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Comparative analysis of the nutritional profiles of five edible macroalgae as sustainable food sources

Beatrice Brix da Costa[1,2*], Andreas Kunzmann[2] and Karin Springer[1]

*Correspondence:
Beatrice Brix da Costa
b.brixdacosta@uni-bremen.de
[1]Marine Botany, Faculty Biology/Chemistry, University of Bremen, BIOM, James- Watt-Straße 1, 28359 Bremen, Germany
[2]Leibniz Centre for Tropical Marine Research, Fahrenheitstraße 6, 28359 Bremen, Germany

Abstract

Seaweed aquaculture holds great promise as a solution to the global challenge of sustainable food production by providing alternative, resilient food sources. This study investigated the nutritional and biochemical profiles of five partially underutilized macroalgal species (*Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, *C. racemosa*, and *Codium taylorii*) to assess their potential as sustainable and nutritious food sources. The proximate composition, including moisture, lipid, carbohydrate and protein content, as well as the fatty acid, pigment, and elemental compositions were analyzed along with antioxidant activity and total phenolic content. All species showed high levels of polyunsaturated fatty acids (PUFAs, 39.3–59.6% of total FAs), especially omega-3 FAs. The green algae exhibited strong antioxidant activities and high total phenolic contents with highest values in *Caulerpa racemosa* (277 mmol Trolox Equivalents (TE) 100 g^{-1} dry weight (DW) and 157 mg Gallic Acid Equivalents (GAE) 100 g^{-1} DW, respectively). The red alga *Botryocladia pseudodichotoma* displayed the comparatively highest lutein content (0.07 mg g^{-1} DW), almost three times higher than in the green algae. Elemental analysis revealed a promising mineral profile of all species, with high levels of essential minerals such as calcium, magnesium, and potassium. The findings highlight the potential of these macroalgae as sustainable and nutritious dietary resources, capable of addressing health and environmental challenges. The study also emphasizes the importance of species diversification in aquaculture, as no single species provides all essential nutrients.

Keywords Antioxidant, Food, Mineral, Pigment, Proximate composition, Phenolic content

1 Introduction

One of the most pressing issues of the 21st is how to feed the world's growing population. Global food production systems are responsible for one-third of the anthropogenic greenhouse gas emissions, primarily from agriculture and related land use activities [1]. Extreme weather events and droughts are already threatening global terrestrial food production yields, as arable land and freshwater sources become increasingly scarce [2].

With terrestrial food production already reaching its limits in some areas, diversifying food sources by tapping into aquatic systems (blue foods) is essential for a resilient and sustainable food supply. In addition, a dietary shift from animal-based to plant-based foods is recognized as a required strategy for achieving more sustainable food production [2]. This transition not only reduces the environmental impact of food production systems by saving resources and reducing greenhouse gas emissions but also contributes to diet-related health challenges. Diets rich in plant-based foods are associated with a lower risk of chronic diseases, such as heart disease and diabetes [3, 4].

Macroalgae, which account for more than 50% of the world's marine and coastal aquaculture products, offer a nutritious and sustainable option for human consumption that meets the goals of both environmental sustainability and improved dietary health [5, 6].

Seaweed aquaculture has emerged as the fastest growing sector within the aquaculture industry, with a remarkable tripling of production over the last two decades [6, 7]. Despite this rapid growth, the sector remains largely dominated by a small number of genera of red and brown macroalgae, with green macroalgae contributing less than 1% to the global production [6, 8]. The reliance on a handful of macroalgae species for commercial production highlights the necessity of exploring new species as potential candidates for sustainable food production. Species diversification can improve productivity, increase genetic diversity and reduce susceptibility to diseases [9, 10].

Macroalgae are known for their excellent nutritional profile, making them a valuable addition to the human diet. There are certain similarities between different groups of macroalgae. For example, they have a low lipid content, but are rich in essential unsaturated fatty acids such as omega-3 fatty acids [11]. Macroalgae are also rich in proteins, vitamins, polysaccharides, and minerals [12, 13]. The chemical composition of macroalgae exhibits significant diversity both between and even within species, influenced by environmental parameters such as temperature, light, nutrient availability, and salinity. This variability contributes to their wide range of bioactive compounds [14]. Including macroalgae in the diet offers several health benefits due to these bioactive compounds, such as pigments and certain polysaccharides with antioxidative properties, or polyunsaturated fatty acids (PUFAs), which contribute to cardiovascular health and immune function [13, 15].

The genus *Caulerpa* has become increasingly popular in recent years, and from 1950 to 2019 it contributed the most to global green macroalgae production (annual average of 6404 t wet weight WW) [16]. *Caulerpa lentillifera* and *Caulerpa racemosa* (also known as "sea grapes" or "green caviar", Fig. 1C, D) are two of the few *Caulerpa* species used for human nutrition, mainly cultivated and consumed in the Indo-Pacific region [17]. Their high nutritional value due to the high content of bioactive compounds such as vitamin C, ß-carotene and flavonoids, as well as their distinctive texture, make precisely these algae increasingly popular as a delicacy worldwide [17–20].

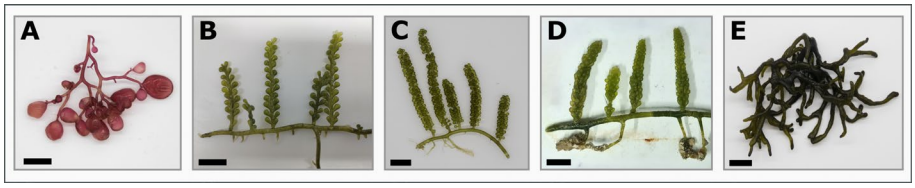

Fig. 1 Investigated macroalgal species. *Botryocladia pseudodichotoma* (**A**), *Caulerpa cylindracea* (**B**), *Caulerpa lentillifera* (**C**), *Caulerpa racemosa* (**D**), and *Codium taylorii* (**E**). Scale bar = 1 cm

Of the two, *C. lentillifera* is the main species produced in commercial aquaculture and primarily cultivated in the Philippines, Vietnam, Taiwan, China, and Japan [21–23]. Moreover, the alga is popular as a biofilter in co-culture systems and has demonstrated bioremediation capacity in aquaculture effluents from various organisms including fish, shrimp and snails [e.g. 24, 25].

While *C. racemosa* is popular in Southeast Asia, the alga has gained notoriety for its invasiveness in other parts of the world. *C. racemosa* has established itself as an invasive species and a major ecological problem in the Mediterranean Sea since 1990 [e.g. 26, 27]. The macroalga is considered one of the most 100 worst invasive species in the Mediterranean [28]. The invasive strain of *Caulerpa racemosa* (*C. racemosa* var. *cylindracea*) has been reclassified and named *C. cylindracea* [26] (Fig. 1B).

Codium is a cosmopolitan genus of green macroalgae that occurs worldwide, with the exception of polar regions [29]. The genus is known for its remarkable phenotypic plasticity. The thalli can form mats or grow upright, either branched or unbranched, and exhibit diverse morphological forms [30]. *Codium* species are used as a food source for cultured abalone, but are also consumed by humans [31, 32]. Their high nutritional value is attributed to the presence of sulfated polysaccharides and other compounds with a variety of bioactive properties, including antioxidant, antibiotic, antiviral, and antitumor activities [e.g. 34–36]. As such, *Codium* is not only one of the most popular edible macroalgae, but is also valued as a delicacy in gourmet cuisines [36].

Botryocladia is a genus of red macroalgae, some species of which are commonly known as red (sea)grapes. *Botryocladia* grows predominantly in shaded sublittoral habitats in warm temperate to tropical seas, although some species are found in colder temperate waters, such as along the Pacific coast of North America and the southern coast of Australia [37, 38]. *Botryocladia* species have small, globular or elongated vesicles arranged along the fronds, giving them a distinctive appearance reminiscent of grape clusters [39]. Despite their interesting morphology, *Botryocladia* species are not well studied. Some species have been studied for their anticoagulant and antidiabetic properties, suggesting promising pharmaceutical uses [40, 41].

As global interest in sustainable and diversified food sources continues to grow, the exploration of new food candidates is critical to meeting the increasing demand for nutrition. Underutilized macroalgae species present a promising solution, with the potential to provide novel and nutritious blue foods while promoting environmentally friendly aquaculture practices. However, there is a lack of comprehensive nutritional data, particularly for species that are not yet established as common food sources.

This comparative analysis aims to fill knowledge gaps regarding the nutritional profiles of lesser-known species and to highlight the potential of green algae.

2 Materials and methods

2.1 Sample material

Specimens of *Botryocladia pseudodichotoma* (Farlow) Kylin and *Codium taylorii* P.C.Silva were purchased 2009 from a German company (Seepferdchen24 Meeresaquaristik GmbH, Visselhövede) and kept in aquaria at the Marine Experimental Ecology (MAREE) aquaculture facilities of the Leibniz Centre for Tropical Marine Research (ZMT) in Bremen, Germany.

Caulerpa cylindracea Sonder specimens were collected off the coast of Tamariu, Spain in the Mediterranean Sea on 12.08.23 at a depth of 5–7 m (41°55'03.5"N 3°12'33.1"E & 41°55'02.9"N 3°12'33.2"E). At the collection sites the water temperature was 25 °C and absolute salinity was 37. Sample collection was supported by staff of the Stolli Divebase. Samples were stored in transparent PVC containers with a moisture sheet to counteract desiccation and transported within 24 h to the ZMT aquaculture facilities where they were placed in aquaria.

Caulerpa lentillifera J.Agardh was collected at the VIJA sea grape farm in Van Phong Bay, Viet Nam (12° 35′ 11.9″ N; 109° 13′ 26.2″ E) in 2019 and transported to the ZMT aquaculture facilities, where they have been cultured since.

Caulerpa racemosa (Forsskål) J.Agardh specimens originate from the Yasawa Islands, Fiji, and were bought at the local market in Suva. Samples were stored in transparent PVC containers with a moisture sheet and transported within 24 h to the University of Bremen, where they were freeze-dried and stored until analysis.

All macroalgae, except for *C. racemosa*, were cultured in glass aquaria (130 × 36 × 80 cm) filled with artificial sea water (RedSea salt, Verneuil dÁvre et d´Iton, France; 25.6 ± 1 °C, absolute salinity of 34.8 ± 0.5). All tanks were supplied with gentle aeration using air stones. Light was provided by light-emitting diode (LED) lamps (Solar Stinger Sunstrip 800 mm, ECONLUX GmbH, Cologne, Germany) in a 12:12 light: dark cycle emitting white light with irradiances of 50 ± 10 µmol photons m^{-2} s^{-1} photosynthetically active radiation (PAR).

2.2 DNA extraction, amplification, and sequencing

Species identification of the macroalgae was achieved through DNA sequence comparisons.

Since the identity of *C. lentillifera* was already confirmed by existing taxonomic information, only the other four species were analyzed.

DNA of fresh samples was isolated using a DNA kit (Plant/Seed Kit ZYMO Research, Germany) and amplified by PCR (Biometra TAdvanced cycler, Analytik Jena GmbH + Co. KG, Germany). 2 µL of DNA extracts were mixed in a total volume of 20 µl containing 10 µL master mix VWR Taq DNA-Polymerase (VWR, /Avantor), 7.5 µL DEPC-water, 0.5 µL $MgCl_2$ (2.0 mM), and 1 µL of each primer. DNA extracts from *C. taylorii* were diluted 1:20 in order to remove PCR inhibitors. The other DNA samples were set undiluted into the PCR due to the low DNA concentration.

tufA primers (Biomers, Germany) were used for *C. cylindracea* and *C. racemosa* and species-specific rbcl primers for *B. pseudodichotoma* and *C. taylorii*. Details of the primers and the PCR conditions can be found in the Appendix (Table A.1).

The quality and size of the PCR products were checked by gel documentation (Biometra Uvsolo TS Imaging System, Analytik Jena GmbH + Co. KG, Germany) on a 2% agarose gel after StainG® dyeing (SERVA, Heidelberg, Germany). The PCR products were purified using either a Monarch® DNA Gel Extraction Kit (New England BioLabs Inc, USA) or ExoSAP-IT© (USB Europe GmBH, Germany) before being subjected to sequencing at StarSeq Mainz.

The obtained sequences were compared to sequences in the Gen Bank® of the National Center for Biotechnology Information (NCBI) using BLAST analysis to identify the respective species.

2.3 Biochemical analysis

Samples were shock-frozen in liquid nitrogen and stored at -80 °C before being freeze-dried for 48 h at 1 mbar (Beta 1–8 LSCbasic, Christ GmbH, Germany). The freeze-dried samples, except the ones for lipid analysis, were ground to powder for 20 s using a FastPrep-24 (MP Biomedicals, Germany).

2.4 Moisture content

Moisture content was calculated by comparing the difference between the initial WW of the samples and the final DW after freeze drying.

$$\text{Moisture } (\%\ \text{WW}) = ((\text{W}_i - \text{W}_f)/\text{W}_i \times)\, 100$$

Where W_i is the initial wet weight of the sample and W_f the weight after drying.

2.5 Carbohydrate content

Total amount of sugars was determined by using the Anthrone Assay [42].

Around 0.03 g of freeze-dried and pulverized sample was suspended in 1.5 mL Milli-Q® water (IQ 7003, Sigma Aldrich/Merck KGaA, Germany). The samples were vortexed and shaken for 15 min before centrifugation (13000 rpm; 5 min; RT). The supernatant containing soluble sugars was used for the assay. To break down the starch, the pellet was heated in Milli-Q water (15 min at 100 °C) and alpha amylase enzyme was added to hydrolysed samples (60 °C for 1 h 15 min). The supernatant was collected after centrifuging (13000 rpm; 5 min; RT) and 96% H_2SO_4 was added. To break down the remaining polysaccharides to glucose, the samples were heated in a dry oven (60 °C, 1 h; 100 °C 30 min).

Samples were measured at 620 nm (Infinite® 200 PRO, Tecan, Switzerland). The concentrations of soluble sugars and starch were calculated based on a sucrose standard curve.

2.6 Lipid content and fatty acid composition

Lipids were extracted following Folch et al. [43] and Hagen [44] using dichloromethane: methanol (2:1) and 0.88% KCl. The weight of the extracted lipids was measured using a scale with an accuracy of 0.01 mg. Total lipid content was expressed as a percentage of dry matter.

The fatty acid (FA) composition was determined by treating subsamples of the lipid extracts with methanol containing 3% concentrated sulfuric acid to obtain methyl ester derivates (FAMEs). The FAs were quantified and identified by gas chromatography (Agilent Technologies, 7890 A, DB-FFAP column, 30 m length, 0.25 mm diameter, Helium as carrier gas). The FAs were identified by retentions times in comparison with peaks of known composition (Supelco 37, Sigma Aldrich/Merck KGaA, Germany).

2.7 Protein content

Protein content was quantified using a modified Lowry assay [45]. 50 mg of dried and ground sample was diluted in 500 µL Dulbecco's Phosphate-Buffered Saline (DPBS) buffer (1:10). After two cycles (4.5 m/s, 20 s, on dry ice) in a FastPrep-24 (MP Biomedicals, Germany) and subsequent centrifugation (10 min, 10000 rpm, 4 °C) the supernatant was mixed with ammonium sulfate in a ratio of 50% (w/v) and incubated for 24 h.

Post-incubation, the mixture was centrifuged again (15 min, 10000 rpm, 4 °C), and the supernatant was discarded. The resulting pellet was resuspended in DPBS. 40 µL of each sample was pipetted into a microwell plate. To each well, 200 µL of Lowry reagent was added, and the plate was incubated for 10 min. Then, 20 µL of Folin-Ciocalteu (FC) reagent was added to each well, followed by an additional 30 min incubation. The absorbance of the samples was measured at 730 nm using a FLUOstar IPTIMA plate reader (BMG Labtech, Germany). Bovine serum albumin (BAS) was used as the standard.

2.8 Pigment composition

Pigments were analyzed following the method described by Wright et al. [46]. Approximately 30 mg of freeze-dried and powdered material was extracted in 1 mL of 90% acetone at 4 °C for 24 h in darkness. The supernatant was filtered (45 µm nylon syringe, Nalgene® Nalge Nunc International, USA) and subsequently analyzed using high-performance liquid chromatography (HPLC, LaChromElite® system, L-2200 autosampler (chilled), DA detector L-2450, VWR-Hitachi International GmbH, Germany). Pigments were separated with a Spherisorb® ODS-2 column (250 mm x 4.6 mm, 5 µm, Waters, Milford, USA) with a LiChrospher®100-RP-18 guard cartridge applying a gradient according to Wright et al. [46]. Peaks of the different pigments were identified at 440 nm and quantified by co-chromatography of the respective standards. The pigment contents are expressed as mg g^{-1} DW.

2.9 Antioxidant activity and total phenolic content

50 mg DW of the samples were dissolved in 1 mL ethanol (70%) and extracted in a water bath (47 °C) for 4 h, being vortexed hourly. Before the analysis, samples were centrifuged for 5 min (2500 g, 20 °C).

The antioxidant activity (AOA) was assessed using a modified ABTS assay described by Re et al. [47]. Initially, a 2.45 mM $ABTS^{\bullet+}$ stock solution was prepared by oxidizing 7.0 mM ABTS with potassium disulfate ($K_2S_2O_8$) over 16 h. An $ABTS^{\bullet+}$ working solution was generated by diluting the stock solution with absolute ethanol until achieving a consistent absorption of 0.7 ± 0.02 at 734 nm using a UV/VIS-spectrophotometer (Thermo Scientific Genesys 140/150, Fisher Scientific GmbH, Germany). 1 mL of the $ABTS^{\bullet+}$ working solution was added to 10 µL of the sample extract and the absorbance was measured at 734 nm after a six-minute reaction time. Trolox served as the standard, and the antioxidant activity was expressed as Trolox Equivalents (TE mmol 100 g^{-1} DW). All chemicals were procured from (Sigma Aldrich/Merck KGaA, Germany).

The total phenolic content (TPC) was quantified using the Folin-Ciocalteu method described by Ainsworth and Gillespie [48], with minor adjustments. 10% (v/v) Folin-Ciocalteu (F-C) reagent and 150 µL of sample extract were mixed using a vortexer. Subsequently, 1.2 mL of Na_2CO_3 (700 mM) was added, and the mixture was incubated in the dark at room temperature for 45 min. Afterwards, the samples were centrifuged (3 min, 5000 rpm, 20 °C), and the absorbance was measured at 765 nm. Gallic acid served as the standard, and the results were expressed as 100 mg Gallic acid equivalents (GAE) g^{-1} (DW).

2.10 Elemental composition

50 mg of freeze-dried and powdered sample as well as Standard Reference Material® 3232 (Kelp powder, "Thallus laminariae") was weighed into a PFA digestion vessel. 5mL HNO3 (69% supra, Roth) and 2.8 mL HCl (32% supra, Sigma Aldrich/Merck KGaA, Germany) were added and the samples were left under a fume-hood until no more reaction was visible. The vessels were then heated up to 50 °C for 1 h, then to 75 °C for another hour, in an EvapoClean Block (AHF Analysentechnik). After closing the vessels tightly, they were heated to 110 °C for 1 h and then left at 130 °C overnight. The next morning, after cooling to room temperature, they were opened and heated up to 110 °C to evaporate the concentrated acid. As soon as just one Milliliter was left, the digested samples were transferred into pre weight PE bottles filled up to 10 mL with 0.5 M HNO_3. The sample extracts were diluted 1:20 for the determination of Ca, Fe, K, Mg, Mn, and P and 1:60 for Na determination. 1 ppm Yttrium was added to all samples as an internal standard.

Elemental analysis was done using a Spectro Ciros Vision inductively coupled plasma optical emission spectrometer (ICP-OES). Calibration was done with a stock solution containing single element standards (Inorganic Ventures) for all the respective elements.

The following wavelengths (in nm) were used: Ca 317.933, Fe 259.941, K 766.491, Mg 279.553, Mn 260.569, Na 589.592, P 213.618, Zn 213.856.

Total carbon (C) and nitrogen (N) contents were analyzed following [49]. 2–3 mg of dried and ground sample was weighed into tin cartridges (6 × 6 × 12 mm) and combusted at 950 °C. Total C and N contents were quantified using an elemental analyzer (Vario EL III, Elementar, Langenselbold, Germany), with Acetanilide (C_8H_9NO) as standard [50]. Concentrations were expressed in mg g^{-1} DW and the C: N ratio was calculated.

2.11 Statistical analysis

All statistical analyses and graphical outputs were performed using R with RStudio [51, 52], along with packages from the tidyverse. Outliers were removed using Grubbs' test, accessible via the GraphPad website (https://www.graphpad.com/quickcalcs/Grubbs1.cfm).

The datasets were tested for normality using QQ plots and the Shapiro-Wilk test ($p > 0.05$), and homogeneity of variance was assessed with Levene's test ($p > 0.05$). Significant differences between the nutritional compounds of the different algae were assessed using analyses of variance (one-way ANOVA), followed by Tukey's *post-hoc* test. Because F-statistic was reported to be robust against moderate violations of normality when the sample size is small [53], the data that were not normally distributed were not transformed.

Summaries of the results of all statistical tests can be found in the appendix (Table A.2).

3 Results

3.1 Species identification

DNA barcoding successfully determined the species of the different macroalgae based on sequence similarity in GenBank (≥ 95%), Table 1.

3.2 Proximate composition

Table 2 provides a summary of the proximate composition, fatty acid profiles and pigment composition, of the five macroalgal species.

Significant differences were observed in the moisture and lipid, and protein content among the species ($p < 0.001$, $p = 0.003$, $p < 0.001$ respectively), whereas the carbohydrate content showed no significant variation. Moisture content ranged from 93.33 ± 0.26% WW in *Codium taylorii* to 96.44 ± 0.13% WW in *Caulerpa lentillifera*. The lipid content varied notably, with the lowest concentration in *Botryocladia botryoides* (0.62 ± 0.05% DW) and the highest in *C. taylorii*. Between the green algae species, no notable difference of lipid concentration was found. *Caulerpa cylindracea* had the highest carbohydrate content with 44.61 ± 14.85% DW.

Protein content ranged from 4.33 ± 0.75% DW in *C. cylindracea* to 16.96 ± 4.48% DW in *C. taylorii*. Significant differences were found between *C. taylorii* and all other algae, except for *Caulerpa lentillifera*.

3.3 Fatty acid composition

All macroalgae exhibited high contents PUFAs ranging from 39.28 ± 1.36% of total fatty acids (TFA) in *B. pseudodichotoma* to 59.59 ± 1.69% in *C. lentillifera* (Table 2). Overall, the green algae had significantly higher PUFA levels than the red alga ($p < 0.001$).

Specifically, the green algae showed high levels of omega-3 FAs (Fig. 2A), particularly 16:3 (n-3) (Hexadecatrienoic acid, HTA) and 18:3 (n-3) (α-Linolenic acid, ALA), with highest levels in *C. lentillifera*, followed by *C. cylindracea* and *C. taylorii* (Table 3). The red alga was distinguished by its significantly high amounts of 20:5 (n-3) (Eicosapentaenoic acid, EPA), making up 25.28 ± 1.57% TFA compared to 1.89 ± 0.05 (*C. taylorii*) to 4.23 ± 0.26% TFA (*C. cylindracea*) in the green algae (Table 3). Omega-6 fatty acid content was highest in *C. taylorii* (19.09 ± 1.65% TFA) and *C. cylindracea* (16.87 ± 0.8% TFA, Fig. 2B).

3.4 Pigment composition

The pigment composition showed several significant differences between the species (Table 2). Chlorophyll *a* content was sevenfold lower in *B. pseudodichotoma* (0.34 ± 0.07 mg g^{-1} DW) than in the other species. Chlorophyll *b* content of the green algae was similarly high as the chlorophyll *a* content ranging from 2.39 ± 0.77 mg g^{-1} DW in *Caulerpa racemosa* to 3.44 ± 0.12 mg g^{-1} DW in *C. taylorii*. ß-carotene was significantly higher in *C. racemosa* (0.39 ± 0.12 mg g^{-1} DW) and *C. taylorii* (0.30 ± 0.05 mg g^{-1} DW) than in the other three species. *B. pseudodichotoma* showed the lowest ß-carotene content (0.04 ± 0.01 mg g^{-1} DW). However, the alga exhibited the highest levels of Lutein

Table 1 Investigated seaweed species with GenBank accession numbers

Species	GenBank
Red algae	
Botryocladia pseudodichotoma	KU687853.1
Green algae	
Caulerpa cylindracea	KY773573.1
Caulerpa lentillifera	nd
Caulerpa racemosa	JN645167.1
Codium taylorii	KP686041.1

Nd = not determined

Table 2 Proximate composition (expressed as % of dry weight, DW), fatty acid composition (expressed as % of total fatty acids, TFA), and pigment composition (in Mg g^{-1} DW) of the five macroalgal species *Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, *C. racemosa*, and *Codium taylorii*.

	Botryocladia pseudodichotoma	Caulerpa cylindracea	Caulerpa lentillifera	Caulerpa racemosa	Codium taylorii
Proximate composition (% DW)					
Moisture*	95.42 ± 0.39^{a}	94.69 ± 0.46^{b}	96.44 ± 0.13^{c}	95.18 ± 0.53^{ab}	93.33 ± 0.26^{d}
Lipids	0.62 ± 0.05^{a}	2.31 ± 0.83^{b}	1.46 ± 0.65^{ab}	nd	2.74 ± 0.79^{b}
Carbohydrates	29.25 ± 5.13^{a}	44.61 ± 14.85^{a}	37.22 ± 5.32^{a}	30.47 ± 4.01^{a}	38.01 ± 14.35^{a}
Proteins	8.28 ± 3.91^{ab}	4.33 ± 0.75^{a}	11.51 ± 2.6^{bc}	7.29 ± 1.8^{ab}	16.96 ± 4.48^{cd}
Fatty acids (% TFA)					
Saturated	48.64 ± 0.67^{a}	40.43 ± 0.94^{b}	34.24 ± 1.25^{c}	nd	33.41 ± 0.64^{c}
Monounsaturated	12.11 ± 0.78^{a}	5.49 ± 0.47^{b}	6.17 ± 0.62^{b}	nd	11.51 ± 0.43^{a}
Polyunsaturated	39.28 ± 1.36^{a}	54.09 ± 1.38^{b}	59.59 ± 1.69^{c}	nd	55.09 ± 0.92^{b}
Pigments (mg g^{-1} DW)					
Chlorophyll *a*	0.34 ± 0.07^{a}	2.44 ± 0.32^{b}	2.25 ± 0.27^{b}	2.22 ± 0.53^{b}	2.81 ± 0.18^{b}
Chlorophyll *b*	-	2.74 ± 0.39^{ab}	2.51 ± 0.38^{ab}	2.39 ± 0.77^{a}	3.44 ± 0.12^{b}
ß-carotene	0.04 ± 0.01^{a}	0.16 ± 0.07^{a}	0.10 ± 0.02^{a}	0.39 ± 0.12^{b}	0.30 ± 0.05^{b}
Lutein	0.07 ± 0.01^{a}	0.02 ± 0.01^{b}	0.02 ± 0.01^{b}	0.03 ± 0.01^{b}	0.04 ± 0.01^{b}
Violaxanthin	-	0.22 ± 0.05^{a}	0.16 ± 0.03^{a}	0.08 ± 0.01^{b}	0.03 ± 0.01^{b}

Significant differences are shown by different letters

Data are mean ± standard deviation, $n = 3–8$. Nd = not determined. * Moisture content as % of wet weight (WW)

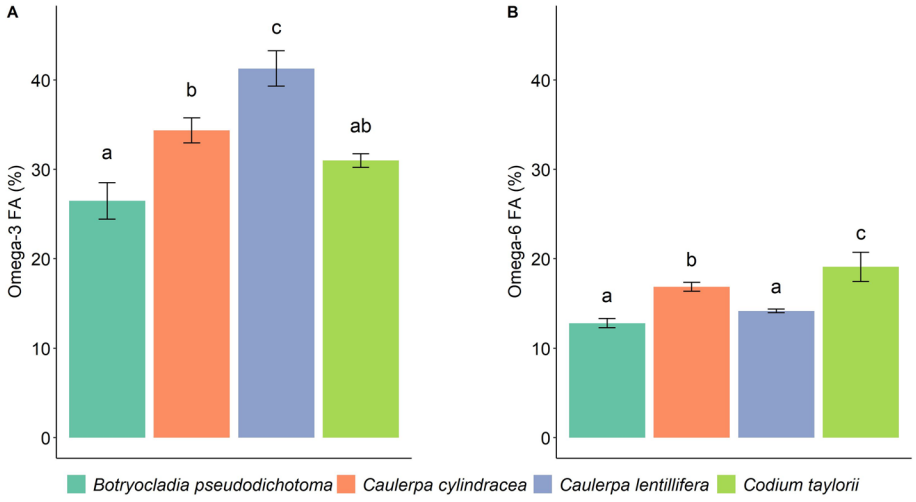

Fig. 2 **A** Omega-3 fatty acid (FA) content (% of total fatty acids, TFA) and **B** omega-6 FA content (% TFA) of the four macroalgal species *Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, and *Codium taylorii*. Significant differences are shown by different letters (One-way ANOVA with post-hoc test, $p < 0.05$). Data are mean ± standard deviation, $n = 3–4$

(0.07 ± 0.01 mg g^{-1} DW). The Violaxanthin contents in *C. cylindracea* and *C. lentillifera* (0.22 ± 0.05 and 0.16 ± 0.03 mg g^{-1} DW, respectively) were significantly higher than in *C. racemosa* and *C. taylorii* (0.08 ± 0.01 and 0.03 ± 0.01 mg g^{-1} DW, respectively).

3.5 Antioxidant activity (AOA) and total phenolic content (TPC)

There was a significant difference of the AOA and the TPC of the macroalgae ($p < 0.001$). The AOA was significantly higher in all green algae than in the red alga (Fig. 3A). Values ranged from 162.45 ± 49.42 mmol TE 100 g^{-1} DW in *C. taylorii* to 277.04 ± 91.83

Table 3 Fatty acid composition in % of total fatty acids (TFA) of *Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, and *Codium taylorii*

Fatty acid (% TFA)	Botryocladia pseudodichotoma	Caulerpa cylindracea	Caulerpa lentillifera	Codium taylorii
12:0	0.19 ± 0.03^{a}	0.03 ± 0.04^{b}	0.03 ± 0.02^{b}	0.39 ± 0.01^{c}
13:0	0.09 ± 0.05^{a}	0.12 ± 0.11^{a}	0.12 ± 0.03^{a}	0.03 ± 0.04^{a}
14:0	6.11 ± 0.34^{a}	3.10 ± 0.90^{b}	2.22 ± 0.84^{b}	2.40 ± 0.18^{b}
15:0	0.61 ± 0.04^{a}	0.29 ± 0.20^{a}	0.28 ± 0.26^{a}	0.78 ± 0.17^{b}
16:0	39.84 ± 0.47^{a}	35.47 ± 1.33^{b}	29.11 ± 2.19^{c}	26.12 ± 0.33^{c}
16:1(n-7)	0.95 ± 0.04^{a}	2.48 ± 0.28^{b}	3.28 ± 0.14^{c}	0.62 ± 0.02^{a}
16:2(n-6)	0.00 ± 0.00^{a}	2.57 ± 0.19^{b}	3.85 ± 0.14^{c}	5.01 ± 0.25^{d}
16:2(n-4)	0.00 ± 0.00^{a}	0.30 ± 0.02^{b}	0.20 ± 0.01^{c}	0.00 ± 0.00^{a}
17:0	0.65 ± 0.10^{ab}	0.46 ± 0.20^{bc}	0.83 ± 0.10^{a}	0.33 ± 0.12^{c}
17:1(n-7)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.06 ± 0.11^{a}	0.01 ± 0.02^{a}
16:3(n-3)	0.00 ± 0.00^{a}	10.55 ± 0.57^{b}	16.42 ± 1.00^{c}	11.11 ± 0.96^{b}
18:0	1.15 ± 0.10^{a}	0.82 ± 0.05^{a}	1.39 ± 0.59^{ab}	2.00 ± 0.06^{a}
18:1(n-9)	8.13 ± 0.39^{a}	1.26 ± 0.15^{b}	1.19 ± 0.04^{b}	10.45 ± 0.45^{c}
18:1(n-7)	3.03 ± 0.48^{a}	1.28 ± 0.09^{b}	0.89 ± 0.06^{bc}	0.38 ± 0.0^{c}
18:1(n-5)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.07 ± 0.11^{a}	0.00 ± 0.00^{a}
18:2(n-6)	1.55 ± 0.13^{a}	7.56 ± 0.23^{b}	9.49 ± 0.20^{c}	10.76 ± 1.0^{c}
18:3(n-6)	0.67 ± 0.11^{a}	1.10 ± 0.05^{b}	0.75 ± 0.08^{a}	1.04 ± 0.09^{b}
18:3(n-3)	0.67 ± 0.23^{a}	14.57 ± 0.65^{b}	18.36 ± 1.16^{c}	15.23 ± 0.92^{b}
18:4(n-3)	0.53 ± 0.40^{a}	1.19 ± 0.08^{a}	0.47 ± 0.04^{a}	1.37 ± 1.46^{a}
20:0	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.05 ± 0.07^{a}
20:1(n-9)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.04 ± 0.06^{a}
20:1(n-5)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.08 ± 0.05^{b}	0.00 ± 0.00^{a}
20:2(n-6)/20:2(n-7)	0.00 ± 0.00^{a}	0.58 ± 0.04^{b}	0.26 ± 0.02^{c}	0.00 ± 0.00^{a}
20:3(n-6)/21:0	0.67 ± 0.03^{a}	0.61 ± 0.08^{a}	0.43 ± 0.02^{b}	0.55 ± 0.06^{ab}
20:4(n-6)	9.90 ± 0.43^{a}	7.02 ± 0.40^{b}	3.17 ± 0.21^{c}	6.48 ± 0.04^{b}
20:3(n-3)	0.00 ± 0.00^{a}	0.16 ± 0.11^{b}	0.22 ± 0.01^{b}	0.00 ± 0.00^{a}
20:4(n-3)	0.00 ± 0.00^{a}	0.07 ± 0.10^{a}	0.13 ± 0.07^{a}	0.07 ± 0.10^{a}
20:5(n-3)	25.28 ± 1.57^{a}	4.23 ± 0.26^{b}	2.11 ± 0.05^{b}	1.89 ± 0.05^{b}
22:0	0.00 ± 0.00^{a}	0.15 ± 0.10^{ab}	0.24 ± 0.03^{b}	1.31 ± 0.17^{c}
22:1(n-9)	0.00 ± 0.00^{a}	0.31 ± 0.44^{a}	0.22 ± 0.39^{a}	0.00 ± 0.00^{a}
22:1(n-7)	0.00 ± 0.00^{a}	0.16 ± 0.12^{ab}	0.36 ± 0.15^{b}	0.00 ± 0.00^{a}
22:2(n-6)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.07 ± 0.07^{a}	0.00 ± 0.00^{a}
22:4(n-6)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.27 ± 0.37^{a}
22:5(n-3)	0.00 ± 0.00^{a}	3.58 ± 0.05^{b}	3.05 ± 0.35^{c}	1.31 ± 0.05^{d}
22:6(n-3)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.52 ± 0.05^{b}	0.00 ± 0.00^{a}

Significant differences are shown by different letters. Data are mean ± standard deviation, $n = 3–4$

mmol TE 100 g^{-1} DW in *C. racemosa*, but was threefold lower in *B. pseudodichotoma* (59.04 ± 18.85 mmol TE 100 g^{-1} DW).

A similar trend was seen in the results of the total phenolic content (Fig. 3B). *B. pseudodichotoma* showed the lowest content (48.36 ± 26.91 mg GAE 100 g^{-1} DW), followed by *C. taylorii* (97.01 ± 7.56 mg GAE 100 g^{-1} DW) and *C. cylindracea* (98.54 ± 9.19 mg GAE 100 g^{-1} DW). The highest total phenolic content was found in *C. racemosa* (156.90 ± 9.34 mg GAE 100 g^{-1} DW). Antioxidant activity and total phenolic content were positively correlated (0.64, $p = 0.002$).

3.6 Elemental composition

Elemental composition varied significantly between the species and can be found in the appendix (Table A.3). All species contained high amounts of minerals with sodium (Na),

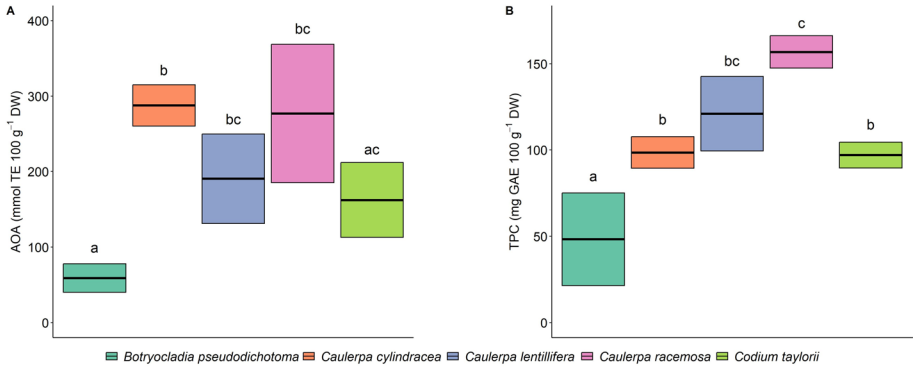

Fig. 3 **A** Antioxidant activity (AOA; mmol Trolox Equivalents/TE 100 g^{-1} dry weight, DW) and **B**) total phenolic content (TPC; mg Gallic acid equivalents/GAE 100 g^{-1} DW) of the five macroalgal species *Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, *C. racemosa*, and *Codium taylorii.* Significant differences are shown by different letters, respectively (One-way ANOVA with *post-hoc* test, $p < 0.05$). Mean (middle bar) ± standard deviation (upper and lower interval), $n = 4$

Table 4 Elemental composition of macro and trace elements of the of the five macroalgal species *Botryocladia pseudodichotoma*, *Caulerpa cylindracea*, *C. lentillifera*, *C. racemosa*, and *Codium Taylorii* and various legumes.

RDI (mg day^{-1})[a]	**Ca**	**K**	**Mg**	**Na**	**Fe**	**Mn**	**Zn**
	1040	**4000**	**325**	**1500**	**13.00**	**1.25**	**10.95**
Macroalgae (mg 10 g^{-1} DW)[b]							
Botryocladia pseudodichotoma	90.08 (9)	859.06 (21)	271.92 (84)	1690.48 (113)	0.42 (3)	0.39 (31)	0.53 (5)
Caulerpa cylindracea	500.33 (48)	130.94 (3)	43.52 (13)	1797.67 (120)	1.16 (9)	0.25 (20)	0.08 (1)
Caulerpa lentillifera	107.50 (10)	115.46 (3)	256.56 (79)	2203.82 (147)	0.38 (3)	0.19 (16)	0.05 (0)
Caulerpa racemosa	270.24 (26)	62.71 (2)	72.36 (22)	960.59 (64)	18.78 (144)	0.28 (23)	0.06 (1)
Codium taylorii	104.84 (10)	66.87 (2)	214.89 (66)	1618.06 (108)	0.61 (5)	1.12 (89)	0.46 (4)
Legumes (mg 100 g^{-1} DW)[c]							
Edamame	60.00 (6)	482.00 (12)	61.00 (19)	6.00 (0)	2.11 (16)	1.01 (81)	1.32 (12)
Lentils	35.00 (3)	677.00 (17)	47.00 (14)	6.00 (0)	6.51 (50)	1.39 (111)	3.27 (30)
Peanuts	92.00 (9)	705.00 (18)	168.00 (52)	18.00 (1)	4.58 (35)	nd	3.27 (30)
Peas	25.00 (2)	244.00 (6)	33.00 (10)	5.00 (0)	1.47 (11)	0.41 (33)	1.24 (11)
Soybeans	197.00 (19)	620.00 (16)	65.00 (20)	15.00 (1)	15.70 (121)	0.55 (44)	0.99 (9)

Values in () represent the % of the recommended daily intake (RDI) based on a serving of 10–100 g dry weight (DW) for macroalgae and the legumes, respectively. Nd = not determined

[a]Recommended daily intake values were obtained from the Deutsche Gesellschaft für Ernährung, Österreichische Gesellschaft für Ernährung [103] and calculated as means for teenagers and adults

[b]Data are mean, $n = 6$. Full data with standard deviations can be found in the appendix (Table A.3)

[c]Data from the National Nutrient Database for Standard Reference of the US Department of Agriculture [104]

calcium (Ca), magnesium (Mg), and potassium (K) being the most prevalent macronutrients. Na was the dominant element in all species, ranging from 96.06 ± 9.28 mg g^{-1} DW in *C. racemosa* to 220.38 ± 10.52 mg g^{-1} DW in *C. lentillifera* ($p < 0.001$).

Ca concentrations also varied significantly between the species ($p < 0.001$). The highest levels were found in *C. cylindracea* (50.03 ± 26.08 mg g^{-1} DW), followed by *C. racemosa* (27.02 ± 10.19 mg g^{-1} DW), while the other algae had calcium contents of around 10 mg g^{-1} DW. *B. pseudodichotoma* showed the highest concentrations of K (85.91 ± 9.33 mg g^{-1} DW), which was 6- to 12-fold higher than in the green algae. Mg content was highest in *B. pseudodichotoma*, *C. lentillifera*, and *C. taylorii* (27.19 ± 1.98, 25.66 ± 1.40, and 21.49 ± 1.10 mg g^{-1} DW, respectively). *C. cylindracea* and *C. racemosa* had significantly lower values of 4.35 ± 0.54 and 7.24 ± 0.28 mg g^{-1} DW, respectively.

Other striking differences of the elemental composition were observed for the contents of manganese (Mn) and iron (Fe). *C. taylorii* showed high levels of Mn with 0.11 ± 0.05 mg g^{-1} DW ($p < 0.001$). Considering the Fe content, *C. racemosa* contained with 1.88 ± 0.60 mg g^{-1} DW 15 to 47-fold more iron than the other algae. The Na: K ratio ranged from 2.00 ± 0.35 in *B. pseudodichotoma* to 24.19 ± 0.88 in *Codium taylorii*. For the tested *Caulerpa* species the Na: K values ranged around 16 ± 4 (Table A.3).

The carbon: nitrogen (C: N) ratio was highest in *C. racemosa* and *C. cylindracea* (8.11 ± 0.44 and 7.37 ± 0.36, respectively).

4 Discussion

4.1 Proximate composition

The proximate composition of the five macroalgae species varied considerably, reflecting the diversity of the species. The high moisture content, ranging from 93 to 96% of fresh weight (FW) is typical of algae, due to their aquatic environment. Despite using the same drying process for all species, significant differences in moisture content were observed. These variations are likely related to species-specific differences in cell structure and composition, which affect their water-holding capacity [54]. Algae with more complex or denser cell walls may retain more water, while those with simpler structures may lose moisture more readily during the drying process.

The carbohydrate content of the species is in line with previous reports for *Caulerpa* and *Codium* species, ranging from 37 to 60% of DW [55, 56] and 42–58% of DW [57], respectively. Carbohydrates make up the largest proportion of the proximate composition of seaweed, serving as both structural and storage components. In addition to their structural functions, seaweed-derived polysaccharides have important applications in the food industry. Polysaccharides such as agar, carrageenan and alginate are extracted from various seaweed species and are widely used as gelling agents, thickeners and stabilizers in food products [58]. This adds to the commercial value of seaweed, not only as a nutritious food source, but also as a source of functional ingredients that can be used in various industrial applications.

The lipid content of all macroalgae species studied was low, which is consistent with the general understanding of marine algae as a low-lipid food source. This observation is consistent with the results of other studies on edible macroalgae [e.g. 12,19,60]. Among the species analyzed, the Chlorophyta species- *Caulerpa cylindracea*, *Caulerpa lentillifera*, *Caulerpa racemosa*, and *Codium taylorii* exhibited slightly higher lipid levels than the red alga *Botryocladia pseudodichotoma*, although overall lipid content remained low. This trend is supported by previous studies reporting similar lipid concentrations in *Caulerpa* and *Codium* species from tropical regions. In particular, the values obtained for the *Caulerpa* species and *C. taylorii* in this study are comparable to the findings of

Kumar et al. [55] and Arakaki et al. [57] for other species within these genera. *B. pseudodichotoma* had the lowest lipid content of all species examined, and the values in this study are lower than those previously reported for other Rhodophyta species [60]. Despite these variations, the low lipid content observed is favorable from a nutritional standpoint, as a low lipid diet is generally recommended to reduce the risk of cardiovascular disease and promote overall health [15].

The protein content differed significantly among the five species. The protein content of the *Caulerpa* species was significantly lower than that reported in previous studies, which indicate a range of 8–19% for different *Caulerpa* species [55, 61]. In contrast, *C. taylorii* showed a relatively high protein content, which is consistent with findings for *C. tomentosum* [62, 63]. The protein content of *B. pseudodichotoma* fell in the middle range, making it a moderate source of protein compared to other algal species.

It should be noted that in many studies the protein content of algae is often calculated by multiplying the nitrogen content by 6.25, however some studies propose lower factors of 5 or 4.14 to be more accurate [64, 65]. However, nitrogen is also a component of other biological molecules, such as DNA and ATP, which means that this method may overestimate the true protein content [19]. Despite this potential overestimation, the protein content of the species analyzed remains comparable to plant-based protein sources such as soybeans and edamame, highlighting the potential of macroalgae as a high-quality plant-based protein source. This finding is particularly relevant given the increasing global demand for sustainable and nutritious plant proteins.

Although the ash content was not directly measured in this study, its estimation provides valuable insight into the mineral content of the algae. Instead, the elemental composition was analyzed in detail and will be discussed in one of the following sections.

4.2 Fatty acid composition

The fatty acid profiles of the algae analyzed were very promising, with more than 50% of the total fatty acids consisting of unsaturated fatty acids, most of which are essential for human health. Among these, PUFAs were particularly prominent in all species. PUFAs cannot be synthesized by humans and are critical for health, playing key roles in reducing inflammation, supporting brain function, and preventing chronic disease [61, 66, 67].

The highest PUFA content was observed in *C. cylindracea* with almost 60% of the total fatty acid content. *C. lentillifera* and *C. taylorii* also showed high levels of PUFA, with approximately 55% of their total fatty acids being polyunsaturated. These levels are significantly higher than those reported in previous studies. Paul et al. [68] reported 47% PUFA content in *C. lentillifera*, and Arakaki et al. [57] found 40% PUFA content in two *Codium* species. Such variability in fatty acid composition is well documented and can be attributed to factors such as seasonal and environmental conditions [15, 69]. Kendel et al. [70] found that the PUFA content of the edible red alga *Grateloupia turuturu* was highest in summer. The high PUFA levels observed in this study may be explained by the fact that the algae were either collected during the summer or cultivated under conditions similar to the summer season.

Among PUFAs, omega-3 fatty acids, particularly eicosapentaenoic acid (EPA) and alpha-linolenic acid (ALA), are of particular importance in human nutrition. Omega-3 fatty acids are known to prevent chronic diseases and are essential for cardiovascular health [66, 67]. In this study, EPA accounted for a quarter of the total fatty acids in *B.*

pseudodichotoma, a finding consistent with previous studies. Dembitsky et al. [71] reported that red algae are generally rich in fatty acids with 20 carbon atoms, such as EPA (20:5 n-3). While the green algae species had lower levels of EPA, they had higher levels of ALA compared to the red algae, highlighting the diverse fatty acid profiles of macroalgae.

Palmitic acid (C16:0) was the most abundant fatty acid in all species, which is in accordance with previous findings. Several studies have detected palmitic acid as a major component of various seaweed species [e.g. 11, 64, 71].

Overall, the fatty acid profiles of the studied species were very promising, highlighting the potential of macroalgae as a good plant-based source of essential fatty acids.

4.3 Pigment composition

The pigment composition of the studied algal species showed high variation, especially with respect to β-carotene and lutein contents. These differences in pigment content could be related to species-specific adaptations to environmental conditions such as light availability and habitat, as pigments such as chlorophylls and carotenoids play a critical role in light harvesting and protection against photooxidative stress [73].

The chlorophyll *a* content did not differ significantly among the Chlorophyta (*C. cylindracea*, *C. lentillifera*, *C. racemosa*, and *C. taylorii*). Results for the chlorophyll *a* content of *C. lentillifera* in this study are comparable to the findings of Paul et al. [68], who reported a value of 2.58 mg g^{-1} DW for the same species. However, *C. racemosa* had a much higher chlorophyll *a* content in their study (5.48 mg g^{-1} DW), which is almost double the value found here, indicating that environmental factors such as irradiance or nutrient availability may have influenced these differences. Chlorophyll *a* is essential for photosynthesis and its production is influenced by the light conditions in the habitat of the alga. In high light environments, macroalgae may produce less chlorophyll *a* as an adaptive mechanism to avoid photodamage caused by excessive light energy [74, 75]. *C. racemosa* was sampled from a high irradiance environment, which may explain the lower chlorophyll *a* content. Additionally, nutrient supply, particularly nitrogen availability, plays a crucial role in chlorophyll synthesis [73]. Studies have shown that increasing nitrogen levels can lead to higher chlorophyll *a* concentrations, whereas nitrogen deficiency typically results in reduced photosynthetic pigment content [76, 77]. Thus, variations in nitrogen availability between sampling sites may also have contributed to the observed differences in chlorophyll *a* content of *C. racemosa* between the study by Paul et al. [68] and the present study.

Chlorophyll *b* content of all green algal species was similar to their chlorophyll a content, a finding that is unusual. Typically, the ratio of chlorophyll *a* to chlorophyll *b* can vary depending on environmental factors such as light quality and nutrient availability. Chlorophyll *b* is an important accessory pigment that not only assists in light absorption, but also has antioxidant properties [78, 79]. The unusual balance between chlorophyll *a* and *b* observed here could be the result of specific adaptations to the light environment, especially since all algae were cultivated in the same tanks, except for *C. racemosa*, which was sampled from a high irradiance environment. This suggests that light conditions may have played an important role in shaping pigment composition.

In this study, the β-carotene content was highest in *C. racemosa* and *C. taylorii*. These values for the green algae are consistent with the findings of Paul et al. [68], but

are significantly higher than those reported by Balasubramaniam et al. [80], who measured a β-carotene content of 0.19 mg g^{-1} DW for *C. lentillifera*. The high β-carotene levels observed in *C. racemosa* may indicate enhanced photoprotection, which is consistent with the high antioxidant activity and total phenolic content found in this species. β-carotene plays a crucial role in protecting cells from oxidative stress, especially under conditions of high light exposure. Reactive oxygen species (ROS), which are produced as by-products of photosynthesis under suboptimal conditions such as excessive light, can cause oxidative damage to cellular components. Antioxidants such as β-carotene act as a defense metabolite by scavenging ROS, thereby minimizing oxidative damage and maintaining cellular integrity [81]. In addition, ß-carotene is a precursor of vitamin A, further enhancing its nutritional value [82].

Another pigment with strong antioxidative capacities is Lutein. Lutein was found in the highest concentrations in the red alga *B. pseudodichotoma*. Its levels were two to three times higher than in the green algal species. These results are consistent with the study by Balasubramaniam et al. [80], who reported the highest lutein content in the red alga *Eucheuma denticulatum* (0.87 mg g^{-1} DW), compared to much lower levels in the brown seaweed *Sargassum polycystum* and *C. lentillifera* (0.12 mg g-1 DW and < 0.02 mg g^{-1} DW, respectively). Lutein is highly valued for its health-promoting properties, including anti-cancer and anti-tumor effects, making it a popular ingredient in cosmetics, pharmaceuticals, and food products [83].

The limited availability of studies on the pigment composition of some of the macroalgal species studied here makes direct comparisons difficult. In addition, methodological differences such as variations in sample preparation, solvents, extraction times and temperatures make comparisons with existing data difficult. These issues highlight the need for more standardized protocols in future research to enable reliable comparisons between studies.

4.4 Antioxidative activity (AOA) and total phenolic content (TPC)

Seaweeds are widely recognized as a rich source of natural antioxidants [e.g. 12,85]. Both antioxidant activity (AOA) and total phenolic content (TPC) were generally higher in the green algae, especially in the *Caulerpa* species. The levels obtained for AOA and TPC in the *Caulerpa* species are in line with previous studies on *C. lentillifera* [25, 85, 86]. This highlights the potential of *Caulerpa* species as a valuable natural source of antioxidants that may contribute to the prevention of oxidative stress-related diseases. Synthetic antioxidants have been linked to potential health risks such as liver damage and carcinogenesis [87, 88]. Macroalgae represent a safer, natural alternative.

No AOA data exists for *B. pseudodichotoma* and *C. taylorii*, which makes it impossible to compare the values of the present study with other studies. Even though comparisons could be made to other red or green macroalgae, such comparisons are difficult due to methodological differences in antioxidant analysis. A wide range of assays, extraction solvents and reference standards are commonly used to measure antioxidant activity, leading to different results [89]. These methodological inconsistencies highlight the need for standardized approaches in future research to improve comparability and better assess the antioxidant potential of macroalgae.

Despite these challenges in comparing AOA values, the TPC results for *C. taylorii* align with findings for *C. fragile* [90], suggesting a similar phenolic composition in

different *Codium* species. The low TPC observed in *B. pseudodichotoma* is also consistent with antioxidant activities of other red algal species e.g. from south Korea [91].

4.5 Elemental composition and C: N ratio

Minerals are essential components of the human diet, because they cannot be synthesized by the human body. More than 95% of daily mineral intake comes from food [92]. Adequate mineral intake plays a critical role in the prevention of chronic and degenerative diseases, including cancer, cardiovascular disease, and neurological disorders [93, 94]. The studied algal species exhibited a promising mineral profile, with significant variations in their elemental composition. A comparison of the macro elements and trace elements of the studied algal species and selected legumes can be found in Table 4.

Sodium was the most abundant element in all five species. This is expected, as the algae grew in saline environments, leading to high sodium accumulation. The sodium content is consistent with previous studies on the mineral composition of various seaweed species [55, 63, 95]. While sodium is essential for normal physiological functions such as maintaining fluid balance and supporting nerve transmission, excessive sodium intake is a known risk factor for hypertension, which can lead to cardiovascular disease [96, 97]. However, seaweeds have the potential to act as a salt substitute in food reformulation. The use of seaweed can reduce sodium intake while increasing the intake of other essential minerals, providing a healthier alternative to salt reduction strategies in processed foods.

Apart from sodium, calcium, magnesium, and potassium were the most prevalent macronutrients in all algae species, highlighting their importance as a mineral source. Calcium is essential for bone health, muscle function, and nerve transmission. This is especially important for vegans and those who do not consume dairy products. The studied algae can provide a significant amount of dietary calcium. *C. cylindracea* had the highest calcium content; a serving of 10 g DW could provide 48% of the Recommended Daily Intake (RDI) for calcium, compared to 19% from soybeans or 9% from peanuts (Table 4).

Magnesium is another essential element, serving as a cofactor in over 300 metabolic reactions, including DNA and RNA synthesis, protein production, and energy metabolism [98]. Magnesium deficiency is closely associated with several chronic diseases [98, 99], making it critical to maintain adequate magnesium intake. *B. pseudodichotoma*, *C. lentillifera*, and *C. taylorii* are particularly high in magnesium, providing up to 84%, 79%, and 66% of the RDI, respectively, which is significantly higher than soybeans (20%) or edamame (19%).

Potassium is essential for maintaining fluid balance, nerve function, and muscle contraction [92]. The red alga *B. pseudodichotoma* had the highest potassium content, with a single serving of the alga meeting 21% of the RDI, a level comparable to legumes, making it an excellent alternative source of this essential nutrient.

The Na: K ratios observed in this study were relatively high compared to previously reported values for macroalgae [15, 96]. However, Paul et al. [68] reported similar values for *C. lentillifera* and even higher values for *C. racemosa*. From a nutritional perspective, a lower Na: K ratio is generally considered more beneficial for human health and high ratios have been associated with hypertension [100]. However, the Na: K ratio of an individual food source does not determine overall nutritional value. When consumed as part

of a balanced diet that includes potassium-rich foods, the overall Na: K ratio can remain optimal. Hence, despite the observed ratios of the macroalgae in the present study, their overall nutrient profile still makes them a valuable addition to a balanced diet.

The results for trace elements such as iron, manganese and zinc were generally in line with previous reports on the mineral content of seaweeds [92, 101]. However, the iron content in *C. racemosa* was significantly higher than expected, probably due to elevated iron concentrations in the surrounding environment. Iron is essential for oxygen transport in the blood and energy metabolism, and seaweeds can be a valuable source of dietary iron, especially for individuals at risk of iron deficiency.

While the mineral content of the species studied may not be sufficient to fully meet the recommended daily intake of essential macro and trace minerals, they do provide significant amounts of minerals such as calcium, magnesium, and potassium, all of which are important for health promotion and disease prevention.

The carbon: nitrogen ratio is a key index for assessing the nutritional quality of food, as it reflects nutrient uptake and assimilation. The carbon pool in algae is mainly used for polysaccharide synthesis, while nitrogen is involved in the production of amino acids, proteins, DNA and ATP [55, 73]. In this study, the C: N ratio in the algae examined was below 10, which is typically considered low and indicates nitrogen-rich conditions. Algae with a low C: N ratio tend to have higher nitrogen content, which is often reflected in higher protein levels. This suggests that these macroalgae are likely to be higher in protein, making them a nutritious option for consumers seeking plant-based protein sources.

5 Conclusion

The consumption of seaweeds as part of a regular diet offers significant health benefits. The five species studied in this research show a strong potential to serve as valuable nutritional resources due to their biochemical composition.

The nutritional profiles of the studied organisms position these seaweeds as important dietary components for supporting human health and preventing chronic diseases. The antioxidant properties of the species studied, especially the green algae, suggest that these macroalgae could serve as excellent sources of natural antioxidants, making them suitable for use in functional foods and nutraceuticals. In addition, the diverse and nutrient-rich mineral profiles of the algae highlight their potential as important contributors to a balanced diet. While no single species provides all essential minerals, the variation in elemental composition between species highlights the importance of consuming a variety of seaweeds to maximize nutritional benefits.

However, it is important to note that these results only provide a snapshot of the nutritional and biochemical composition, as chemical diversity can vary significantly both between and within species due to abiotic factors such as light, temperature and nutrient availability. This variability highlights the need for further studies to fully capture the nutritional potential of seaweeds under different conditions. Moreover, understanding the effects of culture parameters that influence the biochemical composition of the algae allows a targeted manipulation and enhancement of specific compounds [85, 102].

Overall, seaweeds provide a natural source of essential nutrients such as antioxidants, minerals, and other health-promoting compounds. Including them in the diet not only

supports overall well-being, but also contributes to the growing interest in blue food candidates as sustainable, nutritious options for the future.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44187-025-00603-3.

Supplementary Material 1

Acknowledgements

The authors would like to thank the Stolli dive base for their assistance with sampling of Caulerpa cylindracea. Also, the staff of the BioLab and ChemLab at ZMT for their technical support with species identification and the analysis of carbohydrates and elemental composition. Our thanks extend to Britta Iken and Sabrina Dorschner from the Marine Botany and Marine Zoology working groups at the University of Bremen for their help with pigment, lipid, and fatty acid analyses, and to Martin Gräve from the Alfred Wegener Institute, Bremerhaven, for his support with fatty acid identification. We also appreciate the contributions of Milena Söhnen for providing Caulerpa racemosa samples and Aljoscha Fuchs for the measurements of antioxidant and protein content and Lara E. Stuthmann for her invaluable support.

Author contributions

BBDC: Conceptualization, Investigation, Formal analysis, Visualization, Methodology, Writing – Original Draft Preparation; AK: Writing – Review & Editing, Supervision; KS: Writing – Review & Editing, Supervision.

Funding

The conduction of this research was supported by the Marine Botany working group of the University of Bremen.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics, approval and consent to participate

This research was conducted in full compliance with national and regional guidelines in accordance with the Nagoya Protocol on Access and Benefit-Sharing. All necessary permits and approvals for the collection, transport, and use of the algae were obtained from the relevant authorities. For specimens purchased from suppliers, all necessary legal and ethical considerations were met.

Competing interests

The authors declare no competing interests.

Received: 25 January 2025 / Accepted: 21 August 2025

Published online: 26 August 2025

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