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Nutritional composition of edible Hawaiian seaweeds

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Abstract

Fresh seaweeds, both wild and cultivated, are commonly eaten as food in the Hawaiian Islands. Before Western contact, *limu* (seaweed) was a regular part of the diet, and is thought to have contributed vitamins and essential mineral nutrients not found in other staple food items. Twenty-two species of edible Hawaiian macroalgae (6 Chlorophyta, 4 Phaeophyta, 12 Rhodophyta) were analyzed for protein, lipid, carbohydrate, ash, caloric, mineral and vitamin content. *Halymenia formosa* and *Porphyra vietnamensis* ranked highest in total protein content among the species analyzed. Most species contained less than 5% crude lipid, although two *Dictyota* species had over 16% crude lipid based on dry weight. Soluble carbohydrates ranged from 4.5 to 39.9% dry weight. Ash values ranged from 22.4% to 64.2%. *Dictyota sandvicensis* and *Monostroma oxyspermum* had caloric content each over 3000 cal g^{-1} ash-free dry weight. All species contained measurable quantities of 11 essential mineral elements. The majority of Hawaiian seaweeds tested contained β-carotene (vitamin A), and *Enteromorpha flexuosa* contained the highest amount of vitamin C (3 mg g^{-1}).

Introduction

In the Hawaiian Islands prior to Western contact (pre-1779), *limu* (seaweed) was a regular part of the diet and accompanied most meals. Traditionally, Hawaiians mixed a variety of seaweeds with raw and cooked fish, shellfish, raw liver, and cooked meat. *Limu* was also a relish with *poi* (made from cooked, mashed taro) (Abbott, 1996). Seaweeds were the people's spices instead of pepper, oregano, mustard or curry (Fortner, 1978), and served as their vegetables before the introduction of such crops as lettuce, onions, cucumbers, and cabbage (Reed, 1907). Seaweeds, through their collection and preparation, provided a special niche for Hawaiian women, who, until the introduction of Christianity (circa 1819) and the fall of the *kapu* (taboo) system, were forbidden to eat many other nutritious food items, including pork, coconuts, turtles, most varieties of bananas, and several species of fish (Abbott, 1978). Seaweeds were also important to Hawaiian culture in rituals, medicine, legends, and in commerce as a valuable item of exchange between coastal and upland families. Nutritionally, marine macroalgae were probably essential in the traditional Hawaiian diet because the *limu* may have contributed vitamins and essential elements not found in the other two staple items: fish and *poi*. Hawaiian seaweeds may have also provided measurable amounts of protein or dietary fiber.

Approximately 500 species of marine macroalgae are known from the Hawaiian Islands (Abbott, 1999). In 1907, Reed compiled a list of 70 edible marine algae or seaweeds used by Hawaiians for food, 40 of which were in general use. Hawaiian common names varied among islands, and in some cases their exact application is no longer known. At present, only 29 species can be identified by both their Hawaiian and scientific names (Abbott, 1996). About 18 species of Hawaiian seaweeds are collected from the wild for home consumption or for sale. Several are being cultivated on aquaculture farms, and a few species are regularly sold fresh at mainstream supermarkets. In 1990, the commercial harvest of wild (sea catch) seaweed in the Hawaiian Islands, mainly *Asparagopsis taxiformis* (Delile) Trevisan, *Codium reediae* Silva, *Gracilaria coronopifolia* J. Agardh and *Gracilaria parvispora* Abbott, was approximately 2480 kg valued at US$17,456 (Department of Land and Natural Resources, 1990), and by 2001, had more than doubled to 6666 kg worth US$38,849 (Department of Land and Natural Resources, 2002). Today, Hawaiian species of macroalgae are consumed daily by people of many diverse ethnic backgrounds.

The high vitamin and mineral contents of edible seaweeds make them nutritionally valuable (Chapman & Chapman, 1980; Arasaki & Arasaki, 1983). In addition to vitamins and mineral nutrients, seaweeds are also potentially good sources of proteins, polysaccharides, and fiber (Lahaye, 1991; Darcy-Vrillon, 1993). Although the chemical content of edible seaweeds from some regions of the world has been documented, research is long overdue on the nutritive value of Hawaiian seaweeds so commonly collected, bought, sold, cultivated and consumed in the Hawaiian Islands. Reed (1907) reported the chemical composition (water, protein, fat, carbohydrates, ash and calories) of three genera of Hawaiian algae: *Ahnfeltiopsis*, *Ulva* and *Gracilaria*. However, she did not describe the methods used for the analyses except that the material was air-dried and tested by a food chemist for the Territory of Hawai'i. Eight Hawaiian seaweed species were analyzed for carbohydrate content by Schwartz (1911). Miller (1927) reported that *limu ʻeleʻele* (*Enteromorpha* sp.) was fairly high in vitamins A and B, but low in vitamin C, and that *limu līpoa* (*Dictyopteris* sp.) was lacking in all three of these vitamins. The iodine content of twelve Hawaiian seaweed species was determined by Harry (1934), ranging from 1980 μg kg^{-1} in *Hypnea* sp. to 411,000 μg kg^{-1} in *Ahnfeltiopsis concinna* (*limu ʻakiʻaki*). Unfortunately, in all of these studies, no record exists of where or when the specimens were collected, and no voucher specimens were kept to help verify what species were actually tested.

There have been no published quantitative studies on the nutritional composition of Hawaiian seaweeds in over 60 years. The aim of this study is to assess the basic nutritional content of edible marine plants. This information will be essential in the search for additional healthy food sources, and in efforts to assess the value of nearshore natural resources in the Hawaiian Islands.

Materials and methods

Collection

Twenty-two species of seaweeds (Table 1) were collected in food-grade plastic bags (approximately 1 kg fresh weight consisting of at least 20 different thalli from each population), and transported to the laboratory in insulated containers. The list of species includes members of the Chlorophyta, Phaeophyta and Rhodophyta. Some of these species were chosen because they are the most popular edible species in the Hawaiian Islands, e.g. *Codium reediae, Asparagopsis taxiformis* and *Gracilaria coronopifolia*. Other species were selected for screening because historically they were common in the Hawaiian diet, such as *Halymenia formosa* and *Laurencia dotyi*. Some species were chosen because of their potential to contain high levels of vitamins or essential mineral nutrients based on studies of related species in other countries, including members of the genera *Enteromorpha*, *Monostroma*, *Ulva, Sargassum*, *Chondrus,* and *Porphyra*. Samples were identified to genus and species based on examination of morphological and anatomical characteristics, and using taxonomic references (Magruder, 1988; Coppejans & Prud'homme van Reine, 1992; Abbott, 1999; De Clerk, 1999). Voucher specimens were selected, photographed, and prepared as dried herbarium specimens deposited in the Bishop Museum Herbarium in Honolulu (BISH). Spinach (*Spinacia oleracea* L.) was purchased from a local grocery store, processed and analyzed simultaneously with the seaweed samples, and served as a familiar vegetable comparison to the seaweeds.

Sample preparation

Within 6 hours of collection, fresh plants were thoroughly washed three times in filtered seawater. Any epiphytic algae, invertebrates, sand or debris were removed. Samples were divided into portions (50–200 g each), spun in a salad spinner for 30 s to remove excess water, and then weighed on a top-loading balance to 0.01g (wet weight). All portions were placed on aluminum foil trays, and dried to a constant weight at 60 °C in an air oven. The key part of this procedure is to dry the sample to a constant weight at a temperature that causes the least modification of chemical

Table 1. Hawaiian edible seaweed species collected and analyzed for nutritional composition. Hawaiian names based on Abbott (1996). RHSF = Royal Hawaiian Sea Farms, KKHH = Ke Kua'aina Hanauna Hou Farm

Species	Hawaiian name	Collection	Location, Island	Date
Chlorophyta				
Caulerpa lentillifera J. Agardh	–	NC043	Hilton Waikaloa, Hawai'i	11.x.02
Codium reediae Silva	*Limu Wāwae'iole*	NC030	RHSF, Hawai'i	12.iii.02
Codium reediae Silva	*Limu Wāwae'iole*	NC034	Kanahā Beach Park, Maui	21.iii.02
Enteromorpha flexuosa (Wulfen) J. Agardh	–	NC020	North Shore, O'ahu	31.i.02
Enteromorpha intestinalis (L.) Nees	–	NC005	Leleiwi, Hawai'i	25.x.01
Monostroma oxyspermum (Kütz.) Doty	–	NC004	Leleiwi, Hawai'i	25.x.01
Ulva fasciata Delile	*Limu Pālahalaha*	NC019	North Shore, O'ahu	31.i.02
Ulva fasciata Delile	*Limu Pālahalaha*	NC035	Mā'alaea Bay, Maui	21.iii.02
Phaeophyta				
Dictyota acutiloba J. Agardh	*Limu Alani*	NC017	Hale'iwa, O'ahu	31.i.02
Dictyota sandvicensis Kütz.	*Limu Alani*	NC016	Hale'iwa, O'ahu	31.i.02
Sargassum echinocarpum J.Agardh	*Limu Kala*	NC027	Onekahakaha, Hawai'i	1.iii.02
Sargassum obtusifolium J.Agardh	*Limu Kala*	NC028	Onekahakaha, Hawai'i	1.iii.02
Rhodophyta				
Ahnfeltiopsis concinna (J.Ag.) Silva et DeCew	*Limu 'Aki'aki*	NC002	Onekahakaha, Hawai'i	16.x.01
Ahnfeltiopsis concinna (J.Ag.) Silva et DeCew	*Limu 'Aki'aki*	NC021	Kona, Hawai'i	10.ii.02
Asparagopsis taxiformis (Delile) Trevis.	*Limu Kohu*	NC038	Kona, Hawai'i	21.iv.02
Asparagopsis taxiformis (Delile) Trevis.	*Limu Kohu*	NC039	Leleiwi, Hawai'i	25.v.02
Chondrus ocellatus Holmes	–	NC015	Leleiwi, Hawai'i	3.i.02
Eucheuma denticulatum (Burman) Collins et Hervey	–	NC022	Kāne'ohe Bay, O'ahu	13.ii.02
Gracilaria coronopifolia J.Agardh	*Limu Manauea*	NC012	RHSF, Hawai'i	20.xi.01
Gracilaria parvispora Abbott	–	NC031	KKHH, Moloka'i	12.iii.02
Gracilaria salicornia (C. Agardh) Dawson	–	NC006	Onekahakaha, Hawai'i	24.x.01
Halymenia formosa Harv. ex Kütz.	*Limu Lepe-o-Hina*	NC029	Mahai'ula Bay, Hawai'i	9.iii./02
Laurencia dotyi Saito	*Limu Līpe'epe'e*	NC042	Lualualei, O'ahu	5.vi.02
Laurencia mcdermidiae Abbott	–	NC041	Lualualei, O'ahu	5.vi.02
Laurencia nidifica J. Agardh	*Limu Mane'one'o*	NC040	Lualualei, O'ahu	5.vi.02
Porphyra vietnamensis Tanaka et Pham	*Limu Pahe'e*	NC026	Onekahakaha, Hawai'i	28.ii.02

composition. The dried samples were then ground into a fine powder (to pass through a 1 mm sieve) using a coffee grinder or analytical mill (IKA^{TM} A11), and then stored in air-tight labeled glass jars in a refrigerator at 4 °C. All chemical analyses were conducted in triplicate on dried ground material weighed on a Mettler balance with readability to 0.1 mg, except in ash determination for which five replicates were used. All values were reported relative to the dry weight of the seaweed. Mean values and standard error (SE = standard deviation/square root of the sample size) were calculated.

Water content of fresh plants

The water content of the fresh material was calculated by subtracting the dried sample weight from the spun wet weight for each of the portions of the total sample.

Ash determination

Ash content was determined by heating the samples for 4 h at 500 °C following the Association of Official Analytical Chemists (1995) methods as modified by Robledo and Freile Pelegrin (1997).

Total protein analysis

The Lowry method was used for protein determination (Lowry et al., 1951; Harrison & Thomas, 1988). The samples were digested in 1 N NaOH, and then allowed to react with an alkaline copper citrate solution and

Folin-Ciocalteau phenol reagent to measure protein concentration colorimetrically based on absorptions at 660 nm in a Beckman Coulter DU 640 spectrophotometer, and compared to a bovine serum albumin standard.

Soluble carbohydrate content
Soluble carbohydrates were extracted from samples in 5% trichloroacetic acid, and concentrations determined by the phenolic sulfuric acid colorimetric method outlined in Dubois et al. (1956) and used on Mexican seaweeds by Robledo & Freile Pelegrin (1997). Percent soluble carbohydrate was calculated based on absorptions at 490 nm in a Beckman Coulter DU 640 spectrophotometer, and compared to a glycogen standard.

Crude lipid analysis
A gravimetric method was used similar to that of Chan et al. (1997) in which crude lipid was extracted in a chloroform-methanol (2:1, v/v) mixture, then purified according to Folch et al. (1957), and evaporated to dryness under a stream of filtered N_2 gas, and weighed.

Caloric value
Pressed pellets of 100–200 mg of dried powder were combusted in a Parr 1425 Semimicro Calorimeter standardized with benzoic acid. Total calories were calculated on an ash-free basis (Carefoot, 1985).

Element analysis
Samples of dried ground material were sent to an independent laboratory for analysis (Waters Agricultural Laboratories, Inc. in Georgia, USA), which uses the official methods of analysis of the Association of Official Analytical Chemists (AOAC) and the Association of Florida Phosphate Chemists. Five of the 22 species were not sent for testing due to insufficient dried material.

Vitamin A, B complex and C analysis
Samples were sent to an independent chemical analysis laboratory (Industrial Labs in Denver, Colorado, USA), which uses methodologies specified by the Association of Official Analytical Chemists, the Institute for Nutraceutical Advancement, the Food and Drug Administration, and the American Association of Cereal Chemists. Vitamin B complex and vitamin C contents were determined using HPLC, and β-carotene content was measured spectrophotometrically. Because of insufficient amount of dried powder, these tests were not run on 5 of the 22 species. *Halymenia formosa* was not analyzed for vitamins because the 'gumminess' of this seaweed interfered with the assays.

Results

The proximate composition and caloric content of the 22 species of edible Hawaiian seaweeds are shown in Table 2. The water content of fresh material ranged from 68.0 to 94.3%. Ash was the most abundant component of dried material in all species, even though none are calcareous. The greatest range in ash values occurred in the Chlorophyta (Figure 1): with values ranging from 22.4% d. wt in *Monostroma oxyspermum* to 64.3% d. wt in *Codium reediae.* Values for the ash content of the Phaeophyta showed a narrower range. The highest values for total protein content were found in two red seaweed species: *Halymenia formosa* (21.2%) and *Porphyra vietnamensis* (16.5%) (Figure 2). The lowest protein values were in *Laurencia* species. Protein contents varied within species between populations (i.e. *Codium reediae*, *Ahnfeltiopsis concinna*, *Asparagopsis taxiformis*). Soluble carbohydrate composition showed the greatest range among the Chlorophyta: *Codium reediae* had the lowest value (4.5%) and *Enteromorpha flexuosa* the highest value (39.9%) (Figure 3). All four brown seaweed species contained low levels of soluble carbohydrates. Values for soluble carbohydrates displayed little intraspecific and intrageneric variation. The lipid content of most species was low, especially the Rhodophyta (all $< 5\%$) (Figure 4). Two species had a markedly higher crude lipid content, *Dictyota sandvicensis* (20.2%) and *D. acutiloba* (16.1%). *Dictyota sandvicensis* and *Monostroma oxyspermum* had the highest energy values, each with over 3000 cal g^{-1} ash-free d. wt, followed by *Porphyra vietnamensis* with 2771 cal g^{-1} ash-free d. wt (Figure 5). *Codium reediae* showed the lowest caloric content.

Values for vitamin A, vitamin B complex and vitamin C analyses are listed in Table 3. Vitamin A (β-carotene) was the only vitamin that consistently appeared in measurable amounts. *Porphyra vietnamensis* contained the highest content of β-carotene (430 IU g^{-1} d. wt) and *Gracilaria coronopifolia* the least (15 IU g^{-1} d. wt). Only *Enteromorpha*, *Monostroma*, *Ulva* and *Eucheuma* showed detectable levels of vit-

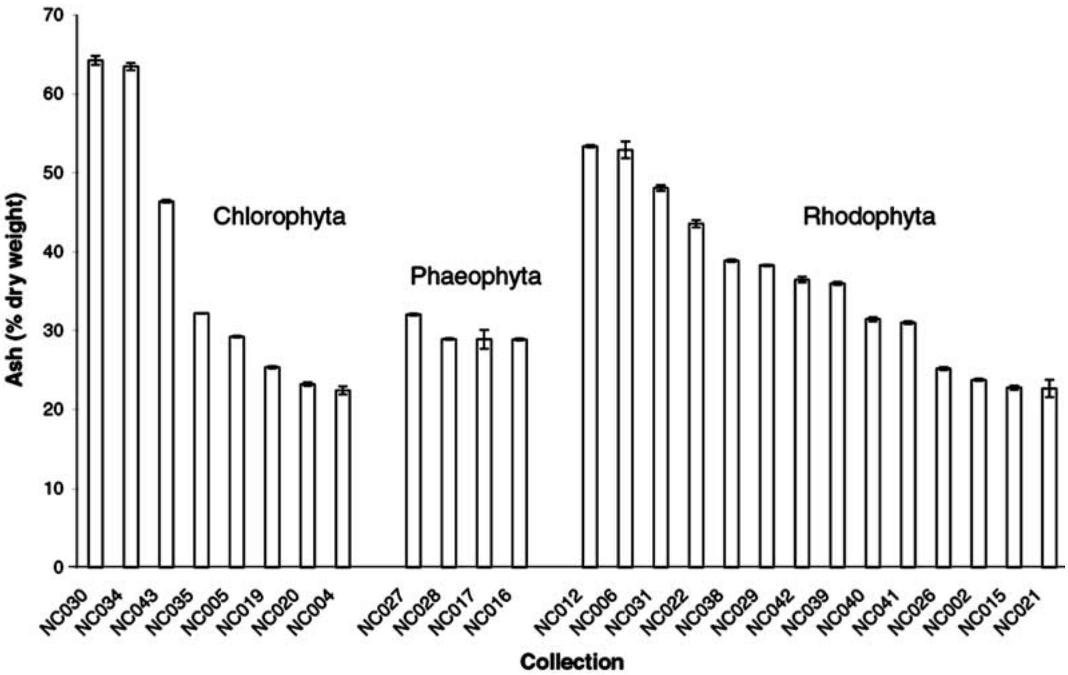


Figure 1. Ash content (% d. wt) of Hawaiian edible seaweeds grouped by division. Mean and SE. n = 5.

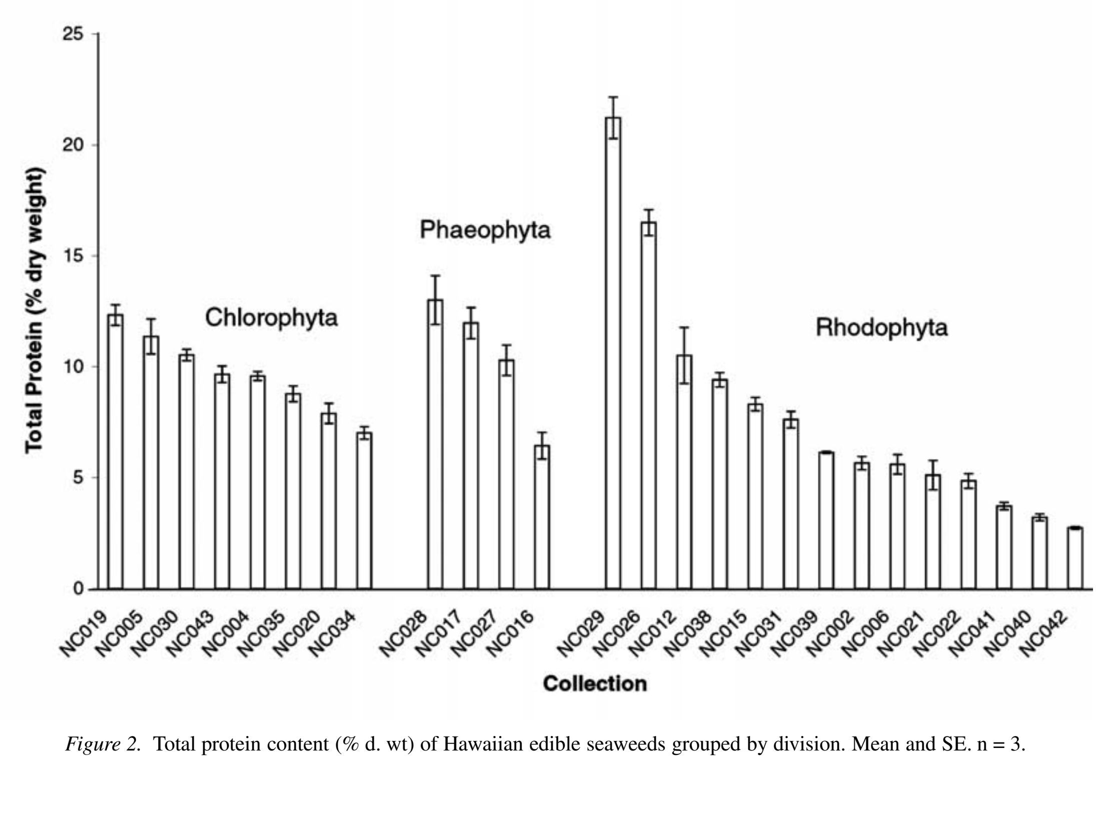


Figure 2. Total protein content (% d. wt) of Hawaiian edible seaweeds grouped by division. Mean and SE. n = 3.

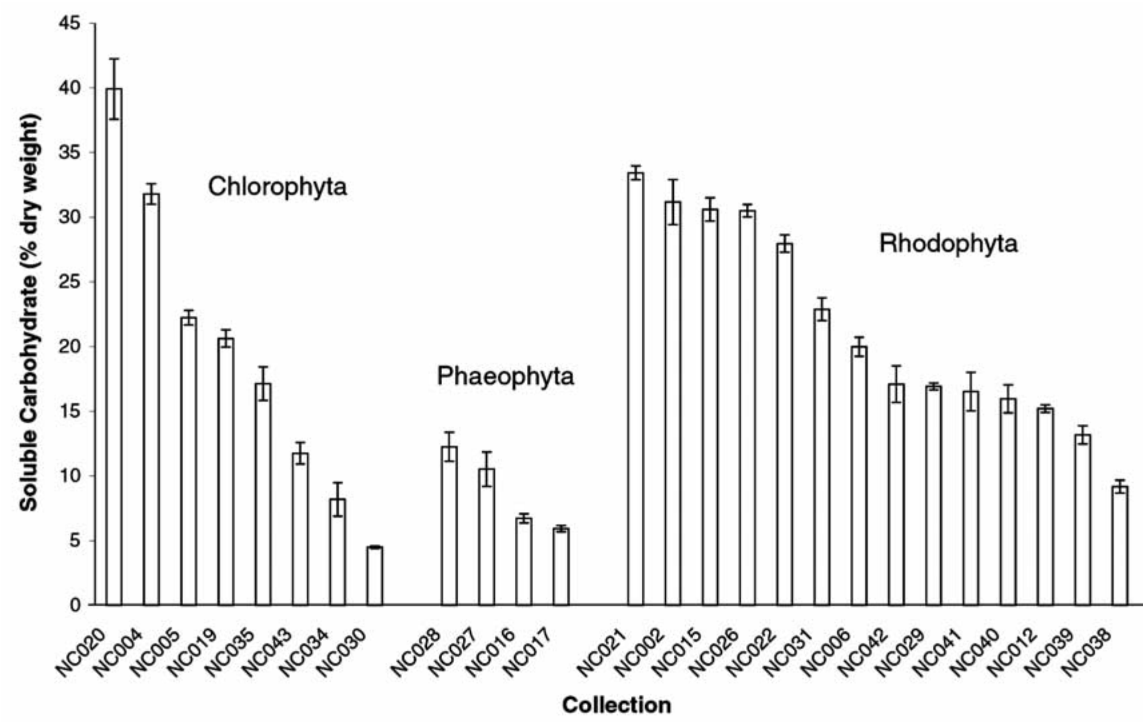


Figure 3. Soluble carbohydrate content (% d. wt) of Hawaiian edible seaweeds grouped by division. Mean and SE. n = 3.

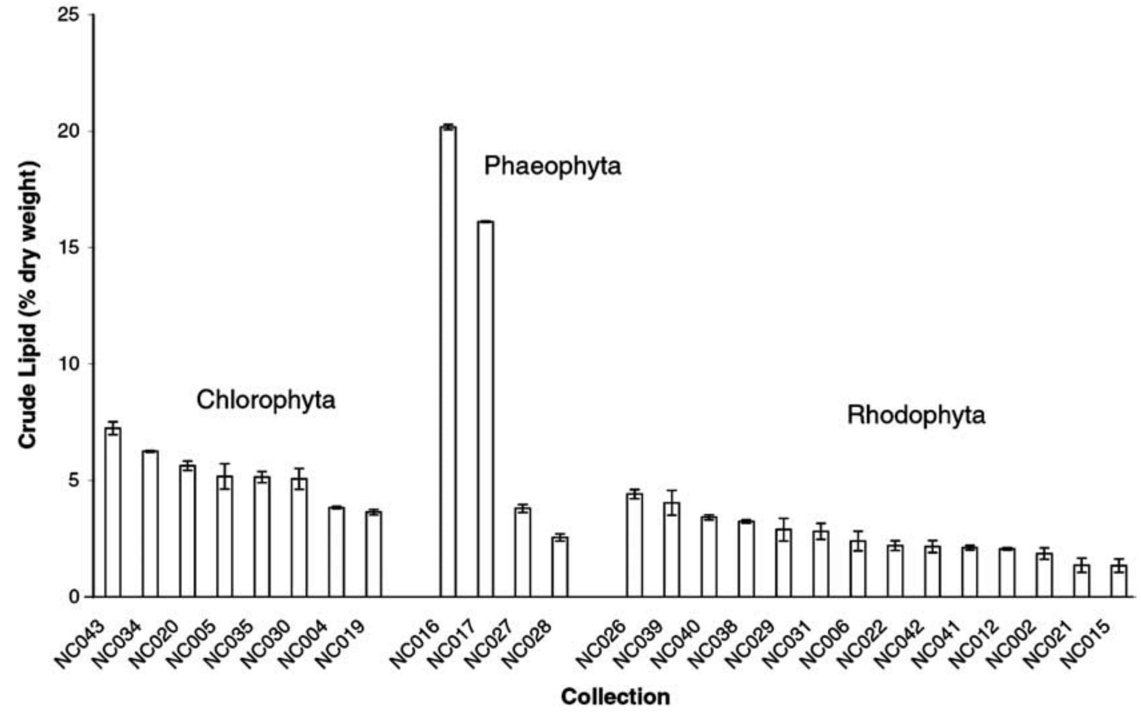


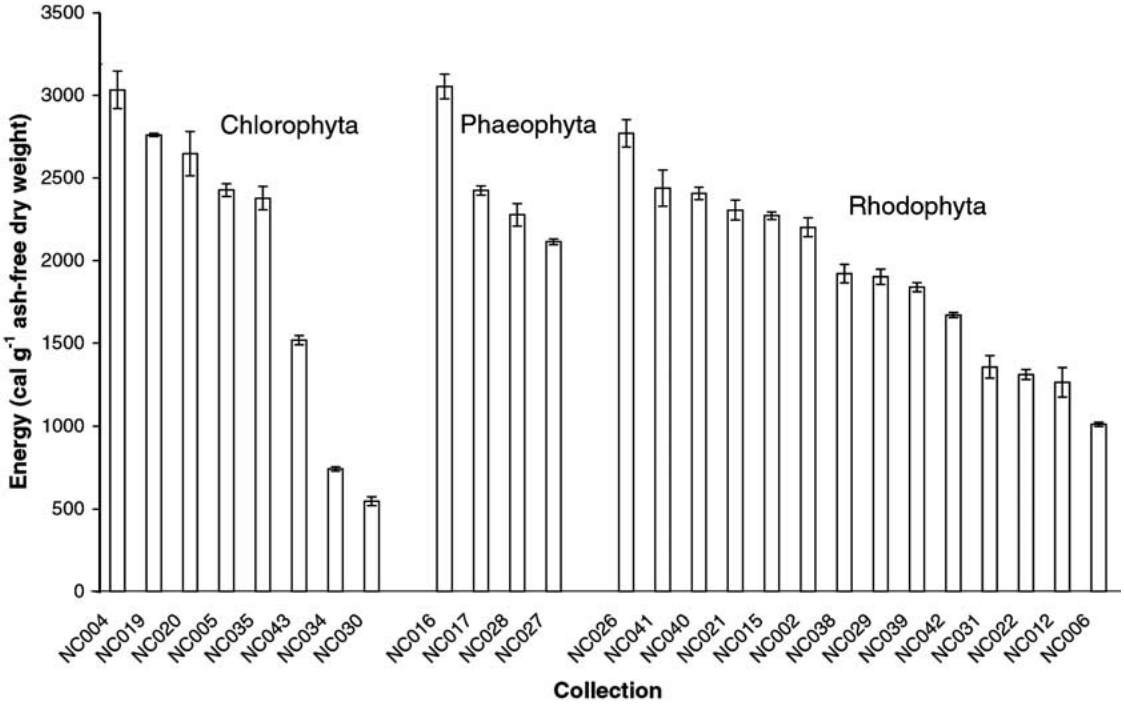
Figure 4. Crude lipid content (% d. wt) of Hawaiian edible seaweeds grouped by division Mean and SE. n = 3.

Table 2. Proximate composition and caloric content of Hawaiian edible macroalgae and spinach. Water content is relative to total fresh weight. Ash, protein, carbohydrate, lipid and energy contents are relative to total dry weight. Mean ± SE: n = 3, except for ash, where n = 5

Species	Collection	Water %	Ash %	Total protein %	Sol. carbo. %	Crude lipid %	Energy cal g^{-1}
Chlorophyta							
Caulerpa lentillifera	NC043	94.0 ± 0.1	46.4 ± 0.2	9.7 ± 0.4	11.8 ± 0.8	7.2 ± 0.3	1517 ± 27.6
Codium reediae	NC030	94.3 ± 0.1	64.3 ± 0.6	10.5 ± 0.3	4.5 ± 0.1	5.1 ± 0.5	547 ± 27.4
Codium reediae	NC034	93.9 ± 0.1	63.5 ± 0.5	7.0 ± 0.3	8.2 ± 1.3	6.3 ± 0.1	741 ± 12.5
Enteromorpha flexuosa	NC020	87.6 ± 0.3	23.2 ± 0.2	7.9 ± 0.5	39.9 ± 2.3	5.6 ± 0.2	2646 ± 134.8
Enteromorpha intestinalis	NC005	93.6*	29.2 ± 0.1	11.4 ± 0.8	22.2 ± 0.6	5.2 ± 0.5	2427 ± 38.5
Monostroma oxyspermum	NC004	92.9 ± 0.6	22.4 ± 0.5	9.6 ± 0.2	31.8 ± 0.8	3.8 ± 0.1	3033 ± 113.3
Ulva fasciata	NC019	83.4 ± 0.4	25.4 ± 0.1	12.3 ± 0.5	20.6 ± 0.7	3.6 ± 0.1	2761 ± 9.9
Ulva fasciata	NC035	86.1 ± 0.2	32.2 ± 0.1	8.8 ± 0.4	17.1 ± 1.3	5.1 ± 0.2	2378 ± 71.1
Phaeophyta							
Dictyota acutiloba	NC017	88.5 ± 0.8	28.9 ± 1.2	12.0 ± 0.7	5.9 ± 0.2	16.1 ± 0.1	2424 ± 28.2
Dictyota sandvicensis	NC016	86.4 ± 0.3	28.9 ± 0.1	6.4 ± 0.6	6.7 ± 0.4	20.2 ± 0.1	3054 ± 75.1
Sargassum echinocarpum	NC027	86.4 ± 0.1	32.0 ± 0.1	10.3 ± 0.7	10.5 ± 1.3	3.8 ± 0.2	2114 ± 17.4
Sargassum obtusifolium	NC028	84.3 ± 0.1	28.9 ± 0.1	13.0 ± 1.1	12.3 ± 1.1	2.6 ± 0.2	2277 ± 67.8
Rhodophyta							
Ahnfeltiopsis concinna	NC002	89.9 ± 0.2	23.8 ± 0.1	5.7 ± 0.3	31.2 ± 1.8	1.9 ± 0.2	2202 ± 56.5
Ahnfeltiopsis concinna	NC021	68.0 ± 0.2	22.7 ± 1.1	5.1 ± 0.7	33.4 ± 0.5	1.4 ± 0.3	2305 ± 60.1
Asparagopsis taxiformis	NC038	87.6*	38.9 ± 0.2	9.4 ± 0.3	9.2 ± 0.5	3.2 ± 0.1	1920 ± 55.6
Asparagopsis taxiformis	NC039	90.3 ± 0.3	36.0 ± 0.2	6.1 ± 0.1	13.2 ± 0.7	4.0 ± 0.5	1838 ± 27.7
Chondrus ocellatus	NC015	77.6 ± 0.5	22.8 ± 0.2	8.3 ± 0.3	30.6 ± 0.9	1.3 ± 0.3	2271 ± 23.4
Eucheuma denticulatum	NC022	89.9 ± 0.2	43.6 ± 0.5	4.9 ± 0.3	28.0 ± 0.7	2.2 ± 0.2	1313 ± 29.7
Gracilaria coronopifolia	NC012	89.4 ± 0.1	53.4 ± 0.1	10.5 ± 1.3	15.2 ± 0.3	2.1 ± 0.1	1266 ± 90.2
Gracilaria parvispora	NC031	90.4 ± 0.1	48.1 ± 0.4	7.6 ± 0.4	22.9 ± 0.9	2.8 ± 0.3	1358 ± 66.4
Gracilaria salicornia	NC006	90.4*	52.9 ± 1.1	5.6 ± 0.4	20.0 ± 0.7	2.4 ± 0.4	1012 ± 12.9
Halymenia formosa	NC029	92.7 ± 0.5	38.3 ± 0.1	21.2 ± 0.9	16.9 ± 0.3	2.9 ± 0.5	1901 ± 46.1
Laurencia dotyi	NC042	89.8*	36.5 ± 0.3	2.7 ± 0.1	17.1 ± 1.4	2.2 ± 0.3	1669 ± 15.0
Laurencia mcdermidiae	NC041	90.7 ± 0.1	31.0 ± 0.2	3.7 ± 0.2	16.5 ± 1.5	2.1 ± 0.1	2437 ± 110.0
Laurencia nidifica	NC040	88.8 ± 0.2	31.4 ± 0.3	3.2 ± 0.2	16.0 ± 1.1	3.4 ± 0.1	2407 ± 37.5
Porphyra vietnamensis	NC026	90.3 ± 0.3	25.2 ± 0.2	16.5 ± 0.6	30.5 ± 0.5	4.4 ± 0.2	2770 ± 81.7
Standard							
Spinacia oleracea	NC00S	92.2*	29.0 ± 0.4	20.3 ± 0.2	2.9 ± 0.1	10.7 ± 0.2	2561 ± 64.6

* Standard error not calculated for this analysis.

amin C. Thiamine (vitamin B_1), riboflavin (vitamin B_2), niacin (B_3), and niacinamide were rarely detectable. The essential major and trace elements contained in 17 species are listed in Table 4. Phosphorus and calcium were present in low concentrations in all species tested. Potassium was the most abundant essential element, followed by sulfur. *Gracilaria coronopifolia* contained the highest potassium content (22.1% d. wt) while *Caulerpa lentillifera* the lowest (0.70% d. wt). Concentrations were similar within species (i.e. *Codium reediae*, *Ulva fasciata* and *Ahnfeltiopsis concinna*), and within genera (i.e. *Sargassum* and *Dictyota*). Within the Phaeophyta, *Dictyota sandvicensis* (608 μg g^{-1} d. wt) and *D. acutiloba* (438 μg g^{-1} d. wt) both exhibited the highest amounts of iron. Among the red algae, *Gracilaria salicornia* was found to be richest in iron (356 μg g^{-1} d. wt) and boron (404 μg g^{-1} d. wt); *Chondrus ocellatus* showed the highest zinc (284 μg g^{-1} d. wt) and copper (39 μg g^{-1} d. wt) values.



pcpc

Figure 5. Ash-free calorific content (calories g^{-1} ash-free d. wt) of Hawaiian edible seaweeds grouped by division. Mean and SE. n = 3.

Table 3. Vitamin A, vitamin B complex, and vitamin C content of Hawaiian edible seaweeds. All values are based on dry weight. Blank values indicate that vitamin content was not detected at the method detection limit. Analyses conducted by Industrial Labs

Species	Collection	β-Carotene IU g^{-1}	Niacin mg g^{-1}	Niacinamide mg g^{-1}	Riboflavin mg g^{-1}	Thiamine mg g^{-1}	Vitamin C mg g^{-1}
Chlorophyta							
Caulerpa lentillifera	NC043	160	2.00	–	–	–	–
Codium reediae	NC030	27	–	–	0.004	–	–
Codium reediae	NC034	36	1.07	–	–	–	–
Enteromorpha flexuosa	NC020	54	–	–	–	–	3.0
Monostroma oxyspermum	NC004	70	–	0.70	–	–	1.3
Ulva fasciata	NC019	180	–	–	0.010	–	2.2
Ulva fasciata	NC035	70	0.66	–	–	–	–
Phaeophyta							
Sargassum echinocarpum	NC027	97	0.09	–	–	–	–
Sargassum obtusifolium	NC028	60	–	–	–	0.06	–
Rhodophyta							
Ahnfeltiopsis concinna	NC002	16	–	–	–	–	–
Ahnfeltiopsis concinna	NC021	40	–	–	–	–	–
Chondrus ocellatus	NC015	30	0.06	–	–	0.09	–
Eucheuma denticulatum	NC022	28	–	–	–	–	2.0
Gracilaria coronopifolia	NC012	15	0.70	–	–	–	–
Gracilaria parvispora	NC031	–	–	–	0.006	–	–
Gracilaria salicornia	NC006	60	–	–	–	–	–
Porphyra vietnamensis	NC026	430	–	–	–	–	–

Table 4. Comparison of selected essential mineral element content in Hawaiian edible macroalgae based on dry weight. Analyses conducted by Waters Agricultural Laboratories, Inc.

Species	Collection	N %	P %	K %	Mg %	Ca %	S %	B $\mu g\ g^{-1}$	Zn $\mu g\ g^{-1}$	Mn $\mu g\ g^{-1}$	Fe $\mu g\ g^{-1}$	Cu $\mu g\ g^{-1}$
Chlorophyta												
Caulerpa lentillifera	NC043	2.39	0.16	0.70	1.65	0.95	1.55	70	17	10	167	6
Codium reediae	NC030	1.80	0.11	0.77	1.72	0.94	4.35	78	3	26	91	1
Codium reediae	NC034	1.94	0.12	0.82	1.70	0.92	3.94	74	3	26	196	1
Enteromorpha flexuosa	NC020	1.27	0.10	1.60	1.17	0.74	3.20	164	6	5	104	3
Monostroma oxyspermum	NC004	2.58	0.35	3.14	1.36	0.58	6.23	52	32	10	142	28
Ulva fasciata	NC019	3.62	0.22	2.87	2.19	0.47	5.24	77	9	12	86	5
Ulva fasciata	NC035	3.74	0.22	3.15	2.94	0.39	5.51	68	6	17	141	1
Phaeophyta												
Dictyota acutiloba	NC017	2.87	0.16	7.26	1.36	1.03	2.21	95	16	12	438	5
Dictyota sandvicensis	NC016	2.69	0.13	5.57	0.91	1.81	1.66	172	13	21	608	5
Sargassum echinocarpum	NC027	1.53	0.14	9.50	1.16	1.31	1.16	106	7	6	92	11
Sargassum obtusifolium	NC028	1.67	0.14	7.90	0.93	1.50	1.41	102	16	15	129	9
Rhodophyta												
Ahnfeltiopsis concinna	NC002	1.46	0.10	3.01	0.75	0.44	7.48	310	22	72	86	3
Ahnfeltiopsis concinna	NC021	1.46	0.11	3.00	0.88	0.49	8.07	320	10	16	72	3
Chondrus ocellatus	NC015	2.62	0.27	2.26	0.92	0.44	7.16	136	284	70	142	39
Eucheuma denticulatum	NC022	0.93	0.08	12.40	0.76	0.45	7.25	212	7	9	112	2
Gracilaria coronopifolia	NC012	3.04	0.38	22.16	0.34	0.18	5.25	244	42	57	136	2
Gracilaria parvispora	NC031	1.48	0.15	16.00	0.49	0.38	3.99	242	8	48	198	3
Gracilaria salicornia	NC006	1.12	0.17	17.97	0.51	0.73	3.95	404	16	10	356	5
Halymenia formosa	NC029	3.29	0.21	4.60	1.25	0.53	5.50	79	22	11	66	4
Porphyra vietnamensis	NC026	2.47	0.25	3.97	0.78	0.29	2.18	32	11	41	154	7

Discussion

Measurable differences in nutritional composition were apparent among the 22 species analyzed. Variation within species was slight. The proximate, mineral and vitamin compositions of the Hawaiian species were comparable to values reported from other parts of the world (see below).

Ash values for these Hawaiian species were similar to values for non-calcified species reported in other studies. However, Hawaiian *Porphyra vietnamensis* had a higher ash content than reported for most other *Porphyra* populations (Portugal et al., 1983; Darcy-Vrillon, 1993; Fan et al., 1993; Cho et al., 1995; Kennish & Williams, 1997). Similarly, the ash values for Hawaiian *Gracilaria* species were higher than the published values for *Gracilaria* from other parts of the world (Burkholder et al., 1971; Portugal et al., 1983; Fan et al., 1993; Robledo & Freile Pelegrin, 1997; Norziah & Ching, 2000).

Halymenia formosa and *Porphyra vietnamensis* ranked highest in total protein content among the Hawaiian species analyzed. These findings were consistent with other studies that reported high protein values for *Porphyra* species (11–44.5%), and *Halymenia* species (8.6–20.9%) (Portugal et al., 1983; Darcy-Vrillon, 1993; Fan et al., 1993; Cho et al., 1995; Kennish & Williams, 1997). Many researchers have assessed protein content of their algal samples by measuring nitrogen (N) content and multiplying it by 6.25. However, nitrogen in seaweeds is a component of many types of molecules in addition to protein, such as DNA and ATP. In comparing results of this study to those obtained by the same Lowry method, which is specific for protein, similar values were seen (Montgomery & Gerking, 1980; Robledo & Freile Pelegrin, 1997; Zemke-White & Clements, 1999). Direct comparisons between Hawaiian species and conspecifics elsewhere were possible for two species: *Ahnfeltiopsis* (= *Ahnfeltia*) *concinna,* and *Eucheuma denticulatum*, and yielded protein values with differences of less than 2% (Montgomery & Gerking, 1980). Although the methodology for protein analysis was not specified in Reed (1907), the protein content values of Hawaiian *Ahnfeltiopsis concinna*, *Gracilaria coronopifolia*, and *Ulva fasciata* showed a similar range (5.6–14.9%) to values for these species in this study.

When comparing carbohydrate content of seaweeds, methods and semantics become an issue. Some researchers measured 'total carbohydrates,' others 'soluble carbohydrates,' still others 'sugars and starches, etc.' In some studies, the carbohydrate content was calculated by subtracting the ash, protein, lipid and moisture from 100%, and in others a colorimetric method was used for analysis. Arasaki & Arasaki (1983) stated that carbohydrates comprise 50–60% of the dry weight of seaweeds. This study measured soluble carbohydrates colorimetrically, and found concentrations ranging from 4.5–39.9% d. wt. Similarly, Kennish & Williams (1997) reported 8.1–33.7% soluble carbohydrates with values for *Enteromorpha*, *Ulva* and *Porphyra* that closely matched ours. Reed (1907) reported non-fiber carbohydrate content (computed by subtraction) of three Hawaiian seaweeds, *Ahnfeltiopsis concinna* (54.9%), *Gracilaria coronopifolia* (58.4%), and *Ulva fasciata* (50.6%), all of which were higher than in this study.

Seaweeds are known to possess low levels of lipids (Arasaki & Arasaki, 1983; Darcy-Vrillon, 1993). Like carbohydrate analyses, a variety of methods have been used to assay total lipids, crude lipids, fats, or the 'ether extract' of seaweeds. Meaningful comparisons can only be made with results from studies that utilize the same procedures. In this study and comparable studies that follow Folch's gravimetric methods and report crude lipid values, most seaweeds consistently contained less than 5% d. wt crude lipid (Montgomery & Gerking, 1980; Qasim, 1986; Chan et al., 1997; Zemke-White & Clements, 1999).

Few studies have examined the caloric content of edible seaweeds. In this study, the values obtained for Hawaiian species of *Caulerpa*, *Enteromorpha*, *Ulva*, *Dictyota*, *Sargassum*, *Ahnfeltiopsis, Eucheuma,* and *Porphyra* agreed with energy values reported for congeneric species (Montgomery & Gerking, 1980; Naidu et al., 1993; Kennish & Williams, 1997). In this study, as in other studies, *Dictyota* and *Porphyra* ranked high (above 2700 cal g^{-1} ash-free d. wt) in caloric content.

According to Arasaki & Arasaki (1983), minerals and vitamins are present in high levels in macroalgae. The majority of the Hawaiian seaweeds tested contained β-carotene (vitamin A) in amounts similar to those reported for comparable genera. Vitamin C occurred in higher concentrations for Hawaiian *Enteromorpha* (3.0 mg g^{-1}) and *Ulva* (2.2 mg g^{-1}) than Japanese *Enteromorpha* (0.10 mg g^{-1}) and *Ulva* (0.10 mg g^{-1}) (Arasaki & Arasaki, 1983). Concentrations of most major essential elements in Hawaiian seaweeds were similar to those reported for congeneric species in other studies (Fan et al., 1993; Cho et al., 1995; Chan et al., 1997; Robledo & Freile Pelegrin, 1997). However, potassium concentrations recorded in Hawaiian *Eucheuma* and *Gracilaria* species were notably higher than values reported for other species in this study and previous studies. Yet, these high potassium concentrations were corroborated by a study in which four Hawaiian *Gracilaria* species from 11 different populations on three different islands consistently contained levels of potassium over 16% d. wt (McDermid & Stuercke, in press). Trace elements varied among Hawaiian seaweeds, and the values often differed greatly in comparison to other published reports. Cho et al. (1995) documented that the trace mineral content of Korean seaweeds differed among sites, and fluctuated monthly at each site.

Spinach is known to have high vitamin, iron, and calcium content (Haytowitz & Matthews, 1984). The analyses of spinach, used as an internal control in this study, showed that ash and water values were well within the range of the macroalgae (Table 2). The protein content of spinach (20.3%) exceeded that in all of the Hawaiian seaweeds, except *Halymenia formosa* (21.2%). Soluble carbohydrate content of spinach (2.9%) was below the lowest algal value. Hawaiian *Porphyra vietnamensis* had 6.4 times more β-carotene than reported for spinach (67 IU g^{-1}), and all Hawaiian seaweeds in this study exceeded the vitamin C content of spinach (Haytowitz & Matthews, 1984).

Asparagopsis taxiformis and *Gracilaria coronopifolia* were two of the seaweeds most favored by ancient Hawaiians. Today, aquacultured *Gracilaria* species (*G. coronopifolia*, *G. parvispora*, *G. tikvahiae* McLachlan) and *Codium reediae*, and wild-harvested *A. taxiformis* are the seaweeds most often sold in markets and used in prepared dishes. None of these showed unusually high nutritional values. Perhaps their appeal to humans is due to other attributes, such as *Gracilaria's* succulent, slightly crunchy texture or *Asparagopsis'* piquant flavor or *Codium's* rich green color. Based on the nutritional qualities found in *Porphyra vietnamensis, Halymenia formosa* and

Monostroma oxyspermum, these native Hawaiian seaweed species not currently in cultivation might be considered for future aquaculture.

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