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Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia

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ABSTRACT: The diet of 84 East Pacific green turtles *Chelonia mydas agassizii*, captured in 2003 and 2004 at Gorgona National Park in the Colombian Pacific, was studied through analysis of lavage samples collected from the lower oesophagus. We identified 5 food diet components, with rank in order of percent dry mass being: tunicates (Salpidae and Doliolidae), red mangrove fruits (*Rhizophora mangle*), algae (Rhodophyta, Chlorophyta, Cyanophyta), small crustaceans (shrimp larvae) and leaves (*Ficus* spp.). Three non-food diet items included coral fragments, shells, and sand/pebbles that were found in large amounts in most retrieved samples. Nutritional analyses were carried out to determine the contribution of diet components to the foraging turtles. Tunicates had the highest protein value (438 g kg^{-1}), followed by algae (174 g kg^{-1}), leaves (170 g kg^{-1}) and mangrove fruits (65 g kg^{-1}). The frequency of retrieved components grouped in animal (including coral), vegetal and sand/pebbles categories did not vary between sampling seasons. The immature East Pacific green sea turtle population at Gorgona National Park showed an omnivorous behaviour, feeding on a range of animal and vegetal components with a bias towards tunicates (Salpidae and Doliolidae). In contrast to the generally herbivorous diet of juvenile green turtles (over 40 cm straight carapace length; SCL), Gorgona's immature population was composed of large juveniles, subadults and a few adults feeding mainly on animal matter. Mean SCL of 86 measured turtles was 58.4 ± 7.8 cm (ranging from 37.0 to 72.9 cm). Mean mass was 28.0 ± 10.7 kg (ranging from 7.5 to 50.5 kg). We speculate that this omnivorous strategy of Gorgona's immature green turtles might provide energetic benefits for continuing long distance migrations to further developmental or mating grounds in the Pacific basin.

KEY WORDS: Green turtle · Black turtle · Feeding ecology · Omnivory · Nutrition · Migration

INTRODUCTION

The genus *Chelonia* includes 2 subspecies: the East Pacific green turtle *C. mydas agassizii* (Boucort 1868) from Baja California to Peru and west to the Galapagos Islands, and the green turtle *C. mydas* (Linnaeus, 1758) in the rest of the world's range (Cliffton et al. 1982, Cornelius 1982, Green 1994). The former is widely distributed along the coasts of North, Central and South America, and is not restricted to coastal waters, occurring in insular and pelagic areas on the eastern side of the Pacific basin (Green 1983, NMFS 1998). The East Pacific green turtle *C. mydas agassizii* is considered to be a melanistic form of the genus *Chelonia*, which is distinguished by its dark greenish, vaulted shape and narrow carapace (Cornelius 1982, Pritchard 1999).

Populations of the East Pacific green turtle have declined in many areas due to increased hunting at breeding sites (Green & Ortiz 1982, Alvarado-Diaz et al. 2001, Seminoff et al. 2002). Incidental capture in artisanal and industrial fisheries has also contributed to the reduction of demographic units in the East Pacific (Alvarado-Diaz & Figueroa 1990, NMFS 1998). The species is currently listed as endangered throughout its range by the IUCN (Hilton-Taylor 2000).

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The green sea turtle is a highly migratory species crossing the border of several countries in the East Pacific while using different habitats during their life cycle (Hirth 1997). According to tag recovery data, migrations for foraging, mating and nesting occur between the northern and southern extremes of the range. Tag recoveries of nesting females tagged on the beaches of Michoacán (México) have been documented from El Salvador, Guatemala, Nicaragua, Costa Rica and Colombia (Alvarado-Diaz & Figueroa 1990). Tag recovery data also indicate that at least part of the East Pacific green turtle population breeding in the Galapagos Islands (Ecuador) is recruited from distant feeding grounds (NMFS 1998). On the other hand, tagged nesters from the Galapagos have been recovered in the coastal waters of Costa Rica, Panama, mainland Ecuador, Peru and Colombia (Green 1984, MacFarland 1984). Studies of migratory routes between nesting and feeding areas of East Pacific green turtles have established the existence of migratory corridors between the Galapagos Islands and the Peninsula of Baja California in Mexico (NMFS 1998). After spending 1 to 10 yr of their post-hatchling life in oceanic habitats, East Pacific green turtles move to shallow coastal waters, where they feed on algae or sea grasses (Mortimer 1982) and mangrove fruits (Limpus & Limpus 2000). Once at these feeding grounds, immature individuals remain associated with specific feeding sites over extended periods, as has been described for green turtles *Chelonia mydas* in Australia (Limpus et al. 1994).

The marine ecosystems of Gorgona National Park in the Colombian Pacific are suitable for the development of diverse species of algae and marine invertebrates (Bula-Meyer 1995). Organic material from continental rivers is dragged by the convergence of surface currents into Gorgona's waters. The insular nearshore habitats of this protected area have been identified as the most important feeding grounds in the Colombian Pacific for resting, growth and sexual development of the East Pacific green sea turtle (Amorocho et al. 2001). Several authors have recognised the importance of insular nearshore habitats for the development of juveniles (e.g. Balazs 1982, Meylan et al. 1994) and for adult foraging (Green 1994, Limpus et al. 1994, Seminoff 2000). It has also been suggested that developmental and feeding habitats may determine the recruitment pattern of juveniles and the timing of adult reproductive cycles (Limpus & Reed 1985).

It is known that green turtles have a strong tendency towards herbivory, changing their diet from carnivorous or omnivorous to herbivorous during their ontogeny (Bjorndal 1980, Mortimer 1982, Garnett et al. 1985, Hirth 1997). The recruitment of *Chelonia* spp. to neritic developmental habitats generally occurs at small sizes of 30 to 40 cm (Musick & Limpus 1997). At a size of about 40 cm carapace length, young green turtles leave pelagic habitats and enter benthic foraging areas, at which time they also switch to their characteristically herbivorous diet (Bjorndal & Bolten 1988, Hirth 1997) and occupy a feeding niche unique among sea turtles (Bjorndal 1997). In several parts of the world adult green turtles (>70 to 100 cm) may feed predominantly on sea grasses (Mortimer 1982, Mendonca 1983) or on algae (Pritchard 1971, Bjorndal 1985, 1997, Green 1994), depending on their abundance. They will also feed on both types of food when these are present in the same area (Read 1991). Variation in diet composition may be a consequence of local availability of food, turtle selectivity and/or type of habitat (Bjorndal 1980, Garnett et al. 1985, Brand-Gardner et al. 1999).

The present study investigated the diet composition and nutritional contribution of food consumed by green turtles *Chelonia* spp. at Gorgona National Park, in order to better understand how sea turtle feeding ecology is affected by features of nearshore foraging grounds.

MATERIALS AND METHODS

Study area. Gorgona National Park (2° 55′ to 3° 00′ N, 78° 09′ to 78° 14′ W) is a 49 200 ha volcanic island located 56 km off the southern Colombian Pacific coast (Fig. 1). The island and the southern islet of Gorgonilla are surrounded by coral reefs (with dominance of *Pocillopora, Psammacora* and *Pavona* spp.), soft corals (*Pacifigorgia, Lobogorgia, Muricea* and *Telesto* spp.), and sandy bottoms, where sea grasses are not present. Water temperature ranges between 26 and 28°C. During the first months of the year marine upwelling brings large amounts of nutrients to Gorgona's marine ecosystems. This is particularly common in January when temperature decreases from 27°C at the surface to 14°C at 15 m depth (INVEMAR 2000). River drainage in Gorgona carries large amounts of terrestrial tropical rainforest vegetation and the waters surrounding the island also receive organic matter supplied by continental rivers of Sanquianga, Satinga, La Tola and Patia. Soft bottoms, rocky coastlines, sandy beaches, coral and soft coral areas make up the marine and coastal ecosystems of Gorgona National Park.

There are 3 species of sea turtles present in this protected area (Rueda 1988). The olive ridley *Lepidochelys olivacea* is the only species that comes ashore to breed on beaches of the southwest side between July and November. Small juveniles of the hawksbill *Eretmochelys imbricata* can be found in the La Azufrada–Playa Blanca coral reefs. However, the most

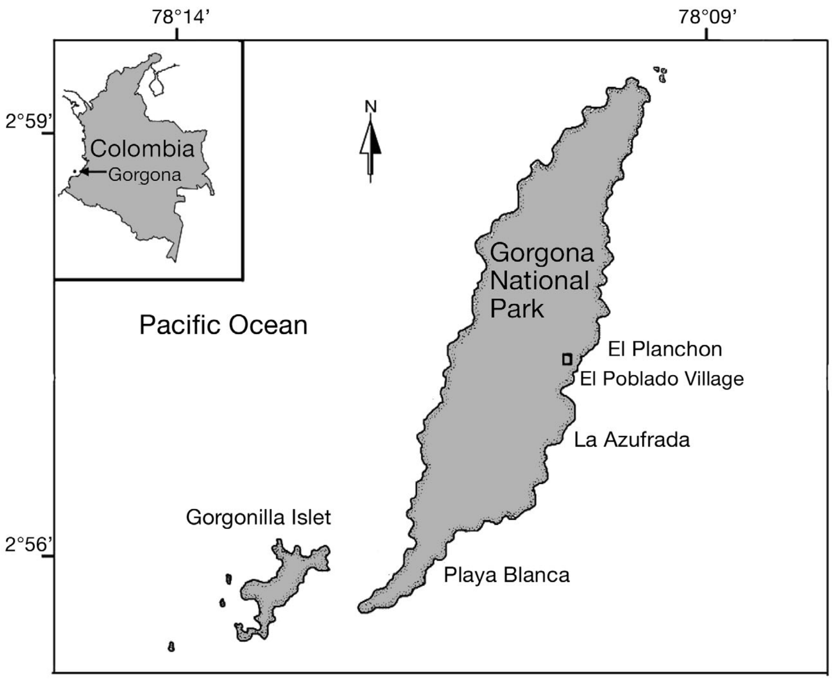

Fig. 1. Map of the study area in the Colombian Pacific, showing coral and sandy habitats at Gorgona National Park

numerous is the East Pacific green turtle *Chelonia mydas agassizii*, which is restricted in the Colombian Pacific to the foraging grounds of Gorgona National Park.

Sampling and content analysis. Four sampling seasons were carried out to assess East Pacific green turtle feeding (October and November 2003, March and July 2004) in coral reefs and sandy bottomed habitats close to the island. Animals resting on the bottom at a depth less than 6 m were captured by hand at night during snorkel surveys of 2 h duration. Body mass was measured using a spring scale. Minimum straight carapace length (SCL) was measured from the nuchal scute to the posterior notch at midline between the supracaudal scutes and width (SCW) at the widest point (Bolten 1999). Sampled turtles were double tagged with Inconel 1005-681S tags (National Band & Tag Co.) in the trailing edge of the front flippers, following standard techniques (Balazs 1999). After obtaining dietary samples in the lab as described below, animals were released within 2 h of being caught with a fluorescent number painted on the carapace, to avoid recapture during the same sampling season.

Food in the mouths of captured animals was collected and oesophageal lavages were performed to recover food samples following the methodology for stomach lavages (Forbes & Limpus 1993). Herein we refer to 'oesophageal' rather than 'stomach' lavages because in East Pacific green turtles, the oesophagus descends to a position just inside the plastron and bends to the left in an S-shaped curve to join the stomach (Wyneken 2001). This anatomical characteristic prevents reaching the crop (muscular specialisation on the base of the oesophagus), with the plastic in-flow and retrieval hoses and actually entering the stomach. In some cases trying to reach the stomach might cause harm to the animal, so the collected material from assessed individuals was recovered from the lower oesophagus, which is lined with sharp and keratinised papillae. These cornified papillae aid in swallowing food (Bleakney 1965) and in retaining small food particles during feeding before they enter the stomach (Smith 1961).

During the lavages we used tubes with diameters relative to the size of the turtle. For animals with a SCL <70 cm, the in-flow and retrieval tubes were both 15 mm external diameter. For animals >70 cm, the in-flow and retrieval tube external diameters used were 15 and 17 mm, respectively. Glycerine was applied to facilitate introduction of the tips of the water in-flow and sample retrieving hoses up to 35 cm into the oesophagus. The mean volume of saltwater flushed through each sampled animal was 4.7 ± 1.4 l. Water was slowly pumped by hand under constant pressure. Seawater was used to filter the retrieved oesophageal contents through a 1 mm sieve. Samples were then sorted following principles of micro stereology (Weibel et al. 1966, Schaefer 1970) and quantified as described by Forbes (1999). Vegetal samples were fixed in 70% ethanol and those of animal origin in 10% formalin. Alimentary samples were taken directly from the beak to assess the composition of the last bite taken by turtles before capture.

Laboratory analyses. We applied 2 techniques to determine the relative volume of each dietary component, as suggested by Forbes (1999):

Water displacement analysis: The entire sieved sample volume and relative sample volume of each food item group were calculated by the method of water displacement in a graduated cylinder. Items with a relative volume >5% in at least one sample were considered a major diet component (Garnett et al. 1985). Food items remaining in the bottom were removed, filtered and weighed for the final analysis.

Final analysis: The procedure applied in this case uses the principles of microstereology and a quantification technique adapted from Forbes (1999). The lavage sample was mixed in a large tray until visually homogeneous, and then a subsample was taken and placed in the bottom of a Petri dish to be viewed through a stereo microscope. A stage mounted template of 1 cm^2 grid divided into 9 'v' shape fields of 40° each was attached underneath the Petri dish and rotated through the entire circumference for identification of dietary components.

Food items were identified and classified to the lowest possible taxonomic category using a combination of available keys for invertebrates, molluscs and botanic species from Gorgona Island and the Pacific mainland. Percent occurrence (%F) for each food group was calculated from the number of samples that contained that food group as a percentage of the total number of samples. Percent dry mass was calculated as the total dry mass of a food group as a percentage of the total dry mass of all the samples combined. The rank of each food group was determined by multiplying its percent occurrence (%F) by its percent dry mass. Proximal analyses were carried out to determine the contribution of the main identified components to the diet of foraging East Pacific green sea turtles.

Statistical analysis. Correlation and regression models were employed to observe the relationship between SCL and CCL of captured individuals. Analyses of variance (ANOVA) tests were conducted to measure variability among principal dietary components, size class and divergence between assessed animals. A post-hoc Ryan–Einot–Gabriel–Welsch multiple means comparison test was used to detect significant differences when indicated by ANOVA. In all analyses results are presented as the mean ± 1 standard deviation.

RESULTS

Size class distribution was estimated following the hatchling, juvenile, subadult, and adult SCL categories defined by Hirth (1997). Although CCL has been suggested as the basic standard length measure for *Chelonia mydas* (Limpus et al. 1994) we took both. Here, we present results of SCL measurements for size class comparisons (Fig. 2), as most studies carried out in East Pacific green turtles report this measure. Of the assessed turtles, there were 83 subadults (40 to 70 cm SCL) plus 3 that were large subadults or small adults (70 to 75 cm SCL). Mean SCL was 58.4 ± 7.8 cm (ranging from 37.0 to 72.9 cm) and mean mass was 28.8 ± 10.7 kg (ranging from 7.5 to 50 kg).

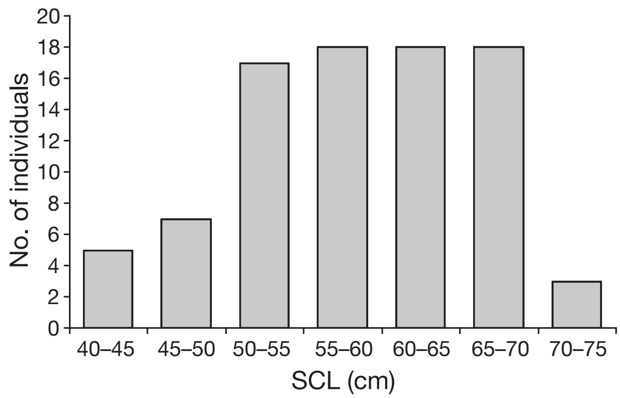

Fig. 2. *Chelonia mydas agassizii.* Straight carapace length (SCL) distribution of 86 East Pacific green turtles captured at Gorgona National Park, Colombia, 2003–2004. In the 70 to 75 cm range, 3 turtles were either large subadults or small adults

Diet composition

Oesophageal contents were collected from a total of 84 of the 86 captured East Pacific green turtles, with 66 from animals captured in the coral reefs of La Azufrada–Playa Blanca and 18 from the sandy bottom habitat of El Planchón. Mean volume of isolated samples retrieved and classified was 15 ± 19 ml (ranging from 1 to 96 ml). Mean wet mass of processed lavage samples was 5.0 ± 2.9 g (ranging from 0.3 to 21.3 g).

Oesophageal contents were classified into 8 groups in recovered samples (Table 1). Tunicates (Salpidae and Doliolidae) were the most frequent item, followed by pieces of red mangrove fruits (*Rhizophora man-*

Table 1. *Chelonia mydas agassizii.* Frequency (%F) and percent dry mass of dietary components retrieved from 84 East Pacific green turtles at Gorgona National Park, Colombia, 2003–2004

Diet component	%F	Dry mass (g)	% Dry mass
Tunicates (Salpidae and Doliolidae)	73.80	86.13	65.95
Mangrove fruit (*Rhizophora mangle*)	69.04	17.24	13.20
Crustaceans (*Penneus* spp.)	63.09	4.78	3.66
Mollusc shells (*Rissoina* spp., *Triphora* spp.)	36.90	1.98	1.52
Leaves (*Ficus* spp., *Ochroma* spp., *Hibiscus* spp.)	29.76	1.79	1.37
Sand and pebbles	28.57	11.89	9.10
Coral (*Pocillopora* spp.)	19.04	1.96	1.50
Marine algae (*Gelidium* spp., *Cladophora* spp.)	17.85	4.83	3.70

gle); crustaceans such as shrimp larvae (*Penneus* spp.) and molluscs (*Rissoina* spp. and *Triphora* spp.). Leaves of terrestrial phanerogams (*Hibiscus tiliaceus, Ochroma pyramidae, Nurolaena lobata, Ficus* spp. *and Clusia* spp.) were the fifth most frequent food group. Sand and pebbles were present in over a quarter of the collected samples. Fragments of coral (*Pocillopora* spp.) and 3 species of algae (*Cladophora panamensis*, *Gelidium pusillum* and *Gelidium bulae*) account for the lowest ranked groups. Stomach and gut contents obtained in a necropsy of a turtle that died from injuries caused by swallowing a fishing hook in the study area corresponded to those found through oesophageal lavages in sampled animals (authors' pers. obs.) The 8 diet groups identified were regrouped into 3 categories: animal (tunicates, crustaceans, molluscs and coral), vegetal (mangrove fruit, leaves and algae) and sand/pebbles. Means of total dry mass per animal by category obtained from ANOVA were: animal 1.12 ± 0.15 g; vegetal 0.2 ± 0.08 g; sand/pebbles 0.1 ± 0.04 g. The nutritional composition of retrieved components (Table 2) indicate that tunicates have the highest content of protein (438.85 g kg^{-1}), P (5.97 g kg^{-1}) and fibre (418.65 g kg^{-1}). Leaves presented a great amount of Ca (19.88 g kg^{-1}), fibre (343.60 g kg^{-1}) and lignin (183.80 g kg^{-1}). Similar amounts of fibre (334.20 g kg^{-1}) and lignin (220.40 g kg^{-1}) were obtained from the red mangrove fruits. Algae account for the highest values of K (9.17 g kg^{-1}), Ca (13.90 g kg^{-1}), Mg (9.59 g kg^{-1}), S (35.98 g kg^{-1}) and ash (176.18 g kg^{-1}).

Dietary components and type of habitat

ANOVA range tests for dry mass of the diet samples of 84 assessed turtles at sandy bottoms of El Planchon and coral reefs of La Azufrada–Playa Blanca showed animal material as the most consumed dietary component; being significantly greater than vegetal and sand/pebbles ($p < 0.0001$) (Table 3). Multiple means comparison of dry mass revealed significant differences between animal material and the other 2 types of dietary components at coral reefs of La Azufrada–Playa Blanca (Fig. 3). ANOVA including types of habitats showed that no significant differences existed between seasons ($p > 0.1290$). No significant relationship was detected between the size class of turtles and the amount of animal or vegetal material ingested.

Table 2. *Chelonia mydas agassizii.* Nutritional contribution based on dry mass of diet components retrieved through oesophageal lavages from 84 East Pacific green turtles at Gorgona National Park, Colombia, 2003–2004. CF: crude fibre, DM: dry mass

Diet component	Protein (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	S (g kg^{-1})	CF (g kg^{-1})	Lignin (g kg^{-1})	Ash (g kg^{-1})	Moisture (g kg^{-1})	DM (g)
Tunicates[1]	252.32	4.85	3.88	2.23	3.38	5.37	418.65			37.40	2.55
Tunicates[2]	438.85	5.97	4.72	9.76	5.90	7.64	376.27			35.65	2.60
Leaves[3]	69.52	0.49	2.70	19.88	4.69	3.75	343.60	177.60	121.86	34.07	11.70
Leaves[4]	170.54	2.27	4.14	10.00	3.41	3.25	406.00	183.80	96.58	32.80	4.50
Algae[5]	174.29	4.24	9.17	13.90	9.59	35.98	284.60	49.80	176.18	38.43	6.35
Mangrove fruit[6]	65.26	0.79	1.77	1.08	0.89	1.20	334.20	220.40	23.70	43.89	31.20

[1]Salpidae, [2]Doliolidae, [3]*Ficus* spp., [4]*Hibiscus* spp., [5]*Gelidium* spp., [6]*Rhizophora mangle*

Table 3. *Chelonia mydas agassizii*. ANOVA using SAS/STAT program of seasonal grouped components retrieved from East Pacific green turtles captured at sandy bottoms of El Planchon and coral reefs of La Azufrada–Playa Blanca of Gorgona National Park in Colombia, 2003–2004 (n = 84)

Source	df	Type III SS	Mean square	*F* Value	p value
Habitat	1	0.096	0.096	0.40	0.5267
Season	2	0.595	0.297	1.23	0.2930
Habitat × Season	2	0.303	0.151	0.63	0.5332
Component	2	17.611	8.805	36.55	<.0001
Habitat × Component	2	0.037	0.018	0.08	0.9244
Season × Component	4	1.740	0.435	1.81	0.1290
Habitat × Season × Component	4	0.683	0.170	0.71	0.5864
Error	207	49.870	0.240		
Corrected Total	224	78.260			

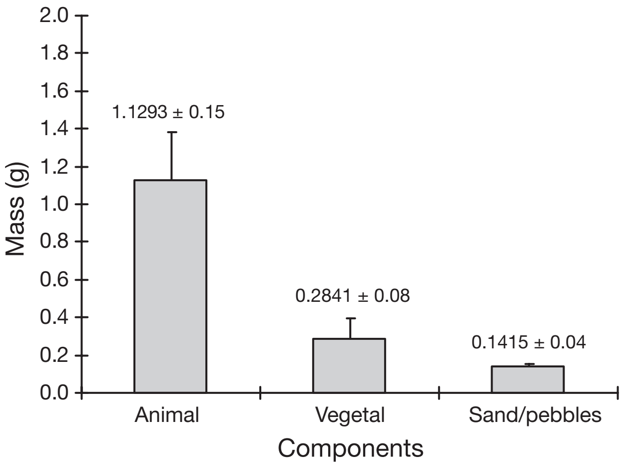

Fig. 3. *Chelonia mydas agassizii.* Multiple means ± SE comparison of dietary components retrieved from 84 East Pacific green turtles at sandy bottomed habitats in El Planchon and coral reefs at La Azufrada–Playa Blanca in Gorgona National Park, Colombia, 2003–2004

DISCUSSION AND CONCLUSIONS

The size distribution of foraging East Pacific green turtles captured at Gorgona National Park corresponded to an immature population almost entirely composed of juveniles, with a small number of large subadults or small adults. Smaller turtles have higher relative energy demands than adults, preferring sheltered areas where net energy expenditure during foraging activities is less than in high-energy oceanic zones (Wikelski et al. 1993). On the other hand, abundant animal material in surface current convergences found in the waters surrounding Gorgona may attract larger individuals that are less dependent on protection provided by coral reefs. A similar difference in mean size of East Pacific green turtles has been observed in the Gulf of California where large animals inhabit deep, high-energy coastlines, while smaller turtles inhabit shallow protected areas (López-Mendilaharsu et al. 2003, Seminoff et al. 2003). The low number of animals caught in sandy bottomed (n = 18) compared with coral (n = 68) habitats does not conclusively show that habitat preference differs with an individual's size class, but 3 juveniles with a CCL average of 47.8 (ranging from 43.3 to 51.7 cm) were recaptured at La Azufrada–Playa Blanca after 7, 12 and 30 months of being tagged (Rodríguez-Zuluaga & Amorocho 2006). This may indicate that small animals spend more time in nearshore protected areas of Gorgona than larger animals.

Although the limitations of the oesophageal lavage method used in this study meant that the total amount of food retrieved from East Pacific green turtles was small, the quantities of the 8 major components recorded are still representative of a larger diet consumed by turtles. The diet of this species at Gorgona National Park was similar to studies carried out in Australia when comparing with the amount of animal material ingested. A total of 63 (26.3%) lavage samples analysed from immature green turtles *Chelonia mydas* at the Moreton Banks and Flathead Gutter, Australia, contained animal material (Read & Limpus 2002). In the Torres Strait, animal material was recorded in 52.3% of the 44 stomach contents analysed from green turtles (Garnett et al. 1985).

These findings do not correspond to the common pattern observed on similarly sized individuals studied in the Eastern Pacific. In the Gulf of California and coast of the Baja peninsula (Mexico), where oesophageal flushing of food components or necropsies for identification of stomach contents has been performed, East Pacific green turtles exhibited a strong tendency toward herbivory, with marine algae comprising 92% of the mean lavage volume (Seminoff et al. 1998), although subadults of East Pacific green turtles in Bahía Magdalena along the coast of Baja California peninsula also forage on non-algal food resources such as red crabs (López-Mendilaharsu et al. 2005) and other chordates (Casas-Andreu & Gómez-Aguirre 1980). Their predominantly herbivorous diet is consistent with other *Chelonia* populations along the Pacific coast of Central America (Mortimer 1982). This trend toward algae and/or sea grasses has also been well documented as a common pattern defining the grazing behaviour of adult green sea turtles *C. mydas*, in the Caribbean (Bjorndal 1980, Mortimer 1982).

On the Pacific coast of South America, the direct observation in the Galapagos Islands (Ecuador) of subadults and adults of the East Pacific green turtle, indicated that they predominantly feed on algae, including *Ulva*, *Padina*, *Gelidium*, *Callithamnion* and *Gracilaria* spp. (Green 1994). However, in coastal waters of Peru, Hays Brown & Brown (1982) found a significant amount of animal matter (molluscs, polychaetes, jellyfish, amphipods, sardines and anchovies) in the stomach contents of subadult and adult green turtles, in addition to algae. This feeding behaviour is similar to the consumption of animal matter by immature foraging turtles assessed at Gorgona National Park, indicating that omnivory might occur in all size classes.

Bjorndal (1997) reported that East Pacific green turtles may have a more carnivorous diet than *Chelonia* of other regions. This might be a consequence of the low presence in the Eastern Pacific of sea grasses and a lack of algal diversity, but an abundance of other prey such as fish, fish eggs, molluscs, crustaceans, polychaetes and jellyfish (Casas-Andreu & Gómez-Aguirre 1980, Fritts 1981, Hays Brown & Brown 1982).

The consumption of a diet with high protein content (tunicates) would result in greater nutrient gain for development to sexual maturity. This has been demonstrated in captive rearing facilities at the Grand Cayman turtle farm, where green turtles consuming higher protein levels grow faster and mature earlier than wild populations (Wood 1974). Green turtles can digest formulated high protein diets with a high degree of efficiency (Wood & Wood 1981) and animal protein may play an important role in the nutrition of this species (Read & Limpus 2002). If we consider nutrient gain as a function of diet quality rather than quantity, it could be that Gorgona's green turtle population are consuming diets high in protein and energy, because they are more useful for non-maintenance purposes, such as growth and reproduction, than diets low in protein and energy. In accordance to Bjorndal (1997), when food types are dispersed, the greater search and handling cost of seeking for a vegetal (algae or sea grass) diet may be greater than the energy gain from a more efficient digestion provided by a good quality mixed diet. Juveniles in this protected area probably acquire more energy feeding on an omnivorous rather than on an exclusively herbivorous diet. Vegetal and animal matter can be found on the surface and within the water column above the coral reefs that turtles use for shelter and resting, thereby avoiding the need to forage far away from the island.

The percent dry mass of tunicates (66%) and invertebrates (4%) in the diet suggests that such food resources make a major contribution of vitamins, trace minerals, or essential amino acids (Bjorndal 1985), and may explain why East Pacific green sea turtles at Gorgona fed mainly on animal matter. Tunicates exhibited high crude fibre contents because they are the only animals able to perform cellulose biosynthesis. Ascidian cellulose synthase may be involved in the formation of the tunic, the cellulose-containing structure that surrounds the surface of the body to protect against predators (Sasakura et al. 2005). Nonetheless, the spatio-temporal patchiness of this resource in terms of seasonal abundance makes red and green algae *Gelidium* spp. and *Cladophora* spp. an alternative supply of food when tunicates become scarce in the foraging grounds.

The occurrence of turtles feeding on terrestrial plants such as *Ficus* spp., *Ochroma* spp., *Hibiscus* spp. and mangrove fruits, *Rhizophora* spp., as a sporadic food source found in the convergence of currents, is evidence of the flow, transformation and use of energy between coastal and marine ecosystems. This could be a strategy of East Pacific green turtles foraging at Gorgona National Park to complement or replace other food items when they are not available. Similar energy flows have been described in the Galapagos (Pritchard 1971) and in Australia (Limpus & Limpus 2000), highlighting the consumption of mangrove leaves and fruits as a substantial and nutritionally important part of green turtle diets.

From personal observation and by inference from diet components, turtles at Gorgona spend time during the day eating within and at the surface of the water column in the current convergences, where ingestion of tunicates, leaves, mangrove fruits and items such as insects, feathers and debris mainly takes place. Sand, pebbles and shells are probably ingested accidentally when foraging at the bottom on coral or on algae attached to the substrate. It is likely that East Pacific green turtles at Gorgona National Park feed predominantly in current convergences where organic matter is abundant, rather than in the sandy and coral habitats in which they were captured. These 2 habitats may perhaps play a more significant role for resting, cleaning and shelter than for feeding purposes.

Although there were no significant differences in the animal–plant composition of the diet of large and small turtles, the former had a tendency towards higher animal consumption, whereas the latter tended to eat more vegetal material. The use of variable food sources (such as tunicates and terrestrial vegetative matter) corresponds to an omnivorous feeding behaviour, which differs from the ontogenetic trend of immature green turtles *Chelonia mydas* to become chiefly herbivorous when entering nearshore feeding habitats. This involves a change in the foraging habits which is very different from grazing on seagrasses or algae. The impact of this opportunistic diet probably enhances the development and productivity of the migratory juvenile and subadult population of East Pacific green turtles feeding at Gorgona National Park. This uncommon dietary shift from herbivory to omnivory would appear to be driven by the nutritional advantage of consuming a protein biased diet that contributes vitamins, minerals and essential amino acids required for growth and rapidly achievement of sexual maturity. The significance of this dietary composition in the context of food availability and energy supply suggests a role of this island as a refuelling station for immature green turtles migrating along this part of the Eastern Pacific coastline. Tagging data shows that, of approximately 250 turtles captured and tagged at Gorgona between 2003 and 2007, only 3 have been recaptured in a subsequent year (authors' unpubl. data), further suggesting a transient, migratory population.

Green sea turtles consistently ingesting a mixed diet (vegetal and animal matter) would almost certainly develop a different microbial community capable of degrading the various complex carbohydrates and proteins required to digest each food item efficiently (Bjorndal 1985). Much research is needed to clarify the relationships between the foraging ecology of sea turtles, nutrition and productivity. To better understand the nutritional effect of the omnivorous diet consumed by immature East Pacific green turtles at Gorgona, further research should focus on the relationship between food selection, nutritional value of a mixed diet intake examining digesta retention time (DRT) and the effect of diet quality (through nutrient limitation), on the productivity and permanence of foraging sea turtles.

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