampled by this approach. Analysis of video data, collected by remotely operated vehicle (ROV), submarine or video sled can gather data on the distribution of fauna over larger areas, and with mobile fauna with more success than grab sampling, although video resolution and illumination can limit the level of taxonomical identification possible (Mortensen et al., 1995; Purser et al., 2009; Schoening et al., 2012). The illumination required to collect video data may also influence faunal behaviour (Trenkel et al., 2004). At CWC reef sites, video studies have focused primarily on occurrence and distribution of sessile species (Mortensen et al., 1995; Henry, 2001; Metaxas and Davis, 2005; Orejas et al., 2008; Purser et al., 2009), with fewer studies quantifying mobile macrofauna across CWC reef microhabitats (Jonsson et al., 2004; Roberts et al., 2008; Le Guilloux et al., 2010; Lessard-Pilon et al., 2010; D'Onghia et al., 2011).

Aside from fish (Mortensen et al., 1995; Costello et al., 2005; Wheeler et al., 2005; Söffker et al., 2011) and the larger crustaceans (> 5 cm) (Mortensen et al., 1995), shrimp are amongst the mobile fauna reported in association with CWC scleractinian corals at northeast Atlantic seamounts (Henry and Roberts, 2007), in the Gulf of Mexico (Cordes et al., 2008; Lessard-Pilon et al., 2010) or with gorgonian corals from Atlantic Canada (Krieger and Wing, 2002;
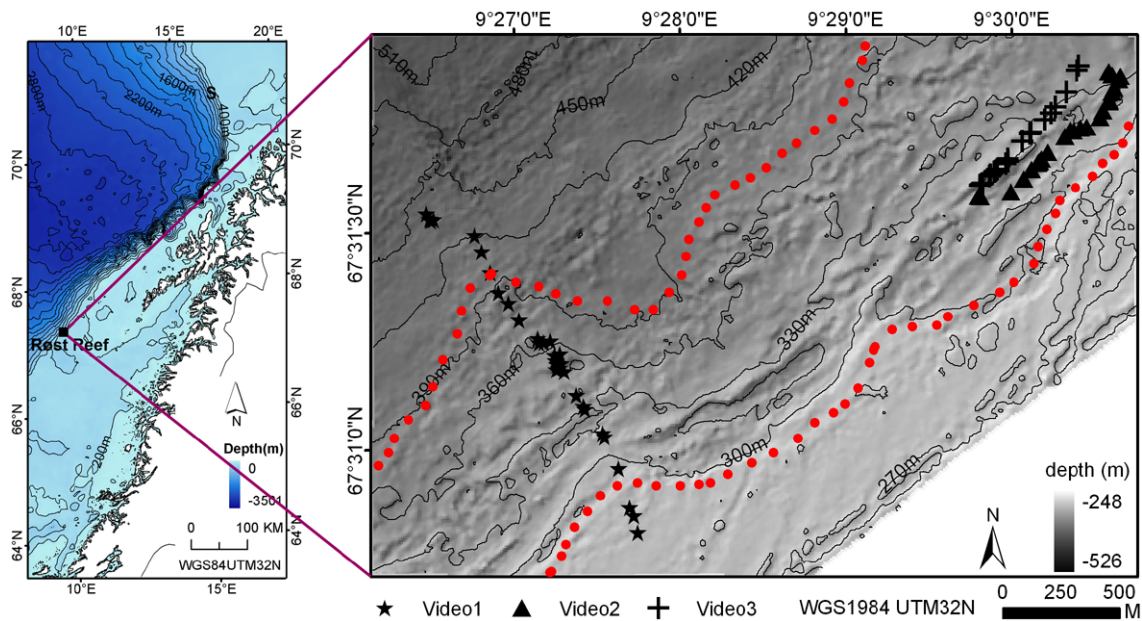
Fig. 3. Bathymetric map showing the location of the Røst Reef on the Norwegian margin, and the location of the three video transects analysed in this study. Red dots delineate reef microhabitat areas.

Buhl-Mortensen and Mortensen, 2004a). From the CWC scleractinian reefs of the Norwegian margin and fjords, *Pandalus borealis*, *Pandalus montagui* (Jonsson et al., 2004), *Pandalus propinquus*, *Lebbeus polaris*, *Eualis gaimardii* and *Caridion gordoni* (Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992; summarised in Mortensen and Fosså, 2006; Jonsson et al., 2004) are the most commonly found shrimp species. The relationship between particular shrimp species and scleractinian or gorgonian corals is uncertain. The hypothesis that shrimp are facultative commensals on the associated coral species has been raised (Buhl-Mortensen and Mortensen, 2004b).

To date, shrimp abundances across the various microhabitats found at CWC reefs have not been studied in detail. Previous video studies reporting densities of mobile fauna associated with microhabitats such as living coral reef, dead coral framework or dead coral rubble have either focused on fauna larger than the majority of shrimp species (Mortensen et al., 1995) or determined densities from discreet patch locations within reefs (Jonsson et al., 2004). In this study we investigate the distribution of shrimp across the CWC microhabitats from video sled data collected at the Røst Reef complex, Norway. The overall aim of the investigation was to see whether or not shrimp abundances were significantly different in the different microhabitats of the CWC reef – such as within and above live *Lophelia pertusa*, or in association with the coral rubble area surrounding the main structural reef. Video data were also collected from the surrounding seafloor non-biogenic microhabitats, such as rubble/pebble covered areas and areas of exposed hard ground. In addition

to quantifying shrimp densities associated with these microhabitats, the spacing of the shrimp within the habitats was also investigated. Here we determined whether shrimp were randomly distributed within a microhabitat, or more prone to either clustering or maintaining a certain spacing distance from each other. By carrying out this distribution analysis we were interested in determining whether or not there may be a behavioural change in shrimp related to the microhabitat.

2 Methods

2.1 Location of study – the Røst Reef

The Røst Reef complex, the largest discovered worldwide to date (Fosså et al., 2002; Nordgulen et al., 2006; Wehrmann et al., 2009; Fosså et al., 2010; Tong et al., 2012a), was the focus of this study. The complex is situated on the edge of the continental shelf, and is marked by vigorous *Lophelia pertusa* scleractinian coral growth on a series of seafloor crests formed by the Trænadjupet landslide during the Cenozoic (Laberg and Vorren, 2000). Between these scleractinian reef crests are regions of coral rubble and areas of low density *Lophelia pertusa* coverage on dead, exposed coral framework (Wehrmann et al., 2009) with the gorgonian coral species *Primnoa arborea* and *Paragorgia arborea* also abundant (Tong et al., 2012a).

2.2 Video data

Data were collected from three video sled traverses (Fig. 3), cross-cutting the coral dense ridge crests, less populated
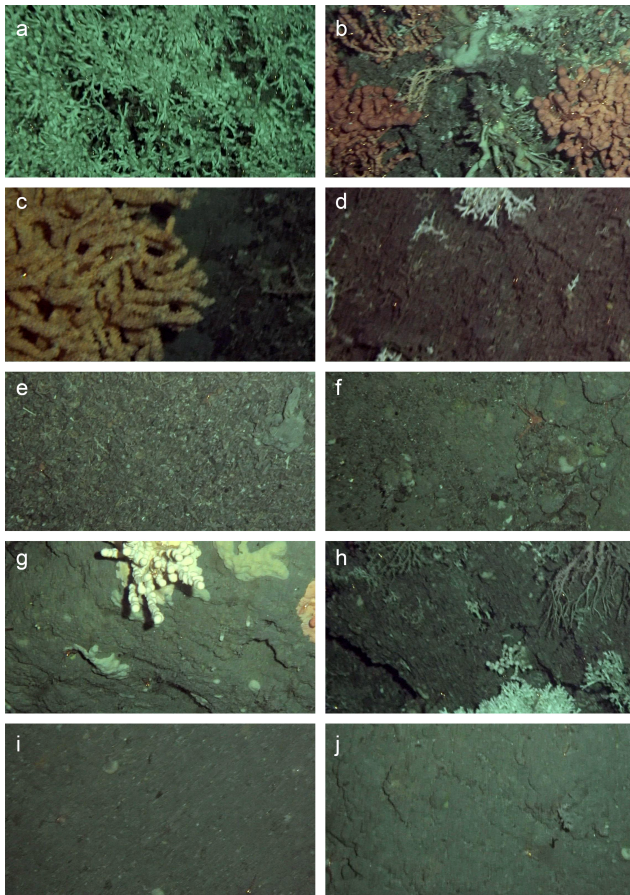
Fig. 4. Habitat categories used in this study. **(a)** Live *Lophelia pertusa*, **(b)** live *Paragorgia arborea* (left and right of image), **(c)** live *Primnoa resedaeformis* (left of image), **(d)** dead scleractinian structure, **(e)** coral rubble, **(f)** gravel/pebbles, **(g)** wall, **(h)** dead gorgonian (right of image), **(i)** soft seabed and **(j)** hard ground.

flanks and sparsely populated intermediate areas during the ARKXXII/1a RV *Polarstern* cruise (Klages and Thiede, 2011) of 2007. The video sled consisted of a metal frame approximately 1 m in area, onto which was mounted two vertically downward facing camera housings and a light source. One camera housing contained a low-resolution camera which could be viewed directly by the winch operator to allow for vertical positioning of the video sled above the seafloor. The second camera housing contained a Sony HD video camera which was used to film the seabed from an altitude of ~ 3 m, with an average area of ~ 1 m^2 (± 25 %) coverage recorded. The video transects were planned to provide data from typical microhabitat categories common at CWC coral reefs on the Norwegian margin (see Sect. 2.3). Video sled transect data have recently been used in a similar ecosystem in the Mediterranean for bethopelagic fauna quantification (D'Onghia et al., 2011).

Two image frames per second were exported from the video camera and imported with a resolution of 1920×1080

pixels into the web-based image annotation platform BIIGLE (Bio-Image Indexing, Graphical Labelling and Exploration) (Ontrup et al., 2009; Schoening et al., 2009; Purser et al., 2009; Bergmann et al., 2011). The seabed overlap of successive image frames was ~ 20 %. The area of seafloor covered by the extracted images was estimated from the assumption that the average diameter of a *Lophelia pertusa* polyp cup is 1 cm (based on box core and submarine samples collected during the cruise). From this analysis, seabed area covered by images containing *Lophelia pertusa* was generally ~ 1 m^2. Throughout the sampling, effort was made to maintain the camera at the same height above the seafloor, and therefore seafloor coverage in images containing no *Lophelia pertusa* was assumed to also be 1 m^2. Prior to analysis, the image frames were checked for suitability, with those covering a seabed area of < 0.75 m^2 or > 1.25 m^2 and those too blurred for analysis discarded – these frames representing images extracted from the video during periods of camera heave, the result of wave action or manual movement of the camera to avoid seafloor obstacles..

2.3 Microhabitat characterisation and shrimp labelling

Ten microhabitat categories were investigated in this study (Fig. 4): live *Lophelia pertusa* (a), live *Paragorgia arborea* (b), live *Primnoa resedaeformis* (c), dead structure (d), coral rubble (e), gravel/pebbles (f), wall (g), dead gorgonian (h), soft seabed (i) and hard ground (j). These microhabitat categories were selected as all were previously reported for the Røst Reef and the Norwegian margin reefs in general (Mortensen et al., 1995; Wehrmann et al., 2009; Tong et al., 2012b).

In each image the main microhabitat category was logged (i.e. that with the greatest seafloor coverage area) via the BIIGLE system. Additionally, presence/absence of each of the other microhabitat categories within each image was also noted.

After identifying each microhabitat in an image, the coordinates of each visible shrimp were also determined. Due to the high reflectivity of the eyes of shrimp, spotting these on the image frames was not a significant problem (Fig. 5). As the video sled filmed the seabed from above, the majority of shrimp were observed from above. The eyes of each shrimp were separated from each other by ~ 5 mm (approx. 5–10 pixels). To assign coordinates for each shrimp individual in an image, the midpoint between the shrimp's eyes was marked into the BIIGLE system as the point location of the shrimp (Fig. 5). Due to the resolution of data, no attempt was made to differentiate shrimp species.

Table 1. Shrimp densities observed across the various habitat categories. Mean and median distance between individual shrimp observed in association with each habitat category are also given. Mean minimum and maximum distances between nearest neighbours are also shown.

Habitat	Number of frames	Shrimps m^{-2}	SD	Mean distance nearest neighbour (mm)	SD	Median distance nearest neighbour (mm)	Mean minimum distance nearest neighbour (mm)	SD	Mean maximum distance nearest neighbour (mm)	SD
Live *Lophelia*	365	24.41	18.64	11.08	5.81	10.07	4.65	4.38	24.45	11.42
Live *Paragorgia*	8	43.00	35.58	10.92	6.22	7.92	3.62	2.29	24.95	13.99
Live *Primnoa*	5	41.60	26.06	10.57	6.23	7.20	4.71	6.08	21.00	8.65
Dead structure	779	8.70	7.80	15.27	11.97	13.54	8.52	10.74	29.79	20.94
Coral rubble	699	1.45	2.52	7.13	13.64	0	5.41	12.57	10.55	19.35
Dead gorgonian	0	0	0	0	0	0	0	0	0	0
Gravel/ pebbles	1330	0.28	0.93	1.5	8.02	0	1.21	7.41	2.10	10.67
Wall	318	1.95	3.38	6.67	12.73	0	4.50	10.68	11.50	20.65
Hard ground	30	0.67	1.94	4.15	11.04	2.26	4.01	10.96	4.43	11.30
Soft sediment	0	0	0	0	0	0	0	0	0	0

2.4 Statistics

2.4.1 Microhabitat category and shrimp density

Video frames used covered a seabed area of $\sim 1\,\mathrm{m}^2$; therefore the number of shrimp logged in each image was assumed to be the minimum number of shrimp m^{-2}. The complexity of microhabitats such as "live *Lophelia pertusa*" or "live *Primnoa resedaeformis*" renders it likely that the surface area available for shrimp to utilise is more extensive than in less complex microhabitats such as "coral rubble". Shrimp individuals may have been obscured from view by coral structure, small overhangs of larger pebbles or coral blocks in some microhabitats. The high heterogeneity of microhabitat categories within CWC reefs has been widely reported (Buhl-Mortensen et al., 2010; Gheerardyn et al., 2010; Tong et al., 2012a), with large variability in habitat complexity often occurring over scales of centimetres or metres. In this study we aim to show statistically whether or not these microhabitat categories are associated with different shrimp abundances.

The 10 microhabitat categories used in this study (see Sect. 2.3) are not of uniform spatial coverage within the Røst Reef. The gorgonian coral species *Paragorgia arborea* and *Primnoa resedaeformis* have a far less extensive spatial coverage than *Lophelia pertusa* (Tong et al., 2012a, b). These differences in coverage can make statistical analysis of video transect data problematic. To address this we grouped together the shrimp abundances observed in association with the various microhabitats into broader categories (with these broader categories covering more comparable spatial areas of reef) for statistical analysis. These broader categories were "live coral" (live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis* habitat categories), "dead coral" (dead structure and dead gorgonian categories), "coral rubble" or "non-biogenic habitats" (gravel/pebble, wall, soft sediment and hard ground categories). To determine whether or not shrimp densities varied significantly between these broader microhabitat categories a one-way ANOVA test with shrimp abundance as the dependant variable and habitat type as the investigated factor (four levels: live coral, dead coral, coral rubble, non-biogenic habitat) was used. Levene's test of homogeneity showed the data to be unequally distributed and therefore the robust Brown–Forsythe's F (Brown and Forsythe, 1974) was reported in the analysis. A Bonferroni post hoc test was used to determine between which of the factor levels (broad microhabitat categories) differences in shrimp density were significant. For the ANOVA and post hoc tests the statistical package SPSS 17.0 was used. Effect size was also determined (ω^2 measure) (Field, 2009).

2.4.2 Local-microhabitat-scale shrimp clustering patterns

By analysing the distances between a shrimp and all its neighbours in a particular image frame a positive/negative association dependent on distance was determined by applying Ripley's L (Ripley, 1976). Ripley's L provides a statistical

Table 2. Table summarising the local (< 40 cm scale) shrimp distribution patterns observed in image frames containing > 20 shrimp. The number of frames taken above the $> 50\%$ live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis* and $> 50\%$ dead structure categories with > 20 shrimp present is indicated. Insufficient shrimp were observed in association with the other habitat categories investigated to allow for computation of Ripley's L.

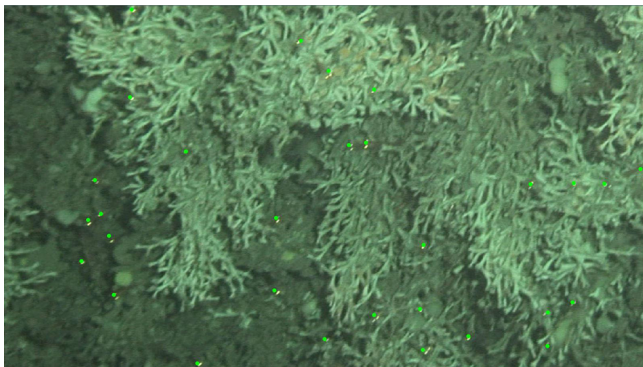| Main habitat	Number of frames	Mean shrimp m^{-2}	SD	Number frame > 20 shrimp m^{-2}	% Frames of habitat	% Frames with shrimp clustering < 10 cm scale	% Frames with shrimp clustering > 10 cm scale	% Frames with regularly spaced shrimp < 10 cm scale	% Frames with regularly spaced shrimp > 10 cm scale	% Frames with no spatial pattern
Live *Lophelia*	365	24.41	18.64	187	51.3	20.3	55.6	31.0	8.6	14.4
Live *Paragorgia*	8	43.00	35.58	5	62.5	40.0	60.0	60.0	20.0	0
Live *Primnoa*	5	41.60	26.06	4	80.0	50.0	75.0	25.0	0	0
Dead structure	779	8.70	7.80	71	9.1	42.6	75.7	10.0	7.1	12.9

Fig. 5. Example frame extracted from the video sled data within the BIIGLE system. A number of slightly blurred shrimp eyes have been labelled in green. The image shows predominantly live *Lophelia pertusa* coral and a number of shrimp within and around the coral structures.

measure for the distribution of point items over different spatial scales. Image frames containing less than 20 shrimp were omitted from this test, as the method requires a minimum number of points (shrimp) for a valid outcome. Confidence envelopes (95 %) were computed by means of Monte Carlo sampling. Deviations from the confidence envelope by points within an image (shrimp locations) allows for rejection of the assumption that the point pattern is random on a particular spatial scale (the spatial scale at which distribution deviates from the confidence envelope) at the confidence level determined. The test also indicates whether or not these deviations represent a clustering of shrimp or a tendency for shrimp individuals to maintain a certain distance from each other. In this study complete spatial randomness was tested, with Ripley's L values computed up to a maximum of 540 pixels (half

the smallest image frame axis, ~ 40 cm), therefore indicating whether there were any trends in distribution (shrimp clustering or spacing) over distances of up to 40 cm.

2.4.3 Habitat complexity and shrimp abundance

In addition to logging the main microhabitat category visible in each analysed image frame, the number of additional microhabitat categories present in an image was also counted. The shrimp densities present in image frames containing 1, 2, 3 or 4+ microhabitat categories was compared with a Kruskal–Wallis test to determine whether or not increase in the number of locally available (< 1 m^2 scale) microhabitat categories had an influence on shrimp abundance.

3 Results

A total of 18 269 shrimp were manually labelled within 3534 analysed images. The main microhabitat category present in each image was identified and the number of shrimp in each image frame logged (Table 1). The median shrimp densities and quartile distribution of these observations is given in Fig. 6. Of the 10 microhabitat categories introduced in Sect. 2.3, eight were predominant habitat categories in at least one image frame. The microhabitat categories "dead gorgonian habitat" and "soft sediment", though present in some images, always had a seafloor coverage of less than at least one other microhabitat category.

3.1 Shrimp densities and microhabitat

There was a significant effect of primary microhabitat category on shrimp abundance, $F(3, 3530) = 503.8$, $p < 0.001$, $\omega^2 = 0.26$ (Brown–Forsythe robust equality of means test
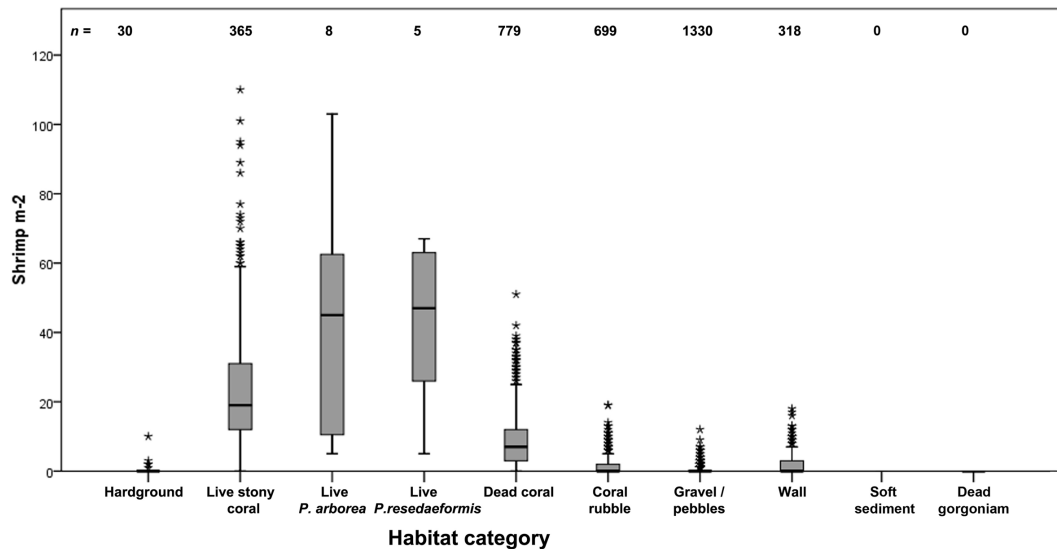
Fig. 6. Box plot showing observed median shrimp densities, quartiles and outliers observed in association with each of the investigated main microhabitat categories.

employed as Levene's test indicated the data to be inhomogeneous). The high ω^2 indicates that the microhabitat category has a large effect on shrimp abundance at the Røst Reef. Bonferroni post hoc tests indicated that shrimp abundances were significantly higher in images containing predominantly live coral ($n = 378$, mean $= 25$, SD $= 19.4$) than in images containing mainly dead coral structure ($n = 779$, mean $= 8.7$, SD $= 7.8$), coral rubble ($n = 699$, mean $= 1.45$, SD $= 2.5$) or non-biogenic microhabitat categories ($n = 1678$, mean $= 0.6$, SD $= 1.8$) ($p < 0.01$). The Bonferroni tests also showed that differences in shrimp abundances were also significant at the same confidence level between images containing predominantly dead coral structure and those containing mainly coral rubble. No significant difference was indicated between shrimp densities observed in images containing predominantly coral rubble microhabitat and those containing mainly non-biogenic microhabitats.

3.2 Patterns of shrimp distribution

The minimum, maximum, mean and median distance between individual shrimp within each microhabitat is given in Table 1. The mean distances to nearest-neighbour scores indicate a generally tighter arrangement of shrimp in association with living coral microhabitats than with dead coral structure or coral rubble microhabitats. Though shrimp tended to be more closely spaced in non-biogenic microhabitats, the low density of shrimp in these microhabitats probably indicates that the few shrimp present are utilising particular microhabitat features (such as pebble overhangs or fissures in a wall) rather than clustering together intentionally.

Sufficient shrimp densities to allow for Ripley's L analysis (> 20 individuals m^{-2}) were observed in 267 image

frames (Table 2). These high densities were only observed in association with live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis* and the dead scleractinian microhabitats. Table 2 shows that within just over 50 % of the images classified as being predominantly live *Lophelia pertusa* microhabitat, > 20 shrimp m^{-2} were observed, with higher percentages of live *Paragorgia arborea* (62.5 %) and live *Primnoa resedaeformis* (80 %) microhabitat image frames also containing shrimp densities of >20 shrimp m^{-2}. Just under 10 % of dead scleractinian structure image frames contained > 20 shrimp m^{-2}. Table 2 shows that on a scale of < 10 cm, shrimp were more negatively associated with their neighbours in live coral microhabitat image frames than in dead coral microhabitat frames. At scales of >10 cm, shrimp were observed to be clustered across all microhabitats, within image frames with > 20 shrimp m^{-2} present.

3.3 Microhabitat complexity and shrimp abundance

Frames containing > 1 microhabitat category had a significantly greater number of shrimp present than those with only 1 microhabitat category present, H (3) $= 1052.54$, $p < 0.01$, Fig. 7. Densities of shrimp in images containing 2, 3 or 4+ microhabitat categories were not significantly different from each other.

4 Discussion

4.1 Shrimp abundance and microhabitat

From the results presented here it would appear that shrimp densities vary across the Røst Reef complex with change in microhabitat category, and that the type of microhabitat
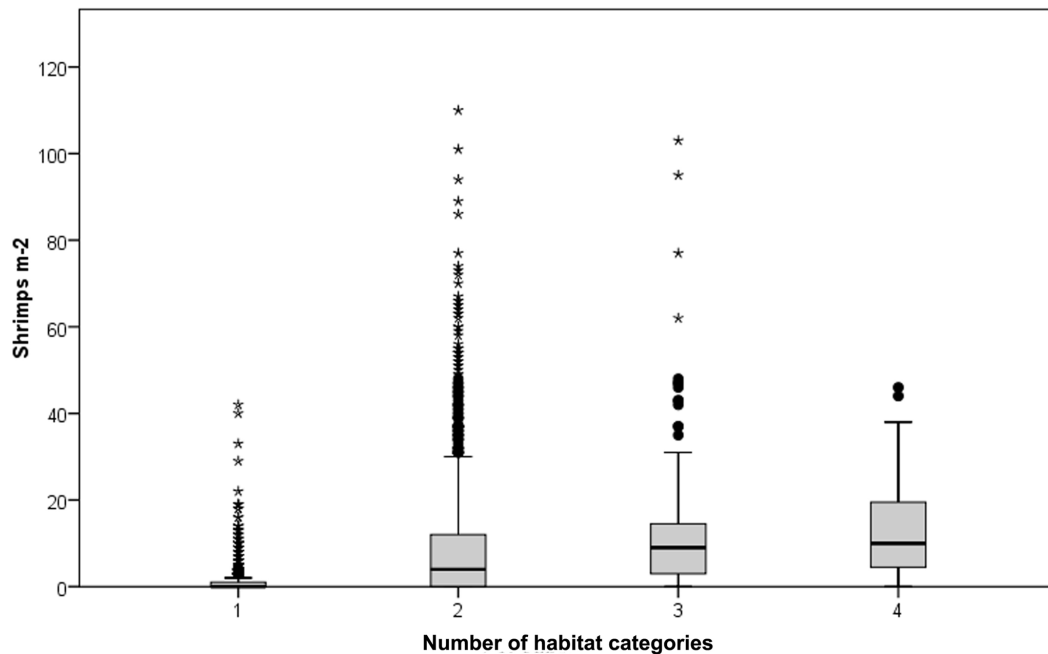
Fig. 7. Box plot showing shrimp densities observed in image frames with differing numbers of microhabitat categories present.

can have a large influence on shrimp density. From the images analysed, shrimp abundances appear highest in regions where the available microhabitat is predominantly live coral, with a mean average density of 25 shrimp m^{-2} (SD = 19.4) recorded. The live reef microhabitat is perhaps the most physically complex (Buhl-Mortensen et al., 2010). Dead coral structure, though still angular and providing physical niches over a range of scales, was associated with shrimp abundances $\sim 60\,\%$ lower than observed in association with the live coral microhabitats (mean shrimp m^{-2} = 8.7, SD = 7.8) . It is unlikely that this difference can be explained by observer bias or shrimp behaviour, given that shrimp eyes were marginally easier to distinguish against dead coral structure than against live coral. Shrimp abundances were lower again in association with the coral rubble microhabitat (mean shrimp m^{-2} = 1.45, SD = 2.5) and non-biogenic microhabitat categories (mean shrimp m^{-2} = 0.6, SD = 1.8). Coral rubble regions of CWC ecosystems consist of small, broken pieces of coral, partially eroded and lying on the seabed. Though this microhabitat contains small structural gaps between fragments which shrimp may occupy, it is difficult to imagine that shrimp utilising these could account for the considerable differences in density observed between this microhabitat and those observed in association with live coral microhabitats. The non-biogenic microhabitat categories, those not dependant on CWC reef development, i.e. hard ground outcrops, gravel/pebble fields and walls, exhibited the lowest abundances of shrimp observed – though some areas of wall microhabitat had densities of several shrimp m^{-2} (Fig. 6). The statistically significant obser-

vation of higher shrimp densities in images containing > 1 microhabitat category is a further indication that increased local heterogeneity may be of benefit to CWC shrimp, as has been observed for shrimp in sublittoral environments (Hewitt et al., 2005).

Whether the shrimp are of benefit to the living *Lophelia pertusa* is not clear from this study. It is possible that they play a useful role in keeping the branches of *Lophelia pertusa* free from accumulating sediment, as has been hypothesised for associated polychaetes (Mortensen, 2001), a process which can lead to tissue damage over time if unchecked (Larsson and Purser, 2011). No attempt was made here to differentiate shrimp species from the video data, and potentially different species could be utilising the live coral and dead coral microhabitats. Spatial partitioning of the reef ecosystem by shrimp species has been reported at tropical coral reefs (Hoeksema and Fransen, 2011). A recent trawl survey done by D'Onghia et al. (2010) comparing species abundances within and outside of CWC reef zones indicated that such partitioning may also be likely at CWC reefs. They report comparable densities of the shrimp species *Aristaeomorpha foliacea* within and surrounding CWC habitat, the complete absence of particular shrimp species, (e.g. *Aristeus antennatus*) from within the reef itself but presence in the surrounding waters, and a 10-times-greater abundance of the commercially significant species *Parapenaeus longirostris* within the living reef structural area. Their paper reports observations from a Mediterranean reef, and the situation may be different on the Norwegian margin. The shrimp species commonly reported to occur within deep Norwegian

waters (Hopkins and Nilssen, 1990) are generally those reported from CWC environments (Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992; summarised in Mortensen and Fosså, 2006; Jonsson et al., 2004) indicating, as commonly reported for sessile fauna, a general lack of endemism in CWC reefs on the Norwegian margin (Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992). Given the great variability in survey methods employed in the reports published to date, however, it is not easy to draw any conclusions on the differences in species densities (or indeed, total shrimp densities) on and off reefs.

Shrimp densities observed in association with *Paragorgia arborea* and *Primnoa resedaeformis* were similar, though the number of frames containing either of these coral species as the predominant microhabitat category were low (Table 1), rendering quantitative statistical analysis difficult. Such comparable densities would not be expected if shrimp were simply utilising the underlying microhabitat (the gorgonian coral) as an elevated surface on which to rest and attain a more favourable position with respect to the prevalent flow conditions, as the growth morphs and vertical colony extent of these gorgonian species is very different. Mortensen and Buhl-Mortensen (2005) indicated that *Paragorgia arborea* and *Primnoa resedaeformis* likely utilise different food sources. *Paragorgia arborea* colonies tend to stand near vertically, facing into the prevalent current and capturing food delivered by the stronger, less turbid currents found tens of centimetres above the seafloor, whereas *Primnoa resedaeformis* colonies may acquire their food supply from more turbid waters found in closer proximity to the seafloor. Possibly the elevated shrimp densities observed on both gorgonian corals are the result of shrimp feeding on material trapped within the mucus secreted by the corals (Patton, 1972), rather than material in the water column. Such a strategy would likely have led shrimp to preferentially occupy *Paragorgia arborea* rather than *Primnoa resedaeformis* – a behavioural trend unsupported by the data here.

The differences in *Lophelia pertusa*, *Paragorgia arborea* and *Primnoa resedaeformis* colony morphologies may account for the differences in shrimp abundances observed in frames containing predominantly these microhabitats. The more flexible gorgonian corals may provide a greater surface area for shrimp to rest on, and/or a more suitable set of refuges for evasion of predators (a behaviour in CWC shrimp hypothesised in Buhl-Mortensen and Mortensen, 2004a). In addition to the gorgonians, scleractinian CWCs also exude mucus as a cleaning agent and potentially as a food-gathering mechanism (Reitner, 2005; Wild et al., 2008; Purser et al., 2010). Should CWC shrimp be utilising material entrapped by the corals as a food source, then some difference in the food value of the mucus or the entrapped material found on scleractinians and gorgonians could explain the minor differences in shrimp densities observed in the coral species' microhabitats (Fig. 6).

Previous studies have investigated megafauna associated with *Paragorgia arborea* and *Primnoa resedaeformis* in western Atlantic waters (Metaxas and Davis, 2005; Buhl-Mortensen and Mortensen, 2005). Buhl-Mortensen and Mortensen (2005) reported on the difficulties involved in quantifying shrimp densities in the vicinity of these gorgonian species by either suction sampling fauna from coral branches or by counting those collected whilst sampling whole coral branches. From video taken by ROV, Buhl-Mortensen and Mortensen (2005) report shrimp densities of 4.8 and 3.1 individuals colony^{-1} in association with *Paragorgia arborea* and *Primnoa resedaeformis* respectively. These density estimates are far lower than those reported in the current study, and made from video data recorded by a more intrusive methodology. In the Gulf of Alaska, Krieger and Wing (2002) reported "hundreds of shrimp eyes" reflected from within the branches of *Primnoa* spp. colonies – although not a strictly quantitative estimate of shrimp density, their rough estimate is comparable with shrimp densities associated with the living gorgonian microhabitats presented here, from the eastern side of the Atlantic. Should protection be the overriding advantage offered by living coral microhabitats over the surrounding dead reef areas, then the complexity and malleability of the *Primnoa resedaeformis* structure may be the most appealing coral microhabitat for smaller shrimp individuals and species. It has been hypothesised that this species is used as a refuge by shrimp < 3 cm in the Gulf of Alaska (Krieger and Wing, 2002). Although in the current study it is not possible to observe statistically significant differences in shrimp abundances between the two investigated gorgonian species, it is quite possible that the video data under-sampled shrimp to a greater degree in frames dominated by *Primnoa resedaeformis* than in frames where the less spatially complex *Paragorgia arborea* coral was in dominance. The spaced, branched morphologies of the gorgonians may offer more useful refuge niches than the more densely packed *Lophelia pertusa* structure, perhaps limiting this microhabitat in usefulness to larger shrimp individuals and species. The number of image frames containing either of the gorgonian species ($n = 5$–8) analysed in this study was far less than frames containing live *Lophelia pertusa* ($n = 365$), so without further study, the hypothesis that higher densities of shrimp are associated with the gorgonian corals should be approached tentatively.

4.2 Shrimp distribution within microhabitats

The observation that shrimp at the Røst Reef preferentially occupy regions of living coral has previously been reported as a likely behavioural trend in mobile CWC reef filter feeders (Buhl-Mortensen et al., 2010), and reported for some shrimp species in the Mediterranean (D'Onghia et al., 2011). Elevated shrimp concentrations observed following direct sampling of associate fauna from within *Lophelia pertusa* living coral structure from the Gulf of Mexico (Cordes et

al., 2008) led the authors to hypothesise that some shrimp species may play a role as cleaners at CWC reefs, as has been observed in tropical reefs (Zann, 1987). At tropical reefs, studies of stomach contents of coral-associated shrimp individuals have indicated a diet consisting of both coral mucus and zooplankton (Patton, 1994). The regular shrimp spacing on the < 10 cm scale (i.e. a tendency to maintain some distance from neighbouring shrimp over distances of less than 10 cm) found in this current study within live coral microhabitats may indicate that individual shrimp require a minimum surrounding space for feeding, or may be a consequence of social interaction (Henry et al., 2013). It is also possible that the regularity of spacing observed is a function of the underlying coral morphology. Given the differences in shrimp densities observed in association with living *Lophelia pertusa* and dead scleractinian structure microhabitats, the feeding hypotheses seem the more likely causes considering that the physical structure of the live *Lophelia pertusa* and dead coral structure microhabitats are not hugely different.

5   Summary

Despite the absence of species-level distribution data and the variation in seabed coverage area of the various microhabitat categories investigated here, it would appear that shrimp densities can vary significantly across Norwegian margin CWC reefs with changes in microhabitat, and that the spacing of shrimp within a microhabitat can also differ between microhabitat categories. The significance of biogenic reef microhabitats for shrimp is very clear, with shrimp densities observed in association with these (live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis*, dead coral structure, coral rubble) in excess of an order of magnitude greater than observed in association with the non-biogenic microhabitats at the Røst Reef (gravel/pebbles, wall, hard ground). What is not clear from this study is whether or not a temporal factor may also determine spatial arrangement and abundances of shrimp within or between microhabitats. The video data used were also of insufficient quality to allow for identification of shrimp to species level, though the image analysis techniques used here would be suitable for differentiating between shrimp species when higher quality video data are available in the future.

Given the high densities of shrimp identified in association with the biogenic microhabitats investigated in this study, it would seem likely that the loss of CWC reefs via anthropogenic activity or otherwise would have a knock-on effect on local fish stocks, in addition to that associated with the loss of structural fish microhabitat. With the high shrimp densities observed here in association with biogenic microhabitats, it would seem likely that the loss of CWC reef ecosystems would result in a drop in local shrimp numbers, and therefore a reduction in prey availability for many fish species.

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