# THE FORAGING ECOLOGY OF THE GREEN SEA TURTLE (CHELONIA MYDAS) ON THE EAST COAST OF HAWAI'I ISLAND

# A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I AT HILO IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN TROPICAL CONSERVATION BIOLOGY AND ENVIRONMENTAL SCIENCES

## JULY 2010

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### DEDICATIONS

This thesis is dedicated to my husband Joshua James Valdez, who has been my strongest supporter through this entire endeavor, and without whom, this project would not have been achievable. And to my daughter Annabelle Cordelia Wills Valdez, who was conceived and grew along side this study. Additionally, with deep love and gratitude, I dedicate this achievement to my grandmother, Anna Buker. Thank you for your everlasting support, compassion, and encouragement. Finally this work is dedicated in honor of my father, Craig Herman Wills; I hope I made you proud.

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granted by the State of Hawaii, Department of Land and Natural Resources. All activities were conducted using approved humane IACUC protocols that constitute provisions of the permits.

#### ABSTRACT

The foraging ecology of the threatened Hawaiian green sea turtle was investigated at Kapoho Bay on the east coast of the island of Hawaii from September 2006-December 2008. The objectives were to: 1) quantify the diversity and abundance of forage material in the habitat, 2) determine the composition of turtle diets, 3) investigate foraging behavior and determine if foraging selectivity was occurring, and 4) evaluate the nutritional content of forage items.

In this study, diet samples were analyzed for 121 individual turtles and 48 turtles were observed while foraging. Comparisons were made between the food items available in the habitat and what the turtles consumed. The habitat sampled was dominated by algae (92%), primarily in the form of algal turf (64%) and macroalgae (13.5%). Rhodophytes dominated the algal assemblage which was comprised of 25 species. Turtle diets were evaluated for short-term and long-term composition using three methods: 1) the bite count method using direct observation of foraging individuals, 2) esophageal lavage, and 3) stable isotope analysis. A total of 16 species of algae, terrestrial grass, and pieces of mangrove propagules were identified from the diet samples. Rhodophytes were most common, comprising 92% of the total pooled diet. Four primary diet items found in the habitat and selected by the turtles were, Amansia glomerata, Gracilaria salicornia, Acanthophora pacifica and Martensia fragilis, all Rhodophytes. The nutritional analysis of forage materials indicated generally that diet selection by turtles was influenced by the protein content, chemical composition and morphological characteristics of the forage material. Rhodophytes were generally higher in protein than Chlorophytes and Phaeophytes, except for a few select species. Implications for further efforts to improve

our understanding of variation in diet and nutrition temporally and spatially are discussed.

Keywords: foraging ecology; green sea turtle; diet; turf algae, Kapoho, Hawaii; stable isotope

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# LIST OF ABBREVIATIONS

FG	Foraging grounds
NG	Nesting grounds
SCL	Straight carapace length
ESA	Endangered Species Act
FP	Fibropapillomatosis
DOF	Direct observation of foraging
ANOVA	Analysis of variance

#### **INTRODUCTION**

Green turtles can be found in tropical and subtropical oceans around the world. Green turtles are the largest members of the family Cheloniidae and the only herbivorous sea turtle species. As young juveniles, green turtles first reside in pelagic waters where prey items are concentrated (Carr 1967*a*, *b*, 1987, Carr and Meylan 1980, Witham 1980, Reich et al. 2007). During this life stage, green turtles are carnivorous, eating small invertebrates (Carr and Meylan 1980, Hirth 1971, Balazs 1980*b*). Immature green turtles undergo a diet and habitat shift by ~40 cm in straight carapace length (SCL) (Hirth 1997) and ~6 kg in body mass (Zug et al. 2001), at which time they recruit to nearshore foraging grounds and become herbivorous. At a size of ~80 cm SCL green turtles become reproductively mature, and begin migrating every few years to their natal beach to nest.

Green turtles are listed as endangered, currently, in the International Union for Conservation of Nature Red Data Book (IUCN 2009) and can also be found in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Still, threats to the species include entanglement and ingestion of marine debris, illegal take of turtles and eggs, and disease such as the tumor causing fibropapillomatosis (FP). The threat that is evermore increasing its impact on sea turtles is the loss of foraging and nesting habitats due to near shore development, such as marina construction, siltation from agricultural runoff, contamination by toxic spills, resort development, and increased vessel traffic (Godley et al. 1998) as well as due to climate change and sea level rise (Baker et al. 2006).

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Green turtle populations have been found to exhibit variation in foraging ecology between habitats (Ehrenfeld 1982, Bjorndal 1999). The availability of food items among FG is known to vary with location and environmental factors (Arthur and Balazs 2008). Geographically separated turtle populations have been found to exhibit different foraging behaviors (Garnett et al. 1985, Brand-Gardner et al. 1999), have distinctly different diets (Arthur and Balazs 2008), and demonstrate FG specific growth rates (Balazs 1980*b*, Bjorndal and Bolten 1988).

It has been suggested that green turtles exhibit two foraging behaviors. Some studies indicate that food items found in green turtle diet samples are primarily associated with the abundance of those forage items in the habitat (Ogden 1976, Bjorndal 1980, Mortimer 1981, Garnett et al. 1985, Ross 1985, Balazs et al. 1987), although some level of selectivity or preference has also been demonstrated (Mortimer 1982, Brand-Gardner et al. 1999). Two requirements have been identified for an animal to selectively choose a food item. First, there must be a variety and abundance of food items in the habitat available to the animal; second, the animal must be able to identify a preferred food item (Leon and Bjorndal 2002, Manly et al. 2002). MacArthur and Pianka (1966) suggested a theory of optimal foraging (modified later by Schoener 1969), that stated that an animal should optimize its energy return per unit of time spent searching for food items. More recent models of foraging optimality have confirmed this theory indicating that animals (including; birds, mammals, reptiles and fish) will select resources of high quality over low quality (Krebs and Davies 1993). Similarly, Bjorndal (1980) found that when given a choice, green turtles will select the food item with the most nutritive quality available. Further evidence suggests selective foraging for certain species or particular growth

stages or portions of plants is occurring (Ross 1985). Studies in Australia (Forbes 1996, Fuentes et al. 2006) and Florida (Gilbert 2005) reported that green turtles demonstrated a preference for certain species and avoidance of others. Other studies have identified that selective grazing for young plants with higher nutritive values, high digestibility and lower epiphyte levels is a trait commonly displayed by the green sea turtle (Bjorndal 1979, 1980, Ogden et al. 1980).

The diet of green turtles varies among populations, although predominantly consists of seagrasses, algae, or both when they are present in the same area (Brand-Gardner et al. 1999). Seagrass predominates as the primary food source throughout most of the green turtles range (Hirth 1971, Mortimer 1982, Garnett et al. 1985). Populations of green turtles that feed solely on seagrasses have been found within a few kilometers of others that forage solely on algae such as off the west coast of Honduras (Carr 1952), Fiji (Hirth 1971), the Torres Strait of Australia (Nietshmann 1984), in the Gulf of Aden (Hirth et al. 1973) and in the Gulf of California (Felger and Moser 1973). Green turtles have been found to forage on marine algae in areas where seagrasses are lacking, like Brazil (Ferreira 1968), Galapagos Island (Pritchard 1971, Carrion-Cortez et al. 2010), the Gulf of California (Felger and Moser 1973) and Hawaii (McDermid and Stuercke et al. 2007, Arthur and Balazs 2008, Russell and Balazs 2009). In areas where green turtles feed heavily upon algae, red algae have been found to occur most often in their diet (Mortimer 1981, Mendonca 1983, Garnett et al. 1985, Balazs et al. 1987, Wershoven and Wershoven 1992, Redfoot 1997, Brand-Gardner et al. 1999, Holloway-Adkins 2001, Gilbert 2005, Arthur and Balazs 2008). This preference for red algae has also been found in fish, mollusks and marine iguanas (Indergaard and Minsaas 1991, Wikelski et al. 1993, Foster and Hodgson 1998). Although research suggests that green turtles feed predominantly on Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyta (brown algae) are also consumed (Garnett et al. 1985, Forbes 1996, Seminoff et al. 2002, Carrion-Cortez et al. 2010). In FG where mangroves are found, mangrove roots (Pritchard 1971), leaves (Pendoley and Fitzpatrick 1999), and propagules or fruit (Limpus and Limpus 2000, Carrion-Cortez et al. 2010) have been found to be consumed. Small amounts of animal material have been found to be commonly consumed as well (Bjorndal 1997, Seminoff et al. 2002, Amorocho and Reina 2007, Carrion-Cortez et al. 2010).

The most highly nutritive and digestible green turtle forage item is seagrass. Seagrasses have a high cellulose structure compared to the low cellulose structure of algae (Percival 1964, Bjorndal 1980). Green turtles guts are as suited for cellulose breakdown as ruminants, allowing a significant source of energy rich volatile fatty acids (Bjorndal 1979). Seagrass also has a high fiber and protein content when compared to marine algae (Bjorndal 1980). Algal species of Rhodophyta tend to have higher protein contents than those of Chlorophyta and Phaeophyta (Indergaard and Minsaas 1991, Wikelski et al. 1993, Foster and Hodgson 1998, Fleurence 1999, McDermid and Stuercke 2003). Red algae also have a higher protein digestibility than green or brown algae (Foster and Hodgson 1998, Wong and Cheung 2001). The microflora of the green turtles' gut are capable of changing to suit different diets, however, a change in these animals' diets or a diet consisting of both seagrass and algae, results in decreased digestive efficiency (Lipkin 1975, Bjorndal 1979).

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Some algae have characteristics that act as defenses against herbivory (Augner 1995). The morphologies and chemical composition of algae can inhibit digestion and reduce their nutritive quality. Some species are difficult to ingest due to coarse, tough texture or spines. The phenolic content of brown algae has been found to be much higher in comparison to species of Rhodophyta and Chlorophyta. Phenolic compounds are naturally derived phytochemicals (antioxidants, flavanoids, phenolic acids, hydroxycinnamic acid derivatives, and lignans) that bind to protein molecules affecting the protein digestibility of the plant (Ragan and Glombitza 1986, Fleurence 1999, Wong and Cheung 2001), as well as causing them to be distasteful (Van Alstyne and Paul 1990). Lignans themselves, form complexes with cellulose, which blocks these carbohydrates from the digestive enzymatic activity (Bjorndal 1980). Even when ingested, green turtles have difficulty fully digesting Phaeophytes, as determined by fecal analysis (Seminoff et al. 2000). Large amounts of algal and invertebrate epiphytes on a food item, which tend to accumulate over time, have been found to discourage foraging as well (Bjorndal 1979, 1980, Ogden et al. 1980).

Understanding feeding behavior and preference is important when evaluating size and growth rates of green turtles. Slow growth rates have been recorded in Australia (Limpus 1979), Florida (Kubis et al. 2009) and Hawaii (Balazs and Chaloupka 2004). The slow growth rates are thought to reflect poor nutrition or density dependent effects on growth which may be due to low availability of prime food sources. Previous studies suggest that high protein diets allow for faster growth and younger reproductive age in green sea turtles (Bjorndal 1980, Wood and Wood 1980, Hadjichristophorou and Grove 1983, Brand-Garner et al. 1999). Diet variation can affect nutrition and growth, as well as age of sexual maturity and fecundity, indicating that diet and nutrition are a major influence on growth and reproduction, and thus to the over all health and sustainability of the species (Carr and Carr 1970, Lipkin 1975, Bjorndal 1979, Bjorndal 1982, Wood and Wood 1980, Hadjichristophorou and Grove 1983, Brand-Gardner et al. 1999).

Stable isotope analysis has become a valuable tool for feeding ecology of marine vertebrates such as cetaceans, pinnipeds and sea turtles (Hobson et al. 1996, Godley et al. 1998, Hooker et al. 2001, Hatase et al. 2002, Biasatti 2004, Seminoff et al. 2006, Reich et al. 2007, 2010). Naturally occurring isotopes are found in elements that have similar properties, different atomic masses, and are resistant to radioactive decay. Stable isotopes are useful because they provide data on food items assimilated over a long period of time, making them less affected by short-term temporal change in diet (Peterson and Fry 1987, Hobson et al. 1996). Stable isotopes carbon  $\delta^{13}$ C and nitrogen  $\delta^{15}$ N of animal tissues undergo predictable changes (i.e. fractionation) with each trophic level (DeNiro and Epstein 1978, 1981, Peterson and Fry 1987). It has been found that the  $\delta$  $^{15}$ N and  $\delta^{13}$  C of consumer tissues is usually (3 to 5‰ and 0 to 1‰ respectively) greater than that of their prey items. The isotope compositions of consumer body tissues are ultimately derived from those found in the diet (DeNiro and Epstein 1978, 1981, Hobson and Clark 1992b. Michener and Schell 1994) making stable isotopes ratios  ${}^{13}C/{}^{12}C$  and  $^{15}$ N/ $^{14}$ N, (expressed as  $\delta^{13}$ C and  $\delta^{15}$ N, respectively) useful dietary tracers (Hatase et al. 2000). The discrimination of stable isotope diet values in consumer tissues is still not fully understood. There are a variety of biochemical factors within the consumer that may affect isotope discrimination such as; the differential excretion of isotopes as food is digested and from respired gassed, isotopic fractionation during amino acid amination

and transamination, and routing of isotopically distinct dietary fractions to specific tissues or tissue components (Peterson and Fry 1987, Hobson and Clark 1992*a*, Ayliffe et al. 2004). A number of external factors also can influence stable isotope discrimination such as; the age (Roth and Hobson 2000), body temperature (Pinnegar and Polunin 1999), digestive strategy (Macrae and Reeds 1980), diet quality (McCutchan et al. 2003, Pearson et al. 2003) and nutritional status (Hobson et al. 1993), of the consumer.

In Hawaii, the green turtle population is increasing, likely due to effective protection of the primary nesting areas and regulations prohibiting the harvesting of this species since 1978 (Balazs and Chaloupka 2004). Balazs and Chaloupka (2006) found that there was a constant level of new nester recruits each year (32% new individuals) indicating that the Hawaiian green turtle population is recovering and could be nearing its foraging habitat carrying capacity (Chaloupka et al. 2008). The Hawaiian green turtle stock is unique in that it is genetically (mtDNA) distinct from other populations in the eastern and western Pacific, being made up of a single primary rookery (Bowen et al. 1992) which is the source of the foraging populations which span more than 2,400 km across the Hawaiian archipelago, but not extending beyond the central Pacific region (Dutton et al. 2008). More than 90% of the population breeds at French Frigate Shoals in the Northwestern Hawaiian Islands (Balazs 1976, 1980, Niethammer et al. 1997). Nesting females range from 80.8 to 106.2 cm SCL (Balazs 1980b), and anywhere from 200-500 females are estimated to nest annually (Chaloupka et al. 2008). Green turtle FG have been identified at many nearshore sites off of the Hawaiian Islands (Balazs et al. 1987, Balazs and Chaloupka 2004, Arthur and Balazs 2008). Green turtles have exhibited substantial FG site fidelity at specific sites throughout the Hawaiian Islands (Balazs 1982,

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Balazs and Chaloupka 2004, 2006, Arthur and Balazs 2008). Although the numbers are increasing, the Hawaiian green turtle stock has been characterized by a lengthy declined in somatic growth rates, a significant spatial and temporal variation in FG specific growth rates of immature green turtles, and a longer expected age until sexual maturity ranging from 35 to 50+ years (25-30yrs Australia) (Zug et al. 2001, Balazs and Chaloupka 2004). It has been noted that FP, the tumor forming disease afflicting green turtles, is prevalent at specific FG throughout Hawaii and may impair the recovery of this once depleted population (Aguirre et al 1998, Balazs et al. 2000, Balazs and Chaloupka 2004, Chaloupka and Balazs 2005, Chaloupka et al. 2009).

Green turtle diet selection has been identified at numerous sites throughout the Hawaiian Islands with 79% of individual diet samples comprised >50% of one item in one study (Arthur and Balazs 2008). The major constituents of turtle diet vary between sites throughout Hawaii indicating that they are also opportunistic feeders (Balazs et al. 1987, Arthur and Balazs 2008). It has also been suggested that turtle diet variation in Hawaii is due to the absence of some favored algal species at a FG indicating that green turtles are able to modify their diets to meet local food availability (Balazs 1980*b*, Russell and Balazs 2009).

Seagrasses have been found in Hawaiian green turtle diet samples, specifically the endemic species of *Halophila hawaiiana*, and *H. decipiens*, however, seagrasses can only be found in a few localized sites such as in Kane'ohe Bay, Oahu; South Moloka'i; and Anini Beach, Kaua'i and has been noted at various sites off the coasts of Kona on the island of Hawaii, Midway Atoll, Pearl and Hermes Atolls and the island of Maui (Balazs 2000, Russell et al. 2003, McDermid et al. 2007). Algae dominate the diets of Hawaiian

green turtles, primarily red algae (Arthur and Balazs 2008). The diets of green turtles in Hawaii have been found to be comprised by more than 250 different species of algae with nine species of algae that have been established as major turtle diet constituents; *Amansia* glomerata, Caulerpa racemosa, Codium spp., Pterocladiella capillacea, Spyridia filamentosa, Turbinaria ornata, and Ulva fasciata (Balazs 1980b, Russell and Balazs 2000, Arthur and Balazs 2008, Russell and Balazs 2009). In addition, three species of exotic algae, *Acanthophora spicifera, Gracilaria salicornia* and *Hypnea musciformis*, are widely consumed (Russell and Balazs 1994, Russell and Balazs 2009).

Gracilaria salicornia has been problematic at a few sites throughout Hawaii for the last few decades due to its proliferation in localized areas causing endemic species to be depleted. This species has a three dimensional growth form, as compared to other alga with two dimensional structures or monospecific stands, which allows it to grow over the top of other benthic organisms (native algae, corals and other invertebrates), thus becoming particularly disruptive and ecologically dominant in some habitats. Gr. salicornia can be found in tidepools, on reef flats, and intertidally to sub tidally up to four meters deep, attached to limestone and basalt substrates. This alga can proliferate into three-dimensional mats, up to 40 cm thick, which are rigidly attached to hard substrata. In calm environments it can also grow in an upright and more freely branching form (Smith et al. 2002). Smith et al. (2002) states that two populations of this species were known to exist on the island of Hawaii before 1950, in Hilo Bay and Kapoho Bay. The origin of these populations is suspected to be tied to ship fouling and/or ballast water from early harbor arrivals in Hilo from the Philippines. Gr. salicornia was intentionally transported from Hilo to Waikiki, Oahu in 1971 and to Kaneohe Bay, Oahu in 1978 for

aquaculture projects that were later abandoned as well as being further introduced from Oahu to Puko'o fishpond, Molokai in the 1980's (Smith et al. 2002). Previous evidence suggests that *Gr. salicornia* has significantly altered benthic community structure and species diversity where it has spread throughout much of Waikiki, and reports suggest that it is now common on much of Molokai's south shore from Kamalo to Kaunakakai. It has been successful at out-competing many other native reef species in localized populations due to its rapid growth rates and its ability to colonize via fragmentation (Smith et al. 2002, Smith et al. 2004). Luckily, the heavy weight of *Gr. salicornia* fragments make lateral spread to different sites less likely (Smith et al 2002).

Kapoho Bay is a known green turtle foraging and resting site and turtle diets were first investigated at this site in 2003 (Arthur and Balazs 2008). Turtles exhibited a monospecific food reliance targeting a few species (*Amansia spp.* and *Gracilaria spp.*) and possibly incidentally ingesting other alga only when it was growing intermixed or in proximity, supporting the theory that Kapoho's green turtles may be selective feeders (Arthur and Balazs 2008). Further investigation at this site was beneficial due to the minimal diet sampling previously (one sampling period, n=7) and the lack of knowledge of the habitat available.

Previously, studies have investigated the foraging ecology of green turtles, but only in recent years have studies began to focus on identification of important food sources through quantitative determination of selection for particular plant species (Forbes 1996, Gilbert 2005, Fuentes et al. 2006). The foraging ecology of green turtles in Hawaii is known to vary spatially and temporally, similarly to other green turtle populations throughout their range, indicating that effective management of these

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endangered and threatened animals can only be guided by an understanding of the foraging ecology and diet of each local population (Ehrenfeld 1982, Bjorndal 1999, Seminoff et al. 2002, Arthur and Balazs 2008, Carrion-Cortez et al. 2010). This study was built on an ongoing study by the Marine Turtle Research Program (MTRP) at NOAA's Pacific Island Fisheries Science Center. The MTRP has studied the green turtle population at Kapoho Bay since 2001. The availability of food items in the foraging habitat at Kapoho Bay was previously unknown prior to this thesis study. The objectives were to: 1) quantify abundance of substrate components in the habitat, 2) determine the composition of the diet of the turtles, 3) investigate foraging behavior and determine if turtles were exhibiting foraging selectivity, and 4) evaluate the nutritional content of the diet.

#### **METHODS**

#### Site description

Kapoho Bay (19° 300' N, 154° 490' W) is located just south of Cape Kumukahi, which is the eastern most point on the island of Hawai'i, USA (Fig 1). The bay ranges in depth from approximately 0.1 m to over 5 m with  $\sim$ 1 m tidal flux. Sea temperature ranges from 23-26° C, with relative humidity ranging from 68 to 86 %. Wind blows offshore about 50% of the time from the westerly-southwesterly direction at speeds of 8 to 13 km per hour. Annual rainfall at Kapoho Bay averages 203 cm with the majority of rainfall (~55%) occurring during the wet season (November-March) (Kapoho Beach Lots, Farm Lots, and Vacationland Estates Wastewater Feasibility Report 2010). The bay is characterized as an exposed reef break with no seasonal change and inconsistent surf (www.surf-forcast.com). The bay has direct surface flow to the Pacific Ocean, with the surrounding land area used by a private residential community with open access to foot traffic and residents. Kapoho Bay includes a shallow rocky fish pond embayment, fringed with mangroves, and a series of protected, geothermally heated pools used by turtles for resting (Arthur & Balazs 2008). The geothermal activity in this area is caused by the high level of volcanic activity at a relatively shallow level below the surface. Warm water temperature is apparent in calm nearshore areas of Kapoho Bay and surrounding brackish water ponds which are connected to the ocean via underground flow which fluctuate with the tide. Due to its location to the volcanically active Kilauea East Rift Zone, Kapoho and surrounding areas have been investigated and drilled

previously for their geothermal properties and since the Kapoho Geothermal Reservoir was discovered in 1976 it has subsequently been tapped for commercial use (Gill 2007).

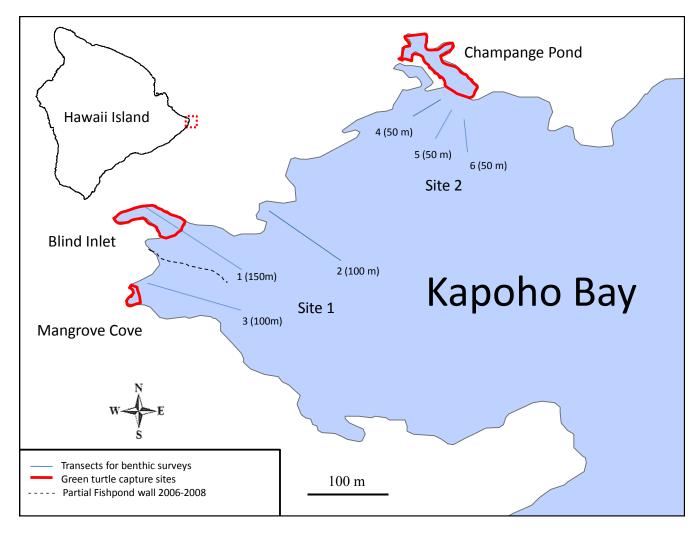


Figure 1. Study sites within Kapoho Bay on the east shore of Hawaii Island.

#### Substrate composition of habitat

Benthic cover surveys were conducted monthly at two sites within the bay (Fig. 1) for a one-year period each (Site 1: Sep. 2007-Aug. 2008, Site 2: Jan. 2008-Dec 2008). The purpose of these surveys was to characterize the abundance of marine plants available to foraging turtles. Multiple sites were chosen for representation of spatial food source variability, however, it can not be excluded that turtles may spend time foraging outside of the surveyed areas. Percent substrate composition was determined using point-intercept method along six designated transects at least 50 m apart ranging in depth from 0.1 m to 3.6 m. Transects 1, 2, and 3 located in Site 1 (depth: 0.1 m-3.6 m), were 150, and 100 m long each, respectively, while transects 4, 5, and 6 located in Site 2 (depth: 0.1 m-3.3 m), were all 50 m in length. Quadrats 0.5 m x 0.5 m with nine intersecting points were placed on the substrate, along the transect, at 10 m intervals. Algae were collected from each point and placed in a bag. Algal biomass was collected quarterly during the sampling period using 10 cm x 10 cm quadrats randomly positioned along the transect while all algae were collected by hand using a scraping tool, and placed in a bag. All algal samples were transported on ice and frozen until identification. When ocean conditions were unfavorable (i.e. storm, high waves and surge), causing >5% loss of biomass sample in the field, substratum samples were taken to the lab, rinsed, scraped, and dried to a constant weight. Vouchers of each specimen collected from the benthic surveys were preserved in the lab and archived as permanent slides and/or as dried herbarium specimens (Tsuda and Abbott 1985). Identification was conducted using a variety of taxonomic keys including Abbott (1999), Abbott and Huisman (2004), and Russell and Balazs (2000). The frequency and percent cover of each substratum

component and each algal phylum present in the habitat were calculated for each season and site using the equations: % Frequency = (# of quadrats containing diet item X 100) / Total # of quadrats; and % Cover = (# of points of diet item in all samples X 100) / Total # of points of all samples.

### **Diet sampling and composition**

### **Direct observation of foraging**

Foraging turtles were observed when encountered within sites. Foraging abundance was recorded using the bite-count method described by Reppert (1960) where a grazing herbivore is observed for a designated amount of time while recording the number of bites taken. A sample of the foraged algae was collected for identification. All algal samples were transported on ice and frozen until identification.

### **Esophageal lavage**

Turtles were captured using scoop nets, closely monitored large-mesh tangle nets, or by hand, while snorkeling (Arthur and Balazs 2008). All captures were carried out by personnel and their assistants of the NOAA Pacific Island Fisheries Science Center, Marine Turtle Research Program. Five sampling periods were conducted (Sep. 20-24<sup>th</sup> 2006, Apr. 28-May 2<sup>nd</sup> 2007, Feb.10-13<sup>th</sup>, Mar. 16-19<sup>th</sup>, and Oct. 12-16<sup>th</sup> 2008). Most of the turtles were caught in shallow water (range 0.1 m to 3.6 m) near shore in three protected pools (Fig. 1; "Blind Inlet" and "Mangrove Cove" within 50 m of benthic transects comprising Site 1 and "Champagne Pond" within 50 m of transects comprising Site 2) where they are found to rest. Upon capture, turtles were checked for existing tags, tagged if no tags were present, weighed, and morphometrics taken. Diet samples were collected by esophageal lavage following the methods of Balazs (1980*a*) and Forbes and Limpus (1993). Turtles were placed on their back with their posterior end slightly elevated. Their mouths were opened with an avian speculum and veterinary mouth gag while plastic tubing, lubricated with vegetable oil, was gently inserted into the esophagus. Water was pumped at low pressure to flush the esophagus and crop producing masticated algae from its mouth which was collected using a silk fine mesh bag. These items were assumed to be from the most recent feeding event. Samples were transported on ice and frozen until analysis.

Diet samples were examined under dissection microscope and identified to the lowest taxon possible and quantified using the principles of microstereology and a Weibel ocular graticule (Weibel et al. 1966, Holloway-Adkins 2001, Arthur and Balazs 2008). Lavage samples were mixed in a petri dish until visually homogenous. An ocular graticule with 80 marked endpoints was used to calculate the relative volumes of each dietary component. A species-area curve was used to determine the appropriate number of fields of view to analyze for each sample. Frequency of occurrence and relative volume was determined for each food type found in all diet samples using the equations: % Frequency = (Number of samples containing diet item X 100) / Total # of samples and; % Volume = (Total volume of diet item in all samples X 100) / Total volume of all samples.

#### Stable isotope analysis

A 3 mm biopsy of epidermis was collected from the inguinal region of each turtle, as well as, triplicate 1 g vouchers of each algal species present along the transects was collected for stable isotope analysis concurrently with the esophageal lavage sampling. The thawed algal samples were processed following the procedure of McDermid and Stuercke (2003). Algae were thoroughly washed three times in 32 ppt salt water to remove any sand or invertebrates. Samples were spun in a salad spinner for 30 s and tamped dry with paper towel to remove excess water. Samples were dried to a constant weight at 60° C in an air oven. The dried samples were then ground and homogenized. Tissue samples were prepared following the methodology of Seminoff et al. (2006), rinsed with distilled water, dried at 60° C for 48 h and then ground with a razor. Between 1.5-2.0 mg dried plant material and 0.5-1.0 mg dried animal material was packed into 5 x 9 mm tin capsules for stable isotope analysis. All samples were analyzed for stable C and N isotopic composition using a Costech<sup>TM</sup> Elemental Analyzer Conflo III coupled to a Thermo<sup>TM</sup> Delta V Advantage Isotope Ratio Mass Spectrometer in the Analytical Laboratory at the University of Hawaii, Hilo. Stable isotope results are presented as deviations from a standard (Pee Dee Belemnite for C and atmospheric nitrogen for N) using the equation:  $\delta X = [R_{sample} / R_{standard}) - 1] 1000$ , where:  $X = {}^{13}C$  or <sup>15</sup>N and  $R = {}^{13}C; {}^{12}C \text{ or } {}^{15}N; {}^{14}N.$ 

Vander Zanden and Rasmussen (2001) found mixing models useful for evaluating contribution of two potential prey sources (A and B) to a predator. In this study, two-source mixing models were used to determine the contribution of two potential food

items (A and B) to the foraging turtles: (Turtle<sub>13C</sub>-(Food Item B<sub>13C</sub>) – (Trophic level)) X 100 / ((Food Item A<sub>13C</sub>) – (Food Item B<sub>13C</sub>)), where trophic level equals: (Turtle<sub>15N</sub> – 2.8 or 3.4 + 1) / 3. The trophic fractionation constant commonly used for predator prey relationships is 3.4‰ based on the Minagawa and Wada (1984), and more recently Vander Zanden and Rasmussen (2001). However, Seminoff et al (2006) found that the trophic fractionation constant specific for green turtle epidermal tissue was  $2.80 \pm 0.11$ . Therefore, mixing models were run for both fractionation constants to be comparable with previous studies.

#### **Forage selectivity**

Pearson's correlations and regression analyses were conducted for season and site to determine if a relationship existed between the abundance of a food item ingested or seen foraged upon, and the abundance of the same item in the habitat. Additionally, Ivlev's electivity index (Ivlev 1961) was used to determine feeding preference and avoidance. The index is used to calculate a value between 1 and -1 for each food item, where 1 = exclusive feeding on the item, 0 = non-selective feeding and -1 = complete avoidance of the item. The formula for calculating the index is:  $E_i = r_i - p_i / r_i + p_i$ , where E is the measure of electivity,  $r_i$  is the relative abundance of food item i, in the lavage sample, and  $p_i$  is the relative abundance of the same item found in the habitat.

#### **Forage protein composition**

For two dates (Feb 2008 and Oct 2008), triplicates of each forage item were dried, ground and homogenized for protein content analysis, following the same procedure as

for samples prepared for stable isotope analysis listed above (Mcdermid and Stuerke 2003). Ten mg of dried ground plant material was transferred into 15 mL centrifuge tubes and 5 mL 1N NaOH was added to each tube and kept at room temperature for ~24 hours. Samples were centrifuged at 500 rpi for 5 minutes. The supernatant was collected for protein measurement following a modified assay of the Lowry method (Lowry et al. 1951). The modified assay reagent contained cupric sulfate, potassium iodide and sodium tartrate in an alkaline sodium carbonate buffer as well the 2N Folin-Ciocalteu reagent. The protein content of the samples was determined by comparing the absorption, read at 660 nm on SpectraMax M2 Plate Reader, for each sample with the standard curve for a known protein content of bovine serum albumin (25-1500 Ug/mL range).

#### Statistical analyses

Data were tested for normality using Ryan Joiner Normality Test. One-way and Two-way ANOVA's utilizing General Linear Models and subsequent Tukey's Multiple Comparisons Tests were used when data was normal or could be transformed. When data could not be transformed, alternate, non-parametric procedures (Kruskal-Wallis Test) were implemented. The factors of season and site were used to determine if seasonal variation and variation between sites exists for benthic cover, biomass, direct observation of foraging, and lavage data. For protein, and isotope data, season was the only factor. An alpha level of 0.05 was used for all statistical tests. Data were statistically analyzed using Minitab (Version 15, Minitab Inc., 2007).

### RESULTS

#### I: Substrate composition of habitat

A variety of algal substrate components (algal turf, fleshy macroalgae, crustose coralline algae and colonial diatoms) and non-algal substrate components (sand, rock, corals, and invertebrate animals) were identified from Kapoho Bay. The algal substrate components comprised the majority of the habitat sampled (Fig. 2, 92% of total cover). Algal turf had the highest percent cover of any substrate component, covering 64% of the habitat sampled, over four times the cover of the second highest substrate component; macroalgae (13.5%) (Table 1). Crustose coralline algae covered 14% of the sampled substrate while diatoms covered 1% (Fig. 3). Non-algal components made up only 8% of the sampled habitat and were categorized separately as non-living and living. Non-living cover (sand and rock) comprised 7% while living corals and living animals together contributed 1% of the total cover (Fig. 2).

# Composition of algal assemblage

Nineteen species of turf algae (Table 2) and eleven species of macroalgae were identified from Kapoho Bay during this study (Table 1, Fig. 4). The relative abundance of the algal substrate components, considered separately, present during this study is shown in Figure 3. The turf sampled at Kapoho Bay was composed of a dense mixture of prostrate species and the early developmental stages of larger macroalgal species. The majority of the algal turf species present were of the division Rhodophyta (55%, Fig. 5). Appendix A1 and 2 lists the algal turf species present at each site, for each, season during sampling. When macroalgae was considered separately, the Rhodophytes comprised 96% of the total cover (Fig. 6). The Chlorophytes comprised only 3% while the Phaeophytes comprised the least with 1% of the total macroalgae. Only four species of macroalgae ever exceeded 5% contribution to the total macroalgal cover (relative abundance) (Fig. 4). These species were all of the division Rhodophyta; *Gracilaria salicornia, Amansia glomerata, Martensia fragilis* and *Acanthophora pacifica* with relative abundance of 68%, 12%, 7% and 6% respectively.

## Temporal and spatial change in algal cover

No significant seasonal change was detected in benthic cover at Kapoho Bay (Two-way ANOVA, p=0.949). The data did indicate, however, a significant difference in the abundance of algal species between Site 1 and Site 2 within Kapoho Bay (Two-way ANOVA, Fig.7, p<0.001). The species that showed significant differences in relative abundance between sites were *Acanthophora pacifica* (Tukey's, p<0.001), *Gracilaria salicornia* (p<0.001), and *Martensia fragilis* (p<0.001). Analysis of individual transects also revealed variation of abundance among species (Tukey's, Appendix B, Fig. 8, p=0.008).

All biomass samples were comprised of turf algae due to random sampling technique. Seasons had no significant effect on biomass data (One-way ANOVA, p=0.739). Biomass varied significantly between sites (One-way ANOVA, Fig. 9, p=0.025) with Site 1 having the highest mean biomass and the highest total biomass by dry weight (Tables 3 and 4). Algal biomass varied significantly (One-way ANOVA, Fig. 10, p=0.017) across the six transects with transect 1 differing significantly from transect 4 (Tukey's p=0.013).

I: <u>Tables</u>

				FO	(%)		
Substrate Component	Relative Abundance (%)	Spring	Summer	Fall	Winter	Site 1	Site 2
Macroalgae	13.52	42.67	41.33	54.00	51.33	63.33	9.44
Rhodophyta	13.32	42.07	37.33	53.33	47.33	60.00	9.44 7.78
Gracilaria salicornia	9.22	40.00 26.67	26.00	36.67	22.00	39.76	-
	9.22 1.64	4.00	26.00	7.33	14.00	59.76 7.14	6.11
Amansia glomerata Mautanaia fuggilia	0.91	3.33	5.33	7.55 4.67	0.67	5.00	0.11
Martensia fragilis							_
Acanthophora pacifica	0.82	1.33	2.67	2.67	8.67	5.48	-
Hypnea spinella	0.20	4.67	1.33		2.00	1.67	1.11
Centroceras clavulatum	0.13	—	-	1.33	2.00	0.95	0.56
Pterocladiella caerulescens	0.06	_	-	0.67	_	0.24	-
Phaeophyta	0.11	_	1.33	0.67	_	0.24	1.11
Dictyota friabilis	0.07	_	1.33	_	_	_	1.11
Sargassum polyphyllum	0.04	_	_	0.67	_	0.24	_
Chlorophyta	0.43	2.67	2.67	_	4.00	3.10	0.56
Bryopsis hypnoides	0.32	2.67	2.67	_	3.33	3.10	_
Cladophoropsis membranacea	0.11	-	-	_	0.67	-	0.56
Algal Turf*	64.06	81.33	89.33	86.67	93.33	84.52	95.00
Crustose Coralline Algae	13.37	46.67	50.67	34.67	43.33	42.86	46.11
Diatoms	0.50	-	4.00	-	-	1.43	_
Rhizophora mangle propagule	0.02	-	-	-	0.67	0.24	_
Coral	0.41	1.33	0.67	3.33	4.00	1.90	3.33
Pocillopora damicornis	0.33	0.67	0.67	2.00	4.00	1.43	2.78
Palythoa caesia	0.06	0.67	-	0.67	-	0.48	
Montipora capitata	0.02	-	-	0.67	-	_	0.56
Living Animals	0.15	0.67	0.67	2.00	-	1.19	_
Tubeworm	0.11	0.67	-	1.33	-	0.71	_
Mantis Shrimp	0.02	-	-	0.67	_	0.24	_
Limpet	0.02	_	0.67	_	_	0.24	_
Non-Living	7.98	24.00	14.00	22.67	14.67	14.05	30.00
Rock	7.64	20.67	12.67	20.67	12.00	10.95	29.44
Sand	0.33	3.33	1.33	2.00	2.67	3.10	0.56

**Table 1.** Relative abundance of substrate components composing the habitat sampled. Frequency of occurrence (FO) is expressed per season and site at Kapoho Bay, Hawaii during this study.

\*Algal turf is comprised of multiple, intermixed species and is difficult to discern and quantify in the field. A complete list of algal turf species present is found in Table 2 and Appendices A1 and A2.

Table 2. The genera and species comprising the algal turf assemblage component, Kapoho Bay, Hawaii.

Rhodophyta	<u>Chlorophyta</u>
Centroceras clavulatum	Chaetomorpha antennina
Chondrocanthus acicularis	Cladophoropsis membranacea
Gelidiopsis intricata	Microdictyon umbilicatum
Gelidiopsis sp	Ulva flexuosa
Gelidium pusillum	Ulva rigida
Hypnea spinella	Valonia aegagropila
Laurencia brachyclados	
Pterocladiella caerulescens	<u>Phaeophyta</u>
Pterocladiella sp	Dictyota friabilis
Tolypiocladia glomerulata	Lobophora variegata

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6		Site 1	Site 2
	Mean n=5,						Season	Mean	Mean
Season	sm n=8	Mean n=5	Mean n=5	Mean n=3	Mean n=3	Mean n=3	Mean	n=63	n=36
		$0.69 \pm$	0.53 ±	$0.29 \pm$	$0.08 \pm$	0.71 ±	$0.56 \pm$	0.41 ±	
Spring	$0.81 \pm 0.15$	0.27	0.28	0.19	0.06	0.26	0.10	0.13	$0.52 \pm 0.16$
		$0.63 \pm$	$0.57 \pm$	$0.31 \pm$	$0.18 \pm$	$0.87 \pm$	$0.63 \pm$	$0.68 \pm$	$0.36 \pm$
Summer	$0.86\pm0.27$	0.22	0.24	0.23	0.11	0.32	0.11	0.13	0.13
		$0.81 \pm$	$0.85 \pm$	$0.09 \pm$	$0.25 \pm$	$0.21 \pm$	$0.59 \pm$	$0.71 \pm$	$0.45 \pm$
Fall	$0.76 \pm 0.29$	0.29	0.30	0.05	0.15	0.09	0.11	0.15	0.16
		$0.24 \pm$	$0.38 \pm$	$0.17 \pm$	$0.81 \pm$	$0.58 \pm$	$0.45 \pm$	$0.81 \pm$	$0.18 \pm$
Winter	$0.59\pm0.16$	0.17	0.33	0.03	0.31	0.32	0.10	0.16	0.06
Transect		0.60 ±	0.63 ±	0.43 ±	0.48 ±	0.51 ±	0.55 ±	0.65 ±	0.38 ±
Mean	$0.58\pm0.12$	0.11	0.14	0.12	0.14	0.17	0.05	0.07	0.07

**Table 3.** Mean ( $\pm$  SE) biomass (mg dry weight per cm<sup>2</sup>) for season, transect and site.

 Table 4. Total biomass (mg dry weight per m<sup>2</sup>) for season, transect and site.

Season	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6	Season Total	Site 1	Site 2
Spring	2.97	1.22	1.90	0.50	2.44	1.73	10.75	11.16	4.98
Summer	4.06	3.43	2.65	0.87	0.24	2.12	13.37	8.42	2.05
Fall	6.84	3.17	2.83	0.92	0.55	2.62	16.93	11.87	1.29
Winter	3.82	4.04	4.26	0.26	0.75	0.63	13.76	9.74	5.31
Transect Total	17.69	11.86	11.64	2.55	3.98	7.09	54.81	41.19	13.62

I: Figures

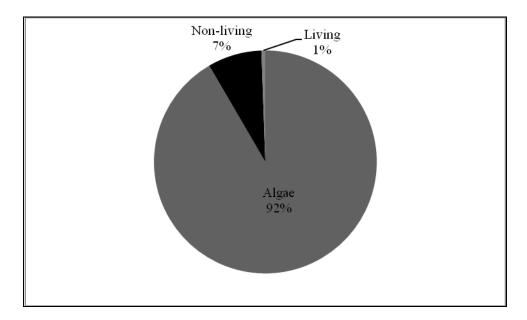


Figure 2. Relative abundance of substrate components at Kapoho Bay during this study.

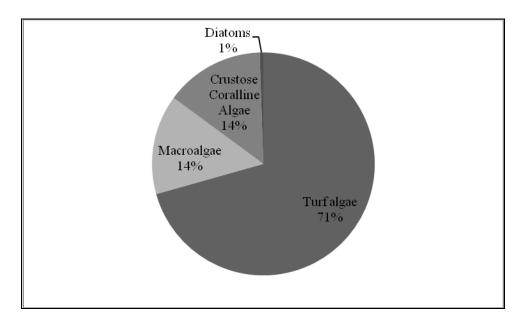


Figure 3. Relative abundance of the algal substrate components at Kapoho Bay during this study.

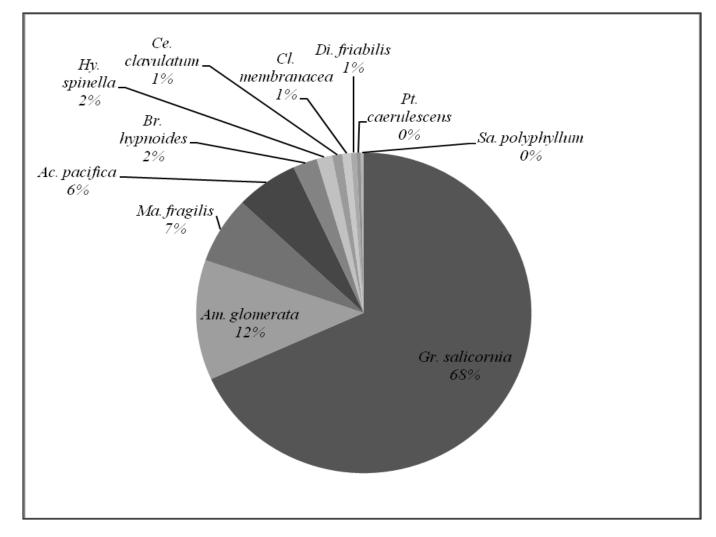


Figure 4. Relative abundance of macroalgal species at Kapoho Bay during this study.

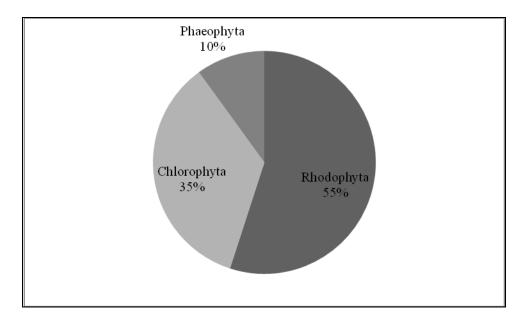


Figure 5. Relative abundance of algal turf species at Kapoho Bay during this study.

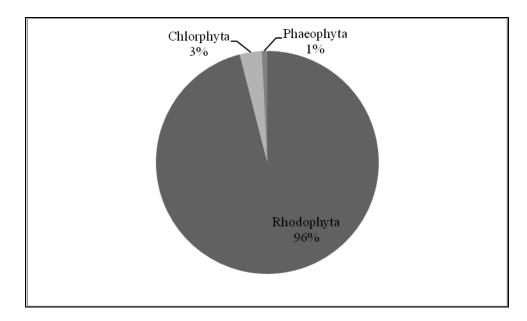


Figure 6. Relative abundance of the macroalgal substrate components at Kapoho Bay during this study

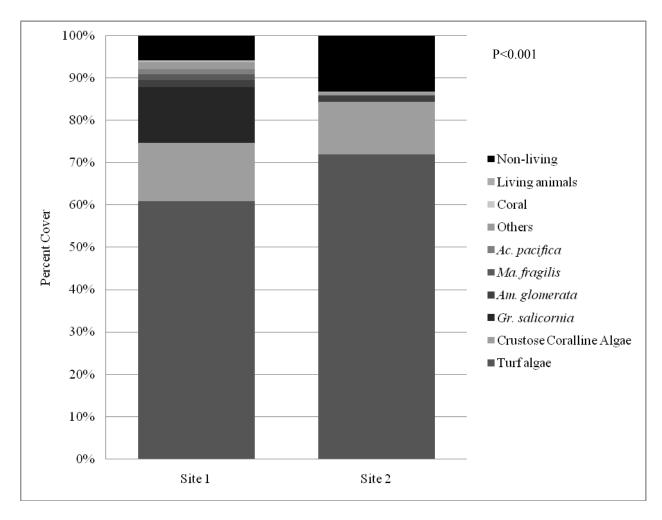


Figure 7. Relative abundance of substrate components at each site within Kapoho Bay during this study.

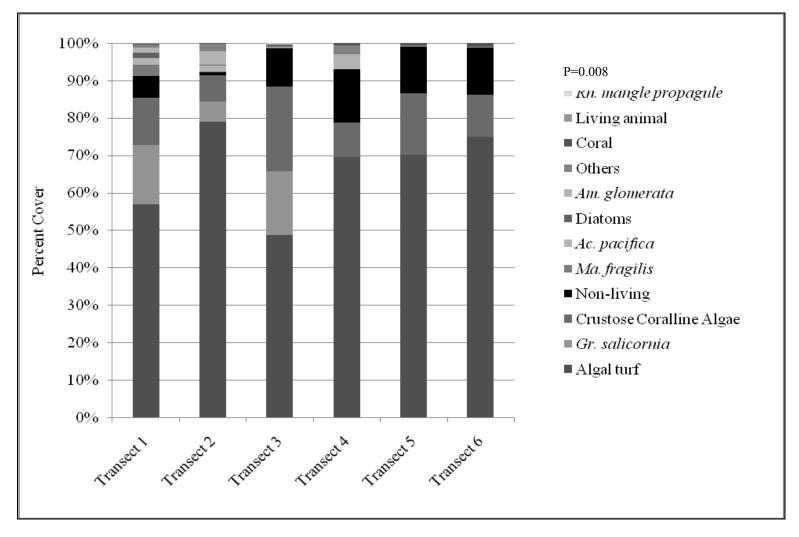


Figure 8. Relative abundance of substrate components within each transect at Kapoho Bay during this study.

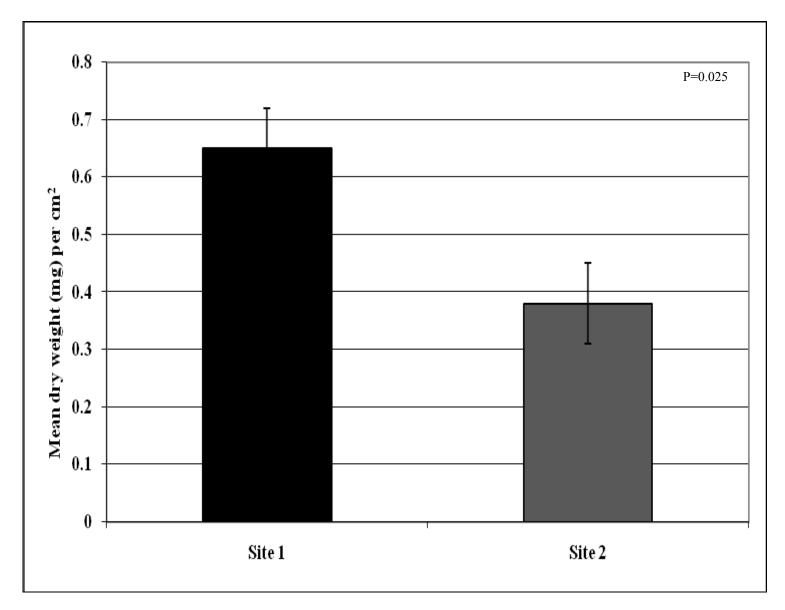


Figure 9. Mean biomass (±SE) for each site within Kapoho Bay during this study.

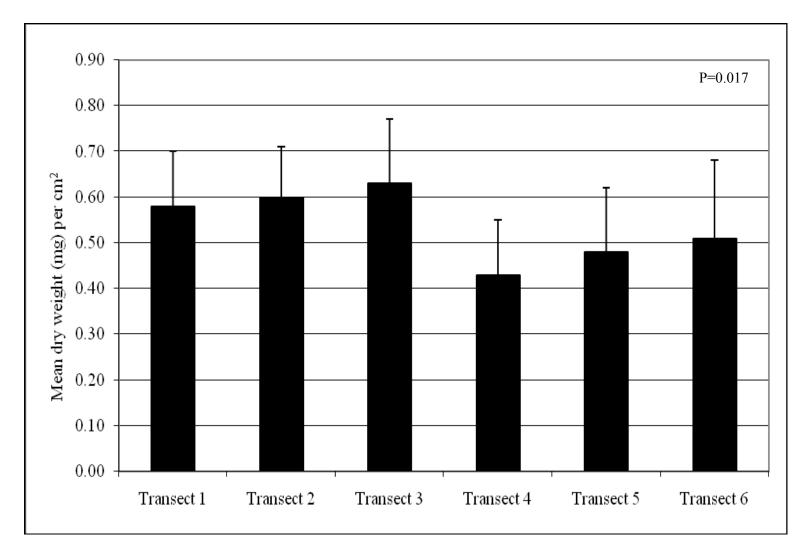


Figure 10. Mean (± SE) biomass for each transect at Kapoho Bay during this study.

#### II: <u>Diet sampling and composition</u>

### **Direct observation of foraging**

Forty eight turtles were observed foraging during this study (34 from site 1 and 14 from site 2). Five species of algae were identified as forage items, however, only four forage items exceeded ( $\geq$ 5% relative abundance or frequency) when the diets were pooled (Fig. 11, Table 5). Two species comprised the majority of food items observed consumed, *Gr. salicornia* (41.9%) and *Am. glomerata* (26.9%). All species of algae observed foraged upon were of the division Rhodophyta. There was a significant difference in abundance of species observed foraged upon between sites within Kapoho Bay (Two-way ANOVA, Fig. 12, p=0.002), but not between seasons (Two-way ANOVA, p=0.233). A Tukey's' test revealed that *Gr. salicornia* was the only alga that was significantly different in amount observed foraged between sites (p<0.001).

### **Turtles sampled**

Diet and/or tissue samples were collected from 121 green turtles captured over the course of five sampling periods. The turtles ranged in size from 36.4 cm to 88.2 cm straight carapace length (SCL) (mean 59.9 cm  $\pm$  0.78). The morphometric measurements for all turtles are shown in Appendix C. Sixty individuals were recaptured during the course of this study, 42 of which were caught twice, 14 were caught three times and 4 were caught four times producing a total of 156 esophageal lavage samples and 181 tissue biopsies (Appendix D). The 60 turtles that were recaptured (# captures at same site/# captures total with site recorded) show fidelity to their capture area 83.6% of the time (Table 6). Out of the 14 turtles caught three times, 92.5% exhibited capture site fidelity; while two turtles caught four times with capture site recorded, both exhibited 93.8% capture site fidelity. No correlation or linear relationship was found between the number of times captured and the recapture rate of turtles at the same resting site (Pearson's 0.897, p=0.291).

## **Esophageal lavage analysis**

Turtles at Kapoho Bay consumed primarily an algal diet (93.6% of total diet) with a few individuals consuming *Rhizophora mangle* propagules and terrestrial grass, tentatively identified as St. Augustine grass (*Stenotaphrum secundatum*), commonly used in coastal areas because of it's tolerance to soils with high salinity (USDA NRCS 2010). A summary of all diet items and their contribution to the diet is shown in Table 7, Appendix E and Fig. 13. In most samples (n=153, 97.4%), one item made up the majority of the relative volume ( $\geq$ 50% of sample). Two lavage samples were comprised dominantly of masticated *Rh. mangle* propagule (1.3%), while one was entirely propagule. Six lavage samples contained terrestrial grass (4%), identified as the major food item, while five were entirely grass. Rocks and shells were found in 12 lavage samples and comprised the majority of one lavage sample.

During this study, sixteen species of algae were identified as food items from lavage samples; however, only four species ever exceeded incidental amounts ( $\geq$ 5%) in the pooled diet of sampled turtles (Table 7, Fig. 13). A total of 145 lavage samples (92.9%, Fig. 14) contained algae as the major food item ( $\geq$ 50% of lavage sample)

with 66 samples (42.3%, Fig. 15) comprised entirely of algae. Lavage samples that consisted primarily ( $\geq$ 50%) of algae were comprised of, *Am. glomerata, Gr. salicornia, Ac. pacifica* and *Ma. fragilis* contributing 43%, 31%, 15% and 8% respectively (Fig. 14). Rhodophytes were the most common diet item encountered, present in 81.3% of all samples and contributing to 92% relative abundance of all food items (Fig. 16). *Am. glomerata* and *Gr. salicornia* were the most important food items for the turtles at Kapoho Bay, representing 38% and 27%, respectively (Fig. 13.), of all items consumed. There was no seasonal variation (Two-way ANOVA, p=0.178) or significance between capture sites (Two-way ANOVA, p=0.703) found in the turtles' diet.

The lavage samples of turtles recaptured at different sampling periods (n=42) indicated variation in diet with 42.2% of recaptured turtles feeding on the same diet item. Out of the 10 turtles lavaged over three sampling periods and the two turtles lavaged four times showed 50% diet fidelity (Table 8, Fig. 18).

One green turtle fecal pellet was collected from the water at Kapoho Bay. This sample contained only one undigested diet component comprising the majority of the pellet, which was identified as terrestrial grass.

### Stable isotope analysis

One-way ANOVA's indicated a significant difference in  $\delta^{13}$ C signatures between algal species (Tukey's, *Ac. pacifica-Ma. fragilis* p=0.046, *Am. glomerata-Gr. salicornia* p=0.028, *Gr. salicornia-Ma. fragilis* p=0.002). There was a significant difference found

in  $\delta^{15}$ N signatures between species (p<0.001). There was also seasonal variation found in the  $\delta^{15}$ N signatures of both algae (p<0.001) and turtle tissues (p=0.003). Three species showed significant variation in  $\delta^{15}$ N signatures between February and October 2008, (Tukey's Fig. 17, *Ac. pacifica* p=0.014, *Br. hypnoides* p=0.002, and *Ma. fragilis* p<0.001). Turtle tissue  $\delta^{15}$ N signatures also varied seasonally with Fall significantly differing from Spring (p=0.004) and Spring significantly differing from Winter (p=0.047).

Two-source mixing models indicated that the percent contribution of each diet item is either 0% or 100% for algal species (Appendix F), indicating that algal species sampled did not have distinct isotopic signatures (Fig. 19). The contribution of *Rh*. *mangle* leaves or propagules to the diet of the turtles ranged from 2.8-29% and 3.2%-31.9%, respectively. Terrestrial grass was found to contribute 0% when prey B items were algae and 68.1-71.1% when prey B items were mangrove. II: Tables

Species	Relative Abundance (%)	Frequency (%)
Gracilaria salicornia	41.9	35.4
Amansia glomerata	26.9	37.5
Martensia fragilis	14.1	12.5
Acanthophora pacifica	14.2	12.5
Gelidium pusillum	2.8	2.1

 Table 5. Pooled observations DOF (n=48) by relative abundance and frequency of occurrence of bites per species.

 Table 6.
 Summary of captured turtles.

# of Times Captured	# Turtles	Site Fidelity (%)
1	61	N/A
2	42	76.9
3	14	92.5
4	4	93.75
Total number of recaptures	60	83.6
Total number of turtles sampled	121	N/A

(Calculated by the number of capture incidences at the same site divided by the total number of captures at any site multiplied by 100).

	Volume		D	6.0	1 (0()
	(%)	_		on of Sam	
Diet Item		Present	$\geq$ 5%	$\geq$ 50%	100%
Algae	93.58	88.52	90.26	92.90	42.30
Amansia glomerata	38.41	31.48	34.46	41.18	50.00
Gracilaria salicornia	26.51	17.05	19.10	29.41	30.56
Acanthophora pacifica	15.41	9.18	10.49	14.38	8.33
Martensia fragilis	8.43	7.54	7.87	7.19	_
Gelidium pusillum	1.08	1.31	1.50	1.31	1.39
Gelidiopsis intricata	0.26	0.98	0.37	-	—
Gelidiopsis sp	1.08	8.20	7.12	0.65	1.39
Hypnea spinella	0.42	3.93	1.50	_	-
Pterocladiella caeurulescens	0.01	0.33	_	-	—
Pterocladiella sp	0.25	0.66	0.75	0.65	_
Tolipiocladia glomerulata	0.02	0.66	_	-	—
Total Rhodophyta	91.88	81.31	83.15	94.16	91.67
Dictyota friabilis	0.83	4.26	4.12	-	_
Turbinaria ornata	0.67	1.64	1.87	_	_
Total Phaeophyta	1.50	5.90	5.99	_	_
Cladophoropsis membranacea	0.17	0.98	1.12	_	_
Valonia aegagropila	0.02	-	_	_	-
Codium sp	0.01	0.33	_	_	_
Total Chlorophyta	0.20	1.31	1.12	_	_
Others	6.42	10.82	9.74	5.84	8.33
Grass	3.94	3.28	3.75	3.92	6.94
Rhizophora mangle propagule	1.45	1.31	1.50	1.31	1.39
Shells/Rocks	1.02	6.23	4.49	0.65	_

**Table 7.** Pooled lavage diet samples from five sampling periods (n=156). Percent volume is the totalpercent that each diet item contributes to the pooled diet. Frequency of occurrence is expressed as theproportion of samples in which the diet item was found and also where it was found to contribute  $\geq$ 5%, $\geq$ 50% and 100% of relative volume.

	# Turtles	# Lavage	Diet Fidelity
# of Times Captured	Lavaged	Samples	(%)
1	58	58	N/A
2	30	60	37.8
3	10	30	50
4	2	8	50
Total number of recaptures Total number of turtles	42	98	42.2
sampled	100	156	N/A

 Table 8.
 Summary of diet fidelity for recaptured turtles.

(Calculated by the number of captures where individual turtle diets contained items previously recorded for the same individual, divided by the total number of diet items found, multiplied by 100).

**II:** Figures

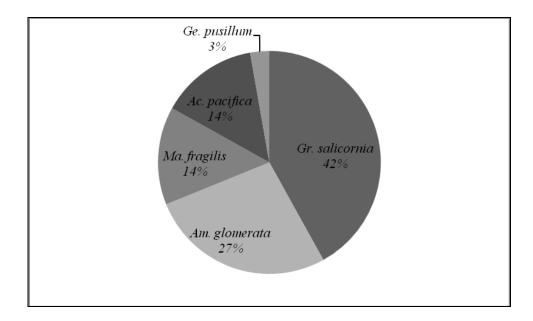


Figure 11. Relative abundance of pooled diet items from DOF at Kapoho Bay during this study.

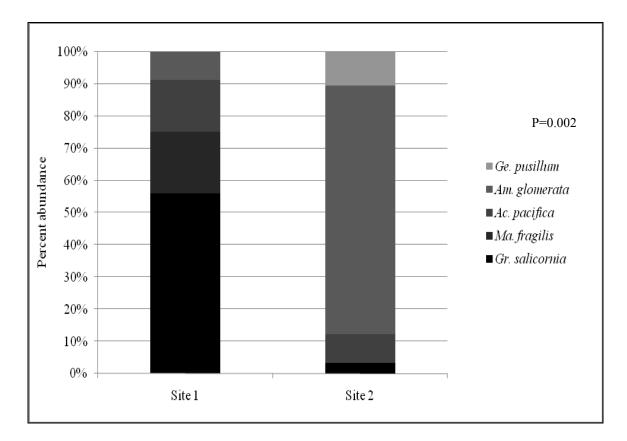
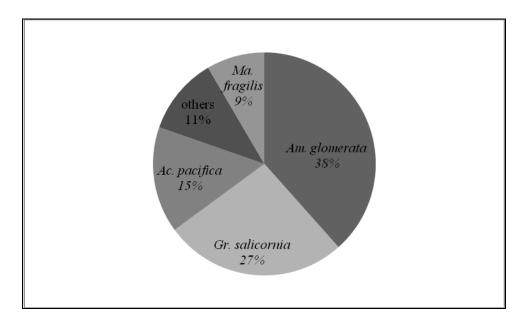


Figure 12. Relative abundance of diet items from DOF within each site at Kapoho Bay during this study.



**Figure 13.** Percent volume of diet items found in lavage samples at Kapoho Bay during this study. The category "others" is all diet items that comprised <5% of the total diet.

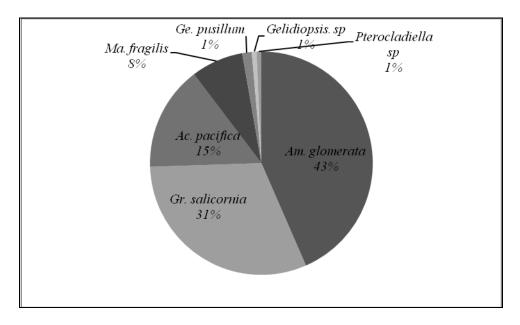


Figure 14. Frequency of occurrence of species in lavages comprised  $\geq$ 50% of algae. All species are Rhodophytes.

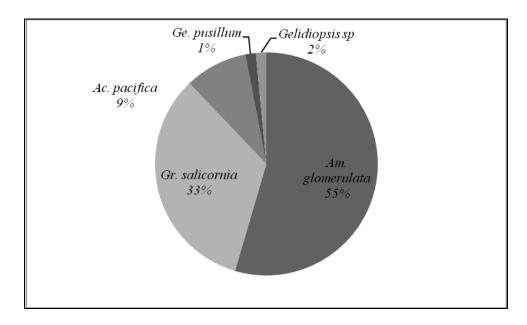


Figure 15. Frequency of occurrence of species in lavages comprised 100% of algae. All species are Rhodophytes.

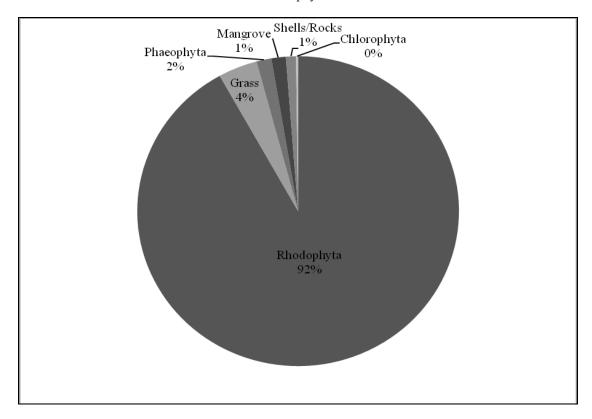


Figure 16. Percent volume of food items in lavage samples by division at Kapoho Bay, Hawaii during this study.

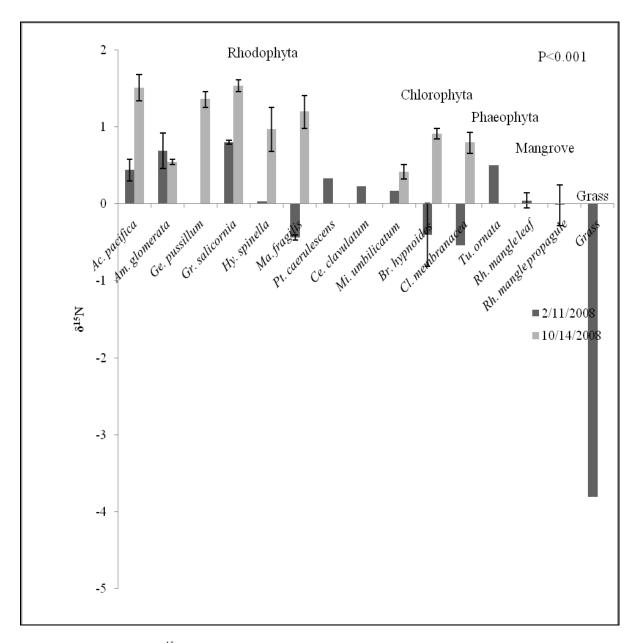


Figure 17. Mean ( $\pm$  SE)  $\delta^{15}$ N isotopic signatures for plants collected during February and October 2008 at Kapoho Bay.

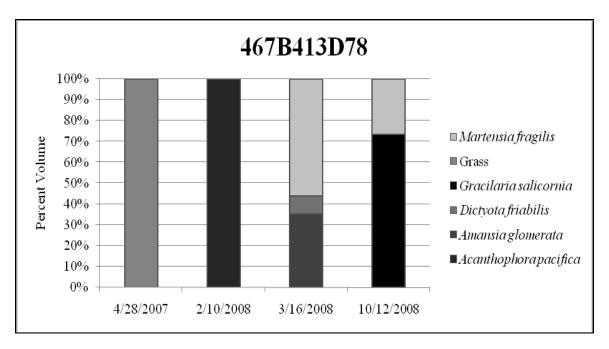


Figure 18a: Lavage composition in percent volume for recaptured turtle #467B413D7

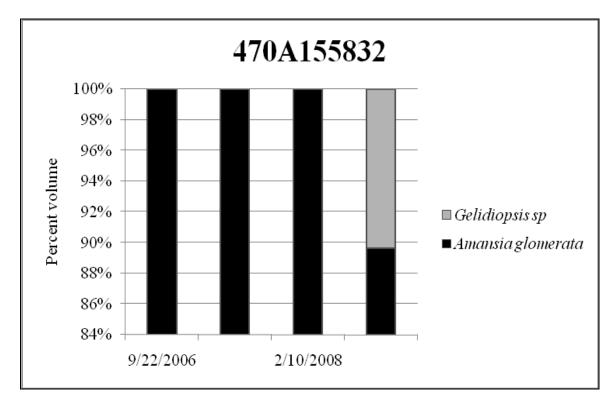


Figure 18b. Lavage composition in percent volume for recaptured turtle #470A155832.

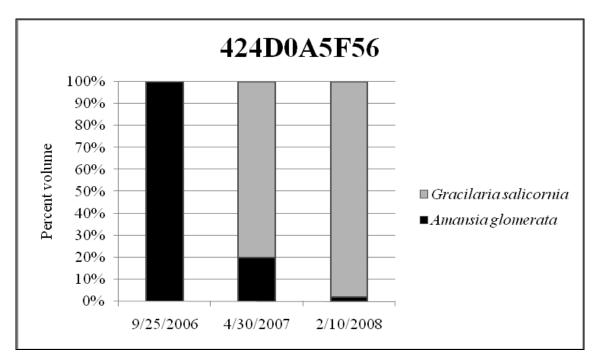


Figure 18c. Lavage composition in percent volume for recaptured turtle #422F1D275A.

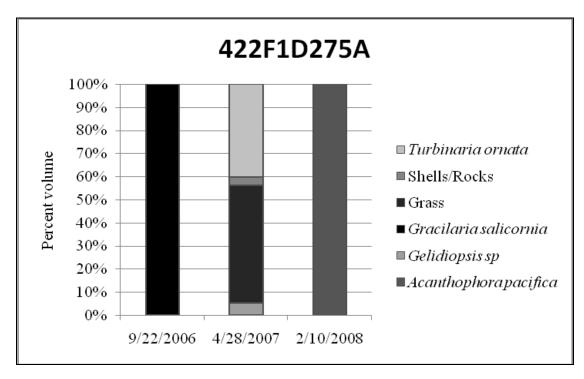


Figure 18d. Lavage composition in percent volume for recaptured turtle #424D0A5F56

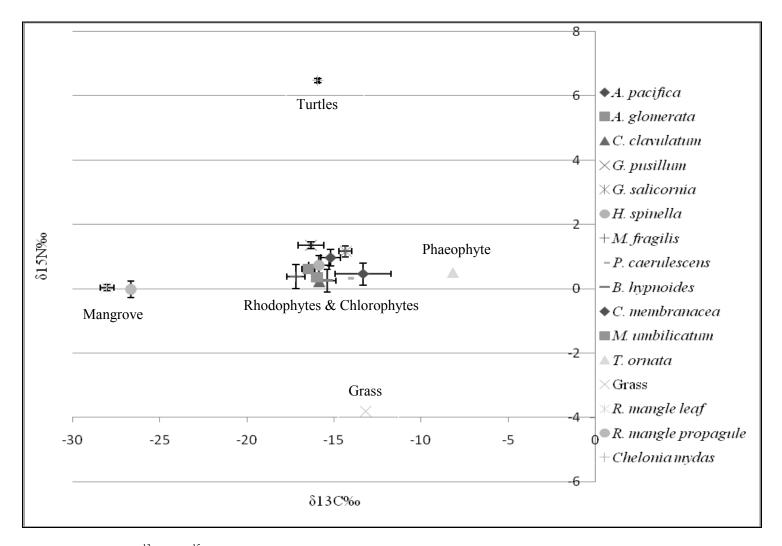


Figure 19. Mean ( $\pm$ SE)  $\delta^{13}$ C and  $\delta^{15}$ N isotopic signatures of *Chelonia mydas* and potential diet items found in the habitat at Kapoho Bay, Hawaii during this study.

#### III: Forage selectivity

A series of correlations found a relationship between the substrate percent cover and the diet percent volume for DOF (Fig. 20, Pearson's=0.681, p=0.003) and esophageal lavage data (Fig. 21, Pearson's=0.679, p=0.003). There was also a significant correlation between the DOF and lavage data (Fig. 22, Pearson's=0.980, p<0.001). There was no correlation or relationship found however, when evaluated by season and site (Table 9). Since the turtles were only consuming algal turf in incidental amounts, the correlations were run a second time excluding algal turf, along with linear regressions, resulting in a stronger significant relationship between the substrate percent cover and diet percent volume for DOF (Fig. 23, Pearson's=0.880, p<0.001, R<sup>2</sup>=77.4%) and less of a significance for esophageal lavage data (Fig. 24, Pearson's = 0.626, p=0.017, R<sup>2</sup>=39.2%).

Ivlev's electivity index was used to determine foraging selectivity of the green turtle population sampled at Kapoho Bay for both DOF (Table 10) and lavage (Table 11) data. For both indices, the species of macroalgae that exceeded 5% of the total pooled diets were included and ranked similarly (*Am. glomerata* 0.86 and 0.90, *Ac. pacifica* 0.86 and 0.8, *Ma. fragilis* 0.85 and 0.76, and *Gr. salicornia* 0.57 and 0.40). All turf species identified from DOF, as well as, species found in lavage samples, ranked a -0.93 and -0.94 respectively, indicating that turf is almost entirely avoided by the turtles. **III: Tables** 

**Table 9.** Results of Pearson's correlations for DOF and lavage data against the benthic cover of the habitat including turf, showing positive but weak correlations indicating a slight relationship between the food items available in the habitat and the same items in the diet. No lavages were conducted during the summer months.

Factor	p-v	alue
	DOF	Lavage
Spring	0.731	0.635
Summer	0.954	-
Fall	0.907	0.856
Winter	0.797	0.657
Site 1	0.831	0.778
Site 2	0.878	0.675

	Electivity
Species	Index
Amansia glomerata	0.86
Acanthophora pacifica	0.86
Martensia fragilis	0.85
Gracilaria salicornia	0.57
Turf	-0.93
Centroceras clavulatum	-1.00
Hypnea spinella	-1.00
Pterocladiella caerulescens	-1.00
Bryopsis hypnoides	-1.00
Cladophoropsis membranacea	-1.00
Dictyota friabilis	-1.00
Sargassum polyphyllum	-1.00
Rhizophora mangle propagule	-1.00
Diatoms	-1.00
Rhodophyta	0.02
Chlorophyta	-1.00
Phaeophyta	-1.00

**Table 10**. Ivlev's Electivity Index of green turtle forage preference and avoidance for DOF data. Determined by formula  $E_i = r_i - p_i / r_i + p_i$ , where  $r_i$  is the relative abundance of prey seen foraged upon and  $p_i$  is the relative abundance of the same prey item in the habitat. The only species of turf seen foraged upon was *Gelidium pusillum* where it found in a thick, dense patch.

Table 11. Ivlev's Electivity Index of green turtle food preference and avoidance for esophageal lavage diet
samples. Determined by formula $E_i = r_i - p_i / r_i + p_i$ , where $r_i$ is the relative abundance of prey item in the
esophagus and p <sub>i</sub> is the relative abundance of the same prey item in the habitat. The genera and species of
turf found in lavage samples were Tolypiocladia glomerulata, Gelidiopsis intricata, Gelidiopsis sp,

Gelidium pusillum, Pterocladiella sp, Valonia aegagropila, and Codium sp.

	Electivity
Species	Index
Turbinaria ornata	1.00
Grass	1.00
Rhizophora mangle propagule	0.97
Amansia glomerata	0.90
Acanthophora pacifica	0.88
Dictyota friabilis	0.80
Martensia fragilis	0.76
Gracilaria salicornia	0.40
Hypnea spinella	0.25
Cladophoropsis membranacea	0.10
Pterocladiella caerulescens	-0.72
Turf	-0.94
Centroceras clavulatum	-1.00
Bryopsis hypnoides	-1.00
Sargassum polyphyllum	-1.00
Diatoms	-1.00
Rhodophyta	-0.02
Chlorophyta	-0.89
Phaeophyta	0.31

III: Figures

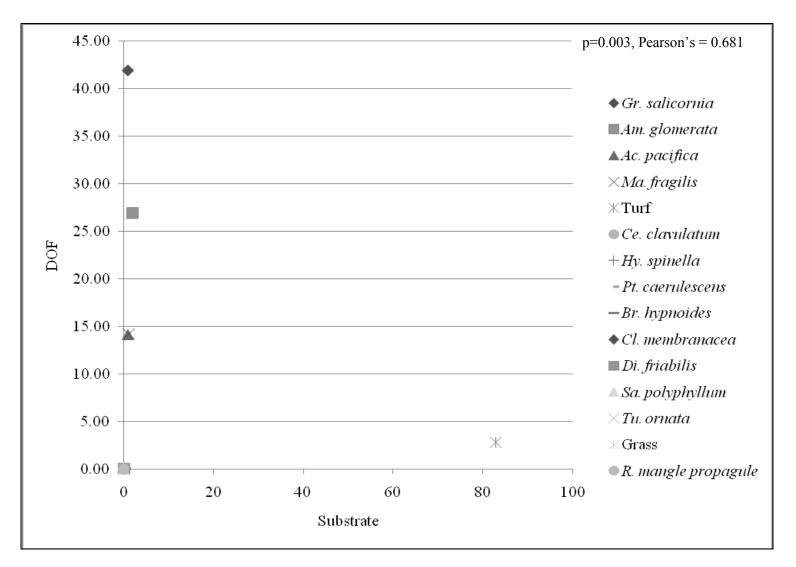


Figure 20. Correlation between relative abundance of edible substrate components (including turf) and food items seen foraged upon (DOF) by turtles at Kapoho Bay during this study.

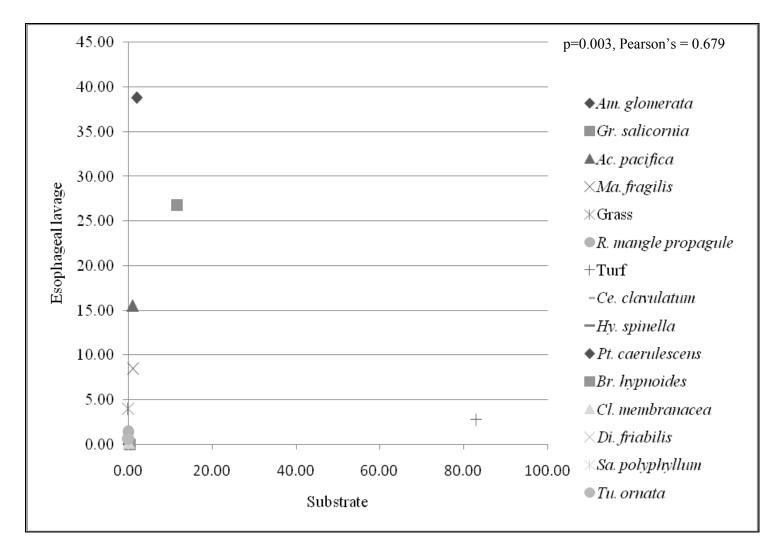


Figure 21. Correlation between relative abundance of edible substrate components (including turf) and food items identified in lavage samples at Kapoho Bay during this study.

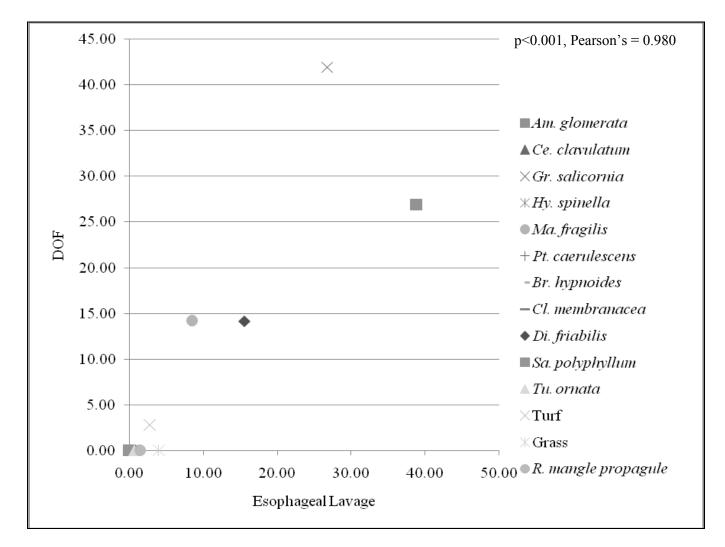


Figure 22. Correlation between relative abundance of food items (including turf) seen foraged upon by turtles and food items identified in lavage samples at Kapoho Bay during this study.

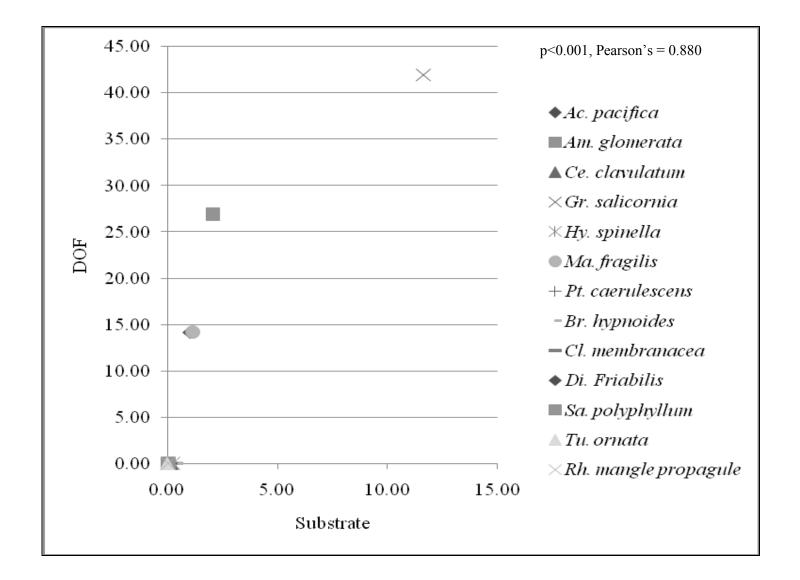


Figure 23. Correlation between relative abundance of edible substrate components (excluding turf) and food items seen foraged upon (DOF) by turtles at Kapoho Bay during this study.

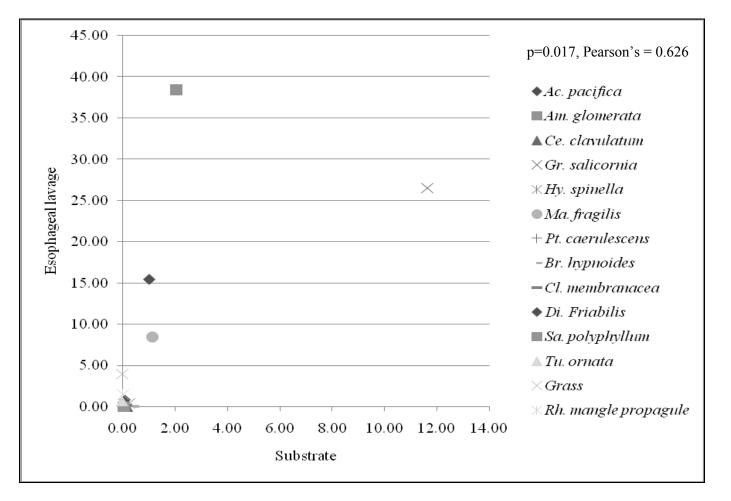


Figure 24. Correlation between relative abundance of edible substrate components (excluding turf) and food items identified in lavage samples at Kapoho Bay during this study.

### IV: Forage nutritional composition

The forage material with the highest protein was grass with 21.9% (mg dry weight) (Table 12). *Rh. mangle* propagules contained only 10.9% protein. Of the divisions of algae, Chlorophyta had the highest protein content (15.2%), Rhodophyta was second (13.7%) and Phaeophyta had the lowest protein content (4.3%).

The algal species with the highest protein content by dry weight were *Br*. *hypnoides*, and *Ce. clavulatum* with 36.8% and 23.8% respectively. The species with the lowest protein content by dry weight were *Tu. ornata* (4.3%) and *Gr. salicornia* (5.7%). Two species of Chlorophyta showed significant seasonal variation in protein content between February and October 2008, *Br. hypnoides* (p=0.006) and *Mi. umbilicatum* (p=0.019) (Fig. 25).

**IV: Tables** 

	Total Protein (%)			
Diet Item	Feb-08	Oct-08	Total Mean	
Rhodophyta	$14.7 \pm 1.6$	$12.6 \pm 1.7$	$13.7 \pm 1.7$	
Centroceras clavulatum	$23.8\pm3.0$	-	$23.8~\pm~3.0$	
Hypnea spinella	$15.1 \pm 1.9$	$21.8\pm5.6$	$18.3\pm3.0$	
Acanthophora pacifica	$18.0 \pm 1.6$	$16.9 \pm 3.3$	$17.5 \pm 1.7$	
Martensia fragilis	$18.0 \pm 1.0$	$15.6\pm0.6$	$16.9\pm0.7$	
Amansia glomerata	$13.1 \pm 1.9$	$8.2\pm0.3$	$10.6 \pm 1.4$	
Pterocladiella caerulescens	$9.0\pm0.7$	-	$9.0\pm0.7$	
Gelidium pusillum	-	$7.2 \pm 0.1$	$7.2 \pm 0.1$	
Gracilaria salicornia	$5.8 \pm 1.0$	$5.7 \pm 0.6$	$5.7 \pm 0.5$	
Chlorophyta	$20.8\pm2.5$	$9.6 \pm 0.8$	$15.2 \pm 1.7$	
Bryopsis hypnoides	$36.8\pm5.5$	$14.4 \pm 1.5$	$25.7\pm5.7$	
Microdictyon umbilicatum	$16.1 \pm 0.9$	$6.4 \pm 0.1$	$10.3 \pm 2.4$	
Cladophoropsis membranacea	$9.5 \pm 1.2$	$8.2 \pm 1.0$	$9.4 \pm 0.7$	
Phaeophyta	$4.3\pm0.2$	-	$4.3\pm0.2$	
Turbinaria ornata	$4.3\pm0.2$	-	$4.3\pm0.2$	
Grass	21.9 *	-	21.9*	
Rhizophora mangle	$13.1 \pm 3.3$	-	$13.1 \pm 3.3$	
Leaf	$15.3\pm6.0$	-	$15.7\pm6.0$	
Propagule	$11.0 \pm 0.5$	-	$10.9 \pm 0.5$	

**Table 12.** Mean ( $\pm$  SE) total protein content relative to total dry weight. n=3, except for grass \*, where n=1.

**IV:** Figures

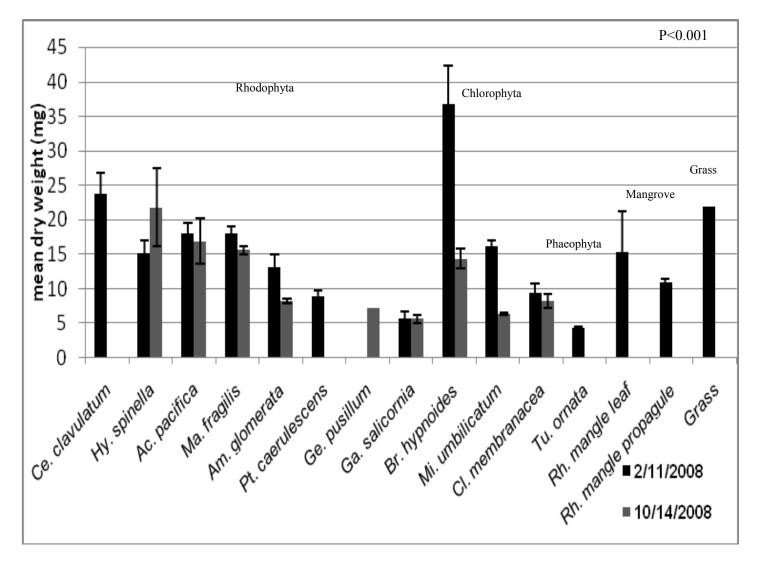


Figure 25. Percent protein content for potential diet items collected during February and October 2008 at Kapoho Bay, Hawaii.

## DISCUSSION

### **Foraging habitat**

The FG at Kapoho Bay are dominated by algae (64% algal turf, and 13.5% macroalgae) with 25 species out of the possible ~500 present in the Hawaiian archipelago (Abbott 1999, Abbott and Huisman 2004), available to foraging turtles. The algal turf (1-3 cm in height) was composed of a dense mixture of interwoven, prostrate species and occasionally the early developmental stages of larger macroalgal species. Species composition varied between sites and among sampling dates as well as demonstrated a variable or patchy distribution within sites. The variability of algal turf at Kapoho Bay is consistent with previous evidence that algal turf can be highly variable among sites in Florida (Forbes 1996), and within Hawaii (Stuercke and McDermid 2004). Of the turf algae available, 60% were Rhodophytes, while 96% of the macroalgal cover was comprised of Rhodophytes consisting of four dominant species; Gr. salicornia, Am. glomerata, Ac. pacifica, and Ma. fragilis. The only nonindigenous alga identified was Gr. Salicornia, which was the most abundant macroalgal species by over five times, indicating that it is the dominant species at Kapoho, and supporting previous evidence that it is successful at out competing local species (Smith et al. 2002, Smith et al. 2004). In this study, the frequency of occurrence of a variety of algal species in the habitat indicates that green turtles have a variety of potential forage items to choose from.

# **Diet composition**

More than 250 species of algae are known to be consumed in some amount by green turtles in Hawaii (Russell and Balazs 2000), however, at Kapoho Bay, the foraging

turtles observed were only ever seen feeding dominantly on four species of red algae. The diet found in the esophageal lavage samples of the turtles was also found to be dominated by algae of the phylum Rhodophyta (81.3%), primarily, the same four species identified from foraging observations. The species of algae that dominated the diet consumed by the turtles at Kapoho Bay were Am. glomerata and Gr. salicornia representing 38% and 27%, respectively, of all items consumed. These results are consistent with Arthur and Balazs (2008) who found green turtle lavage samples at Kapoho to be entirely comprised of *Amansia* and *Gracilaria* in August of 2003. These findings are also consistent with previous studies on foraging ecology of green turtles where red algae is dominantly eaten, such as Florida (Forbes 1996, Redfoot 1997, Holloway-Adkins 2001, Gilbert 2005), Nicaragua (Mortimer 1981), Mexico (Seminoff et al. 2002), Australia (Brand-Gardner et al. 1999, Fuentes et al. 2006), and Hawaii (Arthur and Balazs 2008). The evidence indicates that the nonindigenous alga Gr. salicornia comprises an important proportion of the green turtle diets at Kapoho. This further supports the evidence that this species has been, and still is, a major diet constituent to green turtles in Hawaii since in was first identified from green turtle diet samples from Kane'ohe Bay, O'ahu, in June of 1979 (Russell and Balazs 2009). The most important native species, in order of their contribution to the turtle's diet, were Am. glomerata, Ac. pacifica, and Ma. fragilis. Both Amansia sp. and Acanthophora sp. have been reported as major dietary components for green turtles in the Hawaiian archipelago previously (Balazs 1980a, Russell and Balazs 2000, Russell and Balazs 2009), while Ma. fragilis, which is rare to see, has been unrecorded in the diet of Hawaiian green turtles prior to this study.

A few individuals were determined to have consumed primarily *Rh. mangle* propagules and grass which were not found in the habitat sampled due to their being terrestrial except for one propagule found wedged (not attached to substrate by roots) under a rock along transect 3, near the mangroves. This can be explained by evidence from previous studies where turtles were found to forage on mangroves while they were submerged at high tide and by extending their head and neck from the water to pick leaves or propagules (Pendoley and Fitzpatrick 1999, Limpus and Limpus 2000, Amorocho and Reina 2007, Carrion-Cortez et al. 2010). Turtles have also recently been seen foraging on terrestrial grass at high tide and being hand fed clumps of grass by visitors at least one site on the island of Hawaii; Carlsmith Beach Park, Keaukaha (*Hawaii Tribune Herald*, Jan. 30, 2009). The incidental (<5% total diet) ingestion of turf species, invertebrates, sand, and other debris in this study is similar to other studies of green turtle diet (Seminoff et al. 2002, Ferreira et al. 2006, Fuentes et al. 2006, Lopez-Mendilaharsu et al. 2008, Carrion-Cortez et al. 2010).

Analysis of stable isotope  $\delta^{15}$ N and  $\delta^{13}$ C signatures revealed that it was not possible with two source mixing models to identify distinct  $\delta^{13}$ C signatures among algal species in the diet. It is known that there is an inability to distinguish between different resources or habitats unless they have distinct isotopic signatures. When resources have similar compositions, the distinction between isotopic signatures is blurred, referred to as the "myopia" by Newsome et al. (2006). These results are consistent with Dawson et al. (2002) which indicated that stable isotopes are useful when distinguishing the physiological pathways and status of resources, but it is not always possible to determine the specific taxonomic identity to food sources. It did confirm that the turtles are indeed consuming the species of macroalgae sampled, however, showed conflicting evidence with diet samples that *Rh. mangle* parts or terrestrial grass are not part of the turtles diet. This contradiction in results could be caused by recent ingestion of materials, not allowing enough time for uptake into the animal tissue, however, that was most likely not the case. Grass was found in lavage samples in April of 2007 and mangrove propagules in February 2008 which were the second and third sampling periods, allowing eight more months of assimilation time and two more sampling periods. The turnover rate for dietary-derived  $\delta^{13}$ C in cellular tissue has been established at ~30 days half life indicating there was sufficient time for grass and mangrove signatures to assimilate into turtle tissues (Hobson and Clark 1992a). It is also indicated that the type of tissue used (epidermis) is of lesser metabolic activity than blood or liver and will allow the organism to retain information longer-term and possibly about previously occupied foraging habitats (Hatase et al. 2002, Hobson and Barlein 2004, Seminoff et al. 2006). This phenomenon may be better explained by the multiple distinct sources of protein (mangrove, grass, algae) causing differential routing of dietary nutrients such as suggested by Seminoff et al. (2006). The loss of heavier or lighter isotopes through the internal processes of digestion and cellular respiration could also be playing a role in this scenario (Tieszen and Fagre 1993, Gannes et al. 1997, Ayliffe et al. 2004, Seminoff et al. 2006) such as seen by Klein Breteler et al. (2002) who found that the utilization of carbohydrates and lipids yield significantly different  $\delta_{13}C$  values, but without further investigation into the isotopic differences among dietary proteins, lipids, carbohydrates and other body-tissues components in this study, it is not possible to determine the relative contributions of these factors to the results of this study.

### Site differences

There is evidence to indicate that there are two ecologically distinct sites within Kapoho Bay showing significant differences in abundance and biomass of algal cover, as well as, in the abundance of algae species from DOF, however, no significance was seen in lavage samples. The differences in diet observed foraged upon among sites within Kapoho Bay may reflect the forage material available at each site as turtles were only observed foraging while within 50 m of the habitat sampled, while lavaged turtles may have spent time foraging outside the habitat sampled. In retrospect, Site 2 may not have been best representative of a prime green turtle foraging area due to the lack of three major species of macroalgae subsequently found in turtle diets during this study. The evaluation of biomass during this study was lacking in that only turf algae were recorded, and not macroalgae, due to random sampling and the small percentage of macroalgae available in the habitat sampled compared to turf algae. It would be valuable for future endeavors to perform a fully comprehensive evaluation of biomass by utilizing a different method for determining biomass as well as investigating canopy heights specifically for the species of macroalgae known to be consumed by turtles at Kapoho Bay.

#### Site fidelity

Recaptured green turtles demonstrated fidelity among capture sites (83.6%) where they were found to rest or forage. The diets of recaptured turtles failed to show strong fidelity with only 42.2% of diets containing the same diet items repeatedly. Previous studies indicate strong philopatric tendencies in green turtles (Bowen et al. 1992), but little evidence of specific foraging or resting site fidelity. Green turtle colonies have been found within a few km of each other foraging on distinctly different diets, either seagrass or algae (Carr 1952, Hirth 1971, Felger and Moser 1973, Hirth et al. 1973, Nietshmann 1984). This could indicate that the composition of the turtle diets may be influenced by foraging site fidelity. Further investigation into specific foraging site fidelity perhaps with use of telemetry and observation of foraging surveys could be a valuable direction for future studies.

## Foraging behavior: selectivity vs. availability

Two foraging strategies have been suggested for green turtles: 1) selective foraging for certain species or particular growth stages or portions of the plant (Mortimer 1982, Ross 1985, Brand-Gardner et al. 1999, Arthur and Balazs 2008) and 2) foraging based on the relative abundance of prey items in the habitat (Ogden 1976, Mortimer 1981, Garnett et al. 1985). In order to claim foraging selectivity exists in an environment, two conditions must be met; there must be a variety and abundance of potential food items in the foraging habitat to allow a choice to the animal, a small number of food items are consumed in comparison to those available and animal movement is limited, indicating that intake requirements can be fulfilled in a relatively small area (Leon and Bjorndal 2002, Manly et al. 2002).

Ivlev's index of foraging preference suggests that the turtles at Kapoho generally select species of Rhodophyte. The species of macroalgae that were most highly foraged were *Am. glomerata*, *Ac. pacifica*, *Ma. fragilis* and *Gr. salicornia*. Taxa of Chlorophyta and Phaeophyta were generally avoided. This may be explained by the presence of green and brown species found most commonly as algal turf (<3 cm), and not as large fleshy macroalgae. The green and brown macroalgal species present were either entirely avoided ranking a -1.00 (*Br. hypnoides, Sa. polyphyllum*) or ranked a 1.00 (*Tu. ornata*)

on Ivlev's index indicating that they are selected for by green turtles. The algal turf species present in the esophageal lavage samples and those which turtles were observed foraging upon were only present in incidental amounts (<5%) and ranked the lowest on Ivley's index, indicating algal turf is almost entirely avoided by the turtles at Kapoho. *Rh. mangle* propagules and grass both ranked 1.00 on the index, however, they were not seen growing in the habitat sampled; only majorly comprising a few lavage samples. Gilbert (2005) found species of eight genera, from both phylums of Chlorophyta and Rhodophyta, to be preferred by green turtles at several sites off the coast of Florida. Genera common to those in this study determined to be selected for were; *Hypnea sp.*, Laurencia sp, Gelidium sp. and Gracilaria sp. It has been suggested that diet preference indices are flawed in that their values depend on the density of food items found in the habitat, and the behavior of the consumer, which can cause artificially high or low values if an item is found in the diet but not the habitat, or vice versa (Chesson 1983). For this reason, comparison of electivity values with those of other studies is difficult unless the habitats studied are similar in forage abundance and diversity. The food items at Kapoho that fell into this caveat were Tu. ornata, terrestrial grass, Rh. mangle propagule, and Di. *friabilis*, as well as, the preference for pooled Rhodophytes, which is likely underestimated due to many genera of Rhodophyta being present in the habitat while only a portion were consumed by the turtles. The similarities found between rankings for DOF and esophageal lavage data should not be overlooked. This suggests that the bitecount method of quantifying herbivory (Reppert 1960), previously used only in terrestrial grazing herbivores, is comparable with the established method of esophageal lavage for green turtle diet analysis (Balazs 1980*a*, Forbes and Limpus 1993), and could be used

when the capture of these animals is not possible, however, the probability for error is greater due to environmental conditions and observer skill.

The abundance of food items in the habitat was weakly correlated to the abundance of the same item in the diet of the turtles at Kapoho Bay providing evidence that they may also be foraging based on what is most available to them. Results indicate that turtles at Kapoho eat primarily a macroalgal diet while ingesting turf algae only in incidental levels, regardless of the fact that turf is the most frequently encountered benthic component comprising more than 64% of the habitat sampled. It may be that the turtles are achieving their nutritive requirements on the available macroalgae alone; therefore, the foraging of turf algae at Kapoho is unneeded by the turtles. When turtle diet from DOF was compared to the available forage material in the habitat, a significant correlation was found (Pearson's=0.681, p=0.003). This is expected because turtles ere only observed foraging within (~50 m) of the habitat sampled. The forage material consumed was primarily macroalgae so a secondary correlation, excluding turf algae, revealed a stronger relationship (Pearson's=0.881, p<0.001, R<sup>2</sup>=77.4%). Esophageal lavage data on the other hand, was more strongly correlated with the habitat when turf algae was included (with turf: Pearsons's=0.679, p=0.003, without turf:

Pearson's=0.626, p=0.017,  $R^2$ =39.2%). At at least one site on the west coast of the island of Hawaii (Koloko), algal turf is a main food source for green turtles, however, turf is the dominant forage material available and the species composition and structure of the turf is very different from Kapoho (Arthur and Balazs 2008). The lack of turf in the turtles diet at Kapoho might be explained by a combination of factors; the nature of the turf at Kapoho having defenses against herbivory, and the substratum making it difficult to

forage upon or less available to the turtles ultimately making it not optimal foraging material. The turf at site 1 tended to grow where the substratum was encrusted with calcium carbonate or coralline algae which usually dislodged and remained connected to the rhizomes and holdfasts of plants when collected, which is the most likely explanation for the presence of rocks and calcium carbonate pieces in the lavage samples. At site 2, the turf grew on substratum that was primarily small, smooth stones which would make foraging by a green turtle nearly impossible without ingesting the entire rock. Rhodophytes comprised 96% of the macroalgae present in the habitat and also comprised 92% of the diet ingested by the turtles. The four most common macroalgal species in the habitat were also the most common species found in the diet. Gr. salicornia and Am. glomerata were the two most common macroalgae, showing strong evidence that the abundance and availability of food items in the habitat may effect foraging. The small percentage of diet items consumed compared to the number available in the habitat, as well as, the presence of items in the diet that are not found in the foraging habitat (i.e. Rh. *mangle* propagule, grass and *Tu. ornata*), adds support to the theory that green turtles at this site exhibit selective foraging behaviors. The results of this study indicate that the diet of green turtles at Kapoho Bay is determined by a combination of selective feeding and abundance of forage material in the environment, which is consistent with the findings that green turtle diet is ultimately driven by the availability of preferred diet items in the habitat (Balazs et al. 1987, Forbes 1996, Carrion-Cortez et al. 2010).

#### Nutritional composition of diet

The species of red algae consumed by turtles at Kapoho tended to have higher protein content than species that were avoided. The alga that was most abundantly consumed, Am. glomerata, had a protein content of 13.1% while Gr. salicornia, which was the second most abundant diet item identified, had the lowest protein content (5.8%) of any other Rhodophyte. This can be explained by the fact that Gracilaria was the most abundant macroalgae in the habitat by far, causing the turtles to forage more heavily on it based on its high abundance and availability. The protein contents found in this study were similar to those found by McDermid and Stuercke (2007) except for two outliers (Br. hypnoides and Ce. clavulatum) which had higher protein levels than have been recorded previously. The results of this study are also consistent with previous studies where members of Rhodophyta were found to generally have higher protein contents than those of Chlorophyta and Phaeophyta (Indergaard and Minsaas 1991, Wikelski et al. 1993, Foster and Hodgson 1998, Fleurence 1999, McDermid et al. 2007). This evidence, except for in the case of Gr. salicornia, generally supports the theory of foraging optimality, in which an animal will optimize its energy return per unit of time spent searching for food items by choosing the most nutritious food item available (MacArthur and Pianka 1966, Bjorndal 1979, 1980).

### Digestibility and herbivory defenses

The morphological characteristics and chemical composition of algae can detour herbivores by inhibiting digestion and reducing their nutritive quality known

as anti-herbivore defenses (Augner 1995). The turtles generally avoided all species of Phaeophyta, Chlorophyta and algal turf. Red algae not only tend to have high protein levels, but also have a higher protein digestibility than green or brown algae (Foster and Hodgson 1998, Wong and Cheung 2001). Of the brown algal species, Sa. polyphyllum was entirely avoided while Tu. ornata, which was seen in low numbers in lavage samples, had the lowest protein content of all other plants sampled. Both species share the morphological characteristics of being tough, coarse, and spiny which may make them difficult to consume. Even when ingested, green turtles have been found to have difficulty digesting Phaeophytes, as determined by fecal analysis (Seminoff et al. 2000). The phenolic content of brown algae has been found to be much higher in comparison to species of Rhodophyta and Chlorophyta, and phenols bind to protein molecules affecting the protein digestibility of the plant (Ragan and Glombitza 1986, Fleurence 1999, Wong and Cheung 2001). Of the three species of Chlorophyta analyzed, Mi. umbilicatum and Cl. membranacea were both only found intermixed in turf, and Br. hypnoides tended to accumulate an obvious amount of epiphytes, small invertebrates and debris. The amount of epiphytes on a food item which accumulates as the plant ages has been found to discourage foraging (Bjorndal 1979, 1980, Ogden et al. 1980). The seasonal variation in protein content of Bryopsis could be explained by this factor as isolating clean macroalgal material from the debris was difficult. Even though the algal turf consisted dominantly of Rhodophytes, turf species may have discouraged foraging due to several factors;, the presence of Phaeophytes, calcified Rhodophytes, and high epiphyte and debris load.

These results indicate that anti-herbivory defenses, such as low digestibility and low nutrient content, play a role in green turtle diet selection at Kapoho Bay.

Mangrove propagules and terrestrial grass constituted a small number of whole lavage samples with grass containing the highest protein content and mangrove propagules containing the second to lowest protein content of all diet items; however they do not seem to be assimilating into the tissues of the turtles. Previous studies on green turtles have found that a decreased digestive efficiency occurs when diets consist of two types of forage material such as seagrass and algae (Lipkin 1975, Bjorndal 1979). The evidence of diet variation in a few of the turtles at Kapoho between algae, mangrove and grass, as well as the undigested grass material identified from the fecal pellet sample suggests that these turtles may be experiencing a decrease in digestive efficiency.

### Health of the turtles and future implications

Diet and nutrition are a major influence on growth and can affect growth rates, age of sexual maturity, and fecundity, in green turtles (Carr and Carr 1970, Lipkin 1975, Bjorndal 1979, 1980, Wood and Wood 1980, Bjorndal 1982, Hadjichristophorou and Grove 1983, Brand-Garner et al. 1999). The foraging population at Kapoho is most likely achieving the intake requirements needed to remain healthy based on visual examinations and morphometrics. The results of this study indicate that in habitats where green turtles forage on algae, an assemblage of red macroalgae may be more important to their nutrition than habitats dominated by Chlorophyta or Phaeophyta. When the evidence of site fidelity is coupled with the decrease in digestive efficiency due to diet variation, it is possible to imagine the drastic effect the loss or degradation of a FG would have on these animals. For effective species conservation and management of green turtle foraging grounds, the knowledge of the diet of each local population is crucial due to variation in the foraging ecology between habitats (Ehrenfeld 1982, Bjorndal 1999). Future studies should consider investigation of, specific foraging site fidelity, temporal and spatial diet variation, forage intake, and nutritional value of diet as beneficial avenues for green turtle foraging ecology and conservation.

	Site 1		
Spring	Summer	Fall	Winter
Rhodophyta	Rhodophyta	Rhodophyta	Rhodophyta
Centroceras clavulatum	Centroceras clavulatum	Centroceras clavulatum	Chondrocanthus acicularis
Chondrocanthus acicularis	Chondrocanthus acicularis	Chondrocanthus acicularis	Gelidiopsis intricata
Gelidiopsis intricata	Gelidiopsis intricata	Gelidiopsis intricata	Gelidiopsis sp
Gelidiopsis sp	Gelidiopsis sp	Gelidiopsis sp	Gelidium pusillum
Gelidium pusillum	Gelidium pusillum	Gelidium pusillum	Hypnea spinella
Hypnea spinella	Hypnea spinella	Hypnea spinella	Pterocladiella caerulescens
Laurencia brachyclades	Laurencia brachyclades	Pterocladiella caerulescens	Pterocladiella sp
Pterocladiella caerulescens	Pterocladiella caerulescens	Tolipiocladia glomerulata	
	Pterocladiella sp		
	Tolipiocladia glomerulata		
Chlorophyta	Chlorophyta	Chlorophyta	Chlorophyta
Cladophoropsis	Cladophoropsis	Cladophoropsis	Cladophoropsis
membranacea	membranacea	membranacea	membranacea
Microdictyon umbilicatum	Microdictyon umbilicatum	Microdictyon umbilicatum	
Ulva rigida	Ulva flexuosa	Valonia aegagropila	
	Ulva rigida		
	Phaeophyta	Phaeophyta	
	Dictyota friabilis	Dictyota friabilis	

Appendix A1. Algal turf composition by season for Site 1.

	Site 2					
Spring	Summer	Fall	Winter			
Rhodophyta	Rhodophyta	Rhodophyta	Rhodophyta			
Centroceras clavulatum	Centroceras clavulatum	Centroceras clavulatum	Centroceras clavulatum			
Chondrocanthus acicularis	Chondrocanthus acicularis	Chondrocanthus acicularis	Chondrocanthus acicularis			
Gelidiopsis sp	Chondrocanthus acicularis	Gelidiopsis sp	Gelidiopsis intricata			
Gelidium pusillum	Gelidiopsis sp	Gelidium pusillum	Gelidiopsis sp			
Pterocladiella sp	Gelidium pusillum	Hypnea spinella	Gelidium pusillum			
Pterocladiella caerulescens	Hypnea spinella	Pterocladiella sp	Hypnea spinella			
	Laurencia brachyclades Pterocladiella caerulescens	Pterocladiella caerulescens	Pterocladiella caerulescens			
<b>Chlorophyta</b> Chaetomorpha antennina Cladophoropsis	Chlorophyta Chaetomorpha antennina Cladophoropsis	Chlorophyta Cladophoropsis membranacea	<b>Chlorophyta</b> Cladophoropsis membranacea			
membranacea	membranacea Microdictyon umbilicatum					
Phaeophyta	Phaeophyta	Phaeophyta	Phaeophyta			
Dictyota friabillis	Dictyota friabillis	Dictyota friabilis	Dictyota friabilis			
Lobophora variegata	Lobophora variegata	Lobophora variegata	Lobophora variegata			

Appendix A2. Algal turf composition by season for Site 2.

Species	Transects	p-value
Acanthophora pacifica	Tran 1-Tran 6	p<0.001
	Tran 2-Tran 6	p=0.004
Amansia glomerata	Tran 2-Tran 3	p=0.012
	Tran 2-Tran 5	p=0.002
	Tran 4-Tran 5	p=0.024
Bryopsis hypnoides	Tran 1-Tran 6	p=0.046
Gracilaria salicornia	Tran 1-Tran 4	p<0.001
	Tran 1-Tran 5	p<0.001
	Tran 1-Tran 6	p<0.001
	Tran 2- Tran 4	p=0.006
	Tran 2- Tran 5	p=0.006
	Tran 2- Tran 6	p<0.001
	Tran 3- Tran 4	p<0.001
	Tran 3-Tran 5	p<0.001
	Tran 3-Tran 6	p<0.001
Martensia fragilis	Tran 1-Tran 3	p=0.015
	Tran 1- Tran 4	p=0.015
	Tran 1-Tran 5	p=0.015
	Tran 1-Tran 6	p<0.001
Turf	Tran 2-Tran 3	p<0.001
Diatoms	Tran 1-Tran 2	p=0.038
	Tran 1-Tran 3	p<0.001
	Tran 1-Tran 4	p<0.001
	Tran 1-Tran 5	p<0.001
	Tran 1-Tran 6	p<0.001

Appendix B. Significant p-values for variation in abundance of species by transect.

	Times	Sampling			
Left Tag	Captured	Period	SCL (cm)	Weight (lbs)	FP?
4452781725	1	4	85	214.5	No
4522415843	1	1	60.9	68.3	No
4523671373	1	1	61.5	75	No
4528376832	1	1	61	77	No
4528682028	1	1	41.3	22.6	No
422D4F4030	1	1	56	58.2	No
422F046E69	1	1	69.2	93.9	No
422F080020	1	3	66.6	95.6	No
422F1B6B14	1	1	67.3	96.1	No
423239081D	1	2	50.8	37.6	No
4235706F07	1	1	54	42.1	No
424D05435C	1	1	71.1	106.3	Yes
424D0E4556	1	1	57.9	63.9	No
42501E1224	1	1	71.1	106.3	Yes
433D34573B	1	1	58.8	76	No
443A185310	1	1	54.1	52.7	No
443A1E2068	1	5	70.4	117	No
44522D2925	1	2	60.7	65.8	No
44524 E0272	1	1	70.3	100.8	No
44525E3057	1	2	47.8	40.1	No
452422733F	1	1	56.2	53.8	No
45266D2528	1	1	65.1	86.6	No
452852255A	1	4	47.4	32.5	No
4529786D26	1	1	60.9	68.3	No
46020F7041	1	2	70.6	122.6	No
4629011A1F	1	2	36.4	14	No
467B425537	1	5	61.4	67.5	No
467C194135	1	3	82.8	183.2	No
47063C1E67	1	2	44.9	25.4	No
4709624 E14	1	2	80.6	150.5	No
470970365D	1	1	69.7	102	Yes
4709792D31	1	4	45.4	32.5	No
47097A2E55	1	4	59	64	No
47097E3742	1	1	75.2	132.3	No
470A054066	1	5	55	57	No
470A082A21	1	2	56.1	57.6	No
470A0D4508	1	5	47.6	35	No

Appendix C. Capture information including morphometrics and FP status of Kapoho Bay green turtles.

470A1C3928	1	3	87.9	185.8	No
470A1F6617	1	5	45.9	30.5	No
470A202227	1	1	47.4	34.3	No
470A2C1116	1	1	73.5	130	No
470A3A3954	1	2	73.3	144.5	No
470B054121	1	1	63	74	No
470B1E7320	1	3	87.9	185.8	No
470B2D720B	1	4	48.9	36	No
470B2F0939	1	5	60.9	67.5	No
470B355629	1	4	60.2	73.5	No
470B460069	1	3	66.4	86.9	Yes
470B4E3459	1	5	64.6	81	No
470B5C3F03	1	3	70.8	126.4	No
470C255862	1	5	81.3	218	No
470C2E4547	1	3	57.9	62.4	No
470C311730	1	2	49.6	38.3	No
470C5C4F48	1	5	48.8	37.5	No
470C636053	1	2	61.1	78.6	Yes
470C7B325B	1	5	75.9	153	No
470C7D2A08	1	1	83.5	171.6	No
470D115B66	1	1	38.6	17.7	No
470D125C18	1	4	53	48	No
MC	1	1	83.1	199.3	No
4351211273	2	1, 3	61.6, 64.9	76.7, 80.5	No
4528653520	2	1, 2	57.4, 58.3	58.5, 59.5	No
4628585733	2	2,4	59.3, 59.9	69.7, 69,	No
4629090167	2	2,4	53.8, 55.4	49.3, 50.5	No
4629147140	2	2,4	46.3, 49.2	37.4, 41.5	No
4709640474	2	4, 5	69.6, 69.8	105, 107	No
4709701836	2	3, 5	68.8, 68.7	97, 108.5	No
422D5F6C03	2	1, 2	59.6, 61.2	70.5, 69.2	No
422D62752C	2	1, 2	63.4, 65	85.5, 87.8	No
422D6A1A4A	2	1, 3	65.9, 65.7	88.5, 87.2	No
422E752F59	2	1, 2	69.2, 69.4	93.9, 93	No
422F0A6613	2	1, 2	50.6, 50.8	40, 37.6	No
423230347F	2	1, 2	57.2, 58	62.2, 65.9	No
42324E6167	2	1, 2	59.6, 61.2	70.5, 69.2	No
4232511C58	2	1, 2	67.3, 67.3	97.8, 96.1	No
42334A1D57	2	1, 2	57.2, 58	62.2, 65,9	No
4234764B11	2	2, 5	56.8, 57.6	60.4, 70	No
423F3A0E72	2	1, 2	70.1, 70.1	110.1, 108.2	No
435B71235D	2	1, 3	61.6, 64.9	76.7, 80.5	No

4422014D05	2	2.3	85.3, 86.2	206.3, 201.7	No
443A113D41	2	1, 2	83.8, 83.8	188.2, 183.8	No
445226301A	2	2, 3	41.6, 44.4	24.7, 30.7	No
44522D2274	2	2, 4	59.4, 61.6	65.7, 73	No
4523274D7D	2	1, 2	59, 59.7	73.7,75.7	No
45265B6E10	2	1, 3	62.3, 62.8	73, 79.1	Yes, No
4526775C15	2	4, 5	87.4, 88.2	220, 246.5	No
45284C0030	2	1, 2	50.8, 52.5	43.4, 48.1	No
45296B2F74	2	1, 3	65.9, 66.8	90, 87.9	No
4607494 E66	2	1, 2	53.5,55	47.1, 50.8	No
467D35257D	2	1, 3	68.9, 71.1	103.9, 112	No
467D3A2A1E	2	1, 5	63.4, 65.6	86.6, 96	No
470A00683B	2	3, 4	58.6, 58.7	64.8, 61.5	No
470A081723	2	1, 2	42, 44.2	22.4, 25.3	No
470A101970	2	4, 5	56.2, 57.7	56.5, 63.5	No, Yes
470A11783D	2	3, 4	47.2, 47.2	33.6, 34.5	No
470A146A6F	2	4, 5	42.3, 53.9	50.5, 56	Yes
470B353A0F	2	1, 2	42.5, 44.6	24.6, 28.1	No
470B39534B	2	3, 4	63.1, 62.9	88.5, 87	Yes
470B523363	2	2, 3	65.6, 66.6	85.2, 84.5	No
470C24635A	2	2, 4	60, 56.6	60.7, 57.5	No, Yes
470C702D4A	2	1, 2	40.4, 43.3	22.4, 26.6	No
470D031748	2	1, 3	66.1, 69.3	91.4, 100.5	No
4359317562	3	3, 4, 5	52.8, 53.1, 53.4	50.4, 50, 54	No
					No, No,
4527336730	3	1, 2, 3	66.5, 67.1, 67.4	89.6, 89.1, 93.4	Yes
422F1D275A	3	1, 2, 3	63.9, 64.7, 66.5	93.2, 92.6, 96	No
424D0A5F56	3	1, 2, 3	58.4, 59.1, NT	65.7, 66.2, 69.3	No
424D2B355D	3	1, 2, 3	60.3, 60.6, 61.3	61.3, 64.9, 67.9	No
4452580B10	3	1, 2, 5	54, 55, 57.7	53.3, 54, 64.5	No
44526A6104	3	1, 2, 3	61, 63.2, 66.2	75.5, 82, 92.1	No
44540F3A17	3		62.2, 64, 66.1	78.9, 82.9, 91.4	No
45240B707C	3	1, 2, 3		88.5, 88.7, 91.9	No
46017C6B14	3		54.3, 56.2, 60.9	53.8, 58.1, 77	No
47071E0900	3		50.5, 52, 54.2		No
470A204473	3	3, 4, 5	, ,	39, 37.5, 42	No
470B4E6B15	3	1, 2, 5	52, 54, 57	41.7, 46.4, 53	No
470C7A7315	3	1, 2, 3	38.6, 41.4, 44.5	· · · ·	No
4500(15500	4	1 2 2 4	65.7, 65.8, 66.5,		NT
4529615532	4	1, 2, 3, 4	66.7	98.5	No
467B413D78	4	2 3 1 5	46.3, 48.9, 48.1, 50.6	31.1, 37.8, 37.5, 44	No
+0/D+13D/8	4	2, 3, 4, 5	50.0	<del>44</del>	INU

			48.8, 50.3, 50.2,	32.5, 39.5, 40.5,	
470A070775	4	1, 3, 4, 5	51.8	45	No
			40.1, 40.6, 42.8,	19.2, 21.3, 25,	
470A155832	4	1, 2, 3, 5	45.8	33	No

	Left Tag	Date	Biopsied?	Lavaged?	Capture Site
1	4452781725	3/19/2008	Yes	Yes	Mangrove Cove
2	4522415843	9/21/2006	Yes	No	Blind Inlet
3	4523671373	9/21/2006	Yes	Yes	Blind Inlet
4	4528376832	9/21/2006	Yes	Yes	Blind Inlet
5	4528682028	9/26/2006	Yes	Yes	Mangrove Cove
6	422D4F4030	9/25/2006	Yes	Yes	Champagne Pond
7	422F046E69	9/25/2006	No	Yes	Champagne Pond
8	422F080020	2/11/2008	Yes	Yes	Champagne Pond
9	422F1B6B14	9/24/2006	Yes	No	Blind Inlet
10	423239081D	4/30/2007	No	Yes	Champagne Pond
11	4235706F07	9/22/2006	Yes	Yes	Champagne Pond
12	424D05435C	9/24/2006	Yes	No	Champagne Pond
13	424D0E4556	9/25/2006	Yes	Yes	Champagne Pond
14	42501E1224	9/24/2006	No	Yes	Champagne Pond
15	433D34573B	9/26/2006	Yes	No	Blind Inlet
16	443A185310	9/24/2006	Yes	Yes	Champagne Pond
17	443A1E2068	10/12/2008	Yes	Yes	Blind Inlet
18	44522D2925	5/1/2007	Yes	No	Champagne Pond
19	44524 E0272	9/23/2006	Yes	Yes	Champagne Pond
20	44525E3057	5/2/2007	Yes	No	Mangrove Cove
21	452422733F	9/24/2006	Yes	Yes	Champagne Pond
22	45266D2528	9/22/2006	Yes	Yes	Blind Inlet
23	452852255A	3/19/2008	Yes	Yes	Mangrove Cove
24	4529786D26	9/21/2006	No	Yes	Blind Inlet
25	46020F7041	5/2/2007	Yes	No	Champagne Pond
26	4629011A1F	4/29/2007	Yes	No	Mangrove Cove
27	467B425537	10/13/2008	Yes	Yes	Mangrove Cove
28	467C194135	2/11/2008	Yes	Yes	Champagne Pond
29	47063C1E67	4/29/2007	Yes	Yes	Champagne Pond
30	4709624 E14	4/30/2007	Yes	No	Blind Inlet
31	470970365D	9/22/2006	Yes	No	Blind Inlet
32	4709792D31	3/18/2008	Yes	Yes	Mangrove Cove
33	47097A2E55	3/18/2008	Yes	Yes	Mangrove Cove
34	47097E3742	9/23/2006	Yes	Yes	Mangrove Cove
35	470A054066	10/14/2008	Yes	Yes	Mangrove Cove
36	470A082A21	5/2/2007	Yes	No	Mangrove Cove
37	470A0D4508	10/14/2008	Yes	Yes	Mangrove Cove
38	470A0D4E59	10/14/2008	Yes	Yes	Mangrove Cove
39	470A1C3928	2/12/2008	No	Yes	Mangrove Cove
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Appendix D. Capture information for turtles sampled at Kapoho Bay.

40	470A1F6617	10/15/2008	Yes	Yes	Mangrove Cove
41	470A202227	9/24/2006	Yes	Yes	Champagne Pond
42	470A2C1116	9/22/2006	Yes	Yes	Blind Inlet
43	470A3A3954	4/28/2007	Yes	No	Mangrove Cove
44	470B054121	9/23/2006	Yes	Yes	Mangrove Cove
45	470B1E7320	2/12/2008	Yes	No	Mangrove Cove
46	470B2D720B	3/18/2008	Yes	Yes	Mangrove Cove
47	470B2F0939	10/15/2008	Yes	Yes	Blind Inlet
48	470B355629	3/16/2008	Yes	Yes	Mangrove Cove
49	470B460069	2/11/2008	Yes	No	Blind Inlet
50	470B4E3459	10/14/2008	Yes	Yes	Mangrove Cove
51	470B5C3F03	2/12/2008	Yes	Yes	Champagne Pond
52	470C255862	10/14/2008	Yes	Yes	Mangrove Cove
53	470C2E4547	2/12/2008	Yes	Yes	Mangrove Cove
54	470C311730	5/2/2007	Yes	No	Mangrove Cove
55	470C5C4F48	10/14/2008	Yes	Yes	Mangrove Cove
56	470C636053	4/28/2007	Yes	Yes	Mangrove Cove
57	470C7B325B	10/13/2008	Yes	Yes	Mangrove Cove
58	470C7D2A08	9/25/2006	Yes	Yes	Blind Inlet
59	470D115B66	9/22/2006	No	Yes	Blind Inlet
60	470D125C18	3/18/2008	Yes	Yes	Mangrove Cove
61	MC	9/23/2006	Yes	Yes	Mangrove Cove
62	4351211273	9/25/2006	Yes	No	Champagne Pond
	4351211273	2/10/2008	Yes	No	Champagne Pond
63	4528653520	9/24/2006	Yes	Yes	Champagne Pond
	4528653520	5/1/2007	Yes	Yes	Champagne Pond
64	4628585733	4/28/2007	Yes	Yes	Mangrove Cove
	4628585733	3/17/2008	Yes	Yes	Blind Inlet
65	4629090167	4/28/2007	Yes	Yes	Blind Inlet
	4629090167	3/18/2008	Yes	No	Mangrove Cove
66	4629147140	4/29/2007	Yes	Yes	Blind Inlet
	4629147140	3/16/2008	Yes	Yes	Mangrove Cove
67	4709640474	3/19/2008	Yes	Yes	Mangrove Cove
	4709640474	10/13/2008	Yes	Yes	Mangrove Cove
68	4709701836	2/11/2008	Yes	Yes	Blind Inlet
	4709701836	10/13/2008	Yes	Yes	Blind Inlet
69	422D5F6C03	9/22/2006	Yes	No	Not Listed
	422D5F6C03	5/1/2007	Yes	No	Champagne Pond
70	422D62752C	9/22/2006	Yes	Yes	Blind Inlet
	422D62752C	5/1/2007	Yes	Yes	Champagne Pond
71	422D6A1A4A	9/24/2006	Yes	Yes	Champagne Pond
	422D6A1A4A	2/12/2008	Yes	Yes	Champagne Pond
			89		

72	422E752F59	9/25/2006	Yes	No	Champagne Pond
12	422E752F59	5/2/2007	Yes	No	Champagne Pond
73	422F0A6613	9/24/2006	Yes	No	Blind Inlet
15	422F0A6613	4/30/2007	Yes	No	Champagne Pond
74	423230347F	9/25/2006	Yes	No	Champagne Pond
/ -	423230347F	4/30/2007	Yes	No	Blind Inlet
75	42324E6167	9/22/2006	No	Yes	Not listed
10	42324E6167	5/1/2007	No	Yes	Champagne Pond
76	4232511C58	9/21/2006	Yes	Yes	Blind Inlet
, 0	4232511C58	4/28/2007	Yes	Yes	Blind Inlet
77	42334A1D57	9/25/2006	No	Yes	Champagne Pond
	42334A1D57	4/30/2007	No	Yes	Blind Inlet
78	4234764B11	5/2/2007	Yes	No	Champagne Pond
	4234764B11	10/14/2008	Yes	Yes	Champagne Pond
79	423F3A0E72	9/23/2006	Yes	Yes	Champagne Pond
	423F3A0E72	4/29/2007	Yes	Yes	Blind Inlet
80	435B71235D	9/25/2006	No	Yes	Not listed
	435B71235D	2/10/2008	No	Yes	Champagne Pond
81	4422014D05	5/2/2007	Yes	No	Blind Inlet
	4422014D05	2/12/2008	Yes	Yes	Blind Inlet
82	443A113D41	9/25/2006	Yes	No	Blind Inlet
	443A113D41	5/1/2007	Yes	Yes	Blind Inlet
83	445226301A	5/2/2007	Yes	No	Mangrove Cove
	445226301A	2/12/2008	Yes	Yes	Mangrove Cove
84	44522D2274	5/2/2007	Yes	No	Mangrove Cove
	44522D2274	3/18/2008	Yes	Yes	Mangrove Cove
85	4523274D7D	9/26/2006	Yes	No	Blind Inlet
	4523274D7D	5/2/2007	Yes	No	Blind Inlet
86	45265B6E10	9/21/2006	No	Yes	Blind Inlet
	45265B6E10	2/11/2008	Yes	Yes	Blind Inlet
87	4526775C15	3/19/2008	Yes	Yes	Mangrove Cove
	4526775C15	10/13/2008	Yes	Yes	Mangrove Cove
88	45284C0030	9/24/2006	Yes	Yes	Champagne Pond
	45284C0030	4/30/2007	Yes	Yes	Champagne Pond
89	45296B2F74	9/26/2006	Yes	No	Blind Inlet
	45296B2F74	2/11/2008	Yes	Yes	Blind Inlet
90	4607494 E66	9/24/2006	Yes	Yes	Champagne Pond
	4607494 E66	5/1/2007	Yes	No	Champagne Pond
91	467D35257D	9/25/2006	Yes	Yes	Champagne Pond
0.2	467D35257D	2/12/2008	Yes	Yes	Champagne Pond
92	467D3A2A1E	9/22/2006	Yes	No	Mangrove Cove
	467D3A2A1E	10/15/2008	Yes	Yes	Mangrove Cove
			90		

93	470A00683B	3/18/2008	Yes	Yes	Mangrove Cove
	470A00683B	2/12/2008	No	Yes	Mangrove Cove
94	470A081723	9/24/2006	Yes	Yes	Champagne Pond
	470A081723	5/1/2007	Yes	Yes	Champagne Pond
95	470A101970	3/19/2008	Yes	Yes	Mangrove Cove
	470A101970	10/15/2008	Yes	Yes	Mangrove Cove
96	470A11783D	2/11/2008	Yes	Yes	Blind Inlet
	470A11783D	3/16/2008	No	Yes	Blind Inlet
97	470A146A6F	3/18/2008	Yes	Yes	Mangrove Cove
	470A146A6F	10/13/2008	Yes	Yes	Mangrove Cove
98	470B353A0F	9/24/2006	Yes	Yes	Champagne Pond
	470B353A0F	5/1/2007	Yes	Yes	Champagne Pond
99	470B39534B	2/12/2008	Yes	Yes	Mangrove Cove
	470B39534B	3/16/2008	No	Yes	Mangrove Cove
100	470B523363	5/2/2007	Yes	No	Blind Inlet
	470B523363	2/12/2008	Yes	Yes	Mangrove Cove
101	470C24635A	5/1/2007	Yes	Yes	Mangrove Cove
	470C24635A	3/17/2008	No	Yes	Mangrove Cove
102	470C702D4A	9/25/2006	Yes	Yes	Champagne Pond
	470C702D4A	4/30/2007	Yes	Yes	Champagne Pond
103	470D031748	9/22/2006	Yes	No	Mangrove Cove
	470D031748	2/12/2008	Yes	Yes	Mangrove Cove
104	4359317562	2/10/2008	Yes	Yes	Blind Inlet
	4359317562	3/16/2008	No	Yes	Blind Inlet
	4359317562	10/12/2008	Yes	Yes	Blind Inlet
105	4527336730	9/21/2006	Yes	Yes	Blind Inlet
	4527336730	5/1/2007	Yes	Yes	Blind Inlet
	4527336730	2/11/2008	Yes	Yes	Blind Inlet
106	422F1D275A	9/22/2006	Yes	Yes	Champagne Pond
	422F1D275A	4/28/2007	Yes	Yes	Blind Inlet
	422F1D275A	2/10/2008	Yes	Yes	Champagne Pond
107	424D0A5F56	9/25/2006	Yes	Yes	Champagne Pond
	424D0A5F56	4/30/2007	Yes	Yes	Champagne Pond
	424D0A5F56	2/10/2008	Yes	Yes	Champagne Pond
108	424D2B355D	9/22/2006	Yes	Yes	Not Listed
	424D2B355D	5/1/2007	Yes	No	Champagne Pond
	424D2B355D	2/11/2008	Yes	Yes	Champagne Pond
109	4452580B10	9/24/2006	Yes	Yes	Champagne Pond
	4452580B10	5/1/2007	Yes	Yes	Champagne Pond
	4452580B10	10/14/2008	Yes	Yes	Champagne Pond
110	44526A6104	9/25/2006	Yes	Yes	Champagne Pond
	44526A6104	4/30/2007	Yes	No	Champagne Pond
			01		-

	1150CAC101	2/11/2000	V	V	C1
111	44526A6104	2/11/2008 9/22/2006	Yes	Yes	Champagne Pond
111	44540F3A17		Yes	Yes	Blind Inlet
	44540F3A17	4/30/2007	Yes	Yes	Champagne Pond
110	44540F3A17	2/12/2008	Yes	Yes	Champagne Pond
112	45240B707C	9/23/2006	Yes	Yes	Champagne Pond
	45240B707C	4/30/2007	Yes	Yes	Champagne Pond
	45240B707C	2/10/2008	Yes	Yes	Champagne Pond
113	46017C6B14	9/22/2006	Yes	Yes	Blind Inlet
	46017C6B14	4/28/2007	Yes	Yes	Blind Inlet
	46017C6B14	10/12/2008	Yes	Yes	Blind Inlet
114	47071E0900	9/22/2006	Yes	Yes	Not Listed
	47071E0900	4/29/2007	Yes	Yes	Champagne Pond
	47071E0900	2/10/2008	Yes	Yes	Champagne Pond
115	470A204473	2/11/2008	Yes	Yes	Blind Inlet
	470A204473	3/16/2008	No	Yes	Blind Inlet
	470A204473	10/12/2008	Yes	Yes	Blind Inlet
116	470B4E6B15	9/24/2006	Yes	Yes	Champagne Pond
	470B4E6B15	5/2/2007	Yes	No	Champagne Pond
	470B4E6B15	10/14/2008	Yes	Yes	Champagne Pond
117	470C7A7315	9/22/2006	Yes	No	Blind Inlet
	470C7A7315	5/2/2007	Yes	No	Champagne Pond
	470C7A7315	2/11/2008	Yes	No	Champagne Pond
118	4529615532	9/26/2006	Yes	No	Blind Inlet
	4529615532	4/28/2007	Yes	Yes	Mangrove Cove
	4529615532	2/12/2008	Yes	No	Mangrove Cove
	4529615532	3/18/2008	No	Yes	Mangrove Cove
119	467B413D78	4/28/2007	Yes	Yes	Blind Inlet
	467B413D78	2/10/2008	Yes	Yes	Blind Inlet
	467B413D78	3/16/2008	No	Yes	Blind Inlet
	467B413D78	10/12/2008	Yes	Yes	Blind Inlet
120	470A070775	9/22/2006	Yes	No	Blind Inlet
	470A070775	2/10/2008	Yes	Yes	Blind Inlet
	470A070775	3/16/2008	No	Yes	Blind Inlet
	470A070775	10/12/2008	Yes	Yes	Blind Inlet
121	470A155832	9/22/2006	Yes	Yes	Champagne Pond
	470A155832	4/29/2007	Yes	Yes	Champagne Pond
	470A155832	2/10/2008	Yes	Yes	Champagne Pond
	470A155832	10/14/2008	Yes	Yes	Champagne Pond

≥5% Lavage	n=	FO (%)
Amansia glomerata	92	34.46
Gracilaria salicornia	51	19.10
Acanthophora pacifica	28	10.49
Martensia fragilis	21	7.87
Grass	10	3.75
Gelidium pusillum	4	1.50
Rhizophora mangle propagule	4	1.50
Gelidiopsis sp	19	7.12
Shells/Rocks	12	4.49
Pterocladiella sp	2	0.75
Cladophoropsis membranacea	3	1.12
Dictyota friabilis	11	4.12
Hypnea spinella	4	1.50
Turbinaria ornata	5	1.87
Gelidiopsis intricata	1	0.37

Appendix E1. Frequency of occurrence of diet items expressed as the proportion of samples in which algae was found to contribute  $\geq 5$  of relative volume.

Appendix E2. Frequency of occurrence of diet items expressed as the proportion of samples in which algae was found to contribute  $\geq$ 50% of relative volume.

≥50% Lavage n=153	n=	FO (%)
Amansia glomerata	63	41.18
Gracilaria salicornia	45	29.41
Acanthophora pacifica	22	14.38
Martensia fragilis	11	7.19
Grass	6	3.92
Gelidium pusillum	2	1.31
Rhizophora mangle propagule	2	1.31
Gelidiopsis sp	1	0.65
Shells/Rocks	1	0.65
Pterocladiella sp	1	0.65

100% Lavage	n=	FO (%)
one item	72	100.00
one algal species	66	91.67
Amansia glomerata	36	50.00
Gracilaria salicornia	22	30.56
Acanthophora pacifica	6	8.33
Grass	5	6.94
Gelidium pusillum	1	1.39
Rhizophora mangle propagule	1	1.39
Gelidiopsis sp	1	1.39

**Appendix E3.** Frequency of occurrence of diet items expressed as the proportion of samples in which algae was found to contribute 100% of relative volume.

Diet item #1	Diet item #2	Acanthophora pacifica	Amansia glomerata	Microdictyon umbilicatum	Bryopsis hypnoides	Cladophoropsis membranacea	Gelidium pusillum	Gracilaria salicornia	Grass	Hypnea spinella	<i>Rhizophora mangle</i> leaf	<i>Rhizophora mangle</i> propagule	Martensia fragilis
Acanthophora pacifica 2.8‰			0.0	0.0	0.0	100.0	0.0	100.0	100.0	0.0	82.2	80.1	0.0
3.4‰			0.0	0.0	0.0	100.0	0.0	100.0	100.0	0.0	83.5	81.5	0.0
Amansia glomerata 2.8‰		100.0		100.0	100.0	100.0	100.0	100.0	100.0	100.0	91.3	90.1	0.0
3.4‰		100.0		100.0	100.0	100.0	100.0	100.0	100.0	100.0	92.7	91.7	0.0
Microdictyon umbilicatum 2.8‰		100.0	0.0		100.0	100.0	0.0	100.0	100.0	100.0	87.5	85.9	0.0
3.4‰		100.0	0.0		100.0	100.0	0.0	100.0	100.0	100.0	88.9	87.5	0.0
Bryopsis hypnoides 2.8‰		100.0	0.0	0.0		100.0	0.0	100.0	100.0	0.0	83.4	81.4	0.0
3.4‰		100.0	0.0	0.0		100.0	0.0	100.0	100.0	0.0	84.7	82.9	0.0
Cladophoropsis membranacea 2.8‰		0.0	0.0	0.0	0.0		0.0	0.0	100.0	0.0	71.8	68.9	0.0
3.4‰		0.0	0.0	0.0	0.0		0.0	0.0	100.0	0.0	72.9	70.1	0.0
Gelidium pusillum 2.8‰		100.0	0.0	100.0	100.0	100.0		100.0	100.0	100.0	90.1	88.8	0.0
3.4‰		100.0	0.0	100.0	100.0	100.0		100.0	100.0	100.0	91.5	90.4	0.0
Gracilaria salicornia 2.8‰		0.0	0.0	0.0	0.0	100.0	0.0		100.0	0.0	77.0	74.5	0.0
3.4‰		0.0	0.0	0.0	0.0	100.0	0.0		100.0	0.0	78.2	75.8	0.0
Grass 2.8‰		0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	71.0	68.1	0.0
3.4‰		0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	72.2	69.4	0.0
Hypnea spinella 2.8‰		100.0	0.0	0.0	100.0	100.0	0.0	100.0	100.0		86.7	85.0	0.0
3.4‰		100.0	0.0	0.0	100.0	100.0	0.0	100.0	100.0		88.1	86.6	0.0
Rhizophora mangle leaf 2.8‰		17.8	8.7	12.5	16.6	28.2	9.9	23.0	29.0	13.3		0.0	2.8
3.4‰		16.5	7.3	11.1	15.3	27.1	8.5	21.8	27.8	11.9		0.0	1.2
Rhizophora mangle propagule 2.8‰		19.9	9.9	14.1	18.6	31.1	11.2	25.5	31.9	15.0	100.0		3.2
3.4‰		18.5	8.3	12.5	17.1	29.9	9.6	24.2	30.6	13.4	100.0		1.4
Martensia fragilis 2.8‰		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	97.2	96.8	
3.4‰		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	98.8	98.6	

Appendix F. Two-source mixing model summary showing percent contribution of food items (A and B).

## LITERATURE CITED

- Abbott, I.A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu, Hawaii. pp. 465.
- Abbott, I.A., and J.M. Huisman. 2004. Marine green and brown algae of the Hawaiian Islands. Bishop Museum Press, Honolulu, Hawaii. pp. 259.
- Aguirre, A.A., Spraker, T.R., Balazs, G.H., and B. Zimmerman. 1998. Spirochidiasis and fibropapillomatosis in green turtles of the Hawaiian Islands. Journal of Wildlife Diseases 34:91-98.
- Amorocho, D., and R. Reina. 2007. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorogona National Park, Colombia. Journal of Endangered Species Research **3**:42-51.
- Arthur, K., and G.H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pacific Science 62(2):205-217.
- Augner, M. 1995. Low nutritive quality as a plant defense: effects of herbivore-mediated interactions. Evolution of Ecology **9**:605-61.
- Ayliffe, L.K., Cerling, T.E., Robinson, T., West, A.G., Sponheimer, M., Passey, B.H.,
  Hammer, J., Roeder, B., Dearing, M.D., and J.R. Ehleringer. 2004. Turnover of carbon isotopes in tail hair and breath CO<sub>2</sub> of horses fed an isotopically varied diet. Oecologia
  139:11-22.

- Baker, J.D., Littnan, C.L, and D.W. Johnston. 2006. Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the Northwestern Hawaiian Islands. Endangered Species Research 4:1-10.
- Balazs, G.H. 1976. Green turtle migrations in the Hawaiian Archipelago. Biological Conservation **9**:125-140.
- Balazs, G.H. 1980*a*. Field methods for sampling the dietary components of green turtles, *Chelonia mydas*. Herpetology Rev. **11**(1):5-6.
- Balazs, G.H. 1980b. Synopsis of biological data on the green turtle in the Hawaiian Islands.US Department of Commerce. NOAA Technical Memorandum NMFS-SWFC-7.Honolulu. pp. 141.
- Balazs, G.H. 1982. Growth rates of immature green turtles in the Hawaiian archipelago. *In*:K.A. Bjorndal, editor. Biology and conservation of sea turtles pp 117-125.
- Balazs, G.H. 2000. Assessment of Hawaiian green turtles utilizing coastal foraging pastures at Palaau, Molokai. *In* K.A. Bjorndal, and A.B. Bolten, editors. Proceedings of a Workshop on Assessing Abundance and Trends for In-water Sea Turtle Populations. US Department of Commerce. NOAA Technical Memorandum NMFS-SEFSC 445, pp. 83.
- Balazs, G.H., and M. Chaloupka. 2004. Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. Marine Biology 145:1043-1059.

- Balazs, G.H., and M. Chaloupka. 2006. Recovery trend over 32 years at the Hawaiian green turtle rookery of French Frigate Shoals. Atoll Research Bulletin **543**:147-158.
- Balazs, G.H., Forsyth, R.G., and K.H. Kam. 1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. NOAA Technical Memorandum NMFS-SWFC-71. pp. 107.
- Balazs, G.H., Murakawa, S.K.K., Ellis, D.M., Aguirre, A.A. 2000. Manifestation of fibropapillomatosis and rates of growth of green turtles at Kaneohe Bay in the Hawaiian Islands. Proceedings of the Eighteenth International Symposium on Sea Turtle Biology and Conservation. Veterinary Medicine and Disease/Oral Presentations pp. 132-313.
- Biasatti, D.M. 2004. Stable carbon isotopic profiles for sea turtle humeri: implications for ecology and physiology. Paleogeography Paleoclimatolgy Paleoecology **206**:203-216.
- Bjorndal, K.A. 1979. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. Advances in Comparative Biochemical Physiology **63**:127-133.
- Bjorndal, K.A. 1980. Nutrition and grazing behavior of the green turtle, *Chelonia mydas*. Marine Biology **56**:147–154.
- Bjorndal, K.A. 1982. The consequences of herbivory for the life history pattern of the Caribbean green turtle. *In:* K. A. Bjorndal, editor. Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, D.C., USA. pp. 111–116.
- Bjorndal, K.A. 1997. Foraging ecology and nutrition of sea turtles. *In:* P.L. Lutz and J.A. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida, USA. pp 199–231.

- Bjorndal, K.A. 1999. Priorities for researching foraging habitats. *In:* K.L. Eckert, K.A.
  Bjorndal, F.A. Abreu-Grobois, and M. Donnely, editors. Research and management techniques for the conservation of sea turtles IUCN/SSC Marine Turtle Specialist Group Publication No. 4, Washington, DC. pp. 12-18.
- Bjorndal, K.A., and A.B. Bolten. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. Copeia **1988**:555–564.
- Bowen, B.W., Meylan, A.B., Ross, J.P., Limpus, C.J., Balazs, G.H., and J.C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchial phylogeny. Evolution **46**(4):865-881.
- Brand-Gardner, S.J., Lanyon, J.M., Limpus, C.J. 1999. Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. Australia. Journal of Zoology **47**:181-191.
- Carr, A. 1952. Handbook of turtles. Comstock Publishing Associates, Ithica, New York. pp. 542.
- Carr, A. 1967*a*. So excellent a fish; a natural history of sea turtles. Anchor Press/Doubleday, Garden City, New York. pp. 249.
- Carr, A. 1967b. Adaptive aspects of the scheduled travel of *Chelonia*. *In:* R.M. Storm, editor. Animal orientation and navigation Oregon State University. Press, Corvallis, pp. 35-55.

- Carr, A. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1:103-121.
- Carr, A., and M.H. Carr. 1970. Modulated reproductive periodicity in *Chelonia*. Ecology **51**:335-337.
- Carr, A. and A.B. Meylan. 1980. Evidence of passive migration of green turtle hatchlings in *Sargassum*. Copeia **1980**:366-368.
- Carrion-Cortez, J.A., Zarate, P., and J.A. Seminoff. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. Journal of the Marine Biological Association of the United Kingdom. pp1-9.
- Chaloupka, M., and G.H. Balazs. 2005. Modeling the effect of fibropapilloma disease on the somatic growth dynamics of Hawaiian green sea turtles. Marine Biology 147:1251-1260.
- Chaloupka, M., Bjorndal, K.A., Balazs, G.H., Bolten, A.B., Ehrhart, L.M., Limpus, C.J., Suganuma, H., Troeng, S., and M. Yamaguchi. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Global Ecology and Biogeography 17:297-304.
- Chaloupka, M., Balazs, G.H., and T.M. Work. 2009. Rise and fall over 26 years of a marine epizooitic in Hawaiian green sea turtles. Journal of Wildlife Diseases 45(4):1138-1142.

- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology **64**(5):1297-1304.
- Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., and K.P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecological Systems **33**:507-559.
- DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta **42**:495-506.
- DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta **45**:341-351.
- Dutton, P.H., Balazs, G.H., LeRoux, A., Murakawa, S.K.K., Zarate, P, and L.S. Martinez. 2008. Composition of Hawaiian green turtle foraging aggregations: mtDNA evidence for a distinct regional population. Endangered Species Research **5**:37-44.
- Ehrenfeld, D. 1982. Options and limitation in the conservation of sea turtles. *In:* K.A. Bjorndal, editor. Biology and Conservation of Sea Turtles Smithsonian Institution Press, Washington, DC, pp. 457-464.
- Felger, R., and M.B. Moser. 1973. Eelgrass (*Zostera marina* L.) in the Gulf of California. Science 181(4097):355-356.
- Ferreira, M.M. 1968. Sobre a alimentacao da aruana, *Chelonia mydas* Linnaeus 1758, ao logo da costa do Estado do Ceara. Arq Est Biol Mar Univ Fed DCeara **8**:83-86.

- Ferreira, B., Garcia, M., Jupp, B.P., and A. Al-Kiyumi. 2006. Diet of the green turtle (*Chelonia mydas*) at Ra's Al Hadd, Sultanate of Oman. Chelonian Conservation and Biology **5**:141-146.
- Fleurence, J. 1999 Seaweed proteins; biochemical, nutritional aspects and potential uses. Trends Food Science Techniques **10**:25-28.
- Forbes, G.A. 1996. The diet and feeding ecology of the green sea turtle (*Chelonia mydas*) in an algal-based coral reef community. PhD thesis, James Cook University of North Queensland. pp. 340.
- Forbes, G.A., and C.J. Limpus. 1993. A non-lethal method for retrieving stomach contents from sea turtles. Wildlife research **20**:339-343.
- Foster, G.G., and A.N. Hodgson. 1998. Consumption and apparent dry matter digestibility of six intertidal macroalgae by *Turbo sarmaticus* (Molusca: Vetigastropoda: Turbinidae). Aquaculture **167**:211-277.
- Fuentes, M.M.P.B., Lawler, I.R., and E. Guyris. 2006. Dietary preferences of juvenile green turtles (*Chelonia mydas*) on a tropical reef flat. Wildlife Research **33**:671-678.
- Gannes, L.Z., Martinez del Rio, C., and P. Koch. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology **78**:1271-1276.
- Garnett, S.T., Price, I.R., and F.J. Scott. 1985. The diet of the green turtle *Chelonia mydas* (L.), in Torres Strait, Australia Wildlife Reserve **12**:102-112.

- Gill, A.T. 2007. Feasibility of a Geothermal Direct Use Enterprise Park in Puna, Hawaii.State of Hawaii, Department of Business, Economic Development and Tourism StrategicIndustries Division. pp 11.
- Gilbert, E. 2005. 2005. Juvenile green turtle (*Chelonia mydas*) foraging ecology, feeding selectivity and forage nutrient analysis. Master's thesis, University of Central Florida.pp. 57.
- Godley, B.J., Guch, A.C., Broderick, A.C., Furness, R.W., and S.E. Solomon. 1998.Interaction between marine turtles and artisanal fisheries in the eastern Mediterranean: a probable cause for concern. Reptila pp. 9-70.
- Hadjichristophorou, M., and D.J. Grove. 1983. A study of appetite, digestion and growth in juvenile green turtles (*Chelonia mydas*) fed on artificial diets. Aquaculture **30**:191-201.
- Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Goto, K., and K. Omuta. 2000.
  Feeding grounds of adult female loggerhead turtles, *Caretta caretta*, in the western North
  Pacific Ocean estimated by carbon and nitrogen stable isotope analyses of egg-yolks. *In*A. Mosier, A. Foley, and B. Brost, editors. Proceedings of the Twentieth Annual
  Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum
  NMFS-SEFSC-477. U.S. Department of Commerce, National Marine Fisheries Service,
  Southeast Fisheries Science Center. Miami, Florida., pp. 55-56.
- Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., and T. Fujiwara. 2002. Size-related differences in feeding habitat use of adult female loggerhead

turtles, *Caretta caretta*, around Japan determined by stable isotope analysis and satellite telemetry. Marine Ecology Progress Series **233**:273-281.

- Hawaii Tribune Herald, 30 Jan 2009. Too close to Honu. <u>www.hawaiitribune-herald.com/articles/2009/01/30</u> Accessed 2 Apr 2010.
- Hirth, H.F. 1971. Synopsis of biological data on the green turtle, *Chelonia mydas*. Food and Agriculture Organization of the United Nations, Rome, pp. 79
- Hirth, H.F. 1997. Synopsis of the biological data on the green turtle, *Chelonia mydas* (Linnaeus 1758). US Fish and Wildlife Service Biological Report **97**:1-120.
- Hirth, H.F., Klikoff, I.G., and K.T. Harper. 1973. Seagrasses at Khor Umaira, People's Democratic Republic of Yemen with reference to their role in the diet of the green turtle, *Chelonia mydas* (Linnaeus) 1758. F.A.O. Fish. Synopsis NO. 85. F.A.O./U.N., Rome. 71:1093-1097.
- Hobson, K.A., and F. Barlein. 2004. Isotopic fractionation and turnover in captive golden warblers (*Sylvia boyrin*): implications for delineating dietary and migratory association in wild passerines. Canadian Journal of Zoology **81**:1630-1635.
- Hobson, K.A., and R.G. Clark. 1992*a*. Assessing avian diets using stable isotopes. I. Turnover in  $_{13}$ C in tissues. Condor **94**:181–188.
- Hobson, K.A., and R.G. Clark. 1992*b*. Assessing avian diets using stable isotopes. II. Factors influencing diet–tissue fractionation. Condor **94**:189–197.

- Hobson, K.A., Schell, D.M., Renoug, D., and E. Noseworthy. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences **53**:528–533.
- Holloway-Adkins, K.G. 2001. A comparative study of the feeding ecology of *Chelonia mydas* (green turtle) and the incidental ingestion of *prorocentrum spp*. Master's thesis, University of Central Florida, Orlando, pp. 132.
- Hooker, S.K., Iverson, S.J., Ostrom, P., and S.C. Smith. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Canadian Journal of Zoology **79**:1442-1454.
- Indergaard, M., and J. Minsaas. 1991. Animal and human nutrition. *In:* M.D. Guiry, and G. Blunden, editors. .Seaweed resources in Europe: uses and potential John Wiley and Sons, Chichester, pp 22-64
- International Union for the Conservation of Nature. 2009. IUCN Red List of Threatened Species, version 2010.1 http://www.iucnredlist.org. Accessed 17 Jun 2010.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, pp 302.
- Kapoho Beach Lots, Farm Lots, and Vacationland Estates Wastewater Feasibility Report.2010. Chapter 2, Physical Environment, Engineering Concepts, Inc. pp 35.
- Klein Breteler, W.C.M., Grice, K., Schouten, S., Kloosterhuis, H.T., and J.S. Sinninghe Damste. 2002. Stable carbon isotope fractionation in the marine copepod *Temora*

*longicornis*: unexpectedly low  $\delta_{13}$ C value of faecal pellets. Marine Ecology Progress Series **240**:195-204.

- Krebs, J.R., and N.B. Davies. 1993. An introduction to behavioral ecology. Blackwell Science pp. 42.
- Kubis, S., Chaloupka, M., Ehrhart, L., and M. Bresette. 2009. Growth rates of juvenile green turtles (*Chelonia mydas*) from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Marine Ecology Progress Series 389:257–269.
- Leon, Y.M., and K.A. Bjorndal. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystem. Marine Ecology Progress Series 245:249-258.
- Limpus, C.J. 1979. Sea turtles of the northern Great Barrier Reef. *In:* M.S. Masri, F.T. Jones, R.A.A. Muzzarelli, and E.R. Pariser, editors. Workshop Series Great Barrier Reef Marine Park Authority (GBRMPA). GBRMPA, Townsville, pp. 336.
- Limpus, C.J., and D.J. Limpus. 2000. Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. Marine Turtle Newsletter **89**:13-15.
- Lipkin, Y. 1975. Food of the Red Sea dugong (*Mammalia sirenia*) form Sinai. Israel Journal of Zoology **24**:81-95.
- Lopez-Mendilaharsu, M., Gardner, S., Riosmena-Rodriquez, R., and J.A.Seminoff. 2008. Diet selection by immature green turtles (*Chelonia mydas*) at Bahi'a Magdalena foraging

ground in the Pacific Coast of the Baja California Peninsula, Mexico. Journal of the Marine Biological Association of the United Kingdom **88**:1-7.

- Lowry, O.H., Rosebrough, N.J., Farr, A.L., and R.J. Randall. 1951. Protein Measurement with the Folin Phenol Reagent. Biological Chemistry **193**:265-276.
- MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. American Nature **100**:603-609.
- Macrae, J.C., and P.J. Reeds. 1980. Prediction of protein deposition in ruminants. *In:* P.J. Buttery and D.B. Lindsay, editors. Protein deposition in animals. Butterworths, London, pp 225-249.
- Manly, B.F.J., Mcdonald, L.L., Thomas, D.L., McDonald, T.L., and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for filed studies. 2<sup>nd</sup> ed. Kuwer Academic Publishers, Boston, pp. 221.
- McCutchan, J.H. Jr., Lewis, W.M. Jr., Kendall, C., and C.C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos **102**:378-390.
- McDermid, K.J., and B. Stuercke. 2003. Nutritional composition of edible Hawaiian seaweeds. Journal of Applied Phycology **15**:513-524.
- McDermid, K.J., Stuercke, B., and G.H. Balazs. 2007. Nutritional composition of marine plants in the diet of the green sea turtle (*Chelonia mydas*) in the Hawaiian Islands.Bulletin of Marine Science 81(1):55-71.

- Mendonca, M.T. 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copiea **4**:1013-1023.
- Michener, R.H., and D.M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. *In:* K. Lajtha and R.H. Michener, editors. Stable isotopes in ecology and environmental science pp 138-157.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of <sup>15</sup>N along food chains: Further evidence and the relation between  $\delta^{15}$ N and animal age. Geochim. Cosmochim. Acta 48: 1135-1140.
- Mortimer, J.A. 1981. The feeding ecology of the West Caribbean green turtles (*Chelonia mydas*) in Nicaragua. Biotropica **13**:49-58.
- Mortimer, J. 1982. Feeding ecology of sea turtles. *In:* K.A. Bjorndal, editor. Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, D.C., pp. 103–109.
- Mortimer, J.A., and A. Carr. 1987. Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). Copeia **1987**(1):103-113.
- Newsome, S.D., Martinez del Rio, C., Bearhop, S., and D.L. Phillips. 2006. A niche for isotopic ecology. Frontiers in Ecology and the Environment **5**:429-436.
- Nietschmann, B. 1984. Hunting and ecology of dugongs and green turtles, Torres Strait, Australia. National Geographic Society Research Reports **17**:625-651.

- Niethammer, K.R., Balazs, G.H., Hatfield, J.S., Nakai, G.L., and J.L. Megyesi. 1997. Reproductive biology of the green turtle (*Chelonia mydas*) at Tern Island, French Frigate Shoals, Hawaii. Pacific Science **51**(1):36-47.
- Ogden, J.C. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquatic Botany **2**:103-16.
- Ogden, J.C., Tighe, S., and S. Miller. 1980. Grazing of seagrasses by large herbivores in the Caribbean. American Zoologist **20**:949.
- Pearson, S.F., Levey, D.J., Greenberg, C.H., and C. Martinez del Rio. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. Oecologia 135:516-523.
- Pendoley, K., and J. Fitzpatrick. 1999. Browsing of mangroves by green turtles in Western Australia. Marine Turtle Newsletter **84**:10-11.
- Percival, E. 1964. Algal polysaccharides and their biological relationships. Proceedings of the international seaweed symposium. **4**:18-35.
- Peterson, B.J.,and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Revue Ecological Systems **18**:293-320.
- Pinnegar, J.K., and N.V.C. Polunin. 1999. Differential fractionation of  $\delta_{13}$ C and  $\delta_{15}$ N among fish tissues: implications for the study of trophic interactions. Functional Ecology **13**:225-231.

- Pritchard, P.C.H. 1971. Galapagos sea turtles-preliminary findings. Journal of Herpetology **5**:1-9.
- Ragan, M.A., and K.W. Glombitza. 1986. Phlorotannins, brown algal polyphenols. *In* F.E.Round, and D.J. Chapman, editors. Progress in phycological research, Biopress Ltd,Bristol 4:130-230.
- Redfoot, W. 1997. Population structure and feeding ecology of green turtles utilizing the Trident Submarine basin, Cape Canaveral, Florida as developmental habitat. Master's thesis, University of Central Florida, Orlando, pp. 72.
- Reich, K.O., Bjorndal, K.A., A.B. Bolten. 2007. The 'lost years' of green turtles using stable isotopes to study cryptic lifestages. Biology Letters **3**(6):712-714.
- Reich, K.J., Bjorndal, K.A., Frick, M.G., Witherington, B.E., Johnson, C., and A.B. Bolten.
  2010. Polymodal foraging in adult female loggerheads (*Caretta caretta*). Marine Biology
  157:113-121.
- Reppert, J.N. 1960. Forage preference and grazing habits of cattle at the Eastern Colorado Range Station. J. Range Manage. **13**:58-64.
- Ross, J.P. 1985. Biology of the green turtle, *Chelonia mydas*, on an Arabian feeding ground. Journal of Herpetology **19**:459-68.
- Roth, J.D., and K.A. Hobson. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction.
  Canadian Journal of Zoology 78:848-852.

- Russell, D.J., and G.H. Balazs. 1994. Utilization of alien alga species by sea turtles in Hawai'i. Pages 93–95 *In:* D.J. Baker and K. Sullivan, editors. Proceedings of the Conference and Workshop on Nonindigenous Estuarine and Marine Organisms (NEMO), Seattle, Washington, pp. 20–23.
- Russell, D.J., and G.H. Balazs. 2000. Identification manual for dietary vegetation of the Hawaiian Green Turtle, *Chelonia mydas*. NOAA Technical Memorandum NMFS-SWFSC-294, pp. 49.
- Russell, D.J., and G.H. Balazs. 2009. Dietary shifts by green turtles (*Chelonia mydas*) in the Kane'ohe Bay Region of the Hawaiian Islands: A 28-year study. Pacific Science 63(2):181–192.
- Russell, D.J., Balazs, G.H., Phillips, R.C., and A.K.H. Kam. 2003. Discovery of the sea grass *Halophila decipiens* (Hydrocharitaceae) in the diet of the Hawaiian green turtle, Chelonia mydas. Pacific Science **57**:393–397.
- Schoener, T.W. 1969. Models of optimal size for solitary predators. American Nature **103**:277-313.
- Seminoff, J.A., Nichols, W.J., Hidalgo, A.R.S. 2000. Movement and home range of the East-Pacific green turtle at a Gulf of California (Mexico) feeding area. Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-477, Orlando, FL, p 36-38.

- Seminoff, J.A., Resendiz, A., and W.J. Nichols. 2002. Diet of east Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, Mexico. Journal of Herpetology 36(3):447-453.
- Seminoff, J.A., Jones, T.T., Eguchi, T., Jones, D.R., and P.H. Dutton. 2006. Stable isotope discrimination ( $\delta^{13}$ C and  $\delta^{15}$ N) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. Marine Ecology Progress Series **308**:271-278.
- Smith, J.E., Hunter, C.L., and C.M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pacific Science 56(3):299-315.
- Smith, J.E., Hunter, C.L., Conklin, E.F., Most, R., Sauvage, T., Squair, C., and C.M. Smith.
  2004. Ecology of the invasive red alga *Gracilaria salicornia* (Rhodophyhta) on O'ahu,
  Hawaii. Pacific Sciences 58(2):325-343.
- Stuercke, B. and K.J. McDermid. 2004. Variation in algal turf species composition and abundance on two Hawaiian shallow subtidal reefs. Cryptogramie **25**:353-365.
- Tieszen, L.L., and T. Fagre. 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO2, bone collagen, bioapatite, and soft tissues. In: Lambert J, Grupe G (eds) Molecular archeology of prehistoric human bone. Springer-Verlag, Berlin pp. 123-135.
- Tsuda, R.T., and I.A. Abbott. 1985. Collection, handling, preservation, and logistics. InM.M. Littler and D.S. Littler (eds.), Handbook of phycological methods, CambridgeUniversity Press, New York 5:67-86.

- United States Department of Agriculture, Natural Resources Conservation Service. 2010. Plants Profile:*Stenotaphrum secundatum* (Walter) Kuntze, St. Augustine grass, National Plant Data Center, plants.usda.gov/java/profile?symbol=STSE Accessed 24 June 2010.
- Van Alstyne, K.A., and V.J. Paul. 1990. The biogeography of polyphenolic compounds in marine macroalgae: temperate brown algal defenses deter feeding by tropical herbivorous fishes. Oecologia 84(2):158-163.
- Vander Zanden, M.J., and J.B. Rasmussen. 2001. Variation in δ<sup>15</sup>N and δ<sup>13</sup>C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography
  46(8) pp. 2061-2066.
- Weibel, E.R., Kistler, G.S., and S.F. Scherle. 1966. Practical stereological methods for morphometric cytology. Journal of Cellular Biology 30:23-38.
- Wershoven, R.W., and J.L. Wershoven. 1992. Stomach content analysis of stranded juvenile and adult green turtles in Broward and Palm Beach counties, Florida. *In:* M.
  Salmon, and J. Wyneken, editors. Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-302.
  pp. 124-126.
- Wikelski, M., Gall, B., and F. Trillmich. 1993. Ontogenetic changes in food intake and digestion rate of the herbivorous marine iguana (*Amblyrhynchus cristatus*, Bell).Oecologia 94:373-379.
- Witham, R. 1980. The "lost year" question in young sea turtles. American Zoologist **20**(3):525-530.

- Wong, K.H., and P.C.K. Cheung. 2001. Nutritional evaluation of some subtropical red and green seaweeds-Part II. In-vitro protein digestibility and amino acid profiles of protein concentrates. Food Chemistry **72**:11-17.
- Wood, J.R., and F.E. Wood. 1980. Reproductive biology of captive green sea turtles, *Chelonia mydas*. In American. Zoology, Behavior and reproductive biology of sea turtles.
  20:499-505.
- Zug, G.R., Balazs, G.H., Wetherall, J.A., Parker, D.M., and S.K.K. Murakawa. 2001. Age and growth of Hawaiian green sea turtles (*Chelonia mydas*): An analysis based on skeletochronology. Fisheries Bulletin 100:117–127.