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

A. Purser[1], J. Ontrup[2], T. Schoening[2], L. Thomsen[1], R. Tong[1], V. Unnithan[1], and T. W. Nattkemper[2]

[1]Jacobs University Bremen, Campus Ring 1, 28759 Bremen, Germany
[2]Bielefeld University, Faculty of Technology, Biodata Mining and Applied Neuroinformatics Group, P.O. Box 100131, 33501 Bielefeld, Germany

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Correspondence to: A. Purser (a.purser@jacobs-university.de)

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Abstract

Cold-water coral reefs are highly heterogeneous ecosystems comprising of a range of diverse microhabitats. In a typical European cold-water coral reef various biogenic habitats (live colonies of locally common coral species such as *Lophelia pertusa, Paragorgia arborea* and *Primnoa resedaeformis*, dead coral structure, coral rubble) may be surrounded and intermixed with non-biogenic habitats (soft sediment, hard-ground, gravel/pebbles, steep walls). To date, studies of distribution of sessile fauna across these microhabitats have been more numerous than those investigating mobile fauna distribution.

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

We found shrimp abundances at the Røst reef to be on average an order of magnitude greater in biogenic reef habitats than in non-biogenic habitats. Greatest shrimp densities were observed in association with live *Paragorgia arborea* habitats (43 shrimp m^{-2}, SD = 35.5), live *Primnoa resedaeformis* habitats (41.6 shrimp m^{-2}, SD = 26.1) and live *Lophelia pertusa* habitats (24.4 shrimp m^{-2}, SD = 18.6). In non-biogenic habitats shrimp densities were < 2 shrimp m^{-2}. We conclude that CWC reef habitats clearly support greater shrimp densities than the surrounding non-biogenic habitats on the Norwegian margin.

1 Introduction

Cold-water coral (CWC) ecosystems have been subjects of 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

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develop over time with the growth of complex biogenic reef structures, formed from the calcium carbonate 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 structural features or found in locations where hydrodynamic conditions assist in the 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 (De mol, 2002; Dorschel et al., 2005; Wheeler et al., 2007). The aragonite skeleton of these 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., 2004; Ross and Quattrini, 2007; Ballion et al., 2012; D'Onghia et al., 2012) shrimp and other crustaceans (Reed et al., 1982; Kreiger and Wing, 2002; 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 in various areas of a reef, or entrapping suspended material in turbidity loops above the reef structure (White, 2007; Wagner et al., 2011). Sediments deposited with the coral structure and the surrounding coral rubble areas provide a further microhabitat 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 at European reefs include *Primnoa resedaeformis* and *Paragorgia arborea* (Herrera et al., 2012; Tong et al., 2012). Growth morphologies of these species differ, with *Primnoa resedaeformis* colonies often comprising a number of branched arms 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 assessing CWC reef biodiversity have changed over the years. Early studies using dredge sampling (Jensen and Frederiksen, 1992) gave way to campaigns employing Van Veen or box core sampling techniques (Henry and Roberts, 2007; Henry et al., 2010). Although these techniques are adept at collecting data on sessile species abundances, mobile fauna are often missed or under-sampled by this approach. Analysis of video data, collected by Remote Operated Vehicle (ROV), submarine or video sled can gather data on the distribution of mobile macrofauna with more success than grab sampling, although video resolution and illumination can limit the level of taxonomical identification possible (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 to date have focused primarily on occurrence and distribution of sessile species (Henry, 2001; Metaxas and Davis, 2005; Mortensen et al., 2008; Orejas et al., 2008; Purser et al., 2009), with a lesser number of attempting quantification of mobile macrofauna across various CWC reef habitats (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 (Costello et al., 2005; Wheeler et al., 2005; Söffker et al., 2011) shrimp are the mobile fauna most commonly reported in association with CWC scleractinian (Henry and Roberts, 2007; Lessard-Pilon et al., 2010) and gorgonian corals (Krieger and Wing, 2002; Buhl-Mortensen and Mortensen, 2004a). Published observations have tended to be qualitative rather than quantitative. Shrimp species reported from Norwegian reefs include *Pandalus borealis, Pandalus montagui*, *Pandalus propinquus* and *Caridion gordoni* (Hopkins and Nilssen, 1990; Jonsson et al., 2004; Buhl-Mortensen and Mortensen, 2004b). The relationship between these shrimp species and scleractinian or gorgonian corals is uncertain. The hypothesis that shrimps are facultative commensals on the associated coral species has been raised (Buhl-Mortensen and Mortensen, 2004b). How shrimp vary in abundance across and between typical

CWC coral microhabitats (live scleractinian coral structure, live gorgonian coral structure, dead coral framework etc) has not to date been investigated in detail. In this study we investigate these patterns in distribution across reef habitat categories found at the Røst reef on the Norwegian margin. Video data collected by ship towed video-sled camera was analysed, with the following two hypotheses tested:

1. Shrimp densities will differ by CWC habitat category.
2. Distribution patterns of shrimp observed at CWC reefs will differ on the local scale (< 50 cm), with change in CWC habitat category.

By testing these two hypotheses, the aim was to increase our understanding of the functioning of CWC reef biodiversity hotspots, and to provide information of possible use for the development of management plans for these areas. This latter aim is particularly prescient given that many CWC reefs in European waters are located in areas of significant human activity, primarily commercial fishing and oil and gas exploration/production (Fosså and Skjoldal, 2010; Söffker et al., 2011). It has been hypothesised that CWC reef ecosystems are highly important refuges for some commercial juvenile fish species (Husebø et al., 2002; Ballion et al., 2012) and that these reefs could also play a role in the lifecycle of other mobile commercial fauna, such as some species of shrimp.

2 Methods

2.1 Location of study – the Røst reef

The Røst reef complex, Norway, one of the most extensive in Norwegian waters (Fosså et al., 2002; Nordgulen et al., 2006; Wehrmann et al., 2009; Tong et al., 2013), was the focus of this study. Permission to conduct video surveys of the reef complex was granted by the Institute of Marine Research (IMR), Norway. 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 Traenadjupet landslide during the Cenozoic (Damuth, 1978). 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 corals *Primnoa arborea* and *Paragorgia arborea* also abundant in some regions of the reef complex (Tong et al., 2012).

2.2 Video data

Data was collected from three video sled traverses (Fig. 3), cross-cutting the coral dense ridge crests, less populated flanks and sparsely populated intermediate areas during the ARKXXII/1a "FS Polarstern" cruise (Klages and Thiede, 2011) of 2007. These video transects were planned to provide data from typical habitat categories common at CWC coral reefs on the Norwegian margin (see Sect. 2.3). Video sled transect data has recently been used in a similar ecosystem in the Mediterranean for benthopelagic fauna quantification (D'Onghia et al., 2011).

A Sony HD video camera was used to film the seabed from an altitude of ~ 3 m, with an average area of ~ 1 m^2 (±25 %) coverage recorded. 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 (BioImage 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 %. Prior to analysis, the image frames were checked for suitability, with those covering a seabed area of $< 0.75\,\text{m}^2$ or $> 1.25\,\text{m}^2$ and those too blurred for analysis, discarded. Following this sorting stage, a set of 3534 image frames remained for analysis. Image coverage estimates were based on the assumption that the average diameter of a *Lophelia pertusa* polyp cup is 1 cm.

2.3 Habitat characterisation and shrimp labelling

Each image frame was inspected in turn in the BIIGLE system. For each image the main habitat category was logged (that with > 50 % coverage of an image frame). Additionally, presence/absence of each of the remaining habitat categories within each image was logged. Ten habitat categories were used (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 hardground (j). These habitat categories were selected as they were all previously reported for the Røst reef (Wehrmann et al., 2009; Tong et al., 2012)

Due to the high reflectivity of the eyes of shrimp, spotting them on the image frames was not a significant problem (Fig. 5). As the video sled filmed the seabed from above, the majority of shrimps observed were observed from above. The eyes of each shrimp individual were distinct bright points separated from each other by ~ 5 mm (approx. 5–10 pixels). The mid-point between the two eyes was marked into the BIIGLE system for every shrimp in every image, with these mid-points representing the point location of each individual within each image frame. In the present study no attempt was made to differentiate particular shrimp species. Fig. 5 shows an example image frame from the dataset within the BIIGLE system, with a number of shrimp positions logged.

2.4 Statistics

2.4.1 Habitat category and shrimp density

The video frames used in this analysis covered a seabed area of ~ 1 m^2, therefore the number of shrimps logged in each image was assumed to be the minimum number of shrimp m^{-2}. Given the complex topography of many of the habitats investigated, further shrimp individuals may have been obscured from view by coral structure, or other features such as the small overhangs of larger pebbles or coral blocks.

The high heterogeneity of habitat categories within CWC reefs on the Norwegian margin has been widely reported (Buhl-Mortensen et al., 2010; Gheerardyn et al., 2010; Tong et al., 2012), with great changes in habitat complexity often occurring over scales of cm or m. In this study we aim to show statistically whether or not these habitat categories are associated with different shrimp abundances.

The ten habitat categories used in this study (see Sect. 2.3) are not of uniform spatial coverage within a particular reef, and can vary greatly in coverage between reefs. The gorgonian coral species *Paragorgia arborea* and *Primnoa resedaeformis* have a far less spatial coverage than *Lophelia pertusa* at the Røst reef (Tong et al., 2012, 2013). This variation in coverage can make statistical analysis of video transect data problematic. To address this problem we decided to group together the shrimp abundances observed in association with the various habitats into broader categories covering more comparable spatial areas of reef for statistical analysis.

We focused our study on shrimp abundance on determining whether or not the abundances observed in association with 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 hardground categories) differed statistically. To do this we ran a one-way ANOVA test with shrimp abundance as the dependant variable and habitat type as the investigated factor (4 levels, live coral, dead coral, coral rubble, non-biogenic habitat). Levene's test of homogeneity showed the data to be unequally distributed and therefore the robust Brown-Forsythe's F (Brown and Forsythe, 1974) used for the analysis. A Bonferroni post-hoc test was used to determine between which of the factor levels (habitat categories) shrimp distribution differences were significant. For the ANOVA and post-hoc tests the statistical package SPSS 17.0 was used. Effects size was also determined (ω^2 measure) (Field, 2009).

2.4.2 Local scale shrimp distribution

By analysing the distances between each shrimp and all its neighbours in a particular image frame (i.e. all the other shrimps in an image) a positive/negative association dependent on distance was determined by applying Ripleys-L (Ripley, 1976). Ripleys-L provides a statistical measure for the distribution of point items over different spatial scales. Image frames containing less than 20 Shrimps were omitted from this test, as the method requires a minimum number of points (shrimps) 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 in this instance) allows 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 tight clustering of shrimps or a tendency for a shrimp individual to maintain a certain distance from other shrimps. 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), so indicating whether there was 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 habitat category visible in each analysed image frame, the number of additional habitat categories present in an image was also counted. The shrimp densities present in image frames containing 1, 2, 3 or 4+ habitat categories was compared with a Kruskal-Wallis test, to determine whether or not increase in the number of locally available ($< 1\,\mathrm{m}^2$ scale) habitat categories had an influence on shrimp abundance.

3 Results

A total of 18 269 shrimp were manually labelled within the 3534 images analysed. The main habitat category present in each image was identified and the number of shrimps in each image frame logged. The number of image frames identified as containing primarily each of the habitat categories, along with the mean average and standard deviation of shrimp densities observed in association with each of these is given in Table 1. The median shrimp densities and quartile distribution of these observations is given in Fig. 6. Of the ten habitat categories outlined in Sect. 2.3, eight were present as the predominant category in image frames. Although some images contained areas of the "dead gorgonian habitat" and "soft sediment" categories, coverage by these was always less than 50 % of an image frame.

3.1 Shrimp densities and habitat category

There was a significant effect of habitat category on numbers of shrimp in each image, $F(3,3530) = 503.8$, $p < 0.001$, $\varpi^2 = 0.26$ (Brown-Forsythe robust equality of means test employed as Levene's test indicated the data to be in-homogenous). The high ϖ^2 indicates that the habitat type 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 habitat 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 habitat and those containing mainly non-biogenic habitat.

3.2 Patterns of shrimp distribution

The minimum, maximum, mean and median distance between individual shrimps across each habitat category is given in Table 1. The mean distances to nearest neighbour scores indicate a generally tighter arrangement of shrimps in association with living coral habitats than with dead coral structure or coral rubble habitats. Though shrimps tended to be more closely spaced in non-biogenic habitats, the low density of shrimps in these habitats probably indicates that the few shrimp present are tending to use the same habitat features (such as pebble overhang or fissure in a wall) rather than clumping together intentionally.

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

3.3 Habitat complexity and shrimp abundance

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

4 Discussion

From the results presented here it is clear that shrimp densities vary across a Norwegian CWC reef habitat with change in habitat category, and that the type of habitat can have a large influence on shrimp density. From the images analysed in this study it is clear that shrimp abundances are highest in regions where the available habitat is predominantly live coral, with a mean average density of 25 shrimps m^{-2} (SD = 19.4) recorded in such image frames. Of the reef habitats surveyed in this study, the live reef habitat is perhaps the most physically complex (Buhl-Mortensen et al., 2010). Dead coral structure, though still very angular and providing many physical habitat niches, was associated with shrimp abundances ~ 60 % lower than observed in association with the live coral habitats (mean shrimps m^{-2} = 8.7, SD = 7.8). It is unlikely that this difference can be explained by observer bias or shrimp behaviour, as shrimp eyes were actually easier to distinguish against dead coral structure than against live coral. Shrimp abundances were lower again in association with the coral rubble habitat (mean shrimps m^{-2} = 1.45, SD = 2.5) and non-biogenic habitat categories (mean shrimps m^{-2} = 0.6, SD = 1.8). Coral rubble regions of CWC ecosystems are commonly made up of small, broken pieces of coral, weathered and eroded and lying on the seabed. Though this habitat contains a number of small structural gaps and features shrimp may occupy, it is difficult to imagine that hiding shrimp utilizing these could account for the great difference in density observed when comparing the abundances observed in association with this habitat and those observed in live and dead coral habitats. The non-biogenic habitat categories, those not dependant on CWC reef development, i.e. hardground outcrops, gravel/pebble fields and walls, were regions with the lowest abundances of shrimps observed – though some areas of wall habitat had densities of several shrimp m^{-2} (Fig. 6). The statistically significant observation of higher shrimp densities in images containing more than one habitat category is a further indication that increased local heterogeneity may be of benefit to CWC shrimps, as has been observed for shrimp in sub-littoral environments (Hewitt et al., 2005).

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 shrimps over distances of less than 10 cm) found in this current study within live coral habitats may indicate that individual shrimps require a minimum surrounding space for feeding, or perhaps 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 habitats reported here, the feeding hypothesis seems the more likely, with the physical structure of the live *Lophelia pertusa* and dead coral structure habitats not being hugely different. 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, 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 habitats. Such local spatial partitioning of the reef ecosystem by shrimp species has been reported at tropical coral reefs (Hoeksema and Fransen, 2011). A recent trawl survey comparing species abundances within and outside of CWC reef zones indicated that this may also be likely at CWC reefs. D'Onghia et al. (2010) report comparable densities of the shrimp species *Aristaeomorpha foliacea* within and surrounding CWC habitat, the complete absence of some shrimp species (e.g. *Aristeus antennatus*) from within the reef itself, and a 10x greater abundance of the commercially significant species *Parapenaeus longirostris* within the living reef structural area.

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 habitat category were few (Table 1). Such comparable densities would not be expected if shrimps were simply utilising the underlying habitat (the gorgonian coral) as an elevating substrate on which to rest and attain a more favourable position with respect to the prevalent flow conditions, as the growth morphs and vertical extent reached by colonies of these two gorgonian species is very different. Mortensen and Buhl-Mortensen (2005) indicated that *Paragorgia arborea* and *Primnoa resedaeformis* likely utilise different food sources, with *Paragorgia arborea* colonies tending to stand near vertically, facing into the prevalent current, capturing food delivered by the stronger, less turbid currents found 10 s of cm 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, as such a strategy would likely have led shrimp to preferentially occupy *Paragorgia arborea* rather than *Primnoa resedaeformis* – a possibility unsupported by the data here.

The differences in colony morphology and polyp spacing of *Lophelia pertusa* and those of *Paragorgia arborea* and *Primnoa resedaeformis* may account for the differences in shrimp abundances observed in frames containing predominantly living corals. Possibly the more flexible gorgonian corals allow a greater surface area for shrimps to rest on, or a more suitable set of refuges for evasion of predators. In addition to the gorgonians, scleractinians such as *Lophelia pertusa* 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 minor difference in the food value of the mucus itself or the entrapped material found on scleractinians and gorgonians could also explain the minor differences in shrimp densities observed by coral species (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 figure is comparable with shrimp densities associated with the living gorgonians in this current study, on the eastern side of the Atlantic.

Should protection be the overriding advantage offered by living coral habitats over the surrounding dead reef areas, then the complexity and malleability of the *Primnoa resedaeformis* structure may be the most appealing coral habitat for smaller shrimp species and individuals. It has been hypothesised that this gorgonian species is used as a refuge by shrimp < 3 cm in the Gulf of Alaska (Kreiger and Wing, 2002). Although from the observations reported 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 the video data under sampled shrimps 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 habitat 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 conclusion that higher densities of shrimp are associated with the gorgonian corals should be approached tentatively.

Despite the absence of species level distribution data and some variation in seabed coverage of the various habitat categories investigated, it is clear from the data presented here that shrimp densities can vary significantly across Norwegian margin CWC reefs with changes in habitat category, and that the local scale patterns in shrimp distribution also change with change in habitat. The significance of biogenic reef habitats for shrimp is also very clear, with shrimp densities observed in association with these (live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis*, dead coral structure, coral rubble) to be in excess of an order of magnitude greater than observed in association with the non-biogenic habitats of the investigated region of the Norwegian margin seafloor (gravel/pebbles, wall, hardground). Though not addressed 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 habitat (Söffker et al., 2011). From the shrimp densities reported here it would seem likely that the loss of CWC reef ecosystems would likely result in a drop in local shrimp numbers, and therefore result in a reduction in prey availability for many fish species.

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Table 1. Shrimp densities observed across the various habitat categories. Mean and median distance between individual shrimps 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
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
Hardground	30	0.67	1.94	4.15	11.04	2.26	4.01	10.96	4.43	11.30

Table 2. Table summarizing the local (< 40 cm scale) shrimp distribution patterns observed in image frames containing > 20 shrimps. The number of frames taken above the > 50 % live *Lophelia pertusa*, live *Paragorgia arborea*, live *Primnoa resedaeformis* and > 50 % dead structure categories with > 20 shrimps present is indicated. Insufficient shrimps were observed in association with the other habitat categories investigated to allow 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 shrimps < 10 cm scale	% Frames with regularly spaced shrimps > 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

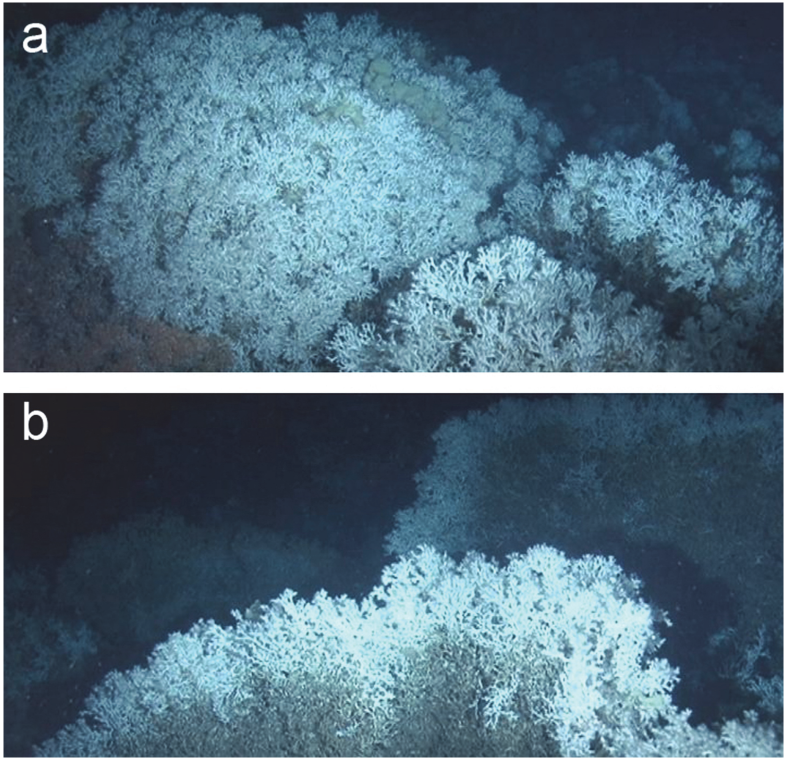


Fig. 1. *Lophelia pertusa* colony at the Røst reef, Norway. **(a)** Typical "cauliflower" growth form at the Røst reef, with live polyps facing into the prevalent current direction. **(b)** The downstream side of the "cauliflower" reef structure. The upper ∼ 25 cm of each "cauliflower" is made up of living *Lophelia pertusa*, the remainder the dead skeletal structure of previous polyp generations. Image courtesy IFM-GEOMAR JAGO team.

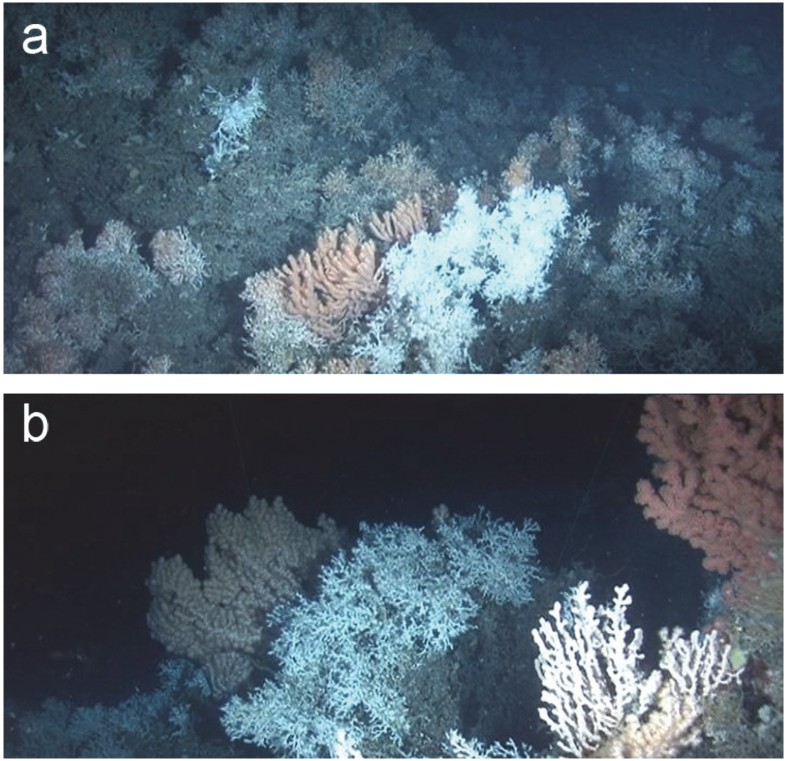


Fig. 2. Typical *Primnoa resedaeformis* and *Paragorgia arborea* colonies at the Røst reef, Norway. **(a)** *P. resedaeformis*, the orange branching gorgonian in the lower centre of the image. Often located in cracks in the *Lophelia pertusa* structure or on the walls of coral blocks. **(b)** Three colonies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

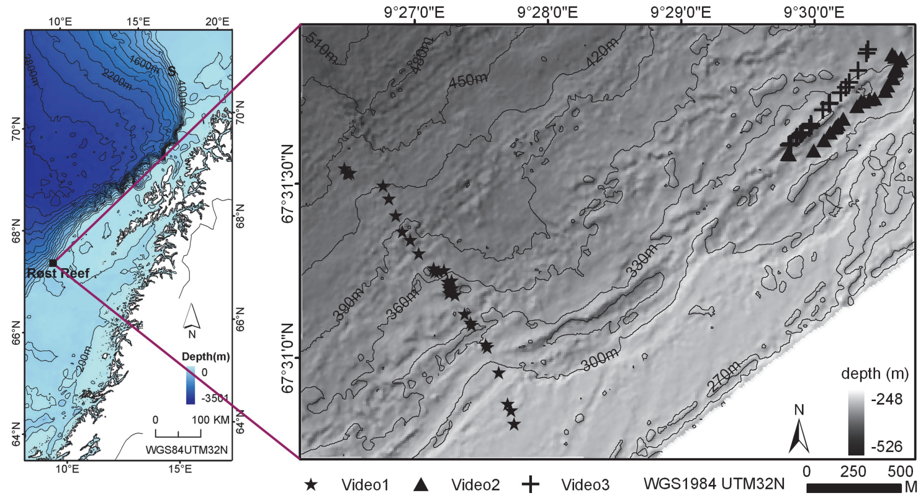


Fig. 3. Bathymetric map showing the location of the Røst reef on the Norwegian margin, and the location of the three video transects analysed in this study.

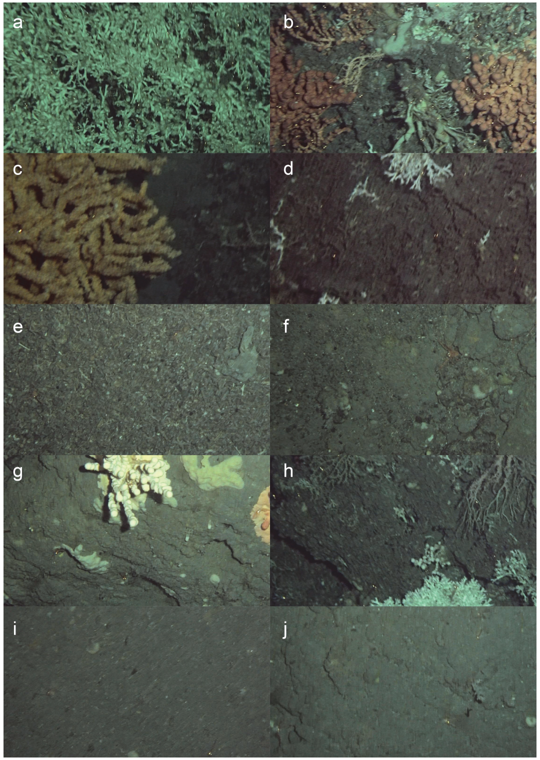
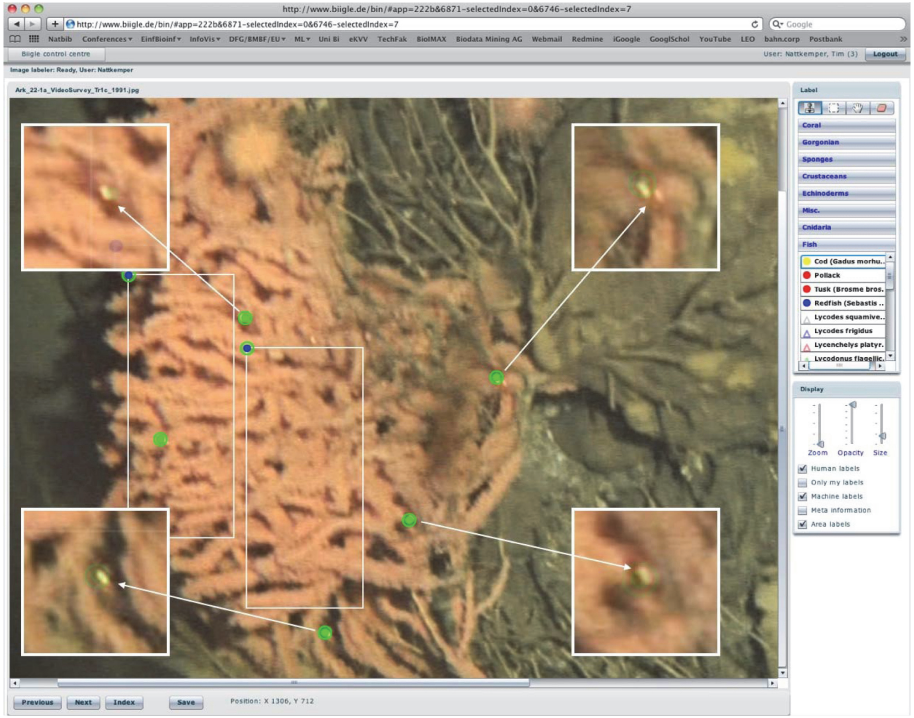


Fig. 4. Habitat categories used in this study. **(a)** Live *Lophelia pertusa*, **(b)** live *Paragorgia arborea* (left and right of image), **(c)** live *Primnoa resedaeformis* (left of image), **(d)** dead scleractinian structure, **(e)** coral rubble, **(f)** gravel/pebbles, **(g)** wall, **(h)** dead gorgonian (right of image), **(i)** soft seabed and **(j)** hardground.



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☑ Human labels
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☑ Machine labels
☐ Meta information
☑ Area labels

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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 *Primnoa resedaeformis* coral, a smaller region of live *Lophelia pertusa* coral and a number of shrimp within and around the coral structures.

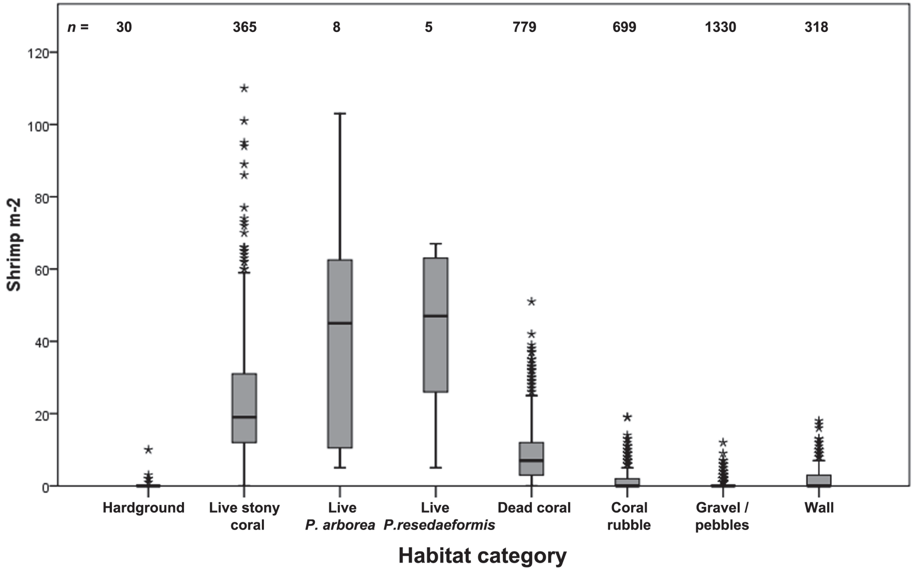

Fig. 6. Boxplot showing observed median shrimp densities, quartiles and outliers observed in association with each of the investigated main habitat categories. No frames contained primarily Dead gorgonian or soft sediment habitats, and these categories are therefore absent from the figure.

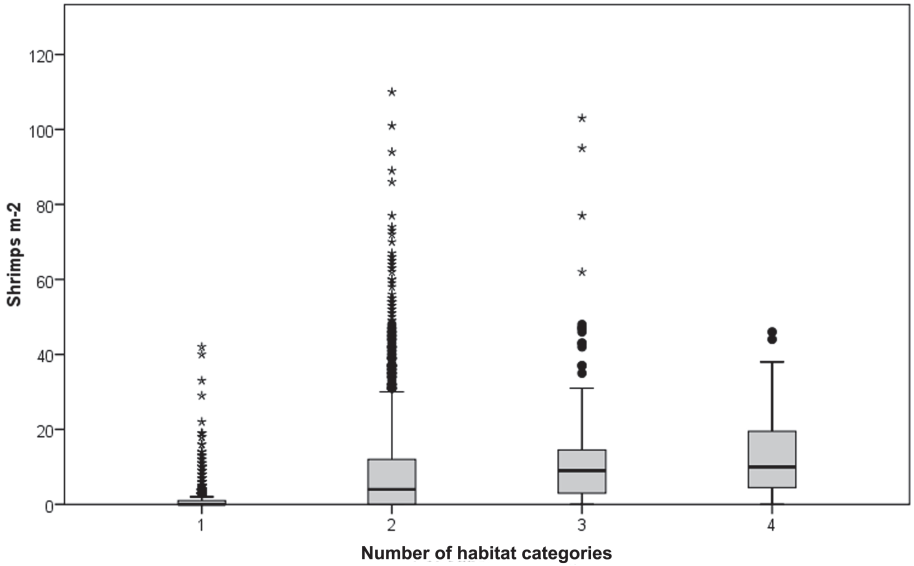

Fig. 7. Boxplot showing shrimp densities observed in image frames with differing numbers of habitat categories present.