Trophic structure of cold-water coral communities revealed from the analysis of tissue isotopes and fatty acid composition

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Running head: Food web structure of cold-water coral reefs

Trophic structure of cold-water coral communities revealed from the analysis of tissue isotopes and fatty acid composition

The trophic structure of cold-water coral reef communities at two contrasting locations, the 800-m deep Belgica Mounds (Irish margin) and 300-m deep Træna reefs (Norwegian Shelf), was investigated using stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and fatty-acid composition analysis. A broad range of specimens, with emphasis on (commercial) fish species, and organic matter sources were sampled using a variety of tools. Irrespective of the environmental and geographical setting, the $\delta^{15}N$ values indicated that the food web encompasses roughly 1.5 to 3 trophic levels. Mobile echinoderms, i.e. sea urchins and sea stars, had highest $\delta^{15}N$ values, indicative of a high trophic position in the food web. The fraction of bacterial fatty acids in reef fauna was generally low (<5%), indicating that enhanced bacterial production in the water column through seafloor seepage of nutrients ('hydraulic theory') does not form a significant energy pathway into the food web. The high fraction of algal and essential fatty acids in reef fauna and fish at both locations indicates a close coupling with surface productivity, but the transport mechanism depends on the hydrographic setting. At Træna, *Calanus* copepods and euphausiids form an additional link between primary production and fish, which is largely absent at Belgica Mounds. At Belgica Mounds, the reef community is primarily supported by phytodetritus, as evidenced by the high contribution of algal fatty acids in faunal tissue and seasonal chlorophyll *a* deposition and marine snow at the reef. The environmental setting of cold-water coral reefs influences the structure of the associated food web.

Keywords: Cold-water coral reefs; food web; carbon isotopes; nitrogen isotopes; fatty acid composition

Introduction

Cold-water corals build carbonate reef structures in the deep-sea (Roberts et al. 2006) that form a substrate for a diverse (Henry & Roberts 2007) and active (Van Oevelen et al. 2009; Wagner et al. 2011; White et al. 2012) reef community. Typical members of this community are the polychaete *Eunice norvegica* (Mueller et al. 2013; Roberts 2005), encrusting and massive sponges (Van Soest & Lavaleye 2005), squat lobsters, soft-corals, gorgonians, hydroids, crabs and sea stars (Duineveld et al. 2007). In addition to these sessile or low-mobility species, demersal, e.g. tusk (*Brosme brosme*) and Norway redfish (*Sebastes viviparus)*, and pelagic, e.g. saithe (*Pollachius virens*), fish species occur in high densities on and around cold-water coral reefs (Biber et al. 2014; Costello et al. 2005; Husebø et al. 2002; Kutti et al. 2015). Although these studies found high fish densities on cold-water coral reefs, it is unclear whether this is related to higher food availability, e.g. a high macrobenthic biomass (Van Oevelen et al. 2009), or related to shelter provided by the physical complexity of the reef (Auster 2005; Husebø et al. 2002). Hence, to better understand the function of cold-water coral reefs it is imperative to unravel the food web structure and take important (commercial) fish species into account.

Cold-water coral communities are supported by phytodetritus (Duineveld et al. 2007; Kiriakoulakis et al. 2004; Van Oevelen et al. 2009), though various studies suggest that also zooplankton contributes to their nutrition (Dodds et al. 2009; Husebø et al. 2002; Kiriakoulakis et al. 2005; Naumann et al. 2011; Van Oevelen et al. 2009). Another organic matter source may be bacterioplankton of which the production is stimulated by mucus release by the cold-water corals (Wild et al. 2008). Deep sponge communities are also capable of chemoautotrophic carbon fixation through symbiotic nitrification (Hoffmann et al. 2009; van Duyl et al. 2008). Finally, classical predatory interactions are relevant for species like carrier crabs, sea stars, sea urchins and tusk (Duineveld et al. 2007; Husebø et al. 2002;

79 Stevenson & Rocha 2013; Van Oevelen et al. 2009).

80 The importance of these various food supply pathways for a cold-water coral reef may
81 be influenced by the environmental setting in which the reef grows (Mienis et al. 2007;
82 Thiem et al. 2006). The interaction of corals mounds with tidal currents may induce
83 downwelling of nutrient-rich surface waters towards the reef mounds (Davies et al. 2009;
84 Duineveld et al. 2012; Soetaert et al. 2016), which may increase the importance of fresh
85 phytodetritus in their nutrition. Other coral mounds may either be too small to induce
86 downwelling or grow in an environment with a unidirectional current or where tidal currents
87 are less prominent. Zooplankton migrates vertically in the water column to feed on
88 phytoplankton during the night and to find shelter from predators in darker deeper waters
89 during the day (Hays 2003). This diel vertical migration pattern was inferred above a cold-
90 water coral reef from a 'rising' backscatter signal at dusk and a 'descending' backscatter
91 signal at dawn in the Gulf of Mexico (Hebbeln et al. 2014; Mienis et al. 2012). Hebbeln et al.
92 (2014) inferred that zooplankton migrated to depths of 500 to 600 m where the cold-water
93 corals are found. Deeper reefs may however be outside the zooplankton migration window
94 and the biomass of zooplankton decreases exponentially with water depth (Angel & de C.
95 Baker 1982). Zooplankton may therefore become progressively less important as a resource
96 for deeper reefs. Hence, cold-water coral communities may be supported through different
97 pathways, but it is not straightforward to decipher the importance of these pathways for a reef
98 food web.

99 Stable isotope measurements of faunal tissue have provided valuable information on
100 deep-sea food web structures including cold-water coral communities (D'Onghia et al. 2010;
101 Duineveld et al. 2007; Kiriakoulakis et al. 2005; Sherwood et al. 2008), since an organism's
102 $\delta^{13}C$ value reflects that of its basal resource, while its $\delta^{15}N$ value is indicative of the trophic

position in the food web. More detailed information on diet composition can be obtained from the composition of individual fatty acids in an organism (Dalsgaard et al. 2003; Kelly & Scheibling 2012). Fatty acids are the main constituents of lipids, which are found in cell membranes and are used as energy storage. Primary producers (Dijkman & Kromkamp 2006), bacteria (Boschker & Middelburg 2002) and zooplankton (Dalsgaard et al. 2003) contain specific individual fatty acids or have a unique fatty acid signature. Consumers of the resources modify these fatty acids only to a limited extent and therefore the fatty acid composition of the consumer is a representative mix of its resources (Iverson et al. 2004). In addition, some fatty acids are coined 'essential', as fish have no or very limited capacity to biosynthesize this group of fatty acids and must obtain them from their diet (Arts et al. 2001; Kelly & Scheibling 2012). Invertebrates have the capacity to synthesize these fatty acids and may therefore form an important link in the food web. Diets of marine organisms can therefore be qualitatively inferred from the concentration and spectrum of its fatty acid composition (Dodds et al. 2009; Kelly & Scheibling 2012).

In this paper, we combine tissue stable isotope and fatty acid composition analysis to investigate food web relations in cold-water coral communities of the Belgica Mounds (Irish Sea) and of the Træna Deep Coral reef field on the Norwegian continental shelf. These study sites are located along the European continental margin and have among the highest densities of cold-water corals around the world (Roberts et al. 2006), but contrast in their environmental setting with differences in water depth, mound size and hydrography. The main goal of this study is to explore the importance of the detrital, zooplankton, bacterial and chemoautotrophic pathways for these cold-water coral communities, with emphasis on demersal and pelagic fish populations.

Materials and methods

Study areas and sampling strategy

The Træna Deep Coral Reef field lies within the regional Marine Protected Area (MPA) and is located south of the Lofoten peninsula on the Norwegian continental shelf on the northern slope of the inner Trænadjupet Trough at 270 to 450 m depth (Fig. 1A). The MPA of 460 km^2 has a high abundance of coral reefs. In a detailed survey of a large part of this region (307 km^2), a total of 1447 long-tailed reefs have been identified from multi-beam bathymetric maps, each being 100-150 m long, 25-55 m wide and on average 7 m high and covering about 2% of the seafloor of the MPA (Lindberg et al. 2004). The hydrography of the Norwegian shelf is influenced by two northward directed current systems. The North Atlantic Current (NAC) transports comparatively warm saline North Atlantic Water (NAW) northward along the continental shelf edge, while the Norwegian Coastal Current (NCC) transports cold, less saline, Norwegian Coastal Water (NCW) northward along the coast. The reefs within the Træna field are aligned parallel to the main current direction with a live *Lophelia pertusa* front that faces the current. The greatest density of coral reefs is found on the southern and western/northwestern edge of a circular depression (Fig. 1A). In addition to the cold-water coral reefs, dense aggregations of demosponges, i.e. *Geodia barretti*, *G. atlantica*, *G. macandrewii*, *Phakellia* spp. and *Mycale* spp., are found in between the reefs (Kutti et al. 2013). Mean bottom water temperature measured in the northern part of the coral MPA (66°58.31 N, 11°07.76 E) was 6.9°C (May 2011) and 7.2°C (March 2010) and salinity was around 35 (35.2 in May 2011 and 35.2 in March 2010). Sampling at the Træna reefs was conducted during various cruises to the northern part of the reef aggregation (Fig. 1A), where the water depth ranges between 270 and 320 m.

Tissue samples of invertebrates and fish of the Træna CWC reefs were collected on a

research cruise that was conducted from 4 to 16 March 2010 with R/V GO Sars. Demersal fish (i.e. *Hippoglossoides platessoides*, *Chimaera monstrosa*, *Phycis blennoides*, *Sebastes viviparus*, *Argentina sphyraena*, *Artediellus atlanticus*, *Trisopterus esmarkii*) were collected using a Campelen 1800 bottom trawl just outside the coral MPA (66°56.65N, 11°29.15E). Krill (i.e. *Meganyctiphanes norvegica* and *Thysanoessa inermis*), cephalopods (*Sepiola atlantica*), shrimps (*Pandalus borealis*) and pelagic fish (i.e. *Maurolicus muelleri*) were collected using a pelagic krill trawl (66°58.24N, 11°27.82E). *Brosme brosme* was caught with a bottom long-line on a research cruise with M/S Atlantic (3-9 March 2010, 66°57.85 N, 11°05.23 E). Samples of *Lophelia pertusa*, suspended matter, zooplankton and *Pollachius virens* were collected between 26 and 31 May 2011 during a cruise with R/V Håkon Mosby. Water samples from 30 and 300 m depth were collected using Niskin water sampling bottles and filtered through Whatmann GF/F filters (5 to 10 litres per filter) to collect suspended matter (66°58.31 N, 11°07.76 E). Zooplankton was sampled (66°58.47 N, 11°05.72 E) using a WP2 plankton net, towed from 100 m depth to the surface, which was subsequently sieved through a 280 and 50 µm sieve to obtain two (large and small, respectively) zooplankton size classes. Microscope investigation later revealed that both size classes contained almost exclusively *Calanus* sp. *Pollachius virens* was caught at 300 m water depth using a long-line (66°58.97 N, 11°05.11 E). *Lophelia pertusa* was collected using the ROV Aglantha (66°58.31 N, 11°07.76 E). Smaller macrofauna was sampled with a square boxcorer (30x30 cm). Long-lines, box cores, plankton hauls and water samples were taken within the dense clusters of reefs at Træna (i.e. <10 m away from the *Lophelia pertusa* framework). Trawling is banned within the coral MPA and was therefore carried out 4 km east of the area (Fig. 1A).

The Belgica Mounds are the southernmost coral mound province of the Porcupine Seabight and are located on the south-eastern slope of the Porcupine Basin (Fig. 1B). The mound province consists of outcropping carbonate mounds on the steepest part of the slope at

a depth of 750 to 850 m and of several isolated mounds (e.g. Galway and Therese Mounds) on the deeper and flatter part of the slope around 950 m depth. The isolated mounds are located in an area of enhanced near-bottom currents, are oriented parallel or slightly oblique to the slope of the margin and are around 1.5 km long and up to 100 m high (Dorschel et al. 2007). Another important feature of the coral mounds at the Rockall and Porcupine continental margin is related to their hydrography, which has a wide spectrum of tidally driven flow that includes bottom-trapped baroclinic motions of diurnal period and semi-diurnal tides (Mienis et al. 2007; Mohn et al. 2014). Tissue samples of invertebrates and fish were collected at Belgica Mounds during the HERMES research cruises with the R/V Pelagia in 2008 and 2009 (51°27'N, 11°45'W at a depth between 836 and 970m). Larger macrofauna was collected with a triangular dredge near the coral reef, while the smaller fauna was sampled with a NIOZ boxcorer with a core diameter of 50 cm. During the 2008 cruise, additional zooplankton and near-bottom suspended particulate matter (SPM) samples were collected. Zooplankton was collected in the upper 200 m of the water column using a vertical net with a mesh size 200 µm. SPM samples were collected with a Stand Alone Pump (SAP, Challenger Oceanic™) mounted on a benthic lander that was deployed at 690 m depth, which filtered a volume of 375 L on a GF/F filter. Two other samples (9 L each) were taken with a CTD rosette sampler in the near-bottom water layer at 890 and 972 m depth and filtered over pre-weighted and muffled GF/F filters. All fauna samples and filters were immediately stored frozen (-20 °C).

In addition, between October 2011 and October 2012, a lander was deployed on Galway Mound (51° 27.099 N, 11° 45.135' W) at a depth of 786 m. The lander was equipped with a near-bottom sediment trap (Technicap PPS4/3), fluorescence sensor (Wetlabs FLNTU) and HD video camera with infrared illumination (custom made at NIOZ). The content of the sediment trap was preserved *in situ* with mercuric chloride. Individual sediment trap samples

covered an exposure time of approximately one month and a total of 12 samples were collected. The samples from the two deployments were analysed for bulk ^{13}C and ^{15}N isotopes and chlorophyll *a* content. The HD video camera took stills on a daily basis, which were analysed for the number of visible aggregates per frame.

Laboratory procedures

Sediment trap samples were analysed for chlorophyll *a* concentration by High Pressure Liquid Chromatography as described in Duineveld et al. (2004). Faunal samples were sorted and identified to the lowest possible taxonomic resolution. Tissue subsamples from individual specimens were taken and analysed for $\delta^{13}C$, $\delta^{15}N$ and fatty acid composition. Subsamples (1-2 mg) for $\delta^{13}C$ and $\delta^{15}N$ analysis were transferred to small silver boats, acidified with 5% HCl to remove inorganic carbon, oven-dried at 60°C, pinched closed and stored frozen before analysis on the Elemental Analyser (EA, Firma Thermo Electron, Flash EA 1112 analyser) that was coupled to a Delta V isotope ratio mass spectrometer (IRMS) for simultaneous measurement of ^{13}C:^{12}C and ^{15}N:^{14}N ratios. Reproducibility of the EA-IRMS analysis was 0.25‰ for ^{15}N and 0.2‰ for ^{13}C. Samples were not lipid-extracted prior to isotope analysis, as this is uncommon for deep-sea invertebrates and the low C:N ratios of these fauna implies that lipid-correction only marginally affects the results (Fanelli et al. 2011). Isotope values are expressed in the δ-notation, which is the per mil (‰) deviation of a sample (R_{sam}, ^{13}C:^{12}C for carbon and ^{15}N:^{14}N for nitrogen) relative to the isotope ratio of a standard material (R_{STD} of carbon is 0.011180, R_{STD} of nitrogen is 0.003677) as $\delta X = (R_{sam}/R_{STD} - 1) \times 1000‰$, with X representing ^{13}C or ^{15}N.

Total lipids were extracted from 10 to 60 mg of wet fauna tissue or 5 g dry sediment using a Bligh and Dyer extraction. The lipid extract was derivatised to volatile fatty acid methyl esters (FAME) and measured for fatty acid concentration on a Gas Chromatograph

coupled to a Flame Ionization Detector (GC-FID) or a Gas Chromatograph coupled to an Isotope Ratio Mass Spectrometer (GC-IRMS) (Middelburg et al. 2000). Fatty acid (FA) data are measured as mg FA/g wet weight, but since the interest in this paper is on the fatty acid composition, the fatty acids are expressed as relative contribution to the total fatty acid pool. This is done to normalize for differences in fatty acid concentrations that are due to different body compositions, although hard body parts were removed from the animal tissues.

Fatty acid biomarkers

The use of fatty acids as individual biomarkers for the identification of food resources is not unambiguous, because some fatty acids have been used as a 'unique' marker for different food sources (Kelly & Scheibling 2012). In this study, we therefore use only fatty acids as specific markers that have been repeatedly used for one single food source and focus on their *relative* abundance. The following fatty acid markers were considered bacteria-specific iC14:0, iC15:0, aiC15:0, iC16:0, iC17:0, aiC17:0 and C18:1ω7c (Alfaro et al. 2006; Boschker & Middelburg 2002; Brett et al. 2006; Howell et al. 2003; Meziane & Tsuchiya 2000), algae-specific C18:3ω3, C20:5ω3 and C22:6ω3 (Alfaro et al. 2006; Boschker & Middelburg 2002; Dijkman & Kromkamp 2006; Ravet et al. 2010) and zooplankton-specific C20:1ω9, C22:1ω9, C22:1ω11 (Alfaro et al. 2006; Dodds et al. 2009; Howell et al. 2003; Ravet et al. 2010). The essential fatty acids are C18:3ω3, C18:ω6, C20:4ω6, C20:5ω3 and C22:6ω3 (Arts et al. 2001). During the sampling at Træna we also obtained zooplankton samples from the water column (see above), to compare the fatty acid profiles of these samples against the selected 'zooplankton' markers found in other organisms.

Multivariate statistics

The summed proportional abundance of specific fatty acid markers of algae, bacteria and zooplankton in reef fauna are analysed with principal component analysis (PCA) with either

248 'site' or 'site + taxa' as grouping factor. When 'site' was used as a group factor, all samples
249 were included in the analysis, because this concerns the whole community. When 'site +
250 taxa' was used as group factor only taxa for which $n>1$ were included in the analysis. The
251 PCAs were performed on arcsine-transformed proportional abundances with the function
252 *prcomp* that is available in R (R Development Core Team 2015). The *prcomp* function uses
253 singular value decomposition, which is a Euclidian-based method. The function *ggbiplot*
254 available in the R package *ggplot2* (Wickham 2009) was used to plot the PCA results and to
255 add normal probability ellipsoids.

256 **Results**

257 ***Træna deep coral reef field***

258 Stable isotope samples from the Træna area are partitioned over 5 organic matter sources, 14
259 reef fauna groups and 10 fish species (Fig. 2A, Table 1). The $\delta^{13}C$ values range from -26.9‰
260 (SPM) to -17.0‰ (sea star *Henricia pertusa*) and $\delta^{15}N$ values range from 5.4‰ (small
261 *Calanus* sp.) to 16.6‰ (*H. pertusa*). The $\delta^{15}N$ isotope values of the on- and off-reef sediment,
262 suspended organic matter, small and large *Calanus* copepods are all lower than those of the
263 reef fauna (Fig. 2A). The associated reef fauna has a $\delta^{13}C$ range of -24.5‰ (*Lophelia*
264 *pertusa*) to -17.0‰ (*H. pertusa*) and a $\delta^{15}N$ range of 8.2‰ (*Lophelia pertusa*) to 16.6‰ (*H.*
265 *pertusa*). The mean isotope value of sponges is relatively high ($\delta^{13}C$ = -18.2‰, $\delta^{15}N$ =
266 15.6‰) and has a large standard deviation. The range of $\delta^{13}C$ values of the fishes (-22.3‰ to
267 -18.1‰) is comparable to that of the reef fauna, but $\delta^{15}N$ values tend to be higher and range
268 from 10.3‰ to 13.6‰. The euphausiids *Meganyctiphanes norvegica* and *Thysanoessa*
269 *inermis* have slightly lower $\delta^{15}N$ values (9.4 and 8.8‰, respectively) as the reef-associated
270 fauna. The sea cucumber *Parastichopus tremulus* and the ophiuroid *Ophiopholis aculeata*
271 also have comparatively low $\delta^{15}N$ values (9.8 and 10.3‰, respectively). Within the

crustaceans, the squat lobster *Munida rugosa* has lowest $\delta^{15}N$ value (10.4‰), followed by the shrimp *Pandalus borealis* (11.9‰) and finally the king crab *Lithodes maja* (12.1‰). Fish have $\delta^{15}N$ values ranging from 10.3‰ for the Norway pout (*Trisopterus esmarkii*) to 13.6‰ for tusk (*Brosme brosme*), which is generally higher as compared to the other reef fauna.

The concentration of total fatty acids (mg C g^{-1} WW) for CWC reef fauna at Træna is variable, but lower than 5% of the wet weight for all organisms, except for the pearlside *Maurolicus muelleri* (7.5%) (Table 3). Other species with a comparatively high fraction of fatty acids are krill *Thysanoessa inermis* (4.9%), fish *Pollachius virens* (1.6%) and both zooplankton size classes (2.9% and 5%). Sediments have lowest (<0.015%) fatty acid fractions, while the holothurian *Parastichopus tremulus* and the crustacean *Lithodes maja* have the lowest fatty acid concentrations among the fauna (<0.06%). No fatty acid data are available for SPM, because the whole filter had to be used for analysis of bulk $\delta^{13}C$ and $\delta^{15}N$.

Bacterial fatty acids are found in all CWC fauna, but the percentage of summed bacterial fatty acids ranges from 1 to almost 20% (Fig. 3A). Sediments, sponges, echinoderms and crustaceans have a higher contribution of bacterial fatty acids (>7 to 20%) as compared to most fish species (1 to 5%). The fatty acid C18:1ω7c dominates the bacterial markers and generally represents >2% of the total fatty acids, while other bacterial markers typically represent <1% (Table 3). The branched short-chained bacterial fatty acid iC14:0 is not detected in many CWC fauna, especially the fish species, but represents 0.7 – 0.9% of the total fatty acid pool in sediments.

Summed algal fatty acids contribute up to 45% of the total fatty acids for the fish species *Chimaera monstrosa* (Rabbit fish), *Hippoglossoides platessoides* (American plaice) and *Trisopterus esmarkii* (Norway pout) (Fig. 3B). Fish species, except for *Brosme brosme* and *Pollachius virens*, have a high algal fatty acid contribution of >32%, as well as *Sepiola*

296 *atlantica*, crustaceans, euphausiids and both *Calanus* size classes. Low algal fatty acid
297 contributions (generally <10%) are found for *Lophelia pertusa*, echinoderms, sponges and
298 sediments. The algal fatty acid C18:3ω3 is hardly found in the CWC fauna, while C16:4ω3
299 and C18:4ω3 generally represent <1% of the total fatty acids (Table 3). A notable exception
300 is the high (~10%) C18:4ω3 content of both *Calanus* size classes. Though variable, the algal
301 markers C20:5ω3 and C22:6ω3 generally dominate the fatty acids of reef fauna.

302 Zooplankton markers generally represent <5% of the total fatty acids, except for
303 *Lophelia pertusa* and *Brosme brosme* (Fig. 3C). The fatty acid C20:1ω9c is found in most
304 CWC fauna and dominates the specific zooplankton fatty acids (0.5 – 3%). The fatty acid
305 C22:1ω11 has the lowest contribution (generally <0.5%), but is found in more fauna than
306 C22:1ω9, although when present, the latter fatty acid contributes between 1 to 3% of the total
307 fatty acid pool.

308 The pattern of summed essential fatty acids (i.e. C18:3ω3, C18:ω6, C20:4ω6,
309 C20:5ω3 and C22:6ω3) resembles that of algal fatty acids, since the dominant fatty acids
310 C18:3ω3, C20:5ω3 and C22:6ω3 overlap between the two fatty acid sets (Fig. 3B, D).
311 However, the contribution of the fatty acid C20:4ω6 is particularly high in *Lophelia pertusa*
312 and *Henricia pertusa*, which raises their total essential fatty acid content substantially (Fig.
313 3D, Table 3).

314 ***Belgica Mounds***

315 Stable isotope samples from Belgica Mounds are partitioned over 33 biotic compartments,
316 including scleractinian and soft corals, sponges, sea stars and 7 fish species (Fig. 2B, Table
317 2). Zooplankton has mean bulk $\delta^{13}C$ and $\delta^{15}N$ values of -20.6‰ and 3.5‰, respectively. The
318 large volume SPM sample taken with the SAPS pump and the two SPM samples from the
319 CTD-rosette were comparable and have a mean bulk $\delta^{13}C$ of -25.7‰ and $\delta^{15}N$ value of

320 5.4‰. Sediment trap samples are slightly higher than the SPM samples and have a mean $\delta^{13}C$
321 of -22.30‰ and a mean $\delta^{15}N$ of 7.0‰. Bulk $\delta^{13}C$ values of the cold-water coral community
322 of the Belgica Mounds range from -22.1‰ (Ophiuroidea spp.) to -12.2‰ (Asteroidea spp.)
323 and bulk $\delta^{15}N$ isotope values range from 6.8‰ (*Lepidion eques*) to 19.6‰ (*Aphrocallistes*
324 sp.) (Fig. 2B). The isotope values of most species range between -22‰ to -16‰ for $\delta^{13}C$ and
325 7‰ to 13‰ for $\delta^{15}N$ (Fig. 2B). *Lophelia pertusa* ($\delta^{13}C$ -18.4‰ and $\delta^{15}N$ 7.6‰) grouped
326 closely with other cnidarians such as *Cirrhipathes* sp. ($\delta^{13}C$ -18.4‰ and $\delta^{15}N$ 7.3‰) and
327 *Madrepora oculata* ($\delta^{13}C$ -18.4‰ and $\delta^{15}N$ 7.3‰). The sponges *Spongosorites* sp. ($\delta^{13}C$ -
328 17.3‰ and $\delta^{15}N$ 7.3‰), Hexactinellida sp. ($\delta^{13}C$ -20.0‰ and $\delta^{15}N$ 12.8‰) and *Aphrocallista*
329 sp. ($\delta^{13}C$ -17.9‰ and $\delta^{15}N$ 19.6‰) have a large variability in their bulk isotope values. Fish
330 species, other than *Lepidion eques*, are not separated by large differences in the $\delta^{13}C$ (range: -
331 16.5 to -18.6‰) and $\delta^{15}N$ values (range: 9.1 to 11.8‰).

332 The total concentration of fatty acids (mg C g^{-1} WW) is highly variable among the
333 reef fauna at Belgica Mounds, but tends to be ≤1% of the wet weight except for the fish
334 species *Epigonus telescopus* (Black cardinal fish) and the crustacean Cirripedia spp. (Table
335 4). Lowest fatty acid concentrations are found for the two sponge taxa *Aphrocalliste* sp. and
336 Hexactinellida sp. The total fatty acid concentration of SPM was 10 µg C L^{-1}.

337 The summed contribution of bacterial fatty acids is >1% and <6% for most CWC reef
338 fauna at Belgica Mounds (Fig. 4A), except for Amphipoda (24%) and the two sponge taxa
339 Hexactinellida sp. (8.6%) and *Spongosorites* sp. (12%). Short-chained and branched fatty
340 acids, especially iC14:0, are not found in all fauna and contribute generally <1% to the total
341 fatty acid pool. A notable exception is that the bacterial fatty acid iC17:0 occurs in
342 appreciable levels in almost all Cnidaria, in particular in *Lophelia pertusa* and *Madrepora*
343 *oculata*, and *Spongosorites* sp. (Table 4). The dominant bacterial marker is C18:1ω7c, which

344 contributes 1% to 6% of the total fatty acid pool.

345 The contribution of summed algal fatty acids ranges from 1% (Asteroidea spp.) to
346 51% for the fish *Coelorinchus caudani* (Fig. 4B). The algal markers C16:4ω3 and C18:3ω3
347 are absent in nearly all reef fauna, with the notable exception of the high C16:4ω3 percentage
348 in *Lophelia pertusa* (2.6%) and SPM (2.3%) (Table 4). The contribution of the fatty acid
349 C20:5ω3 differs considerably among species with values <3% for *Spongosorites* sp., Salpidae
350 sp. and the echinoderms Asteroidea spp. and *Cidaris* sp., but >17% for *Cirrhipathes* sp.
351 (Spiral wire coral), the octopus *Bathypolypus bairdii* and the polychaete *Eunice norvegica*.
352 The fatty acid C22:6ω3 generally dominates the algal markers, but is particularly high in
353 echinoderms, molluscs and most fish species with contributions of 10 to 40%.

354 Zooplankton markers are low in abundance (generally <2%) (Fig. 4C). Two of the
355 zooplankton fatty acids, i.e. C22:1ω9 and C22:1ω11, are found in only a few organisms
356 (Table 4), although a high C22:1ω11 content of ≥2% is detected in the CWC *Lophelia*
357 *pertusa* and *Madrepora oculata*. The fatty acid C20:1ω9c is found in nearly all samples and
358 in a high content in *Echinus* sp. and Asteroidea spp. and two cnidarians *Anthomastus* sp. and
359 *Cirrhipathes* sp.

360 The summed essential fatty acids contribute substantially to the total fatty acid pool of
361 the reef fauna, with most contributions >20% (Fig. 4D). Essential fatty acids seem to
362 concentrate in fish, where the contribution is >30%, except for *Neocyttus helgae* (20%) (Fig.
363 4D).

364 The mooring-mounted fluorescence sensor shows a comparatively low fluorescence
365 signal throughout the year (Fig. 5A), while chlorophyll *a* deposition in the sediment trap
366 increases from undetectable quantities in winter to 0.14 ng m^{-2} d^{-1} in May. Following this
367 spring deposition peak, chlorophyll *a* deposition remains detectable through the remainder of

368 the year (Fig. 5B). Aggregates, as countable on the HD video camera stills, are largely absent
369 in the winter months (Fig. 5C, left inset), but aggregate density increases markedly from
370 March to May (Fig. 5C, right inset) with peak values of >40 visible aggregates per still
371 image. The abundance of aggregates on the still images decreases again towards July and
372 August.

373 ***Multivariate analyses of fatty acid compositions***

374 The PC1 and PC2 of the PCA of the summed specific algal, bacterial and zooplankton fatty
375 acids explain a total of 84.9% of the variance, respectively (Fig. 6). The first axis relates to
376 increasing bacterial relative to algal markers, while the second axis discriminates the
377 abundance of zooplankton markers. The Belgica Mound samples were primarily separated on
378 the PC1 axis. Most Belgica Mound samples did not separate strongly and the normal
379 probability ellipsoid is centred on the summed algal fatty acids. The PCA separates the Træna
380 samples primarily on the PC1 axis by algal and bacteria fatty acids and to a lesser extent on
381 the PC2 axis by zooplankton fatty acids (Fig. 6). The samples from Træna however, were
382 more diverse than the samples from Belgica Mounds, resulting in a broader normal
383 probability ellipsoid as compared to Belgica Mounds.

384 The PC1 and PC1 axes of the PCA plot of Cnidarians explain a total of 85% of the
385 variance (Fig. 7A). The Cnidarian samples from Træna consist exclusively of *Lophelia*
386 *pertusa* and are separated from the Belgica Mounds samples, because of the higher
387 zooplankton fatty acid contribution in their tissue (Fig. 7A). The PCA performed on the
388 Cnidarian species (Fig. 7B) shows that species from Belgica Mounds typically have more
389 specific algal (e.g. *Cirrhipathes* sp.) or bacterial (e.g. *Gorgonian* spp.) fatty acids in their
390 tissues as compared Cnidarians from Træna. The PCA of all fish samples, with PC1 and PC2
391 together explaining a total of 92.5% of the variance, shows that the fish samples from Belgica

Mounds closely cluster together at the variable denoting high algal contributions (Fig. 7C). In contrast, the fish samples from Træna are separated by all three variables, resulting in a broad normal probability ellipsoid. Separate fish species at Træna however have narrow isotopic ellipsoids, so that the broad overall composition is clearly related to different species, each with specific compositions. For instance, *Brosme brosme* is characterised by a high contribution of zooplankton fatty acids, while *Sebastes viviparus* has a high contribution of algal fatty acids (Fig. 7D).

Discussion

The trophic base of cold-water coral reef communities

Our results indicate that the trophic base of reefs of Træna and in particular of Belgica Mounds is strongly dominated by algae, or more likely, phytodetritus. The fatty acid C22:6ω3 was used as marker for feeding on fresh phytodetritus by abyssal copepods by Bühring & Christiansen (2001). The percentage of C22:6ω3 in the reef fauna of Træna and Belgica Mounds was similar to the abyssal copepods, suggesting a dependence on relatively fresh phytodetritus. Thiem et al. (2006) suggested that the transport of fresh phytodetritus to Norwegian reefs is maintained by high primary production on the shelf and along the shelf break that is subsequently transported to the seafloor with the aid of 1) eddies and small fronts that are generated by the bottom topography and 2) a semi-permanent front between the North Atlantic Water and the Norwegian Coastal Current that generates local down-welling. In contrast, the interaction of tidal flows with bottom topography is likely important for the transport of fresh phytodetritus to the Belgica Mounds. Mohn et al. (2014) applied a hydrodynamic model to this region and found that an oscillatory tidal flow interacting with the mound topography promotes the transport of fresh phytodetritus to Belgica Mound reefs. Interestingly, the fluorescence signal at Belgica Mounds is low throughout the year, which

seemingly contradicts the dependence of reef fauna on fresh phytodetritus. In apparent contradiction, the chlorophyll *a* deposition flux is higher in April to June, which indicates an input of fresh phytodetritus in spring. The observed aggregate abundance is mirrored in the chlorophyll *a* deposition flux and we therefore suggest that fresh phytodetritus arrives as aggregates that are not detected by the fluorescence sensor. Likely, the detection volume of the fluorescence sensor is too small to reliably sense the aggregates.

The relative contribution of algal fatty acids in reef fauna provides information on the dominant primary producer supporting the food web. The algal marker C20:5ω3 is a diatom marker, while C22:6ω3 is specific for dinoflagellates (Dijkman & Kromkamp 2006; Kelly & Scheibling 2012). The ratio of these fatty acids signifies their relative importance as primary resource, in which a C20:5ω3/C22:6ω3 ratio of >1 is diatom-dominated and a ratio of <1 is dinoflagellate-dominated (Alfaro et al. 2006; Budge & Parrish 1998; Dalsgaard et al. 2003). The C20:5ω3/C22:6ω3 ratio is predominantly <1 in reef fauna from both Træna and Belgica Mounds, indicating a dinoflagellate dominance at the base of the food web. Dinoflagellates dominate over diatom abundance along the Norwegian shelf (Slagstad et al. 1999) and this dominance has increased in the last two decades (Edwards et al. 2006). In the Atlantic Ocean and along the Irish coast, dinoflagellates and diatoms dominate the phytoplankton community (Painter et al. 2010; Raine et al. 2002), but dinoflagellates may outcompete diatoms (Henson et al. 2012). Evidently, the dinoflagellate dominance in the upper water column is transferred to both reef systems.

The food web of Træna is supported by a broader range of food sources as compared to Belgica Mounds. The $\delta^{15}N$ and $\delta^{13}C$ values of *Lophelia pertusa*, when using fractionation values of 2 - 4‰ for $\delta^{15}N$ and 0 - 1‰ for $\delta^{13}C$ that are typical for deep-sea stable isotope studies (Fanelli et al. 2011; Iken et al. 2001; Petursdottir et al. 2008), suggest that *Calanus*

copepods are an important resource at the Træna reef. The importance of *Calanus* copepods is confirmed from the relatively high fraction of zooplankton markers in *L. pertusa*. It is important to note that Mueller et al. (2014) showed *de novo* synthesis of the 'zooplankton' fatty acid C20:1ω9c in a physiological study with stable isotopes. This cautions against the use of 'only' zooplankton markers to determine the importance of copepods in diets of cold-water corals without sampling zooplankton directly and stable isotope analysis. The $\delta^{13}C$ and $\delta^{15}N$ values of other reef fauna are too high as compared to *Calanus* copepods to suggest that the latter contributes significantly to their nutrition. Most reef fauna mirrors the fatty acid profile of the euphausiid species *Meganyctiphanes norvegica* and *Thysamoessa intermis* that were caught near the reefs. These euphausiids are the dominant krill species on the Norwegian Shelf (Dalpadado 2006) and are apparently an important resource for the reef food web. Indeed, the lights of the Campod videocamera had to be shut off regularly during surveys of the Træna reefs, because the view was blocked by swarms of euphausiids (T. Kutti, pers. obs.).

At Belgica Mounds, zooplankton $\delta^{15}N$ isotope values are >4‰ lower than the reef fauna, suggesting a limited importance of zooplankton for the food web. Other lines of evidence support this. Images from the moored-camera show no visible zooplankton around the reefs, sediment trap deployments repeatedly show no or very low numbers of 'zooplankton swimmers' on the filters (G. Duineveld, pers. obs.) and concentrations of typical zooplankton fatty acids, i.e. C20:1ω9c, C22:1ω9, C22:1ω11 are low (generally <1%) in most reef fauna. A notable exception to this latter argument are cnidarians, including *Lophelia pertusa*, which have a comparatively high C20:1ω9c content as compared to the other reef fauna. As mentioned above, this does not necessarily indicates feeding on zooplankton, because *L. pertusa* may synthesize this fatty acid. The depth of the reefs at Belgica Mounds probably implies that they are outside the zooplankton migration window,

465 which causes zooplankton to be of low importance to the reef food web.

466 The proportion of bacterial markers in most reef-associated fauna was low, especially
467 when compared to those deep-sea systems that are primarily supported by bacterial
468 symbionts (Ben-Mlih et al. 1992; Colaço et al. 2007; Phleger et al. 2005). Two pathways may
469 explain how bacterial production would contribute to the diets of a reef community. The
470 'hydraulic theory' hypothesizes that coral reef communities are supported by seafloor
471 seepage of reduced chemical species (e.g. H_2S and methane), which provide energy for
472 pelagic or symbiotic microbes that in turn supports reef communities (Hovland et al. 2012).
473 Alternatively, mucus released by cold-water corals and subsequent stimulation of bacterial
474 production in reef water (Wild et al. 2008) could elevate the importance of bacterial carbon
475 for the reef community. Chemosynthetic support of a food web can be identified from
476 depleted faunal $\delta^{13}C$ and $\delta^{15}N$ values, but isotope values from both reefs are too high for a
477 possible chemosynthetic basis of the food web (Van Gaever et al. 2006). The low
478 contribution of bacterial fatty acids indicates that support by pelagic bacterial production is
479 less important than that of phytodetritus and zooplankton, especially for fish. A notable
480 exception here are benthic crustaceans and echinoderms. Here bacterial contributions may be
481 elevated through feeding on sedimentary detritus, which is rich in bacterial fatty acids.

482 ***Pathways within the coral-reef food webs***

483 A high variability was observed in the $\delta^{15}N$ and $\delta^{13}C$ values of sponges at Træna and Belgica
484 Mounds (Fig. 2, 8), but also at other deep-sea locations (Duineveld et al. 2007; Iken et al.
485 2001). Sponges are holobionts, hosting a diverse community of microbial symbionts in their
486 tissue that may represent up to 35% of the total sponge biomass (Weisz et al. 2008). The
487 deep-water sponges at Træna and Belgica Mounds have among the highest contributions of
488 bacterial fatty acids of all fauna, suggesting that they have abundant associated microbes.

Deep-water sponges are known to efficiently retain bacterioplankton (Yahel et al. 2007) and take up dissolved organic carbon (van Duyl et al. 2008). However, deep-water sponges are also capable of nitrification, denitrification, annamox and nitrogen fixation (Hoffmann et al. 2009), which are microbial-mediated metabolic pathways that will draw $\delta^{15}N$ and $\delta^{13}C$ values of sponge tissue away from values that are typical for heterotrophic feeding on suspended particulate or dissolved matter. From our results, we cannot identify which metabolic processes are active, but the large variability in $\delta^{15}N$ and $\delta^{13}C$ values of individual sponges suggests a high diversity in carbon and nitrogen (re)cycling pathways. A complex carbon and nitrogen cycling combined with the dominance of sponges at many cold-water coral reefs (Van Soest & Lavaleye 2005) and their high filtration capacity (Kutti et al. 2013; Yahel et al. 2007) suggests that sponges may significantly influence the biogeochemistry of the reef water. Furthermore, deep-sea sponges take up coral-derived DOM and make this available to higher trophic levels by transforming it into particulate detritus (Rix et al. 2016).

The range in $\delta^{15}N$ values for fauna at both reefs is restricted to ~5‰ at Træna and ~7‰ at Belgica Mounds. This $\delta^{15}N$ range indicates that organisms differ by only 1.5 to 2.5 trophic steps in both food webs (assuming a $\delta^{15}N$ trophic fractionation factor of 3‰). It is important to note that large predatory fish are not included in our study, but a relatively flat food web is consistent with reports from Rockall Bank in the eastern Atlantic (Duineveld et al. 2007), Santa Leuca di Maria in the Mediterranean Sea (Carlier et al. 2009) and western Atlantic reefs off the coast of Canada (Sherwood et al. 2008).

Deposit and suspension feeders occupy the lowest trophic level at both locations, including cold-water corals and other cnidarians, stalked barnacles, holothurians and suspension-feeding ophiuroids. At Belgica Mounds however, several deposit or suspension feeders such as hydroids, the bivalve *Hiatella arctica* and holothurians have a comparatively high $\delta^{15}N$ value. While this may indicate feeding at a higher trophic level, it is more likely

514 that these species exploit more refractory organic matter and associated bacteria that
515 temporarily resuspends from the seafloor (Davies et al. 2009; Iken et al. 2001). Similarly,
516 benthic crustaceans have high $\delta^{15}N$ values, a comparatively high percentage of bacterial fatty
517 acids and a lower fraction of algal fatty acids, which indicates detritus feeding in both reef
518 food webs.

519 The sea urchin *Cidaris* sp. and sea stars (Asteroidea spp.) have among the highest
520 $\delta^{15}N$ values at both reefs. This is consistent with other cold-water coral reefs, where a snow
521 crab (Canada, Sherwood et al. 2008), sea star (Mediterranean, Carlier et al. 2009) and sea
522 urchin (Irish margin, Duineveld et al. 2007) had highest $\delta^{15}N$. These species are mobile
523 predators with a broad diet spectrum including sponges, polychaetes and bivalves and the
524 high $\delta^{15}N$ values is therefore related to its high trophic position in the food web (Emson &
525 Young 1994; McClintock 1994; Wieczorek & Hooper 1995). Stevenson and Rocha (2013)
526 documented that four sea urchin species actively predate on living *Lophelia pertusa* and
527 *Madrepora oculata*. The $\delta^{15}N$ difference between echinoids and cold-water corals is however
528 >4‰, indicating that corallivory is not the main feeding mode of echinoderms.

529 Fish species at Træna included several (commercially relevant) demersal and pelagic
530 species. The pelagic species *Maurolicus muelleri*, *Pollachius virens* and *Sebastes viviparus*
531 often have a diet consisting of *Calanus* copepods, euphausiids and fish (Bundy et al. 2011;
532 Carruthers et al. 2005; Husebø et al. 2002; Jaworski & Ragnarsson 2006; Petursdottir et al.
533 2008). The 6.5‰ difference in $\delta^{15}N$ between *Calanus* copepods and *M. muelleri* is too large
534 for *Calanus* to be their main prey item. Instead, euphausiids are likely more important based
535 on the $\delta^{15}N$ values and the high abundance of the algal fatty acid marker C20:5ω3 in both
536 euphausiids and *M. muelleri*. *Pollachius virens* often occurs in high abundance near the cold-
537 water coral reefs (Husebø et al. 2002; Kutti et al. 2015) and euphausiids are often an
538 important prey item (Carruthers et al. 2005; Jaworski & Ragnarsson 2006). The 3‰

539 difference between the $\delta^{15}N$ value of *P. virens* and euphausiids is consistent with feeding on
540 krill, but the low contribution of C22:6ω3 in *P. virens* is at odds with this feeding mode. An
541 alternative diet may involve feeding on fish from soft-bottom sediments such as *Ammodytes*
542 sp. (Sand lance) (Carruthers et al. 2005). Stomach content studies of *S. viviparus* indicated
543 that *Calanus* copepods are a main diet component (Bundy et al. 2011). At Træna, we could
544 analyse only one specimen for $\delta^{15}N$, but the 7‰ difference in $\delta^{15}N$ indicates that *Calanus* sp.
545 are not their main diet. Husebø et al. (2002) found that reef-associated *S. viviparus* had more
546 predatory copepods (*Euchaeta* spp.) in their stomach, which may explain the high $\delta^{15}N$ of *S.*
547 *viviparus* reported here. Stomach content studies of demersal fish species that were sampled
548 here, e.g. *Chimaera monstrosa*, *Brosme brosme* and *Phycis blennoides*, often have a diverse
549 diet of benthic fauna including polychaetes, small amphipods and squat lobster (*Munida* sp.)
550 (Bergstad et al. 2003). Our isotope and fatty acid data do not allow identifying a dominant
551 food source from such a wide spectrum, but $\delta^{15}N$ values of demersal species are elevated as
552 compared to pelagic species (e.g. *Trisopterus esmarkii*) and so their feeding is probably
553 linked to secondary production of the reef-associated fauna community. The high biomass of
554 reef fauna may therefore explain the high abundance of demersal fish species at Træna (Kutti
555 et al. 2015).

556 Fish sampled at Belgica Mounds are mostly non-commercial demersal species, of
557 which *Lepidion eques* and *Guttigadus latifrons* are associated with the coral framework
558 (Biber et al. 2014; Soffker et al. 2011). *Lepidion eques* occurs on both slope sediments and
559 cold-water coral reefs (Biber et al. 2014; Soffker et al. 2011), but the low $\delta^{15}N$ value of *L.*
560 *eques* is at odds with their suspected feeding on epi-and hyperbenthic crustaceans (Mauchline
561 & Gordon 1980). Limited diet information is available for the non-commercial demersal
562 species *Cataetyx alleni*, *Coelorinchus caudani*, *Gaidropsarus vulgaris* and *G. latifrons*, but
563 they seem to feed opportunistically on benthic and epibenthic prey including polychaetes,

564 shrimps, amphipods, crabs and small fish (Blaber & Bulman 1987; Carrasson & Cartes
565 2002). Indeed, the elevated $\delta^{15}N$ value and fatty acid composition (i.e. dominance of
566 C22:6ω3, low contribution of C20:4ω6 and C20:5ω3, and a near absence of zooplankton
567 fatty acids) indicates feeding on crustaceans from the coral reef food web. Algal and essential
568 fatty acids are highest in the fish from Belgica Mounds and as these fatty acids are retained in
569 pelagic food webs (Kainz et al. 2004), we infer that benthic fauna form a trophic link to the
570 demersal fish at Belgica Mounds.

571 In conclusion, we show differences in the trophic structure of two cold-water coral
572 reefs that contrast in their environmental setting. Phytodetritus is at the base of both coral-
573 reef food webs, but we speculate that the mechanism that drives the coupling of the reef food
574 web with surface productivity differs between locations and depends on the hydrography.
575 The resource spectrum that was utilised by the food web at Træna was much broader than at
576 Belgica Mounds, as *Calanus* copepods and euphausiids likely migrate to the depths of the
577 reefs and provide a conduit for the transfer of phytoplankton to the reef food web and
578 associated pelagic fish. The coral reefs at Belgica Mounds are several hundreds of meters
579 deeper than Træna and lack this zooplankton contribution. Instead, the reef food web at
580 Belgica Mounds is primarily supported by phytodetritus, which is transferred to demersal fish
581 that feed on benthic fauna of the reef food web.

582 **References**

583 Alfaro AC, Thomas F, Sergent L, Duxbury M. 2006. Identification of trophic interactions
584 within an estuarine food web (northern New Zealand) using fatty acid biomarkers and
585 stable isotopes. Estuarine Coastal and Shelf Science 70:271-286.
586 Angel MV, de C. Baker A. 1982. Vertical distribution of the standing crop of plankton and
587 micronekton at three stations in the Northeast Atlantic. Biological Oceanography 2:1-
588 30.
589 Arts MT, Ackman RG, Holub BJ. 2001. "Essential fatty acids" in aquatic ecosystems: a
590 crucial link between diet and human health and evolution. Canadian Journal of
591 Fisheries and Aquatic Sciences 58:122-137.
592 Auster PJ, 2005. Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts
593 JM, editors. Cold-Water Corals and Ecosystems. Berlin: Springer-Verlag, p 747-760.
594 Ben-Mlih F, Marty JC, Fialamedioni A. 1992. Fatty-acid composition in deep hydrothermal
595 vent symbiotic bivalves. Journal of Lipid Research 33:1797-1806.
596 Bergstad OA, Wik AD, Hildre O. 2003. Predator-prey relationships and food sources of the
597 Skagerrak deep-water fish assemblage. Journal of Northwest Atlantic Fishery Science
598 31:165-180.
599 Biber MF, Duineveld GCA, Lavaleye MSS, Davies AJ, Bergman MJN, van den Beld IMJ.
600 2014. Investigating the association of fish abundance and biomass with cold-water
601 corals in the deep Northeast Atlantic Ocean using a generalised linear modelling
602 approach. Deep-Sea Research Part II -Topical Studies in Oceanography 99:134-145.
603 Blaber SJM, Bulman CM. 1987. Diets of fishes of the upper continental-slope of eastern
604 Tasmania: content, calorific values, dietary overlap and trophic relationships. Marine
605 Biology 95:345-356.
606 Boschker HTS, Middelburg JJ. 2002. Stable isotopes and biomarkers in microbial ecology.
607 FEMS Microbiology Ecology 40:85-95.
608 Brett MT, Muller-Navarra DC, Ballantyne AP, Ravet JL, Goldman CR. 2006. Daphnia fatty
609 acid composition reflects that of their diet. Limnology and Oceanography 51:2428-
610 2437.
611 Budge SM, Parrish CC. 1998. Lipid biogeochemistry of plankton, settling matter and
612 sediments in Trinity Bay, Newfoundland. II. Fatty acids. Organic Geochemistry
613 29:1547-1559.

614 Bühring SI, Christiansen B. 2001. Lipids in selected abyssal benthopelagic animals: links to
615 the epipelagic zone? Progress in Oceanography 50:369-382.
616 Bundy A, Link JS, Smith BE, Cook AM. 2011. You are what you eat, whenever or wherever
617 you eat it: an integrative analysis of fish food habits in Canadian and U.S.A. waters.
618 Journal of Fish Biology 78:514-539.
619 Carlier A, Le Guilloux E, Olu K, Sarrazin J, Mastrototaro F, Taviani M, et al. 2009. Trophic
620 relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca,
621 Ionian Sea). Marine Ecology Progress Series 397:125-137.
622 Carrasson M, Cartes JE. 2002. Trophic relationships in a Mediterranean deep-sea fish
623 community: partition of food resources, dietary overlap and connections within the
624 benthic boundary layer. Marine Ecology Progress Series 241:41-55.
625 Carruthers EH, Neilson JD, Waters C, Perley P. 2005. Long-term changes in the feeding of
626 *Pollachius virens* on the Scotian Shelf: responses to a dynamic ecosystem. Journal of
627 Fish Biology 66:327-347.
628 Colaço A, Desbruyeres D, Guezennec J. 2007. Polar lipid fatty acids as indicators of trophic
629 associations in a deep-sea vent system community. Marine Ecology-an Evolutionary
630 Perspective 28:15-24.
631 Costello MJ, McCrea M, Freiwald A, Lundälv T, Jonsson L, Bett BJ, et al., 2005. Role of
632 cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald
633 A, Roberts JM, editors. Cold-Water Corals and Ecosystems. Berlin: Springer-Verlag, p
634 771-805.
635 D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, et al. 2010. Effects of
636 deep-water coral banks on the abundance and size structure of the megafauna in the
637 Mediterranean Sea. Deep-Sea Research Part II-Topical Studies in Oceanography
638 57:397-411.
639 Dalpadado P. 2006. Distribution and reproduction strategies of krill (Euphausiacea) on the
640 Norwegian shelf. Polar Biology 29:849-859.
641 Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W. 2003. Fatty acid trophic
642 markers in the pelagic marine environment. Advances in Marine Biology 46:225-340.
643 Davies AJ, Duineveld GCA, Lavaleye MSS, Bergman MJN, Van Haren H, Roberts JM.
644 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the
645 cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex.
646 Limnology and Oceanography 54:620–629.

647 Dijkman NA, Kromkamp JC. 2006. Phospholipid-derived fatty acids as chemotaxonomic
648 markers for phytoplankton: application for inferring phytoplankton composition.
649 Marine Ecology Progress Series 324:113-125.
650 Dodds LA, Black KD, Orr H, Roberts JM. 2009. Lipid biomarkers reveal geographical
651 differences in food supply to the cold-water coral *Lophelia pertusa* (Scleractinia).
652 Marine Ecology Progress Series 397:113-124.
653 Dorschel B, Hebbeln D, Foubert A, White M, Wheeler AJ. 2007. Hydrodynamics and cold-
654 water coral facies distribution related to recent sedimentary processes at Galway
655 Mound west of Ireland. Marine Geology 244:184-195.
656 Duineveld GCA, Jeffreys RM, Lavaleye MSS, Davies AJ, Bergman MJN, Watmough T, et
657 al. 2012. Spatial and tidal variation in food supply to shallow cold-water coral reefs of
658 the Mingulay Reef complex (Outer Hebrides, Scotland). Marine Ecology Progress
659 Series 444:97-115.
660 Duineveld GCA, Lavaleye MSS, Berghuis EM. 2004. Particle flux and food supply to a
661 seamount cold-water coral community (Galicia Bank, NW Spain). Marine Ecology
662 Progress Series 277:13-23.
663 Duineveld GCA, Lavaleye MSS, Bergman MJN, De Stigter H, Mienis F. 2007. Trophic
664 structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in
665 relation to the near-bottom particle supply and current regime. Bulletin of Marine
666 Science 81:449-467.
667 Edwards M, Johns DG, Leterme SC, Svendsen E, Richardson AJ. 2006. Regional climate
668 change and harmful algal blooms in the northeast Atlantic. Limnology and
669 Oceanography 51:820-829.
670 Emson RH, Young CM. 1994. Feeding mechanism of the brisingid starfish *Novodinia*
671 *antillensis*. Marine Biology 118:433-442.
672 Fanelli E, Cartes JE, Papiol V. 2011. Food web structure of deep-sea macrozooplankton and
673 micronekton off the Catalan slope: Insight from stable isotopes. Journal of Marine
674 Systems 87:79-89.
675 Hebbeln D, Wienberg C, Wintersteller P, Freiwald A, Becker M, Beuck L, et al. 2014.
676 Environmental forcing of the Campeche cold-water coral province, southern Gulf of
677 Mexico. Biogeosciences 11:1799-1815.
678 Henry LA, Roberts JM. 2007. Biodiversity and ecological composition of macrobenthos on
679 cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine

680 Seabight, NE Atlantic. Deep-Sea Research Part I-Oceanographic Research Papers
681 54:654-672.
682 Henson S, Lampitt R, Johns D. 2012. Variability in phytoplankton community structure in
683 response to the North Atlantic Oscillation and implications for organic carbon flux.
684 Limnology and Oceanography 57:1591-1601.
685 Hoffmann F, Radax R, Woebken D, Holtappels M, Lavik G, Rapp HT, et al. 2009. Complex
686 nitrogen cycling in the sponge *Geodia barretti*. Environmental Microbiology 11:2228-
687 2243.
688 Hovland M, Jensen S, Indreiten T. 2012. Unit pockmarks associated with *Lophelia* coral reefs
689 off mid-Norway: more evidence of control by 'fertilizing' bottom currents. Geo-Marine
690 Letters 32:545-554.
691 Howell KL, Pond DW, Billett DSM, Tyler PA. 2003. Feeding ecology of deep-sea seastars
692 (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Marine Ecology
693 Progress Series 255:193-206.
694 Husebø Å, Nøttestad L, Fosså JH, Furevik DM, Jørgensen SB. 2002. Distribution and
695 abundance of fish in deep-sea coral habitats. Hydrobiologia 471:91-99.
696 Iken K, Brey T, Wand U, Voigt J, Junghans P. 2001. Food web structure of the benthic
697 community at the Porcupine Abyssal Plain (NE Atlantic): A stable isotope analysis.
698 Progress in Oceanography 50:383-405.
699 Iverson SJ, Field C, Bowen WD, Blanchard W. 2004. Quantitative fatty acid signature
700 analysis: A new method of estimating predator diets. Ecological Monographs 74:211-
701 235.
702 Jaworski A, Ragnarsson SA. 2006. Feeding habits of demersal fish in Icelandic waters: a
703 multivariate approach. ICES Journal of Marine Science 63:1682-1694.
704 Kainz M, Arts MT, Mazumder A. 2004. Essential fatty acids in the planktonic food web and
705 their ecological role for higher trophic levels. Limnology and Oceanography 49:1784-
706 1793.
707 Kelly JR, Scheibling RE. 2012. Fatty acids as dietary tracers in benthic food webs. Marine
708 Ecology Progress Series 446:1-22.
709 Kiriakoulakis K, Bett BJ, White M, Wolff GA. 2004. Organic biogeochemistry of the Darwin
710 Mounds, a deep-water coral ecosystem, of the NE Atlantic. Deep-Sea Research Part I-
711 Oceanographic Research Papers 51:1937-1954.
712 Kiriakoulakis K, Fisher E, Wolff GA, Freiwald A, Grehan A, Roberts JM, 2005. Lipids and
713 nitrogen isotopes of two deep-water corals from the North-East Atlantic: inital results

and implication for their nutrition. In: Freiwald A, Roberts JM, editors. Cold-Water Corals and Ecosystems. Berlin: Springer-Verlag, p 715-729.

Kutti T, Bannister RJ, Fosså JH. 2013. Community structure and ecological function of deep-water sponge grounds in the Traenadypet MPA-Northern Norwegian continental shelf. Continental Shelf Research 69:21-30.

Kutti T, Fosså JH, Bergstad OA. 2015. Influence of structurally complex benthic habitats on fish distribution. Marine Ecology Progress Series 520:175-190.

Lindberg B, Christensen O, Fosså JH, 2004. The geologic and morphologic setting of the Træna reef area based on high resolution acoustic data, Journal. University of Tromsø.

Mauchline J, Gordon JDM. 1980. The food and feeding of the deep-sea morid fish *Lepidion eques* (Gunther, 1887) in the Rockall Trough. Journal of the Marine Biological Association of the United Kingdom 60:1053-1059.

McClintock JB. 1994. Trophic biology of Antarctic shallow-water echinoderms. Marine Ecology Progress Series 111:191-202.

Meziane T, Tsuchiya M. 2000. Fatty acids as tracers of organic matter in the sediments and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Marine Ecology Progress Series 200:49-57.

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR. 2000. The fate of intertidal microphytobenthos: An in situ ^{13}C labelling study. Limnology and Oceanography 45:1224-1234.

Mienis F, de Stigter HC, White M, Duineveld G, de Haas H, van Weering TCE. 2007. Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. Deep-Sea Research Part I-Oceanographic Research Papers 54:1655-1674.

Mienis F, Duineveld GCA, Davies AJ, Ross SW, Seim H, Bane J, et al. 2012. The influence of near-bed hydrodynamic conditions on cold-water corals in the Viosca Knoll area, Gulf of Mexico. Deep-Sea Research Part I-Oceanographic Research Papers 60:32-45.

Mohn C, Rengstorf A, White M, Duineveld G, Mienis F, Soetaert K, et al. 2014. Linking benthic hydrodynamics and cold-water coral occurrences: A high-resolution model study at three cold-water coral provinces in the NE Atlantic. Progress in Oceanography 122:92-104.

Mueller CE, Larsson AI, Veuger B, Middelburg JJ, van Oevelen D. 2014. Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. Biogeosciences 11:123-133.

748 Mueller CE, Lundälv T, Middelburg JJ, van Oevelen D. 2013. The symbiosis between
749 *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm
750 assimilation. Plos One 8:e58660.
751 Naumann MS, Orejas C, Wild C, Ferrier-Pages C. 2011. First evidence for zooplankton
752 feeding sustaining key physiological processes in a scleractinian cold-water coral.
753 Journal of Experimental Biology 214:3570-3576.
754 Painter SC, Lucas MI, Stinchcombe MC, Bibby TS, Poulton AJ. 2010. Summertime trends in
755 pelagic biogeochemistry at the Porcupine Abyssal Plain study site in the northeast
756 Atlantic. Deep-Sea Research Part II-Topical Studies in Oceanography 57:1313-1323.
757 Petursdottir H, Gislason A, Falk-Petersen S, Hop H, Svavarsson J. 2008. Trophic interactions
758 of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable
759 isotope analyses. Deep-Sea Research Part II-Topical Studies in Oceanography 55:83-
760 93.
761 Phleger CF, Nelson MM, Groce AK, Cary SC, Coyne KJ, Nichols PD. 2005. Lipid
762 composition of deep-sea hydrothermal vent tubeworm *Riftia pachyptila*, crabs
763 *Munidopsis subsquamosa* and *Bythograea thermydron*, mussels *Bathymodiolus* sp. and
764 limpets *Lepetodrilus* spp. Comparative Biochemistry and Physiology Part B:
765 Biochemistry and Molecular Biology 141:196-210.
766 R Development Core Team, 2015. R: A language and environment for statistical computing,
767 Journal. R Foundation for Statistical Computing, Vienna, Austria.
768 Raine R, White M, Dodge JD. 2002. The summer distribution of net plankton dinoflagellates
769 and their relation to water movements in the NE Atlantic Ocean, west of Ireland.
770 Journal of Plankton Research 24:1131-1147.
771 Ravet JL, Brett MT, Arhonditsis GB. 2010. The effects of seston lipids on zooplankton fatty
772 acid composition in Lake Washington, Washington, USA. Ecology 91:180-190.
773 Rix L, de Goeij JM, Mueller CE, Struck U, Middelburg JJ, van Duyl FC, et al. 2016. Coral
774 mucus fuels the sponge loop in warm- and cold-water coral reef ecosystems. Scientific
775 Reports 6:18715.
776 Roberts JM. 2005. Reef-aggregating behaviour by symbiotic eunicid polychaetes from cold-
777 water corals: do worms assemble reefs? Journal of the Marine Biological Association
778 of the United Kingdom 85:813-819.
779 Roberts JM, Wheeler AJ, Freiwald A. 2006. Reefs of the deep: The biology and geology of
780 cold-water coral ecosystems. Science 312:543-547.

781 Sherwood OA, Jamieson RE, Edinger EN, Wareham VE. 2008. Stable C and N isotopic
782 composition of cold-water corals from the Newfoundland and Labrador continental
783 slope: Examination of trophic, depth and spatial effects. Deep-Sea Research Part I-
784 Oceanographic Research Papers 55:1392-1402.
785 Slagstad D, Tande KS, Wassman P. 1999. Modelled carbon fluxes as validated by field dta
786 on the north Norwegian shelf during the productive period in 1994. Sarsia 84:303-317.
787 Soetaert K, Mohn C, Rengstorf A, Grehan A, van Oevelen D. 2016. Ecosystem engineering
788 creates a direct nutritional link between 600-m deep cold-water coral mounds and
789 surface productivity. Scientific Reports 6:35057.
790 Soffker M, Sloman KA, Hall-Spencer JM. 2011. *In situ* observations of fish associated with
791 coral reefs off Ireland. Deep-Sea Research Part I-Oceanographic Research Papers
792 58:818-825.
793 Stevenson A, Rocha C. 2013. Evidence for the bioerosion of deep-water corals by echinoids
794 in the Northeast Atlantic. Deep-Sea Research Part I-Oceanographic Research Papers
795 71:73-78.
796 Thiem O, Ravagnan E, Fosså JH, Berntsen J. 2006. Food supply mechanisms for cold-water
797 corals along a continental shelf edge. Journal of Marine Systems 60:207-219.
798 van Duyl FC, Hegeman J, Hoogstraten A, Maier C. 2008. Dissolved carbon fixation by
799 sponge-microbe consortia of deep water coral mounds in the northeastern Atlantic
800 Ocean. Marine Ecology Progress Series 358:137-150.
801 Van Gaever S, Moodley L, de Beer D, Vanreusel A. 2006. Meiobenthos at the Arctic Håkon
802 Mosby Mud Volcano, with a parental-caring nematode thriving in sulphide-rich
803 sediments. Marine Ecology Progress Series 321:143-155.
804 Van Oevelen D, Duineveld GCA, Lavaleye MSS, Mienis F, Soetaert K, Heip CHR. 2009.
805 The cold-water coral community as hotspot of carbon cycling on continental margins: a
806 food web analysis from Rockall Bank (northeast Atlantic). Limnology and
807 Oceanography 54:1829–1844.
808 Van Soest RWM, Lavaleye MSS. 2005. Diversity and abundance of sponges in bathyal coral
809 reefs of Rockall Bank, NE Atlantic, from boxcore samples. Marine Biology Research
810 1:338-349.
811 Wagner H, Purser A, Thomsen L, Jesus CC, Lundälv T. 2011. Particulate organic matter
812 fluxes and hydrodynamics at the Tisler cold-water coral reef. Journal of Marine
813 Systems 85:19-29.

814 Weisz JB, Lindquist N, Martens CS. 2008. Do associated microbial abundances impact
815 marine demosponge pumping rates and tissue densities? Oecologia 155:367-376.
816 White M, Wolff GA, Lundälv T, Guihen D, Kiriakoulakis K, Lavaleye M, et al. 2012. Cold-
817 water coral ecosystem (Tisler Reef, Norwegian Shelf) may be a hotspot for carbon
818 cycling. Marine Ecology Progress Series 465:11-23.
819 Wickham H, 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
820 Wieczorek SK, Hooper RG. 1995. Relationship between diet and food availability in the
821 snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. Journal of
822 Crustacean Biology 15:236-247.
823 Wild C, Mayr C, Wehrmann L, Schöttner S, Naumann M, Hoffmann F, et al. 2008. Organic
824 matter release by cold water corals and its implication for fauna-microbe interaction.
825 Marine Ecology Progress Series 372:67-75.
826 Yahel G, Whitney F, Reiswig HM, Eerkes-Medrano DI, Leys SP. 2007. In situ feeding and
827 metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate
828 fjord with a remotely operated submersible. Limnology and Oceanography 52:428-440.
829

Table 1. List of examined species of the reef food web of the Træna deep coral reef field. The species abbreviation (Abbr) is used in Table 3 and in Figures 2A and 3, *n* indicates the number of replicate specimens analysed for stable isotopes as presented in Fig. 2A.

Abbr	Taxon	Species	Common name	n
Bra_Bra	Brachiopoda	Brachiopoda sp.	lampshell	1
Cep_Sep	Cephalopoda	*Sepiola atlantica*	Little cuttlefish	2
Cni_Lop	Cnidaria	*Lophelia pertusa*	Deepwater white coral	4
Cop_lar	Copepoda large	*Calanus* sp. (>280 um)	copepod	2
Cop_sma	Copepoda small	*Calanus* sp. (>50 um)	copepod	2
Cru_Lit	Decapoda	*Lithodes maja*	Norway king crab	1
Cru_Mun	Decapoda	*Munida rugosa*	squat lobster	3
Cru_Pan	Decapoda	*Pandalus borealis*	Northern shrimp	7
Ech_Bon	Echiura	*Bonellia* sp.	Green spoonworm	1
Ech_Hen	Asteroidea	*Henricia pertusa*	sea star	4
Ech_Oph	Ophiuroidea	*Ophiopholis aculeata*	brittle star	2
Ech_Par	Holothuroidea	*Parastichopus tremulus*	sea cucumber	1
Eup_Meg	Euphausiacea	*Meganyctiphanes norvegica*	Northern krill	6
Eup_Thy	Euphausiacea	*Thysanoessa inermis*	krill	1
Pis_Arg	Pisces	*Argentina sphyraena*	Argentine	1
Pis_Art	Pisces	*Artediellus atlanticus*	Atlantic hookear sculpin	3
Pis_Bro	Pisces	*Brosme brosme*	Tusk	12
Pis_Chi	Pisces	*Chimaera monstrosa*	Rabbit fish	2
Pis_Hip	Pisces	*Hippoglossoides platessoides*	American plaice	3
Pis_Mar	Pisces	*Maurolicus muelleri*	Silvery lightfish	2
Pis_Phy	Pisces	*Phycis blennoides*	Greater forkbeard	2
Pis_Pol	Pisces	*Pollachius virens*	Saith	2
Pis_Seb	Pisces	*Sebastes viviparus*	Norway redfish	1
Pis_Tri	Pisces	*Trisopterus esmarkii*	Norway pout	6
Por_Dem	Porifera	Demospongia spp.	mix of large sponges	18
Tun_Asc	Tunicata	*Ascidia* sp.	sea squirt	1
SPM	Suspended matter	Suspended particulate matter		2
Sed_cwc	Sediment cwc	Sediment coral reef		6
Sed_off	Sediment off	Sediment off-reef		2

834 Table 2. List of examined species of the cold-water coral reef food web at Belgica Mounds.
835 The species abbreviation (Abbr) is used in Table 4 and in Figures 2B and 4, *n* indicates the
836 number of replicate specimens analysed for the stable isotopes as presented in Fig. 2B.

Abbr	Taxon	Species	Common name	n
Biv_Hia	Bivalvia	*Hiatella arctica*	Wrinkled rockborer	2
Cep_Bat	Cephalopoda	*Bathypolypus bairdii*	Spoonarm octopus	2
Cni_Act	Cnidaria	*Actinauge* sp.	anemone	1
Cni_Ant	Cnidaria	*Anthomastus* sp.	soft coral	2
Cni_Cir	Cnidaria	*Cirrhipathes* sp.	Spiral wire coral	2
Cni_Gor	Cnidaria	gorgonian spp.	gorgonian	3
Cni_Hyd	Cnidaria	Hydrozoa spp.	hydroid polyp	3
Cni_Lei	Cnidaria	*Leiopathes* sp.	Black coral	3
Cni_Lop	Cnidaria	*Lophelia pertusa*	Deepwater white coral	3
Cni_Mad	Cnidaria	*Madrepora oculata*	Zigzag coral	3
Cru_Amp	Amphipoda	Amphipoda sp.	sandhopper	1
Cru_Bat	Decapoda	*Bathynectes* sp.	crab	3
Cru_Car	Decapoda	Caridea spp.	shrimp	3
Cru_Cir	Cirripedia	Cirripedia spp.	barnacle	3
Cru_Mun	Decapoda	*Munida* sp.	squat lobster	5
Ech_Ast	Asteroidea	Asteroidea spp.	sea star	3
Ech_Cid	Echinoidea	*Cidaris* sp.	sea urchin	2
Ech_Ech	Echinoidea	*Echinus* sp.	sea urchin	-
Ech_Oph	Ophiuroidea	Ophiuroidea spp.	brittle star	2
Hol_Pso	Holothuroidea	*Psolus* sp.	sea cucumber	1
Gas_Cal	Gastropoda	*Calliostoma* sp.	top snail	3
Pis_Cat	Pisces	*Cataetyx alleni*	deep-sea bythitid fish	2
Pis_Coe	Pisces	*Coelorinchus abditilux*	grenadier	1
Pis_Cor	Pisces	*Coryphaenoides rupestris*	Roundnose grenadier	1
Pis_Epi	Pisces	*Epigonus telescopus*	Black cardinal fish	1
Pis_Gai	Pisces	*Gaidropsarus vulgaris*	Three-bearded rockling	3
Pis_Gut	Pisces	*Guttigadus latifrons*	deep-sea morid fish	1
Pis_Lep	Pisces	*Lepidion eques*	North Atlantic codling	1
Pis_Neo	Pisces	*Neocyttus helgae*	oreo	1
Pol_Eun	Polychaeta	*Eunice norvegica*	bristle worm	3
Pol_Hes	Polychaeta	Hesionidae sp.	bristle worm	3
Por_Aph	Porifera	*Aphrocallistes* sp.	glass sponge	3
Por_Hex	Porifera	Hexactinellida sp.	glass sponge	1
Por_Spo	Porifera	*Spongosorites* sp.	demosponge	3
Tun_Sal	Tunicata	Salpidae sp.	salp	1
SPM	Susp. part. mat.			3
Trap	Sediment trap			12
Zoo	Zooplankton			2

Table 3. Total fatty acid concentration (mean ± standard deviation in mg C g^{-1} WW, except for *Lophelia pertusa* which is in mg C g^{-1} DW [skeleton + tissue]) based on 'n' specimens, and percentages (mean ± standard deviation) of bacterial, algal and zooplankton fatty acids of species of the cold-water coral reef food web at the Træna deep coral reef field. The essential fatty acid markers are given in 'bold' or are listed under 'Essential fatty acids'. For taxa abbreviations see Table 1, '-' means not detected.

Taxa	Concentration		Bacterial markers (%)						Algal markers (%)					Zooplankton markers (%)			Essential fatty acids (%)	
	mg C / g WW	n	iC14:0	iC15:0	aiC15:0	iC17:0	aiC17:0	C18.1ω7c	C16:4ω3	**C18:3ω3**	C18:4ω3	**C20:5ω3**	**C22:6ω3**	C20:1ω9c	C22:1ω9	C22:1ω11	C18:2ω6c	C20:4ω6
Bra_Bra	0.44±0.1	3	-	-	-	0.67±1.17	-	2.83±0.25	0.42±0.73	-	-	3.93±1.14	10.74±2.67	1.7±2.95	-	-	0.43±0.75	4.25±2.03
Cep_Sep	9.38±6.79	2	-	-	-	0.31±0.08	-	1.8±0.24	0.19±0.26	-	0.09±0.13	15.79±1.82	34.77±1.03	1.64±0.46	-	0.09±0.13	0.4±0.16	1.78±0.69
Cni_Lop	1.03±0.34	4	0.05±0.02	0.1±0.05	0.03±0.01	0.61±0.39	0.19±0.02	0.18±0.01	0.21±0.02	-	0.23±0.18	0.34±0.04	1.01±0.13	5.76±6.73	1.85±0.15	0.2±0.07	1.11±0.07	12.08±3.34
Cop_lar	28.57±3.04	2	-	0.3±0	0.26±0	-	-	0.52±0	0.37±0.01	2.78±0	10.73±0.04	2.54±0.65	12.8±2.05	0.4±0.01	0.28±0.39	-	1.16±0	0.29±0.05
Cop_sma	49.64±7.88	2	0.02±0.02	0.15±0.16	0.23±0	-	0.09±0.03	0.5±0.07	0.3±0.06	2.54±0.15	9.48±0.84	1.29±1.13	13.28±0.93	0.33±0.08	1.27±1.8	-	0.92±0.19	0.21±0.06
Cru_Lit	0.54	1	-	-	-	-	-	7.71	-	-	-	7.06	5.44	-	-	-	-	6.27
Cru_Mun	3.23±1.06	2	-	-	-	0.37±0.01	0.09±0	4.71±0.09	0.94±0.07	-	0.2±0.03	17.72±0.42	17.71±0.13	1.05±0.1	-	-	1.19±0.1	2.15±0.03
Cru_Pan	2.9±0.68	6	-	0.1±0.05	-	0.47±0.18	0.13±0.11	5.93±0.44	0.21±0.13	-	0.12±0.07	13.28±1.17	16.67±2.71	0.58±0.15	-	0.08±0.13	0.91±0.15	1.42±1.62
Ech_Hen	0.89±0.48	3	0.34±0.33	2.1±0.89	0.83±0.26	1.85±0.69	0.57±0.22	11.29±3.14	0.39±0.43	-	-	1±0.36	0.52±0.07	-	-	-	0.75±0.56	7.62±6.63
Ech_Oph	8.58±10.27	4	0.17±0.12	1.17±0.29	0.65±0.25	0.72±0.15	0.18±0.14	3.23±1.23	0.18±0.24	-	2.71±1.3	6.05±4.15	2.42±1.74	5.35±2.14	-	0.23±0.26	1.25±0.31	2.08±0.99
Ech_Par	0.2	1	-	3.75	2	4.08	-	3.76	-	-	1.29	3.42	3.91	-	-	-	-	11.04
Eup_Meg	3.43±0.85	3	-	0.08±0.13	-	0.31±0.12	-	3.42±0.32	0.3±0.07	-	0.46±0.54	7.41±2.14	25.57±3.57	1.04±0.27	-	0.14±0.24	1.51±0.29	0.87±0.18
Eup_Thy	48.54±65.07	2	-	0.08±0.11	-	0.52±0.74	-	5.65±2.32	0.32±0.45	-	2.41±0.85	16.91±2.33	18.68±17.55	0.09±0.13	-	0.22±0.31	1.98±1.32	0.17±0.24
Pis_Arg	1.99±0.55	2	-	0.08±0.11	-	0.26±0.03	-	2.75±0.29	0.34±0.04	-	0.32±0.15	4.65±0.49	29.95±11.26	0.64±0.14	-	0.5±0.07	1.01±0.18	1.17±0.09
Pis_Art	1.62±0.84	3	-	-	-	0.71±0.26	0.09±0.15	3.89±2	0.12±0.1	-	-	8.01±3.16	25.8±15.3	0.53±0.21	-	0.08±0.13	0.83±0.17	5.96±0.83
Pis_Bro	3.88±2.46	6	0.04±0.15	0.18±0.03	0.02±0.02	0.29±0.05	0.13±0.08	0.41±0.86	0.08±0.03	-	0.06±0.06	0.03±0.05	12.98±4.36	10.14±3.49	3.09±4.06	5.64±4.29	1±0.14	3.34±0.72
Pis_Chi	2.9±0.49	2	-	-	-	0.68±0.16	0.17±0.06	3.98±0.09	0.58±0.13	-	-	6.29±0.56	34.94±1.92	0.47±0.04	-	0.22±0.01	0.44±0.02	4.3±0.33
Pis_Hip	1.45±0.31	3	-	-	-	0.58±0.26	-	2.86±1.84	-	-	-	12.41±2.37	29.66±9.95	0.68±0.22	-	0.2±0.17	1.33±0.56	7.81±0.72
Pis_Mar	75.49±0.64	3	-	0.4±0.09	0.14±0.02	0.48±0.08	0.08±0.01	1.81±0.57	0.23±0.05	-	0.74±0.2	29.42±1.07	4.49±0.52	-	-	0.28±0.14	0.97±0.05	0.2±0.05
Pis_Phy	1.8±0.35	2	-	-	-	0.33±0.13	-	2.93±0.27	0.06±0.09	-	0.13±0.04	4.77±6.75	31.4±3.69	1.59±0.86	-	0.56±0.35	0.77±0.04	6.54±3.35
Pis_Pol	16.28±1.04	2	-	-	-	-	-	4.31±1.16	-	0.68±0.43	0.67±0.19	1.07±0.46	1.24±1.75	0.73±0.46	-	-	1.34±0.8	2.59±0.18
Pis_Seb	8.15±8.89	3	-	0.04±0.06	0.01±0.02	0.25±0.02	-	1.8±0.29	0.04±0.06	-	0.37±0.07	7.94±1.08	24.2±21.02	0.4±0.35	0.75±1.3	0.28±0.25	3.38±0.33	1.83±0.62
Pis_Tri	4.28±0.66	2	-	0.08±0.11	-	0.21±0.01	-	2.24±0.91	0.23±0.03	-	0.29±0.13	8.19±0.73	35.99±1.81	0.74±0.19	-	1.99±2.34	0.73±0.09	1.14±0.48
Por_Dem	0.67±0.48	17	0.14±0.27	1.85±1.77	1.49±1.42	1.24±1.31	1.26±1.98	4.41±2.38	0.73±1.1	0.24±0.53	1.07±1.6	2.1±2.31	5.27±7.22	1.06±0.91	-	0.5±0.98	0.38±0.4	0.75±0.8
Sed_cwc	0.01±0.004	6	0.68±0.38	2.63±0.66	3.07±0.56	2.35±0.79	0.71±0.38	5.93±2.59	-	-	0.59±0.52	0.4±0.63	1.88±1.48	2.66±3.26	2.1±1.49	-	0.59±0.33	3.24±2.15
Sed_off	$0.009±1{\cdot}10^{-6}$	2	0.94±0.01	2.99±0.16	3.41±0.07	3.03±0.11	0.94±0.07	8.07±0.85	-	-	0.65±0.92	-	1.68±0.13	1.89±2.68	2.13±0.07	-	0.32±0.45	5±0.54
Tun_Asc	0.41±0.58	3	-	-	-	-	-	9.59±5.73	-	-	1.61±2.78	4.08±4.41	12.5±6.13	-	-	-	-	14.31±9.37

Table 4. Total fatty acid concentration (mean ± standard deviation in mg C g^{-1} WW, except for *Lophelia pertusa* which is in mg C g^{-1} DW [skeleton + tissue]) based on 'n' samples, and percentages (mean ± standard deviation) of bacterial, algal and zooplankton fatty acids of taxa of the reef food web at Belgica Mounds. Essential fatty acids are in 'bold' or are listed under 'Essential fatty acids'. For taxa abbreviations see Table 2, '-' means not detected.

Taxa	Concentration		Bacterial markers (%)						Algal markers (%)					Zooplankton markers (%)			Essential fatty acids (%)	
	mg C / g WW	n	iC14:0	iC15:0	aiC15:0	iC17:0	aiC17:0	C18:1ω7c	C16:4ω3	**C18:3ω3**	C18:4ω3	**C20:5ω3**	**C22:6ω3**	C20:1ω9c	C22:1ω9	C22:1ω11	C18:2ω6c	C20:4ω6
Biv_Hia	1.34±0.51	2	-	-	-	0.49±0.09	-	0.94±0.42	-	0.12±0.16	0.39±0.17	8.81±12.47	15.11±0.15	0.35±0.01	-	-	2.01±0.15	9.85±2.98
Cep_Bat	0.87±0.13	2	-	-	-	-	-	1.33±0.13	-	-	-	19.62±5.32	30.64±4.88	-	-	-	-	7.89±1.04
Cni_Act	1	1	-	-	-	0.89	-	2.49	-	-	-	13.95	10.96	2.54	-	-	0.44	1.53
Cni_Ant	0.74±0.62	4	-	-	-	0.14±0.28	-	3.15±0.99	-	-	0.24±0.47	5.56±4.88	3.94±1.85	3.46±0.46	-	-	0.36±0.45	22.3±10.67
Cni_Cir	2.31±1.05	3	-	0.07±0.12	-	0.38±0.04	-	1.33±0.53	-	-	0.13±0.22	23.1±1.23	0.87±0.71	3.09±2.68	-	-	0.05±0.09	5.69±2.26
Cni_Gor	1.86±1.23	3	-	0.29±0.25	0.58±0.59	2.3±2.04	0.03±0.06	2.24±0.28	-	-	-	5.44±1.23	3.25±0.67	0.82±0.22	-	-	0.81±0.28	12.29±2.36
Cni_Hyd	11.09±3.21	3	0.26±0.09	0.62±0.2	0.29±0.09	0.74±0.16	0.28±0.08	2.52±0.11	-	-	-	3.4±1.61	4.08±2.98	0.43±0.05	-	-	0.95±0.32	3.37±2.54
Cni_Lei	8.46±2.01	3	-	0.05±0.08	-	0.44±0.03	-	3.68±0.23	-	-	-	14.3±0.78	0.63±0.22	1.19±0.11	-	-	0.92±0.18	2.33±0.79
Cni_Lop	0.81±0.76	3	-	0.11±0.2	-	1.17±0.76	-	2.58±0.04	2.61±4.53	-	0.29±0.51	7.27±6.29	4.71±3.29	2.04±1.97	-	2.24±3.87	0.82±0.72	2.52±1.55
Cni_Mad	1.81±1.13	3	-	0.04±0.06	-	1.33±0.87	0.03±0.06	1.59±1.25	0.1±0.18	-	0.19±0.32	8.58±7.37	5.79±1.1	1.84±2.15	0.57±0.99	1.87±3.23	0.97±0.39	5.34±3.65
Cru_Amp	92.36	1	-	-	0.06	-	-	24.44	-	-	1.49	6.61	9.55	0.43	-	-	1.22	1.26
Cru_Bat	1.85±0.61	3	-	-	-	0.48±0.02	0.06±0.1	2.42±0.47	-	-	0.15±0.13	9.12±15.8	15.9±1.24	-	-	-	1.29±0.14	6.11±1.62
Cru_Car	2.34±0.34	2	-	-	-	0.29±0.01	-	5.61±0.65	-	-	0.18±0.26	16.31±2.15	15.94±1.83	0.14±0.02	-	-	0.88±0	2.97±0.45
Cru_Cir	27.67±25.36	3	-	0.25±0.05	-	-	-	1.81±0.18	-	0.26±0.45	0.6±1.04	4.64±8.04	10.21±1.4	0.34±0.02	-	-	1.08±0.17	0.61±0.27
Cru_Mun	3.5±0.77	5	0.09±0.21	0.52±1.14	-	0.25±0.05	0.08±0.02	0.81±1.53	0.03±0.02	-	0.14±0.02	-	14.93±1.96	1.11±0.41	0.05±0.08	0.38±0.43	0.64±0.37	13.72±1.7
Ech_Ast	0.37±0.09	3	0.8±1.24	0.22±0.08	0.14±0.13	0.09±0.09	0.05±0.05	1.8±0.65	0.02±0.04	-	-	0.03±0.04	0.92±0.38	1.84±3.18	-	-	0.08±0.13	17.48±3.85
Ech_Cid	0.34±0.04	3	-	0.07±0.06	-	0.3±0.27	-	3.82±0.91	-	-	-	2.22±2.23	0.5±0.86	0.45±0.77	-	-	0.11±0.1	16.67±14.35
Ech_Ech	0.56	1	-	-	-	0.63	-	1.58	-	-	-	9.29	4.26	7.69	-	-	0.29	22.8
Ech_Oph	6.82±0.45	2	0.21±0.11	0.52±0.16	0.42±0.18	0.27±0.38	0.1±0.02	3.21±0.37	-	-	1.8±0.44	12.83±1.26	3.05±0.36	0.75±0	-	-	0.78±0.14	2.78±1.58
Gas_Cal	2.8±0.13	3	-	-	0.03±0.05	0.34±0.13	0.28±0.06	3.73±0.22	-	-	-	5.23±4.56	1.59±0.17	0.07±0.13	-	-	1.26±0.34	16.03±1.41
Hol_Pso	0.91	1	-	0.35	-	-	-	1.29	-	-	-	13.55	5.74	0.81	-	-	0.27	23.53
Pis_Cat	1.83±0	2	-	-	-	0.51±0.07	-	3±0.26	-	-	-	5.71±0.52	32.41±7.07	0.22±0.31	-	-	1.04±0.04	3.06±0.59
Pis_Coe	1.22	1	-	-	-	-	-	1.21	-	-	-	8.49	42.88	-	-	-	0.42	6.65
Pis_Epi	32.36	1	-	-	-	0.22	-	3.03	-	-	-	23.22	8.59	2.04	-	-	0.77	0.82
Pis_Gai	1.61±0.63	3	-	-	-	-	-	2.08±0.23	-	-	-	6.45±0.49	31.7±4.35	0.13±0.22	-	-	0.6±0.07	3.86±0.01
Pis_Gut	1.1±0.1	2	-	-	-	-	-	1.23±0.08	-	-	-	7.45±1.94	30.88±2.93	-	-	-	0.77±0.04	2.53±0.21
Pis_Lep	0.78±0.19	4	-	-	-	0.08±0.17	-	1.88±0.31	-	-	0.07±0.13	3.94±2.96	29.45±2.73	0.08±0.17	-	-	0.6±0.18	3.03±1.38
Pis_Neo	1.81	1	-	-	-	0.3	-	2.23	-	-	-	7.17	10.58	1.02	-	-	0.82	1.81
Pol_Eun	2.81±0.66	2	-	0.07±0.1	0.05±0.07	0.24±0.07	-	1.92±0.31	-	-	0.52±0.15	17.48±1.82	6.86±0.61	0.51±0.02	-	-	1.05±0.01	4.24±0.72
Pol_Hes	10.85±9.64	3	-	0.06±0.05	-	-	-	3.7±0.34	-	-	0.37±0.48	6.65±6.1	17.54±4.55	0.32±0.04	-	-	1.52±0.34	0.73±0.33
Por_Aph	0.17±0.04	3	-	-	-	-	-	1.25±2.16	-	-	-	5.93±4.08	33.35±26.02	-	-	-	-	4.67±4.3
Por_Hex	0.15	1	-	-	-	-	-	8.62	-	-	-	8.41	3.47	-	-	-	2.04	5.9
Por_Spo	1.01±0.75	3	-	-	2.4±0.68	3.53±2	0.76±0.43	5.44±0.75	-	-	-	0.14±0.25	4.84±6.33	-	-	-	0.08±0.15	-
SPM	0.01±0.01	3	-	0.15±0.26	0.45±0.48	-	-	3.47±0.54	1.54±1.39	-	-	-	2.77±3.91	0.14±0.25	-	-	4.13±0.95	1.37±1.46
Tun_Sal	0.41±0.26	3	-	0.67±0.67	0.64±0.67	0.49±0.43	-	0.96±0.88	-	-	1.65±2.86	2.93±5.07	10.15±10.58	0.08±0.14	-	-	0.99±0.93	1.16±1.1

Figure 1. Sample locations at (A) the Træna Deep Coral Reef field indicated as black dots and the white box shows the border of the Træna MPA on the Norwegian shelf (inset) and (B) the Belgica Mounds province on the Irish margin (inset map) with the investigated coral mound enclosed in a white square.

Figure 2. Mean (± standard deviation) $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values for various organic matter sources, reef fauna and fishes at Træna (A) and Belgica Mounds (B). Samples are sorted alphabetically with fish species highlighted in red. Abbreviations for panel A can be found in Table 1 and for panel B in Table 2.

Figure 3. Proportion of (A) summed bacterial fatty acids, (B) summed algal fatty acids, (C) summed zooplankton fatty acids and (D) summed essential fatty acids of species of the Træna deep coral reef field. Errors bars indicate standard deviation calculated from the replicate samples indicated in Table 3. See Table 1 for abbreviations.

Figure 4. Proportion of (A) summed bacterial fatty acids, (B) summed algal fatty acids, (C) summed zooplankton fatty acids and (D) summed essential fatty acids of species of the Belgica Mounds. Errors bars indicate standard deviation calculated from the replicate samples indicated in Table 4. See Table 2 for abbreviations.

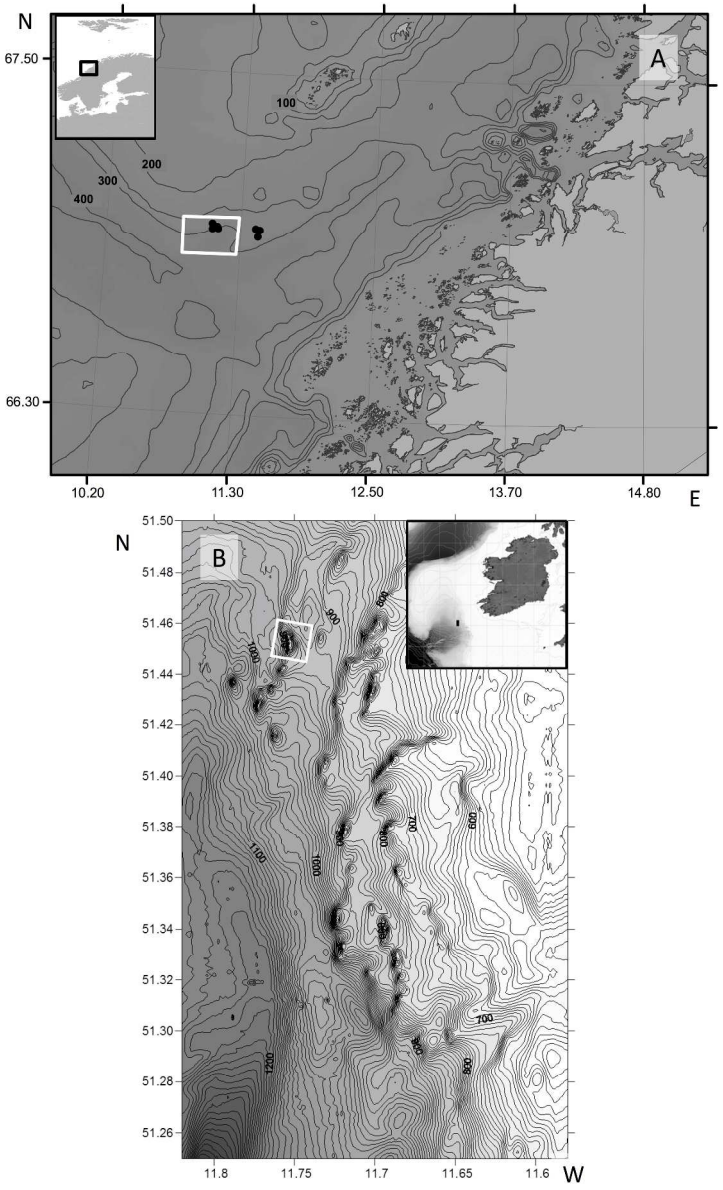
Figure 5. Time series from October 2011 to October 2012 of A) fluorescence signal (in relative units), B) chlorophyll *a* deposition (ng m^{-2} d^{-1}) in the sediment trap and C) number of visible aggregates on a still image. The inset figure on the left shows image from period with no visible aggregates (2-Nov-2011) and inset figure on the right shows an example image from period (2-May-2012) with

visible aggregates in the picture (i.e. the whitish specks in the dark top part of the inset figure).

Figure 6. PC1 and PC2 plot of the principle component analysis of the summed specific fatty acids for algae, bacteria and zooplankton with sites Træna and Belgica mounds as group factor. Normal distribution ellipsoids are indicated.

Figure 7. PC1 and PC2 plots of the principal component analysis of the summed specific fatty acids for algae, bacteria and zooplankton for A) Cnidarian samples with sites Træna and Belgica Mounds as group factor, B) Cnidarian samples with sites and taxa as group factor, C) Pisces samples with sites Træna and Belgica Mounds as group factor, D) Pisces samples with sites and taxa as group factor. Normal distribution ellipsoids are indicated. Abbreviations in the legends of subplot B and D are denoted as "TR_" for Træna and "BM_" for Belgica Mounds followed by the taxa abbreviation, which can be found in Table 1 and 2 for Træna and Belgica Mounds, respectively.

Figure 8. $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of individual sponge samples at the Træna coral reef (open symbols) and Belgica Mounds (closed symbols).



Sample locations at (A) the Træna Deep Coral Reef field indicated as black dots and the white box shows the border of the Træna MPA on the Norwegian shelf (inset) and (B) the Belgica Mounds province on the Irish margin (inset map) with the investigated coral mound enclosed in a white square.

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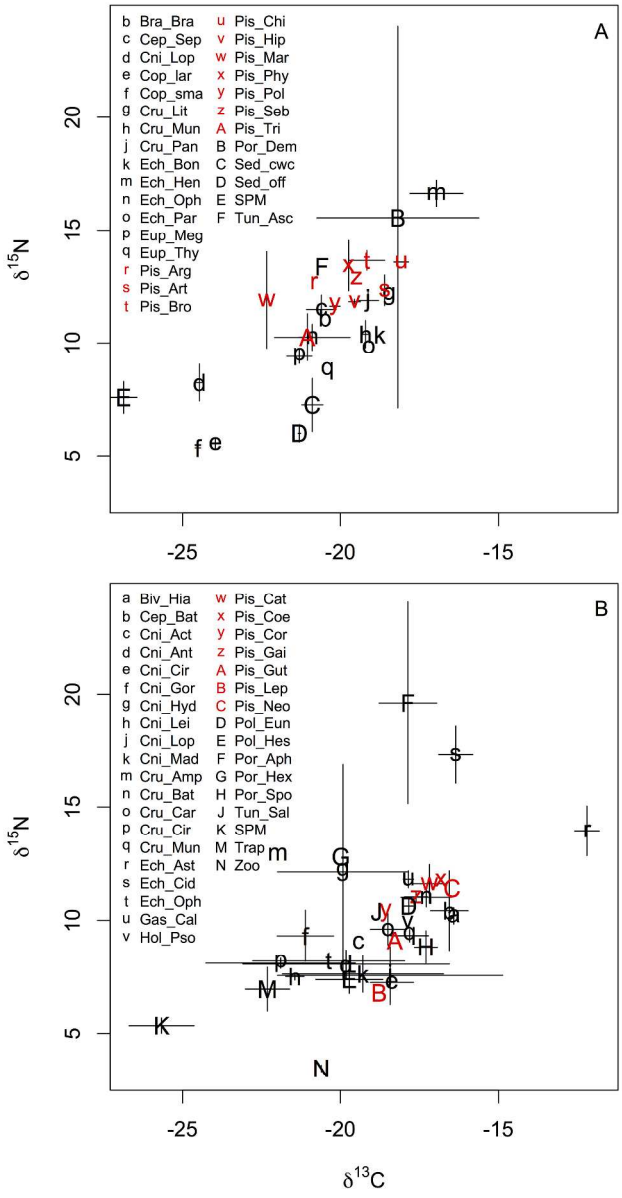
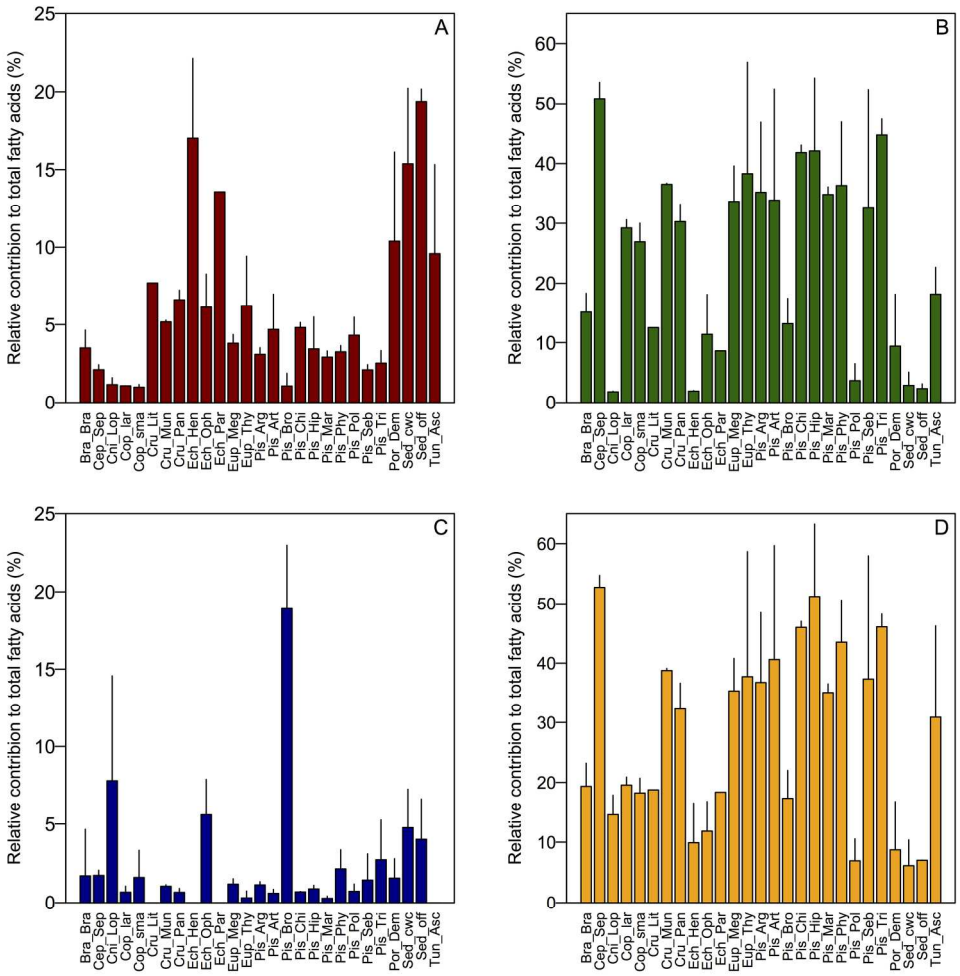


Mean (standard deviation) $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values for various organic matter sources, reef fauna and fishes at Træna (A) and Belgica Mounds (B). Samples are sorted alphabetically with fish species highlighted in red. Abbreviations for panel A can be found in Table 1 and for panel B in Table 2.

275x397mm (300 x 300 DPI)



Proportion of (A) summed bacterial fatty acids, (B) summed algal fatty acids, (C) summed zooplankton fatty acids and (D) summed essential fatty acids of species of the Træna deep coral reef field. Errors bars indicate standard deviation calculated from the replicate samples indicated in Table 3. See Table 1 for abbreviations.

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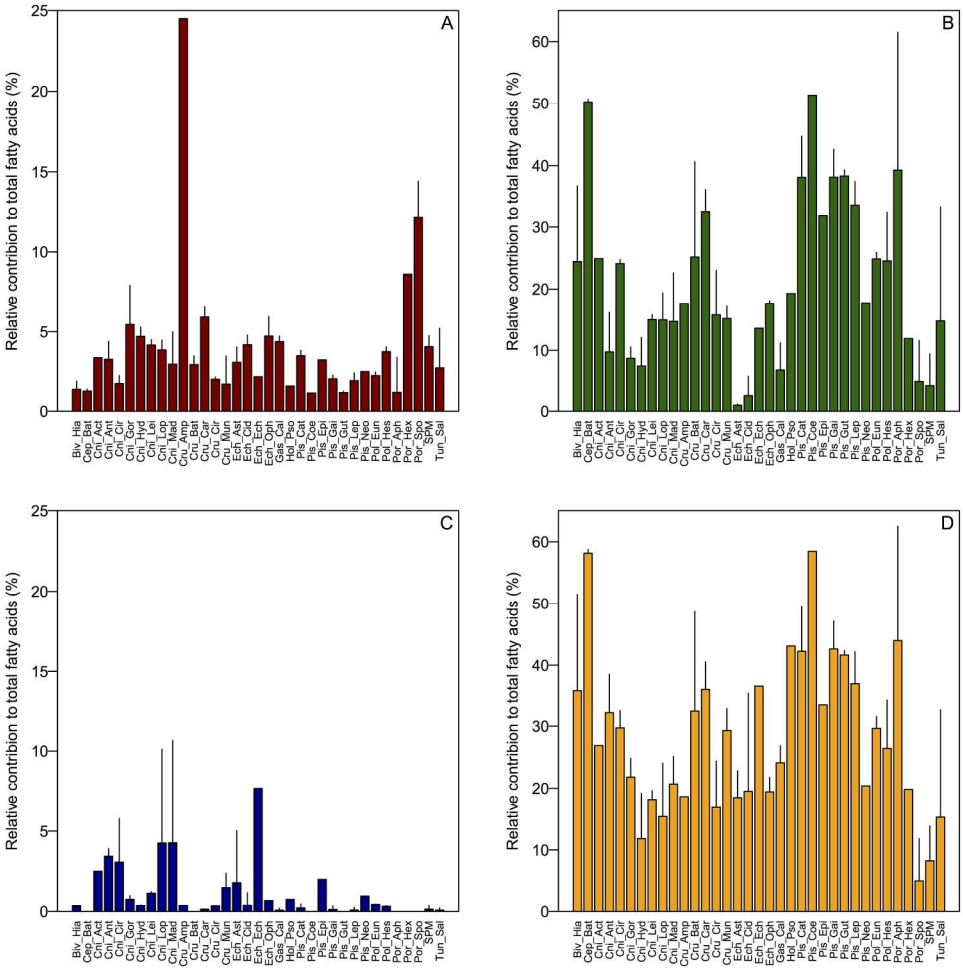
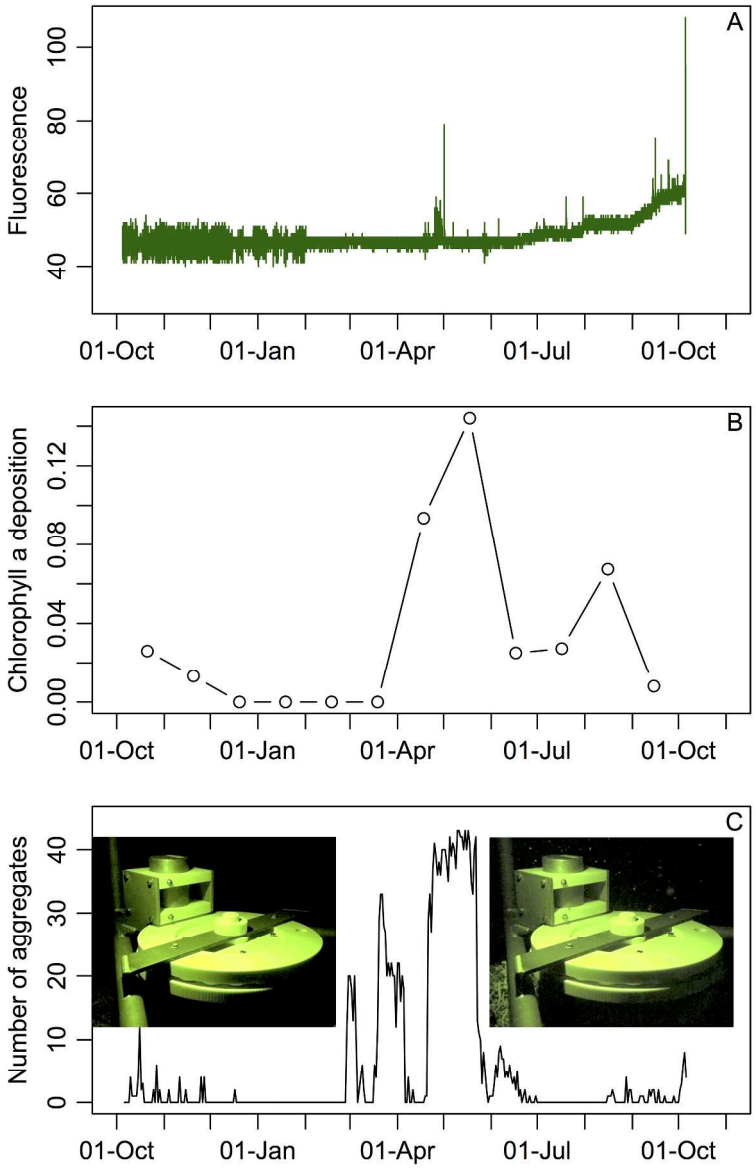


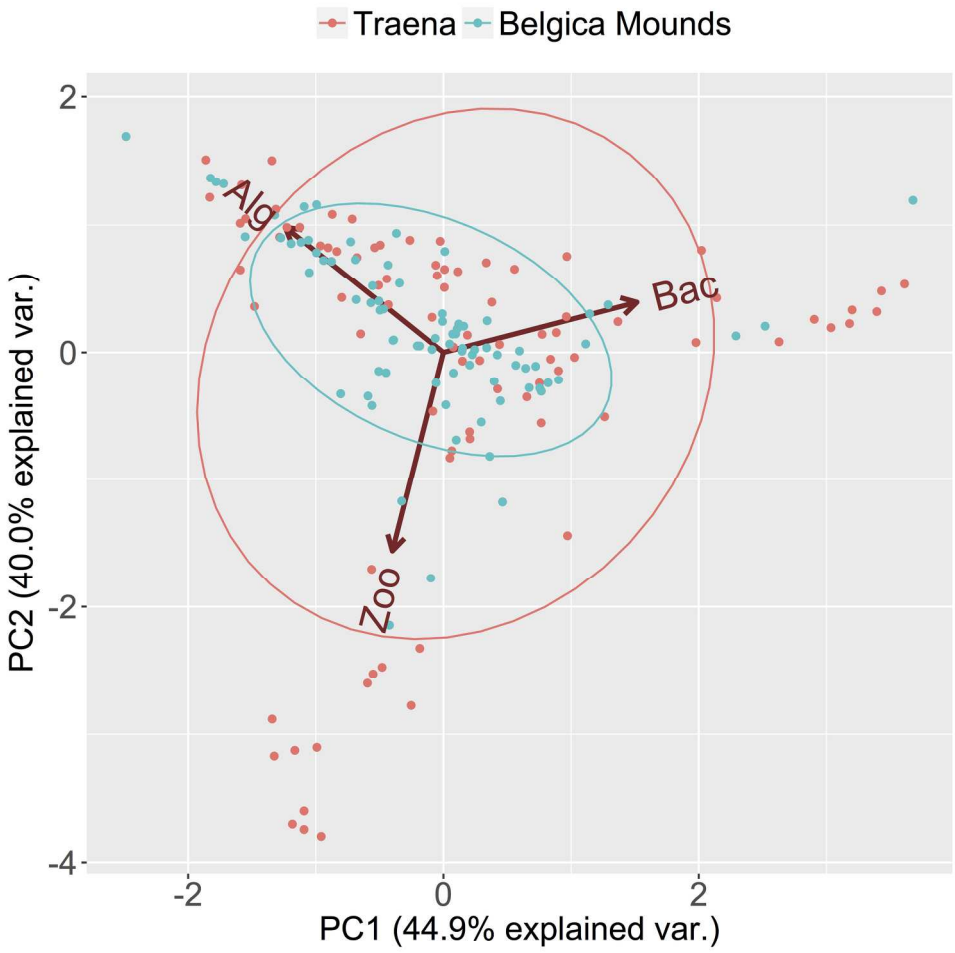
Proportion of (A) summed bacterial fatty acids, (B) summed algal fatty acids, (C) summed zooplankton fatty acids and (D) summed essential fatty acids of species of the Belgica Mounds. Errors bars indicate standard deviation calculated from the replicate samples indicated in Table 4. See Table 2 for abbreviations.

228x228mm (300 x 300 DPI)



Time series from October 2011 to October 2012 of A) fluorescence signal (in relative units), B) chlorophyll *a* deposition (ng m^{-2} d^{-1}) in the sediment trap and C) number of visible aggregates on a still image. The inset figure on the left shows image from period with no visible aggregates (2-Nov-2011) and inset figure on the right shows an example image from period (2-May-2012) with visible aggregates in the picture (i.e. the whitish specks in the dark top part of the inset figure).

203x325mm (300 x 300 DPI)



PC1 and PC2 plot of the principle component analysis of the summed specific fatty acids for algae, bacteria and zooplankton with sites Træna and Belgica mounds as group factor. Normal distribution ellipsoids are indicated.

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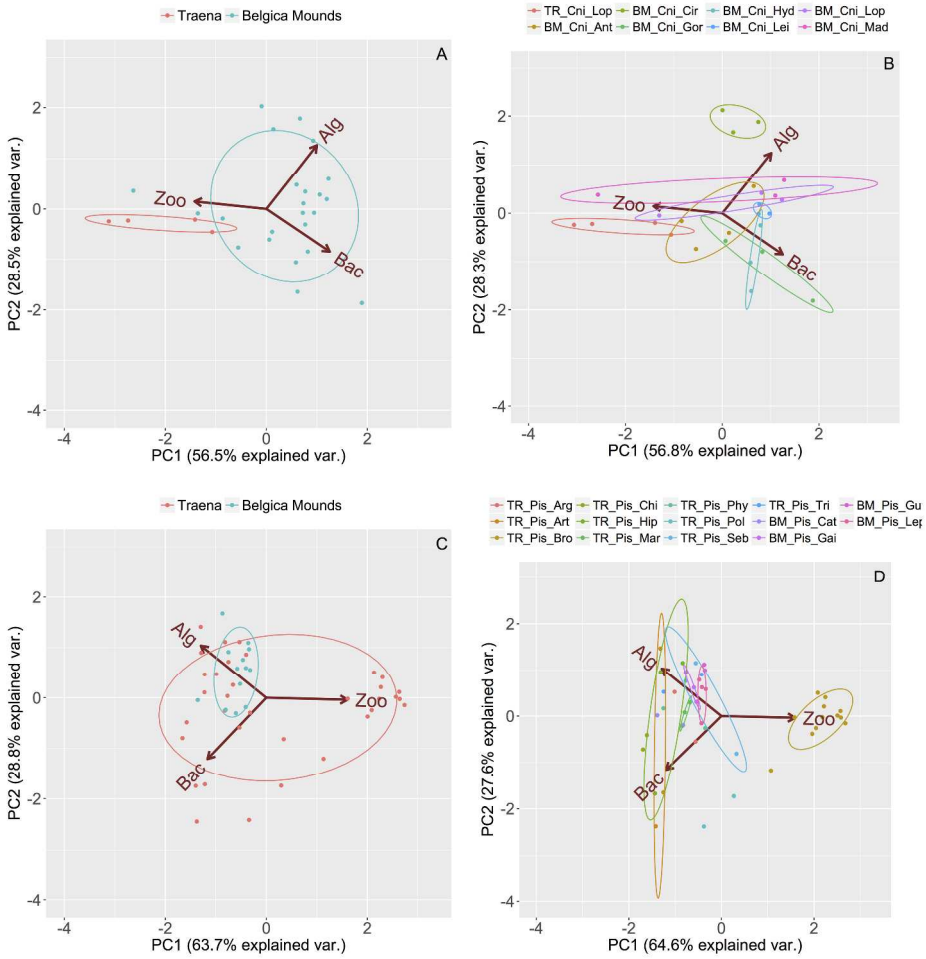

PC1 and PC2 plots of the principal component analysis of the summed specific fatty acids for algae, bacteria and zooplankton for A) Cnidarian samples with sites Træna and Belgica Mounds as group factor, B) Cnidarian samples with sites and taxa as group factor, C) Pisces samples with sites Træna and Belgica Mounds as group factor, D) Pisces samples with sites and taxa as group factor. Normal distribution ellipsoids are indicated. Abbreviations in the legends of subplot B and D are denoted as "TR_" for Træna and "BM_" for Belgica Mounds followed by the taxa abbreviation, which can be found in Table 1 and 2 for Træna and Belgica Mounds, respectively.

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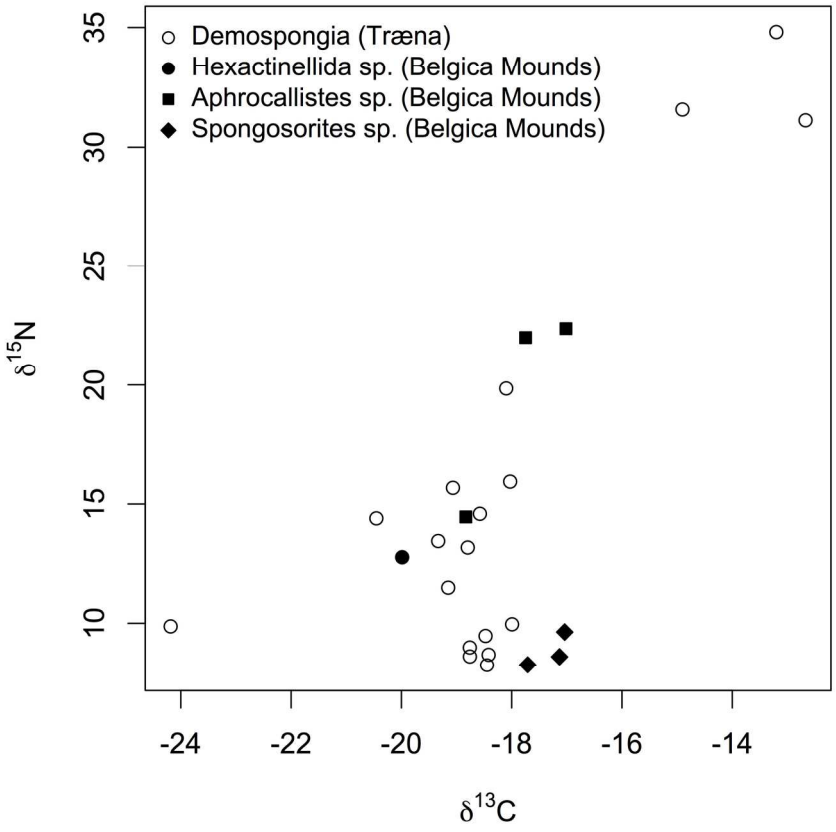

$\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of individual sponge samples at the Træna coral reef (open symbols) and Belgica Mounds (closed symbols).

177x177mm (300 x 300 DPI)