Effect of Environmental Physico-Chemical Parameters on the Biochemical Composition of Wild Icelandic *Laminaria digitata* and *Saccharina latissima* (Laminariaceae, Phaeophyceae)

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ABSTRACT

As global demand for algae products continues to rise, development of efficient cultivation methods for these resources becomes ever more essential. However, to date, there is still little known about how macroalgae respond to their environment, particularly in regard to fluctuations in their biochemistry. To address this, research was conducted which compared levels of biochemical components in two indigenous brown marine macroalgae species (*Laminaria digitata* and *Saccharina latissima*), wild harvested from two study sites located in Iceland. Results of these analyses were then mapped to the following environmental physico-chemical variables present at each of the respective sites: seawater chemistry (i.e., pH, salinity, total phosphorus, orthophosphate-P, nitrate-N, nitrite-N, ammonium-N, and dissolved oxygen), climatological data (i.e., relative humidity, sea surface temperature, air temperature, wind speed, and atmospheric pressure), tide depth, and daylight duration.

The findings showed sea surface temperature to be strongly correlated to both carbohydrates (positively) and proteins (negatively) in both *L. digitata* and *S. latissima* at each site, and therefore could potentially be a key driver in macroalgae biochemical production. In addition, possible secondary, modulating variables were identified, such as total phosphorus and nitrate-N in the case of carbohydrates. The presence of these modulators, in combination with optimal sea surface temperatures may enable peak levels of biochemicals to be achieved. However, their degree of influence may be limited to certain thresholds, outside of which, more of an inhibitory effect may be observed. It was also noted that site specific environmental physico-chemical factors may have a greater influence on algae biochemical variability than genetic familiarity.

1. Introduction

World-wide, marine macroalgae are well known as a natural resource for valuable biochemical components, such as carbohydrates, proteins, lipids, vitamins, and minerals (Kumar et al., 2008; Holdt and Kraan, 2011; Tanna and Mishra, 2019). In their dried powdered form, or as concentrated extracts, they are often used as versatile ingredients in the manufacture of a large variety of products, from cosmetics to cattle feed, and even biofuel (Kim, 2015). In the year 2020, a record combined global fisheries and aquaculture production of 214 million tonnes of biomass, wet weight (WW) was seen (FAO, 2022). Of this total, 36 million tonnes (16.82%) were made up of seaweeds alone, comprising 31 species, and 97.5% of which came from aquaculture (16.5 billion USD) (FAO, 2022). The increasing use for these materials is reflected in their supply, where trade of algae saw an almost 17-fold increase between 1976–2020 (FAO, 2022). It is clear that as

demand for macroalgae based products continues to rise, greater pressure will be placed on suppliers to scale-up their production, in order to meet consumer expectations (Langford et al., 2021).

The majority of global macroalgae production originates from aquaculture in Asia. Conversely, American and European production only make up around 5% and 4% (respectively) of total cultivated seaweed production, with the remainder generally being harvested from wild stocks (Cai et al., 2021). In the European/North-Atlantic region, brown macroalgae species are the most commercially exploited, however, further research is required for the development of more efficient culturing techniques (Kim et al., 2017). Some of the specific challenges identified for the N-Atlantic include development of culture strains for the region and anticipating environmental factors that could be affected by climate change in the near future (Kim et al., 2017; AMAP, 2018). In the N-Atlantic, current research efforts are focused on seasonal seaweed growth performance and chemical composition in different environments or geographical locations (Forbord et al., 2020; Manns et al., 2017), mitigating fouling species (Forbord et al., 2020), and identification of suitable aquaculture locations through studies on seawater quality (Broch et al., 2019). It is also clear by efforts such as MACROSEA, in Norway (https://www.sintef.no/projectweb/macrosea/publications/), and the Safe Seaweed Coalition, in France (https://safeseaweed.linaia.online/), that seaweed aquaculture is of significant economic and ecologic importance for the N-Atlantic region and beyond, and so the continuation of fundamental research is essential.

Of the brown marine macroalgae, both *Laminaria digitata* and *Saccharina latissima* are almost ubiquitously found in the low intertidal and subtidal regions along the coastlines in the N-Atlantic. As a result, they are some of the most studied, harvested, and cultivated macroalgae species in the region. Both *L. digitata* and *S. latissima* are rich sources of polysaccharides, such as alginate, mannitol, laminarin, and fucoidan (Kostas et al., 2017), as well as proteins and defensin-like peptides (Ganesan et al., 2021; Bleakley and Hayes, 2017). Additionally, although present in the lowest concentrations of all the main primary metabolites (0.3%–5%), algal lipids have nonetheless been the subject of much research (Salehi et al., 2019). Furthermore, macroalgae secondary metabolites have also been researched, particularly in relation to prospecting "bio-inspired" pharmaceuticals. Most notably, glycoglycerolipids, phospholipids, sterols, and carotenoids have been found to display promising antioxidant, anti-inflammatory, and anticancer properties (Holdt and Kraan, 2011). Nevertheless, beyond any commercial value these algal proteins, carbohydrates, and lipids may have, as primary metabolites (or biochemical components) they have a critical role in biological functions during the algae's life cycle, and are known to be influenced by seasonal fluctuations, induced by a combination of both intrinsic and extrinsic factors (Vadas Sr et al., 1992).

From an aquaculture perspective, it is imperative that the quality of raw material harvested be of a sufficiently high standard to allow production to be both economically viable and environmentally sustainable (Zhang and Thomsen, 2021). As such, many studies have investigated seasonal changes in marine macroalgae and their chemical compounds, with an aim to determine optimal biomass harvesting regimes (Conolly and Drew, 1985; Martinez et al., 2012; Schiener et al., 2015; Ji et al., 2016). Studies on brown algae from Sweden, Scotland, Denmark, Norway, and Iceland show that timing of seasonal fluctuation in biochemical components and periods of growth are impacted by geographical location (Vilg et al., 2015; Schiener et al., 2015; Manns et al., 2017; Sharma et al., 2018; Forbord et al., 2020). The onset of change in composition is generally delayed in the northern regions compared to the study sites in the south (Forbord et al., 2020), likely driven by key environmental limiting factors such as temperature and day length. However, while *L. digitata* and *S. latissima* exhibit similar seasonal fluctuations in biochemical components between locations, differences in environmental variables appear to influence the extent of fluctuation in algal biochemistry (Schiener et al., 2015; Manns et al., 2017; Forbord et al., 2020). Few, however, take a holistic approach in considering the simultaneous impact of multiple key environmental physico-chemical variables on individual algal biochemical components, irrespective of seasonality. Such information may prove important for understanding the role of algae biology in wild harvesting, or cultivation site selection, as well as for fine-tuning controlled environmental conditions in land-based tank cultivation.

In 2019, Iceland harvested a total of 17,533 tonnes WW of brown algae (0.05% of global macroalgae production), all of which was from the wild. This was made up of 15,551 tonnes of *Ascophyllum nodosum*, 84 tonnes of *Laminaria hyperborea*, and 1898 tonnes of *L. digitata* (Cai et al., 2021). Compared to other N-Atlantic countries, which harvested brown algae during the same year, the following total values were reported: in Norway (163,197 tonnes WW), France (51,476 tonnes WW), and Ireland (29,542 tonnes WW) (Cai et al., 2021). In contrast, it appears as though the macroalgae industry in Iceland may still be in its infancy. Interestingly, a large proportion of this macroalgae originated from cultivation within these countries, whereas in Iceland, there is currently none. Even so, its unique mid N-Atlantic location and dynamic marine habitats, including strong currents, high nutrient availability, variety of temperature gradients, and a rich biodiversity, offer ideal conditions for coastal cultivation of macroalgae (Geddie and Hall, 2020). In light of this, the Icelandic government is currently updating its legislation and policies to accommodate this potentially lucrative industry. The aim being to avoid possible environmental impact resulting from mismanagement and overexploitation within a presently under regulated industry. Nevertheless, current, and predicted effects of climate change may dramatically alter marine environments (e.g., greater prevalence of biofouling as a result of increased infiltration of invasive species - Sorte et al., 2010; Micael et al., 2021), as a result of such phenomena as desalination, acidification, and warming of the oceans (Doney et al., 2012), and so the continuity of suitability of natural sites for macroalgae cultivation remains uncertain.

It is well known that a variety of biotic factors can have profound effects on macroalgae communities. For example, microfouling, grazing, and parasitic epi- and endophytes, present within the surrounding habitat can severely inhibit growth, and can cause disease, or even death, to individuals or entire populations (Korpinen et al., 2007). Moreover, competition for space and resources within the same species (intraspecific), as well as from other species and organisms (interspecific) is also challenging (Carpenter, 1990). Influence from environmental (abiotic) factors may also severely affect the ability of macroalgae to thrive, or even survive under certain conditions. For example, extremes in parameters such as hydrodynamics, desiccation, light (both irradiance and duration), temperature, salinity, and seawater chemistry (esp. pH and nutrient concentrations), can equally be as disruptive as biotic disturbances (Lalegerie et al., 2020).

The goal of this study was to investigate macroalgae/abiotic relationships. The results of which could then be used in the development of small-scale cultivation methods, to optimise yields of valuable bioactive components, via the manipulation of controlled environmental variables in land-based conditions. This study aims to go beyond identification of general seasonal variation in algae chemical composition. Instead, it tries to pinpoint specific physico-chemical variables (or combinations thereof), associated with both seasonality and site location as (obvious and non-obvious) potential key drivers of algal biochemicals within a given species.
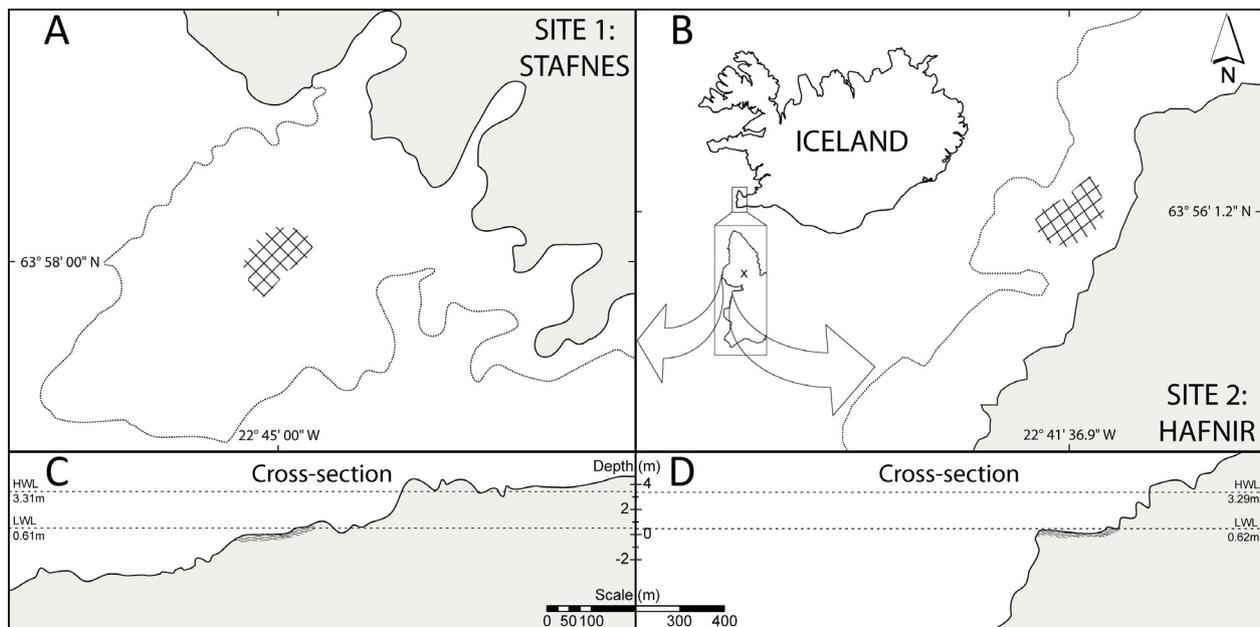
Fig. 1. Location of study site 1: Stafnes (A), and study site 2: Hafnir (B), within Iceland's Southern Peninsula (B inset). Cross-section of study sites 1 (C) and 2 (D) illustrate area topography in relation to the average (year) depth of the high water levels (HWL) and low water levels (LWL) as heavy dashed lines. "X" indicates the location of the weather station (kvk #4018) used in the study (B). Shaded area is land; light dashed lines represent the extent of intertidal zone (A & B); hatched area indicates collection point.

2. Materials and methods

2.1. Sampling locations

Previous investigations revealed that both of the chosen study sites are areas rich in biodiversity. In particular, an abundance of macroalgae species such as *Pelvetia canaliculata*, *Fucus spiralis*, *Fucus vesiculosus*, *A. nodosum*, *Fucus serratus*, *Mastocarpus stellatus*, *P. palmata*, *S. latissima*, and *L. digitata* were noted (Ingólfsson, 2006). As such, the areas were identified as sites of interest for further investigation, as well as potential harvesting areas. According to Munda (1972a), the characteristics of the two study sites appeared to be representative of many similar sites located throughout Iceland, being richly biodiverse with macroalgae species (Munda, 1975). For these reasons, as well as their ease of access and close proximity, the sites were chosen for the current study. Unfortunately, little in the way of specific oceanographic data relating to the sites, such as occurrence of upwelling, were available. Even so, currents of 10–20 cm · s^{-1} have been observed in the SW of Iceland (van Aken, 1995), and mean sea surface temperatures (SST) of 6.3 °C, with average hottest (12.7 °C), and coldest (0.54 °C) values were calculated from historical data (1969–2013), supplied by the Marine and Freshwater Research Institute, Iceland [dataset](MFRI, 2021).

2.1.1. Study site 1

The site was a moderately exposed rocky shore in Stafnes, Sandgerði, Iceland (63°58'00" N, 22°45'00" W) (Figs. 1A & 1C). Huge boulders scattered throughout the site dominated the landscape, forming numerous rock pools, and acted as substrate for a variety of macroalgae species. The intertidal zone spread wide across the foreshore, with a long and shallow cross-shore incline, forming a shelf-like structure, being strongly exposed to wind as it stretched out towards the sea. Average low water level (LWL) at low tide was 0.61 m, and high water level (HWL) at high tide was 3.31 m [dataset](Tide-forecast, 2017). Occasional wave heights of

approx. 1–2 m were noted, with the collection area usually being submerged to a depth of 3–4 m at high tide. A small, rarely used, harbour was adjacent to the site, and the lay of the land was flat. Samples of wild *L. digitata* and *S. latissima* were harvested between September 2014–August 2015, at low tide, at a depth of 1–3 m, within an area located approx. 500 m from the shore.

2.1.2. Study site 2

The second site was a heavily exposed area of rocky shore located 4.53 km southeast of site 1, within Hafnir, Iceland (63°56'1.2" N, 22°41'36.9" W) (Figs. 1B & 1D). A thin strip of sandy beach gave way to a mixture of small pebbles and large rocks. The intertidal zone was wide and continuous along the foreshore, but with a cross-shore area which quickly descended towards the waterline and beyond. The site experienced occasional wave heights of approx. 4 m and had a water depth of 3–6 m at high tide. Average low water level (LWL) at low tide was 0.62 m, and high water level (HWL) at high tide was 3.29 m [dataset](Tide-forecast, 2017), with the collection area usually submerged to a depth of 4–6 m at high tide and strongly exposed to the waves. Just west of the collection area was a large man-made seawall of huge boulders, which made the site appear uneven in many places. Samples of wild *L. digitata* and *S. latissima* were harvested between September 2016–August 2017, at low tide, at a depth of 1–3 m, within an area located approx. 100–150 m from shore.

2.2. Macroalgae sampling and preparation

Approximately 1–2 kg of fresh biomass WW of each study species were collected on a monthly basis, at low tide, from site 1 (Figs. 1A & 1C), and 2 (Figs. 1B & 1D).

Harvesting involved cutting the algae at least 20 cm above the holdfast, with sampled thallus consisting of a mixture of both frond and stipe only (Sjøtun and Gunnarsson, 1995). Size and maturity were not determined for any sample. All samples were transferred in coolers to the laboratory within one hour.

Biomass of each species were briefly washed with deionised water to remove any epiphytes, sand, and debris. Excess water was removed by padding dry with a paper towel, before tissue samples were cut into approximately ∼1 cm^2 pieces, thoroughly mixed, weighed into 500 g lots, and packed into polythene bags (Adams et al., 2009). Each bag represented a single species, collected during a particular harvest month, and were stored at −86 °C, within 3 h of collection (Coaten, 2014).

2.3. Seawater sampling and preparation

1000 mL wide-mouth high-density polyethylene (HDPE) seawater sample collection bottles, and their lids, were cleaned with detergent in a laboratory glassware washer, rinsed with deionised water, soaked in a hot (60 °C) 37% HCl (ACS reagent) acid bath (10 mins, repeated thrice), filled with dilute 30% HCl (Suprapur$^®$), rinsed and filled with ultra-pure deionised water, and then sealed in polythene bags (Crompton, 2006).

A total of 4 l of seawater per sampling were simultaneously collected from the tide inflow at each site during macroalgae collection. Seawater collection bottles were drained of deionised water and rinsed thrice with fresh seawater in the field, prior to final collection of a sample (Dore et al., 1996). Water samples were not prefiltered. Bottles were filled with no head space before being transported to the laboratory in a cooler.

Within two hours of collection, dissolved oxygen (DO), pH, and salinity measurements of the seawater samples were performed (see method details below). Afterwards, samples were decanted into 500 mL wide-mouth HDPE storage bottles, which had been pre-treated in the same manner as the collection bottles. Storage bottles were filled approximately 2/3, to prevent freezing out around the lids, before being stored upright at −20 °C (Dore et al., 1996).

2.4. Macroalgae analyses

The following analyses are commonly used to estimate the relative amounts of total moisture, ash, organic matter (OM), lipids, carbohydrates, and proteins present within algae (Laurens et al., 2012). Unless otherwise stated, samples were homogenised whilst still frozen, before immediately undergoing analyses when once thawed (Adams et al., 2009). Analyses were conducted every three months on the previous three months samples.

2.4.1. Total moisture
Analyses followed Association of Analytical Communities (AOAC) method 930.04 (Latimer, 2012). Results were expressed as % total moisture (WW).

2.4.2. Total ash and organic matter
Ash analyses followed AOAC method 930.05 (Latimer, 2012). Results were expressed as % total ash (minerals) of biomass dry weight (DW). OM was calculated as 100% - ash value (%) = OM value and was also expressed as % total OM (DW).

2.4.3. Total proteins
Analyses followed Barbarino and Lourenço (2005), using a modified Lowry method. Bovine serum albumin (USP) was used as the reference standard, and absorbance was measured at 750 nm, using a UV/Visible Spectrophotometer. Results were expressed as % total proteins (DW).

2.4.4. Total carbohydrates
Analyses followed Saha and Brewer (1994), applying the phenol/sulphuric acid method. D-(+)-Glucose (USP) was used as the reference standard, and absorbance was measured at 490 nm, using a UV/Visible Spectrophotometer. Results were expressed as % total carbohydrates (DW).

2.4.5. Total lipids
Analyses followed AOAC method 945.16 (Latimer, 2012), where crude lipids were extracted from defrosted algae biomass (WW) using petroleum ether (EMSURE$^®$) in a Soxhlet apparatus, before being quantified via their mass. Results were expressed as % total lipids (DW).

2.5. Seawater analysis

The following methods are used to determine relative chemical values within seawater samples, such as pH, salinity, and DO, as well as concentrations of the following nutrients: total phosphorus (TP), orthophosphate (OP), nitrate, nitrite, and ammonium (Strickland and Parsons, 1972; Grasshoff et al., 2009).

Stored samples remained frozen at −20 °C, in darkness, until 4–12 h before analyses, when they were completely thawed using a room temperature water bath (Dore et al., 1996). Sets of samples were analysed every three months and represented the previous three months.

In accordance with the World Ocean Database 2018 (WOD18), the standard unit of $\mu mol \cdot kg^{-1}$ was applied to the quantification of seawater chemicals (Boyer et al., 2018). In addition, nutrients were expressed in terms of equivalents of their corresponding primary nutrients, nitrogen (N) or phosphorus (P) (i.e., nitrate-N, nitrite-N, ammonium-N, and OP-P) (ICES, 2012).

2.5.1. pH and absolute salinity
Measurements were taken using a marine monitoring system and data logger, with attachable temperature, conductivity, and pH probes. Both conductivity and pH readings were automatically temperature compensated, and pH readings were also auto adjusted to conductivity. Results were expressed as pH, and salinity (conductivity) was in terms of Absolute Salinity (S_A, as $g \cdot kg^{-1}$), in accordance with TEOS-10 (Pawlowicz, 2013); calculated using RStudio with package "gsw"- version 1.0–6 (Kelley and Richards, 2021).

2.5.2. Dissolved oxygen
Measurements were taken using a DO meter. Results were expressed as DO $\mu mol \cdot kg^{-1}$.

2.5.3. Total phosphorus and orthophosphate
Determination of OP concentrations followed Taguchi et al. (1985). Determination of TP concentrations were achieved by first subjecting samples to a potassium persulphate (99.99% trace metals basis) digestion under autoclavic conditions (Jeffries et al., 1979; Patton and Kryskalla, 2003), then following the method for OP determination. A stock solution of potassium dihydrogen phosphate (ACS) was used as the reference standard, and absorbance was measured at 710 nm, using a UV/Visible Spectrophotometer. Results were expressed as OP-P $\mu mol \cdot kg^{-1}$ and TP $\mu mol \cdot kg^{-1}$.

2.5.4. Nitrate and nitrite
Determination of nitrate concentrations followed Doane and Horwáth (2003). Step 1. Determinations of nitrite were achieved by first eliminating native nitrite as per Bajic and Jaselskis (1985), then following the method for nitrate determination. Step 2. Nitrite concentrations were calculated via the following equation: results from step 2 - results from step 1 = nitrite concentration. A stock solution of sodium nitrate (ACS), converted to nitrite via the method of step 1, was used as the reference standard, and absorbance was measured at 540 nm, using a UV/Visible Spectrophotometer. Results were expressed as nitrate-N $\mu mol \cdot kg^{-1}$ and nitrite-N $\mu mol \cdot kg^{-1}$.

2.5.5. Ammonium

Determination of ammonium concentrations followed Kanda (1995). A stock solution of ammonium sulphate (ReagentPlus® - dried for 24 h at 60 °C prior to use) was used as the reference standard, and absorbance was measured at 670 nm, using a UV/Visible Spectrophotometer. Results were expressed as ammonium-N μmol $\cdot$ kg^{-1}.

2.6. Physical environment measurements

The following climatological data were obtained online from an Icelandic Meteorological Office (IMO) weather station close to the sites: Relative humidity (RH, as %), air temperature (AT, as °C), wind speed (WS, as m $\cdot$ s^{-1}), and atmospheric pressure (AP, as mb) [dataset](IMO, 2021). This station (IMO code: kvk #4018) was located at Keflavíkurflugvöllur - Keflavík international airport (63°58'53.5" N, 22°37'40.8" W); 6.19 km east of site 1, and 5.69 km northeast of site 2 (Fig. 1B - insert) and had been in continuous operation since 1952. Therefore, historical data [dataset](IMO, 2021) was used to calculate monthly averages relating to 1-, 10-, and 60-year cycles. Also, daily SSTs (as °C), were accessed [dataset](MFRI, 2021), and expressed as monthly averages during times of collection at each site.

Additionally, tide depth (TD, as m; represented as monthly averages of daily difference between high and low tide - nearest values were for Sandgerði harbour), and daylight duration (daylight, as h; represented as monthly averages of daily difference between sunrise and sunset), were gathered using an online database [dataset](Tide-forecast, 2017), for each site, during the given study time frames.

2.7. Statistical analyses

With the exception of TD and daylight duration (calculated as monthly averages of daily variance), all other analyses and measurements were conducted or recorded in triplicates, with data presented as means with standard deviation ($\pm SD$) of the replication ($n = 3$). Further statistical analytical methods utilised the following software: Soft Independent Modelling of Class Analogy - SIMCA® - version 17.0.0.24543, International Business Machines corporation - IBM®, Statistical Package for the Social Sciences - SPSS® Statistics - version 26.0.0.0, and R - version 4.1.0, using RStudio - version 1.4.1103, in conjunction with relevant packages.

2.7.1. Analysis of variance

Using SPSS®, two-way analysis of variance (ANOVA) with repeated measures, were conducted on biochemical component data from *L. digitata* and *S. latissima* collected from sites 1 and 2, to identify statistically significant seasonal variations, both in terms of harvest time and species, over the two 12-month periods. In addition, variations in environmental physico-chemical variables recorded between sites were also tested.

Data initially underwent assessment to determine the presence of outliers and normality, and where necessary, Greenhouse–Geisser or Huynh-Feldt corrections were applied. Post-hoc analyses with Bonferroni adjustment through pairwise comparisons, were then used to identify specific statistically significant differences between species and sites.

2.7.2. Correlation matrix analysis

Data underwent initial pre-treatment using SIMCA®, consisting of Pareto scaling of all values and a logarithmic transformation of independent (X) variables. Correlation matrices were then generated for whole year data models, which were used to identify relationships between levels of algae biochemical components and variations in environmental physico-chemical parameters in the form of a correlation matrix analysis (CMA). Findings were compared against those obtained through the use of R via RStudio with the "cor" and "rcorr" functions to generate correlation data (Pearson's correlation coefficient) and related p values. Results were visualised using package "corrplot" - version 0.90 (Wei et al., 2021), and where found to be statistically significant, were annotated with asterisks to indicate the degree of such (i.e., * = $p < 0.05$, ** = $p < 0.01$, or *** = $p < 0.001$).

Both single species (i.e., one species at one site) and combined inter- and intraspecific three-way matrices were created from two-way CMAs, thereby simultaneously depicting algal biochemical components as correlated with one another, as well as with seawater chemistry, and physical environment measurements. In addition, physico-chemical CMAs were conducted which compared only seawater chemistry and physical environment variables at each respective site. This was done to identify the presence of possible correlations (and covariance) between these environmental physico-chemical parameters.

3. Results

3.1. Descriptive statistics

Individual algal biochemical components were used to identify seasonal trends between each sampled species at both sites. This was achieved by combining direct comparisons of intra- and interspecific data with results of the ANOVA (SI, Figs. S1 & S2 A-D and Tables S1 & S2).

Average carbohydrate content was higher in *S. latissima* at 64.2 ± 1.5 and 66.8 ± 8.2% DW compared to *L. digitata* at 63.2 ± 1.8 and 66.6 ± 6.5% DW at sites 1 and 2, respectively (Figs. S1 & S2 A). Both species exhibited considerably larger fluctuations in carbohydrate between months at site 2.

Highest yearly average content of ash was observed in *S. latissima*, 22.3 ± 1.1 and 20.5 ± 5.1% DW at site 1 and 2, respectively (Fig. S2 B). Yearly average for *L. digitata* was 22.2 ± 0.7 and 19.2 ± 4.0% DW at sites 1 and 2, respectively (Fig. S1 B). Monthly fluctuation in ash content was observed to be larger for both species from site 2, reaching an overall 27.3 ± 2.2% DW in *L. digitata* and 9.4 ± 1.3% DW in *S. latissima*.

*L. digitata* had higher yearly average protein content of 7.6 ± 1.6 and 7.2 ± 1.4% DW compared to *S. latissima* 5.0 ± 1.5 and 5.3 ± 1.1% DW at sites 1 and 2, respectively (Figs. S1 & S2 C). Both species exhibited annual fluctuations in protein content, reaching highest values between February and April in both cases.

Lipid content was 3.6 ± 0.6 and 2.6 ± 0.7% DW in *S. latissima*, compared to 3.0 ± 0.4 and 2.5 ± 0.5% DW in *L. digitata*, at sites 1 and 2, respectively (Figs. S1 & S2 D).

3.2. Correlation matrix analyses

3.2.1. Single species and combined (inter- and intraspecific) correlations within and between sites

Three-way single species CMAs (i.e., algae biochemical components correlated to one another, seawater chemistry, and environmental factors) from sites 1 and 2 are shown in SI, Fig. S3 A-D. Summaries of these CMAs (i.e., displaying statistically significant correlations only) were then compared with the results of the relative combined inter- and intraspecific CMAs (Fig. 2A-D), as shown in Figs. 3 & 4A-D.
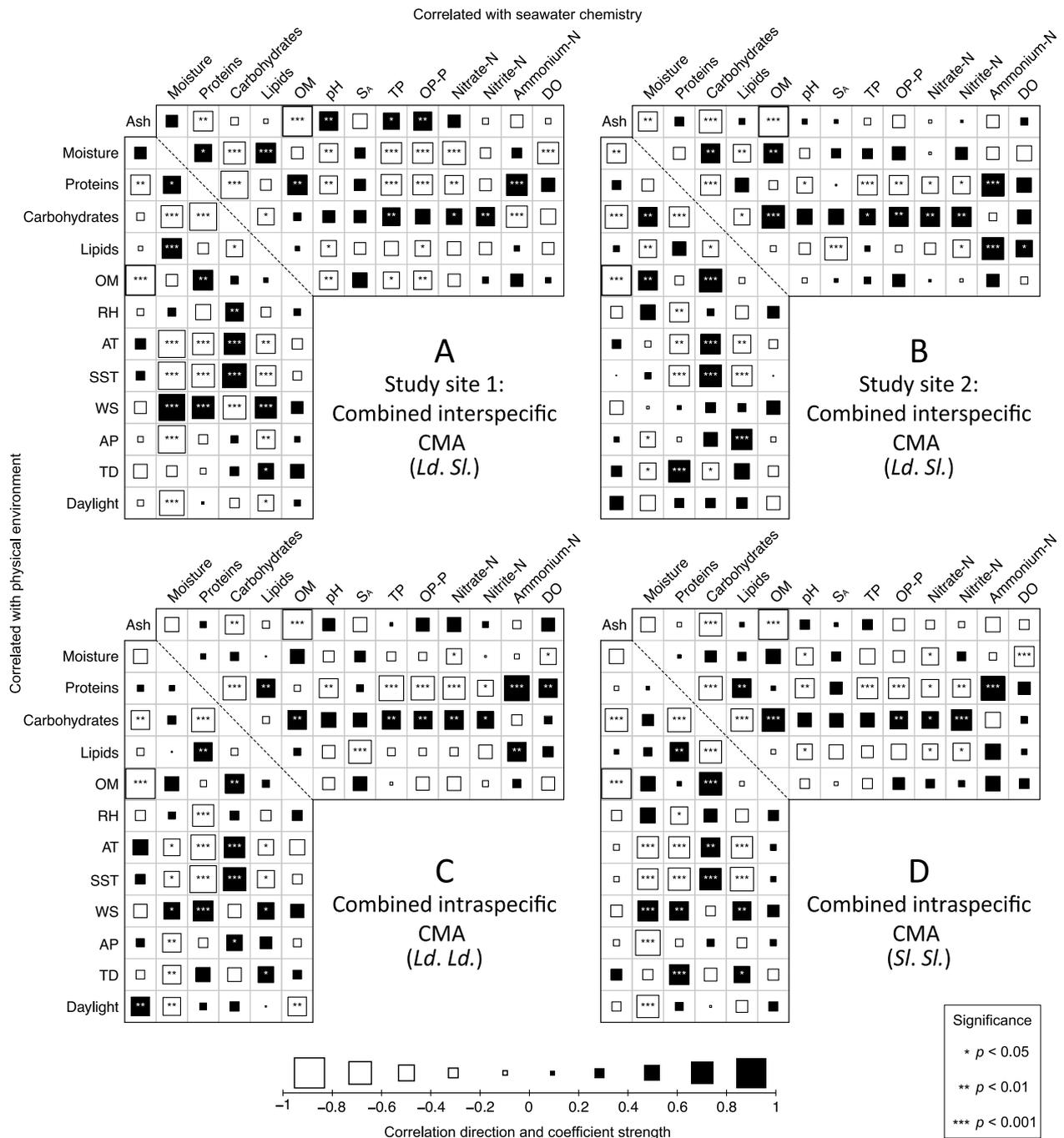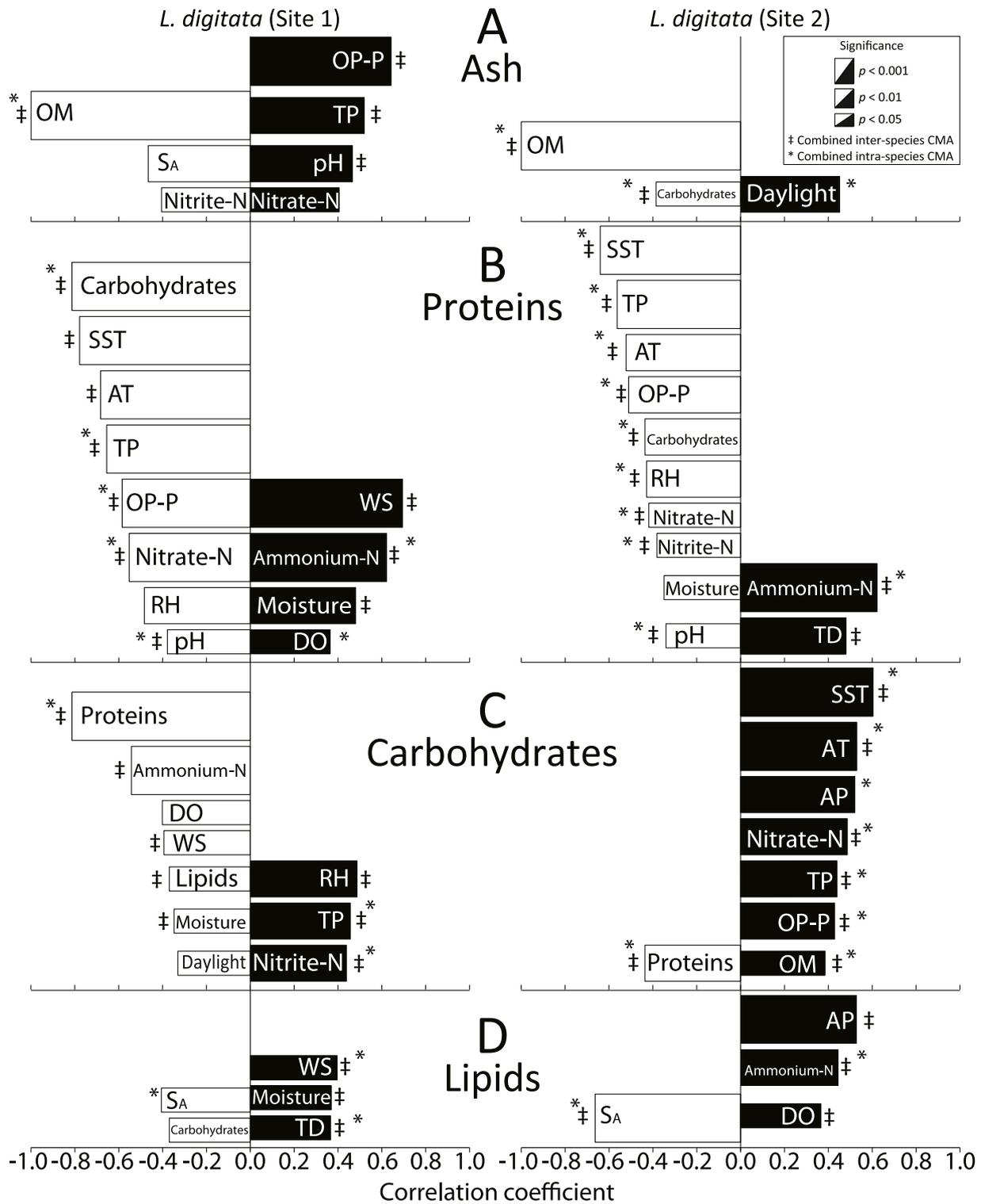
Fig. 2. Three-way combined interspecific CMA *(L. digitata* and *S. latissima)* for study site 1: Stafnes (September 2014–August 2015) (A), combined interspecific CMA *(L. digitata* and *S. latissima)* for study site 2: Hafnir (September 2016–August 2017) (B), combined intraspecific CMA *(L. digitata* and *L. digitata)* for study sites 1 and 2 (C), and combined intraspecific CMA *(S. latissima* and *S. latissima)* for study sites 1 and 2 (D). Depicts direction (+/-), strength, and significance of correlation coefficients between algae biochemical components, seawater chemistry, and physical environment data collected. .

3.2.1.1. L. digitata.

3.2.1.1.1. Ash and organic matter. Figs. 2 and 3A Single species CMAs shared only a strong negative correlation between ash and OM, which was also in agreement with both combined inter- and intraspecific CMAs. The single species CMA from site 1 shared positive correlations with OP-P, TP, and pH with its corresponding combined interspecific CMA, but no further similarities in relation to the combined intraspecific CMA. However, single species CMA from site 2 not only shared an additional negative correlation to carbohydrates in regard to its corresponding interspecific CMA, but also a positive correlation with daylight, which was also noted in the combined intraspecific CMA. Note:

Correlations for OM are the same as for ash, but with reversed values.

3.2.1.1.2. Proteins Figs. 2 and 3B Single species CMAs from both sites shared the following negative correlations: carbohydrates, SST, AT, TP, OP-P, nitrate-N, RH, and pH. Individual CMAs were also in agreement in regard to a positive correlation with ammonium-N. All of these relationships agreed with results found in the combined interspecific CMAs from each site. Furthermore, individual CMA from site 1 shared positive correlations with WS and moisture with its combined interspecific CMA, whereas individual CMA from site 2 shared an additional negative correlation to nitrite-N and RH, and positive correlation

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Fig. 3. Correlation coefficient summaries for biochemical components ash (A), protein (B), carbohydrate (C), and lipid (D) present within *L. digitata* at study site 1: Stafnes (September 2014–August 2015) and study site 2: Hafnir (September 2016–August 2017), in relation to one another, seawater chemistry, and physical environment. ‡In agreement with combined interspecific (within sites) CMAs. *In agreement with combined intraspecific (between sites) CMAs.

to TD with its combined interspecific CMA. Interestingly, with the exception of TD, the combined intraspecific CMA followed every corresponding correlation found between the single species CMA

at site 2 and combined interspecific CMA. However, for site 1, the combined intraspecific CMA only corresponded to negative correlations with carbohydrates, TP, OP-P, nitrate-N, and pH,

and positive correlations to ammonium-N (also with additional positive correlation to DO, which was not noted in the combined interspecific CMA).

3.2.1.1.3. Carbohydrates Figs. 2 and 3C Single species CMAs did not share any further negative correlations between the two sites. However, individual CMAs shared a positive correlation with TP, which were also in agreement with combined interspecific CMAs from each site. Individual CMA from site 1 shared negative correlations with ammonium-N, WS, lipids, and moisture, as well as additional positive correlations with RH and nitrite-N with its combined interspecific CMA, whereas individual CMA from site 2 shared additional positive correlations to SST, AT, nitrate-N, OP-P, and OM, with its combined interspecific CMA. As in the case of proteins, the intraspecific CMA was in full agreement with the single species CMA at site 2, with the addition of positive correlation to AP, which was not seen in the combined interspecific CMA. Even so, for site 1, the combined intraspecific CMA only agreed with a negative correlation with proteins, and positive correlations to TP and nitrite-N.

3.2.1.1.4. Lipids Figs. 2 and 3D Single species CMAs shared only S_A as a negative correlation between the two sites and did not share any positive correlations. Only individual CMA from site 2 shared this negative correlation to S_A with its combined interspecific CMA, along with positive correlations with AP, ammonium-N, and DO. However, individual CMA from site 1 only shared positive correlations to WS, moisture, and TD, as compared to its combined interspecific CMA. Here, the combined intraspecific CMA only shared positive correlations with WS and TD at site 1, and ammonium-N at site 2, and a negative correlation to S_A at both sites, although this correlation was not seen in the combined interspecific CMA at site 1.

3.2.1.2. S. latissima.

3.2.1.2.1. Ash and organic matter. Figs. 2 and 4A As with *L. digitata*, single species CMAs shared only the strong negative correlation between ash and OM between the two sites, as confirmed by both the combined inter- and intraspecific CMAs. In addition, neither site displayed any positive correlations. However, single species CMA from site 1 shared an additional negative correlation with proteins with its combined interspecific CMA, whereas the single species CMA from site 2 shared additional negative correlations to carbohydrates and moisture with its combined interspecific CMA. With the combined intraspecific CMA, only one additional agreement was noted - negative correlation with carbohydrates at site 2. Note: Correlations for OM are the same as for ash, but with reversed values.

3.2.1.2.2. Proteins Figs. 2 and 4B Single species CMAs shared the following negative correlations between the two sites: carbohydrates, SST, AT, TP, and OP-P. An agreement of positive correlations with both ammonium-N and lipids were noted. Apart from lipids, all these relationships were also in agreement with the combined interspecific CMAs from each site. Furthermore, individual CMA from site 1 shared negative correlations with pH and nitrate-N, and positive correlations with OM and WS with its combined interspecific CMA, whereas individual CMA from site 2 shared an additional negative correlation to nitrite-N and RH, and positive correlation to TD with its combined interspecific CMA. The combined intraspecific CMA agreed with all corresponding correlations with the single species CMAs (both positive and negative) at both sites, with an additional positive correlation to lipids, not seen in the combined interspecific CMA.

3.2.1.2.3. Carbohydrates Figs. 2 and 4C At both sites, single species CMAs shared negative correlations with lipids and proteins, as well as a positive correlation with SST, all of which agreed with both corresponding combined inter- and intraspecific CMAs. The single species CMA from site 1 shared negative correlations with WS, proteins, lipids, moisture, and ammonium-N as

well as additional positive correlations with AT, PT, and nitrite-N with its combined interspecific CMA. However, only positive correlations with AT and nitrate-N (with an additional positive correlation with OP-P, which was not noted in the combined interspecific CMA), were seen when compared to the combined intraspecific CMA. Whereas the single species CMA from site 2 shared negative correlations with proteins and lipids, and further positive correlations to OM, nitrate-N, and moisture, as compared to its combined interspecific CMA. All of which, except the positive correlation with moisture, were also seen in the combined intraspecific CMA.

3.2.1.2.4. Lipids Figs. 2 and 4D Single species CMAs shared the following negative correlations between the two sites: carbohydrates, SST, and AT. No positive correlations were shared. These relationships were in agreement with both their respective combined inter- and intraspecific CMAs. Furthermore, the single species CMA from site 1 shared negative correlations with AP, daylight, and OP-P, and positive correlations with WS and moisture with its combined interspecific CMA. Out of these correlations, only the one with WS (with an additional positive correlation with proteins, not previously seen in the combined interspecific CMA), was shared with the combined intraspecific CMA. Whereas individual CMA from site 2 shared an additional negative correlation to nitrite-N and S_A, as well as a positive correlation to ammonium-N, as compared to its combined interspecific CMA. Of these, only the correlation with nitrite-N was shared with the combined intraspecific CMA. In addition, the intraspecific CMA showed positive correlations with proteins at both sites, not previously seen in the combined interspecific CMA.

3.3. Physico-chemical environment analyses

3.3.1. Species/component response to physico-chemical variability

Results of graphs which plotted algal biochemical components against seasonal physico-chemical variability, revealed strong seasonal trends between biochemical/variable pairs (either directly or inversely). Interestingly, applying a theoretical 1-month time lag to the physico-chemical variables, appeared to further emphasise the relationships between these variables and corresponding biochemical components (Figs. 5 & 6A-D).

3.3.1.1. Sea surface temperature with carbohydrates and proteins (Fig. 5). Results of the two-way ANOVA (repeated measures) indicated SST to be statistically significantly different between the sites. SST at each site showed not only a strong positive relationship with carbohydrates (Fig. 5A-B), but also a strong negative relationship with proteins (Fig. 5C-D), in both species, and throughout the year. However, site 1 had significantly lower SST (corresponding with higher levels of proteins in both species), whereas site 2 had significantly higher SST (corresponding with higher levels of carbohydrates in both species).

3.3.1.2. Total phosphorus and nitrate-N with carbohydrates (Fig. 6). Results of the two-way ANOVA (repeated measures) indicated TP and nitrate-N to be statistically significantly different between the sites, and that both TP (Fig. 6A-B) and nitrate-N (Fig. 6C-D) showed direct relationships with carbohydrates, in both species, at each site. Interestingly, both variables were statistically significantly higher at site 1, however, the highest levels of carbohydrates in both species were recorded at site 2.

3.3.2. Comparison of physico-chemical correlations within and between sites

Seawater chemistry and physical environment measurement data was used to create environmental physico-chemical CMAs for each site (Fig. 7A-B). These were used to identify statistically significant interactions between the physico-chemical variables
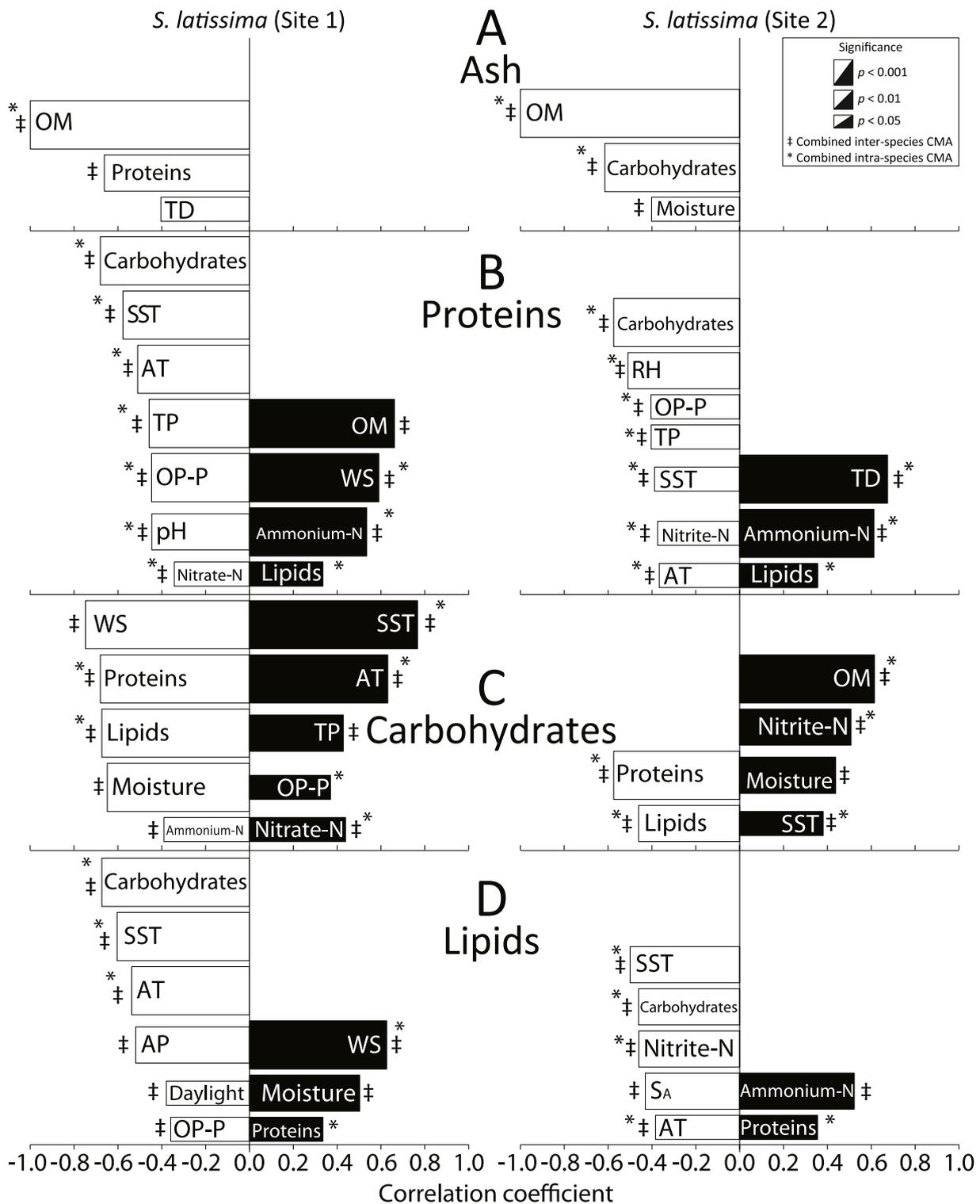
Fig. 4. Correlation coefficient summaries for biochemical components ash (A), proteins (B), carbohydrates (C), and lipids (D) present within *S. latissima* at study site 1: Stafnes (September 2014–August 2015) and study site 2: Hafnir (September 2016–August 2017), in relation to one another, seawater chemistry, and physical environment. ‡In agreement with combined interspecific (within sites) CMAs. *In agreement with combined intraspecific (between sites) CMAs.

and to reveal possible indirect correlations with algal components.

Only statistically significant correlations (i.e., $p < 0.05$) are described. Also, to avoid repetition, correlated pairs are recorded just once, although in many cases, their action should be considered as two-way (see SI, Fig. S4).
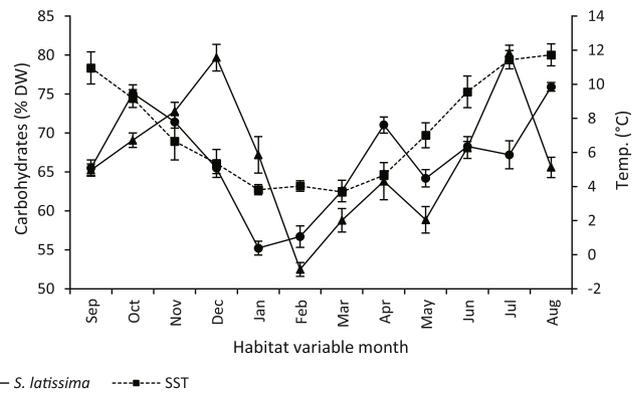
3.3.2.1. Seawater chemistry correlated to one another and physico-chemical measurements.

3.3.2.1.1. Total phosphorus Both sites shared negative correlations with ammonium-N and WS, and positive correlations with OP-P, nitrate-N, AT, SST, AP, and daylight. At site 1 nitrite-N and TD were positively correlated (both significant), although
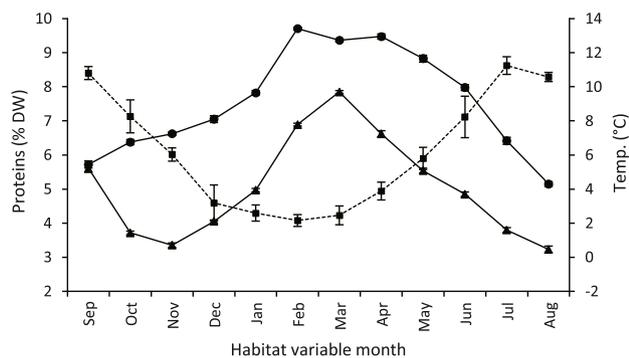
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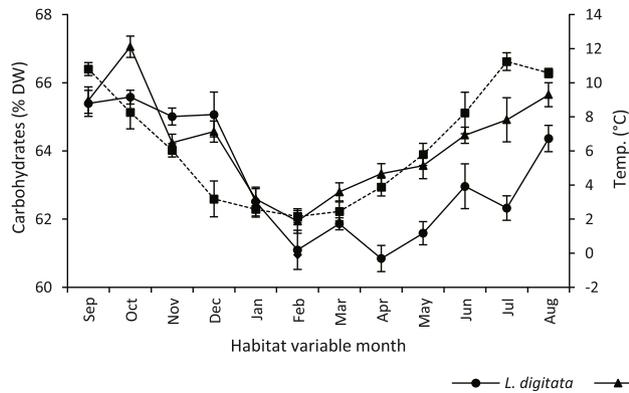
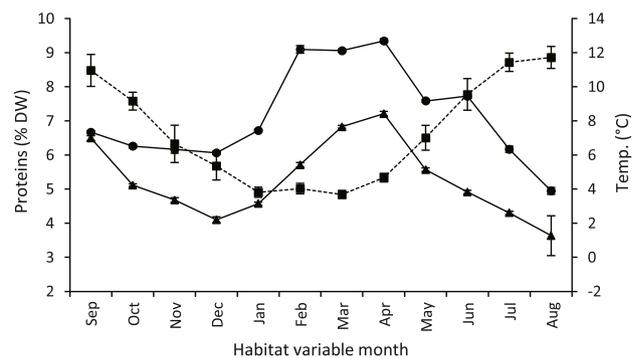**Fig. 5.** Comparison of component variation in *L. digitata* and *S. latissima* to seasonal variation of environmental factors - namely SST. Total carbohydrates and SST from study site 1: Stafnes (September 2014–August 2015) (A), total carbohydrates and SST from study site 2: Hafnir (September 2016–August 2017) (B), total proteins and SST from study site 1 (C), total proteins and SST from study site 2 (D). Yields expressed as a percentage biomass (DW); data points are averages of independent triplicates; *error bars* indicate ±SD. Result of two-way repeated measures ANOVA for SST between study sites is also provided.

in site 2 they were negatively correlated (TD being significantly so). Moreover, at site 1 there was a negative correlation with nitrite-N (significant), but in site 2 the same correlation is positive (non-significant).

3.3.2.1.2. Orthophosphate - P Both sites shared negative correlations with ammonium-N and WS, and positive correlations with nitrate-N, AT, SST, AP, and daylight. Nitrite-N and TD in site 1 were seen to be respectively negatively and positively correlated (both significant), but in site 2 they were respectively positively and negatively correlated (both significant).

3.3.2.1.3. Nitrate - N Both sites shared negative correlations with ammonium-N and WS, and positive correlations with AT, SST, AP, and daylight. Both sites showed DO and RH to be positively correlated, however, these were only seen to be significant in sites 2 and 1 respectively. Nitrite-N and TD in site 1 were seen to be respectively negatively and positively correlated (both significant), but in site 2 the relationship was reversed.

3.3.2.1.4. Nitrite - N Both sites shared negative correlations with ammonium-N and TD, and a positive correlation with DO. Both sites also showed negative correlation with WS, but only in site 2 was this seen as significant. Site 2 showed positive correlations with AT, SST, and daylight (all significant), however, site 1 showed these same variables as being negatively correlated (all non-significant).

3.3.2.1.5. Ammonium - N Both sites shared negative correlations with RH, AT, and SST, and positive correlations with DO and WS. Both sites also shared a positive correlation to AP, although this was only significant in site 2. Site 2 showed TD to be

positively correlated (significant), but in site 1 it was negatively correlated (non-significant).

4. Discussion

4.1. Physico-chemical seasonality and variable correlations

In the current study, analysis of average monthly physical environment data RH, AT, WS and AP showed similarities, between sites and years, as well as with the 10- and 60-year averages. All of which fell within the ±SD of these longer term data sets, as well as being comparable to results found in other publications. For example, average seawater values of pH, TP, and S_A closely resemble those reported in local studies (Stefánsson and Ólafsson, 1991; Aas and Hojerslev, 2001; Johnson et al., 2007, 2008; Jónasdottir et al., 2008). Even so, the following average seawater chemistry measurements at both sites appeared to be higher than published: nitrite-N at site 1 (0.3 ± 0.2) and 2 (0.4 ± 0.3), compared to Jónasdottir et al. (2008) (0.02 ± not mentioned (NM) μmol · kg^{-1}), ammonium-N at site 1 (0.6 ± 0.2) and 2 (0.6 ± 0.3), compared to Johnson et al. (2007, 2008) (0.1 ± 0.1 and 0.3 ± NM μmol · kg^{-1}), and DO at site 1 (296.2 ± 19.0) and 2 (298.3 ± 16.7 μmol · kg^{-1}), compared to Hoogakker et al. (2016) (234.6 ± NM O_2 μmol · kg^{-1}). However, these variations may be a result of differences in sample methodology and location. For instance, both Jónasdottir et al. (2008) and Johnson et al. (2008), collected open ocean samples across the Iceland–Scotland ridge, thereby making it difficult to directly compare against coastal
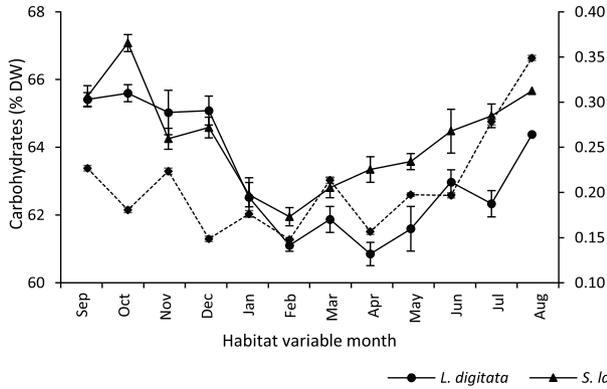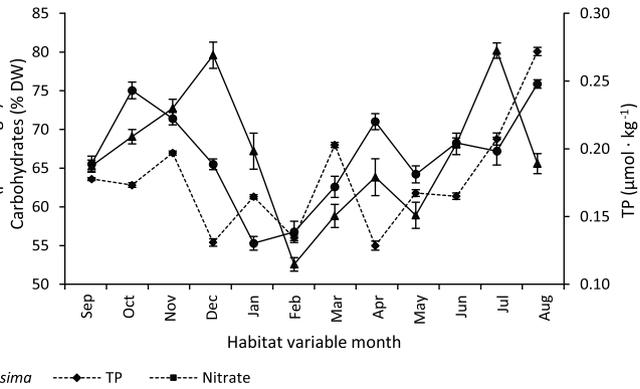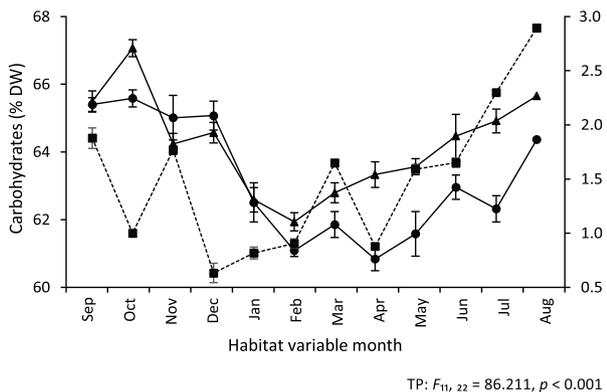
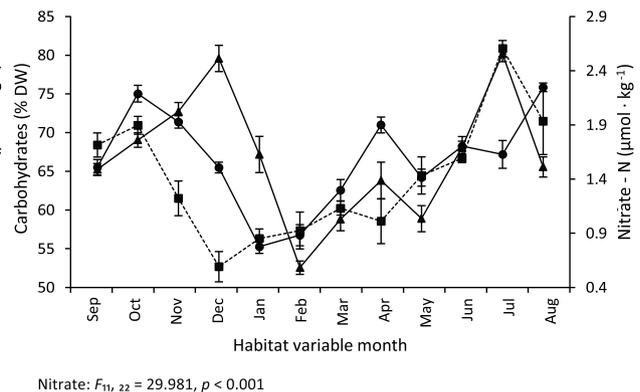**Fig. 6.** Comparison of component variation in *L. digitata* and *S. latissima* to seasonal variation in sea water chemistry - namely TP and nitrate-N content. Total carbohydrates and TP from study site 1: Stafnes (September 2014–August 2015) (A), total carbohydrates and TP from study site 2: Hafnir (September 2016–August 2017) (B), total carbohydrates and nitrate-N from study site 1 (C), total carbohydrates and nitrate-N from study site 2 (D). Yields expressed as a percentage biomass (DW); data points are averages of independent triplicates; *error bars* indicate ±SD. Result of two-way repeated measures ANOVA for both TP and nitrate-N between study sites is also provided.

samples taken during this study. Furthermore, any differences may also be attributed to the effects of coastal upwelling, where nutrient rich deep waters are brought to the offshore sea surface via wind (Takahashi et al., 1993). One recent local study appeared to only touch upon the subject of upwelling, simply stating that the locality of Iceland within the Northern Hemisphere, combined with an eastward flow along its south coast, is likely to be conducive to upwelling conditions (Logemann et al., 2013). Nevertheless, research specifically modelling the effect of topography on coastal upwelling and nutrient exchange, showed that the presence of a gradual cross-shore slope (such as found at site 1), could result in enhanced nutrient availability, through the formation of multiple upwelling centres inshore. Conversely, the absence of such a slope (as in the case of site 2), is more likely to cause regular (unimpeded) coastal upwelling, leading to a more homogenous gradient of nutrients (Song and Chao, 2004). This may explain both differences in seawater nutrient measurements at each site and observed variations in intraspecific comparisons. The intensity of upwelling is known to be correlated to both regional and local variation in kelp biomass, productivity, and ecological dynamics, within temperate and tropical waters (Velimirov et al., 1977; Graham et al., 2007; Pérez-Matus et al., 2017; Rothman et al., 2017).

In the present study, all seawater/seawater correlations were noted as being two-way (either directly or indirectly), which perhaps could be explained by the generation, or natural transformation of one nutrient type to another (Froelich et al., 1982;

Meeder et al., 2012), or may be indicative of their involvement in other processes, such as photolysis (Zafiriou and True, 1979). Environment/environment correlation actions are also two-way (directly), with the exception of TD/daylight, and S_A. Conversely, all environment/seawater correlation actions are one-way (i.e., physical variables influencing seawater chemistry), eliciting either a direct or indirect influence. Numerous physico-chemical interactions are most likely occurring between different biotic and abiotic variables simultaneously within the sites. Some requiring a period of acclimation (e.g., 14 days in the case of physical damage and UV exposure in temperate *L. hyperborea*) (Halm et al., 2011), whilst others involve response lags, such as those seen in stress responses (e.g., rapid desalination or herbivory in temperate *F. vesiculosus*) (Biber et al., 2004; Rohde and Wahl, 2008). Correlations may also either be one- or two-way in their action (see SI, Fig. S4), or may result from direct, indirect, or multi-factor relationships with the algal biochemical components. This is in alignment with Lüning and tom Dieck (1989), who suggested that primary ecological factors and environmental signals may be involved in directing seasonal growth rates and triggering reproductive processes.

Complicating matters further is the possibility that the biological processes of the organisms present at the sites may also be contributing to chemical variations in the seawater, in the form of waste products and metabolites (Carlucci et al., 1970; Pfister et al., 2019). In addition, both sites are exposed, being subject to such influences as tides, storms, nutrient upwelling, etc., which
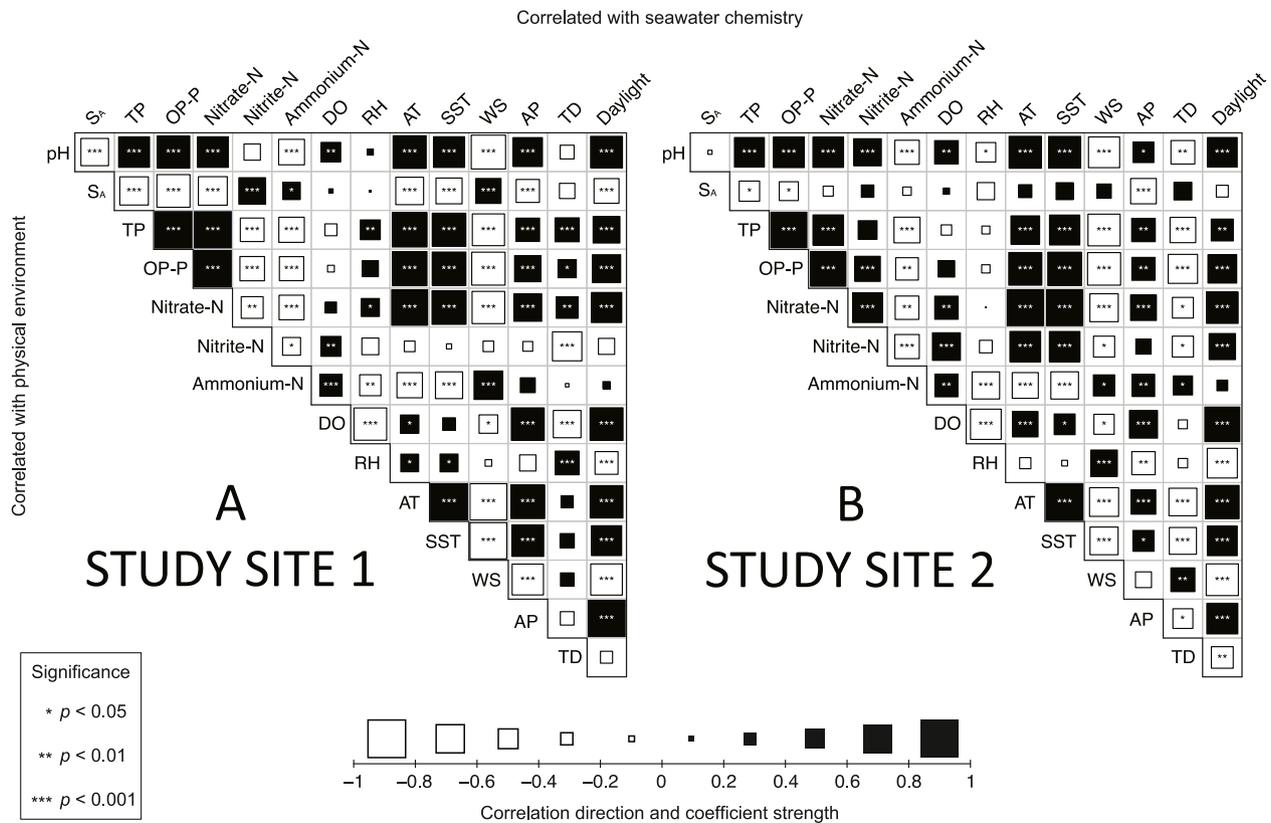
Fig. 7. Correlation matrix for environmental physico-chemical variables (seawater chemistry with physical environment) at study site 1: Stafnes (September 2014–August 2015) (A), and study site 2: Hafnir (September 2016–August 2017) (B). Depicts direction (+/-), strength, and significance of correlation coefficients between seawater chemistry and physical environment data.

may further facilitate fluctuations in seawater chemistry values (Sheppard et al., 2009).

Another fundamental factor affecting both sites is temperature. Historical SST data revealed an 0.5 °C increase in the yearly average SST over a period of 44 years (1969–2013). Despite the relatively small increase over this period, repercussions of ocean warming as a consequence of climate change should not be overlooked. One study, which examined changes in North Atlantic SST between 1982–2010, found an increased rate of 0.5 °C decade^{-1} around Iceland (Taboada and Anadón, 2012). While some macroalgae species will thrive as ocean temperature continues to rise, the net result will likely lead to population migration, loss in biodiversity, and even extinction of key species within marine ecosystems (Ji et al., 2016).

These revelations highlight a high level of complexity, as not only direct correlations between components and variables may exist, but so too indirect (or more subtle) relationships should be considered. Therefore, a hypothesis which proposes more of a modular type biosystem regulation, similar to that suggested by Chang et al. (2022), in the case of phytoplankton, may need to be considered. As such, the presence of key drivers of biochemical modulation (such as temperature and light) alone may be insufficient in ensuring optimal component concentrations. Instead, adequate levels of (multiple) secondary factors (e.g., seawater nutrients) may also need to be present, essentially acting as "effectors", by activating or inhibiting interactions (either directly or indirectly) via feedback loops.

4.2. Species seasonality and component correlations

Chemical composition of both temperate and tropical brown alga is subject to recurrent seasonal fluctuations (Black, 1950;

Thom, 1984; Renaud and Luong-Van, 2006; Polat and Ozogul, 2013; Schiener et al., 2015; Garcia-Vaquero et al., 2021). Here, algal lipids, carbohydrates, proteins, and minerals, concurred with previous temperate brown algae studies, with a deviation of no greater than 10% of biomass (DW $\pm SD$) (Munda, 1972b; Heffernan, 2015; Schiener et al., 2015; Tibbetts et al., 2016; Garcia-Vaquero et al., 2021). Two exceptions were proteins (Munda, 1972a; Tibbetts et al., 2016; Schiener et al., 2015), and lipids (Munda, 1972a; Heffernan, 2015), which were slightly lower and higher, respectively, than documented average. Both species at each site appeared to follow similar seasonal trends (SI, Figs. S1 & S2 A-D). However, site 2 (Hafnir) showed a significantly higher yearly average and a greater seasonal variability of total carbohydrates (*S. latissima*), whereas site 1 (Stafnes) had higher yearly averages of both proteins (*L. digitata*) and lipids (*S. latissima*). These findings may signify a natural variation between different years and/or may be as a result of subtle differences in environmental physico-chemical parameters at each of the locations, highlighting the impact of temporal and spatial variation in kelps. This is supported by Dayton et al. (1992), where a variety of tropical kelp (Southern California) were evaluated on their ability to recover from various disturbances (e.g., seasons, storms, herbivory, competition etc.). It is known that a species' biochemical composition and its intensity of intrinsic factor fluctuations are impacted by habitat structure, including location (D'Este et al., 2017), changes in biodiversity (Boyer et al., 2009), and presence of invasive species as seen in tropical species (Piazzi and Balata, 2009). Additionally, environmental conditions, such as temperature (Manns et al., 2017), salinity (Jie et al., 2016), and seawater nutrient composition and availability (Roleda and Hurd, 2019), are also likely to have an impact. As such, it is possible that populations from different geographical locations may

vary in biochemical composition at a single time point. A good example of this locally is demonstrated by Forbord et al. (2020), where latitude was seen to play a significant role in both biomass yield and protein content, as realised through its presentation of seasonal and spatial variation in biochemical components of wild *S. latissima* and *L. digitata* in SW Iceland.

The findings of this research not only support those seen in earlier studies involving temperate and tropical brown algae by Marinho-Soriano et al. (2006) and Balboa et al. (2016) but are also comparable to the current study's results in terms of protein content in *S. latissima*, when harvested at high latitudes (69°N, Norway), under similar yearly SST fluctuations. Interestingly, at lower latitudes, *S. latissima* has been shown to express different protein trends, peaking during hottest months (Forbord et al., 2020). This presents a good example of adaptation to local conditions known in the genus *Laminaria* (Bartsch et al., 2008), and underlines the need to study the biology of local populations of brown kelps prior to committing to cultivation and harvesting efforts. In addition to SST, seawater nutrients OP-P and TP, were noted as being negatively correlated, whilst ammonium-N was positively correlated to proteins within, and between, both studied species. Similar combined correlations (i.e., negative OP-P and positive ammonium-N), in relation to phycobiliproteins, were reported in the red alga *Gracilaria domingensis* (Pereira et al., 2012). The positive correlation with ammonium-N could be explained by parallel findings seen in some temperate green and red algae, which favour a rapid conversion to amino acids, rather than storing it within cells (Taylor and Rees, 1999). This would indicate a possible direct link between this metabolite and physico-chemical variables. Interestingly, and in agreement with both the combined inter- and intraspecific CMAs, all single species CMAs showed a strong negative correlation between proteins and carbohydrates. This was shared with the general findings in relation to *S. latissima* from the Faroe Islands (Bak et al., 2019), and in temperate kelps off the west coast of Ireland (Garcia-Vaquero et al., 2021). This suggests that this inverse relationship may be seasonally induced (i.e., highest levels of proteins in winter and spring, and lowest in summer and autumn, with carbohydrates following an opposite accumulation trend.

Conversely, carbohydrates were positively correlated to temperature, which was in agreement with a Danish study on *L. digitata* and *S. latissima* (Manns et al., 2017), but at the same time was also negatively correlated to ammonium-N. This concurs with the general hypothesis that algal polysaccharide content increases in response to a critical decrease in cell nitrogen levels (Atkinson and Smith, 1983). These polysaccharides are thought to be then stored for later use as an emergency energy source during times of low daylight and nutrient availability (Lüning and Pang, 2003). Another (or possibly concurrent) explanation for this interaction may simply be due to the fact that ammonium-N and protein are positively correlated, whereas proteins and carbohydrates are negatively correlated. Therefore, logically, carbohydrates and ammonium-N would also be negatively correlated. Another interesting finding was that in both species the location had an impact on whether carbohydrates correlated with nitrite-N or nitrate-N, moreover, these correlations were reversed between *L. digitata* and *S. latissima*. Nitrogen is available as a seawater nutrient in several inorganic and organic forms (i.e., nitrate, nitrite, ammonium, and urea), each of which undergo dynamic chemical conversion from one form to another at varying rates and concentrations, depending on seasonal and environmental conditions (Roleda and Hurd, 2019). For example, in the case of nitrate-N, research suggests that some macroalgae species appear to favour certain forms of nutrients depending on the season. This is thought to be due to energy intensive assimilation of some nutrients (e.g., nitrate), and so these are reserved for when environmental conditions make these options more viable, such as

during periods of higher temperatures and light intensity during the summer months as seen using the example of temperate brown algae (Phillips and Hurd, 2003).

As in the case of proteins, lipids were also negatively correlated with both AT and SST, but only in *S. latissima*. These results, at least in regard to *S. latissima*, agreed with findings of former studies, which show both temperate and polar kelps to be highly sensitive to extremes in temperature (Li et al., 2020; Machado et al., 2019). As a result, even a small increase in temperature (2 °C) within a short period of time, is likely to evoke a reaction which manifests as an opposing reduction in lipid content in tropical brown algae (Wernberg et al., 2016a,b), possibly as a survival response. Further studies suggest that simultaneous changes in both light and temperature may be more pertinent to biochemical variability, rather than temperature alone (Schmid et al., 2021). However, this does not explain why similar lipid/temperature correlations were not found within the studied *L. digitata* populations of the current study.

Similar studies, conducted in other countries, have also found much variation between samples. One study in particular, compared the elemental compositions, fatty acid profiles, and lipidomes of *S. latissima* samples from France, Norway, and the UK. Results showed a distinctive variability between the samples, reinforcing the importance of the relationships between site-specific environmental conditions and algal biochemical composition. In addition, it also discovered that the lipidome profiles were so unique, that potentially they could be used as a "phytochemical fingerprint," to trace samples back to their original geographical locations (Monteiro et al., 2020).

Of particular interest was that more similarities of correlations between algal biochemical components, and environmental physico-chemical variables were noted interspecifically from the same site, than intraspecifically at different sites. This was surprising as one might expect intraspecific specimens to respond/behave more alike on account of genetic familiarity. Nevertheless, these findings are good examples of the exceptional adaptability intertidal organisms display to relatively harsh environmental conditions such as irradiation, as seen in tropical brown algae (Delgado et al., 1995), and salinity (Kirst, 1990), as well as emersion and desiccation, as noted in temperate and tropical brown algae (Schonbeck and Norton, 1979; Oates, 1985).

4.3. Species response to environmental physico-chemical parameters

The importance of temperature in biological systems is axiomatic, owing to its essential role in regulation of chemical reactions, enzyme activity, and nutrient assimilation (Roleda and Hurd, 2019). It is possible that in addition to the seasonal effect of temperature, other driving factors may be involved, such as the relationship each of the algae biochemicals have with nitrogen-based nutrients. These cyclical rhythms are likely linked to the macroalgae's life cycle, maturity, and size, as well as to mechanisms that ensure their survival under changing environmental conditions throughout the seasons, as seen in polar, temperate, and tropical kelps (Lüning, 1988, 1991, 1994; Lüning and tom Dieck, 1989; Makarov et al., 1999; Chow, 2012). Kain (1989) applies the concept of "season responders and anticipators" to subtidal algae species. However, *L. digitata* and *S. latissima* possess characteristics of both categories. For example, both species appear to be highly responsive in growth and reproduction in relation to favourable environmental conditions (such as optimal light irradiation), which is typical of season responders. They also appear to be strategic in the production and storage of specific polysaccharides (in particular laminarin), to ensure over-winter survival (a trait more typical of a season anticipator). This would suggest that either the categorisation is too simplistic, or that the

environmental triggers and biological mechanisms behind these responses may be much more complex.

TP and nitrate-N showed positive correlations with carbohydrates, and yet differing levels of these components were seen between sites (Figs. 3 & 4C). One explanation could be that site 1 nutrient levels, which on average were higher than site 2, may have surpassed a certain threshold, above which an inhibitory effect (either directly or indirectly) may have occurred in relation to kelp carbohydrate levels via negative feedback regulation (van der Molen et al., 2018). Furthermore, it is possible that other physico-chemical factors may either be absent, or present in insufficient levels within site 1, resulting in suboptimal carbohydrate biosynthesis. This suggests that even though the potential availability of nutrients may be high in the surrounding seawater, this may not necessarily translate to simultaneous accessibility within the macroalgae. In addition, improved clarity of physico-chemical and algae biochemical component relationships attained through application of time lag highlight delay reactions between external stimulus and internal responses, as commonly noted in biological systems as part of the adaptation process (Tu and Rappel, 2018). For example, evidence of acclimation in polar and temperate kelps have been reported in relation to changes in water temperature (Davison, 1991; Wiencke et al., 1993; Machalek et al., 1996; Eggert, 2012), nutrient concentrations (Stengel and Dring, 1998), and daylight (Gómez et al., 1995; Gómez and Wiencke, 1997).

Another important point is that of origin. Much of what has already been discussed has focused on possible adaptation of the studied species to their current locations. A study by Bolton (2010), strongly suggests that the Laminariales first originated from the cold-temperate regions of the Northwest Pacific. Although likely to have favoured cooler waters, these early kelps may also have been able to tolerate higher temperatures for brief periods. Subsequent evolution of these ancestral kelps possibly diversified into the 4 families of Alariaceae, Costariceae, Laminariaceae, and Lessoniaceae during the Miocene. Some species then migrated to the N-Atlantic, before eventually settling in either the Northern (Alariaceae, Costariceae, Laminariaceae) or Southern hemisphere (mostly Lessoniaceae). Although much still needs to be confirmed regarding the exact origins and dispersion of these organisms, it is clear that a better understanding of macroalgae can be gained through learning their historical evolution.

4.4. Future research

Results of this study revealed a wealth of potential future research in areas of which the current research has only been able to touch upon. It is, therefore, highly recommended that any further work goes beyond the generalised categories of biochemicals (such as total carbohydrates, proteins, and lipids). By focusing on relationships between environmental physico-chemical variables and specific biomolecules of commercial interest (e.g., primary metabolites such as polysaccharides, peptides, and triglycerides, and secondary metabolites such as pigments, polyphenols, osmolytes, etc.), high value compounds could be produced in consistently higher yields.

It would also be advantageous to conduct transplantation experiments, where live specimens of *L. digitata* and *S. latissima* would be translocated from one study site to another, or even to a new site or another country altogether. The relocated specimens would then be closely monitored for changes in biochemical components, which may indicate phenotypic adaptation to their new habitat. In addition, controlled laboratory experimentation, employing land-based (tank) cultivation, would be essential to both confirm identified component/physico-chemical interactions, as well as help define limitations of physico-chemical manipulation on peak production of target algal biomolecules.

5. Conclusion

As interest in the N-Atlantic for algae cultivation increases, coupled with demand for specific high value algal biochemicals, this paper, therefore, proposes an alternative approach to traditional cultivation methods be considered. This includes addressing essential needs of algae species through a greater understanding of their interactions with their environment. Initial assessment of potential wild or aquaculture sites would help determine the most suitable species to target or cultivate, in relation to corresponding physico-chemical conditions, along with indicating their optimal harvesting schedule/s. Alternatively, land-based tank cultivation of macroalgae species could be bespoke by artificially adjusting the physico-chemical environment to trigger and ensure optimal levels of algal components. This type of cultivation is well known to be costly (i.e., in terms of space, water, and energy), at least initially. Therefore, it would be essential to focus on the production of high-value components, in sufficient yields and purity, for such systems to be economically viable. One advantage of developing such a method in Iceland, is that it benefits from relatively low-cost energy, derived from a sustainable source (geothermal power), which could be used in both the cultivation and processing stages of manufacture (Thorarinsdottir et al., 2017).

According to the results of this study, temperature (specifically SST) was strongly correlated to both carbohydrates (positively) and proteins (negatively), in both *L. digitata* and *S. latissima*. As such, it was regarded as a possible key driver in macroalgae primary metabolite production. Additionally, both TP, and nitrate-N may play a role of modulating nutrients (in particular in the production of carbohydrates), but only within a certain range, above which, an inhibitory action may be seen. Surprisingly, it appeared that the influence of a site specific physico-chemical environment may have a greater effect on algae component variability than does genetic predisposition, with different species responding more alike in terms of their interactions with their environment within the same site, than the same species at both sites.

In order to fully appreciate the relationship between these algae and their surrounding environment, it is essential that further research be conducted, to both confirm, and add to the findings of this paper. Furthermore, a model which includes a more complex interplay of exogenous and endogenous physico-chemical factors (including variables outside of those studied in this investigation), displaying both direct and indirect actions, may be required for the conclusions of this research to be applied practically.

CRediT authorship contribution statement

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary information

Supplementary Information (SI) related to this article can be found online at https://doi.org/10.1016/j.rsma.2023.102839.

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