

**Macroalgae distribution among varying glacial fjords as an indicator of light
and nutrient availability**

by

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ABSTRACT

Arctic macroalgae (kelp) are critical primary producers, contributing significantly to a wide variety of ecosystem services. Kelp extent has been predicted to increase due to decreasing sea ice cover that increases light reaching the coastal ocean. However, climate change-induced factors, such as increasing coastal turbidity and glacier melt, could also impact kelp growth in the Arctic. This thesis examines the role that light and nutrient availability play in understanding kelp cover and depth extent. This study used GoPro videos to determine kelp cover and depth extent as well as macroalgae samples to determine the nutritive state of kelp within two Greenlandic fjords. Results reveal significant turbidity and nutrient gradients throughout the fjords. Where light was limited due to glacial discharge and resuspension of sediments, kelp growth at depth was limited; and where there was increased light availability, kelp cover was greater. Additionally, kelp located nearest the marine-terminating glacier had greater nitrogen concentration than kelp located further from the marine-terminating glacier or the land-terminating glacier, revealing the influence of estuarine circulation on nutrient availability. Where light and nutrients were abundant, kelp biomass and subsequent production was greatest. Additionally, we concluded that sea urchin grazing provided an additional influence with light on kelp depth extent and distribution in both shallow and deep waters. These results are necessary and important to consider when assessing kelp distribution and change, both now and into the future.

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CONTRIBUTION OF AUTHORS

The manuscript in chapter 3 titled “Macroalgae distribution among varying glacial fjords as an indicator of light and nutrient availability” was accomplished through the combined efforts. As the first author, I was responsible for data sampling, processing and analysis, as well as manuscript writing. Dr. C.J. Mundy fostered the idea for the project, and provided significant input along every step of the way including interpretation of the manuscript. Dr. Mikael Kristian Sejr offered valuable input and support, as well as analysis of nutrient samples. Rakesh K. Singh provided satellite estimates of light attenuation. Mie H.S. Winding provided the generous use of the Greenland Institute of Natural Resources laboratory and boats during the sampling period. Lastly, all authors will review and revise the manuscript prior to submission to *Arctic Science*.

CHAPTER 1.0: INTRODUCTION

1.1 Motivation

The current warming of the Arctic Ocean and atmosphere is causing well-documented melt and retreat of sea ice, glaciers, ice sheets and permafrost (Bintanja, 2018; Jansen et al., 2020; Rantanen et al., 2022; Walsh, 2014). This decrease in sea ice cover/glacier extent and thickness has implications for primary producers, including kelp, potentially increasing the length of their growing season due to increased light penetration and therefore photosynthesis (Krause-Jensen & Duarte, 2014; Leu et al., 2015; Meredith et al., 2019; Windsor et al., 2015). Kelp play a significant role in the Arctic marine food web, providing a food source at the base of the food chain (Christie et al., 2009; Schoenrock et al., 2018). Additional services include provision of habitat and shelter through wave reduction, refuge from ultraviolet radiation and predators, and a function as blue carbon, through carbon sequestration and burial within the ocean floor (Christie et al., 2009; Krause-Jensen et al., 2012; Krause-Jensen & Duarte, 2016; Schoenrock et al., 2018).

The rapid reduction of sea ice cover in the Arctic has the potential to allow for kelp to expand their distribution laterally and vertically due to increased light availability (Goldsmit et al., 2021; Krause-Jensen & Duarte, 2014). However, climate change also has the effect of increasing turbidity near rivers and glaciers and creating unstable shoreline that could counteract some of the predicted kelp expansion, potentially leading to shoaling depth limits (Bartsch et al., 2016; Bonsell & Dunton, 2018; Filbee-Dexter et al., 2019; Szeligowska et al., 2021).

Therefore, to improve these kelp distribution predictions under a warming climate, it is important to better understand their response to environmental change. Influential factors such as light, nutrients, substrate, temperature, salinity and urchin grazing are all known variables of kelp

growth (Aumack et al., 2007; Blicher et al., 2007; Henley & Dunton, 1997; Filbee-Dexter et al., 2022; Marambio & Bischof, 2021). However, there is still a knowledge gap as to how kelp may be affected by changes to these variables within complex fjord environments. The research presented in this thesis seeks to increase our knowledge of the drivers of kelp distribution in Arctic fjordic environments. By considering this, we will be better equipped to understand changes occurring in other coastal regions around the globe to predict long term changes at the ecosystem level and enable more effective marine protection strategies.

1.2 Research Objective

It is suggested that kelp represent integrators of annual light and nutrient availability. Kelp cover and depth extent were analyzed within the Nuuk fjord system in Greenland, in relation to light availability, nutrient concentration, and kelp biochemical composition. The objectives of this thesis with their accompanying hypotheses are as follows:

- 1) To classify kelp cover and depth distribution among Nuup Kangerlua and Ameralik Fjords.

H: Stations in close proximity to the glaciers will have disproportionately less kelp cover and extent than stations located farther from the glaciers.

- 2) To relate photosynthetically active radiation (PAR) availability in relation to turbidity and kelp distribution.

H: The increase in kelp extent associated with an increasing open water period with light will be limited to areas of low turbidity, or little change to current turbidity levels.

- 3) To relate the nutritive status of kelp (carbon and nitrogen content) to the kelp distribution.

H: All other things being equal, under greater nutrient supply kelp will have greater production (via growth and lower C:N ratio).

While it is hypothesized that stations located nearest to glacier discharge will have disproportionately less kelp extent and cover versus stations farther from the glacier discharge due to higher turbidity and therefore light attenuation in the prior; it is suggested that kelp with greater nutrient access through glacial estuarine circulation will have lower C:N ratios.

1.3 Thesis Structure

This thesis is composed of four chapters in a sandwich style format. The introductory section states the significance of the research, the objectives, and outline of the thesis. Chapter two provides the necessary background and theory to provide a foundation of knowledge to understand the research contained within the thesis. Chapter three focuses on the thesis objectives where the influence of light and nutrient availability on kelp coverage and distribution are analysed. Additionally, regional comparisons of kelp distribution are discussed to better understand implications of climate change throughout the Arctic region. Background on the study location and sampling methods are provided within the manuscript. This work will be compiled into a manuscript and submitted for peer-review to the journal, *Arctic Science*.

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Lastly, chapter four provides a summary of the thesis, conclusions and recommendations for future work. Reference to literature is appended as the final pages of each chapter.

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CHAPTER 2.0: LITERATURE BACKGROUND

2.1 Introduction

The vast underwater kelp forests from polar to subtropical coastlines provide extensive ecosystem services. These influential primary producers provide an important source of energy for higher up trophic levels and well as provision of habitat and shelter (Christie et al., 2009; Norderhaug et al., 2003; Norderhaug et al., 2005). Kelp growth and expansion in the Arctic is largely limited due to light and nutrient availability (Castro de la Guardia et al., 2023; Chapman & Lindley, 1980; Chapman et al., 1978; Codispoti et al., 2013). A background literature review is provided to introduce the reader to the subject of this thesis. I begin with a discussion describing the water masses and currents of the West Greenland region as well as describe fjord and glacier anatomy and general influence. I then provide background on kelp anatomy, ecosystem services, and the primary factors influencing kelp growth and expansion including various acclimation strategies. Lastly, I address the current state of kelp distribution around the Arctic, divided into the Canadian, Nordic and Greenland regions.

2.2 Fjords and Currents

2.2.1 West Greenland Currents and Water Masses

Baffin Bay is characterized by its semi-enclosed basin and cyclonic circulation with input waters from the Arctic Ocean and the Northwest Atlantic (Hamilton & Wu, 2013). The West Greenland Current (WGC) flows along the West Greenland shelf (depth of 100-500 meters) into the Nuuk fjord system; which includes the two fjords focused on in this thesis, Nuup Kangerlua and Ameralik fjords (Myers & Ribergaard, 2013; Stuart-Lee et al., 2021). The top layer within Nuup Kangerlua is characterized by low salinities (<5) from fresh water glacial melt and land runoff. The intermediate layer is composed of cold subglacial freshwater that ascends upon release at

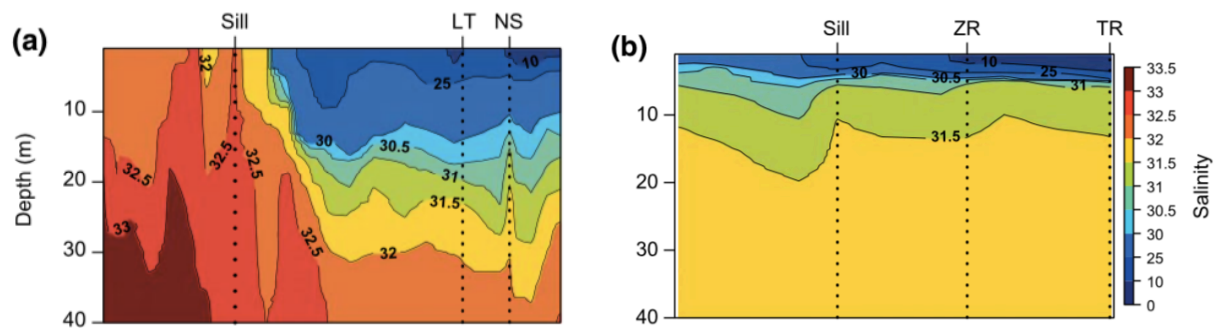
depth due to its low density, while ascending, it mixes with more salty waters which halts its rise (Juul-Pedersen et al., 2015; Mortensen et al., 2011). Beneath this layer is the sill water region formed by mixing water masses in the outer sill region. Lastly, basin waters inflow during the winter and spring with mixtures of coastal and subpolar waters (Mortensen et al., 2011). Within the Ameralik Fjord the upper water mass is composed of warmer, less saline Atlantic and Irminger Sea waters with additional freshwater coastal inflows from the presence of a land-terminating glacial river (Stuart-Lee et al., 2021). Bottom waters of the fjord originate from the WGC Polar waters and are composed of cold salty water (Myers & Ribergaard, 2013; Ren et al., 2009).

2.2.2 Fjord/Glacier Anatomy and Influence

Carved by glacial ice excavation, fjords are often considered the “transition” zone between terrestrial ecosystems and open ocean with additional cryosphere and atmospheric interactions. Therefore, fjords in mid to high latitude regions have received significant attention as an Aquatic Critical Zone due to their high vulnerability during climate fluctuations (Bianchi et al., 2020). Fjords are characterized by long, narrow, steep, deep and often sinuous estuaries, where salt and freshwater interact (Snedden et al., 2012).

Glaciers can be characterized into two types. (1) Tidewater or marine-terminating glaciers have a terminus that extend out into the fjord waters. These glaciers produce much of their meltwater discharge near the sea floor, this freshwater of lower density rises, resulting in mixing and entrainment as it makes its way higher in the water column (Figure 2.1 a). Additionally, mass loss can occur through subaerial melting or calving events (Bianchi et al., 2020; O’Leary & Christoffersen, 2013). Estuarine circulation driven by density facilitates both horizontal and

vertical transfer of heat, nutrients and plankton throughout the fjord (Hopwood et al., 2018). (2) Land-terminating glaciers in contrast lack this circulation mechanism and meltwater is generated through subaerial melting, and therefore are characterized by more stratified water columns due to meltwater and sediment release into the surface waters (Bianchi et al., 2020; Meire et al., 2017; Ren et al., 2009) (Figure 2.1 b). It is important to note that marine-terminating glacier retreat will eventually result in land-terminating glaciers, as is occurring in light of increasing Arctic temperatures (Torsvik et al., 2019).



Error! Bookmark not defined. **Figure 2.1. a)** A vertical salinity profile through Nuup Kangerlua. Lake Tasersuaq (LT) and Narsap Sermia (NS) represent points of land-terminating and marine-terminating glacier input, respectively. **b)** A vertical salinity profile through Young Sound. Zackenbergl River (ZR) and Tyroler River (TR) represent land-terminating glacier river inputs (Meire et al., 2017; CC by 4.0 <https://creativecommons.org/licenses/by/4.0/>).

2.3 Kelp

2.3.1 Anatomy

Kelp, in the order Laminariales, are a marine primary producer that most often reside in regions of rocky substrate where they can attach their holdfast, often along shallow coasts (Bolton, 2010; Schiel & Foster, 2015). They can form large dense stands referred to as kelp forests. Of interest are the large brown algae which include dominant pigments of fucoxanthin and chlorophyll *c* (Garcia-Perez et al., 2022). Kelp are composed of a haptera or holdfast, finger like projections, anchoring the kelp to the ground; as well as a stipe (stem-like structure) and blade (lamina). The

meristem is the stipe/blade junction where much of the kelp elongation takes place (Figure 2.2; Schiel & Foster, 2015). Majority of carbon fixation occurs in the blade as opposed to the meristem region (Wiencke et al., 2006).

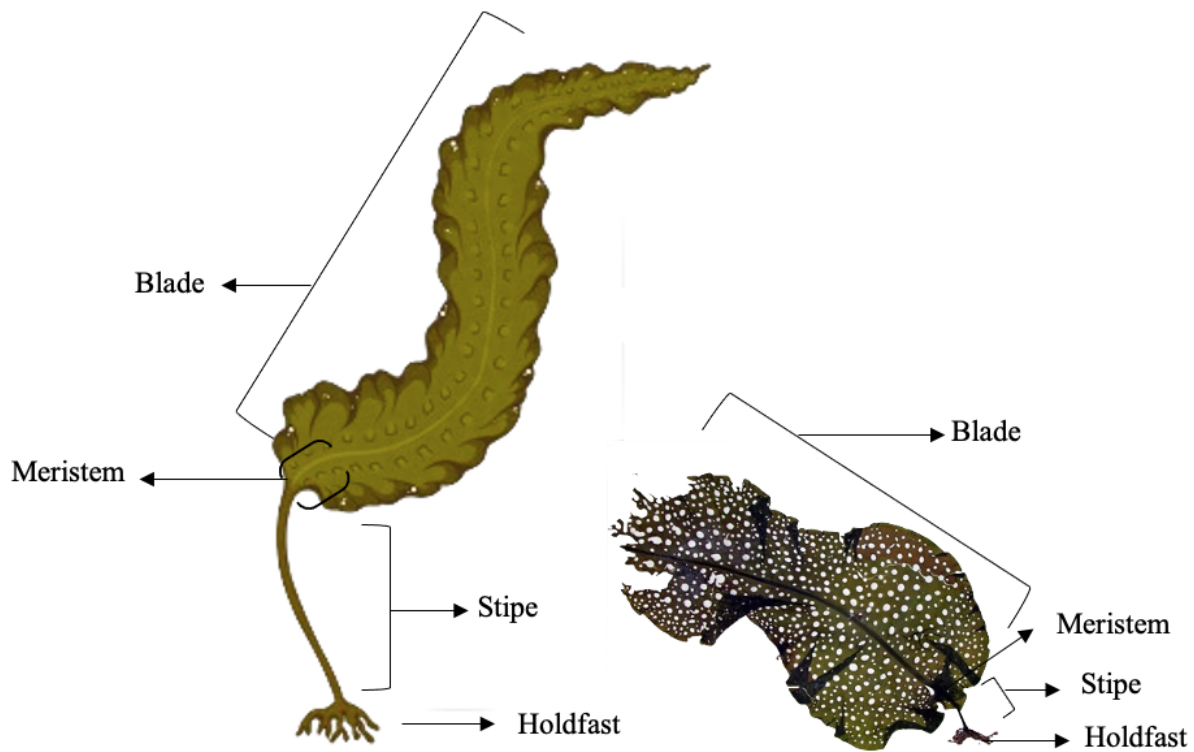
Laminaria solidungula is the only kelp species truly endemic to the Arctic environment. Other kelp species that may reside in the north include *Agarum clathratum*, *Alaria elliptica*, *Alaria esculenta*, *Alaria oblonga*, *Eualaria fistulosa*, *Laminaria digitata*, *Laminaria hyperborea*, *Nereocystis luetkeana*, *Saccharina latissima*, *Saccharina longicruris*, *Saccharina nigripes* and *Saccorhiza dermatodea* (Filbee-Dexter et al., 2019; Scheschonk et al., 2019).

Kelp have the ability to maintain blade tissue and persist throughout winter (unlike ephemeral pelagic and sea ice microalgae), magnifying its importance. A common species, *S. latissima*, also known as sugar kelp, have large thin blades and long stipe between 0.5 and 11 m, resulting in a high canopy, allowing it to outcompete low lying species for light and nutrient absorption (Bolton, 2010; Dayton, 1985; Nielsen et al., 2014; Wernberg et al., 2019). *S. latissima* annually sheds its second blade which degrades in April after new blade initiation occurs in early December. Majority of its growth occurs in late winter through July, fueled in part by stored carbohydrates as well as light as it becomes more readily available as the winter sea ice begins to melt (Dunton, 1985; Henley & Dunton, 1995). An average lifespan for *S. latissima* is between 2 and 5 years however other kelp species may live up to 10 years (Handå et al., 2013; Schaal et al., 2012; Zhang & Thomsen, 2019).

Another common species, *Agarum clathratum*, has similar anatomy to that of *S. latissima*, however, differences include, a shorter stipe of < 1 m, wide midrib, blades that are crinkled and become thicker with age, and a distinctive hole pattern (Figure 2.2) (Choi & Kim, 2012; Gagnon

et al., 2005; Wernberg et al., 2019). Being a low-lying understory and deep growing kelp species, *A. clathratum* is more shade-tolerant than other fast growing species such as *S. latissima* (Wernberg et al., 2019). Significant winter growth for both species gives a head start and therefore, competitive advantage over annual species that only start their growth in summer (Mann, 1973).

Kelp reproduce by releasing spores which disperse by currents and internal waves before settling nearby on the sea floor (Dayton, 1985). Spore survival to gametogenesis can be limited by a range of factors including, temperature, light intensity, photoperiod, nutrient availability, sexual pheromones and culture density (Bolton & Levitt, 1985; Ebbing et al., 2020; Hsiao & Druehl, 1971; Martins et al., 2017; Morita et al., 2003; Reed, 1990). Some kelp release spores at the top of their blade to increase distance of dispersal, while some release nearest the substratum to increase potential fertilization (Dayton, 1985). The spores then become male and female gametophytes whose sperm can fertilize the egg. A higher density of gametophytes has a greater chance for successful fertilization (Dayton, 1985; Schiel & Foster, 2015; Visch et al., 2019).



Error! Bookmark not defined.**Figure 2.2.** Diagram of *S. latissima* (left) (Modified image from Rowe-Jerome, n.d.) and *A. clathratum* (right) (Modified image from Saunders, 2023; © Saunders 2023, with permission).

2.3.2 Ecosystem Services

Understanding kelp distribution becomes of increased significance when considering the value and ecosystem services that kelp forests can provide. Being a primary producer at the base of the food chain, kelp serve as a food source for many species, which in turn provide energy to higher trophic levels (Hynes et al., 2021; Lorentsen et al., 2010 Norderhaug et al., 2005). Kelp grazers include fish, crustaceans, mollusks, echinoderms and detritivores, many of which are of importance to the fisheries market by providing jobs, income and food for humans (Bologna & Steneck, 1993; Pineiro-Corbeira et al., 2022). Additionally, kelp farming is an increasing trend which allows kelp to be grown as a food source for humans and agriculture, as well as used as an

organic fertilizer (Erickson et al., 2012; Goecke et al., 2020; Lei, 2021; Meng et al., 2020; Thorsen et al., 2010; Zheng et al., 2016).

Kelp provide habitat and shelter to a wide variety of species including fish, mammals and invertebrates (Christie et al., 2009; Lorentsen et al., 2010). By absorbing and decreasing the influence of waves, kelp provide refuge from open waters and predators while also decreasing land erosion (Eckman et al., 1989; Loevas & Torum, 2001). Their large canopy can provide shade for creatures against harmful ultraviolet radiation as well as serve as important nursery grounds (Teagle et al., 2017).

Kelp also play a significant role in nutrient cycling as well as bioremediation, through the transfer and exchange of inorganic and organic matter, which is imperative to keep ecosystems in equilibrium (Eger et al., 2023; Hardison et al., 2010). Furthermore, kelp have the ability to sequester surface ocean carbon dioxide to the benthic environment, serving an important function as blue carbon and regulating pH levels to benefit calcifying species (Krause-Jensen et al., 2015). Once dislodged from their original coastal environment due to storms and strong currents, kelp may float to open seas, encounter little disturbance from predators, and subside to the deep ocean floor (Krause-Jensen et al., 2012; Krause-Jensen & Duarte, 2016; Queiros et al., 2019).

2.3.3 Influential Factors of Kelp Growth

Light and Turbidity

Light availability is the main limiting factor for primary production in the Arctic (Codispoti et al., 2013; Henley and Dunton, 1997). This is accentuated due to sea ice cover and the extreme solar cycles experienced in the region, making photosynthesis near impossible throughout winter (Tremblay & Gagnon, 2009). As annual sea ice cover decreases with a warming environment, the

associated increase in open water periods with light will increase light-limited photosynthesis that could potentially intensify kelp production and depth extent (Clark et al., 2013; Krause-Jensen et al., 2014. Krause-Jensen et al., 2019). In fact, the number of open water days was observed to be the best predictor of kelp distribution along an Arctic latitudinal gradient in Greenland (Krause-Jensen et al. 2012). Filbee-Dexter (2022) also detected increased kelp biomass with reduced sea ice cover. Furthermore, Castro de la Guardia et al. (2023) found that a longer open water period with light led to deeper growing kelp. However, these relationships do not consider changes to turbidity. Castro de la Guardia et al. (2023) highlighted 2 locations; Nuuk and Itilleq, that did not experience the same relationship with light as the other Arctic regions. These locations had a long open water period with light but a more shallow depth extent. I suggest that the dissimilar pattern detected at the Nuuk and Itilleq stations are linked to higher suspended sediment in these regions. For instance, decreasing sea ice cover and glacier extent with increased precipitation could enhance erosion and run-off, leading to greater re-suspension, turbidity and thus light attenuation within coastal regions. These changes will act to decrease light availability and therefore photosynthesis with depth due to particulate absorption and scattering of light. Therefore, increasing turbidity may result in decreased kelp depth distributions despite longer open water periods with light.

As previously mentioned, melting marine-terminating glaciers can input freshwater at depth, causing buoyant plumes containing glacial discharge. These plumes can be extremely turbid in nature and limit light penetration at the depth of the plume once it reaches neutral buoyancy depth (when plume density equals ambient density) or maximum height depth (when plume vertical velocity equals zero) (Baines, 2002). These plumes may not always reach the surface and may be more spatially distributed, and therefore can limit light penetration at various depths in

the water column (De Andrés et al., 2020; Slater et al., 2017). Land-terminating glaciers on the contrary release glacial discharge along the land surface (Figure 2.3), verses at depth below a floating ice shelf, limiting light availability even at shallow depths (Hopwood et al., 2018; Sole et al., 2011; Spurkland & Iken, 2011; Szeligowska et al., 2021). These plumes from both marine- and land-terminating glaciers can have negative effects on the benthic environment, not only through limitation of light, but also limiting nutrient uptake by burial, or unstable slopes that could limit kelp hold-fast securement (Farrow et al., 1983; Lyngby & Mortensen, 1996; Spurkland & Iken, 2011).

A study by Dunton (1985) found that *S. latissima* undergoes significant growth from April to July when light availability increases, due to decreasing sea ice cover. Since light availability is greatest in summer, much photosynthesis occurs at this time and is stored as carbohydrate reserves which can be used to fuel growth throughout the year (Henley & Dunton, 1995). Intensified sediment discharge increasing light attenuation near glaciers may lower rates of photosynthesis and subsequent decrease of carbon stores, limiting growth throughout the year (Aumack et al., 2007; Swanson & Fox, 2007). This is likely to restrain kelp expansion near high turbidity areas including near sedimentary depositing glaciers (Filbee-Dexter et al., 2019; Holding et al., 2019; Huovinen et al., 2020; Krumhansl et al., 2014).

Cold water kelp have an estimated minimum light requirement of growth between ~ 30 and $96 \text{ mol photons m}^{-2} \text{ yr}^{-1}$ (Bartsch et al., 2016; Borum et al., 2002; Castro de la Guardia, 2023; Chapman & Lindley et al., 1980; Dunton, 1990). Some kelp use shade adaptation strategies to allow deeper penetrating kelp higher photosynthetic efficiency in negligible light conditions (Blain & Shears, 2019; Borum et al., 2002; Wiencke et al., 2006). Such strategies include

increasing the quantity of photosynthetic pigments to allow for more efficient carbon fixation (e.g., chlorophyll *a*, chlorophyll *c*, fucoxanthin; Blain & Shears, 2019; Gómez et al., 2009). Timing of growth and lowering rates of respiration during cold winter months are both useful strategies. Maximum growth in late winter/spring can be fueled using carbohydrate reserves accumulated from the preceding summer and also take advantage of more abundant nutrient availability during the winter (Dunton, 1985; Henley & Dunton, 1995). While the maximum rate of photosynthesis often decreases within light-limited conditions, the aforementioned photoacclimation strategies increase kelp photosynthetic efficiency by enhancing their ability to capture and use photons, thus, optimizing thallus growth rates and survival (Blain & Shears, 2019).

It must also be mentioned that shallow water kelp receive high light penetration and are restricted by possibility of oversaturation. These kelp can exhibit physiological strategies to avoid photo-inhibition through the addition of high light quenching pigments (e.g. xanthophyll; Borum et al., 2002; Gómez et al., 2009; Ralph & Gademann, 2005; Rodrigues et al., 2000).



Figure 2.3. EOSDIS NASA worldview photo (July 27, 2022) of the Nuuk Fjord region emphasizing sedimentary influence from land-terminating glaciers (white initials), Saqqap Sermersua (SS), Kangilinnguata Sermia (KS) (drains from the GrIS), Qamanaarsuup Sermia (QS) and Naajat Kuuat (NK). Marine-terminating glaciers (black initials) include Narsap Sermia (NS), Akullersuup Sermia (AS) and Kangiata Nunaata Sermia (KNS).

Nutrients and Mixing

In addition to light, nitrate is recognized as the main yield-limiting nutrient for marine primary production in the Arctic (Codispoti et al., 2013; Henley & Dunton, 1997; Peters et al., 2019; Rugiu et al., 2021; Tremblay et al., 2015). New nutrients are supplied to the Arctic from rivers and currents originating from bordering seas. Nutrients are further mixed into surface waters through internal wave mixing, storms, coastal mixing caused by variation in bathymetry (e.g. fjord sill/glacier upwelling), and convection which effectively disperses a strong halocline. Due

to increased strength and frequency of storms and reduction of sea ice beyond the shelf break, mixing and halocline disturbance are predicted to increase, potentially increasing nutrient supply to surface waters (Hopwood et al., 2018; Schiel & Foster, 2015; Tremblay & Gagnon, 2009). However, this may be balanced by stratification from increased melt and freshwater run off, impeding vertical nutrient supply (Moore et al., 2013; Sallée et al., 2021).

Marine-terminating glaciers are found to support greater primary production within their fjord versus that of land-terminating glacier fjords due to freshwater glacial melt release hundreds of meters below the water's surface driving fjord-wide circulation. Rising glacier freshwater melt drives entrainment of nutrient filled waters from the bottom ocean layer, providing access to new nutrients in the euphotic zone throughout the summer (Hopwood et al., 2018; Magorrian & Wells, 2016; Meire et al., 2017; Mortensen et al., 2011). This circulation also increases nutrient availability by reducing stratification in the surface layers (Cape et al., 2019; Meire et al., 2017; Spurkland & Iken, 2011; Szeligowska et al., 2021). In contrast, land-terminating glaciers lack this circulation mechanism and are more heavily influenced by river discharge where high turbidity and increased surface stratification can decrease vertical mixing, decreasing benthic algal photosynthesis via nutrient and light limitation (Ribeiro, et al., 2017; Szeligowska et al., 2021).

These nutrient rich waters found among marine-terminating glaciers can influence kelp production, and therefore, greater nutrient availability through circulation with minimal turbidity could result in increased kelp in these regions (Aure et al., 2007; Henley & Dunton, 1997). We can note the internal kelp nitrogen concentration (% dry weight) for maximum macroalgae growth is ~1.7%, with a critical minimum for growth at 1% (Henley & Dunton, 1997; Pedersen

& Borum, 1996). Increased nitrogen supply and absorption can support greater chlorophyll production within the kelp and therefore photosynthetic activity (Chapman et al., 1978; Rugiu et al., 2021). Subglacial mixing is not only expected to increase macroalgae production, but also phytoplankton production due to increased access to nutrients within the photic zone (Aure et al., 2007; Juul-Pedersen et al., 2015; Meire et al., 2017). Amplified phytoplankton production could have negative implications for resource availability for benthic species (Krause-Jensen & Sand-Jensen, 1998; Lorenzen, 1972; Markager & Vincent, 2001).

Nutrient uptake by kelp can be influenced by faster water motion via minimizing the boundary layer between kelp and water for more efficient diffusion of nutrients (Hurd, 2017; Hurd, 2000). Additionally, water motion via drag forces may intensify productivity by increasing dissolved inorganic carbon uptake (Hurd, 2017). Water mixing in the Arctic near polynyas and tidal currents can indirectly increase kelp production by increasing annual light available for photosynthesis, in areas that otherwise would have been sea ice covered (Bluhm et al., 2022). Low canopy kelp species such as *A. clathratum* and *L. digitata* are better equip to experience wave surges than high canopy kelp which may experience breakage at high velocities (Kawamata, 2001; Kraemer & Chapman, 1991).

Functioning of the kelp, including photosynthesis, acclimation strategies and growth all rely on the ability to acquire nitrogen, which is limited in the Arctic. Therefore, some acclimation strategies have been acquired. Some Arctic kelp have the ability to store nitrogen when ambient levels are high; often in winter, and access those reserves later on for growth, similar to the process of using stored carbon reserves for growth (Chapman & Lindley, 1980; Dunton & Schell,

1986). Additionally, kelp internal nitrate reserves can be supplemented through the use of labile organic nitrogen compounds (Korb & Gerard, 2000).

Substrata

Kelp are often found on rocky substratum, including bedrock, boulders, cobbles or biogenic material, such as shells or muscles where they can attach their holdfast securely (Wernberg et al., 2019). However, some kelp are able to attach to smaller pebbles and even sand; for example, *S. latissima*, *L. solidungula*, *L. digitata*, *D. aculeata* and *A. esculenta* were observed growing on both rocky and sandy substrate, an advantage over other species such as *A. clathratum* which more frequently only grow on rocky substrate (Filbee-Dexter et al., 2022; Hop et al., 2016; Spurkland & Iken, 2011). Therefore, substrate can limit kelp species diversity (Spurkland & Iken, 2011).

However, kelp growing on sandy substrate and more sedimentary environments can face challenges. For example, kelp with a less secure holdfast are more prone to detachment as the result of unstable slopes resulting in soil creep or from storms and waves, with increased significance as decreasing sea ice exposes kelp to such affects (Farrow et al., 1983; Filbee-Dexter et al., 2022; Filbee-Dexter & Scheibling, 2012). Additional challenges of sedimentary environments include burial which can limit carbon and nutrient availability and limit kelp recruitment (Devinny & Volse, 1978; Lyngby & Mortensen, 1996; Mohr et al., 1957).

Temperature and Salinity

Kelp are predominantly found in cold-temperate and polar waters. *L. solidungula* has a temperature growth optimum in waters of 5 to 10°C and *S. latissima* in 10 to 15°C (zoospore germination optimum between 2 and 12°C), however Arctic kelp can be found in a wide range of

temperatures, between -1.5 and 20°C (Gomez et al., 2009; Müller et al., 2008; Wernberg et al., 2019; Wiencke et al., 2006).

To combat the cold harsh environment, evolution of cold shock and anti-freeze proteins allow the photosynthetic electron transport chain to function at near freezing temperatures. Accumulation of unsaturated fatty acids prevent stiffening of membrane lipids (Breeman, 1988; Fernández et al., 2020; Gómez et al., 2009; Wiencke et al., 1994). Photosynthesis in light limiting conditions takes advantage of low temperatures to reduce respiration to maintain net carbon gain (Henley & Dunton, 1997; Scheschonk et al., 2019). These adaptations have allowed kelp to photosynthesize similarly in 5°C and 15°C waters (Davison et al., 1991).

Increased warming is predicted to result in a poleward migration of kelp species (Goldsmith et al., 2021) and has already been observed (Koch et al., 2013; Wernberg et al., 2011). While species such as *S. latissima* may benefit from a small increase in temperature, endemic species such as *L. solidungula* could see a more constricted distribution. The distribution of *A. clathratum* appears to be expanding more northward due to its eurythermic and low light adaptations (Duarte et al., 2018; Filbee-Dexter et al., 2022; Goldsmith et al., 2021; Simonson et al., 2015). Temperature may also indirectly affect kelp by affecting their coastal habitat through erosion, sea ice/glacial melt and freshwater influence, which have been shown to influence kelp distribution (Marambio & Bischof, 2021).

The Arctic experiences strong salinity changes and gradients due to freshwater input from rivers, glaciers and increasing precipitation. Although kelp tend to have limited survival and recruitment in low salinity regions, they can potentially adapt. Mannitol, a product of photosynthesis, regulates kelp to reduce osmotic stress by maintaining intracellular homeostasis (Diehl et al.,

2020; Iwamoto & Shiraiwa, 2005; Kirst, 1990). Goldsmit et al. (2021) suggests increasing temperature and decreasing salinity to be two of the three main factors regulating kelp distribution in the Arctic. *S. latissima* spore settlement was found to be greatest under cooler temperatures and high salinity (9°C/31) compared to warmer temperatures and low salinity (12°C/26) (Lind & Konar, 2017). However, *S. latissima* survives better under low salinity pressures than does *A. clathratum*, with peak occurrence and cover around 29 and 31, respectively (Goldsmit et al. 2021).

Grazing Pressures

Kelp supply food to a wide range of grazing species including amphipods, gastropods, echinoderms, decapods and fish species (Christie et al., 2009; Dayton, 1985; Harris et al., 1984; Leonard, 1994). Kelp experience some of the strongest grazing pressures from sea urchins, particularly *Strongylocentrotus droebachiensis* which is dominant in Arctic environments (Blicher et al, 2007). Intense urchin grazing has the potential to destructively graze away all kelp in an area, creating urchin barrens (Filbee-Dexter & Scheibling, 2017; Ling et al., 2009). Sea urchin abundance is associated with presence of hard substrate and food supply (Bluhm et al., 1998; Hop & Wiencke, 2019). Their diets are composed of dominantly fresh algae or detritus. Blicher et al. (2007) observed a decline in growth performance of *S. droebachiensis* along a south-north gradient in Greenland, corresponding to the length of the open water period and subsequent food availability (Blicher et al, 2007). In addition to food and substrate, there are a wide range of factors that may contribute to high urchin density; for example, a decline in urchin predators, high recruitment during favorable environmental conditions, higher grazing in warmer temperatures and an increase in range expansion due to climate change (Bernstein et al., 1981; Himmelman & Steele, 1971; Ling et al., 2009; Mann et al., 1984; Sivertsen et al., 2006).

Urchins have been found to have highest densities in shallow depth limits, from 1 to 11.4 m in Disko Fjord as well as other areas of Greenland (Krause-Jensen et al., 2012; Krause-Jensen et al., 2019). While off the eastern coast of Canada, urchin dominance was found between the depths of 40 and 85 m with presence down to 140 m (Filbee-Dexter & Scheibling, 2017). An acclimation strategy unique to *A. clathratum* is their ability to produce and release phenolic compounds that detour urchin grazing. This gives *A. clathratum* a competitive advantage over other species, such as *S. latissima*, which are more susceptible to grazing (Gagnon et al., 2005; Vadas, 1977).

2.4 Pan-Arctic Kelp Distribution

With Arctic coasts responsible for one-third of the world's total coastline, there is considerable habitat for kelp growth to occur (Figure 2.4) (Filbee-Dexter et al., 2019; Lantuit et al., 2012; Piepenburg, 2005). Various regions of the Arctic reveal differences in kelp distribution and will be categorized below into sections of Canadian, Nordic (including; Denmark, Norway, Iceland) and Greenlandic Arctic regions according to the AMAP boundary line (observed in Figure 2.4).

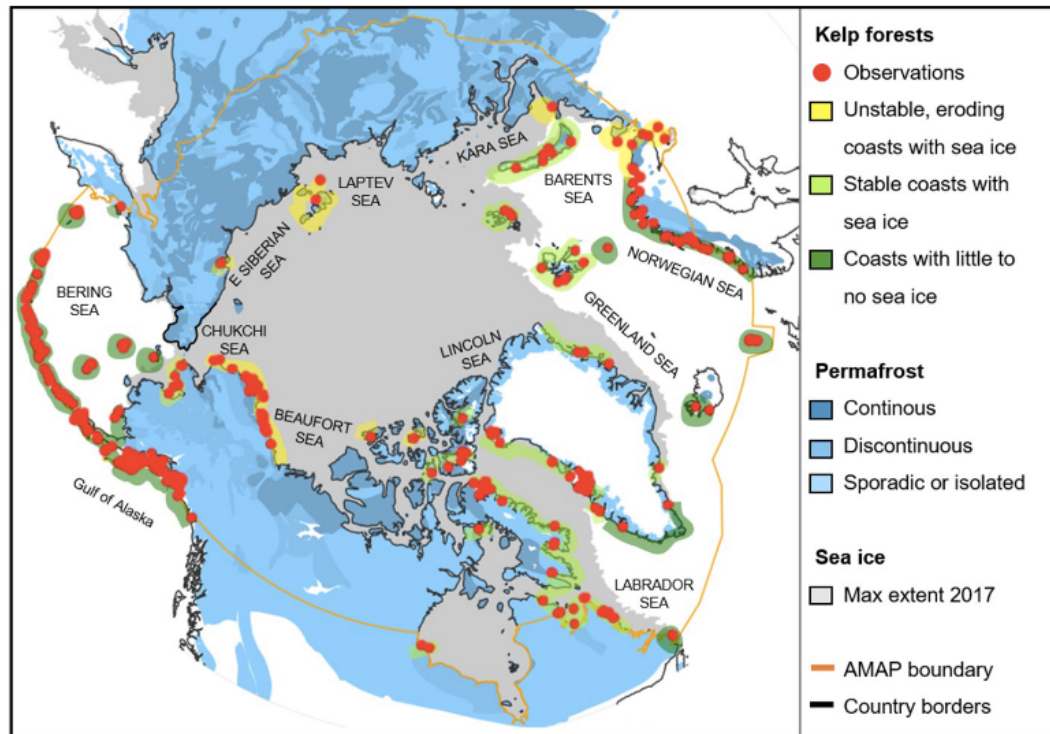


Figure 2.4. Pan-Arctic kelp distribution within the AMAP Arctic boundary line. Kelp observations shown in red (Reprinted from Arctic kelp forests: Diversity, resilience and future, 172, Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M., & Pedersen, M. F., page. 3, © 2019, with permission from Elsevier).

2.4.1 Canadian Arctic

The Canadian Arctic holds 10% of the World's coastline, making it a potentially significant contributor to Arctic kelp growing along near-shore environments (Filbee-Dexter et al., 2022).

Eastern Canadian Arctic surveys described by Filbee-Dexter et al. (2022) revealed the most dominant kelp species to be *A. clathratum*, found frequently at more northern sites, while *S. latissima* and *L. solidungula* were more numerous at southern stations where light availability was greater due to less sea ice. Average total kelp cover was 40.4% ($\pm 29.9\%$ SD), with dominant coverage at depths 10 to 15 m. Using the dataset reported in Filbee-Dexter et al. (2022) to develop a predictive based model, Goldsmit et al. (2021) determined additional factors impacting growth and distribution including temperature and salinity. Along depth transects perpendicular

to shore, kelp cover around Southampton Island increased down to 20 m and decreased down to 50 m (Castro de la Guardia et al., 2023). The Canadian Archipelago kelp distribution had similar species and depth extent, with greatest coverage from 10 to 30 m with a maximum depth of 40 m. At the 10 to 15-m isobath, Filbee-Dexter et al. (2022) reported high cover of *S. latissima*, *L. solidungula* and *A. esculenta* observed among sandy or pebble substrate, whereas *A. clathratum* dominated rocky substrate. Using the depth distribution dataset, increased open water days with light was the strongest indicator for kelp growth (Castro de la Guardia et al., 2023).

Kelp biomass varies regionally, as opposed to latitudinally, suggested to be because of convoluted coastline, variation in substrata, low saline inputs, suspended sediments and complex mixing. Nutrients in the surface waters are low and have been negatively correlated to kelp abundance (Filbee-Dexter et al., 2022). However, Bluhm et al. (2022) observed higher kelp density related to strong tidal currents, which was linked to greater nutrient access and therefore highlights the need to improve our knowledge on this aspect of growth. It is significant to note that the southeast coast of Canada has extensive sea urchin barrens with little vegetation present (Filbee-Dexter et al., 2022).

2.4.2 Nordic Arctic

The most dense kelp forests of the Nordic countries are found along the coasts of Norway and southern Iceland; with kelp appearing on all rocky coastline including eastern Svalbard, and the Faroe Islands (Kvile et al, 2022). The Norwegian coast experienced a *S. latissima* crash in the 1990's likely due to the effects of heat stress. While some areas have recovered and been repopulated, the majority of once forested *S. latissima* areas have not recovered (Moy & Christie, 2012; Sogn Andersen et al., 2019). The coasts of Kongsfjorden are composed of both hard and

soft bottom with the presence of glacial fjords. In glacial fjords such as Kongsfjorden, Hop et al. (2016) found an increase in kelp biomass gradients from inner fjord to outer fjord. Biomass was related to distance and depth from the inner fjord. High turbidity near glacier outlets minimized kelp biomass in these regions; this is similar to other fjord systems which have recorded a gradual shift in kelp zonation towards shallow depth limits (Bartsch et al., 2016). Only *S. latissima* was found to survive on sandy substrate deep in the fjord. At glacier sites *S. latissima* and *L. digitata* dominate, at non glacier sites there was additional coverage of *A. esculenta* (Ronowicz et al., 2020). Similar to other regions of the Arctic, increased kelp occurs where there is a decrease in sea ice with elevated temperatures (Hop et al., 2016; Filbee-Dexter et al., 2022; Krause-Jensen et al., 2012). In addition to these variables, Kvile et al. (2022) found kelp to favour depths less than 30 m and higher wave fetch.

Sea urchins do persist around areas of the Nordic Arctic, favoring high latitude regions (67.5°N and further north), shallow waters and low mean summer temperatures. Additional factors for urchins in this area include low maximum and high minimum current speeds and low wave exposure. Of note, lower urchin densities can favor kelp recovery (Fagerli et al., 2013; Rinde et al., 2014).

2.4.3 Greenland

Kelp follows a decrease in biomass and extent from south to north (64°-77°N) along the Greenland coast due to sea ice cover and warmer waters (Krause-Jensen et al. 2012). Greenland is characterized by fjords and glaciers and experiences high spatial variability among glacier-induced turbidity plumes that can limit primary production in some regions, where clearer waters in other areas allow for kelp growth (Hudson et al., 2014; Lund-Hansen et al., 2018; Stuart-Lee

et al., 2021). As mentioned previously, glacier fjords are unique in their ability to limit primary production through turbidity, yet can also increase it via estuarine circulation and upwelling of nutrients (Cape et al., 2019; Meire et al., 2017). Due to thick sea ice and ice scour throughout the year, Young Sound fjord has low kelp biomass with a depth extent down to 20 m (Borum et al., 2002). Similarly, Nuup Kangerlua fjord has greatest observed kelp density from 0 to 10 m (39.6% average cover) and subsequently decreasing from 10 to 20 (22% average cover) and 20 to 30 m (7.2% average cover) (Ager et al., 2023). Disko Bay, Greenland had kelp growing down to 61 m and even deeper further offshore. These sites are characterized by clear waters with rocky substrate and low urchin density (Filbee-Dexter, 2019). In addition to turbidity influence, urchins are also present throughout the Greenland coastline (Blicher et al., 2007). Therefore, some kelp growth patterns can be explained more regionally as opposed to latitudinally.

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CHAPTER 3.0 MACROALGAE DISTRIBUTION AMONG VARYING GLACIAL FJORDS AS AN INDICATOR OF LIGHT AND NUTRIENT AVAILABILITY

This paper was prepared for submission to peer review in *Arctic Science*. The work represents the core data chapter of my thesis and as first author, it was conducted, analysed, and reported by myself.

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ABSTRACT

Macroalgae play an important part in the coastal ecosystem as a key food source, provision of habitat for a wide variety of species, and sequestering carbon to the bottom of the ocean.

Previous studies suggested that the climate change-induced decreasing sea ice cover in the Arctic is expected to increase kelp distribution. However, warming temperatures also can result in increased glacier melt, runoff, and coastal turbidity that will likely have a negative influence on kelp distribution. In this study we investigate how glacier-induced turbidity and nutrient dynamics could influence the proposed kelp expansion. We analyzed the underwater light and nutrient environment in relation to coverage and depth extent of kelp forests in the Nuuk, Greenland fjords. Reduced light intensities were observed with increasing proximity to glacier fronts, with large subsurface sediment plumes at > 10 m depths within a marine-terminating glacier fjord (Nuup Kangerlua), and at the surface of a land-terminating glacier fjord (Ameralik). Light availability explained up to 56% of observed kelp coverage. Nutrient availability only appeared to influence kelp nearest to the marine-terminating glacier front where kelp nitrogen content was significantly greater relative to other areas, likely due to the upwelling circulation of the fjord. Additionally, high urchin density near the entrance of the glacier fjords suggested an

influence on kelp depth, which confounded the relationship between light availability and kelp depth extent. We conclude that turbidity, via light limitation, and urchin grazing can counteract the expansion of kelp under a decreasing sea ice cover. However, areas with significant nutrient availability sustained by marine-terminating glacier upwelling are suggested to allow for significant kelp production above subsurface turbidity plumes. This greater production is likely to decrease with the retreat of marine glacier termini onto land.

3.1 INTRODUCTION

Climate warming in the Arctic is occurring two to four times faster than the global average (Bintanja, 2018; Jansen et al., 2020; Rantanen, et al., 2022; Walsh, 2014). Intimately linked to this warming is a decrease in sea ice cover, both in extent and thickness, prompting an increase in marine pelagic primary production (Arrigo & Van Dijken, 2015; Stroeve et al., 2014). However, changes will not be limited to phytoplankton, with predicted impacts on ice algae as well as benthic macroalgae (Krause-Jensen & Duarte, 2014; Leu et al., 2015). Though often overlooked, benthic macroalgae, specifically kelp, are extremely influential primary producers in coastal ecosystems. Kelp support a portion of the Arctic marine food web (Christie et al., 2009; Krause-Jensen & Duarte, 2016; Schoenrock et al, 2018), while playing a vital role for other organisms via provision of habitat and shelter, as well as regulation of pH levels to benefit calcifying species (Schoenrock et al, 2018). By decreasing wave action and providing shade against ultraviolet radiation, kelp forests offer refuge to a wide variety of species (Christie et al., 2009). Through the sequestration of surface ocean carbon dioxide to the bottom ocean, kelp may also serve an important function as blue carbon. For example, kelp often become dislodged from their original coastal environment due to storms and strong currents where they can float to open seas, encounter little disturbance from predators, and eventually subside to the deep ocean floor

(Krause-Jensen et al., 2012; Krause-Jensen & Duarte, 2016). The rapid thinning and retreat of sea ice cover in the Arctic region has led to the prediction for kelp to expand their distribution laterally and vertically due to increasing light availability (Krause-Jensen & Duarte, 2014). However, increasing turbidity near rivers, unstable shoreline and melting glaciers may counteract some of this predicted kelp expansion, potentially leading to shoaling depth limits in some coastal environments (Bonsell & Dunton, 2018; Filbee-Dexter et al., 2019).

It is important to recognize that not only sea ice is decreasing at an alarming rate, but so too is the Greenland ice sheet. Rising temperatures exacerbating glacial melt are driving coastal change along the west coast of Greenland (Meredith et al., 2019). This coast is crucial to Greenland's export income and traditional hunting of marine mammals (Meire et al., 2017). Freshwater discharge by glacial melt can influence nutrient supply and turbidity of the water column that can influence primary productivity (Bartsch et al., 2016; Ørberg et al., 2018; Włodarska-Kowalczyk & Pearson, 2004).

Marine-terminating glaciers can exhibit strong mixing patterns due to rising freshwater plumes released subsurface along the glacial terminus. This density driven mixing entrains new nutrients brought up from deep in the water column, enhancing surface primary production within the fjord (Cape et al., 2019; Meire et al, 2017; Spurkland & Iken, 2011; Szeligowska et al., 2021). However, subsurface turbidity plumes may also be produced (Matsuno, et al., 2020; Paulsen & Robson, 2019; Spurkland & Iken, 2011; Szeligowska et al., 2021). Similar to marine-terminating glaciers, increased turbidity is also associated with land-terminating glaciers. In contrast, glacial melt flowing from land spreads highly stratified sediment plumes at the surface that increase light attenuation and impede vertical mixing of new nutrients from depth within these fjord types

(Bartsch et al., 2016; Szeligowska et al., 2021). Therefore, with increasing melt rates and a retreat of glacial termini landward, light attenuation and nutrient availability may limit kelp distribution into the future (Bartsch et al., 2016; Huovinen et al., 2020; Szeligowska et al., 2021).

The Greenland Ice Sheet (GrIS) has accelerated its mass loss rates by ~14% since 1985-1999 through increased surface meltwater runoff and ablation (via calving and submarine melting) of marine-terminating outlet glaciers, making it the single largest contributor to sea level rise (King et al., 2020). An outlet for the GrIS is the Nuuk fjord system. This fjord is experiencing significant sea ice loss, being ice free throughout the majority of the year apart from the inner most region of the fjord (~7 months ice cover). Marine- and land-terminating glaciers feed into the system, making it a unique location to study kelp distribution and its potential response to ongoing change, as it represents the future of many glacial systems (Meire et al., 2016; Meire et al., 2017; Motyka et al., 2017). Here we investigate macroalgae distribution in two contrasting glacial fjords: one with a dominant marine-terminating glacier, Nuup Kangerlua fjord, and one with a land glacier terminus, Ameralik fjord. We demonstrate that turbidity and urchin grazing can impact kelp depth extent, with a strong potential for a decreased kelp distribution with ongoing warming of the Nuuk fjord system.

3.2 METHODS

3.2.1 Study Region

The area of study is the fjordic region surrounding Nuuk, Greenland located at 64.18°N, 51.74°W. Nuup Kangerlua fjord is one of the largest fjord systems in the world at 190 km in length with an estimated 2089 km² of underlying bottom area (Meire et al., 2017; Mortensen et al., 2011; Storr-Paulsen et al., 2004). The Nuup Kangerlua fjord system contains three marine-

and three land-terminating glaciers connected to the GrIS, Kangiata Nunaata Sermia being the largest marine-terminating glacier in the fjord which has a grounding depth of 250 m (Mortensen et al., 2011; Winsor et al., 2015). Ameralik fjord, located just south of Nuuk is ~75 km long and receives land-terminating glacier meltwater delivered from Naajat Kuuat river from the GrIS. This fjord often remains ice free throughout the year and is warmer, more saline and more stratified in comparison to Nuup Kangerlua due to the lack of influence from marine-terminating glaciers (Stuart-Lee et al., 2021).

Sampling was conducted throughout the Nuup Kangerlua and Ameralik fjords from 3 to 17 August 2022. Greenland Institute of Natural Resources “Avataq” and “Aage V Jensen II” motorboats were used for sampling. Stations were selected based on bottom depth and proximity to shore along a gradient, and spread approximately 5 to 7 km apart into the fjord for a total of 26 stations (Figure 3.1). Each station was composed of a perpendicular to coast transect, comprised of 6 sampling depths at 5, 10, 15, 20, 25 and 30 m. The minimum target depth of 5 m was set due to logical constraints of vessel draft and proximity to land, the maximum depth of 30 m was set as kelp was often not present deeper.

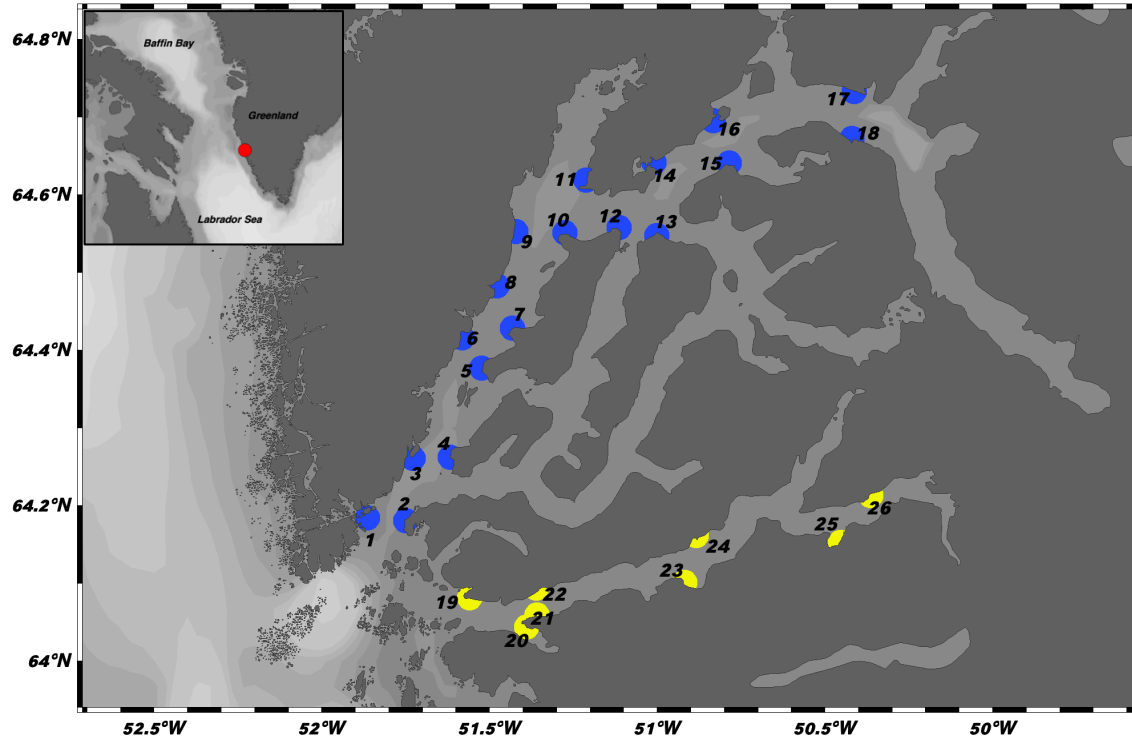


Figure 3.1. Nuuk Fjords, Greenland, containing Nuup Kangerlua (blue stations 1-18) and Ameralik fjords (yellow stations 19-26).

3.2.2 Sample Collection

To estimate kelp distribution, a GoPro camera (HERO6 Black) and flashlight were attached to a weighted fin-stabilized frame (Group B inc.) and lowered by hand to approximately 2 m above the ocean floor to collect 2 minutes of video at each sampling depth (Filbee-Dexter & Scheibling, 2017). The camera field of view was estimated at 6.19 m² (L x W; 2.75 x 2.25 m), as measured when held 2 m above the seafloor. Hydrographic and light profiles were collected using a conductivity, temperature and depth (CTD) sonde (RBR concerto), housed with a LI-193 spherical photosynthetically active radiation (PAR; 400-700 nm) sensor (Li-COR) and deployed by hand at 10 and 30 m bottom depths along each transect. Using a custom built 360° drag rake, 2-3 *S. latissima* kelp were retrieved from all stations where available for collection at the 10 m

bottom depth. Mature intact kelp were selected and kept in a dark cooler until processing later that day.

Using a Niskin bottle (5 L), water samples were collected at surface and 10-m depth increments from the 10 m and 30 m bottom depth sites; nutrient samples were filtered immediately. Water collection for total suspended solids (TSS) and chlorophyll *a* samples were only collected from the 30 m bottom depth at 10-m depth increments. These water samples were stored in a triple rinsed opaque Nalgene bottle and filtered at the end of the day.

3.2.3 Light Estimates

Using the CTD profile from the 30-m bottom depth, euphotic depth was defined as the depth receiving 1% surface PAR calculated using Beer-Lambert's law (Ryther, 1956). Removing ~1 to 5 m from the upper water column to eliminate any artifacts from the boat, a downwelling diffuse attenuation coefficient, K_d^{PAR} , was determined as the exponential slope of PAR verses depth, from the CTD profiles collected in August 2022. It is noted that a distinct difference in K_d^{PAR} was observed between the upper (~0-15 m) and lower (~15-30 m) water column at stations 17 and 26. Subsequently, an average between the upper and lower K_d^{PAR} estimates were used for additional calculations.

To determine incoming light throughout the year, shortwave incoming radiation data (*SW*) was retrieved from the Greenland Ecosystem Monitoring Database (GEM) – ClimateBasis Nuuk as a 5-minute average ($W m^{-2}$). *SW* data were converted to PAR using the following equation (1).

$$PAR^{0+} = \sum_{5min} SW \times 0.46 \times 4.57 \times 300 \quad (1)$$

where PAR^{0+} is PAR just above the ocean's surface. In this equation, PAR is assumed a fraction of SW , equal to 0.46 (Kvifte et al., 1983). $W\ m^{-2}$ were converted to $\mu mol\ photons\ m^{-2}\ 5\ min^{-1}$ using a conversion factor of 4.57 (Sager and McFarlane, 1997), then converted from seconds to 5-minute estimates by multiplying by 300 seconds. These 5-minute estimates were then integrated over one day. To take into account reflection at the atmosphere-ocean interface, we assumed an 8% mean loss of light (i.e., $PAR^{0-} = 0.92 \times PAR^{0+}$; Bélanger et al, 2013; Morel, 1991). To estimate light attenuation throughout the year, monthly K_d^{PAR} estimates were acquired from 2018-2022 MODIS Aqua L1A satellite data using methods described in Singh et al (2022). Monthly averages over the 5 years were calculated. If all 5 years had missing data for a month, we used annual medians. If more than half the monthly values were annual medians (specifically, stations 17, 19, 24, 22, and 26; see Figure 3.1), K_d^{PAR} was interpolated using the 8 closest data points in all directions surrounding the station ($2.22 \times 2.22\ km$ area). We note that K_d^{PAR} does not include November-January due to negligible light conditions.

Due to high August 2022 K_d^{PAR} estimates relative to that measured in August 2022 K_d^{PAR} , all K_d^{PAR} values were corrected by dividing the slope of the linear regression between the two variables with a forced intercept of 0. The resultant relationship was $K_d^{PAR} = 1.24\ K_d^{PAR}$ (i.e., all K_d^{PAR} estimates were divided by 1.24) (Figure 3.2). Note that station 26 was an outlier, and therefore, not included in the correction relationship.

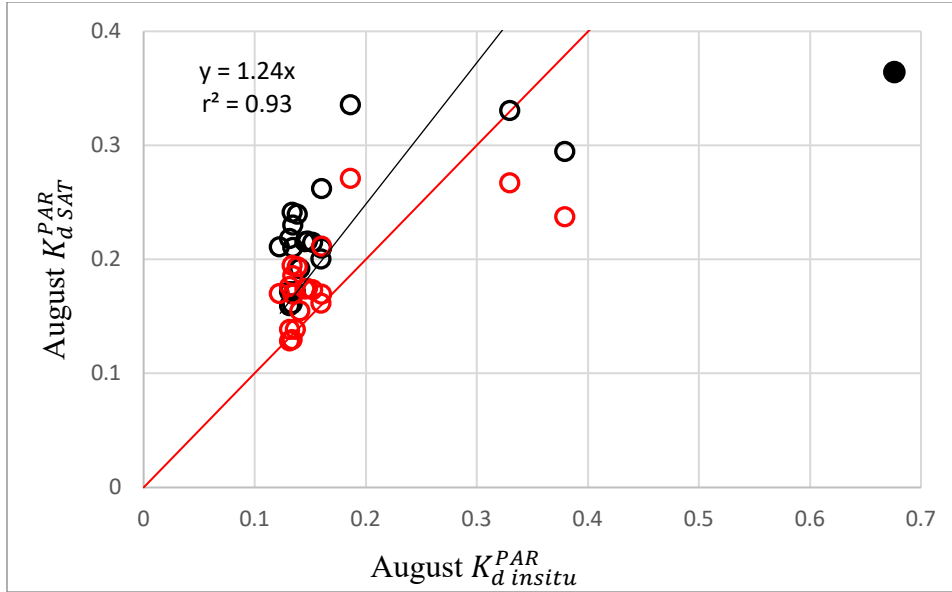


Figure 3.2 Measured August 2022 K_d^{PAR} versus satellite-derived August 2022 $K_d^{PAR}_{SAT}$ indicated by black open circles. The black line is a least squares linear fit (forced with a 0 intercept) used for the correction of the satellite estimates (see text). The open red circles indicate the corrected values of estimated August 2022 $K_d^{PAR}_{SAT}$ that were used for calculations. The red line is a 1:1 line. The filled black circle is station 26 and is noted as an outlier.

Hereinafter, all reported K_d^{PAR} values provided were calibrated using the above procedure.

Daily-integrated PAR at depth ($iPAR_z$) was then calculated using PAR^0 and monthly K_d^{PAR} or $K_d^{PAR}_{insitu}$ to determine light throughout the year ($iPAR_{z-year}$) or for August 2022 ($iPAR_{z-Aug}$), respectively.

3.2.4 GoPro and Kelp C:N Analysis

The GoPro videos were analysed as a point observation of percent of kelp relative to the sea floor to determine kelp percent cover along a depth gradient (Krause-Jensen et al, 2012). Three still images were selected from each video and analysed in MuliSpec64 (2019.08.19). Poor quality GoPro videos were not included in analysis. The still images were selected first based on overall best representation of the entirety of the video and selecting an image from the beginning, middle and end of the video. Using a supervised classification scheme, images were placed in

one of two classes, kelp cover or sea floor to determine kelp cover as a percent (0-100%). Where sand was covering the kelp, extra caution was taken to ensure correct classification to eliminate flawed class diagnoses.

Following methods of Castro de la Guardia et al. (2023) and Krause-Jensen et al. (2012), kelp depth extent for 1, 10, 50 and 80% coverage was defined as the deepest depth occurrence of where this percent was visible. Linear interpolation between sampled 5 m depth intervals was used to estimate depth extent. However, when the 30 m depth (maximum recorded depth) had greater than 1% kelp cover, depth extent estimates were made using linear extrapolation including points that allowed for the best fit of the natural progressive decrease of kelp cover at that station.

In addition to kelp coverage and depth extent, videos were analysed for high and low canopy, kelp species, sea floor substrata and urchin density. High canopy was defined by the presence of a buoyant stipe, seemingly extended off the seafloor, with the strong likelihood that more kelp was present underneath the canopy, as per Castro de la Guardia (2023). Low canopy was defined by low-lying kelp species (with no stipe presence) or if stipes were present, they were not buoyant and kelp remained low lying on the seafloor. Substrata estimates assumed that the visible substratum was representative of the entire image, even when only a small percent was visible (<10%). Substrata was categorized as “sandy” or “rocky”, and where both types were present, “mixed”. Urchins were manually counted in each of the 3 selected still images following Ager et al. (2023) and Filbee-Dexter and Scheibling (2017). Using the assumption that the field view of the camera was 6.19 m², urchin density (number m⁻²) was estimated. It is noted that

urchins could be present underneath high kelp canopy, and therefore, our density estimates are likely conservative.

Measurements of length and width of collected *S. latissima* samples were measured at the blade's longest and widest points and used to determine blade area ($L \times W$). Using a punch (1.27 cm diameter), kelp blades were cored at the meristem and center of the blade. The cored kelp samples were placed into pre-burnt (5 h at 450 °C) tinfoil packets and preserved in a -20°C freezer. To determine carbon (C) and nitrogen (N) levels of the kelp, samples were thawed (~30 mins) and weighed to determine wet weight (WW) of the core. Samples were then placed in the oven and dried at 60°C for 48 hours and weighed again to determine dry weight (DW). The dried kelp was then crushed and 3 replicate samples of ~300-500 µg of kelp were placed in a tinfoil capsule where C and N contents were quantified on a SerCon 20-22 Stable Isotope Ratio Mass Spectrometer coupled with Europa EA-GSL Sample Perception System. The values of carbon and nitrogen were corrected based on blank values and sample weight, then averaged between the 3 replicates.

To calculate *S. latissima* biomass (g WW m^{-2}) at the 10 m depth, the blade area was divided by the kelp corer area ($1.3 \times 10^{-4} \text{ m}^2$) and multiplied by the core wet weight (WW). The average WW of kelp per station was then multiplied by the percent *S. latissima* cover at the 10 m depth. To calculate production ($\text{g C m}^{-2} \text{ yr}^{-1}$), we used WW biomass to C conversion ratios of 0.16 WW:DW and 0.32 DW:C, determined from our data averages. These conversion ratios were similar to ratios used by Filbee-Dexter et al. (2022) of 0.21 and 0.30, respectively. This production estimate is considered to be for one year of growth, as there was no evidence of the previous year's growth.

3.2.4 Water Data Analysis

To determine nutrient concentrations, 15-ml pseudo-duplicate samples were directly taken from the Niskin bottle and filtered through a 25-mm pre-combusted (5 h at 450 °C) GF/F filter into acid washed and triple rinsed vials and frozen at -20°C. Nutrient concentrations were determined at the Aarhus University in Denmark. After reduction to NO in hot vanadium chloride, concentrations of nitrate (NO₃) and nitrite (NO₂) were determined as NO on a NOx analyzer (Model 42C, Thermo Environmental Instruments).

Two subsamples for chlorophyll *a* concentration were collected by filtering ~300-500 mL of sample seawater through a 25-mm GF/F, wrapped in tinfoil, and frozen at -80°C until analysis. For analysis, chlorophyll *a* filters were placed in 20-mL scintillation vials with 90% acetone for extraction of pigments over 18-24 hours at 4 °C in the dark. Florescence of the extracted sample was measured before and after acidification with approximately 0.2 mL of 5% HCl using a Turner Designs Trilogy Fluorometer (Version 1.7). Protocols and chlorophyll *a* concentration determination followed that of JGOFS (1994).

Two subsamples for total suspended solids (TSS) determination were collected by filtering approximately 1000-2000 mL of seawater onto a 47-mm Whatman ProWeigh filter, which was air dried for ~1 hour and then frozen at -20°C. Later, samples were dried in an oven at 75°C for 24 hours and weighed. Initial filter weight was subtracted from the weight of the filter with sample and divided by the volume of filtered sample to determine the concentration of TSS (mg L⁻¹; Neukermans et al., 2012).

3.2.6 Statistical Analysis

All analyses were performed in R (RStudio 2022.07.2), or in Excel using the data analysis tool. Normality of the data was assessed using a Shapiro-Wilk test. A Bartlett test was run to determine equal or unequal variances. Based on results from these initial assumption tests, an ANOVA (F-statistic) or Kruskal-Wallis test (non-parametric; H-statistic) was used to assess the differences in group means, where heteroscedasticity was observed, a student's t-test (T-statistic) was used. Post-Hoc Tukey Kramer test or Dunn's (Bonferroni adjusted p values) test were performed to compare means within groups when necessary. Paired T-test (T-statistic) or Wilcoxon signed ranks test (Z-statistic; non-parametric) were used to compare carbon and nitrogen values between meristem and blade samples of individual kelp. When comparing nominal variables, a Chi-squared test of independence was used. For all tests, p values ≤ 0.05 were considered significant and ns (not significant) implies a p value >0.05 . Spearman Rank correlation was used to determine the degree of association between variables used in stepwise multiple linear regression analysis (Table S1). For multiple linear regression analysis, using z-score standardization, data were rescaled onto a common scale to reduce the effects of multicollinearity for more equivalent comparison among variables. The stepwise linear regression iteratively included or excluded variables based on the models adjusted r^2 improving by at least 0.05 while assuring the model had a p value ≤ 0.05 . All values are presented as mean $\pm$ standard deviation unless otherwise stated.

3.3 RESULTS

3.3.1 Environmental Characteristics

*Temperature, salinity & chlorophyll *a**

Four sub-regions throughout the fjords were identified based on environmental and regional differences observed in the upper 30-m hydrographic profiles (Figure 3.3). Nuup Kangerlua had significant temperature (°C) and salinity gradients throughout its fjord, and contained three of the four identified sub-regions (Table 3.1 and Figure 3.4). Temperature decreased deeper into Nuup Kangerlua, with means of $3.84 \pm 0.43^{\circ}\text{C}$ at the entrance (EN), $2.22 \pm 0.28^{\circ}\text{C}$ in mid Nuup (MN) and $1.16 \pm 0.27^{\circ}\text{C}$ in deep Nuup (DN). Ameralik (AM) was the warmest of the two fjords with an average of $4.90 \pm 0.66^{\circ}\text{C}$. Salinity decreased from EN towards DN with salinities of, 30.6 ± 0.7 , 28.8 ± 0.9 and 26.4 ± 1.1 , respectively. Ameralik was the most saline of the four identified sub-regions at 31.3 ± 1.0 . Significant differences in temperature and salinity were observed between AM and MN, as well as AM and DN. Within Nuup Kangerlua, significant differences in temperature and salinity were observed between EN and DN sub-regions. Chlorophyll *a* concentration averaged $1.16 \pm 0.76 \mu\text{g L}^{-1}$ throughout the fjords and was not significantly different between regions (Table 3.1 and Figure 3.4).

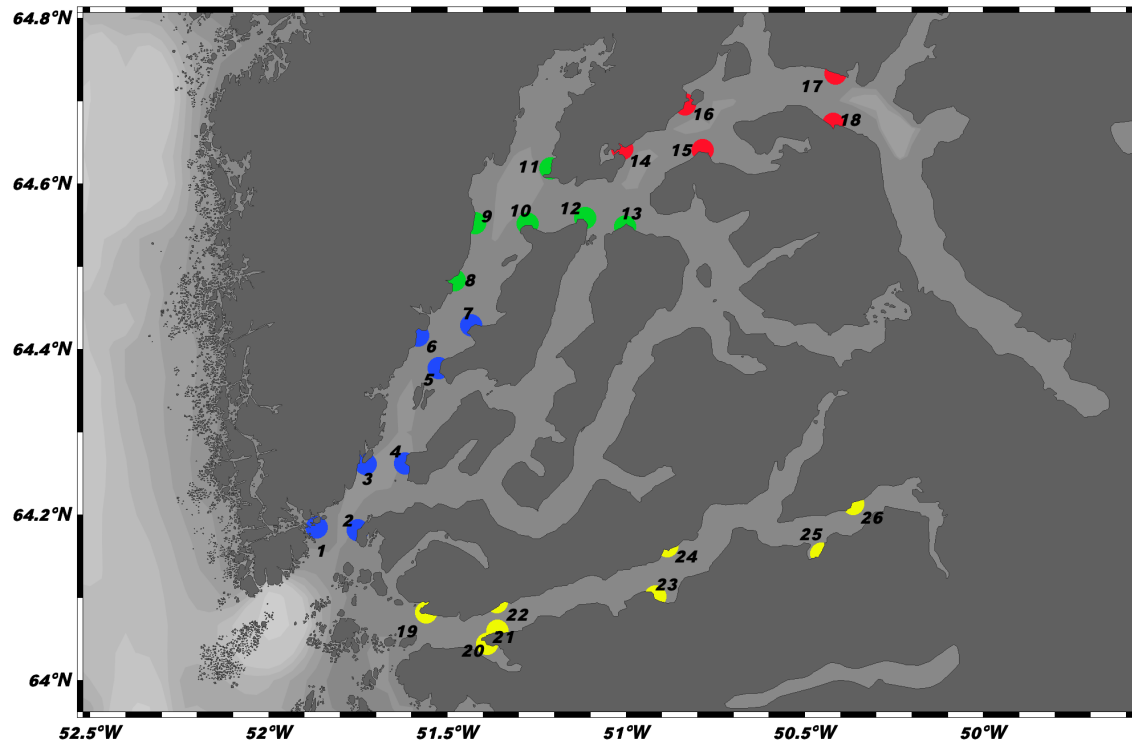
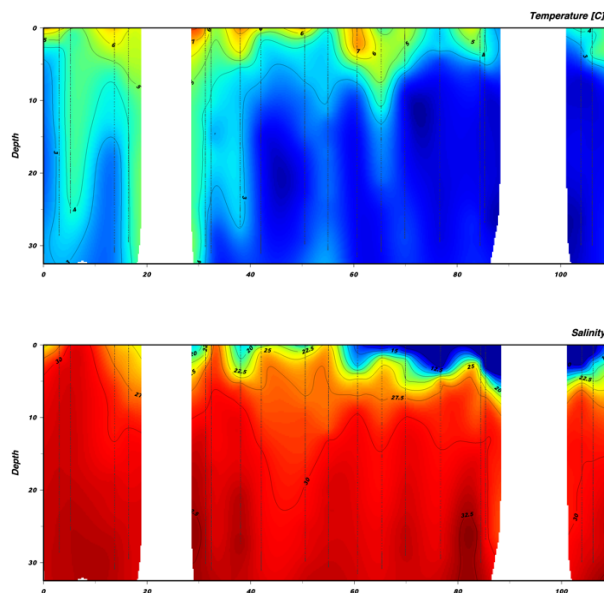
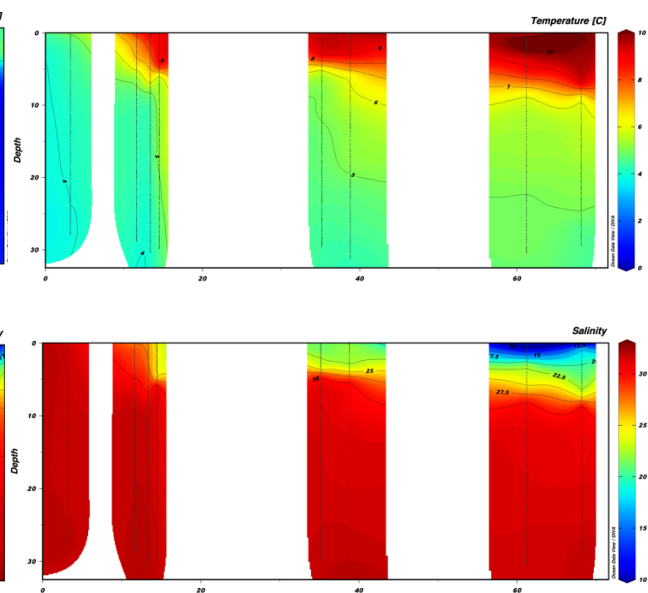


Figure 3.3 The four identified sub-regions of the Nuuk fjords examined. Nuup Kangerlua entrance stations (EN) in blue, mid stations (MN) in green, and deep stations (DN) in red, and Ameralik (AM) stations in yellow.

a)



b)



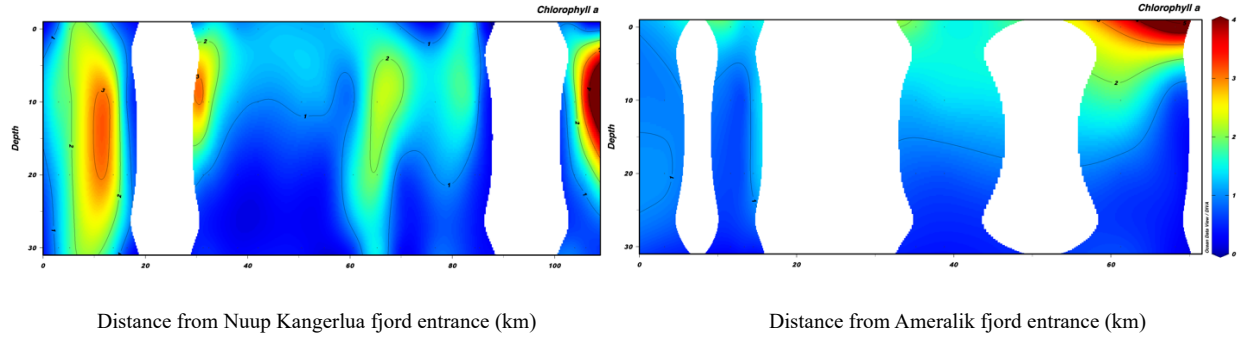


Figure 3.4 a) Nuup Kangerlua and **b)** Ameralik fjord CTD temperature (°C), salinity, and chlorophyll *a* (µg L⁻¹) profiles from 0 – 30 m.

Table 3.1 Average and standard deviations of water column (0-30 m) temperature, salinity, chlorophyll *a*, TSS, nitrate, euphotic depth, K_d^{PAR} and K_d^{PAR} for stations in each sub-region (see Figure 3.3 for sub-region locations). ANOVA or Kruskal Wallis results with F or H statistics, respectively, and p values for differences between groupings. Statistically significant results (p value ≤ 0.05) are bolded. EN stands for entrance to Nuup Kangerlua, MN for mid Nuup Kangerlua, DN for deep Nuup Kangerlua and AM for Ameralik fjord.

Variable	Group				ANOVA or Kruskal Wallis		Post-HOC p values					
	EN (n=7)	MN (n=6)	DN (n=5)	AM (n=8)	F or H test	P-value	EN vs. MN	EN vs. DN	MN vs. DN	EN vs. AM	MN vs. AM	DN vs. AM
Temperature(°C)	3.84 ± 0.43	2.22 ± 0.28	1.16 ± 0.27	4.90 ± 0.66	H-test $\chi^2_3 = 22.61$	<0.0001	ns	0.03	ns	ns	0.006	<0.0001
Salinity	30.6 ± 0.7	28.8 ± 0.9	26.4 ± 1.1	31.3 ± 1.0	H-test $\chi^2_3 = 19.49$	0.0002	ns	0.02	ns	ns	0.03	<0.0001
Chlorophyll <i>a</i> (µg L ⁻¹)	1.39 ± 0.47	1.04 ± 0.41	1.07 ± 0.40	1.11 ± 0.29	F _{3,22} = 1.07	ns	-	-	-	-	-	-
Total Suspended Solids (mg L ⁻¹)	12.7 ± 2.2	11.0 ± 1.7	18.5 ± 7.7	13.2 ± 2.9	H-test $\chi^2_3 = 7.81$	0.05	ns	ns	0.03	ns	ns	ns
Nitrate (µmol L ⁻¹)	1.98 ± 0.42	2.53 ± 0.86	3.79 ± 0.76	0.95 ± 0.54	H-test $\chi^2_3 = 18.44$	0.0004	ns	ns	ns	ns	0.03	<0.0001
Euphotic Depth (m)	33.8 ± 3.2	30.1 ± 1.8	16.9 ± 6.9	29.9 ± 8.2	H-test $\chi^2_3 = 14.4$	0.002	ns	0.001	ns	ns	ns	ns
K_d^{PAR} (m ⁻¹)	0.138 ± 0.015	0.154 ± 0.009	0.319 ± 0.148	0.181 ± 0.113 m	H-test $\chi^2_3 = 14.39$	0.002	ns	0.001	ns	ns	ns	ns
K_d^{PAR} SAT-year (m ⁻¹)	0.169 ± 0.017	0.173 ± 0.020	0.227 ± 0.046	0.200 ± 0.031	H-test $\chi^2_3 = 12.53$	0.006	ns	0.003	ns	ns	ns	ns

3.3.2 Light Attenuation

Averaged TSS estimates from EN, MN, DN, and AM were, 12.7 ± 2.2 , 11.0 ± 1.7 , 18.5 ± 7.7 and 13.2 ± 2.9 mg L⁻¹, respectively, with a significant difference only observed between MN and DN (Figure 3.5 and Table 3.1). In Nuup Kangerlua fjord the euphotic depths from EN, MN and DN were 33.8 ± 3.2 , 30.1 ± 1.8 and 16.9 ± 6.9 m, respectively, while in Ameralik fjord, the euphotic depth averaged 29.9 ± 8.2 m. It is noted that all Ameralik stations had a euphotic depth greater than 30 m with the exception of station 26, nearest to the land-terminating glacier, which had a euphotic depth of 9.98 m. DN had a significantly shoaled euphotic depth compared to EN (Table 3.1).

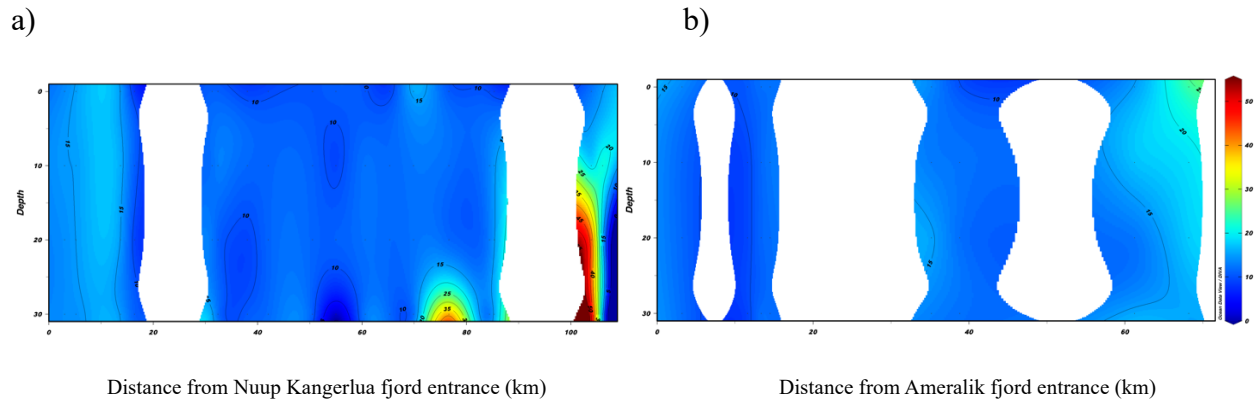


Figure 3.5 a) Nuup Kangerlua and **b)** Ameralik fjord total suspended solids (mg L⁻¹) profiles sampled at surface, 10, 20 and 30 m.

$K_{d\text{ in situ}}^{PAR}$ measured at each station was significantly related to TSS in the water column ($r^2 = 0.69$, $p < 0.0001$). $K_{d\text{ in situ}}^{PAR}$ was highest nearest the glacier discharge in both fjords and decreased towards the entrance of both fjords. The decrease in average $K_{d\text{ in situ}}^{PAR}$ within Nuup Kangerlua from EN, MN and DN was 0.138 ± 0.015 , 0.154 ± 0.009 and 0.319 ± 0.148 m⁻¹, respectively, with a fjord average of 0.193 ± 0.108 m⁻¹. Station 17 and 18 had the greatest attenuation at 0.546 and 0.380 m⁻¹, respectively. In Ameralik fjord, station 26 had the highest value at 0.462 m⁻¹ with

other K_d^{PAR} estimates ranging from 0.134-0.153 m⁻¹ and a fjord average of 0.181 ± 0.113 m⁻¹.

DN K_d^{PAR} differed significantly from EN (Table 3.1). Overall, the Nuuk fjord system had an average K_d^{PAR} of 0.189 ± 0.108 m⁻¹. Light attenuation within the fjords did not show a significant linear relationship to chlorophyll *a* concentration.

Monthly averaged (2019-2021) incoming light ($iPAR^0$) for the Nuuk fjord area is presented in Figure 3.6, which along with K_d^{PAR} , were used to determine calculations of $iPAR_{z-year}$, available light at depth over an annual period. K_d^{PAR} from spring (March-May), summer (June-August), fall (Sept-Oct) and winter (Feb), averaged 0.171 ± 0.030 , 0.196 ± 0.047 , 0.220 ± 0.049 and 0.171 ± 0.033 m⁻¹. It is noted that K_d^{PAR} reached its maximum in fall while incoming light peaked in spring/summer. Overall, the Nuuk fjord system K_d^{PAR} averaged of 0.190 ± 0.036 over an annual period.

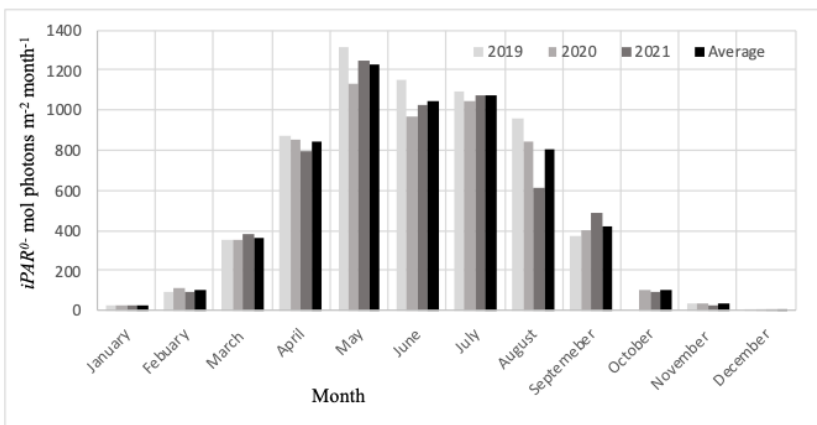


Figure 3.6 Incoming $iPAR^0$ for each month from 2019-2021.

3.3.3 Nutrient Dynamics

Nutrient availability throughout the two fjords varied significantly. An increasing trend was observed in the Nuup Kangerlua fjord with 0-30 m averaged nitrate concentrations of 1.98 ± 0.48 , 2.53 ± 0.86 , and $3.79 \pm 0.76 \mu\text{mol L}^{-1}$ from entrance to deep sites, respectively. Both DN and MN sub-regions had significantly greater nitrate than that of AM, which averaged $0.95 \pm 0.54 \mu\text{mol L}^{-1}$ (Table 3.1 and Figure 3.7). In contrast, nitrate concentration in Nuup Kangerlua fjord averaged $2.66 \pm 2.18 \mu\text{mol L}^{-1}$.

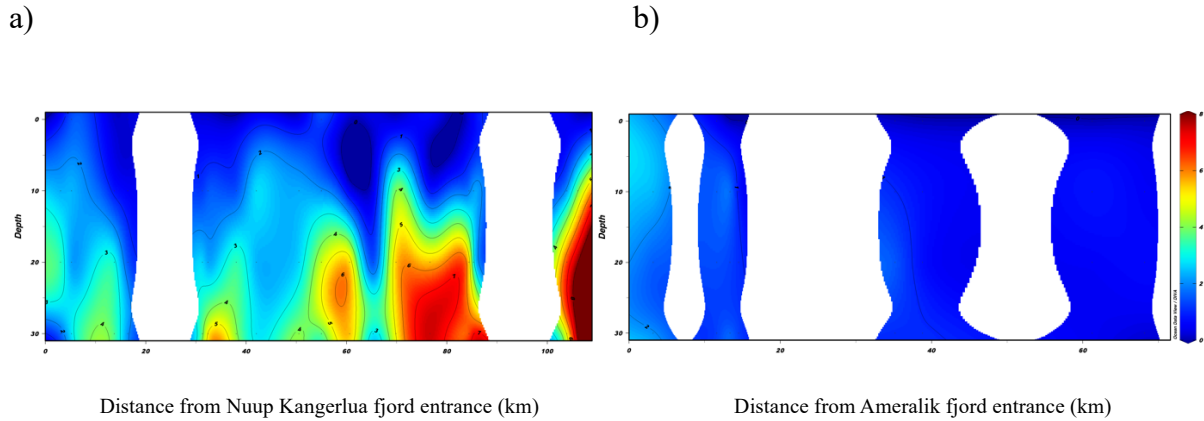


Figure 3.7 a) Nuup Kangerlua and **b)** Ameralik nitrate ($\mu\text{mol L}^{-1}$) profiles.

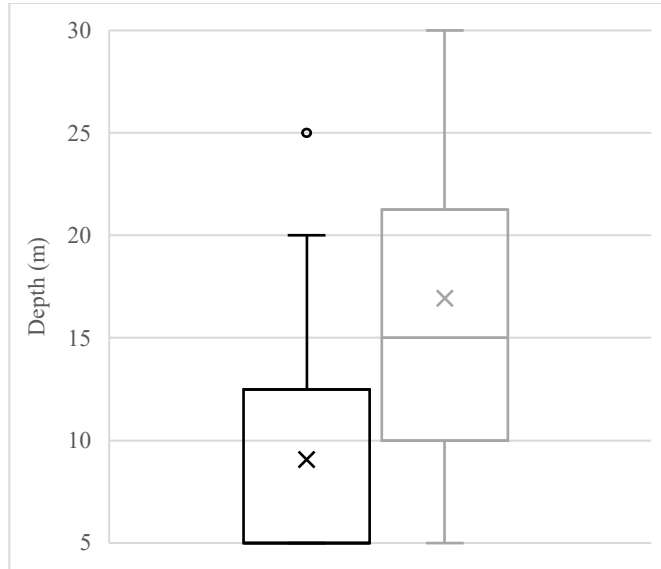
3.3.4 Kelp Distribution

Kelp Species Trends

The kelp assemblages were predominantly composed of high canopy *Saccharina latissimi* and low canopy *Agarum clathratum* species. Other kelp species had minimal coverage (<50%) and were only observed at stations 1, 2, 3 and 10 at the 5 m depth. Sampling depths where *S. latissimi* dominated (greater percent cover than *A. clathratum*) had significantly greater percent kelp cover (median = 63.7%) than depths where *A. clathratum* dominated (i.e., *A. clathratum* had a greater percent cover than *S. latissima*) (median = 26.7%) (H-test $\chi^2_1 = 13.79$; $p = 0.0002$). *A. clathratum* dominated at 70 sampled depths while *S. latissima* only dominated at 37 (Figure 3.8 a). Nuup Kangerlua fjord had greater percent *S. latissima* cover with a mean of $19.3 \pm 33.1\%$ from 0-30 m, while Ameralik fjord had a mean of $3.23 \pm 9.26\%$ (H-test $\chi^2_1 = 7.61$; $p = 0.006$). There was also a significant difference in *A. clathratum* cover between fjords with Nuup Kangerlua averaging $12.9 \pm 22.5\%$ and Ameralik averaging $22.9 \pm 26.1\%$ (H-test $\chi^2_1 = 9.65$; $p = 0.001$). Furthermore, the average depth of *S. latissima* dominance was significantly shallower

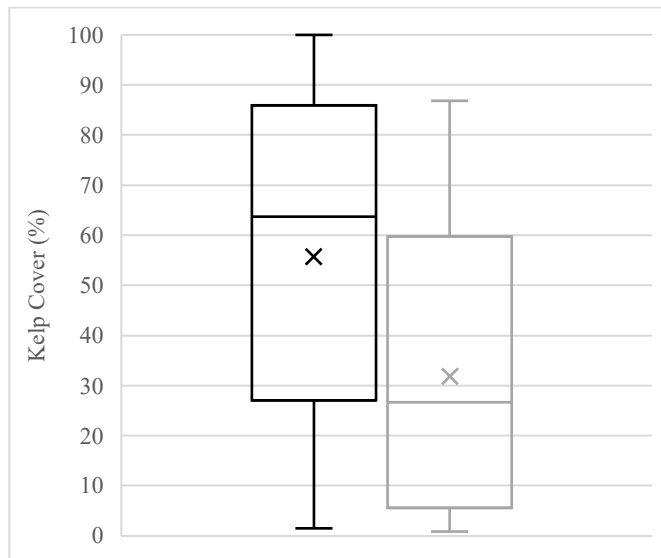
than the average depth of *A. clathratum* dominance, with averages of 9.05 ± 5.12 and 16.9 ± 7.09 m, respectively (H-test $\chi^2_1 = 28.71$; $p < 0.0001$) (Figure 3.8 b).

a)



S. latissima *A. clathratum*

b)

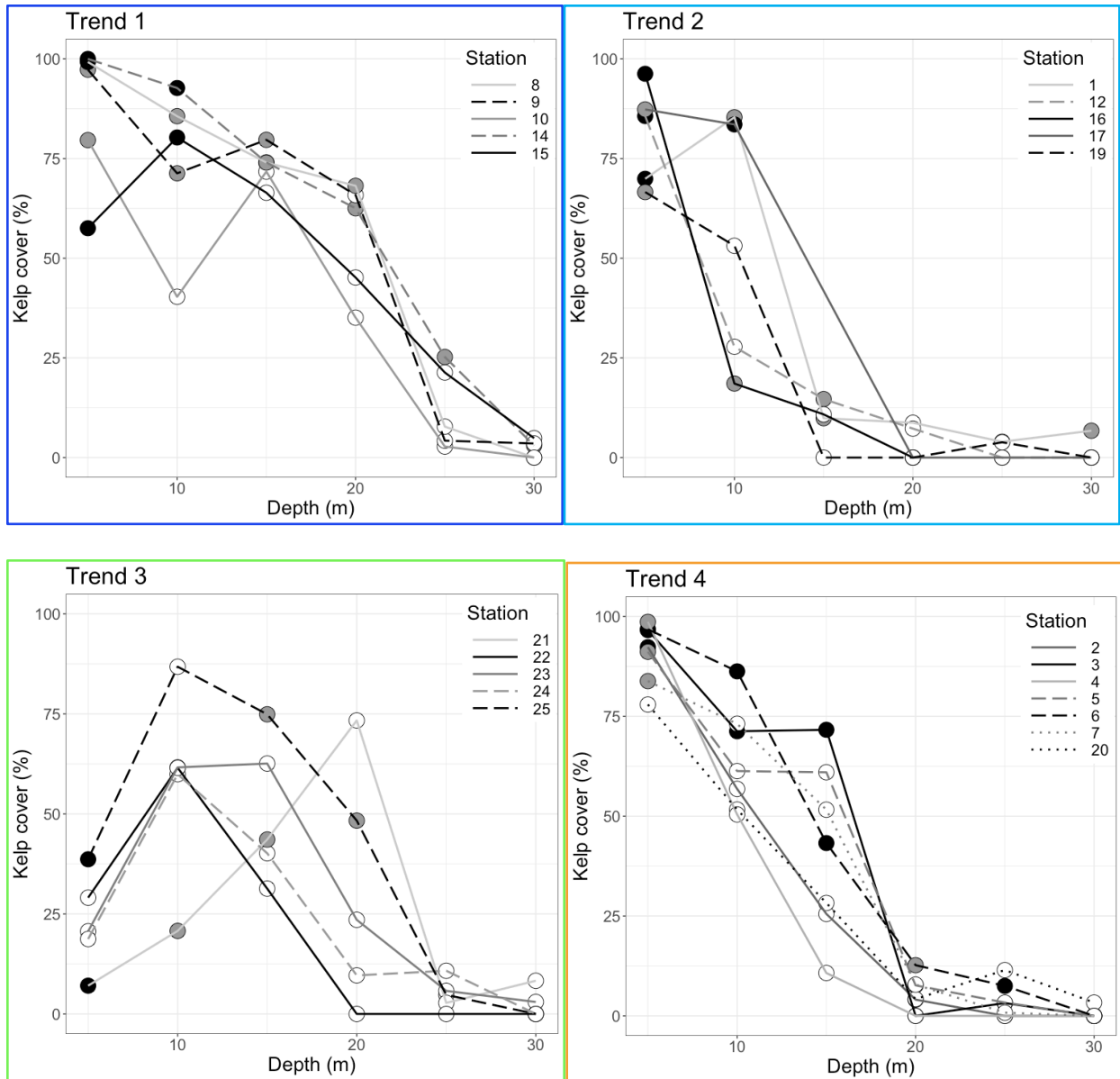


S. latissima *A. clathratum*

Figure 3.8 a) Boxplot of the percent kelp cover of the dominate kelp species **b)** Boxplot of the depth of the dominate kelp species *S. latissima* (black) and *A. clathratum* (grey). Boxplots include the 25th and 75th percentiles, maximum and minimum, dot reveals outlier point, central line depicts the median (at 5 m for *S. latissima* figure b) and the “x” reveals the mean. Numbers in parenthesis show the number of samples.

Kelp Distribution Trends

Kelp within the Nuup Kangerlua and Ameralik fjords have been characterized into 5 visually different trends based on percent kelp cover, kelp depth extent, and high or low canopy (Figure 3.9). Stations 8, 9, 10, 14, and 15 formed trend 1 located in the middle of Nuup Kangerlua and were characterized by high canopy cover at shallow depths, with continuing dense cover of >40% kelp at 20 m bottom depth. Trend 2 made up of stations 1, 12, 16, 17, and 19 were more dispersed, with some stations near the entrance and some located more interior within Nuup Kangerlua fjord. These stations were characterized by a rapid decrease of ~60% kelp at 10-15 m, with little to no kelp past the 15 m depth. Stations 21 through 25 composed trend 3 and were all located within the Ameralik fjord, which had <40% kelp cover at 5 m and an increase to >60% cover between 10 and 20 m, followed by a rapid decrease at greater depths. Trend 4 consisted of stations 2 through 7 and station 20. These stations were located near the entrance of the fjords and were characterized by a trend of >80% cover at 5 m with steady decline, and <15% kelp at 20 m. Trend 5, included stations 11, 13, 18 and 26 which had <40% low canopy kelp at all depths. These stations were spread out between the fjords.



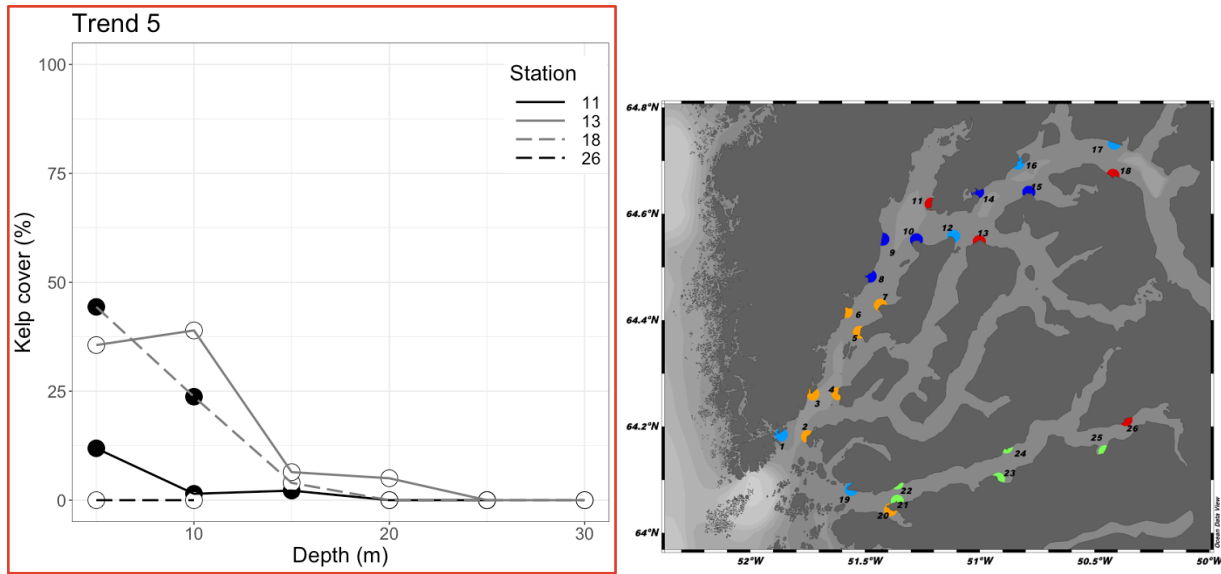


Figure 3.9 Trend 1 (dark blue), Trend 2 (light blue), Trend 3 (green), Trend 4 (orange) and Trend 5 (red) color corresponds to the station colors on the map. Black circles indicate high canopy cover (most often *Saccharina latissima*), white circles indicate low canopy cover (most often *Agarum clathratum*), grey circles indicate the presence of both high and low cover.

Variables of Kelp Percent Cover

Mixed substrate was the dominant substrate type accounting for 70 out of 156 images classified. Of the remaining images, 43 were classified as rocky, 29 as sandy and 14 as unidentified due to inadequate video or canopy cover masking the sea floor. There was no significant impact of substrate on kelp percent cover (H-test $\chi^2_2 = 3.07$; $p = 0.22$).

Simple linear regression was examined for relationships of kelp cover versus temperature, salinity, chlorophyll *a* concentration, nitrate concentration, $iPAR_{z-year}$ and urchin density (Table S2). Of significance, percent kelp cover was most related to $iPAR_{z-year}$ ($r^2 = 0.43$, $p < 0.0001$). Relationships against salinity ($r^2 = -0.16$, $p < 0.0001$), chlorophyll *a* ($r^2 = 0.15$, $p < 0.0001$) and nitrate concentration ($r^2 = -0.11$, $p < 0.0001$) were also observed. With respect to *S. latissima*, percent cover was most related to $iPAR_{z-year}$ ($r^2 = 0.35$, $p < 0.0001$) and salinity ($r^2 = -0.23$, $p < 0.0001$). *A. clathratum* cover was not strongly ($r^2 < 0.05$) related to any of the 6 variables.

Stepwise linear regression was run using the same variables to see how they interact together to explain percent kelp cover (temperature, salinity, urchin density, $iPAR_{z-year}$ and nitrate concentration). Of the 6 variables examined, $iPAR_{z-year}$, temperature and nitrate were significant in the final model which explained 54% of the variation in kelp percent cover within the Nuuk fjord system (Table 3.2). The same variables were significant to explain kelp cover in the final model specific to Nuup Kangerlua fjord, explaining 62% of the variability. Specific to *S. latissima* percent cover, the final stepwise regression model selected all variables, excluding salinity, to explain 57% of the variability in the Nuuk fjord (Table 3.3). When only considering Nuup Kangerlua fjord, the model selected $iPAR_{z-year}$, temperature, nitrate and urchin density to explain 56% of the variability in *S. latissima* cover. No significant findings were observed for kelp cover specific to *A. clathratum* or Ameralik fjord (model $r^2 < 0.50$).

Table 3.2 Stepwise linear regression models predicting kelp cover for **a)** the Nuuk fjords and for **b)** Nuup Kangerlua fjord. Regression coefficients (B), standard error of B , t values and level of significance (p) are presented.

a)	Co-efficient (B)	Std. Error of B	t value	p	Model r^2
(Intercept)	64.1	8.85	7.25	< 0.0001	0.54
$iPAR_{5\text{-year}}$	0.028	0.003	10.6	< 0.0001	
Temperature	-9.47	1.58	-6.00	< 0.0001	
Nitrate	-7.81	1.70	-4.60	< 0.0001	
b)					
(Intercept)	55.3	9.83	5.63	< 0.0001	0.62
$iPAR_{5\text{-year}}$	0.033	0.004	9.29	< 0.0001	
Temperature	-9.83	2.20	-4.47	< 0.0001	
Nitrate	-6.10	1.80	-3.39	0.0001	

Table 3.3 Stepwise linear regression models predicting *S. latissima* cover for **a)** the Nuuk fjords and for **b)** Nuup Kangerlua fjord.

a)	Co-efficient (B)	Std. Error of B	t value	p	Model r^2
(Intercept)	43.7	8.16	5.36	< 0.0001	0.57
$iPAR_{5\text{-year}}$	0.021	0.002	8.86	< 0.0001	
Temperature	-9.63	1.35	-7.12	< 0.0001	
Chlorophyll a	7.08	3.22	2.20	0.03	
Nitrate	-7.15	1.44	-4.97	< 0.0001	
Urchin Density	-1.43	0.46	-3.10	0.002	
b)					
(Intercept)	41.3	9.90	4.17	< 0.0001	0.56
$iPAR_{5\text{-year}}$	0.025	0.004	6.91	< 0.0001	
Temperature	-7.47	2.36	-3.17	0.002	
Nitrate	-6.14	1.81	-3.39	0.001	
Urchin Density	-1.68	0.667	-2.52	0.01	

Regional comparisons of kelp depth extent

Kelp depth extent and light availability was explored on a wider spatial scale by comparing our data to published data from western Greenland and offshore Disko Bay from Krause-Jensen et al. (2012; 2019) and Southampton Island (SHI) from Castro de la Guardia et al. (2023) (Figure 3.10). We identified that western Greenland and the Nuuk fjords had a similar depth extent and light availability for 1, 10 and 50% kelp cover (Table 3.4). Depth extent varied between Nuuk and SHI, as well as Nuuk and Disko Bay. SHI had a significantly deeper depth extent across all levels of kelp cover. At 10, 50 and 80%, Nuuk had greater light availability than SHI. These 4 regions 1, 10, 50, and 80% kelp cover had a similar trend of increasing kelp cover with decreasing depth and increasing light availability. At the 1% kelp cover, Nuuk, west Greenland and SHI had similar light availabilities. While Nuuk and west Greenland had similar August light attenuation estimates of 0.189 ± 0.108 and $0.175 \pm 0.019 \text{ m}^{-1}$, respectively ($T(29) = 0.644$, $p = 0.5$); attenuation was significantly lower around SHI at $0.138 \pm 0.040 \text{ m}^{-1}$ in comparison to Nuuk ($T(35) = 2.19$, $p = 0.02$).

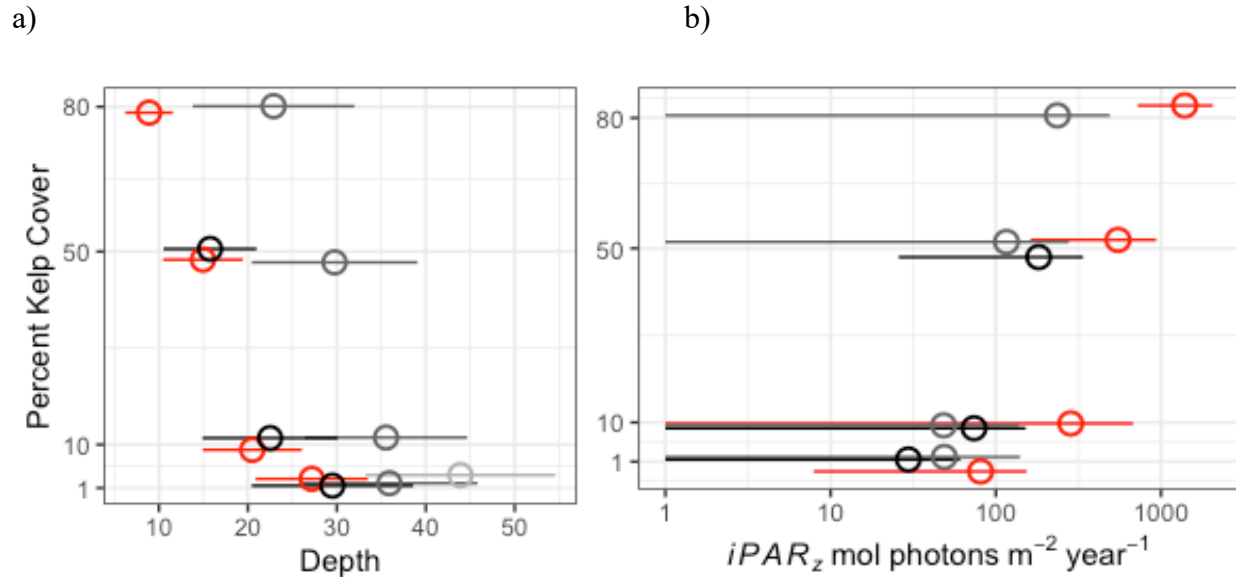


Figure 3.10 1, 10, 50 and 80% kelp cover against **a)** mean maximum depth extent (m) **b)** underwater light environment; $iPAR_{z-year}$ (mol photons $m^{-2} year^{-1}$) (note x-axis log scale). Included kelp forests; Nuuk fjords (red), western Greenland (black), Southampton Island (dark grey) and Offshore Disko Bay (light grey). Western Greenland did not have data for the 80% kelp cover. Disko Bay data was only available for 1% kelp cover, with no available light attenuation estimates to determine $iPAR_{z-year}$, data from Krause-Jensen et al. (2019). Western Greenland data in supplemental materials of Krause-Jensen (2012). Southampton data from supplemental materials Castro de la Guardia et al. (2023).

Table 3.4 Average and standard deviations of light availability ($iPAR_{z-year}$; mol photons $m^{-2} year^{-1}$) and depth extent (m) of 1, 10, 50 and 80% kelp cover for the regions of Nuuk, West Greenland (WG), Southampton Island (SHI) and Disko Bay (DB). ANOVA or Kruskal Wallis results with F or H statistics and p values for differences between groupings. Not available values are indicated as N/A.

	Region				ANOVA or Kruskal Wallis		Post Hoc Dunn Test		
	Study Region; Nuuk	West Greenland (WG)	South-ampton Island (SHI)	Disko Bay (DB)	F-test or H-test	P value	Nuuk vs. WG	Nuuk vs. SHI	Nuuk vs. DB
Depth Extent (m)									
1%	27.2 ± 6.3	29.5 ± 9.1	35.9 ± 9.9	43.9 ± 10.7	H-test $\chi^2_3 = 22.31$	< 0.0001	ns	0.02	<0.0001
10%	20.5 ± 5.6	22.5 ± 7.6	35.5 ± 9.1	N/A	F _{2,43} = 20.05	< 0.0001	ns	<0.0001	N/A
50%	15.0 ± 4.5	15.8 ± 5.2	29.8 ± 9.3	N/A	H-test $\chi^2_2 = 17.3$	0.0002	ns	0.0001	N/A
80%	8.89 ± 2.68	N/A	22.9 ± 9.09	N/A	H-test $\chi^2_1 = 12.32$	0.0004	N/A	0.0004	N/A
Light Availability (mol photons m⁻² yr⁻¹)									
1%	80.8 ± 72.9	29.6 ± 31.3	48.8 ± 91.4	N/A	H-test $\chi^2_2 = 6.35$	0.04	ns	ns	N/A
10%	284 ± 393	73.8 ± 78.1	48.3 ± 89.5	N/A	H-test $\chi^2_2 = 13.305$	0.001	ns	0.001	N/A
50%	549 ± 387	182 ± 156	116 ± 160	N/A	H-test $\chi^2_2 = 13.374$	0.001	ns	0.002	N/A
80%	1390 ± 668	N/A	236 ± 253	N/A	H-test $\chi^2_1 = 12.615$	0.0004	N/A	0.0004	N/A

3.3.5 *Saccharina latissima* Biomass

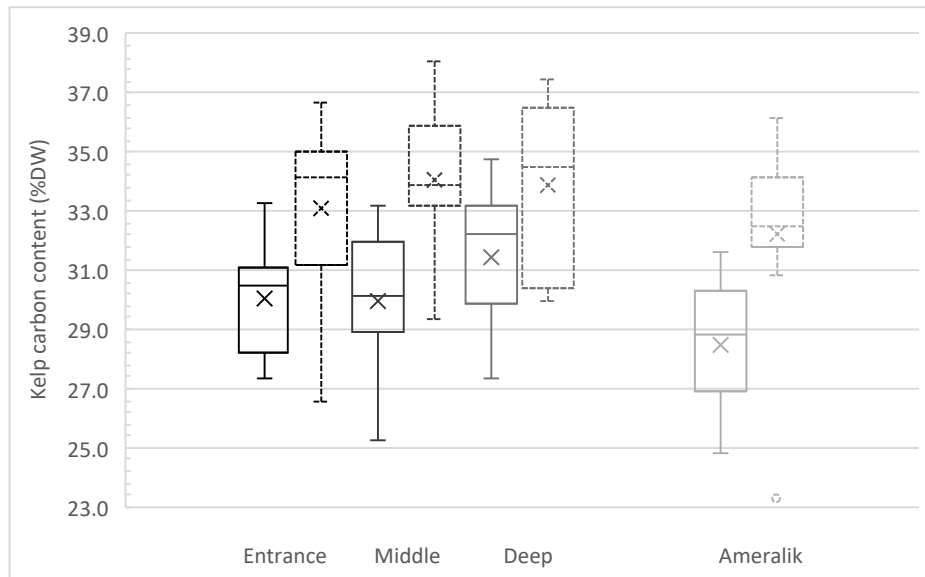
Kelp Carbon and Nitrogen Contents

Changes in *S. latissima* carbon (C) and nitrogen (N) content (% DW) throughout the Nuuk fjords are shown in Figure 3.11. There was a significant difference between mean carbon in the center of the blade ($33.4\% \pm 2.81$) and the meristem ($30.0\% \pm 2.34$) (Z-test = -5.37, $p < 0.0001$) within Nuup Kangerlua. A similar difference was observed in Ameralik fjord where the carbon content averaged $32.2\% \pm 3.48$ in the center of the blade and $28.5\% \pm 2.27$ at the meristem (Z-test = -2.21, $p = 0.03$). There was a significant difference in meristem carbon content ($F_{3,49} = 3.13$, $p = 0.03$) throughout the fjord sub-regions, where kelp in DN had a higher mean carbon content ($31.5\% \pm 2.39$) than kelp in Ameralik fjord ($28.5\% \pm 2.27$; Tukey post hoc; $p = 0.02$).

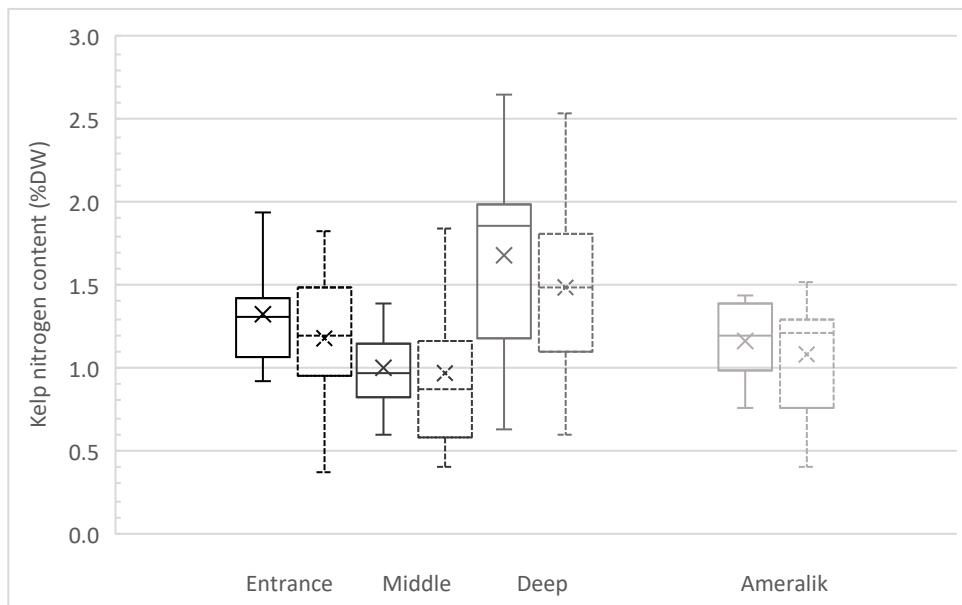
There was a significant difference between nitrogen in the center of the blade (1.18 ± 0.49) and that of the meristem (1.32 ± 0.44) in Nuup Kangerlua ($T(41) = -2.89$, $p = 0.006$). Ameralik fjord had a mean nitrogen content of $1.08\% \pm 0.35$ in the blade and $1.16\% \pm 0.25$ in the meristem, with no significant difference between core location samples ($T(9) = -0.90$, $p = 0.39$). Nitrogen was significantly different in the blade throughout the fjord ($F_{3,52} = 3.36$, $p = 0.03$), specifically between MN (0.964 ± 0.437) and DN (1.48 ± 0.57 ; $p = 0.02$). Nitrogen in the meristem also differed throughout the fjord (H-test $\chi^2_3 = 15.22$; $p = 0.002$), specifically between the EN (1.33 ± 0.28) and MN (1.00 ± 0.22 ; $p = 0.04$), and MN and DN (1.69 ± 0.58 ; $p = 0.001$). There was no significant linear relationship between kelp nitrogen content verses water column nitrate concentrations (blade $r^2 = 0.02$, $p = 0.34$; meristem $r^2 = 0.06$, $p = 0.07$).

There was a significant difference between meristem and blade C:N (g:g) ratios in both Nuup Kangerlua ($T(41) = 4.60$, $p < 0.0001$) and Ameralik fjords (Z-test = -2.21 , $p = 0.03$). The decreasing and increasing nitrogen trend throughout Nuup Kangerlua was also reflected in the C:N ratio. Averaged blade C:N ratios of 35.8 ± 17.0 , 46.9 ± 19.2 and 27.8 ± 15.6 were observed in EN, MN and DN, respectively, while that in AM was 36.6 ± 18.7 . A significant difference was observed between sub-regions (H-test $\chi^2_3 = 9.12$; $p = 0.03$), specifically between MN and DN ($p = 0.02$). Meristem C:N ratios averaged 23.4 ± 4.5 , 31.4 ± 7.7 and 22.0 ± 11.8 in EN, MN and DN, respectively, while that in AM was 25.8 ± 7.0 . The meristem ratio was found to significantly differ among sub-regions (H-test $\chi^2_3 = 13.51$; $p = 0.004$), specifically between MN and DN ($p = 0.002$).

a)



b)



c)

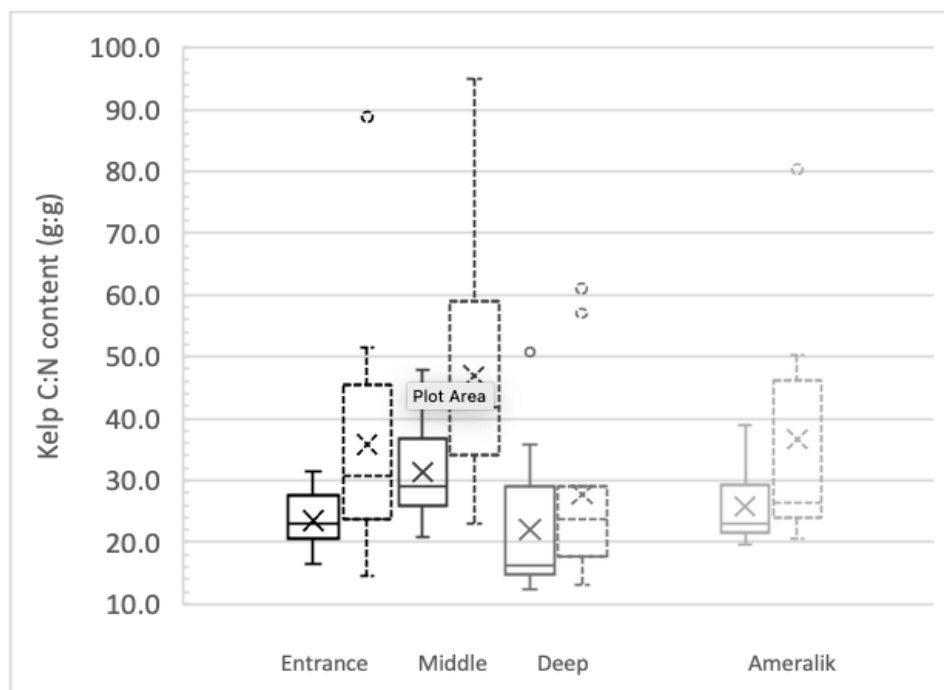


Figure 3.11 Boxplots of *S. latissima* **a)** carbon (% DW) **b)** nitrogen (% DW) and **c)** C:N (g:g) content for entrance (black), middle (dark grey) and deep sub-regions of Nuup Kangerlua (grey), as well as Ameralik fjord (light grey). Solid lines indicate meristem samples, dashed lines indicate samples taken from the center of the blade.

Biomass and Production

Averaged biomass (g WW m⁻²) of *S. latissima* at 10 m bottom depth increased throughout Nuup Kangerlua fjord at 80.5 ± 119 (EN), 104 ± 157 (MN) and 488 ± 217 (DN) g WW m⁻². AM had a much lower average biomass of 28.5 ± 56.9 g WW m⁻². There was a significant difference between the 4 sub-regions (H-test $\chi^2_3 = 9.57$; $p = 0.02$), specifically, DN and AM ($p = 0.03$). *S. latissima* production (g C m⁻² yr⁻¹) at 10 m bottom depth also increased throughout Nuup Kangerlua fjord with averages of 4.12 ± 6.08 (EN), 5.30 ± 8.04 (MN) and 24.99 ± 11.1 (DN) g C m⁻² yr⁻¹. The production average for Ameralik fjord was 1.46 ± 2.91 g C m⁻² yr⁻¹. Similar to biomass estimates, production differed significantly between the 4 sub-regions (H-test $\chi^2_3 = 9.57$; $p = 0.02$), specifically between DN and Ameralik ($p = 0.03$).

3.3.6 Urchin Influence

Environmental variables

Urchin density was significantly different between sites with different substrates (H-test $\chi^2_2 = 12.09$; $p = 0.002$). Specifically, urchin density was higher with rocky substrate compared to sandy ($p = 0.002$). No linear relationship was found between urchin density and physical variables such as temperature, salinity, or depth. Furthermore, there was no difference in urchin density between fjords, however, there was a significant difference between mean urchin density and sub-region (H-test $\chi^2_3 = 26.55$; $p < 0.0001$), specifically between DN and all other sub-regions (EN, $p < 0.0001$; MN, $p = 0.004$ and AM, $p = 0.0004$).

Kelp

Figure 3.12 illustrates the relationship between percent kelp cover and transmitted PAR to the ocean floor. The relationships revealed increasing kelp cover with increasing light availability, followed by a decrease at greater intensities for sites with high urchin densities (Figure S1). For the month of August (Figure 3.12 a), the logarithmic model explained 44% of the variability when urchin density was low. When urchin density was high, a polynomial fit was more appropriate, as kelp cover does not continue to increase despite greater light availability, this model explained 61% of the variability. When the same kelp cover was compared against light availability throughout the year, the logarithmic model explained 56% of the variability in kelp cover when urchin densities were low, and when urchin densities were high a polynomial fit explained 50% of the variability (Figure 3.12b).

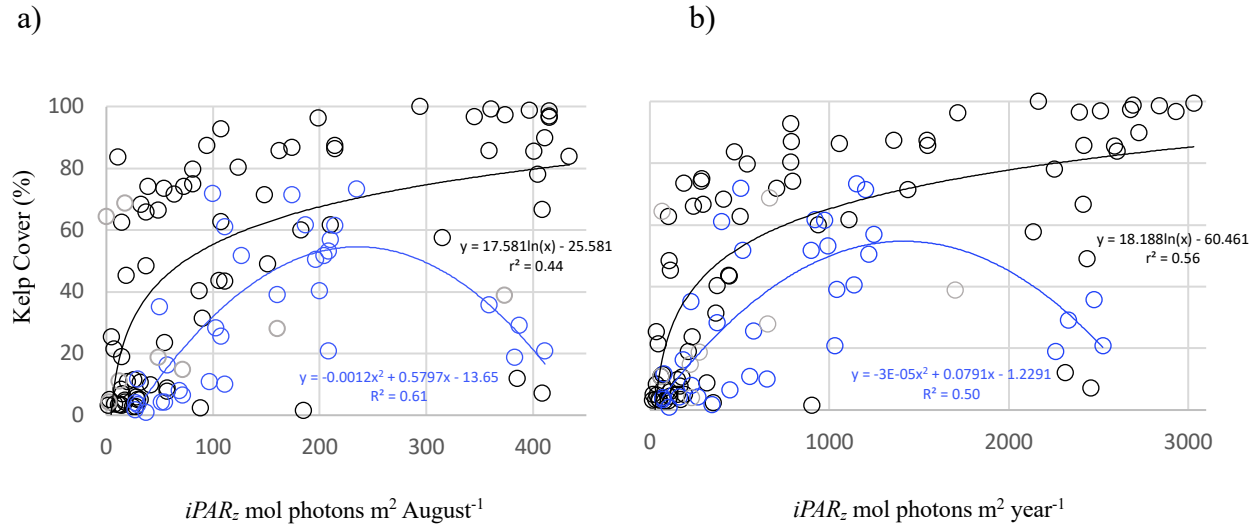


Figure 3.12 Percent kelp cover verses integrated transmitted PAR to the ocean floor **a)** for August ($iPAR_{z-Aug}$) and **b)** throughout the year ($iPAR_{z-year}$). Black indicate low urchin presence (<1 urchin m^{-2}), blue indicate high urchin presence (>1 urchin m^{-2}), grey indicates unknown urchin presence. Note: Kelp cover of 0% was not included.

When urchin density was high (>1 urchin m^{-2}), *S. latissima* cover was significantly lower at $1.51 \pm 5.98\%$ than when urchin density was low (<1 urchin m^{-2}) at $21.5 \pm 34.3\%$ (H-test $\chi^2_1 = 14.51$; $p = 0.0001$) (Figure 3.13 a). However, urchin density did not significantly influence *A.*

clathratum which had an average of $19.9 \pm 23.9\%$ when urchin presence was high and $14.4 \pm 24.5\%$ when urchin presence was low (H-test $\chi^2_1 = 2.84$; $p = 0.09$) (Figure 3.13 b).

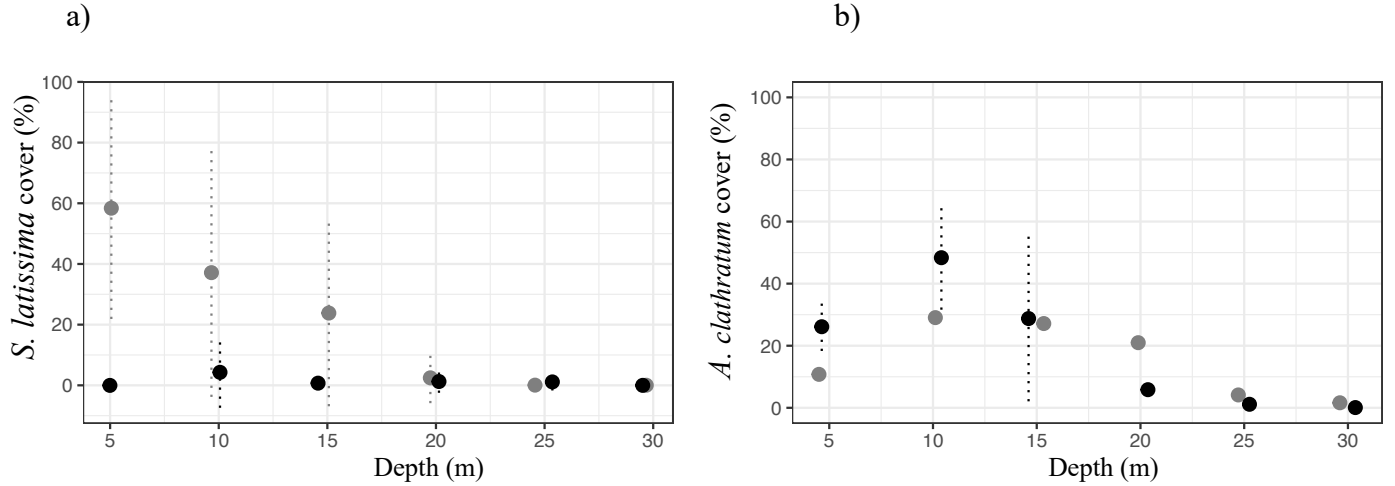


Figure 3.13 a) *S. latissima* b) *A. clathratum* percent cover plotted against depth (m). Black circles indicate high urchin presence (>1 urchin m^{-2}), grey circles indicate low urchin presence (<1 urchin m^{-2}).

3.3 DISCUSSION

3.4.1 Light Availability

Limitations

K_d^{PAR} for all stations were overestimations compared to K_d^{PAR} *insitu*, with the exception of station 17, 18, and 26, which were underestimated. Light attenuation measured at the surface is not always an accurate description of the entire water column. For example, station 17 had a subsurface sediment plume at 15 m depth, and therefore, the surface light attenuation was lower than within the plume (Figure 3.14). Satellite estimates of light attenuation were derived from natural light scattered back to the satellite from surface waters, a recognized limitation of using satellites to estimate light attenuation within highly turbid regions (Singh et al., 2022).

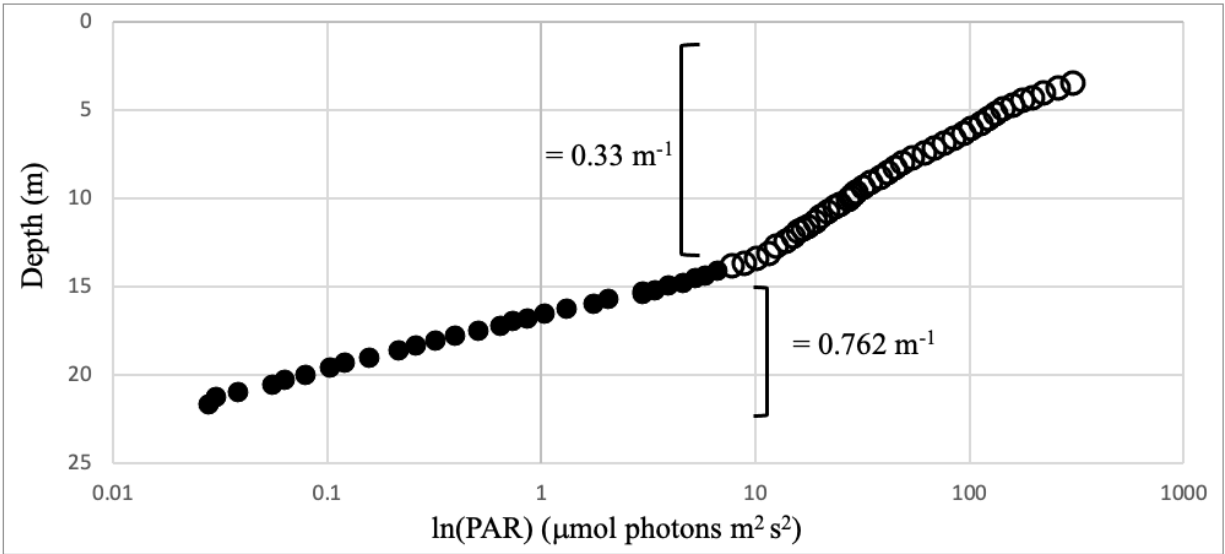


Figure 3.14 Station 17 light profile throughout the water column. Note the difference in K_d^{PAR} at the surface (open circles) and at depth (closed circles) in the water column. Note the log x-axis.

Influence on Nuuk fjord kelp distribution

The Nuuk fjords kelp species were dominated by *Saccharina latissima* and *Agarum clathratum*, similar to that of other Arctic/subarctic regions (Filbee-Dexter et al., 2019; Filbee-Dexter et al., 2022; Goldsmit et al., 2021; Krause-Jensen et al., 2012; Krause-Jensen et al., 2019). *A. clathratum* was the deepest growing species due to its shade-tolerant adaptations while *S. latissima* was more dominate in shallow regions due to its relatively higher light requirements (Krause-Jensen et al., 2019; Sakanishi et al., 2022; Wernberg et al., 2019).

Light availability strongly influenced kelp distribution patterns throughout the fjord system. High light attenuation with increasing proximity to glacier outlets was a function of increased total suspended solids. Lack of available light led to lower kelp cover and a more shallow depth limit in both fjord systems. However, close to the glacial terminus in Nuup Kangerlua fjord, kelp cover at the surface was high (despite a surface attenuation of 0.33 m^{-1} ; Figure 3.14) followed by

a strong drop in kelp cover below 10 m. Upwelling near marine-terminating glaciers can create subsurface sediment plumes (De Andrés et al., 2020), which we observed at depth (15-30 m) in Nuup Kangerlua, with considerably less sediments and a lower attenuation coefficient observed in the surface waters from 0-15 m. In contrast, greater surface light attenuation in Ameralik fjord led to minimal kelp cover near its land-terminating glacier sediment plume. Thus, while Niedzwiedz and Bischof (2023) described a reduction in the glacier plume area influence as marine-terminating glaciers became land-terminating, our results suggest vertical location of the plume could outweigh the associated impact on kelp distribution. However, $iPAR_{z-year}$ alone explained only 43% of kelp cover in the Nuuk fjords, revealing that light availability can only partially explain kelp cover in the fjords.

Regional comparisons

The minimum underwater light requirement for kelp growth (expressed as 1% kelp cover) in Nuuk was estimated at 80.8 ± 72.9 mol photons $m^{-1} yr^{-1}$, which was not significantly different from west Greenland or Southampton Island, and fell in the previously reported range of $\sim 30-96$ mol photons $m^{-1} yr^{-1}$ for cold water laminarians (Bartsch et al., 2016; Borum et al., 2002; Castro de la Guardia et al., 2023; Chapman & Lindley et al., 1980; Dunton, 1990). Furthermore, our average depth extent of 27.2 ± 6.3 m was similar to other areas of west Greenland (29.5 ± 9.1 m) and deeper compared to more northern Arctic regions ranging between 5 and 20 m (Borum et al., 2002; Bartsch et al., 2016; Dunton 1990; Krause-Jensen et al., 2012). This finding can be explained in part by the more southern latitude (i.e., greater annual insolation) of Nuuk and decreased sea ice cover as suggested by Krause-Jensen et al. (2012). However, our depth extent was significantly shallower than SHI (35.9 ± 9.9 m) and offshore Disko Bay, Greenland (43.9 ± 10.7 m). A similar comparison was made by Castro de la Guardia et al. (2023) who highlighted 2

stations (Nuuk and Itelleq) from Krause-Jensen et al. (2012) that had a much shallower depth extent despite a longer open water period with light. The difference is most likely due to turbidity, where we showed that K_d^{PAR} was significantly greater in Nuuk verses that of SHI. Similarly, Bartsch et al. (2016) conducted a study in Kongsfjorden, Svalbard and found that despite a decrease in sea ice cover, many kelp species did not increase their depth extent due to increased light attenuation. While decreasing sea ice cover has been predicted to increase kelp cover and extent in the Arctic, turbidity is a limiting factor, despite, and even more so as a result of, an increasing number of ice-free days per year (Bosnell & Dunton, 2021; Bosnell & Dunton, 2018; Li et al., 2020; Spurkland & Iken, 2011). Therefore, turbidity and associated increased light attenuation has the potential to counteract the impact of decreasing sea ice cover on kelp depth extent.

Light availability has a clear influence on kelp distribution, both in this study and throughout the Arctic. However, it is significant to note that while having a lower light attenuation, stations near the fjord entrances did not observe a deeper depth extent and in some cases had lower cover at the surface. The following explores other factors that could influence kelp distribution.

3.4.2 Kelp Nutrient Dynamics

Our kelp C content estimates fell within previously reported ranges of 24 to 40% (Gevaert et al., 2001; Krause Jensen et al., 2012; Nielsen et al., 2014). It is important to note that carbon reserves peak in late summer, and therefore our reported mean kelp C content of $30.0\% \pm 2.34$ (meristem) and $33.4\% \pm 2.81$ (blade) are likely reflective of maximum annual levels (Gevaert et al., 2001). Observed greater C content within the kelp blade is commonly observed as C exceeds 32%, often in late summer when assimilation exceeds utilization (Gevaert et al., 2001; Henley & Dunton,

1995). This stored carbon can be transported to the meristem to fuel growth throughout the year (Gevaert et al., 2001; Henley & Dunton, 1997). Kelp N content observed in our study are similar to previous studies along Greenland coasts, ranging between 0.77 and 3.16% (Krause Jensen et al., 2012; Neilsen et al., 2014). In contrast to carbon, nitrogen in the meristem and the blade varied spatially throughout the sub-regions, with peak kelp N content within DN, nearest to the marine glacier terminus. Previous research suggests that kelp require a minimum content of 1.7% N to sustain maximum macroalgae growth (Pedersen & Borum, 1996), which only kelp deepest in Nuup Kangerlua fjord were able to attain. Stations in the middle of the fjord were closer to a critical minimum N content required for growth, estimated at 1% (Henley & Dunton, 1997), suggesting the possibility of nitrogen limitation on kelp growth in the Nuuk fjord system. These results are similar to those from Krause-Jensen et al. (2012), who also found higher N content in kelp near glacier termini.

In line with these results, our observations also showed a significantly greater nitrate availability deeper in the fjord, a function of the circulation mechanism within a marine-terminating glacier fjord shown to enhance phytoplankton production throughout summer (Meire et al., 2017; Juul Pedersen et al., 2015). In contrast, nitrate concentrations in the land-terminating glacier fjord, Ameralik, were significantly less, where strong surface stratification minimizes mixing (Stuart-Lee et al., 2021). Higher kelp N content near the entrance of the Nuup Kangerlua fjord was likely due to increased mixing near the sill (Meire et al., 2017), as evidenced by decreased temperature and salinity stratification of the water column, as well as increased chlorophyll *a* concentration.

As carbon remained steady across the fjord system, the kelp C:N content ratio response was mainly a function of N content. The C:N ratios ranged between 23 and 38, consistent for kelp

growing in coastal waters (Henley & Dunton, 1995; Henley & Dunton, 1997; Nielsen et al., 2014; Nielsen et al., 2016). However, it has been suggested that a C:N ratio above 15 is a indication of nitrogen limitation (Hanisak, 1983; Strong-Wright and Taylor, 2022), again suggesting that kelp throughout the Nuuk fjords were potentially nitrogen limited, including deep Nuup kelp, despite higher relatively nitrate availability.

Our method to determine biomass and production was limited by the image-based estimate, not accounting for overlapping layers of canopy and assumed sampled blades represented an annual growth period. Our average production estimate of $8.06 \pm 11.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ fell within production estimates made for other Arctic regions, where Southampton Island ranged from $23.1 - 67.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Filbee-Dexter et al., 2022), and Young sound, Greenland averaged around $0.1\text{-}2.0 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Borum et al., 2002; Gomez et al., 2009). Biomass and subsequent production at 10 m were significantly greater deep in Nuup Kangerlua fjord. As mentioned earlier, fjord circulation was likely responsible for the greater production following evidence of lower C:N ratio and greater nitrate concentrations. However, the subsurface turbidity plume limited kelp production lower in the water column, even when nitrate concentrations were abundant. It is likely our multiple linear regression analysis selected against nitrate to explain kelp cover due to the complex trade-off between nutrient and light availability on kelp growth, evidenced deep in the Nuup Kangerlua fjord.

3.4.3 Urchin Grazing

Strong and abrupt decreases in kelp were observed at stations that had adequate light and nutrient availability, specifically at stations located near the entrance of the fjords. Urchin density was greatest with increased distance from the glaciers. High sedimentation rates near glaciers

resulting in sandy substrate was shown to negatively impact mobile invertebrate abundances (Blicher et al., 2007; Traiger & Konar, 2018), which helps to explain the decreased urchin presence further in the fjord. It is likely that in shallow waters, fast *S. latissima* growth is able to out compete urchin grazing; however, light-limited growth of *S. latissima* in deeper waters can result in a more noticeable sea urchin impact on kelp cover (Filbee-Dexter et al., 2022; Mann, 1973; Norderhaug & Christie, 2009). Accordingly, Ager et al. (2023) suggested that sea urchins could potentially decrease the macroalgae cover in Nuup Kangerlua fjord by 15%. Therefore, urchin grazing provides the best explanation for the shallow depth limit (<15-20 m) of kelp near the entrance of both fjords.

An influence of urchin grazing can also help explain the trend observed throughout the Ameralik fjord, where kelp cover decreased at 5 m. Significantly less cover of *S. latissima* in Ameralik fjord was most likely a function of the negative relationship between *S. latissima* and urchin density. In contrast, *A. clathratum* was more abundant in Ameralik fjord with no discernable urchin impact, likely due to a combination of urchin grazing avoidance measures and less competition by the faster growing high canopy species, *S. latissima* (Filbee-Dexter et al., 2022; Gagnon et al., 2005). Therefore, we suggest urchin grazing impacted species composition. While urchin density means between the two fjord systems were similar, Filbee-Dexter et al. (2022) suggested increased grazing and reproduction rates of urchins were associated with increased temperatures. Therefore, the significantly greater temperatures observed in Ameralik fjord likely resulted in greater impact of urchin grazing at shallow depths in the fjord.

Krause Jensen et al. (2012) stated that the strength of the relationship of kelp depth extent versus days of open water with light decreases when longer than 255 days a year, linked to an interplay

of local regulating factors that can influence kelp growth. Such factors included pressure from sea urchin grazing, which was also observed for other areas of west Greenland (Krause-Jensen et al., 2019). Here, we conclude that urchins provide a confounding effect with light on kelp depth extent and distribution, both in shallow and deep waters.

3.4.4 Additional Considerations

Kelp depth extent could also be influenced by glacial iceberg scour. Station 15 and 18 had signs of possible glacial scour, with scattered fragments of kelp visible on the seafloor. Increased marine-terminating glacier retreat can increase iceberg calving, which has the ability to scour the ocean floor, with potential of iceberg grounding (Borum et al., 2002; Gutt, 2001). This could play a role in limiting kelp extent near glacial calving zones.

We did not consider spatial variability in currents throughout the fjords, yet kelp growth can be influenced by water motion. Specifically, lower kelp growth rates have been observed in areas where water motion is either too slow, limiting nutrient or inorganic carbon uptake, or too fast which can cause structural damage to the kelp thallus (Hurd, 2017; Hurd, 2000; Kraemer & Chapman, 1991; Kregting et al., 2015; Kvile et al., 2022).

3.5 CONCLUSION

Within this study of the Nuuk fjord system, we showed greater turbidity and decreased light availability nearest to glacier discharge, which led to limited kelp growth and cover, particularly below 10 m. However, increased upwelling near the Nuup Kangerlua fjord marine-terminating glacier likely led to increased nitrate availability, which resulted in kelp above the subsurface turbidity plume having greater biomass and production than other sub-regions. These results highlighted that both light and nutrient availability impacted kelp cover and growth in the area. A

third factor influencing kelp cover was sea urchin grazing that impacted species compositions and depth extent towards warmer and less turbid waters within the Nuuk fjord system. We note when urchin densities were low, $iPAR_{z-year}$, dependent on incident PAR, depth, and water clarity was able to explain up to 56% of kelp cover, which was dominated by *S.latissima*.

Meire et al. (2017) showed that marine-terminating glaciers in Nuup Kangerlua fjord provided greater nitrate to the surface by upwelling and drove greater primary production in the form of phytoplankton. Our study built on this to show macroalgae are also impacted by this access to greater nitrate within the same fjord system. However, the benthic environment presents complex factors differing from the pelagic, with high turbidity limiting light at depth for photosynthesis, while in areas of lower turbidity, urchin grazing provided a negative influence on kelp accumulation.

The IPCC states that surface temperatures in the Arctic have increased by 6°C above the 1981-2010 average, leading to exceptional sea ice and glacial mass loss (Meredith et al., 2019). In particular, marine-terminating glaciers are predicted to become land-terminating into the future (Torsvik et al., 2019). Although just a case study, our contrasting results from the two fjord types suggest that this change will likely decrease surface light and nutrient availability, while potentially leading to an increased urchin grazing impact associated with increased fjord temperatures. Ultimately, the impact on kelp distribution and growth within the Nuuk fjord system would be negative. These findings highlight the concept that warming of the Arctic will not necessarily lead to an increased kelp distribution and that we need to continually advance our understanding of processes controlling kelp growth to better predict the potential response for this critical primary producer.

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CHAPTER 4.0 CONCLUSIONS AND RECOMMENDATIONS

CHAPTER 4.1 CONCLUSIONS

This thesis focuses on a study conducted in the Nuuk, Greenland fjord system. Fjords present a dynamic growing environment for kelp with a wide range of benefits and challenges. This region is characterized by glacial melt, both terrestrial runoff from land-terminating glaciers releasing sediment at the surface of the water, creating strong stratification, as well as deep water melt from marine-terminating glaciers, resulting in an upwelling of cold, fresh, nutrient rich waters with sediment plumes found at depth (De Andrés et al., 2020; Hopwood et al., 2018; Meire et al., 2017; Slater et al., 2017).

This thesis examined 26 transects throughout two differing fjord environments to observe how kelp cover and depth extent were impacted within varying growing conditions, such as land- and marine-terminating glacier influence. Light attenuation significantly increased deeper into Nuup Kangerlua, similarly, ambient nutrient levels also increased, presumably due to marine-terminating glacier upwelling. The circulation mechanism in Nuup Kangerlua provides a unique nutrient rich growing environment. In general, kelp biomass and production increased in areas of overlap between lower light attenuation and higher nitrate concentration. Nearest to marine-terminating glacier influence, kelp were able to thrive above the turbidity plume at < 15 m bottom depth, however below the plume, inadequate light availability limited kelp growth. However, nearest the land-terminating glacier in Ameralik fjord, where the turbidity plume was released along the surface, kelp growth was unattainable even in shallow water depths.

We note that $iPAR_{z-year}$ dependent on incident PAR, depth, and water clarity was able to explain up to 56% of kelp cover when urchin densities were low, supporting previous findings linking

increased light availability with increased kelp production and depth extent (Krause Jensen et al., 2012; Castro de la Guardia et al., 2023). While Nuuk's more limited sea ice cover, is receiving greater annual insolation than other Arctic regions, the analysis in this thesis revealed that Nuuk had a more shoaled depth extent. This thesis proposes that the reason for this observation is likely due to higher turbidity levels found throughout the Nuuk fjords. We suggest turbidity near glacier outlets, as is expected to increase with climate change, may limit kelp growth. However, in areas where light and nutrient availability were sufficient, kelp at times was often still limited. It is suggested that sea urchin grazing provides a confounding effect with light on kelp depth extent and distribution, both in shallow and deep waters.

This conclusion highlights the importance of light availability, nutrient abundance and urchin density on kelp distribution and has application for other marine- and land- terminating glacier systems as well as to the greater Arctic, which is under unprecedented pressures due to warming. The research presented in this thesis builds upon Arctic studies showing increasing turbidity could counteract some of the predicted kelp expansion associated with a decreasing ice cover, potentially leading to shoaling depth limits by providing estimates of the minimum underwater light requirement for kelp growth and maximum kelp depth extent (Bartsch et al., 2016; Bonsell & Dunton, 2018; Filbee-Dexter et al., 2019; Szeligowska et al., 2021). The data presented in this thesis can be applied to understand changes occurring in other coastal regions around the globe experiencing increased turbidity due to factors including, but not limited to, glacial discharge, as well as regions of increased erosion, river run off and, or various mixing patterns. This new information improves our understanding of the ecosystem and will assist in more effective marine protection strategies that could feed into modelling efforts of kelp along Arctic coasts with fluctuating environments or where fieldwork may not be possible.

CHAPTER 4.2 RECOMMENDATIONS

The research presented in this thesis builds upon a kelp distribution baseline for Arctic regions, and is an important step in understanding kelp coverage and depth extent response to physical variables of the water column in coastal environments. Here I present some recommendations on how the study presented in this thesis could be improved.

- 1) The MODIS Aqua satellite data used in this research had a spatial resolution of 1 km.

Using Sentinel 2 of higher spatial resolution of 10-60 m could allow for greater accuracy and fine-scale mapping when estimating water turbidity as many studies have already shown (Caballero et al., 2018; Caballero & Stumpf, 2020; Maimouni et al., 2022; Sebastián-Frasquet et al., 2019). This would be beneficial for transitional ecosystems like fjords where turbidity can vary significantly spatially. However, measurements of turbidity at various depths will provide a more accurate description of how turbidity plumes are situated in the water column, unable to be measured by satellites. Often such measurements could be acquired through deployment of a mooring with turbidity, PAR and/or CTD sensors. However, fjord environments are problematic as icebergs continuously flow out of the fjord, scouring and crushing anything in their track. Therefore, I propose a community monitoring strategy to sample water for turbidity measurements to better determine light availability throughout the year.

- 2) Shortwave radiation data acquired from the Greenland ecosystem monitoring website was used to determine incoming light throughout the year. However, only one station in Nuuk collects such data, yet it was applied to the entirety of the fjord system. It is worth acknowledging that the fjord system is very dynamic and has very different climatic conditions throughout. Anecdotal evidence reveals that deep within the fjord was often

sunny and warm, while the same day near the entrance of the fjord was cloudy with cooler temperatures. Therefore, additional climate monitoring located deep in the fjord could be beneficial to determine variation in incoming light.

- 3) Additional suggestions for kelp sampling are proposed. The kelp in this study were only sampled from the 10 m bottom depth at one point in time. Kelp sampled from additional depths as well as different seasons of the year will allow comparison of kelp coverage, varying light acclimation strategies and nutritive state throughout the year based on carbon and nitrogen contents. Furthermore, kelp ages and stipe length could be measured to provide insight as to various environmental or historic events. For example, younger forests may be recovering from urchin grazing or ice scour. Additionally, stipe length could provide insights of light conditions (Gundersen et al., 2021; Pedersen et al., 2012). Kelp quadrat samples acquired by divers could be ideal as to provide more accurate and comparable biomass and production estimates, able to account for canopy cover overlap and direct measurements of wet weight.
- 4) Lastly, trapping is suggested as a cost effective, reliable and more accurate suggestion of measuring urchin density in comparison to counts via video footage (James et al., 2016). This method could allow the size of the urchin to be determined which can provide helpful insight to both urchin and kelp forest health (Pearce et al., 2005; Siikavuopio et al., 2012). Divers could be another suitable method for urchin collection.

To better understand the distribution of kelp throughout the Arctic as a whole, here we present recommendations for future studies.

- 1) As marine-terminating glaciers have the ability to both increase and decrease primary production, more research should be aimed at understanding the thresholds of increased dissolved inorganic nitrogen availability versus the influence of subsurface turbidity plumes. Few studies, if any, have shown the impact of subsurface turbidity plumes on kelp, while the study in this thesis highlighted the importance of this factor. Therefore, more research on this topic is needed. With marine-terminating glaciers expected to become land-terminating into the future, more research surrounding how limited upwelling and mixing and how runoff at the surface has the potential to eliminate kelp growth even in shallow regions is needed. Furthermore, study regions should also be selected based on alternative factors that can increase turbidity besides glacial discharge, this may include regions experiencing erosion, river runoff or various mixing patterns that may limit light availability by differing systems.
- 2) It is important to increase insitu kelp observations and light measurements to better our understanding on the minimum underwater light requirements for growth. This can provide direct measurements to aid in understanding how the environment impacts kelp coverage and depth extent, and to quantify how light availability varies regionally throughout the Arctic to predict future changes.
- 3) We suggest that studies take extra effort in not only addressing the coverage and depth extent of kelp, but to understand distribution based on individual kelp species to understand how future changes to the Arctic may affect various kelp species differently.
- 4) Lastly, more study is needed to see how biological influence of sea urchin grazing as well as disease, which may spread from more southerly locations and influence kelp coverage and depth extent in a warming Arctic.

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SUPPLEMENTARY MATERIALS

Table S1. Spearman Rank Correlation matrix (used to determine relationships to kelp percent cover at each sampled depth) for temperature, salinity, nitrate, urchin density and $iPAR_{z-year}$. Showing correlation coefficient, r , with bold values when the correlation is significant ($p \leq 0.05$). Variables were normalized to reduce the dominant effect of variables with large ranges.

	Temperature	Salinity	Nitrate	Urchin density	Chl a	$iPAR_{z-year}$
Temperature	x	x	x	x	x	x
Salinity	0.03	x	x	x	x	x
Nitrate	-0.79	0.28	x	x	x	x
Urchin density	0.12	0.31	0.13	x	x	x
Chl a	0.13	-0.42	-0.18	0.03	x	x
$iPAR_{z-year}$	0.30	-0.64	-0.35	-0.01	0.61	x

Table S2. Simple linear regression of explanatory variables of kelp percent cover, as well as for *S. latissima* and *A. clathratum* separately. Bolded values are significant ($p \leq 0.05$).

Variable	Simple linear Regression		
	Kelp % cover	<i>S. latissima</i> % cover	<i>A. clathratum</i> % cover
Temperature	$r^2 = 0.01$ $p = 0.22$	$r^2 = 0.0002$ $p = 0.86$	$r^2 = 0.03$ $p = 0.02$
Salinity	$r^2 = -0.16$ $p < 0.0001$	$r^2 = -0.23$ $p < 0.0001$	$r^2 = 0.0002$ $p = 0.85$
Urchin density	$r^2 = -0.01$ $p = 0.21$	$r^2 = -0.05$ $p = 0.01$	$r^2 = 0.02$ $p = 0.08$
$iPAR_{z-year}$	$r^2 = 0.43$ $p < 0.0001$	$r^2 = 0.35$ $p < 0.0001$	$r^2 = 0.02$ $p = 0.10$
Nitrate	$r^2 = -0.11$ $p < 0.0001$	$r^2 = -0.07$ $p = 0.0009$	$r^2 = -0.03$ $p = 0.03$
Chlorophyll a	$r^2 = 0.15$ $p = 0.0001$	$r^2 = 0.12$ $p = 0.002$	$r^2 = 0.02$ $p = 0.19$

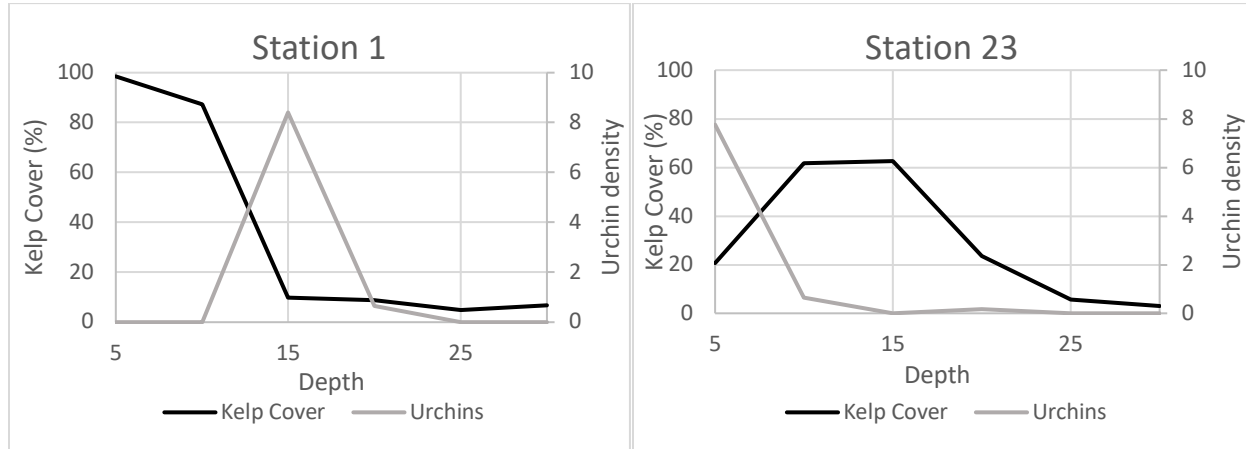


Figure S1. Kelp cover (%) (black line) by depth and urchin density (urchins m⁻²) (grey line) by depth for **a)** a Nuup Kangerlua entrance station (St.1) **b)** and an Ameralik station (St.23).