Green turtle *Chelonia mydas* foraging ecology at 25° S in the western Atlantic: evidence to support a feeding model driven by intrinsic and extrinsic variability

Luciana R. Gama[1,2], Camila Domit[1,*], Matt K. Broadhurst[3,4],
Mariana M. P. B. Fuentes[5], Russell B. Millar[6]

[1]**Laboratório de Ecologia e Conservação, Centro de Estudos do Mar, Universidade Federal do Paraná, Av. Beira Mar s/n, 83255-000, Pontal do Sul, Paraná, Brazil**

[2]**Programa de pós-graduação em Biologia, Universidade Estadual de Londrina, Londrina, Paraná, Brazil**

[3]**New South Wales Department of Primary Industries, Fisheries Conservation Technology Unit, PO Box 4321, Coffs Harbour, New South Wales 2450, Australia**

[4]**Marine and Estuarine Ecology Unit, School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072, Australia**

[5]**Department of Earth, Ocean and Atmospheric Science, Florida State University, Tallahassee, Florida 32306, USA**

[6]**Department of Statistics, The University of Auckland, Private Bag 92019, Auckland 1010, New Zealand**

ABSTRACT: Long-term temporal variation in juvenile *Chelonia mydas* foraging ecology and key intrinsic/extrinsic explanatory factors were assessed at the southwestern Atlantic tropical–temperate transition zone. During a 7 yr period, 120 stranded *C. mydas* (30 to 62 cm curved carapace length; CCL) were collected from beaches in Paraná, adjacent to the World Heritage listed Paranaguá estuarine complex (PEC). The digestive tracts of these specimens were excised and evaluated for dietary contents and morphology. A total of 12 items/groups were found, but mainly comprised *Ulva* sp. (43 % of specimens), *Sargassum* sp. (28 %), *Halodule wrightii* (26 %), *Avicennia schaueriana* (26 %), *Gracilaria domingensis* (22 %), unidentified angiosperms (21 %) and cephalopod beaks (8 %). Nearly 70 % of all *C. mydas* had ingested marine debris. Proportionally more items occurred in the stomach, followed by the intestines and oesophagus. Canonical analysis of principal coordinates revealed several trends, including a negative relationship between CCL and cephalopod consumption, and strong short- and long-term temporal associations with different herbivorous foods. The latter manifested as (1) more *H. wrightii* consumed during the wet season, and other species (but especially *A. schaueriana* and *Sargassum* sp.) during the dry; and (2) a diet change between 2008–2010 and 2012–2014, with a shift towards *Ulva* sp. in the latter period (particularly in 2013). The observed extrinsic variation was attributed to environmental perturbations associated with El Niño, and anthropogenic impacts associated with dredging that started in 2010 in the PEC and which affected foraging habitats. The results reaffirm the foraging variability of *C. mydas*, but also demonstrate that sufficient time-series data are required to adequately describe the ecology of the species as a precursor to management actions that conserve regional populations.

KEY WORDS: Brazil · *Chelonia mydas* · Conservation · Diet · Foraging · Life history

INTRODUCTION

Globally, 6 of the 7 species of sea turtles are listed by the IUCN as either Vulnerable or Endangered, and all have varying levels of intra-specific population concern (IUCN 2014). Universal threats include anthropogenic impacts caused by pollution, coastal development, habitat degradation, climate change and especially fishing mortality (Bugoni et al. 2001, Moore et al. 2013). The latter impact is recognized as

one of the main contributors towards the decline of several species, including *Chelonia mydas*, which has a life cycle that spans tropical and subtropical seas, occupying neritic habitats synonymous with most of the world's fishing effort (Wallace et al. 2013).

As with any species of concern, effective conservation actions towards *C. mydas* are predicated by assessments of key behavioural strategies (especially predator–prey relationships and foraging strategies) and any associated variability (Cardona et al. 2009, Hamann et al. 2010, Santos et al. 2015). However, an obvious difficulty with ecological studies of endangered marine species (such as *C. mydas*) is the inability to destructively sample through stratified and randomized surveys (Underwood 1981). Several approaches have been used to explore the foraging ecology of sea turtles; each with various benefits and limitations (Hatase et al. 2006). Specifically, telemetry (Makowski & Seminoff 2006) and stable isotope analysis (Reich et al. 2007, Cardona et al. 2009, 2010) can provide good data on foraging areas, trophic levels, migratory patterns and nutrient absorption, but are limited to broad assessments of feeding ecology (Jones & Seminoff 2013). Further, these methods require considerable resources and are inherently limited by low replication. Oesophageal lavage has been more commonly used, however this technique precludes sampling the entire digestive tract (Forbes 1999, López-Mendilaharsu et al. 2005, Reisser et al. 2013).

Perhaps the simplest method for studying sea turtle diet and foraging ecology is to use stranded specimens, particularly in areas of intense fishing activity and subsequently adequate sample sizes (Santos et al. 2015). Deceased turtles that are promptly autopsied offer unique, inexpensive data; not only for describing most of their diet, but also other intrinsic characteristics (e.g. sequential digestive tract contents and size) that are often inaccessible via other sampling methods (Forbes 1999). Key limitations in using stranded specimens can include insufficient knowledge of prior health and the absolute time of death, although both issues can be addressed through the observed condition of the animal. Another potential issue is the decomposition (and elimination) of some dietary items, although provided that animals are promptly sampled, it should be possible to identify most digestive contents.

All 4 methods above have been used to study the foraging ecology and movements of *C. mydas* and collectively have demonstrated considerable variability (Burkholder et al. 2011, Jones & Seminoff 2013, Santos et al. 2015). In general, young *C. mydas* (<25 cm curved carapace length, CCL) remain in

oceanic waters as omnivores, but with a bias towards faunal consumption (Bjorndal 1997, Jones & Seminoff 2013). Once juveniles reach ~25 to 35 cm CCL, they typically recruit to neritic habitats and shift towards a herbivorous diet, which is maintained into adulthood (>75 cm CCL) (Bjorndal 1997).

While these feeding habits are often consistent throughout ontogenetic development, they are by no means definitive. For example, studies conducted in the southern Bahamas, southern Australia, northwestern Africa and the Gulf of California found that some neritic juveniles (<44 cm CCL) had a considerable carnivorous component to their diet (Arthur et al. 2008, Cardona et al. 2009). Similarly, in oceanic waters off Japan and in the South Atlantic, a dietary bias towards macrozooplankton and other invertebrates has been observed for some juvenile *C. mydas*, while individuals 34 to 75 cm CCL often are incidentally caught on pelagic longlines baited with cephalopods or teleosts (Hatase et al. 2006, Parker et al. 2011, González Carman et al. 2012, 2014).

Similar dietary variation has been observed across more regional latitude gradients, including in the Caribbean and southwestern Atlantic; a broad area characterised by large numbers of juveniles inhabiting shallow and sheltered habitats. Typically, individuals in the tropics (from the Caribbean to northeastern Brazil) are herbivorous, often presenting a relatively small coastal home range when feeding on macrophytes and seagrasses (Reich et al. 2007, Santos et al. 2015). Conversely, *C. mydas* in the tropical–temperate zone have a more flexible diet and a larger home range (González Carman et al. 2012). Moreover, depending on subtle regional habitat variations (including food availability), *C. mydas* can have either benthic or pelagic foraging strategies (Santos et al. 2015).

Irrespective of small-scale regional subtleties, during the winter most temperate-based individuals in the southwestern Atlantic migrate to the tropics where they consume regionally abundant seagrasses or marine algae (Guebert-Bartholo et al. 2011, González Carman et al. 2012). However, some juveniles remain in the temperate zone, or even migrate further south and predominantly maintain an omnivorous diet and/or continuously migrate between oceanic and coastal zones following a mainly pelagic foraging strategy (Bugoni et al. 2003, González Carman et al. 2012, Reisser et al. 2013).

Several authors have postulated that the observed differences in *C. mydas* diet and movements could reflect either intrinsic and/or extrinsic variables, such as metabolism rates, genetic origins and resource availability, or possibly be a consequence of regional

water temperature and/or seasonality (Hatase et al. 2006, Southwood & Avens 2010, Santos et al. 2015). An important ancillary consideration is that *C. mydas* inadvertently consumes marine debris (more so than the other 6 sea turtle species) which could also confound their natural habits and/or feeding behaviour (Schuyler et al. 2012, Santos et al. 2015).

While the above hypotheses for *C. mydas* are coherent, they remain somewhat speculative, primarily because of poor sample sizes and/or temporal distributions, as well as a lack of standardization among digestive tract assessments due to different methodologies, including qualitative and quantitative measures which are responsible for large-scale gaps in spatio-temporal comparisons. In a recent review, Santos et al. (2015) attempted to quantify some of the factors affecting *C. mydas* diet in the southwestern Atlantic (encapsulating several of the above patterns), but because the data were mostly limited to isolated (opportunistic) sampling, their interpretation precluded the identification of patterns beyond broad environmental relationships. To date, no studies have assessed the relationships between feeding ecology and environmental parameters in a confluence of habitats (off-shore reefs, estuaries and bays) in one region across broad temporal scales.

We aimed to address the above shortfall in this study by first quantifying long-term (over 7 yr) temporal trends in the diet of juvenile *C. mydas* at 25° S latitude (southern Brazil)—the tropical–temperate transition zone characterised by the greatest temporal variation in environmental parameters—and any key intrinsic or extrinsic explanatory factors. To complement this objective, we also considered the collected information in conjunction with spatially separated studies (e.g. Guebert-Bartholo et al. 2011, Santos et al. 2015) to propose a broader model of variability affecting feeding habits.

MATERIALS AND METHODS

Study area

Weekly surveys for dead, stranded *Chelonia mydas* were conducted between July 2008 and June 2014 along 40 km of coastal and estuarine beaches in Paraná (between 25° 34′ and 25° 52′ S), southern Brazil (Fig. 1). This area, and especially the Paranguá estuarine complex (PEC; Fig. 1), is considered to be a foraging ground for immature, neritic-stage *C. mydas* that use seagrass meadows and some estuarine and coastal islands and reefs for feeding throughout the year (Guebert-Bartholo et al. 2011). The area is also exposed to considerable anthropogenic impacts, including dredging within the PEC and adjacent artisanal fishing effort from active (penaeid trawling) and passive (gillnetting and hook-and-line) gears (López-Barrera et al. 2012, Silva et al. 2013)—none of which have bycatch reduction devices, nor associated technology to mitigate landed sea turtle mortalities (Silva et al. 2013).

Data collected

Each collected specimen was assessed *in situ* for its decomposition stage (as per Wyneken 2001) and any obvious interactions with fishers (i.e. dermal net or rope marks, amputations, knife wounds or entangled mesh; modified from Moore et al. 2013). Specimens were then measured for curved carapace width (CCW) and CCL to the nearest mm before being transported to the laboratory, where the digestive tract was excised whole. Data were collected on the weight (to
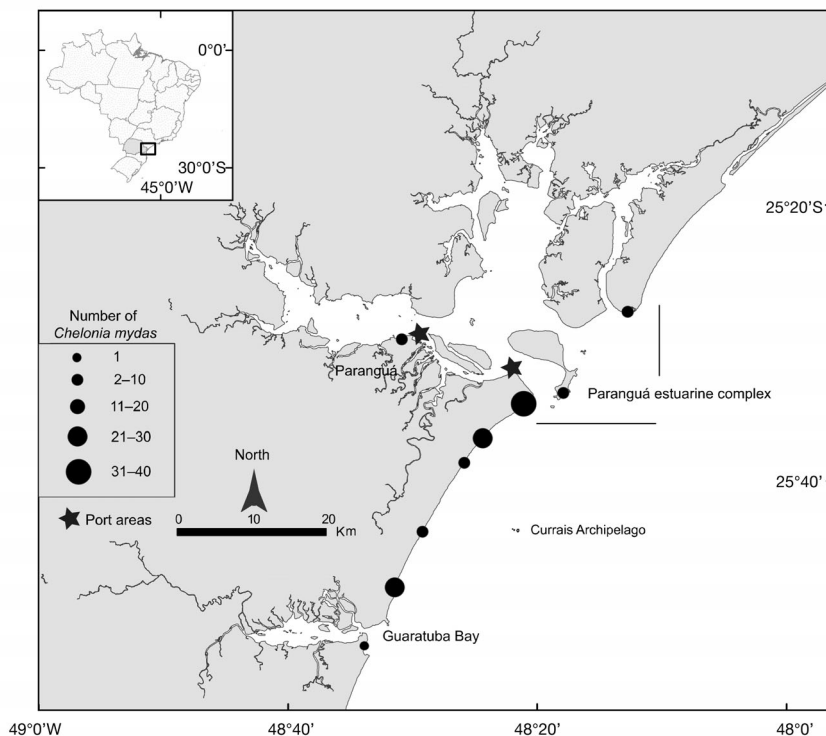

Fig. 1. *Chelonia mydas* sampling sites in Paraná, southern Brazil

the nearest 0.01 g using a precision scale), displaced volume (to the nearest 1 cm^3 using appropriate water-filled cylinders) and length (to the nearest 0.1 cm) of the entire (full) digestive tract, and then subdivisions of the oesophagus, stomach and intestines. All digestive tract contents (including food, sand, shells, faeces, water and marine debris) were removed and the empty subdivisions reassessed for mass and volume as above, and used to calculate the totals for the entire digestive tract. Sexes were determined only for fresh specimens via gonad histology analysis (Rosa 2009, Andrade 2012).

More than 90% of the separated floral and faunal contents were preserved using either 4 or 10% formalin (invertebrates were stored in 70% alcohol and glycerin), prior to identification to either species or genus using a stereomicroscope and assessment of individual weights and volumes as above. Similarly, the total weight and volume of debris in the digestive tract and each subdivision were quantified (as above), before being separated and categorized broadly according to type (simple plastic, rigid plastic and other types of debris) and colour (coloured or transparent).

In addition to the quantitative intrinsic data describing morphology and digestive tract contents, several categories of environmental data were collected (or associated) for each *C. myda*s. These data included date of collection, specific location, monthly sea surface temperature (obtained at 25° 30′ S, 48° 40′ W from MoBIS/Seadata: http://oceancolor.gsfc.nasa.gov/cms/) and rainfall (in mm from the Paranaguá meteorologic station at 25° 31′ S, 48° 30′ W; by SIMEPAR, www.simepar.br, respectively). Rainfall data were aggregated each month into early wet (October, November and December; with a total monthly mean ± SD during the sampled years of 204.65 ± 68.81 mm), late wet (January, February and March; 339.34 ± 92.02 mm), early dry (April, May and June; 151.93 ± 44.05 mm) and late dry seasons (July, August and September; 149.71 ± 73.80 mm).

Data analyses

Multivariate techniques were applied to the vector of food composition data measured for each *C. mydas*. In particular, permutational MANOVA (PERMANOVA; Anderson 2001) was used to determine the relationships between consumed items and various explanatory terms, including the extrinsic factor variables of 'season', 'year' and the quantitative intrinsic variables 'CCL' and 'empty digestive

tract weight'. The multivariate distance between vectors of food composition was calculated as the Bray-Curtis distance applied to fourth-root data.

The statistically significant explanatory variables were subsequently used in a canonical analysis of principal coordinates (CAP; Anderson & Willis 2003) to further explore and visualize the relationship with food type. These multivariate methods were implemented using functions within the R package 'vegan'. Univariate mixed-effects analyses were used to further investigate the strength of relationships, using the 'lme4' function in R package 'lmer'.

The same sequence of analyses as above was repeated for the multivariate response vectors consisting of the weight of the empty digestive tract, and the entire weights of food or debris. In this case, the explanatory variables no longer included empty digestive tract weight.

RESULTS

The sampled period (2008 to 2014) was characterised by considerable intra- and inter-annual variability among rainfall patterns and sea surface temperatures, affected by extreme climatic events within the El Niño (i.e. hotter and wetter than average summers and winters) and La Niña (cooler and dryer than average summers and winters) classifications (estimated by the Oceanic Niño Index, ONI). Specifically, a moderate El Niño effect was recorded from June 2009 to May 2010, followed by strong and weak La Niña in July 2012 and onwards (Fig. 2). Beyond variable fishing effort (see next section), other notable anthropogenic impacts included sustained dredging in the Port of Paranaguá from 2010 onwards (APPA environmental administration office pers. comm.) which maintained considerable sediment suspension throughout the PEC (dredging environment impacts are described by Bray 2008).

Specimens

In total, 120 *Chelonia mydas* were sampled across 7 yr and 4 seasons; most during the dry seasons, and especially between May and July (Fig. 3), which coincided with high bottom-set gillnet effort. There was limited variability in the spatial distribution of specimens, with many found either within or near the southern mouth of the PEC (Fig. 1). A total of 22 *C. mydas* (18%) had visible impacts from fishing interactions, including dermal net marks, amputa-
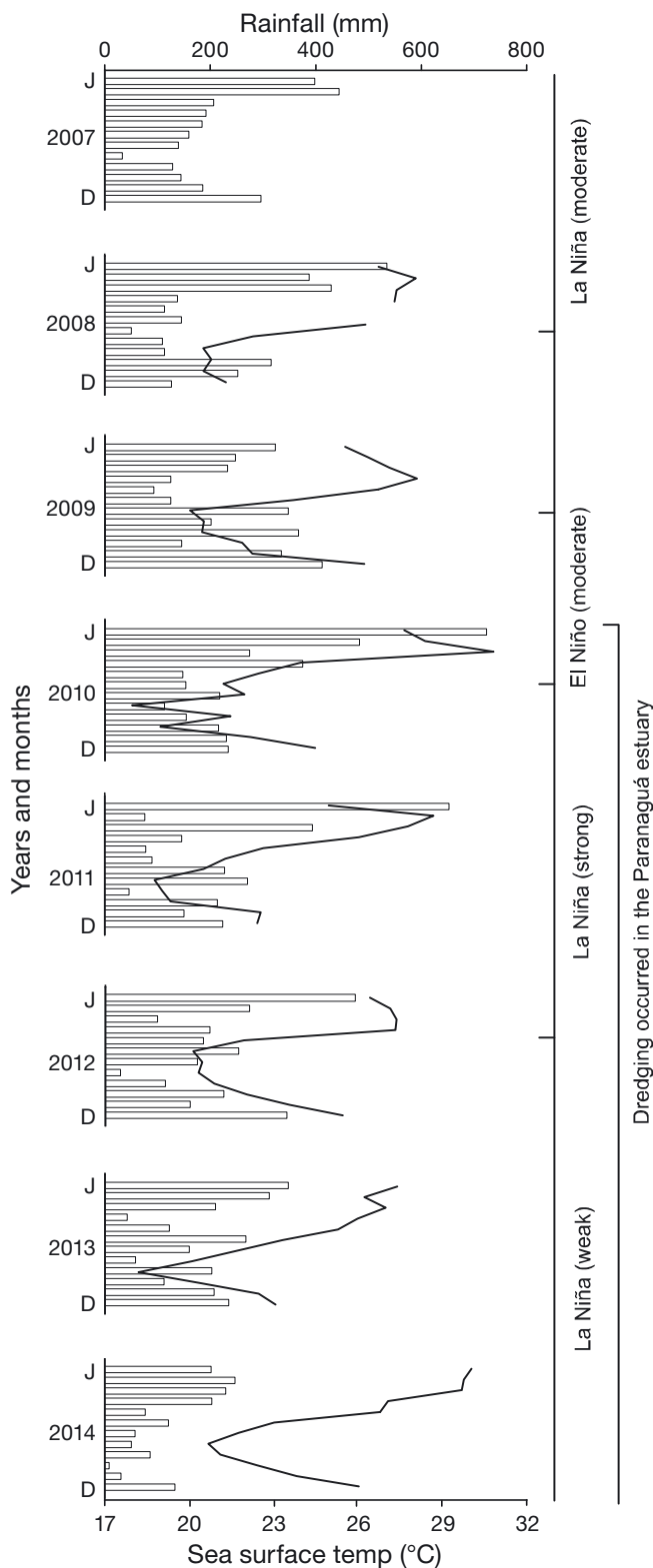
Fig. 2. Monthly rainfall (histograms) and sea surface temperatures, and periods of La Niña or El Niño events and dredging of the Paranaguá estuarine complex for the sampled years
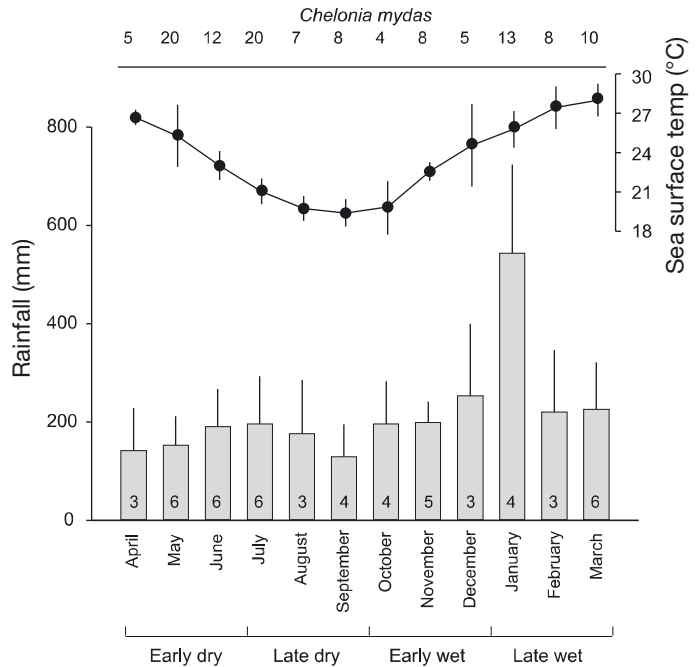

Fig. 3. Monthly mean (±SD) rainfall and mean sea surface temperatures for only those months (numbers in the histogram) during which *Chelonia mydas* (number above the histogram) were collected pooled across the sampled years (2008 to 2014). Dry and wet seasons are delimited

tions or knife wounds. Sizes ranged between 30 and 62 cm CCL (40.00 ± 6.29 cm) and 28 and 55 cm CCW (36.51 ± 5.66 cm), with minimal differences among seasons and years, and with a fairly even distribution of fresh (n = 49), bloated (43) and decayed (27) states (one specimen was not assessed for status). Although no quantitative data were collected, owing to the generally high water and air temperatures, decomposition to a decayed state was estimated at fewer than 7 d. Sex could only be determined for 24 individuals, but there was a bias towards females (17 vs. 7, $\chi^2 = 4.16$, $p < 0.05$). Across all individuals, the mean total digestive tract, oesophagus, stomach and intestine lengths were 383.24 ± 168.43, 16.13 ± 6.40, 28.33 ± 8.38, and 339.50 ± 159.34 cm, respectively. Digestive tract lengths were not considered further because of co-linearity with weights.

Diet

A total of 11 food groups were recorded, including species of Chlorophyta, Rhodophyta, Phaeophyceae, Macrophyta (including the unique seagrass species recorded along the Paraná coast, *Halodule wrightii*)

and cephalopods (Table 1). Most *C. mydas* (68%) also consumed marine debris; typically plastic (96%), much of which (87%) was coloured (Table 1). Of the nutritional items, *Enteromorpha* sp., *Pyropia* sp. and *Rhizoclonium* sp. were least abundant (only found in up to 5 specimens, and only during 2009/2010), and were excluded from the multivariate analyses (Table 1). Ten *C. mydas* had ingested cephalopod beaks, all of which were oceanic species, including *Chirotheutis veranyi* (n = 6), *Illex argentinus* (n = 1), and *Histioteuthis* sp. (n = 1). Three other cephalopod beaks were identified as belonging to the Suborder Oegopsina, but the species were not identified. Excluding cephalopod beaks, *Ulva* sp. and marine debris (all of which were most abundant in the intestines), there were relatively greater weights of items in the stomach, followed by the intestines and oesophagus (Table 1).

Variability in food composition

For the assessed food items, PERMANOVA yielded statistically significant effects of both CCL and year (p > 0.05). Although exploratory ordination plots showed a clear effect of season, it was not significant (p = 0.055). The exploratory plots showed that early and late wet seasons had nearly identical relationships with food composition, as did early and late dry. Consequently, the 4 seasons were combined into only 'dry' and 'wet', and the PERMANOVA was refitted, resulting in statistically significant seasonal grouping (p < 0.01).

CAP analysis was applied to the food compositions using the statistically significant explanatory variables (CCL, years and dichotomous season) found by the PERMANOVA (Fig. 4). The length of the arrows in the biplot demonstrates the strength of association

Table 1. Mean (±SD) weights and volumes (ranges in parentheses) of nutritional items and marine debris found in the oesophagus, stomach, intestine and total digestive tract of 120 *Chelonia mydas* sampled from beaches along the Paraná coast between 2008 and 2014. n: no. of *C. mydas* with the item

| Item	n	Oesophagus Weight (g)	Stomach Weight (g)	Intestine Weight (g)	Total digestive tract Weight (g)	Volume (cm^3)
Chlorophyta						
Ulva sp.	51	15.88 ± 31.98 (0.00–119.18)	56.75 ± 85.27 (0.00 ± 383.27)	210.34 ± 377.67 (0.00–1900.00)	284.40 ± 458.05 (0.00–2000.00)	259.44 ± 405.03 (0.00–1700.00)
Enteromorpha sp.	1	0	6,52	0	6,52	1,4
Rhizoclonium sp.	5	0.20 ± 0.27 (0.00–0.50)	0.08 ± 0.17 (0.00–0.40)	0.40 ± 0.54 (0.00–1.00)	0.69 ± 0.29 (0.40–1.00)	0.78 ± 0.30 (0.40–1.00)
Rhodophyta						
Lobophora sp.	8	0.68 ± 0.99 (0.00–2.51)	0.96 ± 1.53 (0.00–4.22)	0.02 ± 0.04 (0.00–0.13)	1.66 ± 1.34 (0.13–4.22)	1.36 ± 2.19 (0.00–4.80)
Gracilaria domingensis	26	6.68 ± 20.34 (0.00–326.63)	29.95 ± 69.31 (0.00–326.63)	13.75 ± 38.08 (0.00–170.00)	50.00 ± 111.95 (0.25–501.63)	46.43 ± 109.76 (0.00–501.63)
Pyropia sp.	2	0.00 ± 0.00 (0–0)	7.85 ± 7.15 (0.70–15.00)	0.00 ± 0.00 (0–0)	7.85 ± 7.15 (0.70–15.00)	0.50 ± 0.50 (0.00–1.00)
Phaeophyceae						
Sargassum sp.	33	0.48 ± 1.48 (0.00–7.04)	10.32 ± 23.58 (0.00–100.00)	5.99 ± 10.41 (0.00–34.49)	16.80 ± 25.73 (0.26–100.00)	15.27 ± 25.83 (0.00–90.00)
Macrophyta						
Halodule wrightii	31	8.69 ± 15.81 (0.00–50.00)	123.37 ± 224.82 (0.00–900.00)	35.45 ± 42.92 (0.00–125.00)	196.36 ± 258.45 (0.00–900.00)	156.05 ± 227.08 (0.00 ± 867.00)
Avicennias chauerina	31	2.08 ± 5.59 (0.00–28.70)	8.64 ± 13.67 (0.00–63.55)	7.78 ± 19.03 (0.00–85.00)	18.49 ± 29.35 (0.00–120.00)	18.83 ± 31.66 (0.00–120.00)
Unidentified angiosperms	25	0.33 ± 1.1 (0.00–5.00)	2.48 ± 5.47 (0.00–27.33)	2.36 ± 7.85 (0.00–38.40)	5.02 ± 9.65 (0.00–38.40)	4.53 ± 9.11 (0.00–39.08)
Cephalopod beaks	10	0.00 ± 0.00 (0.00–0.00)	1.25 ± 2.01 (0.00–4.50)	2.19 ± 2.42 (0.00–7.50)	3.44 ± 1.96 (1.42–7.50)	2.32 ± 1.25 (0.80–5.00)
Marine debris	82	0.36 ± 2.04 (0.00–17.85)	3.59 ± 12.87 (0.00–82.92)	6.28 ± 13.09 (0.00–93.80)	10.23 ± 18.10 (0.25–93.80)	4.28 ± 8.76 (0.00–50.40)
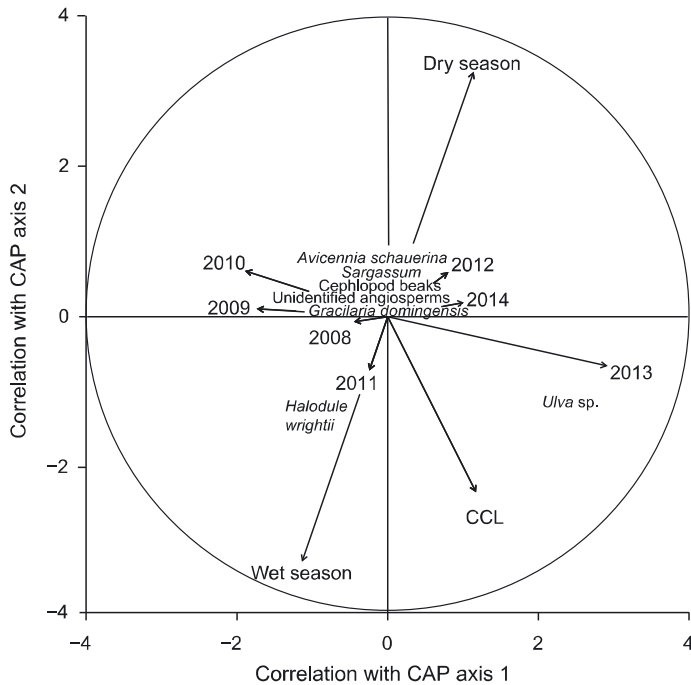
Fig. 4. Canonical analysis of principal coordinates biplot of the relationships between food composition and season (wet vs. dry), years (2008 to 2014) and curved carapace length (CCL) of *Chelonia mydas*

between the respective covariate and the first 2 principal coordinates. Food types that lie away from the centre of the plot indicate a positive association with arrows pointing in their direction. Specifically, *C. mydas* consumed *H. wrightii* during the wet season while most other food, but especially *Avicennia schaueriana* and *Sargassum* sp., were observed in digestive tracts during the dry season (Fig. 4). Of particular note, the association between year and food type appeared to reverse between the years 2008–2010 and 2012–2014, with a greater shift towards *C. mydas* consuming *Ulva* sp. in the latter period, particularly during 2013 (Fig. 4).

Univariate mixed-effects analyses were applied to the various food components, each with CCL and seasons as fixed effects, and years as random. These analyses largely confirmed the CAP conclusions (Fig. 4). In particular, the wet season grouping was strongly positively associated with *H. wrightii* ($p < 0.01$) and negatively associated with *A. schaueriana* ($p < 0.05$). CCL was positively associated with *Ulva* sp. ($p < 0.05$) and to a lesser extent with *H. wrightii* ($p < 0.1$). In addition, CCL was negatively associated with cephalopod beaks ($p < 0.05$). The random effect of year was significant for *Ulva* sp. ($p < 0.001$), but not for all other food types ($p > 0.05$).

Digestive tract composition

PERMANOVA detected significant effects of CCL and year ($p < 0.05$), but not seasonal grouping ($p > 0.05$) on the digestive tract variables. CCL and years were utilized as covariates in the subsequent CAP analysis (Fig. 5). Of note, the biplot indicated that the weight of food in the digestive tract was positively associated with CCL and tended to be greater in 2013 (i.e. *C. mydas* had more food in their digestive tract; Fig. 5). Univariate analyses detected strong positive associations between CCL and both the empty digestive tract weight and the weight of food ($p > 0.05$). These 2 digestive tract variables also had significant random year effects ($p < 0.05$). None of the assessed factors explained significant variability in the weight or the presence of marine debris in the digestive tract ($p > 0.05$).

DISCUSSION

This study represents one of the few attempts to quantify temporal variation in the diet of juvenile *Chelonia mydas* (30 to 62 cm CCL) and explore potential explanatory factors. In doing so, our results support existing models of flexibility among intrinsic
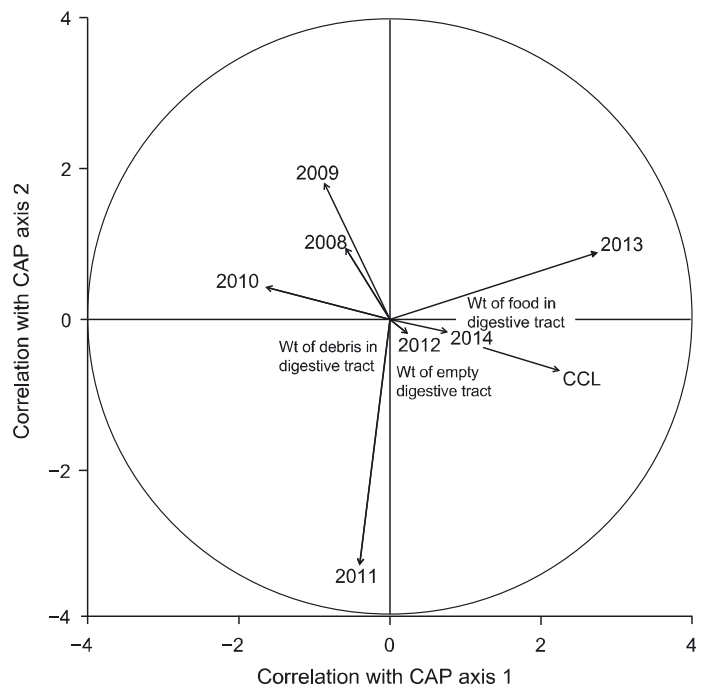

Fig. 5. Canonical analysis of principal coordinates biplot of the relationships between digestive tract weight (of food and marine debris and when empty), years (2008 to 2014) and curved carapace length (CCL) of *Chelonia mydas*

(e.g. CCL) and extrinsic influences (environmental factor fluctuations) (Hatase et al. 2006, Cardona et al. 2009, González Carman et al. 2012, Santos et al. 2015), but based on the observed temporal variation in the latter, also clearly underscore the need for long-term data to adequately understand sea turtle foraging ecology. The temporal variation in diet among *C. mydas* can be discussed by considering the underlying environmental conditions, and used to propose effective conservation actions in response to various anthropogenic impacts.

Prior to postulating the mechanisms contributing towards the observed diet variability, the limitations of the collected data warrant consideration. In particular, unlike telemetry and stable isotope studies, the data describing *C. mydas* diets here were restricted to single points in space and time, precluding individual time-series information and limiting our interpretations to a population level. Further, while we are confident that even the most decayed individuals were sampled within a short time after death (e.g. a maximum of 7 d), it is impossible to determine the longer-term spatial origin of individuals, or to quantify any dietary items that might have been rapidly eliminated (e.g. gelatinous macroplankton). A key assumption of our approach is that most *C. mydas* were actively feeding in the immediate geographic vicinity of stranding.

The above hypothesis is not unreasonable considering that all of the various flora observed in the digestive tract of *C. mydas* were regionally abundant (especially in the PEC) at their times of death (Lana et al. 2001, Guebert-Bartholo et al. 2011, Sordo et al. 2011, Pellizzari et al. 2014). Earlier studies demonstrated, that owing to a confluence between northern warm (i.e. the Brazil current) and southern cold currents (the Falklands current), the PEC and adjacent coast provide vast vegetated areas including mangrove forests (encompassing *Avicennia schaueriana*), *Halodule wrightii* meadows and rocky islands with beds of algae, such as the macrophytas *Gracilaria domingensis* and *Ulva* sp., throughout the year (Lana et al. 2001, Sordo et al. 2011, Pellizzari et al. 2014). Such characteristics indicate that the area has historically been an important foraging ground for *C. mydas* between temperate and tropical waters (Guebert-Bartholo et al. 2011, González Carman et al. 2012, López-Barrera et al. 2012).

Equally important, the presence of most items (all of which have previously been recorded in *C. mydas*; Seminoff et al. 2002, Fuentes et al. 2006, Hatase et al. 2006, Arthur et al. 2008, Cardona et al. 2009, Guebert-Bartholo et al. 2011, Nagaoka et al. 2012, Vélez-

Rubio et al. 2014, Santos et al. 2015) in all subdivisions of the digestive tract, but with a bias towards the stomach and intestines suggests that the stranded animals were actively assimilating regionally available food prior to mortality. The observed gastric spatial separation of food (and associated temporal consumption information) not only supports positive animal health, but also demonstrates the utility of evaluating the entire digestive tract over other methods that assess stomach contents alone (e.g. oesophageal lavage).

Cephalopod beaks were the only non-regional digestive tract items observed, although all species (classifications) occur in adjacent oceanic waters (Velez-Rubio et al. 2014); this was reiterated by their location in the intestines, which indicated consumption well before beach stranding and perhaps either prior to neritic recruitment or during oceanic incursions that are often described for small juveniles in temperate zones (González Carman et al. 2012, Velez-Rubio et al. 2014). In support of the general model describing age-specific dietary requirements, there was a significant negative relationship between CCL and cephalopod ingestion (Bjorndal 1980, Jones & Seminoff 2013); an observation explained by the greater protein requirements of *C. mydas* in their early life stage (Cardona et al. 2009). Such requirements, along with more homogeneous oceanic waters, probably superseded any broader environmental influence on diet (e.g. observed among the herbivorous items) in smaller juvenile *C. mydas*.

Among the larger juvenile *C. mydas* (mainly >40 cm CCL), beyond their propensity to consume significantly more food in proportion to their size, it is clear that both short- and long-term temporal variability strongly affected their foraging ecology. Such variability encompassed predictive seasonal, annual and possible anthropogenic effects, which can be considered independently and also interactively. In particular, there were considerable seasonal differences in rainfall and sea surface temperature at our sampled location, which likely had strong direct and indirect effects on the abundance of dietary items. Warm water and nutrients are required to promote the growth of seagrasses such as *H. wrightii* (Creed 1999, Sordo et al. 2011) — reflecting a preference for these foods during the wet season, with *C. mydas* probably feeding at the oceanic limit of the PEC, using a benthic foraging strategy.

Conversely, seagrass is considerably less abundant during the dry and cooler seasons, and as a response, *C. mydas* shifted their diet to other, more readily

available flora, demonstrating a pelagic foraging strategy. Specifically, similar to the mechanism supporting some *C. mydas* migrations to the tropics, the dry period in large tropical–temperate transition-zone estuaries like the PEC is associated with strong nutritive currents that positively affect the growth of some algae and the presence of other species such as *Sargassum* sp. that often float in the water column (Leite & Turra 2003). Seed dispersal by *A. schaueriana* also occurs regionally during the dry season. These species flourish throughout the inner PEC and adjacent coastal areas which, combined with a relatively greater salinity would facilitate *C. mydas* accessibility to what is considered energetic food. However, such habitat-specific food diversity probably also increased the risk of fishing-gear interactions (considering that greater injuries and mortality were recorded during this season) owing to artisanal fishers seeking to concomitantly exploit more abundant teleost resources (López-Barrera et al. 2012).

The mechanisms affecting the seasonal availability of flora, and ultimately *C. mydas* diet, may extend to broader differences among years, including the climatic effects associated with El Niño and La Niña. For example, during 2007/2008, the El Niño and La Niña sequences were mild. However, during 2009 and part of 2010, there was a moderate El Niño (ONI: +2) with a greater-than-normal wet summer and associated increases in turbidity, which may have negatively impacted seagrass growth and abundance (including *H. wrightii*) and resulted in the observed diet shift to other foods.

Concurrent with El Niño, extensive dredging commenced in the Paranaguá port area during early 2010, exacerbating turbidity and homogenizing hydrological processes throughout the estuary. Such effects have been described as negatively impacting seagrass (e.g. owing to turbidity; Erftemeijer & Robin Lewis 2006), but less so for algal richness and biomass because these species grow on different substrates and habitats (e.g. rocky islands, sand banks and reefs at the PEC mouth and adjacent coast). In the absence of abundant seagrasses, *C. mydas* can consume a variety of algae that still provide a high caloric value, but which have a relatively low volume, which may explain the observed tendency for a lower weight of food in the digestive tract during the aforementioned period.

The El Niño was immediately superseded by a La Niña event (2010 to 2012; ONI −2 and −1; CPTEC 2015) which, owing to cooler temperatures, can also reduce seagrass growth and biomass (Pollard & Greenway 2013, Petus et al. 2014) and affect the availability of other food items, driving *C. mydas* feeding behaviour during these years to be more similar to the model described for dry seasons. It is also likely that by 2012 the sustained dredging had protracted impacts, possibly causing sediment and chemical contaminant suspensions, which, when deposited over meadows restrict seagrass growth but increase suitable habitat for *Ulva* sp.; a resistant and relatively more productive genus in polluted areas (Erftemeijer & Robin Lewis 2006) that was consumed in large quantities by *C. mydas*, especially in 2013. Similar environmental extremes have been reported to affect the migratory patterns of the congeneric sea *Chelonia agassizii* off Peru (Quiñones et al. 2010). Additional data might provide insight into some of the impacts that could occur as climate change progresses.

Although a lack of information (including non-assessed/unidentified potential explanatory variables) means that the underlying mechanisms for diet shifts remain somewhat speculative, the observed temporal variability in *C. mydas* diet reiterates the importance of long-term data to effectively understand foraging ecology. For example, isolated sampling across the same seasons in the PEC prior to dredging or El Niño in 2010 (2004 to 2008) would provide vastly different conclusions to those based on sampling in 2013. Such limitations warrant consideration when drawing inferences from opportunistic studies that involve the isolated accumulation of stranding data. Clearly, regional hydrological and climatic processes and the availability of certain food types are key drivers for foraging behaviour, and because of calorific differences (i.e. the energetic requirement to feed and digest an item vs. its nutritional benefits), would ultimately affect growth, migrations, habitat use and overall *C. mydas* health.

The observed diet variability and the associated foraging strategies also provide insight into possible future responses to anthropogenic impacts (including climate change) and ways that unwanted interactions might be mitigated. The proposed model implies that greater environmental extremes, caused by natural or anthropogenic factors, are likely to affect food availability and habitat use by juvenile *C. mydas*, and also that their early developmental stage (or age) will be an important factor affecting their diet pattern. Such information might be used to delineate appropriate protected areas and management actions, and mitigate possible short- and median-term impacts caused by dredging or fishing. As one example, if dredging processes increase and seagrass availability decreases in the PEC, *C. mydas*

might be expected to frequent nearby rocky islands and reefs where algae will be available, which would overlap with considerable artisanal fishing effort. Clearly, understanding foraging habitats combined with modern monitoring methods (e.g. satellite tags and stable isotopes) will improve our capacity to support *C. mydas* conservation efforts.

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