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Seasonal effect on the biochemical composition of Atlantic seaweeds cultivated in integrated multitrophic aquaculture

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ABSTRACT

Seaweeds are recognized as sustainable food sources rich in nutrients and bioactive compounds, but their composition is highly influenced by seasonality. This study evaluated the biochemical profiles of *Ulva* sp., *Fucus vesiculosus*, *Porphyra dioica*, and *Palmaria palmata* cultivated in integrated multitrophic aquaculture across different seasons. Results showed marked seasonal and species-specific fluctuations. *Porphyra* exhibited the highest protein content, except in spring. *Ulva* was richer in lipids and magnesium across all seasons. *Palmaria* displayed lowest sodium-to-potassium ratios (<1), considered beneficial in reducing the risk of cardiovascular diseases. The distinct seasonal shifts in carbohydrate composition suggest each species adapts its polysaccharide metabolism. All species contained relevant essential amino acids and essential fatty acids contents. Red seaweeds showed high content of omega-3 eicosapentaenoic acid and phycobiliproteins, highlighting their functional potential. These findings demonstrate that seasonal variability shapes the nutritional and bioactive composition of seaweeds, offering opportunities to optimize biomass production for targeted applications.

1. Introduction

Promoting healthy and sustainable diets with minimal ecological footprints has become a priority in the transition towards more sustainable food systems, particularly in the face of a rapidly growing global population and rising food demand. In this context, marine macroalgae (commonly known as seaweeds) are attracting increasing interest beyond Asian countries as natural and sustainable sources of essential nutrients and bioactive compounds with associated health benefits. This has led to their growing consumption as sea-vegetables and their incorporation into the food industry as functional ingredients (Holdt and Kraan, 2011; Mendes et al., 2022; World Bank, 2023). Seaweeds are plant-based low-calorie sources of protein, dietary fibres, minerals (iodine, potassium), and vitamins, exhibiting balanced essential amino acids (EAA) and polyunsaturated fatty acids (PUFA) profiles. Their applications in the food sector range from improving

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rheological and nutritional properties of food matrices to providing bioactivities or serving as natural colorants (Garcia-Perez et al., 2023). Seaweeds occur naturally in marine environments and have traditionally been harvested from wild stocks. However, they can also be cultivated through aquaculture systems, offering important advantages in terms of sustainability, biomass availability and quality control. In particular, integrated multitrophic aquaculture integrated multitrophic aquaculture (IMTA) that promotes the cultivation of aquatic organisms from different trophic levels (*e.g.* finfish and seaweed) (Chopin et al., 2001; Rusco et al., 2024), allowing the absorption of excess nutrients by algae contributing to the reduction of potential environmental impacts, such as eutrophication while allowing increased algal biomass yields. Food safety and quality of IMTA produced seaweed has been validated (Mac Monagail and Morrison, 2019), as exemplified by the company ALGAplus (Ria de Aveiro, Portugal). Despite the nutritional advantages offered by seaweed, their production and consumption in Europe remain low when compared to countries such as South Korea, China and Japan (Mendes et al., 2022). This gap reflects not only differences in dietary traditions but also a limited characterization of Atlantic seaweeds, highlighting the need for robust data on the nutritional profiles and seasonal variability of Atlantic seaweeds to support targeted production and increase consumption in Europe.

Seasonal variations within biomass composition are reported for wild (Sampath-Wiley et al., 2008; Schmid et al., 2014; Villares et al., 2013), and farmed seaweed (Benjamin et al., 2025; Da Costa et al., 2019; Forbord et al., 2020; Laramore et al., 2022; Marinho et al., 2015; Moreira et al., 2020; Roleda et al., 2019). The different seasons of the year translate into changes in environmental factors, such as temperature, light, salinity and nutrient concentration (Lüning and tom Dieck, 1989; Mudlaff et al., 2025), which can also vary geographically (Forbord et al., 2020). These fluctuations are known to trigger physiological mechanisms that influence the biosynthesis, structure, and functionality of compounds (Dewan et al., 2025; Harnedy and FitzGerald, 2011). Although it is possible to minimize the seasonal effects with controlled cultivation conditions in aquaculture systems, there are inevitable shifts in the environment that may impact the composition of biomass produced outdoor (Barbier et al., 2019; Sclodnick et al., 2024). These shifts have also been observed in land-based IMTA cultivation systems, as reported in *Ulva lacinulata* and *Gracilaria vermiculophylla* (Barceló-Villalobos et al., 2017; Sousa et al., 2025).

Among edible seaweeds, *Ulva* spp. (sea lettuce) is a valuable marine crop, commercially produced worldwide due to its wide range of applications across the food value chain, including human food, feed, biostimulants and food packaging (Hofmann et al., 2024). Several studies have reported pronounced seasonal variations in the biochemical composition of both wild and farmed *Ulva* spp., affecting key nutritional components such as proteins, carbohydrates and lipids in either wild and farmed seaweeds (Benjamin et al., 2025; Jansen et al., 2022; Moreira et al., 2020; Qarri and Israel, 2020). These seasonal patterns are highly dependent on geographic location, environmental conditions and cultivation systems, highlighting the need for species- and context-specific characterisation. *Fucus* spp. (wracks) is another edible seaweed, recognised for its high nutritional value seaweeds, particularly for their dietary fibre and mineral content (Catarino et al., 2018) They have been historically used as food, primarily in East Asian countries, but also in some coastal regions of Western Europe and Alaska, in the Azores islands (Catarino et al., 2018; Patarra et al., 2011). Seasonal variations have been observed mainly in wild collected *Fucus* spp reporting increase in the production of fatty acids (FAs) during spring and summer compared to winter, and higher total polyphenolic content, which translated in higher antioxidant activities, in summer (Almeida et al., 2021; Mendes, 2017; Paiva et al., 2018; Pereira et al., 2021; Schmid et al., 2014; Villares et al., 2013). Regarding farmed *Fucus* sp. was showed higher levels of esterified PUFA in spring compared to winter (Da Costa et al., 2019).

Porphyra spp. (Atlantic-Nori or Laver) and *Palmaria palmata* (Dulse) represent two red edible seaweeds highlighted for their high protein content and rich source of eicosapentaenoic acid (EPA), phycobiliproteins and associated bioactive properties (Čmiková et al., 2024; Katra and Grembecka, 2025). These species have been traditionally consumed by Atlantic coastal communities for centuries (Mendes et al., 2022). Evidence on seasonality is mostly documented for wild populations (Galland-Irmouli et al., 1999; Groenigen et al., 2022; Lafeuille et al., 2023; Sampath-Wiley et al., 2008). For instance, seasonal variations influence wild *P. palmata* revealing higher protein content during winter and spring (Galland-Irmouli et al., 1999). Concomitantly, there is evidence on how seasonal variations affect the composition of farmed *Porphyra* and *P. palmata*. Namely, in farmed *Py. yezoensis* from Korea a decrease in protein and increase in carbohydrate, lipid, and ash contents from winter to spring (Jung et al., 2016), and gradual decrease in amino acids from fall to spring, and a spring peak for dietary fibres (Shin et al., 2013).

Unravelling the impact of seasonal variations on the biochemical composition of edible seaweeds is essential to fully exploit their nutritional potential and to optimize their applications in the food and nutraceutical industries. Studies conducted to date highlight the absence of long-term chemical analysis comprising seasonal variability, particularly in seaweeds grown in outdoor land-based IMTA systems. This study investigates the impact of seasonal variations on the nutritional composition of four edible seaweed, *Ulva* sp., *F. vesiculosus*, *P. dioica*, and *P. palmata*, cultivated in Portugal in a land-based IMTA system. Samples of *Ulva* sp., *F. vesiculosus* and *P. dioica* were collected across all four seasons, whereas *P. palmata* was produced from autumn to spring, as this species cannot tolerate the high temperatures reached at the farm during the summer season in Portugal. A biochemical characterization was performed, including proximate composition analysis and profiling of minerals, carbohydrates, amino acids, fatty acids and pigments, to disclose season-specific biochemical profiles.

2. Materials and methods

2.1. Seaweed biomass

Fresh seaweeds were supplied by ALGAplus S.A. (production site in Ria de Aveiro coastal lagoon, mainland Portugal, 40° 36′ 43″ N, 8° 40′ 43″ W), a land-based IMTA system integrated with seabass and seabream. Seaweed biomass was collected at the end of each production cycle. The biomass is produced in outdoor conditions exposed to natural variations of light and temperature (air and water). Cultivation conditions such as initial stocking density and water renewal rates were similar throughout the year and consistent with the company's internal commercial protocols. Season is operationalized as the harvest month that differs by seaweed species (Table 1), according to their ideal cultivation periods and the company’s cultivation management: *Ulva* sp., *F. vesiculosus* and *P. dioica* were collected in autumn (October 2023), winter (January 2024), spring (May 2024) and summer (July 2024 except for *P. dioica* collected in September 2024). *Palmaria palmata* biomass was collected during its seasonal production cycle in autumn (November 2023), winter (January 2024) and spring (March 2024). The production cycles for all seaweeds across seasons lasted approximately 1–2 weeks, and all experimental batches were cultivated under comparable operational conditions throughout the study period. Throughout production, visual quality controls were performed, and the seawater temperature (°C), salinity (ppt) and photosynthetically available radiation (PAR; μmol.m^{-2} s^{-1}) were monitored using a LI−250A light meter equipped with a LI−193 spherical underwater quantum sensor (Table 1). PAR values correspond to the daily peak average measurements. Lower PAR values were registered during *P. dioica* summer cultivation cycle due to forest fire events. After collection, samples were washed with food-safety compliant seawater (the same used in cultivation, that is further filtered and sterilized - UV and ozone). Afterwards, samples were frozen at −80 °C, freeze-dried and milled into a fine

Table 1
Environmental conditions registered for each season during the cultivation period of the collected biomass, including water temperature (°C), salinity (ppt), irradiance (μmol m^{-2} s^{-1}) and photoperiod (h). Measurements correspond to daily peak average values and were recorded at a fixed point within the seaweed cultivation system and represent means±standard deviation (n = days in cultivation).

Season	Month and year (species cultivated)	Water temperature (°C)	Salinity (ppt)	PAR (μmol.m^{-2} s^{-1})	Photoperiod (h)
Autumn	October 2023 (*Ulva* sp., *F. vesiculosus, P. dioica)*	20.4 ± 1.8	27.1 ± 2.5	931.4 ± 729.1	11.2 ± 0.9
	November 2023 (*P. Palmata*)	15.8 ± 1.5	26.5 ± 2.8	869.7 ± 681.4	10.1 ± 0.5
Winter	January 2024 (all seaweed)	13.4 ± 1.5	24.5 ± 2.3	786.4 ± 501.4	9.5 ± 0.3
Spring	March 2024 (*P. palmata*)	15.0 ± 2.0	23.4 ± 2.4	1555.7 ± 794.6	11.7 ± 0.5
	May 2024 (*Ulva* sp., *F. vesiculosus, P. dioica)*	20.0 ± 1.9	30.3 ± 0.9	2674.9 ± 409.4	13.9 ± 0.4
Summer	July 2024 (*Ulva* sp., *F. vesiculosus)*	23.6 ± 1.6	36.7 ± 0.2	2444.6 ± 431.4	14.8 ± 0.3
	September 2024 (*P. dioica*)	19.7 ± 1.3	36.2 ± 0.6	1210.3 ± 1006.7*	12.7 ± 0.6

* lower irradiance was registered in summer *P. dioica* due to intense forest fires

powder. All results herein were described as dry weight biomass (DW biomass) corresponding to freeze-dried biomass.

2.2. *Determination of ash content*

Ash content was determined through gravimetry by burning 50 mg of the sample dry biomass at 550 ºC for 4 h, in a muffle furnace (NABERTHERM, LE62K17N1). After the combustion of the biomass, the weight difference resulted in the ash content. All analyses were performed in triplicate, and the average values were used for data interpretation.

2.3. *Minerals analysis*

Mineral analysis was performed according to the microwave-assisted acid digestion procedure as previously described by (Moreira et al., 2025), using CEM MARS 6 Microwave Acid Digestion Method Compendium for plant tissue. Each seaweed sample was first precisely weighed at 0.5 g and put into a digestion vessel. After adding 10 mL of strong nitric acid, the liquid was gently stirred and allowed to settle for about 15 min before the vessel was closed. The MARS ONE system was employed in the digesting process. The heating protocol included applying power in the 900–1800 W range without stirring, maintaining a pressure of 800 psi, escalating the temperature to 200 °C over 15 min, and keeping it there for another 15 min. The digested samples were allowed to cool completely to room temperature (RT) and subsequently transferred to 50 mL Falcon tubes, which were adjusted to a final volume of 50 mL with ultrapure water. The mineral composition of each digested sample was determined by ICP-OES system (Optima 7000 DV ICP-OES, PerkinElmer, USA). Nitrogen, air, and argon served as carrier gases. External calibration curves were generated in 5% (v/v) HNO3 using a certified multi-element standard solution (UCP−3-mL; REF: P2-MEB687579, Inorganic Ventures, USA) for zinc (Zn; 213.857 nm), phosphorus (P; 214.914 nm), manganese (Mn; 257.610 nm), iron (Fe; 259.939 nm), magnesium (Mg; 279.077 nm), calcium (Ca; 317.933 nm), copper (Cu; 324.752 nm), selenium (Se; 196.026 nm), sodium (Na; 589.592 nm), and potassium (K; 769.896 nm). Each sample was extracted in triplicate.

2.4. *Carbohydrates and alditols analysis*

Neutral sugars from *Ulva* sp., *F. vesiculosus*, and *P. palmata* were analysed as their alditol acetates by gas chromatography with flame ionization detection (GC-FID), using 2-deoxyglucose (1.0 mg.mL^{-1}) as the internal standard (Ferreira et al., 2020). The seaweed biomasses (1–2 mg) were firstly subjected to a pre-hydrolysis with a 72% solution of H_2SO_4 (w/w) for 3 h at room temperature with occasional stirring. Then, a hydrolysis step was performed with 1 M H_2SO_4 solution for 2.5 h at 100 °C for glycosidic bonds cleavage. The resulted monosaccharides were reduced with a 15% $NaBH_4$ solution (w/v) in 3 M NH_3, for 1 h at 30 °C and acetylated with acetic anhydride for 30 min at 30 °C, using methyl-imidazole as a catalyst. Free alditols of *F. vesiculosus* were also analysed by their conversion into their respective alditol acetates by acetylation, using 2-deoxyglucitol (1.0 mg.mL^{-1}) as internal standard.

The neutral sugars content of *P. dioica* was analysed by reductive hydrolysis followed by acetylation, according to literature (Stevenson and Furneaux, 1991), due to the instability of the 3,6-anhydro-galactose (AnGal) residues in acidic media. Thus, a 3 M solution of trifluoroacetic acid and the reducing agent borane−4-methylmorpholine complex (MMB, 80 mg.mL^{-1}) were used to simultaneously hydrolyse and reduce the neutral sugars, for 1 h at 120 ºC, preventing nGal monosaccharide residues from acidic degradation. The samples were cooled down followed by addition of MMB (80 mg.mL^{-1}) and 2-deoxyglucose (1.0 mg.mL^{-1}) as internal standard. After solvents evaporation at reduced pressure, glacial acetic acid was added followed by acetylation with acetic anhydride for 30 min at 30 °C, using methyl-imidazole as catalyst.

The alditols acetates were analysed using GC-FID (Perkin Elmer Clarus 400) equipped with a DB−225 column (30 m length, 0.25 mm internal diameter, 0.25 μm film thickness). The injector and the detector were set to 220 °C and 240 °C, respectively. The oven temperature program began at 220 °C, held that temperature for 7 min, and then increased to 240 °C at a rate of 10 °C.min^{-1}. The hydrogen carrier gas flow rate was 1.7 mL.min−1. The samples were also injected in a gas chromatograph coupled to a mass spectrometer (Shimadzu GC–MS QP2010) equipped with a ZB−5HT capillary column (30 m length, 0.25 mm internal diameter, and 0.25 μm film thickness) to confirm the identification of the sugar residues. The oven temperature program began at 140 °C, increasing to 180 °C at 5 °C.min^{-1}, held for 1 min, and then increasing to 280 °C at 10 °C.min^{-1}. Helium was used as the carrier gas at a flow rate of 0.86 mL.min^{-1}. Samples were injected in split mode, with the injector temperature set for 250 °C. The GC was connected to an Agilent 5973 mass quadrupole selective detector, operating with an electron impact mode at 70 eV, and scanning the range *m/z* 80–400 in a 1 s cycle in a full scan mode acquisition.

The uronic acids (UA) contents in all seaweeds were determined using the *m*-phenylphenol colorimetric method (Silva et al., 2024). Briefly, after pre-hydrolysis, the samples were hydrolysed in 1 M H_2SO_4 for 1 h at 100 °C. The hydrolysed samples were diluted threefold with distilled water and to a 0.1 mL of each sample, 1 mL of 200 mM boric acid prepared in 98% H_2SO_4 was added. The mixture was shaken and heated at 100 °C for 10 min. After cooling on ice, 20 μL of *m*-phenylphenol was added, the samples were transferred to a microplate and the absorbance was measured at 520 nm (BioTek - Eon Microplate Reader). A calibration curve of D-galacturonic acid (0–100 μg.mL^{-1}, 7 calibration points) was performed and the results were expressed as GalA equivalents.

2.5. Elemental analysis and protein estimation

The CHN composition (Table S1) was determined by elemental analysis (Vario EL III®, Elemental Analyser System; GmbH, Hanau, Germany) according to the procedure provided by the manufacturer. The total protein was determined by multiplying the percentage of nitrogen by the factor 5 (Angell et al., 2016). This nitrogen conversion factor 5 is specific for seaweed protein content determination, however, it is important to note that the standardized methods applied in the food industry often use the universal 6.25 factor. All analyses were performed in triplicate, and the average values were used for data interpretation.

2.6. Amino acids profile

The total amino acid content of the different seaweed biomasses grown across the seasons was determined by acid hydrolysis as previously described (Moreira et al., 2025). Two mL of 6 M HCl (Sigma-Aldrich, Inc., St. Louis, USA) were added to 100 mg of each seaweed sample in SPME vials, followed by vortexing. Oxygen was removed from SPME vials through N_2 stream injection, and the vial was covered. The sealed vials were heated to 115 °C in an oven for 20 h and cooled at room temperature after hydrolysis. Then, 5 mL of ultra-pure water was used to dilute the hydrolysed samples, and 10 M NaOH was used to lower the pH down to 3.5. The resulting solution was filtered (0.22 µm filter) and diluted with Mili-Q water.

The total amino acids were detected and measured using liquid chromatography coupled with a high-resolution fluorescence detector. The chromatographic separation was performed with a Sigma Aldrich's Chromolith® Performance RP18e column (100–4.6 mm) following the elution program: starting 10% eluent B, ramped up to 100% eluent B, and then 10% eluent B returned, and a flow rate starting at 0.9 mL.min^{-1} and increasing to 1.2 mL.min^{-1}. Total elution lasted 55 min. The excitation and emission wavelengths for the fluorescence detection were set at 356 nm and 445 nm, respectively, with a sensitivity factor of 1. Data was collected at a rate of 2 Hz, with the light mode set to "Standard." The temperature of the chromatographic column was maintained at 25 °C throughout the analysis.

For HPLC analysis with fluorescence detection the following solutions were prepared as detailed previously (Moreira et al., 2025): a) internal standard (IS) solution containing homoserine (Sigma-Aldrich, USA) 0.01 g in 0.1 M HCl (200 mg.L^{-1}); b) borate (H_3BO_3) buffer (pH 9.5); c) Reagent A: 3 mL of the IS solution was combined with 100 µL of mercaptoethanol (Fluka Analytical, USA) and 0.5 g of sodium tetraphenylborate (Merck, Germany), diluted to 25 mL with borate buffer, and further diluted tenfold with 0.1 M HCl to 20 mg.L^{-1} working solution.; d) Reagent B: 0.6 g of iodoacetic acid (Sigma-Aldrich, USA) dissolved in 15 mL of borate buffer, further diluted to 20 mL with borate buffer, and adjusted to pH 9.5 with 4 M NaOH; and e) reagent C: 0.175 g of o-Phthalaldehyde (OPA) (Sigma-Aldrich, USA) dissolved in 5 mL of methanol, followed by the addition of 0.5 mL of mercaptoethanol, then diluted to 25 mL of borate buffer and degasified with N_2 stream.

A calibration curve was prepared from a stock solution of 100 mg.L^{-1} amino acids in 0.1 M HCl (1–30 mg L^{-1}).

2.7. Lipid analysis

2.7.1. Lipid extraction

Lipids were extracted from 250 mg of freeze-dried biomass of each seaweed using a modified Bligh & Dyer's method (Bligh and Dyer, 1959; Da Costa et al., 2019). The biomass was mixed with 3 mL of dichloromethane (DCM):methanol (MeOH) (1:2, v/v), vortexed for 2 min and incubated for 30 min at room temperature with occasional vortex. Then, DCM was added making a DCM:MeOH proportion of 1:1 (v/v). Centrifugation followed at 2000 rpm for 10 min and the organic phase was collected. This process was repeated three additional times, and the combined organic phases were dried under a nitrogen (N_2) stream. The dried extract was re-dissolved 2 mL of DCM:MeOH (1:1, v/v) following Mili-Q water addition to a final proportion of (1:1:0.9, v/v/v). The mixture was vortexed for 2 min and then centrifuged at 537 *g* for 10 min. The organic phase was collected, and the aqueous phase was re-extracted with DCM twice. The combined organic phases were then filtered using a paper filter (WhatmanTM) and dried under a N_2 stream. The lipid extracts were transferred to pre-weighed amber vials, weighed, and stored at -20 °C until further analysis. The total lipid content was then determined gravimetrically and expressed as a percentage of freeze-dried (DW biomass).

$$\text{Lipid content (\% of DW biomass)} = \frac{\textit{Weight of lipid extract (mg)}}{\textit{Weight of biomass (mg)}} * 100$$

2.7.2. Fatty acids analysis by gas-chromatography mass spectrometry

Fatty acid analysis of the different seaweeds lipid extracts was performed through alkaline trans-esterification to obtain fatty acid methyl esters (FAMEs). Lipid extracts were combined with an internal standard solution (1.0 µg.mL^{-1} of methyl nonadecanoate in *n*-hexane), followed by the addition of KOH solution (2.0 M in MeOH), and 2 min vortex. Then, a saturated NaCl solution was added, and the mixture was centrifuged at 2000 rpm for 5 min. The upper organic phase was collected and dried under a stream of N_2.

FAMEs were re-dissolved in *n*-hexane (99%) for GC-MS analysis. A volume of 2 µL was injected into a GC-MS equipped with a DB-FFAP column as previously described (Conde et al., 2025). The injector and detector temperatures were set at 220 °C and 230 °C, respectively. The carrier gas was helium at a flow rate of 1.4 mL.min^{-1}. The oven temperature program was as follows: starting at 58 °C (held for 2 min), followed by a linear increase to 160 °C at a rate of 25 °C min^{-1}, then a linear increase of 2 °C min^{-1} to 210 °C, and finally a 20 °C min^{-1} increase until reaching 225 °C (held for 15 min). The GC-MS system was coupled with an Agilent 5973 Network Mass Selective Detector (Agilent Technologies), operating in electron impact mode (70 eV) and scanning m/z range of 50–550 in a 1-second cycle in full-scan mode acquisition. The data acquisition software was GCMS5977B/Enhanced MassHunter.

The acquired data were analysed using the software Agilent MassHunter Qualitative Analysis 10.0. FAMEs were identified by comparing their retention times and mass spectra with those of standards (C6–C24, Supelco 37 Component FAME Mix) and databases (“Lipid Web” and the NIST Library). Raw areas were then used to perform semi-quantification by calculating the amount of each FA considering a response factor equal to 1. Results were expressed as absolute amounts per biomass (mg.g^{-1} DW BIOMASS). Nutritional quality indices, atherogenic index (AI) and thrombogenic (TI) index, were calculated, in accordance with the formulas previously reported (Šimat et al., 2015).

2.8. Pigment analysis

2.8.1. Chlorophylls and carotenoids analysis

The carotenoids (i.e. β-carotene, canthaxanthin, zeaxanthin, fucoxanthin, neoxanthin, violaxanthin, astaxanthin, and lutein) and chlorophylls were extracted from 5 mg freeze-dried biomass using organic solvents, methanol and acetone, according to Couso et al. (2012), Schüler et al. (2020). Solvents were added until complete extraction and cell disruption obtained from glass bead-milling. The quantification of carotenoids was conducted from methanolic extracts using high-performance liquid chromatography (Chromaster System, Hitachi, VWR), along with a diode array detector (5430 DAD, Hitachi, VWR) and a Purospher® STAR RP-18 chromatographic column (Merck, 250 x 2.1 mm, 5 µm). The analysis was performed at a temperature of 27 °C, with a flow rate of 1 mL/min over a duration of 40 minutes, and an injection volume of 50 µL. Compound identification took place at a wavelength of 450 nm, using standards for comparison. The concentrations of the carotenoids were calculated based on their respective calibration curves (Couso et al., 2012; Schüler et al., 2020).

Additionally, the chlorophyll content was determined spectrophotometrically from acetone extracts, with concentrations calculated according to the equations established by Lichtenthaler and Wellburn (1983). All analyses were performed in triplicate, and the average values were used for data interpretation.

2.8.2. Phycobiliproteins analysis

The extraction of phycobiliproteins was carried out from seaweed biomass using distilled water and a solid-liquid extraction (SLE) ratio of 0.03 g biomass *per* mL of solvent. SLE was performed using a mechanical rotor at 80 rpm for 30 min, followed by centrifugation of the biomass for 20 min at 21380 *g*. After centrifugation, the supernatant was collected for subsequent analysis, while the pellet was resuspended in fresh solvent and the extraction repeated. This procedure was repeated until the supernatant no longer exhibited absorbance at the characteristic wavelengths. All extractions were performed in triplicate.

The absorbance spectra of the various extracts were measured using a UV–Vis microplate reader (SpectraMax) over a wavelength range of 230 to 700 nm. The typical absorption wavelengths are 565 nm for phycoerythrin and 615 nm for phycocyanin, and quantification was performed using standards R-phycoerythrin and C-phycocyanin (Sigma-Aldrich). All samples and standards were assayed in duplicate.

2.9. Statistical analysis

The statistical analysis was performed to identify significant differences between seasons for each seaweed. Univariate statistical analyses were performed using GraphPad Prism 8.0.1. software. The Shapiro−Wilk test was performed to verify normality of the dataset. When normality was observed, significant differences between groups were evaluated using One-Way ANOVA with Tukey's post hoc test, considering differences significant at p-value < 0.05. Whenever normality was not verified, the Kruskal-Wallis test, followed by Dunn's post-hoc comparisons was employed.

3. Results and discussion

3.1. Proximal composition

The effects of seasonality on the biochemical composition of *Ulva* sp., *F. vesiculosus, P. dioica* and *P. palmata* were assessed to determine how season-related environmental patterns affect the nutritional quality of these edible seaweeds. The proximal composition was evaluated by determining the content of ash, protein, and lipids, and total carbohydrates (the latter estimated by difference), of different seaweeds cultivated in autumn, winter, spring and summer. The results are summarized in Fig. 1 and Table S2 in the Supplementary materials.

The crude protein content differed between each seaweed species and across seasons. The highest amount of protein content was detected in *P. dioica* (seasonal range: 15.7–30.8%), particularly during winter, followed by *P. palmata* (15.3–20.1%) with higher content in both autumn and winter, *Ulva* sp. (10.5–20.8%), and *F. vesiculosus* (8.2–12.2%) both peaking in winter. The protein content reported here is generally within the values previously reported for the studied species, also cultivated in the same land-based system, except for *P. palmata* harvested in winter (Nova et al., 2023). These findings are consistent with the known nutritional profile of red and brown seaweeds which typically show high and low protein content, respectively (Alloyarova et al., 2024; Čmiková et al., 2024; MacArtain et al., 2007). Consequently, the studied red seaweeds, *P. dioica* and *P. palmata*, with a consumption of 5 dried g/day can be an excellent alternative source of high-quality protein namely for plant-based diets (Jiménez-González et al., 2023), while also offering a sustainable process as seaweed cultivation does not require fresh water or arable land, with advantages over traditional high-protein crops, such as soybean (Bleakley and Hayes, 2017). Regarding seasonal effects, we observed higher amounts of protein in winter for all seaweeds, except for *P. palmata,* which peaked slightly earlier in autumn (November harvest vs. October for other species). Although fish effluents from the land-based IMTA system

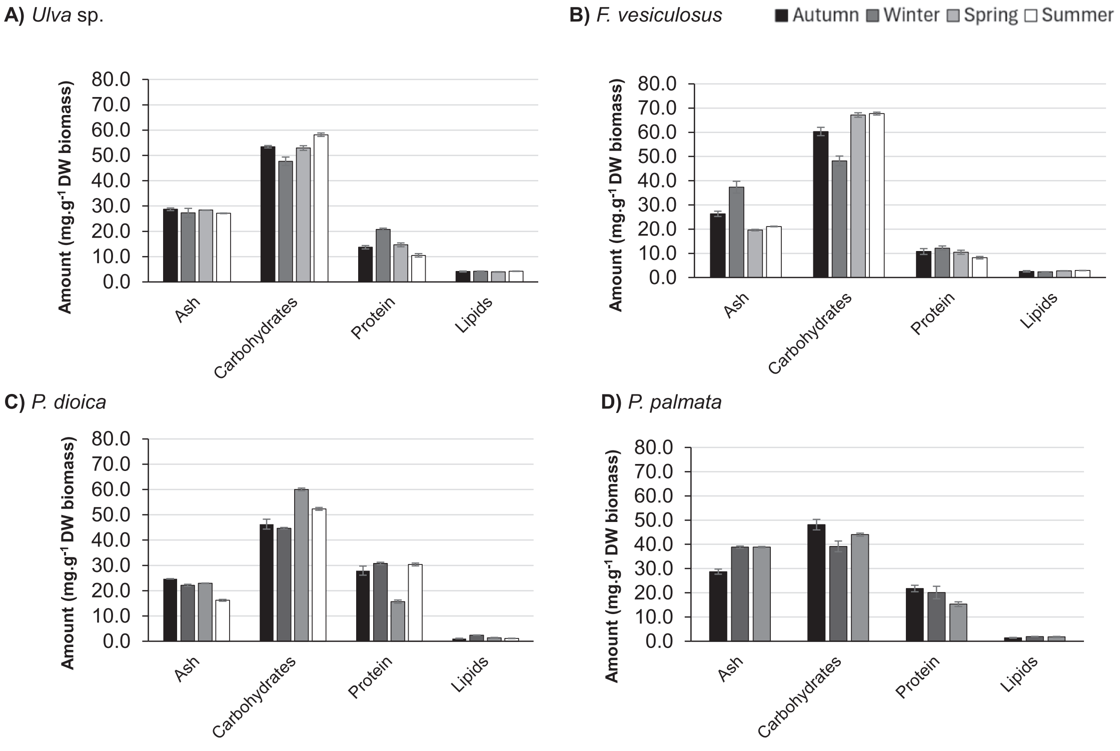

Fig. 1. Proximal composition, including the content of ash, crude protein, carbohydrates (estimated by difference), and lipids, expressed as percentage (%) of freeze-dried (DW) biomass of seaweed cultivated in the different seasons: A) *Ulva* sp., B) *F. vesiculosus*, C) *P. dioica* and D) *P. palmata*. Values are the mean ± standard deviation ($n = 3$). Statistical analysis is presented in Supplementary Table S2.

provided a year-round nutrient input, the water renewal via the *Ria de Aveiro* tides introduces a significant seasonal cycle (Garcia-Perez et al., 117). Seasonality plays a role in the protein content of seaweeds, driven by environmental nutrient availability and growth cycles. During the low light and temperature months of autumn and winter, seaweeds actively accumulate nitrogen and synthesize proteins (Roleda and Hurd, 2019). Conversely, the rapid growth triggered by increased light in spring and summer leads to the depletion of these stored reserves, resulting in a significant decrease in protein concentration. This trend has been observed for *Ulva* sp. cultivated in the same land-based IMTA system (Queirós et al., 2021), and in *U. fenestrata* (Toth et al., 2020), where protein content was higher in biomass grown under low temperatures and light. Knowledge of these variations allows the tailored production of seaweed biomass with higher protein content, in this case, through cultivation and harvesting during winter.

High carbohydrates contents were observed across all seaweeds, which varied between species and were slight influenced by season (Fig. 1). Overall, winter harvested biomass revealed a lower content compared with the other seasons. In *Ulva* sp., carbohydrates peaked in summer and decreased during winter, while showing similar levels in spring and autumn. Similarly, *F. vesiculosus* reached higher carbohydrates content in spring and summer, while the lowest was observed in winter. *Porphyra dioica* had higher contents in spring followed by summer, while *P. palmata* in autumn followed by a decrease in winter. Carbohydrate synthesis is generally promoted by high light intensity, elevated temperatures, and reduced nitrogen availability (Marinho-Soriano et al., 2006). However, periods of rapid growth tend to favour the production of structural polysaccharides, whereas slower growth phases promote the accumulation of storage polysaccharides. Previous studies indicated that seasonal changes can influence the carbohydrates content as observed in *F. vesiculosus* (Rickert et al., 2016), where summer biomass registered higher amounts of carbohydrates compared to spring. These seasonal changes are consistent with environmental factors which include temperature and nitrates availability (Olsson et al., 2020). As previously discussed, the limited light in winter restricts growth, and favours storage of both protein and carbohydrate reserves. Contrarily, the warmer seasons are associated to rapid vegetative growth which may cause a dilution effect, such as the drop in *Ulva* sp. carbohydrates observed during the spring growth peak, but also increase carbon fixation with photosynthesis, explaining the rise of carbohydrates in the remaining species during spring. One study reported greater production of carbohydrates in *U. prolifera* biomass under higher (25 °C) rather than lower temperatures (15 °C) (Li et al., 2019), as opposed to what we reported in the present study. This suggests that species-specific physiology and/or other geographical and environmental factors, such as temperature, may have affected their content.

All seaweeds showed a low lipid content compared to protein and carbohydrates contents, as established for seaweeds (MacArtain et al., 2007). The lipid content of each seaweed is within the amounts previously reported (Da Costa et al., 2018, 2019; Lopes, Melo, et al., 2019; Lopes, Moreira, et al., 2019). *Ulva* sp. achieved the highest amount across the four seasons (4.0–4.2%), while *P. dioica* showed the lowest lipid content (1.1–2.4%). Regarding seasonal effects, the amount of lipids maintained relatively stable across the different seasons, except for *P. dioica* which registered its highest content in spring and lowest in autumn. A previous study has indicated higher lipid content in winter compared to spring in *F. vesiculosus* (Da Costa et al., 2019), although this was not observed in the present study. This may be due to seaweed-specific variations associated with fluctuations in environmental factors, such as light intensity, temperature, and weather conditions (e.g., sunny versus rainy days or heat waves). These variations, often linked to seasonal and climatic changes, can influence the typical lipid content of seaweeds, highlighting the need for routine monitoring and analysis to obtain a more accurate understanding of their biomass quality.

In summary, the results of proximal composition emphasize that fluctuations of environmental factors that are not controlled during production (e.g. irradiance and seawater temperature) across different seasons influence the biochemical composition of seaweeds. The response is specific to species as dictated by underlying nutrient physiology and environmental growth conditions. Beyond proximal composition, understanding how the detailed biochemical parameters, such as minerals, amino acids, monosaccharides, fatty acids and pigments, vary between species and across different seasons is crucial to determine their nutritional benefits for the use of these seaweeds as functional foods, ingredients, and nutraceuticals. The following sections will provide a detailed characterization of the profile of these components.

3.2. Seasonal variations in minerals profiles

The minerals profile of the four different seaweeds was determined, allowing the identification of 13 minerals comprising phosphorus (P), magnesium (Mg), sodium (Na), potassium (K), calcium (Ca), iron (Fe), zinc (Zn), nickel (Ni), cobalt (Co), boron (B), manganese (Mn), copper (Cu) and aluminium (Al) (Fig. 2 and Tables S3-S6 from Supplementary materials). The most abundant minerals observed in each seaweed, including Fe, P, Mg Na and K, are represented in Fig. 2. Elements like Zn, Ni, Co, B were identified in trace amounts ($<0.53\ \mathrm{mg.g^{-1}}$ of DW biomass) in all seaweeds, while Mn and Cu were only detected in a relevant amount ($>1.00\ \mathrm{mg.g^{-1}}$) in *P. palmata* (Supplementary Tables S3-S6).

Dietary minerals play a central role in human health, and adequate intake has been associated with a reduced risk of chronic and degenerative diseases, including cardiovascular and neurodegenerative disorders, cancer, and premature aging (Meng et al., 2019; Sales et al., 2017; Tako, 2019). Seaweeds are particularly rich in essential minerals, which underpins their potential applications as functional foods and nutraceutical ingredients (Circuncisão et al., 2018). However, their mineral composition is highly species-dependent and subject to environmental conditions, such as temperature, salinity, and nutrient availability (Circuncisão et al., 2018). In this study, each of the four investigated seaweed species exhibited distinct mineral profiles that were further modulated by seasonal fluctuations. This variability highlights the potential to strategically harvest seaweed biomass at specific times of the year to obtain optimal mineral compositions, thereby enabling the development of products designed to address targeted nutritional needs.

Na and K were the predominant minerals in all species analyzed, except for *Ulva* sp., which also included higher amounts of Mg. This agrees with previous studies on biomass from the same production system reporting Na and K as the principal minerals in *U. rigida*, *P. dioica*, and *P. palmata*, reflecting similar dynamics across species (Campos et al., 2022; Nova et al., 2023). In *Ulva* sp., Na and K levels peaked in summer, while in *F. vesiculosus* spring biomass was characterized by elevated Na and reduced K compared to other seasons. For *P. dioica*, both Na and K were lowest in winter, whereas *P. palmata* exhibited maximum Na in autumn and particularly high K in winter. An intake of Na below 2 g/day is considered safe and adequate, while the Dietary Reference Value (DRV) of K is set at 3.5 g/day for adults, as reported by the European Food Safety Authority (EFSA) (European Food and Safety Authority, 2025). Given these reference values, moderate consumption of *P. palmata* could be included in a high K plant-rich diet, which is considered beneficial for the general population, and currently also considered for patients with chronic kidney disease, contrary to what has been previously reported (St-Jules and Fouque, 2022). Excessive Na intake is linked to hypertension, a major risk factor for cardiovascular disease, whereas high K intake has protective effects (Morrissey et al., 2020). Consequently, the Na:K molar ratio is considered a key dietary indicator, with values close to 1.0 regarded as beneficial (Circuncisão et al., 2018). In the present study, *Ulva* sp. (1.43–2.29), *F. vesiculosus* (1.52–1.61) and *P. dioica* (1.9–3.09) generally showed ratios < 2, except for *F. vesiculosus* harvested in spring (12.06). The red seaweed *P. palmata* consistently showed ratios < 1, indicating the mineral composition of

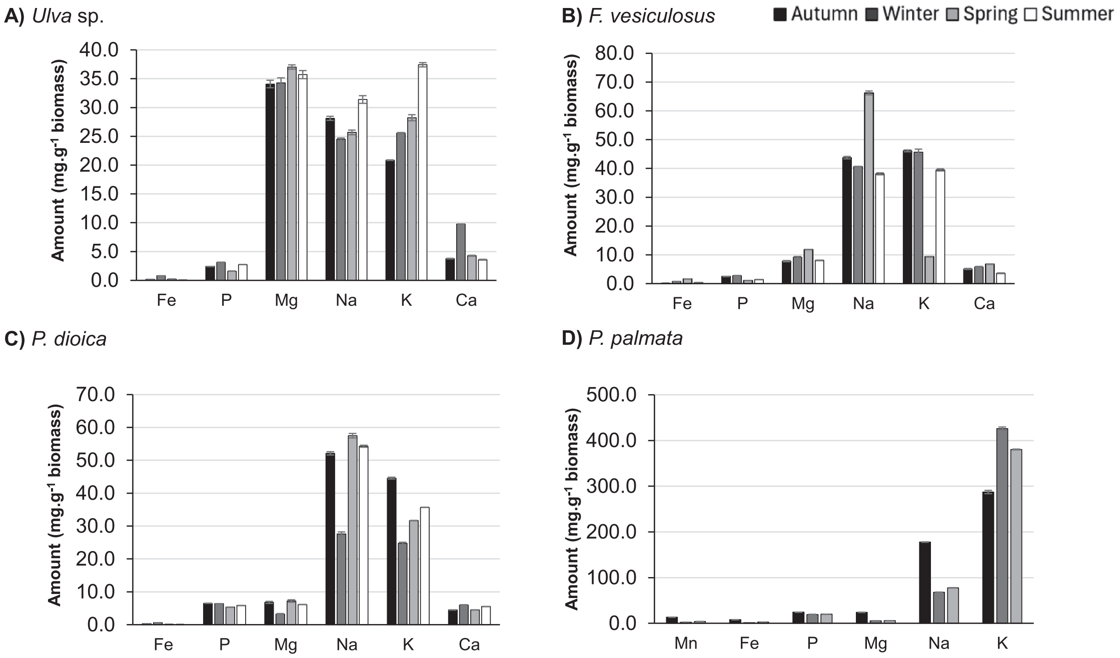

Fig. 2. Composition of the most abundant minerals (mg·g^{-1} DW biomass) seaweed cultivated in the different seasons: A) *Ulva* sp., B) *F. vesiculosus*, C) *P. dioica* and D) *P. palmata*. Values are the mean ± standard deviation (SD) of three replicates (n = 3). Detailed mineral composition and results of statistical analysis are presented in Supplementary Tables S3-S6.

this seaweed as beneficial against cardiovascular diseases. These results were below those reported for those registered for common foods, namely cheese (4.94), preserved and tinned fish (3.64), processed meat (2.77), and pizza, crackers, and other salty snacks (3.31) (Malavolti et al., 2021). Although these comparisons are indicative and depend on serving size and moisture content, this reinforces the nutritional potential of seaweeds as functional foods and ingredients.

Mg was the predominant mineral in *Ulva* sp., revealing a stable composition throughout the year, with values in the same range to those previously reported (26.95–39.92 mg·g^{-1} of DW biomass) (Queirós et al., 2021), while the remaining seaweeds showed consistently lower values of Mg. In *F. vesiculosus*, higher amounts of Mg were observed in spring compared to autumn, while in *P. dioica* spring biomass showed higher Mg content than winter biomass. *Palmaria palmata* showed a different trend with higher Mg content in autumn compared to the remaining seasons. This mineral supports muscle and nerve function as it is essential for the human body as a cofactor of several metabolic reactions (Volpe, 2013). Deficiency in Mg is related to the development of several chronic diseases such as migraine headaches, Alzheimer's disease, stroke, hypertension, cardiovascular disease and type 2 diabetes Mellitus (Volpe, 2013). The stable content of Mg in *Ulva* sp. throughout the year supports the use of this biomass as a functional food.

Beyond Na, K, and Mg, it is noteworthy that other detected elements, such as Fe and Mn (among others), are also essential for the human body (Śliwińska et al., 2018). While these minerals were consistently low across *Ulva* sp., *F. vesiculosus* and *P.* dioica, in *P. palmata* we observed relevant amounts of Fe and Mn in autumn harvested biomass, namely 7.99 and 13.36 mg.g^{-1} DW biomass. Although seaweeds present a relevant mineral profile, further research is still required, particularly concerning mineral bioavailability (Circuncisão et al., 2018). Overall, our findings demonstrate that seaweeds provide species-specific and season-dependent mineral profiles, with Na, K and Mg as dominant elements. Seasonal variability highlights the need to account for harvest time in evaluating their nutritional potential. For example, winter would be an optimal season to harvest K-enriched biomass of *P. palmata*. Importantly, the favourable Na:K ratios, particularly in *P. palmata*, support the use of seaweeds as functional ingredients in food formulations aimed at improving mineral intake and promoting cardiovascular health.

3.3. Seasonal variation in carbohydrates profile and free alditols

The carbohydrates profile was determined for *Ulva* sp., *F. vesiculosus*, *P. dioica*, and *P. palmata* cultivated in different seasons along the year (Fig. 3 and Table S7-S8 from Supplementary materials). Besides the observed seasonal variation of the carbohydrate content, this analysis allowed to predict the fluctuation of the different polysaccharides present in the seaweeds biomass.

The total amount of monosaccharides, quantified after acidic hydrolysis of polysaccharides, ranged between 23.5% and 33.4% (w/w) DW biomass in *Ulva* sp., 25.0–32.4% (w/w) DW biomass in *F. vesiculosus,* 21.7–35.4% (w/w) DW in *P. dioica*, and 33.4–39.8% (w/w) DW biomass in *P. palmata* (Table S7). In *Ulva* sp., total polysaccharides decreased during spring, while remain stable in the other seasons. Contrarily, *F. vesiculosus* and *P. palmata* reached higher carbohydrates content in spring. *P. dioica* had higher contents in spring and winter. Seasonal changes can influence the carbohydrates content in seaweed as observed in *F. vesiculosus* (Rickert et al., 2016), where summer biomass registered higher amounts of carbohydrates compared to spring. One study reported in *U. prolifera* greater production of carbohydrates in biomass under higher (25 °C) rather than lower temperatures (15 °C) (Li et al., 2019). Environmental factors that may contribute to these changes include temperature, light intensity, and nutrient availability (Olsson et al., 2020). Such seasonal variations are influenced not only by the seaweed species, but also by the nature of the polysaccharide, since structural and storage polysaccharides have distinct biological roles in the seaweed growth.

The distinct carbohydrates profiles reflect a very characteristic polysaccharide composition of each species studied, with seasonal variations that are consequently species-specific. Although the following inferences are based on monosaccharide composition and do not confirm polymer identity or sulfation patterns. The most abundant monosaccharides identified in *Ulva* sp. were glucose (Glc) and uronic acids, which decreased in spring compared to the other seasons. Uronic

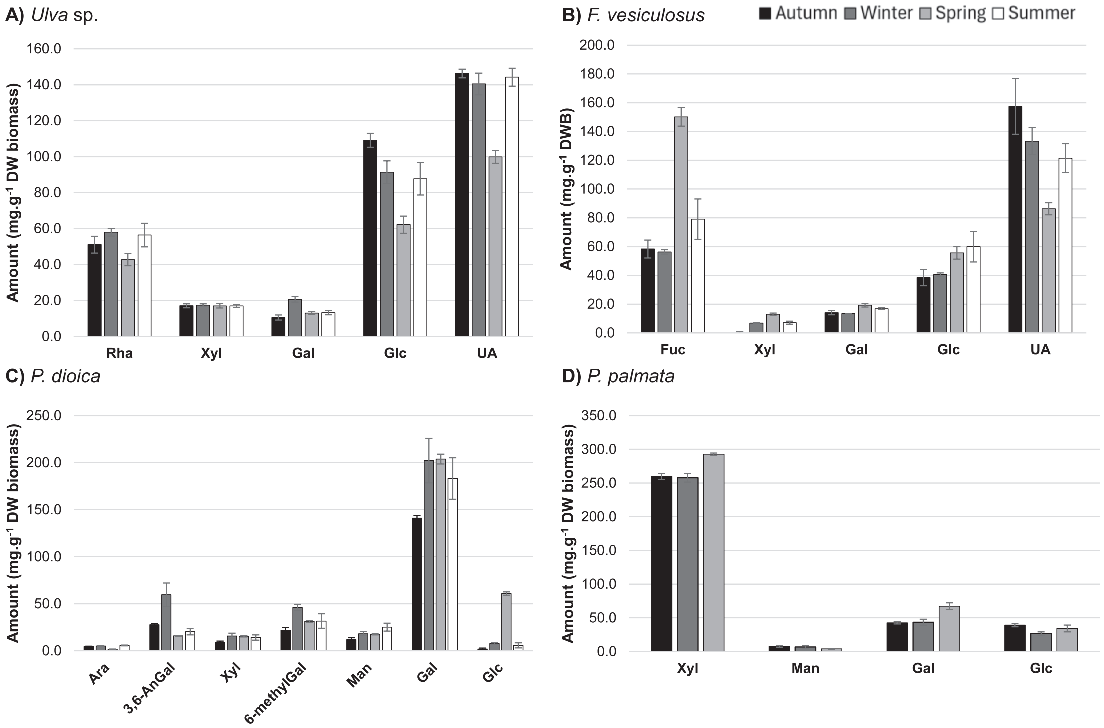

Fig. 3. Carbohydrates composition (mg·g^{-1} DW biomass) of seaweed cultivated in the different seasons: A) *Ulva* sp., B) *F. vesiculosus*, C) *P. dioica* and D) *P. palmata*. Values are the mean ± standard deviation (SD) of three replicates (n = 3). Rha – rhamnose; Fuc – fucose; Ara – arabinose; AnGal – 3,6-anhydrogalactose; Xyl – xylose; 6-methylGal – 6-*O*-methylgalactose; Man – mannose; Gal – galactose; Glc – glucose; UA – uronic acids. Detailed carbohydrates composition and results of statistical analysis are presented in Supplementary Tables S7-S8.

acids, together with rhamnose and xylose residues, are known components of the ulvans, the most predominant cell wall polysaccharides in *Ulva* genus (Aguilar-Briseño et al., 2015). Minor amounts of glucose and galactose are also often reported as part of ulvan polysaccharides, but their occurrence as a component or as a contaminant of ulvan is still unclear (Kidgell et al., 2019). Most of the glucose residues found in *Ulva* sp. are possibly part of cellulose and starch, also characteristic of *Ulva* species (Wahlström et al., 2020). Among the polysaccharides found in *Ulva* sp., ulvans are particularly relevant, as they have been associated with multiple health benefits, such as immunomodulating, anti-hyperlipidemic and anticancer (Kidgell et al., 2019). In this study, the ulvan content was lower only during the spring season, which is in accordance with literature as ulvan content often decreases in spring when rapid growth occurs and increases in summer or autumn when growth slows and storage compounds accumulate (Robic et al., 2009).

Fucus vesiculosus exhibited high levels of fucose (Fuc), which peaked in spring, and uronic acids, which were highest in autumn and winter. The uronic acids are attributed to the presence of alginate, a linear acidic polysaccharide composed of β−1,4-D-mannuronic acid and α−1,4-L-guluronic acid, while fucose is the mainly constituent of fucoidans, a sulphated heterogeneous polysaccharide, that may still contain minor amounts of other sugar residues, namely uronic acids, xylose, galactose, mannose, and glucose (Oliveira et al., 2017). In particular, fucoidans have been related with several bioactivities, such as anti-cancer (Oliveira et al., 2017), anti-inflammatory (Wang et al., 2023), and immunomodulatory (Apostolova et al., 2020). The higher fucose content and lower uronic acids content observed in spring suggest that the production of fucoidans was favoured over alginates in this season. Accordingly, spring is the most favourable season for harvesting fucoidans-rich, when the seaweed growth is active (Konstantin et al., 2023). Despite other potential applications, alginates are mainly used as food additive due to their gelling properties (Abka-khajouei et al., 2022). Glucose residues, which show slightly higher levels in spring and summer in accordance with literature (Konstantin et al., 2023), are likely components of β-laminarans, composed of a linear backbone of β−1,3-D-glucopyranose residues, and cellulose (Circuncisão et al., 2024).

In addition, free mannitol was also detected in *F. vesiculosus,* showing higher amounts during summer (95.1 mg.g^{-1}, Table S8). The accumulation of mannitol during the summer season is attributed to its direct relationship with the photosynthetic activity of the alga. Consequently, higher solar radiation and increased temperatures enhance photosynthesis, leading to greater mannitol accumulation (Konstantin et al., 2023). This sugar alcohol (mannitol) can be used to replace sucrose due to their sweet taste, it is half as sweet and the calorific value is 1.6 kcal/g, and consequently it suitable to produce sugar-free and reduced-calorie products (Hamid et al., 2015). Mannitol is partially digested in the intestines and does not induce hyperglycemia, being particularly important to diabetic-driven foods.

The carbohydrate profile of *P. dioica* revealed high amounts of galactose with lower contents of 3,6-anydroGal, 6-methylGal, Man, Xyl, Glc, and Ara, which is in accordance with the carbohydrates reported for *Porphyra* species (Nova et al., 2023). A notable increase in 3,6-anhydrogalactose (3,6-AnGal) occurred during winter, while Glc increased in spring. The high amount of Gal and 3,6-AnGal is related to the presence of porphyrans, a cell wall polysaccharide related to agarose, composed of a linear backbone of 3-linked β-D-galactose units with alternating 4-linked α-L-galactose−6-sulfate, 3,6-anhydro-α-L-galactose units or 6-*O*-methyl-D-galactose units (Isaka et al., 2015; Priyan Shanura Fernando et al., 2019). Glucose residues may be associated with floridean starch (amylopectin-like glucan), the primary storage carbohydrate found in red algae. This carbohydrate acts as the main carbon and energy reserve, usually accumulate under conditions favourable for photosynthesis (spring and summer) and being metabolized when energy demand increases. Besides their use as gelling and texturizer food additive, porphyrans have been found to have several biological activities, such as antioxidant and anti-inflammatory and prebiotic effects (Isaka et al., 2015; Wang et al., 2023).

The carbohydrates of *P. palmata* were mostly composed by Xyl and Gal whose contents were found higher during spring. The amount of Xyl is related to the presence of xylans typically observed in this red seaweed, namely mix-linked β-(1→3)/β-(1→4)- ᴅ-xylans, as the main cell-wall constituent (Coelho et al., 2025; Deniaud et al., 2003). Xylans have been demonstrated as a fermentable fiber with prebiotic activity, modulating gut microbiota by enhancing short-chain fatty acid production (Allsopp et al., 2020). Galactose residues found in a *P. palmata* are possible constituents of low molecular weight carbohydrates, mainly floridoside (α-ᴅ-galactopyranosyl-(1–2)-glycerol) (Rødde et al., 2004), while glucose residues are part of floridean starch (Stévant et al., 2020). Floridoside has also potential benefits in human health, namely antioxidant (Niu et al., 2020) and anti-inflammatory effects (Kim et al., 2013).

3.4. Seasonal variation in amino acid composition

The amino acid composition (g.100 g^{-1} DW biomass) of *Ulva* sp., *F. vesiculosus*, *P. dioica* and *P. palmata* farmed across different seasons is presented in Table 2 and Table S9-S12 from Supplementary materials. A total of seventeen amino acids were identified comprising seven essential amino acids, namely isoleucine (Ile), leucine (Leu), lysine (Lys), methionine (Met), phenylalanine (Phe), threonine (Thr) and valine (Val), and ten non-essential amino acids (NEAA), including alanine (Ala), arginine (Arg), asparagine (Asn), aspartic acid (Asp), cysteine (Cys), glutamic acid (Glu), glutamine (Gln), glycine (Gly) and serine (Ser) and tyrosine (Tyr). Tryptophan (Try) was not detected in the present work due to the use of acidic hydrolysis, which prevents accurate measurements of this amino acid (Mæhre et al., 2014).

All amino acids reported here have been previously detected in these seaweeds, although variations in the amount of each amino acid were observed (Laramore et al., 2022; Machado et al., 2020; Mæhre et al., 2014). These differences are most probably associated with the specific growth conditions of each seaweed and the production in a land-based IMTA system compared to natural environmental variability of wild seaweeds (Gao et al., 2022; Idowu et al., 2023; Lorenzo et al., 2017). The effect of seasonal harvesting on the amino acid profile of *U. rigida* produced in a land-based IMTA system revealed similar amounts of each amino acid to the results reported herein, although the authors also detected histidine (His) and proline (Pro) which were not detected in this study (Machado et al., 2020).

Appreciable differences were observed among the seaweed species in the concentration of individual amino acids, as well as the total content of essential amino acids and non-essential amino acids (Table 2). The observed seasonal variations in these amino acids suggest that environmental fluctuations across seasons can alter the amino acids profile, in agreement with earlier studies for *Ulva* spp. (Laramore et al., 2022). The amino acid composition is key in assessing the protein quality of foods within the human diet, particularly to ensure an adequate intake of essential amino acids (Machado et al., 2020). These amino acids cannot be synthesized by the human body and must therefore be obtained through dietary sources. Increasing concerns regarding environmental sustainability have led to a gradual shift from diets rich in animal-based proteins toward diets containing alternative and more sustainable protein sources. These diets tend to include plant-based proteins, which often provide lower proportions of essential amino acids of total amino acid composition, namely soy (27%), pea (30%) and corn (32%) (Gorissen et al., 2018). Seaweed proteins contain significant amounts of essential amino acids, accounting for almost 30–40% of their total amino acid composition (Matos et al., 2024). Our results indicated that the essential amino acids proportions differed between the four seaweeds ranging from 47% to 53% in *Ulva* sp., 39–49% in *F. vesiculosus*, 36–45% in *P. dioica* and 37–40% in *P. palmata*. Seasonality also affected the proportion of essential amino acids revealing higher percentages in winter (*Ulva* sp. and *P. palmata*), as well as in spring (*F. vesiculosus*) and summer (*P. dioica*). The proportion of essential amino acids reported in the present study are comparable to those of animal-based proteins, namely whey (43%), milk (39%) and eggs (32%) (Gorissen et al., 2018), thus supporting the use of land-based IMTA cultivated seaweeds as protein alternatives to animal-based diets. As mentioned previously, seasonal harvesting can be tailored to obtain biomasses with higher essential amino acids ratios providing high-quality protein that could support alternative diets, such as vegetarian and vegan diets. For example, *P. dioica* harvested in summer shows a higher EAA proportion compared to other seasons thus highlighting summer as a potential selected season for the harvest of EAA-enriched biomass.

3.5. Seasonal variation in fatty acid profile

The profile of esterified fatty acids (FA) was identified for *Ulva* sp., *F. vesiculosus*, *P. palmata* and *P. dioica* from land-based IMTA production (Fig. 4 and Table S13-S16 from Supplementary materials).

In *Ulva* sp., the most abundant FA throughout each season were consistently FA 18:4 $n-3$, FA 16:0, and FA 16:4 $n-3$ (Fig. 4), which is in agreement with previous studies (Lopes, Moreira, et al., 2019). Regarding the impact of seasonality, higher absolute amounts of all PUFA were observed in summer, autumn and winter biomasses compared to spring. In contrast, the PUFA/SFA ratio was higher in winter biomass supporting previous works that indicated higher abundances in PUFA in *Ulva* species harvested in winter (Moreira et al., 2020). Considering the individual FA of interest, the absolute amount of stearidonic acid (SDA, FA 18:4 $n-3$) was high in autumn, winter and summer biomasses. This PUFA is produced by desaturation of α-linolenic acid (ALA, 18:3 $n-3$), also high in this seaweed, and represents a key intermediate of the biosynthesis of EPA and docosahexaenoic acid (Prasad et al., 2021). As the conversion of ALA to SDA is a slow step in EPA synthesis, some studies have suggested dietary SDA as a promising bypass to obtain higher amounts of EPA, for example, the supplementation of SDA can raise the levels of EPA in red blood cells more efficiently than ALA supplementation (Lemke et al., 2013). In addition, SDA can significantly reduce pro-inflammatory parameters, such as nitric oxide production in macrophages stimulated with pro-inflammatory stimulus, showing anti-inflammatory effects (Sung et al., 2017). The seasonal variations observed in *Ulva* sp. suggest autumn, winter and summer as ideal seasons to harvest functional biomass with anti-inflammatory properties.

Regarding *F. vesiculosus*, the most abundant FA across the four seasons were FA 18:1 $n-9$ and FA 20:4 $n-6$. This profile is in accordance with the FA pattern reported for this seaweed (Da Costa et al., 2019). Seasonal variations indicate a higher amount of PUFA in the summer, followed by autumn, with spring showing a lower level of PUFA. A higher PUFA/SFA ratio was observed in winter compared to other seasons, as determined previously (Da Costa et al., 2019). The highest amounts of oleic acid (FA 18:1 $n-9$) were observed in autumn and summer. This monounsaturated FA is typically present in high abundances in olive oil and can reduce the risk of coronary heart disease by 20–40% through the reduction of LDL-cholesterol levels (Lopez-Huertas, 2010). Other health benefits from oleic acid include improving insulin sensitivity reducing the risk of type 2 diabetes (Palomer et al., 2018). Thus, summer and autumn are the most suitable seasons for harvesting *F. vesiculosus* biomass enriched in oleic acid.

The red seaweeds *P. dioica* and *P. palmata* were characterised by high amounts of FA 20:5$n-3$, as reported previously for these two seaweeds (Da Costa et al., 2018; Lopes et al., 2019). The highest amounts of EPA were observed in the biomasses harvested during winter. The seasonal effects on the FA composition of *P. dioica* and *P. palmata* grown in land-based IMTA was not explored before, although a previous study on wild harvested biomass reported higher amounts in summer compared to autumn (Schmid et al., 2014), which was not observed herein. The highest amounts of EPA were observed in the biomasses harvested during winter. Eicosapentaenoic acid is highly regarded for its health benefits as it is a precursor of anti-inflammatory and pro-resolving

Table 2
Amino acids content (g.100 g^{-1} DW biomass) of *Ulva* sp., *F. vesiculosus*, *P. palmata* and *P. dioica* harvested in four different seasons. This analysis includes both essential (threonine, valine, methionine, phenylalanine, isoleucine, leucine, and lysine) and non-essential (aspartic acid, glutamic acid, cysteine, asparagine, glutamine, glycine, arginine, alanine, and tyrosine) amino acids. Values are three replicates mean ± standard deviation (n = 3). The results of statistical analysis are presented in Supplementary Tables S9-S12.

Amino acids	*Ulva* sp.				*Fucus vesiculosus*				*Palmaria palmata*			*Porphyra dioica*			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Autumn	Winter	Spring	Summer
Ala	0.81 ± 0.02	0.00 ± 0.00	3.81 ± 0.07	1.02 ± 0.02	0.76 ± 0.00	0.89 ± 0.03	0.81 ± 0.03	0.78 ± 0.00	0.99 ± 0.00	0.81 ± 0.00	1.62 ± 0.02	0.20 ± 0.01	2.38 ± 0.09	1.25 ± 0.07	3.12 ± 0.02
Arg	1.39 ± 0.02	1.92 ± 0.02	2.14 ± 0.04	1.75 ± 0.00	0.97 ± 0.48	0.55 ± 0.01	1.39 ± 0.05	1.34 ± 0.00	1.14 ± 0.00	1.14 ± 0.00	1.12 ± 0.02	0.49 ± 0.00	2.23 ± 0.07	5.41 ± 0.53	1.81 ± 0.02
Asn	*n.d*	*n.d*	*n.d*	*n.d*	0.00 ± 0.00	2.16 ± 0.04	0.00 ± 0.00	0.66 ± 0.00	*n.d*	*n.d*	*n.d*	2.89 ± 0.02	2.03 ± 0.07	0.00 ± 0.00	1.54 ± 0.03
Asp	1.36 ± 0.02	2.44 ± 0.03	2.64 ± 0.03	1.71 ± 0.02	1.97 ± 0.00	1.29 ± 0.02	1.36 ± 0.02	1.3 ± 0.01	1.62 ± 0.02	1.34 ± 0.00	2.69 ± 0.02	5.79 ± 0.02	2.58 ± 0.06	0.86 ± 0.10	3.04 ± 0.01
Cys	1.08 ± 0.02	0.00 ± 0.00	0.13 ± 0.00	1.33 ± 0.03	1.00 ± 0.00	0.00 ± 0.00	1.07 ± 0.03	1.03 ± 0.00	0.97 ± 0.00	0.97 ± 0.00	0.97 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.01	2.39 ± 0.03
Glu	1.27 ± 0.02	2.09 ± 0.02	2.32 ± 0.03	1.63 ± 0.02	1.18 ± 0.00	2.41 ± 0.03	1.27 ± 0.03	1.22 ± 0.00	1.53 ± 0.00	1.25 ± 0.00	2.51 ± 0.02	3.57 ± 0.02	2.2 ± 0.08	1.21 ± 0.09	2.84 ± 0.01
Gln	*n.d*	*n.d*	*n.d*	*n.d*	*n.d*	*n.d*	*n.d*	*n.d*	1.91 ± 0.01	1.56 ± 0.00	3.15 ± 0.01	1.97 ± 0.00	0.27 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Gly	1.09 ± 0.01	1.91 ± 0.03	2.21 ± 0.04	1.36 ± 0.01	1.03 ± 0.01	1.84 ± 0.04	1.09 ± 0.02	1.05 ± 0.00	1.31 ± 0.01	1.09 ± 0.01	2.20 ± 0.02	2.49 ± 0.02	1.66 ± 0.06	1.50 ± 0.16	2.22 ± 0.22
Ser	0.27 ± 0.01	2.33 ± 0.03	2.23 ± 0.03	0.22 ± 0.00	0.16 ± 0.00	0.00 ± 0.00	0.27 ± 0.01	0.17 ± 0.00	0.21 ± 0.00	0.17 ± 0.00	0.34 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.39 ± 0.03
Tyr	1.61 ± 0.02	1.23 ± 0.02	1.15 ± 0.02	2.03 ± 0.01	1.51 ± 0.00	0.86 ± 0.02	1.61 ± 0.04	1.55 ± 0.01	1.95 ± 0.00	1.59 ± 0.00	3.22 ± 0.02	0.08 ± 0.00	1.04 ± 0.04	0.70 ± 0.07	3.61 ± 0.02
NEAA	8.86 ± 0.04	11.91 ± 0.05	16.64 ± 0.25	11.03 ± 0.02	8.57 ± 0.46	10.00 ± 0.19	8.87 ± 0.22	8.66 ± 0.61	11.63 ± 0.02	9.92 ± 0.00	17.71 ± 0.18	17.48 ± 0.02	14.39 ± 0.49	11.05 ± 0.97	20.22 ± 1.05
Thr	1.66 ± 0.02	1.44 ± 0.03	1.54 ± 0.04	1.77 ± 0.48	1.55 ± 0.00	0.74 ± 0.02	1.66 ± 0.06	1.60 ± 0.00	*n.d*	*n.d*	*n.d*	0.00 ± 0.00	0.00 ± 0.00	0.9 ± 0.08	3.08 ± 0.53
Val	1.38 ± 0.01	1.59 ± 0.02	1.86 ± 0.03	1.73 ± 0.00	1.30 ± 0.00	1.31 ± 0.04	1.38 ± 0.04	1.32 ± 0.00	1.68 ± 0.01	1.35 ± 0.01	2.73 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	1.04 ± 0.10	3.08 ± 0.02
Met	1.78 ± 0.02	2.28 ± 0.04	0.54 ± 0.02	2.24 ± 0.01	1.67 ± 0.00	0.59 ± 0.02	1.79 ± 0.05	1.72 ± 0.01	1.17 ± 0.02	1.77 ± 0.00	1.52 ± 0.01	3.74 ± 0.02	2.26 ± 0.07	0.34 ± 0.03	3.96 ± 0.04
Phe	0.63 ± 0.01	1.75 ± 0.02	0.64 ± 0.02	0.82 ± 0.01	0.59 ± 0.01	1.02 ± 0.03	0.63 ± 0.03	0.6 ± 0.01	0.78 ± 0.01	0.64 ± 0.01	0.96 ± 0.47	2.03 ± 0.02	1.27 ± 0.05	0.81 ± 0.07	1.44 ± 0.02
Ile	1.29 ± 0.01	1.37 ± 0.02	1.58 ± 0.03	1.24 ± 0.00	1.33 ± 0.00	0.85 ± 0.03	1.28 ± 0.05	1.37 ± 0.01	1.36 ± 0.00	1.28 ± 0.01	2.55 ± 0.02	3.02 ± 0.02	1.21 ± 0.05	0.66 ± 0.08	1.37 ± 0.01
Leu	1.25 ± 0.02	2.39 ± 0.03	1.78 ± 0.04	1.57 ± 0.01	0.84 ± 0.47	1.09 ± 0.03	1.25 ± 0.05	1.20 ± 0.01	1.51 ± 0.00	1.22 ± 0.02	2.52 ± 0.02	0.19 ± 0.01	2.46 ± 0.08	1.74 ± 0.15	2.78 ± 0.01
Lys	0.39 ± 0.01	1.27 ± 0.02	0.83 ± 0.03	0.50 ± 0.01	0.38 ± 0.01	0.81 ± 0.03	0.39 ± 0.02	0.38 ± 0.02	0.46 ± 0.01	0.39 ± 0.01	0.78 ± 0.02	0.87 ± 0.48	1.98 ± 0.07	0.83 ± 0.08	0.87 ± 0.06
EAA	8.38 ± 0.10	12.09 ± 0.11	8.76 ± 0.20	9.87 ± 0.49	7.66 ± 0.44	6.41 ± 0.19	8.38 ± 0.29	8.18 ± 0.03	6.96 ± 0.02	6.66 ± 0.02	11.05 ± 0.46	9.84 ± 0.52	9.18 ± 0.33	6.32 ± 0.58	16.59 ± 0.54

Abbreviations: Ala – alanine; Arg – arginine; Asn – asparagine; Asp – aspartic acid; Cys – cysteine; Glu – glutamic acid; Gln – glutamine; Gly – glycine; Ser – serine; Tyr – tyrosine; Ile – isoleucine; Leu – leucine; Lys – lysine; Met – methionine; Phe – phenylalanine; Thr – threonine; Val – valine; EAA – essential amino acids; NEAA – non-essential amino acids; n.d. – not detected.

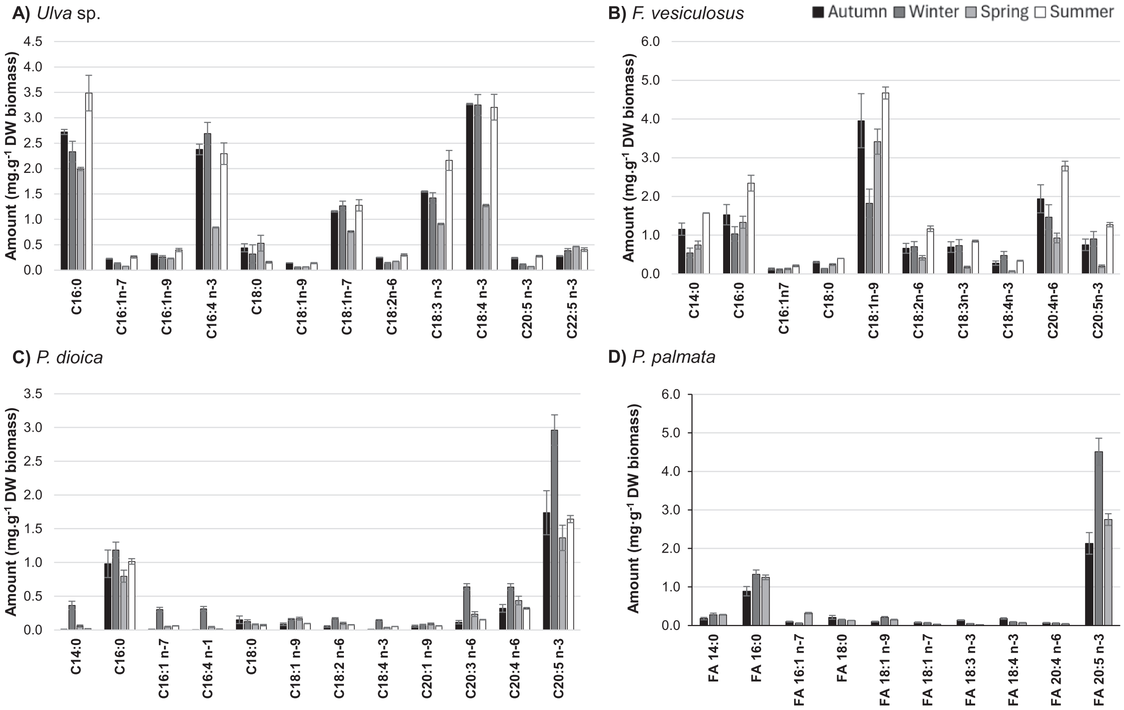

Fig. 4. Profile of the most abundant fatty acids composition (mg·g^{-1} DW biomass) of seaweed cultivated in the different seasons: A) *Ulva* sp., B) *F. vesiculosus*, C) *P. dioica* and D) *P. palmata*. Values are the mean ± standard deviation (SD) of three replicates (n = 3). Detailed fatty acid profile and results of statistical analysis are presented in Supplementary Tables S13-S16.

mediators capable of positively modulating inflammation (Calder, 2006). This omega−3 FA is also important for the neurological development and maintenance of cardiovascular health (Simopoulos, 1991). The current source of EPA in human nutrition is seafood,

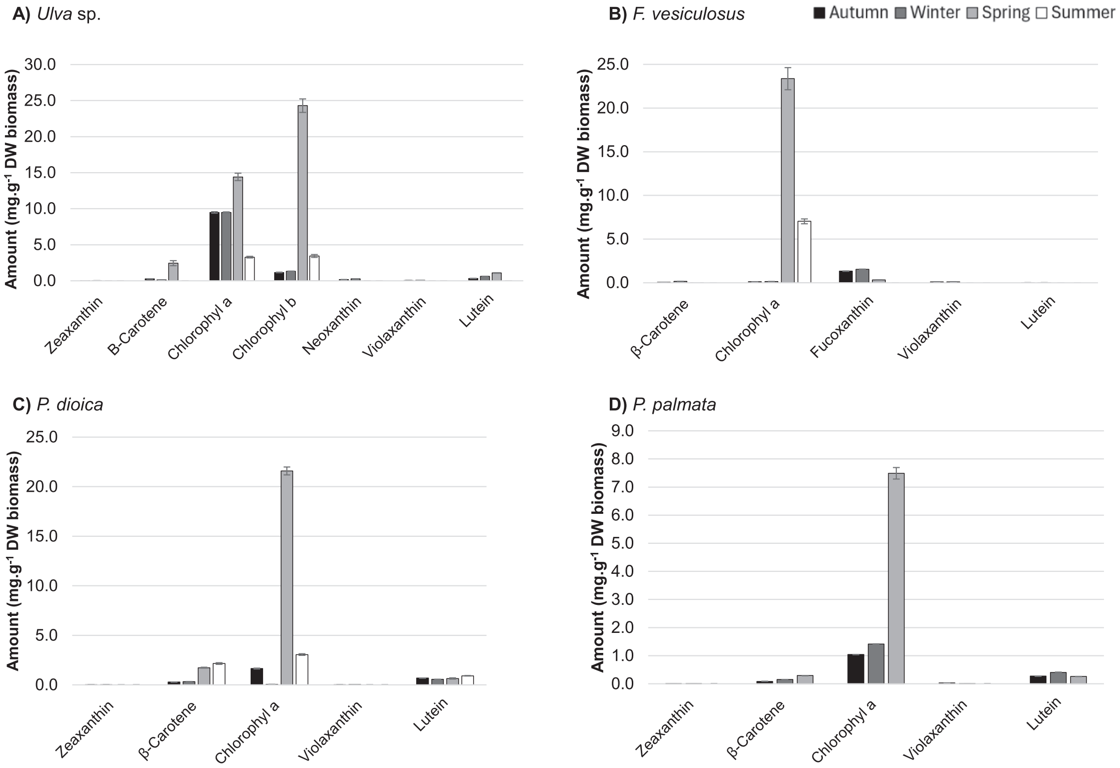

Fig. 5. Profile of the most abundant pigments (mg.g^{-1} DW biomass) identified for *Ulva* sp., *F. vesiculosus*, *P. dioica* and *P. palmata* along the seasons. The values represent the mean ± standard deviation (SD) of three replicates (n = 3). Detailed pigments profile and results of statistical analysis are presented in Supplementary Tables S17.

particularly fish and fish oil, which is not accessible to every consumer due to dietary preferences and geographical location (Wells et al., 2017). EPA-derived from seaweed, namely *P. dioica* and *P. palmata*, offer natural alternatives for this healthy FA that are vegetarian and vegan-friendly and can be obtained through sustainable aquaculture.

The lipid quality indices atherogenic index (AI), thrombogenic index (TI) and hypo/hypercholesterolemic ration (h/H) were determined to evaluate the potential cardiovascular health benefits of the FA from these four seaweeds. These indices reflect the nutritional quality based on fatty acid composition and enable to predict the impact of seaweed lipids in reducing the risk of atherogenic plaques and blood clots formation (Šimat et al., 2015). They have been used previously to assess this potential in fish, microalgae, and seaweed (Conde et al., 2021; Lopes et al., 2020; Rueda et al., 2001). Our results indicate AI and TI values < 1 and relatively high h/H values (Supplementary Table S13-S16), supporting the potential of these seaweeds foods to provide cardiovascular benefits (J. Chen and Liu, 2020), with consistent lower values in *Ulva* sp., *P. dioica* and *P. palmata*. All seasons revealed AI and TI values < 1 supporting year-round production of seaweed biomass with beneficial lipids The values of AI and TI reported in this study are comparable to those reported for seafood and fish (Rueda et al., 2001), as well as other algae (Conde et al., 2021; Lopes et al., 2020).

3.6. Seasonal variation in pigments

The pigment profiles, including chlorophylls and carotenoids, of Ulva sp., F. vesiculosus, P. palmata and P. dioica (Fig. 5 and Table S17 from Supplementary materials), and phycobiliproteins of *P. dioica* and P. palmata (Fig. 6 and Table S18 from Supplementary materials) were evaluated across different seasons. The pigments varied by species and season, linked to the physiological adaptation of each seaweed group to the environmental fluctuations (light and temperature) in the IMTA system.

3.6.1. Chlorophylls and carotenoids

Chlorophyll *a* was the primary photosynthetic pigment detected in all seaweeds with marked seasonality and consistently achieved the highest amount in spring harvested biomass, exceeding the typical chlorophyll range reported for seaweed (up to 5 mg.g^{-1} of DW) (Osório et al., 2020). This is likely attributed to the combined effect of extraction method and nutrient rich IMTA cultivation (Ashkenazi et al., 2022; Figueroa et al., 2010; Garcia-Perez et al., 2022). The spring peak present in all species also reflects a seasonal photoacclimation enhanced by increased light intensity and photoperiod (Henley and Ramus, 1989; Lüning Seaweeds: 1991; Marques et al., 2021). The subsequent decline in chlorophyll observed in summer is driven by photo-oxidative stress and pigment degradation, through excessive light and thermal stress, which may diminish the organoleptic and nutritional quality of the biomass (Raven and Hurd, 2012). Chlorophyll *b* was exclusive to *Ulva* sp. (1.14–24.30 mg.g^{-1} of DW) peaking in spring (Z. Chen et al., 2023). Our findings were in accordance to literature for *Ulva* spp., *Fucus spiralis* and related species (Ashkenazi et al., 2022; Garcia-Perez et al., 2022; Ismail, 2017). Due to their blue-green color, chlorophylls are valuable as natural food colorants (E140 and E141), a trend driven by consumer demand for clean-label products (Solymosi and Mysliwa-Kurdziel, 2017). They also possess a wide diversity of health-promoting effects from antioxidant, anti-inflammatory and anti-cancer properties, supporting their value as functional ingredients (Solymosi and Mysliwa-Kurdziel, 2017) (Manzoor et al., 2024). The substantial amounts of chlorophylls in spring-harvested *Ulva* sp., *F. vesiculosus* and *P. dioica* biomasses highlights this season as an optimal harvesting period to produce chlorophyll-enriched biomass, supporting strategies for tailored cultivation and valorization.

Total carotenoid content was species-specific and seasonally dependent, influencing the biomass potential as a source of high-value antioxidants. The carotenoid content in both *Ulva* sp. (0.80–3.54 mg. g^{-1} DW biomass) and *F. vesiculosus* (0.34–2.46 mg.g^{-1} DW biomass), peaked in spring and winter, respectively. Both species showed near absence in summer. These trends reflect strategies that transition from light-harvesting efficiency to photoprotection (K. Lüning, 1991; Raven and Hurd, 2012; Schmid et al., 2017) and are reported in seaweed (Guihéneuf et al., 2018). The near-absence in summer for these species is likely due to photo-oxidative degradation driven by excessive light and thermal stress. In contrast, *P. dioica* (1.50–3.06 mg.g^{-1} DW biomass), showed its highest carotenoid accumulation in summer. This peak is characterized by high levels of β-carotene and lutein, indicating their crucial role in photoprotection to cope with the increased solar stress and high temperatures (Huang et al., 2024). *P. palmata* exhibited relatively stable, lower carotenoid levels across seasons (0.49–0.68 mg g^{-1} DW biomass), in comparison to the remaining species. These concentrations align with values reported for wild harvested *P. palmata* (0.10–0.80 mg.g^{-1} DW) (Dobychina et al., 2020; Morgan et al., 1980).

Carotenoids are high-value compounds in rising demand as nutraceuticals, food additives, and natural food colorants (Eismann et al., 2020). They possess antioxidant properties that have been regarded as beneficial to reduce the risk of chronic inflammation, heart disease

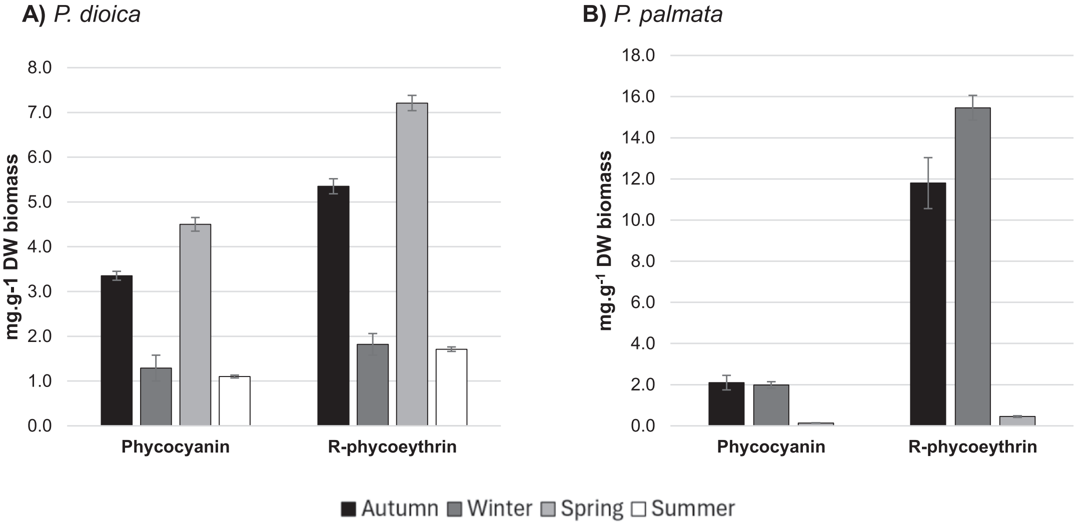

Fig. 6. Content of phycobiliproteins (mg·g^{-1} DW biomass) present in *P. dioica* and *P. palmata* cultivated in the different seasons. Values are the mean ± standard deviation (n = 3).

cancer, and Alzheimer's disease (Guedes et al., 2011). Lutein, for instance, represented as the most abundant carotenoid in *Ulva* sp. (0.00–1.08 mg.g^{-1} DW biomass) and *P. palmata* (0.26–0.40 mg.g^{-1} DW biomass), is associated with improvement in vision and cognitive function, as well as fertility (Eggersdorfer and Wyss, 2018). Similarly, β-carotene, which was the most abundant carotenoid observed in *P. dioica* (0.28–2.15 mg.g^{-1} DW biomass)*,* has shown similar benefits, while also providing anti-inflammatory properties (Kaulmann and Bohn, 2014). The most abundant carotenoid observed in *F. vesiculosus* was fucoxanthin, valued for its anti-obesity and anti-cancer properties (Krinsky and Johnson, 2005). Most carotenoids are obtained from chemical synthesis due to advantages from production costs, although they are less effective as health-promoting compounds (Eggersdorfer and Wyss, 2018). This drives the high demand for carotenoids from natural sources and vegetable origins, positioning seaweed as an additional alternative and sustainable source.

3.6.2. *Phycobiliproteins*

Red seaweeds are characterized by the presence of high-value phycobiliproteins, such as *R*-phycocyanin and *R*-phycoerythrin, which are used as natural colorants and functional ingredients with antioxidant properties (Echave et al., 2022; Gantt, 1975). We determined the content of these phycobiliproteins in *P. dioica* and *P. palmata* grown across different seasons (Fig. 6 and Table S18 from Supplementary materials).

R-phycoerythrin was abundant in both seaweeds with species-specific seasonal patterns. We observed that *P. palmata* exhibited values ranging from 0.45 to 15.46 mg.g^{-1} DW biomass, with the highest concentrations in autumn and winter, consistent with previous reports (Guihéneuf et al., 2018; Martínez and Rico, 2002). This low-light adaptation during winter (Dring, 1981; Gantt and Cunningham, 2001) translates to a winter-harvest advantage from a food processing perspective, where the biomass provides a more concentrated pigment yield, reducing the volume of raw material needed for extraction. In contrast, the amount of R-phycoerythrin in *P. dioica* (1.71–7.21 mg.g^{-1} DW biomass) was highest in both autumn (October harvest) and spring, this is tied to the initiation of its rapid vegetative growth, maximizing energy capture during active biomass accumulation (Roleda and Hurd, 2019). The subsequent decline in summer biomass reflects degradation of pigments as previously explained. Our findings are consistent with reported seasonal patterns in Atlantic *Porphyra* spp. (Guihéneuf et al., 2018; Korbee et al., 2005). *R*-phycoerythrin is of particular interest as a natural red food colorant, while also displaying bioactive properties such as antioxidant, antitumoral, and antidiabetic activities (Thiviya et al., 2022). The seasonal enrichment of *R*-phycoerythrin in winter-harvested *P. palmata* and spring-harvested *P. dioica* highlights opportunities for tailored biomass cultivation and harvesting strategies to maximize pigment yields. *R*-Phycocyanin content also showed clear seasonal and species-specific variations, reflecting its role as an auxiliary light-harvesting pigment. In *P. palmata*, phycocyanin ranged between 0.14–2.10 mg.g^{-1} DW biomass, peaking in autumn, and ranging between 1.10–4.50 mg.g^{-1} DW biomass in *P. dioica*, achieving the highest levels in spring. This blue phycobiliprotein represents another high-value compound, combining applications as a natural food colorant with reported health-promoting effects, including anti-obesity, and anti-neurodegenerative activities which are valued in the nutraceutical market (Thiviya et al., 2022).

The distinct seasonal dynamics of phycobiliproteins in these two species further underscore the importance of strategic harvesting windows to maximize the yields of these specific functional compounds, thereby enhancing the nutraceutical and biotechnological potential of these red seaweeds. Moreover, the degradation of these pigments during the summer months not only reduces the nutritional value of the biomass but may cause discoloration of the blades, which may make summer-harvested biomass be less desirable for premium whole-food applications such as Atlantic-Nori and Dulse flakes.

4. Conclusion

This study contributed to the long-term knowledge of species-specific seasonal variations in the biochemical composition of land-based IMTA farmed seaweeds, with implications for nutrition and functional food applications. All studied seaweeds were characterized by notable levels of carbohydrates and proteins, with *P. dioica* exhibiting the highest overall protein levels during winter and high in late-summer seasons. The studied species generally showed low Na-to-K ratios, except for *F. vesiculosus* harvested in spring, which could offer potential protective effects cardiovascular diseases. *Ulva* sp. also presented high levels of Mg during spring, an essential cofactor for several metabolic reactions. Each seaweed was characterized by a specific monosaccharide profile associated to the presence of bioactive polysaccharides, namely ulvans in *Ulva* sp. across summer, autumn and winter, and fucoidans in *F. vesiculosus* in spring harvested biomass, that have been associated in the literature with anti-cancer and immunomodulatory properties. Essential amino acids were present in proportions compared to animal-based proteins (>35%), suggesting their potential as alternative sources of proteins. Fatty acid analysis of the different seaweeds indicated the presence of lipids with health benefits, namely SDA in *Ulva* sp., which maintain stable high levels in summer, autumn and winter biomasses, and EPA in *P. dioica* and *P. palmata*, that peaked in winter, both with anti-inflammatory properties. Valuable amounts of carotenoids were identified across the different seaweeds, as well as bioactive phycobiliproteins in *P. dioica* and *P. palmata* highlighting the functional properties of the seaweed biomass harvested in winter. Despite seasonal shifts were observed, these variations cannot be attributed to the influence of a specific environmental factor. The biochemical composition is likely influenced by the combination of several variables (e.g. temperature, light intensity, photoperiod and salinity), which vary between each season. In this sense, IMTA enables a structured and partially controlled production strategy, enhancing biochemical consistency compared to open water cultivation, while remaining subject to some seasonal environmental variability. Year-round production is also species-dependent. For instance, it is not currently achieved for *P. palmata* under outdoor conditions at ALGAplus, as this species does not grow at the higher temperatures that occur during the summer. Further studying is necessary to understand the impact of environmental variations across different months to further consolidate and validate the seasonal shifts in composition observed herein.

The biomasses obtained across different seasons can find different applications according to consumers nutritional requirements. Overall, these findings highlight the importance of tailored production and harvesting of different edible seaweeds for production of biomass with targeted bioactive compounds and to develop premium biomass tailored for niche markets.

CRediT authorship contribution statement

Margarida Martins: Writing – review & editing, Validation, Investigation, Data curation. **Joana Batista:** Writing – review & editing, Investigation, Data curation. **Ventura Sónia P. M.:** Writing – review & editing, Validation, Investigation, Data curation. **Mariana Neves:** Writing – review & editing, Investigation, Data curation. **Manuela E. Pintado:** Writing – review & editing, Validation, Funding acquisition. **Diana Lopes:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Inês Oliveira:** Writing – review & editing, Validation, Investigation, Data curation. **Ana Rita Pais:** Writing – review & editing, Investigation, Data curation. **M. Rosário Domingues:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Data curation, Conceptualization. **Helena R. Rocha:** Writing – review & editing, Investigation, Data curation. **Conde Tiago Alexandre Alexandre Teixeira de Sousa:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Ana**

M. Gomes: Writing – review & editing, Validation. **Moreira Ana S. P.:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Hugo Pereira:** Writing – review & editing, Validation, Investigation, Data curation. **Madalena Caria Mendes:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Marta Coelho:** Writing – review & editing, Validation, Investigation, Data curation. **Helena Abreu:** Writing – review & editing, Validation, Investigation, Data curation. **Kayane Oliveira:** Writing – review & editing, Investigation, Data curation. **Ana Ramos:** Writing – review & editing, Validation, Investigation, Data curation. **Alexandra Conde:** Writing – review & editing, Investigation, Data curation. **Cláudia Nunes:** Writing – review & editing, Validation, Investigation, Data curation. **Maria Salvador:** Writing – review & editing, Investigation, Data curation. **Manuel A. Coimbra:** Writing – review & editing, Validation, Funding acquisition. **Andreia S. Ferreira:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jfca.2026.109098.

Data availability

Data will be made available on request.

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