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Study of the chemical composition of edible red macroalgae *Grateloupia turuturu* from Brittany (France)

Claire Denis [a], Michèle Morançais [a], Min Li [a], Estelle Deniaud [a], Pierre Gaudin [a], Gaëtane Wielgosz-Collin [a], Gilles Barnathan [a], Pascal Jaouen [b], Joël Fleurence [a,*]

[a] Mer Molécule Santé, EA 2160, Université de Nantes, Pôle Mer et Littoral, 2 rue de la Houssinière, BP 92208, 44322 Nantes Cedex 3, France
[b] Laboratoire de Génie des Procédés Environnement Agro-alimentaire (GEPEA), UMR CNRS 6144, Université de Nantes, Pôle Mer et Littoral, 37 Boulevard de l'Université, BP 406, 44602 Saint-Nazaire Cedex, France

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ABSTRACT

The chemical composition and its seasonal variation of the red seaweed *Grateloupia turuturu,* an invasive macroalgae from Brittany, France, were investigated. Size, ash, protein, lipid, dietary fibre (soluble, insoluble and total), protein pigment (R-phycoerythrin, R-phycocyanin), and fatty acid content were measured in *G. turuturu* samples collected over 1 year (2006). The average size of this seaweed was 32.0 cm long and approximately 5.0 cm wide, while the size of the thallus was maximal in June (in length and width). On the dry weight basis, this alga was constituted of more than 18% ash, about 23% protein, 2.6% lipids, and approximately 60% dietary fibre. The most abundant fatty acids were palmitic acid and eicosapentaenoic acid (52% and 12% of the fatty acid fraction, respectively). The study of seasonal variations showed that the best period to collect the seaweed for food use is between February and June.

1. Introduction

In Asian countries, especially Japan, China and Korea, there is a long tradition of seaweed consumption (Nisizawa, Noda, Kikuchi, & Watanabe, 1987). The species used as sea vegetables are mainly red and brown algae (Dawczynski, Schubert, & Jahreis, 2007). In Europe, particularly in Norway and France, seaweeds are mainly harvested for the production of hydrocolloids such as alginates, agar or carrageens (Kaas, 1998). These polysaccharides are used as food additives for their thickening properties (McHugh, 2003). In France, seaweeds are also used as sea vegetables or ingredients. However, the consumption of seaweeds is subject to specific regulation (Mabeau & Fleurence, 1993) and the details of the chemical composition and its variations of a species are required to obtain authorisation for its use in human nutrition. The determination of the biochemical composition is also the first step in assessing the nutritional value of a seaweed used as a food product (Darcy-Vrillon, 1993). Currently, only four red seaweed species are authorised for human consumption (Mabeau & Fleurence, 1993), whereas 300 red seaweeds have been identified in Brittany.

In recent years, there has been a rapid expansion on the French Atlantic coast of an invasive species belonging to the red seaweed family (Simon, Ar Gall, & Deslandes, 2001). This species, *Grateloupia turuturu* Yamada, is a native of Japan. It now constitutes an important resource on this part of French coast, but has not been significantly exploited. In Japan, this seaweed is commonly used as a sea vegetable (Fujiwara-Arasaki, Mino, & Kuroda, 1984), but its chemical composition has been only partially described. Moreover, the only data available were collected from *G. turuturu* samples harvested on the Japanese coast. Studies performed on other algae clearly show that the chemical composition varies according to the species, geographic area, season or environmental conditions (Ito & Hori, 1989). Therefore, the evaluation of the chemical content of *G. turuturu*, collected in France, and its seasonal variation appears an essential step in improving current knowledge of the characteristics of this seaweed. It is also a useful way to promote the exploitation of this marine resource in Europe as a sea vegetable or an ingredient.

The aim of this study was to measure the chemical composition, ash, protein, total lipids, fatty acids, dietary fibre, and phycobiliproteins of *G. turuturu* in order to compare this species with other edible seaweeds. Moreover, the seasonal variation in the chemical

Abbreviations: fw, fresh weight; dw, dry weight; FA, fatty acids; PUFA, polyunsaturated fatty acid(s); FAME, fatty acid methyl ester(s); R-PE, R-phycoerythrin; R-PC, R-phycocyanin; GC–MS, gas chromatography–mass spectrometry; SE, standard error.

* Corresponding author. Tel.: +33 (0)2 51 12 56 50; fax: +33 (0)2 51 12 56 68.
E-mail address: joel.fleurence@univ-nantes.fr (J. Fleurence).

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composition was also investigated during one year to determine the best period for harvesting.

2. Materials and methods

2.1. Samples

The thalli of *G. turuturu* were collected in 2006 from the intertidal zone at Piriac-sur-Mer (17°22′N–2°33′E; Atlantic coast, France). The length and the width of 80 blades were measured each month. Epiphytes were removed then samples were successively rinsed with seawater, tap water and distilled water. The rinsed thalli were frozen immediately and freeze-dried (Edwards Super Modulyo, Thermo Electro Corporation, Waltham, MA, USA). The algal sample obtained was ground in liquid nitrogen. The resulting powder (dry weight) was used for different analyses.

2.2. Ash content

Total ash was determined by incineration of 0.5 g of freeze-dried algal material in an oven at 450 °C for 5 h. The ash content was expressed as a percentage of dw.

2.3. Total protein content

The organic nitrogen content was quantified by the Kjeldahl method (Miller & Miller, 1948) and an estimate of the total protein content was calculated by multiplying the nitrogen content by a factor of 6.25 (Lourenco, Barbarino, De-Paula, da S. Pereira, & Marquez, 2002).

The algal powder was homogenised with phosphate buffer (20 mM, pH 7.1). This procedure and the maximum of subsequent manipulations were performed at low temperature (4 °C). After centrifugation at 25,000*g* and 4 °C for 30 min, the supernatant was analyzed for phycobiliprotein content. The R-phycoerythrin (R-PE) and R-phycocyanin (R-PC) concentrations were determined spectrometrically using the Beer and Eshel (1985) equation.

2.4. Total lipid and fatty acid content

Total lipids were extracted with a mixture of dichloromethane: methanol (2:1, v/v) (Folch, Lees, & Stanley, 1957). NaCl (5%) was added to the aqueous phase to improve phase separation. The lipid content was determined by the gravimetric method.

Total lipids were saponified with 2 N ethanolic potassium hydroxide. The unsaponifiable matter was separated, and the remaining aqueous fraction acidified. Fatty acids were recovered by *n*-hexane extraction. Fatty acid methyl esters (FAME) were obtained by transmethylation (40 min under reflux with 6% methanolic hydrogen chloride) and analyzed by gas chromatography (GC, Agilent model 6890 series II) linked to an Agilent 5973 series network mass selective detector (i.e. 70 eV) equipped with an Agilent model 5973 N selective quadrupole mass detector. A GC procedure was required to analyze the FAME distribution of these samples. A CP-Sil 5 CB low bleed MS capillary column (60 m × 0.25 mm i.d., 0.25 μm phase thickness; Chromopack, Middelburg, The Netherlands) was used and the carrier gas was helium (1 ml min^{-1}). The column temperature was programmed from 200 °C to 340 °C at 8 °C/min; the final temperature was maintained for 15 min. FAME in the sample were identified by comparing their mass spectra with those of standards purchased from Sigma–Aldrich (St. Quentin, Fallavier, France). The results are expressed as a percentage of total FAME.

2.5. Total dietary fibre analysis

An enzymatic–gravimetric procedure for the total dietary fibre analysis was used (Fleury & Lahaye, 1991; Prosky, Asp, Schweizer, DeVries, & Furda, 1988). The dry powder sample and blank were incubated with heat stable α-amylase (Termamyl 120L, Novozymes Corp., Bagsvaerd, Denmark) at pH 6.0 for 25 min at 100 °C, then digested with protease (at pH 7.5, 30 min, 60 °C) (*Bacillus licheniformis*, subtilisine Carlsberg, Sigma, St. Louis, MO, USA) and finally with amyloglucosidase (at pH 4.5, 30 min, 60 °C) (E.C. 3.2.1.3, *Aspergillus niger*, Sigma). The insoluble material was recovered by filtration on fritted glass and the residue was washed successively with ethanol and acetone. Soluble dietary fibres were precipitated in 70% ethanol before drying overnight at 4 °C. After filtration, precipitates were rinsed and washed like the insoluble material. Samples were dried overnight at 40 °C.

2.6. Statistical analysis

Statistical analyses were conducted with the SigmaStat 3.1 version software for Windows. One-way analyses of variance were used (ANOVA). Significant difference at $p < 0.05$ between the months was determined by the Student–Newman–Keul's posthoc multicomparison test (SNK).

3. Results and discussion

3.1. Size and proximate composition

The size and the composition of *G. turuturu* are given in Table 1. The mean size of the thalli was 31.7 ± 2.9 cm in length and 4.8 ± 0.7 cm in width. The dry matter represents 9.5 ± 0.2% of the fresh weight (fw). This value is lower than those reported for other red seaweeds such as *Palmaria palmata* which were included between 11% and 22% of wet weight (Morgan, Wright, & Simpson, 1980). These levels were observed after dehydration in a drying oven. The efficiency of the freeze drying process used for drying *Grateloupi*a samples probably explains the value recorded. On the dry weight (dw) basis, the composition of *G. turuturu* was 18.5 ± 0.6% ash, 22.9 ± 2.0% total proteins, 2.6 ± 0.1% total lipids and 60.4 ± 2.3% total dietary fibre. The ash level is in agreement with that described for *P. palmata* (Marrion et al., 2005) and close to that reported for *Gracilaria changgi* (Norziah & Ching, 2000). However, it is higher than that described for the edible red seaweed *Porphyra* sp. (Nori) (Marsham, Scott, & Tobin, 2007).

The protein content (23% dw) is near to that recorded for *G. turuturu* (20% dw) by Fujiwara-Arasaki et al. (1984). It is also close

Table 1
Size and proximate chemical composition of *Grateloupia turuturu*.

	Grateloupia turuturu
Length[c]	31.7 ± 2.9
Width[c]	4.8 ± 0.7
Dry weight[a]	9.5 ± 0.2
Ash[b]	18.5 ± 0.6
Total protein	22.9 ± 2.0
Total lipid[b]	2.6 ± 0.1
Total dietary fibres[b]	60.4 ± 2.3
Soluble fibres[b]	48.1 ± 1.0
Insoluble fibres[b]	12.3 ± 1.2
R-PE[b]	0.30 ± 0.03
R-PC[b]	0.033 ± 0.003

Means ± SE (n = 6–12).
[a] % fw.
[b] % dw.
[c] cm.

Table 2
Fatty acid composition of *Grateloupia turuturu*.

Fatty acid	Annual mean	February	April	June	August	October	December
C14:0	5.3 ± 0.3	3.9	5.1	5.8	6.1	5.3	5.7
C15:0	1.1 ± 0.2	1.4	1.9	1.1	1.0	0.2	0.9
C16:0	51.7 ± 1.5	44.4	53.3	53.1	53.2	54.4	51.9
C18:0	9.2 ± 3.7	3.7	3.3	4.2	23.3	2.4	18.3
C16:1 ω7	1.7 ± 0.2	1.9	2.1	1.2	1.0	1.8	2.3
trans C16:1	1.1 ± 0.2	1.4	1.5	0.5	0.6	1.7	–
C18:1 o > 9	6.2 ± 0.3	5.4	6.2	6.7	5.1	7.0	6.4
C18:1 ω7	2.8 ± 0.4	2.2	2.9	1.8	2.6	4.6	2.6
C18:2 ω6	1.9 ± 0.5	2.0	2.0	2.5	1.0	1.7	2.3
C18:3 ω3	0.8 ± 0.2	1.2	0.9	1.2	0.4	1.0	0.4
C20:4 ω6	4.4 ± 0.8	4.6	4.3	6.0	1.7	6.9	2.8
C20:5 ω3	12.0 ± 3.1	24.1	14.3	13.0	2.6	12.8	5.2
3-OH-C_{17}	2.1 ± 0.5	3.4	2.2	2.4	–	0.2	–
∑ ni	0.8 ± 0.2	0.3	–	0.5	1.4	–	1.2
Saturated fatty acid	67.4 ± 4.5	53.5	63.7	64.2	83.7	62.3	76.8
Monounsaturated	11.6 ± 0.8	11.0	12.6	10.1	9.3	15.1	11.3
PUFAs	19.1 ± 3.8	31.8	21.5	22.8	5.6	22.3	10.7
PUFAs ω6	6.3 ± 0.9	6.6	6.3	8.5	2.7	8.6	5.1
PUFAs ω3	12.8 ± 3.2	25.3	15.2	14.2	3.0	13.7	5.6
Ratio ω6/ω3	0.6 ± 0.1	0.3	0.4	0.6	0.9	0.6	0.9
Total lipids[a]	2.6 ± 0.1	2.6	2.8	3.0	2.5	2.1	3.3

Methyl ester (%), mean ± SE (n = 6); PUFA, polyunsaturated fatty acids; ∑ ni: not identified FA (>0.2%).
[a] Total lipids % dw.

to those (22% dw) reported for the edible seaweed *P. palmata* collected in France during the spring (Galland-Irmouli et al., 1999; Morgan et al., 1980) and authorised as sea vegetables. Concerning the phycobiliproteins, R-PE and R-PC concentrations are 0.30 ± 0.03 and 0.033 ± 0.003% of dry weight, respectively (Table 1).

The lipid content was established as 2.6% of the dry weight (Table 1). This level lies between those reported for *Porphyra umbilicalis* (3.4% dw) and *P. palmata* (1.6% dw) (Fleurence, Gutbier, Mabeau, & Leray, 1994). The fatty acid (FA) composition is given in Table 2. The FA fraction was constituted by about 68% saturated FA, 12% monounsaturated acids and 19% PUFA. The level of saturated FA is higher than those described for *G. turuturu* (33–40% of the FA fraction) by Hotimchenko (2002). The most abundant fatty acid was palmitic acid (C16:0) which constitutes nearly 52% of the FA fraction (Table 2). This result is different from that reported in the same species (Hotimchenko, 2002) and it is also higher than those reported for edible red seaweeds such as *P. umbilicalis* or *P. palmata* (Fleurence et al., 1994). *G. turuturu* also contains PUFA such as C18:2ω6 (linoleic acid), C18:3ω3 (linolenic acid), C20:4ω6 (arachidonic acid) and C20:5ω3 (eicosapentaenoic acid), which have already been reported in other seaweeds (Dawczynski et al., 2007; Sanchez-Machado, Lopez-Cervantes, Lopez-Hernandez, & Paseiro-Losada, 2004). Eicosapentaenoic acid, which represents 12% of the FA fraction, is the main PUFA. This value is lower than those previously reported for *G. turuturu*, which was 22.6% for C20:5ω3 (Hotimchenko, 2002), and for *Porphyra* (nearly 50% of the FA fraction) (Noda, 1993). Such variations in the FA composition can be attributed to both environmental conditions and genetic status (Nelson, Phelger, & Nichols, 2002).

Moreover, it is the first time that 3-hydroxy C_{17} FA was identified in *G. turuturu* (Table 2). Until now, the 3-hydroxy short-chain acids were known as typical bacterial FA.

The level of dietary fibre was especially high (60.4% dw) with a content of soluble fibre close to 48% of the dry weight (Table 1). Similar results have already been reported for *Ulva lactuca* and *Durvillaea antarctica*, which contain 60% and 71% of dietary fibre, respectively (Ortiz et al., 2006). The total dietary fibre of *G. turuturu* is higher than those described for some brown seaweeds such as *Laminaria digitata* (40% dw) (Fleury & Lahaye, 1991), *Himanthalia elongata* (32% dw) or *Ascophyllum nodosum* (47% dw) (Bobin-Dubigeon et al., 1997), which are consumed in France as sea vegetables. It is also greater than those described for common foods such as brown rice, carrots or bananas (MacArtain, Gill, Brooks, Campbell, & Rowland, 2007) and close to those of whole soy (Jiménez-Escrig & Sanchez-Muniz, 2000). Nearly 50% of the dry weight of *G. turuturu* appeared to be constituted by soluble fibre. This is higher than the levels reported for by-products from *Kappaphycus* and cabbage (16.8% dw) or sugar beet pulp (25% dw) (Mabeau & Fleurence, 1993). The insoluble fibre constituted 12.4% of the dry weight. This value is close to that reported for *P. palmata* (11.2%) (Marrion et al., 2005).

3.2. Seasonal variations

3.2.1. Thallus size and dry weight

The morphological variations of thalli are reported in Table 3. The variations in length were greater than those in width. The maximum size of the thallus was observed in June and the minimum in August (Table 3). This thallus regression during August has already been observed by Simon et al. (2001) in *G. turuturu* harvested at Carantec (Brittany). According to these results, the best

Table 3
Mean seasonal variation in the thallus size of *Grateloupia turuturu* (means ± SE) (n = 80).

2006	Length (cm)	Width (cm)
January	23.6 ± 0.8	3.2 ± 0.1
February	26.1 ± 0.9	4.2 ± 0.1
March	28.2 ± 1.1	4.8 ± 0.2
April	36.2 ± 1.5	6.7 ± 0.3
May	44.5 ± 1.8	8.6 ± 0.4
June	52.5 ± 1.8	9.9 ± 0.4
July	42.7 ± 1.6	6.6 ± 0.3
August	20.7 ± 0.8	2.7 ± 0.2
September	27.8 ± 0.7	2.5 ± 0.1
October	26.5 ± 1.0	2.2 ± 0.1
November	28.9 ± 0.8	3.0 ± 0.1
December	24.3 ± 0.9	2.9 ± 0.1

Table 4
Seasonal variation in the chemical composition of *Grateloupia turuturu* (means ± SE).

2006	Dry weight[A] (n = 10)	Ash[B] (n = 15)	Proteins[B] (n = 4)	Lipids[B] (n = 8)	Insoluble fibres[B] (n = 4)	Solubles fibres[B] (n = 4)
January–February	9.72 ± 0.50[a]	16.16 ± 0.14[a]	27.50 ± 1.08a	2.43 ± 0.35[a]	8.99 ± 0.70[a]	49.27 ± 1.79[a]
March– April	9.29 ± 0.20[a]	17.16 ± 0.37[a,b]	26.41 ± 1.03[a]	2.31 ± 0.24[a]	9.11 ± 0.33[a]	43.95 ± 0.80[a]
May–June	8.90 ± 0.19[a]	19.41 ± 0.41[d]	20.31 ± 1.97[b]	2.87 ± 0.18[a]	12.81 ± 1.13[b]	44.11 ± 2.33[a]
July–August	9.44 ± 0.26[a]	18.01 ± 0.37[b,c]	14.06 ± 1.21[c]	2.46 ± 0.13[a]	16.54 ± 1.52[b]	45.99 ± 2.59[a]
September–October	10.15 ± 0.34[a]	19.81 ± 0.32[d]	22.34 ± 2.19[a,b]	2.42 ± 0.29[a]	12.98 ± 1.09[b]	46.66 ± 2.39[a]
November–December	9.33 ± 0.56[a]	19.01 ± 0.52[c,d]	23.91 ± 0.90[a,b]	2.78 ± 0.38[a]	11.79 ± 0.15[b]	49.49 ± 1.13[a]

Significant differences at $p < 0.05$ are indicated with different letters (a–d).
[A] % fw.
[B] % dw.

period for harvesting *G. turuturu* biomass for food processing is during the spring. This corresponds to the greatest growth both in length and width. In addition, the thallus appearance, which is normally brown-purple during this season, becomes yellowish in August and it breaks easily. This phenomenon has also been reported previously (Simon et al., 2001) and shows that the end of summer is not a good period to obtain a product of acceptable quality for both the food industry and consumers. The dry weight ranges from 9.3% to 10.2% of the fresh weight (Table 4) but no significant difference is observed during the year.

3.2.2. Ash, proteins, phycoerythrin and phycocyanin

The ash level varies between 16.2% and 19.8% of the dry weight of *G. turuturu* (Table 4), with an annual average of 18.5 ± 0.6% (Table 1). The variation recorded (5%) is lower than that described for the edible red seaweed *P. palmata* (12%) (Hagen Rødde, Vårum, Larsen, & Myklestad, 2004).

Contrary to other compounds, the proteins were subject to large variations during the year (Table 4). The maximal concentration (nearly 30% dw) was recorded during winter and the beginning of spring, and the minimal concentration (nearly 15% dw) during July and August. This type of seasonal variation, with a maximum in winter and a minimum in summer, is similar to that observed for *P. palmata* (Galland-Irmouli et al., 1999; Morgan et al., 1980). The R-phycoerythrin concentration variation was comparable to that of total proteins, with a minimal concentration in August and September (around 0.1% dw) and a maxima in January (around 0.5% dw) (Table 5). The variation in R-phycocyanin concentration follows the seasonal changes of R-phycoerythrin concentration (Table 5). The minimum concentration is recorded in summer (0.01% dw) and the maximum in January (0.05% dw). These data are in agreement with previous results that show a decrease in the total protein concentration in summer related to the destruction of phycobiliproteins (Galland-Irmouli et al., 1999). Consequently, the best period to harvest *G. turuturu* as a protein or phycoerythrin source is the end of winter and the beginning of spring (Tables 4 and 5).

Table 5
Seasonal variation in phycobiliproteins (R-phycoerythrin and R-phycocyanin) (means ± SE) (n = 4).

2006	R-phycoeryhtrin (% dw)	R-phycocyanin (% dw)
January	0.52 ± 0.01[a]	0.044 ± 0.005[a]
February	0.23 ± 0.03[c,d]	0.028 ± 0.003[a]
March	0.31 ± 0.04[b]	0.033 ± 0.008[a]
April	0.28 ± 0.03[b,c]	0.035 ± 0.002[a]
May	0.36 ± 0.02[b]	0.041 ± 0.001[a]
June	0.23 ± 0.01[c]	0.024 ± 0.002[a,b]
July	0.19 ± 0.02[d]	0.027 ± 0.001[ab]
August	0.10 ± 0.02[e]	0.013 ± 0.002[b]
September	0.15 ± 0.01[e]	0.019 ± 0.002[b]
October	0.39 ± 0.03[b]	0.037 ± 0.007[a]
November	0.37 ± 0.03[b]	0.043 ± 0.002[a]
December	0.37 ± 0.05[b]	0.039 ± 0.006[a]

Significant differences at $p < 0.05$ are indicated with different letters (a–e).

3.2.3. Lipids and fatty acids

There are no variations in the lipid content during the year (Table 4). The highest content of saturated fatty acids was observed in August and the lowest in February (Table 2). In contrast, the highest unsaturated FA content was reported in February (43% of total FA) and the lowest in August (nearly 15% of total FA). The ω3 eicosapentaenoic acid, the most interesting FA in terms of nutrition, content varied between 2.6% and 24% of the FA fraction (Table 2) and its highest concentration was reported in February. The higher levels of arachidonic acid were mainly observed from the end of winter until June (Table 2).

3.2.4. Dietary fibre

No variations in soluble fibre were observed during the year (Table 4). This is not the case for insoluble fibre, for which lower levels are recorded during winter and the early spring. Thus, the best period for the use of *G. turuturu* as a source of insoluble fibre appear to be from May to December.

4. Conclusion

The edible red seaweed *G. turuturu*, harvested on Brittany coasts (France), was analyzed for its seasonal variations of chemical composition and potential nutritional value. *G. turuturu* is characterised by its richness in dietary fibre (nearly 60% dw) and therefore appears to be a good source of food fibre for human consumption. This is very interesting because the beneficial effect of fibre on health is already well-known (Jiménez-Escrig & Sanchez-Muniz, 2000). This seaweed is also rich in proteins, like *P. palmata*, another red alga now authorised in France as a sea vegetable. Its lipid content is low, like all red seaweeds used in human nutrition, and its eicosapentaenoic acid content is similar to those reported for edible red seaweeds such as *Chondrus cripus* or *Gracilaria verrucosa* (Fleurence et al., 1994).

The study of seasonal variations shows that the best period to harvest this species for food products seems to be from February to June. This corresponds to the period when most of the relevant criteria, including biochemical composition (e.g. proteins and FA), total dietary fibres and seaweed appearance, are optimal. Further studies (e.g. amino acid and mineral composition) are, however, necessary to improve our knowledge of the nutritional value of this species, traditionally consumed as a vegetable by Japanese people.

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References

Beer, S., & Eshel, A. (1985). Determining phycoerythrin and phycocyanin concentrations in aqueous crude extracts of red algae. *Australian Journal of Marine Freshwater Research, 36*, 785–792.

Bobin-Dubigeon, C., Hoebler, C., Lognoné, V., Dagorn-Scaviner, C., Mabeau, S., Barry, J.-L., & Lahaye, M. (1997). Chemical composition, physico-chemical properties, enzymatic inhibition and fermentative characteristics of dietary fibres from edible seaweeds. *Sciences des Aliments, 17*, 619–639.

Darcy-Vrillon, B. (1993). Nutritional aspects of the developing use of marine macroalgae for the human food industry. *International Journal of Food Science and Nutrition, 44*, S23–S25.

Dawczynski, C., Schubert, R., & Jahreis, G. (2007). Amino acids, fatty acids, and dietary fibre in edible seaweed products. *Food Chemistry, 103*, 891–899.

Fleurence, J., Gutbier, G., Mabeau, S., & Leray, C. (1994). Fatty acids from 11 marine macroalgae of the French Brittany coast. *Journal of Applied Phycology, 6*, 527–532.

Fleury, N., & Lahaye, M. (1991). Chemical and physico-chemical characterisation of fibers from *Laminaria digitata* (Kumbu Breton): A physiological approach. *Journal of Science of Food and Agriculture, 55*, 389–400.

Folch, J., Lees, M., & Stanley, G. H. S. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry, 226*(1), 497–509.

Fujiwara-Arasaki, T., Mino, N., & Kuroda, M. (1984). The protein value in human nutrition of edible marine algae in Japan. *Hydrobiologia*(116/117), 513–516.

Galland-Irmouli, A. V., Fleurence, J., Lamghari, R., Luçon, M., Rouxel, C., Barbaroux, O., Bronowicki, J. P., Villaume, C., & Guéant, J.-L. (1999). Nutritional value of proteins from edible seaweed *Palmaria palmata* (Dulse). *The Journal of Nutritional Biochemistry, 10*(6), 353–359.

Hagen Rødde, R. S., Vårum, K. M., Larsen, B. A., & Myklestad, S. M. (2004). Seasonal and geographical variation in the chemical composition of the red alga *Palmaria palmata* (L.) Kuntze. *Botanica Marina, 47*(2), 125–133.

Hotimchenko, S. V. (2002). Fatty acid composition of algae from habitats with varying amounts of illumination. *Russian Journal of Marine Biology, 28*(3), 218–220.

Ito, K., & Hori, K. (1989). Seaweed: Chemical composition and potential food uses. *Food Reviews International, 5*(1), 101–144.

Jiménez-Escrig, A., & Sanchez-Muniz, F. J. (2000). Dietary fibre from edible seaweeds: Chemical structure, physicochemical properties and effects on cholesterol metabolism. *Nutrition Research, 20*(4), 585–598.

Kaas, R. (1998). The seaweed resources of France. In A. T. Crichley & M. Ohno (Eds.), *Seaweed resources of the world* (pp. 233–244). Yokusuka, Japan: Japan International Cooperation Agency.

Lourenco, S. O., Barbarino, E., De-Paula, J. C., da S. Pereira, L. O., & Marquez, U. M. L. (2002). Amino acid composition, protein content and calculation of nitrogen-to-protein conversion factors for 19 tropical seaweeds. *Phycological Research, 50*(3), 233–241.

Mabeau, S., & Fleurence, J. (1993). Seaweed in food products: Biochemical and nutritional aspects. *Trends in Food Science & Technology, 4*(4), 103–107.

MacArtain, P., Gill, C. I. R., Brooks, M., Campbell, R., & Rowland, I. R. (2007). Nutritional value of edible seaweeds. *Nutrition Reviews, 65*(12), 535–543.

Marrion, O., Fleurence, J., Schwertz, A., Guéant, J.-L., Mamelouk, L., Ksouri, J., & Villaume, C. (2005). Evaluation of protein in vitro digestibility of *Palmaria palmata* and *Gracilaria verrucosa*. *Journal of Applied Phycology, 17*(2), 99–102.

Marsham, S., Scott, G. W., & Tobin, M. L. (2007). Comparison of nutritive chemistry of a range of temperate seaweeds. *Food Chemistry, 100*(4), 1331–1336.

McHugh, D. J (2003). A guide to the seaweed industry. In *FAO, fisheries technical paper no. 441* (pp. 105). Rome: Food and Agricultural Organization of the United Nations.

Miller, G., & Miller, E. (1948). Determination of nitrogen in biological materials. *Analytical Chemistry, 20*, 481–488.

Morgan, K. C., Wright, J. L. C., & Simpson, F. J. (1980). Review of chemical constituents of the red alga *Palmaria palmata* (Dulse). *Economic Botany, 34*(1), 27–50.

Nelson, M. M., Phelger, C. F., & Nichols, P. D. (2002). Seasonal lipid composition in macroalgae of the northeastern Pacific Ocean. *Botanica Marina, 45*, 58–65.

Nisizawa, K., Noda, H., Kikuchi, R., & Watanabe, T. (1987). The main seaweed foods in Japan. *Hydrobiologia, 151–152*(1), 5–29.

Noda, H. (1993). Health benefits and nutritional properties of nori. *Journal of Applied Phycology, 5*(2), 255–258.

Norziah, M. H., & Ching, C. Y. (2000). Nutritional composition of edible seaweed *Gracilaria changgi*. *Food Chemistry, 68*(1), 69–76.

Ortiz, J., Romero, N., Robert, P., Araya, J., Lopez-Hernández, J., Bozzo, C., Navarrete, E., Osorio, A., & Rios, A. (2006). Dietary fiber, amino acid, fatty acid and tocopherol contents of the edible seaweeds *Ulva lactuca* and *Durvillaea antarctica*. *Food Chemistry, 99*(1), 98–104.

Prosky, L., Asp, N.-G., Schweizer, T. F., DeVries, J. W., & Furda, I. (1988). Determination of insoluble, soluble and total dietary fiber in foods and food products: interlaboratory study. *Journal of the Association of Official Analytical Chemists, 71*(5), 1017–1023.

Sanchez-Machado, D. I., Lopez-Cervantes, J., Lopez-Hernandez, J., & Paseiro-Losada, P. (2004). Fatty acids, total lipid, protein and ash contents of processed edible seaweeds. *Food Chemistry, 85*(3), 439–444.

Simon, C., Ar Gall, E., & Deslandes, E. (2001). Expansion of the red alga *Grateloupia doryphora* along the coasts of Brittany (France). *Hydrobiologia, 443*, 23–29.