Spatial and Temporal Variability of Carbohydrate Compositions in Cultivated *Alaria marginata, Nereocystis luetkeana*, and *Saccharina latissima*

by

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Dedication

To Cayman Ben Jardell:

This thesis is dedicated to the late Cayman Ben Jardell, my younger brother. Through his vibrant enthusiasm for life, confidence in taking on challenges, and yearning for adventure, Cayman was, and continues to be, a profound inspiration in my life.

Abstract

Carbohydrates derived from Laminariales (kelp), including polysaccharides and sugar alcohols, present significant market opportunities for nascent mariculture industries. These carbohydrates can enhance crop biomass value through extractive processing, with applications in medicine, manufacturing, health supplements, and bio-plastics. The relative abundance and composition of carbohydrates in kelp can vary depending on species, life history, tissue type, season, and environmental conditions. In Alaska, mariculture of kelp focuses on three species: *Alaria marginata*, *Nereocystis luetkeana,* and *Saccharina latissima*. This study assessed the relative abundance of carbohydrates (glucan, mannitol, alginate, and fucoidan) in these species, as well as the sulfate content of fucoidan and the ratio of mannuronic to guluronic acids in alginate (M:G ratio) as proxies of chemical attributes for these carbohydrates. Samples were collected from commercial farm sites in the Kodiak Archipelago, Prince William Sound, and Southeast Alaska between April and June of 2023. Carbohydrate composition was analyzed using high-performance anion-exchange chromatography with pulsed amperometric detection. Composition varied among species, where on a dry mass basis, *A. marginata* had the highest average contents of fucoidan and alginate, while *S. latissima* had the highest average glucan content. Fucoidan was the only measured component to have consistent trends over time across sites for all species. Inconsistency in trends over time across sites for biochemical components was most notable in *A. marginata*. Seawater temperature was the most consistent environmental predictor across species, having a moderate, negative correlation the M:G ratio in all species and a moderate, positive correlation with fucoidan in *A. marginata* and *S. latissima*. Of the species studied, *S. latissima* harvested in June may have the highest potential for extractive processing in Alaska. This species had a balanced composition of valuable carbohydrates, high consistency across sites, and high potential yield from a relatively large fraction of solids in wet biomass combined with generally high wet mass growth. This study highlights the complex variability of carbohydrate compositions in kelp and provides the first detailed assessment of *A. marginata*, *N. luetkeana,* and *S. latissima* in Alaska.

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1. Introduction

For millennia, the unique properties of marine macroalgae have been utilized across the globe for sustenance, fabrication, and medicine. These practices continue in our modern era (Cannell, 1993; Chen et al., 2020; Salehi et al., 2019). For example, historical consumption of macroalgae is recorded from Aboriginal Australians (Thurstan et al., 2018), Indigenous peoples of the Pacific Northwest (Turner, 2003), Gauls of Armorica (Anis et al., 2017), and ancient Japan (Nisizawa, 1987). Moreover, examples of macroalgae used as a material rather than food include 17th-century glass manufacturing in Western Europe (Levring, 1969) and Aboriginal Australians' construction of fish traps, nets, and storage vessels (Ross, 2009; Thurstan et al., 2018). In regard to medicinal properties, macroalgae have been used throughout history as a cure for goiter in ancient China (Wang et al., 1999), a remedy for joint pain in Rome (Pérez-Lloréns et al., 2023), a gastrointestinal medicine by Indigenous people of the Pacific Northwest (Turner, 2003), and were featured in medieval Islamic medicinal texts (Yavuz, 2024).

Today, there is an increasing practice of cultivating macroalgae, comprising 97% of global production, while the remaining portion is primarily sourced from industrial wild harvests (Cai et al., 2021). East and Southeast Asian countries lead biomass production, with most cultivated macroalgae catering to the regional demand for direct food consumption but also contributing to the production of animal feed and the extraction of hydrocolloids, such as carrageenan and agar. The latter are crucial for processed food ingredients, manufacturing, and scientific research (Cai et al., 2021). In addition to east Asian countries, Norway, the United States, and Chile contribute to the hydrocolloid industry through farmed and wild-harvested macroalgal biomass, specifically targeting alginate (Cai et al., 2021). The demand for macroalgal biomass is steadily rising, fueled by growing interest in extractive biochemical products for applications in food ingredients, sustainable material manufacturing, pharmaceuticals, and cosmetics (Cannell, 1993; Chen et al., 2020; Grand View Research, 2021; Salehi et al., 2019; Zia et al., 2015).

Marine macroalgae contain a plethora of biochemical components including lipids, amino acids, proteins, phenolic compounds, ash, and carbohydrates (Parjikolaei et al., 2016). While lipids typically constitute less than 5% of dry mass (DM) in macroalgae, they play essential roles in cellular functions, energy storage, and signaling (Nelson et al., 2002; Ragonese et al., 2014; Schmid et al., 2017). Amino acids, in both free and polypeptide forms, are integral for nitrogen storage, metabolism, and physiological stress responses (Lalegerie et al., 2019; McGlathery et al., 1996; Raven & Hurd, 2012). Protein content varies among taxa, with chlorophytes and rhodophytes generally exhibiting higher concentrations than phaeophytes (O' Brien et al., 2022). Phenolic compounds, important secondary metabolites, provide functions, such as protection against UV radiation and act as antioxidants (Gómez & Huovinen, 2010; Rice-Evans et al., 1997). Phenolic content, usually less than 2% of dry mass, is often highest in phaeophytes due to the prevalence of phlorotannin (Celis-Plá et al., 2016; Farghl et al., 2021; Tierney et al., 2010).

Macroalgae also contain a significant amount of inorganic salts, metals, and minerals, collectively known as 'ash,' with Na^+ and K^+ ions contributing largely to this pool (Karsten et al., 1991; Schiener et al., 2015). Ash content varies widely among taxa, typically ranging from 20% to 40% of dry mass, but can be as low as 3% or as high as 89% in certain species (Alghazeer et al., 2022; Garcia-Oliveira et al., 2020; Renaud & Luong-Van, 2006). Additionally, macroalgae are rich in carbohydrates, including structural and energy-storing polysaccharides (Percival, 1979). Phaeophyceae generally have the highest relative abundance of carbohydrates among the macroalgal groups, contributing up to 50% of dry mass (Li et al., 2021). Carbohydrate biochemistry varies significantly among macroalgal taxa and are key for maintaining the structure of cell walls (Deniaud-Bouët et al., 2014; Percival, 1979).

Phaeophytes, the focus of this study, possess an array of cell wall polysaccharides within three major families: cellulose, alginate, and fucoidan (Chen et al., 2020; Deniaud-Bouët et al., 2014, 2017; Kadam et al., 2015). Cellulose, a beta-glucan polymer of glucose, forms a crystalline structure within the extracellular matrix (ECM), although it constitutes a smaller proportion of cell wall biomass compared to terrestrial plants (Collén et al., 2013; Deniaud-Bouët et al., 2014). Alginate, a non-branching polysaccharide composed of D-mannuronic (M) and L-guluronic (G) acids, is abundant in the ECM, forming gel-like structures crucial for mechanical support (Percival, 1979; Plazinski, 2011). Fucoidan, primarily composed of L-fucose, exhibits considerable molecular diversity, and is classified into homo-fucans and hetero-fucans, depending on the fucose purity of their backbone structure (Deniaud-Bouët et al., 2014, 2017).

The ECM's composition is pivotal for phaeophyte physiology, regulating ion flux, protecting cells from stress, and facilitating cellular cohesion (Halat et al., 2020; Mariani et al., 1985; Niklas & Newman, 2013). The ECM consists of highly organized layers, including an inner skeleton, where cellulose fibrils are cross-linked by fucoidan, and an outer amorphous embedding matrix, both with abundant alginate (Davis et al., 2003; Deniaud-Bouët et al., 2014). These components confer unique structural properties, influencing the ECM's overall chemical and mechanical characteristics. Although cellulose constitutes only a small fraction of dry mass, it contributes significantly to cell wall tensile strength (Deniaud-Bouët et al., 2014). Alginate and fucoidan, both negatively charged polysaccharides, play crucial roles in ion binding, affecting viscosity and adaptive physiology against mechanical forces (Gwon et al., 2015; Kloareg et al., 1986, 1987; Kloareg & Quatrano, 1988). Fucoidan's cation-binding properties protect against toxic heavy metals and desiccation stress (Andrade et al., 2010; Percival, 1979). Aside from cell wall polysaccharides, phaeophytes also produce mannitol and laminarin as primary metabolites for energy storage and metabolism (Chen et al., 2020; Percival, 1979). Mannitol's water solubility and non-toxic nature enable its transfer among cells, balancing osmotic potential without toxic ion accumulation (Davison & Reed, 1985; Kirst, 1990). Meanwhile, laminarin, stored within cells, serves as a long-term energy reserve crucial for seasonal growth patterns (Scheschonk et al., 2019).

Understanding the carbohydrate composition and variability among phaeophytes requires consideration of morphological, genetic, evolutionary, and environmental factors (Bruhn et al., 2017; Manns et al., 2017; Schiener et al., 2015). *In situ* sampling, particularly of Laminariales species (i.e., kelp), has provided insights into species-specific compositions, which can vary over time, both within and among seasons (Bruhn et al., 2017; Manns et al., 2017; Schiener et al., 2015). Tissue differentiation, tissue age, and reproductive maturity significantly impact carbohydrate composition (Mak et al., 2013; Kloareg & Quatrano, 1988; Starko et al., 2018). Additionally, phaeophytes can actively regulate carbohydrate composition and molecular structure in response to environmental conditions, such as nutrient availability and water motion (Manns et al., 2017; Torode et al., 2016; Venegas et al., 1993).

Seasonal trends in carbohydrate content often align with the functional roles of these molecules. Mannitol and laminarin, associated with photosynthetic activity, often peak at the end of summer, corresponding with increased irradiance (Gagné et al., 1982). Mannitol also serves as a compatible solute to balance osmotic potential, in response to changing salinity (Dittami et al., 2011; Westermeier et al., 2012). However, seasonal trends in cell wall polysaccharides are more variable due to diverse environmental correlates. Although regional differences exist, fucoidan content often peaks in summer (Bruhn et al., 2017; Qu et al., 2019). For instance, different populations of *Laminaria digitata* exhibit contrasting seasonal patterns in fucoidan content, highlighting the role of local environmental factors (Bruhn et al., 2017). Similarly, peak alginate content varies among species and regions, reflecting complex environmental interactions (Schiener et al., 2015). In addition to environmental correlates, underlying biological processes, such as seasonal maturation, can impact the timing of peak fucoidan content (Mak et al., 2013).

Phaeophyte carbohydrates are increasingly recognized for their diverse commercial applications in food, manufacturing, and health products. Alginate, a food-safe hydrocolloid, finds utility as an emulsifier, thickener, and stabilizer in various food products, bio-plastics, medical bandages, dental molds, and slow-release pharmaceutical formulations (Aderibigbe & Buyana, 2018; Batista et al., 2019; Khalid et al., 2015; Qin et al., 2018). Fucoidans are sought after in pharmaceuticals, nutraceuticals, and cosmetics for their antibacterial, antioxidant, antiviral, and anti-tumor properties (Elizondo-Gonzalez et al., 2012; Marudhupandi & Kumar, 2013; Maruyama et al., 2006; Rocha De Souza et al., 2007). Meanwhile, laminarin exhibits anticoagulant and antioxidant properties (Deniaud-Bouët et al., 2017; Kadam et al., 2015; Tsiapali et al., 200l; Yamaguchi et al., 1966), and mannitol serves as a diabetic-safe sweetener and pharmaceutical agent (Chukwuma et al., 2019; Shawkat et al., 2012).

Efforts to cultivate native kelp species, particularly in regions like Alaska, are expanding rapidly, driven by the growing kelp mariculture industry (Heidkamp et al., 2022; Stekoll, 2019). Kelp farming in Alaska encompasses *Alaria marginata*, *Nereocystis luetkeana*, and *Saccharina latissima.* Except for *S. latissima*, these species have received only limited attention in research, with most studies focused on improving hatchery or in-ocean production with emphasis on growth and biomass (Stekoll et al., 2024; Stekoll et al., 2021). While these studies aid in increasing production efficiency, uncertainty remains in market opportunities for these marine crops (Kim et al., 2019; McKinley Research Group, LLC, 2021; Rinker et al., 2021). The research herein aims to enhance the understanding of marketable attributes and inform potential cultivation practices to increase the extractive biochemical value of these kelp species (Jönsson et al., 2020). Given the potential market opportunities for polysaccharide extracts, this study assessed the variability in carbohydrate composition, including total glucose (as a proxy for laminarin), fucoidan, alginate, and mannitol content in *A. marginata*, *N. luetkeana*, and *S.*

latissima grown in different commercial farm sites over 90 days in spring and summer. The analysis also included other compositional components, such as protein, ash, and dry mass fraction, as well as proxies for carbohydrate quality, including the mannuronic acid to guluronic acid (M:G) ratio and the sulfate content of fucoidan (sulfation). The influence of environmental factors, such as temperature, irradiance, salinity, water motion, and nutrient levels (dissolved inorganic nitrogen and orthophosphate) on these carbohydrate metrics were also considered.

Overall, it was expected that the relative proportion of each carbohydrate type would change over the sampling period and vary among species due to both endogenous factors (i.e., physiology and morphology) and exogenous factors (i.e., environmental conditions). Regarding variability due to environmental conditions, it was expected that temperature and irradiance would correlate positively with glucan content, while salinity would correlate negatively with fucoidan content. Salinity was also expected to correlate positively with mannitol content, and that relative water motion would correlate positively with alginate content. Additionally, all measured carbohydrates were hypothesized to correlate negatively with ambient nutrient concentration. The M:G ratio was expected to decrease over time, with a positive interaction with relative water motion. It was further expected that salinity would correlate negatively with the sulfate content of fucoidan, and the dry mass fraction would increase over time, regardless of environmental conditions.

2. Methods

2.1 Study Sites

Sampling occurred at five commercial kelp farm sites in Alaska: two in Southeast Alaska (SE), two in Prince William Sound (PWS), and one in the Kodiak Archipelago (Table 1, Figure 1). All farms used catenary systems, where multiple lines seeded with kelp ran parallel with a consistent distance between them (Figure 2). This distance varied across farms, as detailed below. The farm site environmental characteristics ranged from semi-protected to heavily protected from wind, waves, and currents, with varying levels of freshwater influence.

Kodiak Site, located adjacent to Woody Island, is semi-protected from strong wave exposure, and has negligible freshwater discharge. This farm had 62 seeded lines spaced 1.2 m apart. PWS Site 1, in Windy Bay, is protected from wind and waves, and has minor freshwater influx. This site had 14 seeded lines spaced 3 m apart. PWS Site 2, located in Simpson Bay, experiences freshwater discharge from Simpson Creek. This farm had 16 seeded lines spaced 3 m apart. SE Site 1, adjacent to Horse Island, is semi-exposed to waves from Stephens Passage on the north and south and is exposed to an interior channel current, with minor freshwater input. This site had 25 seeded lines spaced 1.5 m apart. Lastly, SE Site 2 in Doyle Bay is protected from wind, strong currents, and waves, with no major freshwater discharge. This farm had 300 seeded lines spaced 3 m apart.

Table 1. Sampled commercial kelp farm site descriptors in Alaska, including site name, farm title, region in Alaska, location name, latitude and longitude, dates of cultivation period (multiple dates occur where these events took place over multiple days and reflect their start and end dates), kelp species at each site sampled for tissue, and dates where sampling of kelp tissue and seawater occurred (with day of year [DOY]).

Site Name	Farm Title	Region	Location	Coordinates	Outplant Date(s)	Harvest Dates	Sampled Species	Sampling Dates	Sampling Dates (DOY)
Kodiak Site	Alaska Ocean Farms LLC.	Kodiak Archipelago	Woody Island	57º 45.999' N 152º 21.334' W	11/28/2022	5/17/2023 - 5/21/2023	*A. marginata, S. latissima*	4/14/2023 4/29/2023 5/15/2023 6/3/2023 6/12/2023 6/28/2023	104 119 135 154 163 179
PWS Site 1	Royal Ocean Kelp Co.	Prince William Sound	Windy Bay	60º 33.732’ N 145º 57.576’ W	10/25/2022	4/29/2023 - 5/10/2023	*A. marginata, S. latissima*	4/3/2023 4/22/2023 5/10/2023 6/3/2023 6/13/2023 6/20/2023	93 112 130 154 164 171
PWS Site 2	Noble Ocean Farms	Prince William Sound	Simpson Bay	60º 40.040’ N 145º 43.120’ W	11/4/2022	4/16/2023 - 5/19/2023	*N. luetkeana S. latissima,*	4/3/2023 4/21/2023 5/6/2023 5/19/2023	93 111 126 139
SE Site 1	Sea Quester Farms	Southeast	Horse Island	58° 14.650’ N 134° 44.100’ W	1/15/2023	4/23/2023 - 6/15/2023	*N. luetkeana S. latissima,*	4/11/2023 4/23/2023 5/10/2023 5/25/2023 6/14/2023 6/27/2023	101 113 130 145 165 178
SE Site 2	Seagrove Kelp Co.	Southeast	Doyle Bay	55 º 25.034’ N 133º 03.137’ W	10/20/2022 - 11/8/2022	4/27/2023 - 5/102023	*S. latissima*	4/3/2023 4/29/2023 6/10/2023	93 119 161

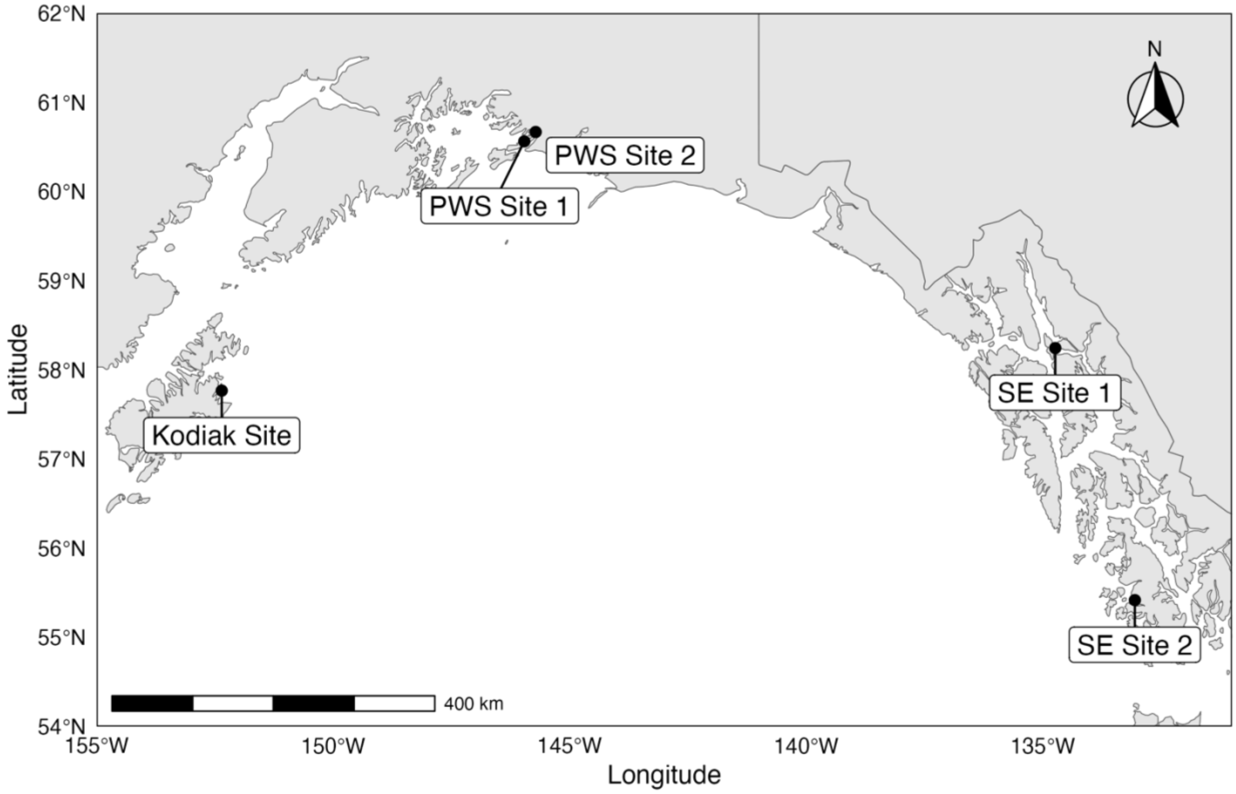

Figure 1. Map of the Gulf of Alaska with the locations of commercial farm sites sampled for kelp in this study. Study regions included the Kodiak Archipelago (Kodiak), Prince William Sound (PWS) and Southeast (SE).

2.2 Sample Collection

Repeated sampling was systematically conducted among the months of April, May and June, 2023, on two 60 m grow-out lines (hereafter called sample lines) per farm (Table 1). *S. latissima* was cultivated at every site, while *A. marginata* and *N. luetkeana* were cultivated at two sites each (Table 1). Sample lines held only one kelp species per line and were positioned in the center of the farms. Each sample comprised a minimum of two adjacent fronds. During each sampling effort, three samples were collected per species from the sample lines (Figure 2). Samples were haphazardly selected from various points along the sample lines, including the middle and both ends. The fronds were carefully detached from their holdfasts and placed into plastic bags on ice for transportation from the farm to a freezing facility.

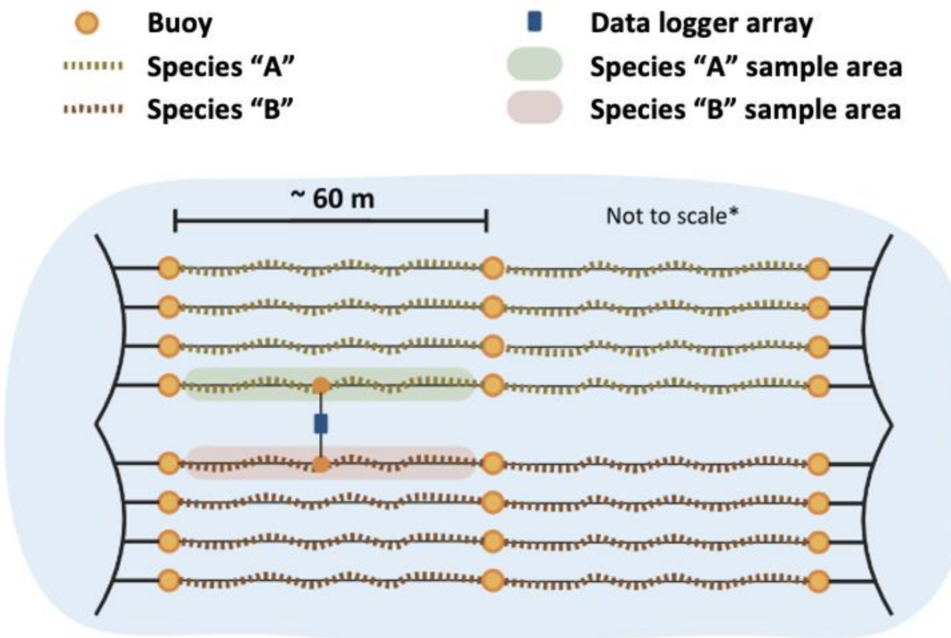

Figure 2. Top-down diagram of an in-ocean catenary system layout with kelp cultivation lines, buoy placement, and data logger array. The diagram features two kelp species and their respective sampling lines. Created with Biorender.com.

Once frozen at -20 °C ± 2 °C, samples were shipped to the Lena Point Fisheries Facility (University of Alaska Fairbanks in Juneau) for further processing (Figure S3). Sampling activities started in early April 2023, and concluded in late June 2023, recurring approximately every two weeks and totaling six sampling efforts per farm, when possible. Discrepancies in sampling consistency occurred across sites due to permit restrictions, weather conditions, and logistical challenges. When possible, sample lines remained in place after surrounding lines were removed for commercial harvest. However, PWS Site 2 was required by permit restrictions to remove all farm equipment from the water by the end of May, restricting sampling efforts to this time.

Frozen samples were weighed on a digital balance (Ohaus Scout Pro, ± 0.1 g), then homogenized in a blender before a maximum of 110 g of wet tissue was placed in a lyophilization flask. The blended material was placed back into a freezer at -20 ^{o}C before being lyophilized in a VirTis Freeze Mobile 25 XL (with manifold), set to operate at -60 ^{o}C and 20 mTorr. Samples remained in the freeze drier for a minimum of 24 h. After weighing the lyophilized biomass, the contents were homogenized using a coffee grinder before sieving through a 500-µm mesh to ensure particle sizes of < 1 mm, congruent with sample preparation criteria for carbohydrate analysis (see section 2.4). After which, the processed biomass was stored at -20 ^{o}C in sealed containers for use in all further tissue composition analyses.

2.3 Environmental Data Collection

Data loggers were situated on a perpendicular line between the two sample lines at each farm site (Figure 2). The logger line also held a logger array, which housed a Hobo Pendant G logger encased in a PVC shield for measuring relative water motion, and a HOBO MX temperature and light logger (Figure 3). The HOBO MX loggers were positioned so the light meters faced towards the surface, while the relative water motion meter hung below the station (Figure 3). The logger array was weighted to hold a position equidistant and at the same relative depth from the sample lines. Data loggers were programmed to record observations in intervals of 10 minutes. Interference with loggers (e.g., lines pulled to the surface) was noted, and the data were excluded from the analyses accordingly. Relative water motion was calculated as the sum of acceleration among the three axes at each sampling point.

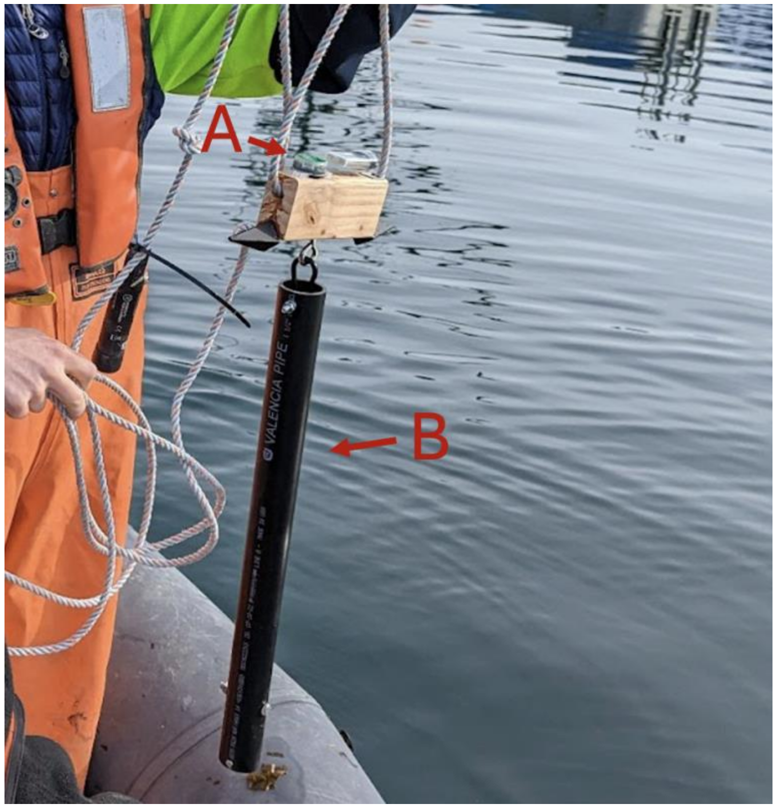

Figure 3. Picture of the logger array system deployed at five kelp farm sites in Alaska between April and June of 2023. A) HOBO MX and B) HOBO Pendant G in a PVC casing. The system was fixed to a sinking line.

Water sampling to determine nitrogen and orthophosphate levels paralleled the frequency of tissue sampling at each site (Table 1). This involved collecting three seawater samples between the two designated sample lines, at a depth approximately corresponding to the placement of sample lines on each farm (typically 2-4 m below the surface). One sample was taken from the midpoint between the lines, while the remaining two were taken from either end. A Science First 1.5 L water sampler was used to collect the samples, which subsequently underwent filtration using a 0.2 μm Polyvinylidene fluoride (PVDF) filter into a 60 ml container. Once filtered, each sample was promptly chilled on ice for transport to a freezing facility.

Water samples were analyzed colorimetrically for ammonium, nitrate, nitrite, and orthophosphate using a Seal Analytical Autoanalyzer 500 with an LED photometer. This analysis was conducted by the NOAA Ted Stevens Marine Research Institute Chemistry Lab.

Nitrate, nitrite, and ammonium were summed to obtain dissolved inorganic nitrogen (DIN). Nutrient concentrations were obtained following the SEAL Analytical methods (Seal Analytical, 2021a; 2021b; 2021c). The autoanalyzer was calibrated for low range nitrate and nitrite (0.08 μM/L to 4 μM/L) with a detection limit of 0.007 μM/L. For ammonium, calibration was in the low range (0.4 – 8 μM/L) with a detection limit of 0.17 μM/L. Samples resulting in below detection limit levels were entered as 0's for analysis.

2.4 Tissue Composition Analysis

Moisture and ash content were measured gravimetrically by oven drying 25 mg ± 2 mg of processed kelp tissue at 60 °C ± 1 °C and combustion at 575 °C ± 25 °C for 24 hours ± 4 hours, respectively. This procedure followed the Determination of Total Solids LAP, where samples were pre-combusted over a Bunsen burner after oven drying and before furnace combustion (Van Wychen & Laurens, 2015). Samples were processed in singlet after ten replicates per species showed a residual standard deviation of less than 5%. A quality control sample was run in triplicate to compare batches. Total solids were calculated from the average frond mass (wet mass) multiplied by the percent mass retained after lyophilization and oven drying at 60 °C ± 1 °C (Van Wychen & Laurens, 2015). Dry mass fraction was calculated as average wet mass / % total solids. Carbon and nitrogen analysis was conducted by the Alaska Stable Isotope Facility at the University of Alaska Fairbanks - Water & Environmental Research Center. The process was conducted via continuous-flow isotope ratio mass spectrometry (CFIRMS). This method utilizes a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific Conflo IV interfaced with a Thermo Scientific DeltaV Plus Mass Spectrometer. Instrument error was < 0.2%. Tissue sulfur content was conducted by the University of California Davis Stable Isotope Facility, where 2.5 mg ± 0.5 mg of processed kelp tissue per sample was analyzed with CFIRMS using an Elementar vario ISOTOPE cube interfaced to an Isoprime PrecisION IRMS. Samples were analyzed in singlet with interspersed laboratory reference material for calibration. Instrument error was < 0.1%.

Carbohydrate composition was analyzed by the National Renewable Energy Laboratory in Golden, Colorado, using high-performance anion-exchange chromatography with pulsed amperometric detection (HPAEC-PAD). This method was used to quantify monomeric units after a two-step sulfuric acid pre-treatment for hydrolyzing polymeric carbohydrates into their respective monomers. The process followed the Determination of Total Carbohydrates in Algal Biomass LAP (Van Wychen & Laurens, 2023). Samples of lyophilized, homogenized tissues were shipped in capped Eppendorf tubes inside Styrofoam insulated containers with cold-packs and were kept frozen when not in transport. Samples of 25 mg ± 2.5 mg of dry algal biomass were run in singlet, with three random samples per batch of 30 run in triplicate, with an allowable standard deviation of up to 0.1% dry mass. An HPAEC-PAD system was used with a CarboPac PA1 column and guard, operated at an injection volume of 10 μL, a flow rate of 1 mL/min and a temperature of 35 °C in the column and detector. The following monosaccharides were analyzed with a limit of quantification of 0.0002 mg/ml: mannitol, fucose, rhamnose, galactosamine, arabinose, glucosamine, galactose, glucose, mannose, xylose, and ribose. The following uronic acids were analyzed with a limit of quantification of 0.002 mg/ml: galacturonic, guluronic, glucuronic, and mannuronic acid. The following standards were used for calibration curves following a series of nine dilution concentrations: D-mannitol (Sigma M4125), L(-) fucose (Sigma F2252), L(-) rhamnose monohydrate (SigmaR3875), D(+) galactosamine hydrochloride (Sigma G0500), D(-) arabinose (Sigma A3131), D(+) glucosamine hydrochloride, (Sigma G4875), D(+) galactose (Sigma G0750), D(+) glucose, (Sigma G7528), D(+) mannose (Sigma M2069), D(+) xylose, (Sigma X1500), and D(-) ribose (Sigma R7500). Correlations between sample monomers and their standard calibration curves were at least 0.999. Uronic acids were corrected for incomplete hydrolysis with correction factors calculated from the recovery fraction of 10 mg of hydrolyzed alginic acid after correcting with the galacturonic calibration curve. All samples were corrected for moisture content with monomers reported on a dry mass basis.

2.5 Polymer Calculations

Calculations for polysaccharides were based on methods by Bruhn et al., (2017). The fucoidan content calculation was as follows: Fucoidan = fucose + galactose + mannose + xylose + glucuronic acid + sulfate. Total sulfate was added to fucoidan calculations. Sulfate was calculated by mass sulfate = (mass sulfur / molar mass sulfur) × molar mass of sulfate ion. Sulfur attributable to protein is assumed to be negligible based on amino acid composition data of *S. latissima* (Marinho et al., 2015). Sulfate mass was subtracted from ash to avoid counting its mass twice. Arabinose was excluded from the fucoidan calculation, as it was below the level of quantification for every sample. Xylose and galactose were excluded, if levels were below detection or quantification levels. Alginate content was calculated as follows: Alginate = mannuronic + guluronic acid (with mannuronic acid quantified as galacturonic acid equivalents). M:G ratio was calculated as mannuronic acid % / guluronic acid %. Percent tissue nitrogen was multiplied by 5 to estimate protein content (Angell et al., 2016).

2.6 Data Analysis

All statistical analyses were performed using R version 2023.06.2+561. Kruskal-Wallis tests paired with Dunn's pairwise tests were used to test for differences in medians of dry mass closure (the sum of quantified components – ash, protein and carbohydrates – divided by the dry mass fraction, expressed as a percent) among species. Linear mixed-effects models were employed to investigate the impact of species, time, and their interaction on various response variables. Each response variable – namely, fucoidan, alginate, glucose, and mannitol (expressed as a percentage of dry mass), as well as the M:G ratio and the degree of sulfation of fucoidan (expressed as a percent mass fraction of fucoidan) – was individually modeled. Interactions were incorporated into the models when found to be statistically significant at an alpha level of 0.05, and subsequently removed if not, following the comparison of Akaike Information Criterion among models (AIC). Site was included as a random intercept effect to accommodate any variability among farm sites. If the random effect explained negligible variance, it was excluded, and a linear model was fit instead.

Intraclass correlation coefficients were utilized to evaluate the proportion of variability explained by the random effect term. T values were utilized for assessing significance, with the absolute value compared against a critical value of 1.98 (two-tailed, 0.05 alpha level). Estimated marginal means were employed to conduct pairwise comparisons between species. Estimates were scrutinized to discern the direction and magnitude of the effects for significant predictor terms. Additionally, predicted linear trends from each model were juxtaposed with scatterplots of actual values over time to assess model accuracy visually. Diagnostic plots, including Q-Q plots for normality, residuals versus fitted values for linearity, and residuals versus predictors for homogeneity of variance, were inspected to verify model assumptions.

Robust linear models were employed when comparing chemical content across collection sites to address residual variability from small sample sizes. Robust linear models were also applied to response variables exhibiting homogeneity of residual variance. In pursuing model simplification, non-significant interactions were removed following AIC comparisons. In cases where samples were gathered from more than two sites, estimated marginal means were utilized for pairwise analysis, facilitating the detection of significant interactions. Natural logarithm transformations were applied to response variables as warranted to achieve normality, guided by examination of residuals versus fitted plots to enhance model fit and meet assumptions. Significance testing was conducted using T values derived from robust linear models, with significance determined as described above. Spearman's rank correlation coefficients were used in assessing correlations among response variables, as well as correlations among environmental predictors and biochemistry metrics. Environmental data were averaged between sampling efforts to balance the number of data points in the predictor variables with the response variables. Only correlation coefficient values greater than $|0.50|$ were included in the results, with moderate correlations defined here as 0.50 to 0.69 and strong correlations ≥ 0.70.

3. Results

3.1 Environmental Conditions at Sites

Kodiak Site showed a fluctuating yet decreasing trend in irradiance from a maximum daily mean of 11.91 klx ± 14.96 klx at day of year (DOY) 109 to a minimum daily mean of 0.01 klx ± 0.02 klx at DOY 180 (Figure 4a, Table S1). Water temperature showed an opposite trend increasing from a minimum daily mean of 3.99 ^{o}C ± 0.13 ^{o}C at DOY 105 to a maximum daily mean of 9.41 ^{o}C ± 0.65 ^{o}C at DOY 177 (Figure 4b). This site had the lowest mean seawater temperature (6.05 ^{o}C ± 1.40 ^{o}C) compared to all other sites (Table S1). Relative water motion at this site could not be measured as the logger was not recovered.

DIN remained consistent throughout the sampling period, with a mean of 5.37 μM ± 1.22 μM (Figure 4c, Table S2). Orthophosphate fluctuated but generally decreased over the sampling period from a mean of 0.94 μM ± 0.05 μM at DOY 105 to a mean of 0.37 μM ± 0.10 μM at DOY 180 (Figure 4d). Salinity also fluctuated, increasing over the study period from a mean of 17.0 ± 3.0 at DOY 105 to a mean of 30.0 ± 1.7 at DOY 180 (Figure 4d).

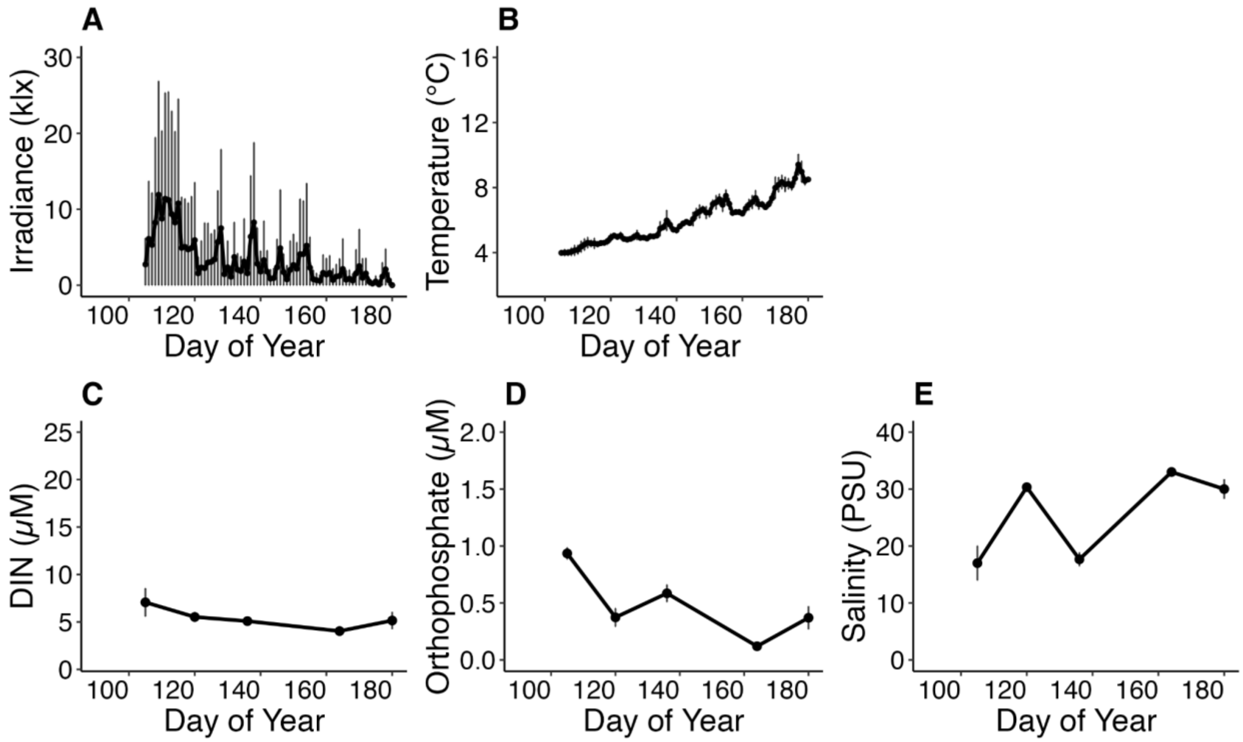

Figure 4. Environmental variables collected from 4/14 to 6/28 (day of year 105 to 180), 2023 at Kodiak Site (commercial kelp farm in Alaska). A) Irradiance, B) temperature, C) dissolved inorganic nitrogen (DIN), D) orthophosphate, and E) salinity. Each point represents a sampling event, the solid line in each graph shows the trend over time, and the vertical lines show one standard deviation.

PWS Site 1 also showed a fluctuating yet overall decreasing trend in irradiance, from a maximum daily mean of 10.63 klx ± 13.04 klx at DOY 111 to a minimum daily mean of 0.19 klx ± 0.39 klx at DOY 172 (Figure 5a). Water temperature showed an opposite trend, increasing from a minimum daily mean of 4.86 ^{o}C ± 0.13 ^{o}C at DOY 95 to a maximum daily mean of 12.40 ^{o}C ± 0.41 ^{o}C at DOY 172 (Figure 5b). Relative water motion increased markedly from a daily mean of 1.14 *g* ± 0.06 *g* at DOY 145 to a daily mean of 1.63 *g* ± 0.05 *g* at DOY 152, before fluctuating with no discernable trend (Figure 4c).

DIN remained relatively consistent throughout the sampling period, with a mean of 4.25 μM ± 1.42 μM (Figure 5d, Table S2). Orthophosphate mirrored DIN and stayed fairly consistent throughout the sampling period, with a mean of 0.14 μM ± 0.13 μM (Figure 5e, Table S2).

Salinity remained consistent for much of the study period but dipped from a mean of 31.0 ± 1.0 at DOY 133 to a mean of 22.7 ± 6.0 at DOY 155 before returning to a mean of 30.7 ± 0.6 at DOY 165 (Figure 5d).

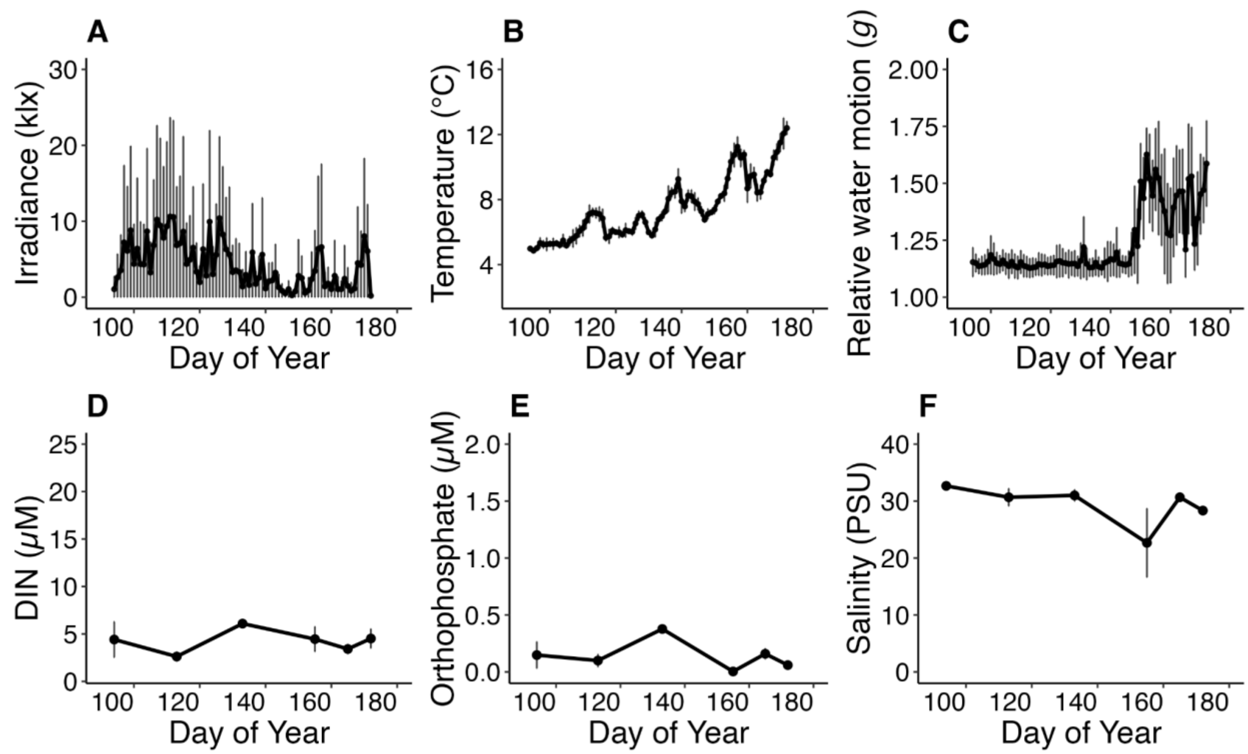

Figure 5. Environmental variables collected from 4/3 to 6/20 (day of year 94 to 172), 2023 at PWS Site 1 (commercial kelp farm in Alaska). A) Irradiance, B) temperature, C) dissolved inorganic nitrogen (DIN), D) orthophosphate, and E) salinity. Each point represents a sampling event, the solid line in each graph shows the trend over time, and the vertical lines show one standard deviation.

Similar to PWS Site 1, PWS Site 2 showed a fluctuating and slightly decreasing trend in irradiance, from a maximum daily mean of 9.43 klx ± 11.26 klx at DOY 107 to a minimum daily mean of 0.04 klx ± 0.10 klx at DOY 140 (Figure 6a). Water temperature showed an opposite trend, increasing from a minimum daily mean of 5.56 ^{o}C ± 0.11 ^{o}C at DOY 94 to a maximum daily mean of 9.67 ^{o}C ± 0.28 ^{o}C at DOY 140 (Figure 6b). Relative water motion stayed relatively consistent for much of the study period, with a mean of 1.13 *g* ± 0.08 *g* (Figure 6c, Table S1). This site had the lowest mean relative water motion compared to all other sites (Table S1).

DIN stayed consistent initially but increased from a mean of 2.36 μM ± 1.34 μM at DOY 127 to a mean of 6.87 μM ± 2.76 μM at DOY 140 (Figure 6d). Orthophosphate stayed relatively consistent throughout the sampling period, with a mean of 0.10 μM ± 0.11 μM (Figure 6e. Table S2). Salinity decreased over the study period and increased in variability from a mean of 31.0 ± 1.0 at DOY 94, to a mean of 13.2 ± 13.3 at DOY 140 (Figure 6f. Table S2). This site had the lowest mean salinity (23.7 ± 9.2) compared to all other sites (Table S2).

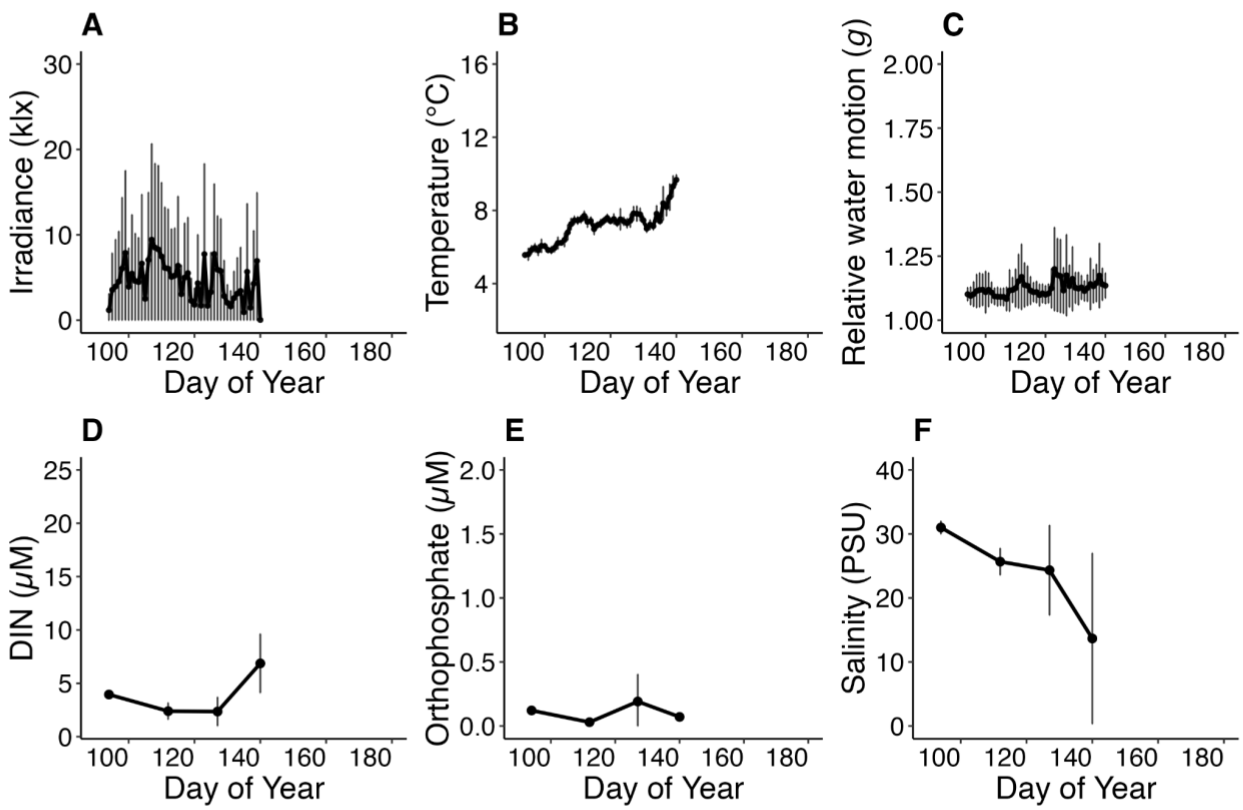

Figure 6. Environmental variables collected from 4/3 to 5/19 (day of year 94 to 140), 2023 at PWS Site 2 (commercial kelp farm in Alaska). A) Irradiance, B) temperature, C) dissolved inorganic nitrogen (DIN), D) orthophosphate, and E) salinity. Each point represents a sampling event, the solid line in each graph shows the trend over time, and the vertical lines show one standard deviation.

SE Site 1 had no discernable trend in irradiance, with a mean of 2.15 klx ± 4.17 klx (Figure 7a, Table S1). Water temperature increased from a minimum daily mean of 4.49 ºC ± 0.09 ºC at DOY 104 to a maximum daily mean of 13.89 ºC ± 0.14 ºC at DOY 177 (Figure 7b.

Table S1). Relative water motion stayed relatively consistent for much of the study period, with a mean of 1.25 *g* ± 0.14 *g* (Figure 7c, Table S1).

DIN fluctuated largely among sample efforts, with a maximum mean of 21.1 μM ± 0.88 μM at DOY 102, and a minimum mean of 2.57 μM ± 0.54 μM at DOY 179 (Figure 7d, Table S2). This site had the highest mean DIN (11.39 μM ± 7.91 μM) compared to all other sites (Table S2). Orthophosphate mirrored DIN in its fluctuating pattern with a maximum mean of 1.69 μM ± 0.02 μM at DOY 102, and a minimum mean of 0.04 μM ± 0.03 μM at DOY 179 (Figure 7e, Table S2). This site had the highest mean orthophosphate (0.84 μM ± 0.68 μM) compared to all other sites (Table S2). Salinity decreased slightly over the study period, with a mean of 33.0 ± 0.0 at DOY 102 to a mean of 21.3 ± 2.1 at DOY 179 (Figure 7f).

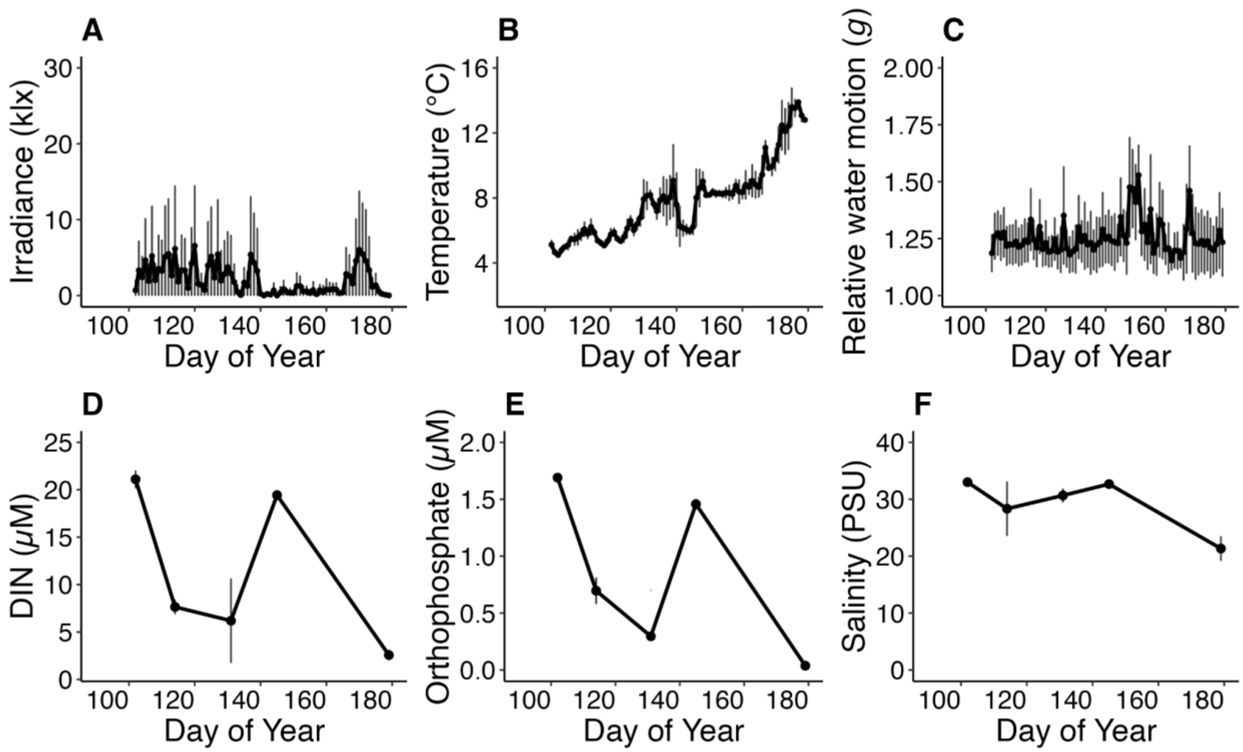

Figure 7. Environmental variables collected from 4/11 to 6/27 (day of year 102 to 179), 2023 at SE Site 1 (commercial kelp farm in Alaska). A) Irradiance, B) temperature, C) dissolved inorganic nitrogen (DIN), D) orthophosphate, and E) salinity. Each point represents a sampling event, the solid line in each graph shows the trend over time, and the vertical lines show one standard deviation.

SE Site 2 contained gaps in environmental data as the logger system was accidentally removed and subsequently reinstalled, while nutrient and salinity data had only two sampling efforts. Similar to SE Site 1, this site showed fluctuating irradiance, with a mean of 1.56 klx ± 3.32 klx (Figure 8a, Table S1). Water temperature increased from a minimum daily mean of 6.09 ºC ± 0.07 ºC at DOY 104 to a maximum daily mean of 12.70 ºC ± 0.40 ºC at DOY 147 (Figure 8b). Relative water motion fluctuated but had no discernible trend for the study period (Figure 8c). This site had the highest mean relative water motion (1.301*g* ± 0.08 *g*) compared to all other sites (Table S1).

DIN dropped slightly between the start and end of study, with a daily mean of 4.44 μM ± 0.02 μM at DOY 98 and a daily mean of 2.81 μM ± 1.20 μM at DOY 162 (Figure 8d). Orthophosphate remained consistent between the start and end of the study, with a mean of 0.38 μM ± 0.07 μM (Figure 8e. Table S2). Salinity remained consistent between the start and end of the study, with a mean of 31.07 ± 0.5 (Figure 8f, Table S2). This site had the highest mean salinity compared to all other sites (Table S2).

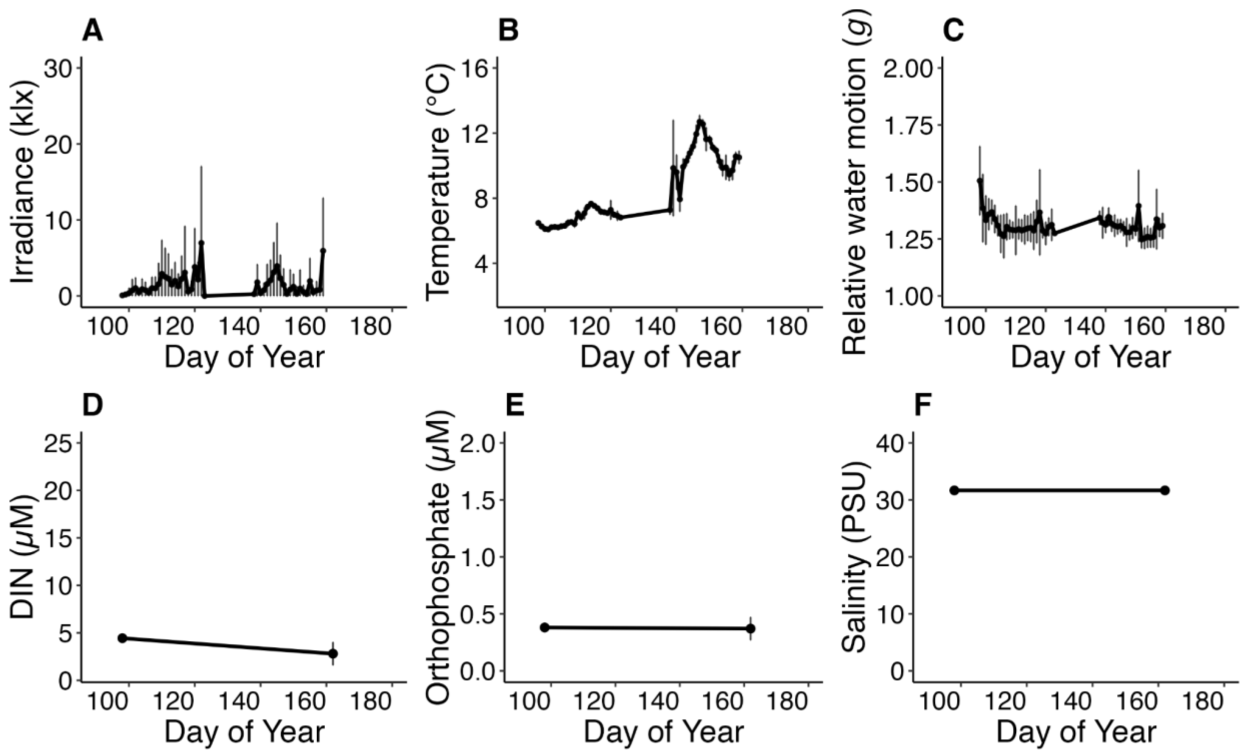

Figure 8. Environmental variables collected from 4/7 to 6/10 (day of year 98 to 162), 2023 at SE Site 2 (commercial kelp farm in Alaska). A) Irradiance, B) temperature, C) dissolved inorganic

nitrogen (DIN), D) orthophosphate, and E) salinity. Each point represents a sampling event, the solid line in each graph shows the trend over time, and the vertical lines show one standard deviation.

3.2 Dry mass closure

In this study, none of the species analyzed achieved a dry mass closure of 100%. The highest dry mass closure recorded was 96.67%, and the lowest was 57.98%, both in samples of *N. luetkeana* (Figure 9). The average dry mass closure varied significantly among species ($p < 0.001$). *S. latissima* exhibited the highest median dry mass closure, with a relatively small interquartile range (IQR) of 86.78 ± 3.25%. *N. luetkeana* had the second-highest median dry mass closure but showed the largest IQR of 84.49 ± 8.55%. In contrast, *A. marginata* displayed the lowest median dry mass closure at 76.66 ± 5.51% (Figure 9).

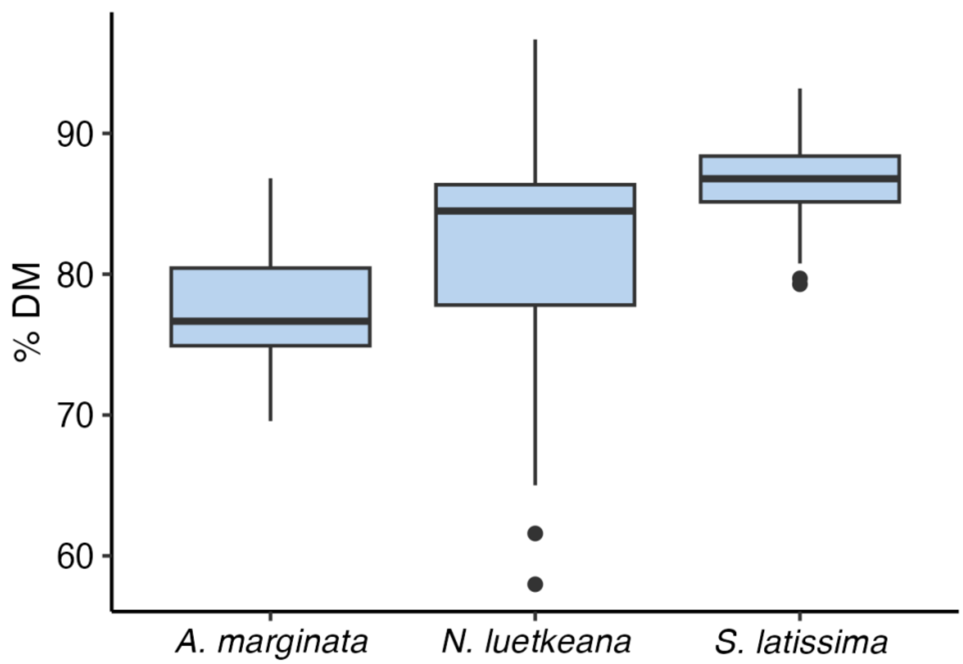

Figure 9. Percent of dry mass accounted for as the sum of quantified components (ash, protein, fucoidan, alginate, glucan, and mannitol) for *Alaria marginata*, *Nereocystis luetkeana*, and *Saccharina latissima* between April and June 2023. Data were combined across commercial kelp farm sites in Alaska (two sites for *A. marginata* and *N. luetkeana*, and five sites for *S. latissima*).

3.3 Dry Mass Fraction

The dry mass fraction (DMF) was significantly higher in *A. marginata* compared to *S. latissima* and *N. luetkeana* ($p < 0.001$). Additionally, *S. latissima* had a significantly higher DMF than *N. luetkeana* ($p < 0.001$; Figure 10a). DOY significantly predicted DMF ($t = 3.723$), with *N. luetkeana* showing a decrease in DMF over time ($t = 3.752$), whereas *S. latissima* and *A. marginata* showed an increase in DMF over time (Figure 10a).

Site-specific trends revealed that the average DMF of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 2.507$), with samples from PWS Site 1 having a 1.41% lower average DMF (Figure 10b). There was a significant correlation between DOY and DMF for *A. marginata* ($t = 3.390$), with an increase of 0.03% per day at both sites (Figure 10b). The average DMF of *S. latissima* did not differ significantly between sites, but there was a significant correlation between DOY and DMF ($t = 2.982$), with an increase of 0.02% per day at both sites (Figure 10c). For *N. luetkeana*, the average DMF differed significantly between PWS Site 2 and SE Site 1 ($t = 4.020$), with samples from PWS Site 2 having a 1.13% higher average DMF on DOY 90 (Figure 10d). There was a significant interaction between DOY and SE Site 1 ($t = 4.367$), where *N. luetkeana* from SE Site 1 decreased in average DMF by 0.01% per day, while *N. luetkeana* from PWS Site 2 decreased by 0.06% per day ($t = 6.151$; Figure 10d).

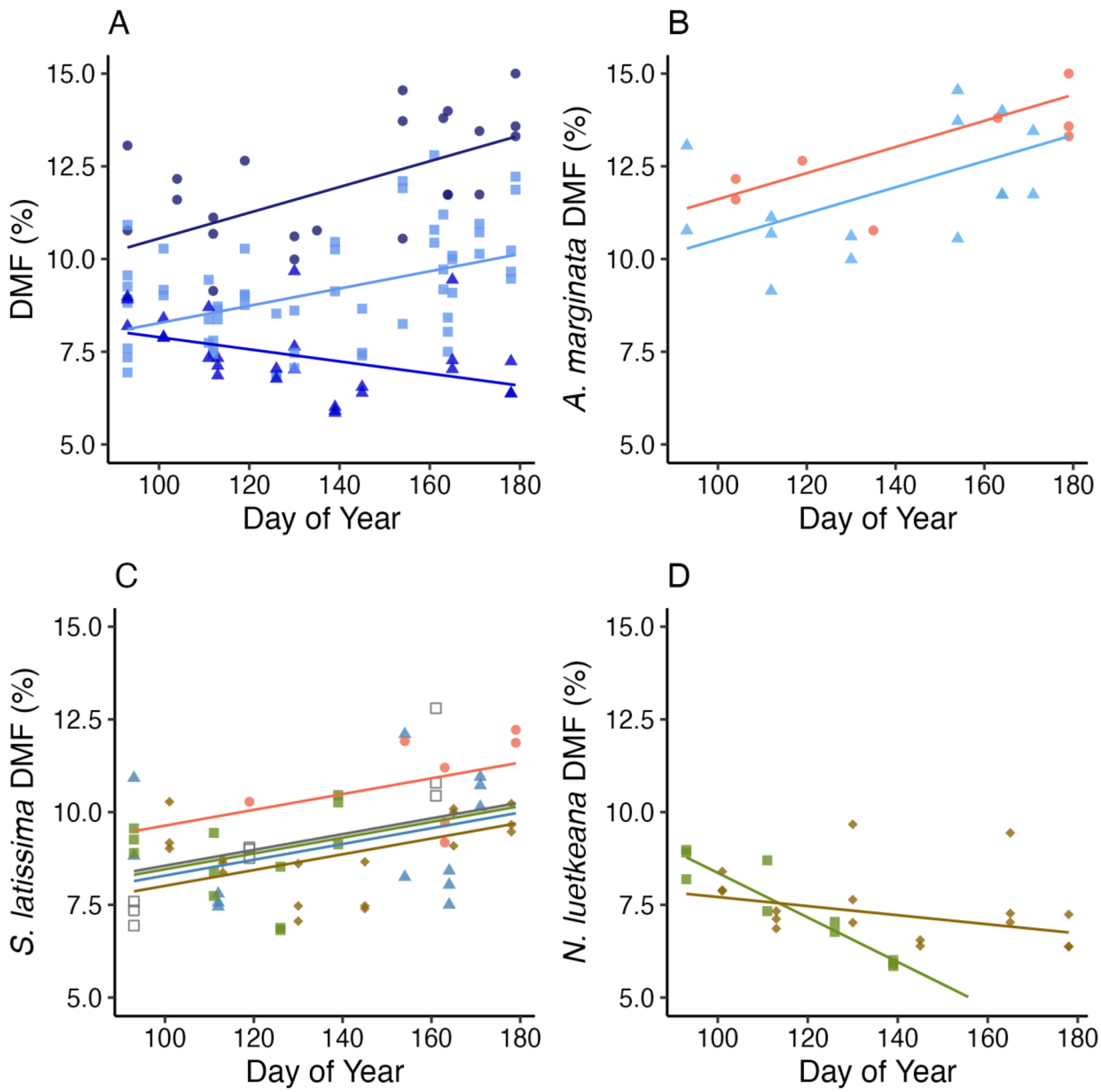

Figure 10. Dry mass fraction of wet biomass (DMF) regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.4 Ash Relative Abundance

Ash content of dry mass was significantly higher in *S. latissima* compared to *A. marginata* ($p < 0.001$) and *N. luetkeana* ($p = 0.008$). Additionally, *N. luetkeana* showed higher ash content than *A. marginata* ($p = 0.005$; Figure 11a). DOY was a significant predictor, with ash content decreasing in all species over the sampling period ($p = 0.005$; Figure 11a).

Site-specific trends revealed that the average ash content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 2.479$), with samples from PWS Site 1 having a 9.36% DM lower average ash content on DOY 90 (Figure 11b). There was a significant interaction between DOY and PWS Site 1 ($t = 2.404$), where *A. marginata* from PWS Site 1 increased in average ash content by 0.01% DM per day, while *A. marginata* from Kodiak Site decreased by 0.14% DM per day ($t = 2.798$; Figure 11b). The average ash content of *S. latissima* was higher at PWS Site 1 than at Kodiak Site, although this was not significant ($p = 0.066$). There was no significant correlation between DOY and average ash content for this species (Figure 11c). The average ash content of *N. luetkeana* did not differ significantly between sites, but there was a significant correlation with DOY ($t = 2.900$), with a decrease of 0.17% DM per day at both sites (Figure 11d).

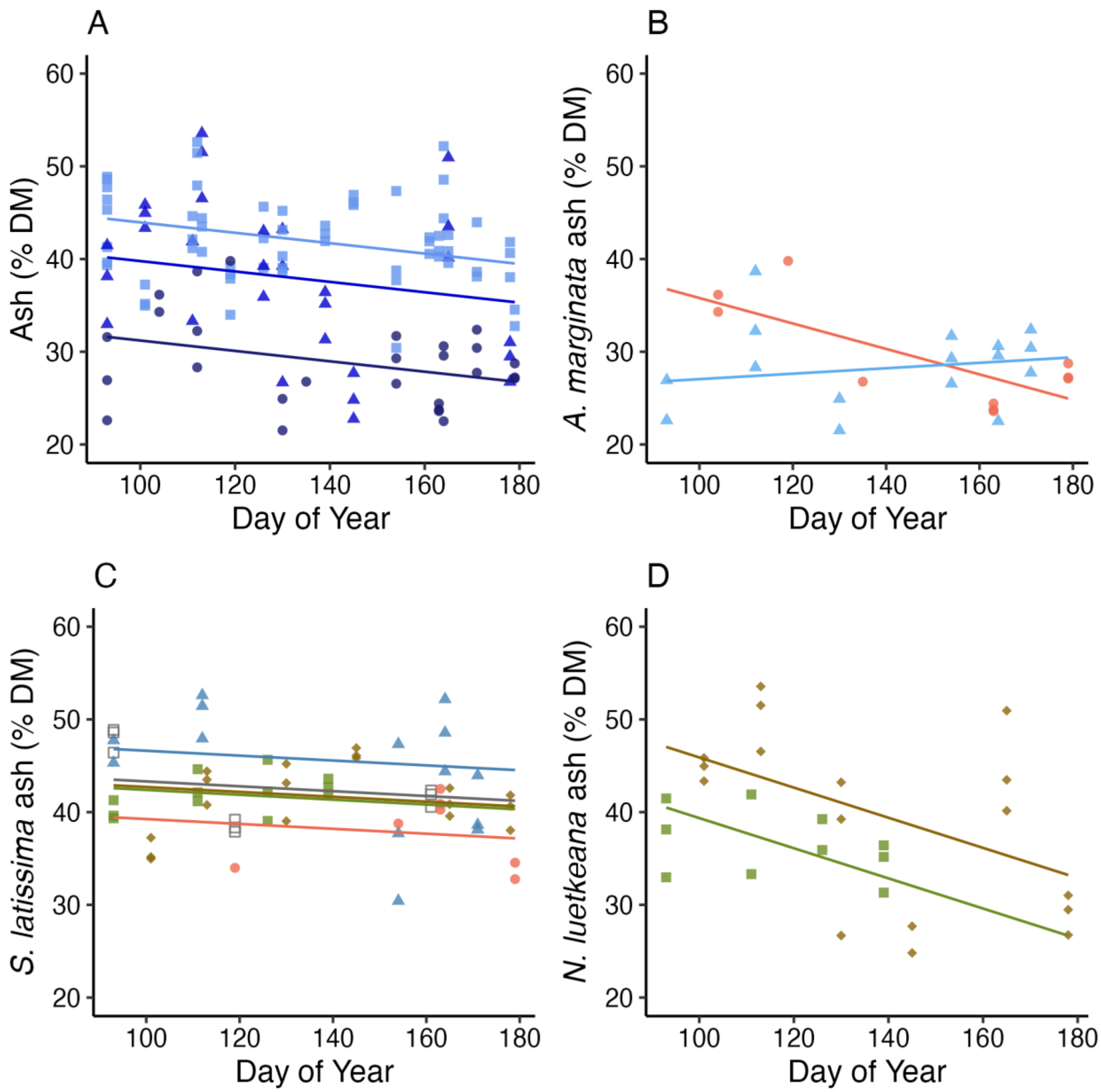

Figure 11. Percent ash content of dry mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.5 Protein Relative Abundance

Protein content of dry mass was significantly lower in *N. luetkeana* compared to *A. marginata* ($p = 0.002$) and *S. latissima* ($p < 0.001$; Figure 12a). DOY was a significant predictor, with protein decreasing in all species over the sampling period ($t = 3.817$; Figure 12a). Site-specific trends showed the average protein content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 6.407$), with samples from PWS Site 1 having a 7.96% DM lower protein content on DOY 90. There was a significant interaction between DOY and site for *A. marginata* ($t = 6.058$), where protein increased on average by 0.01% DM per day at PWS Site 1, and decreased on average by 0.12% DM per day at Kodiak Site ($t = 7.501$; Figure 12b). On DOY 90, the average protein content of *S. latissima* was significantly higher at the Kodiak Site compared to PWS Site 2, PWS Site 1, and SE Site 2 ($p < 0.001$, $p = 0.001$, and $p < 0.001$, respectively). Additionally, protein content in *S. latissima* was significantly higher at SE Site 1 compared to SE Site 2, PWS Site 1, and PWS Site 2 ($p < 0.001$). *S. latissima* from PWS Site 1 also showed significantly higher average protein content than those from SE Site 2 ($p < 0.001$) (Figure 12c). Significant interactions were also detected between DOY and sites. At Kodiak Site, SE Site 1, and SE Site 2, average protein content in *S. latissima* decreased by 0.11%, 0.04%, and 0.01% DM per day, respectively ($t = 3.342$, $t = 1.961$, $t = 2.456$). In contrast, at PWS Site 2, *S. latissima* increased by 0.01% DM per day ($t = 2.805$). The interaction between DOY and *S. latissima* from PWS Site 1 decreased by 0.04% DM per day on average, however this was not significant ($t = 1.823$; Figure 12c). Additionally, the average protein content of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 3.416$), with samples from PWS Site 2 having a 2.83% DM lower average protein content. There was no significant correlation between DOY and average protein content for *N. luetkeana* (Figure 12d).

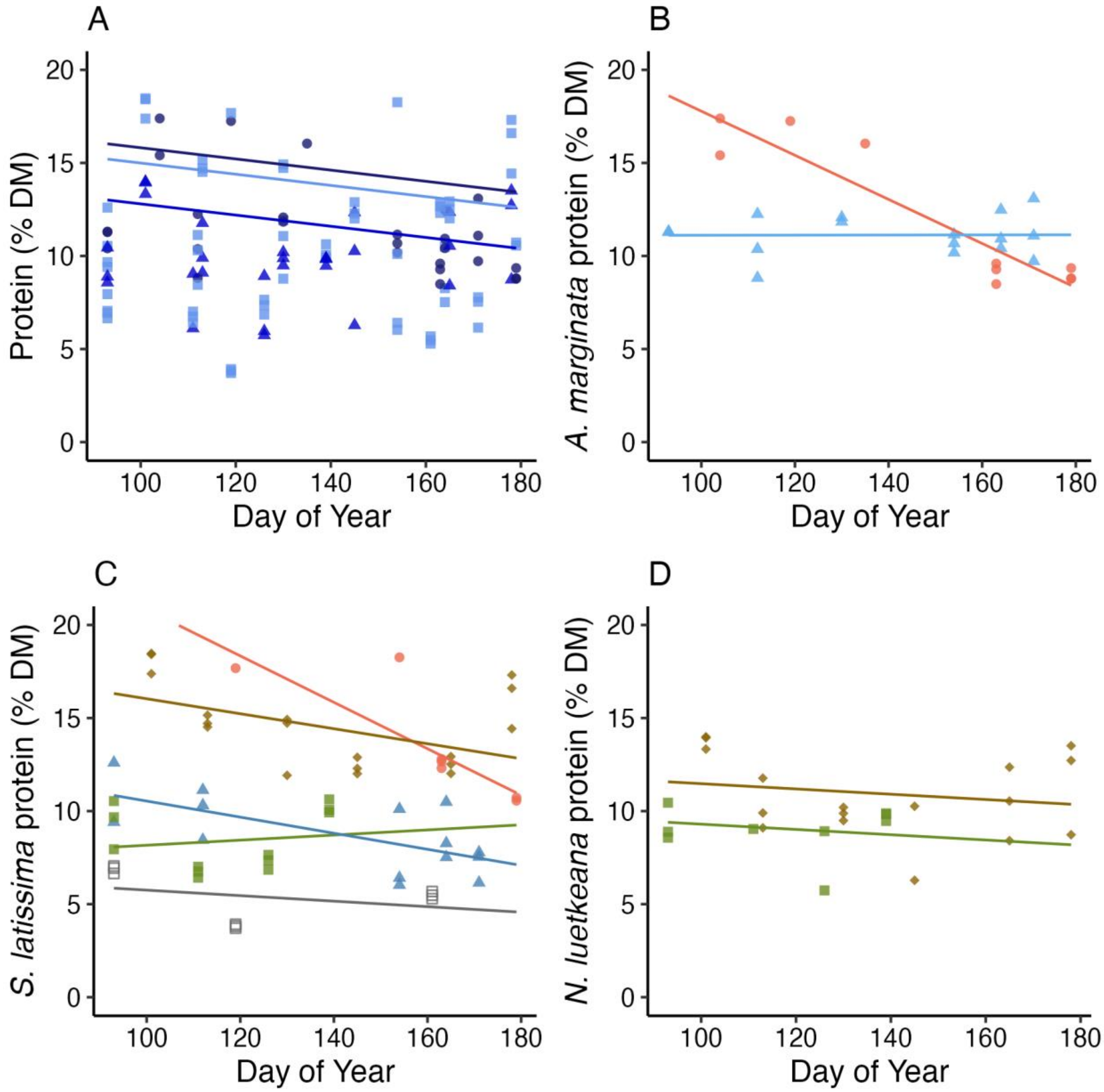

Figure 12. Percent protein content of dry mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.6 Fucoidan Relative Abundance

Fucoidan content of dry mass was significantly higher in *A. marginata* compared to *S. latissima* ($p = 0.005$) and *N. luetkeana* ($p < 0.001$). Additionally, *S. latissima* had significantly higher fucoidan content than *N. luetkeana* ($p < 0.001$) (Figure 13a). DOY did not significantly predict fucoidan content in *A. marginata* or *N. luetkeana*. However, there was a significant interaction between DOY and *S. latissima* ($t = 2.658$), where fucoidan content increased over the sampling period (Figure 13a).

Site-specific trends showed the average fucoidan content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 4.821$), with samples from PWS Site 1 having a 1.03% DM higher content (Figure 13b). Average fucoidan content of *A. marginata* increased by 0.01% DM per day at both sites (Figure 13b), however this correlation was not significant ($t = 1.900$). The average fucoidan content of *S. latissima* did not differ significantly between sites (Figure 13c). However, there was a significant correlation between DOY and average fucoidan content for this species ($t = 6.134$), with an increase of 0.02% DM per day at all sites (Figure 13c). The average fucoidan content of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 3.560$), with samples from PWS Site 2 having a 0.88% DM higher fucoidan content (Figure 13d). Average fucoidan content of *N. luetkeana* increased by 0.01% DM per day at both sites (Figure 13d), however this correlation was not significant ($t = 1.876$).

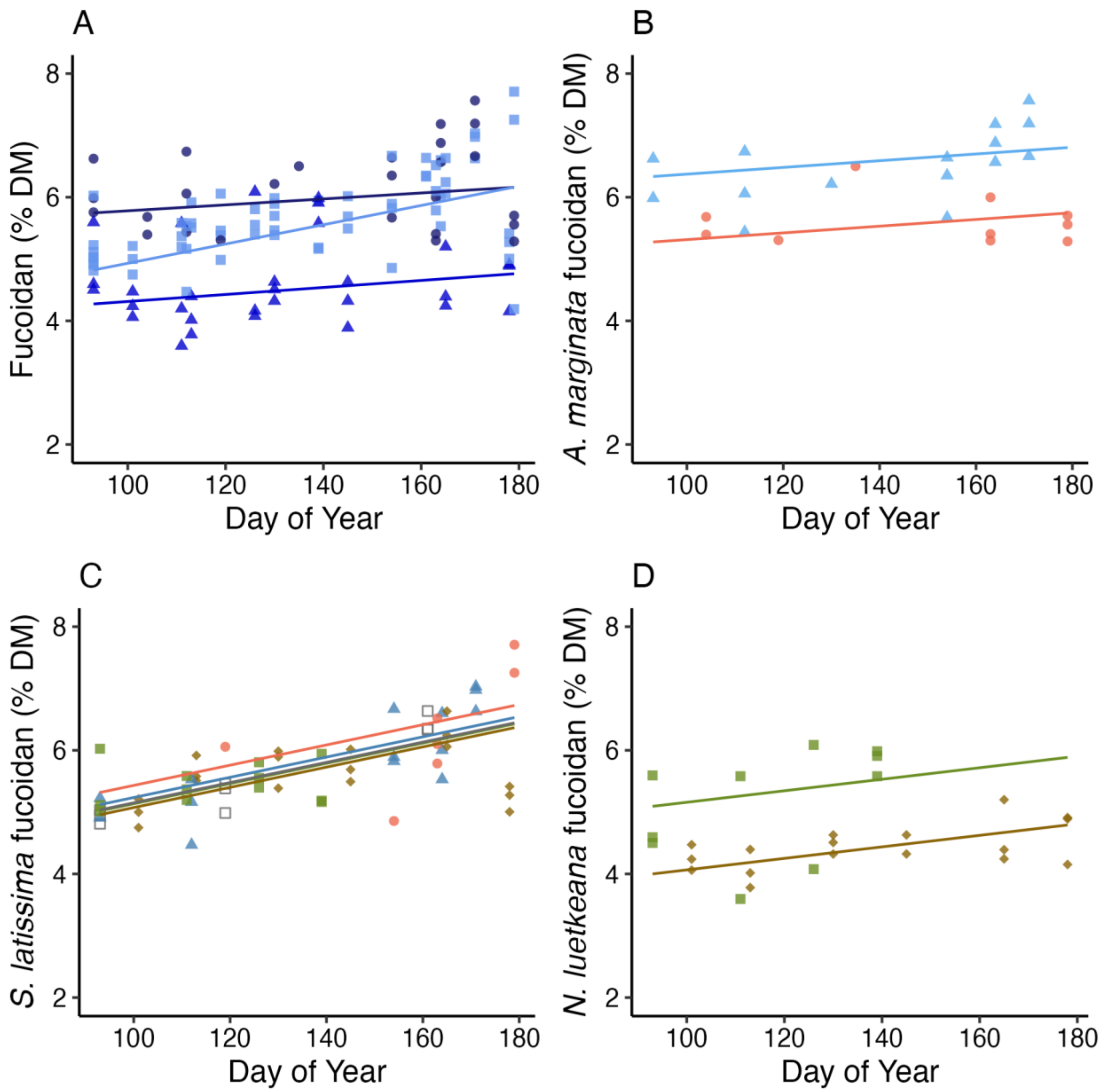

Figure 13. Percent fucoidan content of dry mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.7 Sulfation of Fucoidan

Sulfation (% sulfate in fucoidan) was significantly higher in *N. luetkeana* compared to *A. marginata* ($p < 0.001$) and *S. latissima* ($p < 0.001$). No significant differences were detected between *A. marginata* and *S. latissima* (Figure 14a). Contrary to other results, DOY was not a significant predictor of sulfation (Figure 14a).

Site-specific trends showed the average sulfation of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 3.365$), with samples from PWS Site 1 having a 12.85% lower sulfation on DOY 90. There was a significant interaction between DOY and PWS Site 1 ($t = 2.517$), where *A. marginata* from PWS Site 1 increased in average sulfation by 0.03% per day, while *A. marginata* from Kodiak Site decreased by 0.09% DM per day ($t = 2.439$; Figure 14b). The average sulfation of *S. latissima* did not differ significantly between sites, nor was there a significant correlation between DOY and average sulfation for this species (Figure 14c). On the other hand, the average sulfation of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 3.830$), with samples from PWS Site 2 having a 6.91% higher average sulfation on DOY 90. There was a significant interaction between DOY and SE Site 1 ($t = 4.362$), where *N. luetkeana* from SE Site 1 increased in average sulfation by 0.06% per day, while *N. luetkeana* from PWS Site 2 decreased by 0.37% per day (Figure 14d).

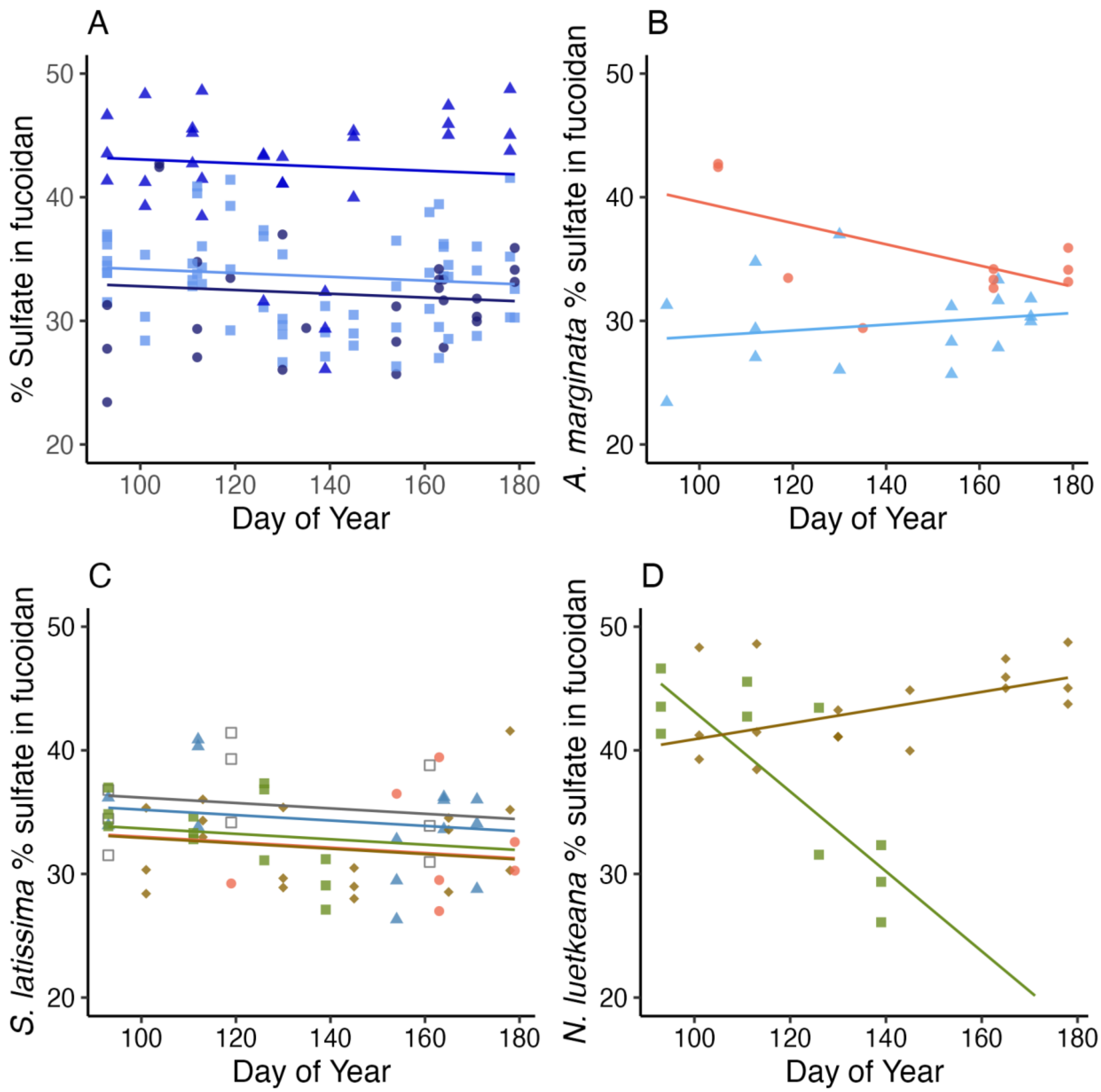

Figure 14. Percent sulfate content of fucoidan regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.8 Alginate Relative Abundance

Alginate content of dry mass was significantly higher in *A. marginata* compared to *N. luetkeana* ($p < 0.001$) and *S. latissima* ($p < 0.001$). *N. luetkeana* and *S. latissima* did not differ significantly (Figure 15a). DOY did not significantly predict alginate content in any species (Figure 15a).

Site-specific trends showed the average alginate content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($p = 0.003$), with samples from PWS Site 1 having a 4.35% DM higher alginate content on DOY 90. There was a significant interaction between DOY and PWS Site 1 ($t = 5.471$), where *A. marginata* from PWS Site 1 decreased in average alginate content by 0.06% DM per day, while *A. marginata* from Kodiak Site increased by 0.10% DM per day ($t = 4.279$; Figure 15b). The average alginate content of *S. latissima* did not differ significantly between sites on DOY 90. However, there was a significant interaction between DOY and SE Site 2 ($t = 2.216$), where *S. latissima* from SE Site 2 increased in average alginate content by 0.06% DM per day (Figure 15c). The average alginate content in *S. latissima* from Kodiak Site and SE Site 1 appeared to decrease over time, although these trends were not significant (Figure 15c). Lastly, the average alginate content of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 4.319$), with samples from PWS Site 2 having a 4.49% DM higher content (Figure 15d). There was no significant correlation between DOY and average alginate content for *N. luetkeana* (Figure 15d).

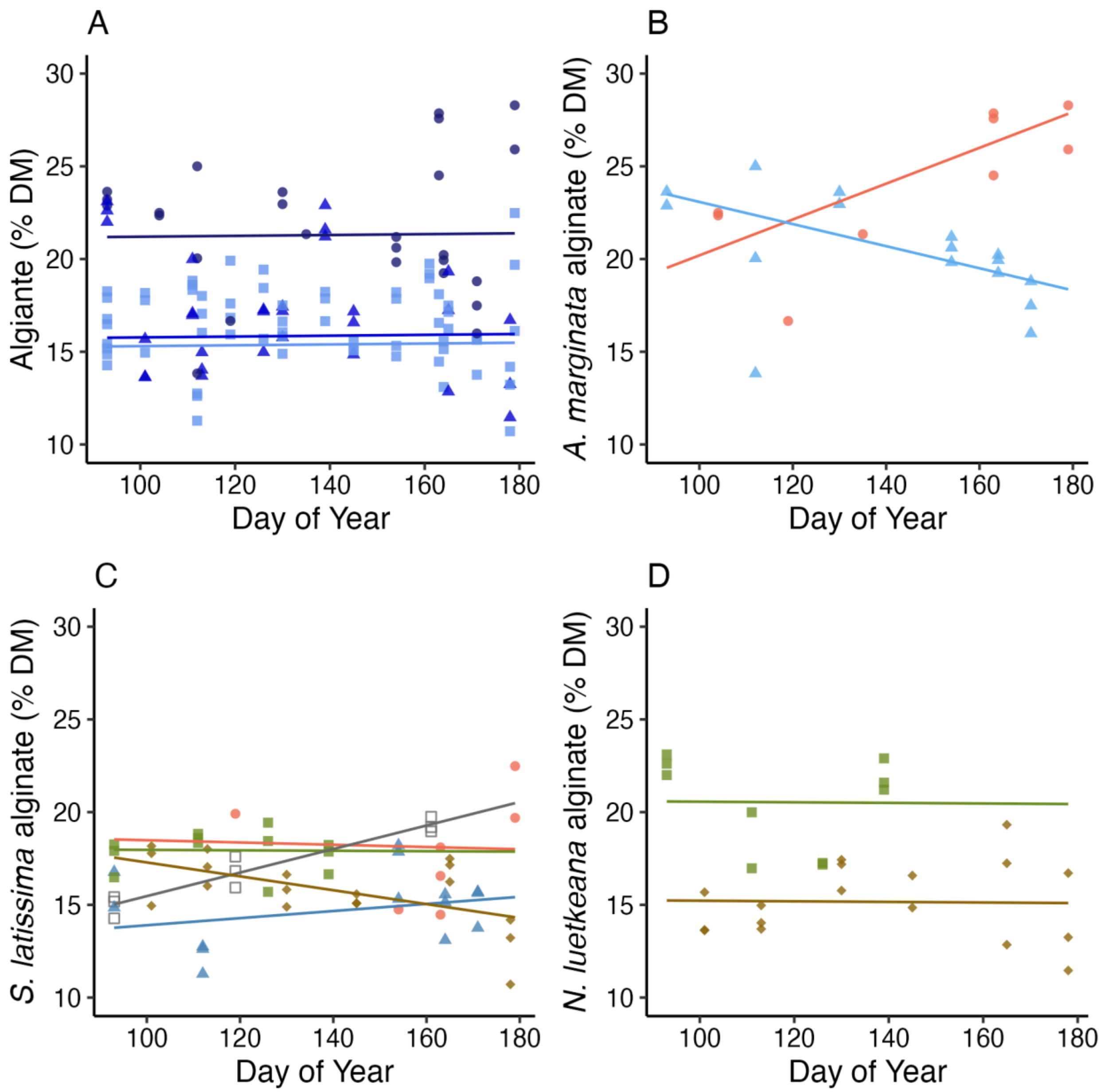

Figure 15. Percent alginate content of dry mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.9 Mannuronic to Guluronic Acid Ratio of Alginate

The M:G ratio was significantly higher in *A. marginata* than in *S. latissima* ($p < 0.001$) and *N. luetkeana* ($p = 0.012$). It was also significantly higher in *N. luetkeana* compared to *S. latissima* ($p = 0.023$; Figure 16a). DOY significantly predicted the M:G ratio, which decreased over the study period in all species ($t = 7.253$; Figure 16a).

Regarding site-specific trends, the average M:G ratio of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 2.741$), with samples from PWS Site 1 having an M:G ratio 2.47 higher on DOY 90. There was a significant interaction between DOY and PWS Site 1 ($t = 2.526$), where the M:G ratio in *A. marginata* decreased on average by 0.03 per day (Figure 16b). For *S. latissima*, the average M:G ratio differed significantly between sites, with samples from PWS Site 1 and SE Site 2 having significantly higher ratios than those from PWS Site 2 ($p = 0.010$ and $p < 0.001$, respectively). The M:G ratio of *S. latissima* from Kodiak Site was higher than PWS Site 2, however this was not significant ($p = 0.076$). Moreover, results show a significant correlation between DOY and average M:G ratio for *S. latissima*, with a decrease of 0.01 per day at all sites ($t = 5.868$; Figure 16c). Lastly, the average ratio of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 5.986$), with samples from PWS Site 2 having a ratio 1.69 lower than those from SE Site 1 (Figure 16d). There was a significant correlation between day of the year and the average M:G ratio ($t = 6.478$), with a decrease of 0.04 per day detected at both sites (Figure 16d).

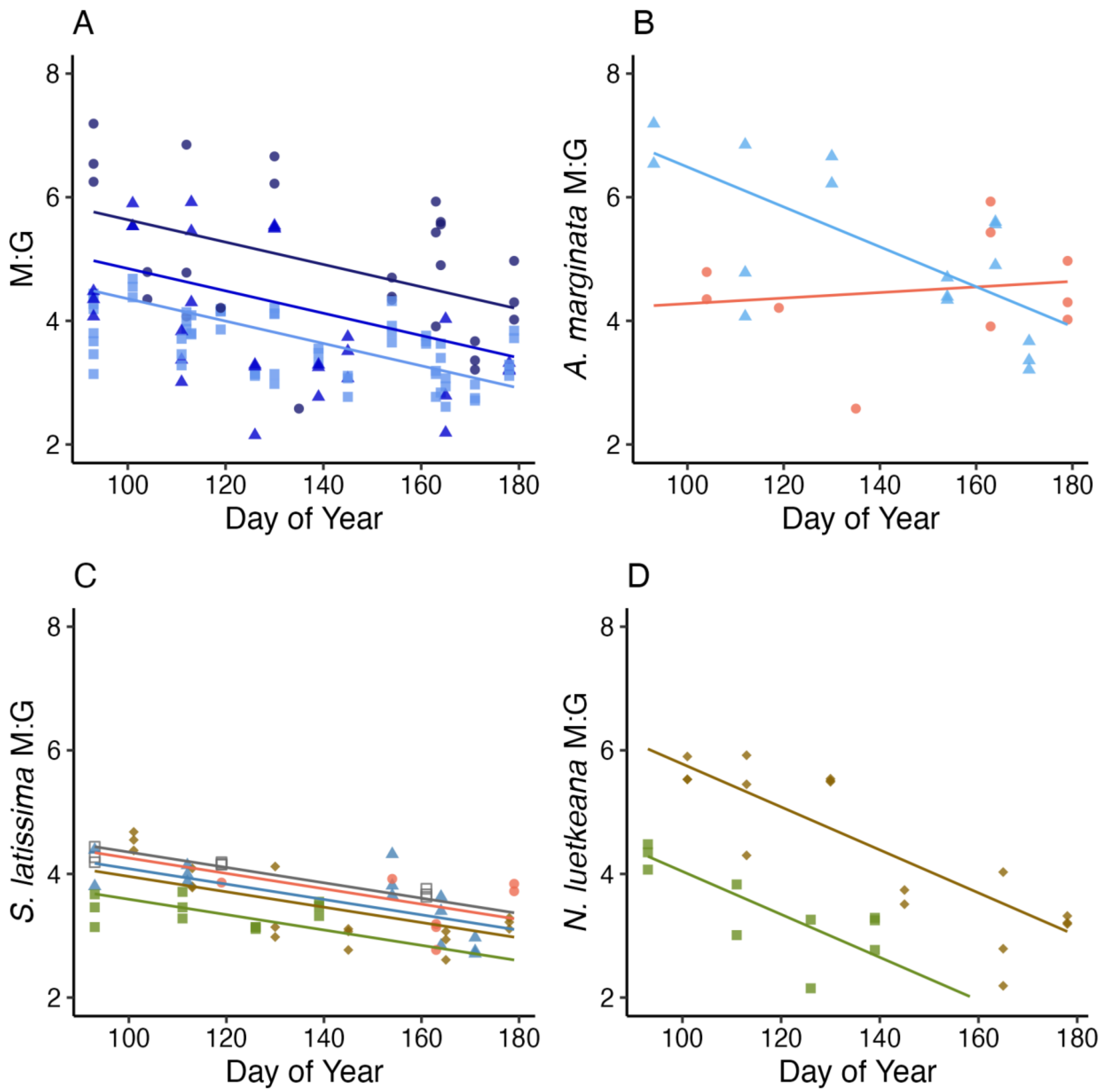

Figure 16. Mannuronic to guluronic acid ratio in alginate regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.10 Glucan Relative Abundance

Glucan content of dry mass was significantly higher in *S. latissima* than in *A. marginata* ($p = 0.001$) and *N. luetkeana* ($p = 0.001$). There was no significant difference in glucan content between *A. marginata* and *N. luetkeana* (Figure 17a). DOY did not significantly predict glucan content in *A. marginata*. However, there was a significant interaction between DOY and *N. luetkeana* ($t = 3.023$), with glucan content increasing over the sampling period. There was an insignificant interaction between DOY and *S. latissima* ($t = 1.847$), which also increased over the sampling period (Figure 17a).

Regarding site-specific trends, the average glucan content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 2.746$), with samples from PWS Site 1 having a 3.74% DM higher content on DOY 90. There was a significant interaction between DOY and PWS Site 1 ($t = 2.241$), where *A. marginata* from PWS Site 1 decreased in average glucan content by 0.01% DM per day (Figure 17b). Furthermore, average glucan in *S. latissima* differed significantly between PWS Site 1 and PWS Site 2 ($p = 0.025$), with samples from PWS Site 2 having a 0.61% DM higher content. There was a significant correlation between DOY and average glucan content for *S. latissima* ($t = 4.542$), which increased by 0.01% DM per day (Figure 17c). The average glucan content was insignificantly different between *N. luetkeana* growing in PWS Site 2 and SE Site 1 ($t = 1.715$), with samples from PWS Site 2 having a 0.11% DM higher content on DOY 90. There was a significant interaction between DOY and site for *N. luetkeana*, where the average glucan content increased by 0.02% DM per day at SE Site 1 ($t = 2.437$), while at PWS Site 2 glucan content increased by 0.05% DM ($t = 3.948$; Figure 17d).

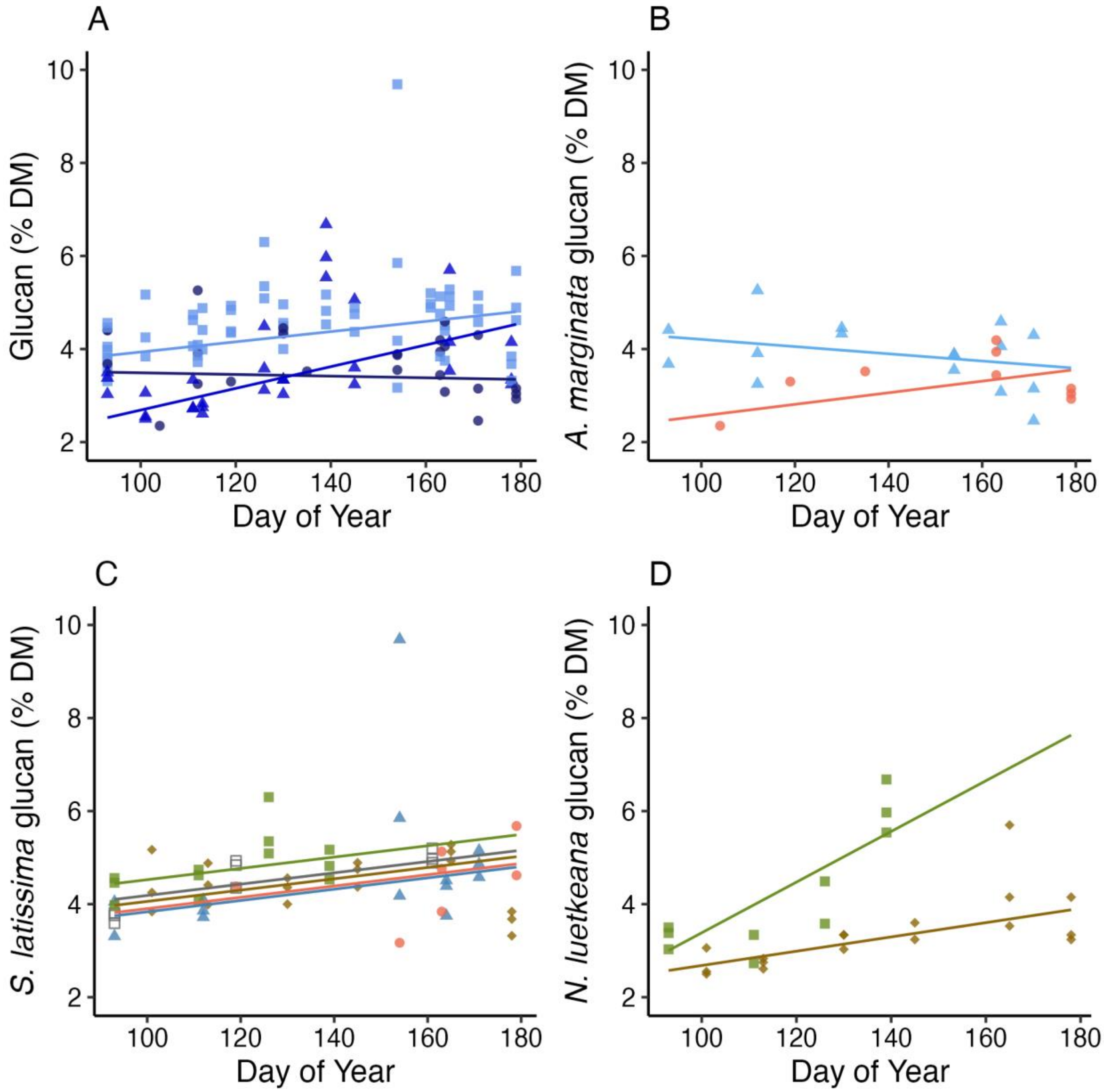

Figure 17. Percent glucan content of dry mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.11 Mannitol Relative Abundance

Contrary to the results obtained for other components, mannitol content of dry mass did not significantly differ among species (Figure 18a). DOY significantly predicted mannitol content, which decreased over the sampling period in all species (Figure 18a). The average mannitol content of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 3.171$), with samples from PWS Site 1 having a 5.38% DM higher content on DOY 90. There was a significant interaction between DOY and PWS Site 1 ($t = 2.839$), where *A. marginata* from this site showed a 0.79% DM decrease in average mannitol content per day (Figure 18b). The average mannitol content of *S. latissima* also differed significantly between sites. *S. latissima* from PWS Site 2 had a higher average mannitol content than Kodiak Site, SE Site 1, and SE Site 2 ($p = 0.004$, $p < 0.001$, and $p < 0.001$, respectively) on DOY 90. Additionally, *S. latissima* from PWS Site 2 significantly interacted with DOY ($t = 2.561$), where the average mannitol content increased by 0.13% DM per day. Although *S. latissima* from SE Site 1 appeared to decrease in average mannitol content over time, this trend was not significant (Figure 18c). Site also influenced the average mannitol content in *N. luetkeana*, where samples from PWS Site 2 and SE Site 1 were significantly different ($t = 2.642$), with those from PWS Site 2 having a 10.09% DM higher content on DOY 90. Results showed a significant interaction between DOY and site for *N. luetkeana* ($t = 2.220$), where those from SE Site 1 decreased by 0.01% DM per day in average mannitol content, while those from PWS Site 2 decreased by 0.19% DM per day (Figure 18d).

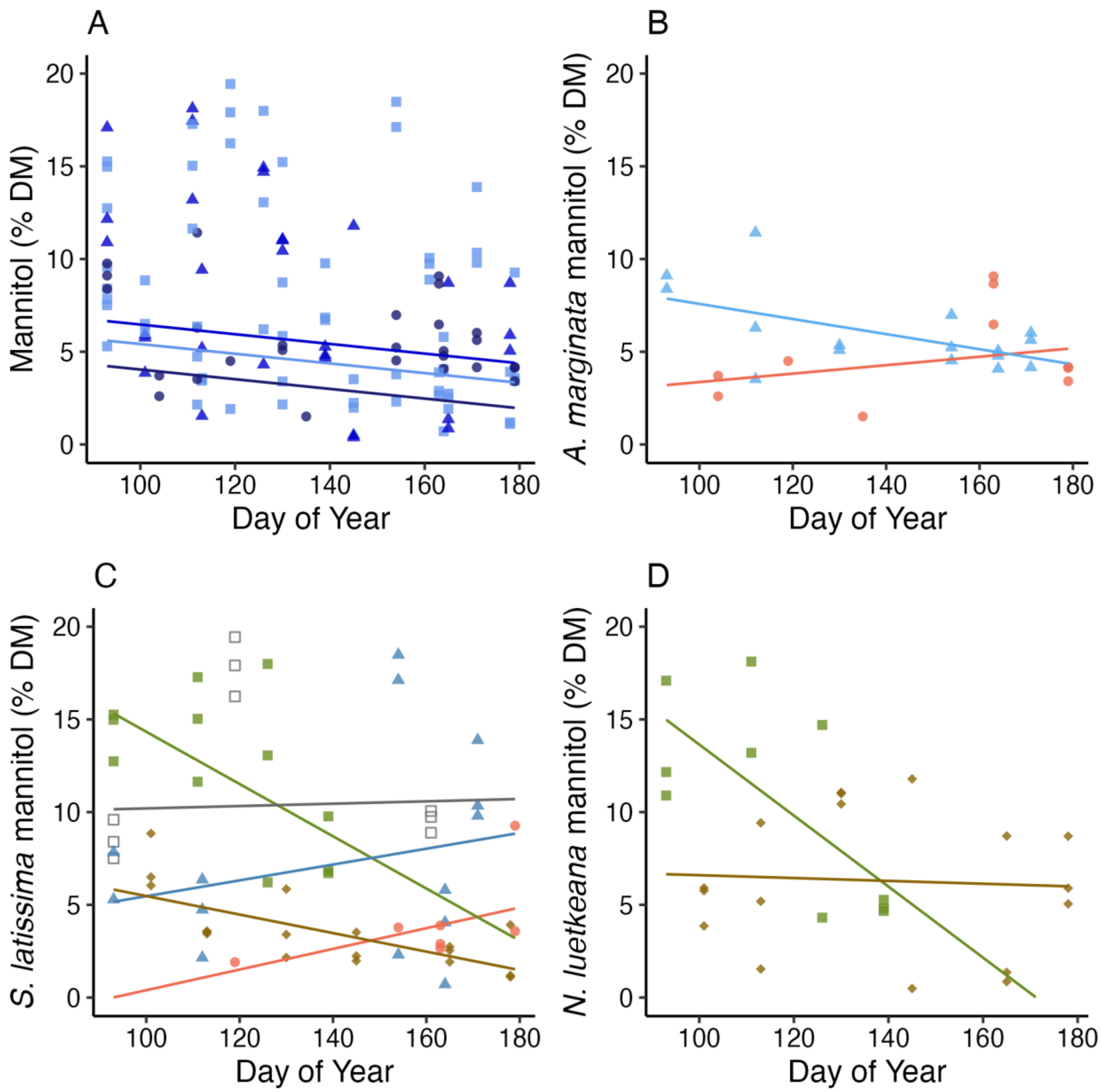

Figure 18. Percent mannitol content of dry mass between April and June, 2023. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*A. marginata*–dark-blue circle–, *N. luetkeana*–medium-blue triangle–, and *S. latissima*–light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.12 Wet Mass

Wet mass was significantly higher in *S. latissima* than in *A. marginata* ($p < 0.001$) and significantly higher in *N. luetkeana* than in *A. marginata* ($p < 0.001$; Figure 19a). DOY was a significant predictor ($t = 3.785$), with values for all species increasing over the sampling period (Figure 19a). The average wet mass of *A. marginata* differed significantly between PWS Site 1 and Kodiak Site ($t = 6.201$), with samples from PWS Site 1 having a lower average wet mass at DOY 90. There was a significant correlation with DOY ($t = 5.297$), with an average wet mass increase of 1.92% per day (Figure 19b). For *S. latissima*, wet mass differed significantly among sites, with those from SE Site 2 having higher values than PWS Site 1 and PWS Site 2 ($p = 0.027$ and $p = 0.001$, respectively). Wet mass at SE Site 1 was significantly lower than at PWS Site 1 and SE Site 2 ($p = 0.017$ and $p < 0.001$, respectively). There was a significant interaction between DOY and SE Site 2, where *S. latissima* from this site decreased in wet mass by 3.31 % per day ($t = 2.078$; Figure 19c). The average wet mass of *N. luetkeana* differed significantly between PWS Site 2 and SE Site 1 ($t = 3.311$), with samples from PWS Site 2 having a lower average wet mass at DOY 90. No correlation was detected with DOY for *N. luetkeana* (Figure 19d).

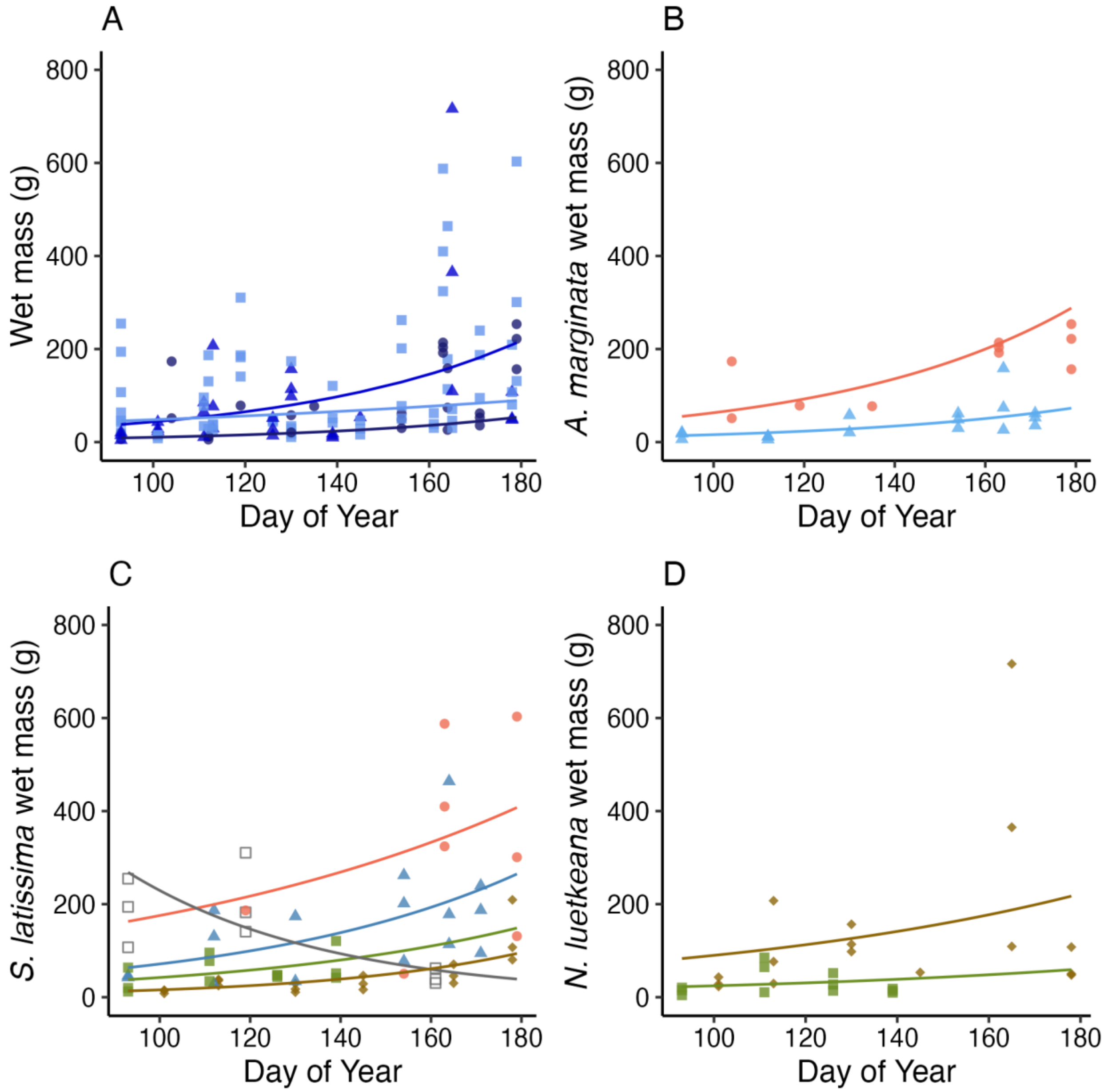

Figure 19. Wet mass regression models. Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. A) All species (*Alaria marginata*–dark-blue circle–, *Nereocystis luetkeana*–medium-blue triangle–, and *Saccharina latissima*– light-blue, square–). B) *A. marginata* (Kodiak Site–red circle–and PWS Site 1–blue triangle–). C) *S. latissima* (Kodiak Site–red circle–, PWS Site 1–blue triangle–, PWS Site 2–green square–, SE Site 1–brown diamond–and SE Site 2–gray open square–). D) *N. luetkeana* (PWS Site 2–green square–and SE Site 1–brown diamond–).

3.13 Correlations Among Components

The strongest correlations among components in *A. marginata* were the positive relationship between wet mass and dry mass fraction (Spearman's rank correlation coefficient, i.e., SRCC = 0.675), and the positive relationship between mannitol and glucan (SRCC = 0.651). Other moderate, positive correlations were observed between M:G ratio and glucan, and between wet mass and sulfation (SRCC = 0.543 and 0.508, respectively). Moderate, negative correlations were observed between ash and glucan, and between ash and alginate (SRCC = -0.565 and -0.514, respectively; Figure 20).

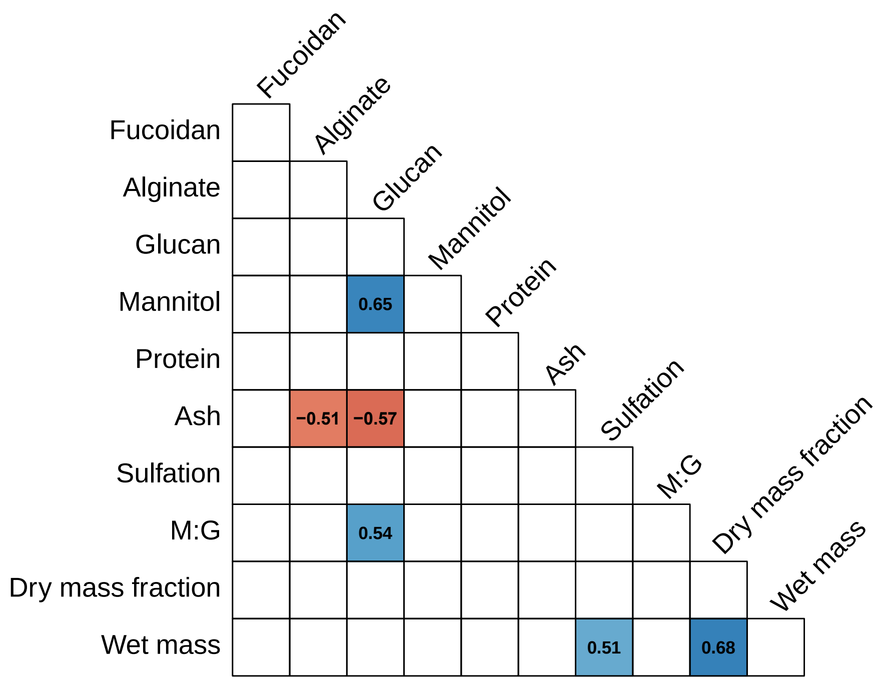

Figure 20. Correlation matrix for *Alaria marginata* between biochemistry metrics (combined data from Kodiak Site and PWS Site 1). Kelp samples were collected from commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviation: ratio of mannuronic to guluronic acids in alginate (M:G). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

The strongest correlation among components in *N. luetkeana* was the negative relationship between M:G ratio and glucan (SRCC = -0.736). Other moderate, negative correlations were observed between protein and mannitol, between protein and alginate, between wet mass and alginate, and between ash and fucoidan (SRCC = -0.571, -0.568, -0.535 and -0.5529, respectively). Moderate positive relationships were observed between alginate and fucoidan, between glucan and fucoidan, and between glucan and alginate (SRCC = 0.672, 0.626 and 0.540, respectively; Figure 21).

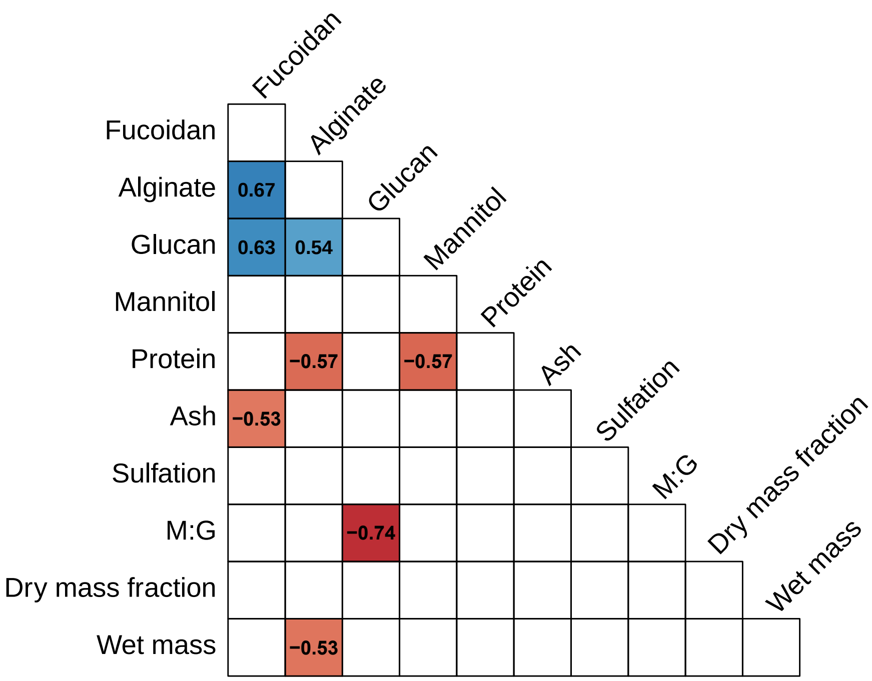

Figure 21. Correlation matrix for *Nereocystis luetkeana* between biochemistry metrics (combined data from PWS Site 2 and SE Site 1). Kelp samples were collected from commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviation: ratio of mannuronic to guluronic acids in alginate (M:G). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

The strongest correlation among components in *S. latissima* was the negative relationship between protein and mannitol (SRCC = -0.752). A moderate, negative correlation was observed between dry mass fraction and ash (SRCC = -0.668). Moderate, positive correlations were observed glucan and alginate, and between glucan and fucoidan (SRCC = 0.606 and 0.603, respectively; Figure 22).

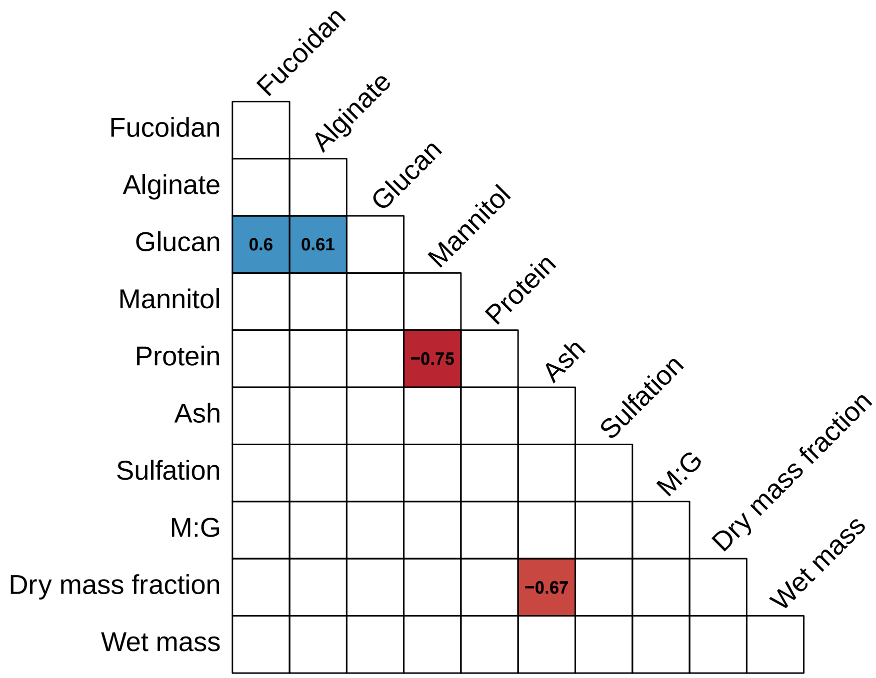

Figure 22. Correlation matrix for *Saccharina latissima* between biochemistry metrics (combined data from all sites). Kelp samples were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviation: ratio of mannuronic to guluronic acids in alginate (M:G). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

3.14 Environmental Correlations

The strongest correlation among environmental predictors and biochemistry metrics for *A. marginata* was the positive relationship between orthophosphate and M:G ratio (SRCC = 0.690). Other moderate, positive correlations were observed between salinity and M:G ratio, between temperature and DMF, between relative water motion and DMF, and between temperature and fucoidan (SRCC = 0.0684, 0.672, 0.632, and 0.522, respectively). Moderate, negative correlations were observed between temperature and M:G ratio, salinity and DMF, between irradiance and DMF, and between temperature and alginate (SRCC = -0.533, -0.531, -0.525, and -0.506, respectively; Figure 23).

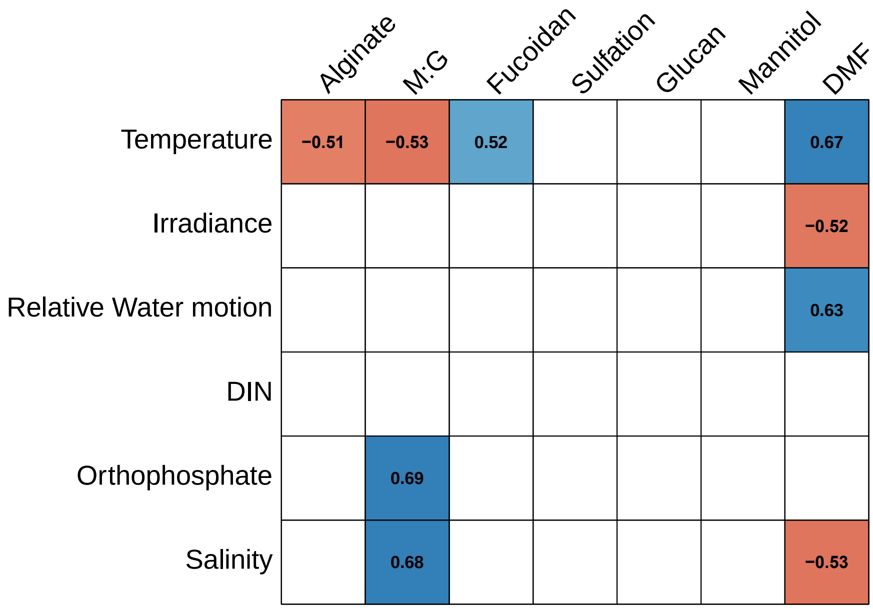

Figure 23. Correlations between environmental predictors and biochemistry metrics for *Alaria marginata* (combined data from Kodiak Site and PWS Site 1). Kelp samples and environmental data were collected from commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviations: dissolved inorganic nitrogen (DIN), dry mass fraction (DMF), ratio of mannuronic to guluronic acids in alginate (M:G ratio). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

The strongest correlation among environmental predictors and biochemistry metrics for *N. luetkeana* was the negative relationship between temperature and M:G ratio (SRCC = -0.726). Moderate, negative correlations were observed between relative water motion and alginate, between DIN and mannitol, and between relative water motion and mannitol (SRCC = -0.586, -0.566, and -0.515, respectively). Moderate positive correlations were observed between temperature and glucan, and between salinity and M:G ratio (SRCC = 0.637 and 0.562, respectively; Figure 24).

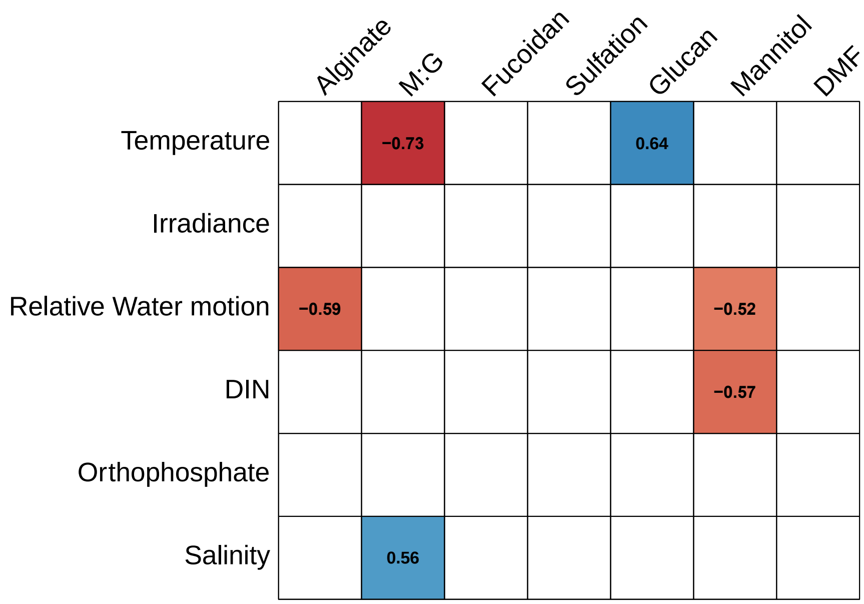

Figure 24. Correlations between environmental predictors and biochemistry metrics for *Nereocystis luetkeana* (combined data from PWS Site 2 and SE Site 1). Kelp samples and environmental data were collected from commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviations: dissolved inorganic nitrogen (DIN), dry mass fraction (DMF), ratio of mannuronic to guluronic acids in alginate (M:G ratio). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

The strongest correlation among environmental predictors and biochemistry metrics for *S. latissima* was the positive relationship between relative water motion and fucoidan (SRCC = 0.681). Another moderate, positive correlation was observed between temperature and fucoidan (SRCC = 0.624). Moderate, negative correlations were observed between temperature and M:G ratio, and between irradiance and fucoidan (SRCC = -0.562 and -0.500, respectively; Figure 25).

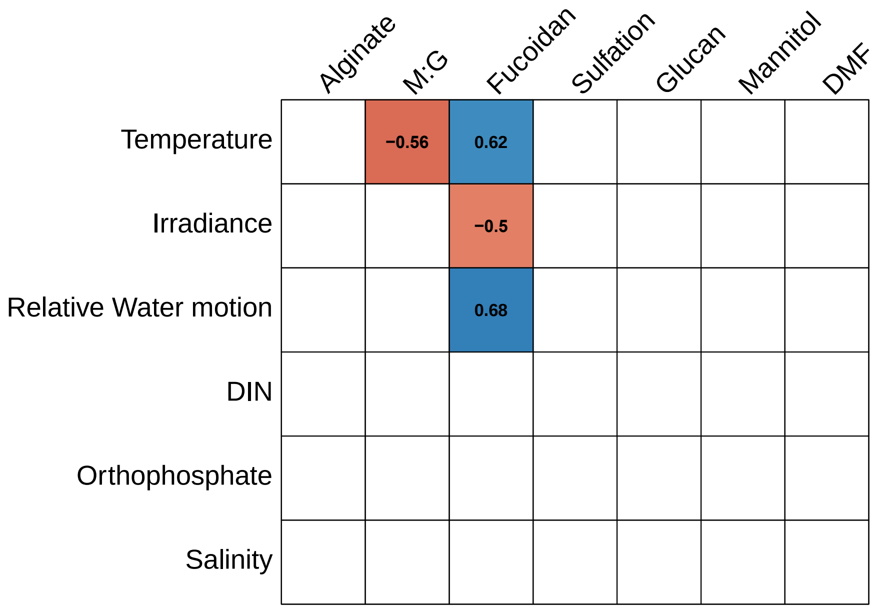

Figure 25. Correlations between environmental predictors and biochemistry metrics for *Saccharina latissima* (combined data from all sites). Kelp samples and environmental data were collected from five commercial kelp farm sites in Alaska between April and June (Day of year 93 to 179), 2023. Abbreviations: dissolved inorganic nitrogen (DIN), dry mass fraction (DMF), ratio of mannuronic to guluronic acids in alginate (M:G ratio). Values indicate Spearman's rank correlation coefficients. Red boxes indicate a negative correlation, and blue boxes indicate a positive correlation.

4. Discussion

Understanding the temporal and spatial dynamics of carbohydrate compositions in kelp is crucial for elucidating their biochemical value in a commercial setting and sheds light on the biological processes that drive their variability. This study explored how farming location affects the relative proportions and proxies of the chemical makeup of carbohydrates in *A. marginata*, *N. luetkeana,* and *S. latissima*. The results support the hypothesis posed in this thesis that carbohydrate proportions change over the potential harvest season and vary among species. Correlations between carbohydrates and environmental factors mostly varied among species, with consistent correlations likely resulting from intrinsic biological processes rather than through cause and effect. This study is the first to examine trends in carbohydrate composition in Alaskan kelp cross spatial and temporal scales.

Variability and temporal trends in recorded environmental variables were expected among sites due to the large geographic range sampled and the known complexities of the Alaska nearshore environment (Batten et al., 2015; Campbell, 2015). Irradiance decreased or showed no noticeable trend over the study season, possibly due to shading by growing kelp biomass surrounding the loggers and/or biofouling on the loggers, which moderately accumulated on much of the logging equipment. Overall, variability of irradiance was high due to changes in cloud cover (Stabeno et al., 2004; Strom et al., 2010). The average seawater temperature differed among sites, but every site showed an increasing trend over the season, consistent with expectations (Royer, 2005). The trend over time in relative water motion at PWS Site 1 was unique in that it abruptly increased, possibly due to boat traffic in the area.

For nutrient data, DIN and orthophosphate were expected to follow a similar pattern between them among sites, with concentrations decreasing in parallel over time (Strom et al., 2006; Umanzor & Stephens, 2023; Kanda et al., 1989). However, this pattern was not observed at every site. De-coupling of these nutrient concentrations at some sites may have been caused by differences in phosphate derived from local terrigenous/riverine sources (Hood & Scott, 2008). Farm sites in Prince William Sound (PWS) were consistent with expectations of geography-driven localized variability. For instance, PWS Site 2 showed an overall decrease in salinity, likely because of snowmelt and a larger watershed at this site than PWS Site 1, which had only one sampling event where the average salinity dropped below 28. It is unclear why Kodiak Site, with the highest exposure to the Gulf of Alaska, showed average salinities down to 17 in April (DOY 105).

Regarding tissue analysis outputs, dry mass closure (mass balance) results had lower values than expected. The exclusion of other components contributing to dry mass from our quantification, such as lipids and phenols, partially explains this gap. However, lipids generally contribute less than 5% and phenols less than 2% of DM (Farghl et al., 2021; Nelson et al., 2002; Tierney et al., 2010). This suggests an under-quantification of one or more analyzed components, which is common when reporting mass balance values. For instance, an effort to understand unaccounted-for components in microalgae using solubility fractions and quantification of major components suggested that many components remained slightly underestimated, along with small polar metabolites that are not accounted for at all, summing to a large proportion of un-quantified biomass (Van Wychen et al., 2021).

Discrepancies in mass balance may also be linked to the method utilized to quantify components. For example, a mass closure study on *Ascophylum nodosum* found high-performance anion exchange with pulsed amperometric detection (HPAEC-PAD) to under-recover glucuronic acid, mannuronic acid, and fucose after incomplete acid hydrolysis when compared to characterization of these sugars with nuclear magnetic resonance spectroscopy (NMR; Trubetskaya et al., 2024). However, this contrasts with a recent study that overestimated carbohydrate values using HPAEC-PAD, resulting in dry mass closures of over 100% (Arlov et al., 2024). Another possibility for the unexpectedly lower dry mass closures may be related to the underestimation of protein. In the present study, protein was calculated based on a conversion factor of 5 applied to tissue nitrogen. However, conversion factors are known to vary among species and over time. A conversion factor of 5 is on the higher end of these estimates and may just as easily be overestimating protein (Angell et al., 2016; Biancarosa et al., 2017; Bruhn et al., 2017). In summary, alginate and fucoidan values might be slightly underestimated given the method used, and species likely differ in their content of biochemicals not quantified in this study.

Dry mass fraction (DMF) indicates moisture capacity, with larger cellular vacuoles (i.e., more internal water mass) correlating with a reduced DMF (Van Ginneken, 2018). Both *S. latissima* and *A. marginata* demonstrated an increase in DMF towards June (DOY 180), contrasting the observed decrease over time in *N. luetkeana*. Black (1950) suggested the accumulation of storage carbohydrates is responsible for variations in DMF as more organic solids accumulate within the same cellular volume. This would explain the trend seen in *S. latissima*, which showed a moderate, positive correlation between DMF and glucan content. Still, no correlation was evident in *A. marginata*, despite the increase in DMF observed in this species. Even more curious is the simultaneous decrease in ash content observed in *N. luetkeana*, as cellular vacuoles serve a crucial function by intracellularly isolating toxic ions, notably Na^+ and Cl^- (contributing to ash content), thereby protecting delicate organelles from their toxic effects (Van Ginneken, 2018). It would be expected that more cellular fluid would equate to a proportional increase in salts to balance osmotic potential, given constant salinity. Although salinity was not constant at either site with *N. luetkeana*, our results show no obvious correlation between the two. It is possible the unique morphology of *N. luetkeana* explains some of these patterns, as rapid stipe growth causes inner cells of the cortex and medulla to stretch and increase their moisture capacity (Smith, 1939). *N. luetkeana* individuals from PWS Site 2 decreased more rapidly in DMF despite showing slower wet mass growth, possibly due to differences in development, whereby PWS Site 2 individuals, being smaller, were lengthening more rapidly than they were increasing in biomass, exacerbating the observed decreasing trend in DMF (Foreman, 1970).

The increasing trend in DMF in *S. latissima* and *A. marginata* coincides with findings from studies conducted on European *S. latissima* (Arlov et al., 2024; Marinho et al., 2015; Schiener et al., 2015). DMF values of *S. latissima* in our study had slightly lower average DMF values than the range of 10-15% DMF commonly observed in previous studies in northern Europe (Arlov et al., 2024; Schiener et al., 2015; Vilg et al., 2015). Consistent with our findings, an increase in DMF was observed in European *S. latissima* from different sites (Ehrig & Alban, 2014). Additionally, *Alaria esculenta* showed higher average DMF values than *S. latissima* in Norway, mirroring our results between *A. marginata* and *S. latissima* (Arlov, et al., 2024). The DMF of *N. luetkeana* from British Columbia peaked in May for both fronds and stipes (Whyte & Englar, 1975), contradicting the significant negative correlation with DOY observed in the present study. However, these values mostly fell within the interquartile range of the median dry mass fraction observed in our study.

The composition of ash in kelp is primarily made up of Na^+ and K^+ ions, crucial components for balancing osmolarity in saltwater (Schiener et al., 2015). Our results found that

A. marginata exhibited the lowest ash content and showed an inverse correlation with alginate content. This supports the notion of smaller vacuoles with thicker cell walls or a higher number of smaller cells than other species. The trend in ash content over time was site-dependent in this species, likely due to differences in alginate investment. *S. latissima* contained the highest average ash content and showed an inverse correlation with storage carbohydrates. The decline in ash content from April (DOY 93) to June (DOY 180) follows a pattern similar to the late-winter, early-spring peak observed in *S. latissima* from northern European waters, indicating consistency with previous studies (Brodhal, 2018; Manns et al., 2017).

The general decrease in tissue nitrogen and protein content observed across species from spring to summer has previously been correlated with decreasing ambient dissolved inorganic nitrogen (DIN), as amino acids are mobilized for tissue growth but cannot be readily replenished (Chapman & Craigie, 1977). Average protein content tended to follow site-specific patterns across species. For example, Kodiak Site had the highest protein content for both *A. marginata* and *S. latissima*, suggesting an influence of local environmental conditions, although specific environmental correlates for protein were not analyzed. Site-specific protein content has been observed in cultivated *S. latissima* in Norway; however, the driver of these differences is unclear (Brodahl, 2018). The availability of DIN among sites does not explain the differences observed in the present study, as even the lower levels of DIN seen in the PWS sites are not likely to limit growth (Fales et al., 2023). Trends over time in wet mass growth opposed trends over time in protein content for both species grown at Kodiak Site and PWS Site 1. However, no correlation was found in any species between wet mass and protein content, and this pattern is not consistent in the literature for cultivated Alaskan *S. latissima* and *A. marginata* (Umanzor & Stephens, 2023). Our results partially support previously described negative correlations between tissue nitrogen and carbohydrates, as protein was inversely correlated with mannitol in *S. latissima*, and inversely correlated with both mannitol and alginate in *N. luetkeana* (Zimmerman & Kremer, 1986).

The declining trend in protein content observed over time across all species in our study is similar to findings in cultivated and wild *S. latissima* from Denmark (Manns et al., 2017). However, the average protein content in our samples was higher compared to observations in Danish kelps, with cultivated species averaging around 10% DM and wild species around 5% DM (Manns et al., 2017). This disparity might partly stem from the protein conversion coefficient of 5 applied to all our samples. In contrast, in Danish *S. latissima*, these coefficients ranged from 2.1 in winter to 5.9 in summer, indicating an increasing association between tissue nitrogen and protein over time (Manns et al., 2017). In *N. luetkeana* from British Columbia, protein content remained relatively stable between April and June, with values comparable to those observed in this study (Whyte & Englar, 1975). Our findings contradict previous research on cultivated Alaskan kelps, where *A. marginata* exhibited significantly higher tissue nitrogen levels than *S. latissima* collected in April, although only one site was assessed in that study (Umanzor & Stephens, 2023).

A. marginata had the highest abundance of fucoidan at the beginning of the sampling period, whereas *S. latissima* was the only species to exhibit a significant increase over time. The abundance of fucoidan in *A. marginata* could be attributed to an adaptation for habitation in the intertidal, a relationship observed in Fucales (Mabeau & Kloareg, 1987). Bruhn et al. (2017) noted a positive correlation between fucoidan content and salinity for wild *S. latissima*, but this correlation was insignificant for *Laminaria digitata*. Salinity did not explain the fucoidan trends observed in our study, however, suggesting a more intrinsic process in this species within the salinity levels observed in our study. Bruhn et al. (2017) also found a significant positive correlation between irradiance and fucoidan content for both species, suggesting that the availability of photo assimilates might be the underlying mechanism. This hypothesis was not supported in our study, as fucoidan showed consistent trends among sites in all species, despite different site-specific trends in mannitol and glucan content over time. Given the surprising decrease in irradiance found in our results across sites, we cannot be confident in the absence of positive correlations found with this predictor in our results. The positive correlation in our results between fucoidan and temperature for *S. latissima* and *A. marginata* is likely a result of these two variables showing the highest consistency in trends rather than a functional relationship. This is consistent with the findings of Manns et al. (2017), who found temperature to be the only significant predictor of biochemical composition.

It is key to highlight that the observed increase in fucoidan content from April to June in *S. latissima* contrasts with the findings of Bruhn et al. (2017), who reported a decrease in average fucoidan content in Danish *S. latissima* from ~5% to ~4.5% DM over the same period. However, direct comparison of values is challenging, as their study did not account for bonded sulfate. Rinker et al. (2021) conducted measurements on crude extractions from farmed Alaskan *A.*

marginata and *S. latissima* (collected from Popof Island and Kodiak Island, respectively), revealing that *S. latissima* had less fucoidan in April and June but more in May than *A. marginata*, with both species exhibiting higher fucoidan content in June compared to April. However, these results are limited in comparability, as only one sample was analyzed per month. Moreover, values of fucoidan content obtained from crude extractions are known to vary widely with extraction methods (Rani et al., 2017; Wang & Chen, 2016). The site-specific average fucoidan contents observed in *A. marginata* and *N. luetkeana* are consistent with localized differences observed in *Ecklonia radiata*, although the mechanism of these differences is unclear (Nepper-Davidsen et al., 2023).

Patterns of sulfate content in fucoidan showed site-dependent trends in both *A. marginata and N. luetkeana*, either increasing or decreasing depending on where the kelp were grown. Instances of increasing sulfate follow observations in *Saccharina sculpera* and *Laminaria japonica* (Honya et al., 1999; Qu et al., 2019). However, both studies sampled only one location. Conversely, sulfate content in *S. latissima* did not change significantly over the sampling period. When assessing the average sulfate content and average fucoidan content for species across sites, the two values appear inverse, a pattern in agreement with Fucales (Fletcher et al., 2017). However, no correlations were observed in our results between these two variables in any species. Although differences in sulfation among locations have been observed in some phaeophytes, including *Sargassum wightii*, *Fucus evanescens*, and even *S. latissima*, differences in trends over time among locations have not been described due to limited temporal sampling at varying sites (Ehrig & Alban, 2014; Eluvakkal & Arunkumar, 2017; Zvyagintseva et al., 2003). Concerning our results, these studies support differences among species in the influence of location on sulfation, where *S. latissima* appears to be driven by consistent, endogenous incorporation of sulfate, contrasting *N. luetkeana* and *A. marginata*, which appear to be site-driven.

The role of sulfate attributed to salinity and desiccation stress tolerance varies in the literature, complicating the distinction between endogenous and exogenous processes. Studies utilizing monoclonal antibodies with varying affinities for sulfated fucoidans found a negative correlation between fucoidan sulfate content and salinity exposure in Fucales species, supporting the idea of sulfate content acting as a mechanism for anti-desiccation stress rather than for osmoregulation (Torode et al., 2015). However, experimentation on a freshwater Ectocarpales strain demonstrated active regulation of sulfate content in polysaccharides through increased production of sulfotransferase enzymes in response to higher salinities, indicating a role of sulfate in osmoregulation (Dittami et al., 2012). In *Laminaria japonica*, genes associated with sulfotransferase production (enzymes involved in sulfate bonding to fucoidan) were up-regulated in response to both reduced salinity and desiccation stress. However, the latter was more pronounced, indicating differing intensities of active regulation between stressors (Lu et al., 2020). In our study, trends in sulfation over time were not consistent with trends in salinity and no correlations were found between these variables, indicating an alternative driver on site-specific patterns. Although *S. latissima* and *A. marginata* were not subject to desiccation stress, larger *N. luetkeana* individuals could reach the surface and experience localized desiccation in the pneumatocyst. This may explain the positive trend in this species grown at SE Site 1 with comparatively larger individuals as indicated by wet mass. In contrast, individuals at PWS Site 2 did not appear to invest as much into highly sulfated fucoidans.

Alginate, providing kelp with flexibility and strength, exhibited significant differences across species, with unclear trends over time. When pooled across sites, *A. marginata* displayed significantly higher alginate contents than *S. latissima* and *N. luetkeana*. One explanation could be *A. marginata*'s typical habitat in intertidal zones and an adaptation to significant wave action (Lindeberg & Lindsrom, 2010). In contrast, *S. latissima* inhabits more sheltered subtidal areas, while *N. luetkeana* remains completely submerged during a portion of its developmental history, despite growing in regions of high water flow. The relationship between high alginate content and wave exposure has been noted for two species of *Durvilleae* (Fucales), with a mid-intertidal species exhibiting significantly more alginate content than one in the low intertidal or subtidal fringe. However, it is unknown if these patterns reflect plastic or intrinsic adaptations (Kelly & Brown, 2000). Overall, these findings support the theory of *A. marginata* having smaller cellular vacuoles with less ash content and either thicker cell walls or smaller cells containing a greater relative proportion of cell wall polysaccharides than the other species in this study.

Our findings on alginate content align with previous studies that observed spatial and temporal variability in kelp species. For instance, Schiener et al. (2015) reported different trends in alginate content between April and June in three species in Scotland from the same location. Similarly, we observed opposing trends in alginate content over time in *A. marginata* and *S. latissima* collected from Kodiak. Zhang & Thomsen (2019) reviewed *S. latissima* carbohydrate compositions and found variable differences in alginate content among locations and growth settings (wild vs. cultivated) from April to June, supporting our observations of site-driven differences, particularly at SE Site 2, which showed a significant increase. However, our results differ from those reported for other Alaskan samples. Compared to our results, Rinker et al. (2021) found lower alginate values for *A. marginata* and *S. latissima*, which may be due to their use of crude extractions rather than chromatography. Conversely, *N. luetkeana* from British Columbia had a similar alginate content to our median value (17.02% DM vs. 16.9% DM in Rinker et al., 2021). However, Whyte & Englar (1975) found that *N. luetkeana* increased in alginate content from April to June, suggesting potential site-dependent trends not captured in our study.

The M:G ratio showed significant differences in values among sites, decreasing consistently over time in *S. latissima* and *N. luetkeana*. These trends follow observations of *S. latissima* grown in lab conditions, where older blades consistently had more guluronic acid (lower M:G ratio; Indergaard et al., 1990). The mechanism proposed is a one-way synthesis pathway of alginates, whereby M-rich alginates are synthesized before modification into G-rich alginates, a process that cannot be directly reverted, but instead relies on alginate-degrading enzymes to break down alginate chains into oligo-alginates before absorption back into the cell to reverse the process (Inoue & Ojima, 2019). Following this explanation, the positive trend in M:G ratio over time observed in *A. marginata* from Kodiak Site represents an interesting case of alginates either accumulating poly G blocks at a lower rate than new alginates are being synthesized, or active degradation of some G-rich alginates. Although peculiar in our results, average monthly M:G ratios did not decrease consistently between *S. latissima* and *L. digitata* grown at different sites in Denmark (Manns et al., 2017). However, limited sample sizes in that study leaves limited confidence in confirming trends over time.

The M:G ratio can affect the gelling properties, viscosity, and mechanical strength of alginates and potentially impact their biological functioning. Studies on extracted alginates have demonstrated increased viscosity with numerous homogenous G units (Smidsrød, 1973), attributed chemically to cation binding, often with $Ca2^{+}$, between poly G blocks on separate alginate chains (Plazinski, 2011). Increased flexibility of macroalgal tissues can decrease mechanical stress loading in wave-exposed environments (Gaylord & Denny, 1997), thus fitting the descending order of average M:G ratios observed for *A. marginata*, an intertidal species, *N.*

luetkeana, which stretches from the subtidal to wave-exposed surfaces, and *S. latissima*, which often inhabits subtidal substrate (Lindeberg & Lindstrom, 2010). Although this pattern hints at intrinsic M:G ratio adaptation among species when averaged, locational differences are present and may represent a secondary effect of ecotype, or cryptic environmental pressures. Ultimately, the role of M:G ratio in regulating thallus tissue mechanics remains incompletely understood. For example, juvenile *Egregia menziesii* grown in water tanks of varying flow rates developed stronger and stiffer blades despite a lower abundance of guluronic acid (Kraemer & Chapman, 1991). Furthermore, conclusions on the gelation properties of alginates in our samples are limited as the M:G ratio is only a proxy and does not account for the proportion of MG blocks that lack the cation-binding properties of GG blocks (Plazinski, 2011).

Finally, fluctuations in storage carbohydrates are linked to the balance between carbon fixation and metabolic demand, making it challenging to discern whether differences in abundance and trends among species over time were due to lower carbon fixation rates or higher metabolic demand. Because cellulose content remains relatively consistent over time in kelp, changes in total glucan content are attributed to laminarin stores (Black, 1950; Schiener et al., 2015). Both *N. luetkeana* and *S. latissima* displayed trends in average glucan content consistent with findings from Danish kelp species. In the latter, glucan increased towards June, indicating carbon fixation outpaced metabolic demand (Manns et al., 2017; Schiener et al., 2015). Contrarily, *A. marginata* from PWS Site 1 decreased in average glucan content over time, opposing observations of a related species, *Alaria esculenta*, which exhibited a steep increase between April and June (Schiener et al., 2015). As wet mass growth was minimal and alginate content decreased in *A. marginata* from this site, it appears some limitation in carbon fixation was present rather than rapid investment into growth and structural carbohydrates. The limitation appears species-specific as glucan content increased in *S. latissima* from the same site. Nevertheless, the cause of such limitation remains unclear.

Laminarin, a long-term energy-storage carbohydrate, accumulates during periods of excess photosynthetic yield (Hatcher et al., 1977; Scheschonk et al., 2019). Its polymerization can be reversed by converting D-glucose units into mannitol for mobilization and eventual respiration (Gómez & Huovinen, 2012; Küppers & Kremer, 1978). This process, observed in *Macrocystis pyrifera*, indicates laminarin accumulation follows a certain threshold of mannitol, utilized after mannitol concentrations decrease (Zimmerman & Kremer, 1986). Mannitol, a simple sugar-alcohol synthesized in the dark reactions as a primary photosynthetic product in brown algae, correlates with photosynthetic ability as a function of light availability (Gravot et al., 2010; Shao et al., 2019). This process is indicated in both species at Kodiak Site, which had parallel trends between mannitol and glucan increasing towards summer, indicating strong photosynthetic performance with excess carbohydrates for long-term storage as laminarin. However, relative mannitol accumulation is complex, as the precursor to mannitol, fructose-6-phosphate, is also used in the biogenesis of other polysaccharides (Chi et al., 2017). In times of sustained growth, mannitol may not accumulate in high quantities due to selective assimilation into structural polysaccharides and high metabolic demand fueled by mannitol catabolism (Chi et al., 2020; Kremer, 1981). Rather than structural polysaccharides, both *S. latissima* and *N. luetkeana* from SE Site 1 showed preferential investment into laminarin as neither had significant differences in mannitol over time, but both increased in glucan content.

Our results revealed no significant differences in average mannitol content among species or over time when averaged across sites, contradicting reported trends of increasing mannitol towards summer and fall (Schiener et al., 2015). While these authors found average mannitol content to differ among species, our observations placed a more significant relationship on geographical location. Although the reported range in mannitol was similar for *S. latissima* from Europe (Schiener et al., 2015), our study reported a lower average. Growth in a mariculture setting can impact mannitol content, as shown in cultivated and wild *S. latissima* from Denmark, where average mannitol content in wild kelp increased steadily. In contrast, cultivated kelp peaked in May and then decreased in June (Manns et al., 2017). A peak of mannitol in May was also found for wild *N. luetkeana* from Bamfield, British Columbia. However, the lack of replicates in that study reduces confidence when applying those findings broadly (Whyte & Englar, 1975). Mannitol also acts as an important organic solute in brown algae, balancing osmotic stress through cytoplasmic accumulation without inferring the toxicity of inorganic ions (Kirst, 1990; Davison & Reed, 1985), contributing to extreme variability in mannitol relative abundance over time in kelp (Schiener et al., 2015; Westermeier et al., 2012). This relationship may partly explain the sharp decrease in mannitol content paired with an increase in glucan content over time in both *S. latissima and N. luetkeana* from PWS Site 2, whereby mannitol was converted into laminarin stores to reduce the number of osmolytes in response to a steady decrease in salinity. However, no significant correlation was found in our data.

In conclusion, this research is a pioneering examination of carbohydrate composition trends in Alaskan kelps across spatial and temporal scales. Findings highlight the complex interplay between biological principles, environmental conditions, and the biochemical makeup of these macroalgae. Locational differences within species are prevalent in many of the biochemical metrics analyzed, but ultimately the driving forces behind these differences could not be confirmed in the present data. Additionally, this study addresses differences in tissue analysis outputs and their impact on mass balance, all of which offer opportunities for future research (see Appendix C). This research contributes to advancing our knowledge about kelp physiology, while providing practical implications for optimizing the cultivation and utilization of these commercially important kelp.

5. Implications for Alaska Mariculture

Carbohydrate extraction from kelp offers potential market opportunities to support the established mariculture industry in Alaska through increased crop value and diversified income streams. This study has outlined both species and site-specific variability in average proportions of valuable carbohydrates and their trends over a potential harvest season. These factors taken together offer insights into species cultivation choices and highlight the importance of farm location for farmers wanting to sell their products to extractive processors in the future and inform processors of the variability to be expected.

Estimated market value for extracted kelp carbohydrates varies based on the purity of the product, demand, and often properties of the carbohydrates rooted in their molecular structure (Zhang & Thomsen, 2019). Alginate accounts for the largest market of any kelp-derived carbohydrates. However, relatively low prices reflect the availability of both internationally and domestically produced alginate from industrial wild harvests (Cai et al., 2021). Although the blocking patterns of uronic acids influence the physical properties of alginate, alginates with both high and low M:G ratios find utility in different circumstances (Costa et al., 2018; FMC Corporation, 2010). In contrast, fucoidan can be highly valuable when refined to a high purity, however, demand is extremely limited due to the challenges faced in commercializing its use in pharmaceuticals (Zayed & Ulber, 2019).

Furthermore, bioactivity, and thus value in pharmaceuticals, is highly dependent on specific chemical attributes, such as the degree of sulfation and branching structure of the molecule (Li et al., 2008). Still, fucoidan is the most valuable carbohydrate, even at moderately pure levels, and demand exists for this carbohydrate in cosmetics and nutraceuticals (Fitton et al., 2015; Zhang & Thomsen, 2019). Similarly, laminarin is moderately valuable in its lesser pure forms, and highly valuable in its pure form, but faces similar challenges in demand to fucoidan (Pramanik et al., 2024; Zhang & Thomsen, 2019). Mannitol is of relatively low value – comparable in value to alginate – due to the availability of this molecule from a wide range of sources, including artificial synthesis (Zhang & Thomsen, 2019; Chen et al., 2020).

Extraction-based kelp bio-refinery operations in Alaska will likely follow a cascading extraction model, in which all components are separated and processed (Nazemi et al., 2021). A techno-economic analysis of enzyme-assisted biorefinery models found raw feedstock composition to be one of the most important parameters affecting profit, along with extraction efficiency (Herrera Barragán et al., 2022). Quality feedstock is a balance between consistency and a favorable composition. As the value of moderate-grade fucoidan and laminarin is several orders of magnitude higher than mannitol and alginate, the relative proportion of these carbohydrates is likely to have a disproportionate impact on feedstock value, despite their lower biomass contribution (Zhang & Thomsen, 2019).

From our results, *A. marginata* and *S. latissima* were comparable in fucoidan content when harvested at the end of June, and both were consistent across sites in their trends overtime. As for glucan (a proxy for laminarin), *S. latissima* increased in content more consistently across sites and showed a higher average glucan content. *N. luetkeana*, having a lower average fucoidan content and site-dependent glucan content appears generally less favorable for carbohydrate extraction. However, the high sulfation content of this species suggests it may contain higher quality fucoidan, although this cannot be confirmed based on the current data. Thus, from a high-value carbohydrate basis, *S. latissima* may be the most suitable crop. Despite its lower value, alginate makes up a considerable amount of biomass, of which *A. marginata* had substantially higher average content. DMF can greatly impact the crop value bound for extractive processing, as biomass with a higher DMF will have more dry mass available for extraction with wet mass held constant. In this regard, *A. marginata* offers the highest DMF of the species studied, making it a strong candidate for extractive processing. However, this species was generally out-performed in wet mass growth by *S. latissima*, where more biomass can be grown on the same amount of line. Thus, the benefits of having a higher DMF must be weighed. Furthermore, both *S. latissima* and *A. marginata* increased consistently in DMF over time, lending well to a later season harvesting in June.

In summary, *S. latissima* may have the highest potential for extractive processing for carbohydrates due to having a generally balanced composition of valuable components, relatively consistent trends across sites, and high potential yields through a combination of the second-highest observed DMF and high potential wet mass production. *A. marginata* offers a favorable composition with high fucoidan and alginate contents, and a high DMF, which could make this a suitable crop with careful site selection and improvements in cultivation techniques to increase wet mass growth. *N. luetkeana* appears to be the least favorable crop due to its lower fucoidan and alginate content, lower DMF, and site-specific variability; however, the high sulfate content observed warrants further investigation into the bioactivity of its fucoidan.

Appendix A: Supplemental material

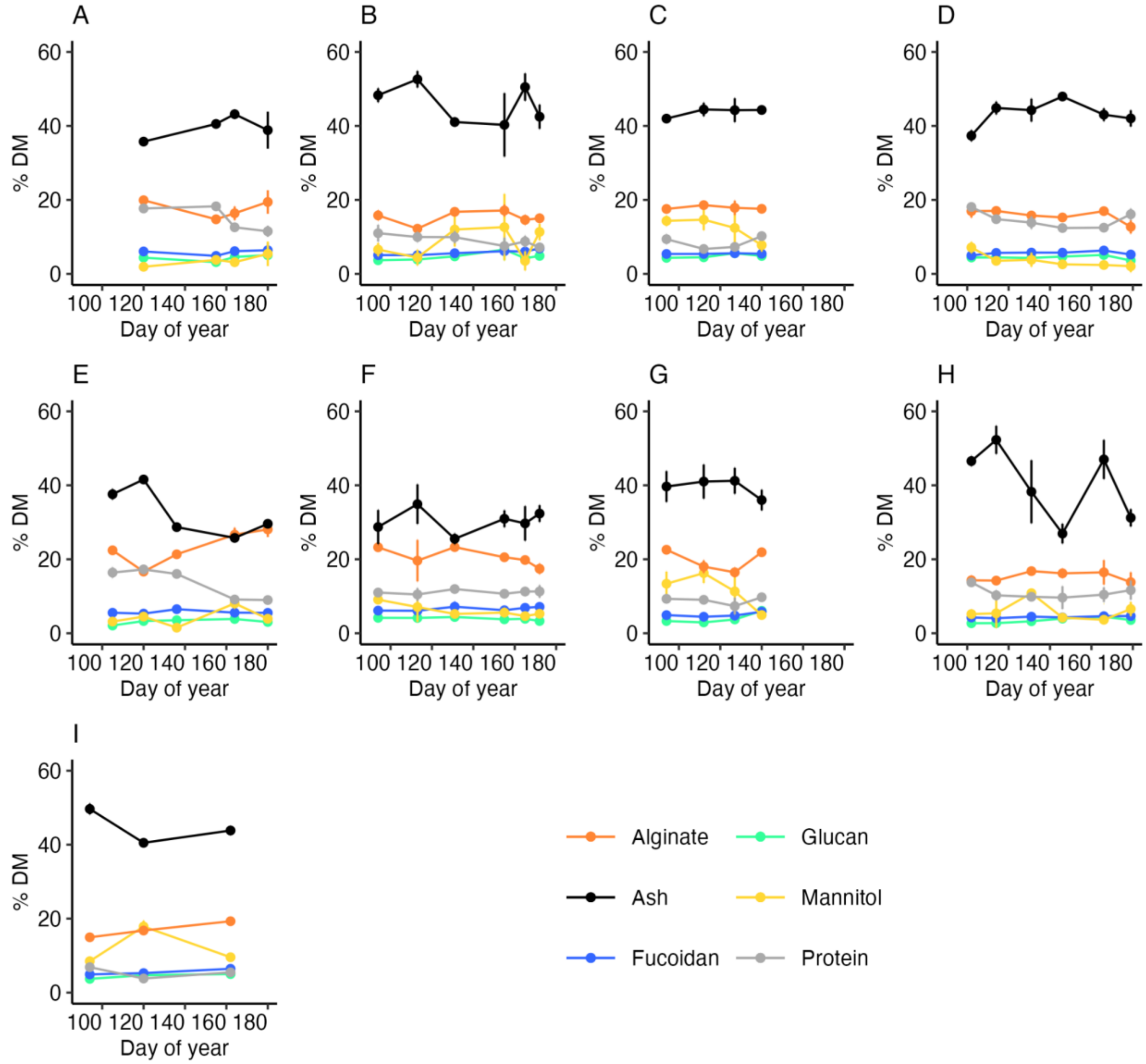

Figure S1. Composition of A) *Saccharina latissima* from Kodiak Site, B) *Saccharina latissima* from PWS Site 1, C) *Saccharina latissima* from PWS Site 2, D) *Saccharina latissima* from SE Site 1, E) *Alaria marginata* from Kodiak Site, F) *Alaria marginata* from PWS Site 1, G) *Nereocystis luetkeana* from PWS Site 2, H) *Nereocystis luetkeana* from SE Site 1 and I) *Saccharina latissima* from SE Site 2 between April and June, 2023. Each point represents a sampling event, the continuous line in each graph shows the trend over time, and the vertical lines show standard deviation.

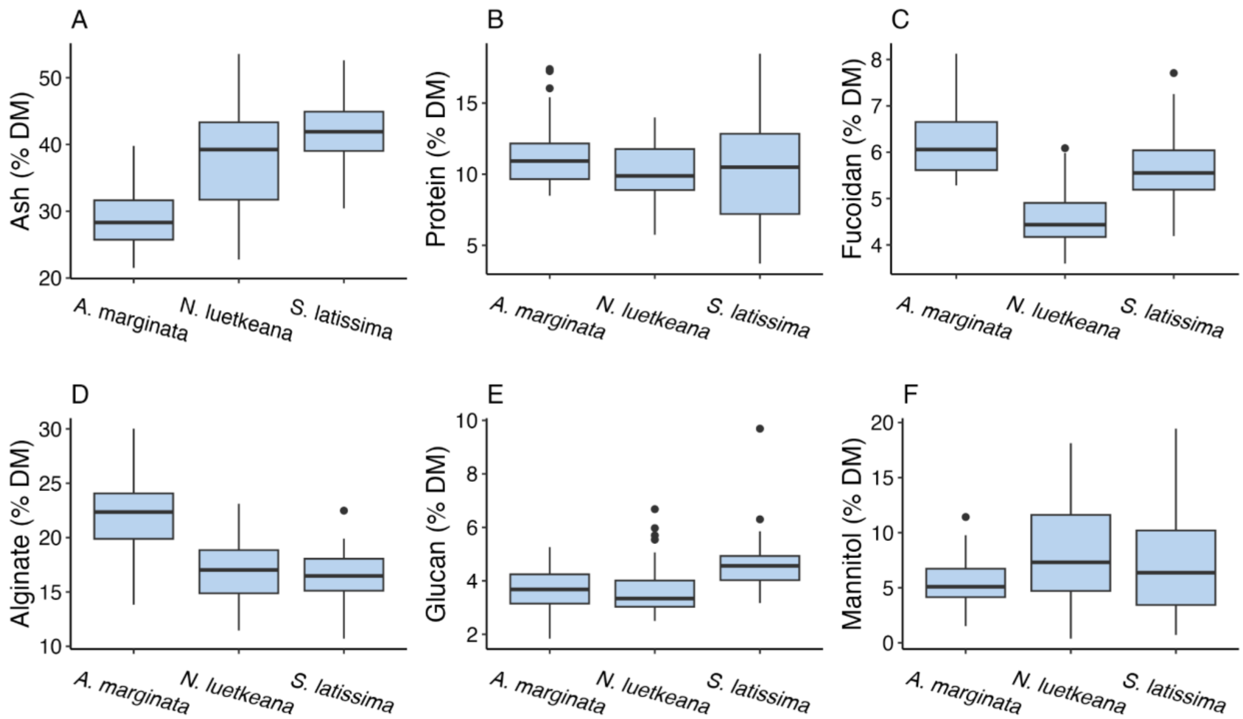

Figure S2. Median values for A) ash, B) protein, C) fucoidan, D) alginate, E) glucan, and F) mannitol, expressed as a percent of dry mass for *Alaria marginata*, *Nereocystis luetkeana*, and *Saccharina latissima* collected from commercial kelp farms in Alaska between April and June, 2023.

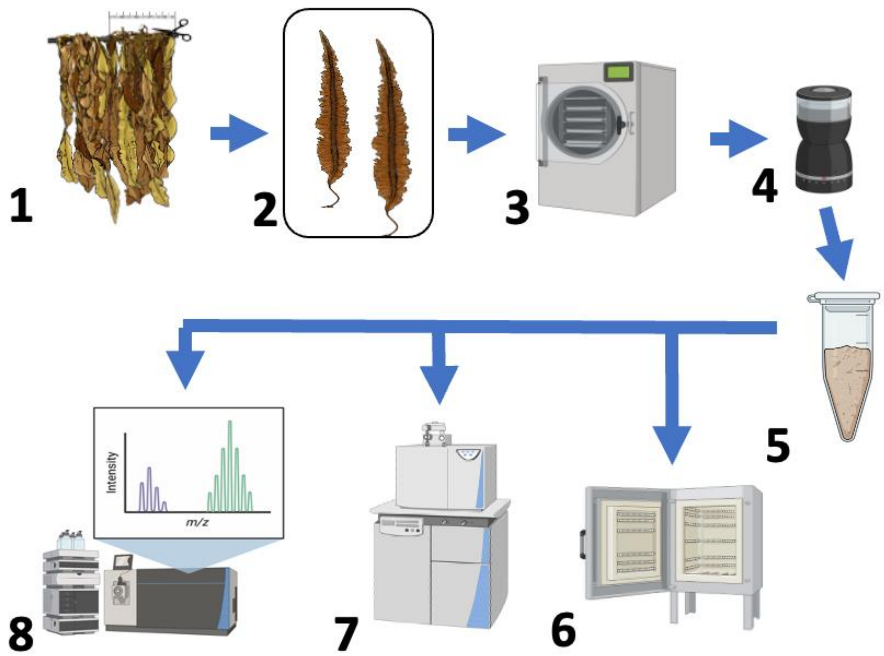

Figure S3. Flowchart of sampling collection, processing, and analysis. 1) Sample collection from farm site, 2) a minimum of two sporophytes taken per sample, 3) samples lyophilized to remove water, 4) samples homogenized and passed through a sieve, 5) a fine powder produced, 6) ash content analysis performed with a muffle furnace, 7) carbon, nitrogen, and sulfate tissue content analysis performed using continuous flow isotope ratio mass spectrometry, and 8) carbohydrate monomer analysis performed using high performance anion exchange chromatography with pulsed amperometric detection.

Table S1. Median, interquartile range (IQR), mean, standard deviation (SD), minimum and maximum values of environmental variables (temperature, irradiance, and relative water motion), for the assessed commercial farms in Alaska (Kodiak Site, PWS Site 1, PWS Site 2, SE Site 1 and SE Site 2) between April and June (Day of year 93 to 179), 2023. Dashes indicate unavailable data.

	Median	IQR	Mean	SD	Min	Max
Temperature (C)						
Kodiak Site	5.83	2.10	6.05	1.40	3.73	10.38
PWS Site 1	7.12	2.66	7.43	1.87	4.59	14.15
PWS Site 2	7.29	1.16	7.15	0.91	4.93	11.07
SE Site 1	7.63	3.22	7.80	2.43	4.33	15.57
SE Site 2	7.51	3.78	8.52	2.13	5.92	15.36
Irradiance (klx)						
Kodiak Site	0.42	3.26	3.33	6.72	0.00	66.03
PWS Site 1	0.92	5.54	4.33	7.20	0.00	64.35
PWS Site 2	1.37	7.24	4.7	6.66	0.00	41.44
SE Site 1	0.26	2.34	2.15	4.17	0.00	62.67
SE Site 2	0.23	1.59	1.56	3.32	0.00	45.51
Relative water motion (*g*)						
Kodiak Site	-	-	-	-	-	-
PWS Site 1	1.15	0.13	1.23	0.18	0.65	1.98
PWS Site 2	1.10	0.08	1.13	0.08	0.88	1.80
SE Site 1	1.23	0.15	1.25	0.14	0.75	2.05
SE Site 2	1.30	0.08	1.31	0.08	0.97	1.98

Table S2. Median, interquartile range (IQR), minimum and maximum of environmental variables (dissolved inorganic nitrogen (DIN), orthophosphate, and salinity) for the assessed commercial farms in Alaska (Kodiak Site, PWS Site 1, PWS Site 2, SE Site 1 and SE Site 2) between April and June (Day of year 93 to 179), 2023.

	Median	IQR	Mean	SD	Min	Max
DIN (µM)						
Kodiak Site	5.26	1.41	5.37	1.22	3.94	8.70
PWS Site 1	3.93	2.61	4.25	1.42	2.06	6.54
PWS Site 2	3.81	2.00	3.89	2.34	1.44	9.23
SE Site 1	8.33	16.04	11.39	7.91	1.99	21.90
SE Site 2	4.21	1.31	3.62	1.17	1.60	4.46
Orthophosphate (µM)						
Kodiak Site	0.46	0.32	0.48	0.29	0.09	0.99
PWS Site 1	0.08	0.14	0.14	0.13	0.00	0.39
PWS Site 2	0.08	0.08	0.10	0.11	0.02	0.44
SE Site 1	0.76	1.40	0.84	0.68	0.01	1.71
SE Site 2	0.36	0.06	0.38	0.07	0.29	0.48
Salinity (PSU)						
Kodiak Site	30.0	13.0	25.6	7.2	14.0	33.0
PWS Site 1	30.5	2.8	29.3	4.0	17.0	33.0
PWS Site 2	26.5	8.0	23.7	9.2	5.0	32.0
SE Site 1	32.0	6.5	29.2	4.9	19.0	33.0
SE Site 2	32.0	0.8	31.7	0.5	31.0	32.0

Table S3. Median, interquartile range (IQR), mean, standard deviation (SD), minimum and maximum of measured values for *A. marginata* and *S. latissima*. Kelp samples were collected from two, and five commercial kelp farm sites in Alaska, respectively, between April and June (Day of year 93 to 179), 2023. Ash, protein, fucoidan, alginate, glucan, and mannitol are expressed as a percent of dry mass. Dry mass (dry mass fraction) is the percent of mass retained after drying wet mass. M:G is the ratio of mannuronic to guluronic acids. Sulfation is the percent of sulfate mass in fucoidan.

	Median	IQR	Mean	SD	Min	Max
A. marginata						
Ash	28.32	5.91	28.87	4.75	21.52	39.79
Protein	10.93	2.51	11.42	2.50	8.49	17.39
Fucoidan	6.06	1.04	6.21	0.76	5.29	8.13
Alginate	22.35	4.19	22.05	3.91	13.83	30.02
Glucan	3.68	1.10	3.64	0.77	1.84	5.26
Mannitol	5.09	2.58	5.69	2.37	1.51	11.42
Dry mass	12.41	2.92	12.51	1.78	9.14	15.32
M:G	4.78	1.63	4.92	1.19	2.58	7.19
Sulfation	31.66	4.97	31.78	4.52	23.41	42.71
S. latissima						
Ash	41.90	5.88	42.01	4.60	32.16	54.16
Protein	10.49	5.65	10.52	3.92	3.71	18.47
Fucoidan	5.55	0.85	5.69	0.69	4.19	7.71
Alginate	16.48	2.94	16.45	2.18	10.71	22.48
Glucan	4.56	0.91	4.60	0.90	3.17	9.69
Mannitol	6.36	6.77	7.68	5.31	0.71	19.44
Dry mass	9.10	2.01	9.31	1.65	6.82	13.36
M:G	3.64	0.93	3.57	0.54	2.61	4.68
Sulfation	33.70	5.82	33.27	3.87	26.32	41.57

Table S4. Median, interquartile range (IQR), mean, standard deviation (SD), minimum and maximum of measured values for *N. luetkeana*. Kelp samples were collected from two commercial kelp farm sites in Alaska between April and June (Day of year 93 to 178), 2023Ash, protein, fucoidan, alginate, glucan, and mannitol are expressed as a percent of dry mass. Dry mass is the percent of mass retained after drying wet mass. M:G is the ratio of mannuronic to guluronic acids. Sulfation is the percent of sulfate mass in fucoidan.

	Median	IQR	Mean	SD	Min	Max
N. luetkeana						
Ash	39.24	11.58	38.09	8.16	22.76	53.56
Protein	9.88	2.88	9.99	2.33	5.74	13.99
Fucoidan	4.43	0.73	4.63	0.68	3.60	6.09
Alginate	17.02	3.97	17.08	3.23	11.46	23.11
Glucan	3.34	0.98	3.67	1.09	2.50	9.69
Mannitol	7.31	6.90	8.17	5.26	0.38	18.12
Dry mass	7.24	1.39	7.41	1.07	5.85	9.67
M:G	3.63	1.99	3.98	1.14	2.15	5.92
Sulfation	43.39	4.21	42.00	5.60	26.09	48.74

Table S5. Carbohydrate monomer composition in *Alaria marginata* and *Saccharina latissima* samples from Kodiak Site in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol %	Fucose %	Galactosamine %	Arabinose %	Glucosamine %	Galactose %	Glucose %	Mannose %	Xylose %	Ribose %	Galacturonic %	Guluronic %	Glucuronic %	Mannuronic %
Alaria marginata	14-Apr	singlet	3.71	0.79	<loq	<loq	<loq	0.77	2.35	0.29	0.23	N/D	N/D	4.20	1.18	18.29
Alaria marginata	14-Apr	triplicate	2.60	0.67	<loq	<loq	<loq	0.81	1.84	0.27	0.20	N/D	N/D	3.86	1.16	18.49
Alaria marginata	29-Apr	singlet	4.50	0.76	<loq	<loq	<loq	0.83	3.30	0.37	0.18	N/D	N/D	3.20	1.38	13.46
Alaria marginata	15-May	singlet	1.51	1.34	<loq	<loq	0.13	0.93	3.52	0.44	0.30	N/D	N/D	5.97	1.58	15.38
Alaria marginata	12-Jun	singlet	9.07	0.96	N/D	<loq	<loq	0.79	4.19	0.38	0.18	N/D	N/D	4.29	1.34	23.30
Alaria marginata	12-Jun	singlet	6.47	0.93	N/D	<loq	<loq	0.69	3.94	0.37	0.17	N/D	N/D	4.02	1.37	23.84
Alaria marginata	12-Jun	singlet	8.67	1.04	<loq	<loq	<loq	0.76	3.44	0.42	0.20	N/D	N/D	4.99	1.52	19.52
Alaria marginata	28-Jun	singlet	4.13	1.01	<loq	<loq	<loq	0.72	3.15	0.45	0.22	N/D	N/D	5.64	1.26	22.65
Alaria marginata	28-Jun	singlet	3.41	1.10	<loq	<loq	<loq	0.82	2.93	0.42	0.22	N/D	N/D	5.66	1.25	24.35
Alaria marginata	28-Jun	singlet	4.18	0.98	<loq	<loq	<loq	0.74	3.04	0.37	0.19	N/D	N/D	4.34	1.09	21.57
Saccharina latissima	29-Apr	singlet	1.91	1.20	<loq	<loq	<loq	0.87	4.38	0.43	0.20	N/D	N/D	4.10	1.59	15.81
Saccharina latissima	3-Jun	singlet	3.78	0.61	N/D	<loq	<loq	0.72	3.17	0.33	0.15	N/D	N/D	3.00	1.27	11.75
Saccharina latissima	12-Jun	singlet	2.65	1.01	<loq	<loq	<loq	0.59	3.84	0.34	0.18	N/D	N/D	4.00	1.58	-
Saccharina latissima	12-Jun	triplicate	2.89	1.51	<loq	<loq	<loq	0.88	5.13	0.49	0.27	N/D	N/D	4.32	1.61	13.78
Saccharina latissima	12-Jun	singlet	3.89	1.24	<loq	<loq	0.15	0.73	4.76	0.44	0.24	N/D	N/D	3.84	1.43	10.63
Saccharina latissima	28-Jun	singlet	3.43	1.29	<loq	<loq	0.16	0.75	4.89	0.47	0.22	N/D	N/D	4.62	1.45	11.50
Saccharina latissima	28-Jun	singlet	3.58	1.86	<loq	<loq	<loq	1.20	5.68	0.48	0.26	N/D	N/D	4.64	1.57	17.83
Saccharina latissima	28-Jun	singlet	9.27	1.85	<loq	<loq	0.14	0.96	4.62	0.45	0.22	N/D	N/D	4.17	1.41	15.52

Table S6. Carbohydrate monomer composition in *Alaria marginata* samples from PWS Site 1 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol	Fucose	Galactosamine	Arabinose	Glucosamine	Galactose	Glucose	Mannose	Xylose	Ribose	Galacturonic	Guluronic	Glucuronic	Mannuronic
			%	%	%	%	%	%	%	%	%	%	%	%	%	%
Alaria marginata	3-Apr	singlet	8.39	1.23	N/D	<loq	<loq	0.99	3.68	0.60	0.50	N/D	N/D	3.03	1.26	19.85
Alaria marginata	22-Apr	triplicate	6.29	1.25	<loq	<loq	<loq	0.94	5.26	0.64	0.53	N/D	N/D	3.18	1.06	21.81
Alaria marginata	22-Apr	singlet	3.52	1.40	N/D	<loq	<loq	0.95	3.25	0.63	0.57	N/D	N/D	3.47	1.21	16.57
Alaria marginata	22-Apr	singlet	11.42	1.07	N/D	<loq	<loq	0.83	3.91	0.52	0.28	N/D	N/D	2.73	0.85	11.10
Alaria marginata	10-May	singlet	5.34	1.54	<loq	<loq	<loq	0.94	4.45	0.61	0.53	N/D	N/D	3.18	1.51	19.78
Alaria marginata	10-May	singlet	5.09	1.36	<loq	<loq	<loq	0.82	4.33	0.56	0.47	N/D	N/D	3.08	1.38	20.52
Alaria marginata	3-Jun	singlet	5.23	1.31	<loq	<loq	<loq	0.94	3.89	0.60	0.45	N/D	N/D	3.62	1.26	17.00
Alaria marginata	3-Jun	singlet	4.53	1.19	<loq	<loq	<loq	0.78	3.55	0.55	0.44	N/D	N/D	3.93	1.26	17.25
Alaria marginata	3-Jun	singlet	6.98	1.33	<loq	<loq	<loq	0.87	3.87	0.58	0.47	N/D	N/D	3.71	1.33	16.12
Alaria marginata	13-Jun	singlet	4.08	1.42	<loq	<loq	<loq	0.97	3.08	0.62	0.51	N/D	N/D	3.26	1.39	15.98
Alaria marginata	13-Jun	triplicate	4.78	1.43	<loq	<loq	<loq	1.01	4.06	0.58	0.46	N/D	N/D	3.06	1.11	17.16
Alaria marginata	13-Jun	singlet	5.04	1.40	<loq	<loq	<loq	1.06	4.59	0.74	0.36	N/D	N/D	3.04	1.18	16.90
Alaria marginata	20-Jun	singlet	6.02	1.52	<loq	<loq	0.17	1.02	4.30	0.61	0.46	N/D	N/D	4.03	1.68	14.77
Alaria marginata	20-Jun	singlet	4.16	1.23	<loq	<loq	0.52	0.77	2.46	0.55	0.46	N/D	N/D	3.67	1.54	12.32
Alaria marginata	20-Jun	triplicate	5.63	1.41	<loq	<loq	0.23	0.95	3.15	0.58	0.46	N/D	N/D	4.15	1.61	13.34

Table S7. Carbohydrate monomer composition in *Saccharina latissima* samples from PWS Site 1 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol %	Fucose %	Galactosamine %	Arabinose %	Glucosamine %	Galactose %	Glucose %	Mannose %	Xylose %	Ribose %	Galacturonic %	Guluronic %	Glucuronic %	Mannuronic %
Saccharina latissima	3-Apr	singlet	5.29	0.84	N/D	<loq	<loq	0.75	3.31	0.43	0.27	N/D	N/D	3.10	0.96	11.76
Saccharina latissima	3-Apr	singlet	7.83	0.96	N/D	<loq	<loq	0.72	4.05	0.44	0.30	N/D	N/D	3.11	0.90	13.66
Saccharina latissima	22-Apr	singlet	4.74	0.98	N/D	<loq	<loq	0.73	3.86	0.46	0.32	N/D	N/D	2.62	0.81	10.13
Saccharina latissima	22-Apr	singlet	6.36	0.95	N/D	<loq	<loq	0.59	3.72	0.42	0.28	N/D	N/D	2.26	0.81	9.02
Saccharina latissima	22-Apr	singlet	2.15	0.99	N/D	<loq	<loq	0.64	4.09	0.45	0.27	N/D	N/D	2.45	0.61	10.17
Saccharina latissima	10-May	triplicate	15.23	1.07	<loq	<loq	<loq	0.66	4.96	0.47	0.32	N/D	N/D	3.08	1.30	12.97
Saccharina latissima	10-May	singlet	8.74	1.35	<loq	<loq	<loq	0.72	4.49	0.48	0.33	N/D	N/D	3.42	1.30	14.08
Saccharina latissima	3-Jun	singlet	2.31	1.25	<loq	<loq	<loq	0.58	4.18	0.49	0.35	N/D	N/D	3.30	1.25	12.03
Saccharina latissima	3-Jun	singlet	17.12	1.50	N/D	<loq	<loq	0.64	5.85	0.52	0.32	N/D	N/D	3.79	1.94	14.42
Saccharina latissima	3-Jun	singlet	18.48	1.61	<loq	<loq	<loq	0.49	9.69	0.55	0.39	N/D	N/D	3.36	1.12	14.50
Saccharina latissima	13-Jun	singlet	0.71	1.11	<loq	<loq	<loq	0.54	3.75	0.46	0.30	N/D	N/D	3.41	1.13	9.70
Saccharina latissima	13-Jun	singlet	4.05	1.33	<loq	<loq	<loq	0.62	4.39	0.50	0.33	N/D	N/D	3.44	1.20	11.70
Saccharina latissima	13-Jun	singlet	5.80	1.51	<loq	<loq	<loq	0.58	4.51	0.47	0.37	N/D	N/D	3.36	1.28	12.20
Saccharina latissima	20-Jun	singlet	9.80	1.45	<loq	<loq	0.22	0.64	4.58	0.46	0.32	N/D	N/D	3.67	1.50	10.09
Saccharina latissima	20-Jun	singlet	13.88	1.55	<loq	<loq	0.19	0.61	4.86	0.44	0.33	N/D	N/D	3.95	1.53	11.75
Saccharina latissima	20-Jun	singlet	10.34	1.76	<loq	<loq	0.33	0.71	5.15	0.50	0.38	N/D	N/D	4.22	1.66	11.42

Table S8. Carbohydrate monomer composition in *Nereocystis luetkeana* and *Saccharina latissima* samples from PWS Site 2 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol	Fucose	Galactosamine	Arabinose	Glucosamine	Galactose	Glucose	Mannose	Xylose	Ribose	Galacturonic	Guluronic	Glucuronic	Mannuronic
			%	%	%	%	%	%	%	%	%	%	%	%	%	%
Nereocystis luetkeana	3-Apr	singlet	17.09	0.73	N/D	<loq	<loq	0.88	3.03	0.33	<loq	N/D	N/D	4.02	0.47	17.98
Nereocystis luetkeana	3-Apr	singlet	10.90	0.86	N/D	<loq	<loq	1.11	3.38	0.39	0.16	N/D	N/D	4.56	0.76	18.55
Nereocystis luetkeana	3-Apr	triplicate	12.16	0.75	<loq	<loq	<loq	0.90	3.50	0.32	0.15	N/D	N/D	4.23	0.48	18.38
Nereocystis luetkeana	21-Apr	singlet	17.45	0.79	N/D	<loq	<loq	0.70	2.72	0.33	<loq	N/D	N/D	3.90	0.48	13.17
Nereocystis luetkeana	21-Apr	singlet	13.20	0.87	N/D	<loq	<loq	0.97	3.34	0.44	0.18	N/D	N/D	4.98	0.72	15.00
Nereocystis luetkeana	21-Apr	singlet	18.12	0.69	N/D	<loq	<loq	0.71	2.73	0.31	<loq	N/D	N/D	3.51	0.24	13.45
Nereocystis luetkeana	6-May	singlet	14.70	0.78	N/D	<loq	<loq	0.68	3.58	0.38	<loq	N/D	N/D	4.03	0.47	13.13
Nereocystis luetkeana	6-May	singlet	4.31	1.10	<loq	<loq	<loq	1.04	4.49	0.59	0.25	N/D	N/D	5.48	1.18	11.78
Nereocystis luetkeana	6-May	singlet	14.92	0.71	N/D	<loq	<loq	0.64	3.12	0.37	0.15	N/D	N/D	3.49	0.48	11.49
Nereocystis luetkeana	19-May	singlet	4.67	1.20	<loq	<loq	<loq	0.96	5.97	0.59	0.23	N/D	N/D	5.34	1.19	17.56
Nereocystis luetkeana	19-May	singlet	5.27	1.29	<loq	<loq	<loq	1.09	6.68	0.63	0.29	N/D	N/D	5.62	1.13	15.58
Nereocystis luetkeana	19-May	singlet	4.81	1.23	<loq	<loq	<loq	0.91	5.54	0.52	0.22	N/D	N/D	5.08	0.91	16.51
Saccharina latissima	3-Apr	singlet	12.74	0.98	N/D	<loq	<loq	0.81	4.46	0.51	0.33	N/D	N/D	4.40	1.16	13.85
Saccharina latissima	3-Apr	singlet	15.26	0.88	N/D	<loq	<loq	0.84	3.98	0.45	0.28	N/D	N/D	4.02	0.93	13.90
Saccharina latissima	3-Apr	singlet	14.98	0.95	N/D	<loq	<loq	0.72	4.56	0.42	0.27	N/D	N/D	3.53	0.91	12.95
Saccharina latissima	21-Apr	singlet	11.64	1.01	N/D	<loq	<loq	0.69	4.74	0.50	0.37	N/D	N/D	4.34	1.15	14.26
Saccharina latissima	21-Apr	singlet	15.03	1.08	N/D	<loq	<loq	0.69	4.06	0.47	0.32	N/D	N/D	3.99	0.93	14.83
Saccharina latissima	21-Apr	singlet	17.28	1.11	N/D	<loq	<loq	0.66	4.62	0.47	0.31	N/D	N/D	4.11	0.96	14.23
Saccharina latissima	6-May	singlet	6.21	1.23	N/D	<loq	<loq	0.62	5.35	0.56	0.40	N/D	N/D	4.69	1.19	14.74
Saccharina latissima	6-May	singlet	13.06	1.12	<loq	<loq	<loq	0.57	5.09	0.48	0.37	N/D	N/D	4.45	0.94	13.99
Saccharina latissima	6-May	singlet	17.99	1.13	N/D	<loq	<loq	0.53	6.30	0.47	0.35	N/D	N/D	3.82	0.94	11.87
Saccharina latissima	19-May	singlet	9.77	1.24	<loq	<loq	<loq	0.58	4.53	0.55	0.35	N/D	N/D	3.85	0.94	12.80
Saccharina latissima	19-May	triplicate	6.84	1.20	<loq	<loq	<loq	0.53	4.82	0.51	0.34	N/D	N/D	4.00	0.98	14.23
Saccharina latissima	19-May	singlet	6.71	1.49	<loq	<loq	<loq	0.62	5.17	0.59	0.41	N/D	N/D	3.99	1.22	13.88

Table S9. Carbohydrate monomer composition in *Nereocystis luetkeana* samples from SE Site 1 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol %	Fucose %	Galactosamine %	Arabinose %	Glucosamine %	Galactose %	Glucose %	Mannose %	Xylose %	Ribose %	Galacturonic %	Guluronic %	Glucuronic %	Mannuronic %
Nereocystis luetkeana	11-Apr	singlet	5.76	0.41	N/D	<loq	0.20	0.81	2.55	0.18	0.08	N/D	N/D	1.98	0.83	11.67
Nereocystis luetkeana	11-Apr	singlet	5.91	0.44	N/D	<loq	0.22	0.91	3.06	0.20	0.09	N/D	N/D	2.40	0.93	13.28
Nereocystis luetkeana	11-Apr	singlet	3.86	0.40	N/D	<loq	0.22	0.84	2.50	0.18	0.10	N/D	N/D	2.08	0.87	11.53
Nereocystis luetkeana	23-Apr	triplicate	9.42	0.47	N/D	<loq	0.17	0.73	2.75	0.20	0.08	N/D	N/D	2.16	0.87	12.81
Nereocystis luetkeana	23-Apr	singlet	5.19	0.48	N/D	<loq	0.20	0.75	2.83	0.20	0.08	N/D	N/D	2.17	0.81	11.85
Nereocystis luetkeana	23-Apr	singlet	1.54	0.44	N/D	<loq	0.19	0.72	2.61	0.18	0.08	N/D	N/D	2.59	0.84	11.11
Nereocystis luetkeana	10-May	singlet	10.44	0.53	N/D	<loq	0.17	0.80	3.34	0.25	0.10	N/D	N/D	2.65	0.97	14.54
Nereocystis luetkeana	10-May	singlet	11.06	0.52	N/D	<loq	0.18	0.78	3.34	0.23	0.10	N/D	N/D	2.42	0.91	13.34
Nereocystis luetkeana	10-May	singlet	11.00	0.48	N/D	<loq	0.17	0.78	3.03	0.23	0.10	N/D	N/D	2.67	1.03	14.76
Nereocystis luetkeana	25-May	singlet	0.38	0.63	<loq	<loq	0.17	N/D	5.06	0.30	0.12	N/D	N/D	4.22	1.08	12.95
Nereocystis luetkeana	25-May	singlet	0.49	0.60	<loq	<loq	0.16	0.62	3.24	0.26	0.12	N/D	N/D	3.13	1.00	11.72
Nereocystis luetkeana	25-May	singlet	11.79	0.52	<loq	<loq	0.15	0.61	3.60	0.27	0.11	N/D	N/D	3.68	1.05	12.90
Nereocystis luetkeana	14-Jun	triplicate	8.71	0.60	<loq	<loq	0.15	0.67	4.15	0.36	0.13	N/D	N/D	3.84	0.98	15.48
Nereocystis luetkeana	14-Jun	singlet	1.36	0.51	<loq	<loq	0.16	0.59	3.53	0.30	0.10	N/D	N/D	3.39	0.84	9.46
Nereocystis luetkeana	14-Jun	singlet	0.86	0.49	<loq	<loq	0.16	0.51	5.70	0.36	0.12	N/D	N/D	5.40	0.90	11.85
Nereocystis luetkeana	27-Jun	singlet	8.70	0.68	<loq	<loq	0.18	0.69	4.15	0.36	0.12	N/D	N/D	3.87	0.90	12.84
Nereocystis luetkeana	27-Jun	singlet	5.90	0.59	<loq	<loq	0.35	0.55	3.24	0.35	0.09	N/D	N/D	2.73	0.71	8.73
Nereocystis luetkeana	27-Jun	singlet	5.05	0.71	<loq	<loq	0.34	0.60	3.34	0.36	0.10	N/D	N/D	3.14	0.75	10.11

Table S10. Carbohydrate monomer composition *Saccharina latissima* samples from SE Site 1 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol %	Fucose %	Galactosamine %	Arabinose %	Glucosamine %	Galactose %	Glucose %	Mannose %	Xylose %	Ribose %	Galacturonic %	Guluronic %	Glucuronic %	Mannuronic %
Saccharina latissima	11-Apr	singlet	8.85	0.74	N/D	<loq	<loq	0.86	4.25	0.36	0.17	N/D	N/D	2.78	1.24	12.17
Saccharina latissima	11-Apr	singlet	6.04	0.67	N/D	<loq	<loq	0.81	3.84	0.34	0.16	N/D	N/D	3.20	1.33	14.58
Saccharina latissima	23-Apr	singlet	3.54	1.06	N/D	<loq	<loq	0.72	4.88	0.35	0.22	N/D	N/D	3.54	1.43	14.47
Saccharina latissima	23-Apr	singlet	3.44	0.83	N/D	<loq	<loq	0.77	3.99	0.37	0.21	N/D	N/D	3.35	1.48	12.67
Saccharina latissima	23-Apr	singlet	3.58	0.91	N/D	<loq	<loq	0.80	4.41	0.36	0.19	N/D	N/D	3.55	1.43	13.50
Saccharina latissima	10-May	singlet	5.85	1.08	N/D	<loq	<loq	0.78	4.56	0.35	0.22	N/D	N/D	3.09	1.37	12.73
Saccharina latissima	10-May	triplicate	2.16	1.02	N/D	<loq	<loq	0.72	4.00	0.37	0.20	N/D	N/D	3.74	1.53	11.15
Saccharina latissima	10-May	singlet	3.40	1.21	N/D	<loq	<loq	0.81	4.36	0.39	0.21	N/D	N/D	4.01	1.58	12.62
Saccharina latissima	25-May	singlet	1.98	1.11	N/D	<loq	<loq	0.70	4.37	0.38	0.21	N/D	N/D	3.67	1.50	11.41
Saccharina latissima	25-May	singlet	3.52	1.23	N/D	<loq	<loq	0.75	4.89	0.40	0.21	N/D	N/D	3.83	1.51	11.75
Saccharina latissima	25-May	singlet	2.24	1.22	N/D	<loq	<loq	0.74	4.75	0.42	0.25	N/D	N/D	4.00	1.55	11.09
Saccharina latissima	14-Jun	singlet	2.54	1.51	<loq	<loq	0.14	0.73	4.93	0.44	0.26	N/D	N/D	4.12	1.39	12.12
Saccharina latissima	14-Jun	singlet	2.74	1.27	<loq	<loq	<loq	0.73	5.13	0.45	0.25	N/D	N/D	4.30	1.39	13.19
Saccharina latissima	14-Jun	singlet	1.92	1.38	<loq	<loq	<loq	0.74	5.28	0.47	0.26	N/D	N/D	4.75	1.55	12.40
Saccharina latissima	27-Jun	singlet	1.11	0.96	<loq	<loq	0.38	0.49	3.32	0.38	0.18	N/D	N/D	2.60	0.92	8.11
Saccharina latissima	27-Jun	singlet	1.19	1.19	<loq	<loq	0.36	0.61	3.68	0.40	0.19	N/D	N/D	3.13	1.13	10.09
Saccharina latissima	27-Jun	singlet	3.92	1.53	<loq	<loq	0.29	0.53	3.84	0.40	0.17	N/D	N/D	3.31	1.04	10.88

Table S11. Carbohydrate monomer composition in *Saccharina latissima* samples from SE Site 2 in 2023. Values are expressed as a % of dry biomass weight. No detection (N/D), below limit of quantification (<loq).

Species	Date	Analytical replication	Mannitol %	Fucose %	Galactosamine %	Arabinose %	Glucosamine %	Galactose %	Glucose %	Mannose %	Xylose %	Ribose %	Galacturonic %	Guluronic %	Glucuronic %	Mannuronic %
Saccharina latissima	3-Apr	singlet	7.51	0.98	<loq	<loq	<loq	0.71	3.59	0.34	0.25	N/D	N/D	2.93	0.87	12.25
Saccharina latissima	3-Apr	singlet	9.59	1.10	<loq	<loq	<loq	0.75	3.81	0.38	0.27	N/D	N/D	2.83	0.88	12.58
Saccharina latissima	3-Apr	singlet	8.40	1.04	<loq	<loq	<loq	0.73	3.76	0.37	0.26	N/D	N/D	2.71	0.79	11.56
Saccharina latissima	29-Apr	singlet	17.91	1.15	N/D	<loq	<loq	0.62	4.35	0.42	0.28	N/D	N/D	3.10	0.81	12.83
Saccharina latissima	29-Apr	singlet	16.24	1.07	N/D	<loq	<loq	0.59	4.84	0.40	0.30	N/D	N/D	3.41	0.84	14.18
Saccharina latissima	29-Apr	singlet	19.44	1.11	N/D	<loq	<loq	0.60	4.93	0.41	0.30	N/D	N/D	3.24	0.86	13.58
Saccharina latissima	10-Jun	singlet	8.89	1.62	N/D	<loq	<loq	0.64	4.89	0.45	0.33	N/D	N/D	4.09	1.02	14.87
Saccharina latissima	10-Jun	singlet	10.06	1.66	N/D	<loq	<loq	0.62	4.97	0.47	0.36	N/D	N/D	4.11	1.10	15.08
Saccharina latissima	10-Jun	triplicate	9.74	1.79	N/D	<loq	<loq	0.63	5.20	0.48	0.36	N/D	N/D	4.15	1.11	15.60

Appendix B: Limitations of This Study

This study aimed to provide novel insights into the carbohydrate composition of several kelp species over both spatial and temporal dimensions, leading to limitations in sampling capacity and variable standardization. We were not able to perform a thorough assessment of environmental correlations due to limited temporal sampling and high variability in both environmental and compositional data. As sampling took place over a broad geographic range from Southeast Alaska, to Kodiak, Alaska, seed stock at each farm reflected local populations. Genetic differences were not considered in this study, possibly confounding the influence of the environment when testing site-specific compositions of the same species. Studies on *A. marginata* and *S. latissima* genetics in Alaska indicate population distinctions at scales of 10 to 100's of kilometers with a history of complex, glacially related extinction, and re-colonization events (Grant & Bringloe, 2020; Grant & Chenoweth, 2021). Genetic influence on carbohydrate composition is limited; however, ecotypes of the same species show different levels of soluble carbohydrates when grown under the same conditions, while correlations have been found among populations in variable temperature/salinity areas and single nucleotide polymorphisms associated with alginate and mannitol production (Guzinski et al., 2020; Olischläger et al., 2014). Other limitations with sampling from commercial farms included differences in farm layout, density of kelp on lines, and time of harvest. The latter resulted in the removal of kelp from lines surrounding the sampling lines during the study period, possibly altering the physical environment. PWS Site 2 was required by their permit to remove all equipment by the end of May, which limited these data when comparing compositions among sites, particularly for *N. luetkeana*.

Appendix C: Future Research

This study sets an outline of temporal trends in carbohydrate composition of three commercially relevant Alaskan kelp species, but did not assess molecular speciation of biochemical constituents and was not able to confidently assess correlations with environmental variables. It is important to understand more detailed aspects of these sugars to inform extraction focused mariculture, as the functioning of these molecules relies on specific chemical properties (Batista, 2019; Li et al., 2008). Fucoidan, for example, is valued for its medicinal and nutraceutical properties; however, these properties vary with molecular structure, including degree of branching and degree of sulfation (Ale et al., 2011; Oliveira et al., 2017). Fucoidan structure and quantity is also known to vary among tissue types; thus, even though *N. luetkeana* had the highest sulfate content in fucoidan, it cannot be determined from this study, if other species have equally, if not higher degrees of sulfation in some of their fucoidans (Mak et al., 2013; Torode et al., 2015). Additional analyses on the species addressed in this study using nuclear magnetic resonance spectroscopy could further our understanding of specific chemical attributes of fucoidan, while monoclonal antibody mapping techniques can inform tissue-specific qualities of fucoidan and increase our physiological understanding (Bilan et al., 2010; Torode et al., 2015). Similarly, the mannuronic to guluronic acid ratio is merely a proxy for gelation capabilities, and understanding variability in molecular weight and uronic acid blocking patterns would be useful to more accurately assess these alginates' potential for extractive processing (Draget et al., 1994; Plazinski, 2011). As for correlations between carbohydrate composition and environmental variables, manipulative experiments in a laboratory setting may allow greater transparency and confidence in these relationships (Bruhn et al., 2017). Understanding the effects of the environment on both quality and chemical structure of kelp carbohydrates is paramount in establishing consistency in biochemical products. Lastly, Alaska contains many species of marine macroalgae, and future research should explore biochemical composition outside of the scope of currently cultivated species (Lindeberg & Lindstrom, 2010).

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