Spatial variation in the foraging behaviour of the Galapagos sea lions (*Zalophus wollebaeki*) assessed using scat collections and stable isotope analysis

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*This study focuses on the comparative analysis of variables related to the trophic niche plasticity in the Galapagos sea lion (*Zalophus wollebaeki*). There is great concern regarding the future of this species, so study of the diet and the way these animals obtain their food is useful to understand and predict their survival possibilities in the long term. The combined use of scat analysis and stable isotopes helps to determine foraging habits of this species in greater detail. The objective of the study was to assess the feeding habits of* Z. wollebaeki *and its space–time variation. The scat analysis (n = 200) gave as a result space–time changes in the foraging strategies of this species. The isotopic values (n = 80) showed differences in relation to foraging grounds ($\delta^{13}C$: P = 0.001), but also suggested an apparent stability in the trophic level of their diet ($\delta^{15}N$: P = 0.084). These results constitute a relevant finding in the evolutionary behaviour of the species, showing that* Z. wollebaeki *has developed a high degree of plasticity in its foraging habits that may improve its survival in a highly demanding ecosystem in terms of limited and fluctuating resources.*

INTRODUCTION

The Galapagos Islands are subject to environmental and oceanographic instability mainly due to the El Niño Southern Oscillation (ENSO), but despite this, they are home to two endemic otariid species: the Galapagos sea lion (*Zalophus wollebaeki*) and the Galapagos fur seal (*Arctocephalus galapagoensis*); species that require a lot of energy to meet their ecological and physiological needs (Costa *et al.*, 2006).

Fluctuations in regional marine productivity and oceanographic disturbances such as the ENSO have resulted in a population decrease of more than 50% for both species over the last 30 yr (Trillmich & Ono, 1991; Heath, 2002). This situation has led the International Union for Conservation of Nature (IUCN) to classify these species as endangered (Aurioles-Gamboa & Trillmich, 2008).

The oceanographic variability of the archipelago causes changes in marine ecosystem dynamics that are reflected from the bottom to the top of the trophic web (Palacios *et al.*, 2006; Schaeffer *et al.*, 2008). These changes cause top predators to respond by diversifying their foraging strategies (Villegas-Amtmann *et al.*, 2008; Baque-Menoscal *et al.*, 2012; Páez-Rosas *et al.*, 2012).

The diversity in foraging habits of marine predators may be caused by both extrinsic and intrinsic factors, including habitat quality, seasonal changes of marine productivity, age, sex and reproductive conditions (Villegas-Amtmann *et al.*, 2011). These changes are more evident in species inhabiting tropical zones, where productivity uncertainty is greater, which, in turn, cause changes in the abundance of prey species (Gentry & Kooyman, 1987).

Traditionally, the study of foraging habits in otariids has been based on analysis of stomach contents and scats. Both techniques are based on the recovery and identification of hard structures, such as fish otoliths and cephalopod beaks, which have a distinctive morphology, permitting prey species to be identified to the species level (García-Rodríguez & Aurioles-Gamboa, 2004; Tollit *et al.*, 2006). Of these techniques, scat analysis is very useful for studying an organism's diet, as a large quantity of samples can be collected quickly without hurting the organism.

This approach has been used to describe the feeding habits of *Z. wollebaeki* at different islands, indicating the consumption of both benthic and pelagic fish and, in smaller proportions, cephalopods (Salazar 2005). The diet consisted primarily of schooling epi-pelagic fishes such as sardines (*Sardinops sagax*) in the western region (Dellinger & Trillmich 1999), and other benthic and pelagic species

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like the sand bass and the bigeye scad (*Paralabrax* spp. and *Selar crumenophthalmus*) at the other end of the archipelago (Páez-Rosas & Aurioles-Gamboa, 2010). Therefore the diet of *Z. wollebaeki* is composed of a wide variety of prey, from both benthic and pelagic environments, which may vary geographically (Salazar, 2005; Páez-Rosas, 2011). Villegas-Amtmann *et al.*, (2008) using satellite telemetry studies and dive records, found different feeding strategies (epipelagic, mesopelagic and benthic) in the rookery of Caamaño located in the central region of the archipelago, suggesting that this species has the ability to diversify its feeding habits to an inter-population and intra-population level.

The isotopic variation analysis of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) has become an important tool for studying the foraging habits of marine predators. This technique allows the researcher to infer the habitat of a consumer ($\delta^{13}C$) (DeNiro & Epstein, 1978) and the trophic level at which it is feeding ($\delta^{15}N$) (DeNiro & Epstein, 1981). Regarding the $\delta^{15}N$, this bioaccumulates between a consumer and its prey (Post, 2002; Bearhop *et al.*, 2004), resulting in an average increase in isotopic enrichment in ^{15}N from 3 to 5‰ between trophic levels (Minagawa & Wada, 1984). A similar effect is produced for $\delta^{13}C$; however, the average enrichment varies from 0.5 to 1‰ between trophic levels (Hobson *et al.*, 1996).

Physicochemical and biological factors determine the differences in baseline $\delta^{13}C$ values between habitats (coastal/ocean or pelagic/benthic), including the isotopic composition and concentration of dissolved CO_2 available to primary producers (Hobson *et al.*, 1996; France, 1995); the taxonomic composition and growth rate of phytoplankton (Fry & Wainwright, 1991; Pancost *et al.*, 1997); and the influence of carbon derived from benthic macrophytes in coastal zones that are ^{13}C-enriched compared to phytoplankton in open-ocean pelagic environments (France, 1995).

The $\delta^{13}C$ values of primary producers may also vary among ocean basins, where pelagic ecosystems in high latitudes typically have much lower $\delta^{13}C$ values than pelagic ecosystems at lower latitudes. This difference is primarily because aqueous (CO_2) is high in colder regions, due to seasonally low photosynthetic rates caused by light and trace metal limitation, vertical mixing of a weakly stratified water column, and the greater solubility of CO_2 leads to lower $\delta^{13}C$ values (Graham *et al.*, 2010). These factors are related to the enzymatic activity of Ribulose-1,5-bisphosphate carboxylase oxigenase (RuBisCO), which catalyzes the CO_2 fixation process to an organic form, and the photorespiration on this substrate by the primary producers, generating a absorption of dioxide carbon into the cells and dissipating energy to the environment (Pancost *et al.*, 1997).

Nitrogen isotope compositions of primary producers set the $\delta^{15}N$ value at the base of the food web and are dependent upon the $\delta^{15}N$ values of their nutrient source (e.g., nitrate, ammonium, N_2). For instance, for offshore waters the $\delta^{15}N$ value of dissolved N_2 is near 0‰, and there is little isotopic fractionation associated with its biological uptake by phytoplankton; N_2-fixation generates organic matter with low $\delta^{15}N$ values (Montoya, 2010).

The latitudinal gradient and oceanographic activity produces changes in $\delta^{15}N$ values at the base of the trophic webs that are reflected in different predators, independent of trophic level (Aurioles-Gamboa *et al.*, 2009); aspects which in turn are linked to the rate of N_2 fixation and denitrification levels in the trophic web (Sigman *et al.*, 2005). This effect may be related to a decrease in the primary productivity of the environment, causing a cascading reduction in the general biomass resource and leading to changes in the importance of the main prey species of the predators to varying degrees, depending on the region (Bearhop *et al.*, 2004; Newsome *et al.*, 2010).

In this study, analysis of scats and stable isotopes in the fur of the Galapagos sea lion, *Zalophus wollebaeki*, were used to determine the degree of complexity in the foraging behaviour of this species at a spatial level.

MATERIALS AND METHODS

The regional biogeography of the Galapagos archipelago proposed by Harris, (1969) and Ruttenberg *et al.*, (2005) was considered to identify a possible spatial pattern in the foraging habits of *Zalophus wollebaeki*. Four breeding rookeries, representing each region, were monitored: Cabo Douglas–Western (0°18′S 91°39′W), Caamaño–Central (0°45′S 90°16′W), Post Office–Southern (01°13′S 90°36′W), and Malecón–Eastern (0°54′S 89°36′W) (Figure 1).

Scat analysis

In March 2009, 50 scat samples were collected in each rookery, with a preference for areas where the females were predominant (55.5%). Each sample was kept in a hermetically sealed plastic bag and labeled with the date and collection site. The samples were sifted with sieves of different mesh size (2.0, 1.2 and 0.7 mm). Structures, including fish otoliths and cephalopod beaks, were collected and used to identify prey species using a stereoscope and specialized literature (García-Godos, 2001; Díaz-Murillo, 2007).

The function proposed by Ferry *et al.*, (1997) and applied in previous studies for this species (Porras-Peters *et al.*, 2008; Páez-Rosas & Aurioles-Gamboa, 2010) was used for estimating the sample size representative of the potential spectrum of prey consumed in each area and season by sea lions. The method consists of calculating the accumulated average and standard deviation of a group of diversity curves generated from prey abundance data, through the Shannon–Wiener *H'* Index (Krebs, 1999). The diversity curves are derived from a function designed in the MATLAB program, which computes 500 permutations at random with all the original data and a 0.05 margin of error. This error is obtained from the data's coefficient of variation and is measured when the accumulated average reaches an asymptote that identifies the appropriate sample size needed to characterize the diet of each rookery.

We used the Index of Importance (IIMPi) to determine the composition of the diet (García-Rodríguez & Aurioles-Gamboa, 2004). The IIMPi measures the importance of prey in each sample unit of scat and includes the probability of finding that prey in a collection of scat. The index generates results from 0 to 1 that are converted into percentages (IIMPi × 100). The degree of trophic overlap between the rookeries was calculated through the Morisita–Horn Index (*Cλ*) (Krebs, 1999), which defines the shared use of food resources between two or more populations (Horn, 1966).
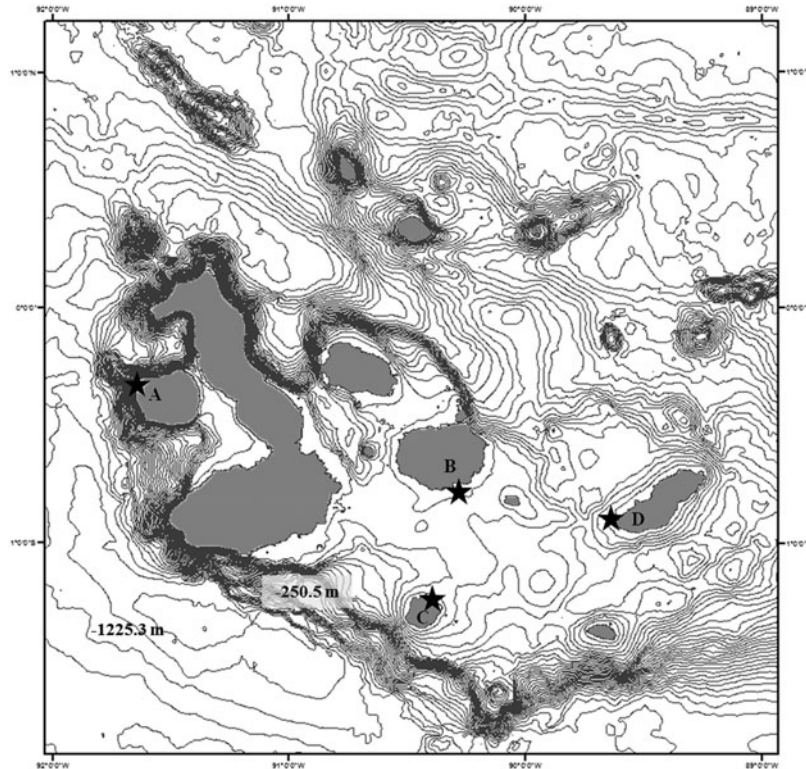
Fig. 1. Collection sites for samples of Galapagos sea lion fur and scat in breeding rookeries: (A) Cabo Douglas (0°18′S 91°39′W) Fernandina Island; (B) Caamaño (0°45′ 90°16′W) Santa Cruz Island; (C) Post Office (01°13′S 90°36′W) Floreana Island; and (D) Malecón (0°54′ 89°36′W), San Cristóbal Island.

Stable isotope analysis

In March 2009 a total of 80 fur samples were collected from pups of approximately two months of age in the four rookeries under study: Cabo Douglas ($n = 20$), Caamaño ($n = 20$), Post Office ($n = 20$), and Malecón ($n = 20$). The age of the pups was calculated based on the growth rate (108 g d^{-1}) reported for this species (Trillmich & Wolf, 2008).

Each sample was rinsed with deionized water to remove residue that interferes with the isotopic signal. Subsequently, the samples were dried in an oven at 80°C for 12 h, and the lipids were extracted using the microwave assisted extraction (MAE) protocol (Microwave Oven Model 1000 MARS 5 × CEM) with 25 ml of chloroform/methanol (1:1) solution (Bligh & Dyer, 1959). This process was applied because the lipids are enriched in ^{12}Crelative to proteins, so in large quantities could negatively skew the isotopic signal of ^{13}C (Tieszen *et al.*, 1983). The sample was homogenized to a fine powder in an agate mortar; then ~0.5 mg of sample was weighed and placed in tin capsules for δ^{15}N and δ^{13}C analysis.

The isotopic ratios were measured using a continuous flow mass spectrometer (20-20 PDZ Europa, Chester, UK) in the Stable Isotopes Laboratory at the University of California at Davis (Davis, USA). The results were expressed in parts per thousand (‰) using the following equation:

$$\delta^{13}C \text{ o } \delta^{15}N = 1000[(R_{sample}/R_{standard}) - 1],$$

where R_{sample} and $R_{standard}$ are ^{13}C/^{12}C or ^{15}N/^{14}N ratios of the sample and standard, respectively. The standards were PDB (Pee Dee Belemnite) for δ^{13}C and the atmospheric N$_2$ for δ^{15}N.

Significant differences in the δ^{15}N and δ^{13}C values between rookeries were evaluated using a nonparametric analysis of variance (Kruskal–Wallis test) along with the Fisher's LSD test for multiple comparisons. Significance was defined as $P < 0.05$ level. Statistica 8.0 software was used to perform the statistical analysis.

RESULTS

Scat analysis

The diversity curves derived from scat samplings in the sea lion rookeries reached the asymptote between 38 and 48 scats, revealing that the sample size established *a priori* in each rookery (50 scats) was sufficient to describe the composition of the diet of *Zalophus wollebaeki* at each site and for that period of time (Figure 2).

Diet composition

Out of the four rookeries sampled, Cabo Douglas (western region) showed the largest trophic spectrum with 16 prey species (15 fish and one cephalopod). The Post Office rookery (southern region) showed 15 prey species (fish only), Caamaño (central region) 14 prey species (13 fish and one cephalopod) and Malecón (eastern region) 12 prey species (fish only). Of these prey 69.3% were identified to the species level, 26.9% to the genus level, and 3.8% to the family level (Table 1).

Several of the prey species were incidental as reflected by their low percentage of importance, therefore, only prey
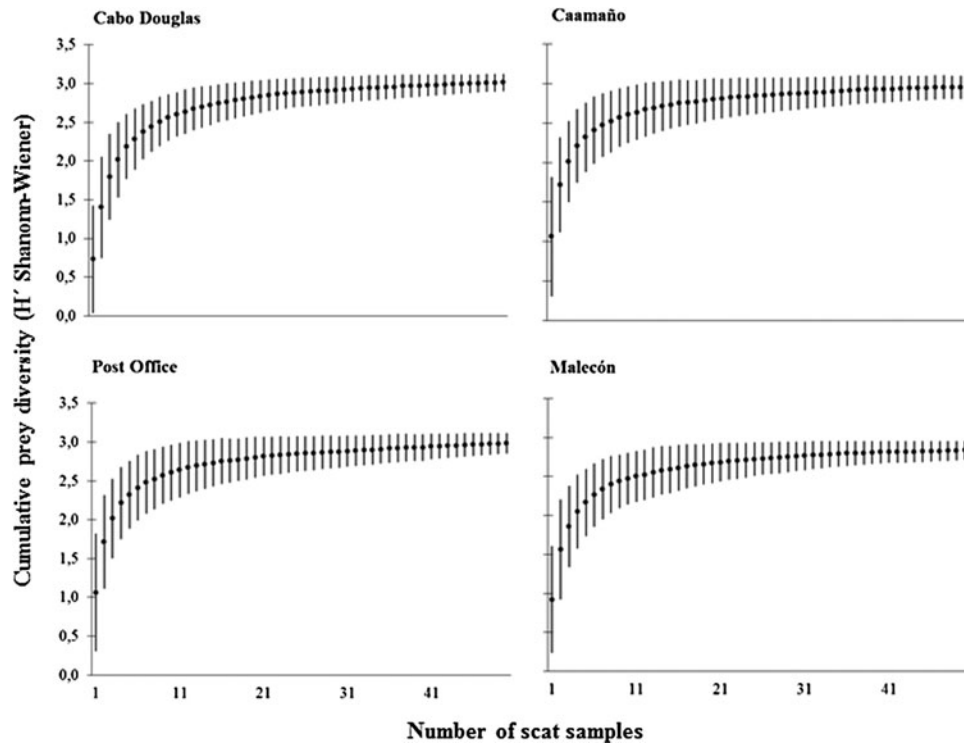
Fig. 2. Prey diversity curves (average ± SD) representing the diet of the Galapagos sea lion. Prey diversity is based on Shannon–Wiener (H′). The curves were generated from abundance data of the prey species identified in scat samples in each rookery.

Table 1. Index of Importance (IIMPi) values of prey identified in Galapagos sea lion scat samples collected in March 2009 in four rookeries of the archipelago.

No.	Prey species	IIMPi (%)				Prey habitat
		Cabo Douglas (Western)	Caamaño (Central)	Post Office (Southern)	Malecón (Eastern)	
1	*Anisotremus caesius*			5.07		Demersal
2	*Alphestes immaculatus*				1.17	Demersal
3	*Caulolatilus* sp.	0.56				Reef
4	*Chilara taylori*	0.97	23.85	6.63		Benthic
5	*Diplectrum* sp.	5.63		0.11		Reef
6	*Haemulon* sp.		0.23			Demersal
7	*Hemanthias* sp.			0.78		Reef
8	*Mastigoteuthis dentata*	0.04				Mesopelagic
9	*Maurolicus muelleri*	29.97				Mesopelagic
10	*Merluccius* sp.	0.29				Epipelagic
11	Myctophidae	48.87	41.67	0.09	4.01	Mesopelagic
12	*Octopus* sp.		0.43			Demersal
13	*Ophichthus triserialis*		1.21	0.30		Demersal
14	*Opisthonema berlangai*	0.77	0.86		31.39	Epipelagic
15	*Opistognatus punctatus*		0.86		12.69	Reef
16	*Otophidium indefatigable*	0.39	11.21	2.06		Benthic
17	*Paralabrax* sp.	0.18	1.84	15.17	34.22	Reef
18	*Paranthias colonus*	1.91	4.48	0.14		Reef
19	*Physiculus talarae*	6.04		1.65	0.67	Benthic
20	*Pontinus clemensi*	4.24		21.55	6.01	Benthic
21	*Pronotogrammus multifasciatus*	0.04	5.75	26.12	0.17	Benthic
22	*Selar crumenophthalmus*		4.89	7.95	5.84	Epipelagic
23	*Serranus aequidens*		0.43		0.83	Benthic
24	*Synodus lacertinus*	0.03		9.10	1.67	Reef
25	*Vinciguerria lucetia*	0.07		3.29	1.34	Mesopelagic
26	*Xenichthys agassizi*		2.30			Reef

species that exceeded 2% in the IIMPi were considered as main prey. Based on this criterion, five main preys were identified in Cabo Douglas; the myctophid fish (Myctophidae) were the most important (48.8%), followed by *Maurolicus muelleri* (29.9%). At Caamaño, seven main prey species were identified, with myctophid fish (41.6%) and *Chilara taylori* (23.8%) as the dominating components in the diet. At Post Office nine main prey species were present, of which *Pronotogrammus multifasciatus* (26.1%) and *Pontinus clemensi* (21.5%) were the most important. The diet of sea lions at Malecón was dominated by *Paralabrax* spp. (34.2%) and *Opisthonema berlangai* (31.3%) (Figure 3).

Spatial trophic overlap

The Morisita–Horn Index ($C\lambda$) (Krebs 1999) indicated that there was no significant trophic overlap between the four rookeries ($C\lambda$ = 0.10 to 0.26) (Table 2), suggesting that the selected *Z. wollebaeki* rookeries representing the distinct regions of the Archipielago had distinct feeding habits.
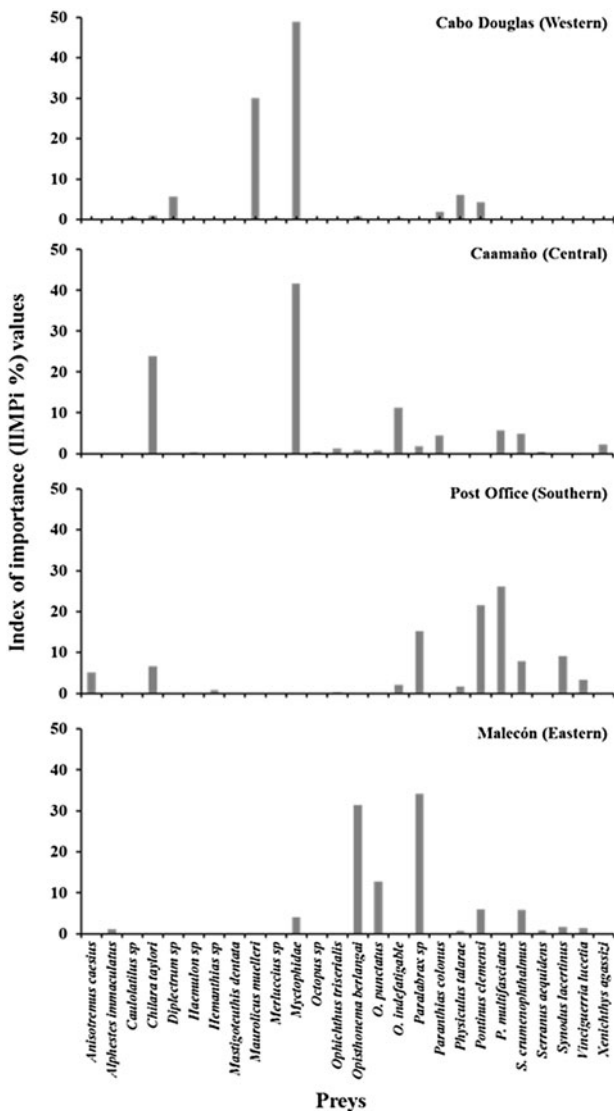

Fig. 3. Index of Importance (IIMPi) values of the main prey (≥1%) identified in Galapagos sea lion scat samples collected in March 2009 in four rookeries representing different regions of Archipelago.

Table 2. Trophic overlap values among Galapagos sea lion rookeries corresponding to different regions of the archipelago. The trophic overlap is based on the Morisita–Horn ($C\lambda$) index. The distance (km) between the analysed pairs of rookeries is shown in parenthesis above the diagonal.

Rookery	Rookeries			
	Cabo Douglas	Caamaño	Post Office	Malecón
Cabo Douglas	–	(162.2 km)	(168.3 km)	(237.8 km)
Caamaño	0.13	–	(51.5 km)	(76.1 km)
Post Office	0.09	0.16	–	(101.1 km)
Malecón	0.10	0.16	0.26	–

Stable isotope analysis

A comparison of $\delta^{13}C$ values among the four sea lion rookeries showed significant differences (Kruskal–Wallis: H $(3,4)$ = 46.81, P = 0.001). Cabo Douglas was significantly different from Caamaño, Post Office and Malecón (all Fisher's LSD: $P < 0.05$) (Figure 4 and Table 3). The $\delta^{15}N$ signal showed a similar trend to the $\delta^{13}C$ values, however the differences between the four rookeries were not significant (Kruskal–Wallis: H $(3,4)$ = 6.64, P = 0.084) (Figure 4 and Table 3).

DISCUSSION

Spatial variation of the foraging habits of *Zalophus wollebaeki*

The observed spatial differences in the diet of the Galapagos sea lion suggests the presence of specific foraging areas with distinct prey components for each rookery where all trophic spectra were represented by a limited group of prey. Cabo Douglas, in the western region, had the greatest diversity of prey species (16), which may have been related to bathymetric conditions (deep waters >2000 m) and the prevalence of blooms in this region of the archipelago (Banks, 2002; Palacios *et al.,* 2006).

Myctophid fish were the main prey of the western and central rookeries of the archipelago (Cabo Douglas and Caamaño, respectively). Myctophids typically migrate from deep waters (300–1200 m), which inhabit during the day, to shallower waters (10–100 m) at night (Nelson, 2006). The broad distribution and abundance of these species makes them one of the main preys of various marine predators
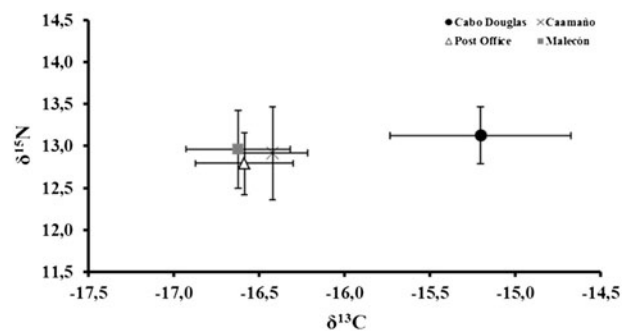

Fig. 4. $\delta^{13}C$ and $\delta^{15}N$ values (mean $\pm$ SD (‰)) from fur samples of Galapagos sea lion pups collected in different rookeries of the archipelago in March 2009.

Table 3. $\delta^{13}C$ and $\delta^{15}N$ values (mean $\pm$ SD (‰)) from fur samples of Galapagos sea lion pups collected in different rookeries of the Galapagos Islands during March 2009.

Rookery	Island	Region	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Cabo Douglas	Fernandina	Western	20	-15.20 ± 0.53	13.12 ± 0.34
Caamaño	Santa Cruz	Central	20	-16.42 ± 0.20	12.92 ± 0.56
Post Office	Floreana	Southern	20	-16.59 ± 0.29	12.79 ± 0.36
Malecón	San Cristobal	Eastern	20	-16.62 ± 0.31	12.96 ± 0.46
	Average			-16.20 ± 0.33	12.94 ± 0.43

(Dellinger & Trillmich, 1999; Osman *et al.*, 2004). However, the complementary preys were different for each site. The second most important prey at Cabo Douglas was the Mueller's pearlside fish (*Maurolicus muelleri*), which is a member of the Sternoptychidae family show similar dial migration as the myctophids (Grove & Lavenberg, 1997). The spotted cusk-eel (*Chilara taylori*) was the most important prey at Caamaño; it is a benthic fish which makes burrows in the sand and requires soft bottom substrates (Grove & Lavenberg, 1997).

The ecological characteristics of the main prey from the southern and eastern rookeries (Post Office and Malecón, respectively) contrast with those of the two above-mentioned regions. The main prey at Post Office was the threadfin bass (*Pronotogrammus multifaciatus*), and at Malecón the sand bass (*Paralabrax* sp). Both species are demersal and tend to prefer rocky substrates near the coast (Grove & Lavenberg, 1997). Similar to the western and central rookeries, the complementary prey distinguished the diet from these sites. The second most important prey at Post Office was the mottled scorpionfish (*Pontinus clemensi*), a demersal species that forms dispersed diurnal and nocturnal shoals, mainly among rocks (Grove & Lavenberg, 1997); also the Galapagos thread herring (*Ophistonema berlangai*) was the second most important prey at Malecón, an epipelagic clupeid that tends to form both small and large shoals close to the coast (Canales *et al.*, 2003).

Our results concur with those of other authors, such as Dellinger & Trillmich, (1999) who stated that the diet of *Z. wollebaeki* in the western rookeries is comprised of sardines (epi-pelagic prey), complemented with some other species such as myctophids (meso-pelagic prey). Our results were also consistent with those of Salazar, (2005), who identified the diet preferences of Galapagos sea lions at distinct rookeries, noting that the central rookeries consumed mainly fish of the families Myctophidae, Clupeidae and Ophidiidae (meso, epi-peleagic and benthic preys), while the southern and eastern rookeries feed on fish from the Serranidae and Clupeidae families, such as threadfin bass, sand bass and Galapagos thread herring (benthic and epi-pelagic prey).

Among other features, the topography of each region of the archipelago seems to influence the foraging preferences of sea lions. For example, the Cabo Douglas rookery (western region) on Fernandina Island, where the continental shelf is shortest and is surrounded by very deep waters (>2000 m) (Banks, 2002), presented the greatest affinity for prey from mesopelagic environments. Conversely, in the rookeries of Post Office (southern region) and Malecón (eastern region) on Floreana and San Cristóbal islands respectively, there is a continental shelf that is shallower than in other parts of the archipelago (~600 m) (Banks, 2002), which allows the sea lions to explore diverse environments and consume demersal and benthic fish.

Trophic overlap

The scat analysis revealed a low trophic overlap between the rookeries, which was expected between Cabo Douglas (western region) and Malecón (eastern region) due to the large distance separating them (237 km). However, these differences were maintained even among the closer rookeries, such as Caamaño (central region) and Post Office (southern region) separated by *ca* 51 km.

Some studies suggest that the Galapagos sea lion may perform foraging trips of approximately 46 km (average) (Kooyman & Trillmich, 1986, Villegas-Amtmann *et al.*, 2008, Páez-Rosas, 2011), so it would be expected that individuals of Caamaño could forage in the same areas as the individuals from the rookeries of Post Office and Malecón, leading to a potential trophic overlap. Nonetheless, there is evidence of specialized trophic behaviour in *Z. wollebaeki* (Villegas-Amtmann *et al.*, 2008; Páez-Rosas & Aurioles-Gamboa, 2010), which may influence the trophic differences observed between Caamaño and the rookeries of Post Office and Malecón.

Spatial isotopic variation

Many factors, such as dietary composition, habitat and oceanographic conditions of the ecosystem, affect the isotopic signal of marine predators (Sigman *et al.*, 2005; Newsome *et al.*, 2010). The $\delta^{13}C$ values from Galapagos sea lions in our study indicate the existence of spatial differences in the sea lion diet around the archipelago, mainly between the western region and the rest of the islands. These findings convey a spatial variation regarding the foraging habitats exploited by the individuals of each region (Hobson *et al.*, 1996; Newsome *et al.*, 2007).

According to the $\delta^{13}C$ values determined for each rookery, we can infer that sea lions from Cabo Douglas (western region), direct their foraging trips toward coastal environments (^{13}C enriched carbon isotope values), unlike sea lions of Caamaño, Post Office and Malecón which feed in oceanic areas (lower ^{13}C values) (Hobson *et al.*, 1996; Newsome *et al.*, 2007). However, a discrepancy occurs upon relating these results with the composition of the diet. Although the main prey species that comprise the diet of Cabo Douglas (Myctophidae and Clupeidae families) are solely pelagic, the principal prey speciess observed in the rest of the rookeries were benthic species (Serranidae and Scorpenidae families). This finding suggests that the carbon isotopic differences

between the rookeries do not result from the diet, but are related to the oceanographic characteristics of each region.

There is some divergence in the equatorial blooms, which are associated with the intensity of the wind and the equatorial sub-stream, causing differences from the equator to the west of the Galapagos Islands (Pak & Zaneveld, 1973). Previous studies that monitored the concentrations of chlorophyll-*a* have suggested that the western region of the archipelago presents an elevated annual production ($10-30$ mg Chl-*a* m^{-3}), while the rest of the archipelago has the lowest average production ($1-5$ mg Chl-*a* m^{-3}) (Banks, 2002; Palacios *et al.,* 2006).

There is an isotopic enrichment in the δ^{13}C values which is produced from the increase in frequency of blooms and the cellular growth rate of phytoplankton (Pancost *et al.,* 1997; Cullen *et al.,* 2001). The elevation in the primary productivity levels generates an increase in phytoplankton biomass and, therefore, its respiration capacity, resulting in high CO$_2$ absorption from the aqueous environment. Phytoplankton blooms tend to enrich the ^{13}C signal, even though the high levels of photosynthesis cause a rapid use and decrease of CO$_2$ (enriched in ^{12}C). In this process, there is discrimination towards ^{13}C, and subsequently the δ^{13}C values are enriched in the primary producers and the higher trophic levels (Bidigare *et al.,* 1997, Schell *et al.,* 1998).

Significant spatial differences were not observed in the δ^{15}N values, which can be explained in three ways: (a) the sea lions of distinct regions consume the same variety of prey species, but in different proportions, resulting in similar δ^{15}N average values (Bearhop *et al.,* 2004; Newsome *et al.,* 2010); (b) the sea lions of these rookeries feed on different prey, but of a similar trophic level (Vander-Zanden & Rasmussen, 1999; Post, 2002); and (c) the sea lions of distinct regions feed in different trophic levels, but these differences are not apparent due to the variability in the isotopic baseline (due to different oceanographic conditions and productivity levels) present in each food web (Aurioles-Gamboa *et al.*, 2009).

Nonetheless, at least two different isotopic areas have been reported in the Galapagos Islands (Aurioles-Gamboa *et al.,* 2009). The first area is located to the west of the archipelago, and the second area is in the southern region. These differences can be associated with topographic characteristics and distinct productivity levels occurring in each area. Our results follow the trend proposed by Aurioles-Gamboa *et al.,* (2009): the Cabo Douglas (western region) and Post Office (southern region) rookeries have higher and lower δ^{15}N values, respectively.

Isotopic differences occur between zones with contrasting oceanographic and topographic characteristics. The majority of deep ocean areas (>2 km) are homogenous in terms of nitrogen sources (nitrates), where the δ^{15}N values are relatively high (approximately 5‰) compared to the shallower areas, where the primary source is the atmospheric nitrogen (N$_2$), which presents lower δ^{15}N values ($\sim-2-0$‰) (Sigman *et al.,* 2005). These factors could be associated with the conditions in the archipelago, where there are spatial differences in levels of upwelling present in the deep zones and in the continental shelf. The western region has the highest productivity and the deepest waters (>2 km) (conditions which generate higher values ^{15}N) compared to the rest of the archipelago (~700 m) (lower values ^{15}N because the main contribution is atmospheric nitrogen), which could

influence biological nitrogen fixation and the denitrification processes of these regions.

The results of this work contribute to our understanding of how a vulnerable species has facilitated its survival by developing foraging strategies that diminish competition in the face of an environment with strong fluctuations in productivity.

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