Journal of Applied Phycology (2025) 37:597–615
https://doi.org/10.1007/s10811-024-03403-x

RESEARCH

Comprehensive analysis of dehydrated edible macroalgae: Volatile compounds, chemical profiles, biological activities, and cytotoxicity

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Received: 18 October 2024 / Revised: 21 November 2024 / Accepted: 22 November 2024 / Published online: 9 January 2025
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Abstract

Seaweeds offer sustainable, low-calorie nutritional options to address global food demand. Their limited use is due to a lack of understanding of their flavor, influenced by volatile organic compounds (VOCs). This study aims to expand knowledge of sensory, bioactive, and chemical properties of edible macroalgae (*Chondrus crispus, Gracilaria gracilis, Porphyra dioica, Pyropia haitanensis, Palmaria palmata,* and *Ulva rigida*) analyzing their VOCs, phenolics, proteins, free amino acids, sugars, and bioactivities. Extracts were obtained using 80% ethanol (25ºC, 60 min). HS-SPME/GC–MS analyses identified distinct compounds, such as 3-methyl-1-butanol, 2-ethyl-1-hexanol, geranylacetone, *trans*-linalool oxide, and trimethylpyrazine in *P. haitanensis*, (*Z*)-4-heptenal in *P. dioica*, octanal, isophorone, heptanoic acid, 2,6-dimethylpyrazine, and tetramethylpyrazine in *P. palmata*, 2-methyl-2-pentenal, 1-pentanol, and 1-hexanol in *G. gracilis*, (*E*)-2-pentenal, (*E*,*E*)-2,4-heptadienal, 5-ethyl-2-furaldehyde, α-terpineol, and α-muurolene in *U. rigida*. Novel compounds were discovered in *P. haitanensis* (20), *P. palmata* (4), *C. crispus* (10), *U. rigida* (14), *G. gracilis* (11), and *P. dioica* (19). Red algae, especially *Porphyra*/*Pyropia* and *P. palmata*, were rich in phenolics, proteins, and sugars. *P. haitanensis* showed the strongest antioxidant and anti-inflammatory properties, while *P. dioica* demonstrated lipid peroxidation prevention. These results, with the safe profile of all evaluated macroalgae, underscore the potential of seaweeds as innovative nutritional and bioactive food ingredients.

Keywords Seaweed · Rhodophyta · Chlorophyta · Innovative foods · Volatile organic compounds · Bioactivity · Cellular assays

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Introduction

One of the most pressing challenges facing society is the need to meet the growing food demands of an ever-expanding global population. By 2050, it is projected that the world's population will reach 9.8 billion people, requiring a 56% increase in calorie consumption compared to 2010 (World Resources Institute 2018). Globally, approximately 795 million people are grappling with undernourishment, and 2 billion suffer from micronutrient deficiencies (FAO et al. 2015), with particularly acute issues in Asia and Africa regions, where population growth is concentrated (Pereira 2020).

At present, nearly half of the world's arable land is allocated to agriculture. However, this practice contributes to 25% of global greenhouse gas emissions, with land-use change emerging as the primary driver (World Resources Institute 2018). Climate change, linked to an increase of natural hazards, poses significant challenges to agriculture, absorbing 22% of the economic impact and affecting crops, livestock production and fisheries (FAO et al. 2015).

Consequently, addressing the global food demand while ensuring food security and environmental sustainability necessitates careful consideration of economic, environmental, and social factors (Lafeuille et al. 2023).

Despite covering 71% of the Earth's surface, oceans contribute a mere 2% to the global demand for food calories (Gierсksky and Doumeizel 2023). Expected to rise by 15% in the next decade, aquaculture has stirred controversy due to its environmental impact (Queirós et al. 2021). Consequently, in the quest for new sources of sustainable foods, the European Union has set forth a plan to double algae production by 2025. This endeavor aims to foster the decarbonization of waters, oceans and seas, thereby mitigating the environmental footprint associated with aquaculture (Kuech et al. 2023). Seaweeds, categorized as low-trophic-level species, exhibit a growth rate conductive to intensive cultivation. They are heralded as one of the most sustainable alternatives for fulfilling global food demand while meeting nutritional requirements with a low caloric value (Pereira 2020). Macroalgae are known for their low fat content and high levels of polysaccharides, fiber, proteins, vitamins, and minerals (Kim and Venkatesan 2015; Cikoš et al. 2020). Recognized as the new "superfoods" (Cikoš et al. 2020), seaweeds have been proposed for the development of innovative, healthier food products such as sodium-reduced, or gluten-free options, while maintaining physicochemical and sensory quality (Yesuraj et al. 2022). Moreover, seaweeds can be integrated into vegan/vegetarian diets as an alternative protein source (Cikoš et al. 2020; Yesuraj et al. 2022), providing a promising approach to meeting the global protein by 2050 with their high content of essential amino acids (Kuech et al. 2023).

Macroalgae flourish in a challenging environment marked by harsh conditions such as temperature fluctuations, salinity, UV radiation exposure, and the presence of pollutants (Cikoš et al. 2020). To thrive in this extreme habitat, they produce a diverse array of secondary metabolites distinct from those found in terrestrial plants (Lomartire and Gonçalves 2023). These compounds include pigments, phenolics, and volatile organic compounds (VOCs) (Goksen 2023). The significant presence of VOCs in seaweeds varies depending on the species and their geographical origin (Figueroa et al. 2023). Among the primary VOCs identified in algae stand out alcohols, carboxylic acids, aldehydes, and ketones (Sánchez-García et al. 2019), recognized for their antimicrobial, antiproliferative, and antioxidant properties (Nunes et al. 2022). VOCs play a pivotal role in defining the aroma of macroalgae, serving as crucial factors in determining food flavor (Sánchez-García et al. 2019). Additionally, they offer a means to evaluate the quality of seaweed and authenticate the presence of specific flavoring substances (Pina et al. 2014; Nunes et al. 2022).

Despite the vast and untapped potential for gastronomic innovation offered by seaweed extracts (Pereira 2020), their limited incorporation into everyday culinary practices is often attributed to a lack of understanding of their flavor and texture (Yesuraj et al. 2022). Furthermore, the sensory properties exhibited in their raw state pose significant barriers to consumption.

Given the limited research on the volatile organic compound (VOC) profiles of macroalgae, this study aims to investigate the volatile organic compound (VOC) profiles of six edible macroalgae post-dehydration to gain a comprehensive understanding of their odor profiles. The goal is to propose these macroalgae as bioactive food ingredients, suitable for integration into regular culinary practices, offering high nutritional value and superior sensory properties. For this purpose, both the chemical composition and biological activity were assessed. Finally, to ensure their safety, the cytotoxic profiles of the edible macroalgae extracts were also assessed.

Materials and Methods

Standards and reagents

Arginine (≥ 98%), bovine serum albumin (BSA) (96%), D,L-glyceraldehyde, Iron(II) sulfate heptahydrate, Folin & Ciocalteu's phenol reagent, gallic acid (≥ 98.0%), L-DOPA, linoleic acid, 5-lipoxygenase from *Glycine max* (soybean), 2-mercaptoethanol, N-(1-naphthyl)ethylenediamine dihydrochloride, ninhydrin, sodium nitroprusside dihydrate (SNP), sucrose (≥ 99.0%), sulfanilamide, and tyrosinase from mushroom were from Sigma-Aldrich (USA); fetal bovine serum (FBS), Dulbecco's Modified Eagle Medium DMEM (1X) + GlutaMAX, AB "Pen Strep" Glico, Hank's balanced salt solution (HBSS) and trypsin from Gibco, Thermo Fisher (Waltham, USA); MTT from Alfa Aesar Chemicals (Haverhill, USA); ascorbic acid was from Fluka Analytical; aldose-reductase (*Homo sapiens,* human) and NADPH from Prozomix (UK). Commercial standards for VOC identity confirmation were supplied by Sigma Aldrich (USA): hexanal (≥ 97.0%), (*Z*)−4-heptenal (≥ 98%), heptanal (≥ 95%), benzaldehyde (≥ 99%), octanal (99%), safranal (≥ 90%), decanal (95%), 1-penten-3-ol (≥ 98%), 3-methyl-1-butanol (≥ 99%), 1-hexanol (≥ 97%), 1-octen-3-ol (≥ 98%), benzyl alcohol (≥ 99.0%), *(E)*−2-octen-1-ol (97%), geranylacetone (≥ 97%), propanoic acid (≥ 99.5%), butanoic acid (≥ 99%), *trans*-linalool oxide (≥ 97.0%), *α*-terpineol (90%), *β*-cyclocitral (≥ 95%), *α*-ionone (≥ 90%), *β*-ionone (≥ 97%).

Macroalga samples

This study focuses on six varieties of edible macroalgae, shown in Fig. S1: the red algae Iris moss (*Chondrus crispus* Stackhouse), Cabelo de velha - Ogonori (*Gracilaria gracilis* (Stackhouse) Steentoft, Irvine & Farnham), Botelho comprido - Dulse (*Palmaria palmata* (L.) F.Weber & D.Mohr), Erva patinha – Atlantic nori (*Porphyra dioica* J. Brodie & L.M. Irvine), and Tan zicai (*Pyropia haitanensis* (T.I.Chang & B.F.Zheng) N. Kikuchi & M. Miyata) , along with the green alga Alface do mar (*Ulva rigida* C.Agardh). All these species, sourced from the Atlantic Ocean along the coasts of Portugal were acquired in a dehydrated state from Algaplus (www.algaplus.pt/). *Pyropia haitanensis* was collected from Thailand and provided by Thai Imex Ltd. Voucher specimens are stored at REQUIMTE/LAQV, Porto.

Extraction process

For the extraction process, the dried macroalgae underwent milling using a Retsch mill (model GM200, 50/60 Hz, 1000 W, 220–240 V). Fractions below 910 µm were specifically chosen as raw materials for extraction. Subsequently, solvent extraction was carried out using the maceration method with a mixture of ethanol:water (80:20, v/v). In brief, 3.0 ± 0.1 g of raw material were placed into an Erlenmeyer flask with 200 mL of solvent and subjected, at room temperature, to a 5-min ultrasounds process (Bandelin Sonorex, Sonorex Super RK514BH, 35 kHz, 215 W). The flask was then transferred to an incubator shaker (RSlab, model RSLAB-7, 50/60 Hz, 30 W, 100–240 V), shielded from light to prevent sample oxidation, and set at 25 °C for 60 min maintaining mechanical stirring at 400 rpm. Upon completion of the extraction, the mixture was filtered and the solid residue was discarded. The ethanol and water fractions in the liquid extracts were eliminated using a rotary evaporator (Heidolph Laborota 4001) at 35ºC and pressure below 70 mbar, resulting in a dry solid extract. To facilitate the subsequent assays, the extracts were redissolved in DMSO, filtered through a PTFE 0.45 µm filter, and stored at −18ºC until analysis. The results are expressed as mg of dried extract per milliliter of the extract solution ($mg_{dry\text{-}extract}\ mL^{-1}$).

Nutrient profile

Total soluble sugars

The determination of total soluble sugars was carried out using a modified version of Nielsen's protocol (Nielsen 2010), employing the phenol-sulfuric method. In brief, the absorbance was measured at 490 nm after combining the sample with a 6.5% (v/v) phenol solution in sulfuric acid. The results, expressed as mg of sucrose equivalent per gram of extract (mg S-Eq g^{-1}), were obtained using a calibration curve constructed with sucrose as standard.

Total protein

The samples were incubated in darkness with Bradford reagent for 5 min and the absorbance was subsequently measured at 595 nm (Bradford 1976). A calibration curve was generated using bovide serum albumin (BSA) and the results are expressed as mg of BSA equivalent per gram of extract (mg BSA-Eq g^{-1}).

Total free amino acids

To assess the overall content of total free amino acids, the ninhydrin reaction method from Sigma-Aldrich with slight modifications was employed (Trigueros et al. 2021). In brief, equal volumes of sample and ninhydrin solution were combined, followed by a 10 min incubation in a boiling water bath and subsequent cooling. Ethanol was added and the absorbance was measured at 570 nm. Arginine was used for constructing a calibration curve, allowing to express the results as mg of arginine equivalent per gram extract (mg ARG-Eq g^{-1}).

Total phenolic content

The determination of total phenolic content (TPC) was carried out following the Folin-Ciocalteu procedure (Singleton et al. 1999). Gallic acid was employed as a standard to express the results as mg of gallic acid equivalent per gram of extract (mg GA-Eq g^{-1}).

HS-SPME/GC-MS for volatile compounds analysis

The detection of volatile organic compounds (VOCs) in macroalgae was performed using an automated headspace solid-phase microextraction (HS-SPME) system coupled with gas chromatography-mass spectrometry (GC-MS). This automated analysis was carried out with a COMBI-PAL system (Varian Pal Autosampler, Switzerland), connected to a 436-GC gas chromatograph (Bruker Daltonics) and a SCION single quadrupole mass spectrometer (Bruker Daltonics). An SLB-5ms (Supelco) fused silica capillary column (30 m x 0.25 mm x 0.25 µm) was utilized for the analysis. The oven temperature was initially set to 40ºC and held for 1 min, then ramped to 250ºC at a rate of 5ºC min^{-1} and held for 5 min. Subsequently, the temperature was further increased to 300ºC at the same heating rate. The total analysis time was 58 min. The detailed acquisition parameters are provided in a previous study (Trigueros et al. 2024a). Briefly, 0.1 g of each sample was transferred to a

20 mL glass vial and incubated 5 min at 45ºC. VOCs were extracted through 30 min incubation at 45°C, with a stirring speed of 250 rpm, a 50/30 µm divinylbenzene/carboxen/polydimethylsiloxane (DVB/CAR/PDMS) fiber (Supelco Inc., USA). The identification of VOCs involved comparing the retention indices (Kovats indices), m/z values, and mass spectra of each peak with literature data and with the National Institute of Standards and Technology (NIST14) reference database. Additionally, identification confirmation was performed with commercially standards, when available. Levels of metabolite annotation was performed as in Viant et al. (2017).

In vitro biological activity screening

Lipid peroxidation activity assay

The evaluation of the impact of algae samples on linoleic acid peroxidation was assessed by adding 5 mM ascorbic acid to a blend of the extract, 20 mM linoleic acid, 0.1 mM Tris-HCl (pH 7.5), and 4 mM iron(II) sulfate heptahydrate. Following incubation at 37ºC for 60 min, 750 µL of ethanol:ether (3:1, v/v) was added, and absorbance was recorded at 233 nm (Trigueros et al. 2024a). The inhibition of lipid peroxidation by the extracts was estimated relative to a control prepared with Tris-HCl buffer (100 mM, pH 7.5).

Aldose-reductase activity assay

The inhibitory potential of each extract against aldose reductase activity was evaluated using a method outlined by Ferreres et al. (2021). In summary, equal volumes of extract, aldose-reductase enzyme solution (1 mg mL^{-1}), and 10 mM D,L-glyceraldehyde were dispensed onto a plate and preincubated at 37°C for 2 min. The reaction was then initiated by the addition of 0.5 mM NADPH and the absorbance at 340 nm was promptly measured. Subsequently, a second measurement was taken after 20 min incubation. This procedure was repeated in triplicate for three independent assays.

Tyrosinase activity assay

The impact of the macroalgae extracts on tyrosinase activity was tracked by monitoring L-DOPA oxidation. In summary, 40 µL of the extract and 40 µL of enzyme solution (100 U mL^{-1}), along with 40 µL of 4.5 mM L-DOPA, were mixed and the oxidation reaction was monitored at 475 nm for 3 min at 20ºC. The sample was substituted with potassium phosphate buffer (50 mM, pH 6.8) to prepare a control for assessing the inhibition capacity of the sample (Trigueros et al. 2024a).

Lipoxygenase activity assay

Linoleic acid oxidation was employed to determine 5-lypoxigenase (5-LOX) activity as previously described (Trigueros et al. 2024a). After mixing the algal extracts with the enzyme solution (100 U mL^{-1}) for 5 min, the oxidation reaction commenced with the addition of 4.18 mM linoleic acid and the absorbance kinetics were monitored at 234 nm for 3 min. A control with phosphate buffer (100 mM, pH 9) was used to estimate the sample's inhibition capacity.

Cellular assays

Cell culture

Human colorectal adenocarcinoma Caco-2 cells and mouse microglia BV2 cells were procured from ATCC (Spain). The cells were cultured in DMEM (1X) + GlutaMAX medium, supplemented with 10% FBS and 1% penicillin-streptomycin, under a humidified atmosphere containing 5% CO_2 at 37°C. Prior to use, the cells were passaged twice. Adherent Caco-2 cells were washed with HBSS upon reaching 70–80% confluence and then trypsinized for subculturing. For experiments, cells were seeded into 96-well plates at a density of 20,000 cells $well^{-1}$ for Caco-2 and 40,000 cells $well^{-1}$ for BV2. The plates were incubated at 37°C for 24 h.

Cell viability assay

The effect of macroalgae extracts on the viability of Caco-2 and BV2 cells was evaluated using the MTT assay as previously described by Ferreres et al. (2021). In brief, serial dilutions of the macroalgae extracts were added to subcultured cell plates and incubated for 24 h at 37ºC. After incubation, the medium was aspirated and replaced with MTT solution. Cell survival was determined by measuring absorbance at 260 nm, with results expressed relative to a control without the extracts. All experiments were performed in triplicate.

Statistical analysis

Statistical analysis was performed using GraphPad Prism 8.4.2 Software. All assays were performed in triplicate and results are expressed as mean ± standard deviation. Significant differences between extracts were confirmed using the Student *t*-test with a two-tailed unpaired method, establishing significance at a p-value < 0.05. Principal component analysis (PCA) was conducted using IBM SPSS Statistics (version 29.0) for Windows and was applied to the total contents of aldehydes, alcohols, ketones, acids, monoterpenes, sesquiterpenes, norisoprenoids, lactones, and pyrazines for each studied macroalgae, aiming to observe the similarities between them.

Results

Nutrient profile composition

Algae are recognized for their outstanding nutritional attributes, offering vitamins, proteins, lipids, polysaccharides, fibers, enzymes, and minerals in higher concentrations compared to land-based food sources (Cikoš et al. 2020; Yesuraj et al. 2022). To further enhance the characterization of the evaluated algae, their nutrient profile, in terms of total sugars, proteins, free amino acids and phenolic compounds, was examined. The results are presented in Table 1. As can be observed, red algae generally exhibited significant higher nutrients content ($p < 0.05$) compared to the green alga (*U. rigida*). *Porphyra/Pyropis* algae have proven to be particularly rich sources of phenolic compounds and protein fractions, including both total protein content and free amino acids. Additionally, *P. palmata* showed the highest sugar content.

Volatile organic compounds (VOCs) identification

Volatile compounds play a crucial role in defining the unique odor and aroma of algae, setting them apart from other culinary ingredients and imparting distinct flavor nuances to dishes (Yamamoto et al. 2014). Forty-seven volatile compounds were identified in the examined macroalgae through HS-SPME/GC-MS analysis. These compounds comprised 14 aldehydes, 10 alcohols, 4 ketones, 8 acids, 2 monoterpenes, 1 sesquiterpene, 3 norisoprenoids, 1 lactone, and 4 pyrazines (Table 2 and Fig. 1). Notably, acids, aldehydes, and alcohols emerged as the predominant compounds present across all six macroalgae varieties. Interestingly, pyrazines were only detected in the *Porphyra* and *Pyropia* species and in *P. palmata*, terpenes were only detected in *P. haitanensis* and *U. rigida*, and lactones were only observed in *P. haitanensis* and *P. palmata* (Fig. 1).

A Principal Component Analysis (PCA) was conducted with data included in Table 2. Fig. 2 depicts the projection of the VOCs profiles of the six macroalgae onto the plane defined by the principal axes PC1 and PC2, containing 69.94% of the total variance. *Pyropia haitanensis* was projected within the quadrant delineated along the negative PC1 and PC2 axes. This positioning is attributed to its elevated levels of pyrazines (**45–46**) and lactones, particularly γ-butyrolactone (**43**). Likewise, *P. palmata* was also positioned along the negative PC1 and PC2 axes, characterized by higher content of lactones (**43**), and ketones (**25–27**). The projection of *U. rigida*, distinctly distant from the other, was displayed across the negative PC1 and positive PC2 axes due to its notable abundance of sesquiterpenes, particularly α-muurolene (**39**), and monoterpenes, specifically α-terpineol (**38**). *Gracilaria*

Table 1 Nutrient profile of studied macroalgae species[a].

	C. crispus			*G. gracilis*			*P. dioica*			*P. haitanensis*			*P. palmata*			*U. rigida*		
Total soluble sugars (mg S-Eq g^{-1})	8.9	±	1.6^{bc}	9.4	±	1.0^{b}	5.6	±	0.5^{d}	6.4	±	0.9^{cd}	22	±	4^{a}	5.7	±	0.9^{d}
Total proteins (mg BSA-Eq g^{-1})	1.09	±	0.08^{c}	1.61	±	0.07^{d}	2.37	±	0.06^{a}	1.00	±	0.03^{c}	0.43	±	0.05^{b}	2.43	±	0.14^{a}
Total free amino acids (mg ARG-Eq g^{-1})	31	±	2^{a}	52	±	3^{e}	193	±	6^{b}	64	±	10^{e}	11.8	±	0.7^{c}	1.4	±	0.3^{d}
Total phenolic content (mg GA-Eq g^{-1})	3.54	±	0.06^{a}	6.5	±	1.4^{b}	14.77	±	0.04^{c}	10.78	±	0.05^{d}	1.76	±	0.03^{e}	1.07	±	0.01^{f}

[a] Values are represented as mean ± SD of three determinations and correspond to mg of standard equivalent per gram of dried macroalgae. Values with different letters in each row are significantly different ($p < 0.05$)

Table 2 Volatile composition of six macroalgae species

Compounds		RT	Most abundant ions (m/z)	R_{match}	RI_T	RI_E	Area $10^{-6} \pm SD$					
							C. crispus	*G. gracilis*	*P. dioica*	*P. haitanensis*	*P. palmata*	*U. rígida*
Aldehydes												
1	Pentanal [L2]	3.71	41/44/58	887	699	-	46 ± 4	74 ± 13	nd	nd	nd	83 ± 10
2	*(E)*−2-Pentenal [L2]	4.72	41/55/83	837	754	-	nd	nd	nd	nd	nd	28 ± 3
3	Hexanal [L1]	5.65	41/44/56	959	-	-	438 ± 16	585 ± 32	81 ± 3	62 ± 6	nd	131 ± 9
4	2-Methyl-2-Pentenal [L2]	6.42	41/69/98	966	837	822	nd	143 ± 34	nd	nd	nd	nd
5	*(Z)*−4-Heptenal [L1]	8.27	41/55/67	925	-	-	nd	nd	11.6 ± 0.4	nd	nd	nd
6	Heptanal [L1]	8.35	41/43/44	926	-	-	nd	52 ± 6	15.0 ± 0.4	nd	nd	21 ± 3
7	*(Z)*−2-Heptenal [L2]	10.04	41/55/83	941	958	948	19 ± 3	nd	nd	12.6 ± 1.4	nd	nd
8	Benzaldehyde [L1]	10.17	77/105	963	-	-	328 ± 24	nd	113.2 ± 1.2	25.9 ± 1.6	117 ± 3	90 ± 7
9	Octanal [L1]	11.40	41/43/57	935	-	-	nd	nd	nd	nd	33 ± 3	nd
10	*(E,E)*−2,4-Heptadienal [L2]	11.68	81	858	1012	1002	nd	nd	nd	nd	nd	179 ± 6
11	5-Ethyl-2-furaldehyde [L2]	12.99	109/124	905	1032	1044	nd	nd	nd	nd	nd	23 ± 2
12	*(E)*−2-Octenal [L2]	13.12	55/70	874	1060	1049	17 ± 3	nd	nd	nd	nd	24.1 ± 1.7
13	2,6,6-Trimethyl-1,3-cyclohexadiene-1-carboxaldehyde (safranal) [L1]	17.39	91/105/107	928	-	-	nd	nd	35 ± 2	59.9 ± 1.7	nd	nd
14	Decanal [L1]	17.52	41/43/57	899	-	-	7.2 ± 2.0	nd	nd	nd	26.8 ± 1.3	nd
Total aldehydes							**855 ± 30[a]**	**854 ± 49[a]**	**256 ± 4[b]**	**160 ± 6[c]**	**177 ± 4[d]**	**579 ± 18[e]**
Alcohols												
15	1-Penten-3-ol [L1]	3.52	57	896	-	-	5.6 ± 0.6	nd	94 ± 3	40 ± 3	nd	70 ± 7
16	3-Methyl-1-butanol [L1]	4.38	55/70	902	-	-	nd	nd	nd	20 ± 2	nd	nd

Table 2 (continued)

	Compounds	RT	Most abundant ions (m/z)	R_{match}	RI_T	RI_E		Area $10^{-6} \pm SD$									
								C. crispus		*G. gracilis*		*P. dioica*	*P. haitanensis*		*P. palmata*		*U. rígida*
17	1-Pentanol [L2]	4.96	41/42/55	936	765	-		nd		127 ± 8		nd	nd		nd		nd
18	*(Z)*−2-Penten-1-ol [L2]	5.02	41/57	919	767	-		nd		nd		50 ± 2	59 ± 2		nd		137 ± 12
19	1-Hexanol [L1]		7.46	56	906	-	-	nd		192 ± 49		nd		nd	nd		nd
20	1-Octen-3-ol [L1]		10.71	57	914	-	-	411 ± 46		1564 ± 523		231 ± 12		296 ± 15	nd		nd
21	2-Ethyl-1-hexanol [L2]		12.22	41/57	884	1030	1020	nd		nd		nd		17.9 ± 0.8	nd		nd
22	Benzyl alcohol [L1]		12.41	77/79/108	923	-	-	129 ± 14		nd		144 ± 6		24.0 ± 1.4	nd		205 ± 6
23	*(E)*−2-Octen-1-ol [L1]		13.39	41/55/57	920	-	-	139 ± 19		199 ± 35		19.8 ± 0.5		42.1 ± 1.3	nd		nd
24	*(E)*−2-Nonen-1-ol [L2]		14.51	41/43/57	848	1081	1094	nd		nd		nd		nd	82.7 ± 0.4		34.7 ± 1.3
Total alcohols										**685 ± 52[a]**	**2082 ± 526[b]**	**539 ± 14[c]**	**499 ± 15[d]**		**82.7 ± 0.4[e]**		**447 ± 15[f]**
Ketones																	
25	*(E,E)*−3,5-Octadien-2-one [L2]		14.19	43/95	912	1073	1083	nd		nd		67 ± 4	51 ± 3		25.84 ± 0.13		107 ± 8
26	3,5,5-Trimethyl-2-cyclohexen-1-one (isophorone) [L2]		15.09	82	897	1124	1113	nd		nd		nd	nd		12.8 ± 0.8		nd
27	2,6,6-Trimethyl-2-cyclohexene-1,4-dione (ketoisophorone) [L2]		15.72	68/96/152	930	1144	1134	40 ± 3		nd		30 ± 2	nd		91.7 ± 1.9		32.0 ± 1.9
28	*(E)*−6,10-Dimethyl-5,9-undecadien-2-one (geranylacetone) [L1]		24.03	41/43/69	931	-	-	nd		nd		nd	56 ± 2		nd		nd
Total ketones										**40 ± 3[a]**	**nd**	**97 ± 4[b]**	**107 ± 4[c]**		**130 ± 2[d]**		**139 ± 8[d]**
Acids																	
29	Acetic acid [L2]		2.79	43/45/60	969	-	-	1365 ± 3		217 ± 30		399 ± 5	794 ± 14		2204 ± 20		108 ± 4
30	Propanoic acid [L1]		3.92	45/73/74	893	-	-	103 ± 5		nd		nd	46.8 ± 0.4		752 ± 15		210 ± 11
31	2-Methylpropanoic acid [L2]		4.95	41/43/73	907	772	-	1054 ± 26		nd		34 ± 5	99.99 ± 0.10		178 ± 4		21 ± 3
32	Butanoic acid [L1]		5.72	60/73	864	-	-	110 ± 3		nd		nd	42 ± 2		249 ± 3		108 ± 9
33	3-Methylbutanoic acid [L2]		7.14	60	923	851	848	5669 ± 320		nd		19.8 ± 1.1	106 ± 13		1111 ± 21		44 ± 10
34	2-Methylbutanoic acid [L2]		7.39	41/57/74	906	861	857	3183 ± 135		nd		20 ± 6	133 ± 4		311 ± 3		50 ± 5
35	Hexanoic acid [L2]		11.07	60/73	939	990	982	1645 ± 321		nd		nd	212 ± 17		285 ± 9		57 ± 8
36	Heptanoic acid [L2]		13.71	45/60/73	819	1078	1068	nd		nd		nd	nd		35.3 ± 1.9		nd
Total acids								**13,129 ± 474[a]**		**217 ± 30[b]**		**473 ± 9[c]**	**1434 ± 26[d]**		**5125 ± 34[e]**		**598 ± 20[f]**

Table 2 (continued)

	Compounds	RT	Most abundant ions (m/z)	R_{match}	RI_T	RI_E	Area $10^{-6} \pm SD$					
							C. crispus	*G. gracilis*	*P. dioica*	*P. haitanensis*	*P. palmata*	*U. rígida*
Monoterpenes												
37	2-[(2*S*,5*S*)−5-Ethenyl-5-methyloxolan-2-yl] propan-2-ol (*trans*-linalool oxide) *L1*	14.02	43/55/59	877	-	-	nd	nd	nd	23.7 ± 0.9	nd	nd
38	2-(4-Methylcyclohex-3-en-1-yl)propan-2-ol (*α*-terpineol) *L1*	17.26	59/93	957	-	-	nd	nd	nd	nd	nd	33.9 ± 1.3
Total monoterpenes							**nd**	**nd**	**nd**	**23.7 ± 0.9[a]**	**nd**	**33.9 ± 1.3[b]**
Sesquiterpenes												
39	(1*S*,4a*S*,8a*R*)−4,7-dimethyl-1-propan-2-yl-1,2,4a,5,6,8a-hexahydronaphthalene (*α*-muurolene) *L2*	25.43	41/91/105	930	1500	1491	nd	nd	nd	nd	nd	12.2 ± 0.6
Total sesquiterpenes							**nd**	**nd**	**nd**	**nd**	**nd**	**12.2 ± 0.6**
	Norisoprenoids											
40	2,6,6-trimethyl-1-cyclohexene-1-carbaxaldehyde (*β*-cyclocitral) *L1*	17.98	67/109	940	-	-	nd	74 ± 20	34.7 ± 1.4	23.5 ± 0.9	nd	nd
41	*(E)*−4-(2,6,6-Trimethylcyclohex-2-en-1-yl)but-3-en-2-one (*α*-ionone) *L1*	23.45	43/93/121	904	-	-	70 ± 10	nd	111 ± 7	77.7 ± 1.7	37 ± 2	nd
42	*(E)*−4-(2,6,6-trimethylcyclohexen-1-yl)but-3-en-2-one (*β*-ionone) *L1*	24.89	43/177	934	-	-	nd	179 ± 47	nd	63 ± 2	nd	nd
Total norisoprenoids							**70 ± 10[a]**	**253 ± 52[b]**	**146 ± 7[c]**	**164 ± 3[d]**	**37 ± 2[e]**	**nd**
Lactones												
43	Oxolan-2-one (*Υ*-butyrolactone) *L2*	8.59	41/42	935	915	901	nd	nd	nd	37.1 ± 1.6	173 ± 5	nd
Total lactones							**nd**	**nd**	**nd**	**37.1 ± 1.6[a]**	**173 ± 5[b]**	**nd**
Pyrazines												
44	2,6-Dimethylpyrazine *L2*	8.79	42/108	883	917	907	nd	nd	nd	nd	22.6 ± 1.6	nd

Table 2 (continued)

	Compounds	RT	Most abundant ions (m/z)	R_{match}	RI_T	RI_E	Area $10^{-6} \pm SD$					
							C. crispus	*G. gracilis*	*P. dioica*	*P. haitanensis*	*P. palmata*	*U. rigida*
45	Trimethylpyrazine [L2]	11.39	42/122	873	1004		993 nd	nd	nd	93 ± 3	nd	
46	3-Ethyl-2,5-dimethylpyrazine [L2]	13.69	135/136	912	1082		1070 nd	nd	30 ± 2	162 ± 7	nd	
47	Tetramethylpyrazine [L2]	13.94	54/136	934	1089		1075 nd	nd	nd	nd	9.1 ± 0.5	nd
Total pyrazines							**nd**	**nd**	**30 ± 2[a]**	**255 ± 7[b]**	**32 ± 2[a]**	**nd**

RT: retention time (min); R_{match}: identification method by the NIST14 Library Database; RI_T: retention index reported in literature (Nunes et al. 2022; Fang et al. 2023) and NIST14 database; RI_E: retention index determined using a commercial hydrocarbon mixture (C8-C20); (Area ± SD) × 10^6 expressed in arbitrary units from three independent assays. [L1] Compound identified by comparison of the RT and MS fragmentation of a commercial reference standard performed under the identical analysis conditions; [L2] Compound identified by spectral MS similarity with the NIST14 database (Viant et al. 2017); nd = not detected. Values with different letters in each row are significantly different ($p < 0.05$)

gracilis was also differentiated from the other macroalgae, being located practically on axis PC2 and positively along PC1 component, essentially due to its notable content of alcohols (**17, 19, 20, 23**). *Porphyra dioica* was projected into the plane defined by the positive PC1 and the negative PC2 axis and *C. crispus* was positioned across the positive PC1 and PC2 axes, both due to its elevated concentration of acids (**29, 31, 33, 34**) and (**29–35**), respectively.

Biological activity screening

Macroalgae have been extensively studied as a rich source of various molecules with antioxidant potential capable of neutralizing free radicals, thereby preventing oxidative damage. To assess the bioactive potential of the six edible macroalgae under study, a screening was carried out to evaluate their antioxidant, anti-tyrosinase, and anti-inflammatory properties. Figure 3 illustrates the ability of the analyzed macroalgae extracts to inhibit lipid peroxidation and to inhibit various targeting enzymes, showing a concentration-dependent trend. Based on the observed experimental results, the *P. dioica* extract revealed the most efficient inhibition capacity against lipid peroxidation (IC_{50} = 0.86±0.06 mg mL^{-1}), while the *P. haitanensis* extract exhibited the highest inhibition activity against aldose-reductase (IC_{50} = 1.00±0.07 mg mL^{-1}) and 5-LOX (IC_{25} = 0.26±0.04 mg mL^{-1}). Conversely, all the evaluated algae exhibited significantly lower inhibition of tyrosinase activity, making it impossible to estimate their IC_{50} values.

Cytotoxicity of the macroalgae extracts

In the final phase of this study, the cytotoxic profile of macroalgae extracts was evaluated on various human cell lines using the MTT assay. Specifically, the effects of the extracts on the viability of human colorectal adenocarcinoma Caco-2 cells and mouse microglia BV2 cells were assessed (Figs. 4 and 5). As shown, none of the extracts caused significant changes in cell viability for either Caco-2 or BV-2 cells across the tested concentration range, where the samples proved their biological activities. These results, compared to a control prepared under identical experimental conditions without the sample, demonstrate the extracts safety, supporting their potential for use in food applications.

Discussion

Volatile organic compounds (VOCs) profiles of edible macroalgae

While numerous studies in the literature have focused on the volatile composition of *PorphyraPyropia* species, there is limited research specifically evaluating VOCs in

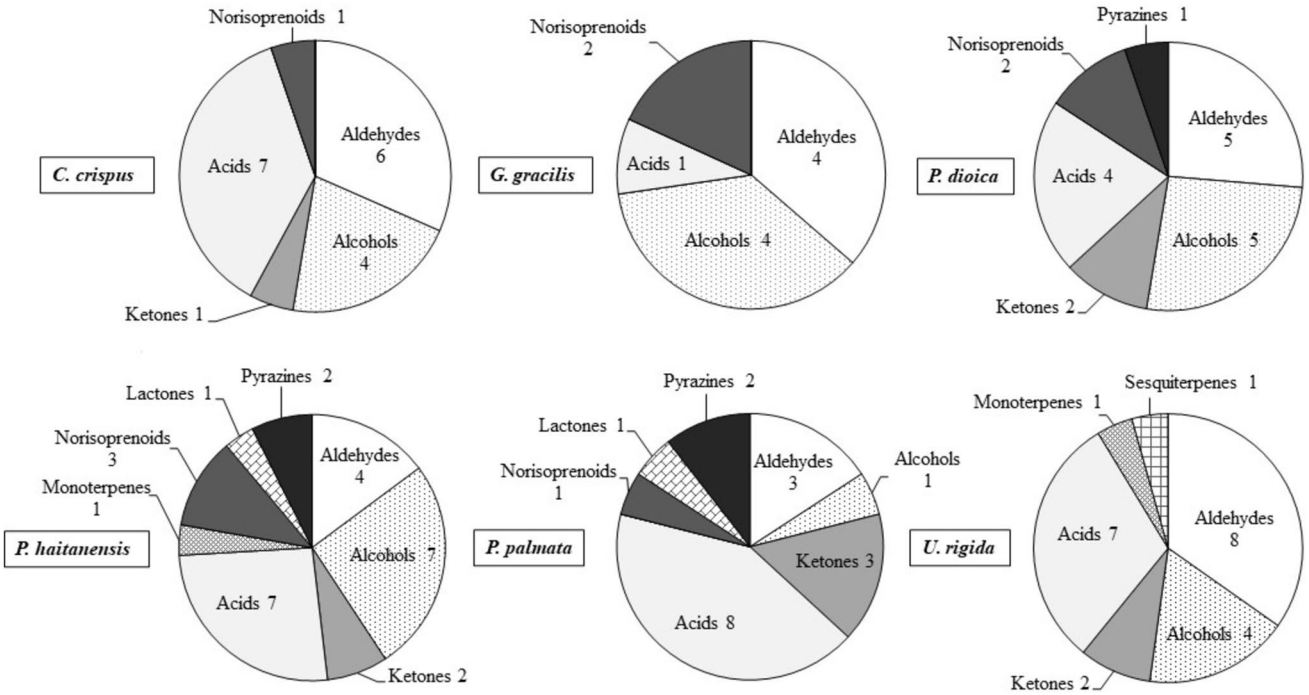


Fig. 1 Total count of volatile organic compounds (VOCs) detected in the six assessed edible macroalgae, calculated as the sum of all the compounds within each chemical compound family

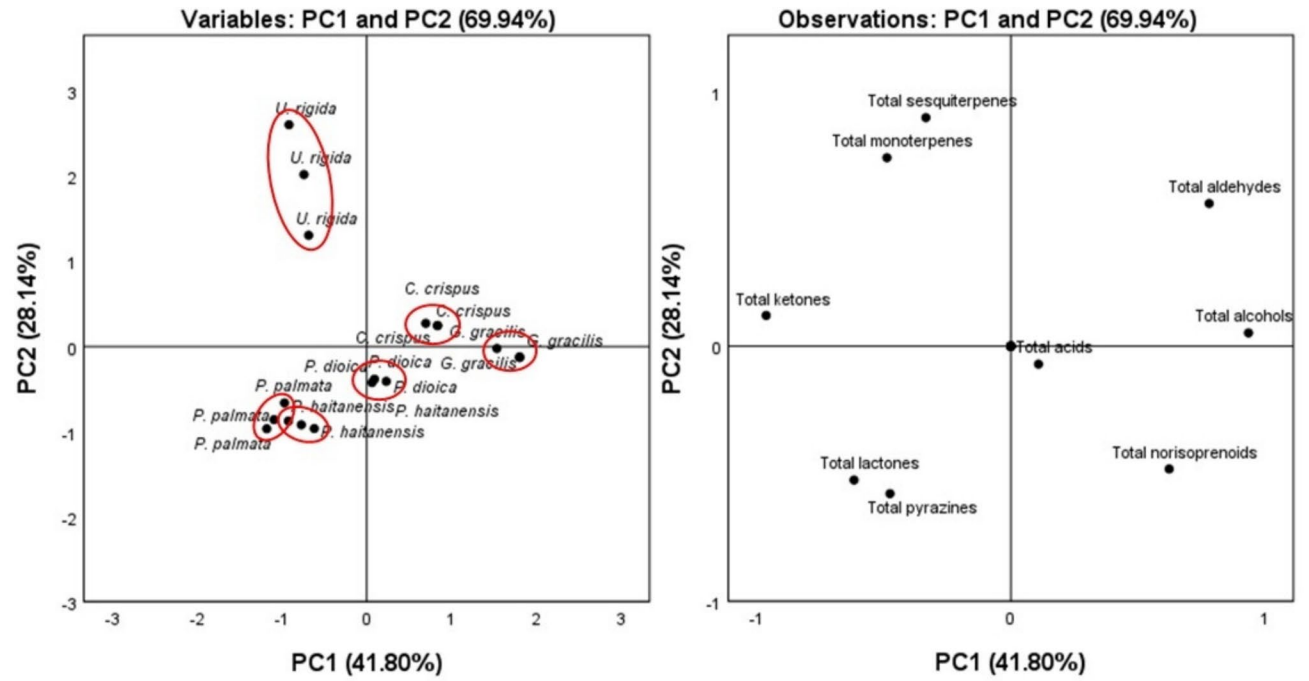


Fig. 2 Projections of *C. crispus, G. gracilis, P. dioica, P. haitanensis, P. palmata* and *U. rigida* and loadings by totals of aldehydes, alcohols, ketones, acids, monoterpenes, sesquiterpenes, norisoprenoids, lactones, and pyrazines contentS, into the plan composed by components PC1 and PC2 containing 69.94% of the total variance. Eigenvalues obtained for PC1 and PC2 were 3.76 and 2.53, respectively

P. haitanensis. Seven volatile compounds identified in this study have been previously documented for *P. haitanensis* (Luo et al. 2014; Chen et al. 2018; Song et al. 2018). However, twenty compounds were reported here for the first time. Among these, seventeen compounds were previously found in algae of the same genera, such as *Pyropia yezoensis, Pyropia tenera* and *Porphyra umbilicalis,* (Shu and Shen 2012; López-Pérez et al. 2017; Garicano Vilar et al. 2020; Rong et al. 2021), while others like 3-methylbutanol (**16**), propanoic acid (**30**), and 2-methylbutanoic acid (**34**) have only been reported in other red algae, namely *P. palmata* and *C. crispus* (Pina et al. 2014; Sánchez-García et al. 2019; Garicano Vilar et al. 2020). The odor descriptors associated with these newly identified VOCs in *P. haitanensis* included herb and sweet (**13**), flower, fruity and sweet (**22**), fruit, mushroom and fat (**25**), sour, astringent and vinegar (**29**), flower (**37**), mint (**40**), flower, raspberry and violet (**42**), caramel and sweet (**43**), and potato and roast (**45**, **46**) (Hu and Pan 2000; Acree and Arn 2004). However, the overall odor profile of *P. haitanensis* would result from the combined contributions of all VOCs, with the most abundant compounds (Fig. S2-3). playing a dominant role. Specifically, *P. haitanensis* was primarily characterized by plant, mushroom (**20**), pungent, and sour **(29)** odor notes (Hu and Pan 2000; Alarcón et al. 2021; Hu et al. 2021; You et al. 2024). Acetic acid **(29)**, a component of vinegar, is commonly used as a condiment (E 260) and as food additive for pickling vegetables and other foods. Additionally, 1-octen-3-ol (**20**), also known as mushroom alcohol due to its characteristic odor, has been approved as food flavouring agent

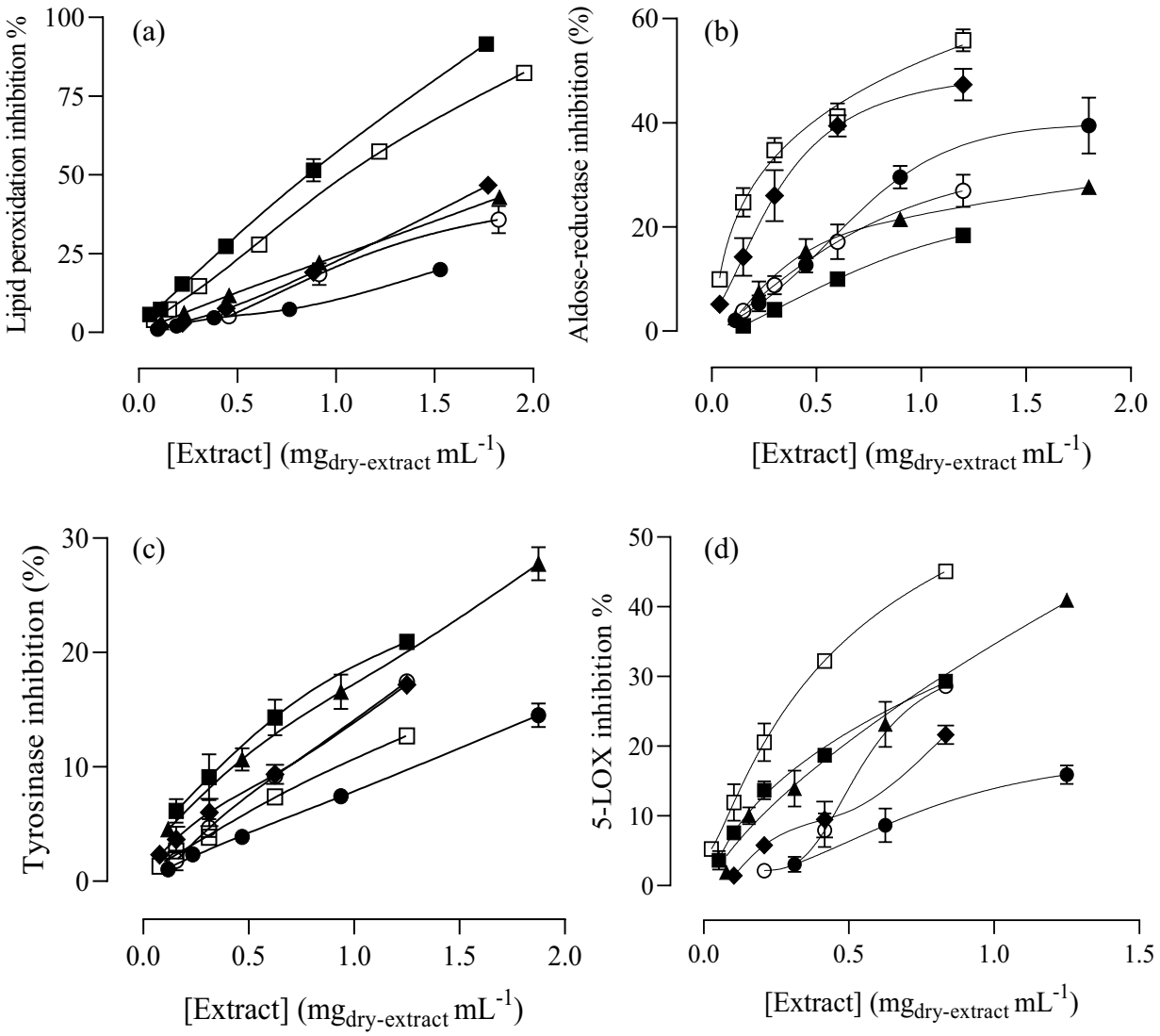


Fig. 3 Effects of the macroalgae ethanolic extracts (○ *C. crispus*, ▲ *G. gracilis*, ● *P. palmata*, ■ *P. dioica*, □ *P. haitanensis*, ◆ *U. rigida*) on the **a)** inhibition of lipid peroxidation, and on the inhibition of the enzymes **b)** aldose-reductase, **c)** tyrosinase, and **d)** 5-lipoxygenase

in the EU by the EFSA without limitations (Bampidis et al. 2020). *Pyropia haitanensis* was the macroalga with highest number of VOCs with 27 compounds identified. Notably, it stood out for its relatively high number of organic acids, alcohols, and aldehydes (Fig. 1). In contrast to the others, *P. haitanensis* exhibited the lowest relative content of aldehydes ($p < 0.05$) (Table 2). Particularly noteworthy was its high content of safranal (**13**), a compound exclusive to this alga and its counterpart *P. dioica*. Regarding alcohols and ketones, 3-methyl-1-butanol (**16**), 2-ethyl-1-hexanol (**21**), and geranylacetone (**28**) were only detected in *P. haitanensis,* and can be considered as specie biomarkers. Additionally, this alga contained the monoterpene *trans*-linalool oxide (**37**), as well as γ-butyrolactone (**43**), also found in *P. palmata*. In addition, it can be highlighted the presence of three norisoprenoids in *P. haitanensis*, namely *β*-cyclocitral (**40**), α-ionone (**41**), and β-ionone (**42**), as well as its high content of pyrazines, being the exclusive source of trimethylpyrazine (**45**).

Compared to *P. haitanensis*, *P. dioica* revealed the identification of 19 volatile organic compounds, where acids, aldehydes, and alcohols constituted over 80% of the total relative amount. The alcohol profile of *P. dioica* closely resembled that of *P. haitanensis*, with a slightly higher relative amount

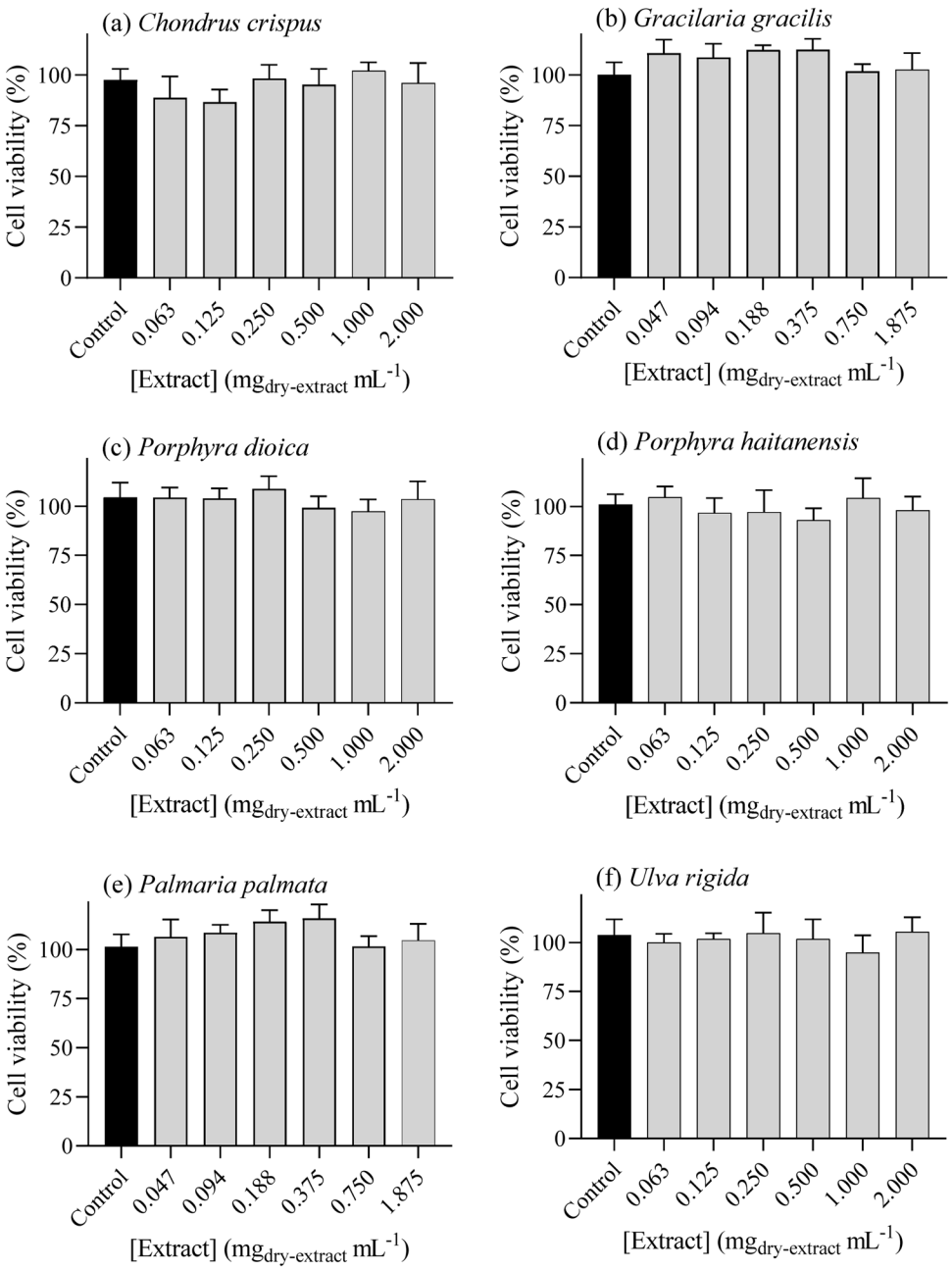


Fig. 4 Impact of the ethanolic macroalgae extracts on the viability of Caco-2 cells. Data are expressed as mean ± SEM ($n = 3$). $p < 0.05$ (*)

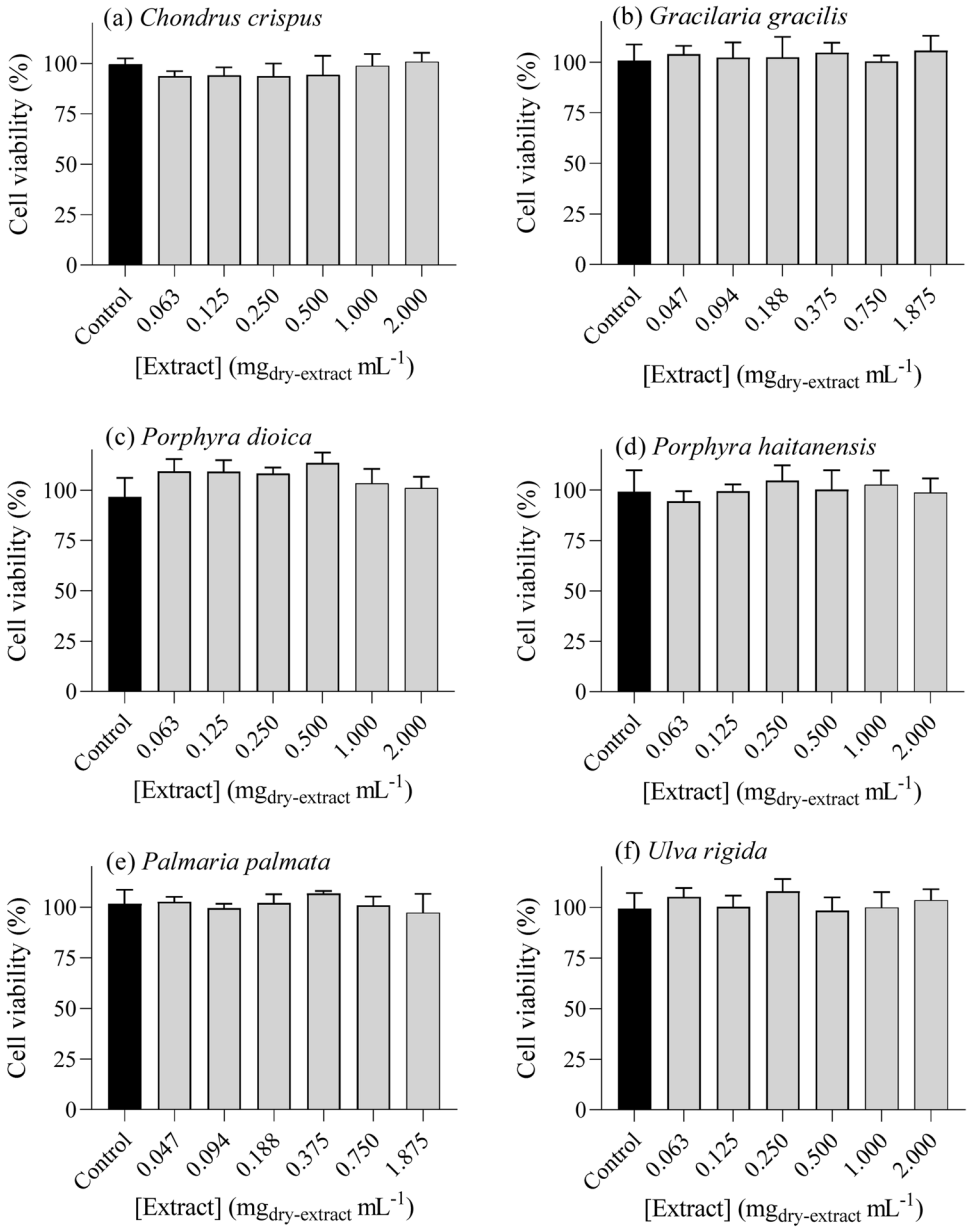


Fig. 5 Impact of the ethanolic macroalgae extracts on the viability of BV2 cells. Data are expressed as mean ± SEM ($n = 3$). $p < 0.05$ (*)

($p < 0.05$), notably standing out 1-penten-3-ol (**15**), which is associated with grassy odor (Hu and Pan 2000). The content of ketones was also quite similar, with a higher content of (*E*,*E*)−3,5-octadien-2-one (**25**) linked to fruit, mushroom, and fat odors (Hu and Pan 2000). Furthermore, comparing with *P. haitanensis* it was outstanding the higher content of *β*-cyclocitral (**40**) and *α*-ionone (**41**). In contrast, *P. dioica* exhibited lower content of acids, only four acids were identified. Among aldehydes, (*Z*)−4-heptenal (**5**) emerged as a distinctive specie marker exclusively detected in *P. dioica*. This compound is associated with biscuit and cream odors while safranal (**13**), also identified in *P. haitanensis*, is related to herb and sweet aromas (Acree and Arn 2004). However, unlike *P. haitanensis*, terpenes and lactones were not identified in *P. dioica*. Moreover, 3-ethyl-2,5-dimethylpyrazine (**46**), associated with vegetal, roasted, and potato odors (Acree and Arn 2004; Aprea 2020) was the unique pyrazine identified in this alga. Based on the most abundant VOCs in *P. dioica* (Fig. S2c), its odor profile aligned with that of *P. haitanensis*, characterized by plant, mushroom (**20**), pungent, and sour (**29**) notes. Additionally, the compound benzyl alcohol (**22**), contributing bitter almond aromas, stood out. Authorized as a food additive (E 1519) by the EFSA (Younes et al. 2019), it is commonly used in bakery wares, cocoa and chocolate products, and liqueurs, such as amaretto. To the best of our knowledge, the VOCs profile of *P. dioica* has not previously explored. Thus, all the compounds identified in this study contribute significantly

to understanding its characterization and offer new perspectives on potential culinary applications of this alga, leveraging the properties associated with these compounds. All of them have been well-documented in algae from the genera *Porphyra* and *Pyropia* (Shu and Shen 2012; López-Pérez et al. 2017; Patra et al. 2017; Garicano Vilar et al. 2020; Rong et al. 2021) and other red algae (Pina et al. 2014; Yuan et al. 2019; Stévant et al. 2020).

Palmaria palmata was identified with a total of 19 VOCs, with organic acids, aldehydes, and ketones being the major identified compounds (Fig. 1). *Palmaria palmata* displayed the second-highest relative content ($p < 0.05$) of acids after *C. crispus* and the highest of ketones along with *U. rigida*. Acetic acid (**29**) was the most abundant compound by far compared to the other identified VOCs (Fig. S3b) and is primarily responsible for the pungent and sour characteristic odor of *P. palmata* (Hu and Pan 2000; Hu et al. 2021). Moreover, heptanoic acid (**36**) was exclusively identified in this alga (Table 2). Regarding ketones, it was noteworthy to highlight isophorone (**26**) as a distinctive chemical marker for this particular alga, as this compound was exclusive to this species. Additionally, the presence of higher quantities of ketoisophorone (**27**) and γ-butyrolactone (**43**) further underscores its significance. Conversely, *P. palmata* was found to present the lowest content of alcohols ($p < 0.05$), being (*E*)−2-nonen-1-ol (**24**) the only alcohol identified. This compound was also found in *U. rigida*, but not previously reported in literature for any algae. Additionally, *P. palmata* exhibited relatively lower content of aldehydes and pyrazines ($p < 0.05$), however compounds like octanal (**9**), 2,6-dimethylpyrazine (**44**), and tetramethylpyrazine (**47**) were uniquely found in *P. palmata*. While VOCs in *P. palmata* have been widely studied (López-Pérez et al. 2017; Garicano Vilar et al. 2020; Stévant et al. 2020; Vilar et al. 2021; Lafeuille et al. 2022), four of the 19 compounds identified in this study were not previously reported. For example, propanoic acid (**30**) was identified but not quantified by Mirzayeva et al. (2021) as the content was below the quantification limit, and López-Pérez et al. (2017) reported no existence of 2-methylpropanoic acid (**31**) in *P. palmata*. 2-Methylbutanoic acid (**34**), identified for the first time in this study, has been found in other red algae, such as *C. crispus* (Pina et al. 2014), while (*E*)−2-nonen-1-ol (**24**), also found in *U. rigida*, has not been previously reported in any algae. Considering these newly identified VOCs, some of the associated odor descriptors for *P. palmata* comprise pungent, soy, rancid, sour, and mold (**30**). Moreover, distinguishing descriptors of *P. palmata* from the other evaluated algae include lemon, green, soap, orange peel, oily, fatty and soapy (**9**), cocoa, meat, medicine, nut, peanut butter, roast, beef and roasted nut (**44**), roasted, green, coffee and cocoa (**47**) (Acree and Arn 2004; Ooi et al. 2022).

Chondrus crispus was highlighted among the six macroalgae due to its significantly higher relative content ($p < 0.05$) of aldehydes and acids, with six and seven identified compounds, respectively (Fig. 1). Noteworthy aldehydes included hexanal (**3**) and benzaldehyde (**8**) (Table 2). Acids, which constituted nearly 90% of the total relative content of identified VOCs in *C. crispus*, were primarily composed of acetic acid (**29**), 2-methylpropanoic acid (**31**), 3-methylbutanoic acid (**33**), 2-methylbutanoic acid (**34**), and hexanoic acid (**35**). Additionally, *C. crispus* exhibited a relatively high content of α-ionone (**41**) and alcohols, with 1-octen-3-ol (**20**), benzyl alcohol (**22**), and (*E*)−2-octen-1-ol (**23**) being the main constituents. Conversely, terpenes, lactones, and pyrazines have not been identified in *C. crispus*, and it presented the lowest content of ketones, with only ketoisophorone (**27**) being identified. Despite the fact that nine of the nineteen identified compounds were already described in *C. crispus* (Pina et al. 2014), some other such as acetic (**29**), propanoic (**30**), butanoic (**32**), and hexanoic acids (**35**), (*Z*)−2-heptenal (**7**), benzyl alcohol (**22**), (*E*)−2-octenal (**12**), (*E*)−2-octen-1-ol (**23**), ketoisophorone (**27**), and decanal (**14**) were described for the first time for this specie. Nevertheless, all these compounds have been previously reported in other algae composition (Horincar et al. 2014; López-Pérez et al. 2017; Chen et al. 2018; Sánchez-García et al. 2019; Yuan et al. 2019; Garicano Vilar et al. 2020; Stévant et al. 2020). Hence, this research contributes to the understanding of *C. crispus* composition and the discovery of new sensorial properties associated with this alga. These properties include odor descriptors such as fat, green, green leaf, nut and walnut (**12**), sweet, roasted, cocoa, rum-like, orange peel, soap and tallow (**14**), rancid and cheese (**32**), pungent, rancid, sour and sharp (**35**) (Acree and Arn 2004; Aprea 2020; Ooi et al. 2022). The dominant odor notes in *C. crispus* are shaped by its major VOCs, such as 1-octen-3-ol **(20)** and acetic acid **(29)**, with the highest levels for the methylated forms of butanoic acid - 3-methylbutanoic acid (**33**) and 2-methylbutanoic acid (**34**) **-** (Fig. S2a), which are linked to cheesy and dairy odors (De Santis and Fidaleo 2022). Regarding potential applications in the food flavoring industry, butyric acid, a compound generally recognized as safe (GRAS) by the FDA, is widely used as a food additive in butter, cheese, caramel, fruit and nuts (Deyo 2005).

Regarding *G. gracilis*, and to the best of our knowledge, this study represents the pioneering investigation into its volatile organic compounds (VOCs) profile. This alga was predominantly characterised by alcohols and aldehydes (Fig. 1) and exhibited a markedly different profile compared to other studied red algae and *U. rigida*. The content of aldehydes was significantly higher, along with *C. crispus* (Table 2). Of particular note was the identification of 2-methyl-2-pentenal (**4**) as a unique compound in *G. gracilis*, known for its green, fruity, brandy and cider-like aromas (Acree and Arn 2004). The content of alcohol was notably greater than that of the other analyzed samples, with 1-octen-3-ol (**20**)

emerging as the major VOC in *G. gracilis* (Fig. S2b). This compound is known for its distinctive plant, mold, earthy odors. Additionally, 1-pentanol (**17**) and 1-hexanol (**19**), two compounds associated with apple, balsamic, bitter almond, flowery, sweet, herbaceous, grass, and woody odor descriptors (Hu and Pan 2000; Aprea 2020; S.- Ooi et al. 2022), were only present in *G. gracilis*. Moreover, it exhibited a higher content of norisoprenoids, mainly *β*-cyclocitral (**40**) and *β*-ionone (**42**). Contrarily to that observed for other macroalgae species, ketones, terpenes, lactones, and pyrazines were not found in *G. gracilis*. Moreover, acetic acid (**29**) was the only organic acid found in this sample. While all of these metabolites have been previously documented in some algae species (Shu and Shen 2012; Horincar et al. 2014; Pina et al. 2014; López-Pérez et al. 2017; Sánchez-García et al. 2019; Garicano Vilar et al. 2020; Yücel et al. 2023), only six were reported in other algae from *Gracilaria* sp. (Yuan et al. 2019; Mirzayeva et al. 2021), thus contributing to broadening the knowledge of the chemical composition and characteristics of *G. gracilis*. Hexanal (**3**), a highly valued compound in the aroma industry known for its fruit, vegetable, and green leaf flavors, was the second most abundant VOC after 1-octen-3-ol (**20**). Hexanal is widely utilized in developing fruity flavors (Ledesma-Amaro and Nicaud 2016). Together, 1-octen-3-ol and hexanal shape the odor profile and potential applications of *G. gracilis* as flavoring agent.

Lastly, *U. rigida* was the unique green alga studied in this work, ranking second after *P. haitanensis* in terms of the highest number of identified VOCs, as depicted in Fig. 1. Among these compounds, 7 acids, 8 aldehydes, and 4 alcohols were determined. This green macroalga showed a notable content of aldehydes and ketones and was characterized by the absence of lactones and pyrazines. Setting itself apart from the other examined red algae, it presented five unique compounds, as outlined in Table 2. Among these unique compounds, it must be mentioned that (*E*)−2-pentenal (**2**) and α-muurolene (**39**) were not previously reported in *U. rigida*. Additionally, 5-ethyl-2-furaldehyde (**11**) was not documented before in any macroalgae prior this study. Interestingly, only 9 out of the total 23 volatile compounds identified in this study have been previously documented in *U. rigida* (Sánchez-García et al. 2019; Yücel et al. 2023). Among these newly discovered VOCs in *U. rigida* evoke a range of odor descriptors including green, apple, bitter almond, pungent (**2**), and wood (**39**). Additionally, the unique VOCs found in *U. rigida*, setting it apart from other evaluated macroalgae, are associated with aromas such as anise, mint, oil, floral (**38**), as well as fat, fried, and nut (**10**) (Acree and Arn 2004; Aprea 2020). The major VOCs in *U. rigida* included hexanal (**3**), benzyl alcohol (**22**), and (*E,E*)−2,4-heptadienal (**10**) (Fig. S3c). Notably, (*E,E*)−2,4-heptadienal is associated with beany odor at low concentrations (< 1,000 ppm) but can produce rancid oil, fishy, and cinnamon-like aromas at higher concentrations (Trindler et al. 2022). Together with minor compounds, these VOCs shape the distinctive odor profile of *U. rigida* and highlight its potential applications as a flavour agent.

Lastly, the PCA analyses revealed that the VOCs profiles of the six studied macroalgae allowed for their differentiation (Fig. 2). Although they shared common compounds, each algae species possessed distinct compounds contributing to individual characteristics and sensory attributes offering potential for the development of innovative recipes. However, although the primary contributors to the distinctive aromas of the six macroalgae evaluated have been identified, the overall flavor of these algae, which arises from complex mixtures of various compounds, cannot be fully attributed to the presence of individual molecules alone (Trindler et al. 2022). Therefore, while this study serves as a valuable starting point for identifying VOCs and their associated odor descriptors in edible macroalgae, further research is needed to assess the specific contribution of these individual components within the complex aroma mixtures.

Biological activity of edible macroalgae

VOCs have garnered attention due to their documented bioactivities, such as their antioxidant properties (Nunes et al. 2022). These algae-derived components have also been linked to anti-bacterial, anti-diabetic, anti-inflammatory, anti-cancer, anti-proliferative, and neuroprotective effects, highlighting their significance as unique bioactive compounds with positive impacts on health (Ferreira et al. 2021). Lipid peroxidation, which directly impacts food quality by causing loss of nutritional value and contributing to diseases such as ageing, atherosclerosis, and cancer, is commonly utilized as an indicator of oxidative stress in human cells and tissues (Patra et al. 2017). The results of the impact of macroalgae extracts on lipid peroxidation were consistent with previously reported data correlating phenolic content with antioxidant activity, as the algae with the highest total phenolic compounds content, accounting for 14.77±0.04 mg g^{-1} and 10.78±0.05 mg g^{-1} for *P. dioica* and *P. haitanensis*, respectively (Table 1), exhibited the highest antioxidant activity (> 80% inhibition on lipid peroxidation at 1.8–2.0 mg mL^{-1} of the extract). Previous studies by other authors have highlighted the antioxidant potential of algae belonging to *Porphyra/Pyropia*. For instance, Patra et al. (2017) assessed the volatile oil extracted from *P. tenera* and similarly noted a great ability to inhibit lipid peroxidation.

Numerous studies have documented the link between insulin resistance and oxidative stress. Indeed, the elevated levels of glucose due to insulin resistance trigger increased aldose reductase activity, leading to depletion of

NADPH. Consequently, cells become more prone to oxidative damage, while also generating glycating agents that compromise antioxidant defenses (Trigueros et al. 2024b). Remarkably, *P. haitanensis* exhibited the highest capacity to inhibit aldose-reductase, with inhibition above 50% at the maximum tested concentration (1.2 mg mL^{-1}). Conversely, *P. dioica* displayed the lowest biological potential (18% at 1.2 mg mL^{-1}), while *U. rigida* achieved the second-highest inhibition rates (47% at 1.2 mg mL^{-1}).

Furthermore, the evaluation of the antioxidant potential of the extracts from the six edible algae was complemented by an assessment of their capacity to inhibit tyrosinase and 5-lipoxygenase (5-LOX). Tyrosinase catalyzes the conversion of monophenols to *o*-diphenols, followed by the oxidation to *o*-quinones, which subsequently polymerize to form melanin. The intracellular accumulation of neuromelanin may contribute to neuronal dysfunction and neurodegeneration, as well as trigger the overexpression of brain tyrosinase, resulting in increased neuromelanin synthesis. In this context, tyrosinase does not serve as a neuroprotective antioxidant agent; rather, it promotes the detrimental accumulation of neuromelanin (Bernardo et al. 2021). The observed algae capacity to inhibit tyrosinase activity appeared rather limited, as inhibition rates below 30% were evident for all the algae tested at the highest concentrations examined (1.25–1.88 mg mL^{-1}) (Fig. 3c). Lipoxygenases play a role in the inflammatory cascade by catalyzing the oxidation of polyunsaturated fatty acids, such as arachidonic and docosahexaenoic acids, into pro-inflammatory compounds, which influence the progression of neurodegenerative diseases (Bernardo et al. 2021). Figure 3d illustrates the algae extracts capacity to inhibit 5-LOX. *Pyropia haitanesis*, previously reported for its anti-inflammatory potential (Qiu et al. 2024), has demonstrated the highest capacity to inhibit the enzyme 5-LOX surpassing 45% inhibition at 0.83 mg mL^{-1}, followed by *G. gracilis* (41% at 1.25 mg mL^{-1}), and *P. dioica* and *C. crispus,* both with 29% inhibition at 0.83 mg mL^{-1}. VOCs shared among these algae (**13**, **41**, **42**), all of which were found in *P. haitanensis*, have been recognized as anti-inflammatory agents (Aloum et al. 2020; Esmaealzadeh et al. 2023), suggesting that they could contribute to the anti-inflammatory properties of these algae.

Cytotoxicity of the macroalgae extracts

With novel VOCs identified for each alga and their bioactive potential confirmed, it becomes essential to assess their impact on the viability of human cell lines to support their use in food formulations. The Caco-2 cell line is commonly used to study how bioactive extracts influence the gastrointestinal epithelium, including their effects on absorption, metabolism, and toxicity (Kumar et al. 2022). As previously noted, none of the extracts demonstrated cytotoxicity in Caco-2 cells (Fig. 4). To the best of our knowledge, the cytotoxic profile on human Caco-2 cells has only been reported for *C. crispus*, with conflicting results. While some studies reported significant cytotoxic effects for methanolic extracts (Alkhalaf 2021), others observed no effects within the tested concentration range (Matin et al. 2024; Premarathna et al. 2024). For the other algae examined, this is the first study investigating their effects on Caco-2 cell viability. Consistent with the findings in this study, negligible cytotoxic effects have been reported for *P. palmata* and *U. rigida* in AGS, A549, and HepG2 human cells (Cassani et al. 2022). Similarly, *P. haitanensis* extracts showed no cytotoxicity below 1.5 mg mL^{-1} in HaCaT cells (Yao et al. 2020). Regarding their effect on BV-2 cells, none of the tested macroalgae significantly ($p < 0.05$) affected cell survival (Fig. 5). The lack of previous studies on the effects of these algae on BV-2 cells, combined with limited research on Caco-2 cells, highlights this study as a foundational step for evaluating their safe applications in the food industry. These findings support the incorporation of macroalgae into food products and the development of formulations with potential health benefits. However, further in-depth studies are necessary to assess the bioavailability of the bioactive compounds and potential interactions among them.

Conclusions

This study presents the volatile organic compound (VOC) profiles of six edible macroalgae, including the red algae *C. crispus*, *G. gracilis*, *P. palmata*, *P. dioica*, and *P. haitanensis*, as well as the green alga *U. rigida.* Notably, this evaluation represents a key novelty of the work, as it reports the VOC profiles of *P. dioica* and *G. gracilis* for the first time, while also identifying new compounds in *C. crispus* (10), *P. palmata* (4), *P. haitanensis* (20), and *U. rigida* (14). This updated characterization expands the unique odor profile for each alga, enhancing their potential use as food additives. The algae, particularly the red species, were also shown to be rich in phenolic compounds, proteins, and sugars, emphasizing their nutritional value. Additionally, bioactivity screening for health-related conditions such as oxidative stress and inflammation revealed significant efficacy. In particular, *P. haitanensis* exhibited potent antioxidant and anti-inflammatory activities through aldose-reductase and 5-LOX inhibition. Moreover, the strong lipid peroxidation inhibition observed in *Pyropia* species further highlights their potential utility in food processing and preservation. A major innovation of this study is the confirmation of the safety profile of the macroalgae extracts, demonstrated by their lack of toxicity to Caco-2 and BV-2 human cells. This study offers a thorough chemical and bioactive characterization of these

macroalgae, offering valuable insights into their potential as functional food ingredients and culinary applications, supported by their proven safety for incorporation into food formulations. However, further research is necessary to assess the bioavailability of the bioactive compounds, their interactions, and the specific contribution of individual components within the complex aroma profiles of the algae

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10811-024-03403-x.

Acknowledgements Ester Trigueros thanks European Union-NextGenerationEU, Ministry of Universities and Recovery, Transformation and Resilience Plan, for the post-doctoral contract through a call from the University of Burgos. Andreia P. Oliveira thanks FCT (Fundação para a Ciência e Tecnologia) for funding through program DL 57/2016 – Norma transitória (DL57/2016/CP1346/CT0015). Paula Guedes de Pinho is supported by a research contract (under Scientific Employment Stimulus) CEECINST/00108/2021/CP2794/CT0001.

Authors' contribution E.T.: Conceptualization, Data curation, Formal Analysis, Investigation, Writing-original draft. F.A.: Validation, Writing – review & editing. P.G. de P.: Validation, Writing – review & editing, Funding acquisition. A.P.O.: Supervision, Validation, Writing – review & editing, Project administration.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This work was supported by PT national funds [FCT/MCTES, Fundação para a Ciência e Tecnologia and Ministério da Ciência, Tecnologia e Ensino Superior] through the project UIDP/50006/2020 and by the projects UIDP/04378/2020 and UIDB/04378/2020 of Research Unit on Applied Molecular Biosciences–UCIBIO, and the project LA/P/0140/2020 from the Associate Laboratory Institute for Health and Bioeconomy–i4HB.

Data availability The data supporting the findings of this study are available within the article and its supplementary information files.

Declarations

Competing interest The authors declare no competing interests.

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References

Acree T, Arn H (2004) Flavornet and human odor space. https://www.flavornet.org/

Alarcón M, Pérez-Coello MS, Díaz-Maroto MC, Alañón ME, Soriano A (2021) Effect of winery by-product extracts on oxidative stability, volatile organic compounds and aroma profile of cooked pork model systems during chilled storage. LWT - Food Sci Technol 152:112260

Alkhalaf MI (2021) Chemical composition, antioxidant, anti-inflammatory and cytotoxic effects of *Chondrus crispus* species of red algae collected from the Red Sea along the shores of Jeddah city. J King Saud Univ Sci 33:101210

Aloum L, Alefishat E, Adem A, Petroianu G (2020) Ionone is more than a Violet's fragrance: A review. Molecules 25:5822

Aprea E (ed) (2020) Volatile compounds and smell chemical (odor and aroma) of food. MDPI, Basel, pp 348

Bampidis V, Azimonti G, Bastos MdL, Christensen H, Kouba M, Durjava MK et al (2020) Safety and efficacy of oct-1-en-3-ol, pent-1-en-3-ol, oct-1-en-3-one, oct-1-en-3-yl acetate, isopulegol and 5-methylhept-2-en-4-one, belonging to chemical group 5 and of isopulegone and α-damascone belonging to chemical group 8 when used as flavourings for all animal species. EFSA J 18(2):e6002

Bernardo J, Malheiro I, Videira RA, Valentão P, Santos AC, Veiga F, Andrade PB (2021) *Trichilia catigua* and *Turnera diffusa* extracts: In vitro inhibition of tyrosinase, antiglycation activity and effects on enzymes and pathways engaged in the neuroinflammatory process. J Ethnopharmacol 271:113865

Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal Biochem 72:248–254

Cassani L, Lourenço-Lopes C, Barral-Martinez M, Chamorro F, Garcia-Perez P, Simal-Gandara J, Prieto MA (2022) Thermochemical characterization of eight seaweed species and evaluation of their potential use as an alternative for biofuel production and source of bioactive compounds. Int J Mol Sci 23:2355

Chen J, Chen Y, Yang R, Luo Q, Chen H, Xu J, Yan X, Shen B (2018) Response to wound-activated stress through a lipid oxidative metabolic pathway in *Pyropia haitanensis*. Algal Res 35:206–214

Cikoš A-M, Coz-Rakovac R, Subaric D, Jerkovic I, Ackar D, Jokic S (2020) Macroalgae in the food industry – Opportunities and challenges. Eng Power 15:14–19

De Santis D, Fidaleo M (2022) Effect of aging pit on volatile compounds and sensory attributes of traditional Italian Fossa cheese. LWT Food Sci Technol 153:112507

Deyo J (2005) Butyric acid. In: Wexler P (ed) Encyclopedia of Toxicology (Second Edition). Elsevier, Chantilly, pp 365–370

Esmaealzadeh D, Ghalibaf AAM, Rad MS, Rezaee R, Razavi BM, Hosseinzadeh H (2023) Pharmacological effects of Safranal: an updated review. Iran J Basic Med Sci 26:1131–1143

Fang R, Zweig M, Li J, Mirzababaei J, Simmonds MSJ (2023) Diversity of volatile organic compounds in 14 rose cultivars. J Essent Oil Res 35:220–237

FAO, IFAD, & WFP (2015) The State of Food Insecurity in the World 2015. Meeting the 2015 international hunger targets: tacking stock of uneven progress. FAO, Rome, pp 1–62

Ferreira M, Teixeira C, Abreu H, Silva J, Costas B, Kiron V, Valente LMP (2021) Nutritional value, antimicrobial and antioxidant activities of micro- and macroalgae, single or blended, unravel their potential use for aquafeeds. J Appl Phycol 33:3507–3518

Ferreres F, Andrade C, Gomes NGM, Andrade PB, Gil-Izquierdo A, Pereira DM, Suksungworn R, Duangsrisai S, Videira RA, Valentão P (2021) Valorisation of kitul, an overlooked food plant: Phenolic profiling of fruits and inflorescences and assessment of their effects on diabetes-related targets. Food Chem 342:128323

Figueroa V, Farfán M, Aguilera JM (2023) Seaweeds as novel foods and source of culinary flavors. Food Rev Intl 39:1–26

Garicano Vilar E, O'Sullivan MG, Kerry JP, Kilcawley KN (2020) Volatile compounds of six species of edible seaweed: A review. Algal Res 45:101740

Giercksky E, Doumeizel V (2023) Seaweed revolution: a manifesto for a sustainable future. Lloyd's register Foundation, London, pp 1–16

Goksen G (2023) Elucidation and quantification health-promoting phenolic compounds, antioxidant properties and sugar levels of ultrasound assisted extraction, aroma compositions and amino acids profiles of macroalgae, *Laurencia papillosa* Ultrason Sonochem 98:106527

Horincar VB, Parfene G, Tyagi AK, Gottardi D, Dinică R, Guerzoni ME, Bahrim G (2014) Extraction and characterization of volatile compounds and fatty acids from red and green macroalgae from the Romanian Black Sea in order to obtain valuable bioadditives and biopreservatives. J Appl Phycol 26:551–559

Hu M, Wang S, Liu Q, Cao R, Xue Y (2021) Flavor profile of dried shrimp at different processing stages. LWT Food Sci Technol 146:111403

Hu S-P, Pan BS (2000) Modification of fish oil aroma using a macroalgal lipoxygenase. J Am Oil Chem Soc 77:343–348

Kim S-K, Venkatesan J (2015) Introduction to Seafood Science. In: Kim S-K (ed) Seafood Science: Advances in Chemistry, Technology and Applications. CRC Press, Boca Raton, pp 1–14

Kuech A, Breuer M, Popescu I (2023) The future of the EU algae sector. European Parliament. https://data.europa.eu/doi/10.2861/218277

Kumar Barbhai MD, Hasan M, Punia S, Dhumal S, Radha Rais N, Chandran D, Pandiselvam R, Kothakota A, Tomar M, Satankar V, Senapathy M, Anitha T, Dey A, Sayed AAS, Gadallah FM, Amarowicz R, Mekhemar M (2022) Onion (*Allium cepa* L.) peels: A review on bioactive compounds and biomedical activities. Biomed Pharmacother 146:112498

Lafeuille B, Francezon N, Goulet C, Perreault V, Turgeon SL, Beaulieu L (2022) Impact of temperature and cooking time on the physicochemical properties and sensory potential of seaweed water extracts of *Palmaria palmata* and *Saccharina longicruris*. J Appl Phycol 34:1731–1747

Lafeuille B, Tamigneaux É, Berger K, Provencher V, Beaulieu L (2023) Variation of the nutritional composition and bioactive potential in edible macroalga S*accharina latissima* cultivated from Atlantic Canada subjected to different growth and processing conditions. Foods 12:1736

Ledesma-Amaro R, Nicaud JM (2016) *Yarrowia lipolytica* as a biotechnological chassis to produce usual and unusual fatty acids. Prog Lipid Res 61:40–50

Lomartire S, Gonçalves AMM (2023) An Overview on Antimicrobial Potential of edible terrestrial plants and marine macroalgae Rhodophyta and Chlorophyta extracts. Marine Drugs 21:163

López-Pérez O, Picon A, Nuñez M (2017) Volatile compounds and odour characteristics of seven species of dehydrated edible seaweeds. Food Res Int 99:1002–1010

Luo Q, Zhu Z, Zhu Z, Yang R, Qian F, Chen H, Yan X (2014) Different responses to heat shock stress revealed heteromorphic adaptation strategy of *Pyropia haitanensis* (Bangiales, Rhodophyta). PLoS ONE 9:e94354

Matin M, Koszarska M, Atanasov AG, Król-Szmajda K, Jóźwik A, Stelmasiak A, Hejna M (2024) Bioactive potential of algae and algae-derived compounds: focus on anti-inflammatory, antimicrobial, and antioxidant effects. Molecules 29:4695

Mirzayeva A, Castro R, Barroso CG, Durán-Guerrero E (2021) Characterization and differentiation of seaweeds on the basis of their volatile composition. Food Chem 336:127725

Nielsen SS (2010) Phenol-sulfuric acid method for total carbohydrates. In: Nielsen SS (ed) Food Analysis Laboratory Manual, 2nd edn. Springer, New York, pp 47–53

Nunes AR, Gonçalves AC, Pinto E, Amaro F, Flores-Félix JD, Almeida A, Guedes de Pinho P, Falcão A, Alves G, Silva LR (2022) Mineral content and volatile profiling of Prunus avium L. (Sweet Cherry) by-products from Fundão Region (Portugal). Foods 11:751

Ooi TS, Ting ASY, Siow LF (2022) Volatile organic compounds and sensory profile of dark chocolates made with cocoa beans fermented with *Pichia kudriavzevii* and *Hanseniaspora thailandica*. J Food Sci Technol 59:2714–2723

Patra JK, Lee SW, Kwon YS, Park JG, Baek KH (2017) Chemical characterization and antioxidant potential of volatile oil from an edible seaweed *Porphyra tenera* (Kjellman, 1897). Chem Cent J 11:34

Pereira L (2020) Characterization of bioactive components in edible algae. Mar Drugs 18:65

Pina AL, Costa AR, Lage-Yusty MA, López-Hernández J (2014) An evaluation of edible red seaweed (*Chondrus crispus*) components and their modification during the cooking process. LWT Food Sci Technol 56:175–180

Premarathna AD, Sooäär A, Ahmed TAE, Rjabovs V, Hincke MT, Tuvikene R (2024) Isolation, structural characterization and biological activities of polysaccharides from *Chondrus crispus*. Food Hydrocoll 154:110131

Qiu S-M, Veeraperumal S, Tan K, Zhong S, Cheong K-L (2024) The in vitro anti-inflammatory mechanism of *Porphyra haitanensis* oligosaccharides on lipopolysaccharide-induced injury in IEC-6 cells. J Funct Foods 112:106005

Queirós AS, Circuncisão AR, Pereira E, Válega M, Abreu MH, Silva AMS, Cardoso SM (2021) Valuable nutrients from *Ulva rigida*: Modulation by seasonal and cultivation factors. Appl Sci 11:6137

Cao R, Hu M, Zhao L, Wang L, Liu Q (2021) Flavor characteristics of different crops of laver (*Porphyra yezoensis*) during one harvest cycle. J Ocean Univ China 20:213–220

Sánchez-García F, Mirzayeva A, Roldán A, Castro R, Palacios V, García-Barroso C, Durán-Guerrero E (2019) Evolution of volatile compounds and sensory characteristics of edible green seaweed (*Ulva rigida*) during storage at different temperatures. J Sci Food Agric 99:5475–5482

Shu N, Shen H (2012) Identification of odour-active compounds in dried and roasted nori (*Porphyra yezoensis*) using a simplified gas chromatography-SNIF technique. Flavour Fragr J 27:157–164

Singleton VL, Orthofer R, Lamuela-Raventós RM (1999) Analysis of total phenols and other oxidation substrates and antioxidants by means of Folin-Ciocalteu reagent. Meth Enzymol 299:152–178

Song Y, Zhao J, Chen J, Luo Q, Yang R, Xu J, Chen H, Yan X (2018) Heat shock-induced metabolic conversion of membrane lipids, fatty acids and volatile organic compounds of *Pyropia haitanensis* under different heat shock time. Phycol Res 66:89–99

Stévant P, Ólafsdóttir A, Déléris P, Dumay J, Fleurence J, Ingadóttir B, Jónsdóttir R, Ragueneau É, Rebours C, Rustad T (2020) Data on the sensory characteristics and chemical composition of the edible red seaweed dulse (*Palmaria palmata*) after dry and semi-dry storage. Data Brief 33:106343

Trigueros E, Sanz MT, Alonso-Riaño P, Beltrán S, Ramos C, Melgosa R (2021) Recovery of the protein fraction with high antioxidant activity from red seaweed industrial solid residue after agar extraction by subcritical water treatment. J Appl Phycol 33:1181–1194

Trigueros E, Benito-Román Ó, Oliveira AP, Videira RA, Andrade PB, Sanz MT, Beltrán S (2024a) Onion (*Allium cepa* L.) skin waste valorization: Unveiling the phenolic profile and biological potential for the creation of bioactive agents through subcritical water extraction. Antioxidants 13:205

Trigueros E, Oliveira AP, Andrade PB, Videira RA, de Pinho PG, Sanz MT, Beltrán S (2024b) Exploring the bioactive potential of algae residue extract via subcritical water extraction: Insights

into chemical composition and biological activity. Food Chem 458:140310
Trindler C, Annika Kopf-Bolanz K, Denkel C (2022) Aroma of peas, its constituents and reduction strategies – Effects from breeding to processing. Food Chem 376:131892
Viant MR, Kurland IJ, Jones MR, Dunn WB (2017) How close are we to complete annotation of metabolomes? Curr Opin Chem Biol 36:64–69
Vilar EG, O'Sullivan MG, Kerry JP, Kilcawley KN (2021) A chemometric approach to characterize the aroma of selected brown and red edible seaweeds / extracts. J Sci Food Agric 101:1228–1238
World Resources Institute (2018) Synthesis report: creating a sustainable food future: a menu of solutions to feed nearly 10 billion people by 2050. World resources Institute, Washington, pp 1–96
Yamamoto M, Baldermann S, Yoshikawa K, Fujita A, Mase N, Watanabe N (2014) Determination of volatile compounds in four commercial samples of Japanese green algae using solid phase microextraction gas chromatography mass spectrometry. Sci World J 2014:289780
Yao WZ, Veeraperumal S, Qiu HM, Chen XQ, Cheong KL (2020) Anti-cancer effects of *Porphyra haitanensis* polysaccharides on human colon cancer cells via cell cycle arrest and apoptosis without causing adverse effects in vitro. 3 Biotech 10:386
Yesuraj D, Deepika C, Ravishankar GA, Rao AR (2022) Seaweed-based recipes for food, health-food applications, and innovative products Including meat and meat analogs. In: Rao AR, Ravishankar GA (eds), Sustainable Global Resources of Seaweeds Volume 2: Food, Pharmaceutical and Health Applications. Springer, Cham, pp 267–292
You S, Tian Y, Zhang W, Zheng B, Zhang Y, Zeng H (2024) Quality properties of fish ball with abalone and its relationship with sensory properties. Food Chem: X 21:101146
Younes M, Aquilina G, Castle L, Engel KH, Fowler P et al (2019) Re-evaluation of benzyl alcohol (E 1519) as food additive. EFSA J 17:e5876
Yuan S, Wu K, Duan Z, Huang Y, Lu Y, Ma X (2019) A sustainable process for the recovery of volatile constituents from *Gracilaria lemaneiformis* in agar production and evaluation of their antioxidant activities. BMC Chem 13:74
Yücel TB, Korkmaz B, Cebeci T, Karaman Ü, Arici YK, Fandakli S, Gül T (2023) Analysis of volatile constituent by hydrodistillation and solid-phase microextraction techniques and antimicrobial and scolicidal activities of essential oil and Soxhlet extracts of *Ulva rigida* grown in Turkey. Chem Biodivers 20:e202300965

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