



Video survey of deep benthic macroalgae and macroalgal detritus along a glacial Arctic fjord: Kongsfjorden (Spitsbergen)

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Abstract

In Kongsfjorden (Spitsbergen), we quantified the zonation of visually dominant macroalgal taxa and of detached macroalgae from underwater videos taken in summer 2009 at six transects between 2 and 138 m water depth. For the first time, we provide information on the occurrence of deep water red algae below the kelp forest and of detached macroalgae at water depth > 30 m. The presence and depth distribution of visually dominant red algae were especially pronounced at the outer fjord, decreased with proximity to the glacial front and they were absent at the innermost locations. Deepest crustose coralline red algae and foliose red algae were observed at 72 and 68 m, respectively. Brown algae were distributed along the entire fjord axis at 2–32 m. Green algae were only present at the middle to inner fjord and at areas influenced by physical disturbance at water depths of 2–26 m. With proximity to the inner fjord the depth distribution of all macroalgae became shallower and only extended to 18 m depth at the innermost location. Major recipients of detached macroalgae were sites at the shallower inner fjord and at the middle fjord below the photic zone at depths to 138 m. They may either fuel deep water secondary production, decompose or support carbon sequestration. Univariate and community analyses of macroalgal classes including detached macroalgae across transects and over depths reveal a considerable difference in community structure between the outermost sites, the central part and the inner fjord areas, reflecting the strong environmental gradients along glacial fjords.

Keywords Arctic fjord · Detached macroalgae · Lower macroalgal depth distribution · Deep sea

Introduction

Macroalgae, as the major primary producers and habitat builders along coastal rocky shores (Duarte and Cebrián 1996; Mann 2000; Christie et al. 2009; Tait and Schiel 2018), constitute a central part of marine shelf ecosystems worldwide. As sunlight is rapidly absorbed by the water column in the marine environment, primary production by macroalgae, microphytobenthos, seagrass or phytoplankton is restricted to the shallow euphotic zone (Gattuso et al. 2006; Ramirez-Llodra et al. 2010).

Besides build-up of biomass, temperate to polar macroalgal forests, which are normally dominated by brown algae of the order Laminariales or Desmarestiales (Lüning 1990), produce macroalgal detritus through incremental blade erosion, detachment of old blades or removal of whole thalli (Krumhansl and Scheibling 2012; Pedersen et al. 2020). The detached macroalgal biomass may therefore fuel secondary production (Ramirez-Llodra et al. 2016) or enter the detrital food chain and carbon cycle via different processes: it may persist as bigger thallus parts or as whole detached thalli where the general form or taxon affiliation of the seaweeds is still visible. We consider both as ‘macroalgal detritus’ in the current investigation. The biomass may further fragment into small particulate organic material (POM) where taxon identity is no longer detectable or dissolve into organic carbon (DOC). This macroalgal detritus may become exported to neighbouring or distant habitats (Fredriksen 2003; Britton-Simmons et al. 2012; Pedersen et al. 2020) contributing to the carbon export into the deep sea (Dierssen et al. 2009; Krause-Jensen and Duarte 2016). Depending on its

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rate of decomposition or burial it may contribute to carbon sequestration (Krause-Jensen et al. 2018) and act as a marine carbon reservoir (Blue carbon; Nellemann et al. 2009; Macreadie et al. 2019; Ortega et al. 2019).

Kongsfjorden in western Spitsbergen is a deep Arctic glacial and sedimentary fjord partially characterized by a steep rocky coast well populated by macroalgae. Macroalgal species composition, biomass and distribution in shallow zones above 30 depths are well known (Hop et al. 2012, 2016; Fredriksen et al. 2014, 2019; Bartsch et al. 2016). Almost 40% of the coastal middle to inner zone of Kongsfjorden between 0 and 30 m depth is covered by macroalgae (Kruss et al. 2017). In total 84 macroalgal species were reported for Kongsfjorden (Fredriksen et al. 2019) and brown algae, especially kelps of the order Laminariales, constitute the majority of the biomass in a depth range between 0 and 20 m (Hop et al. 2012, 2016; Bartsch et al. 2016). There is a clear distributional gradient along the fjord axis varying with substrate type and distance to the glacial fronts. Species with a wider biogeographical distribution are typically broadly spread along the fjord axis (Hop et al. 2016). Whilst the majority of macroalgal communities is restricted to hard bottom locations, in the inner bay of Kongsfjorden some soft bottom areas support macroalgae, primarily on drop stones (Hop et al. 2016; Fredriksen et al. 2019).

Whilst most green algae grow in the littoral zone, the majority of brown algae are located in the upper sublittoral followed by red algae which dominate greater depths (Hop et al. 2012) although lowest depth extension has not been revealed yet. In contrast to this detailed information, the depth distribution of macroalgae > 30 m and of the amount and occurrence of detrital macroalgae is virtually unknown, mostly due to the inaccessibility of the habitat and of diving depth limits. Whilst detached macroalgae may strongly influence the underlying soft bottom communities, the accumulation rate of detached macroalgae at deeper parts of the fjord is unknown as is the effect on the food web structure (Molis et al. 2019).

The objectives of our study thus was (i) to gain knowledge on the distribution of visually dominant macroalgal species or taxon groups beyond the depth limit of 30 m and (ii) to determine the amount and spatial occurrence of macroalgal detritus in Kongsfjorden. A remote video approach via a systematic analysis of georeferenced video transects was accomplished. The footage was recorded across the shore at different locations along the fjord axis, dominated by rocky substrate and also soft sediments and spanning a depth range between 2 and 138 m. Two of the selected sites are located at the northern shorelines and had previously been sampled by Hop et al. (2012, 2016) and Bartsch et al. (2016), but only at shallower depths. At the southern shore four video transect sites are located. Part of this area has been investigated before by air-borne hyperspectral imaging

and acoustic imaging providing a different resolution and not being able to detect macroalgal detritus (Volent et al. 2007; Kruss et al. 2017). All information was collated into a geographical information system (GIS) and resulting shape files are accessible on PANGEA and may serve for future applications.

Materials and methods

Study area

The study was performed in Kongsfjorden (78° 59 N, 11–12° E) at the western coast of Spitsbergen (Fig. 1). The coastal habitats of Kongsfjorden contain a mixture of hard and soft bottom substrates. Central and outer Kongsfjorden is dominated by outcrops of bedrock with a thin-sediment cover (Howe et al. 2003). At the inner part of the fjord, a large glacial complex contributes freshwater influx through melting and calving. Along with the raise in freshwater input by the glacial run-off, the concentration of suspended inorganic matter is increasing towards the inner fjord resulting in soft bottom-dominated areas (Svendsen et al. 2002). All deep fjord sites below 250 m are sedimentary in nature (Howe et al. 2003).

Data collection

In June 2009, the remotely operated vehicle (ROV) ACHILLE M4 (Institut Polaire Français Paul Emile Victor IPEV, France) recorded video transects at six coastal locations of Kongsfjorden, Spitsbergen stretching between 2 and maximal 138 m (Fig. 1). Four transects were located at the south shore along the length axis of the fjord (Kongsfjordneset, Brandal, Prince Heinrich Island, Tyskahytta). Two further transects investigated the steep bedrock of Hansneset with a west–east orientation 50 m apart from each other (Hansneset 1 and Hansneset 2). The ROV was operated on-board the research vessel Teisten (Kings Bay AS, Norway) connected by a cable as described in Laudien and Orchard (2012). The ship's navigation was recorded every two seconds by a GPS in WGS 84 (EPSG 4326). During the ROV dives, the ship drifted with a speed limited to 0.5 knots. The ROV operated along the same vector and at about the same forward speed as the ship. The video transects were georeferenced by means of the ship coordinates. Although offset between ship and ROV was not exactly quantifiable, we assume only a negligible inaccuracy, since the ROV was operated with the same speed as the ship. Sample points were removed, when the ship drifted slower than the ROV, e.g. when the ship was turning or passing locations with steep bedrock.

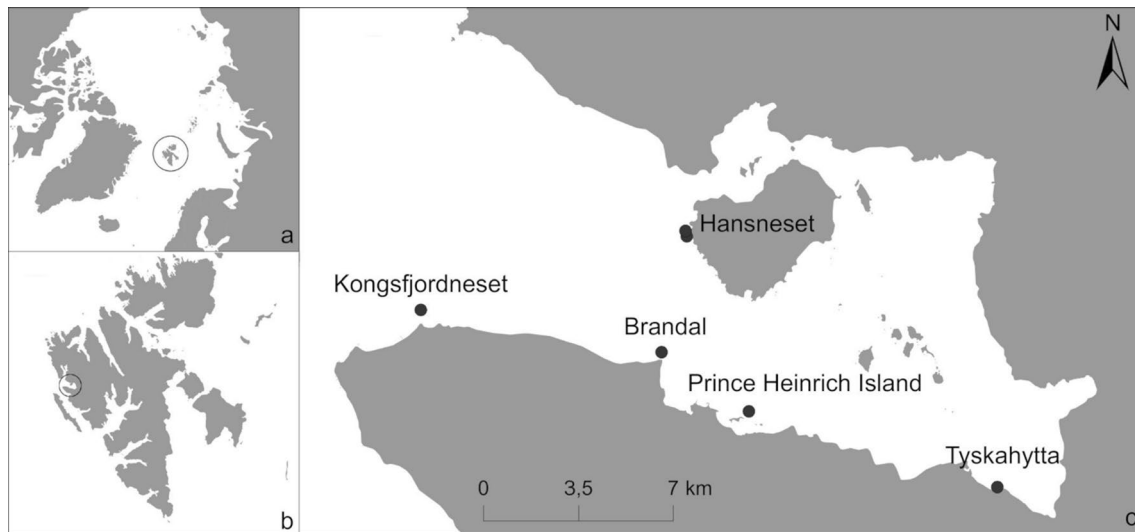


Fig. 1 **a** The Arctic, **b** Spitsbergen and **c** Kongsfjorden, with position of transects (black dots), (data EuroGeographics, Norwegian Polar Institute and Norwegian Mapping Authority)

The video camera SONY HVR-A1E HDV 1080i fitted with a 300-m Extreme Vision Lens was equipped with two halogen lights providing the broad illumination. On most ROV images, three laser pointers were visible, two arranged in a 3-cm horizontal distance and one in a 2-cm vertical distance resulting in a marked area of 6 cm² providing the spatial reference of the captured images. When laser pointers were not visible, an estimation of the area was achieved by comparing frames with a similar distance to the camera. In case the distance also was not directly visible, the scale was subjectively estimated through size of dominant flora or fauna on the images. Unfortunately, laser spots were switched off at Kongsfjordneset and Hansneset 1. Since Hansneset 2 was filmed with a similar estimated distance from the sea floor, the mean area per frame from this transect was used for area estimation of Kongsfjordneset and Hansneset 1. As a precise spatial reference was not possible over all transects, we analysed the percent cover of the frames without a relation to the ground area. The mean frame size was approx. 70–80 × 70–80 cm. Besides the video footage, the ROV measured water depth every other second. The accuracy of the depth sensor is ± 1 m or maximum ± 2 m at deeper points (D. Fleury, IPEV, personal communication).

Spatial analysis

The georeferenced data (date, depth, coordinates) of all transects were linked to the timecode of the video and imported into the geographical coordinate system (GIS) ArcGIS 10.6.1 (ESRI 2011) by an R-Script (Pehlke) and projected to *North Pole Lambert Azimuthal Equal Area (EPSG 102017)*. The course of the ship and hence the spatial orientation as

well as the length of transects were evaluated and illustrated on a map (Online Resource 2). The ROV-born depth data were used to map elevation profiles for transects and to analyse correlation between macroalgal distribution and depth. Gaps in GPS positioning and depth data (e.g. when the sea bed was steep) were closed by linear interpolation. Furthermore, a digital elevation model of Kongsfjorden was created from a point shape file given by the Norwegian Mapping Authority with a resolution of 10 × 10 m. With the help of this digital elevation model ROV depth data were cross-validated before start of analysis.

Every 5 m we extracted coordinates from transects (R script Pehlke) to achieve a representative sampling pattern of the seabed. The corresponding video timecode was extracted with the help of GIS. This considerably facilitated data evaluation and improved the systematic sampling of the video frames.

We consider the Kongsfjorden GIS as a start to establish a geodatabase which encloses geodata and metadata of any formats. It provides useful background information for other researchers who would like to see where transects were located and the geographical information may enhance the repeatability of the investigation in the future.

Image analysis

Each transect was analysed every 5 m. At Tyskahytta (see Fig. 1), we only considered macroalgal coverage every 10 m, since the environment and the biodiversity of the benthic cover was rather constant over distance. The Software Avidemux 2.7 (Mean, France) was used for deinterlacing, video frame extraction, sharpening (Avidemux filter Yadif)

and formatting the frames (images) to bitmap files. When the frame was unsuitable due to turbulence of the seabed or the camera was covered by macroalgae thalli, the next appropriate frame was used. The substitute image was scrutinized to ensure it represented a comparable area of the sea bed. The extracted images were analysed using ImageJ 2 software and its plugin GRID (Rueden et al. 2017). A raster was placed over each frame such that every grid cell was covering 5% of the frame (20,736 pixel²). Each frame was scored according to presence/absence and percent cover of visually dominant macroalgal taxa and categorical groups, detached macroalgae or part of them (macroalgal detritus) and visible substrate type. Macroalgal taxa were identified after Klekowski and Weslawski (1995) and Pedersen (2011). As many species or groups of species could not be determined to species level on the images, we estimated the coverage in the next broader categories: kelp (Laminariales), filamentous brown algae, foliose red algae, filamentous red algae, crustose coralline red algae, foliose green algae [this is probably *Ulvaria obscura* which is the only blade like Ulvales species reported for Kongsfjorden (Fredriksen et al. 2019)] and filamentous green algae (*Acrosiphonia* spp.). In addition to these categories, whenever possible kelp was further discriminated into *Alaria esculenta*, digitate kelp spp. [*Laminaria digitata* and *Hedophyllum nigripes* are grouped together as they are not distinguishable by their external morphology (Dankworth et al. 2020)], *Laminaria solidungula* and *Saccharina latissima*. In the case of filamentous brown algae Chordariaceae spp., which may comprise *Dictyosiphon foeniculaceus*, *Chordaria flagelliformis* and *Stictyosiphon tortilis* were distinguished from the two *Desmarestia* species (*D. aculeata* and *D. viridis*) and from *Halosiphon tomentosus*. Foliose red algae were further discriminated into *Ptilota* spp. (may comprise *Ptilota gunneri* and *P. serrata* according to Fredriksen et al. 2014), *Coccotylus truncatus* and *Phycodryx rubens* (for details see Table 2 in Results). Macroalgae were classified as detached when a free holdfast was visible, they were overturned and not in their usual orientation or when only fragments of the thalli were present. The presence and cover of sea urchins were recorded separately. Substrate was broadly classified into soft bottom, soft bottom with drop stones, hard bottom and hard bottom with silt. Whenever visible, the percent cover of rocky substrate (hard bottom substrate or drop stones) was estimated. Locations with high macroalgal cover, where it was impossible to estimate the substrate type, were assigned to hard bottom by default as a dense macroalgal vegetation does not grow on soft bottom (Wulff et al. 2009). The percent cover of all groups and substrate classes was estimated in 5% increments with 1% cover for minimum coverage: 0%, 1%, 5%, 10%, 15%, etc. up to 100%.

Elevation profiles for each transect were generated and categorized into 2-m-depth zones

(0–2 m, > 2–4 m, > 4–6 m, etc.) and frames from one depth zone and transect were considered as pseudo-replicated images. Depending on the slope of the sea ground, the number of replicates per depth zone n was varying ($n = 0–41$). For every depth zone and transect mean percent cover for macroalgae in total as well as for each algae group (kelp, filamentous brown algae, foliose red algae, filamentous red algae, coralline red algae, foliose green algae and filamentous green algae) along with the cover of detached macroalgae was calculated.

Statistical analysis

Multivariate analysis

A cluster analysis based on the mean cover data per 5-m-depth zones of macroalgae groups (kelp, filamentous brown algae, foliose red algae, filamentous red algae, coralline red algae, foliose green algae and filamentous green algae) and detached macroalgae per transect was performed using a Bray–Curtis similarity matrix from square root-transformed data (Bray and Curtis 1957; Clarke et al. 2014). A depth of 45 m was chosen as a lower limit, since macroalgal vegetation was mainly constricted to shallower areas. Results are presented in form of a non-metric multi-dimensional scaling (nMDS) plot. To identify the key groups which contributed most to the dissimilarity between depth zones and transects a SIMPER analysis was performed (PRIMER v5; Plymouth Marine Laboratory, Clarke and Gorley 2006).

Univariate analysis

Differences in percentage kelp and detached macroalgae cover, as the major classes we were interested in, were tested. As transects were not replicated, 2-factor ANOVA's without replication were performed with arcsine-transformed data with fixed factors, Transect and Depth, followed by Tukey HSD post hoc tests (R, R Core Team 2021). As homogeneity of variances was not achieved throughout (Levene's test), we decreased the significance level to $p = 0.01$ to decrease the possibility of a Type I error. As data were not uniformly present for both cover classes over all transects and depths, we only compared those transects and depths with matching data. In conclusion, differences in mean percentage kelp cover were tested between 6 and 30 m categorized in 2-m-depth zones for the transects Kongsfjordneset, Hansneset 1 and 2 and Brandal. For mean percentage cover of detached macroalgae, differences were tested for shallower depths between 6 and 22 m for Kongsfjordneset, Hansneset 1 and 2, Brandal and Tyskahytta and for greater

depths between 24 and 56 m for the transects Kongsfjordneset, Hansneset 1 and 2 and Brandal.

Results

Transect metadata

The lengths of the six georeferenced video transects varied between 560 and 1485 m (Table 1). The transect at Kongsfjordneset covered the longest distance up to the inner glacial front (24 km), followed by Hansneset 1 and 2 (16 km), Brandal (15 km), Prince Heinrich Island (11 km) and Tyskahytta (2 km). Depths ranged between 2 and 138 m, with the deepest transect being at Brandal and the shallowest at Tyskahytta (Table 1). In total, 907 images have been analysed covering an area of approx. 520 m². The resulting analysed area of each depth range as well as the number of replicates per depth interval per transect are listed in Online Resource 1.

Macroalgal taxa

Overall, 16 macroalgal taxa or groups were identified from video frames along the six transects in Kongsfjorden which are depicted in Fig. 2. The depth distribution across transects is given in Table 2. Foliose green algae occurred only at the inner fjord mainly in the upper range of the sublittoral down to 16 m depth. Filamentous green algae (*Acrosiphonia* spp.) were present at Prince Heinrich Island, Tyskahytta, and Hansneset 1 and at Brandal between 2 and 26 m. The perennial kelp *Alaria esculenta* and *Saccharina latissima* as well as the filamentous brown algae *Desmarestia* spp. were present in all transects from the shallow sublittoral down to 30 m and 32 m, respectively. Perennial digitate kelps (2–24 m) were observed at Hansneset 1 and 2 and Kongsfjordneset only. The annual brown algae Chordariaceae spp. and *Halosiphon tomentosus* occurred exclusively at Brandal in shallow waters down to 10 m or 14 m, respectively.

Laminaria solidungula, the only Arctic endemic kelp species, was only observed at Prince Heinrich Island between 22 and 24 m depth. The perennial red algae *Coccolytus truncatus* (12–48 m) and *Phycodrys rubens* (2–68 m) occurred only at Hansneset 1 and 2 and Prince Heinrich Island. The pseudo-perennial red alga *Devaleraea ramentacea* (4–14 m) and perennial *Ptilota* spp. (20–34 m) were just present at Hansneset. A filamentous red alga, possibly of the genus *Polysiphonia*, occurred exclusively at Kongsfjordneset and Prince Heinrich Island between 10 and 40 m. Crustose coralline red algae were visible at Kongsfjordneset and Hansneset at almost every depth (4–72 m) and occasionally at Prince Heinrich Island. In conclusion, 10 macroalgal taxa or groups were found at Hansneset 1, followed by Prince Heinrich Island (9) and by Hansneset 2 (8), Brandal (7) and Kongsfjordneset (6) and fewest number of macroalgal taxa/groups were observed at Tyskahytta (5).

Depth distribution of macroalgal groups and detached macroalgae across transects

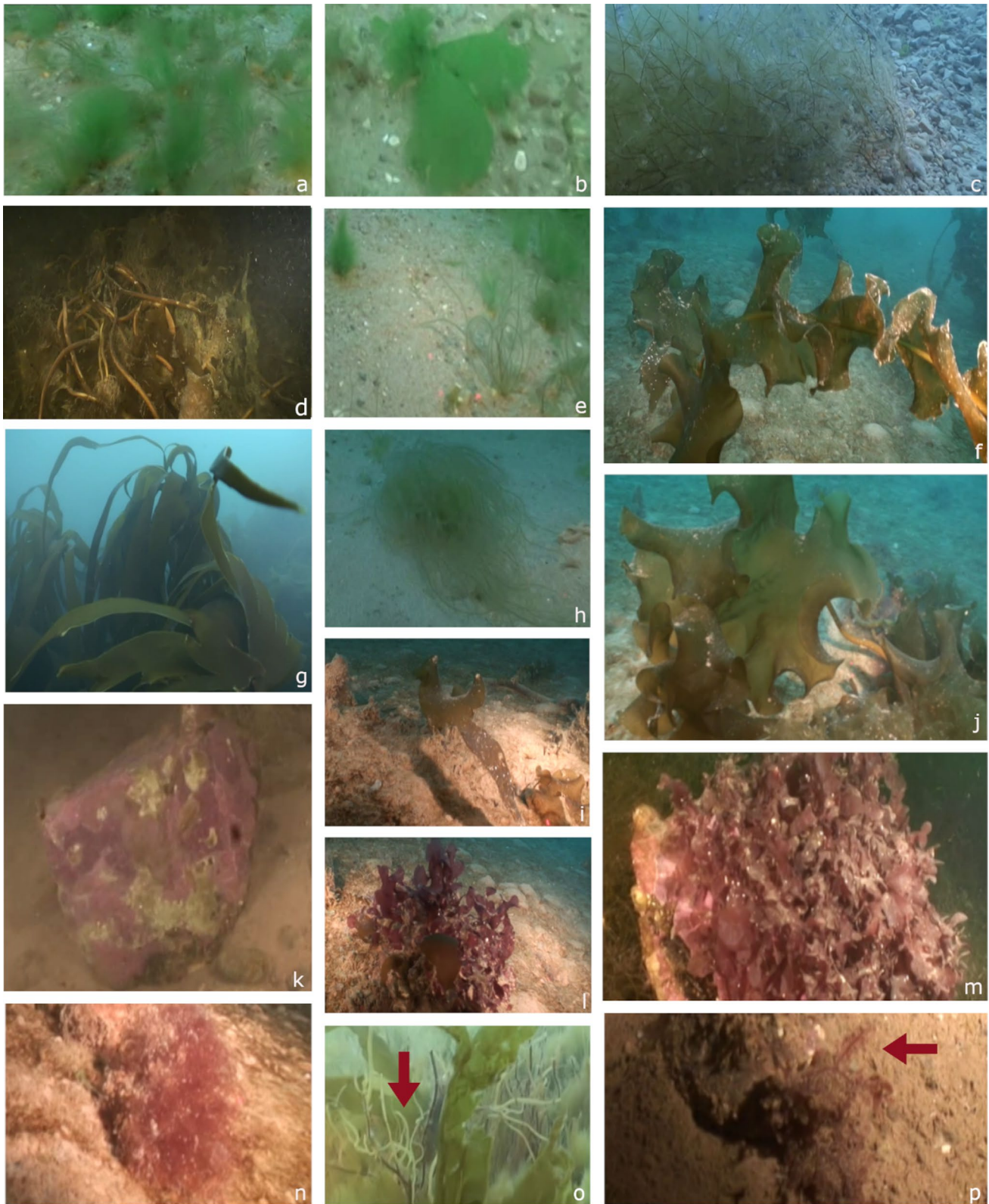
The mean macroalgal cover varied throughout the fjord and the two major depth ranges above and below 30 m. The relative contribution of macroalgae groups and detached macroalgae is depicted in Fig. 3. The coverage of macroalgae, visible hard bottom substrate or drop stones was evaluated in classes along depth gradients for each transect. Figure 4 shows the mean macroalgal percentage cover of the sea floor as well as the cover of hard bottom in 2-m-depth intervals and Online Resource 1 provides mean values.

At the outer location, Kongsfjordneset and the more exposed northern locations Hansneset 1 and 2, the total macroalgal cover at 2–30 m depth was highest (53–57%), whilst the southern and inner locations Brandal, Prince Heinrich Island and Tyskahytta had a low coverage (23, 37, 7%, respectively) in the depth range 4–(24)30 m. Mean cover of attached macroalgae > 30 m depth was generally low with a maximum of 10% at Kongsfjordneset and a minimum at Brandal, where no attached macroalgae were found > 30 m. Filamentous brown algae were distributed along the entire

Table 1 Metadata information of Kongsfjorden macroalgal video analyses: transect names: Hansneset 1 (HN1), Hansneset 2 (HN2), Kongsfjordneset (KN), Brandal (BL), Prince Heinrich Island (PHI)

Transect	Date	Distance [km]	Length [m]	Depth range [m]	Bottom substrate
KN	16.06.2009	24	855	6–60	Hard bottom
HN1	15.06.2009	16	565	2–72	Hard bottom partly covered with silt
HN2	15.06.2009	16	645	6–56	Hard bottom partly covered with silt
BL	17.06.2009	15	1100	4–138	Soft bottom interspersed with drop stones
PHI	16.06.2009	11	560	14–46	Soft bottom interspersed with drop stones
TH	17.06.2009	2	1485	6–24	Soft bottom partly interspersed with drop stones

and Tyskahytta (TH), date of video shooting, distance from inner glacial front (Kongsvegen and Kronebreen glacier), length of video recording, depth range and bottom substrate at location



ford axis < 30 m (4–11%) and even occurred > 30 m at Kongsfjordneset, Hansneset 1 and 2 and Prince Heinrich Island (< 2%). Filamentous brown algae were also present

at Hansneset between 54 and 60 m. However, attachment to the substrate was not verifiable. Whilst kelp were only present < 30 m depth in all transects with an overall mean

Fig. 2 Representative images of identified macroalgal taxa and detached macroalgae from videos at the different transects in Kongsfjorden 2009: **a** Filamentous green algae (possibly *Acrosiphonia* sp.), **b** bladed Ulvales sp. (possibly *Ulvaria obscura*), **c** *Desmarestia* sp., **d** pile of detached macroalgae (mostly kelp and filamentous brown algae) at Brandal at a depth of approximately 130 m, **e** *Halosiphon tomentosus*, **f** *Alaria esculenta* (characteristic midrib clearly visible), **g** digitate kelp (= *Laminaria digitata* and/or *Hedophyllum nigripes*), **h** Chordariaceae spp. (potential mixture of *Dictyosiphon* sp., *Chordaria* sp. and *Stictyosiphon tortilis*), **i** *Laminaria solidungula*, **j** *Saccharina latissima*, **k** Crustose coralline red algae, **l** *Coccolytus truncatus*, **m** *Phycodrys rubens*, **n** filamentous red alga, **o** *Devaleraea ramentacea* (red arrow) and **p** *Ptilota* sp. (red arrow)

cover at this depth range of 2–35%, visible red algal cover (foliose and filamentous red algae together) and crustose coralline red algae increased relative to the total macroalgal cover > 30 m depth (Fig. 3). At Kongsfjordneset, the rocky substrate was densely covered by visible crustose coralline red algae due to a lack of cover algae. Kelp was only growing in patches encircled by filamentous brown algae (*Desmarestia* spp.). In shallower waters (< 15 m), sea urchins were highly abundant surrounding those kelp patches. The Hansneset sites showed a high cover of filamentous and foliose red algae (HN1: 9% < 30 m, 1% > 30 m, HN2: 9% < 30 m, 3% > 30 m), whilst at the inner sites a low cover of red algae was observed (Fig. 3).

Green algae were only observed in the middle to inner fjord (Hansneset 1, Brandal and Tyskahytta) < 30 m depth and were highest at Brandal with 5%. The detailed qualitative description of the depth distribution of macroalgal groups and taxa exhibited in Fig. 4 is available in Online Resource 3.

In contrast to the low coverage of attached macroalgae > 30 m depth, detached macroalgae were observed at each transect in this depth range (Fig. 2), but also with lower coverages < 30 m at middle to inner transects Hansneset 1, Brandal, Prince Heinrich Island and Tyskahytta. Cover of detached macroalgae showed a clear gradient between outer (absent) and inner fjord (increasing) and generally increasing with depths. At Hansneset 1 and 2, a mean maximum cover of 8% of detached algae (mostly kelp, filamentous brown algae and foliose red algae) was observed between 4 and 72 m, whilst at Kongsfjordneset, detached macroalgae were nearly absent with only 1% coverage at 56–58 m (Fig. 4). At Prince Heinrich Island, detached macroalgae (mostly kelp and filamentous brown algae) were present with up to 13% coverage at 16–46 m. At Tyskahytta, detached macroalgae (mostly kelp) were observed at every depth and coverage was relatively high (4–11%) compared to that of attached macroalgae. Most detached macroalgae (mostly kelp and filamentous brown algae) were present at Brandal where they covered a remarkable area of the sea floor \geq 24 m depth occasionally reaching 40% cover and increasing to 66% at 132 m. Figure 2d depicts an example of piles of detached

and disintegrating kelp material visible at several sites at Brandal.

The differences in kelp cover as a proxy for a mature kelp forest and of detached macroalgae as a proxy for detritus pathways were also evaluated quantitatively between transects and along depths. The mean kelp cover was significantly different over the depth gradient and between transects (Table 3). The kelp cover at Hansneset 2 over all depths was highest reaching 100% between 6 and 14 m and therefore was significantly higher than at all other transects where kelp cover was maximally 62.5% at Hansneset 1, 30% at Brandal and 7.5% at Kongsfjordneset (Tukey post hoc test, $p < 0.01$). Interestingly, the kelp cover at Prince Heinrich Island at 14–16 m was unusually high with 98% but was excluded from statistical analysis due to missing data at shallower depths. Although kelp cover was significantly different over the depth gradient (Table 3), no significant differences amongst depth zones were revealed in the post hoc test.

The mean coverage of detached macroalgae between 6 and 22 m and between 24 and 56 m depth across transects were significantly different between transects, but not over the depth range (Tables 4 and 5). There were almost no detached macroalgae at Kongsfjordneset, Hansneset 1 and 2 and Brandal between 6 and 22 m, whilst the mean cover of detached macroalgae at Tyskahytta in this depth zone was significantly higher compared to all other transects reaching up to 10% (Tukey post hoc test, $p < 0.01$). At both Hansneset sites and Brandal, detached macroalgae mostly occurred below the kelp forest deeper than 24 m with a significantly higher cover at Brandal reaching up to 33% (Tukey post hoc test, $p < 0.01$). Prince Heinrich Island was not included in this analysis due to insufficient depth data for this transect.

Community analysis

Similarity of macroalgal group composition (kelp, filamentous brown algae, foliose red algae, filamentous red algae, coralline red algae, foliose green algae and filamentous green algae) along 9 depth horizons between 0 and 45 m per transect is visualized via a non-metric multi-dimensional scaling (nMDS) plot in Fig. 5 and support the qualitative description given above. All depth zones of Kongsfjordneset are clearly separated from all other transects and depth horizons. Results of a SIMPER analysis (all details in Online Resource 4) show that the mean high cover of visible coralline red algae contributed with 35–52% to the differences of Kongsfjordneset to all other transects. The soft bottom locations Brandal and Tyskahytta are also clearly separated and more similar to each other than to the other transects. SIMPER results show that cover of macroalgal detritus and kelp contributed mainly to the dissimilarity of Brandal and Tyskahytta to the other transects (15–31%, 13–33%, respectively).

Table 2 Depth distribution and occurrence of macroalgal taxa and broader macroalgal groups (in bold) along 6 transects in Kongsfjorden 2009: Hansneset 1 (HN1), Hansneset 2 (HN2), Kongsfjordneset (KN), Brandal (BL), Prince Heinrich Island (PHI) and Tyskahytta (TH)

	KN	HN1	HN2	BL	PHI	TH	Depth [m]
Filamentous green algae (<i>Acrosiphonia</i> spp.)	–	2–14	–	4–26	18–20	6–18	2–26
Foliose green algae (<i>Ulva</i> sp.)	–	–	–	8–16	–	6–16	6–16
Filamentous brown algae	6–30	2–28	14–32	4–30	14–32	6–18	2–32
<i>Desmarestia</i> spp. (<i>D. aculeata</i> and <i>D. viridis</i>)	6–30	2–28	14–32	4–30	14–32	6–18	2–32
Chordariaceae spp. (<i>Dictyosiphon</i> sp., <i>Chordaria</i> sp., <i>Stictyosiphon tortilis</i>)	–	–	–	6–10	–	–	6–10
<i>Halosiphon tomentosus</i>	–	–	–	10–14	–	–	10–14
Kelp species	6–16	2–18	6–30	4–30	14–24	6–18	2–30
<i>Alaria esculenta</i>	6–16	4–16	10–30	4–28	16–20	6–12	4–30
Digitate kelp spp. (<i>Laminaria digitata</i> / <i>Hedophyllum nigripes</i>)	6–8	2–18	6–24	–	–	–	2–24
<i>Laminaria solidungula</i>	–	–	–	–	22–24	–	22–24
<i>Saccharina latissima</i>	6–12	6–14	10–30	4–30	14–22	6–18	6–30
Crustose coralline red algae	6–60	4–72	14–32	–	20–44	–	4–72
Foliose red algae	–	2–68	14–56	–	18–44	–	2–68
<i>Coccolytus truncatus</i>	–	12–48	20–22	–	18–22	–	12–48
<i>Phycodrys rubens</i>	–	2–68	14–56	–	20–44	–	2–68
<i>Ptilota</i> spp. (<i>P. serrata</i> and <i>P. gunneri</i>)	–	26–28	20–34	–	–	–	20–34
Filamentous red algae	10–40	4–14	–	–	18–36	–	4–40
Indet species 1	10–40	–	–	–	18–36	–	10–40
<i>Devaleraea ramentacea</i>	–	4–14	–	–	–	–	4–14

The nMDS plot furthermore reveals that macroalgal composition, even in the applied broad groups, varies along depth gradients for every transect (Fig. 5). The SIMPER analysis shows that mean cover of brown algae (kelp and filamentous brown algae) was the primary factor to explain the dissimilarity between shallower sites (0–20 m) characterized by high brown algae coverage and deep sites down to 45 m with low coverages (19–37%, Online Resource 4). The deeper sites (20–45 m) are mostly differentiated by the dissimilarity of cover of detached macroalgae and visibility of coralline red algae (23–45%, 24–27% contribution to dissimilarity, respectively).

Discussion

Macroalgal distribution along the depth gradient and fjord axis

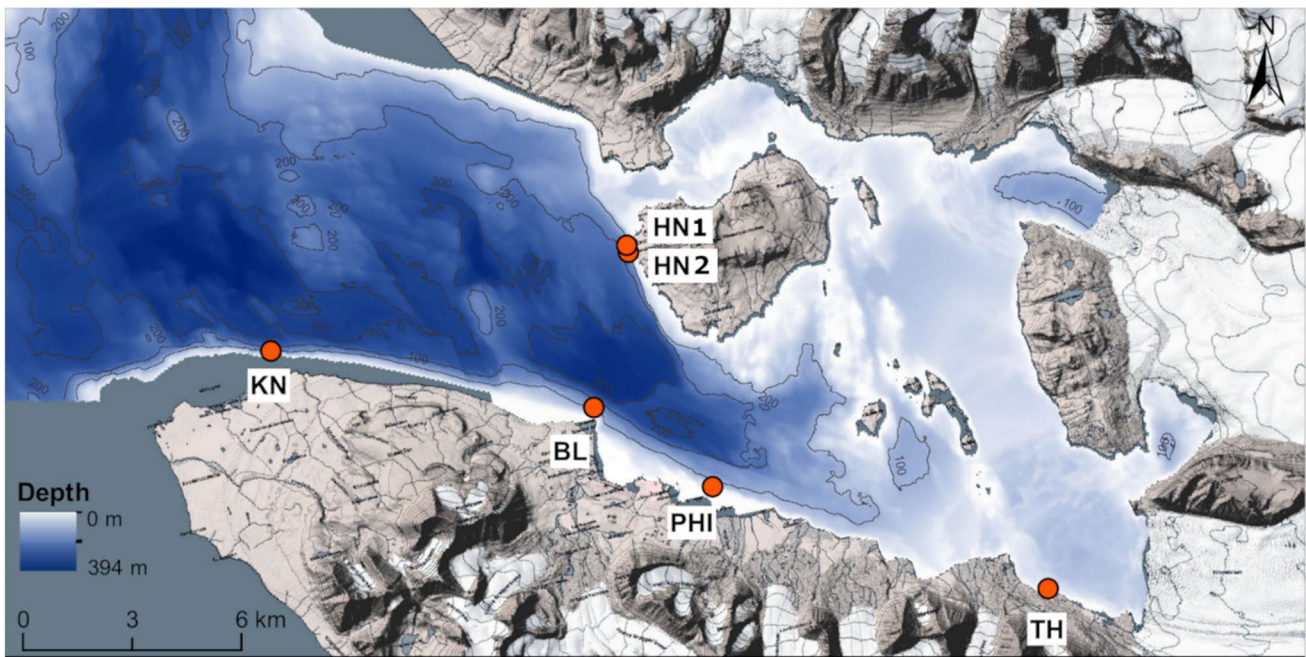
This study for the first time investigated the coastal benthic macroalgal community and the distribution of macroalgal detritus of Kongsfjorden over a vast area at greater depth complementing the detailed information available for the shallow sublittoral of the fjord.

The inclination of the sun angle and strong seasonality of the light in the Arctic (Pavlov et al. 2019) lead to a relatively lower annual sum of available light for macroalgae

compared to temperate regions (Kirk 1994). However, macroalgae can grow at great depths here. Thus far, the deepest record of kelp in the Arctic was deeper than 60 m in Disko Bay (Krause-Jensen et al. 2019), Greenland. The deepest unidentified abundant macroalga growing attached to drop stones at a depth of 166 m was reported by Meyer and Sweetman (2015) in outer Raudfjorden, northern Spitsbergen. For Kongsfjorden, coralline red algae were reported to grow at 75 m depth in 2009 (Laudien and Orchard 2012). Our observations stretching over continuous wider areas confirm that these depth values are not single observations, but a vast red algal vegetation may exist below the shallow sublittoral kelp forest at sites where rocky substrate is available.

Apparently, the location along the fjord axis has an important influence on macroalgal cover and species composition which was shown here and has been reported earlier for the shallow sublittoral (Hop et al. 2016). The inner location Tyskahytta is greatly influenced by glacial melt limiting both light penetration (Pavlov et al. 2019) and available hard substrata. Sedimentation is one major factor inhibiting algal growth and recruitment (Eriksson and Johansson 2005; Zacher et al. 2016) and changing osmotic conditions due to freshwater discharge (Hanelt et al. 2004) require a high physiological acclimation potential of macroalgae (Karsten 2007; Zacher et al. 2009; Spurkland and Iken 2011b).

Green algae were most prominent at the middle to inner fjord at the upper sublittoral corresponding to the study of



Macroalgal cover

subdivision by groups above and below 30 m with the total percent cover [mean ± SD]

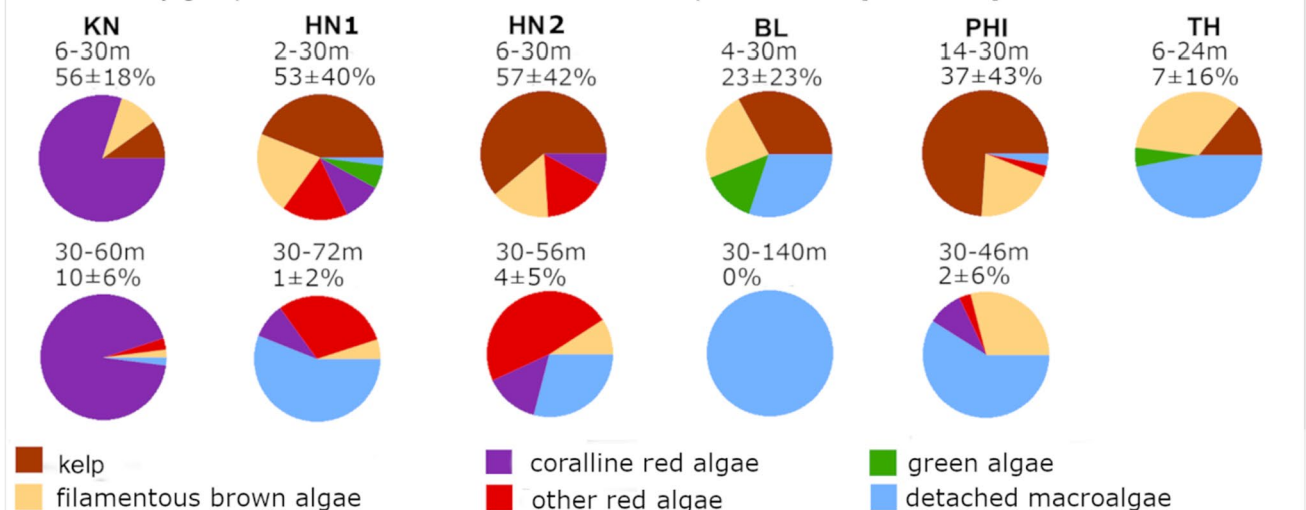


Fig. 3 Above: digital elevation model of Kongsfjorden with 100-m interval isobaths (Norwegian Mapping Authority) and sampling sites: Brandal (BL), Hansneset 1 (HN1), Hansneset 2 (HN2), Kongsfjordneset (KN), Prince Heinrich Island (PHI) and Tyskahytta (TH).

Below: total macroalgal cover of the sea floor (mean ± standard deviation, $n=25-163$) is given per transect separated by 2 depth horizons (< and > 30 m). Relative percentage distribution of macroalgal groups and detached macroalgae is exhibited by pie charts

Hop et al. (2016) from 1996 to 1998. In our study, especially *Acrosiphonia* spp. was present in areas of high physical disturbance either through sedimentation (inner fjord: Tyskahytta) or ice scour (Hansneset). *Acrosiphonia* is an annual opportunistic species, known to be well adapted to ice-scouring. It can survive the winter as microscopic stage or as rhizoidal cushion and quickly recolonizes ice free areas when light levels increase in spring (Hop et al. 2002).

The cover of brown algae (Hop et al. 2016; Kruss et al. 2017) highly varied amongst transects and across the depth gradients. They formed especially dense forests in the middle fjord down to 20 m and therefore probably contributed most to the amount of detached macroalgae or only occurred as single individuals at locations influenced by glacial discharge. Whilst digitate kelps needed rocky substrate, *Desmarestia* spp., *S. latissima* and *A. esculenta* were also observed at soft bottom locations on drop stones. In

Fig. 4 Coverage of visually dominant macroalgal groups and detached macroalgae along six transects in Kongsfjorden in 2009: **a** Kongsfjordneset, **b** Hansneset 1, **c** Hansneset 2, **d** Brandal, **e** Prince Heinrich Island, **f** Tyskahytta; mean percentage coverage per transect and 2-m-depth intervals (the values at the x-axis mark the respective lower depth value of the depth intervals) as well as mean cover of hard bottom substrate or drop stones (grey points). *n*: no data, *cna*: cover of crustose coralline red algae was not possible to quantify. Number of replicates per depth interval and per transect is listed in Online Resource 3

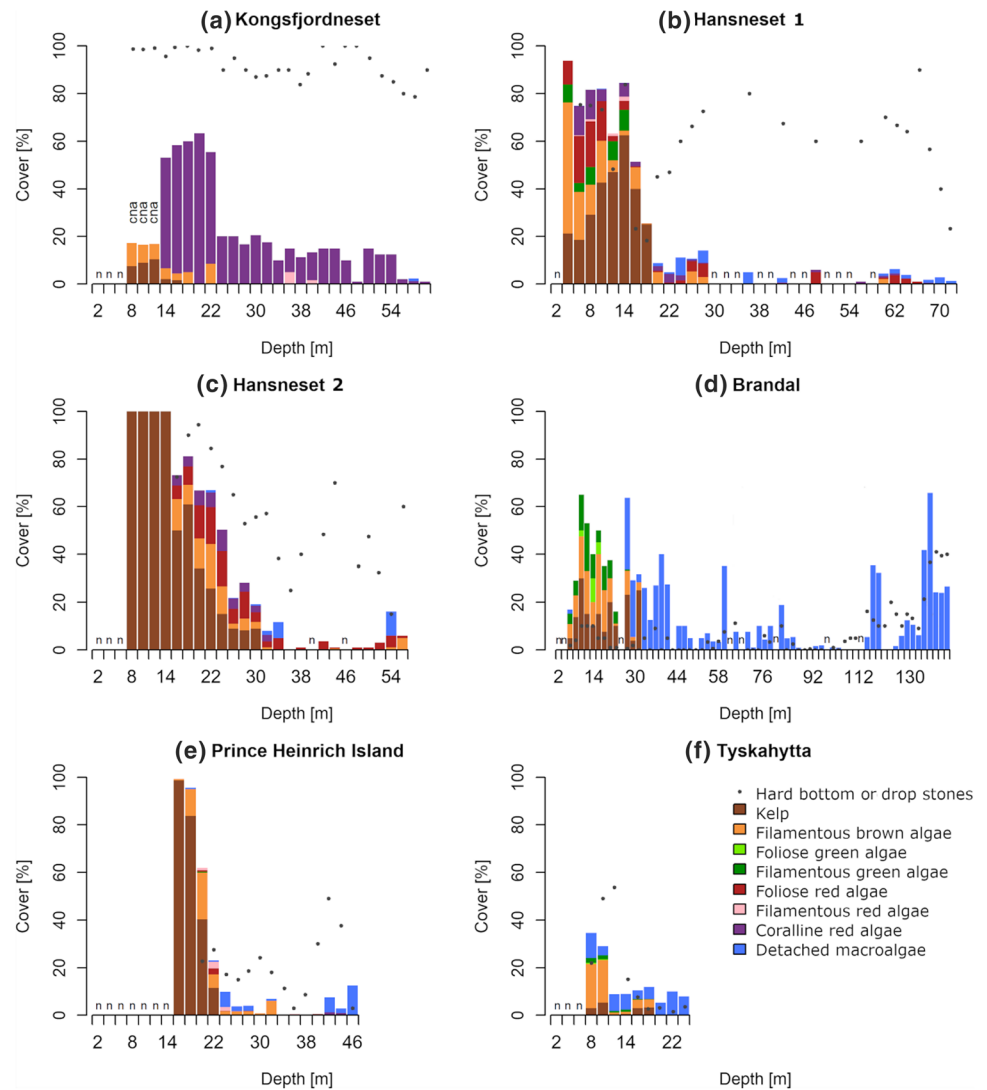


Table 3 Statistical analysis for the effects of depth (6–30 m) and transects (Brandal, Kongsfjordneset, Hansneset 1 and 2) on the coverage of kelp (two-way ANOVA without replication)

Factor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Transect	3	12,177	4059	17.52	<0.0001
Depth	10	8924	892	3.85	0.002

The significance level was lowered to $\alpha=0.01$ due to partially inhomogeneous data

df degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* *F*-statistic

sub-Arctic Alaska *S. latissima* was the only kelp able to grow on soft substrates as they can attach to small gravel (Spurkland and Iken 2011a; Hop et al. 2012).

The only Arctic endemic species present in the fjord, *L. solidungula*, had a very narrow distribution and was just found as small single individuals at Prince Heinrich Island. In studies 11–12 years before and 3–4 years

Table 4 Statistical analysis for the effects of depth (6–22 m) and transects (Brandal, Kongsfjordneset and Hansneset 1 and 2, Tyskahytta) on the coverage of detached macroalgae (two-way ANOVA without replication)

Factor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Transect	4	1247	312	92.04	<0.0001
Depth	7	47	7	1.99	0.09

The significance level was lowered to $\alpha=0.01$ due to partially inhomogeneous data

df degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* *F*-statistic

after our investigation, this species was only present in the middle zone including the station Hansneset < 10 m in the understory of big kelps (Bartsch et al. 2016; Hop et al. 2016). Thus, *L. solidungula* is not abundantly growing in Kongsfjorden, whilst in northern and north-eastern Svalbard (Hinlopenstredet, Nordaustlandet) many

Table 5 Statistical analysis for the effects of depth (24–56 m) and transects (Brandal, Kongsfjordneset and Hansneset 1 and 2) on the coverage of detached macroalgae (two-way ANOVA without replication)

Factor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Transect	3	1496	489	10.3	<0.0001
Depth	5	377	76	1.56	0.23

The significance level was lowered to $\alpha=0.01$ due to partially inhomogeneous data

df degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* *F*-statistic

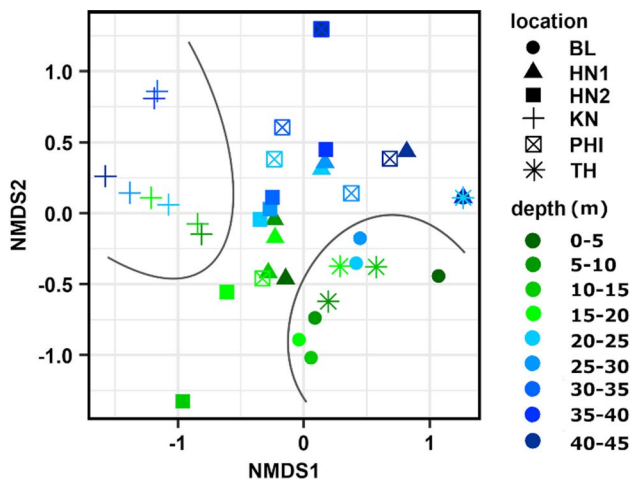


Fig. 5 Non-metric multi-dimensional scaling (nMDS) plot exhibiting similarity of the mean cover of macroalgae groups (kelp, filamentous brown algae, foliose red algae, filamentous red algae, coralline red algae, foliose green algae and filamentous green algae) and of detached macroalgae per transect and 5-m-depth zones using a Bray–Curtis similarity matrix from square root-transformed data. Brandal (BL), Hansneset 1 (HN1), Hansneset 2 (HN2), Kongsfjordneset (KN), Prince Heinrich Island (PHI) and Tyskahytta (TH). Stress=0.1. The grey lines help to visualize the different relative community compositions of outermost KN and of sedimentary influenced BL and TH to central transects HN1, HN2 and PHI

specimens < 1 m total length were abundantly growing in between other kelps between 5 and 30 m (Belseth 2012). As this species requires low light, low temperature and high salinities for the completion of its life cycle (Tom Dieck 1992; Roleda 2016; Muth et al. 2021), it may possibly disappear in Kongsfjorden if seawater temperatures and freshwater input will further rise.

Interestingly, in our study no *Saccorhiza dermatodea* was visually obvious. This annual kelp-like species was commonly present down to 13 m depth in 1996/98 (Hop et al. 2012) and was also recorded in 2012/13 at Hansneset (Bartsch et al. 2016). Its absence in our investigation rather suggests confusion with *Saccharina latissima* or less physical disturbance in 2009 than an upward shift. The general shift

of the lower depth distribution of kelps to shallower depth detected between 1996/1998 and 2014 at Hansneset (Bartsch et al. 2016) was not yet noticeable in our study. We identified dominant digitate kelp even at 16 m depth and also abundant *S. latissima* at depth to 30 m.

At the outermost and exposed site Kongsfjordneset which is characterized by steady bedrock, a dense kelp bed was expected (Lüning 1990). The observed barren ground with a high percentage of crustose coralline red algae was regarded as a proxy for grazing pressure by sea urchins. One key organism substantially feeding on macroalgae is the green sea urchin *Strongylocentrotus droebachiensis*. It rapidly increased in density at outer Kongsfjorden since 1993 (Hop et al. 2002; Beuchel and Gulliksen 2008) and was also observed abundantly (1–20%) at Kongsfjordneset in this study. The only bigger brown algae present at Kongsfjordneset in our study were pockets of *A. esculenta* and *Desmarestia* sp. As *Desmarestia viridis* produces and stores sulphuric acid, it effectively deters grazing by sea urchins, thereby creating a local refuge for kelp and associated communities (Molis et al. 2009).

The slow growing low light tolerating coralline red algae (Vásquez-Elizondo and Enríquez 2017) have only recently been recognized as important ecosystem engineers for the Arctic (e.g. Jørgensbye and Halfar 2017). Their depth distribution recorded for Kongsfjorden is similar to the northernmost coralline algae of Svalbard, recorded at Nordaustlandet in 78 m depth (Teichert et al. 2012) or to those from Greenland recorded at 77 m depth (Jørgensbye and Halfar 2017). As video recordings may hinder detection of coralline red algae or other small macroalgae beneath a dense canopy of cover algae, we can only assume that sites with abundant kelp or red algal cover are potentially rocky and also provide habitats for crustose coralline red algae. Data interpretation thus must be seen in this context.

Dense red algal vegetation at Hansneset and the low cover of foliose and filamentous red algae at all other stations at the south coast may indicate that this bushy red algae require hard substrate and a low sedimentation environment. For cold temperate zones, information on the depth distribution of *Phycodryis* or other foliose red algae is scarce. Reported depth limits range between 23 and 50 m (Sears and Cooper 1978; Vadas and Steneck 1988; Pedersén and Snoeijis 2001; Mikhaylova 2019) but recordings of exact lower depth limits are often hampered by depth limitations of SCUBA diving. Thus, these deep water observations in Kongsfjorden are of special significance and may have an overlooked ecological importance. Schmidt et al. (2021) hypothesize that deep water foliose red algae mats in the Mediterranean Sea are a yet undescribed ecosystem engineer that provides a multitude of ecological niches. If we consider that *Phycodryis* becomes up to 4 years old, a tetrasporophyte may release up to 550,000 tetraspores or female gametophytes up to 120,000

carospores per individual (Schoschina 1996) and houses up to 7583 individuals of epifaunal species per 100 g fresh weight (Lippert et al. 2001), the role of deep water foliose red algae for the Arctic food web and macroalgal carbon cycling might be considerable, but remains unknown.

Detached macroalgae

The majority of local macroalgal primary production in fjord systems is exported to deep sites in northern Norway (Filbee-Dexter et al. 2018; Pedersen et al. 2020). In the Arctic, in western Spitsbergen deep water, macrobenthic fauna primarily relies on macroalgal detritus (Sokołowski et al. 2014; Renaud et al. 2015) but the extent of macroalgal detritus export has never been quantified for Kongsfjorden. The extensive kelp beds observed in the middle of the fjord and also at coastal sites such as Kapp Mitra (Hop et al. 2016) regularly produce at least the annual biomass of the kelp blades as macroalgal detritus. The kelp blades become either detached in spring when new growth is initiated (Lüning 1990), continuously erode over the year (Krumhansl and Scheibling 2011; Pedersen et al. 2020), or biomass is released in the form of millions of spores over winter from several kelp species in Kongsfjorden (Bartsch, pers. observation). Besides that, kelp and macroalgal thalli in general may become detached through wave action after storms (Krumhansl and Scheibling 2012) or through ice-scouring. Although there exist some mapping studies (Volent et al. 2007; Kruss et al. 2017), the precise extent of kelp stands along the fjord axis and thus the amount exported to connected sedimentary habitats is unknown. As the total fresh standing stock biomass of kelps at Hansneset ranged between approx. 2 and 13 kg fresh weight m^{-2} in 2012/13 (Bartsch et al. 2016), this might be in the same range as reported from other more temperate sites. In eastern Canada, the annual detrital production from the erosion of kelp blades increased linearly with kelp bed biomass and ranged from 0.5 to 1.71 kg dry weight m^{-2} (150–513 g C m^{-2}) across sites (Krumhansl und Scheibling 2011). In the Northeast Atlantic, high export rates (> 98% across the study sites) of the annual production of kelp detritus were demonstrated (approx. 4.70 kg fresh weight m^{-2} or 301 g C m^{-2} , Smale et al. 2021). As kelp blades only slowly decompose, this suggests a great potential for long distance transport of this biomass (de Bettignies et al. 2020; Pedersen et al. 2021).

During this study we demonstrated for the first time that considerable detrital macroalgal biomass is present in deep recipient sites below the kelp zone in Kongsfjorden distant from their production sites; this was especially pronounced at Brandal. The inner shallow location of Tyskahytta seems to be an additional recipient of detached macroalgae. The transportation of kelp material into deep sites and the inner fjord by currents probably is a continuous process as video

frames often showed material with different signs of degradation. Due to the rotational Coriolis effects, Atlantic and Arctic water masses enter fjords on west Spitsbergen along the southern shores. In our case study, incoming water masses have to pass Brandal and have to exit along the northern shore (Howe et al. 2003; Pawłowska et al. 2017). As deep trenches facilitate the transport of detached macroalgae to the deep sea (Vetter and Dayton 1998), the deep central fjord basin, which is located in proximity to the Brandal transect (Howe et al. 2003) and which is clearly visible in the newly established digital elevation model for Kongsfjorden (Fig. 3), may be an ideal location for deposition of detritus.

Outlook

The Arctic contains a vast potential habitat for marine macrophytes. The impact of climate change is predicted to be dramatic for the Arctic due to the increased absorption of solar radiation accompanied by sea ice loss and the inflow of ocean heat from lower latitudes (Meredith et al. 2019). Increasingly warmer conditions may result in the northward expansion of boreal macroalgae and fauna (Arrigo et al. 2008; Krause-Jensen and Duarte 2014) and may also fuel primary production of many Arctic macroalgae which currently often thrive at sub-optimal temperature conditions (Iniguez et al. 2016; Franke et al. 2021) except for Arctic endemic species (e.g. Roleda 2016). As the ongoing glacier melting will increase turbidity and sedimentation in the near future, productivity of the macroalgal communities in Arctic fjords is expected to first become reduced (Traiger and Konar 2018; Filbee-Dexter et al. 2019). All these processes are expected to impact the carbon subsidy of deep sea Arctic areas, since kelp forests and deep fjord habitats are closely linked by the seasonal production of algal detritus (Filbee-Dexter et al. 2018).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-022-03072-x>.

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Author contributions All authors contributed to the study conception and design. CW planned and conducted the data collection. Data analysis was performed by KS. KZ and IB contributed analytical tools and statistics. KJ and HP contributed to GIS. HP contributed to R. The first draft of the manuscript was written by KS and all authors commented

on previous versions of the manuscript. The revised version was rewritten by KS and IB and all authors read and approved the manuscript.

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Data availability The videos recorded and analysed during the current study as well as a shape file with all georeferenced data points of the transects with the information on bottom substrate, cover of macroalgal groups and detached macroalgae are available on PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.927141>). Both R scripts to link the georeferenced data of all transects to the timecode of the video and import it into the geographic coordinate system as well as to extract coordinates from transects are available in the GitHub repository of the FACE-IT project.

Declarations

Conflict of interest The authors have no conflict of interest to declare that are relevant to the content of this article.

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