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Chemical profiling of the Arctic sea lettuce *Ulva lactuca* (Chlorophyta) mass-cultivated on land under controlled conditions for food applications

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ABSTRACT

The increasing use of seaweeds in European cuisine led to cultivation initiatives funded by the European Union. *Ulva lactuca*, commonly known as sea lettuce, is a fast growing seaweed in the North Atlantic that chefs are bringing into the local cuisine. Here, different strains of Arctic *U. lactuca* were mass-cultivated under controlled conditions for up to 10 months. We quantified various chemical constituents associated with both health benefits (carbohydrates, protein, fatty acids, minerals) and health risks (heavy metals). Chemical analyses showed that long-term cultivation provided biomass of consistently high food quality and nutritional value. Concentrations of macroelements (C, N, P, Ca, Na, K, Mg) and micronutrients (Fe, Zn, Co, Mn, I) were sufficient to contribute to daily dietary mineral intake. Heavy metals (As, Cd, Hg and Pb) were found at low levels to pose health risk. The nutritional value of *Ulva* in terms of carbohydrates, protein and fatty acids is comparable to some selected fruits, vegetables, nuts and grains.

1. Introduction

Seaweeds (=macroalgae) are classified into three major groups according to their chlorophyll and accessory pigments: green (chlorophytes), brown (phaeophytes) and red (rhodophytes). They are marketed as processed and unprocessed product and have an annual commercial value of more than USD 6 billion (FAO, 2018). Seaweed extracts are commonly used in preparing foods and the direct consumption of seaweeds has existed for centuries in the diets of East Asian and Pacific Island societies. With the popularization of health-food industry, the use and inclusion of seaweeds in Western diets, which traditionally been limited to artisanal practices and coastal communities has recently gained wider consumer interest (Cherry, O'Hara, Magee, McSorley, & Allsopp, 2019). This interest is anchored on the presence of macronutrients, micronutrients, and bioactive compounds, which possess therapeutic potential in disease prevention in humans (Déléris, Nazih, & Bard, 2016). These compounds include polysaccharides, pigments, fatty acids, polyphenols and peptides and may contribute to the development of functional foods and nutraceuticals. The functional traits of these bioactive compounds include antioxidant, antibacterial, anticancer, antidiabetic, antitumor, antiviral, anti-inflammatory and anticoagulant properties (Vonthron-Sénécheau, 2016). Despite an increasing interest in health benefits of whole seaweeds, extracted bioactive components, and seaweed-based food products in humans, the potential adverse effects of edible seaweeds, including those related to ingestion of excess iodine and heavy metals, among others, requires detailed analysis and risk assessment (e.g. Li et al., 2018; Roleda et al., 2018, 2019; Cherry et al., 2019).

Ulva lactuca is a green seaweed species commonly known as sea lettuce. *Ulva* is a cosmopolitan genus found growing on rocky shores

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and reef flats around the world. Under other conditions, various species of *Ulva* are indicators of ecological disturbances, e.g. green tides or algal blooms (Li et al., 2018), which can occur as a consequence of anthropogenic activities such as extensive aquaculture, agriculture, industry, and sewage disposal. Timely, algal green tide biomass harvested in the Yellow Sea, China, has been successfully processed into biofuel (Zhuang et al., 2012). The utilization of *Ulva* biomass, both wild and cultivated, can further be enhanced by mining the potential riches of the species as source of bioactive compounds, food, feed and fertilizer (Dominguez & Loret, 2019).

Since the launching of the New Nordic Cuisine in 2004, a manifesto signed by 12 influential and leading chefs from Finland, Sweden, Norway, Denmark, Iceland, Greenland, and the Faroe Islands that promotes the use of local ingredients and produce from Nordic climates, landscapes, and waters, the Nordic chefs have been looking for hidden gastronomic treasures in seaweeds (Mouritsen, Rhatigan, & Pérez-Lloréns, 2019). The most interesting seaweed species available in the North Atlantic that the chefs are now bringing into the Nordic cuisine include dulse (*Palmaria palmata*), oarweed (*Laminaria digitata*), tangleweed (*Laminaria hyperborea*), sugar kelp (*Saccharina latissima*), winged kelp (*Alaria esculenta*), and various wracks (*Fucus* spp.) as well as sea lettuce or string lettuce (*Ulva* spp.) (Mouritsen et al., 2019). The European market for seaweeds, primarily for culinary uses, has been increasing at 7–10% growth rate per year and with an estimated wholesale value of approximately EUR 24 million in 2013 (Organic Monitor, 2014).

Cultivation of *Ulva* in Northern Norway intended for the local culinary use (Bladet Vesterålen, 2016) was financially supported by the Nordland County through the Interreg Botnia Atlantica Programmes (Nordland fylkeskommune, 2018). Considering the seasonal occurrence of wild *Ulva* spp. in spring and summer, one of the objectives of the project is to produce *Ulva* year around under laboratory condition to provide continuous supply of fresh biomass to local restaurants. The taxonomy for the genus *Ulva* is challenging (e.g. Herrero, Brurberg, Ojeda, & Roleda, 2020). Different and/or the same species could exhibit a different or similar gross morphology (Fig. 1). In this regard, it is important to molecularly identify the species for cultivation because chemical composition of seaweed could vary between species, season, and origin i.e. site of collection (e.g. Roleda et al., 2018, 2019).

To access the food quality of *Ulva*, most studies have exclusively looked into the essential and/or toxic elements (e.g. Pérez et al., 2007; Smith, Summers, & Wong, 2010; Astorga-España, Rodríguez Galdón, Rodríguez Rodríguez, & Díaz Romero, 2015; Desideri et al., 2016), sugars (e.g. Robin, Chavel, Chemodanov, Israel, & Goldberg, 2017; Yaich et al., 2011), amino acids (e.g. Dave & Parekh, 1978; Biancarosa et al., 2017), and fatty acids (e.g. Schmid et al., 2018; Dellatorre, Avaro, Commendatore, Arce, & de Vivar, 2020). Only few studies look into multiple parameters of different chemical composition (e.g. minerals, heavy metals, amino and fatty acids) of edible seaweeds in general and *Ulva* in particular (e.g. Mæhre, Malde, Eilertsen, & Elvevoll, 2014; Peña-Rodriguez, Mawhinney, Ricque-Marie, & Cruz-Suárez, 2011).

This study aimed at assessing the nutritional quality of the edible sea lettuce *U. lactuca* mass-cultivated on land in northern Norway. A chemical profile was determined for each of the four strains by quantifying various constituents related to health benefits for humans. In addition, contaminants (e.g. heavy metals) were determined to estimate potential health risks associated with the consumption of sea lettuce. We hypothesize that there are significant differences in the chemistry of different strains of *U. lactuca*. Results of the study are essential for assessing the food applications of the species to ensure consistent high food quality. Moreover, the chemical composition of *U. lactuca* investigated in this study were compared to those of other *Ulva* species from different locations around the world and to those of selected fruits, seeds, vegetables, vegetable oils, nuts and grains to obtain a broader picture about sea lettuce as raw material for food applications.

2. Materials and methods

2.1. Collection and strain selection for medium-scale cultivation

Different thalli of green seaweed belonging to the genus *Ulva* were collected during late spring and early summer of 2016 in Andøya and Bodø, Nordland, Norway. Collection from specific habitat or site was assigned a collection (i.e. strain) number, separately packed, and brought to the laboratory for cultivation. After preliminary growth experiments (briefly described below), four strains were selected for mass propagation for food application (Fig. 1). These were strain #03 and #06 (collection site and date: Andøya, 11 April 2016; lat/long: 69.1077°N, 15.9667°E), strain #10 (collection site and date: Bodø, 9 May 2016; lat/long: 67.2754°N, 14.5696°E), and strain #12 (collection site and date: Andøya, 22 June 2016; lat/long: 69.1070°N, 15.9712°E). A single blade from each strain was cut into several pieces (approx. 20 cm disc diameter) and clonally propagated.

Using batch cultivation in 250 mL flasks, growth rates of different strains of *Ulva* were measured under different environmental conditions inside a walk-in growth chamber (data not shown). Thereafter, fast growing strains were selected and grown in an indoor cultivation facility using 65.5 L (60.5 × 38 × 37 cm, length × width × height, with seawater outlet at 28.5 cm) and 483 L (177 × 91 × 40 cm, length × width × height, with seawater outlet at 30 cm) capacity tanks. Culture tanks were fed with continuous flow of seawater (3.5×10^{-5} m^3 s^{-1} flow rate) sourced from 200 m depth of the nearby fjord with average nutrient concentration of 10.03 ± 0.22 μM NO_3^-, 0.15 ± 0.02 μM NO_2^-, 3.78 ± 6.60 μM NH_4^+, 0.79 ± 0.15 μM PO_4^{3-}. An irradiance of 100 μmol photons m^{-2} s^{-1} (photosynthetically active radiation, E_{PAR}, 400–700 nm) at 12:12 light:dark photoperiod were provided using fluorescent lamps. The water temperature was maintained at 15 °C. Under continuous cultivation, algal growth takes place under steady-state conditions; that is, growth in a constant environment occurs at a constant rate. At maximum standing stock, seawater volume to seaweed biomass ratio was 0.5 L: 1 g for the 65.5 L tanks and 6 L: 1 g for the 483 L tanks. Regardless of the volume: biomass ratio, growth rate measured ranged from 25 to 30% day^{-1} (Aluwini & Roleda, 2017). During the 8–10-month cultivation period, 50–75% of the biomass were harvested either weekly or fortnightly. Collected samples were frozen at −80 °C, freeze-dried and ground to 120 μm grain size. Homogenized samples of each strain collected were analyzed for various chemical constituents as described below.

2.2. Species identification

Ground samples from above were also used for the molecular identification of the species. Genomic DNA was extracted using the DNeasy® Plant Mini Kit (Qiagen ®) according to the manufacturer's recommendations. A fragment of the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit gene (*rbcL*) approximately 1200 bp in length was amplified using the SH F1 and SH R4 primers as described by Heesch et al. (2009). The fragments were sequenced in both directions (GATC Biotech, Germany), and sequences were trimmed and assembled using the DNASTAR SeqMan software. The consensus sequence was used for species identification by BLAST search in GenBank. The rbcL fragments from the four algal strains resulted in sequences of 1170 bp after trimming. The sequences of all four strains were identical; they were also identical to several specimens of *Ulva lactuca* in GenBank. All identified nucleotide sequences were deposited in the GenBank database under the accession numbers MT338526, MT338527, MT338528 and MT338529 corresponding to the four different strains in Fig. 1 and will be called *U. lactuca* strain #03, #06, #10 and #12 (i.e. UL#03, UL#06, UL#10 and UL#12), respectively.

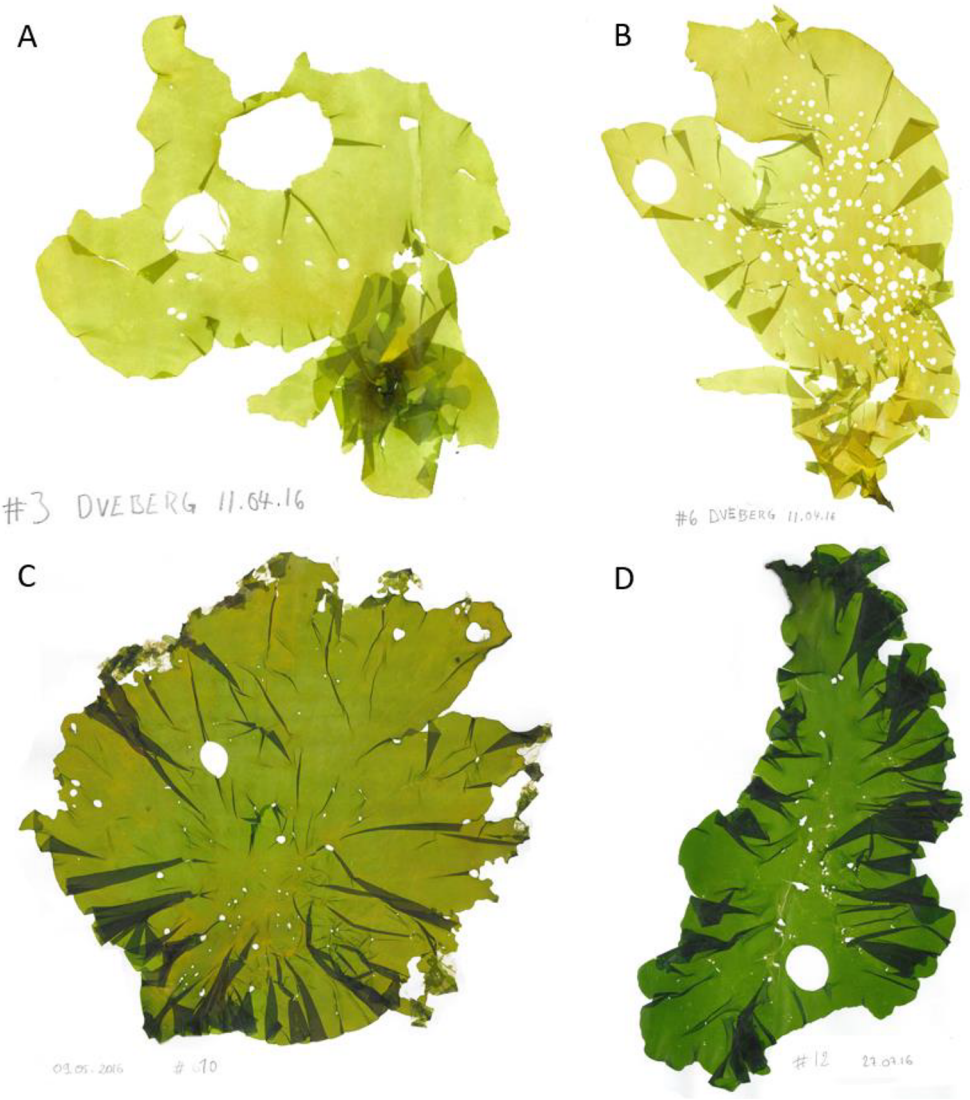

Fig. 1. Morphology of *Ulva lactuca* strains cultivated for food application: A, B and D from Andøya and C from Bodø, northern Norway corresponding to strains UL#03, UL#06, UL#12 and UL#10, respectively.

2.3. Tissue elemental analysis

Ground samples of dried algal biomass were sent to Mikroanalytisches Laboratorium Kolbe (Oberhausen, Germany), a microanalytical lab that provides professional service with regard to elementary analyses. Twelve elements, i.e. Carbon, Nitrogen, Phosphorus, Iodine, Calcium, Sodium, Potassium, Magnesium, Zinc, Iron, Copper and Manganese were analyzed using standard methods and procedures (https://www.mikro-lab.de/?lang=en). Briefly, tissue C and N were measured using a CHN analyzer (MikroCube, Elementar Analysensysteme GmbH, Langenselbold, Germany). Tissue P was determined using a modified vanadate/molybdate method (so-called yellow method): P was identified and quantified by an UV/VIS photometer (Specord 50Plus, AnalytikJena AG, Jena, Germany). Iodine was quantified as iodide via an ion chromatography (883 Basic IC Plus, Metrohm AG, Herisau, Switzerland). Other elements were determined using atomic absorption spectroscopy (AAnalyst 200 AA Spectrometer, Perkin Elmer, Inc., Waltham, MA 02451, USA). Heavy metal content, i.e. total As, Cd, Hg and Pb, were determined by ICP-MS (Agilent 7500ce, Waldbronn, Germany) described in Roleda et al. (2019).

2.4. Ash content

The macroalgae ash content was determined using a standard ash test at 550 °C, according to the procedure described in EN ISO 18122:2015 (ISO, 2015).

2.5. Monosaccharides analysis

Trimethylsilyl (TMS) derivatization of monosaccharides was performed according to Sweeley, Bentley, Makita, and Wells (1963). Briefly, 500 μg (± 10%) dry macroalgae powder samples and 30 μg of inositol, used as internal standard, together with standards of nine monosaccharides (D-Arabinose [Ara], D-Rhamnose [Rha], D-Fucose [Fuc], D-Xylose [Xyl], D-Mannose [Man], D-Galactose [Gal], D-Galacturonic acid [GalA], D-Glucose [Glc], D-Glucuronic acid [GlcA], each at 10, 20, 50 and 100 μg) were methanolysed by 2 M HCl/MeOH at 85 °C for 24 h in glass tubes. The tubes were cooled down and the solvent was evaporated at 40 °C under the stream of nitrogen. After 3 rounds of washing with methanol and evaporation in the stream of nitrogen, silylation was carried out using Tri-sil reagent (3–3039,

SUPELCO) at 80 °C for 20 min. Solvent was evaporated under a stream of nitrogen and pellet was dissolved in 1 mL hexane and filtered through glass wool. This filtrate was evaporated to the final volume of 100–200 µl of which 0.5 µl was analyzed by gas chromatography mass spectrometry (GC–MS) (7890A/5975C; Agilent Technologies, Kista, Sweden) according to Gandla et al. (2015). Silylated monosaccharides were separated on a J&W DB-5MS column (30 m length, 0.25 mm diameter, 0.25 µm film thickness) (Agilent Technologies, Kista, Sweden) with the oven program: 80 °C followed by a temperature increase of 20 °C min^{-1} to 140 °C for 2 min, then 2 °C min^{-1} to 200 °C for 5 min, then 30 °C min^{-1} to 250 °C for 5 min. The total run time was 47 min.

2.6. Amino acids and ammonium analysis

Amino acids and ammonium were extracted according to Näsholm, Sandberg, and Ericsson (1987). Samples of dry macroalgae powder (100 mg) were suspended in 80% ethanol and allowed to stand for 15 min. Samples were centrifuged at 3000 g for 5 min and the supernatant was collected. Pellets were re-extracted three times and the supernatants combined. The supernatants were then evaporated under reduced pressure and re-suspended in Milli-Q water. Amino acids were then derivatized using the Waters AccQ-Tag Ultra Derivatization kit following the manufacturer's instructions (Waters, 1993). The internal standard (nor-valin, 100 mmol N L^{-1}) was added to aliquots of samples or standards. The derivatized amino acids were analyzed by reversed phase liquid chromatography using an Ultra High Performance (UHPLC) system with a Tunable UV (TUV) detector (Waters, Sollentuna, Sweden). The separation of individual amino acids and ammonium was performed with an AccQ-Tag TM Ultra C18 column. Eluent A was 99.9% formic acid and eluent B was 10% acetonitrile. The gradient used was: 0–5.74 min 99.9% A, declining to 90.9% A from 5.74 to 7.74 min, to 78.8% A at 8.24 min and then to 40.4% A at 8.74 min, before re-equilibration with 99.9% A from 8.74 to 9.54 min. The flow rate and column temperature were 0.6 mL min^{-1} and 55 °C, respectively (Inselsbacher, Öhlund, Jämtgård, Huss-Danell, & Näsholm, 2011).

2.7. Total lipids analysis

The total crude lipids were extracted using a single-step method of Axelsson and Gentili (2014). Briefly, a 2:1 chloroform: methanol (v/v) solution was added to the 10 mg (± 20%) dry macroalgae powder samples, vortexed for 2 min, and 0.73% sodium chloride solution was added to achieve 2:1:0.8 ratio, chloroform: methanol: water (v/v/v). Phase separation was achieved by centrifugation at 350 g for 2 min. Lipid phase was recovered and washed twice with chloroform and further centrifuged. Subsequently, samples were vacuum dried in a multievaporator (Syncore® Polyvap, Büchi Labortechnik AB, Flawil, Switzerland) at 40 °C, 120 rpm, and 275 mbar for 3 h. Total lipids content per dry weight was determined gravimetrically and samples were stored at −20 °C until further use in fatty acid methyl esters (FAMEs) quantification and characterization.

2.8. Fatty acid methyl esters analysis (FAMES)

Different triglycerides (TAGs) in the total crude lipid extract were separated from other lipid types and non-lipids fractions using solid phase extraction (SPE). SPE separation was performed using a modified method of Danielewicz, Anderson, and Franz (2011). SPE cartridges (HyperSep™ Silica, Thermo Fisher Scientific, Hägersten, Sweden) were primed with hexane, and the crude lipid extract was dissolved in hexane before loading in the cartridge. An 80:20:1 mixture of hexane: diethyl ether: acetic acid (v/v/v) was used as mobile phase for TAGs elution. The elute was vacuum dried in a multievaporator at 40 °C, 120 rpm, and 275 mbar, overnight. Thereafter, the dry elute was transmethylated according to Lage and Gentili (2018). Briefly, the transmethylation reaction i.e. the conversion of TAGs to FAMEs was carried out in 1% sulfuric acid in dry MeOH, at a temperature of 80 °C for 2 h. Prior to the reaction, toluene was added, and the mixture was vortexed and fluxed with gaseous nitrogen to avoid oxidation. After transmethylation, 5% NaCl aqueous solution and hexane was added in equal proportions, and the hexane phase was recovered after centrifugation. The aqueous phase was washed twice with hexane. To dry the recovered hexane phase, a 2% potassium bicarbonate solution was added, followed by addition of anhydrous sodium sulfate. The mixture was incubated at room temperature for 5 min, and the organic phase was recovered. The hexane layer was vacuum dried in a multievaporator at 40 °C, 120 rpm, and 275 mbar overnight. FAMEs dry samples were stored at −20 °C until gas chromatography (GC) analysis. FAMEs extracts were dissolved in heptane and injected into a TRACE™ 1310 (Thermo Fisher Scientific, Hägersten, Sweden) GC system equipped with flame ionization detector and a 30 m FAMEWAX column (Restek Corporation, Bellefonte, Pennsylvania, USA) with I.D. 0.32 mm and 0.25 µm film thickness. Injection volume was 1 µl with a split ratio and flow of 11 and 8 mL min^{-1}, respectively. The carrier gas was nitrogen, with a fixed flow of 1.5 mL min^{-1}. The temperature program was as follows: initial temperature 195 °C, increased to 240 °C at 1.8 °C min^{-1} and held at this temperature for 2.8 min. Total runtime was 29 min. FAMEs peaks were identified by the comparison of their retention time with authentic standard by GC and quantified by normalization to the internal standard methyl pentadecanoic acid (C15.0).

2.9. Data handling and statistical analysis

Chemical constituents were determined in duplicates or triplicates; the average value of these technical replicates was considered one independent (biological) replicate (n). Biological variance was estimated by random sampling at various time points during the course of the experiment; depending on strain, sampling was conducted three to five times over eight to ten months of biomass production (i.e. n = 3–5), analysis of elemental composition was carried out once (n = 1). Results are presented as means and their one standard deviation of n = 3–5, except for elemental composition. *Effects* of the explanatory variable 'strain' on each 'chemical constituent' (i.e. response variable) were determined by 1-way ANOVAs followed by Tukey HSD test to find *a posteriori* homogeneous sub-groups of means that differed significantly at $\alpha \leq 0.05$ (a *post hoc* test was required for lipid and MUFA contents only). For most data, values followed a normal distribution (Shapiro-Wilk tests: $P > 0.05$) and variances were homogeneous (Levene test: $P > 0.05$). Multi-way ANOVAs were not applied since the experimental design was not fully orthogonal. Statistical analyses were carried out using R (https://www.r-project.org/); data were plotted with SigmaPlot® version 14.

3. Results

3.1. Macroelements, micronutrient, heavy metals, and ash content

Concentrations of various chemical components were similar for the four strains of *U. lactuca* investigated; the intraspecific or strain specific variability observed was marginal. The macroelements varied from 303.5 to 340 mg (g DW)$^{-1}$ for C, 33.2 to 45.8 mg (g DW)$^{-1}$ for N and 2.4 to 4.1 mg (g DW)$^{-1}$ for P (Table 1). The variations in the essential nutrients Ca, Na, K, and Mg among different *U. lactuca* strains were negligible (Table 1), where the difference between the high and low values was as miniscule as 0.03% (Ca) to 0.52% (Na).

Iodine exhibited the highest variability; concentrations ranged from 1.00×10^{-2} mg (g DW)$^{-1}$ (UL#12) to 8.07×10^{-2} mg (g DW)$^{-1}$ (UL#06). The micronutrients Fe, Zn, Cu, and Mn examined varied considerably by a factor of up to 2.8 (Table 1). Heavy metals considered toxic (As, Cd, Hg, and Pb) showed variations by a factor of 1.8 and 2.8

Table 1
Macroelements, micronutrients and heavy metals [mg (g DW)$^{-1}$] of *Ulva lactuca*, and in comparison with other *Ulva* species from various regions. Bold values represent highest concentration. Other studies reported are [1]Mæhre, Malde, Eilertsen & Elvevoll, 2014; [2]Phaneuf, Côté, Dumas, Ferron & LeBlanc, 1999; [3]Desideri et al., 2016; [4]Pérez et al. 2007; [5]Astorga-España, Rodríguez Galdón, Rodríguez Rodríguez & Díaz Romero, 2015; [6]Sun, Liu, Jiang & Yang, 2019; [7]Smith, Summers & Wong, 2010.

	Norway, this study				Norway[1]		Canada[2]	
	UL#03	UL#06	UL#10	UL#12	Ulac	Uint[§]	Ulac	Uint[¶]
Macroelements								
Carbon	337.6	303.5	**340.7**	316.7				
Nitrogen	**45.8**	41.6	45.2	33.2				
Phosphorus	3.3	2.4	4.1	2.5	0.5	1. 2		
Calcium	1.7	1.6	1.5	1.8	3.5	5.5		
Sodium	21.7	18.9	17.1	**22.3**				
Potassium	17.0	17.0	17.8	15.7				
Magnesium	14.9	16.7	15.8	15.6	26.0	15.0		
Micronutrients								
Iron	0.6	0.3	0.6	0.3	0.2	6.0	2.5	**7.0**
Zinc	1.40×10^{-2}	0.87×10^{-2}	0.90×10^{-2}	0.50×10^{-2}	0.80×10^{-2}	2.50×10^{-2}	3.30×10^{-2}	3.82×10^{-2}
Copper	2.03×10^{-2}	1.1×10^{-2}	$\mathbf{2.63 \times 10^{-2}}$	1.60×10^{-2}	0.60×10^{-2}	0.49×10^{-2}	1.92×10^{-2}	2.27×10^{-2}
Manganese	1.43×10^{-2}	0.77×10^{-2}	0.53×10^{-2}	0.73×10^{-2}	1.10×10^{-2}	13.0×10^{-2}	40.9×10^{-2}	15.6×10^{-2}
Iodine	1.80×10^{-2}	8.07×10^{-2}	1.30×10^{-2}	1.00×10^{-2}	2.1×10^{-2}	13.0×10^{-2}	$\mathbf{13.6 \times 10^{-2}}$	2.27×10^{-2}
Heavy metals								
Arsenic	n/a	6.39×10^{-3}	11.3×10^{-3}	9.10×10^{-3}	7.90×10^{-3}	4.90×10^{-3}	6.00×10^{-3}	7.20×10^{-3}
Cadmium	n/a	0.21×10^{-3}	0.26×10^{-3}	0.15×10^{-3}	0.10×10^{-3}	0.12×10^{-3}	0.22×10^{-3}	0.28×10^{-3}
Mercury	n/a	traces	traces	traces	traces	traces		
Lead	n/a	0.59×10^{-3}	1.10×10^{-3}	0.40×10^{-3}			1.64×10^{-3}	3.20×10^{-3}

	Italy[3]*		Argentina[4]		Chile[5]		China[6]	New Zealand[7]
	Ulac	Uint[†]	*Ulva* sp. (3 sites)		*Ulva* sp.	Uint[¶]	Ufas	Usten
			Min.	Max.				
Macroelements								
Carbon								
Nitrogen								
Phosphorus	3.4	**6.6**	1.8	3.0	1.9	2.7	0.7	2.7
Calcium	4.8	2.3	7.1	**13.1**	4.0	9.1	12.9	12.9
Sodium					9.8	19.3	14.1	1.9
Potassium	12.5	**25.7**			11.1	19.5	11.2	7.9
Magnesium			27.7	**31.7**	18.3	14.1	7.7	
Micronutrients								
Iron			0.2	0.5	0.7	1.5	1.5	1.2
Zinc	3.46×10^{-2}	3.17×10^{-2}	1.74×10^{-2}	3.13×10^{-2}	1.62×10^{-2}	3.08×10^{-2}	5.58×10^{-2}	$\mathbf{6.10 \times 10^{-2}}$
Copper	2.31×10^{-2}	1.01×10^{-2}	0.17×10^{-2}	0.38×10^{-2}	0.70×10^{-2}	0.79×10^{-2}	1.98×10^{-2}	1.10×10^{-2}
Manganese	$\mathbf{63.7 \times 10^{-2}}$	3.17×10^{-2}	0.81×10^{-2}	5.14×10^{-2}	2.72×10^{-2}	8.60×10^{-2}	4.90×10^{-2}	19.3×10^{-2}
Iodine	6.37×10^{-2}	2.81×10^{-2}						2.7×10^{-2}
Heavy metals								
Arsenic	2.80×10^{-3}	$\mathbf{15.4 \times 10^{-3}}$	2.98×10^{-3}	5.61×10^{-3}				1.88×10^{-3}
Cadmium		$\mathbf{3.50 \times 10^{-3}}$	0.17×10^{-3}	1.03×10^{-3}			1.00×10^{-3}	
Mercury								$\mathbf{0.10 \times 10^{-3}}$
Lead	6.70×10^{-3}	1.30×10^{-3}	0.82×10^{-3}	1.72×10^{-3}			$\mathbf{10.3 \times 10^{-3}}$	1.83×10^{-3}

Species are: Ulac- *Ulva lactuca*; Uint- *Ulva intestinalis*; Ufas- *Ulva fasciata*; Usten- *Ulva stenophylla.* The *Ulva fasciata* identification of Sun et al. (2019) is deemed uncertain.
*Samples bought from specialty store, origin not specified.
[§]Reported as *Enteromorpha intestinalis*. Currently accepted name is *Ulva intestinalis*.
[¶]Reported as *Enteromorpha* sp. The genus *Enteromorpha* is now *Ulva*.
[†]Misreported as *Ulva/Enteromorpha* and/or *Ulva enteromorpha*.

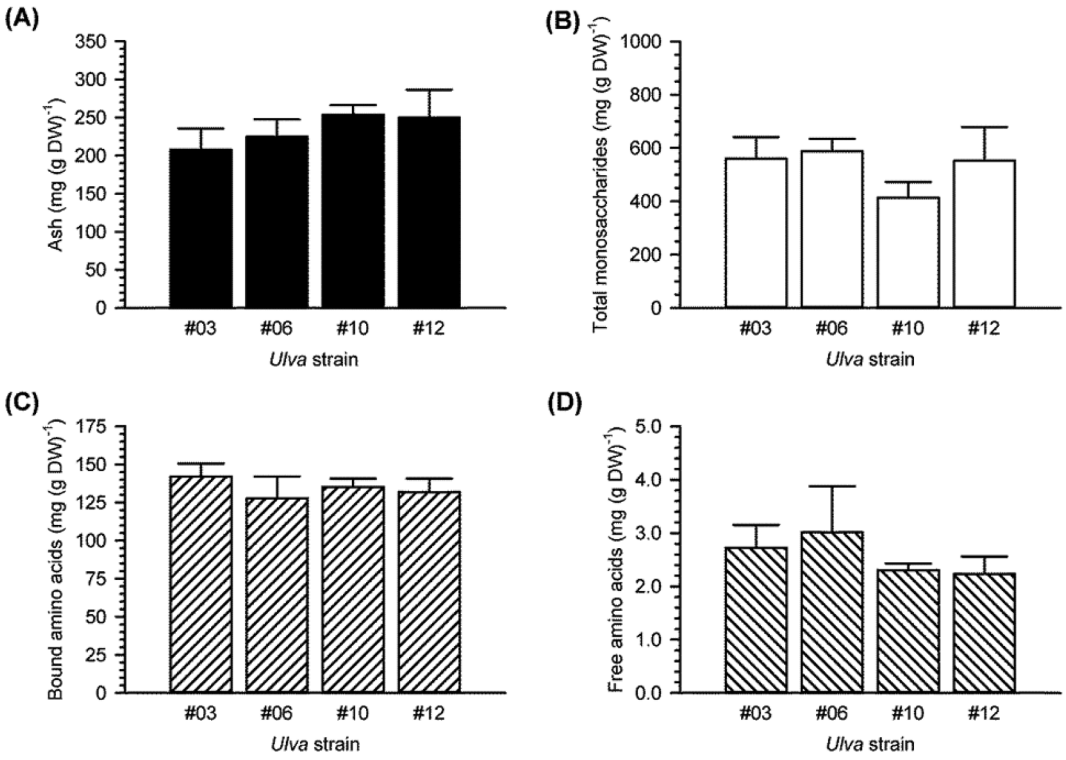

Fig. 2. (A) Total ash content, (B) total sugar content, and (C) bound and (D) free amino acids of different *Ulva* strains. Statistical analyses showed no significant variations in ash, sugar and amino acids among different strains.

for As and Pb, respectively. On the other hand, concentrations of Cd were similarly low for all strains [0.02 – 0.03 mg (g DW)$^{-1}$] and Hg was present only in traces. Similar to most elements, ash contents differed only marginally from 207.8 ± 27.7 (UL#03) to 253.8 ± 12.5 mg (g DW)$^{-1}$ (UL#10) (1-way ANOVA: $F(3,12) = 2.487$, $P = 0.110$: Fig. 2A).

Concentrations of macroelements, micronutrients and heavy metals for the four strains of *U. lactuca* investigated here were similar, i.e. the same order of magnitude, to those reported in the literature for most constituents (Table 1).

3.2. Monosaccharides

Nine different monosaccharides were detected: D-Arabinose, D-Rhamnose, D-Fucose, D-Xylose, D-Mannose, D-Galactose, D-Galacturonic acid, D-Glucose, D-Glucuronic acid (Supplementary Data, Table S1) and similar contents of each monosaccharide were observed for the four *U. lactuca* strains (1-way ANOVAs: $P > 0.05$). Total sugar, presented as sum of monosaccharides (Fig. 2B), ranged from 414.2 mg (g DW)$^{-1}$ (UL#10) to 588.2 mg (g DW)$^{-1}$ (UL#06) (1-way ANOVA: $F(3,12) = 2.959$, $P = 0.075$).

3.3. Amino acids

Total amino acids (AAs) and the fraction of essential (EAA) and non-essential (NEAA) are shown in Table 2. In general, the fraction of NEAA was higher (approximately 82 mg (g DW)$^{-1}$) than the fraction of EAA (approximately 54 mg (g DW)$^{-1}$) for all *U. lactuca* strains, and no statistically different concentrations were detected (1-way ANOVAs: $P > 0.05$). The majority of AA (approximately 134 mg (g DW)$^{-1}$, Fig. 2C) were bound, whereas the concentration of free AA was lower by two orders of magnitude (approximately 2.5 (mg g DW)$^{-1}$, Fig. 2D). Overall, amino acid profiles did not differ statistically between *U. lactuca* strains (1-way ANOVAs: $P > 0.05$). The most prominent EAA is Leucine and NEAAs are Aspartate, Alanine and Glutamate. Miniscule amount of ornithine and γ-aminobutyric acid were found in the free AA fraction while ammonium is measured in both bound and free AA fractions (data not shown).

Table 2
Total amino acid (AA) content in mg (g DW)$^{-1}$ of different *Ulva* strains and results of 1-way ANOVAs. Data are presented as means ± SD (n = 3–5).

Ulva strain	Total AA content	Essential AA content	Non-essential AA content
#03	144.7 ± 8.5	58.5 ± 4.2	86.2 ± 4.4
#06	130.8 ± 13.8	51.4 ± 6.1	79.4 ± 7.8
#10	137.5 ± 5.6	54.1 ± 2.5	83.4 ± 3.2
#12	134.1 ± 9.1	54.2 ± 3.4	79.9 ± 5.8
$F(3,12)$	1.424	1.852	1.221
P	0.284	0.192	0.344

3.4. Total lipids and FAMES

Total lipids varied from 97.42 ± 13.74 mg (g DW)$^{-1}$ (UL#03) to 130. 92 ± 16.28 mg (g DW)$^{-1}$ (UL#12) (Fig. 3A) and the lipid content of strain UL#12 was significantly higher than that of strain UL#03 (1-way ANOVA: $F(3,12) = 4.112$, $P = 0.032$: Tukey HSD: UL#03 < UL#12, $P < 0.05$). From the total lipids, total FAMES was minimal ranging from 2.16 ± 2.54 mg (g DW)$^{-1}$ (UL#10) to 7.44 ± 4.33 mg (g DW)$^{-1}$ (UL#03) and did not differ statistically (1-way ANOVA: $F(3,12) = 2.881$, $P = 0.078$: Fig. 3B). The following fatty acids detected were saturated fatty acids [SFA: C14:0, C18:0, C16:0, C20:0, and C22:0], monounsaturated fatty acid [MUFA: C16.1 and C18.1] and polyunsaturated fatty acid [PUFA: Omega-6 C18:2 and C18:3 (n-6), and Omega-3 C18:3 (n-3)] (Supplemental Data, Table S2). As shown in Fig. 3C, the fraction of SFA was highest for all strains (58–72%). The fraction of PUFA was similar for the four *U. lactuca* strains (19–26%): by contrast, MUFA varied considerably and were significantly highest for UL#03 (17%) and lowest for UL#12 (4%) (Supplemental Data, Table S3).

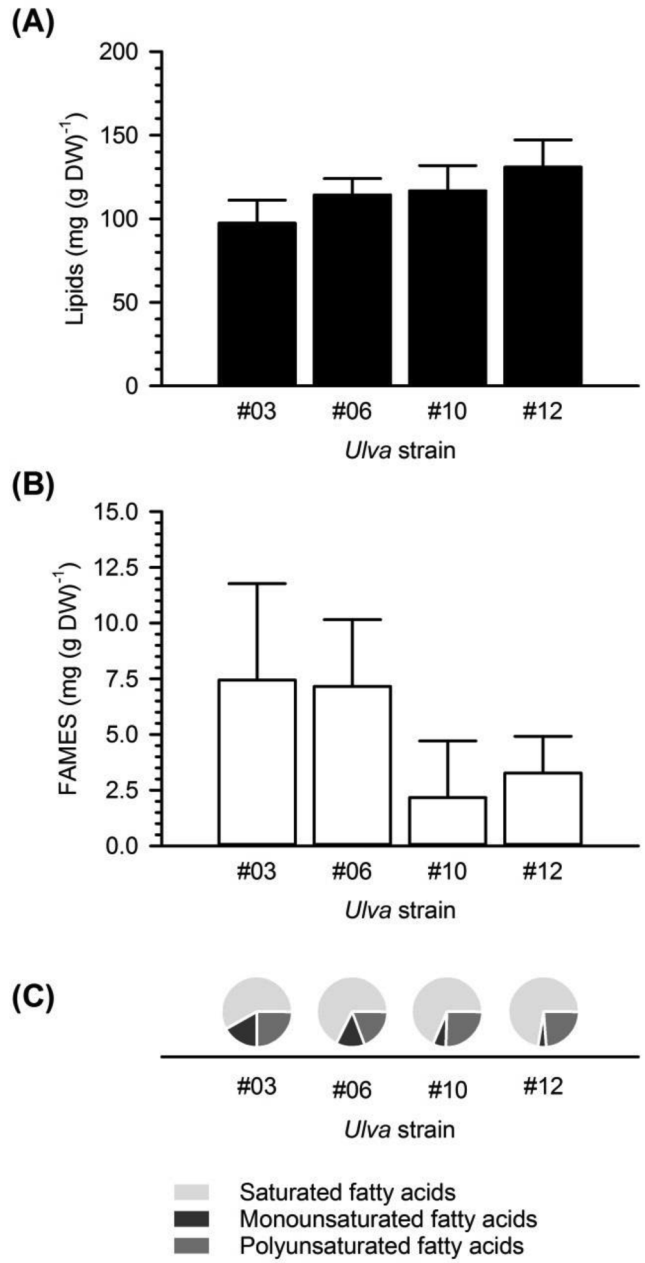

Fig. 3. (A) Total lipid content, (B) total fatty acid content (as FAMES) and (C) proportion of saturated, monounsaturated and polyunsaturated fatty acids (of FAMES) of different *Ulva* strains. Statistical analysis showed significant difference in lipids (1-way ANOVA: $F(3,12) = 4.112$, $P = \mathbf{0.032}$; post hoc: #03 ≤ #06 = #10 ≤ #12; #03 < #12) but not in FAMES.

4. Discussion

Marginal variability in different chemical constituents was observed among different strains of *U. lactuca* mass-cultivated in the land-based culture facility, which is contrary to our hypothesis. Interestingly, our findings indicated that the nutritional value of sea lettuce was not compromised under long-term controlled laboratory cultivation. The nutritional qualities of Arctic sea lettuce from Norway are *at par* with other species/strains from other regions of the world.

4.1. Macroelements, micronutrient, heavy metals, and ash content

The macroelements P, Na, K and Mg of the cultivated sea lettuce were within the range of the reported values for the same and other *Ulva* species (Table 1). The Ca is, however, in the low range (Table 1). This can be attributed to the fact that tank cultivation produced clean biomass i.e. devoid of epiphytes, invertebrates, and calcareous particles common in wild harvested samples, which can contribute to higher Ca and other impurities.

For the micronutrient, Cu among different *Ulva* species/strains were comparable. Fe content was also relatively comparable, except for the high value reported in Canada (Table 1; Phaneuf, Côté, Dumas, Ferron, & LeBlanc, 1999). Conversely, Zn, Mn, and I were the three micronutrients that exhibited the highest variability between different species/strains of *Ulva* sourced from different regions of the world (Table 1). Lowest and highest values reported were 0.50×10^{-2} and 6.10×10^{-2} mg (g DW)$^{-1}$ for Zn; 0.53×10^{-2} and 63.70×10^{-2} mg (g DW)$^{-1}$ for Mn; and 1.0×10^{-2} and 13.6×10^{-2} mg (g DW)$^{-1}$ for I, respectively.

Heavy metal contents (As, Cd, Pb) in *U. lactuca* from Norway were similarly low as the reported values for *Ulva* species from other regions. High As and Cd were present in processed *Ulva intestinalis* of unknown origin bought from a specialty store in Italy (Desideri et al., 2016). The highest Pb was reported in the uncertainly identified *Ulva fasciata* from China (Sun, Liu, Jiang, & Yang, 2019). Hg is of minimal concern as most studies reported only traces are present in *Ulva* spp. except for *Ulva stenophylla* from New Zealand (Smith et al., 2010). On the other hand, the ash content of wild *Ulva lactuca* from Tunisia ([195.9 mg (g DW)$^{-1}$]; Yaich et al., 2011) is comparable to those measured in this study [235.15 mg (g DW)$^{-1}$].

Looking into the potential adverse effects of consuming edible seaweeds i.e. related to the ingestion of excess iodine and heavy metals, we compared *U. lactuca* (this study) to those of the iodine and heavy metal contents of three edible seaweeds *Palmaria palmata*, *Alaria esculenta*, and *Saccharina latissima* collected from the same biogeographic region of northeastern Atlantic.

The mean iodine content of *U. lactuca* was 3.04×10^{-2} mg (g DW)$^{-1}$; this is significantly lower compared than that of red (e.g. *Palmaria palmata*: 0.18 mg (g DW)$^{-1}$) and brown seaweeds (e.g. *Saccharina latissima*: 4.65 mg (g DW)$^{-1}$, *Alaria esculenta*: 0.53 mg (g DW)$^{-1}$; Roleda et al., 2018). By contrast, wild collected *Ulva* species from Ireland contained iodine at the same order of magnitude as those observed in this study, although iodine contents of wild seaweeds may strongly vary with season (Nitschke, Walsh, McDaid, & Stengel, 2018).

The mean total As content in *U. lactuca* [8.93×10^{-3} mg (g DW)$^{-1}$] is comparable to that of red seaweed *P. palmata* [8.84×10^{-3} mg (g DW)$^{-1}$] but significantly lower compared to the brown seaweeds *Alaria esculenta* [56.94×10^{-3} mg (g DW)$^{-1}$] and *Saccharina latissima* [69.79×10^{-3} mg (g DW)$^{-1}$] (Roleda et al., 2019).

Moreover, the Cd of *U. lactuca* [0.21×10^{-3} mg (g DW)$^{-1}$] was also lower compared to the above three species, which ranges from 0.6 to 1.6×10^{-3} mg (g DW)$^{-1}$; however, the Pb present in *Ulva* [0.70×10^{-3} mg (g DW)$^{-1}$] was slightly higher compared to the above three species measuring only 0.20×10^{-3} mg (g DW)$^{-1}$ (Roleda et al., 2019).

A health risk assessment conducted on the consumption of *P. palmata*, *A. esculenta*, and *S. latissima* suggested that these seaweeds pose a low risk for humans with regard to iodine (Roleda et al., 2018) and heavy metals (Roleda et al., 2019). Considering that the iodine and heavy metal contents of *U. lactuca* observed in this study is less than or mostly comparable to the above three species, sea lettuce from Norway cultivated on land can also be safely consumed in allowable daily ration without trepidation on the potential adverse effect.

4.2. Monosaccharides

Total sugar of cultivated *Ulva lactuca* ranges from 414.2 to 588.2 mg (g DW)$^{-1}$. This is significantly higher compared to the total monosaccharide of *U. lactuca* from Tunisia [272 mg (g DW)$^{-1}$] (Yaich et al., 2011) and of unknown *Ulva* species from Israel [68.10 – 159.29 mg (g

DW)$^{-1}$] (Robin et al., 2017). The huge variations between these studies is most likely related to methodological differences rather than related to species-specificity, temporal or spatial variations in sugar content of particular seaweed species.

4.3. Amino acids

The mean total amino acids (TAA) of cultivated *Ulva lactuca* in this study [136.8 mg (g DW)$^{-1}$] is comparable to those of the wild *U. lactuca* [175 mg (g DW)$^{-1}$] and *U. intestinalis* [131 mg (g DW)$^{-1}$] collected from Bodø, Nordland county (Biancarosa et al., 2017). On the other hand, wild *U. lactuca* collected south of Bodø in Sør-Trøndelag county measured slightly lower TAA [101.5 mg (g DW)$^{-1}$] (Mæhre et al., 2014). Surprisingly, cultivated *Ulva clathrata* measured 6× higher TAA ranging from 764 to 804 mg (g DW)$^{-1}$ (Peña-Rodriguez et al., 2011). The huge variation between *U. clathrata* and the two other *Ulva* species could be attributed to species-specific difference in protein synthesis. Previously, the rare compounds ornithine and γ-ominobutyric acid were also reported five different species of *Ulva*, including *U. lactuca* (Dave & Parekh, 1978).

4.4. Total lipids and FAMES

Total lipids (TL) of two *Ulva* species collected from Patagonia, Argentina measured 75.8 and 90.7 mg (g DW)$^{-1}$ for *Ulva* sp.1 and *Ulva* sp.2, respectively (Dellatorre et al., 2020). These values are lower compared to our cultivated *U. lactuca* measuring 97.4 – 130.9 mg (g DW)$^{-1}$. The corresponding total fatty acids (TFA) reported for the two Patagonian *Ulva* species at 10.9 and 24.0 mg (g DW)$^{-1}$ were surprisingly higher compared to those observed in this study ranging from 2 to 7.3 mg (g DW)$^{-1}$. These values, however, fall within the lower range of TFA reported in three other *Ulva* species i.e. *U. australis*, *U. compressa*, and *U. stenophylloides* from cool temperate Australia ranging from 5 to 19 mg (g DW)$^{-1}$ (Schmid et al., 2018). Conversely, another study on tropical Australian Ulvales showed higher TFA in other *Ulva* species *U. clathrata* [11.53 mg (g DW)$^{-1}$], *Ulva flexuosa* [29.31 mg (g DW)$^{-1}$] and *Ulva rigida* [21.39 mg (g DW)$^{-1}$] (Gosch, Magnusson, Paul, & de Nys, 2012). The high variability in TL and TFA contents within the same genus is most likely due to species specificity, and spatial (i.e. biogeographic regions) and seasonal variations in environmental factors. Notably, we observed an inverse relationship between TL and TFA contents in different strains of *Ulva lactuca* (Fig. 3a and b). The same trend, i.e. decreasing fatty acid with increasing total lipid content, was also observed by Gosch and coworkers (2012) in all three major taxonomic groups of seaweeds. Further comparison showed that brown seaweeds (phaeophytes) had the highest TL and TFA contents, followed by green (chlorophytes) and red (rhodophytes) seaweeds (Gosch et al., 2012). On the other hand, the FA composition of the Patagonian *Ulva* species have higher proportion of PUFA > MUFA > SFA (Dellatorre et al., 2020), which is contrary to the proportion of FAs observed in cultivated *Ulva lactuca* i.e. SFA > PUFA > MUFA. Comparison with other studies proved difficult where fatty acid compositions were reported as % of TFA, but the TFA values were not reported (e.g. Mæhre et al., 2014; Peña-Rodriguez et al., 2011). To be able to compare results among different studies, it is imperative to standardize data reporting.

In this study, we measured 13–65× higher TL compared to TFA. The huge difference between TL and TFA contents have also been observed in other studies (e.g. Gosch et al., 2012; Dellatorre et al., 2020). This difference can be attributed to different analytical methods used (Lage & Gentili, 2018). For example, during crude lipids extraction, other compounds of non-lipid origin i.e. characteristic of biological samples can likely be co-extracted and measured gravimetrically leading to an overestimated TL. On the other hand, FAMEs analysis entails lipid purification, transmethylation and GC-FID analysis. Thereafter, only FAMEs peaks that can be positively identified against the retention time of the known standard are integrated, thus providing an accurate quantification.

4.5. Comparative nutritional value of Ulva and selected fruits, vegetables, nuts and grains

The cultivated sea lettuce *U. lactuca* biomass are rich in sugars containing on the average 528.9 mg (g DW)$^{-1}$; however, the sugar content of some fruits exceeded this concentration (Supplementary Data, Table S4). The fruits that contain higher sugar includes litchis with 835 mg (g DW)$^{-1}$, and in decreasing amount of sugar are the following: mango, melon, grapes, figs, plum, peach, watermelon, cherries, apple, apricot, pineapple, persimmons, nectarine, blueberries and pear with 601.6 mg (g DW)$^{-1}$ (Supplementary Data, Table S4). Interestingly, selected vegetables, nuts and grains have much lower sugar contents compared to sea lettuce. For example, representative of the above crops with the highest sugar contents are cabbage [457.8 mg (g DW)$^{-1}$], pistachio [79.6 mg (g DW)$^{-1}$], and rye [11.7 mg (g DW)$^{-1}$], respectively.

The total protein content, i.e. measured as total amino acids, of sea lettuce is on the average 136.8 mg (g DW)$^{-1}$. This value is comparable to the protein contents of other green vegetables e.g. celeriac, celery, Brussels sprout, broccoli and endive at 125.0, 151.0, 157.1, 158.9, 201.3 mg (g DW)$^{-1}$, respectively. However, other vegetables contain 2–3× higher protein e.g. lettuce, asparagus, spinach and mushrooms at 308.9, 324.5, 332.6 and 408.2 mg (g DW)$^{-1}$, respectively. Conversely, fruits have much lower protein contents, ranging from a low of 18.0 mg (g DW)$^{-1}$ in apples to a high of 117.3 mg (g DW)$^{-1}$ in blackberries (Supplementary Data, Table S4).

On the average, the total lipids contents of sea lettuce is 114.85 mg (g DW)$^{-1}$, which is minimal compared to lipids in nuts that are on the average contain 5× higher (Supplementary Data, Table S4). For example, pecan, pistachio and cashew nuts have 746.0, 462.8 and 462.6 mg (g DW)$^{-1}$ total lipids, respectively. The remaining foods presented in Table S3 have on the average [21.7 mg (g DW)$^{-1}$] lesser total lipids compared to our sea lettuce; total lipids concentration ranges from a high in chickpea with 68.3 mg (g DW)$^{-1}$ to a low in sweet potato with 2.2 mg (g DW)$^{-1}$.

Consistent with total lipids, the total fatty acids (FA) content is also higher in nuts with values of 711.0, 439.6 and 415.9 mg (g DW)$^{-1}$ for pecan, pistachio and cashew nut respectively. The mean total FA of sea lettuce is miniscule at 4.6 mg (g DW)$^{-1}$. However, this is higher compared to the total FA of sweet potato [1.4 mg (g DW)$^{-1}$], potato [3.5 mg (g DW)$^{-1}$], and pear [3.8 mg (g DW)$^{-1}$], and comparable to cassava [4.9 mg (g DW)$^{-1}$], persimmons [5.1 mg (g DW)$^{-1}$], rice [6.3 mg (g DW)$^{-1}$], and cranberries [6.6 mg (g DW)$^{-1}$]. Other than nuts, chickpea has the highest total FA at 52.9 mg (g DW)$^{-1}$ (Supplementary Data, Table S4).

The saturated FA of sea lettuce consist > 50% of its total FA; the same was observed in the proportion of saturated FA in the total FA of pumpkin (74.7%), sweet potato (57.1%) and bananas (51.7%). Generally, most fruits, vegetables and grains have a higher proportion of polyunsaturated FA, which could be as high as 80% of the total fatty acids content, e.g. in blackberries and raspberries (both at 81.9%). Conversely, nuts (cashew, pecan, and pistachio) have a higher proportion of monounsaturated FA, i.e. > 50% of the total FA content. Some fruits like plum and apricot also have higher monounsaturated FA, which constituents 69.1% and 62.2% of the total FA content (% values were calculated from supplementary data in Table S4).

The sea lettuce *U. lactuca* showed a fatty acids profile with a good distribution of saturated, monounsaturated and polyunsaturated including omega 3 and 6 FAs compared to seed oils, fruits, and vegetables (Supplementary Data, Table S2).

The individual fatty acid profile of sea lettuce is interesting. For example, its gamma-linolenic acid (C 18:3n-6/omega 6) is higher compared to hempseeds oil but lower than that of black currant seeds

oil. On the other hand, its alpha-linolenic acid (C 18:3n-3/omega 3) is comparable to those of rape seed oil, black currant seed oil, and walnut, and much higher than those of soybean oil, corn oil, sunflower oil, and olive oil. Only chia seed oil, hempseed oil, and the broccoli and cauliflower florets have higher omega 3 (Supplementary Data, Table S2).

The stearic acid (C 18:0) and palmitoleic acid (C 16:1) of the sea lettuce is higher compared to different seed oil, nut, and vegetables. On the other hand, the palmitic acid (C 16:0) of the sea lettuce is slightly lower yet comparable to the vegetables broccoli and cauliflower florets, but higher compared to different seed oils and nut (Supplementary Data, Table S2).

Despite the relatively low total FAMEs content, expressed as mg (g DW)$^{-1}$, in the sea lettuce (Fig. 3 and Table S4), the FAME profile is balanced and of nutritional importance. Hence, sea lettuce can be used as complementary food item as traditionally practiced for centuries in many Asian countries.

The mean ash content of *Ulva lactuca* is relatively high at 234.15 mg (g DW)$^{-1}$. However, this is comparable to the ash content in spinach [200 mg (g DW)$^{-1}$] and endive [227.1 mg (g DW)$^{-1}$]. All other food items listed have lower ash contents, varying from a low of 7.2 mg (g DW)$^{-1}$ in rice to a high of 164.1 mg (g DW)$^{-1}$ in celery (Supplementary Data, Table S4).

Considering the sugar, amino and fatty acids, and mineral contents of sea lettuce in particular and edible seaweeds in general, the use of raw (fresh) or processed (dried or milled) seaweed products provides natural and functional constituent in enriching foods, i.e. to add flavor, aromas, spice, consistency, color and natural minerals to enhance food quality and gastronomic experience.

5. Conclusion

Contrary to our hypothesis, there was no strain specific variability observed in the chemical composition of the sea lettuce *U. lactuca* propagated under controlled condition. The long-term cultivation also did not generate negative impacts on its nutritional quality. In fact, the Arctic sea lettuce from Norway possessed a comparable excellent nutritional quality compared to species/strains from other regions of the world, and was observed to have consistent high food quality.

Entrepreneurs can basically cultivate sea lettuce in a closed system anywhere in the world to provide fresh products or raw materials to restaurants using seaweed in their cuisine. Production lines can be established in the cities, close to the market to minimize transport cost and carbon footprint.

CRediT authorship contribution statement

Michael Y. Roleda: Funding acquisition, Project administration, Supervision, Visualization, Conceptualization, Methodology, Investigation, Writing - original draft, Data curation, Formal analysis. **Sandra Lage:** Investigation, Writing - review & editing. **Daniel Fonn Aluwini:** Funding acquisition, Investigation. **Céline Rebours:** Funding acquisition, Project administration, Supervision, Conceptualization, Investigation. **May Bente Brurberg:** Resources. **Udo Nitschke:** Formal analysis, Visualization, Writing - review & editing. **Francesco G. Gentili:** Funding acquisition, Resources, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodchem.2020.127999.

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Corrigendum to "Chemical profiling of the Arctic sea lettuce *Ulva lactuca* (Chlorophyta) mass-cultivated on land under controlled conditions for food applications" [Food Chemistry, 341 (2021) 127999]

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Due to a current name change, European '*Ulva lactuca* L.' is now recognised under the name *Ulva fenestrata* Postels & Ruprecht (Hughey et al., 2019).

In this regard, the title of this publication should read "Chemical profiling of the Arctic sea lettuce *Ulva fenestrata* (Chlorophyta) mass-cultivated on land under controlled conditions for food applications". Moreover, reference to the sea lettuce species in this study should be *Ulva fenestrata* throughout the manuscript.

It is essential to push for the correct identification of the species because this has wider implications on the use of different species of sea lettuce for food.

The authors would like to apologise for any inconvenience caused.

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