Figure 1. Hawaiian green turtle grazing on terrestrial grass at high tide, Keaukaha Beach Park, 3 October 2011.

Nonnative Seashore Paspalum, *Paspalum vaginatum* (Poaceae), Consumed by Hawaiian Green Sea Turtles (*Chelonia mydas*): Evidence for Nutritional Benefits[1]

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Abstract: The Hawaiian green turtle, *Chelonia mydas* Linnaeus, is a marine herbivore known to feed on sea grasses and seaweeds. On the east side of the island of Hawai'i, at high tide, green turtles have been observed feeding on a terrestrial, salt-tolerant turfgrass: seashore paspalum, *Paspalum vaginatum* Swartz, first introduced to the Hawaiian Islands in the 1930s. The role of this grass in green turtle nutrition is unknown. *Paspalum vaginatum* samples were collected at Keaukaha Beach Park, Hilo, and analyzed for nutritional composition (percentage water, percentage ash, caloric value, C : N ratio, percentage protein, and percentage lignin). In addition, two red seaweeds, *Pterocladiella capillacea* (Gmelin) Santelices & Hommersand, a common food source for green turtles, and *Ahnfeltiopsis concinna* (J. Agardh) Silva & DeCew, an abundant high-intertidal species sometimes consumed by turtles, were analyzed for comparison. In contrast to the two seaweed species, *Paspalum vaginatum* contained approximately half the ash; 300–1,500 more calories/g ash-free dry weight; three to four times greater total protein; and 3–19 times higher lignin content. Green turtles in Hawai'i may opportunistically consume *P. vaginatum* because of its local abundance and/or its high protein and caloric content. In foraging areas where native macroalgal species have declined and/or turtle carrying capacity has been reached, green turtles may exploit new foods, such as seashore paspalum, and perhaps mitigate decline in somatic growth rates and body condition.

The diet of green turtles (*Chelonia mydas* Linnaeus), the largest marine herbivore in the Hawaiian archipelago, includes more than 275 species of macroalgae, two species of sea grasses, and several species of Cyanobacteria (Russell and Balazs 2000, Russell et al. 2003). Ten species of macroalgae, *Amansia glomerata* C. Agardh, *Caulerpa racemosa* (Forsskål) J. Agardh, *Codium* spp., *Pterocladiella capillacea* (Gmelin) Santelices & Hommersand, *Spyridia filamentosa* (Wulfen) Harvey, *Turbinaria ornata* (Turner) J. Agardh, *Ulva fasciata* Delile, *Acanthophora spicifera* (Vahl) Børgesen, and *Hypnea musciformis* (Wulfen *in* Jacquin) Lamouroux, and the sea grass *Halophila hawaiiana* Doty & Stone dominate the diet of the Hawaiian green turtle (Balazs 1980, Russell and Balazs 1994, Arthur and Balazs 2008), some of which have high caloric, carbohydrate, protein, and vitamin A content (McDermid et al. 2007). One factor in food preference of green turtles may be nutrient composition in marine plants (Balazs 1980, McDermid et al. 2007).

Hawaiian green turtle diet may not be limited to marine macrophytes. Since 2008, green turtles have been observed foraging on terrestrial grass on Hawai'i and Moloka'i Islands (G.H.B., unpubl. data; Ashley 2010). Wills (2010) reported terrestrial St. Augustine grass, *Stenotaphrum secundatum* (Walter) Kuntze, in a small proportion of esophageal

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lavage samples from green turtles at Kapoho Bay, Hawai'i Island. Russell et al. (2011) noted numerous cases in which Hawaiian green turtle stomachs contained unidentifiable, partially digested terrestrial grass. In a similar study, 23% of the stomach contents of 39 turtles in Peru contained salt grass, *Distichlis spicata* (L.) Greene (Hays Brown and Brown 1982). Wild green turtles in Hilo, on the windward coast of the island of Hawai'i, have been repeatedly observed grazing at high tide on partially submerged terrestrial grass (Family Poaceae), *Paspalum vaginatum* Swartz or seashore paspalum (Figure 1), apparently ignoring their favored algal food species, *Pterocladiella capillacea* (Rhodophyta), growing on adjacent rocks at the 0 m tide level.

A diet of terrestrial grass might add greater than normal lignin concentrations to a turtle diet. Lignin, a chemical compound that stiffens and fortifies plant cell walls, is found primarily in terrestrial plants and sea grasses, and at low concentrations in some algae (Martone et al. 2009). Lignin forms chemical complexes between cellulose and hemicellulose that block digestive enzymes from breaking apart the structural carbohydrate, making it more difficult to digest (Bjorndal 1980). However, green turtles carry out active hindgut fermentation to assist in fiber digestion (Bjorndal 1979), similar to processes found in horses (Church 1971), sheep, and cattle (Moir 1968). Green turtles could be said to be "preadapted" to digest terrestrial grasses if they encounter them during foraging.

Paspalum vaginatum is a stoloniferous, perennial, semiaquatic, salt-tolerant grass, globally distributed on warm temperate to tropical coasts and in brackish marshes (Wagner et al. 1990). *Paspalum vaginatum* is known as seashore paspalum, as well as biscuit grass, silt grass, saltwater couch, *grama de costa* (Spanish), *herbe rampante* (French), *kambutu* (Fiji), *matie* (Marquesas Islands), *mauku ta'atai* (Cook Islands), *mosie kalalahi* (Niue), *mutia* (Samoa), *wujoojkatejukjuk* (Marshall Islands), and many other local common names. Although the type specimen was collected in Jamaica in 1788, it is unclear whether this species is native to the Americas, Europe, and/or South Africa (Graeme and Kendal 2001). *Paspalum vaginatum* was introduced in the Hawaiian Islands as a cultivated plant (St. John 1973). The first vouchered record of this species in Hawai'i was collected by Fosberg at Kailua Beach, O'ahu, at the edge of brackish water in 1936 (Bishop Museum Herbarium collection no. 13182). Various cultivars of this grass species have been introduced and used extensively for groundcover in coastal landscaping, athletic fields, home lawns, and golf courses (Graeme and Kendal 2001, Brosnan and Deputy 2008), as well as erosion control, wetland restoration, and oil and gas well site reclamation (Gates 2003). Seashore paspalum is now a naturalized species in the Hawaiian Islands and can form dense mats in and around ponds, marshes, coastal streams, tidal estuaries, anchialine ponds, beaches, taro patches, and lagoons (Englund et al. 2001). In ecologically sensitive areas, seashore paspalum is considered an aggressive pest and an invasive, high risk, alien species (Graeme and Kendal 2001, Daehler et al. 2004, PIER 2013) because *P. vaginatum* can outcompete native coastal plant species and alter the physical environment, flora, and fauna of wetlands, estuaries (Shaw and Allen 2003, Graeme 2005, Siemens 2005), and unique anchialine ponds (R. Warshauer, pers. comm., 2012). Wild geese, manatees, cattle, and goats are reported to feed on *P. vaginatum* (Graeme and Kendal 2001, Suyama et al. 2007); however, the role of this grass in green turtle nutrition is unknown.

The purpose of this study was to determine the nutritional value of seashore paspalum during different seasons of the year at a green turtle foraging site. In addition, we hypothesized that *P. vaginatum* would have lower water content, higher ash, greater energy, higher protein, and higher lignin content in comparison with two red seaweeds in the same area, *Ahnfeltiopsis concinna* (J. Agardh) Silva & DeCew, an abundant high-intertidal species sometimes a component of green turtle diets, and *Pterocladiella capillacea*, a commonly consumed species in the intertidal zone.

MATERIALS AND METHODS

Collection

Two species of macroalgae and one species of grass (see Table 1) were collected from Keaukaha Beach Park in Hilo, Hawai'i (latitude: 19° 44′ 06″ N, longitude: 155° 02′ 55″ W). Plant material was collected by hand (between 35 and 153 g fresh weight), haphazardly, with each sample 1–2 m apart, and stored in food-grade plastic bags. Samples were placed in a freezer within 30 min of collection to preserve nutrients. Six samples of each alga and 12 samples of grass were collected in February 2012 (winter); three samples of grass were collected again in May 2012 (spring), August 2012 (summer), and November 2012 (fall). *Pterocladiella capillacea* was selected because it is a major dietary item for the Hawaiian green turtle (Balazs 1980), and *Ahnfeltiopsis concinna* because of its abundance in the high intertidal zone at the study site, proximal to seashore paspalum. The algae were identified using morphological and anatomical characteristics, with Abbott (1999) as a taxonomic reference. The grass species was identified using inflorescence and vegetative characteristics according to Wagner et al. (1990).

Sample Preparation

All the samples were shaken dry and placed in an aluminum tray. Samples were not rinsed so as to mimic turtle grazing habits. Wet weight was measured using an analytical balance. All portions were placed in a drying oven at 60°C and dried to a constant weight. Dried samples were then ground into a fine powder using an analytical grinding mill (IKA A11) and stored in individual, labeled, air-tight glass jars in a refrigerator at 4°C. Ash, C : N, protein, and lignin values were reported relative to the dry weight of the plant material; calories were based on ash-free dry weight. Analyses of the dried, powdered sample were performed with three or more replicates at the University of Hawai'i (UH) Hilo Analytical Laboratory, unless otherwise noted.

Sample Analyses

The percentage water content of the fresh material collected in February 2012 was calculated by subtracting the dried sample weight from the shaken wet sample weight. The difference was divided by the wet weight and the result multiplied by 100.

Ash content was determined by incinerating 95.0–100.0 mg of dried sample for 5 hr at 500°C in acid-washed vials following the procedure outlined by the Association of Official Analytical Chemists (1995). The ash represents inorganic salts and minerals within the plant.

Samples were prepared for C : N analysis by folding 5.0–6.0 mg of fine powdered, dried sample into a tin capsule (Costech) using a method to assure that no sample was lost and no air pockets formed within the capsule. Samples were then placed in a combustion system (Costech 410 Elemental) to determine carbon and nitrogen content.

Protein determination was done using the Lowry method (Lowry et al. 1951). Dried samples were digested in 1 N NaOH and allowed to react with alkaline copper citrate solution and Folin-Ciocalteau phenol reagent. Absorption of the solution was measured at 500 nm and 660 nm in a spectrophotometer (Thermo Scientific GENESYS 20) and compared with a bovine serum albumin standard. The standard curve for bovine serum albumin showed a clean, linear relationship between protein concentration and absorption at 660 nm. The Kjeldahl method for determining protein was also used. The total nitrogen (determined during C : N analysis) was multiplied by 6.25 (Association of Official Agricultural Chemists 1965).

All February samples were combusted in a calorimeter (Parr 6200) in the UH Hilo Chemistry Department using 1.0–1.5 g of dry powder. If dried powder could not be formed into pellets, the sample was placed inside the crucible with the combustion wire lying across the top of the sample. Total calories were calculated on an ash-free basis. Samples of *P. vaginatum* from May, August, and November were sent to Rajesh Jha, Department of

Human Nutrition, Food, and Animal Sciences, UH Mānoa, for analysis.

Samples (5.0–10.0 g of dried powder) were sent to the Agricultural Diagnostic Service Center at the College of Tropical Agriculture and Human Resources, UH Mānoa, for analysis. Samples were analyzed using a fiber analyzer (ANKOM 200), following ANKOM technology method 8.

All data were tested for homogeneity of variances and passed Bartlett's and Levine's tests for equal variances. A one-way analysis of variance (ANOVA) with a Tukey comparison was used to identify significant differences for each response (percentage water, percentage ash, C:N ratio, percentage protein, energy, and percentage lignin).

RESULTS

Nutritional composition of *Paspalum vaginatum*, *Pterocladiella capillacea*, and *Ahnfeltiopsis concinna* is listed in Table 1. Samples of *P. vaginatum* showed no significant seasonal variation in ash, C:N, protein, or lignin. Based on this lack of variation among seasons, all *P. vaginatum* data (winter, spring, summer, and fall) were combined to obtain overall mean values for ash, C:N, protein, and lignin for comparison with other species. However, the caloric value of springtime ($\bar{x} = 4{,}324$ cal/g ash-free dry wt) and summer ($\bar{x} = 4{,}281$ cal/g ash-free dry wt) samples was significantly higher than winter ($\bar{x} = 3{,}910$ cal/g ash-free dry wt) or fall samples ($\bar{x} = 3{,}507$ cal/g ash-free dry wt) ($F = 66.47$, df = 30, $P < .01$).

Water content data were collected on fresh samples only in February 2012: all had high percentage water values. There was a significant difference ($F = 8.82$, df = 23, $P < .02$) among the species (Table 1). The *P. vaginatum* and *Pt. capillacea* showed the highest water content, with a mean value of 77.5% and 77.8%, respectively. *Ahnfeltiopsis concinna* showed the lowest water content, with a mean of 68.0%.

Ash represents the inorganic salt and mineral content of a plant. Seashore paspalum's overall ash content ($\bar{x} = 11.8\%$ dry wt) was half that of the other species tested (Figure 2*A*) and significantly different ($F = 60.64$, df = 32, $P < .01$).

C:N ratios were highest for seashore paspalum and *A. concinna* (Figure 2*B*). The overall C:N ratio of seashore paspalum ($\bar{x} = 23.2$) was significantly greater than that of *Pt. capillacea* ($\bar{x} = 14.2$) ($F = 8.43$, df = 32, $P < .01$).

Lowry method results showed a significant difference ($F = 39.05$, df = 32, $P < .01$) among *P. vaginatum* and the seaweed species

TABLE 1

Nutritional Content of Samples (Mean ± Standard Deviation)

Species	Date Collected	Sample Size	Water %	Ash %	C:N	Protein %	Energy (cal/g)	Lignin %
Paspalum vaginatum	Winter 2 Feb. 2012	12	77.49 ± 5.9 a	12.08 ± 2.2 a	23.12 ± 6.3 a	16.41 ± 5.5 a	3,910 ± 156 b	11.08 ± 1.8 a
Paspalum vaginatum	Spring 8 May 2012	3	—	11.10 ± 0.1 a	19.50 ± 0.03 a	20.98 ± 0.4 a	4,324 ± 259 a	14.91* a
Paspalum vaginatum	Summer 31 Aug. 2012	3	—	12.35 ± 0.2 a	25.31 ± 1.7 a	17.31 ± 0.1 a	4,281 ± 75 a	11.16* a
Paspalum vaginatum	Fall 14 Nov. 2012	3	—	11.09 ± 0.3 a	25.22 ± 0.9 a	16.22 ± 1.4 a	3,507 ± 208 c	13.36* a
Pterocladiella capillacea	Winter 2 Feb. 2012	6	77.80 ± 3.5 a	22.64 ± 6.0 b	14.15 ± 1.0 b	5.95 ± 1.5 b	3,220 ± 193 c	3.69 ± 0.6 b
Ahnfeltiopsis concinna	Winter 2 Feb. 2012	6	68.04 ± 3.1 b	23.72 ± 1.0 b	21.53 ± 6.0 a,b	4.98 ± 0.9 b	2,846 ± 60 d	0.62 ± 0.2 c

Note: Water content is relative to fresh weight. Ash, protein, carbohydrate, C:N, and lignin are relative to dry weight. The values for energy are based on ash-free dry weight. Different letters within a column indicate significant differences ($P < .001$).

* Standard deviation not calculated because $n = 1$.

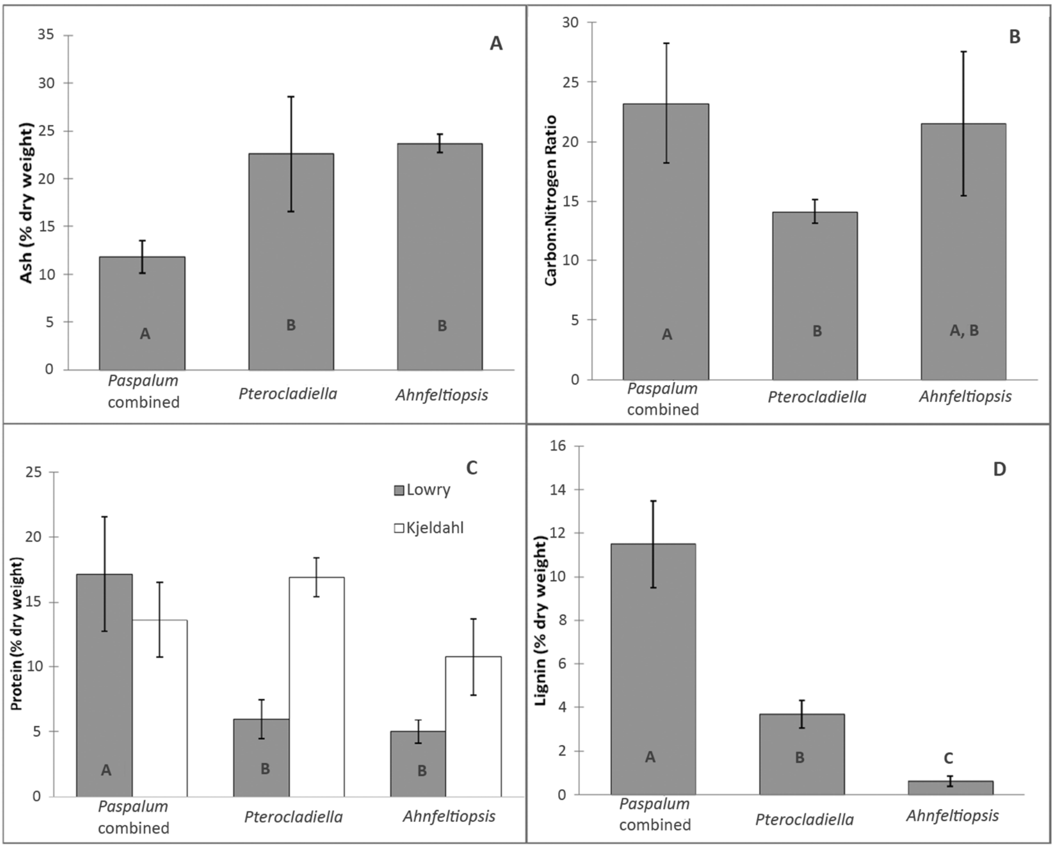

FIGURE 2. Comparisons of ash (percentage dry weight), C:N ratio (dry weight), total protein (percentage dry weight), and total lignin (percentage dry weight) using combined *Paspalum vaginatum* data. Means sharing a common letter are not significantly different, based on Tukey's comparison ($P < .001$). Error bars represent standard deviation. $n = 21$ for *P. vaginatum* (except for lignin $n = 15$); $n = 6$ for *Pterocladiella capillacea* and *Ahnfeltiopsis concinna*.

tested (Figure 2*C*). *Paspalum vaginatum* had a mean overall protein content of 17.2% dry wt; whereas mean protein values for *Pt. capillacea* and *A. concinna* were 6% and 5%, respectively. The Kjeldahl method based on nitrogen content generally indicated higher protein values than the Lowry method, probably because nitrogen occurs in many biological molecules of an organism, not just protein (Figure 2*C*).

There was a significant difference in caloric content ($F = 66.47$, $df = 30$, $P < .01$) among *P. vaginatum* samples and the seaweed species (Table 1). *Paspalum vaginatum* collected in spring 2012 showed the highest energy value ($\bar{x} = 4{,}324$ cal/g ash-free dry wt) and *A. concinna* the lowest ($\bar{x} = 2{,}846$ cal/g ash-free dry wt).

Paspalum vaginatum contained significantly higher amounts of lignin ($F = 130.67$, $df = 26$, $P < .01$) in comparison with *Pt. capillacea* and *A. concinna* (Figure 2*D*). Overall lignin content in seashore paspalum ($\bar{x} = 11.5\%$ dry wt) was more than three times that of *Pt. capillacea* ($\bar{x} = 3.7\%$ dry wt) and about 19 times the mean percentage lignin for *A. concinna* ($\bar{x} = 0.62\%$ dry wt).

DISCUSSION

Values determined in this study for water, ash, total protein, and energy content of

Paspalum vaginatum, *Pterocladiella capillacea*, and *Ahnfeltiopsis concinna* agreed with values reported in previous studies (McDermid and Stuercke 2003, Robinson et al. 2004, McDermid et al. 2007, Suyama et al. 2007), with two exceptions for *Pt. capillacea* (higher ash and lower protein measured in this study), which could be a result of differences in the location of collections or age of thalli. We found little seasonal variation in nutritional composition of *P. vaginatum* at Keaukaha Beach, Hilo. However, caloric content did vary among the seasons, perhaps because in spring and summer *P. vaginatum* has new growth or developing inflorescences and/or seeds with higher protein or lipid content. In comparison with the macroalgae growing at the same site, *P. vaginatum* contained similar water content, half the ash content, greater caloric value, higher percentage protein, a comparable C : N ratio, and higher lignin content.

One of the most commonly consumed species by green turtles in the Hawaiian Islands is *Pt. capillacea* (Balazs 1980, Russell and Balazs 1994). The selection of food species by the Hawaiian green turtle may be determined by energy and nutrients, as well as accessibility, abundance, and concentrations of natural chemical deterrents (Balazs 1980, Bjorndal 1985, Garnett et al. 1985, Forbes 1996, Russell et al. 2003). Green turtles may also choose their food based on toughness, texture, or taste (McDermid et al. 2007). In Florida, Bjorndal (1980) observed turtles selectively grazing on plots of the sea grass *Thalassia testudinum* Banks ex König, which exhibited lower lignin and higher protein content. Immature green turtles in Moreton Bay, Australia, selected food species with lower levels of fiber and higher levels of nitrogen (Brand-Gardner et al. 1999). Therefore, green turtles, like some marine herbivorous fish, may base their food choices on digestibility of cell wall carbohydrates and energy content (Montgomery and Gerking 1980, Zemke-White and Clements 1999). The hindgut microflora populations in green turtles vary in their ability to ferment the cell wall carbohydrates of marine macroalgae versus those of sea grasses, and this may be another factor in diet selection (Bjorndal 1985, Bjorndal et al. 1991). *Paspalum vaginatum* could provide more energy and more protein per gram per bite than *Pt. capillacea* for Hawaiian green turtles, especially if the turtles harbored microflora adapted to metabolize the complex structural carbohydrates in this terrestrial grass.

Ironically, *Paspalum vaginatum*, an invasive, alien, semiaquatic grass, appears to be a nutritious alternative food source for the native Hawaiian green turtle, which is protected under state law and the Federal Endangered Species Act of 1973 as amended. Green turtles in Hawaiʻi are exhibiting flexibility in their diets, in the face of slow maturation rates at some locations (Balazs and Chaloupka 2004), and dedicated fidelity to foraging territories (Balazs 1980, Wills 2010), no matter how marginal. Russell and Balazs (1994, 2009) previously documented "dietary shifts" as native seaweed stocks declined and alien macroalgae became more plentiful in the Hawaiian Islands. Similarly, when cyclones and flooding destroyed sea grass meadows in the Great Barrier Reef, Australia, in early 2011, researchers reported that the majority of surviving turtles in their study sites near Townsville had made a dietary shift and were feeding on red algae (Bell and Ariel 2011). Hawaiian green turtles are the iconic example of a population whose resiliency and recovery are linked to the plasticity of its foraging strategy—exploitation of new food sources (Russell and Balazs 2009). At some foraging areas in Hawaiʻi, green turtle carrying capacity has been reached, thereby explaining a decline in somatic growth rates and body condition in recent years (Balazs and Chaloupka 2004, Wabnitz et al. 2010), which could be mitigated by the use of new food sources. Green turtles may opportunistically consume invasive *P. vaginatum* because of its increasing abundance in traditional turtle foraging areas and/or its high protein and caloric content. *Paspalum vaginatum* along the Keaukaha shoreline is primarily accessible to turtles only at high tide, but elsewhere on the island, in brackish-water fishponds (e.g., Kīholo) and anchialine ponds (e.g., in Kaʻū), *P. vaginatum* and other terrestrial plants growing at the water's edge are available to foraging turtles at other tidal phases.

The consumption of *Paspalum vaginatum* may be further evidence of members of an evolutionarily antique species, *Chelonia mydas*, demonstrating their adeptness at adapting their foraging strategies in response to human-induced changes in their environment. To predict the response of green turtles to future changes in the coastal zone, studies are needed to determine the amount of seashore paspalum being consumed relative to other dietary items; the ability of hindgut microflora to ferment terrestrial grass, which influences its digestibility; and the number of turtles that forage on terrestrial grass at Keaukaha and elsewhere in the Hawaiian Islands.

Note in Proof: In December 2014, the necropsy (#25126) by USGS of a turtle from the Leleiwi area, adjacent to our study site, revealed approximately 2 kg of *Paspalum* sp. in the gastrointestinal tract, "from stem to stern" (T. Work personal communication) (Figure 3).

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FIGURE 3. *Paspalum* sp. filled the gastrointestinal tract (esophagus and crop shown here) of a Leleiwi turtle, necropsied by Thierry Work, USGS, December 4, 2014. Photo by Devon Francke, NOAA PIFSC.

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