

Influence of structurally complex benthic habitats on fish distribution

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ABSTRACT: This study examined the relationship between demersal fish distributions and benthic habitats in the Trænadjupet marine protected area (MPA) on the Norwegian continental shelf. Using a towed video system, multiple pairs of plots with varying densities of cold-water coral mounds and sponges were examined, as well as control plots containing neither of these taxa. A total area of 130 000 m² was surveyed along 16 and 12 linear transects in 2009 and 2010 respectively. The most numerous demersal fish were *Sebastes viviparus* and *Trisopterus esmarkii*, followed by *Brosme brosme*, *Chimaera monstrosa* and *Micromesistius poutassou*. Analyses indicated that *T. esmarkii* and *M. poutassou* exhibited very general patterns of habitat selection whereas *C. monstrosa*, *S. viviparus* and *B. brosme* appeared to be more specialized in their selection of habitat. *C. monstrosa* was abundant in the sponge-beds and unstructured seabed, and appeared only rarely in the coral habitats. The occurrence of cold-water coral mounds and sponges seemed to mainly influence the distribution of *S. viviparus* and *B. brosme*, which were twice as abundant in areas with structurally complex sponge and coral habitats than in the unstructured flat seabed at all spatial scales examined (i.e. <3 m to 2 km). None of the fish species examined in Trænadjupet were confined to only one of the habitats examined, thus the study confirmed facultative use of cold-water corals and sponges as fish habitats on the Norwegian continental shelf.

KEY WORDS: NE Atlantic · Sponge grounds · Cold-water corals · Demersal fish · Habitat association · *Sebastes viviparus* · *Brosme brosme* · *Lophelia pertusa*

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INTRODUCTION

Demersal fish distributions reflect evolved adaptations and ongoing interactions with several biotic and abiotic factors that may vary in time and act at a range of spatial scales. The role of benthic habitat in determining fish distributions has relatively rarely been studied (but see Auster et al. 2003, Uiblein et al. 2003, van der Kooij et al. 2011, D'Onghia et al. 2010, 2012). However, this information is of central interest because it could help facilitate the development of more robust distribution models underlying stock assessments, and the implementation of ecosystem-based approaches in the management of anthropogenic activities (Olsen et al. 2010, Johnson et al.

2013). Of considerable interest in this process is to establish what has been coined 'essential fish habitats', i.e. waters and benthic habitats necessary to fish either for spawning, breeding, feeding or growth to maturity (see Rosenberg et al. 2000) or 'important fish habitats', i.e. habitats that contain significant proportions of a fish population (see Auster 2005). The preferential protection of such habitats may contribute to maintaining the long-term viability and production of fish populations.

The tendency of structurally complex habitats and transitional zones between distinct habitats to attract a higher abundance, biomass and diversity of fauna is well documented in community ecology (Wiens 1976, Pearson & Rosenberg 1978, Macreadie et al. 2010).

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Video surveys from the NW Atlantic and NE Pacific oceans have confirmed that structurally complex benthic habitats (such as boulder fields, coral gardens and sponge fields) often support higher abundances of temperate demersal fish than unstructured, flat seabed (Auster et al. 2003, Laidig et al. 2009, Miller et al. 2012). However, there is variability in the specific responses of different fish species and of different ontogenetic stages to the benthic habitat. In particular, structurally complex benthic habitats seem to be important in determining the local scale distribution of some demersal rockfish and redfish species (Auster et al. 2003, D'Onghia et al. 2010, 2012, Miller et al. 2012) and are used by some species especially during the early stages of the life cycle. Juvenile redfish, *Sebastes* spp., are known to use boulders, cerianthids and sponges for shelter (Auster et al. 2003, Freese & Wing 2003). Baillon et al. (2012) found that larvae of the redfishes *S. fasciatus* and *S. mentella* use sea-pens as habitats. Redfish juveniles and larvae are, however, widespread and are also known from other habitats (Auster et al. 2003, Moser & Boehlert 1991); hence the importance of this relationship for recruitment to the populations of redfish is unknown.

Cold-water coral (CWC) ecosystems built by the scleractinian *Lophelia pertusa* and sponge fields dominated by Geodiidae sponges are widespread on the Norwegian continental shelf and upper slope between 100 and 400 m depth (Fosså et al. 2000, 2002, Mortensen et al. 2001, Klitgaard & Tendal 2004). Together with the rocky outcrops associated with the shelf break and the slopes of banks and troughs, these ecosystems offer a diversity of structurally complex benthic habitats for demersal fish. Little is known about the habitat requirements of the demersal fish inhabiting the Norwegian continental shelf; however, underwater video surveys (Freiwald et al. 2002, Costello et al. 2005) and a semi-quantitative long-line survey (Husebø et al. 2002) have shown that CWC ecosystems tend to support a high diversity and density of demersal fish from the family Gadidae, with *Gadus morhua* (cod), *Pollachius virens* (saithe), *Melanogrammus aeglefinus* (haddock), *Brosme brosme* (tusk), *Molva molva* (ling) and the family Sebastidae, i.e. *Sebastes norvegicus* (golden redfish) and *S. viviparus* (Norway redfish) being among the fish species most commonly observed. In particular, it has been suggested that CWCs are preferred habitats for *Sebastes* spp. and *B. brosme*. Based on observations of gravid females of the redfish *S. norvegicus* and *S. viviparus* around coral mounds, and the assumption that the 3D structure of the coral framework offers protection against preda-

tors, it has been suggested that CWC ecosystems may function as spawning areas for these species (Fosså et al. 2002, Costello et al. 2005). The high abundance of associated invertebrates in CWC ecosystems (Mortensen & Fosså 2006) indicates that they may function as suitable foraging areas for adult *B. brosme* that mainly prey on benthic invertebrates (Husebø et al. 2002, Kutt et al. 2014). The demersal fish most often recorded in CWC habitats are all widely distributed in the NE Atlantic and occur all along the Norwegian shelf, shelf break and fjords north of 62°N. Research performed so far indicates that these species exhibit a facultative use of the CWC habitat (Husebø et al. 2002, Kutt et al. 2014). Fish occurrence in sponge-beds on the NE Atlantic continental shelves has not been thoroughly documented (but see Kutt et al. 2014), therefore the importance of sponge-beds as fish habitat has not yet been assessed.

The objective of this study was to investigate if, and to what extent, demersal fishes aggregate in CWC and sponge habitats. We aimed to supplement earlier observations by providing new and improved scientific data at relevant spatial scales. This was achieved by collecting underwater video data in several replicated areas with structurally complex coral mounds and sponge fields, and in non-complex areas at similar depth and within a limited geographical area (300 km²). Benthic habitats were delineated at 3 different scales (habitat, sub-habitat and microhabitat), and associations were assessed by comparing the use versus availability of benthic habitats at these 3 spatial scales (sensu Hall et al. 1997). If a species was observed more often than could be expected with a random distribution in a specific habitat, then that habitat would be defined as 'preferred'. Coral occurrence was treated as a categorical variable to provide an overall simple presentation of the results and to facilitate comparisons of the results from the Trænadjudupet marine protected area (MPA) with CWC areas containing mounds of dissimilar morphology.

MATERIALS AND METHODS

Study area

Trænadjudupet is a cross-shelf trough cutting 100 km into the continental shelf of Norway south of the Lofoten archipelago (Fig. 1) (Ottesen et al. 2005). In a 300 km² area surrounding a circular depression in the inner part of the trough, 1447 small isolated *Lophelia pertusa* mounds have been mapped using

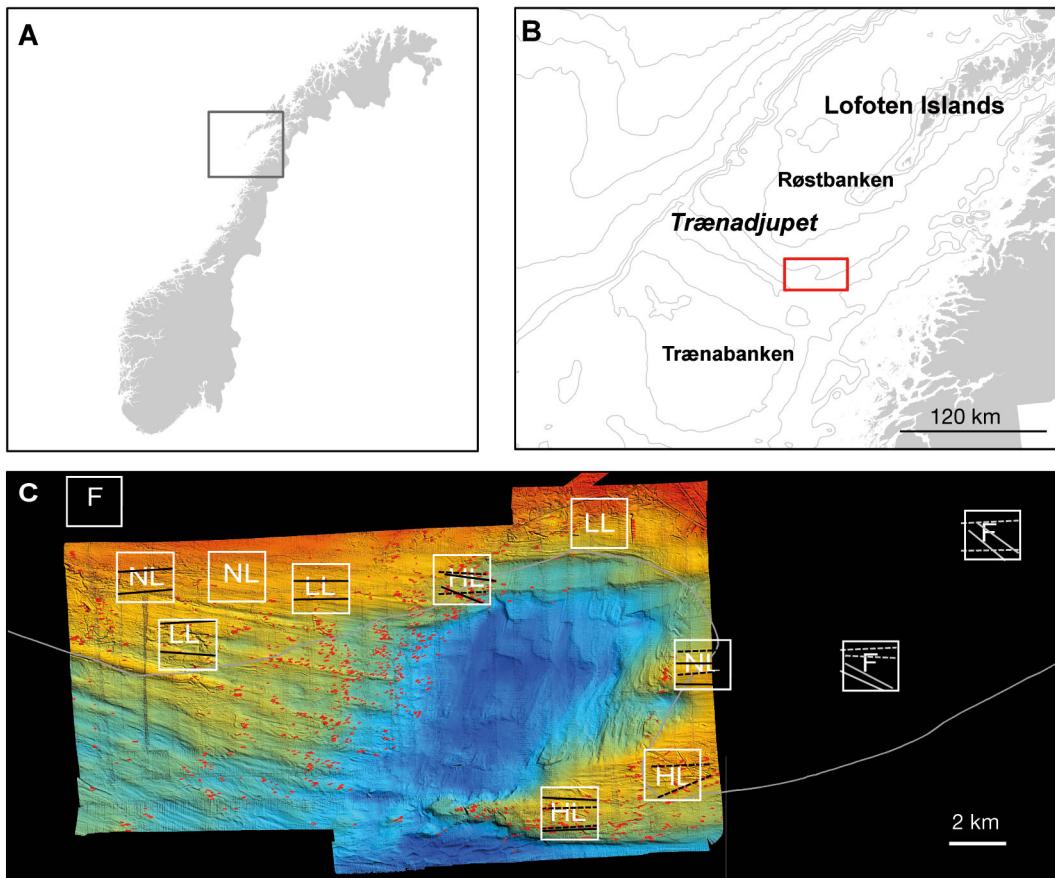


Fig. 1. (A) Study area in (B) the inner part of the cross-shelf trough Trænadjupet coral marine protected area (MPA), northern Norwegian continental shelf. (C) Multi-beam bathymetric map of the MPA showing the individual tailed *Lophelia pertusa* mounds in red (Lindberg 2004, Fosså & Alvsåg 2004) and the areas studied outlined in grey boxes. HL: areas with a high density of coral mounds and sponges; LL: low density of coral mounds and sponges; NL: no coral mounds but with sponges; F: control areas of unstructured flat seabed without large epifauna. Lines within boxes mark the path of the underwater video transects. Solid lines: 2009 transects; dashed lines: 2010 transects; grey line: 300 m depth contour. Note: control areas are outside the MPA borders

underwater video and multi-beam bathymetry (Lindberg 2004). The mounds are 100 to 150 m long and 25 to 55 m wide, with an elevation above the surrounding seabed of up to 12 m (Fig. 2). The mounds are aligned parallel to the main current direction with a head-end containing lobes of live *L. pertusa* colonies facing the current (Fig. 3). In the densest areas, mounds cover up to 10% of the seabed. The study area also contains large sponge-fields of the type recognized as boreal 'ostur' (Klitgaard & Tendal 2004, Kutti et al. 2013, Fig. 4). Hydrographically, the area is dominated by the water masses and flow patterns associated with the Norwegian Coastal Current, which is divided in 2 and directed westwards around Trænabanken and Trænadjupet, often reaching velocities in excess of 30 cm s^{-1} (Sætre & Mork 1981). Bottom trawling has been banned since late 2009 in a $13 \times 23 \text{ km}$ area constituting the Trænadjupet MPA.

Field measurements

On 2 cruises, one occurring from 12 to 20 June 2009 on RV 'H Mosby' and the other from 4 to 16 March 2010 on RV 'GO Sars', underwater videos were recorded to determine habitat associations of demersal fish. Depth ranged between 260 and 320 m. In 2009, 16 transects each of 2 km length were investigated. The transects were equally distributed in 2 plots ($2 \times 2 \text{ km}$) with a high density of coral mounds and sponges (HL), 2 plots with low density of coral mounds and sponges (LL), and 2 plots with no coral mounds but with a high density of sponges (NL) (Fig. 1). Four control transects were positioned on unstructured, sandy seabed (F) (Fig. 1). In 2010, 12 transects of 2 km were investigated with 2 transects in each of 3 plots of HL, 1 plot of NL and 2 plots of F. All transects were run parallel to the

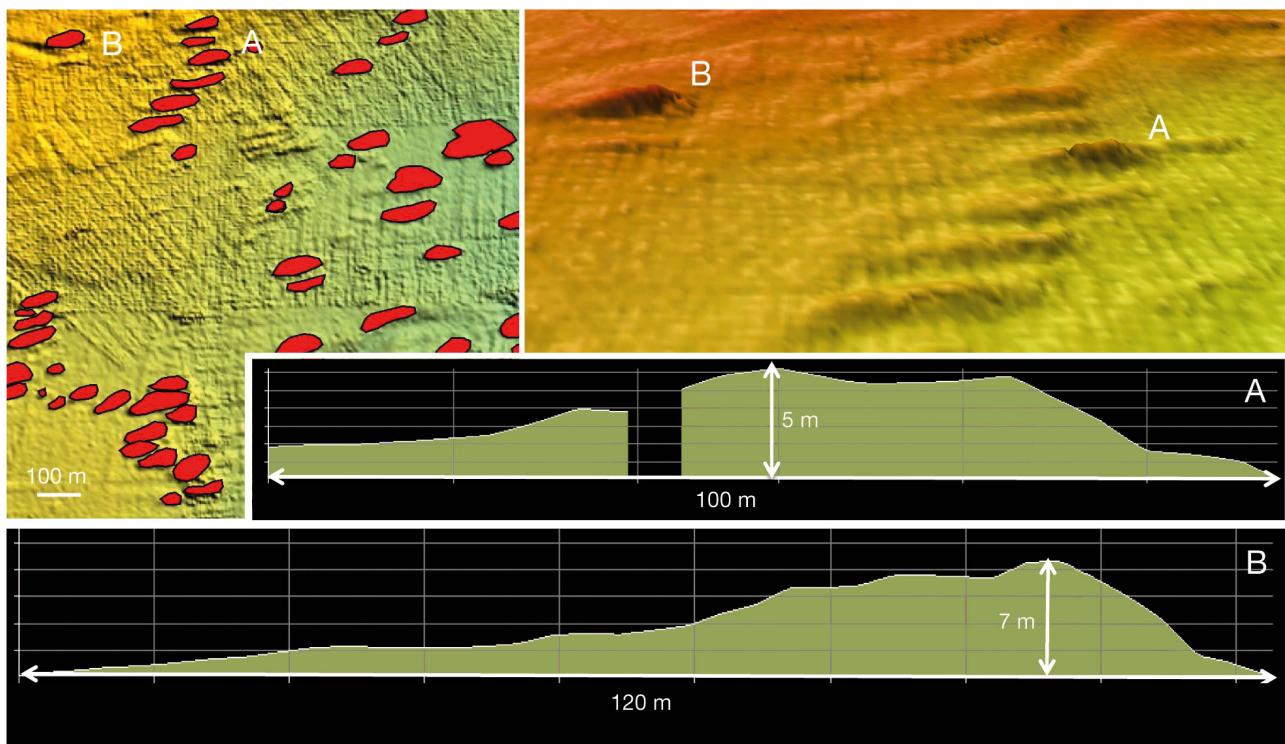


Fig. 2. Multi-beam bathymetric map of the Trænadjudpet *Lophelia pertusa* mounds in the north-westernmost HL (high density coral and sponge) plot (see Fig. 1). The 3D image shows 7 small elongated coral mounds, and the cross-sections show dimensions of 2 of the mounds (A and B). Mound A is 100 m long × 30 m wide × 5 m high (break in profile due to poor echosounder return signal); mound B is 120 × 30 × 7 m

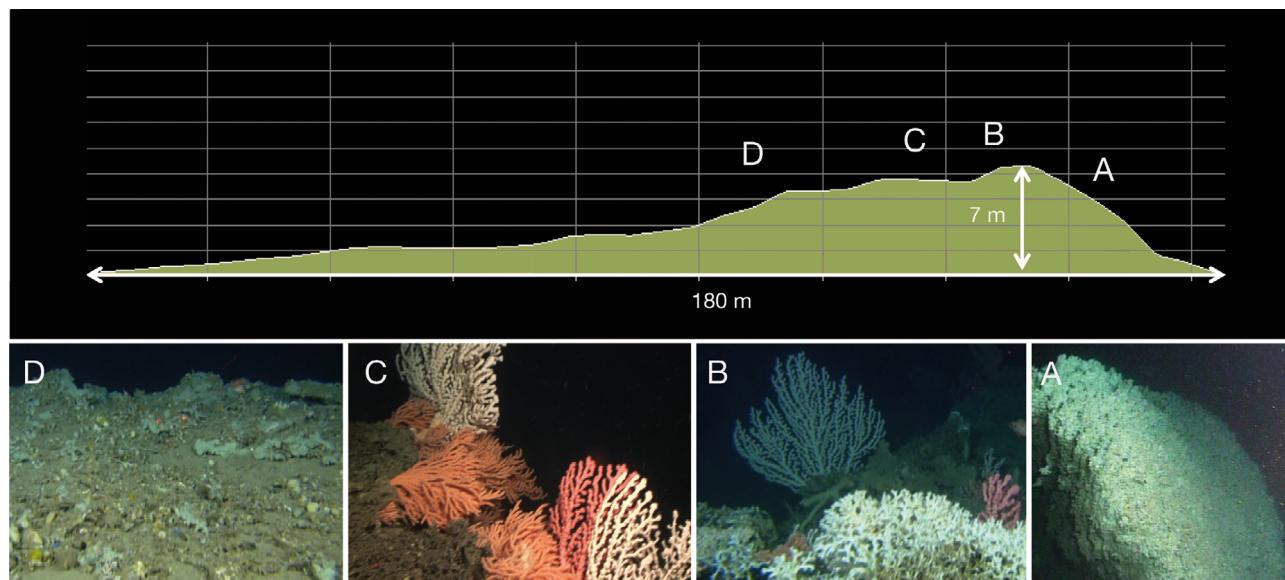


Fig. 3. Cross-section and schematic presentation of the elongated *Lophelia pertusa* cold-water coral mound from Trænadjudpet marine protected area, as identified from multi-beam bathymetry and underwater video. Mounds are partitioned into 4 zones: (A) a head-end with large, consecutive lobes of live *L. pertusa* facing into the dominant current direction, (B) a zone with both live and dead *L. pertusa* with scattered colonies of the gorgonians *Paragorgia arborea* and *Primnoa resedaeformis*, (C) a sediment-clogged dead coral framework, with gorgonians and small sponges and (D) a tail end consisting of coral rubble, sediment and small epifauna (Mortensen & Lepland 2007). Zones (A) and (B) encompass the reef head (RH) sub-habitat, characterized by high substrate complexity (1–5 m); zones (C) and (D) make up the reef tail (RT), with low substrate complexity (0.1–0.5 m)

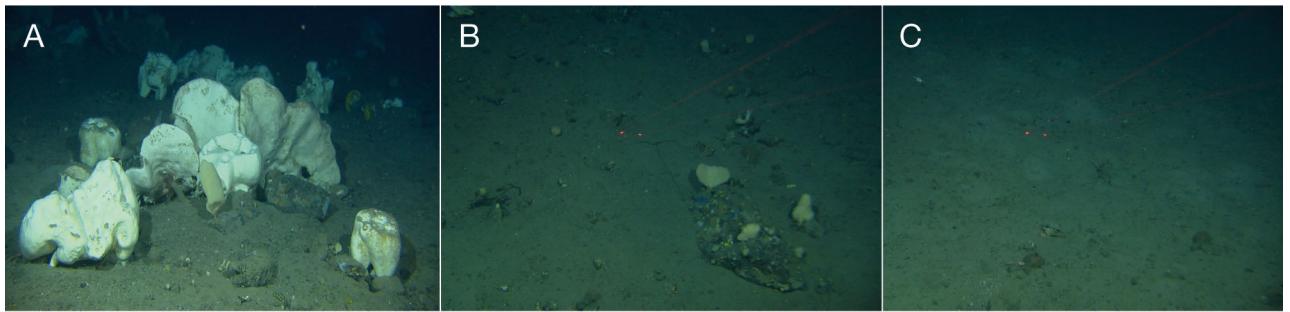


Fig. 4. Sub-habitats present between the elongated *Lophelia pertusa* cold-water coral mounds in Trænadjupet as identified from underwater video. (A) Dense sponge fields (SF) dominated by sponges from the Geodiidea family; (B) sparse sponge communities (SS) typically with *Phakellia* spp. and *Mycalia* spp. growing attached to drop stones and gravel; and (C) unstructured seabed (No) with no large epifauna and no substrate complexity. Laser points are 10 cm apart

predominant current direction, but the start position of the transect within each plot was randomly selected.

The underwater video footage was obtained with a towed video platform (Campod) equipped with high definition (HD) camera, 2 × 400 W HMI lights, depth sensor, altimeter and laser scaling (Bellec et al. 2009, Mortensen et al. 2009). The position of the video was obtained via a transponder accurate to about 2% of the water depth. The platform was towed along pre-defined linear transects at a speed of 0.7 to 1.0 knots, with a winch operator ensuring that the camera was kept 3 m above the seabed. The camera was set in a slightly forward tilted angle to increase the field of view.

Video annotation

Using the software VideoNavigator (©IMR), video footage was classified and recorded in 3 different layers: a biota component, a surface geology component, and a water column component that included the fishes observed. Records were associated with a specific position via the time code. Distance was calculated from the recorded positions. The field of view was estimated from the laser scale and altitude measurements. This information was subsequently used to estimate the area sampled (Bellec et al. 2009, Mortensen et al. 2009).

The biota component included large (>10 cm), 3D structure-forming invertebrates such as sponges and corals. These were identified and counted. The surface geology component recorded the percentage cover of the dominating substrate categories: (1) cobble, (2) pebble, (3) gravel, (4) sand, (5) mud, (6) coral rubble, (7) dead coral framework, (8) live coral

framework and (9) sediment-clogged dead coral framework. Boulders were registered individually and not as a percentage cover. Slope inclination and substrate complexity were continuously classified as (1) flat (0 to 5°), (2) sloping (5 to 30°), (3) steeply sloping (30 to 45°), (4) vertical (45 to 90°) and (5) overhanging (>90°) for slope inclination, with the categories (1) none (0 m), (2) low (0 to 2 m), (3) medium (2 to 5 m) and (4) high (>5 m) for substrate complexity.

All fish were identified to species level and counted. The behavior of the fish was classified as (1) no locomotion, (2) hovering/station-holding, (3) slow forward movement, (4) medium speed swimming and (5) fast swimming (modified from Auster et al. 1995, Costello et al. 2005). Co-occurrence between fish and a particular microhabitat was recorded if an object was in the same video frame as the fish. The distance of the fish to the nearest object (such as corals, sponges or boulders) was recorded using total body lengths of the fish as length scale. Distance to bottom for each fish was recorded as (1) fish touching the bottom, (2) fish less than 1 body length from the bottom and (3) fish more than 1 body length from the bottom.

Assessment of spatial variation in fish abundance

Benthic habitats were delineated using 3 spatial scales, termed habitat (2 km), sub-habitat (5 to 100 m) and microhabitat (<3 m); fish-habitat relationships were then assessed at these scales. In the analyses, only non-schooling fishes were included because schooling fish (i.e. *Pollachius virens*) often aggregated around the video platform preventing accurate estimation of undisturbed density.

Habitat

To determine large-scale habitat associations, all fish were identified and counted along each 2 km transect, and the density of each species within each plot was computed. The exact number of individual coral mounds within each plot was derived from the multi-beam bathymetric maps. The HL plots each contained 63 to 47 individual coral mounds, while the LL plots each contained 20 to 12 individual coral mounds. The abundance of sponges at the plot level was not known for all plots, and therefore associations between fish distribution and sponge density was not assessed this level. Large-sized demosponges were, however, present in all HL, LL and NL plots but were absent from the F plots. In 2009, differences in fish abundance between 8 plots distributed among the 4 different habitat types (i.e. HL, LL, NL and F), were assessed using a 2-way ANOVA. In 2010, differences in fish abundance between 6 plots distributed among 2 habitat types (i.e. HL and F or NL) were assessed. Means for significant factors in the ANOVA were compared using Tukey's HSD test. To ensure that the data met the assumptions of the statistical analyses, the data were checked for homogeneity of variance (using Levene's test) and normality (using Q-Q plots of residuals) prior to analyses. Statistical analyses were carried out using the program R (version 2.15.3, stats-package).

Sub-habitat

Areas of the seabed along the transects were classified *a posteriori* into 5 sub-habitats: reef head (RH), reef tail (RT) (Fig. 3), dense sponge fields (SF), sparse sponge fields (SS) and unstructured flat seabed (No) (Fig. 4), using a combination of surface geology components, records of substrate complexity and slope and the occurrence of large structure-forming macrofauna. The RH sub-habitat consisted of the highly complex front or head of the reef containing live and dead *Lophelia* colonies, while the RT sub-habitat consisted of the lower relief, sediment-clogged dead *Lophelia* framework and coral rubble tail. Two different sponge sub-habitats were discerned: SF, with high abundances of Geodiidae sponges and a substrate complexity of 0.5 to 1 m, and SS, composed of smaller sponges, in particular fan shaped sponges growing on boulders, with a lower substrate complexity. The No sub-habitat consisted of unstructured, flat areas of the seabed. Sub-habitat patches <5 m in length were not recorded.

Densities of fish were estimated by dividing the total number of specimens observed by the area of the associated sub-habitat for each transect. For frequent species such as *Sebastes viviparus* and the gadoid *Trisopterus esmarkii* (Norway pout), the difference between observed and expected fish occurrence was used to assess associations between the fish and all 5 sub-habitats (chi-squared test). The number of fish encounters of the gadoids *Brosme brosme* and *Micromesistius poutassou* (blue whiting) and the chimaerid *Chimaera monstrosa* (rabbit fish) was low ($N = 38$ to 50), and so relationships between fish occurrence and particular sub-habitat features were assessed by comparing the difference between observed and expected fish occurrences in only 3 sub-habitats (chi-squared test): RH and RT were merged into a single coral mound sub-habitat, SF and SS communities were merged into a single sponge sub-habitat, and No remained as the third sub-habitat. A random distribution of species was assumed for all tests. Statistical analyses were carried out using the program R (version 2.15.3, stats-package).

Micro-habitat and vertical migrations

Fish distribution around microhabitat features was assessed by examining differences in the recorded distance between individual fish and the nearest object (such as corals, sponges or boulders). A preference of the fish for specific objects and the behavior of the fish (activity and proximity to the seabed) was also examined. For vertical migrations, diurnal differences in the abundance of the 5 species near the bottom were assessed using a Wilcoxon rank sum test.

RESULTS

Species abundances

A total area of ~130 000 m² was surveyed along 16 and 12 linear transects in 2009 and 2010 respectively (Table 1). The most numerous species observed in 2009 were *Sebastes viviparus* and *Trisopterus esmarkii*, with 617 and 699 encounters respectively, followed by the much less abundant *Brosme brosme*, *Chimaera monstrosa* and *Micromesistius poutassou* with less than 50 records each. In 2010, the most numerous species were *S. viviparus* and *T. esmarkii* with 367 and 336 encounters respectively, followed again by *B. brosme*, *C. monstrosa* and *M. poutassou*.

Table 1. Sampling effort expressed as the area surveyed and the relative frequency of occurrence of each sub-habitat type in 2009 and 2010. RH: reef head; RT: reef tail; SF: dense sponge field; SS: sparse sponge field; No: unstructured flat seabed

Sub-habitat	2009		2010	
	Area (m ²)	Percent	Area (m ²)	Percent
RH	400	0.5	1800	4
RT	5700	7	3900	8
SF	23 500	29.5	7900	16
SS	30 800	39	28 100	58
No	18 900	24	6800	14
Total area	79 300	100	48 500	100

with about 50 records each. Unidentifiable juvenile fish were observed 214 times. *Pollachius virens* was observed frequently in both 2009 and 2010 but could not be accurately enumerated due to its tendency to aggregate around the video platform. In both years, *Lophius piscatorius* (angler) from the family Lophiidae, *Sebastes norvegicus* and *Lycodes* spp. (eel-pout) from the family Zoarcidae were encountered in very low numbers (1 to 3 specimens). In total, 8 adult specimens could not be identified. The density of *S. viviparus*, *T. esmarkii*, *B. brosme* and *M. poutassou* in the study area was similar in June 2009 and March 2010, while the density of *C. monstrosa* was slightly higher in 2010 compared to 2009 (*t*-test, $p < 0.05$) (Table 2).

Habitat use

Habitat scale (2 km)

In 2009, the point estimates of *S. viviparus* and *B. brosme* were higher in structurally complex than in non-complex habitats (Table 2), however, variability was high and the density differences between habi-

tats were not statistically significant. The density of *Trisopterus minutus*, *C. monstrosa* and *M. poutassou* did not seem to be related to the structural complexity of the seabed. However, the density of *T. minutus* differed significantly between the NL and LL habitats (Tukey's HSD post hoc test, $p = 0.033$). For this species, there was also a significant difference in density between the examined plots ($F = 27.23$, $p = 0.0001$).

In 2010, significant differences in fish densities were observed between the 2 habitat types examined for the 4 species. The densities of *S. viviparus* and *B. brosme* were 2 times higher in the HL habitats compared to NL or F habitats (ANOVA, $F = 14.63$, $p = 0.009$ and $F = 6.32$, $p = 0.046$ respectively) (Table 2). The opposite pattern was observed for *C. monstrosa* and *Trisopterus esmarkii*, which were twice as abundant in NL and F habitats compared to HL habitats ($F = 50.07$, $p = 0.040$ and $F = 9.97$, $p = 0.019$ respectively). However, for these species there was also a significant plot effect ($F = 21.77$, $p = 0.001$ and $F = 19.38$, $p = 0.001$ respectively), indicating that other, unknown factors may be equally important in regulating their distribution. *M. poutassou* density did not differ between the coral and the non-coral habitats but varied significantly between plots ($F = 8.6$, $p = 0.011$). No significant differences in density between habitats were observed for juvenile fish present in the study area.

Sub-habitat scale (5 to 100 m)

All transects crossed several sub-habitats but sampling effort was not uniformly distributed across the sub-habitats (Table 1). In both years, a higher density of *S. viviparus* was found in sub-habitats with medium to high substrate complexity, i.e. RH and SF, compared with sub-habitats with low or no substrate complexity (chi-squared test, $p < 0.001$; Table 3,

Table 2. Standardized average abundance of fish (ind. 10 m⁻² ± SE) observed in high (HL), low (LL), no coral (NL) and unstructured sandy seabed (F) habitats in Trænadjupet coral marine protected area, June 2009 and March 2010 (NL and F data were pooled in 2010 due to low sample sizes)

Species	2009				2010	
	HL	LL	NL	F	HL	NL + F
<i>Sebastes viviparus</i>	0.144 ± 0.045	0.146 ± 0.036	0.123 ± 0.061	0.087 ± 0.035	0.144 ± 0.026	0.069 ± 0.018
<i>Trisopterus minutus</i>	0.200 ± 0.030	0.163 ± 0.026	0.228 ± 0.044	0.191 ± 0.061	0.191 ± 0.068	0.378 ± 0.157
<i>Brosme brosme</i>	0.006 ± 0.002	0.003 ± 0.0005	0.002 ± 0.001	0.003 ± 0.0009	0.008 ± 0.002	0.003 ± 0.0011
<i>Chimaera monstrosa</i>	0.004 ± 0.001	0	0.003 ± 0.001	0.003 ± 0.001	0.003 ± 0.0007	0.007 ± 0.0016
<i>Micromesistius poutassou</i>	0.006 ± 0.002	0.002 ± 0.001	0.009 ± 0.008	0.006 ± 0.002	0.003 ± 0.0008	0.004 ± 0.0023
Fry	—	—	—	—	0.049 ± 0.0287	0.001 ± 0.0009

Fig. 5). The pooled data showed that the frequency of occurrence of *B. bromse* in sub-habitats with high and medium substrate complexity (i.e. coral mounds and sponge-beds) was significantly higher than occurrences of the same species on unstructured seabed for both years (Table 4). The occurrence of *C. monstrosa* was clearly associated with specific habitats (chi-squared test, $p < 0.001$). No specimens were observed in the coral sub-habitat on either of the sampling occasions (i.e. 2009 and 2010); it was only observed in sponge sub-habitats and the unstructured seabed.

T. esmarkii was randomly distributed in 2009 but occurred more frequently in the unstructured sub-habitat than in sub-habitats with high and medium substrate complexity (i.e. coral mound and sponge-beds) in 2010 (chi-squared test, $p < 0.001$; Table 3, Fig. 5). The frequency of occurrence of *M. poutassou* was associated with the sponge and unstructured sub-habitats both years (chi-squared test, $p < 0.02$, Table 4, Fig. 5). The juvenile fish that were present in the study area only in March 2010 occurred with equal abundance in all sub-habitats.

Microhabitat scale (<3 m)

Individuals of *S. viviparus* were always observed hovering or with a slow forward movement. They were often positioned very close to the seabed, but less so in the RH sub-habitat (where they were often found hovering above or in front of the reef head) than in the other sub-habitats examined. Overall, 84% of the individuals observed were associated with 3D structures, with sponges having the largest incidence of associated individuals (48%), followed by corals (30%).

Fig. 5. Standardized abundance ($\text{ind. } 10 \text{ m}^{-2}$) of *Sebastes viviparus*, *Trisopterus esmarkii*, *Brosme brosme*, *Chimaera monstrosa* and *Micromesistius poutassou* observed in the 5 sub-habitats (see Table 3 for abbreviations) examined in the Trænadjupet in 2009 and 2010 respectively.

Whiskers are standard error

Table 3. Percent difference between observed and expected occurrences of *Sebastes viviparus* and *Trisopterus esmarkii* in the 5 sub-habitats (RH: reef head; RT: reef tail; SF: dense sponge field; SS: sparse sponge field; No: unstructured sandy seabed) identified in Trænadjupet evaluated using a chi-squared test. Expected values are based on the sampled area of each sub-habitat and assume a random distribution of fish. Differences are significant at $p < 0.05$

Species	Year	RH	RT	SF	SS	No	χ^2	p
<i>Sebastes viviparus</i>	2009	2	7	5	-4	-9	14.7	0.005
	2010	11	-2	12	-17	-4	45.9	<0.001
<i>Trisopterus esmarkii</i>	2009	-1	-3	0	2	2	2.4	ns
	2010	-3	-2	-12	0	18	34.5	<0.001

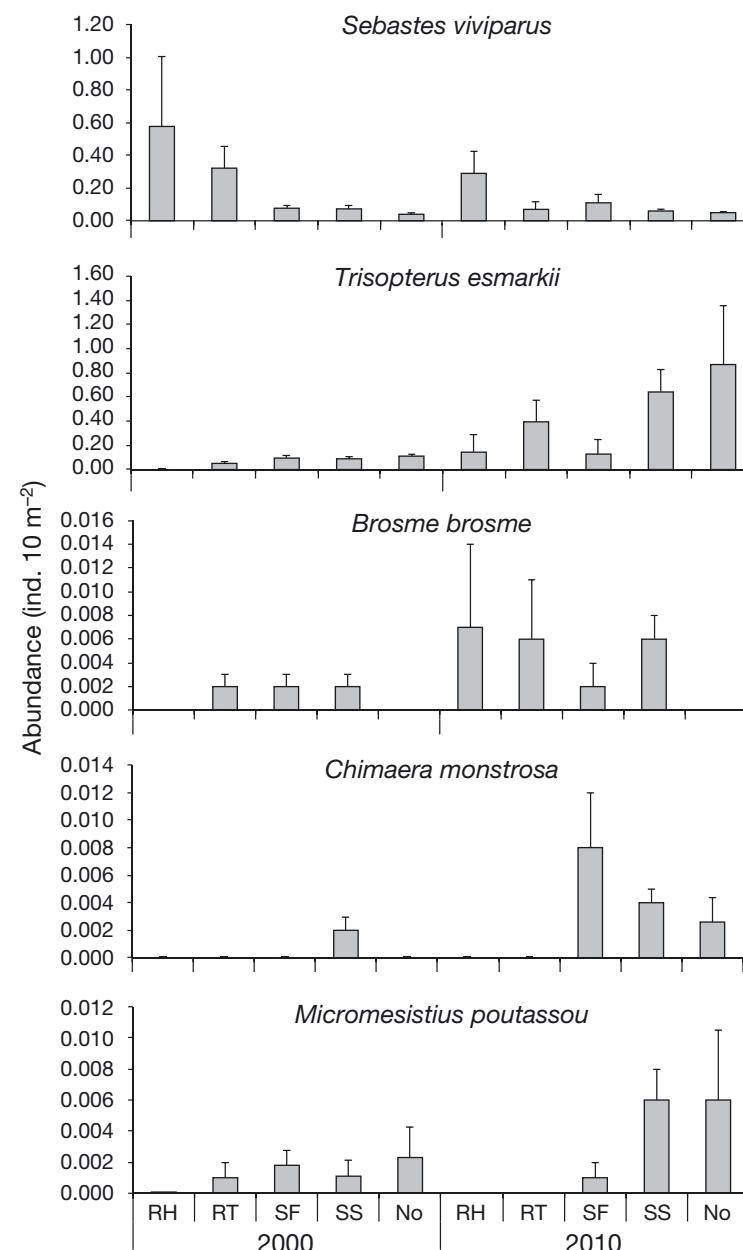


Table 4. Percent difference between observed and expected occurrences of *Brosme brosme*, *Chimaera monstrosa* and *Micromesistius poutassou* in 3 pooled sub-habitats of Trænadjupet evaluated using a chi-squared test. Expected values are based on the sampled area of each sub-habitat and assume a random distribution of fish. Differences are significant at $p < 0.05$

Species	Year	Coral	Sponge	Unstructured	χ^2	p
<i>Brosme brosme</i>	2009	3	15	-17	16.3	<0.001
	2010	2	12	-14	16.3	<0.001
<i>Chimaera monstrosa</i>	2009	-9	32	-23	47.1	<0.001
	2010	-12	9	3	13.7	<0.001
<i>Micromesistius poutassou</i>	2009	-3	14	10	8.1	0.017
	2010	-12	8	4	14.0	<0.001

Fewer individuals were associated with 3D structures in sub-habitats with low or no substrate complexity than in sub-habitats with high or medium substrate complexity (Table 5). The distance between the 3D structures and the fish was generally quite large (average 2.8 body lengths across all sub-habitats), and larger in the RH than in the other sub-habitats (Table 5).

Individuals of *B. brosme* were all observed either station-holding or moving slowly along the seabed, either touching the bottom or positioned <1 body length above the seabed. Overall, 90% of the observed *B. brosme* specimens were associated with a particular microhabitat, with boulders having the largest incidence of associated individuals (50%) followed by massive sponges (24%) and stones with fan shaped *Phakellia* sp. or *Mycale* sp. sponges (15%). Individuals not associated with any microhabitat were found only in the SS sub-habitat. Distance to the nearest 3D structure was similar in all sub-habitats with an overall mean distance of 0.6 fish body length.

C. monstrosa was always observed swimming at slow or medium speeds, with most individuals observed <1 body length above the seabed. Overall, 76% of the observed *C. monstrosa* were associated with a particular microhabitat, with boulders with

sponges having the largest occurrence of associated individuals (41%), followed by boulders (32%) and massive sponges (27%). Microhabitat associations did not appear to be directly dependent on the availability of a 3D object, as more individuals were found in proximity to a 3D structure in the No sub-habitat than in the SS community (Table 5). The mean distance to the nearest 3D object was 2.0 body lengths.

T. esmarkii was always observed station-holding or with a slow forward movement, positioned equally often <1 body length off the seabed as >1 body

length above. Overall, 36% of the individuals observed were associated with 3D objects, with boulders and sponges having the largest numbers of associated individuals (45 and 44% respectively). The mean distance between 3D structure-forming objects and fish was 4.7 body lengths (Table 5).

M. poutassou was mostly observed with a slow forward movement, positioned <1 body length off the seabed. Overall, 60% of the individuals observed were associated with objects at the seabed, with the proportion of associated individuals being higher in sub-habitats with more 3D structures available (Table 5). The distance between objects and fish was 2.3 body lengths and was similar in all sub-habitats examined.

Diurnal vertical migrations

At the latitude investigated here, there is a major seasonality in day length. In June 2009, in 24 h of daylight, there was little or no variation in the number of *T. esmarkii* observed during the course of the day (Fig. 6). However, in March 2010 (sunrise at 06:00 h and sunset at 17:00 h), clear indications of a diurnal vertical movement of individuals were seen,

Table 5. Micro-habitat associations of fish in the 5 different sub-habitats examined. RH: reef head; RT: reef tail; SF: sponge field; SS: sparse sponges; No: unstructured seabed; TL: total length

	Percentage of individuals associated with 3D features					Distance to microhabitat (in fish TL)				
	RH	RT	SF	SS	No	RH	RT	SF	SS	No
<i>Sebastes viviparus</i>	100	47	98	76	16	6.1	2.0	2.0	2.0	2.0
<i>Trisopterus esmarkii</i>	100	50	31	43	22	6.0	3.5	5.6	4.1	3.5
<i>Brosme brosme</i>	100	100	100	84	0	0	0.4	0.5	0.7	-
<i>Chimaera monstrosa</i>	-	-	83	34	66	-	-	2.9	1.9	0.6
<i>Micromesistius poutassou</i>	-	100	63	65	33 ^a	-	1	3.8	2.3	1 ^a

^aOnly 2 individuals

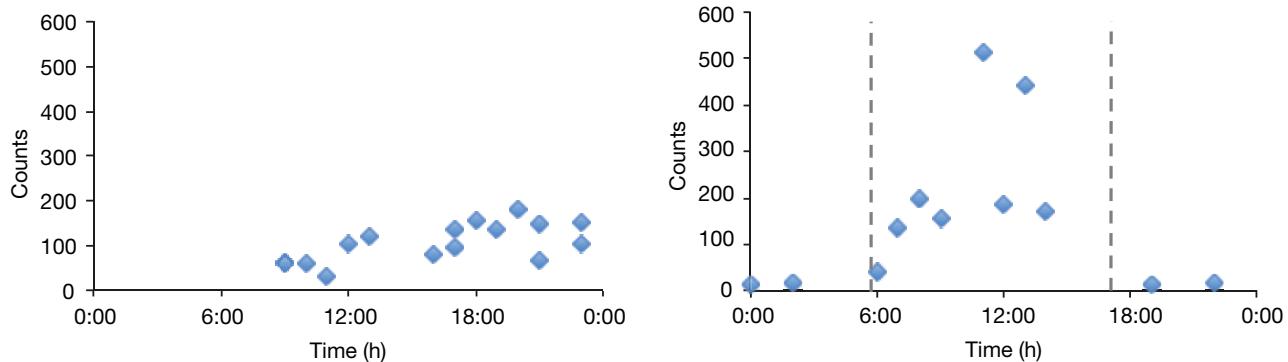


Fig. 6. Counts of *Trisopterus esmarkii* along a 2 km video transect in relation to the time of day: 2009 (left) and 2010 (right). Dashed lines in the 2010 diagram: dawn and dusk

with significantly more specimens occurring in the near-bottom layer in daytime transects compared to nighttime transects (Wilcoxon rank sum test, $W = 35$, $p = 0.0025$). There were no differences in the abundance of *S. viviparus*, *B. bromse*, *C. monstrosa* or *M. potassou* between daytime and nighttime transects, either in 2009 or 2010.

DISCUSSION

General fish distribution patterns

The local-scale habitat selection analyses showed that 2 of the 5 most common species in the Trænadjupet coral MPA, i.e. *Trisopterus esmarkii* and *Micromesistius poutassou*, displayed very general patterns of benthic habitat selection, whereas 3 other species (*Sebastes viviparus*, *Bromsme bromse* and *Chimaera monstrosa*) appeared to be more specialized residents of particular benthic habitats. All 5 species, however, utilized multiple habitats (see *in situ* photographs in Fig. 7), and the general conclusion from this comparatively extensive 2 yr study is that the dominant demersal fish of the northern Norwegian shelf are on the generalist side of a specialist-generalist gradient. As observed in other subareas of the NE Atlantic, these fish are facultative users of the sponge and CWC habitats (Husebø et al. 2002, Costello et al. 2005, Söfker et al. 2011, Biber et al. 2014). This contrasts with results from the continental margin of the southeastern USA, where the existence of obligate relationships between some demersal fish species and CWC habitats have been proposed based on assessments on a similar local spatial scale as that applied in this study (Ross & Quattrini 2007). The overall abundance of the species in the Trænadjupet MPA was similar during both sampling periods, suggesting limited seasonal variation as also found by

van der Kooij et al. (2011) in a similar shelf environment of the NE Atlantic. The exception was *C. monstrosa*, which was twice as abundant in March 2010 as in June 2009, possibly reflecting migration from deeper (>400 m) to shallow areas in spring and summer to deposit egg capsules (Pethon 1998).

Habitat preference

The occurrence of CWC mounds and sponges seemed to influence the large (2 km), small (5 to 100 m) and micro-scale (<3 m) distributions of *S. viviparus* and *B. bromse*, which were twice as abundant in areas with structurally complex sponge-fields and CWC habitats as in habitats with unstructured, flat seabed. The disproportional use of these benthic habitats compared to their availability clearly indicated that for these 2 common demersal fish species, CWC mounds and sponge-fields are preferred habitats (sensu Hall et al. 1997). The preference of *S. viviparus* for inhabiting sponge and coral habitats concurs with findings from the continental shelf seas of the NW Atlantic and NE Pacific oceans, in that demersal redfish and rockfish species often preferably inhabit structurally complex habitats (Auster et al. 2003, Laidig et al. 2009, Miller et al. 2012). Recent *in situ* video surveys from the southern Icelandic shelf have also confirmed this tendency for 2 of the redfish species common in the NE Atlantic (i.e. *S. norvegicus* and *S. viviparus*). They occur more abundantly in the complex structure of boulder fields, CWC mounds and lava fields compared to the unstructured flat seabed of the surrounding shelf (Grabowski et al. 2012, Ragnarsson & Burgos 2012). *Sebastes* spp. have been reported resting by erect sponges (Freese & Wing 2003), however, this is the first study quantifying this association. The observation that *B. bromse* occurs in higher abundances in

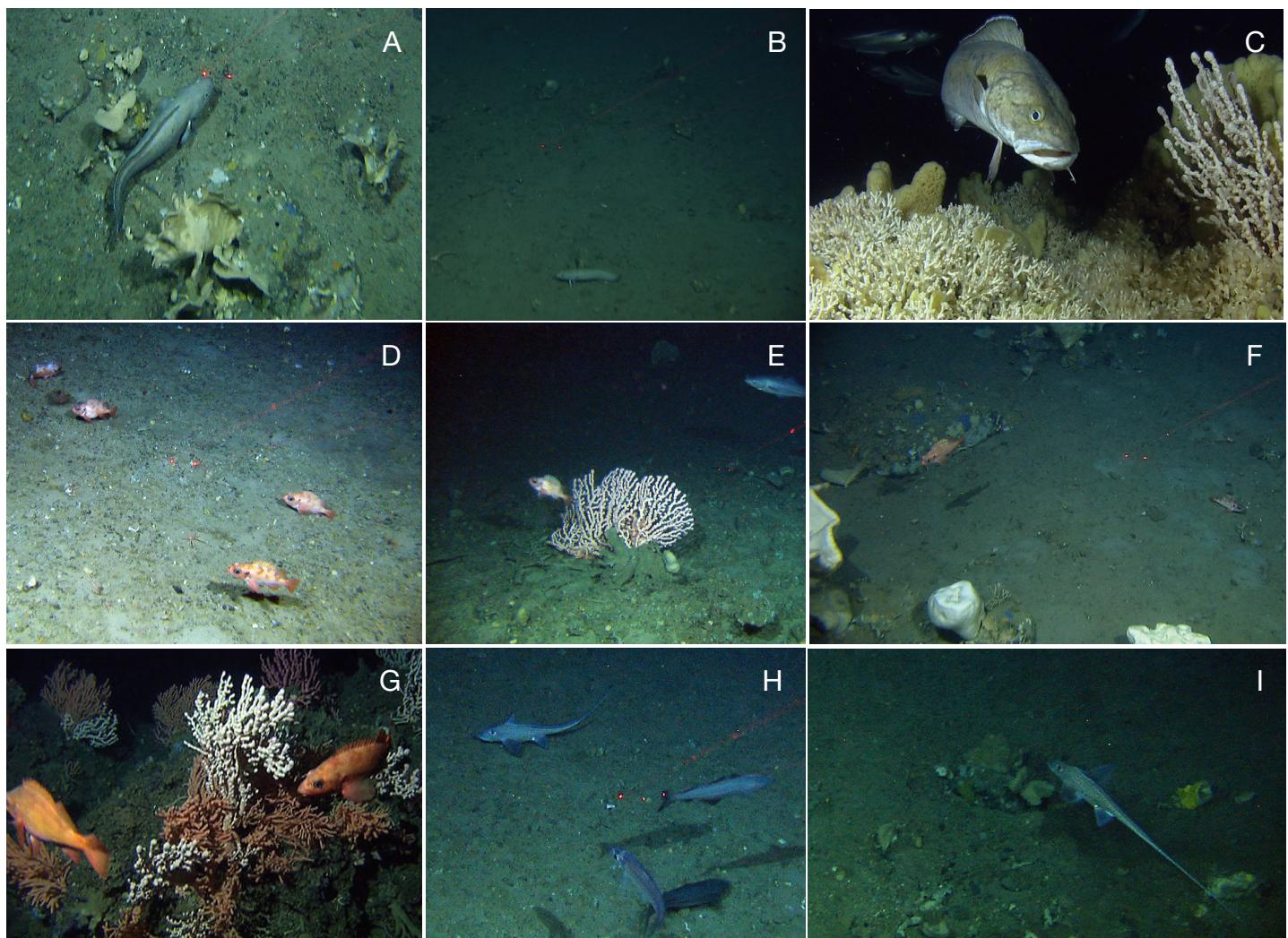


Fig. 7. Example *in situ* photographs of dominant demersal fish species in the cold-water coral, sponge and unstructured benthic habitats of the Trænadjudpet marine protected area (MPA). (A) *Brosme brosme* among sponges, (B) *B. brosme* on unstructured flat seabed, (C) *B. brosme* in the head of the coral mound, (D) *Sebastes viviparus* on unstructured flat seabed, (E) *S. viviparus* next to a gorgonian coral on the tail of the coral mound, (F) *S. viviparus* in the sponge fields, (G) *S. viviparus* among gorgonian corals in the head of the coral mound, (H) *Chimaera monstrosa* on unstructured flat seabed, (I) *C. monstrosa* in a sponge field. Distance between laser points = 10 cm

structurally complex habitats than in unstructured flat seabed is in line with observations from boulder fields and CWC mounds on the Icelandic shelf (Ragnarsson & Burgos 2012), CWC habitats on the mid Norwegian shelf (Husebø et al. 2002), deep CWC habitats off Ireland (Biber et al. 2014) and with observations from the NW Atlantic where *B. brosme* have been reported to preferentially inhabit octocoral gardens, deep boulder reefs and other hard, rough and rocky substrates while being rare on unstructured sandy seabed (COSEWIC 2003, Auster 2005, Auster & Lindholm 2005). For *Sebastes* spp. (probably primarily *S. viviparus*) and *B. brosme*, the framework of the CWCs, sponges and boulders appears to repre-

sent ecologically equivalent habitats (Auster 2005). It is probable that structurally complex seabed habitats support substantial proportions of the adult populations of these species and that the local scale abundance (i.e. from 1 m to 2 km) is closely linked to the accessibility of such habitats. On the Norwegian shelf, structured habitats such as CWC ecosystems (Fosså et al. 2000, 2002, Mortensen et al. 2001), sponge-fields (Klitgaard & Tendal 2004), boulder fields, drumlins, moraine ridges and other rocky outcrops often associated with the shelf break and the slopes of banks and troughs (Lindberg 2004, Ottesen et al. 2005) are common and patchily distributed on the shelf.

Habitat quality

There are several reasons why fish might be associated with a particular habitat that might differ between areas and season depending on, for example, predator and food availability. *B. brosme* is a widely distributed top predator that feeds mainly on benthic macrofauna and demersal fish (Bergstad 1991, Husebø et al. 2002, Kutti et al. 2014). The species probably inhabits CWC mounds and sponge-field habitats because they are favorable feeding areas with an elevated density of its main prey items, such as squat lobster *Munida sarsi*, shown previously to be common in coral rubble (Mortensen et al. 1995), and a generally high diversity of associated infauna prey among the coral mounds (Mortensen & Fosså 2006, Roberts et al. 2006) and sponges (Klitgaard 1995). Adult *S. viviparus* feed mainly on small crustaceans and fish (Hureau & Litvinenko 1986) and may benefit from the dense aggregations of amphipods, euphausiids and shrimps that are frequently observed on the underwater video around CWC mounds (Costello et al. 2005, Ross & Quattrini 2007, Purser et al. 2013, <https://love.statotil.com>). In areas with rapidly changing bottom topography (such as Trænadjupet), cross-shelf currents will generate horizontal divergence and increased particle availability in the benthic boundary layer for the suspension feeding fauna by accelerating bottom current speed (Thiem et al. 2006). Hydrodynamics can also be important in regulating the distribution of zooplankton prey and thereby indirectly, the distribution of planktivorous fish (Slagstad & Tande 1996, Samuelsen et al. 2009). It is therefore possible that the positive relationship observed between demersal fish abundance and the structurally complex benthic habitats in this study may be partly coincidental rather than functional. The fact that fewer individuals of *B. brosme* and *S. viviparus* were associated with 3D structures in the SS compared to the SF habitats supports this view.

In both sampling seasons, the rabbit fish *C. monstrosa* occurred in high numbers in the structurally complex sponge-fields and on the unstructured seabed but never on the CWC mounds. Thus for this species, small-scale (10 to 100 m) habitat selection appeared more specialized, and CWCs and sponges did not seem to represent ecologically equivalent habitats. These results were surprising since in a parallel baited long-line study of the fish community in the Trænadjupet, the catch rates of *C. monstrosa* could be closely linked to the local scale (i.e. 1 to 2 km) occurrence of CWC mounds but appeared un-

related to sponge density (Kutti et al. 2014). Bait attraction into habitats not normally used may have influenced the long-line distribution outcome, however, the mismatch between the results of these 2 studies could also be explained if *C. monstrosa* is associated with the heterogeneous mixed habitat formed by the patchily distributed CWC mounds (Lindberg 2004) and the intervening sponge-fields (Kutti et al. 2013) rather than the actual mounds or the sponge-beds as such. Habitat edges are known to attract higher abundances of certain marine fish species (Smith et al. 2008, Macreadie et al. 2010, Grabowski et al. 2012), which may be related to a greater food availability at patch edges (e.g. Macreadie et al. 2010). High abundances of *C. monstrosa* have previously been documented on the Spanish continental shelf in the heterogeneous seascape of the shelf break, where rocky outcrops co-occur with patchily distributed sponge and non-framework building coral fauna (Sánchez et al. 2008). The small mouth of *C. monstrosa* is endowed with crushing plates, enabling it to feed on bivalves, small amphipods, caridea (shrimps) and anomurans (Mauchline & Gordon 1983, Bergstad et al. 2003, Moura et al. 2005), taxa that are highly diverse both within the sponge-beds (Klitgaard 1995) and the CWC *Lophelia pertusa* mounds (Mortensen & Fosså 2006, Roberts et al. 2006). However, the ventral position of the small mouth makes feeding within the actual *Lophelia pertusa* framework impossible, restricting feeding to the soft-sediment available in the unstructured seabed habitats as well as between the sponges in the sponge-bed habitat. *C. monstrosa* is slow-moving, but nevertheless highly mobile and thus the variability in responses shown by this species to the presence of CWC mounds, sponge-beds, unstructured plain seabed and the edges surrounding these habitats may be, in part, be a function of the scale of sampling (Biber et al. 2014).

Scale dependency

In Trænadjupet, the patchy distribution of CWC mounds, sponge-fields and their intervening edges create locally very heterogeneous environments (Lindberg 2004, Kutti et al. 2013). Demersal fish often respond to the presence of such habitat variation, and for tropical reef and stream fish communities, the spatial scale is often included in the assessments of fish-habitat relationships (Munday et al. 1997, Munday 2002, Chittaro 2004). In this study as well, the spatial scale proved to be vital in resolving these

relationships. The planktivorous fish *T. esmarkii* and *M. poutassou*, which are thought to be only temporarily associated with the benthic system due to diel vertical migrations (Torgersen et al. 1997, Johnsen & Godø 2007), appeared to be randomly distributed at large (1 to 2 km) spatial scales, but as habitat specialists when the benthic habitat was delineated using smaller (5 to 100 m) spatial scales. The only species for which clear vertical migration patterns were documented during this study, *T. esmarkii*, was only very rarely associated with microhabitat features and was also found in the highest abundances in low or no complexity sub-habitats.

As with recent *in situ* observations from the Irish continental shelf (Söfftker et al. 2011), we found no links between the presence of CWC habitats and the local scale distribution of *M. poutassou*. However, while Söfftker et al. (2011) suggested that a larger scale link between the distribution of *M. poutassou* and CWC mounds could still exist on the Irish shelf due to very high pelagic production at some mounds (White et al. 2005), we found no evidence of such a relationship. On the contrary, in a parallel acoustic survey of fish distributions on the northern Norwegian shelf, it was concluded that mesopelagic fish such as *Clupea harengus* (Atlantic herring) from the family Clupeidae and *M. poutassou* are associated mainly with deeper oceanic water masses as they occur in high numbers on the shelf break but only very rarely in quantities detectable using acoustics in Trænadjupet (authors' unpubl. data). Interestingly, we found that on smaller spatial scales, *M. poutassou* appeared to avoid coral habitats while showing a preference for sponge as well as unstructured habitats. Whether this is a result of coincidence or active habitat choice of the individuals remains unconfirmed by this study.

Implications for management

There is growing evidence that several temperate demersal fish have specific habitat requirements, however, little is known about the function of the habitat specialization and the effect of the absence of such apparently preferred habitats. For one, habitats may be particularly valuable and even essential if they are used for breeding, spawning or as nurseries (see e.g. Rosenberg et al. 2000). An important function of structurally complex shallow tropical ecosystems, such as coral, mangroves and sea-grass beds, is indeed that they serve as nursery areas for juvenile fish (Nagelkerken et al. 2000, 2002, Mumby et al. 2004)

and as such have been shown to be vital for the attainment of large populations of some commercially harvested species (Nagelkerken et al. 2002). Apart from the recent findings of redfish *Sebastes fasciatus* and *S. mentella* larvae in deep sea-pen fields (Baillon et al. 2012), a few observations of gravid female redfish *S. norvegicus* and *S. viviparus* around cold-water coral mounds (Fosså et al. 2002, Costello et al. 2005) and the observations of juvenile redfish (*Sebastes* sp.) using boulders, cerianthids and sponges for shelter (Auster et al. 2003, Freese & Wing 2003), there have been few indications that structurally complex benthic habitats have a similarly important function for the early life stages of commercially harvested temperate demersal fish. On the contrary, several studies have noted the apparent lack of juvenile fish in structurally complex CWC ecosystems (e.g. Costello et al. 2005, Ross & Quattrini 2007). Our study corroborates these findings, with equally many juvenile fish observed in all examined habitats. Among species that are not commercially harvested (in Norway), *Galeus melastomus* (blackmouth catshark) from the family Scyliorhinidae appears to be using CWC ecosystems as spawning grounds although it is not known to what extent. Henry et al. (2013) reported higher trawl catches of this shark near coral habitats in the Mingulay Reef complex and multiple observations of shark egg cases within the *Lophelia* framework. In a longline fishing study of the Trænadjupet coral MPA, *G. melastomus* catch rates were twice as high in coral habitats as in unstructured flat seabed, supporting the view that CWC could be used for breeding, spawning or as nurseries by this species (Kutti et al. 2014).

Specific habitats may be considered particularly valuable or important if the density of adult individuals within that habitat is comparatively high and/or if the habitat covers a substantial area of the distributional range of a fish population (Auster 2005). This study showed that within the Trænadjupet MPA, a substantial part of the adult populations of *B. brosme* and *S. viviparus* inhabited the complex habitats of the coral mounds and sponge-fields. However, based on the fact that CWC and sponges occur very patchily (Fosså et al. 2000, Klitgaard & Tendal 2004) and cover only 0.5 to 1 % of the total area of the Norwegian continental shelf (Fosså et al. 2000), the importance of these habitats on a regional scale is probably less than is often assumed (see Kutti et al. 2014 for *B. brosme* catch statistics). Indeed, CWC and sponge habitats might be expected to have only a small influence on these demersal fish populations as these fish do inhabit alternative structurally complex

and non-complex habitats (COSEWIC 2003, Auster 2005, Auster & Lindholm 2005, Grabowski et al. 2012, Ragnarsson & Burgos 2012). To date, recruitment variation and commercial harvesting history are probably primary sources of abundance variation of these species (e.g. redfish, Planque et al. 2012). However, in the NW Atlantic, climate change and rise in seawater temperatures is predicted to result in reduced availability of structurally complex habitats and an exacerbation of the population decline caused by commercial harvesting of *B. brosme* (Hare et al. 2012). Furthermore, the role of the Trænadjupet coral MPA in providing a refuge for commercial fish species harvested by trawls comparable to that of the Santa Maria di Leuca coral province in the Mediterranean Sea (D'Onghia et al. 2010, 2012) remains unconfirmed by this study.

CONCLUSIONS

This study found positive relationships between the presence of structurally complex CWC mounds and/or sponge fields and the abundance of 3 of the 5 most common demersal fish in the Trænadjupet MPA, northern Norwegian shelf. *Sebastes viviparus* and *Brosme brosme* both showed clear associations with the CWC and sponge habitats at all spatial scales examined, while *Chimaera monstrosa* was associated with sponge habitats and unstructured seabed but was absent from the CWC habitats. None of the species examined were confined to a single habitat, thus the study confirmed prior assumptions that the demersal fish of the Norwegian shelf are on the generalist side of the specialist-generalist gradient and are facultative inhabitants of the CWC and sponge habitats. While this study suggests that the importance of CWC and sponge fields for the fish populations on the Norwegian shelf could be less than is often assumed, the wider ecological value of CWC and sponge ecosystems remains far from fully understood.

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