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NUTRITIONAL COMPOSITION OF MARINE PLANTS IN THE DIET OF THE GREEN SEA TURTLE (*CHELONIA MYDAS*) IN THE HAWAIIAN ISLANDS

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ABSTRACT

In the Hawaiian Islands, seaweeds and seagrasses are eaten by green turtles, *Chelonia mydas* Linnaeus. Sixteen macroalgal species (7 Chlorophyta, 2 Phaeophyta, 7 Rhodophyta), two seagrass species, and multi-specific algal turf from turtle foraging areas on four different islands were analyzed for proximate (protein, lipid, carbohydrate), water, ash, energy, amino acid, vitamin, and mineral content. *Pterocladiella capillacea* (Gmelin) Santelices and Hommersand, a prominent dietary item, and *Rhizoclonium implexum* (Dillwyn) Kützing, an infrequently consumed species, ranked highest in total protein content. Most species contained < 10% crude lipid. Soluble carbohydrates ranged from 3.2%–39.9% dry weight. Ash values ranged from 13.7%–81.4% dry weight. Energy content of *P. capillacea* was over 14 kJ g^{-1} ash-free dry weight. All species tested contained measurable quantities of 11 minerals. Vitamin A (β-carotene) was detected in all marine plants tested; most contained Niacin (B_3); and *Enteromorpha flexuosa* (Wulfen) J. Agardh had the highest amount of vitamin C (3 mg g^{-1}). Samples contained measurable amounts of all essential amino acids, except for tryptophan. These data provide new information about Hawaiian green turtle feeding ecology and factors that may influence somatic growth rates.

The green turtle (*Chelonia mydas* Linnaeus) is the most common sea turtle and the largest marine herbivore in the Hawaiian Islands (Balazs, 1980; Balazs and Chaloupka, 2004a). Over 275 species of marine algae, and two seagrass species have been reported in crop and stomach samples from Hawaiian green turtles (Balazs, 1980; Balazs et al., 1987; Russell and Balazs, 1994a, 2000; Russell et al., 2003). Ten seaweed genera and one seagrass genus form the majority of the green turtle diet in the Hawaiian Islands (Arthur, 2005). Green turtles in the Hawaiian Islands show fidelity to foraging grounds on specific reefs (Balazs, 1982), and are substantially site-specific, except for migrations to and from breeding grounds at French Frigate Shoals in the Northwestern Hawaiian Islands (Balazs and Chaloupka, 2004a,b). In the Caribbean, green turtles feed primarily on seagrasses in "grazing plots" (Bjorndal, 1980; Mortimer, 1981; Thayer et al., 1982; Mendonça, 1983; Thayer et al., 1984; Bjorndal, 1985, 1996), and seaweeds form the bulk of the diet only in certain habitats (see review in Mortimer, 1982; Bjorndal, 1985, 1996; Garnett et al., 1985; Forbes, 1996; Seminoff et al., 2002). The nutritional value and digestibility of the Caribbean seagrass, *Thalassia testudinum* Banks ex König (Bjorndal, 1980; Vicente et al., 1980; Dawes and Lawrence, 1983; Dawes, 1986), and 15 species of seaweeds at Heron Reef, Australia (Forbes, 1996) have been well-documented, but this important aspect of the feeding ecology of Hawaiian green turtles is lacking.

The Hawaiian green turtle metapopulation represents a distinct genetic stock (Dutton, 2003), and has increased in numbers since protection under the U.S. Endangered Species Act began in 1978 (Balazs and Chaloupka, 2004b). However, the Hawaiian green turtle stock is characterized by a long-term decline in somatic growth rates of immature turtles, significant spatial and temporal variation in immature growth rates

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that are foraging ground-specific, and a high expected age-at-maturity ranging from 35 to 50+ yrs, compared to 25–30 yrs in some Great Barrier Reef populations (Zug et al., 2001; Balazs and Chaloupka, 2004a; Chaloupka et al., 2004). Environmental conditions (e.g., sea surface temperature fluctuations, coastal flooding events, habitat quality), density-dependent effects, food stock dynamics, and forage type differences have been suggested as explanations for variation in somatic growth patterns (Bjorndal et al., 2000; Balazs and Chaloupka, 2004a; Chaloupka et al., 2004). The findings that captive-raised green turtles fed high protein, easily digestible diets grow faster than wild turtles (Wood and Wood, 1977a,b, 1981; Bjorndal, 1985), reach sexual maturity earlier, and produce more eggs annually per female (Wood and Wood, 1980), imply that nutrition has an important role in green turtle growth, reproduction, and long-term viability of the species. Variation in fecundity of wild Caribbean and Surinam populations of green turtles has been credited to differences in diet: seagrass vs algae (Bjorndal, 1982). Nesting numbers of green turtles have been correlated with food availability in the months prior to breeding (Limpus and Nichols, 1988; Broderick et al., 2001). Balazs (1982) attributed differences in growth rates of juvenile Hawaiian green turtles from different islands to dietary differences. Differences in the fatty acid composition of depot fat in young Hawaiian green turtles has been linked to differences in length of time on benthic foraging grounds, and to differences in primary dietary components: the red macroalga, *Pterocladiella capillacea* (Gmelin) Santelices and Hommersand vs the seagrass, *Halophila hawaiiana* Doty and Stone (Seaborn et al., 2005). Other than the fatty acid profiles for these two marine plants, and total dietary fiber content (McDermid et al., 2005), the nutritional composition of marine plants consumed by Hawaiian green turtles has not been determined. The purpose of this study was to analyze the proximate composition (protein, carbohydrate, and lipid), as well as water, ash, energy, mineral, vitamin, and amino acid content of the most common seaweed and seagrass food items at important foraging grounds to provide new information about the feeding ecology of Hawaiian green turtles, and factors that may influence somatic growth rate patterns.

Materials and Methods

Collection.—Sixteen species of macroalgae and two species of seagrasses were collected (approximately 1 kg fresh weight when possible) from 13 different recognized turtle foraging areas (Balazs, 1980): intertidal and subtidal sites on the islands of Hawaii, Maui, Oahu, and Midway Atoll (Table 1; Fig. 1). The list of species includes members of the Chlorophyta, Phaeophyta, Rhodophyta, and Magnoliophyta. Species were chosen because they are consumed by the green turtle, *C. mydas* (Russell and Balazs, 2000). Species were collected during months when they were abundant at the selected foraging areas. Another dietary item, algal turf: densely packed, multispecific assemblages of caespitose seaweeds growing in clumps or tufts < 3 cm in height (Stuercke and McDermid, 2004), was sampled haphazardly in triplicate each month from October 2002 to August 2003 at an additional turtle foraging area, Kaloko-Honokōhau National Historical Park, Hawaii. All specimens were placed in food-grade plastic bags and transported to the laboratory in insulated containers. Samples were identified to genus or species based on examination of morphological and anatomical characteristics and using taxonomic references (Abbott, 1999; Abbott and Huisman, 2004). Voucher specimens were selected, photographed, and deposited in the Bishop Museum Herbarium in Honolulu (BISH).

Sample Preparation.—Within 6 hrs of collection, fresh material of macroalgae and seagrasses was thoroughly rinsed three times in filtered seawater, and any remaining epiphytic

Table 1. List of Hawaiian seaweed and seagrass species consumed by the green turtle, *Chelonia mydas*, analyzed for nutritional composition.

Species	Collection #	Collection site	Date collected
Chlorophyta			
Caulerpa lentillifera J. Agardh	NC043	Waikoloa Dolphin Pens, Hawaii	Oct. 11, 2002
Cladophora vagabunda (L.) Hock	NC036	Māʻalaea, Maui	Mar. 21, 2002
Codium hawaiiense Silva and Chacana	NC045	Corsair Wreck, Midway	Sept. 21, 2002
Codium reediae Silva	NC034	Kanahā, Maui	Mar. 21, 2002
Enteromorpha flexuosa (Wulfen) J. Agardh	NC020	Papaʻiloa, Oahu	Jan. 31, 2002
Rhizoclonium implexum (Dillwyn) Kützing	NC044	Hilton Waikoloa Lagoon, Hawaii	Oct. 11, 2002
Ulva fasciata Delile	NC035	Māʻalaea, Maui	Mar. 21, 2002
U. fasciata	NC019	Papaʻiloa, Oahu	Jan. 31, 2002
Phaeophyta			
Dictyota acutiloba J. Agardh	NC017	Haleʻiwa, Oahu	Jan. 31, 2002
Sargassum echinocarpum J.Agardh	NC027	Onekahakaha, Hawaii	Mar. 1, 2002
Rhodophyta			
Acanthophora spicifera (Vahl) Børgesen	NC023	Kaneohe Bay, Oahu	Feb. 13, 2002
Ahnfeltiopsis concinna (J. Agardh) Silva and DeCew	NC002	Onekahakaha, Hawaii	Oct. 16, 2002
Amansia glomerata C. Agardh	NC047	Leleiwi, Hawaii	Dec. 9, 2002
Gracilaria salicornia (C. Agardh) Dawson	NC025	Kaneohe Bay, Oahu	Feb. 13, 2002
Hypnea musciformis (Wulfen in Jacquin) Lamouroux	NC033	Kanahā, Maui	Mar. 21, 2002
H. musciformis	NC018	Laniākea, Oahu	Jan. 31, 2002
Laurencia nidifica J. Agardh	NC040	Lualualei, Oahu	June 5, 2002
Pterocladiella capillacea (S. G. Gmelin) Sant. and Homm.	NC014	Punaluʻu, Hawaii	Jan. 2, 2002
Magnoliophyta			
Halophila decipiens Ostenfeld (leaves + petioles)	NC037a	Kāhala, Oahu	April 19, 2002
H. decipiens (roots + rhizomes)	NC037b	Kāhala, Oahu	April 19, 2002
Halophila hawaiiana Doty and Stone (leaves + petioles)	NC024a	Kaneohe Bay, Oahu	Feb. 13, 2002
H. hawaiiana (roots + rhizomes)	NC024b	Kaneohe Bay, Oahu	Feb. 13, 2002

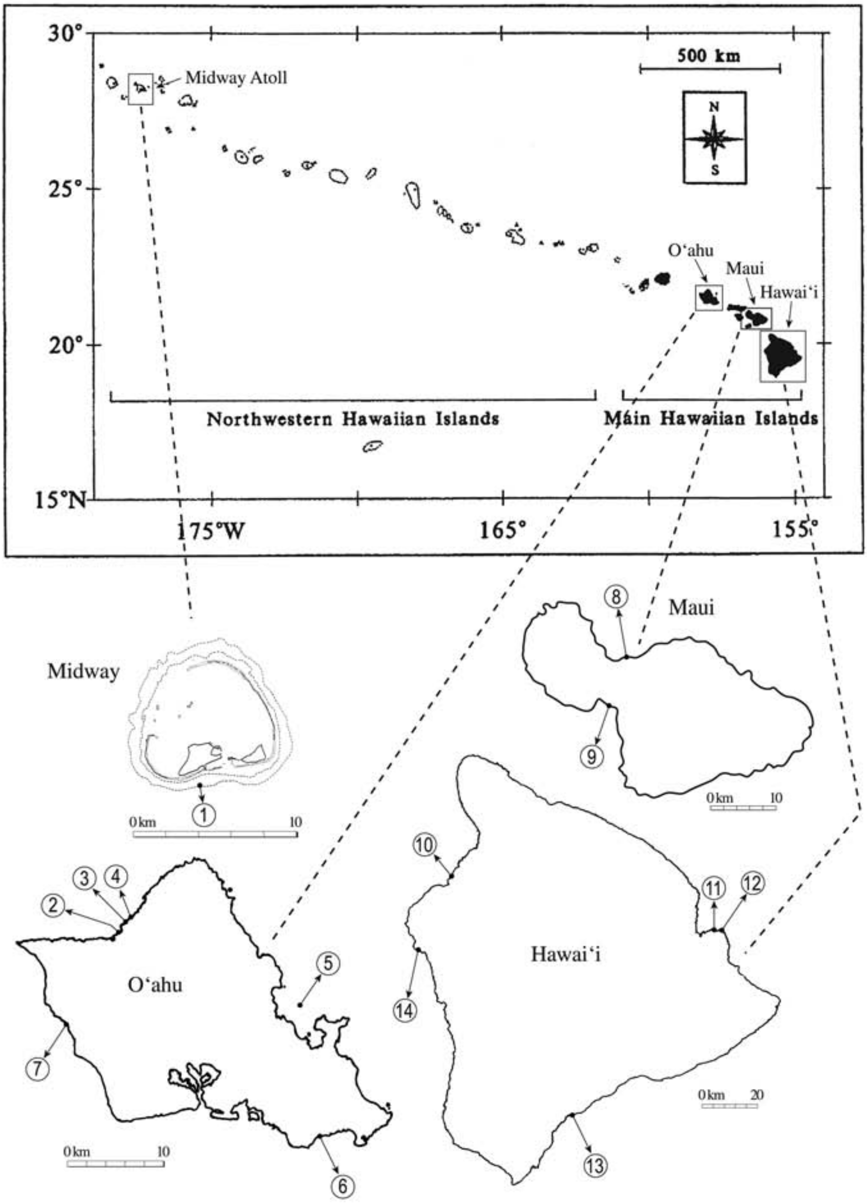

Figure 1. Hawaiian Archipelago with locations of collection sites numbered in order from north to south, clockwise around islands: 1 = Corsair Wreck, 2 = Hale'iwa, 3 = Papa'iloa, 4 = Laniākea, 5 = Kaneohe Bay, 6 = Kāhala, 7 = Lualualei, 8 = Kanahā, 9 = Mā'alaea, 10 = Waikoloa Dolphin Lagoon, 11 = Onekahakaha, 12 = Leleiwi, 13 = Punalu'u, 14 = Kaloko-Honokōhau National Historical Park.

algae, invertebrates, sand, and debris removed by hand. Seagrass specimens were divided into the above-ground (leaves, petioles) and below-ground (rhizomes, roots) parts, for comparison of results with previous studies. Turf samples were also rinsed three times in filtered seawater to remove as much sand, debris, and invertebrates as possible, but were not hand-cleaned. All samples were divided into portions (50–200 g each), spun in a salad spinner for 30 s to remove excess water, and then weighed (wet weight). All portions were placed on aluminum foil trays, and dried to a constant weight at 60 °C in an air oven. 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™ A11), and then stored in air-tight labeled glass jars in a refrigerator at 4 °C which maintained moisture content below 5.5%. All chemical analyses were conducted in triplicate on dried ground material, except in ash determination for which five replicates were used. All values were reported relative to the dry weight of the seaweed and seagrass, except energy values, which were based on an ash-free dry weight.

Composition Analyses.—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 content was determined by incinerating the samples for 4 hrs at 500 °C following the Association of Official Analytical Chemists (1995) methods as modified by Robledo and Freile Pelegrin (1997).

The Lowry method was used for total protein determination (Lowry et al., 1951; Harrison and Thomas, 1988). The samples were digested in 1 N NaOH, 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 carbohydrates were extracted from samples in 10% 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 and 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.

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, purified according to Folch et al. (1957), evaporated to dryness under a stream of filtered N_2 gas, and weighed.

Pressed pellets of 0.1–0.2 g of dried powder of each sample were combusted in a Parr 1425 Semimicro Calorimeter standardized with benzoic acid. Benzoate was added to ground samples when necessary to help form pellets and allow total combustion. Total calories were calculated on an ash-free basis (Carefoot, 1985), and converted to kJ g^{-1} using the formula: kcal × 4.184 = kJ. Energy content was not determined for the turf samples, because the pellets fell apart and did not undergo complete combustion, even after adding benzoate.

Samples were sent to an independent chemical analysis laboratory (Industrial Labs in Denver, Colorado, USA) that uses methodologies as 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 content of the seaweed samples was determined using HPLC, and β-carotene content was measured spectrophotometrically. Because of insufficient amount of dried sample, these tests were not run on four of the 16 species of algae, on the two seagrass species, nor on the algal turf.

Samples of dried ground material were sent to an independent laboratory (Waters Agricultural Laboratories, Inc., Georgia, USA) that uses accepted methods of analysis of the Association of Official Analytical Chemists (AOAC) and the Association of Florida Phosphate Chemists. Not all of the samples were tested for minerals because of insufficient available dried material.

Sixteen seaweed species, two seagrass species, and four turf samples were sent to an independent laboratory for amino acid analysis (Protein Chemistry Laboratory, at Texas A&M University, USA). This lab reports 16 naturally occurring amino acids by first subjecting the solid sample to a 6 N HCl liquid-phase hydrolysis. Additionally, tryptophan is determined using a 5 N NaOH hydrolysis, which is optimized for this specific amino acid. The lab then uses a Hewlett Packard AminoQuant II system that analyzes peptides and proteins by pre-column derivatization of hydrolyzed samples with o-phthalaldehyde (OPA), which reacts with primary amino acids and 9-fluoromethyl-chloroformate (FMOC), which reacts with secondary amino acids. The rapid reaction of both reagents produces a highly fluorescent and UV-absorbing isoindole derivative, which is then separated by reverse phase HPLC. The derivatized amino acids are identified by UV absorbance with a diode array detector or by fluorescence using an in-line fluorescence detector. The amounts of amino acids recovered are presented as percent of dry weight of the sample.

Results

The water content of fresh seaweeds and seagrasses consumed by Hawaiian green turtles ranged from 67.0% to 94.0% (Table 2). Ash was usually the most abundant component of the dried material in all species, except *Enteromorpha flexuosa*, *Ahnfeltiopsis concinna*, and *P. capillacea*. The highest values for total protein content were found in *Rhizoclonium implexum* (13.9% dry weight) and *P. capillacea* (13.4% dry weight). The two lowest protein values were found in the below-ground portion (roots and rhizomes) of the seagrass, *Halophila decipiens* (2.5% dry weight), and in the red seaweed, *Acanthophora spicifera* (2.6% dry weight). Soluble carbohydrate composition ranged from 4.3% to 39.9% dry weight. Most species contained < 10% crude lipid, except for *Cladophora vagabunda* (11.8% dry weight) and *Dictyota acutiloba* (16.1% dry weight). *Enteromorpha flexuosa*, *Ulva fasciata*, *D. acutiloba*, *Laurencia nidifica*, and *P. capillacea* had the highest energy values, each with over 10 kJ g^{-1} ash-free dry weight. Below-ground parts of the seagrass, *H. hawaiiana,* showed the lowest energy content.

Vitamin A (β-carotene) was the only vitamin that consistently appeared in measurable amounts (Table 3). *Rhizoclonium implexum* contained the highest amount of β -carotene (330 IU g^{-1} dry weight). Only *E. flexuosa* and *U. fasciata* showed detectable amounts of vitamin C, 3.0 mg g^{-1} dry weight and 2.2 mg g^{-1} dry weight, respectively. Nine of the seaweeds tested contained Niacin (B_3). Niacinamide was found in *P. capillacea* (0.3 mg g^{-1} dry weight). Only *U. fasciata*, sampled from Oahu, contained a detectable amount of Riboflavin (B_2), 0.01 mg g^{-1} dry weight. Sulfur and potassium were the most abundant minerals in most of the species (Table 4); whereas, phosphorus was present in low concentrations in all species. Among the trace elements, boron and iron had the highest values in the seaweed and seagrass samples. Measurable amounts of all 17 amino acids assayed, except tryptophan, were found in the seagrass and seaweed samples (Table 5).

Turf samples from Kaloko-Honokōhau National Historical Park, Hawaii consisted of 20 different algal genera (Table 6). Variation in monthly ash, protein, soluble carbohydrate, and crude lipid content of the turf samples (Fig. 2) was assessed using balanced ANOVA after Ryan-Joiner's test confirmed normality and Barlett's test verified equal variances. Soluble carbohydrate data were log transformed to achieve homogeneity of variances. Tukey's pairwise comparison was employed to determine where the differences existed between sampling dates. Ash (P = 0.017, F = 3.07, df = 29) and soluble carbohydrate (P = 0.002, F = 4.51, df = 29) content differed significantly over time. For ash, only the values in November 2002 and February 2003 were significantly different from each other; whereas, soluble carbohydrate values for October 2002 differed significantly from those of January, February, May, and June 2003. Total protein and crude lipid content of turf showed no significant difference among months. No clear seasonal trends in nutritional composition of the algal turf were evident. Ash was the most abundant component of the dried turf (mean values 58%–78.8% dry weight); mean total protein values were < 6.5% dry weight; mean crude lipid content was also consistently low (1.1%–3.1% dry weight). Measurable

Table 2. Mean (± standard error) proximate, water, ash, and energy content of Hawaiian marine plants consumed by green turtles. Water content is relative to total fresh weight. Ash, protein, carbohydrate, and lipid values are relative to total dry weight. The values for energy are based on ash-free dry weight. A = leaves + petioles, B = roots + rhizomes. n = 3 for all analyses, except n = 5 for ash.

Species	Collection #	Water (%)	Ash (%)	Total protein (%)	Soluble carbohydrate (%)	Crude lipid (%)	Energy (kJ g^{-1})
Chlorophyta							
Caulerpa lentillifera	NC043	94.0 ± 0.04	46.4 ± 0.2	9.7 ± 0.4	11.8 ± 0.8	7.2 ± 0.3	6.35 ± 0.12
Cladophora vagabunda	NC036	89.5 ± 0.3	34.2 ± 0.2	12.3 ± 0.2	12.1 ± 0.5	11.4 ± 0.4	9.39 ± 0.10
Codium hawaiiense	NC045	—	51.7 ± 0.2	4.0 ± 0.3	27.4 ± 0.4	2.6 ± 0.3	4.18 ± 0.11
Codium reediae	NC034	93.9 ± 0.1	63.5 ± 0.4	7.0 ± 0.3	8.2 ± 1.3	6.1 ± 0.2	3.10 ± 0.05
Enteromorpha flexuosa	NC020	87.6 ± 0.3	23.2 ± 0.2	7.9 ± 0.4	39.9 ± 2.3	5.6 ± 0.2	11.07 ± 0.56
Rhizoclonium implexum	NC044	86.0 ± 0.2	35.5 ± 0.1	13.9 ± 0.6	9.0 ± 0.4	8.3 ± 0.2	8.13 ± 0.06
Ulva fasciata	NC019	83.4 ± 0.4	25.4 ± 0.1	12.3 ± 0.5	20.6 ± 0.7	3.6 ± 0.1	11.55 ± 0.04
Ulva fasciata	NC035	86.1 ± 0.2	32.2 ± 0.1	8.8 ± 0.4	17.1 ± 1.3	5.1 ± 0.2	9.95 ± 0.30
Phaeophyta							
Dictyota acutiloba	NC017	88.5 ± 0.8	28.9 ± 1.2	12.0 ± 0.6	5.9 ± 0.2	16.1 ± 0.03	10.14 ± 0.12
Sargassum echinocarpum	NC027	86.4 ± 0.1	32.0 ± 0.1	10.3 ± 0.7	10.5 ± 1.3	3.8 ± 0.2	8.85 ± 0.07
Rhodophyta							
Acanthophora spicifera	NC023	91.8 ± 0.1	36.6 ± 0.1	2.6 ± 0.1	31.5 ± 1.1	2.4 ± 0.2	7.85 ± 0.17
Ahnfeltiopsis concinna	NC002	67.0*	23.8 ± 0.1	5.7 ± 0.3	31.2 ± 1.8	1.9 ± 0.2	9.21 ± 0.24
Amansia glomerata	NC047	79.8 ± 0.3	38.0 ± 0.6	12.3 ± 0.4	20.3 ± 1.1	3.7 ± 0.5	8.12 ± 0.32
Gracilaria salicornia	NC025	90.1 ± 0.2	49.5 ± 1.4	3.9 ± 0.4	24.6 ± 0.6	1.5 ± 0.1	6.05 ± 0.22
Hypnea musciformis	NC033	90.0 ± 0.2	43.5 ± 0.4	11.1 ± 0.2	16.1 ± 0.2	3.9 ± 0.1	7.01 ± 0.16
Hypnea musciformis	NC018	89.9 ± 0.3	39.9 ± 1.8	11.6 ± 0.7	19.9 ± 1.0	1.9 ± 0.2	7.71 ± 0.08
Laurencia nidifica	NC040	88.8 ± 0.2	31.4 ± 0.3	3.2 ± 0.2	16.0 ± 1.1	3.4 ± 0.1	10.07 ± 0.16
Pterocladiella capillacea	NC014	75.4 ± 0.5	13.7 ± 0.3	13.4 ± 0.3	33.2 ± 0.3	2.3 ± 0.5	14.70 ± 0.49
Magnoliophyta							
Halophila decipiens A	NC037a	92.1*	48.1 ± 0.9	6.2 ± 0.1	4.3 ± 0.4	5.1 ± 0.4	4.58 ± 0.09
Halophila decipiens B	NC037b	92.5*	43.2 ± 0.6	2.5 ± 0.1	8.2 ± 0.3	3.1 ± 0.1	5.15 ± 0.11
Halophila hawaiiana A	NC024a	88.5 ± 2.6	37.7 ± 0.1	9.2 ± 0.4	9.9 ± 0.3	3.8 ± 1.2	7.10 ± 0.12
Halophila hawaiiana B	NC024b	90.3 ± 0.8	53.5 ± 1.6	5.6 ± 0.4	18.2 ± 0.2	2.9 ± 0.2	2.91 ± 0.11

* Standard error not calculated for this analysis because n = 1

Table 3. Vitamin A and B_3 content of Hawaiian seaweeds consumed by green turtles. All values are based on dry weight. Blank values indicate that vitamin content was not detected at the method detection limit.

Species	Collection #	β-carotene (A) IU g^{-1}	Niacin (B_3) mg g^{-1}
Chlorophyta			
Caulerpa lentillifera	NC043	160	2
Cladophora vagabunda	NC036	93	1.64
Codium hawaiiense	NC045	30	0.8
Codium reediae	NC034	36	1.07
Enteromorpha flexuosa	NC020	54	—
Rhizoclonium implexum	NC044	330	3
Ulva fasciata	NC019	180	—
Ulva fasciata	NC035	70	0.66
Phaeophyta			
Sargassum echinocarpum	NC027	97	0.09
Rhodophyta			
Acanthophora spicifera	NC023	51	—
Ahnfeltiopsis concinna	NC002	16.2	—
Gracilaria salicornia	NC025	230	0.08
Hypnea musciformis	NC033	66	1.26
Pterocladiella capillacea	NC014	170	—

amounts of 17 amino acids were found in the algal turf (Table 7). Histidine, methionine, and tryptophan had the lowest concentrations in all turf samples. Aspartic acid and glutamic acid were the most abundant amino acids in the turf samples.

Discussion

Approximately 500 species of marine macroalgae are known from the Hawaiian Islands (Abbott, 1999), over half of which are known to be consumed by Hawaiian green turtles (Russell and Balazs, 2000). However, Balazs (1980) reported nine species of algae as major dietary components of green turtles in the Hawaiian Archipelago: *Amansia glomerata*, *Caulerpa racemosa*, *Codium* spp., *P. capillacea*, *Spyridia filamentosa*, *Turbinaria ornata*, and *U. fasciata*. *Acanthophora spicifera* and *Hypnea musciformis*, two introduced red seaweeds, have since been added to that list of major food sources (Russell and Balazs, 1994a,b). In a recent analysis of diet samples, genera that comprised > 50% of the combined esophagus and anterior crop samples, included *Halophila*, *Acanthophora*, *Centroceras*, *Gelidiella*, *Gracilaria*, *Hypnea*, *Pterocladiella*, *Amansia*, *Cladophora*, *Codium*, and *Dictyosphaeria* (Arthur, 2005). Four of the major food species, *A. glomerata*, *H. musciformis*, *P. capillacea*, and *U. fasciata* were among the highest in energy, soluble carbohydrate, protein, and vitamin A content, as well as certain minerals and amino acids. However, although extremely abundant throughout much of the range of the Hawaiian green turtle, and common in turtle diets (Arthur, 2005), *A. spicifera* did not show any notably high nutritional values. Although *Codium* is common in turtle foregut samples, *Codium hawaiiense* and *Codium reediae* had conspicuously low energy content: < 4.2 kJ g^{-1} ash-free dry weight. In a previous study (McDermid and Stuercke, 2003), two foliose red seaweeds consumed by humans, *Halymenia formosa* Harvey ex Kützing (a large, frondose, sub-

Table 4. Comparision of selected minerals in Hawaiian marine plants consumed by green turtles. Values are based on dry weight. A = leaves + petioles, B = roots + rhizomes

Species	Coll. #	N %	P %	K %	Mg %	Ca %	S %	B ppm	Zn ppm	Mn ppm	Fe ppm	Cu ppm
Chlorophyta												
Caulerpa lentillifera	NC043	2.39	0.16	0.70	1.65	0.95	1.55	70.17	16.70	9.85	166.70	6.30
Cladophora vagabunda	NC036	3.74	0.20	3.15	2.94	0.39	5.51	68.00	6.00	17.00	14.00	1.00
Codium hawaiiense	NC045	0.88	0.06	0.97	1.84	1.00	6.51	63.75	11.84	3.58	39.22	3.36
Codium reediae	NC034	1.94	0.12	0.82	1.70	0.92	3.94	74.00	3.00	26.00	196.00	1.00
Enteromorpha flexuosa	NC020	1.27	0.10	1.60	1.17	0.74	3.20	164.00	6.00	5.00	104.00	3.00
Rhizoclonium implexum	NC044	4.73	0.23	11.60	0.88	0.58	2.11	107.00	60.04	10.42	236.00	18.17
Ulva fasciata	NC035	3.74	0.22	3.15	2.94	0.39	5.51	68.00	6.00	17.00	141.00	1.00
Ulva fasciata	NC019	3.62	0.22	2.87	2.19	0.47	5.24	77.00	9.00	12.00	86.00	5.00
Phaeophyta												
Dictyota acutiloba	NC017	2.87	0.16	7.26	1.36	1.03	2.21	95.00	16.00	12.00	438.00	5.00
Sargassum echinocarpum	NC027	1.53	0.14	9.50	1.16	1.31	1.16	106.00	7.00	6.00	92.00	11.00
Rhodophyta												
Acanthophora spicifera	NC023	1.22	0.02	1.51	0.15	0.95	5.47	249.00	5.00	3.00	154.00	5.00
Ahnfeltiopsis concinna	NC002	1.46	0.10	3.01	0.75	0.44	7.48	309.94	21.50	71.68	85.77	3.10
Gracilaria salicornia	NC025	0.70	0.16	18.30	0.47	0.96	5.35	442.00	6.00	3.00	79.00	2.00
Hypnea musciformis	NC033	3.39	0.25	2.34	0.60	0.31	6.82	179.00	7.00	12.00	145.00	2.00
Hypnea musciformis	NC018	3.21	0.40	2.36	0.65	0.69	7.56	196.00	7.00	9.00	26.00	4.00
Pterocladiella capillacea	NC014	3.62	0.27	4.61	0.37	0.42	1.91	265.53	10.33	15.98	132.69	8.23
Magnoliophyta												
Halophila hawaiiana A	NC024a	2.31	0.42	2.02	1.62	1.80	1.16	689.00	11.00	12.00	213.00	5.00
Halophila hawaiiana B	NC024b	0.90	0.18	1.73	1.73	11.82	0.91	498.00	7.00	12.00	516.00	3.00

Table 5. The amino acid content of Hawaiian marine plants consumed by green turtles. Values are expressed as % of dry weight. A = leaves + petioles, B = roots + rhizomes

Species	Coll. #	Asx*	Glx	Ser	His	Gly	Thr	Ala	Arg	Tyr	Val	Met	Phe	Ile	Leu	Lys	Pro	Trp
Chlorophyta																		
Caulerpa lentillifera	NC043	0.79	0.88	0.31	0.11	0.49	0.36	0.42	0.41	0.18	0.47	0.09	0.41	0.37	0.57	0.40	0.24	0.16
Cladophora vagabunda	NC036	1.79	1.86	0.70	0.18	0.76	0.62	0.82	0.83	0.55	0.81	0.13	0.77	0.60	1.48	0.78	0.78	0.00
Codium hawaiiense	NC045	0.34	0.43	0.18	0.00	0.22	0.11	0.20	0.14	0.09	0.18	0.02	0.13	0.12	0.49	0.14	0.18	0.00
Codium reediae	NC034	0.74	0.77	0.34	0.09	0.40	0.24	0.37	0.28	0.19	0.35	0.08	0.27	0.22	0.85	0.28	0.48	0.05
Enteromorpha flexuosa	NC020	0.61	0.69	0.28	0.09	0.33	0.21	0.45	0.23	0.12	0.30	0.07	0.24	0.18	0.67	0.17	0.43	0.03
Rhizoclonium implexum	NC044	1.87	1.51	0.44	0.11	0.54	0.32	0.50	0.80	0.29	0.50	0.07	0.47	0.36	0.95	0.64	0.60	0.06
Ulva fasciata	NC035	1.65	1.99	0.84	0.80	1.09	0.70	1.08	1.26	0.54	0.76	0.19	0.77	0.52	1.45	0.61	0.75	0.03
Ulva fasciata	NC019	1.45	1.57	0.63	0.37	0.78	0.63	1.16	0.74	0.28	0.80	0.10	0.67	0.52	0.84	0.69	0.45	0.13
Phaeophyta																		
Dictyota acutiloba	NC017	2.58	1.52	0.47	0.10	0.48	0.39	0.61	0.59	0.32	0.49	0.21	0.50	0.41	1.11	0.39	0.66	0.00
Sargassum echinocarpum	NC027	0.64	1.26	0.23	0.57	0.27	0.19	0.39	0.27	0.14	0.27	0.09	0.25	0.23	0.58	0.20	0.47	0.00
Rhodophyta																		
Acanthophora spicifera	NC023	0.44	0.46	0.19	0.05	0.15	0.19	0.21	0.17	0.07	0.19	0.05	0.16	0.14	0.28	0.21	0.16	0.05
Ahnfeltiopsis concinna	NC002	0.44	0.49	0.26	0.04	0.30	0.16	0.23	0.47	0.26	0.20	0.06	0.20	0.14	0.53	0.33	0.47	0.04
Amansia glomerata	NC047	0.98	0.92	0.32	0.11	0.38	0.31	0.47	0.41	0.15	0.45	0.03	0.33	0.31	0.51	0.58	0.43	0.12
Gracilaria salicornia	NC025	0.19	0.24	0.10	0.03	0.20	0.07	0.13	0.18	0.06	0.11	0.03	0.09	0.81	0.43	0.10	0.37	0.03
Hypnea musciformis	NC033	1.66	1.84	0.94	0.18	0.74	0.76	0.87	2.23	0.57	0.85	0.31	0.74	0.90	1.45	0.96	0.92	0.24
Hypnea musciformis	NC018	1.45	1.52	0.60	0.14	0.62	0.56	0.72	1.87	0.49	0.82	0.27	0.70	0.86	1.31	0.84	0.74	0.20
Laurencia nidifica	NC040	0.87	0.94	0.38	0.10	0.40	0.35	0.39	0.42	0.41	0.40	0.10	0.34	0.32	0.78	0.57	0.36	0.05
Pterocladiella capillacea	NC014	1.06	1.62	0.53	0.13	0.41	0.44	0.57	0.46	0.24	0.49	0.11	0.48	0.39	0.64	0.76	0.30	0.11
Magnoliophyta																		
Halophila decipiens A	NC037a	0.63	0.92	0.37	0.09	0.46	0.22	0.86	0.45	0.20	0.31	0.03	0.32	0.25	0.82	0.30	0.56	0.09
Halophila decipiens B	NC037b	0.20	0.23	0.01	0.03	0.18	0.05	0.23	0.13	0.05	0.08	0.02	0.07	0.06	0.27	0.07	0.07	0.07
Halophila hawaiiana A	NC024a	0.61	1.32	0.28	0.11	0.30	0.24	1.29	0.33	0.14	0.39	0.07	0.34	0.32	0.54	0.28	0.47	0.12
Halophila hawaiiana B	NC024b	0.21	0.70	0.12	0.05	0.19	0.07	0.47	0.15	0.07	0.11	0.03	0.09	0.09	0.38	0.11	0.36	0.11

*Asx = aspartic acid, Glx = glutamic acid, Ser = serine, His = histidine, Gly = glycine, Thr = threonine, Ala = alanine, Arg = arginine, Tyr = tyrosine, Val = valine, Met = methionine, Phe = phenylalanine, Ile = isoleucine, Leu = leucine, Lys = lysine, Pro = proline, Trp = tryptophan

Table 6. Genera comprising the algal turf collected at Kaloko-Honokōhau National Historical Park, Hawaii.

Rhodophyta	Chlorophyta
Acanthophora	*Cladophora*
Anotrichium	*Enteromorpha*
Caulacanthus	*Rhizoclonium*
Centroceras	*Ulva*
Ceramium	*Valonia*
Coelothrix	
Chondria	
Gelidiella	
Gelidium	
Hypnea	
Jania	
Polysiphonia	
Pterocladiella	
Taenioma	
Tolypiocladia	

tidal species) and *Porphyra vietnamensis* Tanaka and Pham (small, ephemeral blades in the splash zone), had higher protein values than any species in this study, but *H. formosa* and *P. vietnamensis* are not reported to be consumed by Hawaiian green turtles. The selection of food species by green turtles probably optimizes nutrient and energy intake, but may also be influenced by species accessibility, abundance, and/or levels of deleterious natural chemical compounds (secondary metabolites) in the seaweeds (Balazs, 1980; Garnett et al., 1985; Forbes, 1996; Russell et al., 2003). Turtles may choose their seaweeds and seagrasses in situ based on toughness, succulence, texture, or taste which might reflect plant age or health. Other food attributes may influence green turtle food selection, for instance, marine herbivorous fish diet choices are based on digestibility of cell wall and storage carbohydrates (Montgomery and Gerking, 1980; Zemke-White and Clements, 1999), as well as nutrient and energy content. In contrast, the key factor in food preference in the tropical herbivorous crab, *Grapsus albolineatus* Lamarck, is algal morphology, rather than nutrient content or digestibility (Kennish and Williams, 1997).

In this study, the seaweeds, seagrasses, and algal turfs known to be consumed by Hawaiian green turtles showed considerable variation in nutritional composition that may be due to species characteristics, as well as the month and location of collection. Differences in nutrient content did not follow a simple pattern based on phylum, pigmentation, or morphology, i.e., a green filamentous seaweed, *R. implexum,* and a red, branched, foliose species, *P. capillacea,* ranked highest in total protein content. In general, members of the Rhodophyta contained high levels of soluble carbohydrates (16.0%–33.2%); however, *E. flexuosa* (Chlorophyta) contained the greatest amount (39.9%). For species of Chlorophyta and Phaeophyta tested, crude lipids ranged from 2.6% to 16.1%; whereas, all lipid values for Rhodophyta were < 4%. Low energy values characterized the two seagrasses (Magnoliophyta), as well as two *Codium* species (Chlorophyta). The extent to which environmental conditions or algal phenology affect the nutritional composition in subtropical seaweeds is not known.

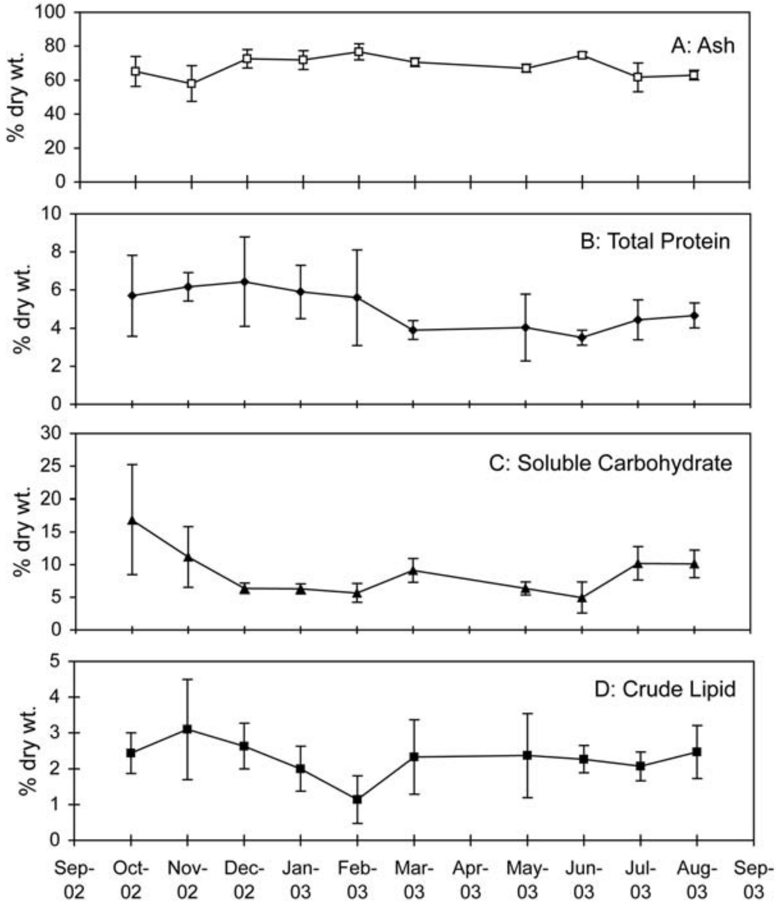

Figure 2. Nutritional composition of algal turf at Kaloko-Honokōhau, Hawaii Island, based on monthly samples (n = 3). Error bars represent standard deviation. (A) mean ash content (% dry weight); (B) mean total protein content (% dry weight); (C) mean soluble carbohydrate content (% dry weight); (D) mean crude lipid content (% dry weight).

Turf samples composed of a mixture of small red and green algae were consistently high in ash content, and low in protein and lipid. The high ash levels in the turf may be a reflection of the abundance of calcareous algae present in the turf, e.g., *Jania*. Although ash and soluble carbohydrate content showed significant variation among months, no clear seasonal pattern in ash, protein, carbohydrate or lipid content of the algal turf was evident. The year-round availability of turf algae at Kaloko-Honokōhau may be more important to foraging turtles than nutritional quality of the turf.

All parts of *Halophila* species are found in turtle forestomach samples; however, it is common to find masses of severed leaves, with only a few rhizomes (D. J. Russell, American Univ. of Sharjah, United Arab Emirates, pers. comm.). Both Hawaiian *Halophila* seagrass species consumed by Hawaiian green turtles had higher ash, lower protein, and lower energy in comparison to the well-known Caribbean seagrass *T. testudinum* eaten by green turtles (Bjorndal, 1980; Dawes and Lawrence, 1983). Vicente et al. (1980) reported values for potassium, phosphorus, and magnesium in

Table 7. Amino acid content of the algal turf collected from Kaloko-Honokōhau National Historical Park, Hawaii. Values are expressed as % of dry weight.

Collection month	Asx*	Glx	Ser	His	Gly	Thr	Ala	Arg	Tyr	Val	Met	Phe	Ile	Leu	Lys	Pro	Trp
November 2002	0.77	0.97	0.32	0.08	0.33	0.27	0.41	0.43	0.15	0.28	0.08	0.29	0.22	0.41	0.40	0.24	0.06
December 2002	0.50	0.66	0.18	0.06	0.23	0.16	0.27	0.29	0.08	0.23	0.04	0.20	0.19	0.28	0.31	0.15	0.08
January 2003	0.39	0.47	0.14	0.03	0.15	0.12	0.19	0.19	0.08	0.13	0.04	0.15	0.10	0.19	0.19	0.12	0.05
February 2003	0.59	0.71	0.19	0.06	0.24	0.18	0.30	0.27	0.10	0.26	0.05	0.21	0.21	0.32	0.31	0.16	0.08

*Asx = aspartic acid, Glx = glutamic acid, Ser = serine, His = histidine, Gly = glycine, Thr = threonine, Ala = alanine, Arg = arginine, Tyr = tyrosine, Val = valine, Met = methionine, Phe = phenylalanine, Ile = isoleucine, Leu = leucine, Lys = lysine, Pro = proline, Trp = tryptophan

T. testudinum that were similar to the levels of these minerals in *H. decipiens and H. hawaiiana*. With respect to other *Halophila* species, the above-ground portions of both Hawaiian species had lower protein and energy content than reported for three Florida species: *H. decipiens, Halophila engelmannii,* and *H. johnsonii* (Dawes et al., 1987, 1989).

Wood and Wood (1977a,b) determined that the essential amino acids and their quantitative requirements (shown in parentheses) for hatchling green turtles include lysine (1.8%), tryptophan (0.22%), methionine (0.5%), valine (1.3%), leucine (1.6%), isoleucine (1.0%), and phenylalanine (1.0%). The amino acid values measured for seaweeds and seagrasses in the present study were all lower than the required amounts for green turtle hatchlings; however, juvenile and adult turtles may have different amino acid requirements. The turf at Kaloko-Honokōhau National Historical Park showed the same pattern of low levels of these essential amino acids. Similar amino acid results for marine algae have been reported by Burkholder et al. (1971), Chan et al. (1997), and Wong and Cheung (2000).

Nutritional composition data provided in this study, in combination with ongoing research on site-specific food selection, ingestion rates, food stock abundance, and growth rates may help explain the low somatic growth rate patterns of Hawaiian green turtles (Balazs and Chaloupka, 2004a), and provide a better understanding of the dynamics of the Hawaiian green turtle stock.

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