

Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands

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The Galapagos Islands are among the most important nesting areas for the green sea turtle, Chelonia mydas, in the eastern Pacific Ocean. In addition, the coastal waters of this oceanic archipelago host many important feeding areas for this species, although little is known about green turtle feeding ecology at these sites. The goal of this study was to identify and quantify the most important items in the diet of the green turtle at the foraging grounds of Bahía Elizabeth, Caleta Derek and Punta Nuñez. Our analysis was based on 65 oesophageal samples from turtles captured in 2006 and 2007. We compared spatial and seasonal composition of diet using non-metric multidimensional scaling analysis (MDS) and analysis of similarity (ANOSIM). Green turtle diet was composed mainly of the algae species Ulva lactuca, Polysiphonia sp., Hypnea sp. and Dictyota sp., and the red mangrove Rhizophora mangle. Turtles also consumed animal matter, mainly cnidarians, albeit to a lesser extent. Content of turtle diets was different among feeding grounds and seasons. The ANOSIM showed that diet composition can differ between foraging grounds using presence/absence of diet items. Even though U. lactuca was the most abundant algae consumed in both seasons, changes in species richness of algae were found between both sampling events, with diet during the warm season more varied than the cold season ($\chi^2 = 16.84$, $df = 6$; $P < 0.05$).

Keywords: eastern Pacific Ocean, black turtle, *Chelonia mydas*, diet, Galapagos Marine Reserve, spatial variation

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INTRODUCTION

Green turtles, *Chelonia mydas*, occur in tropical and subtropical regions throughout the world's oceans. Due to overexploitation of eggs and turtles as food source and, to a lesser extent, incidental mortality related to marine fisheries and degradation of marine and nesting habitats, populations have declined throughout the world (Groombridge & Luxmoore, 1989; NMFS, 1998; Seminoff, 2004; Koch *et al.*, 2006). Green turtles are currently listed as endangered in the *International Union for Conservation of Nature Red Data Book* (IUCN, 2009) and are included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Despite a worldwide increase in research and conservation of green turtles, their foraging biology and habitat requirements remain poorly understood (Bjorndal, 1997).

Like most sea turtles, green turtles are migratory and use a wide range of broadly separated localities and habitats during their lifetime (Hirth, 1997). Upon leaving the nesting beach, it has been hypothesized that hatchlings begin an oceanic phase, perhaps floating passively in major current systems (gyres) for several years (Carr & Meylan, 1980; Carr, 1987; Reich *et al.*, 2007; Arthur *et al.*, 2008). In neritic habitats,

green turtles feed primarily on algae and/or seagrass, with diet composition varying between feeding areas. In the Hawaiian archipelago (Balazs, 1980) and in Bahía de los Ángeles (Gulf of California, Mexico) (Seminoff *et al.*, 2002), they feed mainly on macroalgae. On the Pacific coast of Baja California Peninsula (Mexico) the diet is dominated by a mixture of algae and seagrasses (López-Mendilaharsu *et al.*, 2005), while in the Caribbean Sea (Bjorndal, 1980, 1985; Mortimer, 1981) and on the Great Barrier Reef in Australia (Fuentes *et al.*, 2006) the green sea turtles feed predominantly on seagrasses.

In the eastern Pacific Ocean (EPO) the most studied feeding grounds for the green turtle are the Baja California peninsula (Mexico) (Cliffon *et al.*, 1982; Seminoff *et al.*, 2002; López-Mendilaharsu *et al.*, 2005), the Gulf of Fonseca (Honduras) (Carr, 1952), Gorgona Island (Colombia) (Amarocho & Reina, 2007), the Galapagos Islands (Ecuador) (Green & Ortiz-Crespo, 1982), and the Paracas Peninsula (Perú) (Márquez, 1990). At many of these sites, green turtles consume large quantities of invertebrate matter in addition to marine algae and seagrasses (Carr, 1952; Hays & Brown, 1982; Seminoff *et al.*, 2002; Amorocho & Reina, 2007). The diet composition at different feeding grounds depends on the availability of resources (Bjorndal, 1980; Ross, 1985; Balazs *et al.*, 1987), and to some extent by foraging preferences, especially for certain species of red algae (Gilbert, 2005; Fuentes *et al.*, 2006; López-Mendilaharsu *et al.*, 2008).

Among the most important areas for green turtles in the EPO are the Galapagos Islands, an oceanic archipelago located ~1000 km west from mainland Ecuador (Green &

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Ortiz-Crespo, 1982; Hurtado, 1984). In addition to hosting a major nesting population, the Galapagos Islands contains important feeding grounds for green turtles, particularly around the archipelago's western islands of Isabela and Fernandina (Green & Ortiz-Crespo, 1982), where high productivity areas are located (Banks, 2002) due to local upwelling (Feldman, 1985). Here and elsewhere, there is a resident population of green turtles which feeds in nearshore neritic foraging habitats (Seminoff *et al.*, 2007). Green & Ortiz-Crespo (1982) and Green (1994) made some comments on the diet composition of the green turtle in the Galapagos Islands. However, they did not carry out an exhaustive study on this issue. Despite the importance of the Galapagos Islands for green turtles, the feeding ecology of this species has been poorly studied.

The purpose of this research was to study the dietary composition of green turtles in the Galapagos Islands, and how it differed spatially and seasonally through oesophagic content analysis. The present study is a contribution to the overall understanding of green turtle diet in the EPO, an ocean region that has been known for hosting the enigmatic invertebrate foraging behaviour of green turtles (Bjorndal, 1997).

MATERIALS AND METHODS

Study site

From 2006 to 2007, we studied green turtles at three feeding areas in the Galapagos Islands. These include Bahia Elizabeth (BE) ($00^{\circ}35'41.1''W91^{\circ}04'10.2''$), Caleta Derek (CD) ($00^{\circ}38'35.9''W91^{\circ}05'33.4''$) in the Western Galapagos

Islands and Punta Nuñez (PN) ($00^{\circ}44'40.7''W 90^{\circ}15'18.3''$) in the Eastern Galapagos Islands (Figure 1). Whereas BE and CD are lagoons (1–5 m deep) with low swell influence, PN is an exposed bay (1–15 m deep) influenced by strong currents and wave action. The sea floor in BE is mainly covered by mud, where turtles are usually observed resting. The sea floor in CD is mainly covered by rocks and small patches of green algae. Adjacent coasts of BE and CD present great cover of the green alga *Ulva* spp. and other turf algae (e.g. *Polysiphonia* sp.). The PN sea floor is covered mainly by mixed patches of *Caulerpa racemosa* and *Hypnea* sp. and smaller patches of *Dictyota* sp. at the external part of the bay.

According to the Galapagos Marine Reserve (GMR) zoning scheme (DPNG & FCD, 1999) these localities are not totally protected. At BE non-extractive (tourism and conservation) activities are allowed, at CD and PN extractive (fishing) and non-extractive activities are allowed (DPNG & FCD, 1999).

Turtle capture and measurement

Turtle capture efforts were conducted at BE in February and August 2006, at CD in August 2006, and at PN in June, September, October 2006 and July 2007. A 100 m net with 30 cm mesh size was used for capturing turtles. Manual captures were also made using snorkel equipment. Upon capture, turtles were transported to a boat where their curved carapace lengths (CCL) were measured (± 0.1 cm) with a measuring tape, from the anterior nuchal scute to the posterior most edge of the carapace.

We grouped turtles according to their size in base on the mean nesting size (MNS) of females that nest on the Galapagos beaches (MNS = 86.7 cm CCL; Zárate *et al.*, 2003).

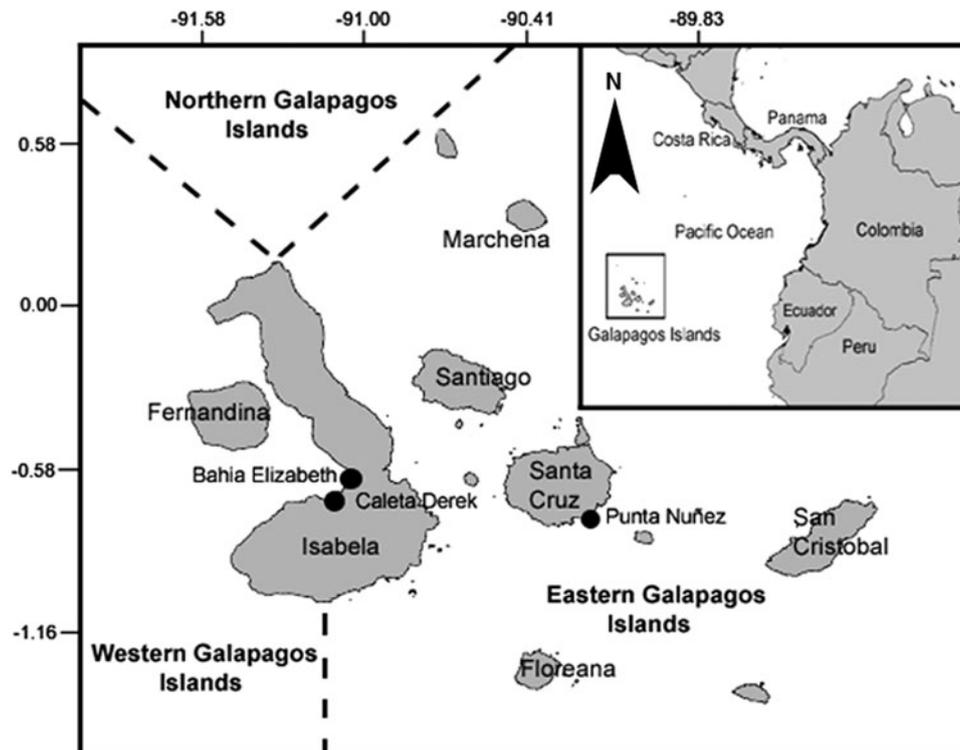


Fig. 1. Galapagos Archipelago. The black points show the study sites of Bahia Elizabeth, Caleta Derek and Punta Nuñez. Hatched lines are divisions of the three ecoregions in Galapagos, according to Spalding *et al.* (2007).

Thus, Group I included all turtles with $CCL < MNS$ (probable immatures), and Group II included all animals with $CCL \geq MNS$ (probable adults). This assignment may represent immature and adult individuals, but there may be some imprecision because all turtles do not necessarily reach maturity at the same size (Limpus & Chaloupka, 1997).

Curved carapace length data were normal ($Z = 1.20$; $P = 0.112$) and homogeneous (Levene = 0.18; $P = 0.834$) so a one-way ANOVA was applied to determine CCL differences between study areas and seasons. This analysis was done with the software SPSS 12.0 (SPSS Inc, Chicago).

Diet study

To analyse the diet we conducted oesophageal lavage to collect recently ingested food from the oesophagus and the anterior stomach region of turtles (Forbes & Limpus, 1993). Turtles were placed on their back, and the mouth was opened using a pry bar until a veterinary mouth gag was inserted to keep it open. A tube lubricated with vegetable oil was inserted in the oesophagus and clean seawater was pumped at low and constant pressure. The procedure lasted no more than five minutes. After the oesophageal lavage, turtles were released in the study area. Diet samples were stored in plastic bags and frozen for later laboratory analysis.

The volume of each sample was determined through measuring water displacement in a graduated cylinder. Each sample was then spread in a Petri dish of appropriate size, and dietary components were identified to the lowest possible taxonomic level according to Taylor (1945), Abbott & Hollenberg (1976), Lobban (1996) and Russell & Balazs (2000). Algae identification was performed using a stereoscope and light microscope. To quantify the relative abundance of the consumed items a 16 squares graticule (each square of 1×1 cm) with 2 mm^2 gradations was located in the bottom of the Petri dish. The relative abundance of food components was determined by the microstereology technique (Schaefer, 1970; Redfoot, 1997). This technique involves counting the number of times a particular item appears over the intersection points of the squares using a stereomicroscope. Thus, the relative abundance represents the points covered by each species. The relative abundance of each food item was estimated using the following formula:

$$\begin{aligned} &\text{relative volume of diet (\%V)} \\ &= \frac{\text{no. of points by diet item}}{\text{total no. points counted for entire sample}} \times 100 \end{aligned}$$

Any diet component with a relative volume $>5\%$ in at least one sample was considered an important item (Garnett *et al.*, 1985; Seminoff *et al.*, 2002; Arthur & Balazs, 2008). For all consumed items with $>5\%$, we calculated the frequency of occurrence (%FO) (Windell & Bowen, 1978):

$$\begin{aligned} &\text{frequency of occurrence (\%FO)} \\ &= \frac{\text{no. samples in which diet item observed}}{\text{total no. of samples}} \times 100 \end{aligned}$$

The weighted resultant index (Rw) was used to establish the most important elements of the diet of the turtles in the three sites. This is a relative importance index that combines

the %FO and the %V and allows us to estimate the order of importance for the entire array of foods ingested:

$$Rw = \frac{1}{\sum Q(V^2 \times FO^2)^{\frac{1}{2}}} \times 100$$

where,

$$Q = \frac{45 - |\theta - 45|}{45}$$

This index can be graphically represented as a function of the θ angle that is calculated using the formula $\tan^{-1}(V/FO)$. This makes it possible to interpret the importance of each item considering the consistency of the %V and %FO. Diet components with a uniform representation of %V and %FO have angles close to 45° . The values of the Rw vary between 0 and 100; food items with values close to 100 represent the most important in the diet, while those closer to 0 represent less important items in the diet (Mohan & Sankaran, 1988).

The similarity of the diet between the study sites and the two sampling events at BE was tested with non-metric multidimensional scaling analysis (MDS) using a Bray–Curtis similarity matrix (presence/absence). This analysis uses a dissimilar measurement function for each pair of samples and expresses it in terms of distance in a multidimensional graphic. A similarity analysis (ANOSIM) was made as well to examine the effect of the sites over the diet component samples. The ANOSIM is a non-parametric permutation analysis applied to a similarity presence/absence matrix from which we could analyse the null hypothesis that there are no differences between sampling events, grouping the sites and samples (Arthur & Balazs, 2008). The MDS and ANOSIM analyses were processed with the software Community Analysis Package (CAP) version 3.0 (Pisces Conservation Ltd).

To analyse how the contribution of relative volume of the principal diet components ($V \geq 5\%$) varied between the two sampling events at BE a comparative histogram was made. Welch ANOVA was applied to determine differences in the consumption proportion of the principal alimentary items in the diet of the turtles in the study sites and between sampling seasons at BE. Welch ANOVA is a variance analysis that considers normal data that does not obey the homogeneity assumption. This analysis was done using the software SPSS version 12.0 (SPSS Inc, Chicago).

RESULTS

A total of 65 green turtles were captured. At BE, of the 33 turtles, 14 were captured in August 2006 (cold season) and 19 were captured in February 2006 (warm season). At CD, 20 turtles were captured in August 2006, while at PN, 14 turtles were captured during 2006–2007.

At BE 97% ($N = 32$) of captured turtles were categorized in Group I ($CCL < MNS$), whereas 3% ($N = 1$) were categorized in Group II ($CCL \geq MNS$). At CD 95% ($N = 19$) of captured turtles were categorized in Group I and 5% ($N = 1$) were categorized in Group II. At PN, 42% ($N = 5$) were categorized in Group I, whereas the remains 58% ($N = 7$) were categorized

in Group II. Significant differences were found between mean size of turtles captured in the three study sites ($F_{2, 64} = 21.44$; $P < 0.01$) (Figure 2). Turtles at PN (mean CCL = 81.02 ± 10.40 cm) were the largest compared to turtles captured at CD (mean CCL = 66.84 ± 10.76 cm) and BE (mean CCL = 59.14 ± 9.31 cm). No significant differences were found in the sizes of turtles captured during warm versus cold seasons ($F_{1, 32} = 1.38$; $P > 0.05$) at BE.

Mean oesophageal sample volume was 3.15 ± 2.00 ml at PN ($N = 12$), 7.21 ± 6.26 ml at CD ($N = 20$) and 5.18 ± 4.67 ml at BE ($N = 14$). Diet components consumed by green turtles in the Galapagos Islands are shown in Table 1. Due to the lack of taxonomic keys for identifying the marine flora of the Galapagos Islands and the high endemism (29%) of algae reported in this area by Garske (2002), most of the algae were only identified to genus level. Green turtles fed mainly on algae (mean relative volume = 82.27%) but also on mangrove (mean relative volume = 5.03%) and animal matter (mean relative volume = 8.75%). In terms of relative abundance, green algae were the major dietary constituent, followed by red algae (Table 1). However, this did not reflect the species richness in the diet (3 species of green algae and 18 species of red algae). Five components were the most important in terms of relative abundance in the diet ($V \geq 5\%$): *Ulva lactuca*, *Polysiphonia* sp., *Hypnea* sp., *Dictyota* sp. and the red mangrove *Rhizophora mangle*. While the algae *Prionitis* sp., *Pterocladia* sp., *Caloglossa* sp., *Anhelftiopsis* sp. and *Centroceras* sp. were only found in small quantities ($V \leq 1\%$).

The ANOSIM showed that diet sample composition can differ between places and seasons, based on the presence and absence of the alimentary components (significance level = 0.10%; $P < 0.01$). However, similarity in diet of green turtles at BE and CD in August is evident according to the MDS analysis (Figure 3). This similarity is attributed to the presence of *U. lactuca*, *Polysiphonia* sp. and *Gelidium* sp. in the diet of turtles at both sites. While differences in the samples compared to PN are principally because of the presence of *Hypnea* sp., *Caulerpa racemosa* and *Dictyota* sp., algae that were only found in the samples from PN.

Although *U. lactuca* was a common item in the diet of turtles from the three study areas, it was ingested in different

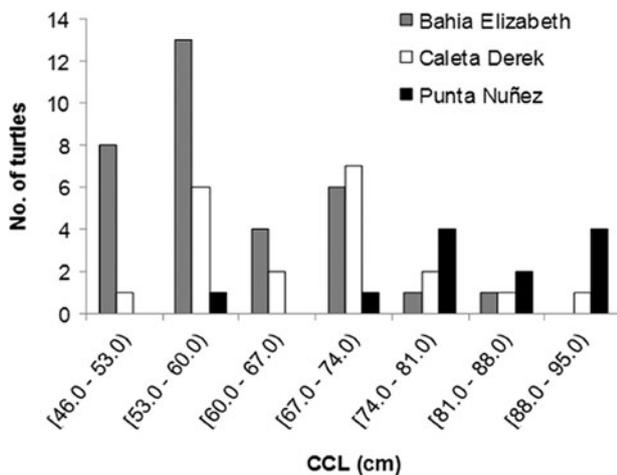


Fig. 2. Size-classes of green sea turtles captured in the three study sites: Bahia Elizabeth ($N = 33$), Caleta Derek ($N = 20$), Punta Nuñez ($N = 12$).

Table 1. Diet of the green sea turtle at three study areas in the Galapagos Islands. Table shows relative abundance of food items (%V \pm standard error (SE)) and frequency of occurrence (%FO). %FO with %V > 5 and %V > 50 represent the percentage of samples in which the diet item was found to contribute more than 5% and 50% of relative volume.

Diet component	Mean %V	SE	%FO	%FO with %V > 5	%FO with %V > 50
Algae					
<i>Ulva lactuca</i>	37.32	4.41	69.23	69.23	44.62
<i>Caulerpa racemosa</i>	3.75	2.24	4.62	4.62	3.08
<i>Codium</i> sp.	2.23	0.92	13.85	12.31	-
Total Chlorophyta	43.31	4.71	73.85	73.85	47.70
<i>Polysiphonia</i> sp.	4.91	1.75	21.54	16.92	1.54
<i>Hypnea</i> sp.	4.89	2.31	10.77	9.23	4.62
<i>Gelidium</i> sp.	3.54	1.09	20.00	18.46	-
<i>Bostrychia</i> sp.	2.88	1.56	13.85	10.77	3.08
<i>Callophyllis</i> sp.	2.58	1.49	4.62	4.62	3.08
<i>Catenella opuntia</i>	2.54	1.39	7.69	7.69	3.08
<i>Halymenia</i> sp.	2.49	1.44	6.15	6.15	3.08
<i>Gymnogongrus</i> sp.	2.23	1.10	12.31	9.23	1.54
<i>Gelidiella</i> sp.	1.42	1.42	1.54	1.54	1.54
<i>Gracilaria</i> sp.	1.18	0.75	7.69	4.62	-
<i>Anhelftia</i> sp.	1.09	0.62	7.69	6.15	-
<i>Coralina</i> sp.	1.05	0.81	6.15	3.08	1.54
No. identified foliious	0.60	0.57	3.08	1.54	-
<i>Prionitis</i> sp.	0.53	0.37	4.62	3.08	-
<i>Pterocladia</i> sp.	0.40	0.26	4.62	3.08	-
<i>Caloglossa</i> sp.	0.38	0.27	3.08	3.08	-
<i>Anhelftiopsis</i> sp.	0.21	0.21	1.54	1.54	-
<i>Centroceras</i> sp.	0.20	0.20	1.54	1.54	-
Total Rhodophyta	33.13	4.21	93.84	72.3	23.07
<i>Dictyota</i> sp.	4.86	2.61	7.69	6.15	4.62
No. identified foliious	0.97	0.97	1.54	1.54	1.54
Total Phaeophyta	5.83	2.75	9.23	7.70	6.15
Vascular plants					
<i>Rhizophora mangle</i>	5.03	1.69	16.92	15.38	1.54
Animal matter					
Cnidaria No. identified cnidarian	4.30	1.78	13.85	13.85	1.54
Hydrozoa: Siphonophora	2.37	1.66	3.08	3.08	3.08
Scyphozoa	1.23	1.23	1.54	1.54	1.54
Nematoda	0.29	0.24	3.08	1.54	-
Annelida Spunalidae	0.25	0.25	1.54	1.54	-
Mollusca Gastropoda	0.25	0.12	7.69	1.54	-
Crustacea Hiperidae	0.06	0.06	1.54	-	-
Total animal matter	8.75	2.64	26.15	23.08	6.15
Other					
Sand	3.52	1.37	18.46	13.85	0.00

proportions (Welch ANOVA $F_{2, 28.81} = 64.01$; $P < 0.001$). The weighted resultant index (Rw) shows that *U. lactuca* is the main food item in the diet of green turtles at BE and CD (Figure 4), with greater prevalence in diet of green turtles at CD (Rw = 98.45). On the other hand, primary diet components according to the Rw at PN were *Hypnea* sp. > *Dictyota* sp. > *Caulerpa racemosa*.

Diet of turtles in the warm season at BE had greater species richness than that during the cold season ($\chi^2 = 16.84$, $df = 6$; $P < 0.05$). Figure 5 shows the comparison of relative abundance of food items that were important ($V > 5\%$) in at least one season at BE. *Ulva lactuca* was the most important item in both seasons and the level of consumption of

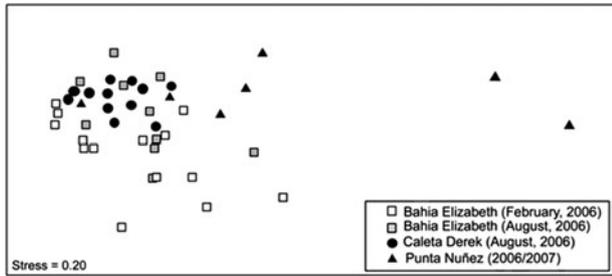


Fig. 3. Two-dimensional multidimensional scaling grouping samples by study site, using a presence/absence matrix of the diet items in the samples ($N = 65$). Points that appear close together show higher similarity in the food items assemblages than those that appear distant.

this item did not change significantly (Welch ANOVA $F_{1, 28.06} = 0.28$; $P > 0.05$).

DISCUSSION

The present study shows that the Galapagos Islands coasts provide a variety of food resources for juvenile and adult green turtles. According to the MNS (86.7 cm CCL) criterion as a proxy threshold for estimating maturity, dominant size-classes of green turtles that aggregate at BE and CD (46–74 cm CCL) corresponded to juvenile individuals, while at PN the size-range (74–95 cm CCL) corresponded to large juveniles and presumed adult individuals. This provides further evidence that green turtles show some degree of ontogenetic habitat preference, with the largest turtles tending to aggregate at higher-energy coastal areas and smaller individuals at shallow protected areas (Seminoff *et al.*, 2003; López-Mendilaharsu *et al.*, 2005; Koch *et al.*, 2007). Ontogenetic habitat shift has been also suggested to occur with loggerhead (*Caretta caretta*) (Tomas *et al.*, 2001) and Kemp's ridley (*Lepidochelys kempii*) turtles (Schmid *et al.*, 2003) which may be a strategy that confers an advantage for

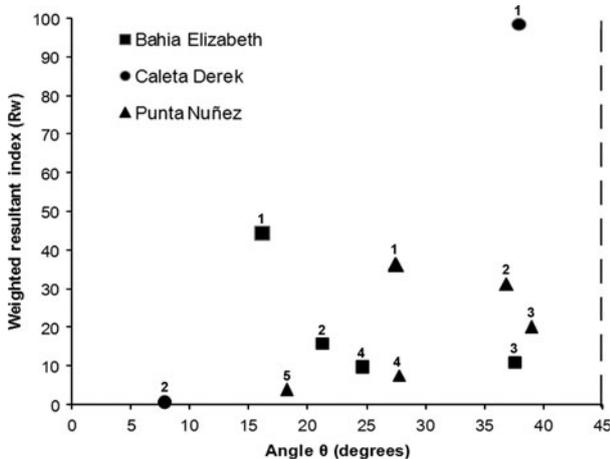


Fig. 4. Importance of the primary food items ($V > 5\%$) consumed by green turtles in three study areas in the Galapagos Islands. Weighted resultant index (Rw) denotes the order of importance of the food items in the diet. Bahia Elizabeth ($N = 14$): (1) *Ulva lactuca*, (2) *Polysiphonia* sp., (3) Hidrozoa, (4) *Rhizophora mangle*; Caleta Derek ($N = 20$): (1) *Ulva lactuca*, (2) *Codium* sp.; Punta Nuñez ($N = 12$): (1) *Hypnea* sp., (2) *Dictyota* sp., (3) *Caulerpa racemosa*, (4) *Ulva lactuca*, (5) *Gelidium* sp.

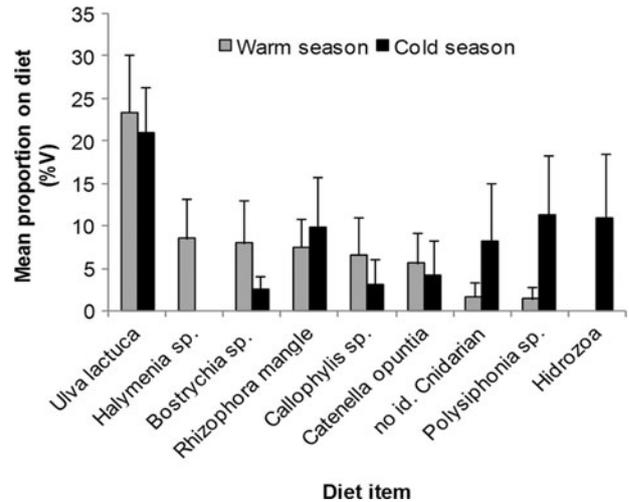


Fig. 5. Mean proportion ($\%V \pm SE$) of major food items ($V > 5\%$) in the diet of the green turtle during two seasons in the Galapagos Islands. This figure represents the two sampling events in Bahia Elizabeth: warm season ($N = 19$) and cold season ($N = 14$).

turtles to increase growth rates (Bjørndal *et al.*, 2000) and survival (Schmid *et al.*, 2003; Koch *et al.*, 2007).

Green turtles in the Galapagos Islands mainly feed on algae. The reports of Green & Ortiz-Crespo (1982) and Green (1994) did not provide a detailed list of the algae species present in the green turtle diet, thereby precluding long term comparisons with the present study. However, we speculate that local significant changes in algae communities (Robinson, 1985; Vinueza *et al.*, 2006) related to strong El Niño Southern Oscillation (ENSO) events during 1982–1983 and 1997–1998, could have induced changes in green turtle diet composition along the time, as have occurred in the Hawaiian archipelago (Russell & Balazs, 2009).

Changes in green turtle diet composition during both seasons at BE are probably due to seasonal changes in vegetation availability. Garske (2002) reported seasonal patterns in the marine flora of the Galapagos Islands, especially in the Western Galapagos region where BE is located.

The diet composition of green turtles may change as the algal biomass and cover decline from the cool to warm season, as has been found with other herbivores that feed on similar algae species (e.g. *Ulva*), such as the marine iguana (*Amblyrhynchus cristatus*) (Shepherd & Hawkes, 2005). Although, biomass of *Ulva* reduces significantly during the warm season (Vinueza *et al.*, 2006) no significant differences were found in its consumption proportion by the green turtle in both seasons, which suggest selection of this resource, yet when it is scarce. But the fact that turtles in the warm season consume a higher diversity of red algae, suggests that in this season turtles consume more food items to complete their food requirements. We also expect seasonal changes in diet composition of turtles that feed at CD and PN, due to changing oceanographic features, particularly because of upwelling processes, which causes differential patterns in algae composition on Galapagos Islands coasts (Garske, 2002).

Algae assemblages that make up the diet of green turtles are different between study sites. Diet composition is more similar at BE and CD, likely due, at least in part to the close proximity of these two sites and the consistency of available algae

(Figure 1). In addition, BE and CD are located in the same region (Western Galapagos Islands) and algae composition may be relatively homogeneous (Garske, 2002). PN is located in the Eastern Galapagos Islands where higher sea surface temperatures occur (Banks, 2002), which causes the observed differences in algae assemblages (Garske, 2002). The fact that site-specific composition of the diet of green turtles varies over a short geographical scale was also reported in the Hawaiian Islands (Arthur & Balazs, 2008). This underscores the adaptive nature of green turtle foraging strategies, which is likely driven by local food availability.

The proportion of green algae in the diet of green turtles reported in the present study is higher than most previous green turtle diet studies. Whereas we found that green algae constituted 43.3% of the diet of green turtles, it is 11.6% in the Hawaiian archipelago (Arthur & Balazs, 2008), 9% on the west coast of the Baja California Peninsula (López-Mendilaharsu *et al.*, 2005), 6.2% in the Gulf of California, Mexico (Seminoff *et al.*, 2002), and 5.11% in Texas, USA (Coyne, 1994), all four sites of which green turtles feed mainly on red algae. Red algae are generally higher in protein and energy content, and digestibility than green algae (especially *Ulva*) (Wong & Cheung, 2001; Rubenstein & Wikelski, 2003), which suggest that green turtle diet in the Galapagos Islands may have less nutritional content compared with turtles in other foraging grounds where they consume red algae at higher extent.

The green turtle, unique among sea turtles in feeding on macroalgae, may be variously stressed by ENSO events in the Galapagos Islands, when algae biomass decline, and only algae of poor food quality persists (e.g. *Ulva* spp.) (Laurie, 1989). Strong ENSO events in the Galapagos Islands have caused drastic declines of growth rates and number of other herbivores, such as marine iguanas (*Amblyrynchus cristatus*) and the 'zayapa' crab *Grapsus grapsus* (Laurie & Brown, 1990; Vinuesa *et al.*, 2006). Despite that no studies have focused on the effect of ENSO on green turtles in the Galapagos Islands, it is suggested that it may profoundly influence green turtle nutrient intake, and consecutively produce a decline of growth rates and a delay of the size-at-maturity. Nutrient deficiencies caused by ENSO can also reduce the reproductive output of green turtles, by not allowing nesting females to reach the required body condition to breed, which may drive interannual variation in nesting numbers, as has been reported at the north coast of Australia (Limpus & Nicholls, 1988).

The green alga *Ulva lactuca* was the preferred food of green turtles in BE and CD, whereas in PN the preferred items were *C. racemosa*, *Hypnea* sp. and *Dictyota* sp. By means of visual surveys on the sea floor in adjacent coasts of CD and BE, it was evident that *U. lactuca* was the most abundant algae, covering most of the rocky bottom, where turtles were usually observed performing feeding activities. In contrast, the most abundant algae species at PN are *C. racemosa*, *Hypnea* sp. and *Dictyota* sp. (Garske, 2002). This coincidence in algal abundance in marine habitats and in our lavage samples suggests that green turtles consume the most readily available food at the foraging areas at which they inhabit. This is consistent with previous findings by Balazs (1980), Garnett *et al.* (1985) and Forbes (1996).

The red mangrove *R. mangle* (mainly shoots) constitutes 5% of the diet of the green turtle in the Galapagos Islands. The consumption of this item by green turtles in the Galapagos Islands was previously reported by Pritchard (1971), and was reported in other foraging areas such as

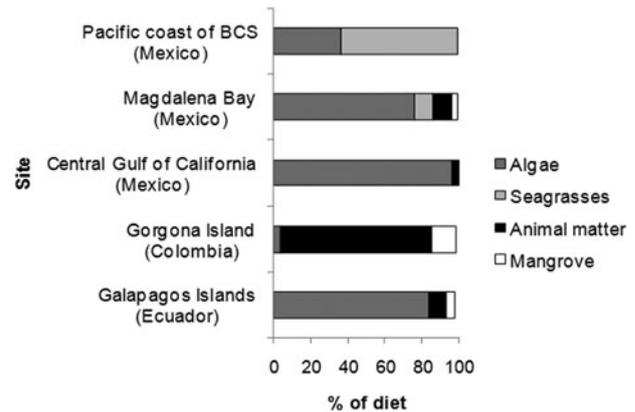


Fig. 6. Proportion (%) of the main diet groups of the green turtle in five foraging grounds along the Eastern Pacific Ocean: Pacific coast of the Baja California Peninsula (López-Mendilaharsu *et al.*, 2005), Magdalena Bay (López-Mendilaharsu *et al.*, 2005), Central Gulf of California (Seminoff *et al.*, 2002), Gorgona Island (Amarocho & Reina, 2007), Galapagos Islands (this study).

Gorgona Island (Colombia) (Amarocho & Reina, 2007) and Australia (Limpus & Limpus, 2000). Somewhat interesting is the fact that the red mangrove is substrate for the epiphytic algae *Catenella opuntia*, *Bostrychia* spp. and *Caloglossa* spp. (Skelton & South, 2002; personal observation), that were consumed by turtles at BE, a site with ample supply of red mangroves around the lagoon. *Catenella opuntia* and *Bostrychia* sp. were consumed in a proportion higher than 5% in the warm season (Figure 5), so they may be target dietary components for green turtles. On the other hand, consumption of red mangrove was higher (> 5%) during the cold season when the consumption of epiphytic species was < 5% (Figure 5), thus it seems that red mangrove consumption is not incidental. This reflects the significance of the red mangrove as a food resource and a foraging habitat for juvenile green turtles at BE.

Turtles in our study also consumed a number of items at trace levels. These items may be incidentally consumed as they could be associated with the substrate of algae preferred by green turtles. Incidental consumption of some species have been reported for green turtles elsewhere (Seminoff *et al.*, 2002; Ferreira *et al.*, 2006; Fuentes *et al.*, 2006; López-Mendilaharsu *et al.*, 2008). In our study, items consumed incidentally may include all species that contribute less than 1% of relative volume in the diet, such as *Prionitis* sp., *Pterocladia* sp., *Anhelfeltiopsis* sp., *Centroceras* sp. and some invertebrates (Table 1). We believe the frequent presence of sand in lavage samples is a consequence of the type of habitat used by green turtles and the result of incidental consumption of substrate material while foraging.

Invertebrates comprised only 8.75% of the total dietary abundance of green turtles in the Galapagos Islands. Only cnidarians (Scyphozoa, Siphonophora) were found at a level that warranted consideration as a major diet item (7.9% of relative volume). Whether these foods were consumed incidentally or purposely remains unresolved. However, even those invertebrate foods found at trace levels (nematodes, annelids, molluscs and crustaceans) may contribute vitamins, minerals and essential amino acids (Bjorndal, 1990) and thus provide nutritional benefits.

The herbivory tendency of the green turtle found in this study, supports the most common feeding pattern of post-

pelagic green turtles (Bjorndal, 1997) and is not consistent with other studies that suggest that green turtles in the EPO may consume high amounts of animal matter (Carr, 1952; Bjorndal, 1997; Amorocho & Reina, 2007) (Figure 6). These spatial differences in diet composition along the EPO suggest that post-pelagic green turtles have the capability to adopt different feeding strategies, possibly in response to local abundance and type of resources.

Conservation implications

The Galapagos Islands coasts provide several habitats that appear to be characterized by unique algae assemblages and different geophysical and oceanographic conditions, which may drive green turtle ontogenetic habitat shifts. Thus, it is important to protect these different habitats as they provide food to complement green turtle's energetic requirements for growth at different maturity stages. Thanks to the GMR zoning scheme, most, although not all, of the green turtle foraging grounds on the Galapagos Islands coasts are totally protected. This zoning scheme divides the coastal line in three subzones according to the allowed human activities. In the case of our study areas, these are not totally protected (see study areas description) which could represent a threat for green turtles.

Despite the great usefulness of the GMR zoning scheme for conservation purposes, it is important to identify critical endangered species habitats for conservation. In the case of areas with high aggregation of green turtles, where tourism activities are allowed, it is necessary to promote better tourism practices and control of boat traffic, as they alter turtle behaviour during resting and feeding activities (González, 2008). These management efforts will assure the continued health of the local green turtle population and will provide an opportunity to continue studying green turtles in a near 'pristine' condition.

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