Review of Chemical Constituents of the Red Alga *Palmaria palmata* (Dulse)

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The data reported in the literature and recent analyses of the composition of Palmaria palmata *(*Rhodymenia palmata*) are compiled and discussed. The reported values have a relatively wide spread ranging from 73–89% moisture and, on a dry weight basis, 12–37% ash, 8–35% crude protein, 38–74% carbohydrate and 0.2–3.8% lipid. Some of the variation can be attributed to seasonal and nutritional conditions.* P. palmata *has potassium, chlorine and sodium as its major mineral constituents and, in comparison to terrestrial fruits and vegetables, is a good source of iron, magnesium, calcium and iodine. Vitamin A (as carotene) and, in the fresh plant, vitamin C, are present in appreciable amounts.* P. palmata *is potentially a high protein food source, and its protein quality rates well with vegetables of good nutritional value. The major polysaccharide is a β-(1 → 3) and β-(1 → 4) linked xylan.* P. palmata *is a natural source of desmosterol.*

Marine plants have been used by man for centuries as food, fodder, fertilizer and sources of chemicals for the pharmaceutical, food and chemical industries. People in the Far East and Polynesia have a long history of eating marine algae as a beneficial supplement to their diets. In contrast, very little seaweed, as such, is eaten in the Western world. An exception is the red alga *Palmaria palmata* (L.) O. Küntze [=*Rhodymenia palmata* (L.) Greville (Guiry, 1974, 1975)], which has been used for centuries in coastal areas of Europe and more recently in northeastern North America (Schachat and Glicksman, 1959; Chapman, 1970; Ffrench, 1974). *P. palmata,* distributed throughout cooler waters of the North Atlantic and North Pacific (Guiry, 1975), is known to local inhabitants more popularly as "Dulse" (Great Britain and North America), "Dillisk" (Ireland), "Söl" (Iceland), "Søl" (Norway), "Goemon à vache" (France), or "Darusu" (Japan) (Butters, 1899; Schachat and Glicksman, 1959; Levring et al., 1969; Dixon, 1973). Interest in *P. palmata* as a food has prompted several studies on its protein, carbohydrate, fat, vitamin and mineral content. In this article we review published information on the chemical composition of *P. palmata,* add some recent data and evaluate its potential as a food source.

CHEMICAL COMPOSITION

Data reported in the literature on the chemical composition of *P. palmata* are from analyses of field-collected material by many independent groups. As a result the considerable variation in some data is probably owing to differences in methodology and to differences in plants, arising from site, seasonal, and population variations. A seasonal pattern is apparent for some constituents, but a lack of detailed information about the environment at the time of collection makes it

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difficult to correlate the effects of environmental parameters on the chemical composition of the plant.

1. Dry weight, ash, major minerals and trace elements

There is a wide range of dry weights (11–22% of wet weight) and ash weights (11.7–36.6% of dry weight) in the literature for field-collected material (Table 1). Although no seasonal data are reported for *P. palmata,* the dry weights of other Rhodophyceae in cold and temperate waters are commonly high in late summer and autumn and low in winter (Vinogradov, 1953). Some ash values show an opposite trend (Young and Langille, 1958). At the Atlantic Regional Laboratory dulse maintained in flowing seawater in tanks under conditions of controlled light and temperature was high in dry matter and low in ash when grown in nitrogen-depleted water, whereas plants fed high levels of nitrate had a low dry matter but high ash content (Morgan et al., 1979; Table 1). The experiments mimicked the high winter and low summer levels of nitrogenous nutrients in seawater which are considered important in promoting variation in the growth and chemical composition of marine benthic algae (Mathieson and Tveter, 1975; Chapman and Craigie, 1977). In addition, a population difference was observed: the lower water content of Dark Harbour dulse relative to Woodward's Cove dulse at Grand Manan Is., New Brunswick (Ocean Science Associates, 1972) was maintained when plants from the two areas were grown under similar culture conditions (Morgan et al., 1979). Munda (1972) reported variation in the dry weight of plants collected from several locations in Iceland (Table 1).

P. palmata contains a variety of mineral elements (Tables 1, 2). Although the data are fragmentary and variable, the elements in highest concentration appear to be chlorine, potassium and sodium (Table 1). The concentrations of potassium and phosphorus are notably high relative to amounts found in other seaweed species (Butler, 1931; Young and Langille, 1958). *P. palmata* is also a rich source of iodine, and radiotracer experiments reveal the halogen occurring mainly in mono- and diiodotyrosine and triiodothyronine (Scott, 1954; André, 1971). The concentrations of alkaline earth elements, when compared with other algae (Bowen, 1956), are relatively low. Of 14 species examined by Mauchline and Templeton (1966) only *P. palmata* had less calcium than was found in the surrounding seawater. The sulfate content is lower than that in seaweeds containing sulfated galactans (e.g., carrageenan) as their primary sugar (Ross, 1953).

Among trace elements, iron, aluminum and zinc occur in the highest amounts (Table 2). In comparing the trace elements present in red and brown algae, Black and Woodward (1957) found relatively high amounts of zinc, vanadium and chromium and low amounts of strontium in *P. palmata.* Their values are much higher than those reported in other studies. Lunde (1970) reinvestigated a number of seaweeds collected from the same area, and found that dulse contained average amounts of copper, manganese, zinc, selenium and iron but low amounts of molybdenum, arsenic, antimony and cobalt. Strontium occurred at lower levels in *P. palmata* and other red algae than in brown algae (Bowen, 1956), whereas the opposite was found for thorium (Strohal and Pinter, 1973).

TABLE 1. DRY WEIGHT, ASH AND MAJOR ELEMENTS OF *Palmaria palmata*.

Site	Month or season	Dry weight, % wet wt.	Ash, % dry wt.	Cl	K	Na	Ca	Mg	P	S	I	Reference
				mg/g dry wt.								
Rhode Island	—	13.7			24.2				3.0			Wheeler & Hartwell, 1893[a]
Brittany, France	—	15.7	36.6		90	22	12.5	5	2.5		0.81	Vincent, 1924[a]
—	—				378[b]	4.9[b]						Bertrand & Perietzeana, 1927[a]
St. Andrews, New Brunswick	June–July	15	26.9		122						0.23	Butler, 1931
Nova Scotia	—				22.2				3.9		1.2	Young, 1948
Halifax, Nova Scotia	May	11.9	26.7				2.4		3.2			MacPherson & Young, 1949
N. Berwick, Scotland	—		21.2							2.3		Ross, 1953
Weymouth, England	—						1.1					Bowen, 1956
N. Berwick, Scotland	January		27.4	97	79	20.7	7.2	3.9	5.6	3.5	0.3	Black & Woodward, 1957
Nova Scotia	July				71	25	4.7				0.08	Young & Langille, 1958
Irish Sea	—		11.7									Culkin & Riley, 1958
Culture	—	20		53	80	1.9						MacRobbie & Dainty, 1958
Irish Sea	—						0.17[c]					Mauchline & Templeton, 1966

TABLE 1. CONTINUED.

Site	Month or season	Dry weight, % wet wt.	Ash, % dry wt.	Cl	K	Na	Ca	Mg	P	S	I	Reference
				mg/g dry wt.								
Iceland	summer	16.4–21.1	25–32.5									Munda, 1972
Grand Manan Is., New Brunswick	summer											Ocean Science Associates, 1972
Dark Harbour		16										
Woodward's Cove		11										
Tank culture												
Dark Harbour		20.1										Morgan et al., 1979
Woodward's Cove		15.4										
Tank culture	High light/ low N	27	14									Morgan et al., 1979
	Low light/ high N	13	31									

Other data (mg/g dry weight): Silicon 10 (Black & Woodward, 1957); Iodine 7.1 (Standford, 1877[a]), 1.2 (Cameron, 1915), 0.008[c] (Kylin, 1929[a]), 0.21 (Bruievich et al., 1933[a]), 0.009[c] (Vinogradov & Bergmann, 1938[a]).

[a] Cited in Vinogradov, 1953.

[b] Expressed as mg/g of ash weight.

[c] Expressed as mg/g of wet weight.

TABLE 2. TRACE ELEMENTS OF *Palmaria palmata*.

Site	Month or season	Fe	Al	Zn	B	Sr	Ti	Mn	Cr	Cu	V	Pb	F	As	Ba	Sn	Co	Ag	Mo	Reference[a]
		μg/g dry weight																		
Brittany, France	—	4,400						12.5												1[b]
—	—						5													2[b]
San Juan Archipelago, Washington	—				46															3
Gulf of Kola	—				131															4[b]
Gulf of Kola	—																			5[b]
Halifax, Nova Scotia	May	250																		6
Iceland	Feb.–Apr.									22										7
Weymouth, England	—					18.8									0.6					8
N. Berwick, Scotland	Jan.	1,355		200		90	100	110	34	48	29	28	15.2			<5	2.6	1.0	0.83	9
Irish Sea	—	252	175							24.4					21					10
Nova Scotia	July			41						26				10			0.13		0.31	11
Irish Sea	—					2[c]									<5[c]					12
Trondheimsfjord, Norway	March	153		143				11		24				13			0.5		0.6	13

Other trace elements (μg/g dry weight): rubidium 1.9[c] (Glebovitch, 1941[b]); Bromine 0.011 (Bowen, 1956); gallium 0.04 (Culkin & Riley, 1958); nickel >2 (Young & Langille, 1958); selenium 0.17, antimony 0.05 (Lunde, 1970); thorium 1.2 (Strohal & Pinter, 1973).

[a] Reference: 1—Vincent, 1924; 2—Kaminskäia, 1933; 3—Igelsrud et al., 1938; 4—Glebovitch, 1941; 5—Borovik-Romanova, 1944; 6—MacPherson & Young, 1949; 7—Pálsson & Grimsson, 1953; 8—Bowen, 1956; 9—Black & Woodward, 1957; 10—Culkin & Riley, 1958; 11—Young & Langille, 1958; 12—Mauchline & Templeton, 1966; 13—Lunde, 1970.

[b] Cited in Vinogradov, 1953.

[c] Expressed as μg/g of wet weight.

2. Vitamins

In general, green and red algae have a higher content of B vitamins than brown algae (Lundin and Ericson, 1955). The amounts found in *P. palmata* are typical for a red alga, although high levels of thiamine (Kanazawa et al., 1966) and niacin (Larsen, 1958) and low levels of vitamin B_{12} (Ericson and Lewis, 1953; Kuceva and Bukin, 1957) have been reported (Table 3). The B_{12} activity is due to at least four factors, three having been identified as cyanocobalamin, pseudovitamin B_{12} and vitamin B_{12S} (Ericson and Lewis, 1953). Studies of ^{60}Co uptake by *P. palmata* have shown that despite a large accumulation of isotope by the plant, vitamin B_{12} was unlabelled (Ericson and Lewis, 1953; Scott and Ericson, 1955). The investigators concluded that B_{12} in the seaweed arises from an exogenous source, possibly from closely-associated bacteria. Biotin-1-sulfoxide is the principal active form of biotin (Larsen, 1961) and nicotinic acid amide of niacin (Larsen, 1958). The influence of season and habitat on vitamin B content of *P. palmata* is not understood. Some data suggest that the concentration of niacin is maximal in spring (Larsen, 1958), vitamin B_{12} in spring and summer (Lundin and Ericson, 1955), while biotin shows no regular seasonal trend (Larsen, 1961).

α-Tocopherol (vitamin E) is the only tocopherol detected in *P. palmata* and other algae, except species of Fucaceae which contain the γ- and δ-homologues as well (Jensen, 1969). The tocopherol content of *P. palmata* is low (Table 3) compared with members of the Fucaceae (Jensen, 1969), with a maximum in late summer and autumn (Brown, 1953). However, dulse contains average to high amounts of vitamin C on a wet weight basis (Lunde and Lie, 1938; Creac'h and Baraud, 1954), again reaching a peak in late summer and autumn (Lunde and Lie, 1938). Other vitamins, including choline (DaSilva and Jensen, 1973), folic and folinic acid (Ericson, 1953) are present in the usual amounts found in a marine alga (Table 3).

Total carotene concentrations approximate vitamin A activity (Tables 10, 11), and in *P. palmata* are generally higher than in other seaweeds (Owen, 1954; Larsen and Haug, 1956). Conditions during the harvest and drying of dulse can severely affect the carotenoid content. Drying in the open during poor weather conditions has resulted in almost complete degradation of the carotenoids within a week (Haug and Larsen, 1957). The degradation is apparently an enzymatic process which is effectively retarded by potassium cyanide or sodium sulfide (Haug and Larsen, 1956b). The loss was also significantly less with rapid artificial drying at 80°C. The carotene content varied throughout the year: Owen (1954) reported appreciably higher values in September than in January, although Haug and Larsen (1957) observed no regular trend (Table 10).

3. Nitrogenous constituents

The total nitrogen content of *P. palmata* on a dry weight basis is high in comparison to other seaweed species (MacPherson and Young, 1949; Munda, 1972), though there is considerable variation in both field-collected (1.8–4.7%) and tank-cultivated (1.3–4.2%) material (Table 4). Seasonality has been demonstrated recently by Chaumont (1978): total nitrogen was highest during winter and early spring and lowest during summer and autumn, a trend reported for other Rhodophyceae (e.g., Mathieson and Tveter, 1975, 1976). Similarly, in tank

TABLE 3. VITAMIN CONTENT OF *Palmaria palmata*.

Site	Month or season	Vitamin C	Choline	Tocopherol	Niacin	Riboflavin	Pantothenic acid	Thiamine	Folic acid	Folinic acid	Vit. B_6	Biotin	Vit. B_{12}	Reference
		μg/g wet wt.	μg/g dry wt.											
—	Feb.–May	220–450												Lunde & Lie, 1938
	Sept.–Jan.	400–500												
Angmagssalik	—	170												Høygaard & Rasmussen, 1939
N. Berwick, Scotland	summer								1.3	0.46				Ericson, 1953
N. Berwick, Scotland	July												0.09	Ericson & Lewis, 1953
Middleton, Ireland	fall			139										Brown, 1953
	winter			22										
—	—												0.10	Ann. Rep. Inst. Seaweed Res., 1954
France	March	520												Creac'h & Baraud, 1954
N. Berwick, Scotland	—												0.24	Scott & Ericson, 1955
Barents Sea	—												0.009	Kuceva & Bukin, 1957
N. Berwick, Scotland	Jan.				28.9	5.3		1.5						Black & Woodward, 1957
Norway	April				83									Larsen, 1958
	Sept.				22									
Norway	—											0.07		Larsen, 1961
Grand Manan Is., New Brunswick	summer				16.9	5.0	4.3	6.3			0.14	0.18	0.028	Kanazawa et al., 1966
Norway	spring			35										Jensen, 1969
Norway	Feb.		2,000											DaSilva & Jensen, 1973

TABLE 4. NITROGEN CONSTITUENTS OF *Palmaria palmata* (% DRY WEIGHT).

Location	Season	Total nitrogen	Alcohol soluble-N	Nitrate-N	Volatile base-N	Amide-N	Free amino acid-N	Residual-N[a]	Crude[b] protein	Reference
N. Berwick, Scotland	January	3.91		0.13	0.01	0.48	0.25	3.28	(24.4)	Channing & Young, 1953
Halifax, Nova Scotia	September	2.08	0.24					1.84	(13.0)	Smith & Young, 1955
France	Spring	3.42	0.84	0.10	0.008			2.58	(21.4)	Citharel & Villeret, 1964
France	Oct.–May	2.4–5.7, av. 4.0	0.5–1.9, av. 1.0	0.03–0.7, av. 0.23				1.7–4.8, av. 3.0	(15.0–35.6, av. 25.0)	Chaumont, 1978
	June–Sept.	1.3–3.1, av. 1.9	0.2–0.8, av. 0.4	0.01–0.04, av. 0.03				0.8–2.3, av. 1.5	(8.1–19.4, av. 11.6)	
Tank culture	high light/low N	1.30	0.24	0.0007				1.06	(8.1)	Morgan et al., 1979
	low light/high N	3.79	0.40	0.02				3.39	(23.4)	

Other crude protein data (% dry weight): (23.1) (Butler, 1931); 20.5–21.6 (Schmidt-Nielsen & Hammer, 1932); (25.3) (MacPherson & Young, 1949); 23.5 (Bender et al., 1953); (21.9) (Ross, 1953); (17–18) (Coulson, 1955); 23.4 (Black & Woodward, 1957); (22.1) (Young, 1964); (22–29) (Schlichting & Purdom, 1969); 11.6–16.3 (Munda, 1972).

[a] Residual-N calculated as difference between total nitrogen and soluble nitrogen, except for data of Channing & Young (1953) where residual-N is the difference between total nitrogen and the sum of nitrate-, volatile base- and amide-N.

[b] Crude protein calculated from the total nitrogen value × 6.25. Values in brackets are cited in reference as % total nitrogen.

TABLE 5. AMINO ACID COMPOSITION OF *Palmaria palmata*.

Amino acid g/100 g dry wt.	Channing & Young, 1953[a]		Smith & Young, 1955[b]		Lyman et al., 1956[c]		Black, 1958[c]		Munda & Gubensek, 1976		Schlichting & Purdom, 1969	
	Dried plant	Crude protein	Dried plant	Crude protein	Dried plant	Crude protein	Dried plant	Crude protein	Dried plant	Crude protein	Dried plant	Crude protein
Alanine	1.85	7.6	0.8	6.1					1.32	7.02	1.64	5.60
Glycine				4.9					1.02	5.43	1.30	4.43
Valine	1.46	6.0	0.7	5.2	1.25	6.04	1.1	6.4	1.05	5.59	1.37	4.68
Leucine	0.71	2.9	0.7	5.3	1.12	5.41	1.1	5.5	1.02	5.43	1.84	6.29
Isoleucine	0.66	2.7	0.5	3.5	0.88	4.25	0.8	4.0	0.67	3.56	1.06	3.62
Serine			0.6	4.4					0.76	4.04	1.21	4.13
Threonine			0.5	4.1	0.89	4.30	0.9	4.4	0.87	4.63	1.04	3.56
Cysteine			+[d]	+					0.0	0.0	0.81	2.76
Methionine			0.1	0.8	0.37	1.79	0.5	2.3	0.39	2.07	2.00	6.84
Aspartic Acid	2.20	9.0	1.1	8.3					1.84	9.99	2.05	6.99
Glutamic Acid	2.37	9.7	1.0	8.0					1.00	5.32	2.36	8.05
Lysine			0.5	4.1	1.49	7.20	1.5	6.9	0.83	4.42	1.63	5.57
Arginine			0.5	4.1	1.08	5.22	1.0	4.8	0.87	4.63	1.37	4.68
Phenylalanine			0.6	4.5	0.81	3.91	0.8	3.2	0.71	3.78	1.44	4.92
Tryptophan			+	+	0.27	1.30	0.2	0.9	0.56	2.98	–[e]	–
Proline			0.5	3.6					0.97	5.16	1.08	3.68
Histidine			0.07	0.5	0.33	1.59	0.3	1.3	0.26	1.38	0.29	0.99
Total nitrogen[f]	3.91		2.08		3.33		3.60		3.01		4.68	

[a] Incomplete analysis.
[b] Analysis of combined amino acids only. Original data expressed as % amino acid nitrogen of total nitrogen in hydrolysate.
[c] Analysis of essential amino acids only.
[d] Detected, but not measured.
[e] Not detected by method used.
[f] % of dry weight.

culture, the nitrogen content rapidly declines when *P. palmata* is grown in nitrogen-depleted water (Morgan et al., 1979).

The earliest amino acid analyses of *P. palmata* were reported by Channing and Young (1953) and Coulson (1953b) who detected 17 common amino acids in paper chromatograms of whole-plant hydrolysates. Coulson also detected the iodoamino acids, 3:5-diiodotyrosine, 3:5-diiodothyronine and thyroxine. Quantitative analysis of certain amino acids in the protein fraction by Channing and Young (1953) showed that the dulse proteins were rich in glutamic and aspartic acids. Subsequent analyses (Smith and Young, 1955; Coulson, 1955; Schlichting and Purdom, 1969; Munda and Gubensek, 1976) confirmed the preponderance of aspartic and glutamic acids, and also found that arginine, glycine, alanine, leucine and valine were present in major amounts (Table 5). Only Schlichting and Purdom reported a high methionine content (2 g/100 g of dry sample), some 3–4 times higher than that found in other studies. Most investigators agree that methionine, histidine, tryptophan and cysteine are present in small quantities (Coulson, 1955; Smith and Young, 1955; Munda and Gubensek, 1976). The prevalence of acidic amino acids and low concentration of basic amino acids in the proteins of *P. palmata* is typical of most other Rhodophyceae examined (Munda and Gubensek, 1976). Two groups studying only the essential amino acids in *P. palmata* (Lyman et al., 1956; Black, 1958) found relatively high amounts of lysine (Table 5).

P. palmata contains a pool of free amino acids and small peptides. Channing and Young (1953) in analyzing the soluble nitrogen fraction of alcohol extracts

reported alanine, aspartic and glutamic acids as the major constituents, while Coulson (1953a) found, in addition, significant amounts of serine and proline, the latter constituting over 50% of the total free amino acids in winter samples of dulse (Citharel, 1966). Proline and glutamic acid were found to be the major free amino acids by Laycock et al. (1979) in dulse grown in tanks in a greenhouse. They discovered the presence of *D*-homocysteic acid, an unusual amino acid not previously reported in a marine alga. Laycock (1979) has since found that partial purification of the alcohol extract on Dowex 50 reveals major amounts of several basic amino acids, including gigartinine and arginine, and the dipeptide L-citrullinyl-L-arginine, not detected in crude extracts by an amino acid analyzer or by electrophoresis. L-citrullinyl-L-arginine may be one of the basic peptides previously referred to in a brief report (Ann. Rep. Inst. Seaweed Res., 1963).

Trace amounts of amines, ammonium salts (volatile base nitrogen, Table 4), and nitrite have been found in the alcohol soluble non-protein fraction (Channing and Young, 1953; Citharel and Villeret, 1964), but concentrations of nitrate as high as 18% of the total nitrogen have been reported (Chaumont, 1978). The data in Table 4 illustrate a considerable seasonal variation in the percentage of soluble nitrogen on a dry-weight basis. Chaumont (1978) records a 2–3-fold increase between summer and winter samples, tissue nitrate levels increasing about 7-fold, while other soluble nitrogen constituents show lesser increases. Winter samples of Nova Scotian dulse are also reported to contain increased amounts of peptides and free amino acids (Smith and Young, 1952). In culture there is a rapid, but transitory, increase in tissue nitrate in dulse following the addition of high (0.5 mM) levels of nitrate (Morgan et al., 1979).

4. Carbohydrates

The most common polysaccharides of red algae contain D- or L-galactose residues in which the galactan units are alternately β-(1 $\rightarrow$ 3)- and β-(1 $\rightarrow$ 4)- linked (Mackie and Preston, 1974). The sugars may be methoxylated or esterified with sulfate. Included in this group are agar, carrageenan, porphyran and furcellaran. The major polysaccharide of *P. palmata,* however, is a water-soluble xylan composed of β-(1 $\rightarrow$ 3)- and β-(1 $\rightarrow$ 4)-linked D-xylose units which contain no sulfate ester or methoxyl groups. This polysaccharide is unlike the xylans of land plants which are usually water insoluble and possess only β-(1 $\rightarrow$ 4)-linked residues. The xylan of dulse also differs from the xylans of green algae which are composed of continuous chains of β-(1 $\rightarrow$ 3)-linked units (Mackie and Percival, 1959; Cerezo et al., 1971).

The water-soluble xylan of *P. palmata* was first isolated by Barry and Dillon (1940), and subsequent chemical analysis, including characterization of the products of enzymic hydrolysis (Howard, 1957), showed it to be an essentially linear molecule of xylose units, with both β-(1 $\rightarrow$ 3) and β-(1 $\rightarrow$ 4) linkages present in the same chain (Barry et al., 1950, 1954; Percival and Chanda, 1950). Only a small proportion of the (1 $\rightarrow$ 3)-linked units are adjacent, the majority being flanked by (1 $\rightarrow$ 4)-linked residues (Manners and Mitchell, 1963). More recent work has revealed two xylans in *P. palmata,* one obtained by extraction with water (xylan I) and the other by subsequent extraction of the residue with 0.1 M sulfuric acid (xylan II) (Bjorndal et al., 1965). The main difference between these xylans is the

TABLE 6. CARBOHYDRATES OF *Palmaria palmata* (% DRY WEIGHT).

Site	Month or season	Isoflo-ridoside	Flor-idoside	Floridean starch	Hexose	Uronic anhydride	Pentose	Total carbo-hydrate	Cellu-lose	Reference
—	—		14.8							Kylin, 1918
St. Andrews, New Brunswick	July								1.5	Butler, 1931
—	Summer				8–11[a]	5–7[a]	41–45[a]			Schmidt-Nielsen & Hammer, 1932
—	—								2.1	Naylor & Russell-Wells, 1934
—	—							45		Young, 1948
France	July		4.0							Henry, 1949
	Feb.		1.9							
N. Berwick, Scotland	—				3.5[b]	3.3[c]	36[b]		2.4	Ross, 1953
N. Berwick, Scotland	Jan.								2.1	Black & Woodward, 1957
—	March		0.4[d]	None						Schachat & Glicksman, 1959
	Sept.–Oct.		2.5–5.4	None						
Washington Coast	—			Small granules						Meeuse et al., 1960
Nova Scotia	—								3.5	Young, 1966
Nova Scotia	July	0.1[e]	5.6[e]							Craigie et al., 1968
France	July–Sept.		16–25[f]							Chaumont, 1978
	Oct.–June		3–8							
Tank culture	low light/high N						29[g]	38[h]		Morgan et al., 1979
	high light/low N						46	74		

[a] Expressed as % of ash-free dry weight.
[b] Hydrolysis with N-sulphuric acid; analysis by means of hypoiodite solution; results calculated to anhydro-hexose or -pentose.
[c] Distillation with 19% HCl and absorption of CO_2 in NaOH.
[d] Expressed as % of wet weight.
[e] Expressed as % of alcohol extracted dry weight.
[f] Measured against galactose.
[g] Extraction with 0.1 N H_2SO_4 at 80°C; analysis by orcinol-$FeCl_3$/HCl method (Mejbaum, 1939); measured against xylose.
[h] Extraction with 0.1 N H_2SO_4 at 80°C; analysis by phenolsulfuric method (Dubois et al., 1956); measured against sucrose.

proportion of β-(1 → 3) and β-(1 → 4) linkages: xylan I contains 71% of β-(1 → 4) and 29% β-(1 → 3) whereas the corresponding figures for xylan II are 62% and 38%. Using 3 M NaOH, Turvey and Williams (1970) extracted a third xylan containing almost exclusively β-(1 → 4) linkages from the skeletal material of the cell wall.

There is disagreement about the molecular size of *P. palmata* xylans. Determinations of the degree of polymerization (DP) by several different methods give DP's ranging from 40–114 (Barry et al., 1950; Manners and Mitchell, 1963; Bjorndal et al., 1965; Sturgeon, 1973). Although the variation likely is due to differences in methodology, the chain length and the proportion of the two types of linkage may vary in the different molecules.

Before the major polysaccharide of *P. palmata* was purified and characterized, floridoside was isolated by Colin and Guéguen (1930). This low molecular weight carbohydrate, 2-O-glycerol α-D-galactopyranoside, is a common reserve product of the Rhodophyceae (Putman and Hassid, 1954). In dulse, floridoside may reach levels as high as 25% of the dry weight (Chaumont, 1978), but lesser amounts (<10%) are usually found (Table 6). Trace amounts of the closely related derivative, isofloridoside (1-O-glycerol α-D-galactopyranoside), have also been reported (Craigie et al., 1968).

Another storage polysaccharide of *P. palmata* is floridean starch, which occurs in characteristically shaped granules. It is composed of chains of α-(1 → 4)- and α-(1 → 6)-linked glucose units, interspersed occasionally with α-(1 → 3)-linkages similar in structure to the amylopectin of higher plants (Percival and McDowell, 1967). Meeuse and co-workers (1960) found only small granules of floridean starch in *P. palmata* collected along the northwest coast of the United States, and considered it a poor source of this material. Schachat and Glicksman (1959), in fact, detected none in both winter and autumn samples, but higher levels apparently occur in older fronds (Myers and Preston, 1959) and in cells of the stipe (Dawson, 1966). A modified cellulose, containing equal amounts of β-(1 → 4)-linked xylose and glucose residues, is synthesized by *P. palmata* in small amounts (Cronshaw et al., 1958; Myers and Preston, 1959; Table 6). Chitin was not detected in the cell wall (Young, 1966).

There is some seasonal variation in concentration of carbohydrate as illustrated in Table 6. Schachat and Glicksman (1959) reported the concentration of floridoside in March was 0.4% (fresh weight) and in September was 5.4%. A recent 12-month study by Chaumont (1978) found that the floridoside content reached a maximum in July and a minimum in November. Several workers (Black et al., 1965; Fuller and Mathieson, 1972; Mathieson and Tveter, 1975) have recorded summer–autumn maxima in the carbohydrate content of other red algae which seem to coincide with the depletion of nitrate from the seawater. Likewise, the carbohydrate content of dulse under greenhouse conditions was 50–80% higher in plants grown in nitrogen-depleted seawater than in plants fertilized regularly with nitrate (Morgan et al., 1979).

5. Lipids

The lipid content of *P. palmata* is low (0.3–3.8% of dry weight), typical for a red alga. The fatty acid constituents were first examined by Lovern (1936) but

TABLE 7. LIPID CONTENT AND FATTY ACIDS OF *Palmaria palmata*.

Site	Month or season	Lipids % dry weight	Fatty acid composition, % saturated		unsaturated		Reference
Aberdeen, Scotland	—		Σ saturated	25	Σ unsaturated	75	Lovern, 1936
			C_{16}	19	C_{18}	20	
			others	6	C_{20}	36	
					others	19	
France	—	0.4–1.6					Henry, 1949
Halifax, Nova Scotia	May	3.8					MacPherson & Young, 1949
N. Berwick, Scotland	—	2.4					Ross, 1953
N. Berwick, Scotland	Jan.	0.3					Black & Woodward, 1957
Isle of Man, England	March		Σ saturated	36.3	Σ unsaturated	58.0	Chuecas & Riley, 1966
			C_{14}	11.9	C_{18}	39.1	
			C_{16}	22.0	C_{20}	11.0	
			others	2.4	others	7.9	
Grand Manan Is., New Brunswick	summer	0.6					Idler et al., 1968
Grand Manan Is., New Brunswick	June–Aug.	0.6–1.7					Idler & Wiseman, 1970
	Sept.–Nov.	0.2–1.1					
Iceland	summer	0.8–1.7					Munda, 1972
Halifax, Nova Scotia	Dec.		Σ saturated	36	Σ monoethylenic	11	Ackman & McLachlan, 1977
			14:0	8.9	18:1ω9	3.6	
			16:0	25.0	others	<7.5	
			others	<2	Σ polyethylenic	53	
					20:5ω3	45.5	
					others	~8	

these data were expanded by Chuecas and Riley (1966) and refined by Ackman and McLachlan (1977) (Table 7). Marine plants afford a greater variety of fatty acids than do most terrestrial plants (Hilditch and Williams, 1964; Wood, 1974) and like animals, accumulate polyethylenic fatty acids of C_{20} and C_{22} chain lengths in the cellular membrane (Ackman, 1964; Hilditch and Williams, 1964; Wagner and Pohl, 1966). There is little difference in the proportions of the three basic types of fatty acids, saturated, monounsaturated and polyethylenic among the three major divisions of benthic marine algae (Rhodophyceae, Phaeophyceae, Chlorophyceae). Palmitic acid (16:0) is the major unsaturated acid and oleic (18:1) the major monoethylenic acid (Chuecas and Riley, 1966; Ackman and McLachlan, 1977). An earlier report (Laur, 1961) of a group of uncharacterized polyethylenic C_{20} acids in *P. palmata* has been confirmed by Ackman and McLachlan (1977). This major group is mainly comprised of 20:5ω3 together with trace amounts of 20:2, 20:3 and 20:4 isomers.

The principal sterol of the unsaponifiable lipid fraction of most red algae is cholesterol (Goodwin, 1974), but dulse is unusual in that it produces desmosterol rather than cholesterol as a major C_{27} sterol (Gibbons et al., 1967; Idler et al., 1968; Idler and Wiseman, 1970; Ferezou et al., 1974; Morisaki et al., 1976; Idler and Atkinson, 1976) (Table 8). Although red algae are capable of synthesizing C-24 alkyl derivatives (which contain one or two extra carbons in the side-chain) they are seldom major products (Ferezou et al., 1974). A list of minor sterols in dulse appears as a footnote to Table 8.

In two short-term studies of the sterol composition of dulse from Grand Manan Island, Bay of Fundy, Idler and co-workers (Idler et al., 1968; Idler and Wiseman, 1970) found a significant but unaccountable variation in the proportion of desmosterol (31–97% of total sterols) and cholesterol (2–92%) from sample to sample, although the largest desmosterol yield occurred in midsummer (Table 8). However, results of a later and more prolonged study from Logy Bay, Newfoundland (Idler and Atkinson, 1976) were different: desmosterol was the major sterol in all samples, but was present in higher amounts than in Grand Manan samples, reaching maximal levels in November–December and May. These differences suggested to the authors that geographical location is an important factor in desmosterol production by dulse.

Hydrocarbons are minor components in *P. palmata*, forming 0.003 and 0.009% of the dry weight in two samples from the east coast of the United States (Clark and Blumer, 1967; Youngblood et al., 1971) and 0.019% in samples collected in the Bay of Fundy (Wright, 1979) (Table 9). In each study n-heptadecane was the predominant saturated hydrocarbon with smaller amounts of n-pentadecane, typical for red algae (Youngblood et al., 1971).

5. *Pigments*

The chlorophyll and biliproteins of *P. palmata* are well characterized. Chlorophyll *a* (Owen, 1954; Bjornland and Aquilar-Martinez, 1976), R-phycocyanin (O'hEocha, 1962; Young, 1970), allophycocyanin (O'hEocha, 1962; Young, 1970), R-phycoerythrin and β-phycoerythrin (O'hEocha, 1960; Young, 1970; van der Velde, 1973a, 1973b) have all been observed. No seasonal data exist on the biliprotein content, but *P. palmata* and other Rhodophyceae growing in shallow,

TABLE 8. STEROLS OF *Palmaria palmata*.

Site	Season or month	Total sterols	Desmosterol	Cholesterol	Desmosterol	Cholesterol	Reference
		mg/100 g dry wt.			% Total sterols		
—	—				99	1	Gibbons et al., 1967
Grand Manan Is., New Brunswick	Summer	10–40	1.2–39	1.1–15	7.7–97.2	2.1–92.3	Idler et al., 1968
France	—				62	27	Alcaide et al., 1968
Rhode Island	—				88	2	Meunier et al., 1970
Grand Manan Is.,	June–Aug.	10–19	8–18	0.5–5.8	39.2–97.2	2.1–30.4	Idler & Wiseman, 1970
New Brunswick	Sept.–Nov.	6–10	1.5–11.9	0.2–2.0	30.6–91.4	3.3–49.2	
France	—				56	20	Ferezou et al., 1974
Japan	—		3	1			Morisaki et al., 1976
Logy Bay, Newfoundland	June–May	~1–78	~1–77	<1			Idler & Atkinson, 1976

Minor sterols (% of total sterols): 22-dehydrocholesterol 0.1–1.7; brassicasterol <0.1; stigmasterol + 24-methylenecholesterol 2.2–6.8; β-sitosterol 0.2–16.2; fucosterol 2.1–3.7 (Idler et al., 1968); β-sitosterol + fucosterol 10 (Meunier et al., 1970); 22-dehydrocholesterol <0.1–1.4; brassicasterol 0–3.8; 22:23-dihydrobrassicasterol 0–9.5; 24-methylenechloesterol 0.4–17.2; β-sitosterol 0–16.2; fucosterol 0–9.8; 28-isofucosterol 0–0.5 (Idler & Wiseman, 1970); 22-dehydrocholesterol 0.7, brassicasterol 1.03; 24-methylenecholesterol 2.3; fucosterol 13; 24-dimethylchola-5,22-diene-3β-ol 0.45; *cycloartanol* 1.0; 31-*nor*-cycloartanol 0.7; 5α-*cholestan*-3β-*ol* <0.1 (Ferezou et al., 1974); 22-dehydrocholesterol; 24-methylenecholesterol; isofucosterol; ligosterol; cholesta-5,25-diene-3β,23-diol (Morisaki et al., 1976).

TABLE 9. HYDROCARBON CONTENT OF *Palmaria palmata*.

Site	Month or season	Hydrocarbon % dry weight	% Composition		Reference
New Hampshire	March	0.0094[a]	n-heptadecane	79	Clarke & Blumer, 1967
			n-pentadecane	~20	
			pristane	trace	
Massachusetts	May	0.003	n-heptadecane	99	Youngblood et al., 1971
			n-pentadecane	~1	
			alkenes	~0.3	
Bay of Fundy	December	0.019	n-heptadecane	96.8	Wright, 1979
			n-pentadecane	2.3	
			alkenes	trace	

[a] % extracted dry weight.

sunlit waters commonly lose their dark-red pigmentation in late summer (MacFarlane, 1968; Edelstein et al., 1970). Laboratory culture work indicates that both high light intensity and nitrogen deprivation are important factors in this loss (Waaland et al., 1974; Neish et al., 1977). Amounts of biliprotein in tank-cultivated dulse range from 26 mg/g dry weight in dark-red, nitrate-fed plants to <0.5 mg/g dry weight in pale-green, nitrogen-starved plants (Laycock, 1979; Table 10). In comparison to biliprotein, amounts of chlorophyll *a* in healthy plants are usually much lower (Table 10). Owen (1954) reports marginally higher values in the autumn than in winter.

P. palmata contains the usual red algal carotenoids, α- and β-carotene and lutein (Table 10), though zeaxanthin, common to most Rhodophyceae, is totally absent (Bjornland and Aguilar-Martinez, 1976). An early report of taraxanthin (Heilbron et al., 1935) has since been shown to be lutein epoxide (Buchecker et al., 1976). The α-carotene/β-carotene ratio ranges from 1.4 to 2.7 (Larsen and Haug, 1956; Bjornland and Aguilar-Martinez, 1976). As noted previously (see Vitamins) the carotenoid yield depends upon the postharvest treatment of dulse. In order to preserve the carotenoid content, the plant must be carefully and rapidly dried.

NUTRITIONAL ASPECTS

Europeans possibly first ate *P. palmata* after observing that shore-grazing animals favored it over other seaweeds (Kingsbury, 1969). According to Icelandic sagas, "söl" has been eaten since at least the 10th century (Hallsson, 1964). The practice came to North America following European settlement and records show that dulse was commercially harvested in the Bay of Fundy area as early as 1876 (Hay, 1886; Farlow, 1891). Today, the commercial trade of dulse no longer flourishes in Scotland, Ireland or England, while in Iceland the harvest is used primarily as cattle feed (Hallsson, 1964). A dulse industry is still active in Atlantic Canada, where amounts harvested over the past 30 years, principally from Grand Manan Island, New Brunswick, range from 21,000–60,000 kg (dry weight) per year (Ocean Science Associates, 1972; Reppert, 1973; Ffrench, 1974; Neish, 1976).

TABLE 10. PIGMENT COMPOSITION OF *Palmaria palmata*.

Site	Month or season	Bili-protein	Chloro-phyll	Total carote-noids	Carotene	Lutein	Reference
		mg/g dry weight		μg/g dry weight			
Helgoland, Germany	July–Aug.				249–285		Seybold & Egle, 1938
N. Berwick, Scotland	Jan.		0.41	108	37		Owen, 1954
	Sept.		0.63	341	115		
Norway	Feb.–June				197–388		Haug & Larsen, 1956a
Norway	Summer				360		Larsen & Haug, 1956
Norway	April–March				230–420		Haug & Larsen, 1957
Norway	May		3.20	800	α80 β30	240	Bjornland & Aguilar-Martinez, 1976
Tank culture	high nitrate	26					Laycock, 1979
	low nitrate	<0.5					

In North America and Europe the frond is eaten raw as a vegetable substitute or is dried and eaten as a condiment or in powdered form (Schachat and Glicksman, 1959; Hallsson, 1964; Chapman, 1970; Ffrench, 1974; Madlener, 1977). In Table 11 the vitamin and mineral contents of dulse are compared with those of several vegetables, fruits and some snack foods. Dulse contains high concentrations of most minerals, particularly sodium, potassium and chlorine. There is also a relatively high calcium, iron and magnesium content, both on a fresh weight and dry weight basis, and the high iodine content means less than 1 g of dulse is sufficient to supply an adult's daily requirement for this element. In this context, dulse contains all trace elements (Table 2) recognized in human physiological processes.

Dulse also compares favorably with many fruits and vegetables as a source of most vitamins (Table 11). The vitamin A content is nearly 50% that of carrots, while vitamin C averages more than 75% of the value for oranges. However, drying and storage of dulse probably destroys much of the vitamin C content and has an adverse affect on most B vitamins. Despite this, dried dulse contains average amounts of thiamine, riboflavin and niacin in relation to other foods though it is a meager source of vitamin B_6 and biotin.

P. palmata is potentially a useful source of protein. Conventionally, protein is expressed as the total (Kjeldhal) nitrogen value × 6.25. Based on nitrogen analyses, some protein values for *P. palmata* are high (>30% of the dry weight; Table 4) and are undoubtedly overestimated because of the presence of nonprotein nitrogen. However, the bulk of nonprotein nitrogen is in the form of amides, peptides and free amino acids, which could enhance the percentage of utilizable amino acids. The protein content of dulse (20–25%) compares favorably with *Porphyra tenera* (28–36%), a red alga popular in the Orient (Chapman, 1970) and with many other high protein foods such as roast beef (25%), canned salmon (20%) and soybean (30%) (Heinz Co., 1956).

The values in Table 12 show that the essential amino acid content of *P. palmata*

TABLE 11. COMPARISON OF VITAMIN AND MINERAL CONTENTS OF *Palmaria palmata* AND OTHER FOODS (MG PER 100 G EDIBLE PORTION).[a]

	Water g	Minerals										Vitamins						
		Na	K	Ca	Mg	Mn	Fe	Cu	P	S	Cl	A[b] IU	B_1	B_2	B_6	biotin	niacin	C
Palmaria palmata,																		
dried	trace	1,740	7,000	560	450	4.5	50	3.0	360	290	7,500	26,600	0.39	0.52	0.014	0.013	3.8	—
fresh	83	295	1,200	95	75	0.8	8.5	0.5	60	50	1,275	4,500	0.07	0.09	0.002	0.002	0.65	38
Apples,																		
dried	20	—	—	24	—	—	1.4	—	42	—	—	0	0.05	0.08	—	—	0.5	6–60
fresh	84	1	116	6	6	0.08	0.3	0.07	10	5	4	90	0.04	0.02	0.10	—	0.2	3–30
Oranges	87	0.3	170	33	10	0.03	0.4	0.08	23	8	4	190	0.08	0.03	0.12		0.2	49
Raisins	24	31	708	78	6	—	3.3	0.2	129	42	103	50	0.15	0.08	—	—	0.5	trace
Carrots,																		
dried	6	—	—	242	—	—	5.9	—	102	—	—	60,000	0.29	0.28	—	—	3.2	11
fresh	89	48	311	41	17	0.25	0.9	0.11	34	21	42	2,000–12,000	0.13	0.06	0.19	—	0.64	4.3
Peas,																		
dried	10	42	880	73	140	1.99	6.0	0.80	397	196	44	370	0.87	0.29	—	0.017	3.0	2
fresh	75	0.9	380	22	27	0.41	2.0	0.23	118	56	33	690	0.30	0.18	0.18	—	1.9	26
Potatoes,																		
dried	7	—	—	25	—	—	3.7	—	103	—	—	400	0.25	0.10	—	—	4.8	26
fresh	87	0.8	410	14	27	0.17	0.8	0.16	52	29	35	40	0.10	0.04	0.2	—	1.0	23
Potato chips	3	340	880	30	—	—	1.9	—	132	—	—	50	0.18	0.11	—	—	3.2	11
Peanuts,																		
roasted	5	2.0	740	74	167	1.51	1.9	0.27	393	377	4	360	0.30	0.15	12.0	0.03	21.6	0

[a] Vitamin and mineral contents of *P. palmata* are an average of values given in Tables 1–3 and 10. Except for vitamin C, chemical analyses of *P. palmata* have generally been conducted on oven-dried material. The fresh weight data are calculated from dry weight values multiplied by a factor of 0.17 (83% moisture). Since drying results in some loss of vitamins the actual fresh weight values may be higher than those given in the table. Data for other foods from *Documenta Guigy* Scientific Tables. 6th edition. Diem, Conrad (Ed.) Geigy Pharmaceuticals. Ardsley, N.Y. 1962. A zero value (0) = no detectable content of the constituent concerned. A dash (—) = no data available.

[b] Vitamin A activity due to naturally-occurring vitamin A and/or carotenes: 1 IU vitamin A = 0.0006 mg β-carotene or 0.0012 mg α-carotene. Vitamin A content of *P. palmata* calculated on basis of α/β ratio = 2.0.

TABLE 12. COMPARISON OF ESSENTIAL AMINO ACIDS OF *Palmaria palmata* AND WHOLE EGG (G/100 G CRUDE PROTEIN).

Amino acid	*Palmaria*[a]	Whole egg[b]	*Palmaria*/egg
Histidine	1.2	—	—
Isoleucine	3.6	6.6	0.55
Leucine	5.1	8.8	0.58
Lysine	5.6	6.4	0.88
Methionine	2.8 (1.7)[c]	3.1	0.90 (0.55)[c]
Phenylalanine	4.1	5.8	0.70
Threonine	4.2	5.1	0.82
Tryptophan	1.3	1.6	0.81
Valine	5.7	7.3	0.78

[a] Average value calculated from data in Table 5.
[b] Reference protein recommended by the joint FAO/WHO Expert Group. World Health Organization, 1965.
[c] Recalculated omitting data of Schlichting and Purdom, 1969.

compares favorably with whole egg protein, except for somewhat insufficient amounts of leucine, isoleucine and possibly methionine. Dulse had the highest protein quality of several marine algae examined by Larsen and Hawkins (1961) and rates well with vegetables of good nutritional value. This is not inconsistent with results of feeding tests with rats (Bender et al., 1953): dulse was found to have a net protein utilization (protein retained per protein ingested) of 42, as compared to 44 for peas and 49 for corn. Lyman et al. (1956) (Table 5) considered dulse sufficiently rich in lysine to compensate for the marked deficiency of this amino acid in feed grains.

The low fat content of *P. palmata* and other marine algae render them as unimportant sources, though the lipids are easily assimilated by man (Johnston, 1966). As is typical for a red alga, the concentration of sterols in dulse is relatively low (0.001–0.08% of the dry weight). However *P. palmata* could serve as a source of desmosterol for the synthesis of pharmacologically important steroids including progesterone (Bernassau and Fetizon, 1975) and 25-hydroxycholesterol, a key intermediate in the synthesis of the biologically active forms of vitamin D_3, 25-hydroxycholecalciferol and 1α,25-dihydroxycholecalciferol (Morisaki et al., 1972; Partridge et al., 1974).

Some of the carbohydrates in dulse are digestible by man. Ptyalin, diastase and other digestive enzymes readily hydrolyze the α-glucose linkage of floridean starch and floridoside (Johnston, 1966). The β-(1 $\rightarrow$ 3)- and β-(1 $\rightarrow$ 4)-linkages of xylan, resistant to human digestive enzymes, are susceptible to degradation by microorganisms (Howard, 1957), and an early report (Swartz, 1911) of the complete disappearance of dulse xylan from the human alimentary tract seems attributable to such bacterial activity; it is unknown to what extent this hydrolyzed material can serve as a useful nutrient source. Pentose-fermenting bacteria of the rumen enable sheep and cattle to make complete us of xylan and other hemicelluloses (Ann. Rep. Inst. Seaweed Res., 1956; Howard, 1957).

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