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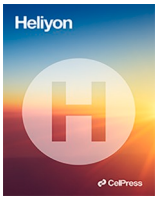

Research article

# Physicochemical properties of wild and cultivated *Saccharina latissima* macroalgae harvested in the Canadian boreal-subarctic transition zone

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ABSTRACT

*Saccharina latissima* is a brown seaweed used as a food ingredient. The aim of this work was to study possible differences between *S. latissima* chemical composition, color, mode of cultivation, harvesting period and site and its environmental conditions. Water temperature, salinity, radiation, and fluorescence were monitored in each harvesting site. Chemical composition of *S. latissima* varied greatly with period and site, with a high content of carbohydrates and ash. Crude protein content varied from 3.7 % to 12.8 %, with a higher concentration observed in wild samples harvested in Bas-St. Laurent (11.1–12.8 %). Cultivated seaweed also presented a high crude protein (12.2 %) and ash (52 % against 27 % in wild samples) concentrations, but crude fiber and carbohydrates concentrations were lower, reaching up to 2.7 and 1.9-fold, respectively, than those in wild seaweeds. *S. latissima* presented a more intense yellow color in June. A trend of darker and more green-colored seaweeds when cultivated in the end of summer was confirmed. Our results suggest that variations in chemical components and chromaticity of this species are probably affected by complex interactions of environmental conditions.

## 1. Introduction

The macroalga *Saccharina latissima* (Linnaeus) is a cosmopolitan temperate/boreal species [1] that is found in protected bays but is less abundant in wave-exposed shores [2]. *S. latissima* is a brown macroalga belonging to the order Laminariales (kelps), also known by its former latin name *Laminaria latissima*, the sugar kelp and kombu royal [3].

*S. latissima* has 33.9–76.0 % (dry weight, d.w.) of readily digested carbohydrates, such as starch, and other polysaccharides that are not readily digested [4,5] whereas crude fibers and hemicellulose can represent 29.3–37.4 % (d.w.) [6]. This species also contain protein (5.1–9.9 %, d.w.; determined by Lowry), ash (22–41 %, d.w.) [7], and, in smaller amounts, lipids (0.8 %, d.w.) [6]. Macroalgae have been used to introduce nutritional value into food products, improving the dietary fiber, peptides, and minerals content. Brown

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algae such as *S. latissima* are considered food ingredients with many health-promoting compounds, such as polysaccharides of complex structures, phlorotannins, fucoxanthin, bioactive peptides [8–12], with applications in the food [13], feed [14,15] and pharmaceutical [8] industries. Fucoidans, an important carbohydrate found in *S. latissima*, have extensive biological activities [9]. Although very promising, great effort is being dedicated to introducing macroalgae into the diets of western countries and explore their potential as novel functional food ingredients [9]. Our research group has demonstrated the relevance of *S. latissima* extracts and bioactive peptides, with demonstrated antioxidant, antimicrobial and anti-hypertensive activities [16–18]. The high iodine content in laminaria species (against 10 times lower iodine content found in Porphyra algae (Nori)) and the presence of epiphytic animals readily attach on the blades and constitute an unwanted food addition, are the main challenges. However, several solutions are being studied, including the determination of specific cultivation conditions and post-harvest treatments [19]. Recent studies have not only explored the nutritional aspect of macroalgae food processing but have also included other essential aspects such as product stability, food matrix compatibility, technological and sensorial properties [9,20]. In a recent study, our group has evaluated the impact of temperature and cooking time on the sensory potential and physicochemical properties of *S. latissima* and *Palmaria palmata* [21].

Color in seaweed-fortified products is also a key factor in the food industry, greatly influencing the final product appearance and acceptance [9]. Natural pigments from algae have been well-recognized for their valuable beneficial effects in food [22,23] and pharmaceuticals [24,25]. Sources of natural pigments can be considered a greener alternative to chemically synthesized colorants [26], while providing nutritional components [27]. The production of natural colorants from algae has been reported to have many advantages such as low cost, simple production, high-yield and environmental-friendly [28]. A drawback is that production may be susceptible to a certain degree of seasonal and site variation [28]. In seaweed, natural pigments and chemical composition is influenced by the production method (wild or cultivated), period of harvest and environmental conditions. Natural variations in environmental conditions are inherent features of all-natural systems, and influence macroalgae biology. Indeed, the production of several secondary metabolites is often related to seaweed's capacity of resisting and developing in harsh environments [10,29]. The chemical composition of macroalgae varies with species [7,30], habitats [31,32], age [33,34] and environmental conditions [35], such as light [36], temperature [37], and nutrients [38–41], and salinity [4,42–45]. The development of structural color in algae is believed to be linked to intrinsic adaptation mechanisms and is influenced by the environmental conditions, especially radiation intensity, influenced by the water turbidity [46].

The influence of environmental factors on the composition and development of macroalgae depends on the combination of many physiological and phenomenological parameters and thus the establishment of associations is complex [7,8,45,47]. However, the comprehension of these associations could improve macroalgae production and quality, contributing to meet the increasing demand of these materials [8,29]. Few associations between environmental parameters (temperature, light intensity, and the concentration of dissolved inorganic phosphorus in seawater) and composition (such as protein and carbohydrate content) [41,48] have been reported.

Although kelp forests are abundant in the infralittoral zone of the Gulf of St. Lawrence (GSL), Nova Scotia and the Gulf of Maine, and mainly dominated by *S. latissima* [1], these wild kelp beds are not harvested [49]. Recently, several kelp culture farms started up in Maine and Québec [50,51]. Despite a renewed interest in this underexploited marine resource, to date, few studies have been conducted on the nutritive value and chemical diversity of macroalgae growing inside the GSL and little is known about their regional differences. In fact, GSL is characterized by a diversity of oceanographic and climatic conditions that may influence the biochemistry of macroalgae. According to Merzouk and Johnson [2], the northwest Atlantic coast of Canada is divided into boreal and subarctic biogeographic regions based on temperature and environmental conditions, and the subarctic region extends south into the GSL, encompassing Labrador, the northern half of Newfoundland, and the northern gulf shore of Québec.

Whilst effects of environmental factors on composition have been reported previously for *S. latissima* in other regions [7,52,53], the associations between harvesting site, period of harvest, chemical composition, and color, for this species, was still not explored. In a recent publication our research group have studied these associations for the red macroalgae *P. palmata* [54], another species relevant to the Canadian boreal area. Thus, this paper proposes the study of chemical composition and color analysis of wild and cultivated *S. latissima* samples, based on the time and origin of the harvest in the Canadian boreal-subarctic transition zone. Additionally, the differences between natural conditions (water temperature, salinity, Photosynthetically Active Radiation (PAR), and CDOM fluorescence and macroalgae proximate compositions were investigated.

## 2. Materials and methods

### 2.1. Chemicals

Alfie Packers Kjeldahl Catalyst Pro-Pac Tablets ($K_2SO_4/CuSO_4$) were purchased from Alfie Packers Inc (Omaha, NE, USA). Sodium hydroxide and sodium sulfate anhydrous of the American Chemical Society (ACS) were purchased from Anachemia Canada Co (Montreal, QC, Canada). Chloroform ($CHCl_3$) was purchased from VWR Analytical (Radnor, PA, USA). α-amylase (E-BLAAM), protease (E-BSPRT), amyloglucosidase (E-AMGDF), and Celite (G-CEL 100) were purchased from Megazyme International Ireland Ltd. (Wicklow, Ireland). Hydrochloric acid ACS-Pur was purchased from Fisher Scientific (Geel, Belgium). 2-(4-morpholino)-ethane sulfonic acid/MES (CAS 145224-94-8) was purchased from Fisher Scientific, (Geel, Belgium). TRIS (hydroxymethyl) aminomethane 9210 was purchased from VWR/Life Science (Solon, OH, USA).

### 2.2. Algal biomass

#### 2.2.1. Wild macroalgae harvesting

Samples were harvested from the coastline of the St. Lawrence River lower estuary (Bas-St-Laurent (BSL) and Côte-Nord (Sept-Îles)) and of the Gaspé Peninsula (Gaspé and Pabos) in the Gulf of St. Lawrence (GSL), between June and July 2015 (Fig. 1). In addition, farmed samples from Îles-de-la-Madeleine (IDM) and Paspébiac (Gaspé Peninsula) (Fig. 1) were included in the analyses, from July and August 2015. Wild kelps were collected from exposed and shallow coastal sites, between the bottom of the intertidal and the top of the infralittoral stage. In Québec, the abrasive effect of the ice and the violent storms between fall and spring causes most large sporophytes are teared off. Thus, most specimens in shallow harvest areas are approximately one year old or less [50].

About 1–4.5 kg (which corresponds to 100–400 g of dried material) of vegetative sporophytes of wild *S. latissima* were collected per harvest site. Only fresh and well-pigmented, intact, and unsoiled young samples, including stipe and fronds, cut above the holdfast, were harvested. All algae samples came from individuals with a total length (blade + stipe) between 1 and 4 m. It was mainly the meristematic zone that was kept for analysis (first 30 cm of blade above the stipe). Naturally, as the size of fronds differ from one macroalgae to another, it is reasonable to estimate that each sample (from 1 kg to 4.5 kg) contained between 20 and 40 specimens (biological replicates). However, a recent study has suggested that genetic differences for algae in Québec are small [56].

#### 2.2.2. Cultivated macroalgae

Farmed *S. latissima* were cultivated on submerged longlines in four marine farms located in the Bay of Paspébiac (Paspébiac, QC, Canada) and in the Bay of Plaisance (IDM, QC, Canada). In Paspébiac, the seedlings were attached to the culture lines in October 2014 and the lines were maintained at a 7 m depth until April 2015 when they were raised to 5 m until harvesting in July 2015. In contrast, the longlines in the Bay of Plaisance were always maintained at a 7 m depth and harvesting took place in August 2015. Further information on the seedling technical details is given in the Supplementary Material (s1). Once the harvested samples were on the boat, macroalgae were placed in an opaque plastic bag and stored in cooler boxes filled with ice packs for transport to the laboratory (4–5 h). In the laboratory, the bags were stored at 4 °C until treatment (12–24 h).

#### 2.2.3. Macroalgae sample preparation

Upon reception, wild and cultivated macroalgae were manually cleaned to remove biofouling (sea snail spawn, encrusting

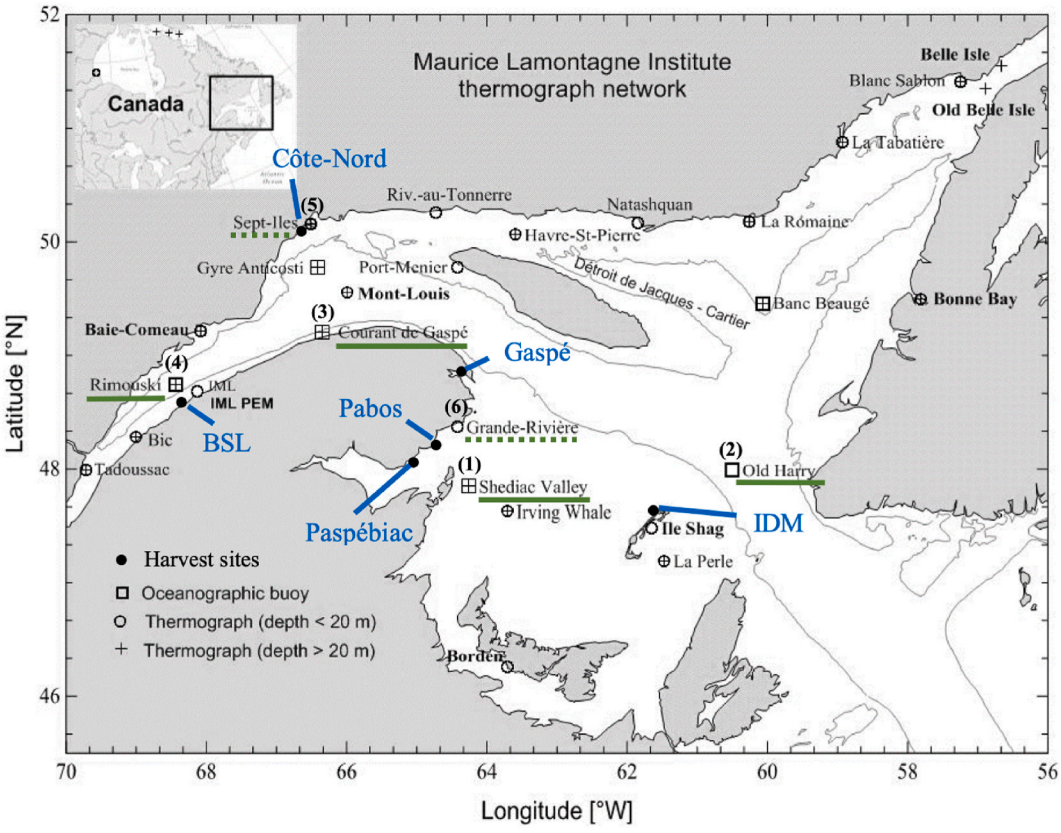


**Fig. 1.** Harvesting sites (●) of the wild and cultivated *S. latissima* samples. Buoy systems (1, 2, 3, and 4) and tide gauges (5 and 6) according to Pettigrew et al. (2017) and Vasconcelos et al. (2022), with modifications [54,55]. IDM: Îles-de-la-Madeleine; BSL: Bas-St-Laurent.

bryozoans, thread algae, etc.) and rinsed with filtered water. Whenever the stipe or apical end of the frond was damaged or covered with dirt, the concerned portion was thrown away.

Macroalgae were oven dried for 48 h (ThermoScientific, HeraTherm/OGS400, Montreal, QC, Canada) at a temperature of 40 °C until the water content was ≤20 %. Water content in samples was determined gravimetrically at 105 °C for 12 h using an incubator until equilibrium. Dried macroalgae were reduced into flakes using a cutter/mixer (Stephan UMC 5 electronic/Hameln, Germany), ground to a fine powder (Thermomix model, Wuppertal, Germany) and stored (4 °C) in vacuum-sealed bags until use. For each sampling site and date, the dried algae were mixed before packing and analyses.

### 2.3. Environmental conditions

Environmental conditions in the dates macroalgae were harvested were monitored every 15 min, from 9 a.m. to 13 p.m. using buoy systems from the Saint Lawrence Global Observatory [57]. These data were provided by the following buoy-based systems: (1) PMZA-VAS Shédiac/47°46.998′N 64° 2′O (June 7 and 10 and July 7); (2) IML 10 Old-Harry/48°0′ N 60° 30′O (June 24 and August 17); (3) IML 7 Courant de Gaspé/49°14.502′N 66° 12′ O (July 12 and 14), and (4) PMZA-RIKI Rimouski/48° 40.002′N 68° 34.998′ O (June 8 and July 15). In addition, two tide measuring stations located in (5) Sept-Iles/50° 11.688′N 66° 22.608′O (July 14), and (6) Rivière-au-Renard (Grande-Rivière)/48° 59.82′N 64° 22.83′O (June 10 and July 7) were used, from which salinity and temperature data were collected. Buoys and tide gauges closest to the harvesting sites (Fig. 1) were used to get the most representative climatic conditions in the corresponding areas. Table 1 demonstrates which buoys and tide gauges were used to represent which harvesting sites.

Water temperature (%C) and salinity (practical salinity unit (PSU)) were measured using an SBE 37-SI/SIP MicroCAT, which is a high-accuracy oceanographic recorder (model SBE 37-SI, Seabird Electronics Inc., Halifax, CA) that was positioned at 0.5 m depth. Surface photosynthetic active radiation (PAR) was monitored using a PAR sensor (model 600Mlin, Satlantic Inc., Halifax, Canada) positioned at 3.10 m depth. PAR data were presented in μmol photon $m^{-2}$ $s^{-1}$. Fluorescence of colored dissolved organic matter (CDOM) was measured using a fluorometer (model CDOM WetStar, Western Environmental Technology Laboratories (Wetlabs) Inc., Philomath, United States) at a depth of 0.5 m, and data were presented in mg $m^{-3}$ (ppb) (Fig. 2). This equipment emits light in the blue wavelength (370 nm) and absorbs light in the ultraviolet (460 nm). All of those sensors are operated, and data is made available for the research community by the Observatoire Global du Saint-Laurent (OSGL) [57].

### 2.4. Chemical composition

Prior to chemical composition determinations, seaweed samples were homogenized. Briefly, 550 g of dried macroalgae samples were placed into a mixer-mortar-grinder (RM 100, Retsch, Newtown, PA, USA), frozen in liquid nitrogen and ground. The resulting seaweed powder was collected in plastic bags, weighed, and stored at 4 °C until use. This procedure was used for both wild and cultivated seaweed samples. Nitrogen content was determined using the Kjeldahl method (AOAC 988.05) [58] and the crude protein was calculated by converting the nitrogen content according to Ref. [59] (N x 4.92). Ash (muffle furnace at 550 °C; AOAC 950.46 [58]) and crude fiber (soluble and insoluble) contents (enzymatic-gravimetric method, AOAC 985.29 [58]), were determined. Crude fiber determination method involves subjecting the sample to a succession of enzymes to remove digestible material, an ethanol precipitation step to isolate non-starch polysaccharides, as well as ash and protein determination. However, an incomplete precipitation in 80 % of ethanol introduces error result in potential losses of polysaccharides [60]. Thus, remaining carbohydrates content (digestible) was obtained by the difference of 100 % - [% crude protein + % lipids + % ash] - % fiber [61].

The lipid concentration was obtained using a modified protocol from Bligh and Dyer [62], according to Schmid et al. [63]. Macroalgae powder (1 ± 0.05 g) was extracted overnight at 25 °C under constant stirring with 21 mL of $CHCl_3$: MeOH and 2.0 mL of $H_2O$. The samples were centrifuged (4 min at 2500×*g*) (Avanti J-E Centrifuge, Beckman Coulter, USA), and the organic phase was pipetted into a glass tube containing glass wool and anhydrous sodium sulfate. The phase containing lipids was recovered using a rotary evaporator (40 °C).

**Table 1**
Harvesting sites, dates, buoy systems (1, 2, 3, 4) and tide gauges (5, 6) used for the collection of environmental data [57], following the schematic representation presented in Fig. 1.

| Month | Site | Buoy system for PAR and CDOM fluorescence data | Buoy system for salinity and temperature data | Harvest dates |
|---|---|---|---|---|
| Wild Seaweeds | | | | |
| June | IDM | Old-Harry | Old-Harry | June 7th, 2015 |
| | BSL | Rimouski | Rimouski | June 8th, 2015 |
| | Pabos | Shédiac Valley | Grande-Rivière | June 10th, 2015 |
| July | IDM | Old-Harry | Old-Harry | July 24th, 2015 |
| | BSL | Rimouski | Rimouski | July 15th, 2015 |
| | Côte-Nord | Courant de Gaspé | Sept-Îles | July 14th, 2015 |
| | Gaspé | Courant de Gaspé | Grande-Rivière | July 12th, 2015 |
| **Cultivated Seaweeds** | | | | |
| July | Paspébiac | Shédiac | Shédiac | July 7th, 2015 |
| August | IDM | Old-Harry | Old-Harry | August 17th, 2015 |

IDM: Îles-de-la-Madeleine; BSL: Bas-St-Laurent; PAR: Photosynthetically Active Radiation; CDOM: Chromophoric dissolved organic matter.

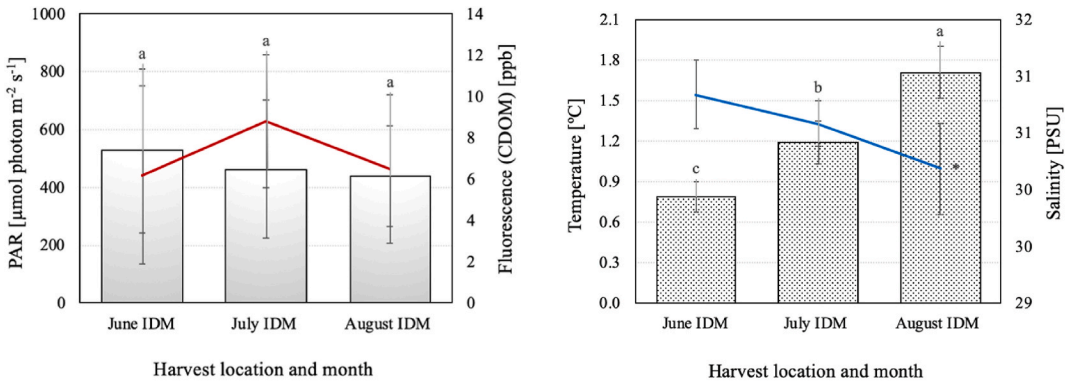


**Fig. 2.** Environmental parameters observed during the harvest days of *S. latissima* according to data from Observatoire Global du Saint-Laurence (OGSL) (2017) [57], referring to: (a) Photosynthetically Active Radiation (PAR), represented in the main axis and bars and fluorescence CDOM (Chromophoric dissolved organic matter) in the second axis represented by the continuous red line and; (b) temperature in the main axis represented by the bars and salinity in the second axis, represented by the continuous blue line, for the site Îles-de-la-Madeleine (IDM). Values are expressed as monthly average between the 11 a.m. and 12 p.m. period ± standard deviation, n = 5 for 30 days. Different letters for each harvesting site indicate significant differences among months ($p < 0.05$). Values are expressed as period monthly average taken between 11 a.m. and 12 p.m. ± standard deviation, n = 5 per day, per month.

All analyses were performed in triplicates except for fiber content, which was carried out in duplicate due to limited sample amount, and all data were reported on a dry weight basis (d.w.).

### 2.5. Color measurement

Macroalgae colors were determined using a colorimeter (Minolta Chroma Meters CR-300, Ramsey, NJ, USA) with a 0.8 mm measuring aperture and a white background. The colorimeter was calibrated against a standard white reference tile (L* = 84.56; a* = +53.42 and b* = - 12.36). Briefly, homogenized samples in powder form were placed in a Petri dish and flattened. Measurements were performed in triplicates on the surface of the powder. Results were reported in terms of lightness (L*) ranging from 0 (black) to 100 (white), while a* and b* are the chromaticity coordinates that indicate color directions: +a* (red); −a* (green); +b* (yellow); and −b* (blue), according to the CIELAB system [64].

### 2.6. Statistical analysis

Data were presented as the mean value ± standard deviation. Environmental data were collected using the period between 11 a.m. and 12 p.m. (Observatoire Global du Saint-Laurent 2017). Five measurements per day (every 15 min), for all days in each month were collected and this monthly average value was reported. Data were analyzed using one-way analysis of variance (ANOVA), followed by post-hoc Tukey-HSD multiple comparison test for samples. For data that did not meet the parametric assumptions of ANOVA

**Table 2**
Chemical composition (g 100 $g^{-1}$ dry weight) of dried *S. latissima* according to the period and harvesting location.

| Month | Site | Chemical compounds | | | | |
|---|---|---|---|---|---|---|
| | | Total Carbohydrates | | Ash | Protein | Lipids |
| | | Carbohydrates | Crude fiber | | | |
| **Wild Seaweeds** | | | | | | |
| June | IDM | $53.30 \pm 0.06^{b}$ | $12.20 \pm 0.05^{g}$ | $27.74 \pm 0.07^{e}$ | $6.37 \pm 0.91^{g}$ | $0.43 \pm 0.01^{c}$ |
| | BSL | $37.06 \pm 1.40^{ed}$ | $17.98 \pm 0.30^{b}$ | $30.89 \pm 1.06^{d}$ | $12.81 \pm 0.30^{a}$ | $1.65 \pm 0.18^{ba}$ |
| | Pabos | $57.72 \pm 0.27^{b}$ | $16.34 \pm 0.04^{d}$ | $23.08 \pm 0.13^{f}$ | $7.26 \pm 0.10^{f}$ | $0.59 \pm 0.11^{c}$ |
| July | IDM | $42.29 \pm 0.77^{c}$ | $19.05 \pm 0.08^{a}$ | $27.40 \pm 0.85^{e}$ | $9.42 \pm 0.11^{d}$ | $1.74 \pm 0.24^{ba}$ |
| | BSL | $43.02 \pm 0.25^{c}$ | $15.02 \pm 0.03^{e}$ | $28.97 \pm 0.22^{ed}$ | $11.07 \pm 0.05^{c}$ | $1.89 \pm 0.10^{a}$ |
| | Côte-Nord | $62.31 \pm 0.36^{a}$ | $18.48 \pm 0.44^{ba}$ | $15.58 \pm 0.09^{g}$ | $3.74 \pm 0.05^{h}$ | $0.42 \pm 0.05^{c}$ |
| | Gaspé | $35.51 \pm 0.16^{e}$ | $13.96 \pm 0.11^{f}$ | $40.63 \pm 0.06^{b}$ | $7.73 \pm 0.06^{e}$ | $2.12 \pm 0.12^{a}$ |
| **Cultivated Seaweeds** | | | | | | |
| July | Paspébiac | $39.36 \pm 0.07^{d}$ | $17.11 \pm 0.28^{c}$ | $35.97 \pm 0.07^{c}$ | $6.41 \pm 0.04^{g}$ | $2.22 \pm 0.28^{a}$ |
| August | IDM | $27.88 \pm 1.27^{f}$ | $7.04 \pm 0.09^{h}$ | $51.74 \pm 1.22^{a}$ | $12.21 \pm 0.11^{b}$ | $1.25 \pm 0.17^{b}$ |

IDM: Îles-de-la-Madeleine; BSL: Bas-St-Laurent. Values are expressed as mean ± standard deviation, n = 3, in g per 100 g of dry weight (%, d.w.). Same letters within the same column indicate non-significant differences ($p < 0.05$).

(normality, by Anderson Darling's and Shapiro Wilk's tests and homoscedasticity, by Levene's and Bartlett's tests), Kruskal-Wallis non-parametric ANOVA test followed by Dunn's test were done to identify which levels or treatments behaved differently from each other. Pearson's correlation coefficient (r) was used to test the relationship between environmental parameters, color measurement and chemical composition. All analyses were performed using R studio (version April 1, 1717, PBC, Boston, MA, USA).

## 3. Results

### 3.1. Chemical composition

Chemical composition of wild and cultivated *S. latissima* collected in the sites evaluated in this work is presented in Table 2. Macroalgae samples water content varied from 5 to 12 % (mass basis). Wild *S. latissima* samples showed a carbohydrate content in the range of 35.5–62.3 % (d.w.) and crude fiber of 12.2–19.1 % (d.w.). Ash content varied from 15.6 % to 40.6 % (d.w.). Crude protein content was within the 3.7–12.0 % (d.w.) range and lipids represented 0.4–2.1 % (d.w.) of the algae composition. Cultivated seaweeds presented a similar composition range, but presented some samples with a higher ash content, reaching 51.7 % (d.w.), and smaller crude fiber (7.0 %, d.w.) and carbohydrates (27.9 %) contents.

Among wild seaweeds collected in the month of June, *S. latissima* from BSL have shown the lowest carbohydrate content (37.1 %, d.w.) and higher crude fiber, ash, crude protein, and lipids content than the algae collected at IDM and Pabos in that same month. In July, *S. latissima* from BSL still presented the higher crude protein content (11.1 %, d.w.) among the algae collected on the other sites, but the lower carbohydrates (35.5 %, d.w.) and crude fibers (14.0 %, d.w.) content was found for Gaspé-collected algae. This sample also had the higher lipids (2.1 %, d.w.) and ashes content (40.1 %, d.w.).

*S. latissima* collected from IDM in June and July have shown statistical difference in composition for all components except for the ashes content (around 27 %). Crude protein, lipids, and crude fiber content increased about 1.5, 4.0 and 1.6-fold and carbohydrates content decreased 1.26-fold when the alga was collected in July instead of June. This effect was not observed for *S. latissima* collected from BSL, that maintained its content of ash and lipids constant between these two months (June and July). Crude protein and crude fiber content were slightly decreased from 12.8 % to 11.1 %, and 17.9 %–15.0 %, respectively. A 1.2-fold increase of carbohydrates in this alga was detected if collected in July.

Finally, differences in composition between wild *S. latissima* from IDM collected in June and July and cultivated *S. latissima* collected on the same site in August indicate that the cultivated seaweed presented a higher crude protein content (12.2 %) compared to the crude protein content in wild seaweeds collected in the same site (6.4–9.4 %). Ash content in cultivated *S. latissima* was also much higher (51.7 % against 27.4–27.7 % in wild samples). Crude fiber and carbohydrates content were lower in the cultivated samples, reaching up to 2.7 and 1.9-fold lower crude fiber and carbohydrate content, respectively, than in wild seaweeds.

### 3.2. Colorimetric measurement results

Chromatic variations were observed in dried macroalgae (Table 3). Irrespective of month of harvest, site and mode of cultivation, *S. latissima* samples presented a lightness value ranging from 40.5 (darker) to 56.5 (lighter), a* parameter varying from −3.2 (green) to 0.67 (red) and b* parameter in the 4.9–9.2 range, indicating a yellowish color.

Among wild *S. latissima* samples harvested in June, the darkest color was found in the seaweed collected at Pabos (49.2 ± 1.3), with luminosity values ranging from 49.2 to 56.5. This sample also had the smallest green and yellow color intensity among the other samples harvested in that month. In *S. latissima* samples harvested in July, a slight decrease in luminosity could be observed (40.5–52.8). A tendency of a greener color in all samples harvested in this month was also observed, whereas the b* parameter did not seem to be different from samples harvested in June.

**Table 3**
Color parameters of dried *S. latissima* according to the period and harvesting location.

| Months | Sites | Color parameters | | |
|---|---|---|---|---|
| | | L* | a* | b* |
| Wild seaweeds | | | | |
| June | IDM | $56.51 \pm 1.41^{a}$ | $-1.83 \pm 0.14^{c}$ | $8.87 \pm 0.27^{ba}$ |
| | BSL | $55.43 \pm 0.29^{a}$ | $-1.30 \pm 0.04^{b}$ | $7.86 \pm 0.63^{b}$ |
| | Pabos | $49.18 \pm 1.26^{c}$ | $-1.04 \pm 0.07^{b}$ | $4.87 \pm 0.37^{c}$ |
| July | IDM | $52.28 \pm 0.86^{b}$ | $-2.86 \pm 0.26^{e}$ | $7.68 \pm 0.81^{b}$ |
| | BSL | $40.48 \pm 1.43^{d}$ | $-2.49 \pm 0.20^{d}$ | $5.79 \pm 0.44^{c}$ |
| | Côte-Nord | $52.79 \pm 0.74^{b}$ | $-2.95 \pm 0.18^{ef}$ | $9.12 \pm 0.62^{a}$ |
| | Gaspé | $52.03 \pm 0.74^{b}$ | $-2.78 \pm 0.12^{ed}$ | $5.73 \pm 0.45^{c}$ |
| **Cultivated seaweeds** | | | | |
| July | Paspébiac | $50.58 \pm 0.39^{cb}$ | $-3.24 \pm 0.11^{f}$ | $9.20 \pm 0.45^{a}$ |
| August | IDM | $48.83 \pm 1.25^{c}$ | $0.67 \pm 0.10^{a}$ | $5.63 \pm 0.41^{c}$ |

Color parameters of the CIELab scale, where L* represents the luminosity, a* the green (−)/red (+) colors and b*, the blue (−)/yellow (+) colors. IDM: Îles-de-la-Madeleine; BSL: Bas-St-Laurent. Values are expressed as mean ± standard deviation, n = 3. Same letters within the same column indicate non-significant differences ($p < 0.05$).

The tendency of darker and more green-colored wild seaweed if harvested later in summer is confirmed when looking at the L* and a* parameters for *S. latissima* samples harvested from IDM and from BSL. Luminosity values decreased 7 % and 27 % and the absolute value of a* increased 1.5 and 1.9-fold for samples of IDM and BSL, respectively.

The luminosity trend is indeed observed for cultivated IDM samples harvested in August, that presented an even lower luminosity, of 48.8, compared to 52.3 in July and 56.5 in June, for wild samples. The a* parameter was, however, quite different, presenting a positive value. The b* value was lower than the wild samples collected at that same site in the previous months. It is important to note that among both cultivated and wild samples, the one with higher a* and b* absolute values were the cultivated seaweed collected at Paspébiac.

### 3.3. Environmental factors

Radiation PAR and CDOM parameters determined at *S. latissima* harvesting sites revealed levels of PAR ranged from 383 μmol photon $m^{-2}$ $s^{-1}$ (BSL, July) to 527 μmol photon $m^{-2}$ $s^{-1}$ (IDM, June) and CDOM values ranged from 1.9 ppb (Pabos, June and Paspébiac, August) to 9.8 ppb (BSL, June), respectively (Table 4). Differences in PAR among the different sites were not detected due to high standard deviation of the measurements, which are typically high in open sea buoyancy systems. On the other hand, differences in CDOM fluorescence were detected and were remarkably higher in June in BSL and lower in Pabos. In July, the highest CDOM fluorescence was detected at IDM and the lower in Paspébiac.

Figs. 2 and 3 show the evolution of environmental parameters in different months, in IDM and BSL, respectively. Differences in PAR in the same place from June to July/August were not detected for any of these two harvesting sites (IDM or BSL). A decrease in fluorescence was detected in BSL in the month of July compared to the previous month.

A clear rise in temperature was observed for both sites with the progression of summer (Figs. 2b and 3b). Salinity varied differently between the two sites, with a decrease detected in August in IDM and no differences detected in BSL from June to July.

Salinity levels in the evaluated sites and months of the study ranged from 25.7 to 30.8 PSU, with a higher salinity detected at IDM. Temperature varied less than 10 °C, from an average of 7.3 °C–15.6 °C between June and July. Seawater temperature in the different harvesting sites were around 7–8 °C in June but increased in July to 8–15 °C.

## 4. Discussion

### 4.1. Chemical composition

Chemical composition of wild and cultivated *S. latissima* evaluated in this study in within the range reported in the literature. Carbohydrates content in *S. latissima* samples of this study were in accordance to previously reported values (35–63 %) [7,10,14,18,65]. Crude fiber concentrations in *S. latissima* vary greatly (7–70 %) [7,14,18,65]. The values obtained in the study belonged to the lower reported range, around 15 %. Ash content was reported well within the reported range (15–40 %) [7,10,18,52,65,66]. Crude protein content was also similar to the reported range for this species, typically varying from 1 % to 17 % [7,10,14,17,18,40,41,52,65,66]. Lipid content in seaweeds was previously reported to be between 0.3 and 2.9 % [10,14,18,65,66]. Some of the samples studied in this work reached 2 %.

Carbohydrate concentrations varied greatly among harvesting sites, with higher levels observed in IDM in June and Côte-Nord in July. However, correlations to environmental parameters collected at the harvesting sites were not found during the period of the study. *S. latissima* cultivated in proximity to salmon (*Salmo salar*) aquaculture in Norway from June throughout the summer, experienced a decrease in the length of the blade followed by loss of biomass that coincided with heavy fouling by epiphytes (bryozoan) [52,67]. These *S. latissima* were deployed at a depth of 8–9 m at experimental locations along the Norwegian coast had a 51.9 % ash content [68]. This bryozoan colonization contributed to the reduction in the carbohydrate concentration in samples [69]. The increase

**Table 4**
Mean values of environmental parameters as a function of the *S. latissima* harvest month.

| Month/Harvest site | Environmental parameters | | | |
|---|---|---|---|---|
| | PAR (μmol photon $m^{-2}s^{-1}$) | CDOM fluorescence (ppb) | Salinity (PSU) | Temperature (°C) |
| June | | | | |
| IDM | $527 \pm 283^{a}$ | $6.2 \pm 4.3^{b}$ | $30.8 \pm 0.3^{a}$ | $7.9 \pm 1.1^{ab}$ |
| BSL | $479 \pm 233^{a}$ | $9.8 \pm 2.4^{a}$ | $26.8 \pm 1.5^{b}$ | $7.3 \pm 1.3^{b}$ |
| Pabos | $486 \pm 270^{a}$ | $1.9 \pm 0.8^{c}$ | $26.9 \pm 0.2^{bc}$ | $8.7 \pm 1.4^{a}$ |
| **July** | | | | |
| IDM | $463 \pm 239^{a}$ | $8.8 \pm 3.2^{a}$ | $30.6 \pm 0.3^{a}$ | $11.9 \pm 1.6^{b}$ |
| BSL | $383 \pm 178^{a}$ | $7.4 \pm 1.8^{b}$ | $27.6 \pm 1.2^{bc}$ | $8.7 \pm 2.0^{c}$ |
| Côte-Nord | $430 \pm 246^{a}$ | $7.3 \pm 1.3^{b}$ | $25.7 \pm 0.3^{d}$ | $11.7 \pm 1.5^{b}$ |
| Gaspé | $430 \pm 246^{a}$ | $7.3 \pm 1.3^{b}$ | $27.4 \pm 0.3^{c}$ | $9.7 \pm 2.5^{bc}$ |
| Paspébiac[a] | $419 \pm 223^{a}$ | $1.9 \pm 0.9^{c}$ | $28.2 \pm 0.3^{b}$ | $15.6 \pm 1.2^{a}$ |

[a] Cultivated samples. IDM: Îles-de-la-Madeleine; BSL: Bas-St-Laurent; PAR: Photosynthetically Active Radiation; CDOM: Chromophoric dissolved organic matter. Values are expressed as period monthly average taken between 11 a.m. and 12 p.m. ± standard deviation, n = 5 per day, per month. Same letters within the same month indicate significant differences ($p < 0.05$).

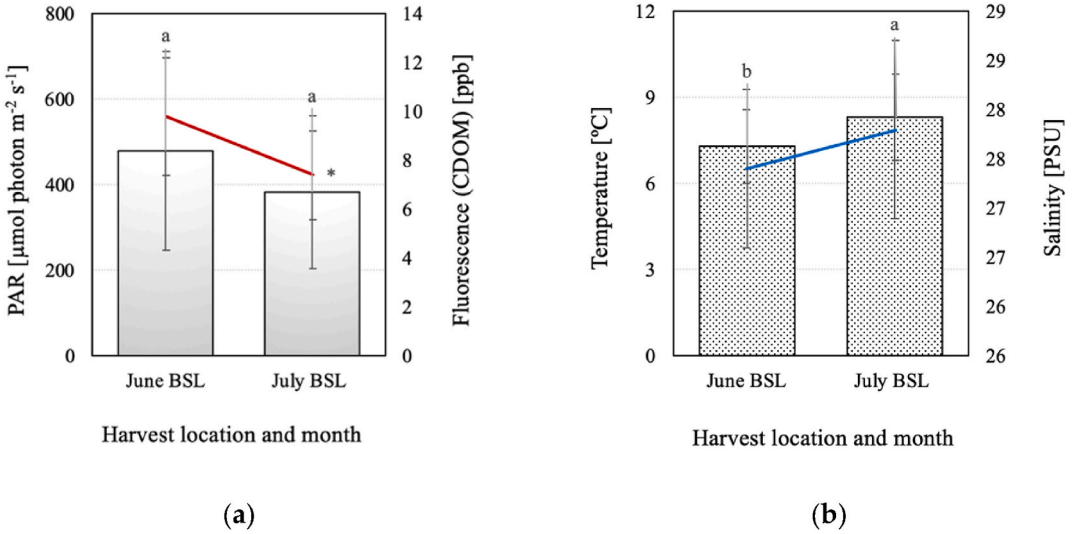


**Fig. 3.** Environmental parameters observed during the harvest days of *S. latissima* according to data from Observatoire Global du Saint-Laurence (OGSL) (2017) [57], referring to: (a) Photosynthetically Active Radiation (PAR), represented in the main axis and bars and fluorescence CDOM (Chromophoric dissolved organic matter) in the second axis represented by the continuous red line and; (b) temperature in the main axis represented by the bars and salinity in the second axis for the site Bas-St-Laurent (BSL). Values are expressed as monthly average between the 11 a.m. and 12 p.m. period ± standard deviation, n = 5 for 30 days. Different letters for each harvesting site indicate significant differences among months ($p < 0.05$). Values are expressed as period monthly average taken between 11 a.m. and 12 p.m. ± standard deviation, n = 5 per day, per month.

in the N concentration of the biomass was represented by the presence of epiphytes. Even though wild samples were rinsed, and most epibionts-covered parts were removed, it is possible that small colonies of bryozoans remained stuck on some fronds. In the culture kelp sampled on August 15 at IDM, *Membranipora membranacea* colonies were covering 20 % of the blade surface, and this may therefore have contributed to the high ash (51.74 ± 1.22 %) and crude protein (12.21 ± 0.11 %) concentrations and the significantly reduced ($p < 0.05$) carbohydrate (27.88 ± 1.27 %) concentration observed (Table 2). Indeed, in the kelp farms of Québec, an encrusting bryozoan (*M. membranacea*) start colonizing cultivated kelp in June and rapidly covers the entire surface of the blades causing accelerated erosion and breakage of the thallus [70]. The coverage of colonies of the bryozoans encrusted in the blades and that are difficult to remove completely were also reported in the Gulf of Maine (USA) [71], in Nova Scotia [72], and Norway [73].

Samples harvested in the BSL showed an increase of carbohydrates between June and July whereas the inverse behavior was observed in the samples from the IDM (Table 2). In this work, algae were harvested in the vegetative sporophyte life cycle stage of the algae. According to studies carried out by SjØtun and Gunnarsson [74], the maximum growth of this species is observed in May, with a marked decline in the growth rate by June. Broch and Slagstad [39] also observed that this species displays a reduced growth in summer (a period when nitrate concentration is low and the plants store carbohydrates) and autumn and the growth increase again from about mid-winter when nitrate is abundant and stored carbohydrates are reused for growth. Indeed, a general increase in sample's carbohydrate content was detected in July in comparison to June, which could indicate that *S. latissima* were storing carbohydrates during summer. Studies of the annual cycles of *Laminaria* (*Saccharina*) *longicruris* growth have demonstrated that during winter, compounds such as carbohydrates are synthesized and accumulate throughout the spring and the summer, which are then consumed during the fall and early winter [75,76].

Lipid concentrations were increased from June to July in IDM and BSL (Table 2). However, it is important to note that for samples with high carbohydrate content (>50 g 100 $g^{-1}$ d.w.), lipid content was low (<1 g 100 $g^{-1}$ d.w.) (Table 2). Research indicates that lipid levels in algae generally increase in winter and spring [77] and decrease in summer [78].

Results found in this work indicate that *S. latissima* collected in different harvesting sites presented distinct compositions. Macroalgae harvest in BSL seems to have a lower content of carbohydrates and higher content of other compounds (fibers, ash, crude protein, and lipids), especially in the month of June. A higher content of lipids and crude protein were also found in algae collected in this site in July. In BSL region, a lower temperature in these two months was detected compared to the other studied sites. Olischläger et al. [37] reported that at low temperatures, the crude protein and lipid contents increase in *S. latissima*. Although the trend of temperature rise is clear from June to August (Figs. 2 and 3), in the samples from IDM, a trend of crude protein concentration increasing with the date and the seawater temperature was observed (6.37 ± 0.91 g 100 $g^{-1}$/June – 9.42 ± 0.11 g 100 $g^{-1}$/July) (Table 2). Marinho et al. [52] reported that crude protein content show marked seasonal variations, with the lowest values recorded in May/July (1.3–1.7 % d.w.) and the highest values recorded in November (9.7–10.8 % d.w.). Conversely, Schiener et al. [7] showed that relative differences in the crude protein content of *S. latissima* on the Isle of Seil/Scotland varied significantly from 9.9 % (March) to 5.1 % (October), with an average crude protein content of 7.1 ± 1.7 %. Compared with the values reported by these authors, the crude protein concentration of the samples collected in a climatic transition zone (IDM and BSL) reached higher levels. It was previously demonstrated that high nutrient availability in BSL enables increased kelp biomass production [79]. In addition, Espinoza and

Chapman [80] showed that *Laminaria longicruris* populations from nitrate-poor and nitrate-rich Canadian regions, grown under identical conditions, accumulate quite different amount of nitrate in their tissues, with plants from nitrate-poor regions showing a much greater ability to accumulate a tissue pool of $NO_3^-$. The differences between these two populations are interpreted as an adaptive response to local nitrate environments [80]. This may explain the higher concentrations of crude proteins in IDM and BSL (probably nitrate-rich region) samples compared to other sites (probably nitrate-poor regions).

### 4.2. Color measurement

*S. latissima* samples evaluated in this study have all showed a negative a* and positive b* values, indicating a tendency towards the green and yellow colors (Table 3). Among all samples, the ones that cultivated samples from IDM (August) were the ones with a stronger brown coloration. Structural color patterns observed in brown algae are complex and research is still incipient [46]. *S. latissima* contains chlorophylls (types a and b) and several carotenoids (specially xanthophylls) with an important proportion of fucoxanthin and neofucoxanthin. The typical brown color of *Phaeophyceae* has been linked to light absorption of the fucoxanthin [81] but several compounds are responsible for the variety of colors found in brown algae, including other carotenoids such as β-carotene, violaxanthin, etc. [28]. The tendency of *S. latissima* harvested in the conditions studied in this work suggests a different adaptation of macroalgae chromaticity in these regions. It is important to note that algae's color was evaluated after stabilization, and that these pre-treatments (drying, grinding and cold preservation) influence their color [82].

The observed decrease in b* absolute value of samples from IDM and BSL from June to July indicate a possible loss of yellow pigments in samples. Ramus [83] found a relationship between light, photosynthetic pigments, and the availability of nitrogen (N) for algal growth. According to this author, if available N was insufficient for growth, pigment concentration was reduced and macroalgae color paled. Investigation of color of *S. latissima* for a longer period could further corroborate these results. Based on the data of this study, *S. latissima* harvested in June would have a higher color intensity and crude protein concentration for most locations. The higher the color in macroalgae, the higher the commercial value, due to the interest in its color compounds [84].

### 4.3. Differences between environmental parameters and S. latissima chemical composition and color

Although differences in PAR were not statistically significant due to the high variability of data collected (Table 4), light availability is known to influence the distribution and color of macroalgae [85–88]. The available light for primary production (photosynthetically available radiation/PAR) is defined as the light that reaches the depth of primary production at all wavelengths of the visible spectrum [88]. *S. latissima* reaches their lower limit of growth at a depth limit where the light level is at maximum of about 0.6–1.2 % of the surface irradiance. This species has a photosynthetic rate that exceeds the respiratory rate (compensation point, $E_c$) at very low irradiance levels, at about 5–8 μmol $m^{-2}$ $s^{-1}$ [81]. Radiation (PAR) data at the harvesting sites indicate a light availability in the order of 100 times superior to $E_c$, indicating that algae had enough light availability. Periods with net photosynthetic rates are required so that seaweeds can grow and reproduce and have enough energy storage to winter, with low light availability [81]. Under low light conditions, plants invest more energy in the synthesis of light-collecting pigments, whereas under strong light the plant synthesizes photosynthetic enzymes, electron chain components, as well as photo-protective structures and activates energy-dissipating mechanisms [81]. *S. latissima*, which are well acclimated to strong irradiance levels, show more pigments of the xanthophyll cycle in spring because of the strong irradiance exposure that happens during this period [89].

Differences in environmental nutrient availability could also have influenced color differences observed in *S. latissima* samples (Table 3). Loss of pigmentation in cultivated kelp has been explained by the lack of nutrient in the environment. Previous studies in the region of Gulf of St. Lawrence shown a nutrient concentration increase at the end of September, with nitrate being the most limiting nutrient during summer, not being replenished before September, when stratification begins to break [90]. As previously commented, macroalgae contains accessory photosynthetic pigments, that, when present in sufficient amounts, blend with, or mask the visual color of chlorophyll A [91]. This fact has been observed in our samples, where a green color was not observed.

Absorption of light by algae is selective and can be influenced by the concentration of suspended particles in the water [92]. During spring and ice break-up, there is an increase in the amount of terrestrial chromophoric dissolved organic matter (CDOM) in coastal areas that may present several biological, chemical and physical effects in marine life [93]. CDOM absorption generally decreases with depth and has shown an inverse relationship to tidal cycles [94]. CDOM distributions can be investigated through the emission of fluorescence, which is an optical characteristic that depends on organic matter concentrations [95]. Substantial light attenuation detected by fluorescence is associated with lower salinities and higher CDOM levels [96]. However, most macroalgae (such as kelps) inhabit the sublittoral, which rarely experience salinity and desiccation stress due to quite stable environmental factors in the deep-water environment [97]. Fluorescence data from this study did not seem to affect composition or color.

Salinity values showed low monthly variation (June to August), with a similar salinity distribution in June and July (Table 4). No clear tendencies were seen in the same site in different months – whereas for IDM a decrease with the progression of months was observed, a stable salinity level was found in BSL (Figs. 2b and 3b). Correlations between salinity levels and composition or color parameters were also not found even though some reports suggest influence in composition. Nielsen et al. [4] have observed decreases in protein and carbohydrate contents in *Laminaria digitata* and *S. latissima* as salinity increased from 20 to 30 PSU. However, differences of such magnitude were not detected in this study.

Temperature was gradually increased with the progress of summer (from June to August) (Table 4 and Figs. 2b and 3b). Temperature is another important factor influencing the biogeographic distribution of macroalgae, especially in polar and cold-temperate regions [85,98]. Steinhoff [99] reported that in the Arctic, macroalgae grow and mature in challenging conditions: ice cover and

abrasion, low light and nutrient availability, and low temperatures; that require exceptional survival strategies. Consequently, during the winter seasons, macroalgae live with photon flux rates that do not meet its energy needs. Energy must then be chemically stored [81]. Recent results have suggested that low temperatures caused metabolic alterations to increase stress performance of *S. latissima* [85]. Thus, the season and algal physiological state are important factors affecting the content of extractable compounds, the relative proportions of lipids, and the levels of particular classes of lipids and pigments [33]. As previously commented, results from our study indicated conflicting tendencies regarding the evolution of lipid content with the months for IDM (Fig. 2b) and BSL (Fig. 3b).

Results of this study show that *S. latissima* from several locations in the Canadian Atlantic shore resulted in seaweed of different composition and color during summer. Data suggest that higher crude protein concentration and color intensity would be reached in *S. latissima* samples harvested in June. Samples from BSL seemed to present the higher crude protein concentrations in the study, during both months studied (June and July). It is important to note that the established relations were done considering environmental data from specific periods and are only valid for the factors and locations studied. As discussed, the elucidation of further associations between composition, color and environmental factors would require a large period of study and the inclusion of other factors such as different algae development stages, water flow, sea water composition and aeration that are closely related to the boundary layer composition and the effective nutrition diffusion and uptake by the algal biomass [14].

## 5. Conclusions

Chromatic variations were observed in the samples of *S. latissima*, showing a higher color intensity in June. Some changes in proximal composition (ash, carbohydrates, lipids, and crude protein contents) were associated with the concentrations of other compounds and temperature. *S. latissima* could be considered as a marine protein source, notably those from the BSL region harvested in June–July, that presented a high crude protein content of 11–13 g 100 $g^{-1}$ (d.w.). Our results also show as well that cultivated *S. latissima* presented similar composition and color properties as did wild samples. Results from this study could be used to determine the best harvest and cultivation sites for target components of commercial interest. Next research in the subject could include a wider period of study, more environmental factors, such as those related to sea composition and water flow and consider the determination of specific pigment concentrations in samples.

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## Data availability statement

Data available in a publicly accessible repository that does not issue DOIs Publicly available datasets were analyzed in this study. This data can be found here: [OGSL (2017) Observatoire Global du Saint-Laurent. Prévisions océaniques. https://ogsl.ca/ocean/ Accessed 15 April 2017, as described in the Methods section].

## CRediT authorship contribution statement

**Margarida Maria Monteiro Vasconcelos:** Conceptualization, Data curation, Formal analysis, Methodology, Validation, Writing – original draft. **Gabriela Vollet Marson:** Formal analysis, Validation, Visualization, Writing – review & editing. **Sylvie L. Turgeon:** Funding acquisition, Resources, Supervision, Writing – review & editing. **Éric Tamigneaux:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Lucie Beaulieu:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, 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

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