

# A jellyfish diet for the herbivorous green turtle *Chelonia mydas* in the temperate SW Atlantic

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**Abstract** Feeding ecology of juvenile green turtles (*Chelonia mydas*) was studied from 2008 to 2011 at Samborombón Bay (35°30′–36°30′S, Argentina), combining data on digestive tract examination and stable isotope analysis through a Bayesian mixing model. We found that animal matter, in particular gelatinous plankton, was consumed in large proportions compared to herbivorous food items such as terrestrial plants and macroalgae. This diet is facilitated by the high abundance of gelatinous plankton in the region, thus confirming the adaptive foraging behaviour of the juveniles according to prey abundance in the SW

Atlantic. To our knowledge, this is the first study to employ this combination of techniques and to conclusively demonstrate that animal matter, in particular gelatinous plankton, is important in the diet of the neritic green sea turtles.

## Introduction

It is widely known and accepted that the green sea turtle (*Chelonia mydas*) exhibits an herbivorous diet during most part of its life (Bjorndal 1985, 1997; Seminoff et al. 2002; Arthur and Balazs 2008; Santos et al. 2011). This unique diet among sea turtles is acquired after an ontogenetic shift that occurs when early juveniles move from oceanic to neritic foraging habitats, change from an omnivorous to a strict herbivorous diet and also from a pelagic to a benthic feeding behaviour (Bolten 2003; Reich et al. 2007; Arthur et al. 2008). This shift is thought to be abrupt and irreversible (Bolten 2003; Reich et al. 2007; Arthur et al. 2008), and it might help turtles be less vulnerable to predators and attain sexual maturity sooner through an increased growth rate (Werner and Gilliam 1984; Bolten 2003; Snover et al. 2010). Recently, a growing body of literature has documented the consumption of animal matter in neritic green sea turtles (e.g. Heithaus et al. 2002; Hatase et al. 2006; Amorocho and Reina 2007; Quiñones et al. 2010; Burkholder et al. 2011; Lemons et al. 2011), thus challenging the paradigm of an abrupt and irreversible shift (Cardona et al. 2009, 2010; González Carman et al. 2012). Yet, whether the diet of neritic green sea turtles includes a substantial portion of animal matter has not been rigorously tested.

Here, we present a case where juvenile green turtles seasonally exploit a neritic habitat in the temperate coast of South America that is unsuitable for an herbivorous diet.

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The Samborombón Bay (35°30′–36°30′S)–in the southwest portion of the Río de la Plata estuarine area, Argentina–lacks macroalgae and seagrass meadows (Boschi 1988; Boraso and Zaiuso 2008). Conversely, several species of fish, molluscs and crustaceans inhabit the area. Particularly abundant is the gelatinous plankton that include species of hydromedusae, scyphomedusae and ctenophores (Mianzan and Guerrero 2000; Mianzan et al. 2001a, b; Alvarez Colombo et al. 2003). After foraging in the Río de la Plata, the juvenile turtles migrate to warmer northern areas that include oceanic waters, indicating that the ontogenetic shift undertaken by the species would not be abrupt and irreversible (González Carman et al. 2011, 2012). Due to the characteristics of the region, we hypothesized that neritic green sea turtles are specifically exploiting animal prey, especially gelatinous plankton.

We investigated the diet of these juveniles by combining two methodologies, digestive tract examination (DTE) and stable isotope analysis (SIA), through a Bayesian mixing model. Several studies in green sea turtles have used DTE to infer diet (e.g. Seminoff et al. 2002; Fuentes et al. 2006; López-Mendilaharsu et al. 2006; Arthur and Balazs 2008; Santos et al. 2011). Results suggest that green sea turtles feed on seagrass and/or macroalgae almost exclusively, establishing the paradigm of strict herbivory. Some invertebrates (such as sponges, snails, polychaetes) were also recorded in the digestive tracts, but in low amounts (Seminoff et al. 2002; Russell et al. 2011). Few studies reported the consumption of considerable amounts of jellyfish. Quiñones et al. (2010) observed the almost exclusive consumption of the jellyfish *Chrysaora plocamia* by East Pacific green turtles (*Chelonia mydas agassizii*) on the coast of Peru during an El Niño event. Since the abundance of macroalgae decreases and jellyfish increases during El Niño events in the region, it is likely that the turtles preyed opportunistically on this jellyfish taking advantage of its great availability when its main food source was absent (Quiñones et al. 2010).

Gelatinous plankton is a neglected food source for several species, including fish, marine mammals and sea turtles (Mianzan et al. 1996, 2001a; Cardona et al. 2012), because its detection during digestive tract examinations is challenging due in part to its rapid digestibility (Arai et al. 2003; Doyle et al. 2007; Burkholder et al. 2011; Cardona et al. 2012). The problem can be overcome using SIA of consumer and prey tissues (e.g. DeNiro and Epstein 1981; Burkholder et al. 2011; Cardona et al. 2012). Compared to DTE, the SIA of turtle tissue reflects a time-integrated diet, with the timescale determined by its metabolic activity (Peterson and Fry 1987). Keratinized tissues (e.g. epidermis) tend to indicate feeding patterns over several months, while fast turnover tissues (e.g. blood plasma) tend to integrate diet over a period of weeks reflecting recent diet

(Hobson 1999; Dalerum and Angerbjorn 2005). In contrast, DTE provides a limited temporal window or “snapshot” into diet trends, which usually results in an incomplete description of an animal’s diet (Hyslop 1980; Burkholder et al. 2011). Furthermore, the SIA gives information on prey effectively assimilated and not only on those consumed (Post 2002). However, some limitations also exist. The SIA does not allow for direct species identification and quantification of prey, and information on the isotopic composition of putative prey is needed to interpret results (Gannes et al. 1998; Post 2002; Burkholder et al. 2011). Therefore, studies like this using both techniques are desirable.

## Materials and methods

### Field methods

Data were collected from 69 juvenile *Chelonia mydas* (62 dead, 7 alive) caught as bycatch in the artisanal gillnet fishery of Samborombón Bay from 2008 to 2011. Body weight ( $W \pm 0.1$  kg) and curved carapace length (CCL  $\pm 0.1$  cm) were measured according to Bolten (2000).

Digestive tract examination was performed for 62 dead *C. mydas*. For the SIA, we sampled the epidermis and muscle from seven dead *C. mydas* and collected epidermis and blood from seven live *C. mydas* following the methodology used by Seminoff et al. (2006). These tissues reflect likely diet on a scale from weeks to several months. Blood plasma reflects diet close to the time of sampling while red blood cells and epidermis integrate food intake for longer periods (Seminoff et al. 2007; Reich et al. 2008; McClellan et al. 2010; Pajuelo et al. 2012). There is no information about the time integrated by the muscle, but in terrestrial mammals, it gives information on the diet over an intermediate time period between plasma and epidermis (Tieszen et al. 1983).

### Laboratory procedures

#### *Digestive tract examination*

Diet samples from the oesophagi and the stomachs were rinsed through a 2-mm-fine-mesh sieve and fixed in a 4 % formalin solution according to Forbes (2000). Food items were identified to the possible lowest taxonomic level with a binocular dissecting scope. Items that could not be identified were grouped into an “unidentified” category. We conducted microscopic investigation (magnification up to 1000x) to identify nematocysts or combs (groups of cilia) characteristic of gelatinous plankton within the contents (Van Nierop and Den Hartog 1984; Frick et al. 2001). The nematocysts found were then classified according to

Mariscal (1974) and Kokelj et al. (1993) and compared to nematocysts present in putative cnidarian prey chosen according to their occurrence and abundance in Samborombón Bay. This material was provided by the Medusozoa Collection of the Coastal Station J. J. Nágera of Mar del Plata National University and the National Institute for Fisheries Research and Development (INIDEP) of Argentina.

#### Stable isotope analysis

Skin, muscle and blood samples (whole blood, red blood cells, blood plasma) were processed in accordance with the methods used in Seminoff et al. (2006). Approximately 0.8–1.2 mg of tissue samples was loaded into sterilized tin capsules and analysed by a mass spectrometer in the Institute of Geochronology and Isotopic Geology (INGEIS) of Buenos Aires University, Argentina. An elemental combustion system Carlo Erba EA1108 interfaced via a ConFlo IV device to a Thermo Scientific Delta V Advantage mass spectrometer was used to obtain  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and C:N ratio data for all samples. The stable isotope ratios of tissue samples were expressed relative to international isotope standards in the following conventional delta ( $\delta$ ) notation in parts per thousand (‰).  $\delta^{13}\text{C}$  is expressed relative to Pee Dee Belemnite (PDB) and  $\delta^{15}\text{N}$  relative to atmospheric nitrogen.

#### Statistics

We calculated the frequency of occurrence (%FO), the total wet weight (%W<sub>tot</sub>) and the individual wet weight (%W<sub>ind</sub>) for each discernible diet item (Hyslop 1980; Arthur and Balazs 2008; Quiñones et al. 2010). Diet information is presented as the mean proportion each item contributed to diet (mean %W<sub>ind</sub> ± one standard error). Frequency of occurrence is expressed as the overall proportion of samples in which a diet item is observed, but also as the proportion of samples where each diet item was ≤5, ≥50 and ≥75 % of %W<sub>ind</sub> to evaluate incidental ingestion (Quiñones et al. 2010). To determine the importance of a food item, we calculated an Index of Relative Importance (IRI) as follows:  $\text{IRI} = \%W_{\text{tot}} * \%FO$ ;  $\%IRI = (\text{IRI}^n / \sum_{n=1} \text{IRI}) * 100$ . This index was modified from the original formulation of Pinkas et al. (1971), since it incorporates weight instead of volume and it does not include the number of food items quantified due to methodological constraints.

Following Burkholder et al. (2011) and Dodge et al. (2011), we applied a post hoc lipid correction factor to the carbon isotope ratios estimated ( $\delta^{13}\text{C}$ ) for all tissues. We corrected according to equation  $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$ , if  $\text{C:N} \geq 3.5$  (Post et al. 2007). After this normalization, the difference between the isotopic compositions of tissues was evaluated through a general linear

model (GLM, McCullagh and Nelder 1989) with a fixed factor (TISSUE, 4 levels) and a random factor (TURTLE, 14 levels). For this comparison, the level epidermis was not differentiated between live and dead turtles. The level whole blood was not included because it expresses the joint value of blood plasma and red blood cells. Post hoc comparisons were then tested through the Tukey's unequal test (Zar 1996) of the software Statistica 6.0. We then evaluated differences between epidermis from live and dead turtles through a general linear model (GLM, McCullagh and Nelder 1989) with a fixed factor (CONDITION OF TISSUE, 2 levels) and a random factor (TURTLE, 14 levels).

To infer the trophic level and the foraging habitats of turtles, the isotopic composition of blood plasma (representing the diet recently acquired) was compared graphically to the isotopic composition of potential prey that occurs in Samborombón Bay. This last information came from a previous study conducted by Botto et al. (2011) and Gaitán (2012) and was also corrected for lipids according to Post et al. (2007). We used diet–tissue (dt) discrimination factors of  $^{13}\text{C}$  and  $^{15}\text{N}$  (plasma tissue:  $\Delta_{\text{dt}}^{15}\text{N} = + 2.92 \pm 0.03 \text{‰}$ ,  $\Delta_{\text{dt}}^{13}\text{C} = - 0.12 \pm 0.03 \text{‰}$ ) estimated by Seminoff et al. (2006).

We then constructed a Bayesian mixing model to estimate the relative contribution of potential prey items to the turtle's diet (Phillips 2001; Phillips and Gregg 2003; Inger et al. 2010; Parnell et al. 2010). SIAR (Stable Isotope Analysis in R, version 4.1.3, Inger et al. 2010; Parnell et al. 2010) was fitted in R (R 3.0.1, R Development Core Team 2013) including isotopic compositions of turtle blood plasma, isotopic compositions of putative prey (Botto et al. 2011; Gaitán 2012) and discrimination factors (Seminoff et al. 2006). SIAR accounts for individual variation in all these input parameters (Inger et al. 2010; Parnell et al. 2010). The criteria to include putative prey in the model were that a given prey (1) was observed in the digestive tracts, (2) had an isotopic composition compatible with the composition of blood plasma according to discrimination factors informed by Seminoff et al. (2006) and/or (3) is abundant in the Samborombón Bay according Acha et al. (2008), Gaitán (2004), Mianzan et al. (2001b), Schiariti et al. (2006) and Schiariti (2008). The model was fit via Markov chain Monte Carlo (MCMC) methods producing simulations of plausible values of dietary proportions of potential prey consistent with the data using a Dirichlet prior distribution (Parnell et al. 2010). The SIAR MCMC was run for 500,000 iterations, discarding the first 50,000 samples according to Inger et al. (2010). The resulting probability density function distributions of the feasible feeding solutions produced by SIAR allowed direct identification of the most probable solution (i.e. the mean value). Upper and lower credibility intervals (1–99 % percentiles) described the range of feasible contribution for each diet item (Inger et al. 2010; Parnell et al.

**Table 1** Items found in the digestive tracts of juvenile green turtles ( $n = 62$ ) in Samborombón Bay, Argentina.

Item	%W <sub>ind</sub>		%FO				%IRI
	Mean	SE	Present	≤5 %W <sub>ind</sub>	≥50 %W <sub>ind</sub>	≥75 %W <sub>ind</sub>	
<b>Animal matter</b>	<b>55.3</b>	<b>4.6</b>	<b>92.1</b>	<b>7.9</b>	<b>57.1</b>	<b>41.3</b>	
Cnidarians							
Jelly like mucous material with nematocysts	47.8	4.6	81.0	3.2	49.1	30.2	
Hydroid polyps	2.4	1.5	27.0	20.6	1.6	1.6	
Total cnidarians	55.6	4.4	88.8				72.5
Molluscs							
<i>Heleobia</i> sp.	1.7	0.5	42.9	31.8			
Eggs of <i>Rapana venosa</i>	1.4	1.0	12.7	9.5	1.6		
<i>Macra</i> sp.	1.1	0.6	22.2	0.1			
Total molluscs	7.9	1.6	52.4				3.1
Chaetopteridae polychaete	0.6	0.6	1.6				~0
Insect body parts	0.2	0.1	7.9	6.4			~0
Anomura crustacean	0.1	0.1	1.6	1.6			~0
Fish eggs	0.1	0.1	1.6	1.6			~0
<b>Plant matter</b>	<b>13.2</b>	<b>3.6</b>	<b>38.1</b>	<b>9.5</b>	<b>14.3</b>	<b>11.1</b>	
Terrestrial plant <i>Spartina</i> sp.	9.0	0.3	33.3	14.3	6.4	6.4	6.9
Macroalgae							
<i>Ulva</i> sp.	2.9	2.0	4.8		4.8	4.8	
<i>Porphyra</i> sp. + <i>Petalonia</i> sp.	0.9	0.3	1.6		1.6		
<i>Rhodomenia</i> sp.	0.1	0.1	1.6				
<i>Gymnogongrus</i> sp.	0.1	0.1	1.6	1.6			
Total Macroalgae	4.2	2.2	9.5				1.4
<b>Other items</b>							
Substrate (shell fragments, stones)	5.5	1.1	66.7	31.8			8.2
Very digested material	6.1	2.4	11.1	4.8	6.4	3.2	1.1
Unidentified material	2.7	1.3	15.9	3.2	1.6		1.4
Liquid	10.9	3.3	17.5		9.5	6.4	5.4

%W<sub>ind</sub> individual wet weight, %FO frequency of occurrence, %IRI index of relative importance, SE one standard error

2010). After running the model, we produced a matrix correlation plot for the posterior distributions of each putative prey. This is a useful diagnostic tool to assess whether the model is performing well as is indicated by low correlations between prey. High negative correlations indicate that the model is struggling to differentiate between prey, whereas high positive correlations indicate that one prey may necessarily require another prey in some proportion so as to balance each other (Inger et al. 2010).

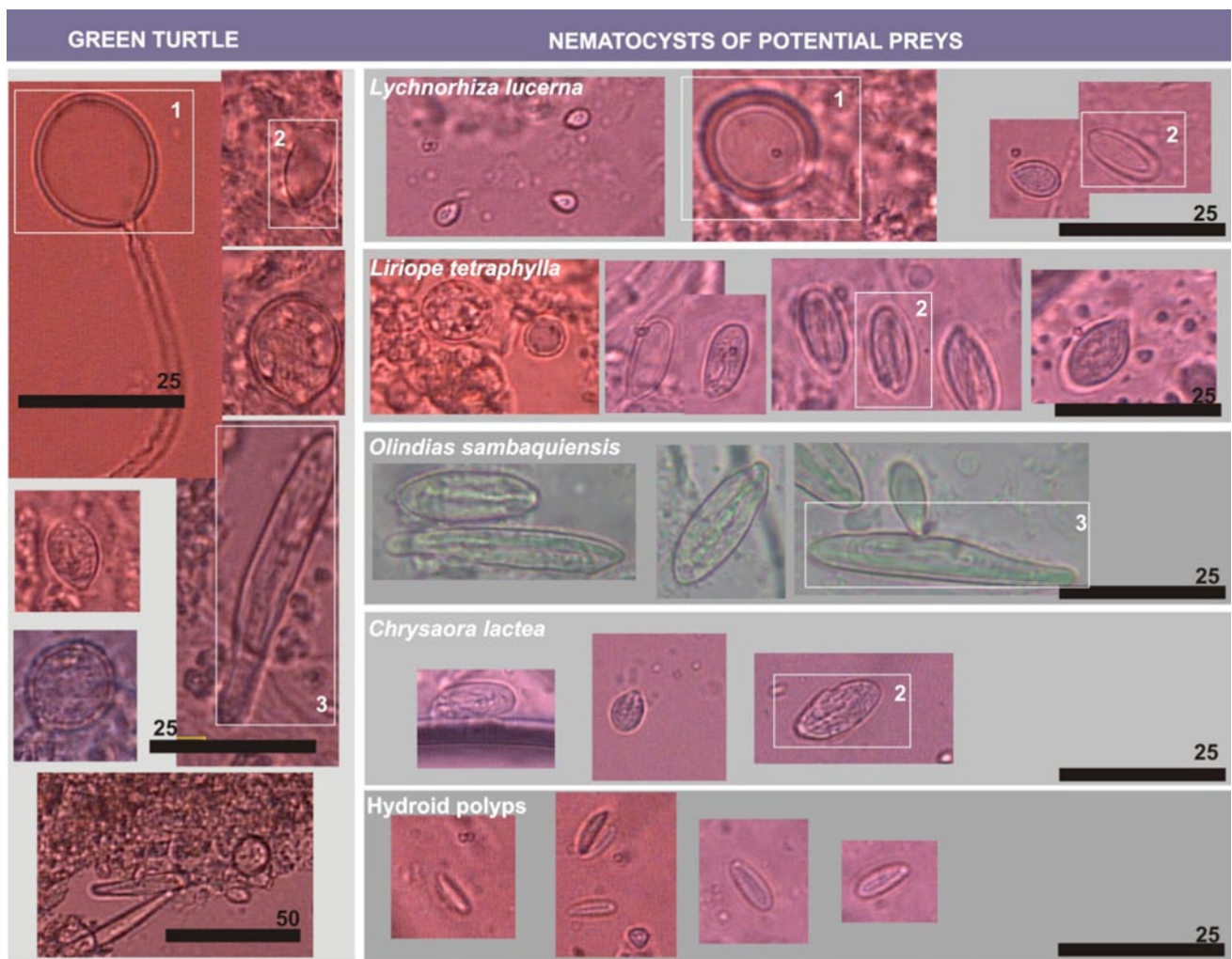
## Results

### Digestive tract examination

Juveniles of *Chelonia mydas* in Samborombón Bay (mean CCL ± SD = 38.5 ± 4.4 cm, range = 31.3–52.2 cm,  $N = 54$ ; mean W ± SD = 6.0 ± 2.9 kg,

range = 2.3–16.8 kg,  $N = 47$ ) have an omnivorous diet, composed mainly of three food items according to their %W<sub>ind</sub>: cnidarians, terrestrial plants and molluscs (Table 1). Cnidarians were by far the most frequent and abundant food item. They were present in 88.8 % of the samples, showed an overall %W<sub>ind</sub> of 55.6 and the highest %IRI of 72.5. They were represented mostly by a jelly like mucous material (that in 30 % of the samples had a %W<sub>ind</sub> > 75) and hydroid polyps (Anthomedusae and Leptomedusae) to a lesser extent (2.4 %). Cnidarians were followed by the terrestrial plant *Spartina* sp. (%IRI = 6.9), present in 33.3 % of the samples and with a %W<sub>ind</sub> of 9.0. Lastly, molluscs (%IRI = 3.1) were present in more than 50 % of the samples and showed an overall %W<sub>ind</sub> of 7.9. They were represented by the gastropod *Heleobia* sp., eggs from *Rapana venosa* and the bivalve *Macra* sp.

The colour of the jelly like mucous material varied between yellow, brown, pink and transparent. No body



**Fig. 1** Comparison between nematocysts found in the jelly like mucous material of green turtle's contents and nematocysts of their putative cnidarian prey in Samborombón Bay, Argentina. The scale

represents 25 and 50  $\mu\text{m}$ . Numbers within frames indicate the same type of nematocysts

structures (such as oral arms or combs) could be identified in the samples. However, the microscopic examination allowed the observation of nematocysts in 78 % of the cases. The observed nematocysts may be associated with at least 4 species of jellyfish: *Liriope tetraphylla*, *Lychnorhiza lucerna*, *Olindias sambaquiensis* and *Chrysaora lactea*. We found nematocysts of the type heterotrichous anisorhiza, which are present in *L. lucerna* (frame 1, Fig. 1), nematocysts of the type mastigophore occurring in *L. lucerna*, *L. tetraphylla* and *C. lactea* (frame 2, Fig. 1), and nematocysts of the type microbasic p-mastigophore present in *O. sambaquiensis* (frame 3, Fig. 1). We did not observe nematocysts belonging to any hydroid polyps.

Macroalgae were uncommon and scarce (%FO = 9.5, %W<sub>ind</sub> = 4.2, %IRI = 1.4; Table 1). *Ulva* sp. was the most abundant and frequent macroalgae species found. Other food items observed included Chaetopteridae polychaetes,

insect body parts, fish eggs and an Anomuran crustacean. Only two *C. mydas* did not contain any food items in their digestive tract.

#### Stable isotope analysis

In general, the isotopic composition of turtle tissues varied with respect to N and/or C (Table 2, Fig. 2). In the case of nitrogen, the muscle and red blood cells were similar to each other, but different from epidermis and blood plasma ( $F = 36.4$ ;  $P < 0.05$ ). Regarding carbon, the epidermis differed from the rest of the tissues ( $F = 142.7$ ;  $P < 0.05$ ). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of epidermis were significantly different between dead and live animals ( $F = 12.3$ ;  $P < 0.05$ ).

Blood plasma of turtles was depleted in  $^{13}\text{C}$ , indicating a neritic foraging habitat. The mean  $\delta^{15}\text{N}$  value was intermediate between the primary (*Mactra* sp.) and secondary

**Table 2** Mean stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for juvenile green turtle tissues and putative prey in Samborombón Bay, Argentina

	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	C:N
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD
<b>Green turtle (14)</b>			
Epidermis (14)	10.3 $\pm$ 1.3 <sup>a</sup>	-16.1 $\pm$ 0.8 <sup>1</sup>	3.5 $\pm$ 0.0
Dead turtles (7)	9.5 $\pm$ 1.0	-15.5 $\pm$ 0.7	
Live turtles (7)	11.1 $\pm$ 1.1	-16.5 $\pm$ 0.2	
Blood plasma (7)	12.1 $\pm$ 1.3 <sup>b</sup>	-17.8 $\pm$ 0.3 <sup>2</sup>	4.9 $\pm$ 0.1
Red blood cells (7)	8.8 $\pm$ 1.6 <sup>c</sup>	-17.8 $\pm$ 0.3 <sup>2</sup>	3.8 $\pm$ 0.0
Muscle (7)	8.9 $\pm$ 0.8 <sup>c</sup>	-17.8 $\pm$ 0.6 <sup>2</sup>	3.9 $\pm$ 0.0
Whole blood (7)	9.4 $\pm$ 1.6	-17.9 $\pm$ 0.3	4.0 $\pm$ 0.0
<b>Planktivorous fish</b>			
<i>Brevoortia aurea</i> (9)	12.8 $\pm$ 0.5	-19.6 $\pm$ 0.5	
<i>Stromateus brasiliensis</i> (8)	16.4 $\pm$ 0.4	-19.4 $\pm$ 1.5	
<b>Non-gelatinous plankton</b>			
<i>Neomysis americana</i> (4)	11.6 $\pm$ 0.3	-17.0 $\pm$ 0.1	
<i>Acartia tonsa</i> (4)	9.7 $\pm$ 0.2	-15.3 $\pm$ 1.2	
<b>Gelatinous plankton</b>			
<i>Liriope tetraphylla</i> (5)	9.1 $\pm$ 2.4	-17.2 $\pm$ 0.8	
<i>Lychnorhiza lucerna</i> (5)	12.2 $\pm$ 0.7	-17.2 $\pm$ 0.2	
<i>Chrysaora lactea</i> (4)	13.0 $\pm$ 0.1	-15.9 $\pm$ 0.5	
<i>Mnemiopsis</i> sp. (8)	13.1 $\pm$ 2.4	-17.2 $\pm$ 0.6	
<b>Benthos</b>			
<i>Macra isabelleana</i> (3)	9.5 $\pm$ 0.6	-18.3 $\pm$ 0.3	
<i>Rapana venosa</i> (3)	12.6 $\pm$ 0.4	-15.3 $\pm$ 0.0	
<b>Terrestrial plant</b>			
<i>Spartina alterniflora</i> (3)	7.9 $\pm$ 0.3	-13.0 $\pm$ 0.1	

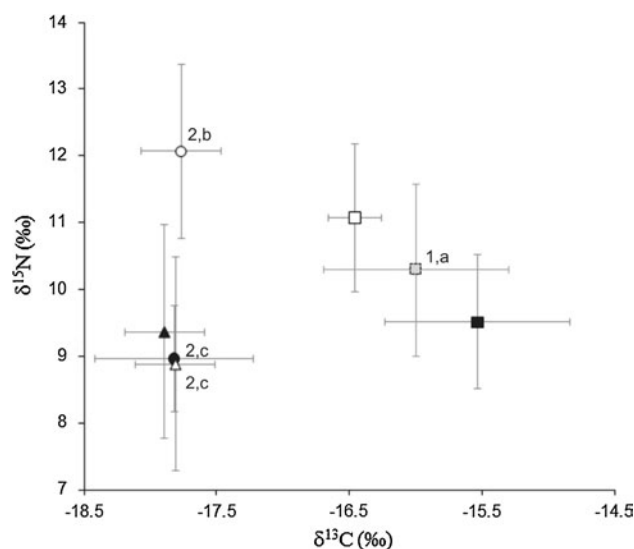
Information on prey came from previous studies (Botto et al. 2011; Gaitán 2012). Letters and numbers indicate a post hoc comparison for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in green turtle tissue, respectively. Numbers between parentheses indicate sample size

SD one standard deviation

consumers (like the mysid crustacean *Neomysis americana* and the planktivorous fish *Brevoortia aurea*, Fig. 3). In this context, putative prey of *C. mydas* in Samborombón Bay were: the hydromedusae *L. tetraphylla* and the bivalve *Macra* sp.

### Mixing model

The model was constructed with the following prey: the jellyfish *L. lucerna*, *C. lactea* and *L. tetraphylla*, the ctenophore *Mnemiopsis* sp., the terrestrial plant *Spartina alterniflora* and the bivalve *Macra* sp., chosen according to results from the digestive tract examinations and stable isotope analysis. The model indicated an animal matter-dominated diet. The gelatinous plankton contributed substantially to the diet of *C. mydas*, with an overall modelled mean proportion of 48.8 % (Fig. 4). In particular,



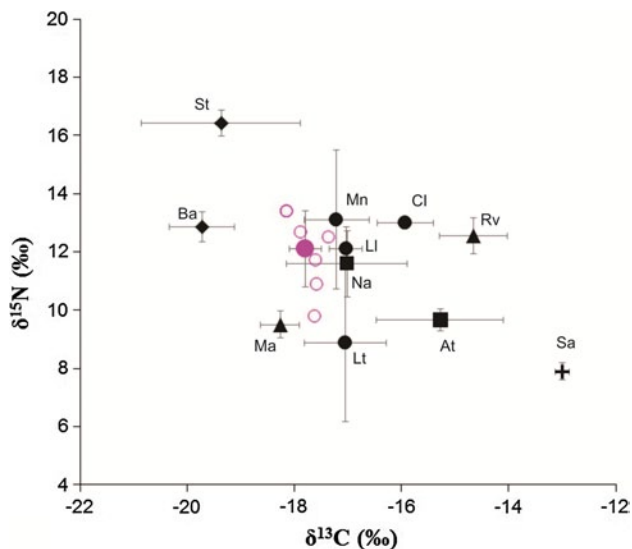
**Fig. 2** Bivariate plot of isotopic values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of blood plasma (open circle), whole blood (full triangle), red blood cells (open triangle), muscle (full circle) and epidermis (open square: live animals; full black square: dead animals; full grey square: live and dead animals) of juvenile green turtles from Samborombón Bay, Argentina. Bars indicate one standard deviation (see values in Table 2). Letters and numbers indicate a post hoc comparison of green turtle tissue for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively

*L. tetraphylla* had a modelled mean proportion of 23.8 % and proportional distributions of feasible contribution ranging from 0.8–55.5 %. *L. lucerna*, *Mnemiopsis* sp. and *C. lactea* would have minor contributions. *Macra* sp. also had an important contribution to the turtle diet with a modelled mean proportion of 47.6 % and proportional distributions of feasible contribution ranging from 17.1–75.5 %. *Spartina alterniflora* had the minimum contribution of all putative prey (mean = 3.5 %, 1–99 % = 0.1–12.6). The matrix correlation plot showed that only the posterior distributions of *L. tetraphylla* and *Macra* sp. were negatively correlated ( $r = -0.67$ ).

## Discussion

### Assessment of diet through a combination of techniques

Through the combined use of DTE and SIA, we determined that juveniles of *Chelonia mydas* have an animal matter-dominated diet while foraging in the study area. Gelatinous plankton was consumed in large proportions compared to herbivorous food items such as terrestrial plants and macroalgae. To our knowledge, this is the first study to employ this combination of techniques and to conclusively demonstrate that animal matter, in particular gelatinous plankton, is important in the diet of the neritic green sea turtles.



**Fig. 3**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of blood plasma for juvenile green turtles ( $n = 7$ ) and their putative prey sampled in Samborombón Bay, Argentina. Pink full circle indicates the mean value and pink open circles the individual values. Squares represent non-gelatinous plankton organisms (Na: *Neomysis americana*, At: *Acartia tonsa*), diamonds are planktivorous fish (St: *Stromateus brasiliensis*, Ba: *Brevoortia aurea*), triangles are benthic organisms (Rv: *Rapana venosa*, Ma: *Mactra* sp.), crosses are terrestrial plants (Sa: *Spartina alterniflora*) and circles are gelatinous plankton organisms (Mn: *Mnemiopsis* sp., Cl: *Chrysaora lactea*, Lt: *Liriope tetraphylla*, Ll: *Lychnorhiza lucerna*). Points indicate the mean value and bars one standard deviation (see values in Table 2)

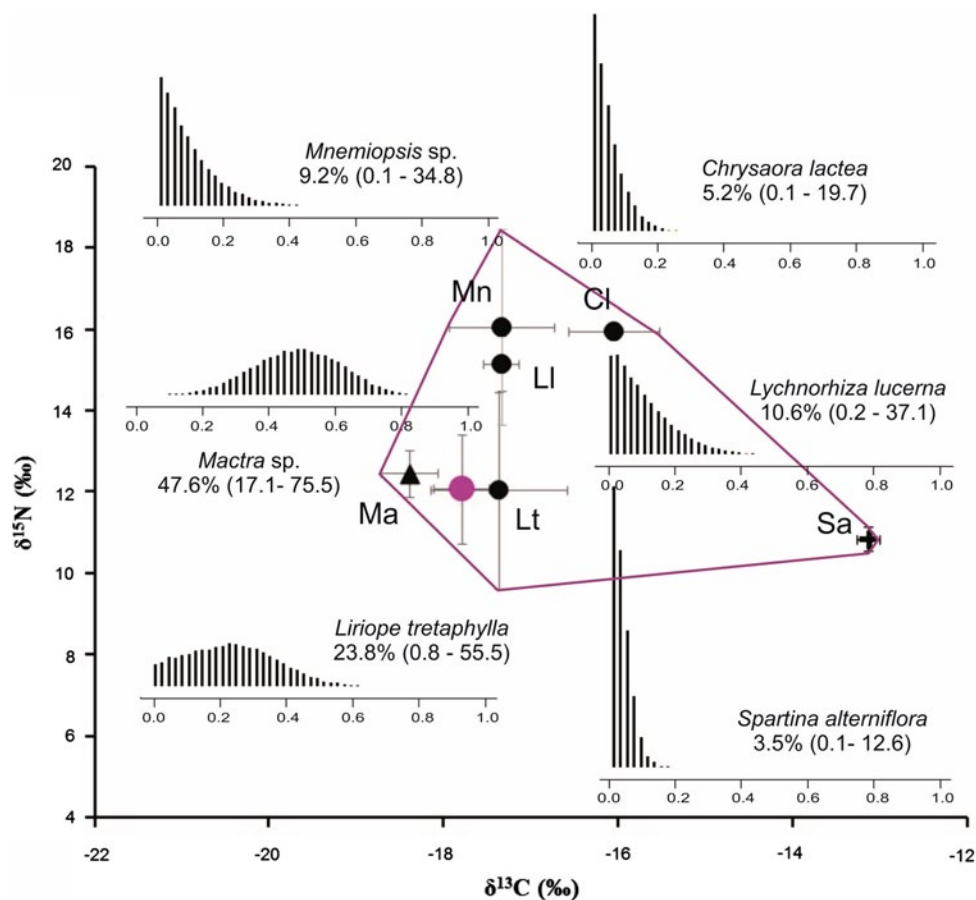
The comparison between the isotopic composition of epidermis and blood plasma (reflecting an early and later diet, respectively) gives insight into the feeding behaviour of *C. mydas*. Since C isotopic values exhibit a latitudinal gradient (Cherel and Hobson 2007), the fact that the epidermis was enriched in  $^{13}\text{C}$  suggests that juveniles occupy northern neritic habitats previous to arrival at the Río de la Plata (Fig. 2). In those habitats, the turtles might have consumed macroalgae. This is suggested by the  $\delta^{15}\text{N}$  value of the epidermis (10.3 ‰), which can be obtained considering a  $\delta^{15}\text{N}$  value of macroalgae in southern Brazil and Uruguay of 7.3 ‰ (Corbisier et al. 2006; Rodríguez Graña et al. 2008) and an epidermis enrichment factor of 2.8 ‰ (Seminoff et al. 2006). Epidermis from live and dead turtles differed in their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. We did not expect this difference because we obtained both types of animals from gillnets set near the coastline. We did not work with dead animals that could have been stranded at the beach for several days or weeks before sampling. Moreover, the time of sampling never exceeded a day, so it is unlikely that a change in skin composition of dead turtles occurs within such a short-time frame. We hope that future research could account for this difference.

Once in the Río de la Plata, the mixing model indicated that the gelatinous plankton contributed ca. 50 % to the diet of turtles, with *L. tetraphylla* as main contributor (Fig. 4). The consumption of gelatinous plankton was confirmed through the observation of nematocysts in the mucous material found in the digestive tracts. The nematocysts we observed are present in the jellyfish *Liriope tetraphylla*, *Chrysaora lactea*, *Olindias sambaquiensis* and *Lychnorhiza lucerna* at least, although we cannot dismiss the consumption of other jellyfish species with the same type of nematocyst that also occur in the area. Burkholder et al. (2011) also observed that the diet of juvenile green turtles from Australia could rely on gelatinous plankton and seagrass as evidenced by the stable isotope values of the epidermis. But, they were not able to confirm the presence of gelatinous plankton through oesophageal lavages.

Other items in the diet of *C. mydas* foraging in the Río de la Plata were molluscs and terrestrial plants. The consumption of the bivalve *Mactra* sp. was determined by DTE and SIA. To date, bivalves have been observed only in the diet of East Pacific green turtles (Seminoff et al. 2002). However, this is the first time that *Mactra* sp. is described as a food source for green turtles. Posterior correlation plots showed a negative correlation between *L. tetraphylla* and *Mactra* sp. distributions suggesting that one or other prey, but not both at the same time, occur. Considering that the gelatinous mucous was most important than *Mactra* sp. in the digestive tract examination (Table 1), it is possible that the amount of gelatinous plankton is underestimated by the model given that the two prey have similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. With respect to the gastropod *Heleobia* sp., its small size (<5 mm) and low % $W_{\text{ind}}$  suggest that it could be consumed incidentally along with another food item, despite being frequently observed. The terrestrial plant *Spartina* sp. was also found in the digestive tracts, although the mixing model did not show evidence that these plants contribute substantially to the nutrition of the turtles. Oesophageal lavages of juveniles from southern Brazil showed consumption of *Spartina alterniflora* and the mangrove *Avicennia schaueriana* (Nagaoka et al. 2012). But, given the high lignin composition of terrestrial plants compared to seagrass (Dawes 1986), it is possible that the consumption of *Spartina* sp. does not lead to a nutritional gain. Besides, *Spartina* sp. would not contribute substantially to the de Río de la Plata food web (Botto et al. 2011).

Mixing models can be sensitive to discrimination factors, elemental concentrations and digestibility of prey. In particular, discrimination factors depend on the species, life stage, tissue analysed and diet isotopic composition (Caut et al. 2009; Bond and Diamond 2011; Vander Zanden et al. 2012). In this study, we used discrimination factors estimated for juvenile green turtles of similar size maintained on a control diet (Seminoff et al. 2006). We did not

**Fig. 4** Results from the SIAR model showing green turtle trophic space formed by its putative prey (plotted values corrected by discrimination factors from Seminoff et al. 2006). Frequency distribution (mean and 1–99 % percentiles) represents feasible proportions of each prey to the diet of the turtles for all solutions. Ma: *Maetra* sp., Mn: *Mnemiopsis* sp., Cl: *Chrysaora lactea*, Lt: *Liriope tetraphylla*, Ll: *Lychnorhiza lucerna*. Points indicate the mean value and bars one standard deviation



used discrimination factors informed by Vander Zanden et al. (2012) because they were estimated for considerably larger animals. We could not account for the differences in C and N concentration or the digestibility of prey, so our results should be interpreted taking these limitations into consideration.

#### Costs and benefits of a gelatinous-dominated diet

Feeding on a low-energy food such as gelatinous prey (Doyle et al. 2007) is not unusual for sea turtles. For example, the leatherback turtle (*Dermochelys coriacea*) relies exclusively on gelatinous plankton (Bjorndal 1997), and it is known to feed on jellyfish in temperate waters (Houghton et al. 2006; Heaslip et al. 2012). Indeed, in the Irish Sea, Houghton et al. (2006) found that jellyfish hot spots were sufficiently consistent in space and time to drive long-term turtle foraging associations. This diet allows the species to undertake vast migrations across world oceans (James et al. 2005; Heaslip et al. 2012).

It seems that leatherbacks compensate for this energetically poor diet with a high consumption rate enabled by high prey availability (Heaslip et al. 2012). Feeding on gelatinous plankton in temperate waters of the SW

Atlantic—especially in the frontal area of the Río de la Plata (Mianzan and Guerrero 2000)—might also provide an opportunity for juvenile green sea turtles to have a high consumption rate of prey. Particularly, the abundance of the scyphomedusae *L. lucerna* can reach high biomass to an extent that a specific fishery may be developed in the region (Schariti 2008). The hydromedusae *L. tetraphylla* can also reach peak abundance of  $1.10^6$  individuals/m<sup>3</sup> during summer and autumn (Mianzan et al. 2000), coinciding with the occurrence of green turtles (González Carman et al. 2011). Indeed, it constitutes the 25 % of zooplankton biomass in dry weight during these months in the Samborombón Bay (Sorarrain 1998; Gaitán 2004). However, finding *L. tetraphylla* as potentially one of the most important prey items for green turtles was still unexpected as these hydromedusae are small (1–3 cm of bell diameter), and it is normally expected that prey size increases with predator size in marine ecosystems (Costa 2009). But even larger animals like adult leatherbacks can prey on small scyphomedusae such as *Linuche unguiculata* where it occurs in great abundance in the tropical waters of the Solomon Islands (Fossette et al. 2011).

Apart from being beneficial if consumed at high rates, preying on gelatinous plankton might be a way to avoid



intraspecific competition. It is possible that juvenile green turtles find high competition rates among conspecifics in northern foraging habitats where seagrass and macroalgae meadows are available and constitute the major part of green turtle diet (López-Mendilaharsu et al. 2006; Guebert-Bartholo et al. 2011). It is known that intraspecific competition decreases growth rate in juvenile green turtles (Bjorndal et al. 2000); therefore, this could be a reason why juvenile green turtles migrate seasonally to temperate habitats.

#### Juvenile green turtle behaviour in the SW Atlantic

Information on the habitat use and foraging ecology shows a putative foraging route used by juvenile green turtles in the SW Atlantic. After having an herbivorous diet in northern habitats, turtles arrive seasonally (from November to May) at the Río de la Plata where they prey on gelatinous plankton. It is possible that only a portion of the population takes advantage of this resource pressed by intraspecific competition. Even though gelatinous plankton is an energetically poor food, it is highly abundant and predictable (in time and space) in the Río de la Plata frontal zone (Mianzan and Guerrero 2000; Mianzan et al. 2001b; Alvarez Colombo et al. 2003). The turtles forage for at least 5 months in the estuarine area (González Carman et al. 2011, 2012). Later, they migrate to northern neritic habitats (e.g. coast of Uruguay and Brazil) to resume an herbivorous diet (López-Mendilaharsu et al. 2006; Guebert-Bartholo et al. 2011). Some animals also overwinter in oceanic areas where a benthic or an herbivorous diet is unlikely (González Carman et al. 2012), but where other gelatinous prey such as salps are available (Mianzan and Guerrero 2000; Mianzan et al. 2001a). Preying on gelatinous plankton should have some benefit at least, considering that some turtles return to the estuary in consecutive years (González Carman et al. 2012). Therefore, a flexible behaviour seems the rule for juvenile green turtles inhabiting the SW Atlantic, confirming that the ontogenetic shift undertaken by the turtles is not necessarily abrupt and irreversible in the region (González Carman et al. 2012).

To continue gaining insights into the foraging ecology and ontogenetic shift of the species, we recommend that future diet studies combine different techniques (e.g. SIA, DTE, underwater observations) to assess the importance of gelatinous plankton as food resource for green turtles throughout the species distribution range.

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