



Fatty acid composition of different morphological structures in the sub-Antarctic kelps *Macrocystis pyrifera* (L.) C. Agardh and *Lessonia flavicans* Bory of the Magellan Ecoregion: Nutritional and biomedical potentials

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Abstract

The sub-Antarctic Magellan Ecoregion is a unique biogeographic area located at the southern tip of South America, which has exceptional marine flora and high endemism. Along the coastline, the ochrophytes *Macrocystis pyrifera* and *Lessonia flavicans* form vital underwater forests that serve as critical habitats, providing shelter, food and breeding grounds for a diverse marine organisms. These algal species are also important components used in the food industry and biomedicine, due to their high lipid, amino acid and fiber content. In this study, we investigated the intra-thallus variation of fatty acids among the different morphological structures (fronds, stipes and holdfast) of *M. pyrifera* and *L. flavicans* collected in Rinconada Bulnes during spring, 2021. The stipes of *M. pyrifera* ($3.73 \pm 1.73\%$) and the fronds of *L. flavicans* ($3.35 \pm 0.97\%$) both exhibited high lipid content. Saturated fatty acids were highest in the holdfast of *M. pyrifera* ($37.82 \pm 0.06\%$) followed by the fronds of *L. flavicans* ($34.30 \pm 0.10\%$). Notably, monounsaturated fatty acids showed higher levels in the holdfast of *L. flavicans* ($46.45 \pm 0.19\%$) followed by the stipes of *M. pyrifera* ($43.04 \pm 0.08\%$). The fronds of both *M. pyrifera* ($32.38 \pm 0.26\%$) and *L. flavicans* ($28.89 \pm 0.23\%$) showed high levels of polyunsaturated fatty acids. These findings provide valuable insight into the intra-thallus variation of fatty acids in different morphological structures of *M. pyrifera* and *L. flavicans*, highlighting their potential nutritional and biomedical importance as the most representative kelps in the Magellan region.

Keywords Phaeophyceae · Fatty acids profile · *Macrocystis* thallus · *Lessonia* thallus · Kelp uses · Biomedical potential, Magellan region

Introduction

Macroalgae increasingly have shown great potential over the years due to their multiple uses and applications, ranging from everyday life to large-scale industries (Ganesan et al. 2019). They contain a significant amount of phycocolloids (e.g. agar, carrageenans and alginates), which are widely used in the food, cosmetic, pharmaceutical and biotechnological industries (Kelly and Brown 2000; Mansilla et al. 2012; Wan et al. 2019; Leandro et al. 2020; Pereira et al. 2021). Several studies demonstrate the benefits of macroalgae as nutraceuticals due to their significant lipid, amino acid and fiber content (Harnedy and FitzGerald 2013; Flachs et al. 2014; Astorga-España

et al. 2017; Athyros et al. 2018; Husni 2018; Afonso et al. 2019; Cikoš et al. 2020), and their potential applications in human health to fight pathologies of high prevalence and public health impact such as cancer, stroke, hypertension, type II diabetes, gastrointestinal disorders, osteoporosis, immune disorders, arthritis and influenza, among others (Mendis and Kim 2011; Collins et al. 2016; Quitral et al. 2019; Do-Amaral et al. 2020).

The sub-Antarctic Magellan Ecoregion (47° - 56° S; 71° - 73° W) of Chile has unique environmental conditions due to its location at the southern tip of South America (Rozzi et al. 2012). The diverse and abundant flora and fauna in this region may be due to the presence of various oceanographic gradients (influenced by the Pacific, Atlantic and Southern Oceans) and substrate types (e.g. sandy beaches, terraces, boulders and pebbles). This region is exposed

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to seasonal changes in abiotic parameters including temperature, salinity, photoperiod and solar radiation, which play a significant role in shaping the ecosystem (Dayton 1985; Silva and Calvete 2002; Ojeda et al. 2014). The high environmental heterogeneity of this region allows the occurrence of a benthic marine flora with high endemism, which hosts the largest reserves of submerged brown alga forests, with a predominance of the species *Lessonia flavicans* Bory, *Lessonia searlesiana* Asensi and de Reviers, *Durvillaea antarctica* (Chamisso) Hariot and *Macrocystis pyrifera* (L.) C. Agardh (Mansilla et al. 2020; Marambio et al. 2020). The last two species have wide dominance and extension, with populations parallel to the coast (30–45 m wide, Mansilla and Ávila 2011). They are considered as ecosystem engineers, forming habitats that provide shelter, food and breeding places for different species of great biological and economic importance in these sub-Antarctic environments (Ramírez 2010; Mansilla and Ávila 2011; Marambio et al. 2020).

Sub-Antarctic macroalgae are exposed to environmental stressors characteristic of high latitudes such as cold temperature, which induces the biosynthesis of unsaturated fatty acids in macroalgae. This is a mechanism of acclimatization to low temperatures (Khotimchenko and Yakovleva 2005; Koch et al. 2016; Barkina et al. 2020; Ho et al. 2021; Chemello et al. 2022). Environmental stress triggers alterations in several physiological processes, generating an increase in reactive oxygen species (ROS); lethal increase in ROS promotes "signaling molecules" originating defensive genes and adaptive responses. These adaptive strategies allow toleration of environmental stress through a set of antioxidant enzymes and metabolites such as polyunsaturated fatty acids (PUFA). These compounds contribute to controlling cellular levels of ROS and minimizing the detrimental effects of oxidative stress, preserving the cellular redox state and homeostasis of organisms, thus controlling internal conditions in the face of environmental changes (Kumar et al. 2014; Chemello et al. 2022).

The lipid composition of macroalgae has attracted considerable interest recently, due to their high PUFA content, particularly α -linolenic (18:3n-3), stearidonic (18:4n-3), arachidonic (20:4n-6) and eicosapentaenoic (20:5n-3) acids, which are essential dietary components in humans and animals (Kendel et al. 2015; Da Costa et al. 2019; Do-Amaral et al. 2020). These PUFA also possess antimicrobial, antiviral, anti-inflammatory and antitumor properties (Kendel et al. 2015; Da Costa et al. 2019; Do-Amaral et al. 2020; Saini et al. 2021; Kargin and Bilgüven 2022) and play a crucial role in the prevention of cardiovascular disease, osteoarthritis and diabetes (Marinho et al. 2015; Da Costa et al. 2019; Pereira et al. 2021; Rocha et al. 2022; Healy et al.

2023). Macroalgae have been suggested as potential candidates for PUFA supply, showing higher concentrations than those found in terrestrial vegetables (Marinho et al. 2015).

Several studies have explored the variation of fatty acids in brown macroalgae, particularly intra-thallus variation. Khotimchenko and Kulikova (2000) analyzed the fronds (upper, middle and lower) of *Saccharina japonica* and reported elevated levels of PUFA (n-6) in the lower zone ($29.8 \pm 1.5\%$) and PUFA (n-3) in the upper zone ($30.7 \pm 2.1\%$) of the frond. Gosch et al. (2015a) conducted a seasonal study over a year, examining intra-thallus variation between sections (end, middle and base) of the species *Spatoglossum macrodontum*. They observed consistently high levels of PUFA in all sections of the species, with a peak in June ($\sim 40\%$), while the basal section exhibited higher monounsaturated fatty acids (MUFA) ($32.16 \pm 0.43\%$) in September. Gosch et al. (2015b) explored the seasonal and intra-thallus fatty acid variation of the species *Dictyota bartayresii* and *Dictyopteris australis* in frond sections (upper and lower; terminal, middle and basal, respectively), finding a slight increase from the upper to lower sections of *D. bartayresii*, with high levels of MUFA ($\sim 30.5\%$) in summer and PUFA ($\sim 37.2\%$) in winter. In the case of *D. australis*, they showed a pattern of increasing MUFA from the terminal to the basal Sect. ($27.3 \pm 10.4\%$) in summer, whereas PUFA did not show an intra-thallus variation pattern and high levels were observed in the middle Sect. ($42.8 \pm 3.4\%$) in winter. Schmid and Stengel (2015) investigated five species of Laminariales (*Alaria esculenta*, *Laminaria digitata*, *Laminaria hyperborea*, *Saccharina latissima* and *Saccorhiza polyschides*) and three species of Fucales (*Ascophyllum nodosum*, *Fucus serratus* and *Himantalia elongata*). They observed a pattern of intra-thallus variation with decreasing MUFA content (from the ends of the fronds towards the holdfast) in the Laminariales species with high levels in *L. hyperborea* ($29.3 \pm 2.2\%$), while an opposite distribution pattern was evident (from the holdfast towards the end of the fronds) for PUFA, with high levels in *L. digitata* ($55.5 \pm 1.4\%$). No distinct distribution pattern was observed in the Fucales species, but high levels of MUFA ($45.4 \pm 1.3\%$) and PUFA ($54.6 \pm 0.9\%$) were found at the fronds ends of *A. nodosum* and *H. elongata*, respectively.

Previous studies conducted at lower latitudes (27° S) of Chile explored fatty acid variation in the brown macroalgae *M. pyrifera* and *D. antarctica* (Ortiz et al. 2006, 2009). However, only Ortiz et al. (2006) specifically investigated the intra-thallus variation in *D. antarctica* (in fronds and stipes), reporting high levels of MUFA ($38.11 \pm 0.12\%$) and PUFA ($34.42 \pm 1.90\%$) in fronds compared to stipes ($29.21 \pm 1.13\%$ and $29.23 \pm 2.20\%$, respectively). Several studies in the Magellan region have analyzed fatty acids in *M. pyrifera*,

D. antarctica and *L. flavicans* (Mansilla and Ávila 2011; Astorga-España and Mansilla 2014; Astorga-España et al. 2017; Santos et al. 2019). However, none of these studies addressed the intra-thallus variation in the most representative kelps of the region.

The rise in chronic diseases over recent decades is a global concern, impacting the quality of life and exerting a significant economic burden on both public and private health systems (Crespo et al. 2020). According to the Chilean Ministry of Health, the Magellan region faces high rates of prevalent diseases like type 2 diabetes mellitus, obesity and hypertension. In fact, 13.4% of the region's population (total population 166,533, National Health Survey, 2016–2017) have been diagnosed with hypertension, and an estimated additional 13% are likely unaware of their condition (Fernandez 2019). Data from the National Health Survey (2016–2017), reveal that 80.2% of the population in Magellan suffers from obesity, attributed to a sedentary lifestyle, high meat consumption and low intake of fruits and vegetables, partly due to the adverse climatic conditions and isolation inherent to a remote and extreme region. However, the Magellan region possesses untapped potential that offers an ideal opportunity to address these prevalent diseases among the local population. The abundant macroalga populations in sub-Antarctic ecosystems, thriving in harsh environmental conditions with constant low temperatures, low irradiance and extended photoperiods, represent a vital source of biomolecules, particularly with high concentration of fatty acids. Understanding these biomolecules is essential for future biomedical research and their potential incorporation into a healthy diet.

Owing to the environmental extremes found in high latitudes, such as permanent low temperatures, it is anticipated that the sub-Antarctic kelps *M. pyrifera* and *L. flavicans* will exhibit higher levels of unsaturated fatty acids compared to other low latitude macroalgae. The aim of this study is to assess the fatty acid concentration in the different morphological structures (fronds, stipes and holdfast) of these two significant kelp species from the sub-Antarctic Magellan Ecoregion, given their potential applications in biomedicine.

Materials and methods

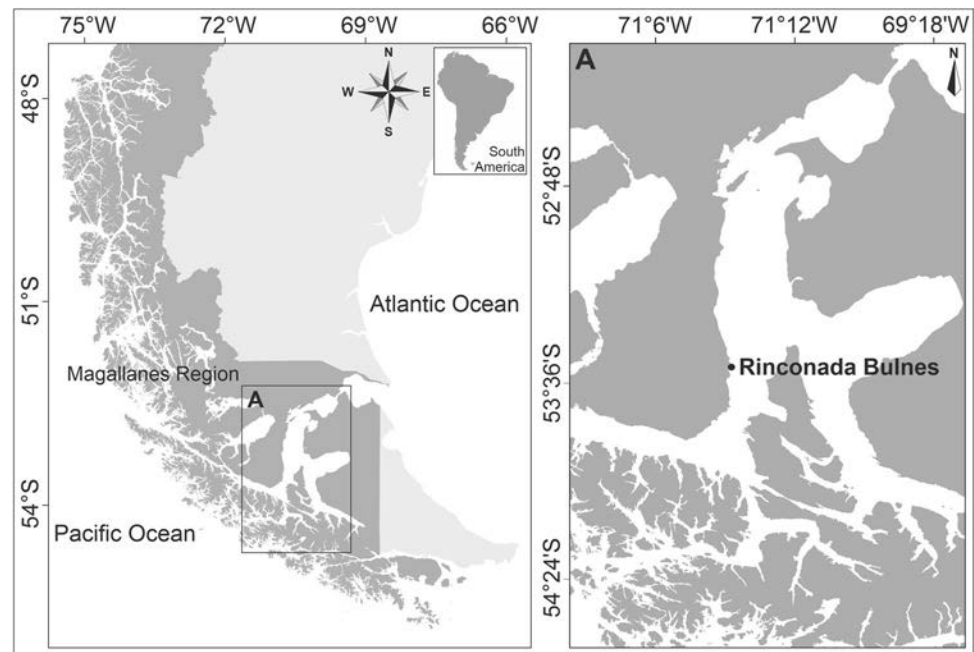
Field sampling Twelve adult individuals (6 individuals for both *M. pyrifera* and *L. flavicans*) were collected at Rinconada Bulnes, Puerto del Hambre (53°35'47.76" S; 70°56'08.52" W), located south of Punta Arenas, Chile (Fig. 1) during spring of 2021. For each species, the collected individuals ranged from 1–1.5 m in length. All samples were transported through a seawater cooler to the Laboratory of Antarctic and sub-Antarctic Marine Ecosystems

(LEMAS) at the University of Magellan. Upon arrival at the laboratory, the samples were carefully separated by structure (fronds, stipes and holdfast), followed by washing with distilled water to remove epiphytes and seawater from the thallus according to Schmid et al. (2018). Subsequently, 300 g of fresh biomass was collected from each thallus structure. The collected samples were then frozen at -80 °C and subsequently lyophilized at -50 °C. For lipid extraction, 30 g of dried biomass per structure of each species was used.

Lipid extraction For lipid extraction, 3.0 g of lyophilized samples were used ($n=9$ for *M. pyrifera* and $n=9$ for *L. flavicans*) following the method described by Bligh and Dyer (1959). Each thallus structure ($n=3$ for both species) was ground through a motor-driven mill (Thomas Scientific) and weighed in 150 mL beakers. Lipids were extracted by adding 10 mL chloroform, 20 mL methanol and 8 mL distilled water in proportions $\text{CHCl}_3:\text{CH}_3\text{OH}:\text{H}_2\text{O}$ (1:2:0.8). The mixture was homogenized for 3 min using an Ultra-Turrax disperser (IKA T25, USA) and the homogenate was filtered under vacuum through Whatman No.1 filter paper. The samples were re-extracted using the same procedure to recover as much extract as possible. The filtrate was transferred to a 100 mL graduated cylinder where its volume was measured and the missing amounts of chloroform and water were immediately added to reach the ratio $\text{CHCl}_3:\text{CH}_3\text{OH}:\text{H}_2\text{O}$ (2:2:1.8). After phase separation and clarification for 10 min, the chloroform phase containing the lipids was extracted using a Pasteur pipette and transferred to a pre-weighed 250 mL flask. The chloroform was evaporated using a vacuum rotary evaporator for 20 min at 45 °C, and the solvents were completely removed under a nitrogen gas stream. The total lipid content was measured gravimetrically and stored in hermetically sealed tubes containing a mixed chloroform: methanol solvent solution with 0.01% butylated hydroxytoluene (BHT) in a nitrogen atmosphere. The tubes were kept in the dark at -80 °C.

Fatty acid esterification The dried lipid extracts were transformed into fatty acid methyl esters (FAME) using the method of Metcalfe et al. (1966), with some modifications to simplify the weighing. Specifically, 20 mg of the sample was weighed in screw-capped test tubes, and 1.5 mL 0.50 M methanol-sodium hydroxide was added. The tubes were tightly stoppered, vortexed, and heated at 100 °C for 5 min. After cooling to room temperature, 2.0 mL of 14% boron trifluoride (BF_3) in methanol (Supelco, USA) was added and the tubes were capped, vortexed, and block heated at 100 °C for 30 min which was followed by the addition of hexane (1.0 mL) and vortex mixing for 30 seg. To facilitate phase extraction, 5.0 mL saturated NaCl was added to the mixture. The solution was centrifuged, and the hexane layer was transferred to a second tube. The methanol–water phase was

Fig. 1 Sampling site of *M. pyrifera* and *L. flavicans* individuals in Rinconada Bulnes (53°35'47.76"S; 70°56'08.52"W), Magellan region, Chile



extracted again with 1.0 mL hexane. The hexane extracts were combined and concentrated to 1 mL under a nitrogen stream before gas chromatographic analysis.

Gas chromatographic analysis The analysis was carried out using an Agilent model 7890B gas chromatograph equipped with an autosampler and a flame ionization detector. The identification of methyl ester fatty acids was performed by comparing their retention times on the Agilent HP-88 column (60 m × 0.25 mm × 0.20 μm) with the retention times of high-purity 37-component FAME MIX standards (Sigma Aldrich, USA). A flow split injection system with a 50:1 vent ratio was used; the carrier gas (H₂) flow rate was 1 mL min⁻¹. The injector temperature was 250 °C, and the detector temperature was 280 °C. The oven temperature program started at 120 °C for 5 min, followed by a ramp of 3 °C min⁻¹ to 220 °C, which was then maintained for 5 min.

Data analysis

Statistical analysis was performed at 95% confidence level ($p=0.05$) using STATISTICA software version 7.1. A factorial analysis of variance (ANOVA) was performed to compare the lipid composition between the factors (species, structure, species-structure) of *M. pyrifera* and *L. flavicans*. When the results were significant ($p < 0.05$), a Tukey test

was performed to verify the significant difference between them. The non-parametric Kruskal–Wallis test (Siegel and Castellan 1988) was used to compare the means of multiple variables, investigating the differences in fatty acids among the structures (fronds, stipes and holdfast) of each macroalga species. This test was chosen due to its ability to handle data without assuming a normal distribution (Kruskal and Wallis 1952), (STATISTICA software, version 7.1). To explore the relationships between the structures (fronds, stipes and holdfast) of *M. pyrifera* and *L. flavicans* and the fatty acid composition, Principal Component Analysis (PCA) (Jolliffe 1986) was employed with the 'factoextra' package in R v4.2.0 (R Development Core Team 2022). A two-way permutational analysis of variance (PERMANOVA) (Anderson 2001) was utilized to assess the differences in fatty acid composition between the macroalga species and their structures (fronds, stipes and holdfasts). PERMANOVA calculated the Euclidean dissimilarity distance between observations pairs using non-transformed data and 9999 permutations. All factors were treated as fixed (Galloway et al. 2012), and the homogeneity of the multivariate dispersion was tested using the PERMDISP function, yielding non-significant results (Anderson and Walsh 2013). Multivariate analysis was conducted using PRIMER 6 v6.1.13 software with the PERMANOVA + v1.0.3 add-on package (Clarke and Gorley 2006) (PRIMER-E, Ltd., UK).

Results

The lipids composition was significantly different between the structures for each species ($p < 0.05$, Online Resource 1). In the case of *M. pyrifera*, the values were found to be more concentrated in the stipes ($3.73 \pm 1.73\%$), followed by the fronds ($2.74 \pm 0.70\%$) and the holdfast ($1.38 \pm 0.08\%$). On the other hand, the lipid composition of *L. flavicans* increased in the following order: holdfast ($1.26 \pm 0.15\%$), stipes ($2.27 \pm 0.66\%$), fronds ($3.35 \pm 0.97\%$), (Online Resource 2).

The three thallus structures of *M. pyrifera* displayed similar percentages ($35.09 \pm 0.11\%$; $35.77 \pm 0.28\%$; $37.82 \pm 0.06\%$) of total saturated fatty acids (SAFA), while the highest percentages of MUFA were found in the stipe ($43.04 \pm 0.08\%$) and the holdfast ($41.65 \pm 0.21\%$), nearly doubling the percentage obtained in the fronds

($26.46 \pm 0.10\%$). Fronds exhibited the highest percentage of PUFA ($32.38 \pm 0.26\%$), followed by stipes ($21.99 \pm 0.17\%$) and holdfasts ($18.24 \pm 0.17\%$), (Fig. 2a). The total SAFA of *L. flavicans* was higher in fronds ($34.30 \pm 0.10\%$) and holdfasts ($32.01 \pm 0.19\%$) than in stipes ($27.59 \pm 0.06\%$), while the total percentage of MUFA was highest in the holdfast ($46.45 \pm 0.19\%$), similar to that found in stipes ($43.64 \pm 0.04\%$), and twice the concentration found in fronds ($29.46 \pm 0.13\%$). The total percentage of PUFA was higher in fronds ($28.89 \pm 0.23\%$) and stipes ($27.71 \pm 0.05\%$) than in holdfasts ($18.39 \pm 0.21\%$), (Fig. 2b). A total of 16 fatty acids, including 6 saturated, 3 monounsaturated and 8 polyunsaturated fatty acids, were identified in the different thallus structures of *M. pyrifera* and 14 fatty acids; 5 saturated, 4 monounsaturated, and 5 polyunsaturated fatty acids were found in its thallus structures of *L. flavicans* (Table 1 and Figs. 3 and 4).

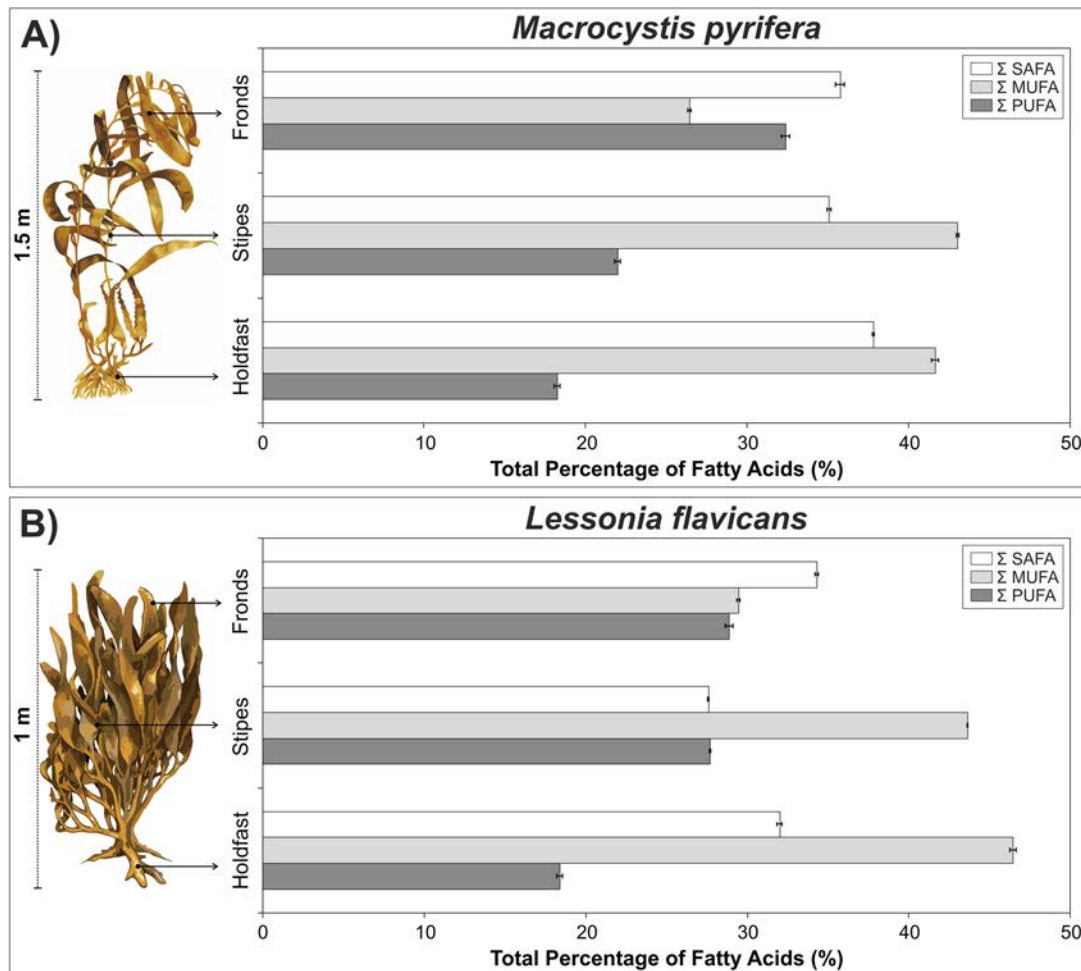


Fig. 2 Total percentage (%) of saturated, monounsaturated and polyunsaturated fatty acids of **A)** *M. pyrifera* and **B)** *L. flavicans* (fronds, stipes and holdfast), in Rinconada Bulnes ($53^{\circ}35'47.76''S$;

$70^{\circ}56'08.52''W$), Magellan region, Chile ($n=9$ for *M. pyrifera* and $n=9$ for *L. flavicans*). Data are given as percentage of total fatty acid content and are presented as mean values of triplicate samples \pm SD

Table 1 Percentage profile (%) of saturated, monounsaturated and polyunsaturated fatty acids in *M. pyrifera* and *L. flavicans* (fronds, stipes and holdfast), Magellan region, Chile. (n=9 for *M. pyrifera*and n=9 for *L. flavicans*). Data are given as percentage of total fatty acid content and are presented as mean values of triplicate samples \pm SD. (-) Not detected

Fatty acids	Chemical formulae	Percentage fronds (mean \pm SD)		Percentage stipes (mean \pm SD)		Percentage holdfast (mean \pm SD)	
		<i>M. pyrifera</i>	<i>L. flavicans</i>	<i>M. pyrifera</i>	<i>L. flavicans</i>	<i>M. pyrifera</i>	<i>L. flavicans</i>
Tridecanoic acid	C13:0	1.26 \pm 0.01	-	-	-	-	-
Myristic acid	C14:0	11.50 \pm 0.05	7.13 \pm 0.02	14.55 \pm 0.06	4.69 \pm 0.01	14.54 \pm 0.12	5.30 \pm 0.2
Pentadecanoic acid	C15:0	1.02 \pm 0.34	-	-	-	0.24 \pm 0.34	0.80 \pm 0.01
Palmitic acid	C16:0	20.82 \pm 0.09	26.05 \pm 0.09	18.55 \pm 0.06	20.48 \pm 0.02	20.74 \pm 0.16	23.83 \pm 0.12
Palmitoleic acid	C16:1n-7	2.82 \pm 0.01	2.21 \pm 0.01	2.69 \pm 0.01	4.40 \pm 0.00	3.99 \pm 0.01	4.98 \pm 0.08
Stearic acid	C18:0	0.56 \pm 0.01	1.05 \pm 0.00	1.04 \pm 0.02	1.00 \pm 0.00	1.28 \pm 0.02	1.01 \pm 0.00
Oleic acid	C18:1n-9c	11.44 \pm 0.06	11.44 \pm 0.04	22.03 \pm 0.05	13.07 \pm 0.00	23.27 \pm 0.18	22.55 \pm 0.10
Linolelaidic acid	C18:2n-6t	0.21 \pm 0.30	-	-	-	-	-
Linoleic acid	C18:2n-6c	4.33 \pm 0.01	4.10 \pm 0.05	4.30 \pm 0.06	6.14 \pm 0.06	4.45 \pm 0.04	7.71 \pm 0.04
Arachidic acid	C20:0	0.63 \pm 0.00	-	0.88 \pm 0.02	1.42 \pm 0.05	1.05 \pm 0.00	0.97 \pm 0.01
Linolenic acid	C18:3n-3	5.69 \pm 0.03	5.53 \pm 0.02	3.35 \pm 0.01	4.04 \pm 0.00	2.23 \pm 0.04	1.57 \pm 0.01
Octadecatetraenoic acid	C18:4n-3	9.42 \pm 0.04	6.59 \pm 0.06	3.80 \pm 0.06	5.16 \pm 0.05	2.32 \pm 0.02	1.96 \pm 0.13
γ -Linolenic acid	C18:3n-6	-	-	-	0.92 \pm 0.01	-	1.82 \pm 0.01
8,11,14-cis-Eicosatrienoic acid	C20:3n-6	0.79 \pm 0.01	-	1.40 \pm 0.13	-	1.45 \pm 0.16	-
Arachidonic acid	C20:4n-6	0.63 \pm 0.02	1.78 \pm 0.06	1.33 \pm 0.02	-	0.69 \pm 0.12	-
5,8,11,14,17-cis-Eicosapentanoic acid	C20:5n-3	10.13 \pm 0.02	10.89 \pm 0.38	7.10 \pm 0.10	11.44 \pm 0.00	5.99 \pm 0.06	5.34 \pm 0.05
Eicosatetraenoic acid	C20:4n-3	1.18 \pm 0.03	-	0.72 \pm 0.05	-	1.12 \pm 0.10	-
11-cis Eicosanoic acid	C20:1n-9	-	-	-	2.83 \pm 0.03	-	2.90 \pm 0.02
Erucic acid	C22:1n-9	12.13 \pm 0.03	15.74 \pm 0.07	18.27 \pm 0.04	23.36 \pm 0.01	14.25 \pm 0.04	16.09 \pm 0.25
Omega 3	Σ n-3	26.42 \pm 4.57	23.01 \pm 4.41	14.97 \pm 2.73	20.65 \pm 4.34	11.65 \pm 2.16	8.87 \pm 1.98
Omega 6	Σ n-6	5.96 \pm 1.57	5.88 \pm 1.58	7.02 \pm 1.59	7.06 \pm 2.29	6.59 \pm 1.64	9.52 \pm 2.88

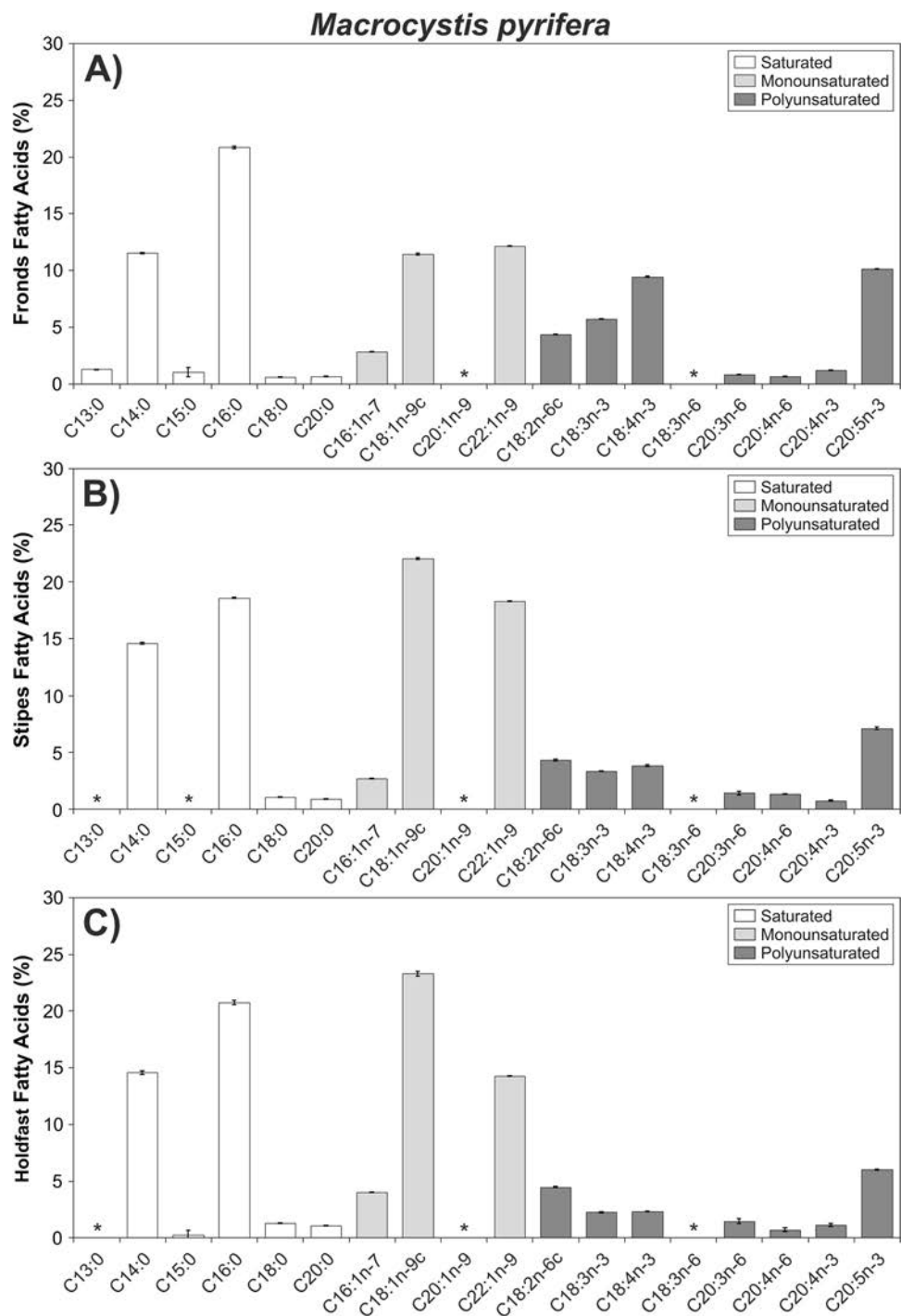
The results for omega-3 and omega-6 and in *M. pyrifera* revealed an increase in omega-3 levels from the holdfast (11.65 \pm 2.16%), stipes (14.97 \pm 2.73%) to the fronds (26.42 \pm 4.57%), while omega-6 levels remained constant across all three structures within a similar range (6.59 \pm 1.64%; 7.02 \pm 1.59% and 5.96 \pm 1.57%, respectively). The omega-6 levels of *L. flavicans* increased from the fronds (5.88 \pm 1.58%), stipes (7.06 \pm 2.29%) to the holdfast (9.52 \pm 2.88%), while omega-3 levels decreased from the fronds (23.01 \pm 4.41%), stipes (20.65 \pm 4.34%) to the holdfast (8.87 \pm 1.98%), (Table 1).

Each of the more abundant fatty acids in the structures of *M. pyrifera* accounted for 10% or more of the fatty acid profile. These fatty acids were C14:0 (11.50 \pm 0.05%), C16:0 (20.82 \pm 0.09%), C18:1n-9c (11.44 \pm 0.06%), C20:5n-3 (10.13 \pm 0.02%) and C22:1n-9 (12.13 \pm 0.03%) in the fronds. In the stipes, they were C14:0 (14.55 \pm 0.07%), C16:0 (18.55 \pm 0.07%), C18:1n-9c (22.03 \pm 0.05%), C22:1n-9 (18.27 \pm 0.04%); in the holdfast they were

C14:0 (14.54 \pm 0.12%), C16:0 (20.74 \pm 0.16%), C18:1n-9c (23.28 \pm 0.18%), and C22:1n-9 (14.25 \pm 0.04%) (Fig. 3, Table 1). The most representative acids in both the fronds and stipes of *L. flavicans* species were C16:0 (26.05 \pm 0.09%; 20.48 \pm 0.02%), C18:1n-9c (11.44 \pm 0.04%; 13.07 \pm 0.00%), C20:5n-3 (10.89 \pm 0.38%; 11.44 \pm 0.00%) and C22:1n-9 (15.74 \pm 0.07%; 23.36 \pm 0.01%), while in the holdfast they were C16:0 (23.83 \pm 0.12%), C18:1n-9c (22.55 \pm 0.10%) and C22:1n-9 (16.09 \pm 0.25%), (Fig. 4 and Table 1).

Statistical analysis revealed significant differences in the fatty acid profile among the three *M. pyrifera* structures (Online Resource 3). In SAFA compounds, both stearic acid (C18:0) and arachidic acid (C20:0) exhibited significant differences ($p > 0.02$) between fronds and holdfasts, with higher values in holdfasts (1.27 \pm 0.02% and 1.05 \pm 0.00%, respectively). Significant differences in MUFA compounds ($p > 0.02$) were found for palmitoleic acid (C16:1n-7) between stipes (2.69 \pm 0.01%) and holdfast (3.99 \pm 0.01%), oleic acid (C18:1n-9c) between fronds (11.44 \pm 0.06%) and

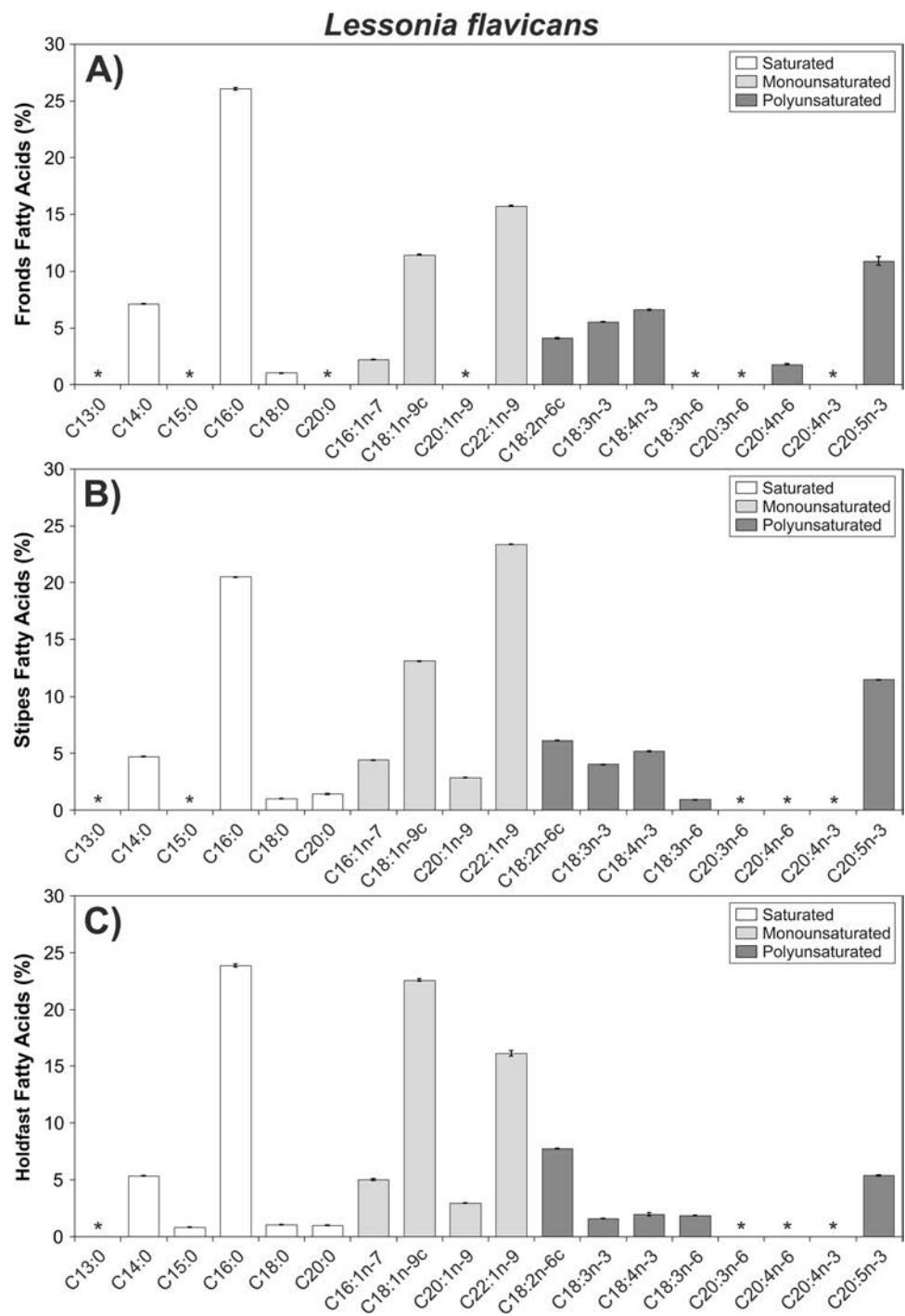
Fig. 3 Percentage (%) of identified fatty acids (saturated, monounsaturated and polyunsaturated) from *M. pyrifera* **A**) fronds, **B**) stipes and **C**) holdfast, in Rinconada Bulnes (53°35'47.76"S; 70°56'08.52"W), Magellan region, Chile (n=9 for *M. pyrifera* and n=9 for *L. flavicans*). Data are given as percentage of total fatty acid content and are presented as mean values of triplicate samples \pm SD. (*) Not detected



holdfast ($23.27 \pm 0.18\%$), and erucic acid (C22:1n-9) between fronds ($12.13 \pm 0.03\%$) and stipes ($18.27 \pm 0.04\%$). Significant differences ($p > 0.022$) were also observed between fronds and holdfast for PUFA compounds linolenic acid (C18:3n-3) ($5.69 \pm 0.03\%$; $2.23 \pm 0.04\%$), octadecatetraenoic acid (C18:4n-3) ($9.42 \pm 0.04\%$; $2.32 \pm 0.02\%$) and eicosapentaenoic acid (C20:5n-3) ($10.13 \pm 0.02\%$; $5.99 \pm 0.06\%$).

Statistical analyses also revealed significant differences among the three structures For *L. flavicans* (Online Resource 4). Significant differences in SAFA ($p = 0.02$) were observed between fronds and stipes for myristic acid (C14:0) ($7.13 \pm 0.02\%$; $4.69 \pm 0.01\%$), palmitic acid (C16:0) ($26.05 \pm 0.09\%$; $20.48 \pm 0.02\%$), stearic acid (C18:0) ($1.05 \pm 0.00\%$; $1.00 \pm 0.00\%$) and

Fig. 4 Percentage (%) of identified fatty acids (saturated, monounsaturated and polyunsaturated) from *L. flavicans* **A**) fronds, **B**) stipes and **C**) holdfast, in Rinconada Bulnes (53°35'47.76"S; 70°56'08.52"W), Magellan region, Chile (n=9 for *M. pyrifera* and n=9 for *L. flavicans*). Data are given as percentage of total fatty acid content and are presented as mean values of triplicate samples \pm SD. (*) Not detected



arachidic acid (C20:0) ($0.00 \pm 0.00\%$; $1.42 \pm 0.05\%$). For MUFA, significant differences ($p > 0.02$) were found between fronds and holdfast for palmitoleic acid (C16:1n-7) ($2.21 \pm 0.01\%$; $4.98 \pm 0.08\%$), oleic acid (C18:1n-9c) ($11.44 \pm 0.04\%$; $22.55 \pm 0.10\%$) and erucic acid (C22:1n-9) ($16.74 \pm 0.07\%$; $16.09 \pm 0.25\%$), respectively. Significant differences ($p > 0.02$) were also observed for eicosanoic acid (C20:1n-9) between fronds ($0.00 \pm 0.00\%$) and stipes ($2.83 \pm 0.03\%$).

For PUFA, significant differences ($p > 0.02$) between fronds and holdfast were observed for linoleic acid (C18:2n-6c) ($4.10 \pm 0.05\%$; $7.71 \pm 0.04\%$), linolenic acid (C18:3n-3) ($5.53 \pm 0.02\%$; $1.57 \pm 0.01\%$), octadecatetraenoic acid (C18:4n-3) ($6.59 \pm 0.06\%$; $1.96 \pm 0.13\%$) and γ -linolenic acid (C18:3n-6) ($0.00 \pm 0.00\%$; $1.82 \pm 0.01\%$). A significant difference ($p > 0.02$) between stipes and holdfast was also found for eicosapentaenoic acid (EPA) (C20:5n-3) ($11.44 \pm 0.00\%$; $5.34 \pm 0.05\%$).

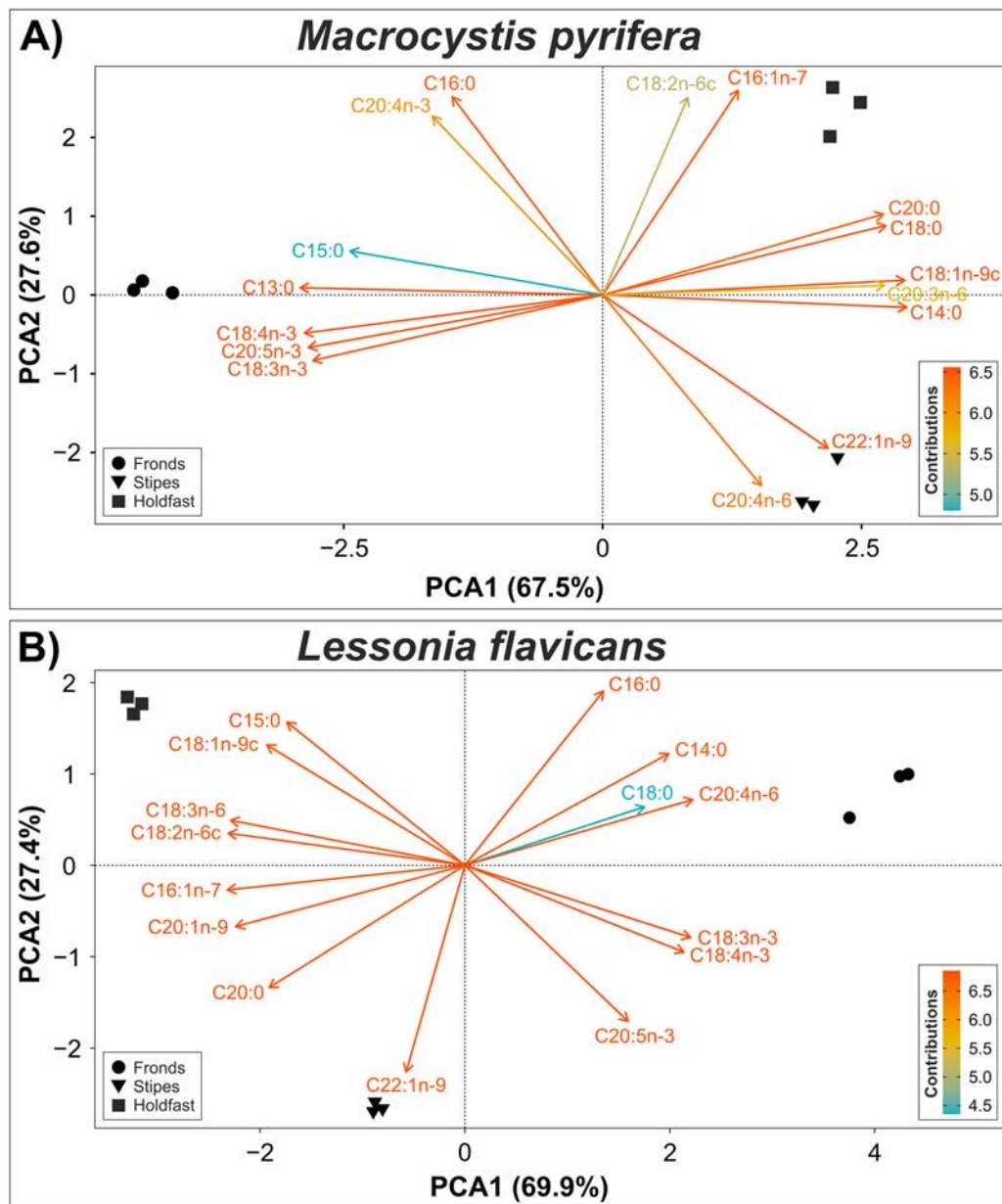


Fig. 5 Principal Component Analysis (PCA) of identified fatty acids (saturated, monounsaturated and polyunsaturated) from **A**) *M. pyrifera* and **B**) *L. flavicans* (fronds, stipes and holdfast), in Rinconada Bulnes (53°35'47,76"S; 70°56'08,52"W), Magellan region, Chile

Due to the significant statistical differences observed, a Principal Component Analysis (PCA) was conducted to examine the clustering of the fatty acids detected in the different structures of *M. pyrifera* and *L. flavicans*. For *M. pyrifera*, PCA1 and PCA2 explained 95.1% of the total variance in the observed variables. The analyses revealed a positive relationship between the fatty acid C13:0 and fronds, C16:1n-7 and holdfasts, and C22:1n-9 and C20:4n-6 with the stipes. The other fatty acids (C16:0, C20:4n-3, C15:0, C18:4n-3, C20:5n-3, C18:3n-3, C18:2n-6c, C20:0, C18:0) exhibited a mixed interaction between the components (PCA1 and

PCA2). The fatty acids C18:1n-9c, C20:3n-6 and C14:0 showed a prominent cluster in the first component (PCA1), but with a mixed interaction between stipes and holdfast. The C15:0 fatty acid had the lowest contribution (approximately 5.0) compared to the other fatty acids analyzed (Fig. 5a). PCA1 and PCA2 explained 97.3% of the total variance in the samples of *L. flavicans*. The analyses revealed a positive relationship between the fatty acids C14:0; C20:4n-6 and the fronds, C15:0; C18:1n-9c, the holdfast and C22:1n-9 the stipes. Fatty acid C16:0 showed mixed interactions between fronds and holdfast, while C18:2n-6c, C18:3n-6,

Table 2 Permutational Multivariate Analysis of Variance (PERMANOVA) showing differences in fatty acid composition between macroalgae species (*M. pyrifera* and *L. flavicans*) and their structures (fronds, stipes and holdfast). Analyses are based on Euclidean distance matrix, type III sum of squares, fixed effects and 9999 permutations. Abbreviations: df, Degrees of freedom; MS, Mean squares

Factor	df	MS	Pseudo-F	p-value
Algae	1	488.47	2721.3	0.0001 ***
Structure	2	434.84	2422.5	0.0001 ***
Algae × Structure	2	93.465	520.7	0.0001 ***
Residuals	12	0.1795		

(*) Indicates significant values at a confidence level of 95% ($p < 0.05$)

C16:1n-7, C20:1n-9 and C20:0 showed mixed interactions between holdfast and stipes. Fatty acids (C20:4n-3, C18:4n-3, C20:5n-3 and C18:3n-3) showed mixed interactions between stipes and fronds. Fatty acid C18:0 had the lowest contribution (4.5) to the components (Fig. 5b).

PERMANOVA was conducted to assess the variation in fatty acid composition within each macroalgae species and to determine significant differences between their thallus structures. The results indicated significant differences ($p > 0.0001$) in fatty acid composition between macroalga species (*M. pyrifera* and *L. flavicans*), between structures (fronds, stipes, and holdfast) and between species and structure (*M. pyrifera* and *L. flavicans*; fronds, stipes, and holdfast) (Table 2).

Discussion

The fatty acid composition in the fronds, stipes, and holdfast of the sub-Antarctic kelps *Macrocystis pyrifera* and *Lessonia flavicans* showed significant variation, particularly in monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA). While saturated fatty acids (SAFA) had similar levels between structures in both *M. pyrifera* and *L. flavicans*, MUFA exhibited a pattern of increasing concentration from fronds ($26.46 \pm 0.10\%$; $29.46 \pm 0.13\%$) to stipes ($43.04 \pm 0.08\%$; $43.64 \pm 0.04\%$) and holdfast ($41.65 \pm 0.21\%$; $46.45 \pm 0.19\%$) for both macroalga species. Conversely, PUFA showed a decreasing pattern from fronds ($32.38 \pm 0.26\%$; $28.89 \pm 0.23\%$) to stipes ($21.99 \pm 0.17\%$; $27.71 \pm 0.05\%$) and holdfast ($18.24 \pm 0.17\%$; $18.39 \pm 0.21\%$) for both species. Similar patterns of variation in fatty acid concentrations were described for *Saccharina japonica* by Khotimchenko and Kulikova (2000), who observed elevated levels ($30.7 \pm 2.1\%$) of PUFA (n3) in the upper zone of fronds. Similarly, Gosch et al. (2015a) observed high levels of MUFA in the basal zone ($32.16 \pm 0.43\%$) of the fronds of *S. macrodontum*, and Gosch et al. (2015b) reported an increase in MUFA from the ends towards the base of *D. bartayresii*, with high levels ($\sim 30.45\%$). Finally, Schmid and Stengel

(2015) also observed a pattern of increased PUFA from the holdfast towards the fronds in Laminariales species, with high levels ($55.5 \pm 1.4\%$) in *L. digitata*. A well-differentiated distribution of PUFA concentrations in the different morphological structures of the thallus is evident in all these studies.

In contrast to other studies with *M. pyrifera* (Schmid et al. 2018, 2020; Biancacci et al. 2022) and *Lessonia corrugata* (Schmid et al. 2018), where high concentrations of PUFA were found, our results showed high levels of MUFA but low levels of PUFA. According to studies by Schmid et al. (2020) in laboratory culture, under two nitrate conditions ($5 \mu\text{M}$ and $80 \mu\text{M}$) and three temperatures (6, 17 and $24 \text{ }^\circ\text{C}$), and by Biancacci et al. (2022) in marine culture lines at two sites with existing aquaculture concessions off the coast of Tasmania, Australia; these studies suggest that elevated PUFA levels may be induced by both the effects of salmon farming and the high nutrient conditions created there, which could lead to increase fatty acid concentrations in macroalgae. The Magellan kelp populations used in this study come from an area with little anthropogenic influence, therefore the fatty acid composition of the macroalgae studied is not influenced by farming systems that generate high nutrient conditions capable of inducing changes in fatty acid composition.

The environmental factors temperature, light, salinity, pH and nutrient availability, as well as habitat conditions, have been reported as parameters that regulate the fatty acid composition of macroalgae (Khotimchenko et al. 2002; Gosch et al. 2015a; Schmid and Stengel 2015; Schmid et al. 2018; Biancacci et al. 2022), resulting in different ranges of survival and adaptability (Schmid and Stengel 2015; Gerasimenko and Logvinov 2016). Variations in fatty acids in different structures of macroalgae are likely related to the morphological, functional and physiological differentiation of these structures, which play roles in growth, photosynthesis and energy storage (Gosch et al. 2015a). This differentiation may lead to a greater number of double bonds (PUFA) for the electron transport activity of the photosystems, especially at low temperatures (Sanina et al. 2008). Apical fronds are meristems with greater photosynthetic capacity compared to the basal structure (holdfast), whose primary function is to support and fix the substrate (Gosch et al. 2015a, b). Vega and Toledo (2018) reported that the chemical composition of macroalgae (proteins, carbohydrates, lipids and fibers) may increase during cold periods, as macroalgae need to enhance their nitrogen fixation rate for reproduction and growth. Macroalgae have to utilize energy to maintain their physiological processes during warm periods, resulting in a loss of nitrogen reserves. Oceanographic parameters have also been described as factors influencing phenotypic plasticity and variation in the chemical composition of macroalgae (Schmid and Stengel 2015; Vega and Toledo 2018).

The fatty acid profiles of *M. pyrifera* and *L. flavicans* exhibited high levels of certain MUFA in all their structures, particularly oleic acid (C18:1n-9c) and erucic acid

(C22:1n-9), especially in the stipes and holdfast. The fatty acid EPA (eicosapentaenoic acid) also stood out in the PUFA profile, despite the low concentrations found. EPA (C20:5n-3) was prominently present in *M. pyrifera* and *L. flavicans* fronds, with significantly higher levels in *L. flavicans* stipes. MUFA and PUFA have been shown to have beneficial effects on human health, including protection against insulin resistance (Mantilla-Mora et al. 2021), improved cardiovascular and coronary health, and improved cognitive performance in children (Cikoš et al. 2020). The high content of MUFA found in *M. pyrifera* and *L. flavicans* supports their role in the following: i) a protective mechanism against insulin resistance by altering cell membrane fluidity, modulating the regulation of transcription factors and influencing the expression of genes related to energy metabolism (Mantilla-Mora et al. 2021); ii) a regulator of lipid membrane fluidity under stress conditions (such as low temperatures), achieved through the expression of genes involved in the control of loacclimatization (Santos et al. 2017); and iii) an important component of a diet that reduces the risk of cardiovascular disease (Lomartire et al. 2021).

The balance between omega-6 and omega-3 fatty acids is of paramount importance for humans, particularly considering the increasing prevalence of processed foods, which reduce omega-3 levels and elevate omega-6 content in the diet, leading to potential effects on health (Melby 2019). The optimal omega-6/omega-3 ratio advocated by the pharmaceutical industry to combat common diseases is believed to range from 1:1 to 4:1 (Melby 2019; Santos et al. 2019). In the present study, a remarkable omega-6/omega-3 ratio of 1:1 was identified in the holdfast of *L. flavicans*, a brown macroalga endemic to the Magellan region.

The sub-Antarctic Magellan Ecoregion holds significant potential for biomedical applications at both regional and national levels. This potential is underscored by the utilization of specific macroalgal biomolecules that have demonstrated noteworthy outcomes in the field of biomedicine. These include: i) Investigation into the antitumor properties of lipid extracts derived from *Mazzaella laminarioides*, showing promising effects on bladder cancer cells (Do-Amaral et al. 2020); ii) The utilization of carrageenan sourced from *Gigartina skottsbergii* as a molecular tool for the early detection of SARS-CoV-2 (Zank et al. 2023) and iii) Ongoing preliminary research, as part of Fabio Méndez's PhD thesis, exploring the impact of lipid extracts from *M. pyrifera* and *L. flavicans* on glucose metabolism. This study encompasses both in vivo research utilizing *Caenorhabditis elegans* models and in vitro investigations using SH-SY5Y neuronal cells.

A novel opportunity emerges to exploit the resource species sustainably, with potential applications in A) healthy food—incorporating *M. pyrifera* into new food recipes can contribute to promoting a balanced diet in local communities

and reduce the risk of obesity within health centers, as demonstrated preliminarily in Astorga-España and Mansilla (2014) and B) nutraceuticals—*M. pyrifera* and *L. flavicans* can be utilized in the form of pills, capsules or syrups, with various beneficial effects including antibacterial, antiviral, anti-inflammatory, anticoagulant and antithrombotic properties.

Finally, this study is the first to compare the fatty acid composition between morphological structures (holdfast, stipes, and fronds) in two highly representative macroalga species from the sub-Antarctic Magellan Ecoregion. The region and the country must intensify efforts in bioprospecting for molecules in sub-Antarctic macroalgae to combat prevalent diseases in a remote natural laboratory with low anthropogenic impact.

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Authors' contributions F.M., wrote the main manuscript text, sample analysis, prepared figures. A.R., sample analysis. F.B., prepared figures. P.G., wrote the main manuscript text. M.F., wrote the main manuscript text. J.Z., wrote the main manuscript text. N.I., wrote the main manuscript text. A.M., wrote the main manuscript text. All authors reviewed the manuscript.

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Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare that the authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

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