

A Comparison of Immature Green Turtle (*Chelonia mydas*) Diets among Seven Sites in the Main Hawaiian Islands¹

Karen E. Arthur^{2,3} and George H. Balazs⁴

Abstract: Understanding resource acquisition and feeding ecology of threatened species is integral to their conservation because diet is intimately linked with growth rate and reproductive output. We examined diets of immature green sea turtles, *Chelonia mydas* (L.), from seven sites on the islands of Hawai'i, O'ahu, Moloka'i, and Lāna'i in January and August 2003. Diet analysis was based on 191 samples collected from 181 live green turtles by stomach lavage. These samples were identified and quantified using dissection microscopy and the principles of microstereology. Diet of green turtles in the Main Hawaiian Islands was dominated by red algae, and diet items most commonly encountered were *Acanthophora spicifera* (an introduced species), *Hypnea* sp., *Pterocladia* sp., and *Cladophora* sp. Sea grasses (*Halophila hawaiiiana* and *H. decipiens*) were an important component of diet in turtles from Kāne'ohe Bay. Content of green turtle diets differed among foraging grounds, and these differences may provide an insight into previously documented differences in turtle growth rates among sites.

GREEN TURTLES, *Chelonia mydas* (L.), are threatened marine reptiles found throughout the world's tropical and subtropical oceans (Pritchard 1997), with distinctive genetic populations structured within oceanic basins (Bowen et al. 1992). Although many Pacific Ocean populations are declining because of

overharvest of adults and eggs (Seminoff 2002), the Hawaiian population is in a state of recovery, with long-term increases in nesting numbers on French Frigate Shoals (Balazs and Chaloupka 2004a, 2006).

The Hawaiian green turtle genetic stock is made up of a number of geographically disparate foraging ground populations within the 132 islands of the Hawaiian archipelago (Balazs and Chaloupka 2004a). Immature green turtles recruit to these inshore foraging habitats at ~35 cm straight carapace length (SCL) and ~6 kg (Zug et al. 2002) where their diet shifts from the omnivorous planktivory of a pelagic turtle to the herbivorous diet of an inshore immature turtle (Bolten 2003). In these inshore foraging habitats, turtles demonstrate high site fidelity and foraging ground specific growth rates (Balazs and Chaloupka 2004b). The turtles are all from the same genetic stock (Bowen et al. 1992); therefore it is likely that these differences in growth rate are based on the availability or quality of food at each foraging ground (Balazs and Chaloupka 2004b).

An understanding of green turtle feeding ecology is integral to their conservation. Not only does diet potentially influence growth

¹The U.S. National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service Pacific Islands Fisheries Science Center provided partial funding and logistical support for this project. All research was conducted under State of Hawai'i Department of Land and Natural Resources Scientific Collecting Permit SCP 2003 04. Manuscript accepted 18 July 2007.

²Centre for Marine Studies, University of Queensland, St. Lucia, Queensland 4072, Australia.

³Corresponding author. Current address: Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, Florida, 34949 (phone: 772-462-0973; fax: 772-461-8154; e-mail: arthur@si.edu).

⁴NOAA, National Marine Fisheries Service, Pacific Islands Fisheries Science Center. 2570 Dole Street, Honolulu, Hawai'i 96822-2396.

rate, but, in turn, growth rate is related to the time it takes turtles to reach maturity (Balazs 1982, Balazs and Chaloupka 2004b). A delay in maturation may decrease survivorship to adulthood and, therefore, reproductive output (Balazs and Chaloupka 2004b). Diet quality or quantity, as controlled by prevailing environmental conditions, have also been correlated with interannual variability in nesting numbers through the availability of forage material during the months and/or years preceding breeding (Limpus and Nicholls 1988, Broderick et al. 2001). Therefore, resource availability and acquisition is also a determinant in reproductive output and population survival.

The diet of post-pelagic green turtles has been described for many populations around the world and consists predominantly of seagrass, macroalgae, and often small amounts of animal material (Bjorndal 1997). Forage items found in their diet are primarily associated with the local availability of those forage items (Bjorndal 1980, Garnett et al. 1985), although some level of selectivity has also been demonstrated (Mortimer 1982, Brand-Gardner et al. 1999). Dietary studies of green turtles in algal-dominated systems indicate that turtles feed predominantly on Rhodophyta (red algae), although Chlorophyta (green algae) and Phaeophyta (brown algae) are also consumed (Garnett et al. 1985, Forbes 1996, Seminoff et al. 2002). In an extensive study of resident turtles at Heron Island, Australia, an algal-based coral reef community, Forbes (1996) found that green turtles demonstrated a preference for certain species and avoidance of undesirable forage material. Preferred species included *Gelidiella* sp. and *Sargassum* sp., and turtles avoided *Halimeda* sp. and *Chlorodesmis* sp. Although there were differences in diet among size classes, all turtles appeared to have a base diet of algal turf that was opportunistically enhanced with desirable monogeneric stands when available.

In the algal-based coral reef system of the Hawaiian Islands, green turtles also feed on algae and seagrass. Of approximately 400 species of algae present in the Hawaiian archipelago (Abbott 1999), only nine species accounted for the majority of green turtle diet

items (Balazs 1980b). In a study of 21 turtles from Pālā'au, Moloka'i, the red alga *Acanthophora specifera* was the most prevalent diet item, but other red algae such as *Amansia glomerata*, *Spyridia filamentosa*, and *Hypnea cervicornis* were also common (Balazs et al. 1987). The seagrasses *Halophila hawaiiiana* and *H. decipiens* are also found in Hawaiian green turtle diets but only from a few locations that provide suitable habitat for seagrass growth (Russell et al. 2003).

In this study, we examined the diet of immature green turtles from the algal-dominated coral reef system of the Main Hawaiian Islands. The specific aim of this research was to characterize the diet of green turtles from geographically disparate foraging ground aggregations within the inhabited islands of the Hawaiian archipelago.

MATERIALS AND METHODS

Seven green turtle foraging locations were examined (Figure 1). These sites were selected to provide a variety of habitat types and known growth rates from foraging aggregations previously assessed during long-term population demographic studies (Balazs et al. 1987, Balazs and Chaloupka 2004b). Each site was sampled during two field trips: 22–31 January and 11–26 August 2003, except for Kapoho, which was sampled only in August 2003 (Table 1).

Two sites on the northeastern coast of O'ahu were sampled: Kāne'ohe Bay (21° 31' N, 158° 51' W) and Kailua Bay (21° 25' N, 157° 44' W). Both sites are relatively shallow bays protected seaward by coral reefs. Pālā'au, on the southern shore of Moloka'i (21° 06' N, 157° 07' W) consists of a broad reef flat fringed by mangroves. The northeastern coast of Lāna'i (20° 55' N, 156° 54' W) features inshore coral reef flats that extend out to the Au'au Channel that separates Lāna'i from Maui and Moloka'i. Three sites were studied on the island of Hawai'i, two sites on the west coast (Kona/Kohala) and one on the east coast. On the Kona/Kohala coast, Kīholo Bay (19° 52' N, 155° 55' W) provides foraging and resting habitat for immature turtles primarily in the Wainānālī'i Lagoon but

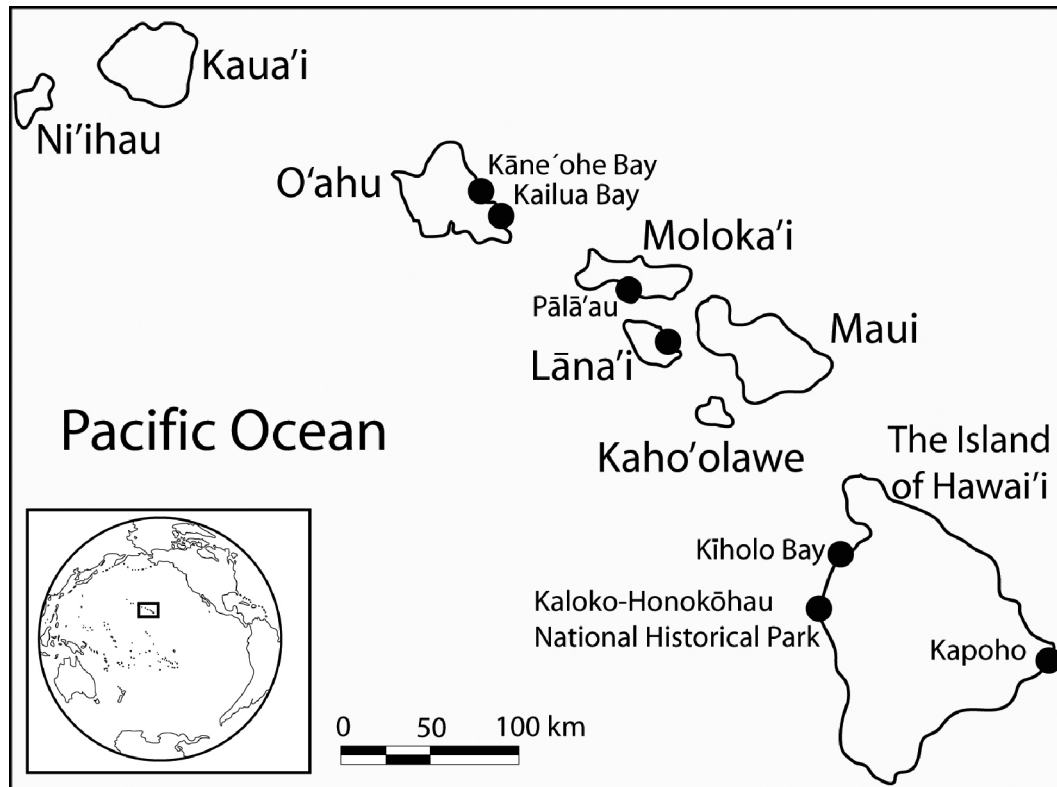


FIGURE 1. The Main Hawaiian Islands. Study sites are denoted by a closed circle (●). Inset map shows locality of the Hawaiian archipelago within the Pacific Ocean.

TABLE 1
Number of Turtles Sampled at Each Site for Each
Sampling Period

Site	January 2003	August 2003 ^a	Total
Kāne'ōhe Bay, O'ahu	16	10 (2)	26
Kailua Bay, O'ahu	16	25 (2)	41
Pālā'au, Moloka'i	15	2 (1)	17
Lāna'i	10	10 (0)	20
Kīholo Bay, Hawai'i	24	20 (4)	44
Kaloko-Honokōhau, Hawai'i	20	15 (1)	35
Kapoho, Hawai'i	—	8 (0)	8
All sites combined	101	90 (10)	191

^a Number in parentheses represents the number of turtles sampled in August that had previously been sampled in January.

also in the mixohaline ancient Hawaiian fishponds adjacent to the lagoon (Balazs et al. 2000, Harrington et al. 2000), and Kaloko-Honokōhau National Historical Park (19° 25' N, 155° 55' W) is the site of an ancient Hawaiian settlement that provides turtle foraging habitat along the rocky inshore reef. The third site on the island of Hawai'i was Kapoho (19° 30' N, 154° 49' W). This site includes a shallow rocky embayment, fringed with mangroves, and a series of protected geothermal-heated pools used by turtles for underwater resting.

Turtles were captured at Pālā'au, Moloka'i, using a nonentangling bullpen net (Balazs et al. 1987, Balazs and Chaloupka 2004b), and at other locations turtles were captured by hand while snorkeling or with the use of scoop nets (Balazs et al. 2000).

The turtles were brought to shore or to a boat to be tagged, weighed, and SCL measured (Balazs et al. 1987). Gender was not determined in this study.

Diet samples were obtained by stomach lavage after the modified methods of Balazs (1980a) and Forbes and Limpus (1993). Turtles were placed on their back, slightly angled with head lower than their body. Their mouth was opened using an avian veterinary speculum and held open with a standard veterinarian canine gag. A plastic tube, lubricated with vegetable oil, was gently inserted into the esophagus, and seawater was introduced at low pressure to the crop to flush out food particles in the esophagus and anterior crop. These items were assumed to be from the most recent feeding event. Samples were immediately frozen and maintained at $<0^{\circ}\text{C}$ until analyzed.

Diet samples were identified and quantified under dissection microscope. Each diet item was identified to the lowest possible taxon. Algae were identified in accordance with Magruder and Hunt (1979), Cribb (1983, 1996), Abbott (1999), Russell and Balazs (2000) and with assistance from Dennis Russell (pers. comm.). Seagrass was also identified in accordance with Waycott et al. (2004). Quantitative assessment of diet was based on the frequency of occurrence of each diet item and its relative volume within each diet. Frequency of occurrence was calculated based on the number of samples in which the diet item was observed:

Frequency of occurrence (%)

$$= \frac{(\text{No. samples in which diet item observed}) \times 100}{\text{Total no. samples}}$$

The relative volume that each diet item contributed to diet was determined using the principles of microstereology (Schaefer 1970) after the modified methods of Forbes (1999) and Read and Limpus (2002). The samples were mixed until visually homogenous and viewed at $\times 7$ magnification, giving a 19 mm field of view. A graticule with 33 marked positions was used to determine the volumetric proportion of each food item by counting the number of points covering each food

type. Ten nonoverlapping fields of view were observed, and a total of 330 points were identified for each sample (Arthur 2005). The relative proportion of each food type present was then calculated by dividing the number of points covering each food type by the total number of points observed for the sample.

Relative volume of diet (%)

$$= \frac{(\text{No. of points covering diet item}) \times 100}{\text{Total no. points assessed for sample}}$$

As a comparison with diet samples, fecal pellets were collected opportunistically along the beaches on the northeastern coast of Lānaʻi and at Kaloko-Honokōhau (Hawaiʻi). Samples from Lānaʻi were collected at the same time as live animal diet sampling and fecal samples from Kaloko-Honokōhau were collected in July 2003. Fecal material was observed under dissection microscope and identified, where possible, as per dietary items. As a result of the breakdown associated with gut passage, it was determined that the relative volumetric analysis used for the diet samples was inappropriate for fecal material (Seminoff et al. 2002) and, therefore, only the frequency of occurrence of each diet item will be considered.

Diet information is presented as the mean proportion each item contributed to diet (\pm standard error) and the frequency with which items were observed in samples. Frequency is expressed as the proportion of samples in which a diet item is observed, where the diet item was $>5\%$ volume, and where it was $>50\%$ volume. A nonmetric multidimensional scaling approach was used to determine whether there was a sampling event and/or site effect influencing the type of food consumed by the turtles. This ordination approach is an iterative procedure that uses a function of dissimilarity measure for each pair of samples and then reconciles these points in terms of distance on a multidimensional plot. In this instance, presence/absence data for taxonomic groupings of diet data were used to assess variations between the two sampling events and between sites. Kapoho was not included in this analysis be-

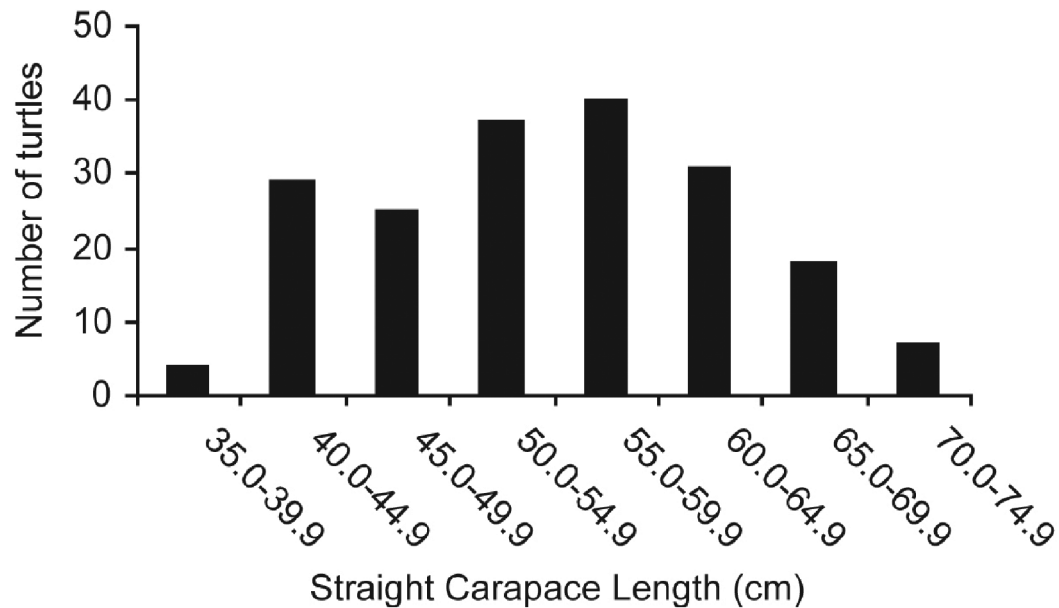


FIGURE 2. Frequency histogram of straight carapace length of turtles captured in the Hawaiian Islands during 2003 for diet analysis ($n = 191$).

cause data for only one sampling event was available. Using Primer 5 (V5.1.2, Primer-E Ltd., Plymouth), a Bray-Curtis similarity matrix was established for all samples, and nonmetric multidimensional scaling was used to produce an ordination of these data. The resulting two-dimensional ordination had a stress level of 0.16. A two-way crossed analysis of similarity (ANOSIM2) was used to assess the effects of site and sampling event on the diet samples. ANOSIM is a nonparametric permutation procedure that is applied to the similarity matrix. A two-way crossed ANOSIM is analogous to a two-way nested analysis of variance (ANOVA) (Clarke and Warwick 1994), and in this case it was used to test the null hypotheses that there was no difference between sites averaged across sampling events and no difference between sampling events using site groups as samples. Statistical significance was accepted at $P < .05$.

RESULTS

In total, 181 green turtles were captured and their stomachs flushed during January and

August sampling events in 2003 to yield 191 diet samples. Ten turtles were sampled in both January and August. All turtles were <75 cm (SCL) in length (Figure 2). The minimum breeding size for green turtles in the Hawaiian Islands metapopulation is 80 cm (Balazs and Chaloupka 2004b). Thus, all animals examined during this study were assumed to be immature.

Table 2 provides a summary of the 191 diet samples from live green turtles captured in the Hawaiian Islands. Green turtles in the Hawaiian Islands have an algal-based diet, with the majority of material found in crop samples from the division Rhodophyta (red algae). Red algae were the most common dietary items encountered (present in 99.5% of samples), and they provided the greatest proportion of the dietary volume, with an average of 78.0% for all sites combined. Chlorophyta (green algae) and Phaeophyta (brown algae) were also common but contributed little quantity to the diet. Sea grass was uncommon and only found in turtles sampled from Kāneʻohe Bay, where it contributed >5% of the dietary volume in all cases where ob-

TABLE 2
Food Items Found in Green Turtle Diets in the Hawaiian Islands

Diet Item	Relative Volume (%)		Proportion of Samples (%)		
	Mean	SE	Present	>5%	>50%
Seagrass					
<i>Halophila decipiens</i>	1.6	0.8	3.1	3.1	1.5
<i>Halophila hawaiiiana</i>	0.6	0.4	2.6	1.5	1.0
Total seagrass	2.1	0.9	5.6	4.6	2.6
Algae					
<i>Acanthophora spicifera</i>	23.7	2.2	49.2	43.6	27.7
<i>Amphiroa</i> sp.	0.1	0.0	5.1	—	—
Family Ceramiaceae	0.4	0.1	15.4	2.6	—
<i>Cerium</i> sp.	0.3	0.1	19.0	1.0	—
<i>Centroceras clavulatum</i>	1.3	0.3	28.2	7.2	0.5
<i>Chondria</i> sp.	<i>T</i>	—	3.1	—	—
<i>Gelidiella</i> sp.	1.0	0.5	4.6	2.1	1.0
<i>Gelidium</i> sp.	<i>T</i>	—	0.5	—	—
<i>Gracilaria</i> sp.	8.6	1.5	32.3	22.1	7.2
<i>Hypnea</i> sp.	11.8	1.3	72.8	39.5	8.2
<i>Laurencia</i> sp.	2.9	0.4	45.1	15.4	—
<i>Amansia glomerata</i>	8.9	1.6	26.2	17.4	8.2
<i>Polysiphonia</i> sp.	0.8	0.3	32.3	2.6	—
<i>Pterocladia</i> sp.	17.8	2.0	52.8	36.9	16.9
Total Rhodophyta	78.0	1.6	99.5	95.9	70.3
<i>Bryopsis</i> sp.	<i>T</i>	—	0.5	—	—
<i>Cladophora</i> sp.	6.7	1.0	63.1	29.7	3.1
<i>Codium</i> sp.	2.5	0.8	13.3	6.7	2.1
<i>Dictyosphaeria</i> spp. (<i>D. cavernosa</i> and <i>D. versluysii</i> combined)	1.1	0.3	25.1	5.6	0.5
<i>Enteromorpha</i> sp.	0.1	—	3.6	0.5	—
<i>Halimeda opuntia</i>	0.5	0.1	12.3	3.1	—
<i>Rhizoclonium grande</i>	<i>T</i>	—	0.5	—	—
<i>Ulva</i> sp.	0.7	0.2	26.2	5.1	—
Total Chlorophyta	11.6	1.3	84.1	45.1	5.6
<i>Dictyota</i> sp.	0.3	0.1	22.1	—	—
<i>Lobophora variegata</i>	0.2	0.1	3.6	1.0	—
<i>Padina</i> sp.	<i>T</i>	—	0.5	0.5	—
<i>Sargassum</i> sp.	0.4	0.2	12.3	1.5	—
<i>Turbinaria ornata</i>	0.8	0.2	12.8	6.7	—
<i>Zonaria</i> sp.	0.4	0.2	1.5	—	—
Total Phaeophyta	1.7	0.3	38.5	9.7	—
Other					
<i>Lyngbya majuscula</i>	0.6	0.2	25.1	3.1	—
<i>Lyngbya semiplena</i>	0.2	0.1	2.1	—	—
<i>Lyngbya porphyrosiphonis</i>	<i>T</i>	—	1.0	—	—
<i>Schizothrix</i> sp.	<i>T</i>	—	0.5	—	—
Total Cyanobacteria	0.7	0.2	27.2	3.1	—
Crustacean	0.1	—	4.6	—	—
Egg mass	<i>T</i>	—	0.5	—	—
Unidentified jellyfish	0.2	0.1	3.6	1.0	—
<i>Stylocheilus</i> sp.	<i>T</i>	—	0.5	—	—
Unidentified white egg mass	<i>T</i>	—	0.5	—	—
Gastropod shell	0.6	0.3	31.8	1.5	0.5
Sponge	<i>T</i>	—	2.1	—	—
Total animal material	0.9	0.3	36.9	2.6	0.5

TABLE 2 (continued)

Diet Item	Relative Volume (%)		Proportion of Samples (%)		
	Mean	SE	Present	>5%	>50%
Terrestrial material	<i>T</i>	—	0.5	—	—
Green plastic	<i>T</i>	—	0.5	—	—
Total miscellaneous	<i>T</i>	—	4.6	—	—
Unidentified material	4.9	0.4	88.2	33.8	—

Note: Diet samples are from seven sites combined ($n = 191$). Mean relative volume (\pm standard error) is the average that each diet item contributes to diet. *T*, trace (mean $<0.1\%$). Frequency of occurrence is expressed as the proportion of samples in which the diet item was found and also where it was found to contribute $>5\%$ and $>50\%$ of relative volume.

served. Cyanobacteria and animal material, such as sponge, were both common in samples (36.4% and 27.2%, respectively) but generally only contributed trace ($\leq 0.1\%$) amounts. Other items observed included

green plastic (found in the diet sample of a turtle from Kailua), and unidentified terrestrial plant material.

Twenty-seven genera of algae and two genera of Cyanobacteria were identified. In

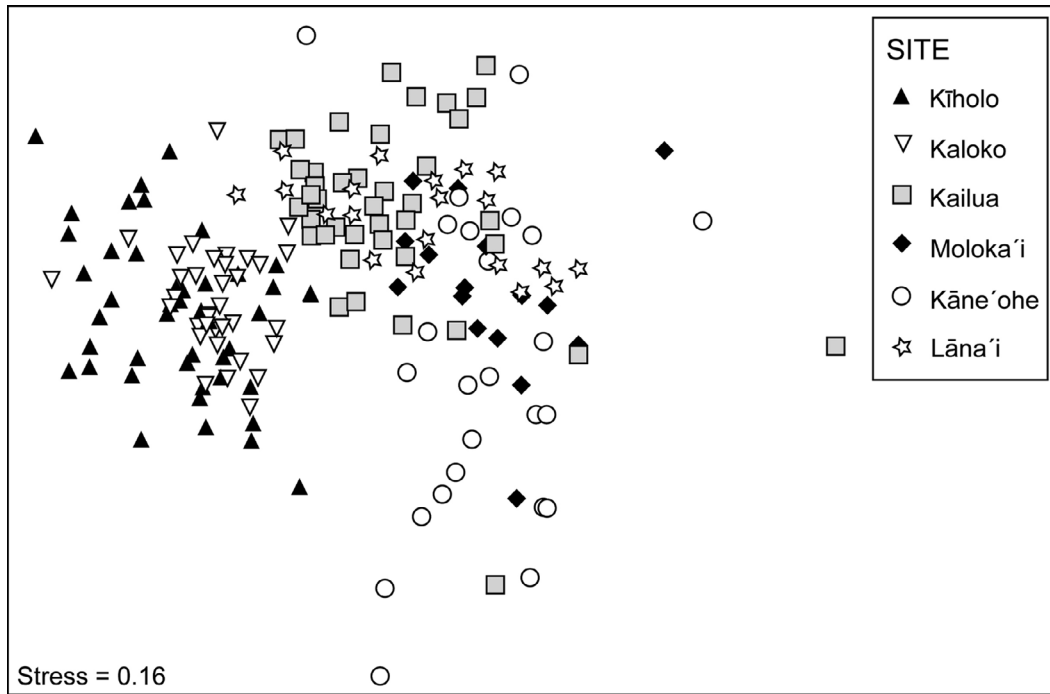


FIGURE 3. Two-dimensional multidimensional scaling ordination showing the grouping of diet samples by foraging site based on the presence/absence of diet items in each sample ($n = 183$). Points that appear closer together are more similar in their algal assemblages than points farther apart. Kapoho was not included in this analysis because it was sampled only during August.

most samples (78.9%), one diet item made up the majority of the relative volume (>50% of sample). Genera that contributed >50% of diet samples included *Halophila* sp., *Acanthophora* sp., *Centroceras* sp., *Gelidiella* sp., *Gracilaria* sp., *Hypnea* sp., *Pterocladia* sp., *Amansia glomerata*, *Cladophora* sp., *Codium* sp., and *Dictyosphaeria* sp.

The two-way crossed ANOSIM indicated that sites could be distinguished from one another using presence/absence of diet items, but no difference was found between the two sampling events at each site (site: global $R = 0.577$, significance level = 0.1%, $P = .001$; sampling event: global $R = 0.269$, significance level = 5.2%, $P = .052$). The similarity in turtle diets was evident in the clumping of the site factor in the multidimensional scaling ordination (Figure 3). This similarity in diet was driven by *Cladophora* sp. and *Pterocladia* sp. in Kīholo Bay and Kaloko-Honokōhau, but by *Acanthophora spicifera* and *Hypnea* sp. at Moloka'i, Lāna'i, Kailua Bay, and Kāne'ohe Bay (Figure 4). Also, the presence of *Halophila decipiens* in Kāne'ohe Bay samples (Figure 4) contributed to the separation of these samples from other sites in the multidimensional scaling ordination (Figure 3). This suggests that there was little seasonal variation in turtle forage material, but that each foraging ground provided different forage suitable for turtle diets.

Five fecal pellets were collected from along the beach at both Lāna'i and Kaloko-Honokōhau. These samples contained 9 and 11 identifiable items, respectively. Undigested diet material included Rhodophyta, Chlorophyta, Phaeophyta, Cyanobacteria, sponge, and monofilament fishing line (Table 3). A greater diversity of algae genera was observed in diet samples from both sites (Lāna'i = 20, Kaloko-Honokōhau = 18) compared with identifiable items observed in fecal pellets. Fleshy red algae, such as *A. spicifera*, which were observed in 90% of diet samples from Lāna'i, were not found in any of the fecal pellets from the same site. Conversely, *Dictyota* sp. and *Sargassum* sp. were observed in fecal material but not in any diet samples from Kaloko-Honokōhau.

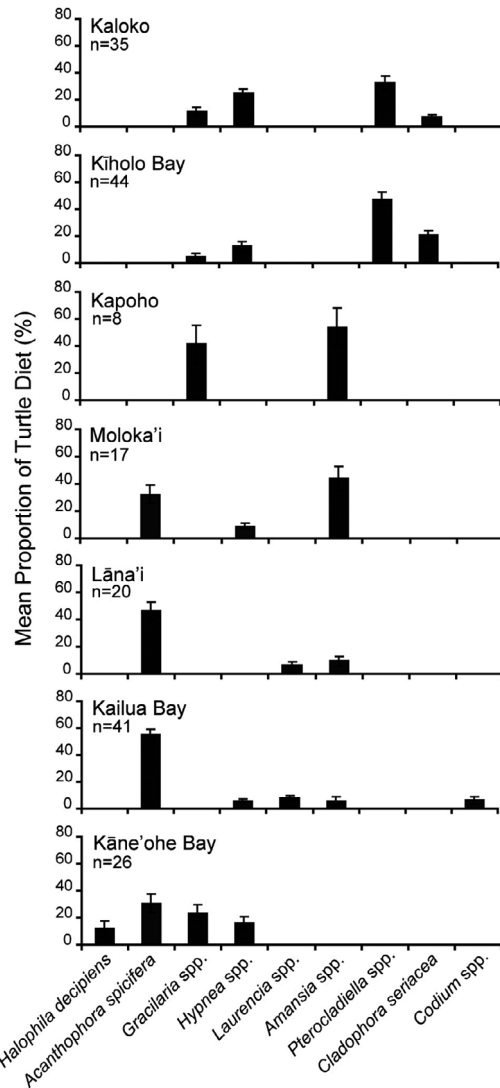


FIGURE 4. Diet of green turtles in the Hawaiian Islands grouped by site ($n = 191$). Diet items contributing an average relative mean volume >1% of diet at each location are shown.

DISCUSSION

Green turtles in the Main Hawaiian Islands, at the southern end of the archipelago, predominantly consume red macroalgae. The corticated red algae dominated diets at most study sites, and some form of red algae was

TABLE 3

Comparison of Frequency of Occurrence of Food Items Observed in Fecal Pellets and Stomach Flush Samples Collected from the Crop of Turtles Captured in Lāna'i and Kaloko-Honokōhau

Diet Item	Frequency of Occurrence (%)			
	Kaloko-Honokōhau		Lāna'i	
	Crop	Fecal	Crop	Fecal
<i>Acanthopora spicifera</i>	5.7	0	90.0	0
<i>Amphiroa</i> spp.	17.1	0	0.0	0
<i>Cerium</i> spp.	54.3	0	35.0	0
<i>Centroceras</i> spp.	54.3	0	30.0	0
<i>Cbondria</i> spp.	2.9	0	5.0	0
<i>Gracilaria</i> spp.	48.6	0	10.0	0
<i>Hypnea</i> spp.	85.7	0	80.0	80
<i>Laurencia</i> spp.	28.6	0	85.0	0
<i>Melanamansia glomerata</i>	5.7	20	65.0	100
<i>Polysiphonia</i> spp.	45.7	20	40.0	0
<i>Pterocladia</i> spp.	77.1	100	25.0	40
Total Rhodophyta	100	100	100	100
<i>Cladophora</i> spp.	97.1	40	50.0	20
<i>Codium</i> spp.	5.7	0	30.0	0
<i>Dictyosphaeria</i> spp.	14.3	40	55.0	80
<i>Enteromorpha</i> spp.	17.1	100	0.0	0
<i>Halimeda</i> spp.	0.0	20	20.0	0
<i>Ulva</i> spp.	62.8	40	100	20
Total Chlorophyta	95.6	100	90.5	80
<i>Dictyota</i> spp.	0.0	20	20.0	0
<i>Sargassum</i> spp.	0.0	20	23.8	0
<i>Turbinaria</i> spp.	2.9	0	30.0	0
<i>Zonaria</i> spp.	0.0	0	5.0	0
Total Phaeophyta	2.2	40	71.4	0
<i>Lyngbya majuscula</i>	20.0	0	50.0	80
Total Cyanobacteria	24.4	0	42.9	80
Egg material	5.7	0	0	0
Jellyfish	0	0	15	0
Sponge	11.4	20	0	20
Fishing line	0	0	0	20

Note: Fecal pellets were collected on the beach at Lāna'i (diet $n = 20$, fecal $n = 5$) and Kaloko-Honokōhau (diet $n = 35$, fecal $n = 5$).

present in 99.5% of samples. The only exception was a sample from Kāne'ohe Bay that was composed entirely of *Halophila decipiens*. The seagrasses *H. decipiens* and *H. hawaiiiana* contributed substantially to the diets of Kāne'ohe Bay turtles, supporting a previous study demonstrating that both species were present in green turtle diets in the Hawaiian

Islands (Russell et al. 2003). The genera of algae encountered most often in diet samples in the study reported here generally reflect those previously reported for the Main Hawaiian Islands (Balazs 1980b, Balazs et al. 1987, Balazs et al. 2000, Russell and Balazs 2000). However, in this study, we have also identified site-specific differences in green turtle diets (Figures 3 and 4).

Although some degree of preference for certain food items has been demonstrated in other green turtle populations (Mortimer 1982, Brand-Gardner et al. 1999), diet selection is ultimately driven by the availability of preferred diet items (Forbes 1996). The differences in diet among sites in the study reported here may reflect the forage material available at each site. For example, the diets of turtles at Kīholo and Kaloko-Honokōhau were similar (Figure 4), and because both sites are located on the Kona/Kohala coast of the island of Hawai'i, similar environmental conditions are likely to be structuring the faunal assemblage and therefore food availability at the two locations.

Diet samples in this study were dominated by a single food item. In 78.9% of samples, one alga or seagrass made up more than 50% of the sample (Table 2). A monospecific food reliance suggests that turtles were targeting specific species and potentially incidentally ingesting other co-occurring algae growing in close proximity. This evidence supports the theory that green turtles are selective feeders (Bjørndal 1980, Mortimer 1982, Brand-Gardner et al. 1999), as was noted by Forbes (1996) at Heron and Wistari Reefs, Australia.

Acanthopora spicifera was common in diets from all sites except on the island of Hawai'i. This alga was accidentally introduced to the Hawaiian Islands in the 1950s (Doty 1961) and colonized successfully and spread quickly (Russell and Balazs 1994, Abbott 1999, Smith et al. 2002). By 1980, *A. spicifera* had become a principal component of turtle diets on Lāna'i and a minor food source for turtles at O'ahu but was not at that time considered a major food source for turtles in the Hawaiian archipelago (Balazs 1980b). Later that decade,

it was reported as a dominant food source both at O'ahu and Moloka'i and present in diet samples from Maui (Balazs et al. 1987). Both *A. spicifera* and *H. musciformis* (another alga introduced to the Hawaiian Islands in the 1970s) became common elements of green turtle diet by the 1990s (Russell and Balazs 1994). In the study reported here, *A. spicifera* was common in the turtles' diet (49.2%) and contributed a substantial proportion of diet at Kāne'ōhe Bay, Kailua, Moloka'i, and on the east coast of Lāna'i. This dietary composition demonstrates the extent to which the alga has spread throughout the Islands. The absence of *A. spicifera* from turtle diets collected from Kapoho and Kīholo on the island of Hawai'i suggests that it has not yet established in these areas. This hypothesis is consistent with a report by Smith et al. (2002) stating that no *A. spicifera* was found at either Kapoho or Kīholo, although *A. spicifera* was reported to be present at Kaloko-Honokōhau in the harbor adjacent to the turtle sampling location. As only two of the 35 turtles from this site consumed *A. spicifera* and only in small quantities, it is believed that the alga is sparse within the foraging area. The diet-switching capabilities of turtles to utilize nonendemic algae species such as *A. spicifera* demonstrate that although green turtles are selective foragers, they are also opportunistic feeders that can adapt to novel food resources.

Not only was *A. spicifera* common in turtle diets, it may also provide an important source of energy. Although many algal species were identifiable in fecal pellets from both Kaloko-Honokōhau and Lāna'i, no *A. spicifera* was observed (Table 3). This was the case even though it was a common component of turtle diet at Lāna'i and present in two samples from Kaloko-Honokōhau. The presence of identifiable diet items in fecal material implies that this alga is not fully digested. Green turtle fecal pellets previously collected in Kāne'ōhe Bay were also found to have identifiable algae present (Balazs et al. 1993), indicating that not all material ingested by Hawaiian turtles is digested and assimilated. In a similar study, conducted in another

algal-dominated foraging ground in the Torres Strait, Australia, no identifiable material was found in fecal pellets (Garnett et al. 1985). Turtles in the region had been feeding on algae of the genera *Hypnea*, *Laurencia*, *Caulerpa*, *Vidalia*, and *Sargassum*. *Hypnea*, *Laurencia*, and *Sargassum* were observed in diets in the study reported here, but only *Hypnea* sp. and *Sargassum* sp. were present in fecal material. This could indicate that digestion efficiency varies among turtle populations or that the structural composition of algae varies between sites. Algal species have plastic morphological traits (Dring 1992), and therefore different environmental conditions could lead the same taxa to have different structural characteristics that may render the algae more or less susceptible to digestion.

Differences in availability in forage material and low digestion efficiency may provide some explanation of the variable growth rates observed among various Hawaiian green turtle foraging aggregations (Balazs and Chaloupka 2004b). To clearly understand this relationship, the abundance and growth rate of forage material, and the nutritional value, digestibility, and foraging costs required to obtain and process these diet items should be quantified. In addition, these parameters should also be considered in terms of the density-dependent effects of a green turtle stock that is currently in recovery (Balazs and Chaloupka 2004 a,b, 2006).

To our knowledge, this is the first time multidimensional scaling has been used to address the feeding ecology of marine turtles, and this technique has provided insight into intrinsic differences between these foraging ground populations. As it is a nonparametric test, it is versatile and capable of analyzing datasets that contain large amounts of information. As such, multidimensional scaling may prove useful in understanding the feeding ecology of other sea turtle populations and addressing issues such as variation between age classes, foraging location, or seasonal variation in feeding ecology.

This is also the first known study to compare the diets of immature green turtles

across multiple sites in the Main Hawaiian Islands. We have demonstrated that although green turtle diets are dominated by red algae, the major constituents of diet vary between sites. Turtles appeared to be selective and opportunistic feeders that target a primary diet item rather than grazing on multiple species. However, these observations were probably ultimately influenced by the availability of forage items within the foraging area.

ACKNOWLEDGMENTS

We thank S. K. K. Murakawa, S. Eames, and C. Hooven for their assistance in logistics and fieldwork. M. Rice and the students from the Hawai'i Preparatory Academy, T. Work, S. Beavers, E. and D. Medeiros, D. Bicoy, M. Chang, B. Puleloa, and B. Morris assisted in the capture and sampling of turtles. We acknowledge D. Russell for his advice in differentiating algae in turtle diet samples and S. Kubis, T. Tucker, G. Antonelis, and the anonymous reviewers for their valuable comments on the manuscript.

Literature Cited

- Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu, Hawai'i.
- Arthur, K. E. 2005. Ecotoxicology of the cyanobacterium *Lyngbya majuscula* and health implications for green sea turtles (*Chelonia mydas*). Ph.D. diss., Centre for Marine Studies, University of Queensland, Brisbane.
- Balazs, G. H. 1980a. Field methods for sampling the dietary components of green turtle *Chelonia mydas*. *Herpetol. Rev.* 11:5–6.
- . 1980b. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Department of Commerce, NOAA-TM-NMFS-SWFC-7, Honolulu.
- . 1982. Growth rates of immature green turtles in the Hawaiian archipelago. Pages 117–125 in K. A. Bjorndal, ed. *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, D.C.
- Balazs, G. H., and M. Chaloupka. 2004a. Thirty-year recovery trend in the one depleted Hawaiian green sea turtle stock. *Biol. Conserv.* 117:491–498.
- . 2004b. Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian archipelago. *Mar. Biol. (Berl.)* 145:1043–1059.
- . 2006. Recovery trend over 32 years at the Hawaiian green turtle rookery of French Frigate Shoals. *Atoll Res. Bull.* 543:147–158.
- Balazs, G. H., R. G. Forsyth, and A. K. H. Kam. 1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. U.S. Department of Commerce, NOAA-NMFS-SWFC 71, Honolulu.
- Balazs, G. H., R. Fujioka, and C. Fujioka. 1993. Marine turtle faeces on Hawaiian beaches. *Mar. Pollut. Bull.* 26:392–394.
- Balazs, G. H., M. Rice, S. K. K. Murakawa, and G. Watson. 2000. Growth rates and residency of immature green turtles at Kiholo Bay, Hawai'i. Pages 283–285 in F. A. Abreu, R. Briseno, R. Marquez, and L. Sarti, eds. *Proceedings of the 18th International Sea Turtle Symposium*, Mazatlán, México, U.S. Department of Commerce, Miami, Florida.
- Bjorndal, K. A. 1980. Nutritional and grazing behaviour of the green turtle *Chelonia mydas*. *Mar. Biol. (Berl.)* 56:147–154.
- . 1997. Foraging ecology and nutrition of sea turtles. Pages 199–231 in P. L. Lutz and J. A. Musick, eds. *The biology of sea turtles*. CRC Press, London.
- Bolten, A. B. 2003. Variation in sea turtle life history patterns: Neritic vs. oceanic development stages. Pages 243–257 in P. L. Lutz, J. A. Musick, and J. Wyneken, eds. *The biology of sea turtles* Vol. 2. CRC Press, Washington, D.C.
- Bowen, B. W., A. B. Meylan, J. P. Ross, C. J. Limpus, G. H. Balazs, and J. C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution* 46:865–881.

- Brand-Gardner, S. J., J. M. Lanyon, and C. J. Limpus. 1999. Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. *Aust. J. Zool.* 47:181–191.
- Broderick, A. C., B. J. Godley, and G. C. Hays. 2001. Trophic status drives inter-annual variability in nesting numbers of marine turtles. *Proc. R. Soc. Lond. B Biol. Sci.* 268:1481–1487.
- Clarke, K. R., and R. M. Warwick. 1994. Changes in marine communities: An approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth, United Kingdom.
- Cribb, A. B. 1983. Marine algae of the southern Great Barrier Reef—Rhodophyta. Watson Ferguson & Co., Brisbane.
- . 1996. Seaweeds of Queensland: A naturalist's guide. The Queensland Naturalists' Club Inc., Brisbane.
- Doty, M. 1961. A possible invader of the marine flora of Hawai'i. *Pac. Sci.* 15:547–552.
- Dring, M. J. 1992. The biology of marine plants. Cambridge University Press, Cambridge, United Kingdom.
- Forbes, G. A. 1996. The diet and feeding ecology of the green sea turtle (*Chelonia mydas*) in algal-based coral reef community. Ph.D. diss., James Cook University, Townsville, Australia.
- . 1999. Diet sampling and diet component analysis. Page 235 in K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly, eds. Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication, Washington, D.C.
- Forbes, G. A., and C. J. Limpus. 1993. A non-lethal method for retrieving stomach contents from sea turtles. *Wildl. Res.* 20:339–343.
- Garnett, S. T., I. R. Price, and F. J. Scott. 1985. The diet of the green turtle, *Chelonia mydas* (L.), in Torres Strait. *Aust. Wildl. Res.* 12:103–112.
- Harrington, K. A., M. R. Rice, and G. H. Balazs. 2000. Habitat use of mixohaline ponds by green turtles at Kiholo Bay, Hawaii. Pages 285–286 in A. Mosier, A. Foley, and B. Brost, eds. Proceedings of the 20th Annual Symposium on Sea Turtle Biology and Conservation, Orlando, Florida. U.S. Department of Commerce, Miami, Florida.
- Limpus, C. J., and N. Nicholls. 1988. The southern oscillation regulates the annual numbers of green turtles (*Chelonia mydas*) breeding around Northern Australia. *Aust. Wildl. Res.* 15:157–161.
- Magruder, W. H., and J. W. Hunt. 1979. Seaweeds of Hawaii: A photographic identification guide. The Orient Publishing Company, Honolulu.
- Mortimer, J. A. 1982. Feeding ecology of sea turtles. Pages 103–109 in K. A. Bjorndal, ed. Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, D.C.
- Pritchard, P. C. H. 1997. Evolution, phylogeny, and current status. Pages 1–28 in P. L. Lutz and J. A. Musick, eds. The biology of sea turtles. CRC Press, London.
- Read, M. A., and C. J. Limpus. 2002. The green turtle, *Chelonia mydas*, in Queensland: Feeding ecology of immature turtles in Moreton Bay, southeastern Queensland. *Mem. Queensl. Mus.* 48:207–214.
- Russell, D. J., and G. H. Balazs. 1994. Colonization by the alien marine alga *Hypnea musciformis* (Wulfen) J. Ag. (Rhodophyta: Gigartinales) in the Hawaiian Islands and its utilization by the green turtle, *Chelonia mydas* L. *Aquat. Bot.* 47:53–60.
- . 2000. Identification manual for dietary vegetation of the Hawaiian green turtle, *Chelonia mydas*. U.S. Department of Commerce, NOAA-NMFS-NFSC, Honolulu.
- Russell, D. J., G. H. Balazs, R. C. Phillips, and A. K. H. Kam. 2003. Discovery of the sea grass *Halophila decipiens* (Hydrocharitaceae) in the diet of the Hawaiian green turtle, *Chelonia mydas*. *Pac. Sci.* 57:393–397.
- Schaefer, A. 1970. Die rechnerischen Unterlagen der Stereologie. *Mikro-Stereol.* 7:3–16.
- Seminoff, J. A. 2002. Global green turtle (*Chelonia mydas*) assessment for the IUCN

- Red List Programme. Report submitted by the Marine Turtle Specialist Group to the Species Survival Commission, Gland, Switzerland (available at www.iucnredlist.org).
- Seminoff, J. A., A. Resendiz, and W. J. Nichols. 2002. Diet of East Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, Mexico. *J. Herpetol.* 36: 447–453.
- Smith, J. E., C. L. Hunter, and C. M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pac. Sci.* 56:299–315.
- Waycott, M., K. McMahon, J. Mellors, A. Calladine, and D. Kleine. 2004. A guide to tropical seagrasses of the Indo-West Pacific. James Cook University, Townsville, Australia.
- Zug, G. R., G. H. Balazs, J. A. Wetherall, D. M. Parker, and S. K. K. Murakawa. 2002. Age and growth of Hawaiian green seaturtles (*Chelonia mydas*): An analysis based on skeletochronology. *Fish. Bull.* 100:117–127.

