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Deep-Sea Research Part I

Community structure of deep fjord and shelf benthic fauna receiving different detrital kelp inputs in northern Norway

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ABSTRACT

Kelp forests produce large amounts of macroalgal detritus, ranging from whole plants to small particles (1 mm). The role of this kelp detritus in fueling deep-sea communities adjacent to healthy kelp forests was investigated in a region in the north of Norway by comparing the community structure and biodiversity of meio-, macro-, and megafauna in two deep (450 m) areas with different expected input of kelp detritus: a deep fjord basin surrounded by kelp forests and the adjacent continental shelf 15 km offshore from the kelp forests. The results showed that, although the fjord received a significantly higher amount of large kelp detritus (i.e. blades) than the shelf area, the amount of small kelp detritus available on the sediment was similar in both areas. There were significant differences in the multidimensional scaling analyses on the community structure for meio-, macro-, and megafauna between the fjord and the shelf. Significant differences were also found in biomass, abundance and biodiversity indices for some groups. However, no clear pattern emerged in the community structure and biodiversity between the fjord and the shelf, and the observed differences could not be linked directly to kelp detritus availability. The similar amounts of small particles of kelp detritus in the fjord and shelf area suggest that kelp detritus can provide organic matter to ecosystems further away than initially hypothesized, thus potentially shaping the structure and functioning of deep benthic communities distant from the kelp forests. Yet, the direct (trophic) links of kelp detritus and the studied benthic fauna need to be further analysed. The results are discussed in relation to current global changes in kelp forest, including regime shifts from healthy kelp reefs to turfs or barren areas, which reduce drastically the amount of macroalgal detritus produced and exported.

1. Introduction

Deep-sea ecosystems (commonly considered below 250 m depth and often coinciding with the shelf break, Thisle, 2003) are characterized by the lack of photosynthetically-available light. Deep-sea communities are thus predominantly heterotrophic, with their metabolism depending on the breakdown of complex organic molecules ultimately derived from photosynthetic production in the euphotic zone (Gage, 2003). This particulate organic matter enters the system through the water column as "marine snow", as well as advected down the margins or as sporadic falls of large parcels of organic matter (e.g. fish, whales, wood and macroalgae) (Ramirez-Llodra et al., 2010). Several biological and environmental factors shape the composition and distribution of deep-sea communities, including depth and its related variables (temperature, pressure, light), topography, habitat type and heterogeneity, food supply, biological interactions, connectivity and food availability (Levin et al., 2010; Smith et al., 2008; Ramirez-Llodra et al., 2010; Rex and Etter, 2010) as well as, increasingly, human impacts including

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climate change (Ramirez-Llodra et al., 2011). Because of the heterotrophic nature of most deep-sea communities, the quantity and quality of food supply to the deep-sea floor plays a major role in shaping not only species composition, but also the spatio-temporal patterns of abundance and species richness (Billett et al., 2001; Stuart et al., 2003; Smith et al., 2008; Costello and Chaudhary, 2017).

The efficient use by pelagic heterotrophs of the labile components in the sinking particulate organic matter (POM) significantly decreases the quality and quantity of the POM through the water column, which, at abyssal depths, can result in important food limitations (Smith et al., 2008). In addition to phytodetritus input, deep-sea communities can use medium to large food falls, including fish, large cetaceans and macroalgae, which provide sporadic but massive pulses of labile organic matter to the seafloor (Vetter and Dayton, 1998; Gage, 2003; Smith and Baco, 2003; Dierssen et al., 2009; Bernardino et al., 2010; Garden and Smith, 2015).

Kelp forests are iconic marine ecosystems that form complex systems along temperate and polar coastlines (Wernberg et al., 2019). They provide a major source of primary production (Krumhansl and Scheibling, 2012a; Mann, 1973) and support high secondary productivity of rich and diverse communities, maintaining high biodiversity and complex functions (Fredriksen, 2003; Norderhaug and Christie, 2011; Teagle et al., 2017). Norway hosts some of the world's largest kelp forests, dominated by *Laminaria hyperborea*, with depth ranges from 0 to 30 m and annual productions ranging from 0.2 to 0.8 kg C m^{-2} y^{-1} (Pedersen et al., 2012; Pessarrodona et al., 2018). The organic matter produced by kelp is either consumed in the kelp forest or exported as detritus. Estimates of detritus export indicate that 80% of the kelp production is exported globally (Krumhansl and Scheibling, 2012a), while it can be as high as 90% in Norwegian kelp forests (Norderhaug and Christie, 2011). This represent significant inputs of carbon to communities outside of the kelp reefs, both shallow and deep (Dierssen et al., 2009), but despite this knowledge, empirical data on the role of kelp detritus fueling adjacent ecosystems is scarce. The few studies available suggest that macroalgae can provide food to otherwise food-limited deep-sea ecosystems (Vetter and Dayton, 1998, 1999; Bernardino et al., 2010; Ramirez-Llodra et al., 2016; Renaud et al., 2015; Fjærtoft, 2018), influence distribution patterns of coastal species (McMeans et al., 2013) by facilitating connectivity (Vanderklift and Wernberg, 2008) and support increased secondary productivity (Schaal et al., 2011). Although there is increasing evidence that kelp and other macrophytes play a central role in fueling adjacent communities (Renaud et al., 2015), a comprehensive understanding of the nature and extent of kelp subsidy to these communities is still lacking (Krumhansl and Scheibling, 2012a) and no such studies exist in deep benthic arctic communities (Filbee-Dexter et al., 2018; Renaud et al., 2015). Understanding this trophic link between shallow-water, highly-productive systems and the more food-limited deep-sea benthos is important in the current situation of changing oceans, where climate-related stressors are driving regime shifts and large scale changes in kelp forests (Lauzon-Guay and Scheibling, 2014; Filbee-Dexter et al., 2016; Ling et al., 2009; Martínez et al., 2018). A recent review of the status of global kelp forests has shown that, for sites with over 20 years of data, 61% of the kelp forests are declining while only 5% are increasing (Wernberg et al., 2019). The declines include shifts to sea urchin barrens, turf reefs and other macroalgal reefs (Filbee-Dexter and Wernberg, 2018), which will consequently result in variations in detritus formation and transport.

In Norway, kelp forests have undergone dramatic regime shifts in the last four decades. Large areas along the west and north coasts of Norway were grazed down by sea urchins in the 1970s, while increasing seawater temperatures and coastal eutrophication have caused a die-back of kelp along the southern coast, leaving about 40% of the former kelp areas as barren grounds (Moy and Christie, 2012). Although barren grounds still persist in the north, there has been a northward trend of kelp recovery from the southern margin of barrens since the 1990s (Norderhaug and Christie, 2009), and a trend of recovery in

localized areas near the Russian border (Christie et al., 2019). These large-scale changes in standing kelp biomass, together with the associated production and export of detritus, are predicted to have profound trophic implications for the structure and functioning of adjacent ecosystems (Krumhansl et al., 2016). The KELPEX project (2016–2018) quantified the production and export of kelp in northern Norway and assessed the effect of kelp detritus in fueling shallow and deep benthic communities adjacent to healthy kelp forests. In this project, we showed that kelp detritus is produced by distal erosion of blades, dislodgement of blades and whole plants, grazing from sea urchins and other fauna, and phenologically-driven whole blade loss in spring (Pedersen et al., 2019). The latter accounts for 58% of the total detrital production, which averaged 0.48 kg C m^{-2} (Pedersen et al., 2019). The project has shown also that 50% of the kelp detritus produced in this study area is retained in the shallows by sea urchins and topography, but that whole blades, stipes and fragments of detritus are abundant in the deep subtidal down to 70 m depth and recorded inside the fjord below 400 m depth (Filbee-Dexter et al., 2018). Detritus can also take the form of small particles (~0.5 mm^2, often as the result of sea urchin shredding (Filbee-Dexter et al., 2019a), which sink two orders of magnitude slower than coarse detritus, and can thus be transported 100s km from the source (Wernberg and Filbee-Dexter, 2018). The aim of the current study, developed within the KELPEX project, was to investigate the benthic communities, including the meio-, macro- and megafauna components, at bathyal depths in Northern Norway, and assess the potential role of the different types of kelp detritus in fueling deep benthic communities. The study area included the mouth of the Malangen fjord surrounded by a healthy kelp reef and the adjacent shelf 15 km away from the kelp (Fig. 1). The project's initial assumptions were:

1. High kelp detritus exported from the kelp reef surrounding the mouth of the Malangen fjord (Filbee-Dexter et al., 2018) will sink to the deep fjord basin and accumulate as kelp graveyards (e.g. Vetter and Dayton, 1998; Britton-Simons et al., 2012; Filbee-Dexter et al., 2018; Krumhansl and Scheibling, 2012a).

2.Such accumulation of kelp will not be found on the shelf site 15 km offshore the kelp reef, and thus the fjord and shelf benthic communities would receive a significantly different input of kelp detritus.

3. Based on Ramirez-Llodra et al. (2016), we predicted that kelp detritus will degrade on the seafloor providing food to benthic fauna and potentially influencing community composition and structure.

4. Previous knowledge indicated that the two study areas (deep fjord basin and deep shelf) have similar environmental conditions and benthic invertebrate communities. The taxa found in both areas are mostly the same (see http://www.mareano.no and Pedersen pers. comm). Bottom water temperature is similar with an annual temperature ranging from 6 to 7 °C, (Falkenhaug et al., 1997), because of the influence of Atlantic water masses which differs from other, colder fjords. The seafloor is composed of sediment (Elvsborg 1979; Keck and Wassmann 1996) and the depth is the same (450 m).

Based on these assumptions, we expected that the higher input of organic matter in the form of kelp detritus to the fjord site would provide a significantly higher amount of energy to the system, potentially supporting one or more of the following community traits: higher total organic matter and total organic carbon in the sediments of the fjord site, higher biomass/biodiversity of the meiofauna community; higher biomass of macro- and megabenthic communities; richer infaunal communities; higher abundance of taxa that can exploit kelp detritus (e. g. grazers, amphipods), modified community structure; modified biodiversity.

2. Material and methods

2.1. Study area and sampling

The mouth of the Malangen fjord has a deep basin (450 m) surrounded by steep walls and healthy kelp forests in the shallows, and a sill
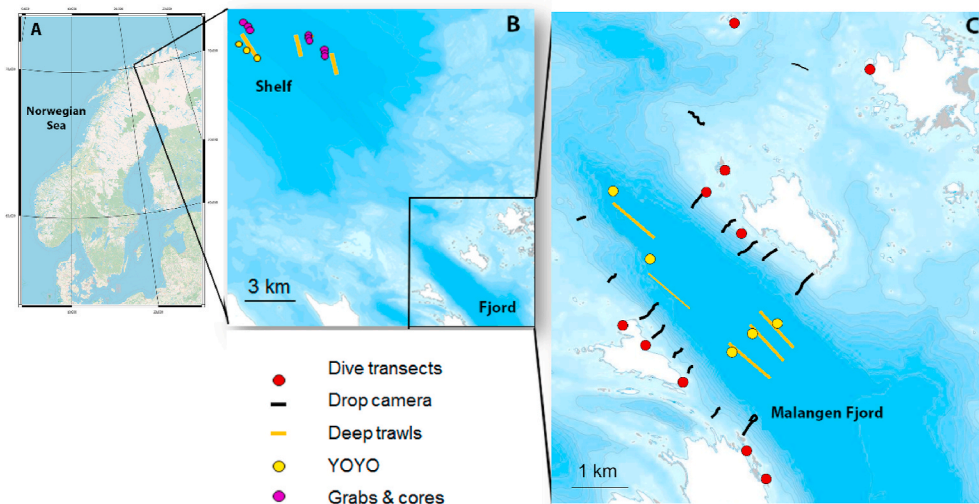
Fig. 1. Map of the KELPEX study area showing the general location of the Malangen fjord (A); the shelf area (B) and the fjord area (C). The location of the scuba-dive transects (red dots) represent also the location of the kelp forest. YOYO: YoYo Camera transects. Grabs & cores: sediment samples taken with a Van Veen Grab and a Gemini corer. Isobaths: 50 m intervals. A detailed table of sample station metadata is available in Supplementary Material (S1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

at 200 m depth separating the basin from the shelf (Fig. 1C). Sampling was conducted during the 2-week KELPEX cruise on board RV Johan Ruud in April-May 2016. Two deep benthic areas with expected different kelp-detritus inputs were studied. The area at the mouth of the Malangen fjord (69°35′N, 17°55′E), referred herein as the "fjord" (Fig. 1C), was assumed to be an area receiving considerable kelp debris falling from the surrounding kelp forests down the steep slopes and accumulating on the deep basin. An area on the shelf, Malangsdjupet referred herein as the "shelf" (Fig. 1B), was selected at a similar depth (450 m) 15 km offshore the Malangen fjord (69°45′N, 17°40′E). We assumed that this area was too far from the kelp forests to receive significant kelp debris. Both areas were known to have similar main environmental parameters. Malangsdjupet (shelf) is a glacial through on the continental shelf (Hald et al., 2011). The shelf and the fjord are influenced by Atlantic dense water with >35 PSU and temperature of about 8 °C forming the bottom water (Hald et al., 2011). The bottom water temperatures during the cruise were 6.4 °C in the fjord area and 6.6 °C at the shelf area (Malangsdjupet). The fjord has frequent (annually) exchange of the bottom layer with Atlantic water (Hald et al., 2011). Above the bottom layer is water from the Norwegian coastal current with salinity between 32 and 35 PSU and temperature between 2 and 13 °C. Freshwater runoff from rivers also influence the surface layer. The seafloor in both areas is composed of fine sediment (Elvsborg 1979; Keck and Wassmann 1996). Prior to the study, species composition and abundance data from the shelf (see http://www.mareano.no) were compared to previous data available from the fjord study area (Pedersen pers. comm), and the overall composition was similar.

To assess the presence of kelp debris on the seafloor, deep-towed YoYo-camera (YYC) surveys were conducted in the two areas. A total of 3 successful transects were conducted on the shelf (3 replicates of 1 site) and 5 in the fjord (5 replicates of 1 site). The transects were ca. 1500 m long, with 50–60 photographs of the seafloor taken per transect. The presence of large kelp particles (visible in the photographs) was recorded, and their biomass estimated using biomass to area relationship (according to Filbee-Dexter et al., 2018). The biomass of small particles of kelp debris (not discernible in the photographs) in each area was quantified from grab samples by re-suspending the kelp particles in water, collecting them with a scoopula and/forceps, placing them on a pre-weighed circular piece of blotting paper to remove excess water, and weighing them in a precise balance (0.001 g).

The meio-, macro- and mega-fauna were sampled in both areas (fjord and shelf) at 3 sites per area. Three to four replicates per site were taken whenever possible (Fig. 1). The meiofauna was sampled with a Gemini

corer containing two tubes with an inner diameter of 80 mm. Nine deployments were made in the fjord and nine on the shelf (3 replicates per site at 3 sites in each area). After collection, sediment cores were sliced into 0–1, 1–2 and 2–5 cm sediment depth layers on board. For each deployment, 1 core was destined for meiofauna identification and preserved separately in a 4% buffered formalin solution lengthened with filtered (32 μm) seawater, and the second core was dedicated to environmental variable analyses and immediately frozen at −20 °C. The macrofauna was collected with Van Veen Grabs (15 in the fjord: 5 replicates per site; 15 on the shelf: 5 replicates per site) of 0.1 m² surface. The grabs were sieved on board with 500 μm and 1 mm sieves and preserved in 4% buffered formalin. The megafauna was sampled with two benthic trawls: an otter trawl (OT) and a beam trwl. The otter trawl has a mouth opening of 18 m width and ca. 8 m height, with a mesh size of 35 mm in the cod-end and 8 mm in the last 1.3 m. This gear samples preferentially highly mobile fauna such as fish. The distance between the trawl doors (45 m) was taken as the effective fishing width for fish that was herded, and the width of mouth opening was taken as the fishing width for invertebrates. Three otter trawls were made on the shelf and 4 in the fjord. The beam trawl had a mouth opening of 2 m and mesh size of 5 mm, sampling efficiently the benthic invertebrate communities. Six beam trawls were made on the shelf and 6 in the fjord. Because of the large sample size in the trawls and large area sampled, no replicated sites were included. Thus, the sampling resulted in 6 replicates of otter trawl samples on the shelf and 4 in the fjord, and 6 replicates of beam trawls on the shelf and 6 on the fjord.

In order to assess the response of mobile megafauna in the deep fjord to experimentally deployed kelp, a time-lapse camera (TLC) was deployed on a free-fall lander. The TLC was mounted on a lander with a plate at seafloor level, where known weights of kelp detritus were added in a mesh bag. A total of six deployments, all representing one site in the fjord area were conducted: 2 control deployments with no kelp on the plate and 4 experimental deployments with kelp. Each deployment lasted 30 h and 1 photograph was taken every 5 min. The kelp (*L. hyperborea*) used in 5 of the kelp deployments were collected from 6 m depth by divers and hung for 6 weeks under a dock in Sommarøy harbour to age. For 1 deployment, kelp was taken from an otter trawl, where it became lightly coated with fish scales and mucus during the sampling process.

2.2. Sample processing

2.2.1. Sediment variables

Sediment grain size distribution was measured using a Malvern Mastersizer hydro 2000 G (0.02–2000 μm size range) and classified according to the Wentworth scale (1922). Grain size, clay % (<4 μm), silt % (4–63 μm), very fine sand % (63–125 μm), fine sand % (125–250 μm), medium sand % (250–500 μm), coarse sand (500–1000 μm) and very coarse sand (1000–2000 μm) were measured. Pigments were extracted from lyophilised sediments by adding 10 ml 90% acetone and concentrations measured with a fluorescence detector after HPLC (High-Performance Liquid Chromatography) separation. The following pigment variables were considered: μg g^{-1} sediment chlorophyll *a*, μg g^{-1} sediment phaeophytin, and μg g^{-1} sediment fucoxanthin for all the sediment layers down to 5 cm. Percentages of total nitrogen (TN) and total organic carbon (TOC) fractions were measured using a Flash EA 1112+ MAs 200 elemental analyser (Thermo Interscience). Sediment total organic matter (TOM) was determined after combustion of the sediment samples at 500 °C.

2.2.2. Meiofauna

Samples for meiofauna characterization were rinsed with tap water over a 1 mm sieve and retained on a 32 μm mesh sieve. Organisms were extracted by density gradient centrifugation (3 × 12 min at 3000 rpm) using the colloidal silica polymer Ludox HS-40 (VINCX, 1996) at a specific density of 1.18 g cm^{-3}. The meiofauna was preserved in 4% formalin and the taxa identified to the lowest taxonomic level possible in the lab. Total meiofauna density (ind. 10 cm^{-2}) and relative abundance were calculated in the 0–5 cm depth layers. For the 0–1 cm sediment layer, the first 110 nematodes were randomly picked out and identified to genus level. Biomass of nematodes is expressed as organic carbon content per area (μg C cm-^{2}) and was directly calculated from the ratio mass spectrometer output as follows: Nematode biomass (μg C/10 cm^2) = (μg C in the cup measured with the EA-IRMS/number of nematodes in that cup) * nematode density (#ind/10 cm^2).

2.2.2. Macrofauna and megafauna

The macrofauna samples collected with the grab were sorted and identified in the laboratory to the lowest taxonomic level possible and all individuals counted. Biomass was measured to the nearest 0.1 g in a precise balance. The megafauna collected from the trawls was sorted on board, identified to the lowest taxonomical level possible, weighted and measured. The biomass and density of each taxon was calculated and standardised by the swept area of each trawl.

2.3. Data analyses

Differences in sediment environmental conditions between fjord and shelf areas were assessed by means of a two-way ANOVA (area and site, the latter one nested in area) for the 0–5 cm layer from the cores. Variables were log-transformed when the assumption of normality was not fulfilled. All variables were normalized prior to analysis. The community structure and biodiversity of each size class (meio-, macro- and megafauna) were analysed separately using multivariate techniques in PRIMER v6 (Clarke and Gorley, 2006) to test for differences in community composition. Environmental conditions (based on sediment variables) and community assemblages for the meio- and macrofauna compartments were linked using the BIO-ENV procedure in PRIMER (999 permutations). Biodiversity indices (Margalef's richness d, ES(n), Shannon-Wiener H′ and Pielou's evenness J′) were calculated with PRIMER. Differences in densities and biodiversity indices between the fjord and the shelf communities were analysed in R (R Core Team, 2018), PRIMER with the PERMANOVA + add-on (Anderson et al., 2008), using *t*-tests when the data were pooled per site (e.g. otter trawl and beam trawl data compared between the fjord and the shelf), ANOVA or non-parametric alternatives when assumptions were violated.

3. Results

3.1. Kelp detritus

Large pieces of kelp detritus (blades) were observed in the 4 YYC transects conducted in the fjord (Fig. 2A), but no kelp was observed in any of the 3 YYC transects conducted on the shelf. In addition, all benthic trawls conducted in the fjord collected large particles of kelp (Mean: 0.570 ± 1.0 g m^{-2}), while almost no kelp was collected in the trawls on the shelf (Mean: 0.087 ± 0.24 g m^{-2}) (Fig. 2B). Small particles of brown macroalgae identified as kelp (0.5–3 mm in diameter) were observed on the sieved grab samples. There were no significant differences in the biomass of small kelp particles between the fjord (mean: 22.6 ± 12.6 g m^{-2}) and the shelf (mean: 15.6 ± 4.8 g m^{-2}) areas (Nested ANOVA, $F_{1,14}$ = 4.02, P = 0.065). These results indicated that, as expected, the large kelp detritus (blades) are mostly retained in the fjord's deep basin adjacent to the kelp forests. However, and in contrast to our initial assumption, the shelf area 15 km off the kelp forest also receives kelp detritus, but here mostly in the form of small particles.

3.2. Sedimentary environmental conditions

All the sediment environmental data (MGS, Clay%, Silt%, very find sand %, fine sand %, medium sand %, coarse sand %, very coarse sand %, fucoxanthin, Chl a, Phaeophytin, TN, TOC, TOC/TN and TOM) is available in the Supplementary Material (S2). No significant differences were found in the amount of fucoxanthin (Fuco) (Nested ANOVA, $F_{(1,18)}$ = 1.015, P = 0.327) and phaeophytin (Phaeo) (Nested ANOVA, $F_{(1,18)}$ = 0.342, P = 0.547) between the fjord and shelf sediment samples, but chlorophyll *a* (Chl a) was significantly higher at the shelf (ANOVA, $F_{(1,18)}$ = 4.997, P = 0.038). Granulometric properties showed a large variation in substrate type, with sediment particles varying from clay to very coarse sand, but the dominant size fractions were silt (57.34% ± 7.8%) and very fine sand (18.3% ± 2.8%) for all samples. Nevertheless, median grain size (MGS) was higher in the fjord than on the shelf (Nested ANOVA, $F_{(1,18)}$ = 55.97, P < 0.001). Average TOC levels were 1.68 ± 0.19% (fjord) and 1.75 ± 0.11% (shelf) but did not differ significantly between both areas (Nested ANOVA, $F_{(1,18)}$ = 2.346, P = 0.143). TN content ranged from 0.28 to 0.30% for fjord and shelf, respectively, and was slightly but significantly higher on the shelf than in the fjord (Nested ANOVA, $F_{(1,18)}$ = 4.923, P = 0.0396). Similarly, TOM levels on the shelf were higher than in the fjord (Nested ANOVA, $F_{(1,18)}$ = 88.25, P < 0.001). These results do not support our expectation of higher total organic matter and total organic carbon in the sediments of the fjord site.

3.3. Meiofauna

3.3.1. Community composition

A total of 15 meiofaunal taxa were sampled in both areas, and their community composition was roughly similar. Nematoda was by far the most abundant taxa (total average of 91 ± 2.7%), followed by Polychaeta (3.9 ± 1.3%), Copepoda (3.5 ± 1.1%) and their Nauplii (1.2 ± 1.0%). Other taxa included Tanaidacea, Kinorhyncha, Cumacea and Ostracoda, which all contributed less than 0.4% to total densities. Average meiofauna densities in the 0–5 cm sediment depth layer were on average slightly higher in the shelf area (958.4 ± 195.6 ind. 10 cm^{-2}) than in the fjord (887.9 ± 84.0 ind. 10 cm^{-2}), but differences were not significant (ANOVA, $F_{(1,15)}$ = 0.5; P = 0.49). Only copepod densities were significantly higher in the fjord than in the shelf samples (ANOVA, $F_{(1,15)}$ = 9.825; P = 0.0068). Meiofauna densities varied with depth in the sediment, depending on the area (significant interaction area x depth in PERMANOVA, Pseudo-F = 10.799, P = 0.001). Within fjord stations, densities increased with depth, while this trend was opposite in shelf stations (Fig. 3).
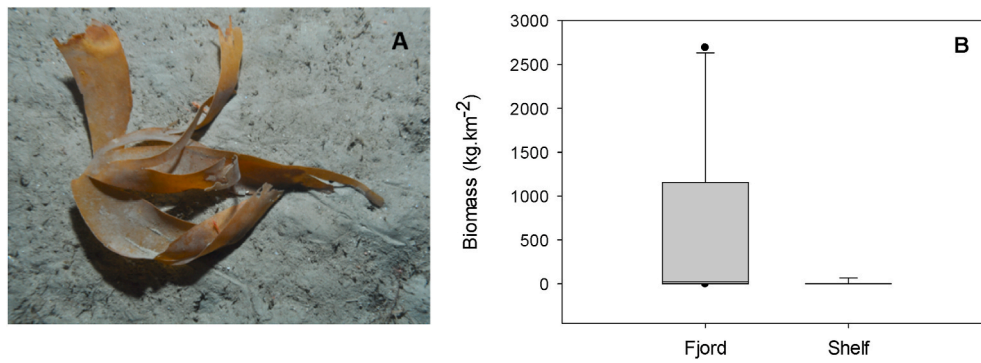
Fig. 2. A. YYC photograph in the fjord at 450 m depth showing a kelp blade on the seafloor. B. Box plot of the biomass of large pieces and blades of kelp collected in the trawls (beam and otter-trawls combined) in the fjord and on the shelf.
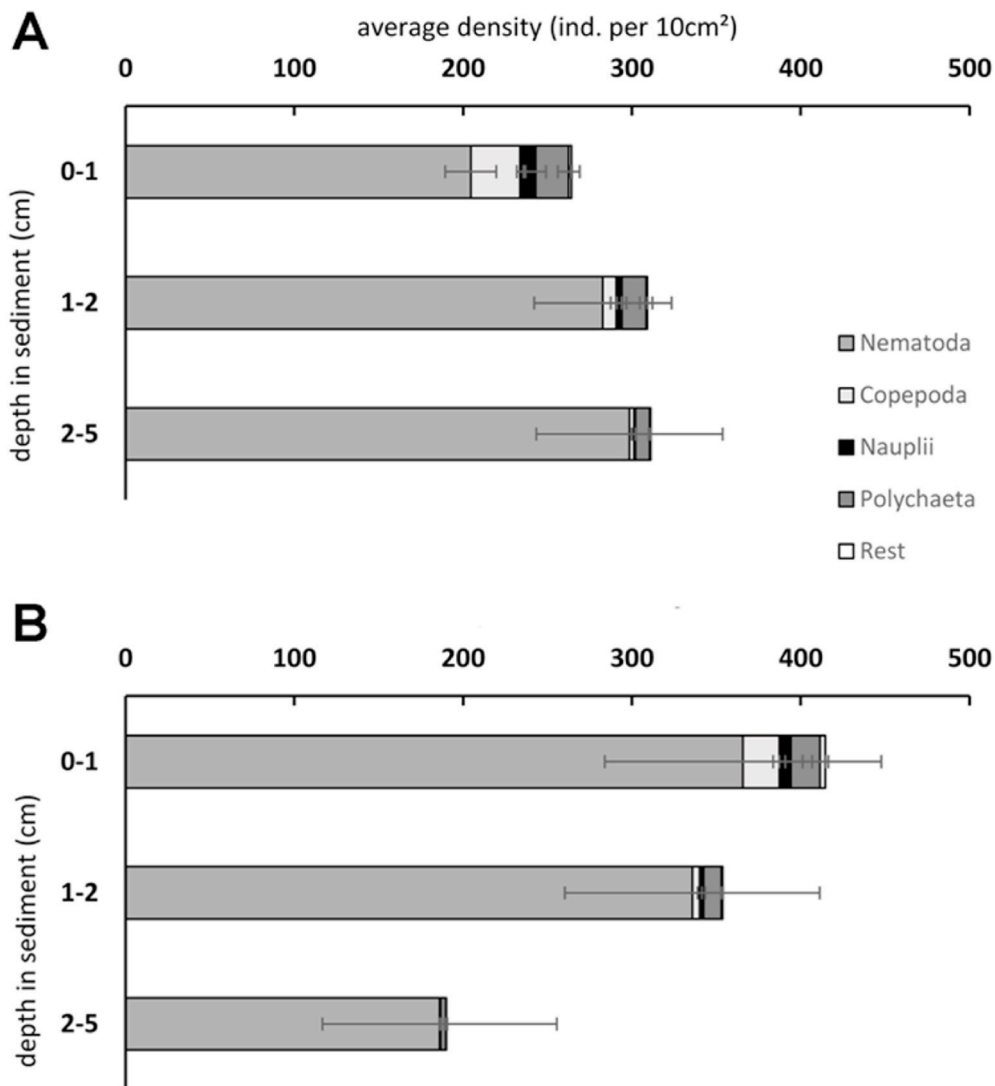

Fig. 3. Vertical profiles of average meiofauna density (ind. 10 cm^{-2}) and community composition in fjord (A) and shelf (B) areas. Error bars denote standard deviation.

3.3.2. Nematode community structure and diversity

In total, 94 nematode genera belonging to 29 families were identified (Supplementary Material S3). The average density of nematodes in the upper 0–1 cm layer was significantly lower in the fjord (204.5 ± 15.2 ind. 10 cm^{-2}) compared to the shelf (365.8 ± 81.9 ind. 10 cm^{-2}) (Wilcoxon rank sum P < 0.001; SI1). Average nematode biomass in the 0–1 cm layer was 29.5 ± 14.4 µg C 10 cm^{-2} (fjord) and 49.1 ± 23.2 µg C 10 cm^{-2} (shelf), with no significant differences between areas (Nested ANOVA: $F_{(1,11)}$ = 3.558; P = 0.0859). Biodiversity was assessed by means of four indices: the expected number of genera EG (65), Shannon diversity (H′), Pielou's evenness (J′) and Margalef's species richness (d). All indices showed slightly elevated values in shelf samples compared to

the fjord, but J′, H′ and EG (65) were also significantly different (Nested ANOVA: J′: $F_{(1,12)} = 5.852$, P = 0.0324; H′: $F_{(1,12)} = 14.834$, P = 0.0023; EG (65): $F_{(1,12)} = 6.922$, P = 0.0219, Fig. 4, Supplementary Material S3).

The nematode community structure was significantly different between the fjord and the shelf areas (PERMANOVA: P (MC) = 0.0065; average dissimilarity ca. 54.2%; Fig. 5). In general, approximately 13–15 genera accounted for 67–80% of total community abundance in both areas. Certain genera such as *Daptonema*, *Dorylaimopsis*, *Paramesacanthion* and *Sphaerolaimus* were abundant in the fjord and not on the shelf, whereas genera such as *Anticoma*, *Halichoanolaimus*, *Neochromadora*, *Paracanthonchus* and *Rhabdodemania* were more abundant on the shelf.

3.3.3. Nematode community and environmental variables

Nine environmental variables (MGS, Silt, Fuco, Chl a, Pheo, TN, TOC, TOC/TN, and TOM) were used to test for relationships with the nematode community composition (as square-root transformed relative abundances) using a BIO-ENV analysis. The BEST Global test indicated that there was a significant relationship between the environmental variables and the nematode genus composition ($\rho = 0.453$; P = 0.002). Mainly MGS and silt fraction in the sediment were important in explaining differences in nematode genus composition (maximum $\rho = 0.453$), followed by a combination of five variables ($\rho = 0.453$),

consisting of MGS, silt, TOM, TOC and Fuco.

3.4. Macrofauna

3.4.1. Community composition

A total of 210 species belonging to 8 phyla (Annelida, Cnidaria, Crustacea, Echinodermata, Mollusca, Nemertea, Phoronida, Sipuncula) were sampled with the Van Veen grab (Supplementary Material S4 provides the species list with mean biomass and density data). In the fjord, biomass was dominated by annelids (38.3%) followed by cnidarians (30.1%) and molluscs (29.4%). In contrast, the shelf macrofauna biomass was mostly composed of annelids (65.4%) and molluscs (32.4%). In terms of macrofauna density, the fjord community was dominated by annelids (79.7%), followed by molluscs (16.0%), with all other groups accounting for less than 3% each. On the shelf, the macrofauna density was dominated by annelids (64.6%), followed by molluscs (24.3%) and sipunculids (5.25%), with all other groups accounting for less than 3% each. Within the annelids, biomass was higher on the shelf (mean: 26.8 ± 12.1 g m^{-2}) than the fjord (mean: 14.5 ± 5.6 g m^{-2}), while density was higher in the fjord (mean: 6913 ± 2768 ind. m^{-2}) than the shelf (mean: 5106 ± 1585 ind. m^{-2}), suggesting that the annelids in the fjord are smaller relative to the annelids on the shelf. The contrary is true for cnidarians, with a higher density on the shelf (mean: 30.0 ± 45.6
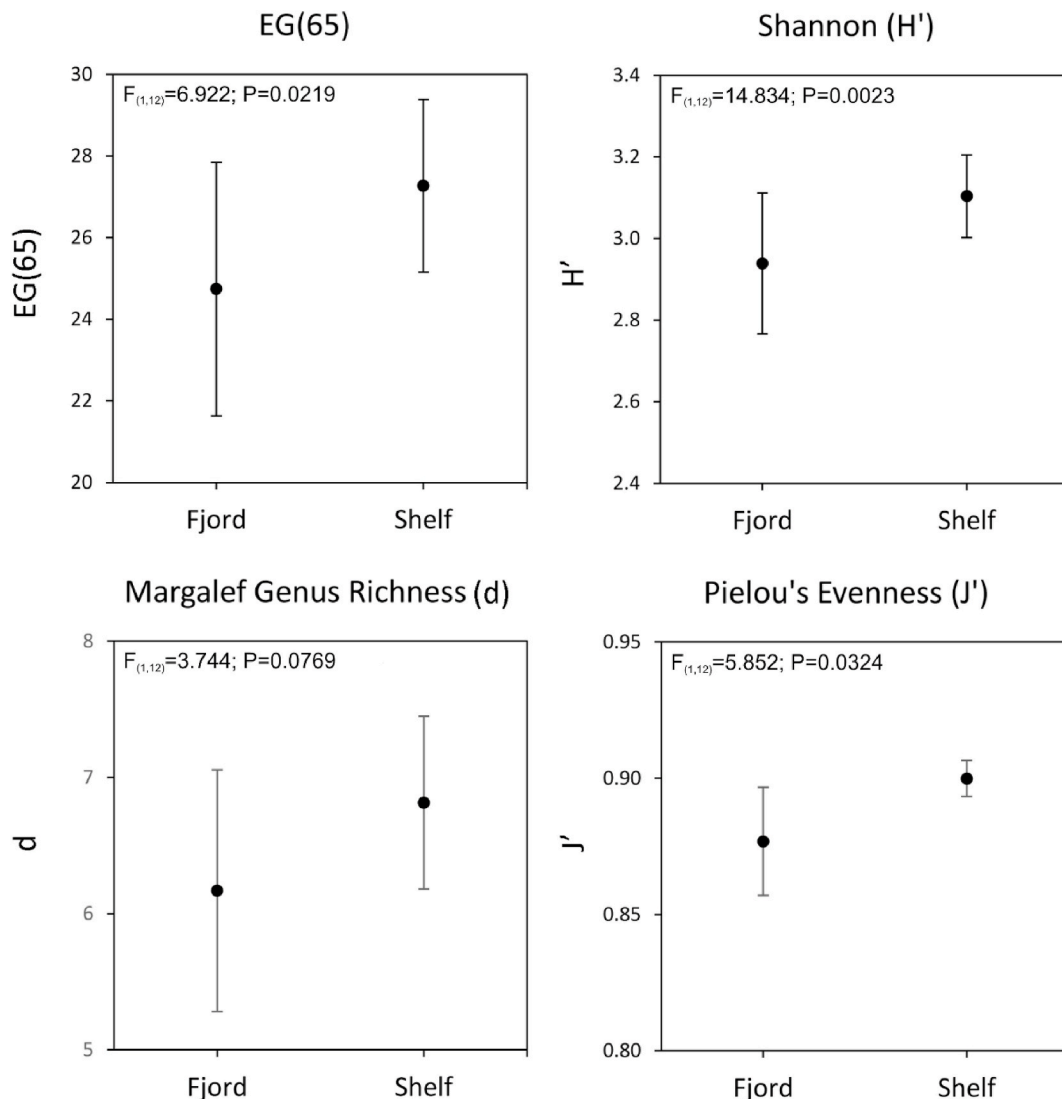

Fig. 4. Average nematode biodiversity indices in fjord and shelf areas. Error bars denote standard deviation. Results of the ANOVA tests are also given for each index.
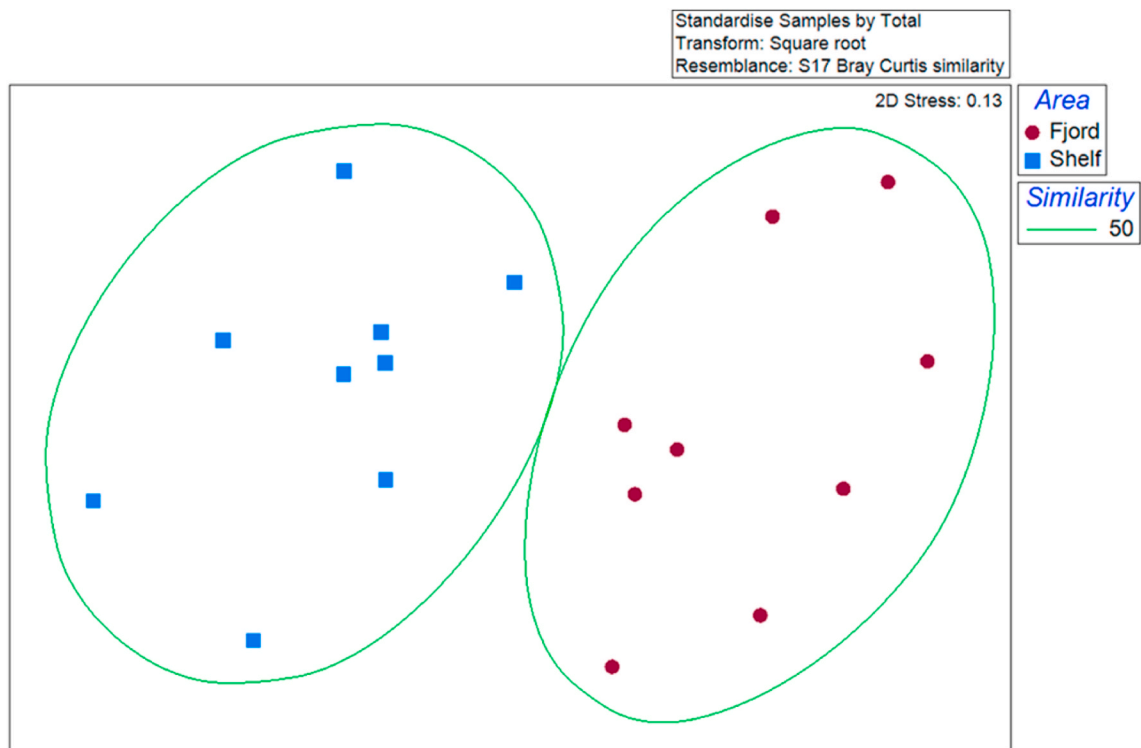
Fig. 5. Multidimensional scaling of nematode community structure based on relative genus abundance (%) from the fjord (circles) and the shelf (squares). Data has been square-root transformed and Bray-Curtis similarity index was used. Line shows 50% similarity.

ind. m^{-2}) than the fjord (mean: 6.7 $\pm$ 16.3 ind. m^{-2}), but higher biomass in the fjord (mean: 11.7 $\pm$ 28.7 g m^{-2}) than the shelf (mean: 0.1 $\pm$ 0.2 g m^{-2}). This suggests that the cnidarians in the fjord are larger than those sampled on the shelf. We found no evidence that taxa that can exploit kelp detritus (e.g. grazers, amphipods) were more abundant in the fjord compared to the shelf.

There were no significant differences in mean density of total macrofauna between the fjord and the shelf (ANOVA: F = 0.33, P = 0.569) (Fig. 6A). However, there were significant differences amongst phyla (ANOVA: F = 76.49, P < 0.005), with density of annelids and molluscs significantly higher than the other groups (Tukey post-hoc test; P < 0.005). There were also significant differences in the interaction phylum*area (F = 2.27, P < 0.05), caused by a significant higher density of annelids on the fjord than the shelf (post-hoc Tukey test, P < 0.05). In terms of total biomass, no significant differences were detected between the fjord and the shelf (ANOVA: F = 0.05, P = 0.819) (Fig. 6B) or in the

interaction phylum*area (ANOVA: F = 1.88, P = 0.084).

3.4.2. Community structure and biodiversity

Clear significant differences were observed in the macrofaunal community structure between the fjord and shelf areas (Fig. 7). The SIMPROF test shows that there is more structure in the samples than could be obtained by chance under the null hypothesis of no group structure (SIMPROF, π = 8.247, P < 0.001) and ANOSIM confirms that there are significant differences in community composition between areas (R = 1; P = 0.002). A SIMPER test shows that the average of the Bray-Curtis dissimilarities in community composition between all pairs of sites is 61.75. The two species contributing most to this dissimilarity were the polychaete *Paramphinome jeffreysii*, which was more abundant in the fjord (64.3% of total abundance) than the shelf (38.1%), and the polychaete *Heteromastus* sp, which was not present in the fjord, but was relatively abundant (23.4%) on the shelf.
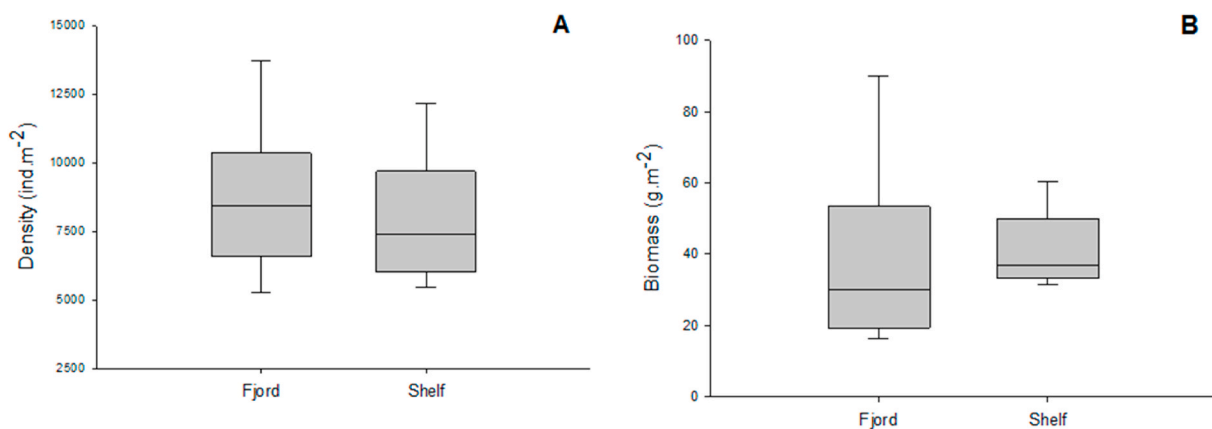

Fig. 6. Box plot of density (A) and biomass (B) of macrofauna from the fjord and shelf areas. Plots show median, first and third quartiles, maximum and minimum values.
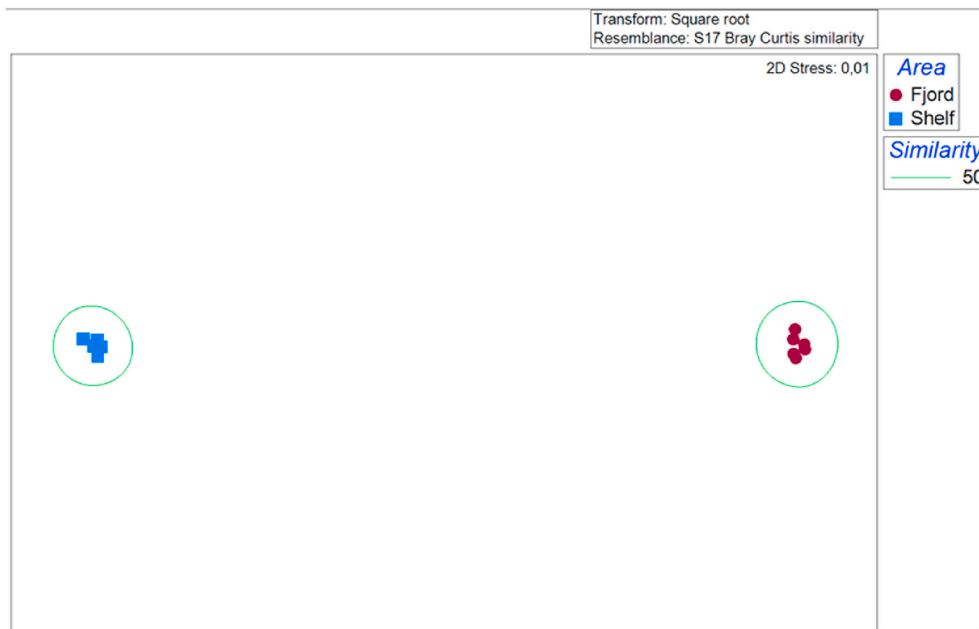
Fig. 7. Multidimensional scaling of macrofaunal community structure from the fjord (circles) and the shelf (squares). Line shows 50% similarity.

In terms of macrofauna biodiversity indices, the expected number of species ES (100), Shannon diversity (H′) and Pielou's evenness (J′) were significantly higher on the shelf than in the fjord, while there were no significant differences in Margalef's species richness (d) (*t*-test, results in Fig. 8).

3.4.3. Community structure and environmental variables

Nine environmental variables (biomass of small kelp particles in sediment; MGS; Fuco; Chl a; Pheo; TN; TOC; TOC/TN; and TOM) were used to test for relationships with macrofauna community composition using a BIO-ENV test. MGS, TOM and TN are the variables that explain better macrofaunal community composition. The results show that the rank correlation coefficient ρ is maximised for MGS (0.71), followed by a
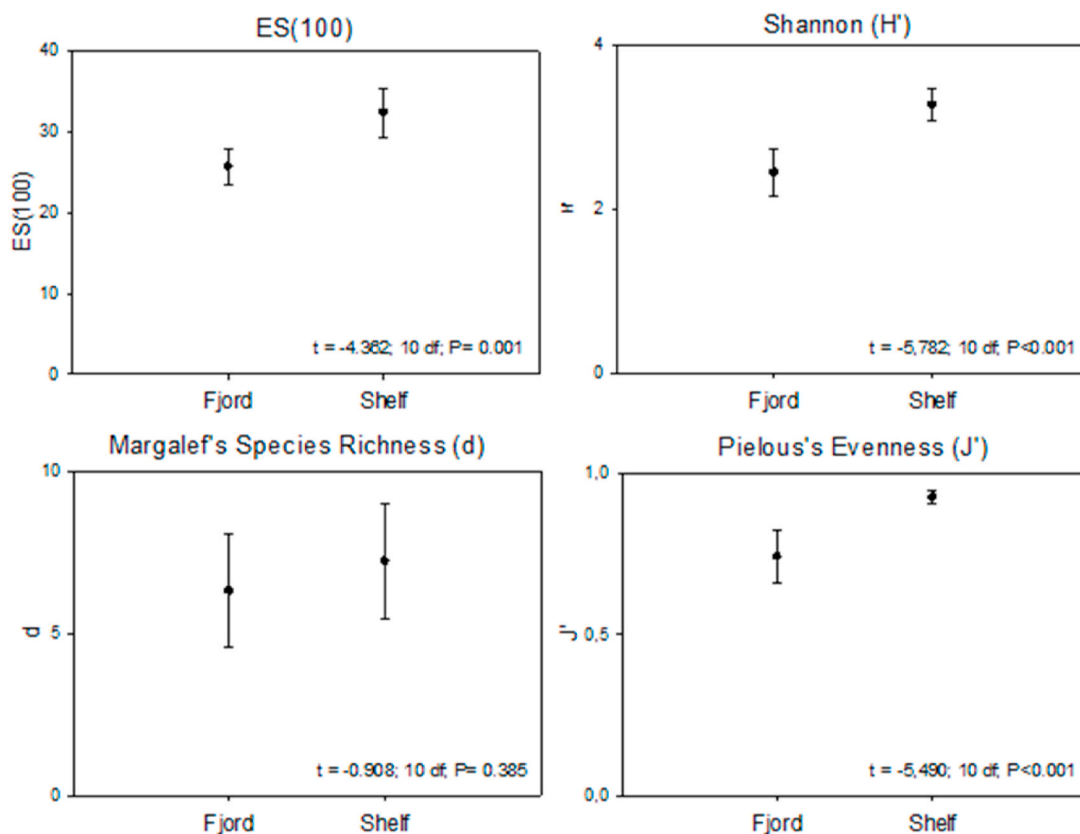

Fig. 8. Average macrofauna biodiversity indices in the fjord and on the shelf. Error bars denote standard deviation. Results of t-tests are also given for each index.

combination of MGS and TOM (p = 0.66), and MGS, TN and TOM (p = 0.61). The first time that small kelp particles are included as an explanatory variable is as the fourth best overall correlation, with a combination of small kelp particles, MGS, TN and TOM (p = 0.58). The BEST Global test confirms that the observed relationship between the macrofauna community structure and the environmental variables is significant (p = 0.713, P < 0.01).

3.5. Megafauna

3.5.1. Community composition

A total of 40 species of megafauna belonging to 7 phyla were sampled with the otter trawl, dominated by fish and chimaera. The beam trawls collected a total of 44 species belonging to 10 phyla, dominated by invertebrates. The supplementary information provides the full species list with mean biomass and density data for the specimens collected with the otter trawl (Supplementary Material S5) and beam trawl (Supplementary Material S6).

Otter-trawl samples: biomass in both areas is dominated by chordates (96.8% in the fjord and 93.1% on the shelf). This is followed by arthropods (2% fjord, 4% shelf), particularly the shrimp *Pandalus borealis* and *Pasiphaea multidentata*. Faunal density in the fjord is dominated in similar proportions by arthropods (50.3%) and chordates (48.8%), while the community of the shelf is dominated by arthropods (79.5%), followed by chordates (19.5%). The high densities of arthropods in the fjord are related to *Pandalus borealis*, *P. montagui* and *Pasiphaea multidentata*, while, on the shelf, most of the arthropods were represented by *P. multidentata*. Within the chordates, *Gadiculus argenteus*, *Micromesistius poutassou* and *Chimaera monstrosa* were more abundant in the fjord than on the shelf.

Beam-trawl samples: biomass in both areas is dominated by echinoderms (72.9% fjord, 76.3% shelf), mostly represented by the holothurian *Pseudostichopus tremulus*. This is followed by chordates (13.1%)

and cnidarians (9.2%) in the fjord, and cnidarians (16.6%) on the shelf. Cnidarians are mostly represented by anemones. Faunal density is dominated by arthropods (57.9% fjord, 49.9% shelf), mostly represented by *Munida sarsi* and *Pontophilus norvegicus*, as well as a high abundance of small, unidentified crustaceans. Nevertheless, a high number of pycnogonids was collected also in the fjord. In the fjord, the echinoderms are the second most abundant phylum (19.9%), followed by annelids (11.8%). On the shelf, echinoderms, molluscs and annelids are similarly abundant (14.6%, 13.2% and 13.0% respectively). There were no significant differences in total biomass and total density between the fjord and the shelf for the communities sampled with any of the gears (OT and BT, *t*-test, P > 0.1) (Fig. 9).

3.5.2. Community structure and biodiversity

Significant differences were observed in the megafaunal community structure between the fjord and shelf areas (Fig. 10), both for the samples collected with the OT and the BT. The SIMPROF test shows that there is more structure in the samples than could be obtained by chance under the null hypothesis of no group structure (OT – SIMPROF, π = 5.517, P < 0.001; BT – SIMPROF, π = 1.831, P < 0.019).

Four biodiversity indices were calculated for the benthic communities from the fjord and the shelf, both for the otter trawl and beam trawl samples. Although there was a trend of higher species richness and biodiversity in the fjord than the shelf communities for both gears, no significant differences were found for any of the four indices for the otter-trawl samples (Fig. 11), while Margalef's species richness (d) and Pielou's Evenness (J′) were significantly higher for the fjord than shelf communities (*t*-test, or Mann-Whitney Rank Sum Test when Normality or Equal Variance tests were not passed; Fig. 12).

3.5.3. Faunal response to deployed kelp detritus

Little faunal response was observed on detrital kelp deployed at 400 m depth with the TLC. The 4 deployments with kelp attracted 4–6
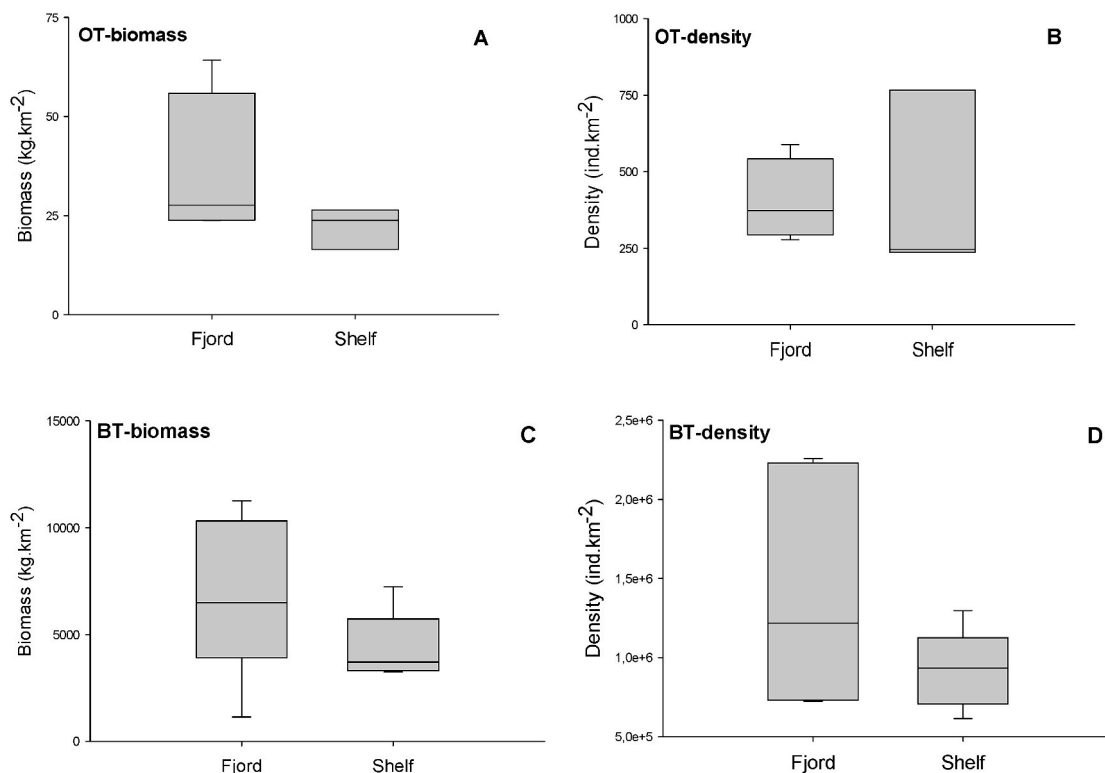

Fig. 9. Box plot of megafauna biomass and density from the fjord and shelf areas. A: biomass collected with the otter trawl (OT). B: density collected with the otter trawl (OT). C: biomass collected with the beam trawl (BT). D: density collected with the beam trawl (BT). Plots show median, first and third quartiles, maximum and minimum values.
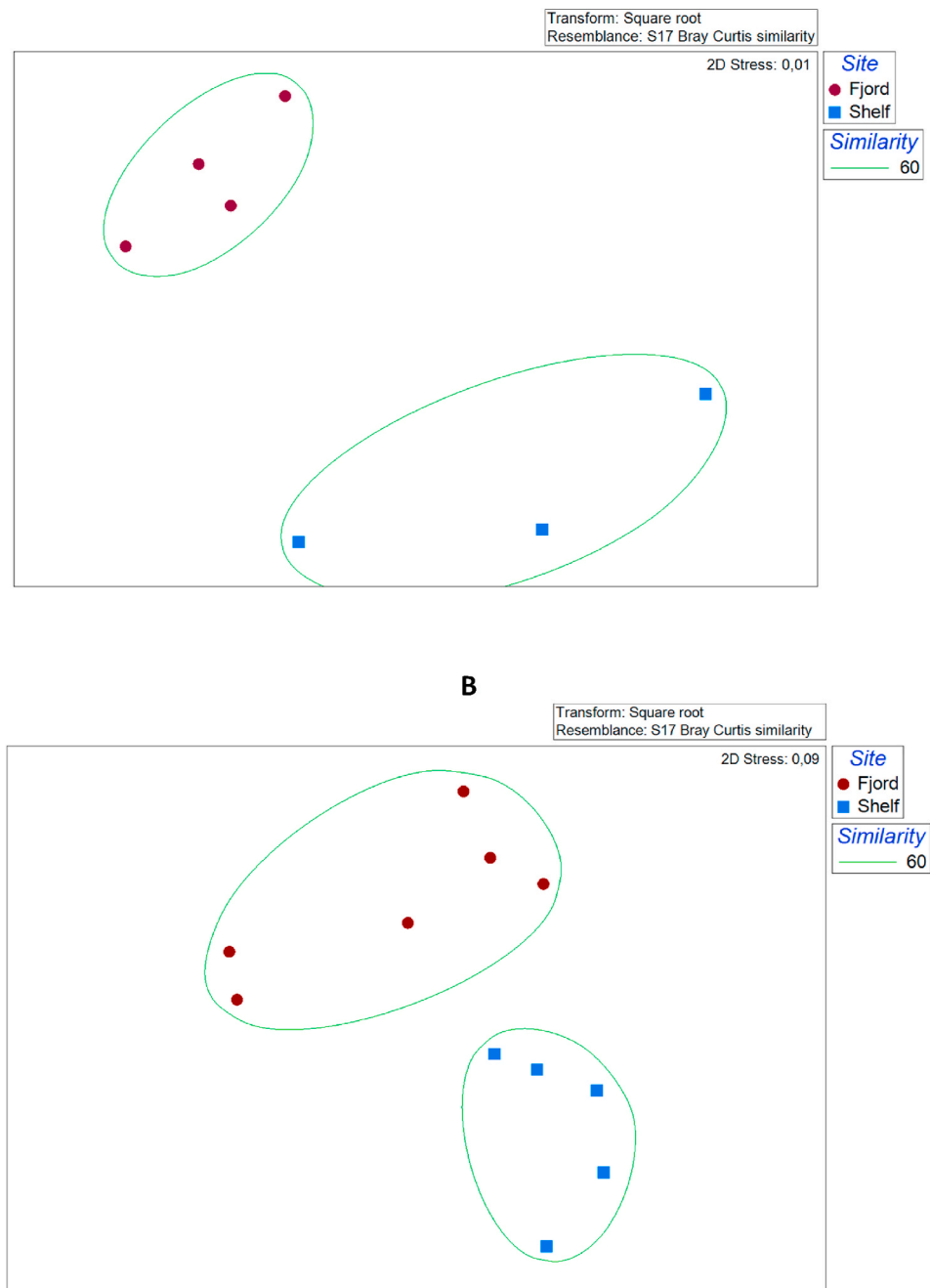
Fig. 10. Multidimensional scaling of megafaunal community structure from the fjord (circles) and the shelf (squares). A. Community sampled with the otter trawl. B. community sampled with the beam trawl. Line represents 60% similarity.

shrimp during each of the 30 h deployments, with shrimp staying on top of the kelp for 12–78 min. Amphipods could be observed on and over the deployed kelp, but with a maximum of 5–10 individuals on the kelp at all times. The two control deployments (without kelp) attracted 3 to 5 shrimp, but these did not stay on the TLC plate for more than 3 min (1 photograph). A small number of amphipods were also observed around the control TLC, but they did not stay on the plate. Although the kelp seemed to retain shrimp and amphipods for longer than the plate with no kelp, it was unclear whether the shrimp and amphipods were attracted to the TLC structure, using the kelp as refuge, or if they were responding to a cue for food. Interestingly, one deployment used detrital kelp that had been collected from the otter trawl and was thus covered with fish mucus. This kelp deployment attracted a high number of amphipods, with over 100 individuals counted on the kelp at the end of the

deployment.

4. Discussion

Particulate and dissolved organic carbon (POC and DOC), also known as detritus, are key components of food sources for benthic communities (Renaud et al., 2015). This is particularly true for most deep benthic ecosystems, where heterotrophic faunal communities depend, ultimately, on the primary productivity in the euphotic zone. The role of phytodetritus in fuelling deep benthic communities has been widely studied (reviewed in Gage, 2003) and large fate of organic falls such as whale falls (Smith and Baco, 2003) and macroalgal falls (Bernardino et al., 2010; McMeans et al., 2013; Vetter and Dayton, 1998) have also been documented. Many studies relate spatial patterns of
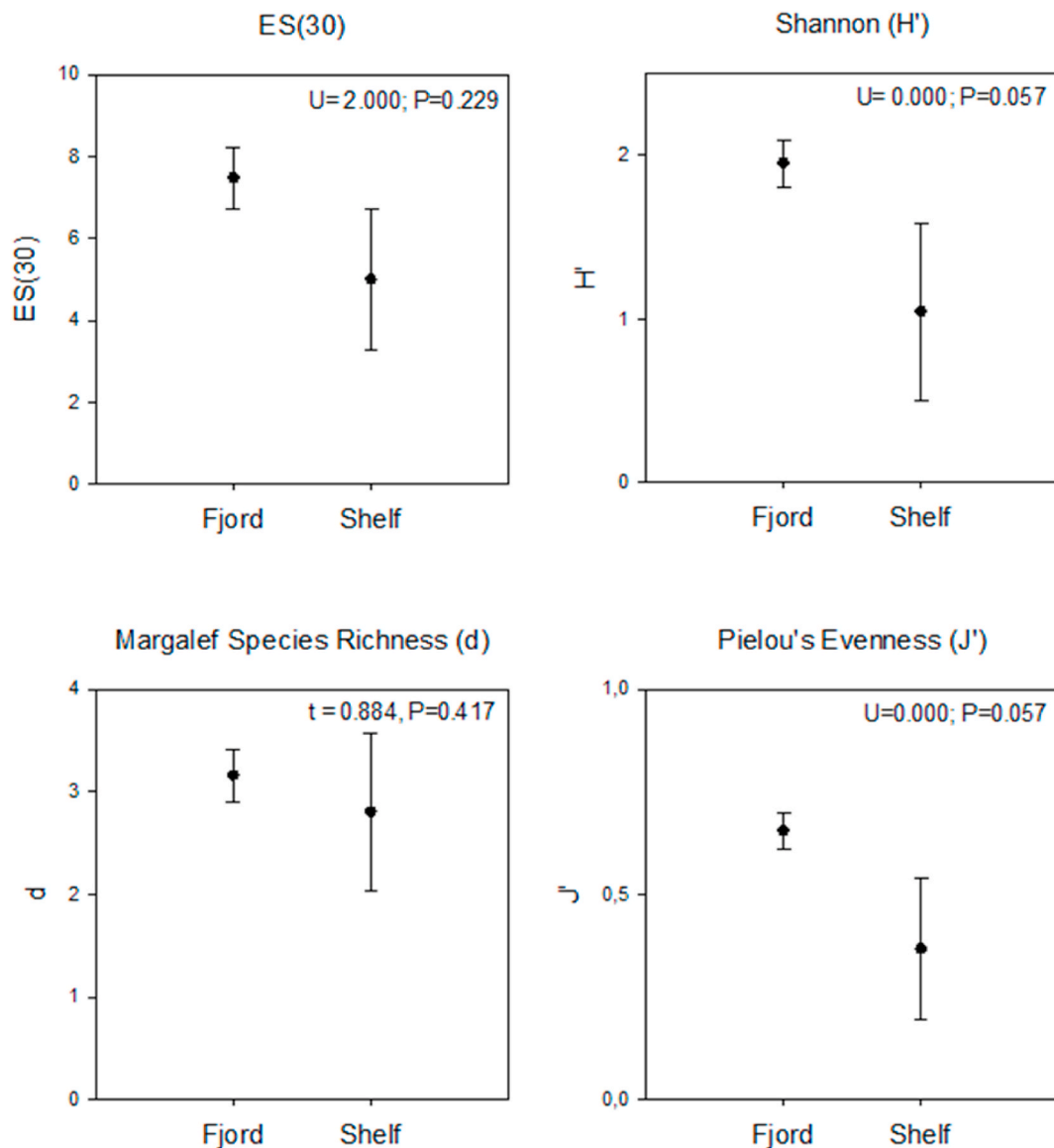
Fig. 11. Average megafauna biodiversity indices for samples collected with the otter trawl in the fjord and on the shelf. Error bars denote standard deviation. Results of t-tests are also given for each index.

benthic faunal abundance and biomass to the input of POC from the surface-lit layers of the ocean (Gage, 2003; Smith et al., 2008). However, and despite the high detrital production rates of kelp in the coastal zone and the evidence that macroalgal detritus reaches deep benthic habitats (Krause-Jensen and Duarte, 2016; Smith, 1981), few studies have investigated the role of kelp detritus (large or small particles) in shaping deep benthic communities (Vetter and Dayton, 1999; Bernardino et al., 2010; Ramirez-Llodra et al., 2016; Renaud et al., 2008). Here, we addressed this question by studying the community structure and biodiversity of the 3 faunal components (meio-, macro- and megafauna) of an upper bathyal region in northern Norway.

The initial study design considered the deep (450 m) basin at the mouth of the Malangen fjord as an area that should receive considerable input of kelp detritus from the abundant kelp forests in the shallows. In comparison, the benthic community on the adjacent continental shelf 15 km offshore, at the same depth and with comparable substrate and temperature, was assumed to receive little input of kelp detritus. A parallel study showed that the seasonal cast of kelp blades in spring results in a short-term resource pulse that is transported over several weeks and can be observed in the shallows, the deep subtidal (down to

80 m) and the deep fjord (450 m) (Filbee-Dexter et al., 2018). This pattern was true for the fjord area. In contrast, on the offshore shelf, large pieces of kelp were not observed on the seabed photographic survey nor collected in the benthic trawls. This was consistent with our expectations and with similar observations that have been reported for a region off California, where large amounts of kelp detritus (in the form of large pieces) were observed in the Carmel submarine canyon, but detritus was negligible on an adjacent shelf area 9 km offshore (Harrold et al., 1998). The authors attribute the low biomass of macroalgae on the shelf area to the slower currents and higher consumption rates by the deep-sea echinoid *Allocentrotus fragilis*.

Yet, in this study, when we considered the accumulation of small-particle kelp detritus, a different pattern emerged. In fact, we showed that the standing biomass of small kelp particles is similar in the two study areas: the shelf and the deep fjord. Wernberg and Filbee-Dexter (2018) analysed the sinking rate of different size-particles of kelp detritus, from whole plants to the small kelp-particles that are produced by sea-urchin grazing. These authors showed that the small kelp-particle detritus sink at significantly lower rates than larger kelp detritus, increasing the dispersal potential of small-particle detritus. A physical
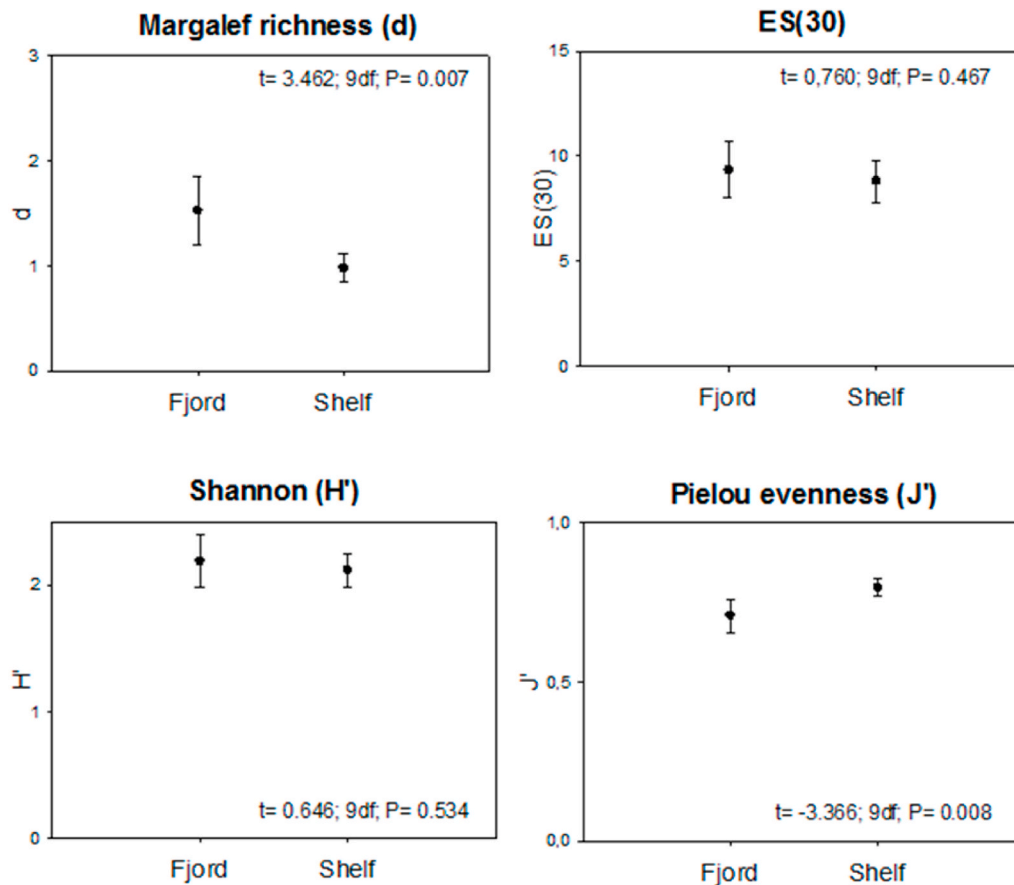
Fig. 12. Average megafauna biodiversity indices for samples collected with the beam trawl in the fjord and on the shelf. Error bars denote standard deviation. Results of t-tests are also given for each index.

model of particle transport in the same region, conducted in parallel to this study, showed that with the oceanographic currents in the region of Malangen fjord and adjacent shelf, the small kelp detritus can be transported tens of kilometres away from the source (Filbee-Dexter et al., 2019a). Our observations of small particle detritus on the surface of the grab samples support the model outcomes and provides evidence that abundant small particles of kelp detritus reach the seafloor on the offshore shelf study area. We did not measure the input of small kelp particles (only the standing biomass on the seafloor), so it is possible that one of our study areas has a higher consumption rate from the benthic fauna than the other, and that the actual kelp input is also higher in that area. However, a key outcome of this study was the rebuttal of our initial hypothesis that the benthic communities on the shelf, away from the kelp forest, would not receive noticeable amounts of kelp detritus. This is a major finding, as it implies that kelp detritus can provide organic carbon to trophic systems far from the kelp source and may be particularly important in subsidising communities that are otherwise food limited, such as the lower bathyal or abyssal regions (Smith et al., 2008).

A number of factors can influence the transport and uptake by fauna of kelp detritus. As POC sinks through the water column, the labile components are utilised by the pelagic microbial and metazoan communities, decreasing the quantity and quality of food that reaches the deep seafloor (Lampitt and Antia, 1997). However, transport and concentration of organic matter can be enhanced by hydrographic processes related to topographic features such as submarine canyons (Fernandez-Arcaya et al., 2017). Canyons act as conduits of particles from the shelf to the deep basins and have been shown to be preferential areas for the transport and accumulation of macroalgae (Harrold et al., 1998; Vetter and Dayton, 1999; Vetter, 1994). Vetter and Dayton (1999) suggest that the observed accumulated macroalgal detritus in canyons off California

sustained and increased megafaunal abundance in the canyon. Harrold et al. (1998) estimated that kelp detritus in the Carmel Submarine Canyon (California) can account from 20% to 83% of the total input of particulate organic carbon to the seafloor. However, the authors indicated that the extent to which this macroalgal carbon input alters benthic communities is still unclear. Bernardino et al. (2010) experimentally deployed large kelp parcels (100 kg) at 1670 m off California. The study showed that kelp-derived organic matter was rapidly transferred to the sediments and utilised by microbes and metazoans, resulting in a significant change in the macrobenthos after 0.25 and 0.5 years. These studies provide evidence of a significant contribution of kelp detritus in the composition of the POC input to the deep seafloor, but the pathways by which this organic matter is used by the fauna needs further analyses.

The few studies that have quantified directly the role of macroalgal detritus in fuelling coastal benthic communities in polar regions used stable isotope analyses and showed that the benthic communities are fuelled by multiple energy channels, including phytodetritus and macroalgae (Dunton, 2001; Dunton and Schell, 1987; McMeans et al., 2013). Little has been done in analysing the assimilation of macroalgal carbon by deep-sea benthic communities, but a recent study in Isfjorden (Svalbard) indicated that macroalgal detritus contributes significantly to the trophic web of benthic Arctic ecosystems (Renaud et al., 2015).

In our study, we found significant differences between the community structures of the meio-, macro- and megafauna benthos in the fjord and adjacent shelf areas with similar environmental conditions (i.e. temperature, salinity, sediment seafloor and depth). However, no direct links between community structure and kelp detritus could be made. Because macrofauna and small-kelp particles were collected together from grab samples, this faunal component provided the best dataset to

assess the role of small-kelp detritus in shaping the benthic community structure. The results indicated that the main environmental factors explaining the observed community structures in the fjord and on the shelf were specific sediment variables: mean grain size of the sediment, total organic matter and total nitrogen. Small kelp particles were included in the set of relevant variables as fourth best correlation, suggesting potential influence of kelp detritus in shaping macrofaunal communities. However, our analyses do not provide direct evidence for this link. For the meiofauna, the main explanatory variables for the differences in nematode genus composition (as the dominant metazoan taxon) were related to sediment particle size rather than kelp-derived organic matter. Nematodes are indeed regarded as grazers of microalgae and bacteria, while predation is also a potentially important feeding strategy (Moens et al., 2005; Moens and Vincx, 1997). However, Riera and Hubas (2003) did found that organic matter derived from stranded macroalgae, mostly *Enteromorpha* sp. and *Fucus spiralis*, was the primary contributor to the assimilated food sources of nematodes in intertidal habitats of Roscoff (France). Empirical evidence for a trophic link between nematodes and macroalga was not observed in this study. One possible explanation for this is that phytoplankton-derived organic carbon may be cycled more rapidly than kelp-derived organic carbon, which can be more refractory and remineralised slower (Bianchi et al., 2018), but additional stable isotope analyses should provide more clear results

The biodiversity indices calculated for meio-, macro- and megafauna did not indicate clear patterns between the fjord and shelf communities. In most cases, the biodiversity indices were not significantly different between the two study sites, and no relation could be made to kelp-detritus input onto the seafloor. In fact, similar amounts of small-kelp detritus particles in both areas would provide similar macroalgal carbon to the meio- and macro-benthic communities in the fjord and the shelf. Based on a previous study in the Oslo fjord (Ramirez-Llodra et al., 2016), we hypothesized that decomposing kelp in large accumulations on the deep seafloor could provide a significant amount of energy to the benthic communities. However, although we observed large kelp detritus (blades) at 450 m on the fjord basin, no dense kelp accumulations (i.e. kelp graveyards) were observed. The observed kelp blades on the seafloor were in a relatively fresh state, and thus not directly available for most fauna (Krumhansl and Scheibling, 2012). Kelp detritus contains structural components that are not easily broken down and require microbial communities to colonise and degrade the material before it becomes nutritionally available for most benthic fauna (Norderhaug et al., 2003). The experimental deployment of kelp parcels with the TLC provided further indications that the benthic fauna was not directly interested in the 6-week old kelp itself. The only TLC deployment that showed a significant attraction to amphipods was the deployment with kelp collected in the otter trawl, and thus with a strong food cue ('rotting fish'). This may indicate slower degradation rates of *L. hyperborea* than have been previously reported for other kelp species (e.g., *S. latissima*, Krumhansl and Scheibling, 2012). We suggest that longer deployments (i.e. months) of kelp on the seafloor, allowing for the kelp to start degrading, and become nutritionally available are needed to ascertain the use of large kelp detritus by deep benthic communitiesy.

5. Forward look

Fluxes of organic carbon in the coastal zone are changing in the Anthropocene, and this will have consequences for benthic communities that rely on coastal sources of organic material. Kelp forests are major sources of coastal production that are undergoing significant changes globally (Krumhansl et al., 2016a; Wernberg et al., 2019). These include shifts to turf algae at many warm range margins and alternations between sea-urchin barrens and kelp forests. Shifts from kelp forests to turf reefs or sea-urchin barrens result in a significant reduction in kelp detritus formation and thus in POC input to the adjacent deep-sea

ecosystems. Temporal simulations projecting a decrease of kelp detritus biomass showed important biomass and trophic changes on the food-web structure (Vilas et al., submitted). In our study area, the expected increase in kelp with the retreat of sea urchins, recently reported by Christie et al. (2019), should result in greater flushing of kelp detritus into deep regions. In addition, increased macroalgal bed growth and spatial distribution predicted for Arctic fjords in relation to sea-ice loss (Filbee-Dexter et al., 2019b; Krause-Jensen and Duarte, 2014), make studying these dynamic processes at high latitudes particularly critical.

Interestingly, our results ran contrary to many of our initial assumptions and findings from other regions on these dynamics. This highlights the number of unknowns that remain regarding how kelp detritus is transported and accumulated on the sea floor, and what post depositional processes are at play in deep habitats. Further studies are necessary to quantify the role of kelp and other macroalgal detritus in fuelling deep benthic fauna in different regions of the world and at different depths, to better predict the response of deep-sea ecosystems to regime shifts in coastal areas driven by climate change or other stressors (e.g. pollution, harvesting). In addition, measuring *in situ* degradation rates will be critical for understanding the fate of this material at depth. In parallel to questions regarding trophic linkages with kelp, regional and global carbon budgets highlight the importance of fjords and other coastal systems as hotspots for carbon burial (Bianchi et al., 2018; Smith et al., 2015). Additional studies are necessary to provide empirical data to the current discussion on the role of kelp and other macroalgal detritus in carbon sequestration (see Krause-Jensen and Duarte, 2016), both regionally and globally.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.dsr.2020.103433.

Contributions

All authors contributed to the research equally. ERL coordinated the project and co-lead the cruise with TP. TP, NM and DV collected the megafauna samples and provided the megafauna dataset. ERL analysed the megafauna data and collected and analysed the macrofauna data with GB. KFD contributed to macrofauna sample collection and led the analyses of kelp fluxes. KG, MVG, AV and FH collected and analysed the meiofauna data. All authors contributed to the writing of the paper. Data is available upon request to the corresponding author.

References

Anderson, M., Clark, M.R., Gorley, R., 2008. PERMANOVA+ for Primer: Guide to Software and Statistical Methods.

Bernardino, A.F., Smith, C.R., Baco, A., Altamira, I., Sumida, P.Y.G., 2010. Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. Deep-Sea Res. Part I Oceanogr. Res. Pap. 57, 708–723. https://doi.org/10.1016/J.DSR.2010.03.004.

Bianchi, T.S., Cui, X., Blair, N.E., Burdige, D.J., Eglinton, T.I., Galy, V., 2018. Centers of organic carbon burial and oxidation at the land-ocean interface. Org. Geochem. 115, 138–155. https://doi.org/10.1016/J.ORGGEOCHEM.2017.09.008.

Billett, D.S., Betta, B., Rice, A., Thurston, M., Galéron, J., Sibuet, M., GAWolff, G.A., 2001. Long-term change in the megabenthos of the porcupine abyssal plain (NE atlantic). Prog. Oceanogr. 50, 325–348. https://doi.org/10.1016/S0079-6611(01)00060-X.

Britton-Simmons, Kevin, Rhoades, Ali, Pacunski, Robert, Galloway, Aaron, Lowe, Alexander, Sosik, Elizabeth, Dethier, Megan, Duggins, David, 2012. Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. Limnology and oceanography 57, 176–184. https://doi.org/10.4319/lo.2012.57.1.0176.

Christie, H., Gundersen, H., Rinde, E., Filbee-Dexter, K., Norderhaug, K.M., Pedersen, T., Bekkby, T., Gitmark, J.K., Fagerli, C.W., 2019. Can multitrophic interactions and ocean warming influence large-scale kelp recovery? Ecol. Evol. 9, 2847–2862. https://doi.org/10.1002/ece3.4963.

Clarke, K., Gorley, R., 2006. Primer. PRIMER-e, Plymouth.

Costello, Mark, Chaudhary, Chhaya, 2017. Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation. Current Biology 27, R511–R527. https://doi.org/10.1016/j.cub.2017.04.060.

Dierssen, H.M., Zimmerman, R.C., Drake, L.A., Burdige, D.J., 2009. Potential export of unattached benthic macroalgae to the deep sea through wind-driven Langmuir circulation. Geophys. Res. Lett. 36, 1–5.

Dunton, K.H., 2001. δ^{15}N and δ^{13}C measurements of antarctic peninsula fauna: trophic relationships and assimilation of benthic seaweeds. Am. Zool. 41, 99–112. https://doi.org/10.1093/icb/41.1.99.

Dunton, K.H., Schell, D.M., 1987. Dependence of consumers on macroalgal (Laminaria solidungula) carbon in an arctic kelp community: ??13C evidence. Mar. Biol. 93, 615–625. https://doi.org/10.1007/BF00392799.

Elvsborg, A., 1979. Late Quaternary sedimentation in a glacial trough on the continental shelf off Troms, northern Norway. Nor. Geol. Tidsskr. 59, 309–325.

Falkenhaug, T., Tande, K., Timonin, A., 1997. Spatio-temporal patterns in the copepod community in Malangen, Northen Norway. Journal of Plankton Research 19 449–468.

Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V.A.I., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A.A., Sanchez, F., Van den Beld, I.M.J., 2017. Ecological role of submarine canyons and need for canyon conservation: a review. Front. Mar. Sci. 4–5. https://doi.org/10.3389/fmars.2017.00005.

Filbee-Dexter, K., Wernberg, T., 2018. Rise of Turfs : a new battlefront for globally declining kelp forests. Bioscience 68. https://doi.org/10.1093/biosci/bix147.

Filbee-Dexter, K., Feehan, C.J., Scheibling, R.E., 2016. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Mar. Ecol. Prog. Ser. 543, 141–152. https://doi.org/10.3354/meps11554.

Filbee-Dexter, K., Wernberg, T., Norderhaug, K.M., Ramirez-Llodra, E., Pedersen, M.F., 2018. Movement of pulsed resource subsidies from kelp forests to deep fjords. Oecologia 187, 291–304. https://doi.org/10.1007/s00442-018-4121-7.

Filbee-Dexter, K., Pedersen, M., Fredriksen, S., Norderhaug, K., Rinde, E., Kristiansen, T., Albretsen, J., Wernberg, T., 2019a. Carbon export IS facilitated BY sea urchins transforming kelp detritus. Oecologia in revisio.

Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K.M., Pedersen, M.F., 2019b. Arctic kelp forests: diversity, resilience and future. Global Planet. Change 172, 1–14. https://doi.org/10.1016/j.gloplacha.2018.09.005.

FjærtoftLønne, Kaja, 2018. Macroalgal detritus: Physical variables and impacts on the benthic macrofaunal community. Master thesis. NTNU 80. http://hdl.handle.net/11250/2504552.

Fredriksen, S., 2003. Food web studies in a Norwegian kelp forest based on stable isotope (δ13C and δ15N) analysis. Mar. Ecol. Prog. Ser. https://doi.org/10.2307/24867089.

Gage, J.D., 2003. Food inputs, utilization, carbon flow and energetics. In: Tyler, P.A. (Ed.), Ecosystems of the Deep Oceans. Elsevier, p. 313.

Garden, C.J., Smith, A.M., 2015. Voyages of seaweeds: the role of macroalgae in sediment transport. Sediment. Geol. 318, 1–9.

Hald, M., Salomonsen, G., Husum, K., Wilson, L., 2011. A 2000 year record of atlantic water temperature variability from the malangen fjord, northeastern north atlantic. Holocene 21, 1049–1059.

Harrold, C., Light, K., Lisin, S., 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. Limnol. Oceanogr. 43, 669–678. https://doi.org/10.4319/lo.1998.43.4.0669.

Keck, A., Wassmann, P., 1996. Temporal and spatial patterns of sedimentation in the subarctic fjord Malangen, northern Norway. Sarsia 80, 259–276.

Krause-Jensen, D., Duarte, C.M., 2014. Expansion of vegetated coastal ecosystems in the future Arctic. Front. Mar. Sci. 1, 77. https://doi.org/10.3389/fmars.2014.00077.

Krause-Jensen, D., Duarte, C.M., 2016. Substantial role of macroalgae in marine carbon sequestration. Nat. Geosci. 9, 737–742. https://doi.org/10.1038/ngeo2790.

Krumhansl, K., Scheibling, R., 2012a. Production and fate of kelp detritus. Mar. Ecol. Prog. Ser. 467, 281–302. https://doi.org/10.3354/meps09940.

Krumhansl, K.A., Okamoto, D.K., Rassweiler, A., Novak, M., Bolton, J.J., Cavanaugh, K. C., Connell, S.D., Johnson, C.R., Konar, B., Ling, S.D., Micheli, F., Norderhaug, K.M., Pérez-Matus, A., Sousa-Pinto, I., Reed, D.C., Salomon, A.K., Shears, N.T., Wernberg, T., Anderson, R.J., Barrett, N.S., Buschmann, A.H., Carr, M.H., Caselle, J. E., Derrien-Courtel, S., Edgar, G.J., Edwards, M., Estes, J.A., Goodwin, C., Kenner, M. C., Kushner, D.J., Moy, F.E., Nunn, J., Steneck, R.S., Vásquez, J., Watson, J., Witman, J.D., Byrnes, J.E.K., 2016. Global patterns of kelp forest change over the past half-century. Proc. Natl. Acad. Sci. Unit. States Am. 113, 13785–13790. https://doi.org/10.1073/pnas.1606102113.

Krumhansl, K., Scheibling, R., 2012. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. fragile. Mar. Ecol. Prog. Ser. 456, 73–85. https://doi.org/10.3354/meps09671Krumhansl.

Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep seas: regional characteristics and temporal variability. Deep-Sea Res. Part I Oceanogr. Res. Pap. 44, 1377–1403. https://doi.org/10.1016/S0967-0637(97)00020-4.

Krumhansl, K.A., Lauzon-Guay, J.-S., Scheibling, R.E., 2014. Modeling effects of climate change and phase shifts on detrital production of a kelp bed. Ecology 95, 763–74.

Levin, L.A., et al., 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. Marine Ecolgy 31, 1–5.

Ling, S.D., Johnson, C.R., Ridgeway, K., Hobday, A.J., Haddon, M., 2009. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Global Change Biol. 15, 719–731. https://doi.org/10.1111/j.1365-2486.2008.01734.x.

Mann, K., 1973. Seaweeds: their productivity and strategy for growth. Science 182, 975–981. https://doi.org/10.1126/science.155.3758.81.

Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J.A., Fordham, D.A., Russell, B.D., Gurgel, C.F.D., Wernberg, T., 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers. Distrib. 24, 1350–1366. https://doi.org/10.1111/ddi.12767.

McMeans, B., Rooney, N., Arts, M., Fisk, A., 2013. Food web structure of a coastal Arctic marine ecosystem and implications for stability. Mar. Ecol. Prog. Ser. 482, 17–28. https://doi.org/10.3354/meps10278.

Moens, T., Vincx, M., 1997. Observations on the feeding ecology of estuarine nematodes. cambridge.org 77, 211–227.

Moens, T., Bouillon, S., Gallucci, F., 2005. Dual stable isotope abundances unravel trophic position of estuarine nematodes. J. Mar. Biol. Assoc. U. K. 85, 1401–1407. https://doi.org/10.1017/S0025315405012580.

Moy, F.E., Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. Mar. Biol. Res. 8, 309–321. https://doi.org/10.1080/17451000.2011.637561.

Norderhaug, K.M., Christie, H.C., 2009. Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar. Biol. Res. 5, 515–528. https://doi.org/10.1080/17451000902932985.

Norderhaug, K.M., Christie, H., 2011. Secondary production in a *Laminaria hyperborea* kelp forest and variation according to wave exposure. Estuar. Coast Shelf Sci. 95, 135–144. https://doi.org/10.1016/J.ECSS.2011.08.028.

Norderhaug, K.M., Fredriksen, S., Nygaard, K., 2003. Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. Mar. Ecol. Prog. Ser. 255, 135–144.

Pedersen, M., Nejrup, L., Fredriksen, S., Christie, H., Norderhaug, K., 2012. Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*. Mar. Ecol. Prog. Ser. 451, 45–60. https://doi.org/10.3354/meps09594.

Pedersen, M.F., Filbee-dexter, K., Fagerli, C.W., Fredriksen, S., 2019. Detrital carbon production and export in high latitude kelp forests. Oecologia in review 1–33.

Pessarrodona, A., Moore, P.J., Sayer, M.D.J., Smale, D.A., 2018. Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. Global Change Biol. 24, 4386–4398. https://doi.org/10.1111/gcb.14303.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martínez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7, 2851–2899. https://doi.org/10.5194/bg-7-2851-2010.

Ramirez-Llodra, E., Rinde, E., Gundersen, H., Christie, H., Fagerli, C.W., Fredriksen, S., Gitmark, J.K., Norling, K., Walday, M.G., Norderhaug, K.M., 2016. A snap shot of the short-term response of crustaceans to macrophyte detritus in the deep Oslofjord. Sci. Rep. 6, 23800. https://doi.org/10.1038/srep23800.

Renaud, P.E., Morata, N., Carroll, M.L., Denisenko, S.G., Reigstad, M., 2008. Pelagic–benthic coupling in the western Barents Sea: processes and time scales. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 2372–2380. https://doi.org/10.1016/J.DSR2.2008.05.017.

Renaud, P.E., Løkken, T.S., Jørgensen, L.L., Berge, J., Johnson, B.J., 2015. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front. Mar. Sci. 2, 31. https://doi.org/10.3389/fmars.2015.00031.

Rex, Michael, Etter, Ron, 2010. Deep-Sea Biodiversity: Pattern and Scale. BioScience 61, 327–328. https://doi.org/10.1525/bio.2011.61.4.17.

Riera, P., Hubas, C., 2003. Trophic ecology of nematodes from various microhabitats of the Roscoff Aber Bay (France): importance of stranded macroalgae evidenced through δ13C and δ15N. Mar. Ecol. Prog. Ser. 260, 151–159.

Schaal, G., Riera, P., Leroux, C., 2011. Microscale variations of food web functioning within a rocky shore invertebrate community. Mar. Biol. 158, 623–630. https://doi.org/10.1007/s00227-010-1586-2.

Smith, S., 1981. Marine macrophytes as a global carbon sink. Science 84 211, 838–840. https://doi.org/10.1126/science.211.4484.838.

Smith, C.R., Baco, A., 2003. Ecology of whale falls at the deep-sea floor. Oceanogr. Mar. Biol. Annu. Rev. 41, 311–354.

Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23, 518–528. https://doi.org/10.1016/J.TREE.2008.05.002.

Smith, R.W., Bianchi, T.S., Allison, M., Savage, C., Galy, V., 2015. High rates of organic carbon burial in fjord sediments globally. Nat. Geosci. 8, 450–453. https://doi.org/10.1038/ngeo2421.

Stuart, C., Rex, M., Etter, R., 2003. Large-scape spatial and temporal patterns of deep-sea benthic species diversity. In: Tyler, P.A. (Ed.), Ecosystems of the Deep Oceans. Elsevier, p. 569.

Teagle, H.A., Hawkins, S.J., Moore, P., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J. Exp. Mar. Biol. Ecol. 492, 81–98. https://doi.org/10.1016/J.JEMBE.2017.01.017.

Thisle, D., 2003. The deep-sea floor: an overview. Ecosystems of the World, V. 28 Ecosystems of the deep ocean. Elsevier, Amsterdam, pp. 5–39.

Vanderklift, M.A., Wernberg, T., 2008. Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia 157, 327–335. https://doi.org/10.1007/s00442-008-1061-7.

Vetter, E.W., 1994. Hotspots of benthic production. Nature 372, 47. https://doi.org/10.1038/372047a0, 47.

Vetter, E.W., Dayton, P.K., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep Sea Res. Part II Top. Stud. Oceanogr. 45, 25–54. https://doi.org/10.1016/S0967-0645(97)00048-9.

Vetter, E., Dayton, P., 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar. Ecol. Prog. Ser. 186, 137–148. https://doi.org/10.3354/meps186137.

Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., Pedersen, Norderhaug, Fredriksen, Wernberg, Ramirez-Llodra, n.d. Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining ecosystem structural and functional traits. Deep Sea Res. II Top. Stud. Oceanogr.

Vincx, M., 1996. Meiofauna in Marine and 15 Freshwater Sediments.

Wentworth, Chester K., 1922. A Scale of Grade and Class Terms for Clastic Sediments. The Journal of Geology 30 (5), 377–392.

Wernberg, T., Filbee-Dexter, K., 2018. Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. Sci. Rep.

Wernberg, T., Krumhansl, K.A., Filbee-Dexter, K., Pedersen, M.F., 2019. Status and trends for the world's kelp forests. In: Sheppard, C. (Ed.), World Seas: an Environmental Evaluation, Vol III: Ecological Issues and Environmental Impacts. Elsevier.

Ramirez-Llodra, Eva, Tyler, Paul A., Baker, Maria C., Bergstad, Odd Aksel, Clark, Malcolm, Escobar, Elva, Levin, Lisa A., Menot, L., Rowden, Ashley A., Smith, Craig R. and Van Dover, Cindy Lee (2011). Man and the last great wilderness: human impact on the deep sea. PLoS ONE: 6(8) Pages: e22588. doi:10.1371/journal.pone.0022588.