Dietary Shifts by Green Turtles (*Chelonia mydas*) in the Kāne'ohe Bay Region of the Hawaiian Islands: A 28-Year Study[1]

Dennis J. Russell[2] *and George H. Balazs*[3]

Abstract: The green turtle, *Chelonia mydas*, has modified its feeding behavior to include the increasing abundance of nonnative algae growing in the greater Kāne'ohe Bay area of O'ahu in the Hawaiian Islands. Changes in diet of the green turtle are correlated with an increase in abundance of seven species of nonnative algae between 1977 and 2005. Turtles were found to be eating 130 species of marine vegetation, and the three most common were the nonnative species *Acanthophora spicifera*, *Hypnea musciformis*, and *Gracilaria salicornia*. These three abundant and nutritious food sources are now an important part of the turtle diet in addition to native species found in and near Kāne'ohe Bay. *Chelonia mydas* behavior has shifted to include these new seaweeds within 10 years of their introduction to the region. The turtles have also gradually included an additional four less-prolific slow-growing nonnative algal species (*Eucheuma denticulatum*, *Gracilaria tikvahiae*, *Kappaphycus striatum*, and *Kappaphycus alvarezii*), but the time it has taken turtles to include these species has been longer, 20–30 years, after the seaweeds were introduced. During this same 28-year time period numbers of *C. mydas* have increased throughout the Hawaiian Islands.

The feeding behavior and diet of the herbivorous green turtle, *Chelonia mydas* (L.), have been the subject of 28 years of research conducted between 1977 and 2005 throughout the Hawaiian Archipelago and especially in the vicinity of Kāne'ohe Bay, Hawai'i (Figure 1). The green turtle has shown a remarkable ability to rebound from decline, largely due to conservation measures, such as protection from harvesting and other forms of take under the U.S. Endangered Species Act, and now the population is recovering (Balazs and Chaloupka 2004*a*, 2006). However, a decline in the somatic growth rates of the turtles indicates that the population may be approaching carrying capacity and now available food may be limiting growth at some locations (Balazs and Chaloupka 2004*b*). Shifts in the diet of the green turtle in Kāne'ohe Bay may be fortuitous for the turtles and their continuing recovery. This paper focuses on the ability of green turtles to modify their feeding behavior and take advantage of additional algal food sources.

Although understanding all aspects of green turtle biology is critical for the recovery of the species (Hirth 1997), one of the more important conservation topics involves turtle feeding behavior, which includes knowledge of the species of algae, sea grasses, animals, and other items *C. mydas* is eating, and eventually protecting the most important foraging sites and food species they are utilizing (Balazs 1980, Hirth 1997, Russell et al. 2003). It has been known for many years that *C. mydas* feeds on a wide variety of marine vegetation (Balazs et al. 1987, Russell and Balazs 1994, Arthur and Balazs 2008). Data from the feeding habits of *C. mydas* have also been used to discover changes in the feeding behavior of *C. mydas*, which include nonnative species in its diet, and to follow the spread of *Hypnea musciformis*, a nonnative species, from its

[1] Manuscript accepted 10 July 2008.
[2] Department of Biology, Chemistry, and Environmental Sciences, American University of Sharjah, P.O. Box 26666, Sharjah, United Arab Emirates (e-mail: drussell@aus.edu).
[3] NOAA, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, Hawai'i 96822-2396.

Pacific Science (2009), vol. 63, no. 2:181–192

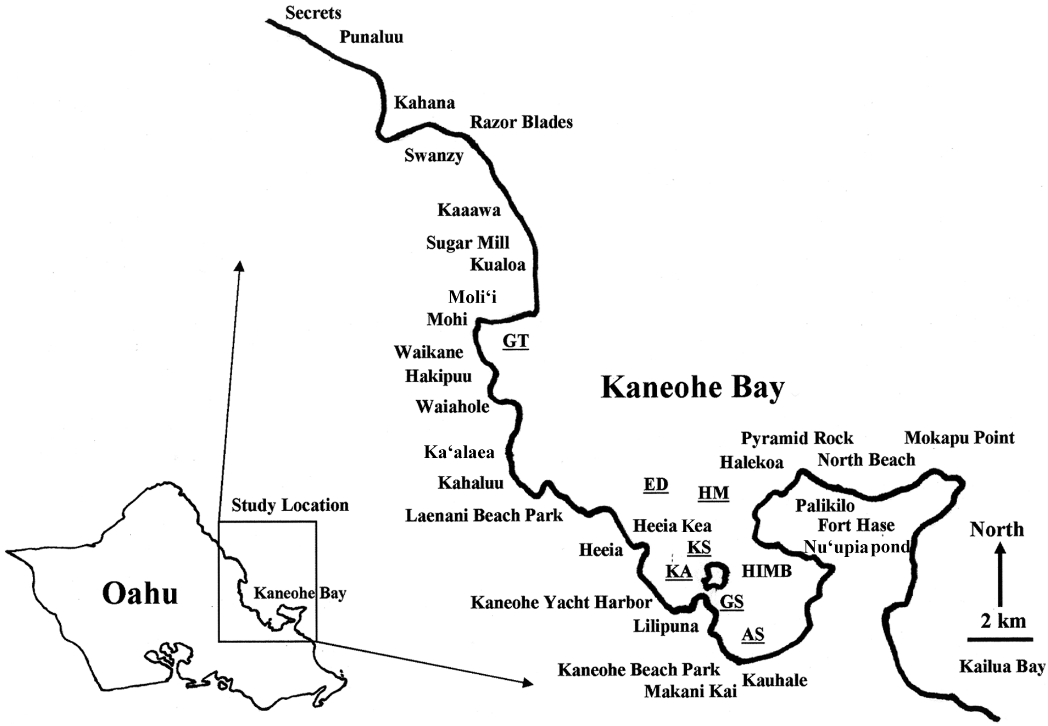

FIGURE 1. O‘ahu, Hawai‘i, showing the location of the study: the Kāne‘ohe Bay region including adjacent shores, the locations where stranded turtles were found, and the initial locations where nonnative algae were introduced. AS, *A. spicifera;* HM, *H. musciformis;* GS, *G. salicornia;* ED, *E. denticulatum;* GT, *G. tikvahiae;* KA, *K. alvarezii;* KS, *K. striatum.*

place of introduction on O‘ahu to the other Hawaiian Islands (Russell and Balazs 1994, Smith et al. 2002). Another study relating to the two sea-grass species *Halophila hawaiiana* and *H. decipiens* revealed that *C. mydas* had adjusted its feeding according to the abundance of these two sea-grass species, and as *H. decipiens* became more abundant the turtles began feeding on it in addition to *H. hawaiiana* (Russell et al. 2003).

Our turtle diet study was initiated in the same decade when several species of marine algae were introduced to Hawai‘i in the 1970s (Russell 1981, 1992, Eldredge and Smith 2001). The greater Kāne‘ohe Bay area was a critical location for the study of green turtle feeding behavior because many of the new transplants of nonnative algal species went directly into Kāne‘ohe Bay (Russell 1983, 1992), and it was known when and where they were introduced (Figure 1). In this paper we investigate the hypothesis that *C. mydas* has modified its feeding behavior to include nonnative, introduced species of algae into its diet as they became more abundant in this well-known turtle foraging location.

MATERIALS AND METHODS

Green turtles feed in foraging locations by nipping off small pieces of algae, sea grasses, and other food items with their beaks, pressing the water out on the roof of their mouth and swallowing. This gives a uniform size to the food items, which can be spread uniformly on a petri plate without further manipulation or maceration. The algae, sea grass, and other material become packed into a crop, a pouch located in the posterior region of the esophagus (Balazs et al. 1998, Work 2000). Diet samples for our study were obtained from stranded dead turtles at the time of necropsy; each sample represents the necropsy of one turtle. Carcasses were salvaged for necropsy through a widely publicized sea turtle stranding research program (Chaloupka et al. 2008). Analysis was done, using SPSS 15.0 (SPSS Inc., Chicago), on 372 samples from turtles found at 31 locations in the Kāne'ohe Bay area (Figure 1) from 1977 to 2005, from Kahana to Mōkapu Point (Figure 1). Sampling was entirely dependent on the finding and reporting of stranded dead turtles, and this led to receiving up to 38 samples each year. The average number of samples received was 12.3/year; during 1982–1984 there were no samples, therefore interpolated data were used for those 3 years.

One 50 ml sample was taken from the crop of each turtle, preserved in 10% formalin/seawater, and analyzed microscopically by D.J.R. (Russell and Balazs 2000). Identification of major algal species and sea grasses was based on the latest knowledge of algae available at the time and later modified to show the most up-to-date taxonomy possible (Phillips and McRoy 1980, Abbott 1999, Abbott and Huisman 2004, Huisman et al. 2007).

The entire 50 ml sample was suspended evenly and poured into a 2 × 14 cm petri plate with 32 squares (2 × 2 cm) etched into the bottom. The sample was examined under a stereomicroscope and the species fragments sorted onto the squares, which were counted and converted into percentages. The percentages represent both the surface area covered by each species and are also a measure of the volume they represent (1.6 ml of sample covers each 2 × 2 cm square). Examination ended when all the trace species were recorded using a compound microscope. Trace species were those that represented less than 1% of the sample. Frequency represents the proportion of samples in which the diet items were observed and the average percentage represents the proportion that the diet species contributed to the total samples.

RESULTS AND DISCUSSION

Green turtles in Kāne'ohe Bay were eating 130 species, mostly marine algae, but also two species of sea grasses (Table 1). Of the 130 species, 81 (62.3%) were found in trace amounts because they either were nearly microscopic or occurred in small amounts and only one to three times out of the total 372 samples (Table 1). *Acanthophora spicifera* was found in more samples (64.0%) than any other species, followed by *Hypnea musciformis* (41.4%) and *Gracilaria salicornia* (37.0%); each of these is a nonnative alga (Russell 1981, 1992). Four additional nonnative algae species were also present in the samples: *Eucheuma denticulatum* (2.2%), *Kappaphycus alvarezii* (1.3%), *Kappaphycus striatum* (1.1%), and *Gracilaria tikvahiae* (0.8%). A few native species were present in nearly all of the samples (98%), but only three nonnative species contributed more than 40% of the amount eaten by the turtles (Figure 2, Table 1). Only 22 species, or 16.9% of the total number of species, accounted for >4% occurrence in the turtles' food items (Table 1). The remaining 108 species were either sparse or microscopic in size and found as trace amounts. The most important native species, in order of their contribution values to the turtle diet, were *Pterocladiella capillacea*, *Codium edule*, *Amansia glomerata*, *Codium arabicum*, *Halophila hawaiiana*, *Dictyosphaeria cavernosa*, and *Spyridia filamentosa*. This indicates that the three nonnative species were contributing an important proportion of the green turtle diet when compared with native species.

The history of algal introductions into Kāne'ohe Bay has been well documented (Russell 1981). *Acanthophora spicifera* was the first nonnative seaweed recorded for the Hawaiian Islands. It entered O'ahu on the leeward side, probably as fouling on a barge from Guam, into Pearl Harbor, in 1950 and by 1954 was found growing on reefs in the Kāne'ohe Bay region. By 1956 it had also spread to Kaua'i and other Hawaiian Islands (Doty 1961). Studies between 1978 and 1993 showed that *A. spicifera* was being utilized by turtles for food and was present in 34% of the 802 turtle samples taken throughout the Hawaiian Islands (Russell and Balazs 1994). By 2005 that quantity had increased to 64% frequency in the samples, and the quantity of

TABLE 1

Algae and Sea-Grass Species Listed in Order of Number of Times They Were Found in Turtle Samples, Their Frequency (% Smp) in 372 Samples, and Average Percentage Amounts or Quantity (Avg %) in the Samples

Species	No. of Times Found	% Sample	Avg %[a] (SD)
**Acanthophora spicifera*	237	64.0%	44.1% (32.8)
**Hypnea musciformis*	154	41.4%	42.0% (32.7)
**Gracilaria salicornia*	138	37.0%	40.9% (33.0)
Codium edule	95	25.5%	32.1% (30.5)
Laurencia nidifica	88	23.7%	12.5% (16.5)
Codium arabicum	78	21.0%	28.9% (30.5)
Amansia glomerata	70	18.8%	30.0% (34.1)
Dictyosphaeria cavernosa	62	17.0%	20.2% (27.6)
Halophila hawaiiana	59	15.9%	24.0% (14.3)
Pterocladiella capillacea	57	15.3%	35.5% (31.3)
Dictyota acuteloba	50	13.4%	8.5% (8.5)
Lyngbya majuscula	49	13.2%	4.0% (3.5)
Spyridia filamentosa	49	13.2%	15.7% (25.7)
Dictyosphaeria versluysii	36	9.7%	5.5% (5.8)
Sargassum echinocarpum	36	9.7%	10.9% (13.2)
Halimeda discoidea	29	7.8%	7.2% (9.6)
Sargassum sp.	29	7.8%	36.3% (32.0)
Gracilaria coronopifolia	25	6.7%	20.8% (28.9)
Sargassum polyphyllum	25	6.7%	12.6% (22.6)
Valonia aegagropila	21	5.7%	3% (2.8)
Halophila decipiens	15	4.0%	28.4% (28.8)
Ulva reticulata	15	4.0%	33.8% (40.0)
Ceramium sp.	14	3.8%	Only trace
Hypnea cervicornis	14	3.8%	23.1% (34.2)
Sphacelaria furcigera	14	3.8%	Only trace
Champia parvula	13	3.5%	16.0% (19.8)
Cladophora sp.	13	3.5%	51.0% (69.3)
Sphacelaria sp.	13	3.5%	Only trace
Turbinaria ornata	13	3.5%	16.5% (20.6)
Codium phasmaticum	12	3.2%	18.5% (16.9)
Dictyota sp.	12	3.2%	Only trace
Gelidium sp.	11	3.0%	29.3% (24.0)
Microdictyon umbilicatum	11	3.0%	6.0% trace
Polysiphonia howeii	11	3.0%	Only trace
Polysiphonia sp.	11	3.0%	Only trace
Laurencia sp.	10	2.7%	6.0% (6.1)
Padina japonica	10	2.7%	3.0% trace
Cladophoropsis sp.	9	2.4%	Only trace
Dictyota friabilis	9	2.4%	18.0% trace
**Eucheuma denticulatum*	8	2.2%	34.6% (31.2)
Gelidium crinale	7	1.9%	1.3% (0.8)
Hypnea pannosa	7	1.9%	22.5% (21.8)
Hypnea sp.	7	1.9%	Only trace
Sphacelaria tribuloides	7	1.9%	1.6% (0.9)
Gelidium puscillum	6	1.6%	35% (trace)
Ulva fasciata	6	1.6%	7.8% (7.8)
Zonaria hawaiiensis	6	1.6%	2.0% (trace)
Hypnea spinella	5	1.3%	Only trace
**Kappaphycus alvarezii*	5	1.3%	11.0% (7.4)
Leviellia jungermannioides	5	1.3%	Only trace
Actinotrichia fragilis	4	1.1%	5.0% (1.4)
Ahnfeltiopsis concinna	4	1.1%	60.0% (45.6)
Bryopsis pennata	4	1.1%	Only trace
Cladophoropsis membranacea	4	1.1%	Only trace
Dictyopteris sp.	4	1.1%	Only trace

TABLE 1 (continued)

Species	No. of Times Found	% Sample	Avg %[a] (SD)
Hincksia indica	4	1.1%	Only trace
Gracilaria sp.	4	1.1%	1.0% (1.0)
**Kappaphycus striatum*	4	1.1%	23.0% (23.6)
Centroceros clavulatum	3	0.8%	Only trace
Codium sp.	3	0.8%	6.7% trace
Dictyopteris plagiogramma	3	0.8%	33.3% trace
Dictyota crennulata	3	0.8%	Only trace
Dictyota divaricata	3	0.8%	Only trace
Gelidiella acerosa	3	0.8%	39.7% trace
**Gracilaria tikvahiae*	3	0.8%	52.7% trace
Laurencia pennata	3	0.8%	14.0% trace
Lobophora variegata	3	0.8%	1.0% trace
Microdictyon sechellianum	3	0.8%	Only trace
Microdictyon sp.	3	0.8%	Only trace
Ulva rigida	3	0.8%	11.3% trace
Ulva sp.	3	0.8%	7.0% trace
Achrochaetium sp.	2	0.5%	Only trace
Bornetella sphaerica	2	0.5%	3.0% trace
Bryopsis sp.	2	0.5%	Only trace
Caulerpa sertularioides	2	0.5%	10.0% trace
Chondria tenuissima	2	0.5%	Only trace
Chondrococcus hornemanni	2	0.5%	Only trace
Cladophora fascicularis	2	0.5%	1.0% trace
Coelothrix irregularis	2	0.5%	42.5% trace
Enteromorpha clathrata	2	0.5%	Only trace
Enteromorpha sp.	2	0.5%	Only trace
Galaxaura fasciculata	2	0.5%	24.5% trace
Halymenia formosa	2	0.5%	5.0% trace
Polysiphonia sparsa	2	0.5%	20.0% trace
Rhizoclonium grande	2	0.5%	Only trace
Sargassum obtussifolium	2	0.5%	70.0% trace
Scytonema pascheri	2	0.5%	Only trace
Alsidium cymatophilum	1	0.3%	10.0% trace
Asparagopsis taxiformis	1	0.3%	5.0% trace
Boodlea composita	1	0.3%	Only trace
Caulerpa racemosa	1	0.3%	Only trace
Cladophora seracea	1	0.3%	Only trace
Codium reedae	1	0.3%	Only trace
Colpomenia sinuosa	1	0.3%	Only trace
Dasya sp.	1	0.3%	Only trace
Ectocarpus sp.	1	0.3%	Only trace
Endarachne binghamiae	1	0.3%	Only trace
Galaxaura sp.	1	0.3%	Only trace
Gelidiopsis variabilis	1	0.3%	Only trace
Chondria sp.	1	0.3%	Only trace
Gracilaria bursapastoris	1	0.3%	Only trace
Grateloupia sp.	1	0.3%	Only trace
Griffithsia sp.	1	0.3%	Only trace
Halimeda sp.	1	0.3%	Only trace
Martensia fragilis	1	0.3%	Only trace
Hypnea nidifica	1	0.3%	Only trace
Jania capillacea	1	0.3%	Only trace
Laurencia cartilaginea	1	0.3%	Only trace
Laurencia obtusa	1	0.3%	Only trace
Liagora sp.	1	0.3%	Only trace
Padina thivii	1	0.3%	Only trace
Pterocladia bulosa	1	0.3%	Only trace

TABLE 1 (continued)

Species	No. of Times Found	% Sample	Avg %[a] (SD)
Rhodymenia anastomosans	1	0.3%	Only trace
Rosenvingea orientalis	1	0.3%	Only trace
Schizothrix calcicola	1	0.3%	Only trace
Siphonocladus tropicus	1	0.3%	2.0% trace
Struvea anastomosans	1	0.3%	Only trace
Tolypiocladia calodictyon	1	0.3%	Only trace
Trichogloea subnuda	1	0.3%	10.0% trace
**Avrainvellea amadelpha*	1	0.3%	Only trace

[a] "Only trace" indicates that the species never occurred in quantities greater than 1%; "trace" with a percentage indicates that the species occurred in one to three samples in quantities greater than 1%, the average of these few samples is given, and in all other samples it was only a trace.

* Nonnative species.

A. spicifera increased from an average of 36.4 to 44.1% of the amount of algae in the samples (Figure 3). *Acanthophora spicifera* consistently made up 10% of the algae in the turtle samples from 1990 to 2005.

Hypnea musciformis was introduced directly into Kāneʻohe Bay from Florida for marine agronomic purposes in January 1974 (Figure 1), and the first turtle crop sample containing *H. musciformis* was discovered in October 1977 (Russell and Balazs 1994). However, it did not become a food item that was found in turtle samples consistently year after year until after 1985, 11 years after it

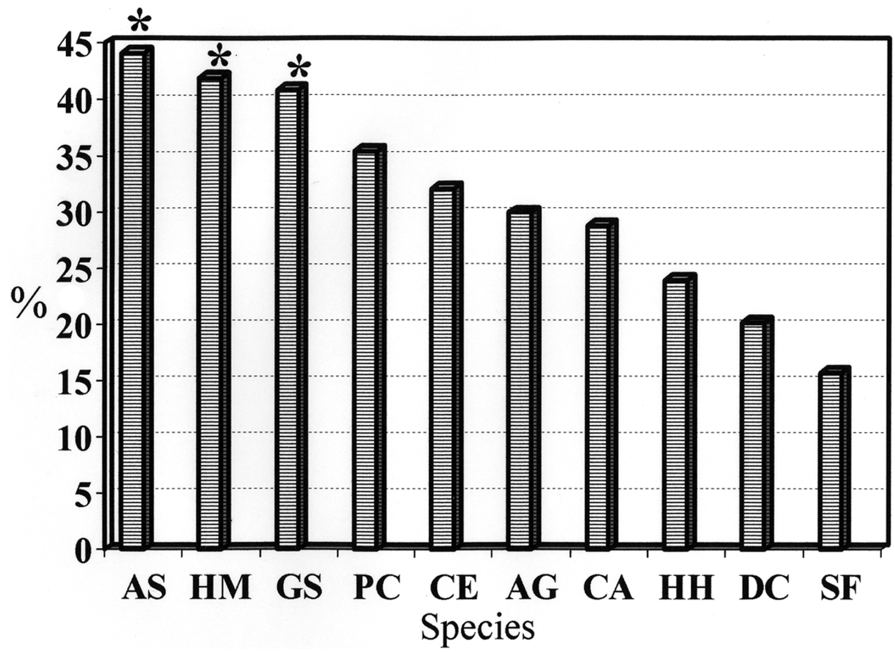

Figure 2. The 10 algal species most commonly found in turtle samples arranged in order of their frequency. Numbers represent the average percentage amounts they contributed to the samples from a total of 372 samples. Asterisks (*) indicate nonnative species: AS, *A. spicifera;* HM, *H. musciformis;* GS, *G. salicornia.* The remainder are native species: PC, *P. capillacea;* CE, *C. edule;* AG, *A. glomerata;* CA, *C. arabicum;* HH, *H. hawaiiana;* DC, *D. cavernosa;* SF, *S. filamentosa.*

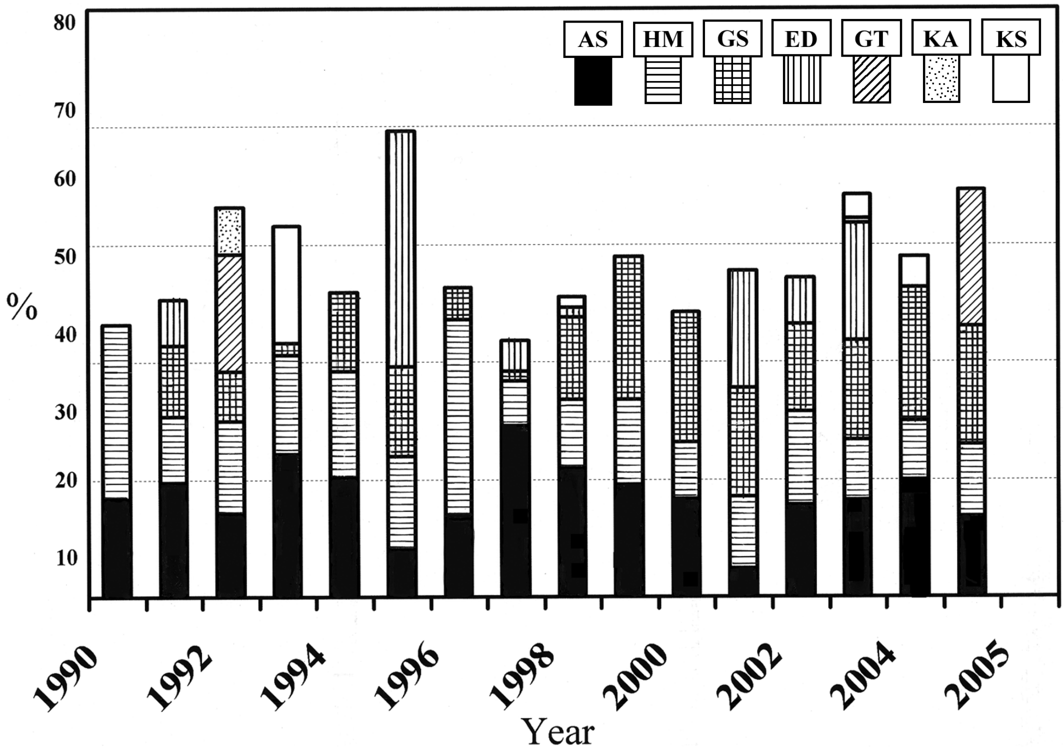

FIGURE 3. First occurrence and subsequent appearances for nonnative algal species in turtle samples. Bars represent the combined proportional contributions to the total average percentage by only the nonnative species in the samples from 1990 to 2005. AS, *A. spicifera;* HM, *H. musciformis;* GS, *G. salicornia;* ED, *E. denticulatum;* GT, *G. tikvahiae;* KA, *K. alvarezii;* KS, *K. striatum*.

was introduced to the bay (Figure 3, Table 2). *Hypnea musciformis* was introduced onto reef flats and has been consistently present in samples and has made up about 5% of the algae in samples from 1990 to 2005 (Figures 1, 3).

Gracilaria salicornia was introduced to Waikīkī, Oʻahu, in April 1971 from Hilo, Hawaiʻi, and later to Kāneʻohe Bay, near Lilipuna pier (Figure 1) in September 1978 (Russell 1981). The first turtle sample con-

TABLE 2

Comparison of Dates Nonnative Algae Were Introduced to Kāneʻohe Bay with Time They Were First Recorded in Crop Samples Taken from *C. mydas*

Species	Date Introduced	First Sample	Established in the Diet	Lag time (yr)
Acanthophora spicifera	1956	1977	1977	?
Hypnea musciformis	Jan. 1974	Oct. 1977	Oct. 1985	11
Gracilaria salicornia	Sept. 1978	June 1991	June 1991	13
Gracilaria tikvahiae	1976	Apr. 1992	Apr. 1992*	16+
Kappaphycus alvarezii	Sept. 1974	Sept. 1992	Sept. 1992*	18+
Kappaphycus striatum	Sept. 1974	Sept. 1993	Apr. 2003*	20+
Eucheuma denticulatum	Oct. 1970	Apr. 1991	Apr. 1997	27

* Species are not yet established and are only sporadic components of the turtle diet.

taining *G. salicornia* was discovered in June 1991 (Figure 3), 13 years after it was introduced to the bay. These data suggest that it takes about 10–13 years for a successful newly introduced nonnative species to become part of the regular (found consistently year to year) diet of *C. mydas*. *Gracilaria salicornia* was found in samples consistently year to year only after 1991 (Figure 3), and after 1999 *G. salicornia* regularly made up about 10% of the algae in the Kāne'ohe Bay area samples.

Eucheuma denticulatum was introduced to Kāne'ohe Bay from the Philippine Islands in October 1970 and planted on several reefs (Figure 1). It was cultivated extensively on Coconut Island (HIMB) in experiments designed to gather data for the propagation of this marine alga to supply seaweed farms throughout the Pacific (Russell 1983). The first turtle sample found with *E. denticulatum* was discovered in April 1991, 21 years later (Figure 3), and it has been in a total of only eight samples during the 15 years to the end of 2005. *Eucheuma denticulatum* is still not abundant in Kāne'ohe Bay and has not spread quickly, when compared with *H. musciformis* and *G. salicornia*, and consequently it has been slow in becoming part of the regular diet of turtles during each year.

Kappaphycus alvarezii was introduced from the Philippine Islands to Kāne'ohe Bay in September 1974 and planted on several reefs (Russell 1983) (Figure 1). It first appeared in turtle samples in September 1992 (Figure 3), 18 years later, and sporadically in only five samples during the 13 years through 2005. Like *E. denticulatum*, it too is still not abundant in Kāne'ohe Bay, has not quickly spread, and is only slowly becoming a part of the turtles' regular diet.

Kappaphycus striatum was introduced to Kāne'ohe Bay from Pohnpei and the Philippines in 1974 and planted on several reefs (Russell 1983) (Figure 1). It first appeared in turtle samples 20 years later, in April 1993 (Figure 3). Since then it has been discovered sporadically and was only found in four samples during the 12 years to 2005. Its appearance in turtle samples was noted in 1993 and then much later again only in 2003 (Figure 3). It was only able to grow well and spread when it was intensely cultivated on a reef on Coconut Island (HIMB) (Figure 1), and after the cultivation activity ended it has remained in only small amounts in isolated patches in the bay. These last three commercially valuable species were released into Kāne'ohe Bay, where they are continuing to survive without cultivation, do not reproduce rapidly, are not abundant, and have not spread to adjacent areas. It has taken about 20 years for the slower-growing species that do not spread quickly, but that are still successful nonnative species, to become an occasional part of the turtles' diet, and they are not yet consistently found in samples every year.

Gracilaria tikvahiae was introduced from Florida to Kāne'ohe Bay in 1976 and has been cultivated in ponds on marine farms near Mōli'i and Mohi (Figure 1) for the purpose of selling it as a fresh vegetable (Russell 1981) . The first time it was discovered in turtle samples was in April 1992 (Figure 3), 16 years later, and it has been found in only three samples during the 13 years since; the last being in August 2005. It has not yet become an established part of the green turtle diet 30 years after it was introduced to Kāne'ohe Bay. This is probably because *G. tikvahiae* is mostly confined to fenced farms, and we have observed that it is located in only a few places near shore adjacent to those seaweed gardens.

Our research shows that green turtles are eventually able to find and utilize newly introduced sources of food as the established algae species become sufficiently abundant in the turtle's foraging locations, although this may take several years.

The diet shift by green turtles toward the abundant nonnative algal species in the Kāne'ohe Bay study area increased from 1977 to 2005 (Figure 4), with the average of nonnative species in turtle crop samples being significantly higher than the native species (Figure 5). The best fit, using natural log transformation, helps visualize the data and shows that the nonnative algae increased and overtook the declining native algae during approximately 1985–1987 (Figure 4). Also, there are relatively few nonnative species contributing a greater amount to the turtle

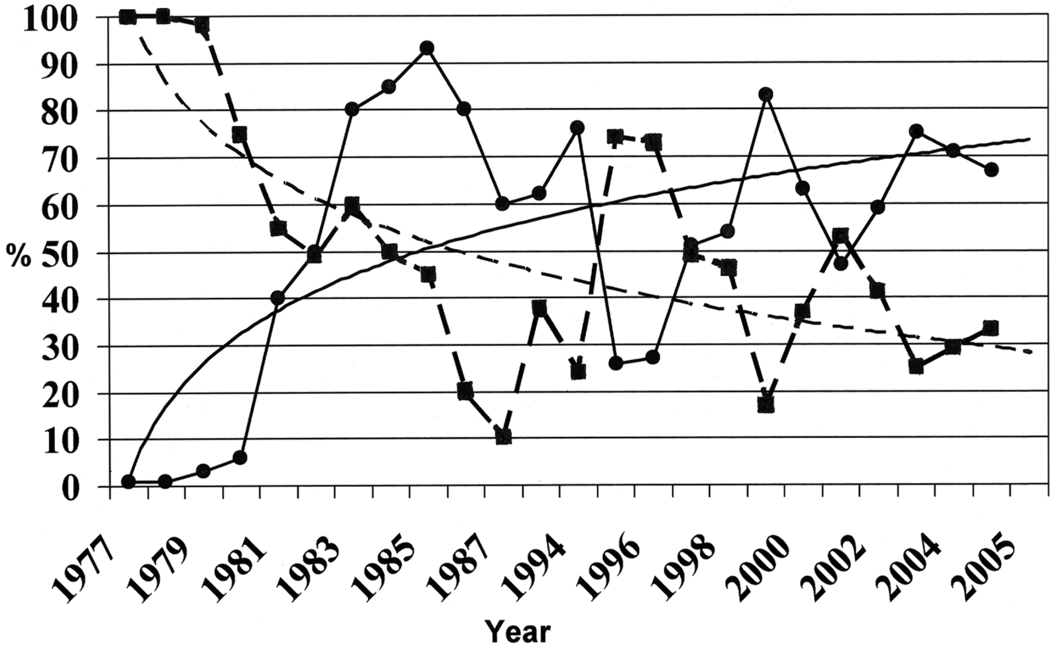

FIGURE 4. Total average frequencies (%) of the nonnative algae (circles) in turtle samples compared with the total average frequencies of the native algae (squares) from 1977 to 2005. Solid line represents the best fit for the nonnative data ($y = 20.67\ln(x) + 5.95$), and the dashed line represents the best fit for the native data ($y = -22.99\ln(x) + 102.5$).

diet from the Kāne'ohe Bay area when compared with the larger number of native species that are each contributing less.

When these data are compared between the small number of nonnative algae and the large number of native algae, the importance of the nonnative species to the diet of the turtles becomes even more apparent (Figure 5). On average, from 1985 to 2005 the five nonnative species composed 58% of the turtles' food, and the 115 native species composed 42% of the food turtles were using in the Kāne'ohe Bay area (Table 1). This means each nonnative species was providing about 11.6% of the food to the turtles, and each native species was only providing 0.4% of their food. The transition by turtles to use these newly introduced food sources occurred between 1980 and 1990 (Figure 4), after which the turtles chose to eat more of the abundant introduced food sources. It took less than 10 years for *Chelonia mydas* to actively modify its diet to include nonnative species of algae as they became more abundant in relation to the available native species (Figures 4, 5).

Abundance alone is probably not the only reason the turtles are utilizing the nonnative species, because preference and nutrition are also important. The native species *Dictyosphaeria cavernosa* and *Dictyosphaeria versluysii*, succulent green algae, are quite abundant in this region (Russell 1981) but are not utilized as much as expected. They represented only 10–17% of the samples and only 5% of the algae present (Table 1). Green turtles in Florida are also selective in what they eat and prefer some algae over others and even avoid eating some algae that are readily abundant and available to them (Gilbert 2005). In the Kāne'ohe Bay region, *Halimeda discoidea*, a highly calcified green seaweed, is also abundant and available to the turtles (Russell 1981) but is seldom present in the samples: 7.8% of the samples and mostly in trace quantities (Table 1). *Padina japonica* is also abundant on the reef and commonly available

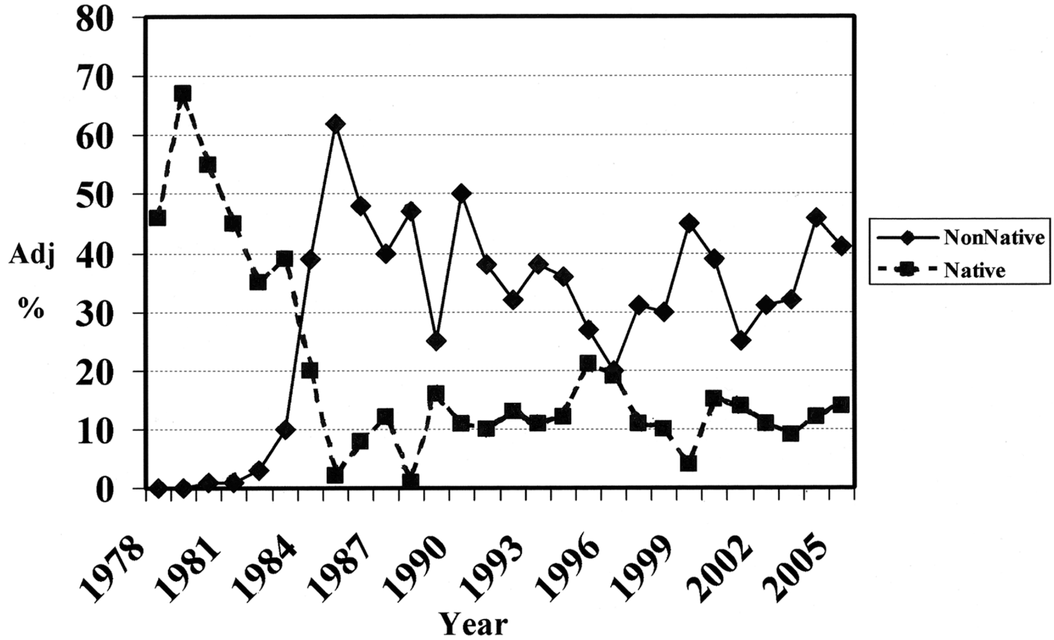

FIGURE 5. Weighted percentages of nonnative algae compared with native algae in the turtle diet. Adjustment was made by dividing the percentage of total algae each year by the number of species that contributed those totals.

to turtles but is utilized only 2.7% of the time and is probably eaten incidentally along with more important food items, since it too is found mostly in trace amounts. *Lyngbya majuscula* is a small filamentous cyanophyte that was found in 13% of the samples, but it was nearly always present in trace amounts (Table 1). It could be an important ingested item related to adverse health effects, even in small amounts, because at times it is known to become toxic and is occasionally present on the reefs in large quantities as a bloom (Arthur et al. 2006).

Gilbert (2005) found that juvenile green turtles in Florida were feeding primarily on *Hypnea* spp., which is similar to what our data show for Hawai'i. Other species found in the diet of Florida turtles also included *Gelidium* spp., which are similar to *Pterocladellia capillacea* in color, texture, and size, as seen in our samples. *Gracilaria* sp. and *A. spicifera* were also common in Florida turtle samples and are also common in the Hawai'i turtle samples (Table 1). *Hypnea* sp., in the Florida study, had a higher nutritional value and was lower in fiber than the less-nutritious species that were not selected by turtles, and the turtles actively avoided those less-valuable species (Gilbert 2005). These results paralleled what was found in Hawai'i but with important differences.

The most common marine plants from turtles found by Arthur and Balazs (2008), in Hawai'i, were *A. spicifera*, *Hypnea* sp., *P. capillacea*, *H. hawaiiana*, *H. decipiens*, and *Cladophora* sp. All of these species were present in our samples, but *C. arabicum*, *C. edule*, and *A. glomerata* were more important in our samples than the two sea-grass species recorded by Arthur and Balazs (2008). However, their study clearly showed that turtles selectively feed on different species in different pastures; therefore variations in turtle diet between study areas are reasonable and expected.

In addition, the nutritional value of the three most common nonnative algae in turtle samples is similar to that of the native species (McDermid and Stuercke 2003, McDermid et al. 2007). These new and abundant nonnative species are now supplying the turtles with an important source of energy and protein in addition to the native species they continue to include in their diet. The diet shift by *C. mydas* to include the introduced algae food sources in the Kāne‘ohe Bay region was a behavior pattern that was repeated every time a newly introduced food source became available to them.

CONCLUSIONS

Important conservation efforts in Hawai‘i have successfully reversed the downward trend for *C. mydas*, and as the population appears to be approaching carrying capacity the importance of protecting and maintaining adequate food in their foraging areas becomes critical. The increasing numbers of green turtles in Hawai‘i (Balazs and Chaloupka 2004*a*, 2006, Hays 2004), are directly a result of conservation measures, and appear to be due to turtles finding, selecting, and using newly introduced supplemental seaweed food resources. Green turtle nesters increased noticeably after 1985 and this was during the same time period that turtles began utilizing the new food sources in the study area foraging grounds (Figure 4). These food sources appear to be contributing to the carrying capacity of the green turtle's habitat and also to its recovery in Hawai‘i.

ACKNOWLEDGMENTS

For long-term contributions to dietary studies of free-ranging green turtles throughout the Hawaiian Islands we sincerely thank the following individuals, agencies, and organizations: Isabella A. Abbott, Karen Arthur, Bridget McBride, Donna Brown, Sallie Beavers, Ursula and Peter Keuper-Bennett, Dart Bicoy, Shandell Brunson, Emily Carlson, Mike Coelho, John Coney, Walter Dudley, Skippy Hau, Leon Hallacher, Stacy (Kubis) Hargrove, Don Heacock, Cody Hooven, Alan Kam, Regina (Luna) Rudrud, Darren Marshall, Karla McDermid, Ed and Diane Medeiros, Sherwood Maynard, Shawn Murakawa, Bob Morris, Irene Nurzia-Humburg, Joy Oliveira, Erin Siebert, Russell Sparks, Bill Puleloa, Jason Turner, Bob Rameyer, Marc Rice, Denise Parker, Thierry Work, State of Hawai‘i Division of Aquatic Resources and Division of Conservation and Resources Enforcement, Marine Option Program (University of Hawai‘i at Mānoa, University of Hawai‘i at Hilo, Maui Community College), the Hawai‘i Preparatory Academy, and the NOAA Hawaiian Islands Humpback Whale National Marine Sanctuary. For valuable review comments and suggestions on the manuscript we express appreciation to George Antonelis, Alan Bolten, Bruce Mundy, Karla McDermid, Stacy (Kubis) Hargrove, and anonymous journal reviewers.

Literature Cited

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu.

Abbott, I. A., and J. M. Huisman. 2004. Marine green and brown algae of the Hawaiian Islands. Bishop Museum Press, Honolulu.

Arthur, K. E., and G. H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pac. Sci. 62:205–217.

Arthur, K. E., C. J. Limpus, C. M. Roelfsema, J. W. Udy, and G. R. Shaw. 2006. A bloom of *Lyngbya majuscula* in Shoalwater Bay, Queensland, Australia: An important feeding ground for the green turtle (*Chelonia mydas*). Harmful Algae 5:251–265.

Balazs, G. H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. NOAA Tech. Memo. NMFS-SWFC-7.

Balazs, G. H., and M. Chaloupka. 2004*a*. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. Biol. Conserv. 117:491–498.

———. 2004*b*. Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian archipelago. Mar. Biol. (Berl.) 145:1043–1059.

———. 2006. Recovery trend over 32 years at the Hawaiian green turtle rookery of French Frigate Shoals. Atoll Res. Bull. 543:147–158.

Balazs, G. H., R. G. Forsyth, and A. K. H. Kam. 1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. NOAA Tech. Memo. NMFS-SWFSC-71.

Balazs, G. H., S. K. K. Murakawa, J. Wyneken, and B. A. Schroeder. 1998. Differences in flipper size and esophagus morphology of green turtles from Hawaii and Florida. Pages 137–139 *in* Proceedings 17th Annual Sea Turtle Symposium, 4–8 March 1997, Orlando, Florida. NOAA Tech. Memo. NMFS-SEFSC-415.

Chaloupka, M., T. M. Work, G. H. Balazs, S. K. K. Murakawa, and R. Morris. 2008. Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian Archipelago (1982–2003). Mar. Biol. (Berl.) 154:887–898.

Doty, M. S. 1961. *Acanthophora*, a possible invader of the marine flora of Hawaii. Pac. Sci. 15:547–552.

Eldredge, L. G., and C. M. Smith. 2001. A guidebook of introduced marine species in Hawaiʻi. Bishop Mus. Tech. Rep. 21.

Gilbert, E. I. 2005. Juvenile green turtle (*Chelonia mydas*) foraging ecology: Feeding selectivity and forage nutrient analysis. M.S. thesis, University of Central Florida, Orlando.

Hays, G. C. 2004. Good news for sea turtles. Trends Ecol. Evol. 19:349–351.

Hirth, H. F. 1997. Synopsis of the biological data of the green turtle *Chelonia mydas* (Linnaeus 1758). U.S. Fish Wildl. Serv. Biol. Rep. 97 (1): 1–120.

Huisman, J. M., I. A. Abbott, and C. M. Smith. 2007. Hawaiian reef plants. University of Hawaiʻi Sea Grant College Program Rep. No. UNIHI-SEAGRANT-BA-03-02.

McDermid, K. J., and B. Stuercke. 2003. Nutritional composition of edible Hawaiian seaweeds. J. Appl. Phycol. 15:513–524.

McDermid, K. J., B. Stuercke, and G. H. Balazs. 2007. Nutritional composition of marine plants in the diet of the green sea turtle (*Chelonia mydas*) in the Hawaiian Islands. Bull. Mar. Sci. 81:55–71.

Phillips, R. C., and C. P. McRoy. 1980. Handbook of seagrass biology: An ecosystem perspective. Garland STPM Press, New York.

Russell, D. J. 1981. The introduction and establishment of *Acanthophora spicifera* (Vahl) Boerg. and *Eucheuma striatum* Schmitz in Hawaii. Ph.D. diss., University of Hawaiʻi, Honolulu.

———. 1983. Ecology of the imported red seaweed *Eucheuma striatum* Schmitz on Coconut Island, Oʻahu, Hawaiʻi. Pac. Sci. 37:87–106.

———. 1992. The ecological invasion of the Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag. and *Hypnea cervicornis* J. Ag. ICES Mar. Sci. Symp. 194:110–125.

Russell, D. J., and G. H. Balazs. 1994. Utilization of alien alga species by sea turtles in Hawaiʻi. Pages 93–95 *in* D. J. Baker and K. Sullivan, eds. Proceedings of the Conference and Workshop on Nonindigenous Estuarine and Marine Organisms (NEMO), Seattle, Washington, 20–23 April 1993. NOAA, Washington, D.C.

———. 2000. Identification manual for dietary vegetation of the Hawaiian green turtle *Chelonia mydas*. NOAA Tech. Memo. NMFS-SWFSC-294.

Russell, D. J., G. H. Balazs, R. C. Phillips, and A. K. H. Kam. 2003. Discovery of the sea grass *Halophila decipiens* (Hydrocharitaceae) in the diet of the Hawaiian green turtle, *Chelonia mydas*. Pac. Sci. 57:393–397.

Smith, J. E., C. L. Hunter, and C. M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pac. Sci. 56:299–315.

Work, T. M. 2000. Sea turtle necropsy manual for biologists in remote refuges. U.S. Geological Survey National Wildlife Health Center Hawaiʻi Field Station.