

Arctic kelp forest decline – a consequence of melting glaciers?

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Abstract

The Arctic archipelago of Svalbard is a hotspot of global warming and many fjords experience a continuous increase in seawater temperature and glacial melt while sea-ice cover declines. In 1996/98 and 2012-14 macroalgal biomass and species diversity were quantified at the study site Hansneset, Kongsfjorden (W-Spitsbergen) in order to identify potential changes over time. In 2021, we repeated the earlier studies by stratified random sampling (1x1 m², n=3) along a sublittoral depth transect (0, 2.5, 5, 10 and 15m) and investigated the lower depth limits of dominant brown algae between 2-20m. The fresh weight maximum was 11.5 kg m⁻² at 2.5m and kelp blades stored 277g carbon m⁻² and 18g nitrogen m⁻² at this depth. Although biomass did not significantly change since 2012/13, the ‘Digitate Kelps’ community (*Laminaria digitata*/*Hedophyllum nigripes*) changed to an *Alaria esculenta* dominated kelp forest in 2021 and a balanced age structure of kelps (juveniles plus many older kelp individuals) was only apparent at 2.5m. In addition, the abundances and lower depth limits of all dominant brown algae declined noticeably over the last 25 years while the deep red algae flora remained stable. As we revealed that biomass allocation to blades, stipes and holdfasts as well as the ability to store blade carbon and nitrogen was kelp species-specific, a pronounced shift in the functionality of the kelp forest had occurred over time. We propose that the observed changes in the macroalgal community are mainly driven by alterations in underwater light climate as in situ data confirmed increasing turbidity and decreasing irradiance since 2012 and 2017, respectively. As a consequence, the overall retreat of the kelp forest to lower depth levels seems to be a result of strong glacial melt and will possibly continue in future with unforeseen consequences for Arctic coasts and their socio-ecological fjord systems.

Title page

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Abstract

The Arctic archipelago of Svalbard is a hotspot of global warming and many fjords experience a continuous increase in seawater temperature and glacial melt while sea-ice cover decline. In 1996/98 and 2012-14 macroalgal biomass and species diversity were quantified at study site Hansneset, Kongsfjorden (W-Spitsbergen) in order to identify potential changes over time. In 2021, we repeated the earlier studies by stratified random sampling (1x1 m², n=3) along a sublittoral depth transect (0, 2.5, 5, 10 and 15m) and investigated the lower depth limits of dominant brown algae 220m. The fresh weight maximum was 11.5 kg m⁻² at 2.5m and kelp blades stored 277g carbon m⁻² and 18g nitrogen m⁻² at this depth. Although biomass did not significantly change since 2012/13, the ‘Digitate Kelps’ community (*Laminaria digitata* / *Hedophyllum nigripes*) changed to an *Alaria esculenta* dominated kelp forest in 2021 and a balanced age structure of kelps (juveniles plus many older kelp individuals) was only apparent at 2.5m. In addition, the abundances and lower depth limits of all dominant brown algae declined noticeably over the last 25 years while the deep red algae flora remained stable. As we revealed that biomass allocation to blades, stipes and holdfasts as well as the ability to store blade carbon and nitrogen was kelp species-specific, a pronounced shift in the functionality of the kelp forest had occurred over time. We propose that the observed changes in the macroalgal community are mainly driven by alterations in underwater light climate as *in situ* data confirmed increasing turbidity and decreasing irradiance since 2012 and 2017, respectively. As a consequence, the overall retreat of the kelp forest to lower depth levels seems to be a result of strong glacial melt and will possibly continue in future with unforeseen consequences for Arctic coasts and their socio-ecological fjord systems.

Keywords

macroalgae, depth zonation, biomass, age structure, time series, Svalbard

Cover letter

Dear Professor Beckerman,

I am pleased to submit our manuscript “Arctic kelp forest decline – a consequence of melting glaciers” for publication in *Ecology and Evolution*.

We aimed to document variations in Arctic kelp forest dynamics which are likely due to global climate change using a unique time series approach. Therefore, the macroalgal community at our sampling site in Kongsfjorden (W-Spitsbergen) was sampled in a standardized manner at three time points spanning over the past 25 years. As the Arctic is substantially affected by warming we expected to observe alterations in the seaweed community and especially kelps as major coastal foundation species over time.

In 2021 the upward shift of the kelp forest and consequently the overall seaweed biomass maximum to the shallow subtidal, which was first observed between 1996/98 and 2012/13, continued. Since the last investigation the kelp forest structure noticeably changed as ‘Digitate Kelps’ and *Saccharina latissima* retreated to the uppermost depth level and *Alaria esculenta* became the dominant seaweed species down to 10m water depth. These alterations in species dominance over time are associated with a functional shift of the kelp forest as we show that each kelp exhibits a species-specific strategy in biomass accretion and thereby carbon allocation. The main driver shaping Arctic macroalgal communities currently appears to be the decrease in water transparency as a consequence of glacier loss and resulting sediment plumes, which was confirmed by *in situ* decreasing PAR and increasing turbidity data.

It is frequently debated if Arctic kelp forests will expand or retreat as sea ice coverage and ice scouring pressure weaken with warming. Our results imply that the habitat for kelp forests along Arctic fjord systems influenced by glacial melt will decline further as long as coastal turbidity and sedimentation continue to

intensify. Our research contributes to the understanding of fjord ecosystem response to climate change and can improve predictions for wider stretches of Arctic coastline.

Thank you for your consideration.

Sincerely,

Luisa Düsedau

Text

Introduction

Submarine algal forests are present along 25% of the world's coastline ranging from temperate to polar regions (Filbee-Dexter & Wernberg, 2018). In the past their northward extension into the Arctic was physically limited by sea ice and low light conditions whereas their distribution towards the equator is restricted by nutrient availability and warm temperatures (Steneck & Johnson, 2013). These forests are formed by large kelps of the brown algae order Laminariales, which are foundation species on rocky shores and serve as important ecosystem engineers and major primary producers (Filbee-Dexter et al., 2019). Worldwide kelp forests are particularly valuable ecosystems that host a high biodiversity of marine life and complex food webs (Krause-Jensen et al., 2012; Teagle et al., 2017).

Caused by ubiquitous global climate change, the Arctic ocean has warmed four times faster than the global average since 1979 (Rantanen et al., 2022). Sea ice loss due to increasing water temperatures has led to a prolongation of the open water period potentially improving growth conditions for Arctic kelps (Krause-Jensen et al., 2012; Sumata et al., 2023). The associated changes of favorable underwater light regime and reduced physical disturbance by ice scraping are predicted to open up new habitats enabling an expansion of kelp forests into the future Arctic (Assis et al., 2022; Krause-Jensen & Duarte, 2014). At the same time, glaciers around the globe are melting rapidly (Hugonnet et al., 2021) and increasing meltwater runoff creates strong turbidity and salinity gradients with potential negative impacts on coastal productivity (Sejr et al., 2022; Jerosch et al., 2019).

Kongsfjorden (western Spitzbergen, Svalbard archipelago) is an example of a well monitored Arctic fjord that experiences strong impacts of climate change and is regarded to serve as a marine high latitude model ecosystem (Bischof et al., 2019b). The hydrography of Kongsfjorden is influenced by cold Arctic water from the East Spitsbergen Coastal Current flowing around the Svalbard shelf and warm saline Atlantic water from the West Spitsbergen Current (Svendsen et al., 2002). To the west Kongsfjorden is open to the Arctic Ocean where the water masses entering through the southern part are mixed with fresh water from glacial meltwater and river runoff before flowing out along the northern coast (Kruss et al., 2017). Reflecting the overall regime shift in the Arctic Ocean (Sumata et al., 2023), Kongsfjorden crossed the tipping point away from cold Arctic winters with persistent thick sea ice coverage in winter 2006 when warm water masses started to enter the fjord all year round (Tverberg et al., 2019). A long time series indicates that the overall seawater temperature and the number of ice-free days along the northwest coast of Svalbard has increased gradually within 30 years since 1980 (Kortsch et al., 2012). Continuous oceanographic measurements suggest that Kongsfjorden has already transitioned to an Atlantic-type fjord as depth averaged temperatures in the inner fjord in summer have increased by 0.26°C/yr since 2010 (De Rovere et al., 2022).

Kongsfjorden is lined by several glaciers at different stages of glacial retreat with four main calving tidewater glaciers and several land-terminating glaciers including Brøggerbreen at the Bayelva river (Pavlov et al., 2019; Svendsen et al., 2002). When freshwater from glacial melt, snow and precipitation enters the fjord in summer, it carries suspended terrestrial particles that form large sediment plumes which alter the spectral composition of the underwater light regime available for macroalgal photosynthesis (Niedzwiedz & Bischof, 2023; Pavlov et al., 2019).

The shallow subtidal of the Kongsfjorden coastline down to 15m depth is densely covered with macroalgal meadows but even at ~70m depth deep-water red algae and crustose coralline algae occur (Schimani et al.,

2022; Kruss et al., 2017). Along the fjord axis multiple kelp forests are present which are strongly impacted by alterations in their environment on the species as well as the community level (Schimani et al., 2022; Bischof et al., 2019a; Hop et al., 2016). In 1996/98 Hop et al. (2012) investigated for the first time the biodiversity and biomass distribution of macroalgae along a depth transect on the rocky shore of Hansneset. They reported a rich kelp forest that was dominated by ‘Digitate Kelps’ (*Laminaria digitata* / *Hedophyllum nigripes*), *Alaria esculenta* and *Saccharina latissima* and overall documented 62 macroalgal species. In 2012-14 the hard bottom community was examined a second time and standards for future monitoring were established by Bartsch et al. (2016) and Paar et al. (2016). In the upper subtidal zone (2.5m) kelp biomass in 2012/13 was significantly 8.2 fold higher compared to 1996/98 and the study revealed that not only the overall biomass maximum but the entire kelp forest had shifted upwards (Bartsch et al., 2016). These changes in the kelp forest community structure were discussed as being likely a consequence of altering abiotic conditions caused by Arctic warming and hence may largely impact coastal ecosystem services (Filbee-Dexter et al., 2019; Bartsch et al., 2016). Furthermore, the responses of different species and life stages of kelps in multi-stressor experiments indicate that some kelp species may benefit from climate change while others will retreat (Niedzwiedz & Bischof, 2023; Diehl & Bischof, 2021; Franke et al., 2021; Roleda, 2016; Zacher et al., 2016).

Despite their ecological importance, Arctic kelp forests are largely understudied and the investigations in Kongsfjorden are a rare example of consistent quantitative monitoring that provide important data for predictions of the future Arctic (Bischof et al., 2019a; Filbee-Dexter et al., 2019; Wernberg et al., 2019). It was therefore the objective of the current study to examine biomass and community development in an Arctic kelp forest spanning over 25 years of Arctic warming. In 2021 we repeated the investigations from 1996/98 (Hop et al., 2012) and 2012-14 (Bartsch et al., 2016) at the Hansneset sampling site and complemented the existing time series (Figure 1). The observed changes in the macroalgal community and new investigations on ecological differences between kelp species provide important insights for the key question, how kelp forests are affected in an Arctic fjord system that is influenced by warming, sea ice retreat and glacial melt.

2. Materials and Methods

Study site

Kongsfjorden is located on western Spitzbergen which is part of the Svalbard archipelago. Blomstrand is its largest island and situated in the center of the Arctic fjord. Until the early 1990s it was a peninsula and connected to the coast of Kongsfjorden by the retreating tidal glacier Blomstrandbreen (Burton et al., 2016; Svendsen et al., 2002). Our study site Hansneset (78°59.101’N, 11°57.793’E, for map see Figure 2) is located on the western side of Blomstrand island. It is a moderately exposed hard-bottom location and consists of steep bedrock with scant sediment cover (Voronkov et al., 2013). Since 2007, the site has remained ice free in winter and is relatively sheltered from occasional drift icebergs from the calving glaciers of the fjord (Lippert et al., 2001; Paar et al., 2016).

Study design

In the present study macroalgal biomass and species distribution investigations from 1996/98 (Hop et al., 2012) and 2012-14 (Bartsch et al., 2016) were repeated between 21 June and 15 July 2021. A detailed overview of response variables and a comparison of methods used in the previous studies is given in Bartsch et al. (2016). To guarantee a comparable dataset and facilitate future monitoring at the study site, the survey methods followed the established protocols given in Bartsch et al. (2016) and Paar et al. (2016). In 2021, two successive diving campaigns were conducted of which the first was a semi-quantitative (visual) investigation on the depth distribution and abundance of dominant brown algae between 2m and 20m depth. In contrast, the second campaign was an extensive quantitative study with complete destructive sampling at 2.5, 5, 10 and 15m depth and multiple associated measurements of the collected material (fresh and dry weight, leaf area index, kelp demography, blade carbon and nitrogen content). In both diving campaigns sampling depths were measured by a bottom timer (Scubapro Digital 330) and afterwards corrected to chart datum (lowest astronomical tide) according to the local tide calendar (<https://www.kartverket.no/en/at-sea/>).

Macroalgal fresh weight and the lower depth distribution of biomass dominant brown algae were analyzed across all three timepoints (this study, Bartsch et al., 2016; Hop et al., 2012). Mean age and density per m² of adult kelps as well as the leaf area index of biomass dominant species or groups was investigated in 2021 and compared to 2012/13 data (Bartsch et al., 2016). Furthermore, new aspects targeting the ecological differences between kelp species (holdfast, stipe and blade dry biomass as well as blade carbon and nitrogen content) were analyzed in the recent study.

In the Arctic and sub-Arctic, two morphologically very similar digitate kelp species (*Laminaria digitata* and *Hedophyllum nigripes*) may grow side by side and only DNA barcoding can reveal secure species identification (Dankworth et al., 2020), which has not been conducted here. Thus, this species complex is referred to as 'Digitate Kelps' throughout this study, although the ecology of these two species is probably quite different (Franke et al., 2021).

Lower depth distribution of dominant brown algal species

The depth distribution of biomass dominant brown algae (Laminariales species, *Sacchoriza dermatodea*, *Desmarestia* spp.) was semi-quantitatively (visually) investigated by scientific divers in five parallel transects off the coastline covering the vertical gradient between 2m and 20m depth. The target distance between transects was 5m and transects were distributed over a horizontal width of approximately 30m. A 1 x 1m quadrat divided into four 50 x 50cm subquadrats was placed on the ground or above the kelps at every depth meter along the transect and species occurrence was documented as attached frequency within each subquadrat. This resulted in a relative frequency of 0 – 4 per depth and transect. Additionally, the visual presence of the species in the close surroundings of each quadrant was documented. In summary this generates in a maximum presence score of 5 for each species per replicate. The target replication was five per depth but due to depth corrections to chart datum this resulted in n = 3–8 for each depth and species. In replicates with more than 50% coverage of kelps, it was not possible to place the quadrat on the ground. Here the depth was corrected by the mean height (78cm) of the local kelp canopy (data not shown). To enable a comparison between the publications of Hop et al. (2012), Bartsch et al. (2016) and the present study, scores were transformed into percentage cover classes and the abundance of species was classified as rare (5-15% [?] score 1-3), common (16-60% [?] score 4-12), subdominant (61-80% [?] score 13-16) and dominant (81-100% [?] score 17-20). In 1996/98 these semi-quantitative classes referred to a combination of biomass and %-coverage values while in 2014 and 2021 a combination of relative frequency and presence/absence data was applied. Furthermore, investigated depth levels varied between time points (1996/98: 20 – 8m; 2014: 20 – 8m; 2021: 20 – 2m) and *Desmarestia* spp. includes *D. aculeata* and *D. viridis* as in Bartsch et al. (2016).

Macroalgal biomass

For the quantitative diving campaign, a main transect was installed in the sublittoral off Hansneset, marking the vertical gradient between 2.5 and 15m depth below chart datum. Proceeding laterally +/-15m from this main transect, complete destructive sampling was performed by scientific diving at 2.5, 5, 10 and 15m depth. At each depth horizon the attached macroalgal biomass of all kelps and understory seaweeds was collected within randomly chosen 1 x 1m quadrats (n = 3). Additional sampling was performed in the infralittoral fringe level (0m) using 50 x 50cm quadrats (n = 3) and data was extrapolated to 1m² before analysis. Algae were sampled in net bags and kept in seawater filled barrels for transport. In the laboratory, biomass samples were stored in flow through seawater tanks before further processing.

Algal material was sorted to species level, blotted dry with cotton towels and fresh weight (FW) as well as dry weight (DW) was determined (Mettler Toledo PB3002_S/FACT Delta Range, Max 600g/3100g, d = 0.01g/0.1g, Germany). Adult kelps were separated into holdfast, stipe and blade prior to weight measurements. Juvenile individuals with a stipe length [?]5cm were weighed as whole individuals. Dry weight of species was recorded after drying over night at 70degC in a drying oven (Termaks, Series TS9000, Model TS9135). Due to logistical reasons, the DW could not be documented for every adult kelp specimen. For adult kelp DW representatives of each species and stipe length category were dried depending on their occurrence to represent the properties of the local kelps as realistic as possible (*Alaria esculenta* : n = 8

(5–15cm, 31–50cm, >80cm); $n = 10$ (16–30cm), $n = 9$ (51–80cm); ‘Digitate Kelps’: $n = 9$ (5–15cm), $n = 10$ (16–30cm, 51–80cm), $n = 14$ (31–50cm), $n = 3$ (>80cm); *Saccharina latissima* : $n = 3$ (5–15cm), $n = 8$ (51–80cm, >80cm)). The resulting regression formulas between FW and DW expressed high determination coefficients (majority $R^2 > 0.9$) and were used to calculate the DW of the remaining specimens (Appendix 1). All adult kelp individuals [?] 2 years collected from 2.5m and 5m depth were analyzed for holdfast, blade and stipe DW as well as blade:stipe DW ratio.

Biomass dominant species were organized in two categories as well as six groups (Kelps: *A. esculenta* , ‘Digitate Kelps’, *S. latissima* ; Understory seaweeds: ‘Other Phaeophyceae’, Rhodophyta, Chlorophyta) and the historical datasets were reanalyzed accordingly for comparison. The following species are classified in the group ‘Other Phaeophyceae’ (brown algae): *Battersia arctica* , *Chorda filum* , *Chordaria flagelliformis* , *Desmarestia aculeata* , *Desmarestia viridis* , *Dictyosiphon foeniculaceus* , *Ectocarpus* sp., *Fucus distichus* , *Halosiphon tomentosus* , *Haplospora globosa* , *Laminaria solidungula* , young *Laminaria* spp., *Pylaiella* sp., *Sacchorhiza dermatodea* , *Scytosiphon* sp., *Sphacelaria plumosa* . In the group of Rhodophyta (red algae) the following species are pooled: *Coccotylus truncatus* , *Cystoclonium purpureum* , *Devaleraea ramentacea* , *Euthora cristata* , *Odonthalia dentata* , *Palmaria palmata* , *Phycodrys rubens* , *Plocamium cartilagineum* , *Porphyra* sp./*Pyropia* sp., *Ptilota* sp., *Rhodomela* sp., *Turnerella penneyi* . Some specimens of *Devaleraea ramentacea* were densely covered by brown *Elachista fucicola* epiphytes which could not be removed but were considered negligible relative to host biomass. The group Chlorophyta (green algae) contains the following species: *Acrosiphonia* spp., *Chaetomorpha melagonium* , *Kornmannia leptoderma* , *Spongomorpha* spp., *Ulva* sp. Calcified coralline algae were present along the depth transect but were excluded from identification as in the previous studies.

Leaf area index (LAI)

The leaf area of all macroalgae collected from the quantitative sampling quadrats was determined from digital photographs (Canon EOS 600D) using black calibration quadrats and the image analysis software ImageJ (Schneider et al. 2012, Version 2.1.0). Single large specimens (e.g. kelps and kelp like brown algae) were recorded individually whereas all specimens of most understory algae per replicate were spread out and photographed together. According to (Luning, 1969), the leaf area index (LAI) is the measured leaf area normalized to 1 m² ground. Samples from 0m were not included in the LAI analysis. For very few adult kelp specimens (*A. esculenta* and ‘Digitate Kelps’: $n = 4$) the leaf area was not measured. In these rare cases, a regression formula between blade DW and leaf area of representatives of each species was calculated (Appendix 1) and applied to the respective specimens.

Age class distribution and density of kelps

To investigate the demographic structure of the Hansneset kelp forest, the age and density of kelp specimens was documented at 2.5, 5 and 10m depth. The seasonal growth rhythm of kelps results in the formation of annual growth rings, which can be used for age determination in adult kelps ((Parke, 1948); for discussion see Bartsch et al., (2016)). The minimum age of kelp individuals was determined by counting the annual growth rings of a thin cross section taken from the stipe just above the holdfast. Small delicate kelp individuals with [?]5cm stipe length and specimens without growth rings were considered juveniles (<1 year old). For a minority of kelp individuals, the age was not recorded (*A. esculenta* : $n = 4$; ‘Digitate Kelps’: $n = 21$; *S. latissima* : $n = 6$) but calculated using a regression formula from stipe length and age following Rinde & Sjøtun (2005) (Appendix 1).

C:N ratio, C and N content

For analyzing the carbon and nitrogen content in the blades of adult kelps, a sub-sample of meristematic discs (o 24mm) was taken for each kelp species across all age classes ([?] 2years – 8years; *A. esculenta*: $n = 11$ (2.5m); $n = 15$ (5m); ‘Digitate Kelps’: $n = 15$ (2.5m); $n = 10$ (5m); *S. latissima* : $n = 15$ (2.5m); $n = 7$ (5m)) from 2.5 and 5 m depths individuals. The blade samples were blotted dry with Kimtech Science precision wipers (Kimberly-Clark Professional, USA), immediately frozen at -80degC and later freeze-dried (freeze dryer: CHRIST, ALPHA 2-4 LD plus with LyoCube 4-8, Germany; pump: vacubrand, chemistry

hybrid pump RC6, Germany). The freeze-dried algal material was ground to powder using a ball mill (Retsch MM40, Germany) and five 3 mm steel beads (frequency 30/s, 1 min). Subsamples of 5-6 mg were weighed into tin cartridges (6 x 6 x 12mm) and the samples were combusted at 950degC following the protocol of Graiff et al. (2015). The total content of C and N was automatically quantified in an elemental analyzer (UNICUBE(r) Elementar Analysensysteme GmbH, Langenselbold, Germany) and acetanilide was used as the standard (Verardo et al., 1990). Individual %carbon, %nitrogen and C:N ratio was analyzed and these data were used to extrapolate the absolute C and N content stored in the DW of kelp blades per m⁻² in 2021.

PAR and Turbidity

PAR (photosynthetically active radiation) and turbidity data were measured year-round with a sampling frequency of 1hz (1sec⁻¹) in the framework of the AWIPEV-COSYNA underwater observatory in Ny Ålesund (UMT 8763953degN, 433992degE, for map see Figure 2). For a detailed description of the AWIPEV-COSYNA underwater observatory see Fischer et al. (2017) and Fischer et al. (2020). Briefly, the system comprises a land-based FerryBox system equipped with various hydrographic sensors receiving water from a remote-controlled underwater pump station at 11m water depth. Additionally, a cable connected (fibre-optic and 240 V power) underwater node system comprises a fixed sensor carrier at 11m water depth (+/- tide) as well as a vertical profiling sensor elevator to the surface. For the here presented analysis, PAR and turbidity data from a CTD (Sea & Sun 90, installed in June 2012) and a PAR sensor (Sea-Bird ECO-PAR, installed in September 2016) mounted at a vertical profiling sensor elevator were used. The profiling sensor elevator performs one full vertical profile from about 11 m to 1 m water depth (+/- tide) every day. After that daily profile, the vertical profiling unit is randomly positioned in one of the five depth strata 9, 7, 5, 3 and 1 m below the water surface for 24h in a way that each depth stratum is sampled once a week. Turbidity was measured in formazine turbidity unit (FTU) and PAR in $\mu\text{mol m}^{-2} \text{s}^{-1}$. All sensors are maintained regularly in a one-year interval. Data gaps due to system maintenance or a sensor failure were compensated by averaging all measurements within the 24h period to a single 24h mean value and subsequently averaging these daily means over one week. Weeks when no PAR and turbidity data were available at all were excluded and Appendix 2 shows the real number of available data weeks for all years. The focus of the present study is PAR and turbidity during the macroalgal growth season in the polar summer and therefore only data from week 8 in March to week 44 in October were included in further analysis.

Statistical analyses

The statistical analyses were performed in R version 4.2.2 ('Innocent and Trusting', R Core Team, 2022). The original data from 1996/98 (<https://doi.org/10.1594/PANGAEA.864321>) and 2012-14 (provided by I. Bartsch) were used for the time series analysis. Due to the logistical constraints of the intensive scuba diving campaign along the sublittoral gradient at Hansneset for all three time points of the time series, only a limited number of replicates was obtained per campaign (1996/1998: n = 2 (0m); n = 3 (5 – 15m); n = 4 (2.5m); 2012/2013: n = 3 (0 and 15m); n = 6 (2.5 – 10m); 2021: n = 3). The homogeneity of variances was tested using the Levene's test before each ANOVA. As the absence of a species or group at a certain depth level results in zero values for that depth, only relevant depth levels were included in the statistical tests.

Time series analysis (1996/98-2012/13-2021): Separate two-factorial ANOVAs were performed to assess the effects of the fixed factors time, depth and their interaction for FW (log + 1 transformed data) and LAI of the biomass-dominant species or groups. When the ANOVA output revealed significant effects, a Tukey HSD post hoc test for uneven n was applied. In case homogeneity of variances could not be achieved by transformation but the results of the two-factorial ANOVA were highly significant, a non-parametric Kruskal – Wallis test followed by a pairwise Wilcoxon rank sum test was performed to test for differences between depth levels. This study focused on investigating changes over time and therefore the differences in species and group FW and LAI across depth levels in 2021 alone were not examined statistically.

Age and density comparison 2013 / 2021: To investigate differences between timepoints and kelp species for the mean age and density per m⁻² at 2.5m and 5m (2013 and 2021: n = 3), separate two-factorial ANOVAs were performed and significant effects were further investigated using a Tukey HSD post hoc test. For the

analysis of mean density per m^2 , data was $\log + 1$ transformed to achieve homogeneity of variances. Juvenile specimens < 1 year were excluded from the statistical analysis.

Adult kelp dry weight and biochemical investigations in 2021: Individual holdfast, blade and stipe DW, blade:stipe DW ratio as well as blade %carbon, %nitrogen and C:N ratio was compared between kelp species and across the relevant depth levels (2.5 – 5m) in 2021. Homogeneity of variances (Levene’s Test) and normal distribution (Shapiro-Wilk Test) could not be achieved through data transformation. The effect of the factors depth and species on the individual parameters were tested in separate non-parametric Kruskal-Wallis tests and by pairwise Wilcoxon rank sum tests with Bonferroni correction to reveal differences between species.

Carbon and nitrogen 2021: Mean extrapolated carbon and nitrogen stored in kelp blade DW per m^2 in summer 2021 was compared between depth levels and kelp species (2.5 and 5m; both $n = 3$) using separate two-factorial ANOVAs.

PAR and Turbidity time series: PAR and turbidity data were quality controlled according to an adapted ARGO standard for stationary sensors (Fischer et al., 2021; Waldmann et al., 2022). To analyze long-term changes and trends over the sampling period, the residuals of the observed weekly PAR and turbidity values to the expected PAR and turbidity values were calculated, using the means of the observed weeks across all years as expected values. The trend-analysis of PAR and turbidity over the sampling period was done by simple linear regression over time using the R base functions “lm” (R Core Team, 2019).

3. Results

Fresh weight

Seaweed biomass along the depth gradient in 2021:

In 2021, a total of 21 biomass dominant macroalgal taxa (11 Phaeophyceae, 6 Rhodophyta, 4 Chlorophyta) were collected along the depth transect. In contrast to the previous studies, six macroalgal taxa were not biomass relevant anymore as they were either absent (Phaeophyceae: *Chorda filum*, *Haplospora globosa*, *Laminaria solidungula*; Rhodophyta: *Cystoclonium purpureum*, *Odonthalia dentata*) or were only encountered in negligible amounts of $< 0.1\text{g FW}$ (Phaeophyceae: *Battersia arctica*). Detailed FW and DW data of single species and sums of groups in 2021 are given in Appendix 3 and Appendix 4, respectively.

In the infralittoral zone (0m) the macroalgal community was most diverse with 15 taxa present and understory seaweed FW (2.2 kg FW m^{-2}), ‘Other Phaeophyceae’ (1.2 kg FW m^{-2}) as well as Rhodophyta (0.9 kg FW m^{-2}) exhibited their maximum biomass. In contrast, the biomass peak of overall seaweed FW ($11.5 \text{ kg FW m}^{-2}$) and kelp FW ($11.3 \text{ kg FW m}^{-2}$) was at 2.5m. At 5 and 10m the kelp species *A. esculenta* (3.6 and 0.9 kg FW m^{-2} , respectively) showed the highest biomass of all seaweeds. Because of the high *A. esculenta* FW, kelps were responsible for 95 and 56% of the overall seaweed FW at 5 and 10m, respectively. At 15 m the ground was almost exclusively covered with Rhodophyta ($0.335 \text{ kg FW m}^{-2}$) and dominated by *Phycodrys rubens* ($0.317 \text{ kg FW m}^{-2}$), while *A. esculenta* ($0.0009 \text{ kg FW m}^{-2}$) was near to its lower distribution limit.

Seaweed biomass timeseries (1996/98-2012/13-2021):

Mean fresh weight (FW) was compared over three time points (1996/98, 2012/13 and 2021) and across the biomass dominant species and groups at relevant depth levels. Figure 3 illustrates the change in FW over time and statistical results of separate two-factorial ANOVAs for the factors time, depth and their interaction on FW are given in Table 1.

Overall seaweed biomass along the depth transect (0 – 15m) exhibited a significant interaction of time x depth ($p = 0.006$). When comparing 2021 data to earlier time points, the seaweed FW maximum at 2.5m was similar to 2012/13 ($14.5 \text{ kg FW m}^{-2}$). In contrast, in 1996/98 the seaweed FW maximum was approx. 50% lower and at 5m (6.7 kg FW m^{-2}), explaining the interaction between time and depth over the three time points. The general pattern of seaweed FW distribution along the depth gradient was the same between 2012/13 and 2021 but very different compared to 1996/98. Additionally, seaweed FW significantly differed along the depth gradient ($p < 0.0001$) as time integrated seaweed FW increased 3.4 fold from 0m to the

maximum at 2.5m (10.3 kg FW m⁻²) and then decreased to 52% (5m), 80% (10m) and 94% (15m) of the maximum, respectively ((2.5 = 5) > (5 = 0) > (0 = 10) > (10 = 15), $p < 0.02$, Tukey test).

As kelp FW (0 - 10m) constituted most of the overall seaweed FW, it showed similar responses and exhibited a significant interaction of time x depth ($p = 0.003$). Between 1996/98 and 2021 kelp FW at 2.5m increased significantly by 6.7 fold from 1.7 to 11.4 kg FW m⁻² ($p = 0.03$, Tukey test). Consequently, the increase and upward shift in kelp FW maximum from 5 to 2.5m, which had already been observed between 1996/98 and 2012/13, remained the same in 2021. This relation is also reflected in significant differences along the depth gradient ($p < 0.0001$) as time integrated kelp FW was 9 and 4 fold higher at 2.5m (9.6 kg FW m⁻²) and 5m (4.2 kg FW m⁻²) than at 0m and 10m (both depths 1.1 kg FW m⁻²), respectively ((2.5m = 5m) > (10m = 0m), $p < 0.007$, Tukey test). In contrast to overall seaweed FW, kelp FW was also affected by the factor time ($p < 0.021$). Depth integrated kelp FW in 2021 (4.4 kg FW m⁻²) was double compared to 1996/98 (2.2 kg FW m⁻²) and slightly lower than in 2012/13 (5.5 kg FW m⁻²) but only the change between the 1st and 2nd study was significant ((2012/13 = 2021) > (2021 = 1996/98), $p = 0.04$, Tukey test).

Same as overall kelp FW, FW of the kelp species *Alaria esculenta* (2.5 – 10m) changed significantly over time ($p = 0.018$) and increased continuously from 0.5 kg FW m⁻² in 1996/98 over 1.2 kg FW m⁻² in 2012/13 to 3.1 kg FW m⁻² in 2021 ((2021 = 2012/13) > (2012/13 = 1996/98), $p = 0.017$, Tukey test).

Similar to *A. esculenta* FW, FW of ‘Digitate Kelps’ (2.5 – 5m) was affected by the factor time ($p = 0.02$), but Tukey Posthoc test did not reveal significant differences between years. Furthermore, ‘Digitate Kelps’ FW changed with depth ($p = 0.002$) and time integrated FW was significantly 4 fold higher at 2.5m (6 kg FW m⁻²) compared to 5m (1.5 kg FW m⁻²) ($p = 0.002$, Tukey test).

Interestingly FW of *Saccharina latissima* (0 - 10m) showed a different trend than *A. esculenta* and ‘Digitate Kelps’ as there was a significant interaction between time x depth ($p < 0.05$). In 1996/98 *S. latissima* FW along the depth transect continuously increased and peaked at 10m (1.2 kg FW m⁻²). This pattern changed in 2012/13 and 2021 as the maximum of *S. latissima* FW was 1.6 fold higher and recorded at 2.5m (both years 2 kg FW m⁻²). Although *S. latissima* FW also changed significantly with depth ($p = 0.04$), these differences were not resolved via Tukey Posthoc test.

Understory seaweeds FW (0 – 15m) differed along the depth gradient ($p = 0.005$) as time integrated understory FW at 0m (1.9 kg FW m⁻²) was significantly 2.6 – 3.5 fold higher compared to 2.5m, 5m and 15m depth (0.7, 0.7 and 0.5 kg FW m⁻², respectively) ((0m = 10m) > (10m = 15m = 2.5m = 5m), $p < 0.03$, Tukey test).

The group ‘Other Phaeophyceae’ (0 – 15 m), which excludes adult kelps, exhibited similar trends as understory seaweeds. There was an effect of depth ($p = 0.01$) as time integrated FW of ‘Other Phaeophyceae’ was significantly 2.6 – 12.8 fold higher at 0m (1.2 kg FW m⁻²) than at 5m, 10m or 15m depth (0.45, 0.4 and 0.1 kg FW m⁻², respectively) ((0m = 2.5m) > (2.5m = 10m = 5m = 15m), $p < 0.05$, Tukey test).

In contrast to ‘Other Phaeophyceae’, the FW of Rhodophyta (0 – 15 m) showed a significant interaction of time x depth ($p = 0.002$). While there were no biomass dominant Rhodophyta at 0m in 1996/98 (Fig. 1), the FW at this depth significantly increased to 0.95 and 0.93 kg FW m⁻², respectively in 2012/13 and 2021 ($p = 0.04$, Tukey test). Furthermore, the change in biomass distribution pattern over time is reflected at 2.5m and 5m where Rhodophyta FW was up to 93.5 fold higher in 1996/98 (0.37 and 0.40 kg FW m⁻²) compared to 2012/13 (0.006 and 0.03 kg FW m⁻²) or 2021 (0.004 and 0.07 kg FW m⁻²). Additionally, there was a significant effect of depth ($p < 0.0001$) as time integrated Rhodophyta FW decreased sharply from 0m (0.7 kg FW m⁻²) to 2.5m and 5m (both 0.1 kg FW m⁻²) followed by an increase at 10m and 15m (both 0.5 kg FW m⁻²) ((0m = 10m = 15m) > (5m = 2.5m), $p < 0.03$, Tukey test).

Chlorophyta were only rarely recorded along the depth transect (1996/98: 2.5m, 5m; 2012/13: 0m; 2021: 0m, 2.5m) and were therefore excluded from the statistical analysis.

Leaf area index (LAI)

Seaweed LAI along the depth gradient in 2021:

The LAI of biomass dominant species and groups in 2021 largely reflected their recorded fresh weight and was different between species, groups and depth levels along the investigated transect (Appendix 5). All seaweed LAI reached its maximum at 2.5m (LAI=8.6) as this depth and 5m (LAI=4) were nearly exclusively inhabited by kelps (both depths 99%). In 2021 *A. esculenta* (LAI=5) had the highest LAI of all seaweed species at 2.5m, followed by ‘Digitate Kelps’ (LAI=2.8) and *S. latissima* (LAI=0.8). At 5m *A. esculenta* reached with 3.2 the highest LAI of all seaweeds, while the LAI of ‘Digitate Kelps’ (LAI=0.3) and *S. latissima* (LAI=0.27) severely declined. The maximum LAI of understory seaweeds in 2021 was recorded at 10m with a LAI of 1.6. At 15m, Rhodophyta (LAI=0.8) were the most prominent group contributing 99% to the all seaweed LAI.

Seaweed LAI comparison between 2012 and 2021:

The LAI was compared between 2012 and 2021 and across the species and groups at relevant depth levels. Figure 4 illustrates the change in mean LAI between the two years and statistical results of the separate two-factorial ANOVAs are given in Table 2. Overall there was no significant interactive effect of time x depth in any of the investigated species or groups and the factor time was only significant for ‘Digitate Kelps’. However, all species and groups exhibited significant differences between depth levels except for *Saccharina latissima* (2.5 – 5m) and ‘Other Phaephyceae’(5 - 15m). Detailed LAI data of species and groups in 2012 and 2021 are given in Appendix 5. Data from 2012 were sampled in 0.25m² frames and extrapolated to 1m².

Overall seaweed LAI (2.5 – 15m) changed significantly along the depth gradient ($p < 0.0001$) and time integrated overall seaweed LAI was maximal at 2.5m (LAI=9) followed by a gradual decrease of 60%, 82% and 85% at 5m (LAI=3.6), 10m (LAI=1.6) and 15m (LAI=1.4), respectively (2.5m > (5m = 10m = 15m), $p < 0.002$, Tukey test).

Similar to the LAI of all seaweeds, LAI of all kelps (2.5 – 5m) exhibited a significant change with depth ($p = 0.009$) and the time integrated maximal kelp LAI of 9 at 2.5m and was significantly 2.6 fold higher compared to 5m (LAI=3.4) ($p = 0.009$, Tukey test).

Interestingly, LAI of ‘Digitate Kelps’ (2.5 – 5m) was the only group which changed significantly over time ($p = 0.018$) as well as with depth ($p = 0.004$). Depth integrated LAI of ‘Digitate Kelps’ was significantly 3.4 fold higher in 2012 (LAI=5.3) compared to 2021 (LAI=1.6) ($p = 0.018$, Tukey test). Time integrated ‘Digitate Kelps’ LAI was significantly 84% lower at 5m (LAI=0.9) compared to 2.5m (LAI=5.9) ($p < 0.004$, Tukey test).

Understory seaweed LAI (5 – 15m) changed significantly along the depth transect ($p = 0.046$), although Tukey test did not reveal significant differences between depth levels.

As Rhodophyta (5 - 15m) contributed most to the understory LAI, this group exhibited similar responses and changed significantly with depth ($p = 0.025$). Time integrated Rhodophyta LAI had its maximum at 15m (LAI=1.3) which was 1.2 fold higher than at 10m (LAI=1.1) and significantly 14.7 fold higher compared to 5m (LAI=0.9) ((15m = 10m) > (10m = 5m), $p = 0.03$, Tukey test).

Lower depth distribution of kelp and kelp-like species over time

A comparison of semi-quantitative data on lower depth distribution and abundances of biomass dominant brown algae species over time is illustrated in Figure 5. An overall upward shift in lower depth distribution limit and a noticeable decrease in species abundance since 1996/98 is evident for all investigated species (*A. esculenta*, ‘Digitate Kelps’, *S. latissima*, *Saccorhiza dermatodea*, *Desmarestia* spp.). This change is especially prominent in ‘Digitate Kelps’ and *S. latissima*. The lower distribution limit of ‘Digitate Kelps’ decreased severely by 10m over time from 15m in 1996/98 over 10m in 2014 to 5m in 2021. Similarly, the recorded depth for lowest occurring *S. latissima* specimens decreased by 7m over time from 16m (1996/98) over 14m (2014) to 9m (2021). For both taxa the shift in abundance which was already observed between the 1st and 2nd study continued in 2021 and these species were not classified as dominant or sub-dominant any more.

In contrast to the other two kelp species, the lower depth distribution limit of *A. esculenta* remained relatively unchanged and varied between 15m (1996/98), 18m (2014) and 13m (2021). However, also *A. esculenta* abundance decreased throughout the investigated time points as the species was sub-dominant at 12m in 1996/98 while this abundance class moved upwards to 8m and 9m in 2014 and 2021, respectively.

Similar to *A. esculenta*, the lowest distribution limits of *Saccorhiza dermatodea* and *Desmarestia* spp. only changed slightly over time. However, despite their stability in depth distribution, these species exhibited a decrease in abundance, which was especially strong in *Desmarestia* spp. While *Desmarestia* spp. had been mostly dominant to sub-dominant in 1996/98 between 20m and 9m, these abundance classes were not recorded at any depth level in 2021.

Age structure and density of kelp species

Age structure and density of the kelp community was investigated along the Hansneset depth gradient (2.5 – 10m) in summer 2013 and 2021 as a proxy for the stability of the environment. The observed pattern of relative age class distribution of all kelps, *A. esculenta*, ‘Digitate Kelps’ and *S. latissima* changed considerably between the two time periods. Data from 2021 are illustrated in Figure 6 and detailed age and density information is given in Appendix 6. As the investigation of other parameters already revealed changes across depth levels, the statistical analysis of mean age (years m^{-2}) and density (ind. m^{-2}) focused on adult ([?] 1 year) kelps and differences between species and time points (Table 3, Figure 7). Detailed data from 2013 were published as Supplement Table S3 in Bartsch et al. (2016).

Relative age class distribution in 2021:

The relative abundance of adult kelps ([?] 1 year) peaked at 2.5m in *A. esculenta*, ‘Digitate Kelps’, *S. latissima* and the overarching group ‘All Kelps’. Furthermore, 2.5m was the only depth with a balanced age structure in 2021. At 5m the relative abundance of juveniles sharply increased to [?] 95% in all three kelp species and the overall kelp density reached its maximum with 690 ind. m^{-2} . This pattern became even more pronounced at 10m where 100% of all ‘Digitate Kelps’ and *S. latissima* individuals were juveniles and *A. esculenta* was the only kelp species for which a few old individuals (5% 4-9years) were present. Compared to the density peak at 5m, the species-specific densities at 10m decreased to mean densities similar to 2.5m but mostly composed of juveniles. Of

Age and density per m^2 of adult kelps between 2013 and 2021:

The age of adult kelps [?]1 year at 2.5m and 5m was significantly different between the three kelp species ($p = 0.004$ and $p = 0.02$, Table 3). At 2.5m the time integrated age of *A. esculenta* (4.2 years m^{-2}) was 1.5 fold higher compared to *S. latissima* and ‘Digitate Kelps’ (both 2.7 years m^{-2}) ($A. esculenta > (S. latissima = \text{‘Digitate Kelps’})$, $p [?] 0.01$, Tukey test). The species-specific age differences became even more pronounced at 5m as the time integrated age of *A. esculenta* remained at 4.2 years m^{-2} and was thereby double of *S. latissima* (2.1 years m^{-2}) and 2.5 fold higher compared to ‘Digitate Kelps’ (1.7 years m^{-2}) ($A. esculenta > (S. latissima = \text{‘Digitate Kelps’})$, $p [?] 0.05$, Tukey test). The age of adult kelps at both depths was not significantly affected by the factor time or the interaction of time x species (Table 3).

Similarly, the density of adult kelps at 2.5m and 5m did not change significantly over time, across species and there was no interactive effect of time x species. An interesting exception is the overall density of adult kelps per m^{-2} at 5m which exhibited differences between years ($p = 0.007$) as species integrated density was significantly 2.5 fold higher in 2013 (17.1 ind. m^{-2}) compared to 2021 (6.8 ind. m^{-2}).

Kelp holdfast, stipe and blade dry weight in 2021

Holdfast, stipe and blade DW, and blade:stipe DW ratio of all adult kelps ([?] 2 years) collected in 2021 was compared between *A. esculenta*, ‘Digitate Kelps’ and *S. latissima* from 2.5m and 5m depth. Figure 8 illustrates the differences between species at 2.5m and 5m. Statistical results of non-parametric Kruskal-Wallis tests for the factors species and depth are given in Table 4.

Holdfast DW of adult kelp individuals [?]2years at 2.5 and 5m depth varied significantly between species ($p < 0.05$) as integrated holdfast DW in ‘Digitate Kelps’ (1.9 ± 1.8 g DW) was 1.2 – 1.6 fold higher than in *S. latissima* (1.6 ± 1.2 g DW) and *A. esculenta* (1.2 ± 1.1 g DW), respectively. Nonetheless, the Wilcoxon test did not reveal significant differences in holdfast DW between species.

Interestingly, stipe DW of adult kelps also varied significantly across kelp species ($p < 0.001$) but, in contrast to holdfast DW, depth integrated stipe DW was highest in *S. latissima* (9.9 ± 4.5 g DW) and *A. esculenta* (9.7 ± 7.2 g DW) while it was significantly lower in ‘Digitate Kelps’ (6.2 ± 6.7 g DW) ($(S. latissima = A. esculenta) > \text{‘Digitate Kelps’}$, $p < 0.002$, Wilcoxon test) (all: mean $\pm$ SD).

Blade DW did neither exhibit significant differences between kelp species ($p = 0.2$) nor across depth levels ($p = 0.7$).

Similar to the stipe DW, the blade:stipe DW ratio of adult kelps was different between species ($p = 0.002$) and changed with depth ($p < 0.001$). In contrast to the other parameters, depth integrated blade:stipe DW ratio in ‘Digitate Kelps’ (4.1 ± 2.8) was significantly 2.1-2.4 fold higher than in *A. esculenta* (2 ± 2.6) and *S. latissima* (1.7 ± 1.4), respectively ($\text{‘Digitate Kelps’} > (S. latissima = A. esculenta)$, $p < 0.001$, Wilcoxon test). Species integrated blade:stipe DW ratio was 2.6 ± 2.2 at 2.5m and 2.7 ± 3.9 at 5m ($p = 0.002$, Wilcoxon test) (all: mean $\pm$ SD).

Kelp blade carbon and nitrogen in 2021

For a random subsample of adult kelps ([?] 2 years) that were investigated for dry weight, additionally the blade %carbon, %nitrogen and C:N ratio was compared across the three kelps and at the depth levels 2.5m and 5m (Table 5, Figure 9). Detailed data for *A. esculenta*, *S. latissima* and ‘Digitate Kelps’ are provided in Appendix 7. Additionally, blade carbon and blade nitrogen DW per m^2 is presented in Figure 10.

Overall, the three parameters %carbon, %nitrogen and C:N ratio in the blades of adult kelp individuals [?]2 years (2.5 – 5m) varied significantly between kelp species (Table 5). However, the factor depth did not exhibit a significant effect on any of the investigated parameters.

Relative carbon content was highest in *A. esculenta* (34 ± 5 %carbon), followed by *S. latissima* (32 ± 5 %carbon) which was itself significantly 1.2 fold higher compared to ‘Digitate Kelps’ (28 ± 5 %carbon) ($A. esculenta > S. latissima > \text{‘Digitate Kelps’}$, $p < 0.03$, Wilcoxon test).

In contrast, relative blade nitrogen in *A. esculenta* (2 ± 0.9 %nitrogen) and ‘Digitate Kelps’ (1.8 ± 0.5 %nitrogen) was similar and significantly 1.4-1.3 fold higher than in *S. latissima* (1.4 ± 0.8 %nitrogen) ($(A. esculenta = \text{‘Digitate Kelps’}) > S. latissima$, $p < 0.02$, Wilcoxon test).

Interestingly, depth integrated C:N ratio in *S. latissima* was 26.5 and thereby significantly 1.3 fold higher compared to *A. esculenta* (19.8) and 1.5 fold higher than in ‘Digitate Kelps’ (17.3) ($S. latissima > (A. esculenta = \text{‘Digitate Kelps’})$, $p < 0.03$, Wilcoxon test) (all: mean $\pm$ SD).

In contrast to the carbon and nitrogen parameters measured per kelp individual, blade carbon and nitrogen per m^2 (2.5 – 5m) were not different between species or depth levels and there was no interactive effect of species x depth (Figure 10). Even though statistical tests did not reveal significant differences, depth integrated blade carbon was highest in blades of *A. esculenta* (82.6 ± 78.1 g C m^{-2}) followed by ‘Digitate Kelps’ (69.3 ± 144.3 g C m^{-2}) and was lowest in *S. latissima* (28.1 ± 28.2 g C m^{-2}). Interestingly, depth integrated blade nitrogen was highest in ‘Digitate Kelps’ (5.1 ± 10.8 g N m^{-2}) and *A. esculenta* (5 ± 5.1 g N m^{-2}) which was 4 fold higher compared to *S. latissima* (1.2 ± 1.1 g N m^{-2}). Overall the blades of adult kelps ([?] 2 years) of the local kelp forest stored 277 ± 123 g C m^{-2} and 18 ± 9 g N m^{-2} at 2.5m in contrast to only 83 ± 34 g C m^{-2} and 4 ± 2 g N m^{-2} at 5m (all: mean $\pm$ SD).

PAR and Turbidity

In situ data from the AWIPEV-COSYNA underwater observatory close to the estuary of the Bayelva river were analyzed over time and used as a proxy for the development of the underwater light conditions in

Kongsfjorden. Residual calculations used for the statistical analysis of changes over time are shown in Figure 11 and associated absolute values are presented in Appendix 8.

Turbidity significantly ($p < 0.001$) increased over time with an average numerical increase of 0.104 FTU units per year (slope per week = 0.002 FTU * average numbers of weeks per year = 52). Even more prominent as the absolute average increase in turbidity per year, however, was the change in the extreme values of turbidity. Starting in 2016, the positive residuals in turbidity significantly increased until 2020 with maximal values in 2019 of up to 70 FTU. In 2021, lower values, similar to the pre-2016 phase were observed. Contrary to the turbidity, the average PAR values per week significantly decreased over time ($p < 0.01$) from 2017 to 2021 with a numerical value of $-0.29 \mu\text{mol m}^{-2} \text{s}^{-1}$ per year. Similar to turbidity, not only the absolute numerical PAR values per week changed but also the seasonal character of the phases with lower photon fluence rates seemed to change. This became especially prominent in 2020 when PAR values lower than the expected mean were measured over the entire year.

4. Discussion

The present investigation indicates that Arctic kelp species are differently affected by the strong changes in environmental conditions that are prevailing along Svalbard's coasts. Within the relatively short time period of 25 years, a community which used to be dominated by 'Digitate Kelps' transformed to an *Alaria esculenta* dominated kelp forest. This change was reflected in high biomasses, leaf area indices and adult densities of *A. esculenta* at 5m and 10m, depth levels from which the other two kelp species, *Saccharina latissima* and 'Digitate Kelps', retreated over time. However, our time series also showed that all investigated kelp and kelp-like species, including *A. esculenta*, decreased their depth distribution and abundance along the depth gradient throughout the years. Additionally, the biomass maximum and the whole kelp forest progressively shifted upwards to the uppermost depth level at 2.5m. This remained the only habitat in which all three prevailing kelp species still had a balanced age structure between juveniles and adults of different age classes characterizing a mature kelp forest while this relationship decreased with depth.

Svalbard experiences considerable impacts of global warming and Kongsfjorden is an Arctic fjord with numerous glaciers in transition (Bischof et al., 2019b). In July and August 1997 temperatures varied around 4°C at Hansneset in the water column down to 20m (Hanelt et al., 2001). In contrast, between 2016 and 2021 the monthly median ocean temperature at 11m depth was 6.1°C in August at Ny Ålesund on the southern coast of Kongsfjorden (Gattuso et al., 2023). At the same site the average water temperature in the surface layer (upper 10m) even reached a maximum of 8.4°C in summer 2020 (<https://dashboard.awi.de/?dashboard=2847>). Over the past decades warming air and water temperatures led to a severe decline of the seasonal sea ice extent and thickness so that in recent winters only the northern part of the inner bay was covered by thin sea ice (Pavlova et al., 2019; Payne & Roesler, 2019; Maturilli et al., 2019). This elongation of the open water period leads to an extension of the vegetation period which theoretically promotes kelp forest depth extension as long as it is accompanied by improved water transparency (Castro de la Guardia et al., 2023). However, our results indicate that this potentially positive effect of less ice scouring and reduced sea ice cover for kelp communities gets overshadowed by the counteracting effects of sediment plumes occurring as a consequence of increasing glacial melt (Niedzwiedz & Bischof, 2023; Payne & Roesler, 2019). Geyman et al. (2022) showed that glaciers on Svalbard (including Kongsfjorden area), retreated substantially over time as a response to warming summer temperatures. The increasing subglacial meltwater discharge of sea-terminating glaciers is suspected to be the main source of the increasing sedimentation in Kongsfjorden (Svendsen et al., 2002). With their long-term analysis of satellite images Konik et al. (2021) revealed that Kongsfjorden experiences the phenomenon of "coastal darkening" as water transparency considerably decreased between 1997-2019. We were able to confirm this trend with in situ measurements from the AWIPEV-COSYNA underwater observatory and provide evidence that the turbidity of the water column has increased over time at this coastal site while light availability for macroalgal photosynthesis decreased. The observed lower turbidity values in 2021 may have occurred due to the comparatively colder spring and summer temperatures in the marine Kongsfjorden ecosystem (<https://dashboard.awi.de/?dashboard=2847>). However, the location of our sensors at the outflow of the Bayelva river is not geographically close to our study site Hansneset and can

therefore only serve as a proxy for the general trend of decreasing light levels with increasing glacial melt throughout Kongsfjorden.

Experimental studies have shown that most kelp species present in Kongsfjorden are capable of coping with increasing water temperatures if they do not surpass 10°C (Diehl & Bischof, 2021; Franke et al., 2021; Tom Dieck, 1993). Thus, the observed increase in summer seawater temperatures (Payne & Roesler, 2019) seemingly do not directly account for the observed changes in kelp structure. However, laboratory studies with early life stages by Zacher et al. (2019) indicated a potential competitive advantage of *A. esculenta* over *L. digitata* under future Arctic warming. *A. esculenta* outcompeted *L. digitata* due to higher growth rates when the two species were co-cultivated at ambient (5°C) and elevated (9-10°C) summer temperatures but not at 15°C where *A. esculenta* gets close to its upper temperature limit (Zacher et al., 2019). The assumed North Pacific origin of the brown algae order Laminariales together with their relatively recent introduction to the Arctic after the last glaciation might be the reason for the generally high temperature tolerances in Arctic kelps (Lüning 1990; Tom Dieck 1993; Adey et al., 2008).

A decreasing annual light budget and the direct and indirect effects of sedimentation are most likely the main abiotic factors causing the observed changes in community dynamics and upwards shift of the kelp forest (Fragkopoulou et al., 2022; Smith et al., 2022). Ecophysiological studies showed that an increase in turbidity and sedimentation can have negative effects on photosynthetic rates of adult kelps (Roleda et al., 2008), germination capacity of spores as well as recruitment success of juvenile kelps (Roleda, 2016; Zacher et al., 2016) and thus on the overall productivity of Arctic kelps. *A. esculenta* spore germination and sporophyte recruitment thereby were less susceptible to sediment loading than *L. digitata* and *S. latissima* (Zacher et al., 2016). Similarly, Niedzwiedz & Bischof (2023) reported that under the current abiotic conditions in Kongsfjorden, with low underwater light availability and enhanced temperatures, *A. esculenta* is in advantage. In contrast to *S. latissima*, *A. esculenta* exhibited low compensation irradiance together with low dark respiration rates and a high carbon content independent of temperature treatments (3°C and 7°C), which support our in situ data (Niedzwiedz & Bischof, 2023). Even though experiments by Diehl & Bischof (2021) suggested that *S. latissima* is especially able to acclimate to an increase in temperature and nutrients as well as a decrease in salinity caused by Arctic glacial melt water, this did not seem to be a competitive factor shaping the current kelp forest at our study site.

Between 1996 and 1998, Hop et al. (2016) extensively investigated the macroalgal distribution at five sites along the axis of Kongsfjorden by combining quantitative destructive samplings with video transects. The authors report that the gradient in abiotic environmental conditions was reflected in highest macroalgal biomass at the outer fjord locations Kapp Mitra and Kapp Guisnez while deepest macroalgal coverage was recorded in the inner fjord at Hansneset (Hop et al., 2016). Since than other studies on macroalgal communities in Kongsfjorden were mostly qualitative, except for Bartsch et al. (2016). According to the hydroacoustic mapping study from 2007, Kruss et al. (2017) showed that the coastline along the southern shore of Kongsfjorden was nearly exclusively covered with large macroalgae until 15m water depth, while further down to 30m macroalgal cover became much less. A video survey performed in summer 2009 (Schimani et al., 2022) also indicated dense kelp forests in the center of Kongsfjorden, including Hansneset, down to 30m. The latter authors assumed that kelp distribution along the fjord axis is controlled by the exposure to glacial melt and available hard substrata (Schimani et al., 2022).

Kelp forests were also investigated in other Svalbard fjords and macroalgal communities showed to be individually shaped by site specific physio-chemical conditions. A hydroacoustic investigation supported by underwater videos compared Isfjorden on the warm west coast of Svalbard and Storfjorden on the colder east coast (Wiktor et al., 2022). Macroalgal communities in both fjords were similar but macroalgal bottom coverage in water depths above 6m was considerably less in Storfjorden than in Isfjorden, assumingly due to higher ice scouring pressure in the colder Arctic fjord (Wiktor Jr et al., 2022). The observed pattern in Storfjorden may be similar to the Hansneset kelp forest from 1996/98 (Hop et al., 2012), whereas the current state (this study) might correspond more to reports from the warmer Isfjorden, also opening to the west coast, with highest macroalgal coverage at shallow water depths. In 2021 the variation between the single

collected replicates from 5m and below was small, indicating a homogenous and undisturbed macroalgal community. In contrast, at 2.5m the samples were largely different, as one replicate was dominated by *A. esculenta*, one by ‘Digitate Kelps’ and the third was mixed but contained fewer adult kelps. This heterogeneity of replicates in the shallow subtidal indicates a heterogenous community exposed to ice scouring. Overall, the observed increase in macroalgal biomass at 0m and 2.5m between 1996/98 and 2012/13 as well as the present investigation provides additional evidence that the reduction of ice scouring pressure continued in 2021 (Bartsch et al., 2016; Hop et al., 2012).

In Hornsund, at the southern tip of Svalbard, kelp forest communities along the fjord axis reflect a strong gradient in abiotic conditions with varying distance to the glacier front (Ronowicz et al., 2020). Compared to Hansneset, total kelp biomass at the Hornsund sites were much lower at 5m and similar at 10m, except for the glacier free site where kelp biomass interestingly increased with depth (Ronowicz et al., 2020). In contrast to our study, ‘Digitate Kelps’ and *S. latissima* were prominent in the glacially exposed kelp forests of Hornsund whereas *A. esculenta* was only present at a site characterized by high water transparency (Ronowicz et al., 2020). Along the coastline of the Eastern Canadian Arctic Filbee-Dexter et al. (2022) reported a positive correlation between the elongation of the open water period and kelp biomass. In contrast to the biomass distribution along the depth transect at Hansneset the latter authors observed an increase in kelp biomass with depth from 5m to 15m across their 55 sites indicating that the influence of ice scouring at lower depths was much more pronounced than in Kongsfjorden. However, our findings of decreasing kelp biomass along the depth gradient were congruent to Smith et al. (2022) who reported a similar pattern for *Laminaria hyperborea* kelp forests in the U.K. which was strongly shaped by decreasing underwater light availability.

The Arctic kelps investigated in our study possess a differential strategy in biomass accretion and thereby carbon allocation to perennial structures of holdfast and stipe and annual formation of blades. While adult ‘Digitate Kelps’ invested most biomass in their holdfast and blades, *S. latissima* and *A. esculenta* individuals expressed highest stipe biomasses. These ecological differences between the three prevailing kelp species have diverse consequences. When abundance and dominance relationships of macroalgal species at Hansneset change over time, the 3D structure of the kelp forest and therefore the habitat conditions for associated species shift accordingly. Epifaunal biodiversity is highest in kelp holdfasts compared to blades and lowest on stipes, but even though species richness is consistent between ‘Digitate Kelps’, *S. latissima* and *A. esculenta* the most commonly associated species vary in a kelp specific manner (Włodarska-Kowalczyk et al., 2009). Consequently, the continuous alteration in biotic and abiotic factors at our study site has indeed already influenced the fauna inhabiting the kelp forest as species abundances, taxonomic composition as well as biomass distribution varied over time (Paar et al., 2016; Niklass, 2022). Paar et al. (2016) showed that the biomass and secondary production of associated macrozoobenthos is strongly associated with macroalgal depth distribution as both parameters were highest in the upper most sublittoral in 2012/13, which represented an inverted pattern compared to 1996/98. At greater depths, where dominant kelps are absent, other macroalgae species like *Desmarestia aculeata*, *Ptilota* spp. and *Phycodrys rubens* also strongly promote epifaunal communities (Lippert et al., 2001; Włodarska-Kowalczyk et al., 2009), indicating their often overlooked important role for Arctic benthic ecosystems. Furthermore, higher trophic levels like fish are influenced by the structure and bottom coverage of habitat forming macroalgae (Brand & Fischer, 2016).

The Arctic flora is characterized by only a small amount of endemic Arctic species compared to those with a wider cold-temperate to Arctic distribution. Wilce (2016) identified only 21 of 161 macroalgal species to be Arctic endemics. In Kongsfjorden, this relation is even smaller as has been outlined by Hop et al. (2012) who noticed that one half of the macroalgal species encountered were truly Arctic to cold-temperate while the other half had even wider distribution ranges and there were only four Arctic endemic species including the kelp *Laminaria solidungula*. Especially this kelp may be negatively impacted by warming waters (Tom Dieck, 1992; Roleda, 2016). We observed that this rare species which had only been present with very small individuals at Hansneset (Bartsch et al., 2016; Hop et al., 2012) was not encountered anymore in our quantitative 2021 samples. However, in other Svalbard fjords *L. solidungula* is still present (Ronowicz et al., 2020; Wiktor Jr et al., 2022). In future, macroalgal species distribution ranges are predicted to shift northwards with an increasing number of Atlantic species potentially spreading into the warming Arctic

while Arctic species retreat (Fredriksen et al., 2019; Krause-Jensen & Duarte, 2014; Kortsch et al., 2012; Weslawski et al., 2010).

Kelp forests contribute strongly to the net primary production and the coastal carbon cycle as carbon is fixed in their biomass through photosynthesis (Krause-Jensen & Duarte, 2016; Pessarrodona et al., 2022; Smale et al., 2022). Pessarrodona et al. (2022) highlighted their ecological importance by stating that the global net primary production of subtidal seaweed forests even exceeds coastal phytoplankton productivity. Smale et al. (2016) reported a wide average carbon standing stock of 721 g C m^{-2} at 5m for *Laminaria hyperborea* kelp forests along the coast of the U.K. Their conversion of biomass to carbon stock was based on the assumption that carbon content makes up $\sim 30\%$ of kelp DW which included also the holdfast and stipe DW (Smale et al., 2016). In contrast, we investigated blade carbon content (Figure 10) and showed that the carbon content differs in a kelp species specific manner (*A. esculenta* 34%, ‘Digitate Kelps’ 27%, *S. latissima* 32%). When applying the same calculation as Smale et al. (2016) to the overall kelp DW collected at Hansneset (Appendix 4) we estimated 489.6 g C m^{-2} at 2.5m and 190.2 g C m^{-2} at 5m. Both values are lower compared to the average of the U.K. kelp forests (Smale et al., 2016). But most importantly our study showed that carbon and nitrogen allocation strategies significantly vary between kelp species as has already recently been shown for *Alaria marginata* and *S. latissima* from Alaska (Umanzor & Stephens, 2022) and cold-temperate kelp species (Gilson et al., 2021). Consequently, the contributions of each kelp species to the overall carbon standing stock in kelp forests can vary according to the relative carbon content in biomass. In this respect the observed change from a ‘Digitate Kelps’ forest into an *A. esculenta* kelp forest reveals a higher potential for carbon allocation in *A. esculenta* blades compared to ‘Digitate Kelps’ blades. This may have even wider consequences for the whole carbon budget of the surrounding waters as there is a continuous release of dissolved organic carbon (DOC) from kelps into the surroundings (Weigel & Pfister, 2021) which may thereby have changed the DOC budget of Kongsfjorden within the last decade.

In Arctic fjords detached macroalgal detritus is transported to deeper locations where they may support secondary production or biological carbon sequestration (Cui et al., 2022; Schimani et al., 2022). Even though not significantly different, mean blade biomass of ‘Digitate Kelps’ (21.4 g DW) from Hansneset was nearly double compared to *A. esculenta* (12 g DW) in 2021 (Figure 8). Considering that kelp blades decay over the seasons and storm waves fragment or even detach the thalli (Krumhansl & Scheibling, 2012) it is likely that the change in species dominance leads to less carbon being exported for local carbon sequestration. Together with the kelp forest retreat at our study site, this might resemble the predicted decline in kelp forest contribution to marine carbon cycles under the negative impacts of increasing water turbidity (Blain et al., 2021). However, the potential contribution of kelp forests in general to natural carbon sequestration remains a controversially discussed topic in current research (Hurd et al., 2022; Krause-Jensen et al., 2022; Smale et al., 2022; Pedersen et al., 2020).

5. Conclusion

In this novel Arctic time series, we report considerable changes in kelp forest dynamics over the past 25 years in Kongsfjorden on Svalbard which are likely the result of global climate change. At our study site kelp demography, biomass and species dominance along the depth transect were influenced by the prevailing counteracting environmental drivers related to Arctic warming (Schlegel et al., 2023). In contrast to proposed assumptions (Assis et al., 2022; Krause-Jensen et al., 2012; Krause-Jensen & Duarte, 2014) we observed a decrease of depth expansion of the investigated kelp forest despite its release from ice scouring pressure and shading by thick sea ice coverage. The documented retreat of the kelp forest to the uppermost depth level reflects the decline of key engineer species exposed to coastal darkening with potentially large impacts on all associated higher trophic levels. As kelp communities represent complex marine ecosystems our investigation aims to serve as an example study that quantifies the negative consequences of increasing glacier loss (Geyman et al., 2022) to facilitate future predictions for wider stretches of Arctic coastline. We propose that in Arctic fjord systems influenced by strong melt water runoff, kelp forest communities will decline further as long as glaciers retreat and coastal darkening intensifies. The effects of the rapidly shrinking Arctic cryosphere on marine primary producers and their highly valuable ecosystem services are extensive and will continue in a

changing future Arctic.

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Tables

Table 1 Results of two-factorial ANOVA for the factors time, depth and their interaction on fresh weight of biomass-dominant species or groups in the relevant depth levels. 1996/1998: n = 2 (0 m); n = 3 (5 – 15 m); n = 4 (2.5 m); 2012/2013: n = 3 (0 and 15 m); n = 6 (2.5 – 10 m); 2021: all depths n = 3

Species/groups	Time	Time	Depth
All seaweeds (0 – 15 m) *	F _{2,39} = 1.457	ns	(F _{4,39} = 25.573) (F _{4,39} = 25.573) (p < 0. 001)

All kelps (0 – 10 m)	$F_{2,33} = 3.401$	$p = \mathbf{0.045}$	$F_{3,33} = 19.883$	$F_{3,33} = 19.883$	$p < \mathbf{0.001}$
<i>Alaria esculenta</i> (2.5 – 10 m)	$F_{2,28} = 4.585$	$p = \mathbf{0.019}$	$F_{2,28} = 1.281$	$F_{2,28} = 1.281$	ns
‘Digitate Kelps’ (2.5 – 5 m)	$F_{2,19} = 4.408$	$p = \mathbf{0.027}$	$F_{1,19} = 13.24$	$F_{1,19} = 13.24$	$p = \mathbf{0.002}$
<i>Saccharina latissima</i> (0 – 10 m)	$F_{2,33} = 0.509$	ns	$F_{3,33} = 3.118$	$F_{3,33} = 3.118$	$p = \mathbf{0.039}$
All understory seaweeds (0 – 15 m)	$F_{2,39} = 0.853$	ns	$F_{4,39} = 4.434$	$F_{4,39} = 4.434$	$p = \mathbf{0.005}$
‘Other Phaeophyceae’ (0 – 15 m)	$F_{2,39} = 0.873$	ns	$F_{4,39} = 3.879$	$F_{4,39} = 3.879$	$p = \mathbf{0.01}$
Rhodophyta (0 – 15 m) *	$F_{2,39} = 0.361$	ns	($F_{4,39} = 9.768$)	($F_{4,39} = 9.768$)	($p = < \mathbf{0.001}$)

ns not significant; in brackets: variances of residuals were still heterogeneous after transformation; * significant depth effect confirmed by nonparametric Kruskal-Wallis test ($p < 0.001$)

Table 2 Results of two-factorial ANOVAs for the factors time, depth and their interaction on the leaf area index (LAI) of biomass-dominant species groups at the relevant depth levels (2012 and 2021: n = 3).

Species/group	Time	Time	Depth	Depth		Time x depth	Time x depth	
All seaweeds (2.5 – 15 m)	$F_{1,16} = 0$	ns	$F_{3,16} = 17.005$	$p < \mathbf{0.001}$	$p < \mathbf{0.001}$	$F_{3,16} = 0.428$	ns	ns
All kelps (2.5 – 5 m)	$F_{1,8} = 0$	ns	$F_{1,8} = 11.587$	$p = \mathbf{0.009}$	$p = \mathbf{0.009}$	$F_{1,8} = 0.308$	ns	ns
<i>Alaria esculenta</i> (5 m)*	$F_{1,4} = 5.87$	ns						
‘Digitate Kelps’ (2.5 – 5 m)	$F_{1,8} = 8.723$	$p = \mathbf{0.018}$	$F_{1,8} = 15.809$	$p = \mathbf{0.004}$	$p = \mathbf{0.004}$	$F_{1,8} = 3.94$	ns	ns
<i>Saccharina latissima</i> (2.5 – 5 m)	$F_{1,8} = 0.501$	ns	$F_{1,8} = 0$	ns	ns	$F_{1,8} = 3.043$	ns	ns
All understory seaweeds (5 – 15 m)	$F_{1,12} = 0.194$	ns	$F_{2,12} = 4.023$	$p = \mathbf{0.046}$	$p = \mathbf{0.046}$	$F_{2,12} = 1.528$	ns	ns
‘Other Phaeophyceae’ (5 – 15 m)	$F_{1,12} = 0.208$	ns	$F_{2,12} = 1.505$	ns	ns	$F_{2,12} = 0.233$	ns	ns
Rhodophyta (5 – 15 m)	$F_{1,12} = 0.148$	ns	$F_{2,12} = 5.099$	$p = \mathbf{0.025}$	$p = \mathbf{0.025}$	$F_{2,12} = 1.716$	ns	ns

ns not significant, * in 2012 *Alaria esculenta* was only present at 5m depth in the small frame size, therefore a one-factorial ANOVA for the factor time was applied

Table 3 Results of two-factorial ANOVAs for the factors time, species and their interaction on the age and density per m⁻² of adult kelps ([?] 1 year) at 2.5m and 5m (2013 and 2021: n = 3).

Parameter	Depth	Time	Time	Species	Species	Time x species	Time x species
Age	2.5m	F _{1,12} = 4.377	ns	F _{2,12} = 8.983	p = 0.004	F _{2,12} = 0.080	ns
	5m	F _{1,12} = 0.222	ns	F _{2,12} = 5.968	p = 0.02	F _{2,12} = 0.038	ns
Density	2.5m	F _{1,12} = 1.061	ns	F _{2,12} = 2.857	ns	F _{2,12} = 1.162	ns
	5m	F _{1,12} = 10.411	p = 0.007	F _{2,12} = 1.155	ns	F _{2,12} = 3.145	ns

ns not significant

Table 4 Results of non-parametric Kruskal-Wallis test for the factors species and depth on the dry weight (DW) of all adult kelp individuals ([?] 2 years) from 2.5 and 5 m depth collected in summer 2021 at Hansneset, Kongsfjorden (Svalbard). *A. esculenta*: n = 75 (2.5 m); n = 43 (5 m); ‘Digitate Kelps’: n = 65 (2.5 m); n = 6 (5 m); *S. latissima* : n = 29 (2.5 m); n = 4 (5 m)

Parameter	Depth			Species		
Holdfast DW	X ² = 0.365	dF = 1	ns	X ² = 6.142	dF = 2	p < 0.05
Stipe DW	X ² = 2.566	dF = 1	ns	X ² = 16.608	dF = 2	p < 0.001
Blade DW	X ² = 0.179	dF = 1	ns	X ² = 2.969	dF = 2	ns
Blade/Stipe ratio	X ² = 9.170	dF = 1	p = 0.002	X ² = 67.011	dF = 2	p < 0.001

ns not significant

Table 5 Results of non-parametric Kruskal-Wallis test for the factors species and depth on blade CN parameters in a random subsample of adult kelp individuals ([?] 2 years) from 2.5 and 5 m depth collected in summer 2021 at Hansneset, Kongsfjorden (Svalbard). *A. esculenta*: n = 11 (2.5 m), n = 15 (5 m); ‘Digitate Kelps’: n = 15 (2.5 m), n = 10 (5 m); *S. latissima* : n = 15 (2.5 m), n = 7 (5 m).

Parameter	Depth			Species		
%carbon	X ² = 2.3538	dF = 1	ns	X ² = 24.556	dF = 2	p < 0.001
%nitrogen	X ² = 0.00374	dF = 1	ns	X ² = 11.189	dF = 2	p = 0.004
CN ratio	X ² = 0.059822	dF = 1	ns	X ² = 11.535	dF = 2	p = 0.003

ns not significant

Appendix

Appendix 1. Regression formulas for the calculation of the following relationships per kelp species (whole thallus) or per parts of them (blade / stipe / holdfast) for fresh weight (FW) : dry weight (DW), stipe length (SL) : age, DW : leaf area index (LAI), whole thallus fresh weight (WT FW) : DW.

Species	x	y	Formula	R ²	n
<i>‘Digitate Kelps’</i>					
Holdfast	FW	DW	y = 0.2021x - 0.035	0.9856	46
Stipe	FW	DW	y = 0.1177x - 0.0146	0.9954	46
	SL	Age	y = 1.0728x ^{0.3231}	0.8552	116
Blade	FW	DW	y = 0.1803x - 2.6118	0.9689	46

Species	x	y	Formula	R ²	n
Whole Thallus	DW	LAI	$y = 46.991x + 211.6$	0.9278	46
	FW	DW	$y = 0.164x - 2.7325$	0.9842	46
<i>Alaria esculenta</i>					
Holdfast	FW	DW	$y = 0.1521x + 0.0382$	0.9745	41
Stipe	FW	DW	$y = 0.1137x + 0.4676$	0.9747	43
	WT FW	DW	$y = 0.0421x - 0.3275$	0.8056	42
	SL	Age	$y = 0.9277x^{0.3877}$	0.7037	142
Sporophyll	FW	DW	$y = 0.2126x + 0.5854$	0.8925	29
Blade	FW	DW	$y = 0.1452x - 0.2493$	0.9802	42
	WT FW	DW	$y = 0.0652x + 0.9214$	0.8871	41
	DW	LAI	$y = 120.79x + 313.89$	0.8893	42
Whole Thallus	FW	DW	$y = 0.1497x + 0.0431$	0.9672	42
<i>Saccharina latissima</i>					
Holdfast	FW	DW	$y = 0.2429x - 0.316$	0.9373	18
Stipe	FW	DW	$y = 0.0899x + 0.952$	0.9156	18
	WT FW	DW	$y = 0.0365x + 1.9363$	0.8235	18
	SL	Age	$y = 0.8107x^{0.3197}$	0.7725	42
Blade	FW	DW	$y = 0.1452x - 0.2746$	0.9556	18
	WT FW	DW	$y = 0.0847x - 2.7372$	0.8538	18
Whole Thallus	FW	DW	$y = 0.1255x + 0.0329$	0.9448	18

Appendix 2. Number of weeks with PAR and turbidity data available in each year obtained from the AWIPEV-COSYNA (Coastal Observing Systems of the Northern and Arctic Seas) underwater observatory off Ny Ålesund, Kongsfjorden. Only the summer period from week 8 (March) to week 44 (October) was considered.

	PAR	Turbidity
Year	n	n
2012		14
2013		24
2014		37
2015		20
2016	3	37
2017	37	31
2018	24	37
2019	37	34
2020	36	22
2021	37	37

Appendix 3. Mean rounded fresh weight (g m^{-2}) $\pm$ standard deviation of all seaweed species and summarized values of species groups at Hansneset, Kongsfjorden in summer 2021 ($n = 3$) at 0 m, 2.5 m, 5 m, 10 m and 15 m depth. Data from 0 m depth referred to 0.25 m^{-2} frames but have been normalized to 1 m^2 here.

Species	0 m	2.5 m	5 m	10 m	15 m
<i>All kelps</i>	911 ± 505	11363 ± 6194	4394 ± 2392	994 ± 123	0.9 ± 0.9
<i>Alaria esculenta</i>	122 ± 71	4828 ± 6192	3571 ± 2318	994 ± 123	0.9 ± 0.9
Digitate kelps	449 ± 234	4504 ± 6688	238 ± 222	0	0
<i>Saccharina latissima</i>	341 ± 587	2031 ± 1562	586 ± 508	0	0

<i>All other Phaeophyceae</i>	1191 ± 542	10 ± 18	149 ± 171	179 ± 248	3 ± 3
<i>Chordaria flagelliformis</i> and <i>Dictosiphon</i> sp.	164 ± 192	0	0	0	0
<i>Desmarestia aculeata</i>	0	0	92 ± 101	157 ± 249	2 ± 3
<i>Desmarestia viridis</i>	0	0	0	0.8 ± 1.4	0.6 ± 1
Ectocarpales	476 ± 351	0	0	0	0
<i>Fucus distichus</i>	549 ± 101	0	0	0	0
<i>Halosiphon tomentosus</i>	0	0.9 ± 1.6	37 ± 59	0.2 ± 0.4	0
<i>Saccorhiza dermatodea</i>	0	10 ± 17	16 ± 14	0	0
<i>Scytosiphon</i> sp.	1 ± 0.9	0	0	0	0
Young <i>Laminaria</i> spp.	0	0	4 ± 3	21 ± 6	0
<i>All Rhodophyta</i>	927 ± 462	4 ± 4	66 ± 59	589 ± 79	335 ± 69
<i>Devaleraea ramentacea</i>	810 ± 430	0	0	0	0
<i>Euthora cristata</i>	0	0	3 ± 3	4 ± 1	6 ± 0.1
<i>Palmaria palmata</i>	40 ± 40	0	0	0	0
<i>Phycodrys rubens</i>	0	0.2 ± 0.2	14 ± 11	446 ± 113	317 ± 51
<i>Ptilota</i> spp.	2 ± 3	4 ± 4	49 ± 47	140 ± 37	18 ± 24
<i>Rhodomela</i> sp.	76 ± 98	0	0	0	0
<i>All Chlorophyta</i>	52 ± 18	86 ± 149	0	0	0
<i>Acrosiphonia</i> sp. and <i>Spongomorpha</i> sp.	23 ± 22	86 ± 149	0	0	0
<i>Chaetomorpha melagonium</i>	0.6 ± 0.6	0	0	0	0
<i>Kornmannia leptoderma</i>	24 ± 34	0	0	0	0
<i>Ulva</i> sp.	4 ± 7	0	0	0	0
All understory seaweeds	2169 ± 1021	100 ± 171	215 ± 178	769 ± 273	338 ± 72
All seaweeds	3080 ± 1233	11463 ± 6247	4609 ± 2308	1763 ± 177	339 ± 71

Appendix 4. Mean rounded dry weight (g m^{-2}) ± standard deviation of all seaweed species and summarized values of species groups at Hansneset, Kongsfjorden in summer 2021 ($n = 3$) at 0 m, 2.5 m, 5 m, 10 m and 15 m depth. Data from 0 m depth referred to 0.25 m^{-2} frames but have been normalized to 1 m^2 here.

Species	0 m	2.5 m	5 m	10 m	15 m
<i>All kelps</i>	123 ± 58	1632 ± 849	634 ± 323	172 ± 18	0.2 ± 0.2
<i>Alaria esculenta</i>	19 ± 12	703 ± 871	532 ± 318	170 ± 18	0.2 ± 0.2
Digitate kelps	62 ± 29	674 ± 1021	32 ± 31	0	0
<i>Saccharina latissima</i>	42 ± 73	254 ± 184	71 ± 61	0	0
<i>All other Phaeophyceae</i>	189 ± 164	0.6 ± 1.1	17 ± 17	29 ± 47	0.4 ± 0.5
<i>Chordaria flagelliformis</i> and <i>Dictosiphon</i> sp.	30.2 ± 39.9	0	0	0	0
<i>Desmarestia aculeata</i>	0	0	13 ± 11	29 ± 47	0.4 ± 0.5
<i>Desmarestia viridis</i>	0	0	0	0.1 ± 0.2	0.1 ± 0.1
Ectocarpales	77 ± 76	0	0	0	0
<i>Fucus distichus</i>	82 ± 73	0	0	0	0
<i>Halosiphon tomentosus</i>	0	0.1 ± 0.1	3.2 ± 5	0.02 ± 0.03	0
<i>Saccorhiza dermatodea</i>	0	0.6 ± 1	1 ± 0.9	0	0
<i>Scytosiphon</i> sp.	0.05 ± 0.05	0	0	0	0
Young <i>Laminaria</i> spp.	0	0	0.3 ± 0.3	2.3 ± 0.4	0
<i>All Rhodophyta</i>	131 ± 129	0.9 ± 1	13 ± 11	115 ± 20	66 ± 14
<i>Devaleraea ramentacea</i>	113 ± 126	0	0	0	0
<i>Euthora cristata</i>	0	0	0.5 ± 0.5	0.5 ± 0.1	0.01 ± 0.01
<i>Palmaria palmata</i>	5.2 ± 7.9	0	0	0	0
<i>Phycodrys rubens</i>	0	0.1 ± 0.1	2.6 ± 2	90 ± 27	62 ± 10
<i>Ptilota</i> spp.	0.1 ± 0.1	0.8 ± 0.9	9.6 ± 9	25 ± 7	3.8 ± 4.9
<i>Rhodomela</i> sp.	12.8 ± 17.4	0	0	0	0

<i>All Chlorophyta</i>	9.3 ± 3.5	0.1 ± 0.2	0	0	0
<i>Acrosiphonia</i> sp. and <i>Spongomorpha</i> sp.	4.4 ± 4.1	0.1 ± 0.2	0	0	0
<i>Chaetomorpha melagonium</i>	0.2 ± 0.2	0	0	0	0
<i>Kornmannia leptoderma</i>	4.1 ± 6.6	0	0	0	0
<i>Ulva</i> sp.	0.6 ± 1.1	0	0	0	0
All understory seaweeds	330 ± 289	1.6 ± 2.2	29 ± 19	144 ± 48	66 ± 15
All seaweeds	452 ± 309	1633 ± 849	664 ± 309	316 ± 34	66 ± 15

Appendix 5. Mean rounded leaf area index ± standard deviation of all seaweed species and summarizing species groups at Hansneset, Kongsfjorden in summer 2012 and 2021 (n = 3) at 2.5 m, 5 m, 10 m and 15 m depth. Data from 2012 refer to 0.25 m² frames but have been normalized to 1 m² here.

Species	Year	2.5 m	5 m	10 m	15 m
<i>All kelps</i>	2012 2021	9.5 ± 0.3 8.6 ± 5	3 ± 2 4 ± 2	0 0.5 ± 0.2	0 0.005 ± 0.004
<i>Alaria esculenta</i>	2012 2021	0 5 ± 6	0.3 ± 0.4 3.2 ± 2	0 0.5 ± 0.2	0 0.005 ± 0.004
Digitate kelps	2012 2021	9 ± 0.6 2.8 ± 4	1.5 ± 1.4 0.3 ± 0.3	0 0	0 0
<i>Saccharina latissima</i>	2012 2021	0.5 ± 0.7 0.8 ± 0.7	1 ± 0.4 0.27 ± 0.2	0 0	0 0
<i>Other</i>	2012 2021	0 0.04 ± 0.07	0.11 ± 0.08 0.15 ± 0.15	0.25 ± 0.25 0.22 ± 0.29	0.1 ± 0.1 0.006 ± 0.006
<i>Phaeophyceae</i>					
<i>Desmarestia aculeata</i>	2021	0	0.02 ± 0.02	0.14 ± 0.22	0.005 ± 0.006
<i>Desmarestia viridis</i>	2021	0	0	0.004 ± 0.007	0.002 ± 0.003
<i>Halosiphon tomentosus</i>	2021	0.005 ± 0.008	0.08 ± 0.13	0.0006 ± 0.001	0
<i>Saccorhiza dermatodea</i>	2021	0.035 ± 0.06	0.01 ± 0.024	0	0
Young <i>Laminaria</i> spp.	2021	0	0.03 ± 0.02	0.07 ± 0.08	0
<i>Rhodophyta</i>	2012 2021	0 0.02 ± 0.01	0.03 ± 0.06 0.14 ± 0.14	0.88 ± 0.87 1.35 ± 0.24	1.8 ± 1.3 0.8 ± 0.6
<i>Euthora cristata</i>	2021	0	0.006 ± 0.004	0.03 ± 0.04	0.0002 ± 0.0004
<i>Phycodrys rubens</i>	2021	0.0005 ± 0.0004	0.06 ± 0.06	0.99 ± 0.26	0.75 ± 0.6
<i>Ptilota</i> spp.	2021	0.015 ± 0.013	0.077 ± 0.078	0.33 ± 0.08	0.06 ± 0.07
All understory	2012 2021	0 0.055 ± 0.08	0.15 ± 0.08 0.29 ± 0.2	1.1 ± 1.1 1.57 ± 0.47	1.9 ± 1.4 0.8 ± 0.6
All seaweeds	2012 2021	9.5 ± 0.3 8.6 ± 5	3 ± 2 4 ± 2	1 ± 1 2 ± 0.2	2 ± 1 0.8 ± 0.6

Species	2.5 m	5 m	10 m	15 m
<i>Alaria esculenta</i>				
Juveniles	1 ± 2	311 ± 383	40 ± 21	3 ± 5
1	0	0	0	0
2	2 ± 3	2 ± 2	0	0
3	6 ± 7	2 ± 2	0	0

4	4 ± 7	5 ± 4	1 ± 1	0
5	7 ± 9	4 ± 5	<1 ± 1	0
6	5 ± 8	2 ± 1	<1 ± 1	0
7	1 ± 1	1 ± 1	0	0
8	0	0	1 ± 1	0
9	<1 ± 1	0	0	0
Digitate kelps				
Juveniles	19 ± 13	135 ± 140	37 ± 10	0
1	2 ± 3	0	0	0
2	8 ± 8	1 ± 2	0	0
3	9 ± 6	1 ± 1	0	0
4	7 ± 13	0	0	0
5	2 ± 3	0	0	0
6	<1 ± 1	0	0	0
<i>Saccharina latissima</i>				
Juveniles	<1 ± 1	224 ± 344	10 ± 9	0
1	<1 ± 1	0	0	0
2	2 ± 1	1 ± 1	0	0
3	6 ± 5	1 ± 1	0	0
4	3 ± 3	1 ± 1	0	0
5	<1 ± 1	<1 ± 1	0	0

Appendix 6. Mean rounded density ± standard deviation per age class of kelp species per m⁻² at Hansneset, Kongsfjorden in summer 2021 (n = 3) at 2.5 m, 5 m, 10 m and 15 m depth.

Appendix 7. Mean rounded %carbon and %nitrogen values ± standard deviation stored in the dry blade biomass of kelp species at Hansneset, Kongsfjorden in summer 2021.

Species	n	%carbon	%nitrogen	C:N ratio
<i>Alaria esculenta</i>				
2.5 m	11	34 ± 5	2.2 ± 1.1	18 ± 7
5 m	15	35 ± 6	1.9 ± 0.6	20 ± 5
10 m	7	37 ± 1	2.7 ± 0.6	
Digitate kelps				
2.5 m	15	27 ± 5	2 ± 0.5	15 ± 6
5 m	10	29 ± 3	1.4 ± 0.2	21 ± 4
<i>Saccharina latissima</i>				
2.5 m	15	32 ± 6	1.3 ± 0.8	29 ± 9
5 m	7	32 ± 3	1.7 ± 0.6	22 ± 11

Figure Legends

Figure 1 Shift in kelp forest biomass and depth distribution over 25 years of Arctic warming at our study site Hansneset in Kongsfjorden, Svalbard. The habitat for kelp communities along Arctic fjord systems declines as the increase in glacial melt intensifies the phenomenon of coastal darkening which prevents the depth extension of key kelp species despite elongation of the open water period. This illustration is based on data from Hop et al. (2012), Bartsch et al. (2016) and the present study.

Figure 2 Study site of the depth transect at the Hansneset kelp forest and location of the AWIPEV-COSYNA underwater observatory in Kongsfjorden, western Spitzbergen. The maps were plotted using the R package ggOceanMaps (Vihtakari, 2022) in R version 4.2.2 ('Innocent and Trusting', R Core Team, 2022).

Figure 3 Fresh weight (FW) m^{-2} of biomass dominant macroalgal species and groups along the depth gradient at Hansneset, Kongsfjorden (Svalbard) over time as indicated by different colors (mean $\pm$ SD; 1996/1998: $n = 2$ (0 m), $n = 3$ (5 – 15 m), $n = 4$ (2.5 m); 2012/2013: $n = 3$ (0 and 15 m), $n = 6$ (2.5 – 10 m); 2021: all depths $n = 3$).

Figure 4 Leaf area index (LAI) of macroalgal species and groups along the depth gradient at Hansneset, Kongsfjorden (Svalbard) in summer 2012 and 2021 (mean $\pm$ SD, $n = 3$) as indicated by different colors. Original sample size differed between 2012 (0.25 m^2) and 2021 (1 m^2). In 2012 no kelps were documented at 10m and 15m due to the small frame size (0.25 m^2 frame).

Figure 5 Changes of abundance and lower depth distribution (relative to chart datum) of biomass dominant brown algae species over time at Hansneset, Kongsfjorden (Svalbard). Absence of data between 2 - 7m in 1996/98 and 2014 is marked in grey. Changes in lower distribution limits are highlighted (red line) and semi-quantitative abundance classes are indicated by color intensity.

Figure 6 Relative age-class distribution of all kelps and single kelp species along the depth gradient (2.5 – 10m) at Hansneset, Kongsfjorden (Svalbard) in summer 2021. Numbers above stacked columns indicate the mean number of kelp individuals per m^2 ($n = 3$). The age of kelp individuals was subsumed into four age classes indicated by color code.

Figure 7 Age and density per m^2 of adult kelps ([?] 1 year) at 2.5m (a, b) and 5m (c, d) at Hansneset, Kongsfjorden (Svalbard) between summer 2013 and 2021. Colors indicate kelp species (mean $\pm$ SD; 2013 and 2021: $n = 3$).

Figure 8 Individual holdfast (a), stipe (b), blade dry weight (DW) (c) and blade:stipe DW ratio (d) of adult kelps ([?] 2 years) collected from 2.5m and 5m depth in Hansneset, Kongsfjorden (Svalbard) in summer 2021. Boxplots represent the median (50th percentile), the interquartile range (25th to 75th percentile), and whiskers the lower (5th) and upper (95th) percentile. Colors of boxplots indicate the three kelp species and single data points from 2.5m (blue circles) and 5m (red triangles) are presented. Significant differences between species are marked with different capital letters (non-parametric Kruskal-Wallis test with pairwise Wilcoxon rank sum tests with Bonferroni correction, *A. esculenta*: $n = 75$ (2.5 m); $n = 43$ (5 m); ‘Digitate Kelps’: $n = 65$ (2.5 m); $n = 6$ (5 m); *S. latissima* : $n = 29$ (2.5 m); $n = 4$ (5 m)).

Figure 9 Individual blade %carbon (a), %nitrogen (b) and C:N ratio (c) in a random subsample of adult kelps ([?] 2 years) collected from 2.5m and 5m depth at Hansneset, Kongsfjorden (Svalbard) in summer 2021 (*A. esculenta*: $n = 11$ (2.5 m), $n = 15$ (5 m); ‘Digitate Kelps’: $n = 15$ (2.5 m), $n = 10$ (5 m); *S. latissima* : $n = 15$ (2.5 m), $n = 7$ (5 m)). Visualization same as Figure 7.

Figure 10 Blade carbon (a) and nitrogen (b) of adult kelps ([?] 2 years) per m^2 at 2.5m and 5m depth at Hansneset, Kongsfjorden (Svalbard) in summer 2021. Colors indicate kelp species (mean $\pm$ SD; $n = 3$).

Figure 11. Long-term change in PAR and turbidity at the AWIPEV-COSYNA underwater observatory off Ny Alesund, Kongsfjorden. Weekly means originate from the daily vertical water column profiles recorded between 11m to 1m depth (+/- tide). The deviation of the observed weekly PAR and turbidity values to the expected PAR and turbidity values is shown. The expected value (zero line) was calculated as the mean of the calendar week across all years. A simple linear regression model (dashed line) was used to analyze the trend in PAR and turbidity change over the years. Only the photosynthetic active period (summer light condition) from week 8 (March) to week 44 (October) was considered.

Appendix 8. Absolute weekly PAR and turbidity values recorded at the AWIPEV-COSYNA (Coastal Observing Systems of the Northern and Arctic Seas) underwater observatory off Ny Alesund, Kongsfjorden. Data for the winter period from week 45 (November) to week 7 (February) not shown.

Data availability statement

The data supporting the conclusions of this article are available on the Zenodo platform: Dusedau, L., Fredriksen, S., Brand, M., Fischer, P., Karsten, U., Bischof, K., Savoie, A., & Bartsch, I. (2023). Kelp forest

biomass, species composition and depth distribution survey at Hansneset in Kongsfjorden, Svalbard [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.10014495>

PAR and turbidity data from the AWIPEV-COSYNA Underwater Observatory in Ny Alesund supporting the findings of this study are available on the AWI dashboard. <https://dashboard.awi.de/?dashboard=3865>

Competing Interests Statement

There is no conflict of interest, all permits regarding sampling were given by Norwegian authorities (Sysselmannen Svalbard).

Author Contribution Indication

All the authors have made substantial contributions to the content of the manuscript.

Luisa Dusedau: Conceptualization (supporting), Data Curation (lead), Formal Analysis (lead), Investigation (equal), Validation (lead), Visualization (lead), Writing – Original draft (lead), Writing – Review & Editing (lead). **Stein Fredriksen:** Investigation (supporting), Supervision (supporting), Validation (supporting), Writing – Review & Editing (supporting).

Markus Brand: Investigation (supporting), Resources (equal), Writing – Review & Editing (supporting). **Philipp Fischer:** Data Curation (supporting), Formal Analysis (supporting), Investigation (supporting), Resources (equal), Visualization (supporting). **Ulf Karsten:** Resources (equal), Writing – Review & Editing (supporting). **Kai Bischof:** Funding Acquisition (lead), Supervision (supporting), Writing – Review & Editing (supporting). **Amanda Savoie:** Supervision (supporting), Writing – Review & Editing (supporting). **Inka Bartsch:** Conceptualization (lead), Investigation (equal), Project Administration (lead), Supervision (lead), Validation (supporting), Writing – Original draft (supporting), Writing – Review & Editing (supporting)

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