LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–16

doi: 10.1002/lno.70056

RESEARCH ARTICLE

Latitude, sea ice, and glaciers are important drivers of submerged vegetation distributions in the Arctic coastal waters along east Greenland

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Abstract

Present study is the first quantitative and coherent presentation of the submerged marine vegetation along the Greenland east coast, from 65.5°N to 76.8°N, based on data obtained from 286 underwater video transects. Based on cluster analysis, four different marine submerged vegetation community figurations were identified: a southern and deeper kelp forest including *Laminaria solidungula* and *Agarum clathratum*, the marine vegetation along the Blosseville coast, seaweed meadows characterized by, e.g., submerged *Fucus distichus*, and high-arctic kelp forest. The habitat figurations were related to and potentially explained by drivers considered to be key for their spatial distribution. The drivers considered were latitude as a proxy for light conditions with stronger seasonality and receding light conditions toward the north, suitable substratum for the marine vegetation to establish and grow, and the sea ice conditions with respect to light attenuation and scouring. Two of the vegetation types were explained by latitude, whereas the two vegetation types identified for the mid segment of the surveyed coastline were considered to be more correlated to local/regional conditions such as the presence of dynamic sea ice and glaciers as well as smaller-sized hard substratum. Some degree of marine vegetation/kelp forest pauperization was observed with increasing latitude, expressed as a decrease in coverage and depth distribution. The vegetation belt was declining from a depth of 34 to 18 m within the northward latitudinal gradient surveyed, although for some species, no change in species-specific maximal depth limits could be observed.

Marine benthic vegetation supports key ecosystem functions, by providing habitats shelter, feeding and nursing grounds for a variety of fauna (Christie et al. 2007), and thereby promote biodiversity, but also climate change mitigation and adaptation (Krause-Jensen et al. 2020; Filbee-Dexter et al. 2019). Therefore, changes in the macroalgal distribution, e.g., toward the north (Kvile et al. 2022), may affect the functioning of the arctic marine ecosystems (Krause-Jensen et al. 2020).

In general, published information regarding the macroalgal communities along the Greenland east coast is scarce. Filbee-Dexter et al. (2019) base to a great extent their presentation on kelp from Greenland on historic information and note that the historical records that they refer to represent a baseline and may not reflect current kelp distributions.

Historically, mainly qualitative floristic studies have been conducted (Supporting Information Table S1). Lund (1959a, 1959b) investigated macroalgal samples collected in the region between the Ittoqqortoormiit area (70.5°N) and Kejser Franz Joseph's Fjord (73.5°N). Even earlier, however, marine macroalgae were collected at different expeditions to Greenland during the 19th century, and were identified and described by Rosenvinge (1893, 1898, 1910, 1933). Only a few, more recent studies of the macroalgal flora were conducted at the north-east coast of Greenland. A study at Mestersvig (72.2°N) (Birklund et al. 2006), which included collections and identifications of macroalgae, supplements the floristic overview, and studies of marine macroalgal biomass and production in

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Associate editor: Ruth Reef

Data Availability Statement: All data will be made available upon request to the corresponding author.

Young Sound (74.4°N) have been performed by Borum et al. (2002), Roberts et al. (2002), and Krause-Jensen et al. (2007) (Supporting Information Table S1).

From these studies, it was clear that communities of macroalgae were present along the east Greenland coastline; however, no information on vegetation types, distribution, and coverage was collected.

Therefore, overall, this study focuses on providing data on the submerged benthic flora along the east coast of Greenland and aims to identify vegetation types, including biodiversity, coverage, and depth distribution in relation to latitude and related drivers.

In this study, which covers the Greenland east coast from 65.5°N to 76.8°N, it is considered that light may be the dominant environmental factor that drives the presence and distribution of macroalgae. Latitudes may be considered as the proxy of light conditions with increasingly strong seasonal light regimes at the northern latitudes (Ljungström et al. 2021).

Therefore, it is expected that coverage and depth penetration will be correlated to latitudes, and that occurrences and coverage of kelp forest will be increasingly limited by light toward the North.

Sea ice may be a proxy for sea temperature but also influences light conditions. Thus, the marked seasonally changing light regime is consolidated by sea ice cover due to its shading effect, also depending on the overlay of snow (Glud et al. 2007), and which may be approximately 9 months of a year in, e.g., Young Sound (Holding et al. 2019). Moreover, melting multi-year ice and glacier run-off may release fine particles into the water column and reduce water transparency, and hence light penetration (Borum et al. 2002; Niedzwiedz and Bischof 2023). The third effect from glacier ice and ice floes may be scouring on shoreline and seabed, damaging the marine vegetation (Gutt 2001; Sejr et al. 2021).

However, independent of the light and temperature, substratum characteristics are additionally important for the distribution and abundance of macroalgal vegetation, and only hard and stable substrate can serve as a base for a rich community of marine, benthic macroalgal communities (Middelboe et al. 1997). Although rocky cliffs are considered the main geology of the Greenland coastline (Young and Carilli 2018), other types of substrata, not stable for macroalgal attachment, such as, e.g., fine grained and alluvial sediments, and moraine deposits as well as sandstone, are often present along the northeast Greenland coasts below the tidal zone (e.g., Clausen et al. 2022, and data herein).

The present study is the first coherent study of the submerged marine vegetation along 1700 km of the Greenland east coast, covering 11° of latitudes (65.5–76.8°N). We present quantitative data on the marine macroalgal vegetation and substratum obtained from 286 underwater video transects accomplished along the east Greenland coastline as well as analyses of potential drivers. The study will thus contribute data to the ongoing studies on the impacts of climate change, but also provide data for the development of the oil spill sensitive atlas for northeast Greenland (Wegeberg et al. 2021).

In addition to the presentation of the macroalgae distribution along the Greenland east coast, we test the following hypothesis:

1. Pauperization of marine vegetation/kelp forest with increasing latitude expressed as a decrease in coverage and depth distribution due to receding light conditions with a stronger seasonal light regime including long periods of complete darkness combined with sea ice (and snow) cover.
2. Glacier ice and sea ice concentration act as drivers for coastal community presence and vegetation community configurations, coverage, and depth penetration.

Materials and methods

In August/September 2016 and August 2017, ship-based surveys were carried out along the east Greenland coastline. In 2016, the survey covered the section from Ittoqqortoormiit (70°N) to Syttenkilometernæsset (76.8°N) (Fig. 1), with the Royal Danish Navy vessel *HDMS Knud Rasmussen* as research platform. For underwater video transect recordings, the vessel's RIB (Rigid Inflatable Boat) and SAR (Search and Rescue) boats was used. Further, the vessel's SCUBA divers assisted in collection of samples. In 2017, the section from south of Tasiilaq (65.5°N) to Ittoqqortoormiit (Fig. 1) was covered using motorboats and a dinghy as platforms for the underwater video transect recordings.

Underwater video recordings and analyses

The underwater videos were recorded along randomly selected transects perpendicular to the coast with an analogue underwater video camera (LH Camera, Underwater Video Systems, https://lh-camera.dk) from shallowest possible water depth to maximum depth of erect macroalgal vegetation, usually within a 3–45 m depth range. The length of transect was sought to be of same depth range for obtaining systematic data, but may on cases be shorter due to, e.g., strong currents that may prohibit lowering of the camera by it being caught by the currents; flat sloping, which may cause very long and thus time consuming transects not providing much new information; and/or unsuitable substrate, e.g., sand flats.

A total number of 286 underwater video transect recordings was obtained, 158 in 2016 and 128 in 2017 (Fig. 1).

The underwater camera was handheld in the 50 m cable connecting the camera to a monitor and video recorder in the boat, ensuring that the camera was in the right depth position and could observe the nature of the macroalgal vegetation. Position and depth were recorded along with the video signal from a built-in GPS in the video case system and an underwater pressure gauge along with the camera. The video camera was towed at a maximum sailing speed of 1 knot at a height above the sea floor or vegetation, which allowed for

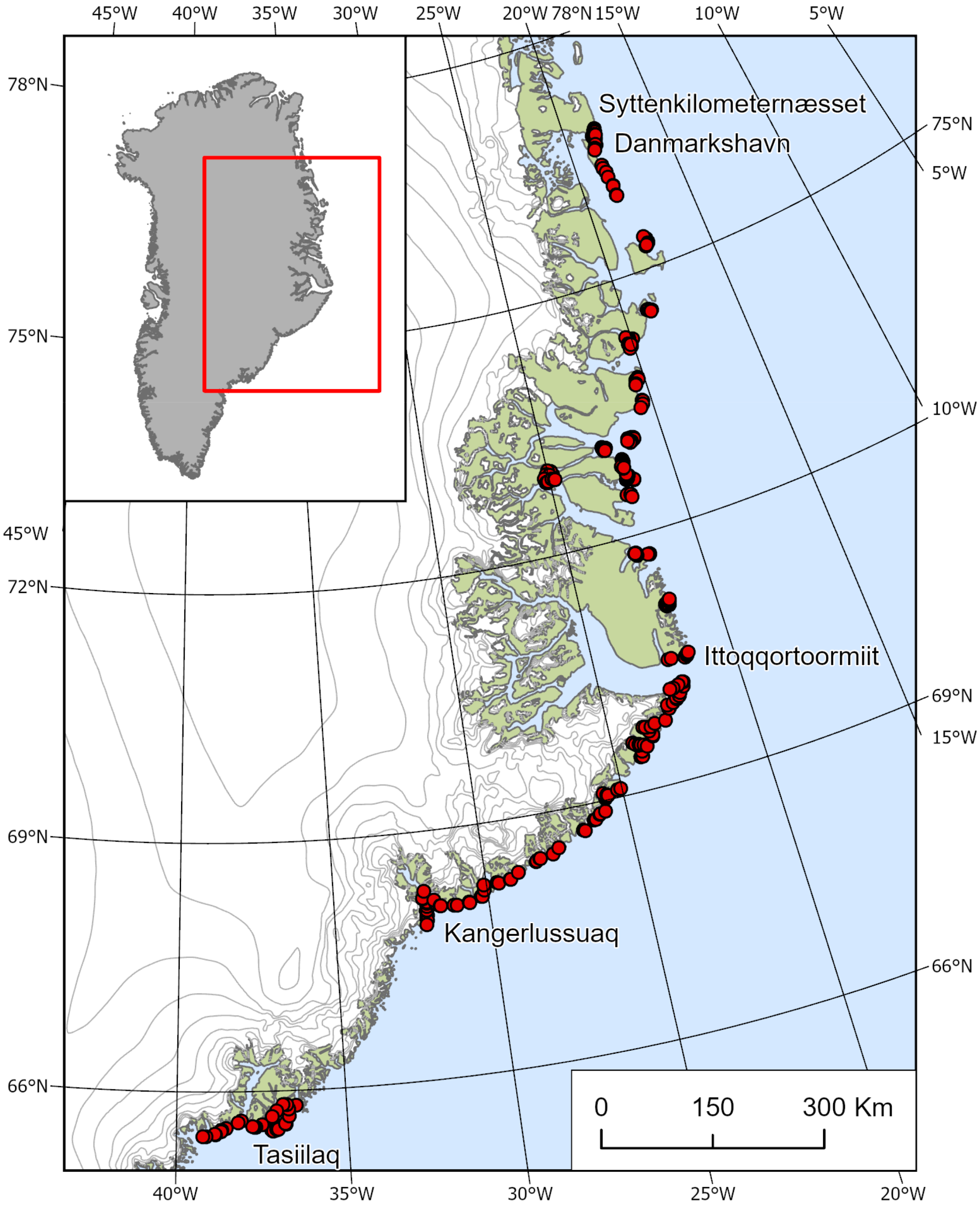

Fig. 1. The study area along the Greenland east coast (red frame in the set-in map), and the locations for all underwater videos obtained from the surveys in 2016 and 2017 (●).

recognition of substratum or algal species (usually < 1 m). The camera components were mounted on a tow-fish, which kept the camera in the towed direction and at an angled position of about 45°. To aid in the recognition of sea floor elements (substratum, flora, fauna), a GoPro camera (GoPro Hero 5) was mounted on the tow-fish in 2017 for improved video quality along with the underwater camera videos, which included the documentation of position and depth from the built-in GPS and depth sensor. The underwater camera videos were recorded as AVI files, and the GoPro files in MP4 format.

Each video recording was analyzed at 1 m depth intervals as an integrated estimation of the percent coverage of macroalgal species or assemblages at the specific depth interval and the seafloor/substratum types (soft, soft/mixed, pebbles, stones, hard/mixed, hard).

The maximal tidal amplitude along the east coast of Greenland is ranging from 1.2 to 1.8 m, and 3.6 m at Tasiilaq in the years of sampling (Nielsen and Ribergaard 2016; Ribergaard 2016). The deviation from the mean tidal level on the specific dates of sampling was less than 1 m (max. 0.9 m at Tasiilaq).

The analyses of the videos were performed by two assessors, and random comparisons were made to assure uniform recognition and identification, as well as macroalgal coverage percent estimations in 1 m depth intervals. Flora and fauna species were identified as far as possible from the video material, in some cases supported by samples obtained by SCUBA divers in 2016.

Species identification

From the videos, species were identified as far as possible, which in particular means large and characteristic species, e.g., the kelp species *Fucus distichus* and *Desmarestia aculeata*, and *Turnerella pennyi*. Further, some species identifications were validated from the SCUBA diver collections, e.g., *Chaetopteris plumosa*, *Coccotylus truncatus*, and *Arcticophycus glacialis*. Regarding *Saccharina* spp., the SCUBA diver collected species were identified as *Saccharina latissima* based on the short length of stipe. As no specimens that unequivocally could be assigned to *S. longicruris* were observed, all sugar kelp specimens were assigned to *S. latissima*. Identifications were based on the literature in Supporting Information Table S1, as well as Pedersen (2011).

In the latitudinal gradient analyses, species not precisely identified (Supporting Information Table S2) were pooled according to main groups (Chlorophyta, Phaeophyceae, Rhodophyta) and morphological groups (filamentous, rotund, blade).

Only visible, erect, and canopy-forming species were registered from the underwater video, as understory vegetation, including crustose algal species, was either not visible on videos or difficult to perceive.

Data processing and analyses

All data analysis calculations and plots were done using the R statistical computing environment (R Core Team 2022).

Video footage

Results of visual analysis of video footage included (for each 1-m interval): (1) positions of transects' initial and terminal points; (2) presence and fraction (%) of area occupied by each algae species big enough to be recognized on the video footage; and (3) type of sediments at each depth identified by visual inspection on video footage, whereas areas with 100% algal coverage and where the bottom was not visible, hard substrate was assumed. All species names were verified with the World Register of Marine Species (WoRMS) (https://marinespecies.org).

Number of days with daylight and ice concentrations

Number of days with daylight was calculated for a latitude of each midpoint of each transect using sunAngle procedure from OCE package (Kelley and Richards 2022).

Sea ice coverage concentrations were acquired from E.U. Copernicus Marine Service Information (https://marine.copernicus.eu/), Arctic Ocean Physics Analysis and Forecast (parameter "Sea ice area fraction"). Dataset contains daily ice concentrations calculated as a fraction of a modeled pixel area (spatial resolution of 12.5 km × 12.5 km) covered with sea ice from summer 2016 to fall 2017. Each transect was assigned with a value of a pixel that contained the midpoint of a given transect.

Depth distribution of dominant species

The shallowest and the deepest depth occurrences of dominant kelp species were fed into the lm procedure in the statistical package R to calculate a linear model to find their correlations with latitude (R Core Team 2022).

Depth range of kelp species from comparable areas and studies was compiled including arctic Canada (Bluhm et al. 2022) and Svalbard (Schimani et al. 2022; Wiktor et al. 2022) (Supporting Information Table S3).

Coverage percentage analyses

Gross mean coverage was obtained as an overall mean coverage on all surveyed areas to the deepest obtained recordings, i.e., including nulls. In addition, the gross mean was obtained for surveyed depths < 30 m to obtain information on the coverage percentage of the vegetation with uniform depth reach. Mean maximal coverage percentage was obtained as the mean of maximal coverage percentages per transect.

Regarding substratum coverage, the gross mean hard substratum coverage was obtained as an overall mean coverage percentage of hard substratum.

Cluster analyses

Characteristic types of marine vegetation (vegetation assemblages) were determined by finding aggregates of species within the dataset using the *k*-means procedure (Hartigan and Wong 1979) on species coverages. First, the optimal number of classes was estimated by performing a number of splits that were set with different *k* parameters (number of expected classes). Second, the best choice was found by comparing the homogeneity of groups by comparing "tightness" of each point cloud, i.e., how close to each other points in one cloud are to each other compared to all other points, in a multidimensional space where each species coverage is a separate dimension. As a result, each cluster is characterized by species being more frequent in one cluster compared with any other. By investigating the distributions of physical parameters within clusters and comparing those with each other, we can infer about the affiliation of the cluster with some specific conditions or lack of it. Herein, we have investigated the frequency of the cluster's occurrence in latitudinal bins, at various substrate types and at various depth levels.

Results

Latitude as proxy for light and ice conditions

Number of days with sun above the horizon correlates almost linearly to the latitude (Supporting Information Fig. S1). Thus, latitudes can be used as a proxy for the light conditions.

Regarding sea ice concentration, the maximal sea ice concentration and its mean along the east coast of Greenland are presented in Supporting Information Fig. S2. South of 66.5°N, the sea ice coverage never reaches 100% during a year, whereas around 67–69°N there may be 100% ice coverage, but only for a short time of the year. At ca. 70°N it changes, and there is a higher degree of ice coverage on a yearly mean reaching approximately 40%. From 71°N, there is almost 100% sea ice concentration year-round along the coast. Thus, sea ice coverage increases with increasing latitudes along the east coast of Greenland.

Substratum distribution

In Fig. 2, the pooled substratum type data are presented as fractions of each substratum type according to latitude bins and three depth intervals: 0–5, 5–10, and 10–50 m. The hard, and stable, substratum types are dominant especially at the lower depths, but also at the lower latitudes, although there are some quite specific areas, where hard bottom is less dominant, which are at 69–70°N, and from 73°N. At 75 and 77°N, hard bottom seems to be quite dominant again at least until 10 m depth (Fig. 2).

Species presence

A full list of the high frequencies (f) of species occurrences including all kelp and fucoid species as well as other dominant species of Phaeophyceae and Rhodophyta, which could be identified with some certainty at least to genus from the underwater videos. Further, the rarely observed and arctic endemic species, *A. glacialis*, is included in the list. In addition, the list includes latitudinal and depth distribution for the entries, as well as weighted mean, min, and max. The list is filtered with the highest frequency species first. For a full list, please consult Supporting Information Table S2.

Macroalgal coverage along a latitudinal gradient and depth range

Overall, the mean coverage of seaweed in the surveyed area reached 18.2% (SD = 15.2), with a mean of maximal coverage observed at one transect reaching 77.7%. When limiting the analysis to the surveyed area within depths < 30 m, the mean coverage rises to 28.9% (SD = 21.3). At hard substratum, which covered 60% of the entire seabed surveyed, mean coverage was 49.0% (SD = 35.6). The maximal coverage was found at 6 m depth; the maximal depth for erect seaweed species reached 48 m (Table 1).

Plotting the coverage percentage along a latitudinal and depth gradient (Fig. 3), dominance of kelp species coverage can be observed at the higher latitudes, whereas the species of Rhodophyta are more conspicuous at the lower latitudes, except from the lowest latitude in the Tassilaq area. The macroalgal coverage percentages reaches 75 to almost 100% in the southerly latitudinal bins but is lower (up to 50%) along the Blosseville coast (68–70°N). The marine vegetation is changing after approximately 68.5°N toward being more mixed with filamentous brown algae ("Other"), as well as robust presence and relatively high coverage percentage of *F. distichus* and *C. plumosa* (Supporting Information Table S2; Fig. 3). At 74°N there is a shift toward a relatively high degree of kelp coverage and at the highest latitudinal bin, the general coverage may reach 75% again, however, at a shallower depth range than in the three most southerly latitudinal bins (64.5–68.5 N).

The red algal species have been observed rather randomly in the most southern latitudinal bins reaching a maximal coverage of 75% at lower depth at 69°N. However, they are more constantly observed with coverage of approximately 25%–8% at depths < 35 m at the northern latitudinal bins from 70°N (Fig. 3).

In general, there is a shift in dominant kelp species from south to north (Fig. 4). In the three most southerly latitudinal bins, the kelp forest is constituted by all six kelp species observed within the investigation and has a coverage of up to 50% and generally a coverage of more than 25% down to 30 m depth (Fig. 4). The most northern limit of *Agarum clathratum* is reached at 68°N, which is just the south part of the Blosseville coast, resulting in a change in the kelp forest composition (Fig. 4; Supporting Information Table S2). From 68.5°N to 70.5°N the kelp species, *Alaria esculenta*, *Laminaria solidungula* and *S. latissima* only constitute up to 25% coverage at 10 m depth, and from 70.5°N to 72.5°N, the coastline only has very little coverage by the kelp species according to present survey (Figs. 3, 4). From the latitude of 72.5°N, the kelp forest is mostly constituted by *L. solidungula*, with increasing coverage of *S. latissima* toward the highest latitudes investigated and with some coverage of *A. esculenta* even at the highest latitudes (Fig. 4).

In general, a gross mean of macroalgal coverage across all transects shows that coverage is highest (> 40%, but < 55%) at depths < 15 m, but deeper than 5 m (Fig. 5). The Chlorophyta species peaks at depths < 10 m and is only observed at depths less than 20 m (Fig. 3). Thus, the gross mean coverage peak is constituted by approximately 20% kelp species, 15% other species, 8% red algal species, and 5% of *Fucus* spp. and *C. plumosa*, respectively (Fig. 5). The decline in coverage toward depth is most pronounced in "Other" species, and at depths reaching 30 m, the macroalgal coverage is constituted mostly by kelp and red algal species; however, it still reaches

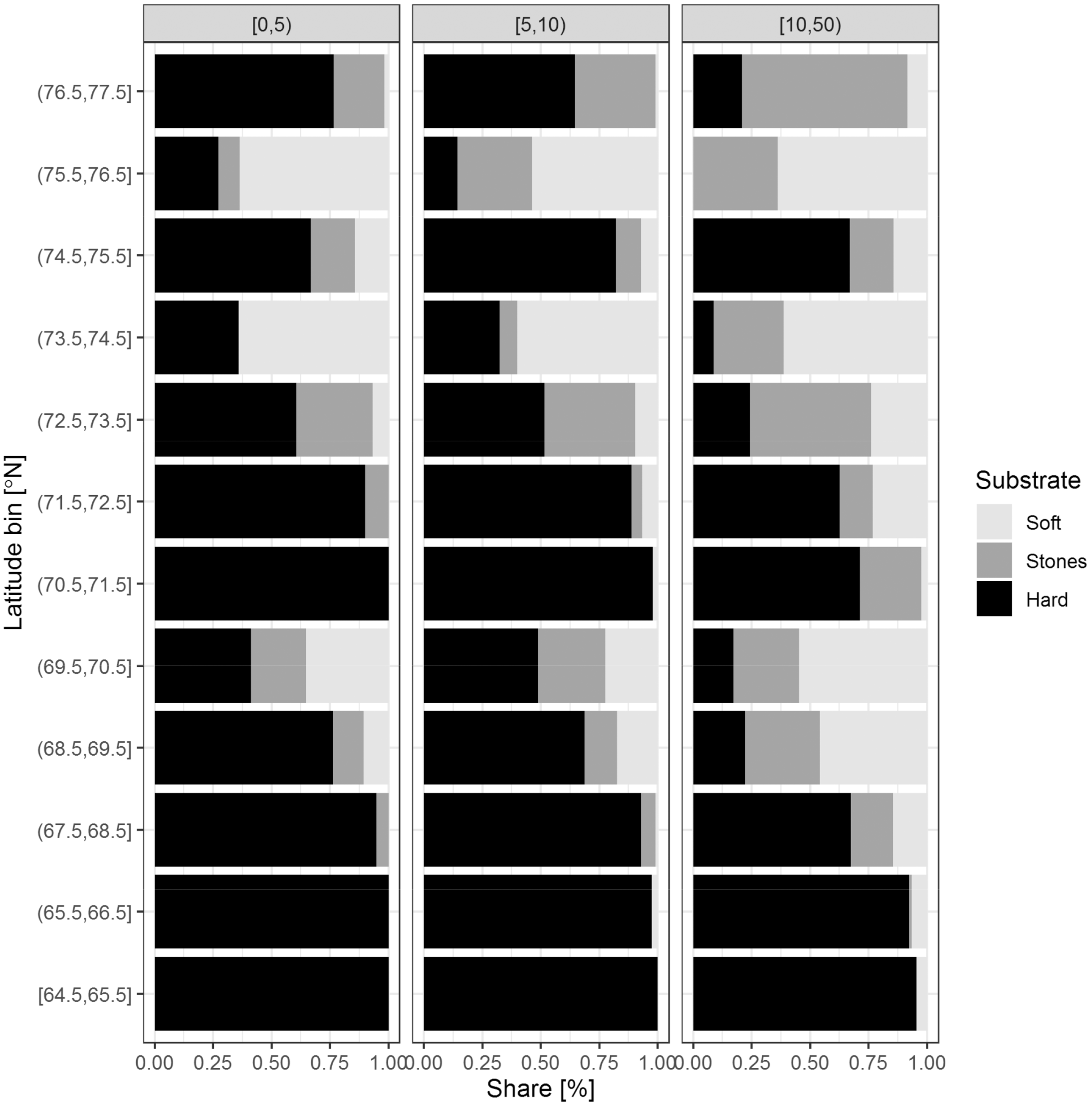

Fig. 2. Sediment type was recorded during visual investigation of gathered footage. Observations were pooled into three depth classes: shallow (0–5 m), intermediate (5–15 m) and deep (> 15 m), and three substrate classes: soft, stones and hard from the substratum categories, soft, soft/mixed, pebbles, stones, hard/mixed, hard. Counts of each substrate class are plotted in respective depth classes in each latitude bin as a fraction of all observations.

almost 30% coverage (Fig. 5). From approximately 30 m, both these algal groups decline toward 50 m, whereas 52 m is the maximal depth for registration of erect macroalgae (*A. clathratum*) on the east coast of Greenland achieved in the present survey (Fig. 5; Supporting Information Table S2).

From considering only kelp forest species, the species depth distribution in the kelp forests generally followed a pattern where *A. esculenta* and *S. latissima* dominated the shallower subtidal zone until approximately 25 m, whereas *L. solidungula* together with *A. clathratum*, when present, dominated the

Table 1. Cool facts of macroalgal and hard substratum coverage as well as depth distribution along the Greenland east coast. Mean and maximal values of coverage (%) and depth range (m) within the surveyed coastline are given.

Gross mean coverage (%)	Gross mean coverage (%) for depths < 30 m	Mean max coverage (%)	Gross mean hard substratum coverage (%)	Max coverage depth (m)	Max depth (m)
18.2 (SD = 15.2)	28.9 (SD = 21.3)	77.7	49.0 (SD = 35.6)	6	48

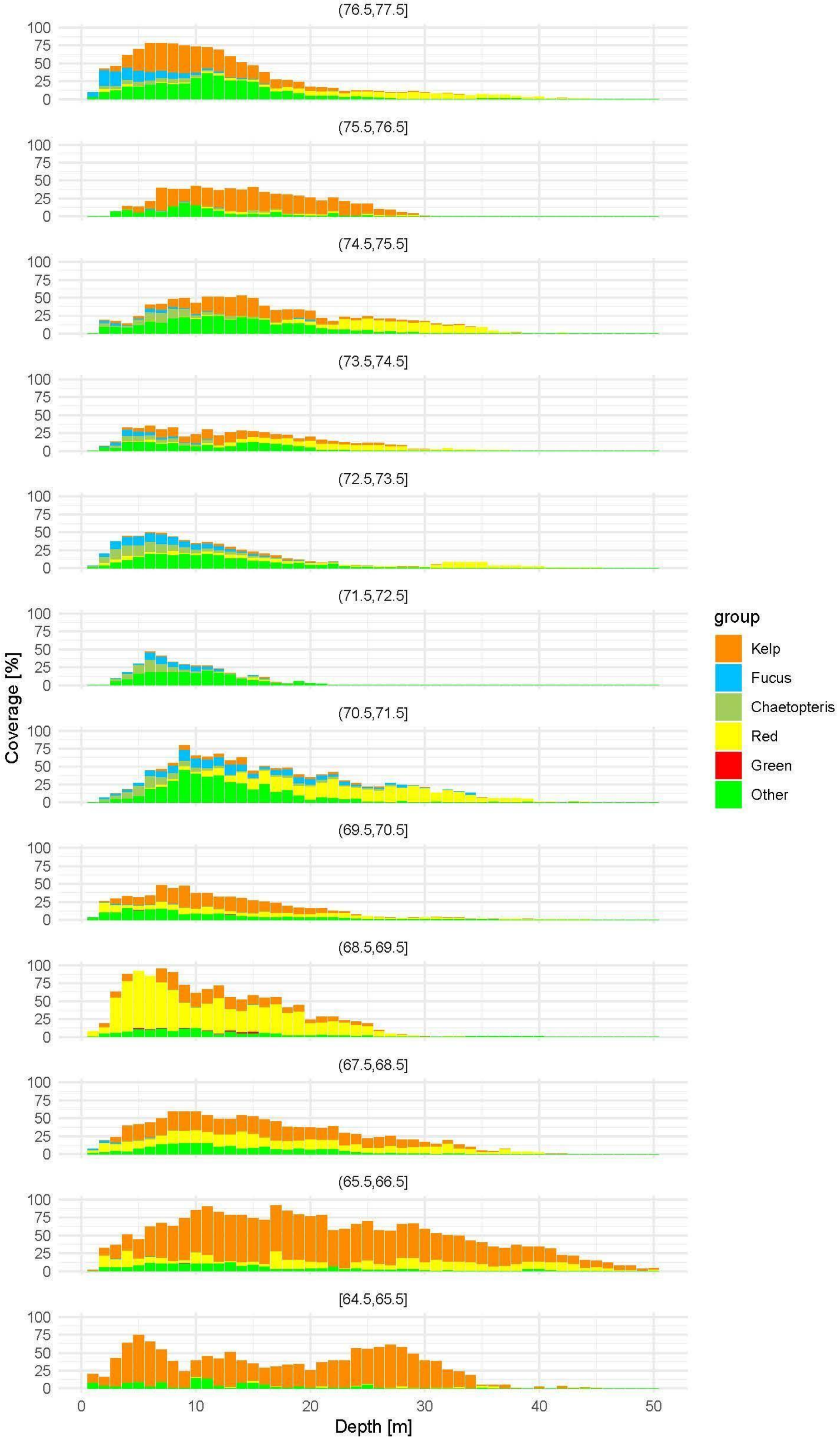

Fig. 3. Distribution of the macroalgal coverage along the latitudinal and depth gradients from 64.5°N to 77.5°N in 1° steps. We have no data from the interval 66.5–67.5°N. Some species with high entry frequencies or of special interest are presented; however, other macroalgal groups were pooled to give an overall presentation.

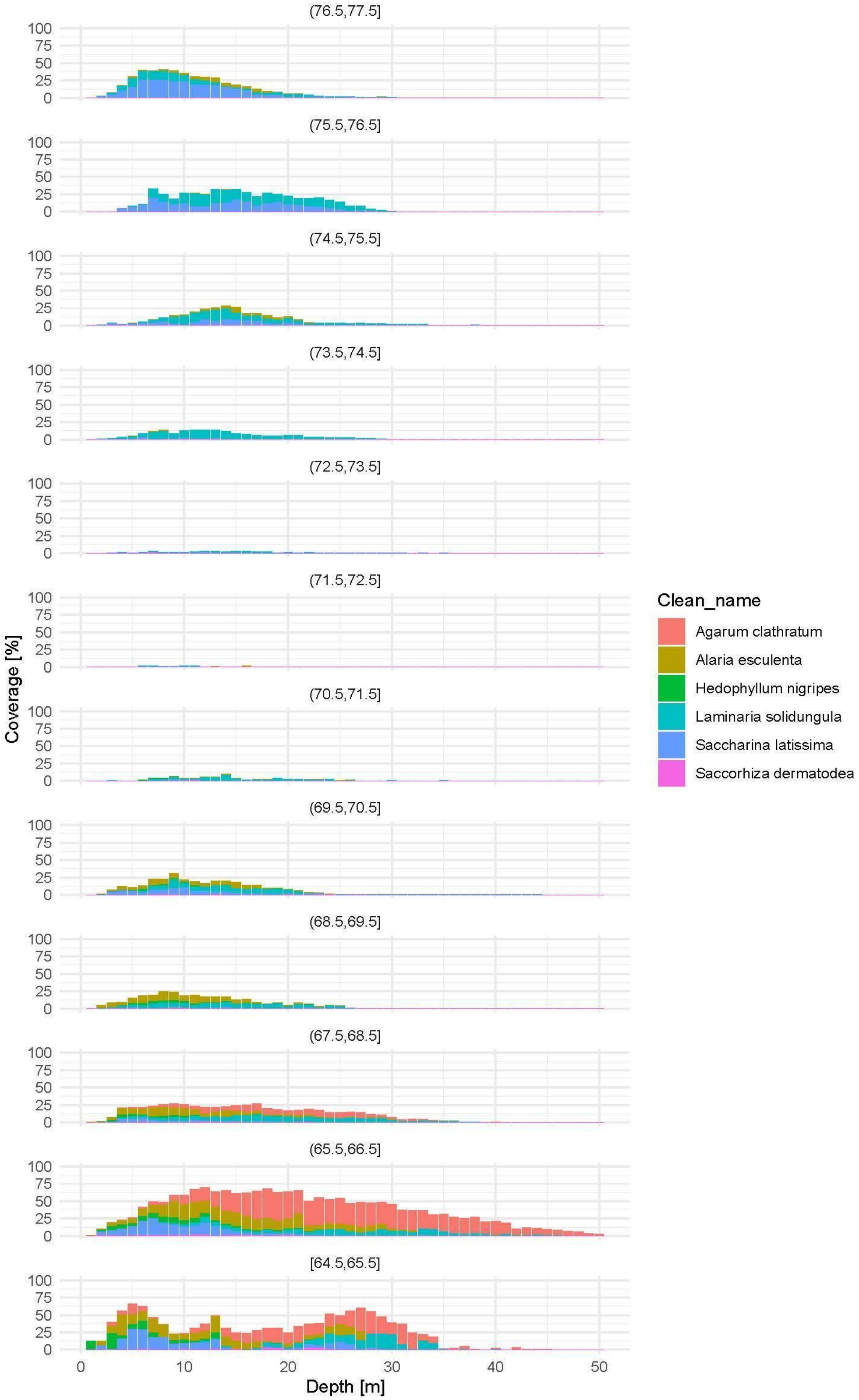

Fig. 4. Distribution of the kelp species coverage along the latitudinal and depth gradients.

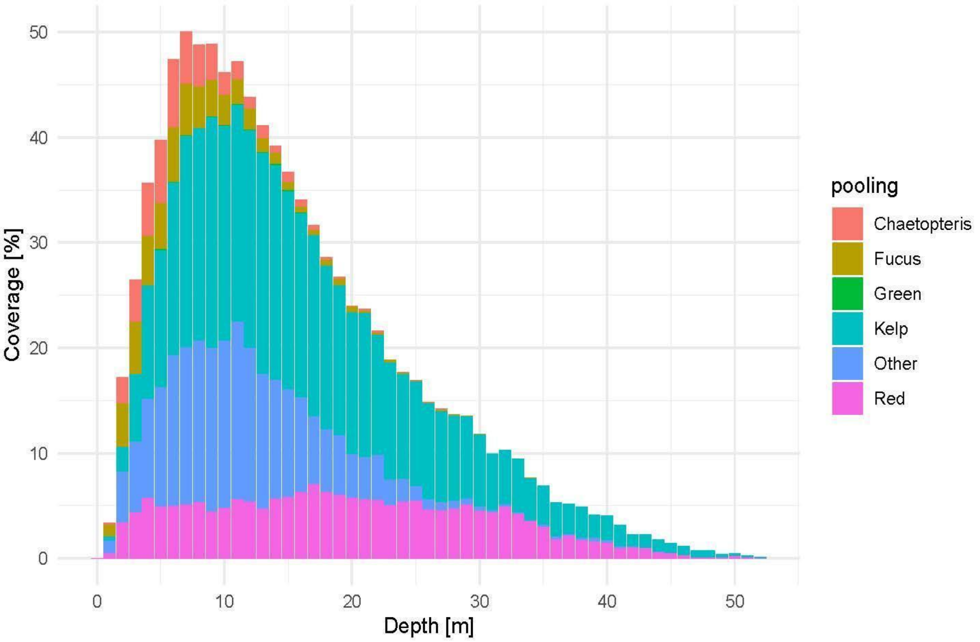

Fig. 5. Coverage (%) of respective algae groups along the depth gradient in all collected transects.

deeper part of the kelp forest until > 30 m. However, the species intermixed and, in some sites, *A. esculenta* and *S. latissima* penetrated to deeper waters (Fig. 4). In general, the depth range for the kelp species is narrowing from 45 m depth at the most southerly latitudinal bin to 32 m depth at the most northern latitudinal bin (Fig. 4). This is expressed by a change in average depth distribution within the kelp species *A. esculenta* and *L. solidungula* that are present along the entire latitudinal gradient investigated (Fig. 4; Supporting Information Fig. S3). For *A. clathratum*, the average maximal depth distribution does not change within the narrow latitudinal range of which the species was registered, i.e., from 65.46°N to 68.28°N (Fig. 4; Supporting Information Fig. S3; Supporting Information Table S2). The average maximal depth distribution of *S. latissima* does likewise not change; however, the average upper depth limit of the species changes from 10 m to ca 5 m depth within the investigated latitudinal range (Fig. 4; Supporting Information Fig. S3). Further, a shift toward a more restricted kelp forest depth distribution with increasing latitudes can be seen from the decrease in depth range of canopy coverage > 10% from 34 to 18 m along the latitudinal gradient (Fig. 4).

Although the coverage of red algal species is higher at the more southerly latitudinal bins (Fig. 3), there is no overall change in the average depth distribution for the erect Rhodophyta species, *C. truncatus* and *T. pennyi*, both reaching great depth ranges down to 45 and 51 m, respectively, within the latitudinal gradient investigated (Supporting Information Fig. S3; Supporting Information Table S2).

Macroalgal vegetation types

To identify significant macroalgal community figurations, vegetation types, a cluster analysis across the entire data set was performed (Supporting Information Fig. S4). Table 2 depicts which species (combination) the 10 clusters from the analysis are defined by, also according to the overarching dendrogram combining clusters, describing vegetation types.

Thus, to test if the marine vegetation clusters also were established by environmental conditions, they were tested according to latitudes, depth, and substratum type (Fig. 6), and their geographical and depth distribution as well as their potential affinity to substratum are compiled in Table 2.

Discussion

Latitudinal distribution

Most of the species are found along the entire investigated area, but *A. clathratum* is restricted to a southern distribution along the Greenland east coast, reaching its northern distribution limit at 68.3°N (Supporting Information Table S2). The species is considered to have a Pacific origin (Bringloe and Saunders 2019), and although it has a temperate distribution in the Pacific Ocean, it also penetrates into the highArctic along the Greenland west coast (Lüning 1990; Guiry and Guiry 2024) and along the Beaufort Sea (Bringloe and Saunders 2019). Thus, it is not likely that low water temperatures alone are limiting the distribution of the species on the Greenland east coast. However, perhaps together with a combination of other environmental factors along the Blosseville coast, e.g., lack of suitable substratum (Fig. 2) and wave

Table 2. List of clusters and the species defining them. Closely aligned clusters are pooled. The species are listed with those mostly defining the cluster (red colors) toward less defining for the cluster(s) (green colors) according to Supporting Information Fig. S4 (heat map). More rarely identified species with entry frequencies of < 1% (Supporting Information Table S2) are in brackets. The environmental conditions, latitudes, depth, and substratum, influencing the establishment of the clusters according to Fig. 6, are included.

Cluster	Vegetation types/species	Latitudes	Depth range	Substratum
1 Blosseville coast	*Polysiphonia* spp *Phycodrys rubens* *Devalerea ramentacea* *Phaeophyceae* (filamentous) *Laminaria solidungula*	The Blosseville coast 68–71°N	Largest coverage at 15–20 m	Mixed substratum
2 + 9 Seaweed meadow	*Fucus distichus* *Chaetopteris plumosa* *Arcticophycus glacialis* *Pylaiella* sp. Species and genera of the families Chordariaceae Scytosiphonaceae within the order Ectocarpales	Northern latitudes 71–77.5°N	0–15 m	Hard substratum, stones
3 Kelp forest	*Hedophyllum nigripes* Rhodophyta (unspecified) *Halosiphon tomentosum* *Laminaria solidungula* *Devalerea ramentaceae* *Ptilota* sp. *Chordaria flagelliformis* Chlorophyta *Agarum clathratum* *Alaria esculenta* *Arcticophycus plantaginea*	Southern latitudes 65–70°N	From shallow waters to the deepest (50 m), declines from 15 to 20 m	Hard and stable substratum including scattered stones on a soft seabed
4 "Rare" species (few registrations)	[*Battersia arctica*] [*Stictyosiphon tortilis*] Phaeophyceae (rotund and unspecified) Rhodophyta (unspecified) *Hedophyllum nigripes* *Halosiphon tomentosum*	All latitudes	Most common from 5 to 15 m	Exclusively at the hard and stable substratum types
5 Not well defined	Chlorophyta Phaeophyceae (unspecified)	All latitudes	Increasing depth	Softer sediment
6 *Laminaria solidungula*	Phaeophyceae (filamentous and unspecified) *Desmarestia aculeata* *Laminaria solidungula*	Northern latitudes 73–74.5°N	Shallow to 15 (20) m	Hard, stable substratum including scattered stones on a soft seabed
7 Green and red algae	*Cladophora rupestris* [*Membranoptera denticulata*]	Restricted to 68.5–69.5°N	*M. denticulata*, 5 m *C. rupestris*, 5–15 m	
8 Red algae, deep	*Coccotylus truncatus* *Turnerella pennyi* Filamentous Rhodophyta	Abundant in restricted areas at 71, 75 and 77°N	Increasing to 30–40 m	
10 Shallow, brown species	[*Chaetomorpha melagonium*] [*Fucus vesiculosus*] *Saccorhiza dermatodea* *Saccharina latissima* *Agarum clathratum* *Alaria esculenta*	South of 66°N	Shallow depths 5–10 m	Hard substratum

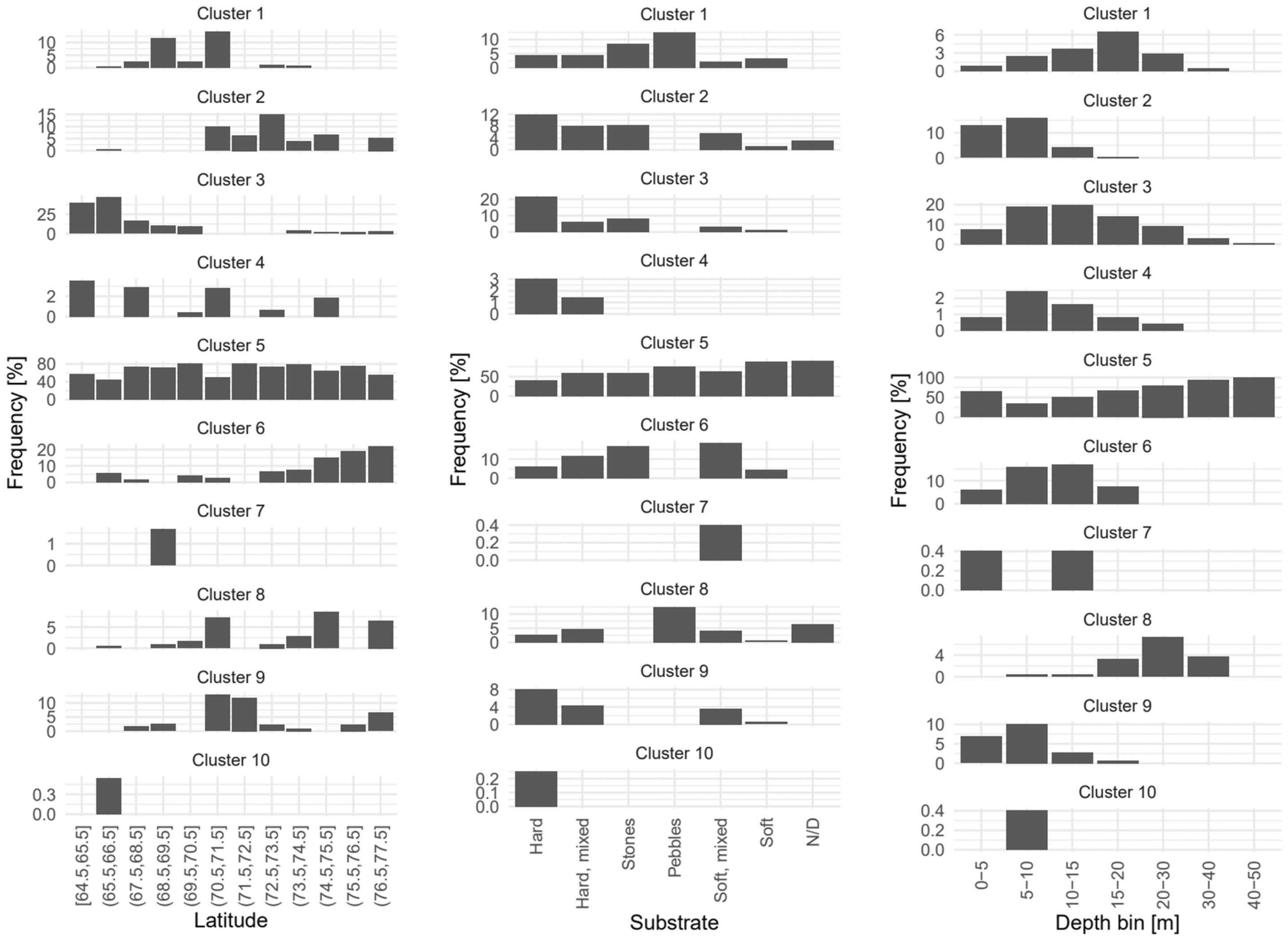

Fig. 6. Bar plots of relative frequencies of each cluster in respective groups: (left) in latitudinal bins; (mid) different substrate categories; (right) at various depths.

exposure, the Blosseville coast may also act as a physical barrier against disseminating further north. However, in addition, in east Greenland, a northward propagation may (further) be constrained by the southward east Greenland Current (Krause-Jensen et al. 2020).

Depth distribution

In general, the depth distributions along the Greenland east coast are comparable with the depth ranges found for kelp species in arctic Canada (Bluhm et al. 2022), and in Svalbard (Schimani et al. 2022) (Supporting Information Table S3). Wiktor et al. (2022) found a more limited depth distribution of kelp species in Svalbard, which they explain by the presence of sea urchins. Kelp forests can be converted to barren grounds caused by intense sea urchin grazing (Christie et al. 2019), which has also been observed along the Greenland west coast (Kjær et al. 2024). However, sea urchins were only randomly observed along the Greenland east coast (present study).

No change in depth limits within latitudes surveyed on the east coast of Greenland can be observed (Fig. 4; Supporting Information Fig. S3), although a trend toward decreasing depth range with increasing latitude was expected due to an increase in length of season with suboptimal light conditions, thus fewer days with sun above the horizon (Supporting Information Fig. S1). However, at random sites, the seaweed vegetation penetrated down to more than 40 m depth (Fig. 4; Supporting Information Fig. S3). Thus, it seems that more local conditions may influence the possibility for some species (*A. esculenta*, *C. truncatus*, *T. pennyi*; Supporting Information Fig. S3) to penetrate to greater depths, e.g., south-directed slope, currents/gyres keeping open water, less water turbidity due to low pelagic primary production or outlet of silt from, e.g., glacier melt water, together with the presence of stable substratum (Fig. 2). In connection with publishing the kelp forest depth record for the North Atlantic in the Disko area in west Greenland, Krause-Jensen et al. (2019) also tested the effect of higher water turbidity at coastal sites vs. offshore sites on depth penetration. They found significantly lower mean depth limits of kelp forests from the coastal sites than at the offshore sites (31 and 43 m, respectively), both being in the same range as found in the present study.

The kelp forest belt with a canopy coverage > 10% is narrowing from reaching a depth of 34 m to 18 m in the north (Fig. 4), which is quite exact in accordance with the range found by Krause-Jensen et al. (2012) for the Greenland west coast within the same latitudinal gradient. They found a depth range, for kelp canopy coverage > 10%, from 24 to 33 m at southern latitudes (64–73°N) to 9–14 m at the most northern latitudes (77–78°N). This suggests that the overall light conditions (including number of days with sun above the horizon and number of days with sea ice cover) may be the main driver of the general kelp forest depth range in Greenland.

Canopy coverage

The maximal cumulative canopy coverage in the present study is found at 6 m (Fig. 4; Table 1), which is in correspondence with the results of Schimani et al. (2022) and Wiktor et al. (2022) for Svalbard (Supporting Information Table S3). The mean maximal coverage on the east coast reached 78%, which is somewhat higher than the range, 5%–62%, found by Filbee-Dexter et al. (2022) in their surveyed area in arctic Canada.

However, the gross mean of 18% canopy coverage found in the present study is about half of the mean of 40% found by Filbee-Dexter et al. (2022). Excluding vegetation coverage nulls from the deepest parts of the transects (> 30) m in the present study results in a mean coverage of 29% (Table 1), which is closer to the Canada findings. Differences in available substratum may explain differences in gross mean coverage, and although the gross mean of substratum type is not given in Filbee-Dexter et al. (2022), they find a clear correlation between hard substratum coverage and, e.g., coverage of *A. clathratum*.

Along the surveyed coastline in east Greenland, hard substratum reached a mean of 63%, although in some areas the stable substratum is less available (Fig. 2). The relatively small mean percentage of canopy coverage is also seen in the work of Kvile et al. (2022). Their prediction of Nordic distribution of kelp forest, including a minimum canopy coverage of *L. solidungula* and *S. latissima* of 50%, which includes the present study data set for east Greenland, applies presence of suitable substratum and sea ice concentration as drivers. They show that the areas where it is predicted that the coverage of the two kelp species will reach a minimum of 50% coverage is quite limited within the same coastline interval as the present study. However, in some areas, other drivers, perhaps with more local implications, also on the substratum, may affect especially the canopy coverage more than depth range as such. For some segments along the Greenland east coast, the coastal waters may be heavily impacted by glacier ice and melt water due to the high number of coastal glaciers. The contribution of glacier ice resulting in ice scouring of seabed and silt from melt water impacts water turbidity and thus light conditions (Niedzwiedz and Bischof 2023), as well as covering hard substratum by sedimentation of particles. Especially along the Blosseville coast, there are numerous glacier outlets (e.g., Catania et al. 2020), and which segment, according to Kvile et al. (Kvile et al. 2022, fig. 3), and Figs. 4 and 5 (latitudinal bins 68–70°N), lack kelp forest canopy reaching high coverage.

Vegetation type distribution and their drivers

From the cluster analyses, a number of vegetation types have been identified, which fit into four segments along the east Greenland coastline, ranging from (1) the Tasiilaq area (65°N) to Kangerlussuaq (68°N) in the south; (2) a segment along the Blosseville coast (68–70°N); (3) from Liverpool Land and up to apx Young Sound (74°N); and (4) the area around Danmarkshavn in the north (77°N) (Figs. 3 and 4).

The southern segment

Cluster 3 represents the southern and deeper kelp forest including *L. solidungula* and *A. clathratum*. This part of the kelp forest resembles the kelp forest at the Greenland south and west coast by the mix of kelp species and the presence of *A. clathratum*. *Agarum clathratum* is a characteristic and dominant component of the kelp forest at more sheltered locations and at greater depths around Tasiilaq (Fig. 3) and at the Greenland south and west coasts (Wegeberg 2007; Kjær et al. 2024). *Laminaria solidungula* is the only kelp species considered arctic endemic (e.g., Bringloe et al. 2020). Filbee-Dexter et al. (2022) describe a similar kelp forest type as the most common community configuration, which was a mixed assemblage of the same species, *A. clathratum*, *A. esculenta*, *L. solidungula*, and including the quite common species in east Greenland, *S. latissima* (Supporting Information Table S2).

Further, a cluster with *Fucus vesiculosus* and the kelp species *Saccorhiza dermatodea*, but not *L. solidungula*, is restricted to low water and the southern latitudes (Cluster 10). *S. dermatodea* is, reputedly, an annual species (Keats and South 1985), and, as such, may be considered opportunistic, colonizing bare grounds where other perennial kelp species are absent from the hard substratum, which absence of other kelp species this cluster is also characterized by. This may be a sign of disturbance, e.g., due to scouring from ice floes in the relatively low waters. In the southern latitudinal bins, the sea ice concentration does not reach 100% at any time of the year (Supporting Information Fig. S2), which may allow for ice floes to drift. The phenomenon of multiyear drift ice along the Greenland east coast, turning Cape Farewell (southernmost tip of Greenland), and continuing up along the Greenland west coast is described in, e.g., Frederiksen et al. (2012).

Blosseville coast

As described above, the Blosseville coast has numerous marine-terminating glaciers, and, as such, the coastal waters are heavily influenced by ice fronts and glacier output, i.e., silty water and glacier ice. Thus, the characteristic kelp forest of this coastline segment is the vegetation type of Cluster 1, which is dominated by *L. solidungula* together with red algal species on a seabed with a mix of substratum types from hard (rock) to pebbles.

It was characteristic that the marine vegetation appeared at 15–20 m depth, and as such the upper meters were considered to possess a very dynamic environment due to impacts from turbid glacier melt water as well as ice scouring together with more unstable substrates from an eroding coastline. Unlike Schimani et al. (2022), who describe a fjord environment and found that the depth for maximal kelp biomass decreased at glacial sites compared to sites not influenced by glacier, the Blosseville coast provides an open and exposed coast. Therefore, the turbid glacier melt water may only impact the lower depths closest to the coast due to dilution. The coastline between Tasiilaq and Kangerlussuaq may also be heavily influenced by glaciers (e.g., Catania et al. 2020), but unfortunately this part of the coastline was not surveyed due to a heavy concentration of sea ice in the year of the survey (2017).

Seaweed meadows

Cluster 2 and Cluster 9 represent the macroalgal species assemblages of what we call here the seaweed meadow, as they are characterized by low vegetation of *C. plumosa* and *F. distichus* and include *A. glacialis* (Cluster 2 + 9). This macroalgal vegetation type was only observed along the coastline between approximately 71°N and 73°N, but similar vegetation was described from the Inglefield Inlet at Qaannaaq (77°N) in northwest Greenland (Wilce 1964). Thus, it seems plausible that the seaweed meadow as a vegetation type is a high-arctic element, both on the east and west coasts of Greenland.

High-arctic kelp forest

In the high arctic, in the extreme north end of the surveyed coastline, kelp forest with relatively high dominance of *L. solidungula* as well as *D. aculeata* was a characteristic marine vegetation element (Cluster 6). The seasonal physiological performance of arctic macroalgae is strongly linked to life strategies of individual species or ecotypes. Dunton (1982) showed that *L. solidungula* relied to a high degree on reserves stored during the 3 months of light for its annual growth in arctic Canada. As discussed by Borum et al. (2002), maintenance of old lamina, and thereby accumulation of surface area of an individual, enhances light and inorganic carbon harvesting, and particularly *L. solidungula*, and to a lesser extent *S. latissima*, can possess up to several lamina generations on the Greenland east coast (Lund 1959a, 1959b; Borum et al. 2002). In temperate regions, the lamina of *S. latissima* from the preceding year's growth is lost successively due to erosion along with the development of the new lamina. In the present study, *L. solidungula* was observed with up to three (sometimes even four) generations of lamina (Supporting Information Fig. S5), which is also described by Rosenvinge (1910) for the east coast.

Another characteristic component of the high-Arctic segment of the east Greenland coastline is the presence of *C. truncatus* and *T. pennyi* as a vegetation type at the larger depths (Cluster 8). Schimani et al. (2022) provide information from Svalbard, as they consider for the first time, the occurrence of deep-water red algae below the kelp forest, which is confirmed by this study, where erect red algal species, *C. truncatus* and *T. pennyi* are found at 45 and 51 m, respectively (Supporting Information Table S2).

The predicted distribution of kelp in the eastern Canadian Arctic, including ice thickness, temperature, and salinity as drivers, showed that it is likely that kelp may expand northwards with climate change (Goldsmit et al. 2021). However, this is with the exception of the distribution of the endemic arctic kelp *L. solidungula*, which is considered to suffer from temperature increase and thus its distribution may shrink from its southern distributional limit (Bischof et al. 2019; Goldsmit et al. 2021; Bringloe et al. 2022). In general, though, Scherrer et al. (2019) found, in their modeling study evaluating alternative causes for climate-induced macroalgal increases in arctic rocky bottom communities in Svalbard, that light is the primary driver of increases in macroalgal coverage, whereas increased seawater temperature plays a secondary role. Hence, the number of days without sea ice cover can be considered a proxy for the annual window of optimal light conditions and the cumulative annual amount of light reaching the seabed. In this respect, e.g., Krause-Jensen et al. (2012) found that the number of days with sea ice cover was the driver of kelp belt depth distribution along the west coast of Greenland being narrower northwards. Also, Filbee-Dexter et al. (2022) found a positive relationship between open water days and macroalgal quantitative and qualitative parameters in the eastern Canadian Arctic.

On the contrary, long-term patterns of benthic irradiance and kelp production, reviewing data from 1979 with present-day data from the Beaufort Sea, Bonsell and Dunton (2018) found no evidence for increased production with a longer sea ice-free period. They explain it by very low light transmittance to the benthic vegetation during the ice-free season as well as wind-driven resuspension of sediments following ice break-up, increasing turbidity and decreasing light penetration to the seabed. They find that the window for optimal light conditions may be in the shoulder seasons for ice break-up and freeze, when intermediate sea ice concentrations reduce wind-driven sediment resuspension (Bonsell and Dunton 2021, 2018).

In the present study, we do find a change in depth distribution of some kelp species, including *L. solidungula*, the species studied by Bonsell and Dunton (2018), along the latitudinal gradient (Fig. 4; Supporting Information Fig. S3). However, we do also find comparable coverages in the south and north extremes of the surveyed coastline, also at lower depth (Fig. 3), even though the number of days above the horizon is decreased from 365 to 252 d (Supporting Information Fig. S1), and there is almost 100% sea ice cover all year (Supporting Information Fig. S2). Thus, there seems to be a high degree of adaptation to the suboptimal light conditions and that sea ice cover may introduce some, to the kelp species, beneficial conditions to the environment, e.g., through dampening of wind effects.

Conclusion

Pauperization of marine vegetation/kelp forest was observed, and their regional averages did decrease to some extent, with increasing latitude, which are expressed as decreases in coverage and depth distribution due to the northwards receding light conditions. The kelp forest vegetation belt, with a canopy coverage > 10%, was narrowing from reaching a depth of 34 to 18 m within the latitudinal gradient surveyed (65.5–76.8°N). However, for some species, no change in maximal depth limits could be observed within these latitudes.

Further, it was found that sea ice concentration may act as a driver for coastal community presence and coverage as a cumulative effect with stronger seasonality in light conditions northwards along the surveyed coastline. In addition, the presence of glaciers, which were most common along the Blosseville coast in the survey area, was considered to have an impact on vegetation type due to glacial meltwater particle plumes increasing water turbidity and decreasing light penetration.

Thus, with respect to the presence of different marine vegetation community figurations, coverage, and depth in areas with different impacts from sea ice concentration, which may not be directly correlated to latitude, four vegetation types were identified. Two vegetation types, the most southern and most northern, were considered to be correlated with latitudes, whereas the two vegetation types identified for the mid segment of the surveyed coastline may have been more correlated to local/regional conditions such as impacts from the presence of dynamic sea ice and glaciers, as well as smaller-sized hard substratum.

Author Contributions

Susse Wegeberg: Conceptualization, Methodology, Formal analysis, Investigation, Resource, Writing – original draft, Funding acquisition, Project administration. Jozef Wiktor: Formal analysis, Writing – review & editing. Jannie Fries Linnebjerg: Formal analysis, Writing – review & editing. Ole Geertz-Hansen: Conceptualization, Methodology, Formal analysis, Investigation, Resource, Writing – original draft.

Acknowledgments

This study has been conducted using E.U. Copernicus Marine Service Information; https://doi.org/10.48670/moi-00001. We wish to wholeheartedly thank the crew on *HDMS Knud Rasmussen* for their extremely professional and efficient assistance in 2016 and aid in transfer between Tasiilaq and Kangerlussuaq in 2017. It was due to their helpful and positive attitude that such a high number of transects over such a long distance were obtained within such a short time (10 d) as well as SCUBA diver collections. Also, the 2017 skippers of *Qaaddaatser* and *Vega* of Tasiilaq and Kummiut, respectively, are likewise thanked for their proactive approach to make the journey safe and field work successful. This study is part of the Northeast Greenland Environmental Study Program, a collaboration between DCE—Danish Centre for Environment and Energy at Aarhus University, the Greenland Institute of Natural Resources, and the Environmental Agency for Mineral Resource Activities of the Government of Greenland.

Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 24 March 2024
Revised 05 January 2025
Accepted 27 March 2025