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Regional and local factors determining green turtle *Chelonia mydas* foraging relationships with the environment

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ABSTRACT: Changes in green turtle *Chelonia mydas* foraging patterns were evaluated within a latitudinal gradient along tropical and subtropical coasts in the southwestern Atlantic and investigated as to how green turtles responded to regional and local changes in their foraging habitats. In addition, we evaluated how changes in feeding ecology caused populations to be more susceptible to various anthropogenic threats. The literature and original diet data of 427 green turtles were analyzed. Turtles from tropical and subtropical reefs exhibited the classic pattern of herbivorous benthic foraging, turtles from estuarine areas exhibited a more generalist diet and pelagic foraging, and turtles from colder reef areas, located between the winter isotherms of 10°C and 20°C, exhibited an omnivorous diet and pelagic foraging strategy. The amount of ingested animal matter was higher in occurrence and abundance in the green turtle diets in the most southern foraging areas. Foraging ecology was influenced by regional (phycogeographical provinces and water temperature) and local (urbanization and rivers) factors. Green turtles exhibited high foraging plasticity, and their importance to the ecosystem was not restricted to their role as herbivores. Green turtles may also have an important role as second-order consumers in certain areas, mainly in the cooler waters at the extremes of their distribution. Foraging plasticity was observed both in the type of diet item and foraging strategy, which implies that there may be variation in the exposure of populations to threats.

KEY WORDS: Sea turtle · Anthropogenic debris · Herbivory · Diet · Conservation

INTRODUCTION

The green turtle *Chelonia mydas* is an Endangered marine turtle species with a circumglobal distribution in tropical and subtropical waters (Seminoff 2004). After hatching, green turtles enter the sea and swim actively offshore until they reach the oceanic zone (Musick & Limpus 1997). The foraging ecology of green turtles in the oceanic phase is poorly known, but studies have revealed that they are omnivorous, with a large representation of animal items in their diet (Witherington et al. 2012). After recruiting to the neritic zone, juvenile green turtles shift to a herbivorous diet, which is a unique diet among marine turtles (Bjorndal 1997). Due to their high grazing capacity, green turtles are classified as megaherbivores, along with sirenians (dugongs and manatees). These animals play an important ecological role in the structuring of communities (Goatley et al. 2012).

Pioneer studies on green turtle diet by Mortimer (1981) and Bjorndal (1980) showed that green turtles feed predominantly on seagrass in the Caribbean, with a relatively low contribution of algae and animal matter. Since these earlier studies on green turtle

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foraging ecology, a number of studies from different habitats and geographical regions have been published (Garnett et al. 1985, Ross 1985, Bjorndal et al. 1991, Forbes 1996, Brand-Gardner et al. 1999, Seminoff et al. 2002a, Bugoni et al. 2003, Fuentes et al. 2006, Arthur & Balazs 2008, Lopez-Mendilaharsu et al. 2008, Arthur et al. 2009, Cardona et al. 2009, Russell & Balazs 2009, Russell et al. 2011, Reisser et al. 2013, González Carman et al. 2014a). These studies showed that green turtle diet varies greatly among geographical regions. In a compilation of diet data from green turtle estuarine foraging areas, Nagaoka et al. (2012) showed that there is large diet variation even when comparing relatively similar habitats. In addition, recent studies using stable isotopes and/or esophageal/stomach content analyses have support the idea that green turtles are not strictly herbivores, demonstrating that in some areas turtles may consume large amounts of animal matter (Amorocho & Reina 2007, Carrión-Cortez et al. 2010, Burkholder et al. 2011, Lemons et al. 2011, Reisser et al. 2013, González Carman et al. 2014a). These studies demonstrate that the foraging ecology of green turtles is not well understood, because the data indicate that variation occurs not only in the diet items among foraging areas, but also the feeding behavior of green turtles within foraging areas.

Understanding the ecological role of green turtles is important for 3 main reasons (Bjorndal & Jackson 2003): (1) to discover the losses in ecosystem structure and function; (2) to understand how environmental changes, natural or human-induced, will affect green turtles; and (3) to assist management and conservation actions, given that the main goal of the Marine Turtle Specialist Group of the World Conservation Union (MTSG) is to restore and maintain marine turtle populations that are capable of fulfilling their ecological roles (MTSG 1995). Despite the many studies on green turtle diets, few studies have attempted to understand factors that may determine turtle foraging relationships with the environment.

Two aspects define the foraging biology of a species: (1) intrinsic factors, such as digestive physiology and behavior; and (2) extrinsic factors, such as abundance, distribution, and quality of the resource (Whelan & Schmidt 2007). Extrinsic factors, such as the distribution and abundance of prey species, are influenced by local and regional processes (Ricklefs 1987); thus, the foraging ecology of a species may vary along its distribution. Understanding the foraging ecology of species is imperative to their conservation because the acquisition of food is directly related to the survival, growth rate and reproductive output (Bjorndal 1985, Balazs 1995). In addition, changes in foraging strategies caused by local and regional processes may force species to face anthropogenic threats according to how turtles use their habitat.

In this study, we analyzed literature and original data from more than 400 green turtles distributed along tropical and subtropical coasts of Brazil and Argentina. The main goal of our study was to evaluate the foraging patterns observed across a broad latitudinal gradient and investigate how green turtles respond to regional and local changes in their foraging habitats. In addition, we evaluated how changes in feeding ecology cause populations to be more or less susceptible to various anthropogenic threats, such as debris ingestion.

MATERIALS AND METHODS

Study area and feeding analyses

We collected diet samples over 3 yr (2010–2013) from 137 green turtles in different habitats along the Brazilian coast (Fig. 1). The curved carapace length (CCL) was measured with a plastic metric tape. We collected diet samples from 43 live turtles and 94 stranded, dead turtles that were located during intensive coastal monitoring efforts. Table 1 provides detailed information from all study areas. Diet samples from live animals (n = 43) were collected according to the standardized method of esophageal lavage (Forbes & Limpus 1993). Diet samples from stranded, dead turtles (n = 94) were obtained by collection of their esophageal and stomach contents. All analyzed turtles exhibited normal health, according to the condition indexes of Walsh (1999). All collected material was preserved in a 4% formalin/seawater solution. Diet items were identified to the lowest possible taxonomic level with the use of magnification, microscopes, and specialized taxonomic keys. We quantified the diet items by their weight (0.1 g) and volume (0.1 ml; via water displacement). Samples of the macroalgae and seagrass items ingested by green turtles were donated to the herbarium of the Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil. In addition to the turtles sampled for this study (n = 137), we used data from an additional 290 green turtles obtained from other studies (Santos et al. 2004, Nakashima 2008, Guebert-Bartholo et al. 2011, Nagaoka et al. 2012, Reisser et al. 2013, González Carman et al. 2014a), resulting in a total of 427 turtles (Table 1). All data were collected according to a standardized method

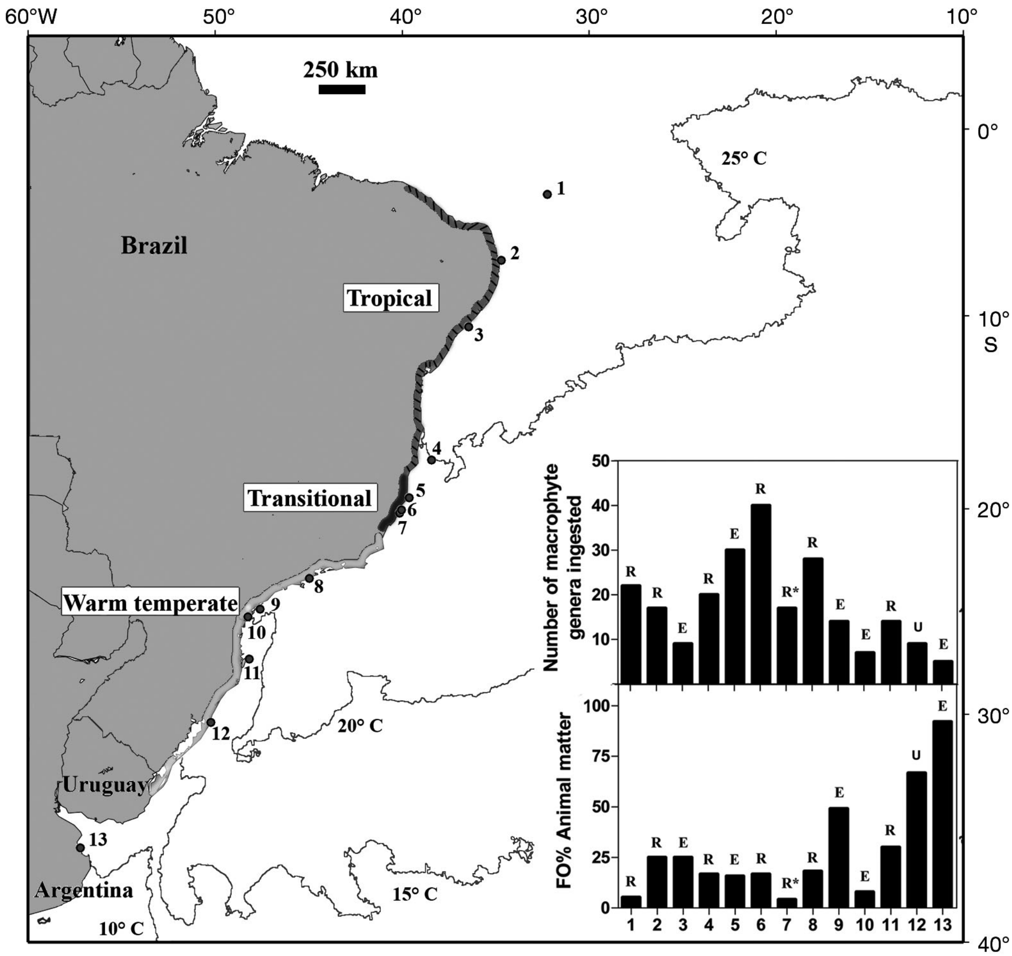

Fig. 1. Study areas of green turtle *Chelonia mydas* diet along the South American Atlantic coast. Brazilian phycogeographic provinces (tropical, transitional zone, and warm temperate) were determined according to Horta et al. (2001). The isotherms are winter isotherms. 1–13: study areas. Also shown are number of macrophyte genera and frequency of occurrence (%FO) of animal matter in the diet in each study area. R: reef; E: estuarine area; R*: reef in a highly urbanized area; U: unconsolidated substrate. Refer to Table 1 for details of study areas

Table 1. Areas, habitats, and methodology used to assess green turtle *Chelonia mydas* diet along the South America, Atlantic coast (sites 1–12 on the Brazilian coast and 13 on the Argentine coast). Data from areas 2 and 9–13 were obtained from other studies, as cited. N: number of individuals; CCL ± SD = mean curved carapace length ± standard deviation; *SD not available. Area numbers are as shown and in Fig. 1. PE: Pernambuco, PB: Paraíba, BA: Bahia, ES: Espírito Santo, SP: São Paulo, PR: Paraná, SC: Santa Catarina

Site	Study area	Habitat	Sample method	N	CCL ± SD (cm)	Reference
1	Fernando de Noronha, PE	Reef	Esophageal lavage	19	50.5 ± 12.5	–
2	João Pessoa, PB	Reef	Stranded turtles	9	61.9 ± 23.5	Santos et al. (2004)
3	Sergipe coast	Estuary	Stranded turtles	17	42.5 ± 19.6	–
4	Abrolhos, BA	Reef	Esophageal lavage	24	52.3 ± 12.4	–
5	Regência, ES	Estuary	Stranded turtles	19	35.4 ± 3.5	–
6	Fundão, ES	Reef	Stranded turtles	24	36.7 ± 7.2	–
7	Vitória, ES	Reef (highly urbanized)	Stranded turtles	23	40.3 ± 6.7	–
8	Ubatuba, SP	Reef	Stranded turtles	11	39.0 ± 6.2	–
9	Cananéia, SP	Estuary	Esophageal lavage	53	36.9 ± 3.8	Nagaoka et al. (2012)
10	Paranaguá Estuary, PR	Estuary	Stranded turtles	76	49.7 ± 7.7	Guebert-Bartholo et al. (2011)
11	Arvoredo Island, SC	Reef	Esophageal lavage	34	49.9 ± 10.4	Reisser et al. (2013)
12	Rio Grande do Sul North coast	Unconsolidated substrate	Stranded turtles	64	40.6*	Nakashima (2008)
13	Samborombón Bay	Estuary	Stranded turtles	54	38.5 ± 4.4	González Carman et al. (2014a)

for esophageal lavage described by Forbes & Limpus (1993) and for analysis of esophageal and stomach contents described by Forbes (1999). Relative wet weight was determined as follows:

$$\text{Weight (\%)} = \frac{\text{Total weight of the diet item of all samples}}{\text{Total weight of all samples}} \times 100 \quad (1)$$

We calculated feeding preference by comparing food item ingestion with food item availability. For preference analysis, we used data collected on 3 reefs; 2 were located in protected areas (Fernando de Noronha Island, reef area 1, and Abrolhos Archipelago, reef area 4), and 1 was located in a highly urbanized area (Vitória, reef area 7). For the highly urbanized area (reef area 7), we used data previously published by Santos et al. (2011). Vegetation surveys were conducted on these reefs in the same period and area where captured green turtles were feeding. These sites present representative flora of the entire macroregion used by these populations as feeding areas. After previous evaluation of sampling efforts, as recommended by Murray et al. (2006), vegetation was assessed using percentage cover; we used 5 quadrats (30 × 30 cm) that were randomly distributed along transects (30 m), placed in substrates with an inclination between 0 and 40°, niches frequently used by these herbivores. Ten transects were evenly distributed over feeding areas representing the dominant phytobenthic structure. All transects were placed in the same area where green turtles were captured during their foraging activities. Diet selection was ascertained using the Waller-Duncan test for rank differences in relation to selection, which indicates the preference of diet items (Johnson 1980). This procedure measures the relationship between the availability of the diet component and the usage of this item in the diet, which is expressed by Tbar values (average rank difference). Tbar < 0 indicates that the diet component was selected, Tbar = 0 indicates that the diet component was consumed in the same proportion of its availability, and Tbar > 0 indicates that the diet component was not selected. However, to provide a more intuitive graphical representation, we used −Tbar values. Feeding preference analysis was conducted using the Prefer 5.1 computer package (USGS 1995).

The Brazilian coast was divided into phycogeographic provinces according to Horta et al. (2001) (Fig. 1). The tropical province presents typically tropical flora and is less abundant in vegetation compared to the Caribbean; the area is located along rocky shores and coral reefs from south Bahia to Piauí State. The warm temperate province has a relatively rich flora compared to the tropical province; it contains many species that are typically found in cold waters. However, the warm temperate area demonstrates a decrease in richness from north to south. This province is characterized by rocky shores with relatively less substrate complexity when compared to the tropical province. Samborombón Bay in Argentina is also located in the warm temperate province (Spalding et al. 2007). The transitional zone is located between these 2 macroregions, and is considered one of the most diverse regions for macroalgal flora along the Brazilian coast (Figueiredo et al. 2008).

Debris ingestion

To evaluate the impact of debris ingestion, we analyzed the entire gastrointestinal system of 244 green turtles to retrieve debris, and gathered debris ingestion data from 274 green turtles from studies that used comparable methods (Nakashima 2008, Guebert-Bartholo et al. 2011, Bezerra 2014, González Carman et al. 2014b, Poli et al. 2014; Table 2). We quantified the ingested debris by weight (0.01 g), volume (0.1 ml; via alcohol displacement), and number of items.

Statistical analysis

We used analysis of similarity (ANOSIM) to evaluate the differences in the participation of floating diet items between turtles from reef areas (1, 2, 4, 6, 8, and 11) and estuarine areas (3 and 5). The Bray-Curtis similarity matrix was generated from the relative weights of floating and benthic items ingested by each turtle. We considered floating items to be terrestrial plant leaves, small pieces of wood, and *Sargassum* spp. with air bladders (floating structure). All marine macrophyte species were considered benthic items, including *Sargassum* spp. when found without air bladders. ANOSIM was also used to evaluate differences in diet items of turtles from different reef areas (1, 2, 4, 6, 8, and 11). For this test, the Bray-Curtis similarity matrix was generated from the relative weight of Rhodophyta, Chlorophyta, Phaeophycea, and seagrasses ingested by each turtle. We used a Kruskal-Wallis test followed by Dunn's multiple comparison test to evaluate the difference in the number of macrophyte genera ingested by individual turtles from the tropical province, transitional zone, and warm temperate province. A Mann-Whitney *U*-test was used to compare the number of ingested macro-

Table 2. Areas used to assess debris ingestion by green turtles *Chelonia mydas* along the South American Atlantic coast (sites 1–12 on the Brazilian coast and 13 on the Argentine coast). Data from areas 2, 9, 10, 12, and 13 were obtained from other studies, as cited. N: number of individuals; CCL ± SD: mean curved carapace length ± standard deviation; *SD not available; –: data not available. Area numbers and state abbreviations are as shown in Table 1 and Fig. 1

Site	Study area	N	CCL ± SD (cm)	Reference
1	Fernando de Noronha, PE	–	–	–
2	João Pessoa, PB	84	56.6 ± 21.5	Poli et al. (2014)
3	Sergipe coast	22	42.6 ± 20.4	–
4	Abrolhos, BA	–	–	–
5	Regência, ES	21	35.1 ± 3.4	–
6	Fundão, ES	81	36.5 ± 4.6	–
7	Vitória, ES	103	39.8 ± 7.4	–
8	Ubatuba, SP	17	38.1 ± 5.4	–
9	Cananéia, SP	66	40.2 ± 8.0	Bezerra (2014)
10	Paranaguá Estuary, PR	76	49.7 ± 7.7	Guebert–Bartholo et al. (2011)
11	Arvoredo Island, SC	–	–	–
12	Rio Grande do Sul North coast	64	40.6*	Nakashima (2008)
13	Samborombón Bay	68	38.5 ± 4.4	González Carman et al. (2014b)

phyte genera between turtles from the 2 reefs located in the transitional zone, a minimally urbanized reef area (Fundão, area 6), and a highly urbanized reef area (Vitória, area 7). We used Spearman's correlation test to evaluate the relationship between the weight and volume of ingested items (diet items and anthropogenic debris).

RESULTS

Green turtles fed mainly on macroalgae in most areas, consuming 79 marine macrophyte genera (see Appendix 1). We found that weight and volume of ingested diet items ($r = 0.98$, $p < 0.01$) and debris ($r = 0.85$, $p < 0.01$) were highly correlated; therefore, we present our data using only weight because this measure is more precise. The high correlation between weight and volume allowed us to make direct comparisons with other research that used debris volume instead of debris weight. In reef and estuarine areas from the central and north Brazilian coast, the consumption of animal matter by green turtles was very low and was mostly composed of macrophyte-associated invertebrates (Fig. 1, Table 3). The amount of animal matter increased in frequency and abundance in the most southern distribution area of the species (Fig. 1). Green turtles from foraging areas located between the winter isotherms of 10°C and 20°C exhibited an intentional ingestion of animal matter, mainly composed of ctenophores and jellyfish (Table 3). This high ingestion of ctenophores and jellyfish not only indicates differences in diet but also differences in foraging strategy. These animals are mostly found in the water column and not in the substrate, similar to most of the ingested macrophytes. A similar pattern in the foraging strategy was found in the estuarine areas from the central and northern Brazilian coast (sites 3, 5, and 9). Turtles from reef and estuarine areas showed a significant difference in the consumption of floating material ($R = 0.53$; $p < 0.01$; Fig. 2). This result indicates that turtles from these areas also exhibited a different foraging strategy: a classic, benthic foraging strategy was found in the reef areas and a more pelagic foraging strategy was found in the estuarine areas.

Turtles from the transitional zone exhibited a significantly richer diet regarding macrophyte genera than turtles from tropical ($p < 0.01$) and warm temperate ($p < 0.01$) provinces, but no difference was found between the 2 provinces ($p > 0.05$; Fig. 1). When we compared the 2 reefs located in the transitional zone, we found that green turtles from highly urbanized reefs (area 7) exhibited a significantly poorer diet regarding macrophyte genera than in turtles from minimally urbanized reef areas ($p < 0.01$). The green turtle diets from highly urbanized reefs were dominated by only 1 genus of Chlorophyta, *Ulva* (Table 4).

Algae were the main diet group from all reef areas (Fig. 3), with a low presence of seagrass except in the Abrolhos reef area (area 4), where *Halodule wrightii* was the main diet item (Table 4). When we compared the diet composition of reef areas using the 4 major macrophyte groups (Rhodophyta, Chlorophyta, Phaeophycea, and seagrasses), we did not find significant differences among the tropical province, transitional zone, and warm temperate province ($R = 0.05$; $p > 0.05$). However, the diet of green turtles from estuarine areas varied greatly with regard to the abundance of the 4 major macrophyte groups (Rhodophyta, Chlorophyta, Phaeophycea, and seagrasses), with a significant difference in the composition of diet between the 2 evaluated estuarine areas ($R = 0.15$; $p = 0.02$; Fig. 3, Table 4).

Table 3. Relative weight of animal matter found in green turtle *Chelonia mydas* diets. R: reef; R*: reef in a highly urbanized area; E: estuarine area; U: unconsolidated substrate. Refer to Table 1 for details on study areas

Isotherm:	>25°C			25–20°C							15–20°C		10–15°C
Habitats:	R	R	E	R	E	R	R*	R	E	E	R	U	E
Study areas:	1	2	3	4	5	6	7	8	9[a]	10[a]	11	12[a]	13
Crustacea	<0.1	–	–	0.4	0.1	<0.1	–	1.4	–	–	–	4.3	0.1
Decapoda	–	–	–	<0.1	0.1	<0.1	–	1.4	–	–	–	4.3	0.1
Isopoda	<0.1	–	–	0.4	–	<0.1	–	–	–	–	–	–	–
Cirripedia	–	–	–	–	–	–	–	–	–	–	–	–	–
Mollusca	–	<0.1	<0.1	–	–	–	–	–	5.8	–	–	9	4.2
Bivalves	–	–	–	–	–	–	–	–	–	–	–	7.6	1.1
Gastropoda	–	<0.1	<0.1	–	–	–	–	–	5.8	–	–	1.0	3.1
Cephalopoda	–	–	–	–	–	–	–	–	–	–	–	0.4	–
Polychaetes	–	<0.1	<0.1	–	–	–	–	0.2	–	–	–	–	0.6
Ctenophora	–	–	–	–	–	–	–	–	–	–	20	–	–
Porifera	–	–	–	–	–	–	–	–	–	–	–	–	–
Bryozoa	–	–	–	–	–	–	–	–	0.4	–	–	–	–
Cnidaria	–	–	<0.1	–	–	–	–	–	1.0	–	–	–	50.1
Jellyfish	–	–	–	–	–	–	–	–	–	–	–	–	47.8
Polyps	–	–	<0.1	–	–	–	–	–	1.0	–	–	–	2.4
Insects	–	–	–	–	–	–	–	<0.1	–	–	–	2.3	0.2
Osteichthyes	–	–	0.1	–	<0.1	–	–	0.1	0.6	–	–	1.0	0.1
Unidentified	–	–	–	–	–	–	<0.1	–	–	2.4	–	0.9	–
Total	**<0.1**	**<0.1**	**0.1**	**0.4**	**0.1**	**<0.1**	**<0.1**	**1.7**	**7.8**	**2.4**	**20**	**17.5**	**55.3**

[a]Mean relative volume instead of mean relative weight

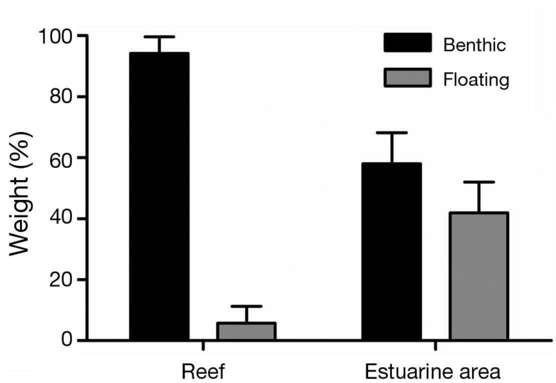

Fig. 2. Mean relative weight and standard error of benthic and floating diet items ingested by green turtles *Chelonia mydas* from reef areas (1, 2, 4, 6, 7, and 8) and estuarine areas (3, 5, and 9; see Fig. 1 for locations of areas)

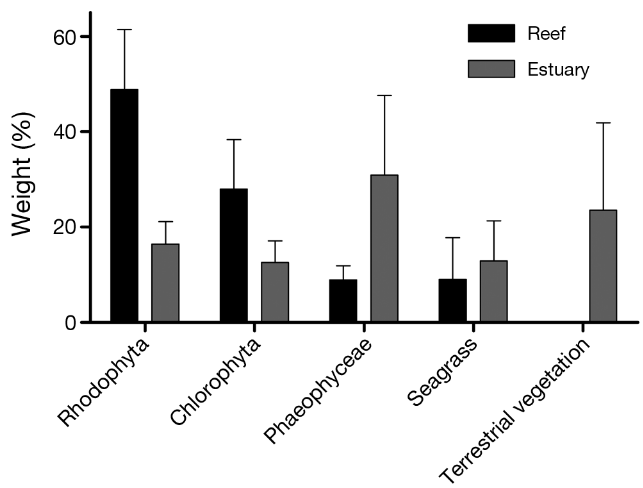

Fig. 3. Mean relative weight and standard error of the major food item groups ingested by green turtles *Chelonia mydas* from reefs and estuarine areas

The main genera found in the green turtle diets were as follows: *Gelidium* spp. (Rhodophyta); *Caulerpa* spp., and *Ulva* spp. (Chlorophyta), with a larger amount of *Caulerpa* spp. in the tropical province and *Ulva* spp. in the warm temperate province; *Sargassum* spp. (Phaeophycea); and *Halodule* sp. (seagrass) (Table 4). The feeding preference analyses showed a common pattern shared by turtles from the 3 reef areas evaluated: a preference for Rhodophyta and seagrasses and the avoidance of Phaeophycea (Fig. 4). The selectivity for Chlorophyta varied among areas.

Table 4. Relative weight of the main marine macrophyte genera found in green turtle *Chelonia mydas* diets. Numbers 1 to 13 denote the study areas. R: reef; R*: reef in a highly urbanized area; E: estuarine area; and U: unconsolidated substrate. Refer to Table 1 for details on study areas

Phycogeographic provinces:	Tropical				Transitional			Warm temperate					
Habitats:	R	R	E	R	E	R	R*	R	E	E	R	U	E
Study areas:	1	2	3	4	5	6	7	8	9[a]	10[a]	11	12[a]	13
Rhodophyta	66.2	93.9	32.5	17.1	15.1	25.8	11.5	56.4	5.6	9.0	20.8	<0.1	0.9
Acanthophora	–	–	–	–	–	–	–	15.5	–	–	–	–	–
Bostrychia	–	–	–	–	–	–	–	–	5.6	–	–	–	–
Bryothamnion	–	–	–	<0.1	<0.1	0.2	–	1.1	–	–	–	–	–
Chondracanthus	–	–	–	–	2.9	9.3	2.7	<0.1	–	–	–	–	–
Cryptonemia	–	3.5	1.0	<0.1	5.5	–	–	–	–	–	–	–	–
Gelidiella	3.0	4.4	–	5.4	–	–	–	<0.1	–	–	–	–	–
Gelidium	2.9	80.5	–	0.4	3.4	9.1	5.6	0.7	–	–	–	–	–
Gracilaria	–	1.7	–	0.5	3.3	4.7	0.5	0.0	–	4.2	–	–	–
Grateloupia	–	–	–	–	–	–	–	1.5	–	–	–	–	–
Halymenia	–	–	31.5	–	<0.1	0.3	2.3	<0.1	–	–	–	–	–
Hypnea	0.6	2.1	–	2.0	<0.1	0.6	<0.1	25.5	–	4.8	4.8	–	–
Laurencia	59.7	0.8	–	<0.1	<0.1	<0.1	–	–	–	–	0.5	–	–
Osmundaria	–	1.0	–	4.3	–	0.2	–	–	–	–	–	–	–
Porphyra	–	–	–	–	–	<0.1	–	0.3	–	–	–	–	0.9
Pterocladia	–	<0.1	–	–	–	1.4	0.1	10.3	–	–	–	–	–
Pterocladiella	–	–	–	–	–	–	–	–	–	–	15.5	–	–
Rhodymenia	–	–	–	4.5	–	<0.1	0.3	0.3	–	–	–	–	–
Wurdemannia	–	–	–	–	–	–	–	1.2	–	–	–	–	–
Chlorophyta	<0.1	5.2	1.9	23.8	16.7	68.6	83.8	26.9	13.0	6.7	41.8	51.8	2.9
Caulerpa	<0.1	5.2	1.9	23.8	8.5	7.3	10.8	0.1	–	–	–	–	–
Cladophora	–	–	–	–	0.6	<0.1	0.7	6.9	–	–	–	–	–
Codium	–	<0.1	–	–	0.1	<0.1	–	–	–	–	41.8	–	–
Enteromorpha	–	–	–	–	–	–	–	–	–	–	–	0.3	–
Gayralia	–	–	–	–	–	–	–	–	5.4	–	–	–	–
Halimeda	<0.1	–	–	–	<0.1	3.7	–	–	–	–	–	–	–
Udotea	–	–	–	–	–	–	–	–	–	–	–	3.7	–
Ulva	<0.1	–	–	–	7.5	57.6	72.3	19.9	7.6	6.7	–	47.8	2.9
Phaeophyceae	20.4	0.7	47.5	3.1	57.1	3.3	<0.1	9.4	–	1.2	13.7	22.8	<0.1
Dictyopteris	14.1	0.4	–	1.4	<0.1	2.3	<0.1	0.5	–	–	0.5	–	–
Lobophora	6.0	0.1	–	0.4	1.0	0.3	–	–	–	–	–	–	–
Sargassum	0.3	0.2	47.5	1.3	56.1	0.7	–	8.9	–	1.2	13.2	22.8	–
Seagrass	7.2	–	18.0	53.2	6.0	0.1	4.4	0.4	2.4	42.9	–	–	–
Halodule	7.2	–	18.0	53.2	6.0	0.1	4.4	0.4	2.4	42.9	–	–	–
Total	**93.8**	**99.8**	**99.9**	**97.2**	**94.9**	**97.8**	**99.7**	**93.1**	**21.0**	**59.8**	**76.3**	**74.6**	**3.8**

[a]Mean relative volume instead of mean relative weight

Debris ingestion

The frequency of occurrence of debris ingestion was high in all areas, with a mean frequency of occurrence of 80.3 %. The frequency of occurrence of debris ingestion and the amount of ingested debris were higher in areas where the abundance of pelagic items, such as *Sargassum* spp. with air bladders, pelagic invertebrates, Osteichthyes, and terrestrial vegetation and invertebrates, in green turtles diets were higher (Table 5). Plastic was the major debris ingested in all areas (Table 5). For detailed information on debris ingestion by turtles from this study, see Santos et al. (2015).

DISCUSSION

The ecological role of green turtles along the coastal study area was mainly associated with their importance as herbivores. However, green turtles exhibited foraging variability, and their importance to the ecosystem was not restricted to their role as herbivores. Green turtles may also play an important role as second-order consumers in certain areas, mainly in cooler waters at the extremes of their distribution. Foraging differences were not only observed in the differences in the types of diet items but also in the foraging strategy, which implies different exposure levels to threats.

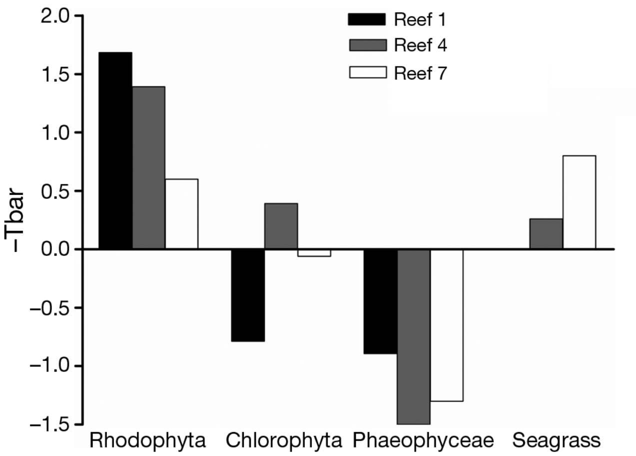

Fig. 4. Diet preference of green turtles *Chelonia mydas* from 3 different feeding areas along the Brazilian coast (reef 1 = protected area, Fernando de Noronha, Pernambuco [PE]; reef 4, protected area, Abrolhos, Bahia [BA]; reef 7, highly urbanized area, Vitória, Espírito Santo [ES]). Diet preference was ascertained using the Waller-Duncan test to rank differences in relation to selection, where higher values of –Tbar indicate the most preferred resource (see 'Materials and methods')

Animal ingestion and foraging strategy

Green turtles were primarily herbivorous in most of their distribution, with a higher ingestion of animal matter at 2 sites in the most southern areas, which are characterized by cooler waters (between 10°C and 20°C isotherms) and a relatively low diversity of algal assemblages (Horta et al. 2001). The animal matter ingested in areas above the 20°C isotherm was considered to be macrophyte-associated invertebrates. In areas south of the 20°C isotherm, the ingestion of animal matter was considered to be intentional. We attribute the higher presence of animal matter in the most southern areas to the interaction of 1 intrinsic factor represented by the physiological constraint of cold water and 2 extrinsic factors, represented by (1) the regional algal variation and (2) the availability of animal matter. Green turtles are ectothermic, and their digestive efficiency is affected by the surrounding water temperature (Bjorndal 1980). The colder temperatures in the most southern areas may lower the ability to efficiently digest vegetation; thus, a diet based only on macrophytes may not provide the energetic requirements to support growth,

Table 5. Relative abundance of benthic and pelagic diet items, anthropogenic debris prevalence (frequency of occurrence, FO%), and abundance (mean weight per turtle), and relative abundance of plastic in all ingested anthroponic debris items found in green turtles *Chelonia mydas*. R: reef; R*: reef in a highly urbanized area; E: estuarine area; U: unconsolidated substrate; –: data not available. Refer to Tables 1 & 2 for details on study areas

Isotherm:	>25°C			25–20°C							15–20°C		10–15°C
Habitats:	R	R	E	R	E	R	R*	R	E	E	R	U	E
Study areas:	1	2	3	4	5	6	7	8	9	10	11	12	13
Benthic items	**93.5**	**99.6**	**52.4**	**96.3**	**38.9**	**97.1**	**99.7**	**85.8**	**29.7**	**63.0**	**63.1**	**66.0**	**12.1**
Benthic macrophytes	93.5	99.6	52.4	95.9	38.8	97.1	99.7	84.2	22.5	60.6	63.1	51.8	4.2
Benthic invertebrates	<0.1	<0.1	<0.1	0.4	0.1	<0.1		1.6	7.2			13.3	7.9
Unidentified invertebrates							<0.1			2.4		0.9	
Pelagic items	**0.3**	**0.2**	**47.6**	**1.3**	**59.9**	**0.7**	**0.0**	**9.0**	**35.7**	**18.1**	**32.2**	**35.1**	**56.9**
Sargassum spp. with air bladders (floating structure)	0.3	0.2	47.5	1.3	56.1	0.7		8.9		1.2	13.2	22.8	
Pelagic invertebrates											20	9	47.8
Osteichthyes			0.1		<0.1			0.1	0.6			1.0	0.1
Terrestrial vegetation and invertebrates					3.8			<0.1	35.1	16.1		2.3	9.0
Marine debris (FO%)	**–**	**15.5**	**70**	**–**	**100**	**64**	**93**	**94**	**70**	**69.7**	**–**	**71.9**	**90.0**
Marine debris (mean weight in grams)	**–**	**–**	**7.7**	**–**	**1.2**	**0.4**	**2.1**	**0.2**	**10.4**	**24.6**[a]	**–**	**5.7**[a]	**2.6**
Plastic abundance (%)	**–**	**–**	**81.9**	**–**	**86.6**	**72.2**	**73.1**	**79.6**	**89.4**	**83.2**	**–**	**–**	**94.0**

[a]Mean marine debris volume in ml instead of mean marine debris weight in grams

forcing these animals to feed on animal matter, which may be more energetic and easily digestible source for juvenile green turtles (Bjorndal 1980, Forbes 1996, Morais et al. 2014). In addition to the results of this study, studies conducted in Pacific waters that showed a higher animal matter content in neritic green turtle diets were also located in areas with relatively low water temperatures (Lemons et al. 2011) or in tropical waters seasonally influenced by cold waters (Amorocho & Reina 2007). Two extrinsic factors may be responsible for the high levels of animal matter ingestion in the colder waters: the relatively smaller abundance of algal assemblages (Horta et al. 2001), which restricts the herbivorous diet (Russell et al. 2011), and the relatively higher availability of jellyfish and ctenophores, which favor the omnivorous diet (Reisser et al. 2013, González Carman et al. 2014a).

Local habitat variation also plays an important role in the diet and foraging strategy of green turtles. We found substantial differences in green turtle foraging ecology between reefs and estuarine areas within the same phycogeographical provinces and water temperature ranges. The green turtles in the estuarine areas deviated from the classical selective feeding strategy found in the reef areas in this study and in many worldwide studies (Fuentes et al. 2006, Arthur & Balazs 2008, Lopez-Mendilaharsu et al. 2008). In the estuarine areas, turtles showed a generalist feeding strategy with a high contribution of floating material. The diet of turtles from estuarine areas may be explained by the poor algal assemblages found in these areas along the Brazilian coast, which is due to the relatively lower salinity and high sediment loads carried by rivers (Horta et al. 2001). Pelagic foraging and generalist feeding behavior found in estuarine areas likely occurs to make better use of local food items because foraging in the water column will maximize the ingestion of terrestrial vegetal matter carried by rivers (Limpus & Limpus 2000, Amorocho & Reina 2007, Guebert-Bartholo et al. 2011, Nagaoka et al. 2012) and detached algae from close reefs. However, turtles may also feed on benthic material depending on the characteristics of the estuarine area, such as the high ingestion of *Halodule wrightii* found in the Paranaguá Estuary (Guebert-Bartholo et al. 2011). Diet items varied greatly among the estuarine areas in our study, which supports the results of green turtle diets from other estuaries compiled by Nagaoka et al. (2012). The high diet variability is most likely related to the high diversity of habitats found within estuarine systems, which are mainly determined by abiotic factors that vary greatly among estuaries, such as the quantity of freshwater input, water circulation, and the rate of geomorphological change (Day et al. 2012).

In the reef areas, green turtles exhibited a diet based mainly on benthic macroalgae, with less variation in their diet when compared to turtles from estuarine habitats. In most areas, the majority of diet items of green turtles was composed of Rhodophyta and Chlorophyta, which agrees with other studies where algae were the main source of food (Hawaii, Arthur & Balazs 2008; México, López-Mendilaharsu et al. 2008). However, the low inclusion of seagrass contrasts with studies from the Caribbean (Bjorndal 1980, Mortimer 1981). The observed differences between turtle diets in the Caribbean and Brazil are most likely related to the relatively low abundance of seagrass along the Brazilian coast. In the majority of the reef areas, we found a diet based mostly on algae; however, we found a mixed diet (algae and seagrass) in 1 reef area (Abrolhos, reef area 4). This mixed diet of seagrass and algae is not expected even when both groups are available (André et al. 2005, Fuentes et al. 2006) because the complex carbohydrates are very different in these 2 groups; thus, a mixed diet may lower the digestive efficiency (Bjorndal 1980). This uncommon diet may be due to the typical macroalgal flora associated with seagrass beds in Abrolhos (Creed & Amado Filho 1999), which may hamper the selective feeding on seagrass by green turtles in this area.

Feeding preference and diet richness

We studied the feeding preference in 3 areas with very different levels of macrophyte availability. Nevertheless, a similar pattern of preference was found: the preference for Rhodophyta algae and the avoidance of Phaeophycea algae. Similar results were also found in studies conducted in Australia (Fuentes et al. 2006) and Arvoredo Island, Brazil (Reisser et al. 2013). However, no preference pattern of Rhodophyta and seagrass was found by Lopéz-Mendilaharsu et al. (2008) in México, with Rhodophyta genera equally distributed among preferred and avoided genera. The overall preference for higher taxonomic groups of macrophytes, such as Rhodophyta and seagrass, may vary among areas due to the differences in the species composition of the assemblage. The preference analysis among the 3 different areas found in our study and the preference or high ingestion of Rhodophyta and seagrass found in other studies (Bjorndal 1980, Mortimer 1981, Seminoff et al. 2002a, Fuentes et al. 2006, Arthur & Balazs 2008, Lopez-Mendilaharsu et al. 2008, Reisser et al. 2013) support the overall preference for Rhodophyta and seagrass by green turtles. The importance of Rhodophyta and seagrass was also found in other marine vertebrate herbivores, such as fish (Montgomery & Gerking 1980) and dugongs (André et al. 2005). The reasons for this preference may be related to the nutritional value and palatability of these groups. However, further studies are needed to better comprehend green turtle feeding preferences. This information is necessary to identify green turtle ecological requirements and to help determine better conservation management strategies.

The richness found in green turtle diets appeared to be related to the richness of diet items in the feeding area; turtles from richer phycogeographical provinces had a significantly richer diet. This result indicates that despite the feeding preferences, green turtles explored a high number of macroalgae genera when a rich algal assemblage was available. This rich diet may be due to the considerable variation in species nutritional composition (McDermid et al. 2007) and that different food items are required to optimize different process of the life cycle, such as growth, survival, and fecundity (Worm et al. 2006).

The identified diet items allowed us to infer the area used by green turtles in their feeding, which is critical to their conservation (Seminoff et al. 2002b). Based on the species ingested, we believe that turtles feed mainly in shallow waters because most of the diet species are commonly found from intertidal depths to depths of 10 m (Litter & Litter 2000). The ingestion of several genera such as *Porphyra* spp., which are common in the high intertidal zone, indicates that turtles may feed in very shallow waters, taking advantage of high tides to better explore the intertidal zone. The use of shallow waters suggested here is corroborated by other studies, which have used different methodologies to show that green turtles are more abundant in shallow feeding areas (Reisser et al. 2013).

Implications for conservation

The implications for conservation derived from our findings can be divided into 2 categories: the implications related to the differences in foraging strategies and the differences in diet items. We found 2 main foraging strategies, benthic and surface, that were related to regional and local habitat variations. The main implication of the variation in foraging strategy is related to the risk of anthropogenic debris ingestion, which represents a major threat to marine turtles (Hamann et al. 2010). Individuals with surface feeding strategies, such as turtles from cold water reefs and estuaries, may have a higher risk of debris ingestion when compared with benthic feeding strategies. The higher risk faced by these turtles is justified because the major component of marine debris is plastic, a positively buoyant material (Derraik 2002). Therefore, turtles that forage in the water column may have a higher chance of encountering plastic material than turtles that feed mainly on benthic species. Turtles from estuarine areas face an even higher risk than other turtles, because, in addition to the pelagic foraging, rivers are among the most important sources of ocean debris (Barnes et al. 2009). Regardless of the foraging strategy, sea turtles from foraging areas located in regions with high human population densities may be at greater risk, because cities are one of the main sources of anthropogenic debris (Barnes et al. 2009), especially in countries with poor quality of waste management (Jambeck et al. 2015).

Herbivorous feeding imposed a nutrient-limited diet for green turtles, which is related to the relatively delayed sexual maturity and reduced reproductive output in green turtles (Bjorndal 1995). Turtles with a more nutritious diet will have relatively high growth rates and reproductive output; therefore, the variability of diet items from different feeding areas may have direct impacts on green turtle conservation (Bjorndal 1985). Our results showed that turtles from estuarine areas may have a low quality diet, due to the relatively higher abundance of land-based vegetal matter carried by the river, such as dead leaves and small pieces of wood, and of *Sargassum* spp. (Phaeophycea), which was avoided by turtles in other foraging areas and may have a low digestibility, as suggested by Seminoff et al. (2002a). The diet found in turtles from estuarine areas may lead to lower growth rates. Coastal degradation may also reduce the diet quality of green turtles because it limits food availability through reduction in the diversity of the macroalgal assemblage (Santos et al. 2011). This nutritional limitation may reduce the recovery of the adult population due to the reduction in growth rates and may favor the development of diseases, such as fibropapillomatosis (Santos et al. 2011). In this manner, the increasing human impact on coastal areas, even without provoking observable death, may have enduring effects on green turtle populations.

A common trait to all green turtles from reefs and estuarine areas, regardless of their diet or foraging strategy, is feeding in shallow waters. This information is important to better manage fishery activities, which are a major threat to marine turtles; the introduced threats are primarily related to the commercial fishing industry (Hillestad et al. 1995, Lutcavage et al. 1997). The shallow feeding areas of green turtles in Brazil make them more susceptible to fishery activities that occur close to the coast, particularly gillnet fisheries, which are commonly used by artisanal fisheries. Therefore, the quantification of mortality caused by artisanal fisheries and work with the local fishery community may be seen as priorities for green turtle conservation.

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Appendix 1. List of marine macrophyte genera found in the diet of green turtles *Chelonia mydas* along the South American coast

Chlorophyta	**Rhodophyta**	**Rhodophyta**
Acicularia	*Acanthophora*	*Gymnogongrus*
Anadyomene	*Acrochaetium*	*Haliptilon*
Boodleopsis	*Amansia*	*Halymenia*
Bryopsis	*Amphiroa*	*Hypnea*
Caulerpa	*Arthrocardia*	*Jania*
Chaetomorpha	*Asparagopsis*	*Laurencia*
Cladophora	*Bostrychia*	*Murrayella*
Cladophoropsis	*Bryothamnion*	*Neosiphonia*
Codium	*Caloglossa*	*Osmundaria*
Derbesia	*Catenella*	*Peyssonnelia*
Enteromorpha	*Centroceras*	*Plocamium*
Ernodesmis	*Ceramium*	*Polysiphonia*
Gayralia	*Champia*	*Porphyra*
Halimeda	*Cheilosporum*	*Predaea*
Rhizoclonium	*Chondracanthus*	*Pterocladia*
Udotea	*Chondria*	*Pterocladiella*
Ulva	*Compsopogon*	*Rhodymenia*
	Cryptonemia	*Thuretia*
Phaeophyceae	*Cryptopleura*	*Tricleocarpa*
Canistrocarpus	*Delesseriaceae*	*Wurdemannia*
Colpomenia	*Digenea*	
Dictyopteris	*Galaxaura*	**Seagrasses**
Dictyota	*Gelidiella*	*Halodule*
Lobophora	*Gelidiopsis*	*Halophila*
Padina	*Gelidium*	*Sebdenia*
Petalonia	*Gigarttina*	
Sargassum	*Gracilaria*	
Sphacelaria	*Gracilariopsis*	
	Grateloupia	

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