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Competition influence in the segregation of the trophic niche of otariids: a case study using isotopic bayesian mixing models in Galapagos pinnipeds

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RATIONALE: The feeding success of predators is associated with the competition level for resources, and, thus, sympatric species are exposed to a potential trophic overlap. Isotopic Bayesian mixing models should provide a better understanding of the contribution of preys to the diet of predators and the feeding behavior of a species over time.

METHODS: The carbon and nitrogen isotopic signatures from pup hair samples of 93 Galapagos sea lions and 48 Galapagos fur seals collected between 2003 and 2009 in different regions (east and west) of the archipelago were analyzed. A PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 continuous flow gas source mass spectrometer was employed. Bayesian models, SIAR and SIBER, were used to estimate the contribution of prey to the diet of predators, the niche breadth, and the trophic overlap level between the populations.

RESULTS: Statistical differences in the isotopic values of both predators were observed over the time. The mixing model determined that Galapagos fur seals had a primarily teutophagous diet, whereas the Galapagos sea lions fed exclusively on fish in both regions of the archipelago. The SIBER analysis showed differences in the trophic niche between the two sea lion populations, with the western rookery of the Galapagos sea lion being the population with the largest trophic niche area.

CONCLUSIONS: A trophic niche partitioning between Galapagos fur seals and Galapagos sea lions in the west of the archipelago is suggested by our results. At intraspecific level, the western population of the Galapagos sea lion (ZwW) showed higher trophic breadth than the eastern population, a strategy adopted by the ZwW to decrease the interspecific competition levels in the western region. Copyright © 2014 John Wiley & Sons, Ltd.

The level of competition for trophic resources is a key factor in facilitating the coexistence of species and, in turn, maintaining the structure of ecological communities.^[1] The various elements associated with the feeding behavior of marine predators, i.e., their feeding area, diving behavior, or diet structure, often differ among closely related species, even at an intraspecific level.^[2,3]

The feeding success of various marine predators is associated with their body size and their diving capacity.^[4] Overall, the diving strategies of marine mammals are determined by their oxygen and fuel stores and the rate of consumption resulting from their metabolism, which can be aerobic or anaerobic.^[4] Morphological characteristics set limits to the physiological behavior of marine predators and are key factors in establishing the trophic strategies of

species.^[4] For example, the diving capacity of fur seals measured in their aerobic dive limit is relatively smaller (1.6 to 1.7 min) than that of sea lions (2.3 to 3.8 min), and this imposes a constraint for the depth of the foraging dives of this species.^[5] Consequently, sympatric species with similar evolutionary origins are exposed to potential trophic overlap, which leads to strong competition for resources and may cause the displacement or loss of these populations.^[5,6]

The Galapagos sea lion (*Zalophus wollebaeki*) and fur seal (*Arctocephalus galapagoensis*) are a good case study because they are endemic species to the Galapagos Islands with similar evolutionary origins (Otariidae family), and the two species are distributed differentially in the archipelago yet coexist in the western region, where they reproduce in sympatric conditions.^[7]

The *Z. wollebaeki* are distributed throughout the archipelago, with their primary settling colonies on the eastern islands (San Cristobal and Española), whereas *A. galapagoensis* exclusively inhabit the western islands (Isabela and Fernandina).^[8] Previous studies suggest that in zones where sympatry exists (Isabela and Fernandina islands), the two species occupy a similar ecological niche with small differences in feeding strategies.^[9,10] However,

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the population tendencies for both otariids have varied considerably in the last three decades.^[8] In the western region of the archipelago, an increase in the population of *A. galapagoensis* and a considerable reduction in the *Z. wollebaeki* population have been observed (D. Páez-Rosas, unpublished data).

The otariids from the Galapagos Islands are one of the few cases of adaptation to a subtropical environment, as in the Archipelago,^[11] where important fluctuations in their primary productivity exist and are driven by oceanographic events, such as the El Niño Southern Oscillation (ENSO),^[12] which has significantly decreased the populations of both species during the last 30 years.^[8,13] This situation has led the International Union for Conservation of Nature (IUCN) to list them as endangered species.^[14]

The feeding habits of the Galapagos pinnipeds have been moderately studied using mainly scat analysis.^[9,15] However, this technique incurs intrinsic temporal biases since it provides a single snapshot of the diet of each individual before sampling, which necessitates the use of complementary techniques.^[16]

In recent years, stable carbon and nitrogen isotopes have become a standard tool for investigating trophic ecology of wild animals, including pinnipeds.^[17,18] Although this technique offers less detailed information on dietary composition than scat analysis, an integrated measure of all assimilated food during a prolonged period of time is obtained.^[19] This technique allows trophic behaviors and feeding zones at the inter- and intra-population levels to be compared given the variations of the isotopic gradient present in the ecosystem.^[20,21]

Carbon isotope ratio variations are associated with different feeding environments or energy sources (costal/oceanic, pelagic/benthic) used by consumers.^[22] For nitrogen, there is a successive increase in this isotope ratio along the trophic web,^[23] which allows the trophic level and amplitude of a species to be evaluated with a greater precision.^[24,25] Isotopic differences follow from one level to another in the trophic web,^[26,27] which becomes enriched with the heavier isotope at each trophic level, from ~3 to 5‰ for $\delta^{15}\text{N}$ values and from ~0.5 to 1‰ for $\delta^{13}\text{C}$ values.^[22,28]

Although the trophic spectrum of the Galapagos otariids has already been described, and although the dominant prey of *Z. wollebaeki* has been identified,^[3] the contribution of the species to the diet has not been evaluated. Currently, bayesian approximation models using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have provided a better understanding of the trophic behavior of species because the models can be adjusted to allow for an imprecise hypothesis, which allows the uncertainty involved in the contribution of the energy sources to be described in probabilistic terms.^[29,30]

In this study, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of pup hair samples from *Z. wollebaeki* and *A. galapagoensis* collected between 2003 and 2009 were analyzed. Stable Isotope Analysis in R (SIAR) and Stable Isotope Bayesian Ellipses in R (SIBER) were used to estimate the percentage contribution of prey species to the diets of both otariids and to determine the habitat usage, niche breadth, and degree of trophic overlap between populations in the regions inhabited by both species in sympatry (Fernandina Island) and the region exclusively inhabited by *Z. wollebaeki* (San Cristobal Island). The analysis determined the possible variability in the trophic specialization levels of these species in two contrasting regions of the archipelago.

EXPERIMENTAL

Study area

The study was conducted in two geographically opposed colonies in the Galapagos Archipelago: to the west, on Cape Hammond–Fernandina Island, where *Z. wollebaeki* (ZwW) and *A. galapagoensis* (Ag) coexist, and to the east, in El Malecon on San Cristobal Island, where only *Z. wollebaeki* (ZwE) inhabits, constituting one of its more populated colonies (Fig. 1). There is a regional difference in the Galapagos Islands with respect to marine productivity; the western region (Fernandina and Isabela islands) exhibits high annual productivity, whereas the rest of the archipelago exhibits a lower mean productivity.^[12] However, in zones near the south-eastern region (San Cristobal and Española islands) there is a higher than average marine productivity.^[31]

Sample collection and processing

Hair samples were collected from 2- and 3-month-old individuals of both species in the Cape Hammond rookery (*Z. wollebaeki*, $n = 43$; *A. galapagoensis*, $n = 48$), and 50 hair samples were collected from *Z. wollebaeki* pups in the El Malecon rookery during the reproductive seasons of 2003, 2004, 2005, 2008, and 2009 (Table 1). Pup age was estimated from the total weight of the individuals and the daily growth rate reported for *Z. wollebaeki* and *A. galapagoensis* (108 g/day and 41 g/day, respectively).^[7]

Pup hair was used because it integrates isotopic information from their *in utero* phase and from the first few months of their life (lactation phase), which makes it possible to track the isotopic signature of adult females from the isotope fractionation that occurs between the mother and pup. For the Galapagos pinnipeds, the isotope fractionation in hair is 0.5‰ for $\delta^{13}\text{C}$ values and 1.7‰ for $\delta^{15}\text{N}$ values.^[32]

Each sample was rinsed with de-ionized water to eliminate any residue that could affect the isotope signature and dried at 80 °C for 12 h. Lipid extraction was performed by Microwave-Assisted Extraction (MAE, microwave oven model 1,000 MARS 5; CEM, Matthews, NC, USA) with 25 mL of a chloroform/methanol solution (1:1). Next, the sample was homogenized with an agate mortar until a fine powder was obtained, from which approximately 1 mg was sampled and placed on a tin capsule (8 mm x 5 mm) for isotopic analysis.

Isotope ratios were measured under continuous flow in a mass spectrometer (20-20 PDZ Europe, Sercon Ltd, Crewe, UK) at the Stable Isotope Laboratory, University of California (Davis, CA, USA). The results are expressed as:^[26]

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left[\frac{R_{\text{sample}}}{R_{\text{standard}}} \right] - 1 \right]$$

where R is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio of the sample and standard, respectively. The standard for $\delta^{13}\text{C}$ values was PDB (Pee Dee Belemnite), and the standard for $\delta^{15}\text{N}$ values was atmospheric N_2 . The results were calibrated with international standards (ammonium sulfate for $\delta^{15}\text{N}$ values and sucrose for $\delta^{13}\text{C}$ values), which generated a standard deviation between the isotopic measurement trials of <0.3% for $\delta^{15}\text{N}$ values and <0.2% for $\delta^{13}\text{C}$ values.

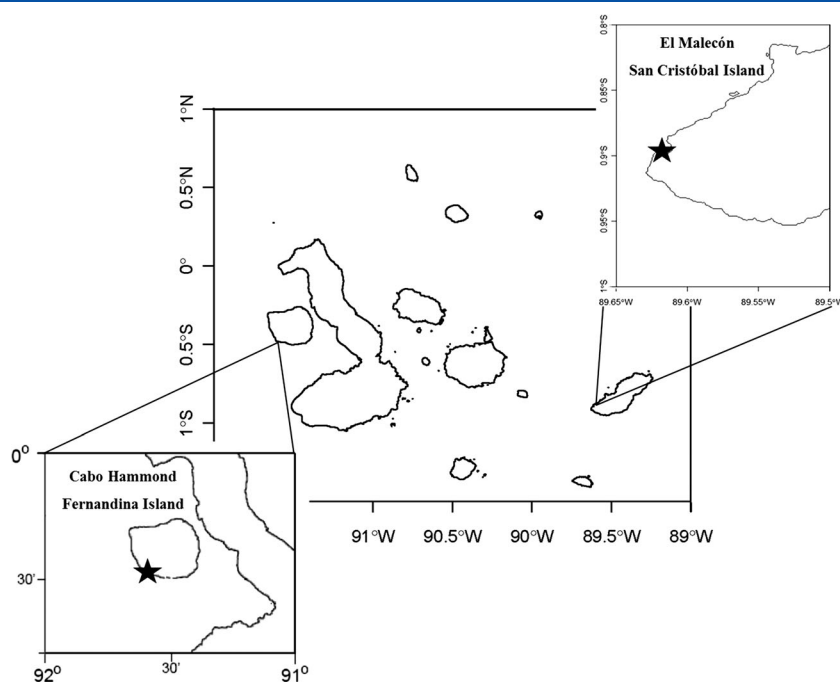


Figure 1. Study area in the Galapagos Islands showing: the rookery where the Galapagos sea lion *Zalophus wollebaeki* and Galapagos fur seal *Arctocephalus galapagoensis* live in sympatry on Fernandina Island: Cabo Hammond (0°28'12\"S, 91°36'59\"W), and the rookery only inhabited by the Galapagos sea lion on San Cristobal Island: El Malecón (0°54'8.1\"S, 89°36'44.1\"W).

Table 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and the C/N ratio (mean \pm SD in ‰) from fur samples of Galapagos otariid pups collected in the western (Fernandina) and eastern (San Cristobal) regions of the archipelago during the years 2003, 2004, 2005, 2008 and 2009

Year	Species	n	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	C/N mass ratio
2003	<i>A. galapagoensis</i>	10	-16.2 \pm 0.3	12.7 \pm 0.4	2.8 \pm 0.1
	<i>Z. wollebaeki</i> (West)	5	-15.8 \pm 0.7	13.1 \pm 0.3	2.8 \pm 0.1
	<i>Z. wollebaeki</i> (East)	10	-16.2 \pm 0.2	12.9 \pm 0.4	2.7 \pm 0.1
2004	<i>A. galapagoensis</i>	10	-16.3 \pm 0.2	12.2 \pm 0.4	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (West)	10	-14.6 \pm 0.3	13.0 \pm 0.4	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (East)	10	-16.4 \pm 0.3	13.2 \pm 0.6	3.6 \pm 0.1
2005	<i>A. galapagoensis</i>	10	-16.7 \pm 0.2	12.7 \pm 0.7	3.1 \pm 0.1
	<i>Z. wollebaeki</i> (West)	10	-15.0 \pm 0.4	13.3 \pm 0.9	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (East)	10	-16.1 \pm 0.3	13.2 \pm 0.7	3.2 \pm 0.1
2008	<i>A. galapagoensis</i>	8	-16.8 \pm 0.4	11.1 \pm 0.6	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (West)	8	-16.5 \pm 0.5	13.1 \pm 0.9	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (East)	10	-16.3 \pm 0.5	13.1 \pm 1.2	3.2 \pm 0.1
2009	<i>A. galapagoensis</i>	10	-17.0 \pm 0.1	12.3 \pm 0.1	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (West)	10	-16.4 \pm 0.3	13.1 \pm 0.6	3.2 \pm 0.1
	<i>Z. wollebaeki</i> (East)	10	-16.9 \pm 0.4	13.0 \pm 0.4	3.2 \pm 0.1

Statistical analysis

The normality and homoscedasticity of the isotopic data were tested using the Shapiro–Wilks and Levene tests, respectively. Statistical differences between the isotopic values occurring in three populations of otariids and among the breeding seasons (years) were assessed using a Kruskal Wallis test and by multiple comparisons of the mean ranks for all groups. The statistical significance is reported in terms of 'p' at the 0.05 level. Statistical analyses were performed using the Statistica 8.0 software (StatSoft, Inc., Tulsa, OK, USA).

Isotopic contribution of prey

Published data of the average isotope values for fish species^[33] and cephalopods,^[34,35] which have previously been identified as important prey in the diet of pinnipeds^[3,9,36,37] (Table 2), were used to construct the trophic structure of the Galapagos Islands female otariids.

The percentage contributions of various preys to the diets of *Z. wollebaeki* and *A. galapagoensis* in the different study zones were evaluated with the bayesian isotope mixing model, SIAR, which has been proposed and implemented by others.^[38,39]

Table 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SD) from different species identified as important prey in the diet of Galapagos fur seals and Galapagos sea lions

Species	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	N° Samples
* <i>Selar crumenophthalmus</i>	-15.9 ± 0.3	11.9 ± 0.7	5
* <i>Anchoa</i> spp.	-16.6 ± 0.4	10.9 ± 0.8	4
* <i>Sardinops sagax</i>	-16.8 ± 0.7	9.8 ± 1.4	8
+ <i>Paralabrax</i> spp.	-15.0 ± 0.1	12.8 ± 0.6	5
+ <i>Pontinus clemensi</i>	-14.9 ± 0.2	13.2 ± 0.3	4
+ <i>Semicossyphus darwini</i>	-14.9 ± 0.1	12.2 ± 0.3	3
^ <i>Dosidicus gigas</i>	-17.7 ± 0.3	9.4 ± 1.3	10
^ <i>Sthenoteuthis oualaniensis</i>	-18.1 ± 0.2	10.4 ± 0.3	3
^ <i>Ommastrephes bartrami</i>	-18.2 ± 0.4	10.0 ± 0.4	6

*Pelagic fish; +Benthic fish; ^Squids.
Data provided by Calle-Moran^[34] and published in Ruiz-Cooley *et al.*^[35] and Páez-Rosas *et al.*^[33]

This model estimates the probability distribution of the contribution of n sources (prey) to a mixture and also evaluates the uncertainty associated with the isotopic values of the sources and predator.^[29] Given the variability in terms of type and the environment of the prey observed in the diet of both species, an inter-annual mixing model was developed to observe the influence of these changes in the global model. The variability in the percentage contribution of each prey to the diets of the otariids throughout the years was determined with the coefficient of variation. The published isotopic fractionations between prey and predator using tissues with similar isotopic integration rate (i.e. muscle of prey and skin of sea lions)^[32,33] were used to perform this analysis.

Niche breadth and trophic overlap

The niche breadth and the degree of trophic overlap of the three populations (*A. galapagoensis* Ag, *Z. wollebaeki* – West ZwW and East ZwE) were estimated from the Convex-Hull area in the bi-dimensional isotopic space of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and evaluated with the standard Bayesian ellipses analysis SIBER. This analysis was conducted with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values corrected by the fractionation factor between the mother and pup for all seasons under study, which allowed the uncertainty of the observed data to be included and could incorporate the inherent error that occurred during the sampling procedure.^[39]

The extension of the trophic niche is represented by the area of the corrected ellipse, which is less influenced by the extreme values that encompass the total area of the polygon. The degree of trophic overlap between populations was calculated as the overlap index of the model SIBER, where a value greater than 1 indicates overlap between species.

RESULTS

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined from 141 hair samples of *A. galapagoensis* and *Z. wollebaeki* pups collected from 2003 to 2009. The C/N ratio in all cases was within the theoretical range established for assimilated proteins (2.8 to 3.8)^[40] (Table 1).

The global average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ estimated for *A. galapagoensis* ($n=48$) were $-16.6 \pm 0.4\text{‰}$ and $12.2 \pm 0.7\text{‰}$, respectively. The global average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from

the populations of *Z. wollebaeki* from the western ($n=43$) and eastern ($n=50$) regions of the archipelago were $-15.6 \pm 0.9\text{‰}$ and $13.1 \pm 0.7\text{‰}$, and $-16.4 \pm 0.5\text{‰}$ and $13.1 \pm 0.7\text{‰}$, respectively.

Significant differences among the populations were found in their isotopic signatures ($\delta^{13}\text{C}$: $H_{(2, 141)} = 29.47$, $P < 0.001$; $\delta^{15}\text{N}$: $H_{(2, 141)} = 38.37$, $P < 0.001$). With respect to $\delta^{13}\text{C}$ values, *A. galapagoensis* was significantly different from the eastern population of *Z. wollebaeki* (multiple comparisons of mean ranks: $P=0.007$), while for $\delta^{15}\text{N}$ values, differences were found between *A. galapagoensis* and both populations of *Z. wollebaeki* (all multiple comparisons of mean ranks: $P < 0.001$). At the inter-annual level, there were no significant differences in $\delta^{15}\text{N}$ values between the *A. galapagoensis* and *Z. wollebaeki* populations ($H_{(4, 141)} = 5.06$, $P = 0.281$); however, the differences in $\delta^{13}\text{C}$ values were significant ($H_{(4, 141)} = 46.18$, $P < 0.001$). The multiple comparison of the mean ranks showed that the years 2003, 2004, and 2005 were significantly different from 2008 and 2009 (all $P < 0.05$).

Prey proportions in the consumer's diet

The global mixing model provides evidence for some predominance of the Humboldt squid (*Dosidicus gigas*) in the diet of Ag, which presented a mean proportion of 35.9% (ranging from 17.1% to 54.3%), followed by sardines (*Sardinops sagax*) as complementary prey (Fig. 2(A)). For ZwW, a clear predominance of benthic fish, such as *Semicossyphus darwini* and *Paralabrax* spp., was evident (mean contribution of 26.7% and 15.5%, respectively) over time (Fig. 2(B)), whereas the diet of ZwE had a more equitable contribution between benthic and pelagic fish, such as *S. darwini*, *Paralabrax* spp., and *S. sagax* (mean contributions of 27.6%, 15%, and 13.1%, respectively) (Fig. 2(C)).

The inter-annual model (Table 3) showed a higher variability with respect to the percentage contribution of prey for Ag (average coefficient of variation (CV) = 29.1%) than for ZwW (CV = 16.3%) and ZwE (CV = 9.9%). In Ag, squid species were ratified as the primary prey in the pinniped diet over time (Fig. 3). *D. gigas* showed the highest mean contribution in 2003 and 2004 (18.4% and 23.2%, respectively), and it was the second in 2005, 2008 and 2009 when *O. bartrami* had the highest mean contributions (23.7%, 23.3% and 28.4%, respectively) (Table 3). However, for the years 2003 and mainly 2004, *S. sagax* represented an important contribution to the Ag diet,

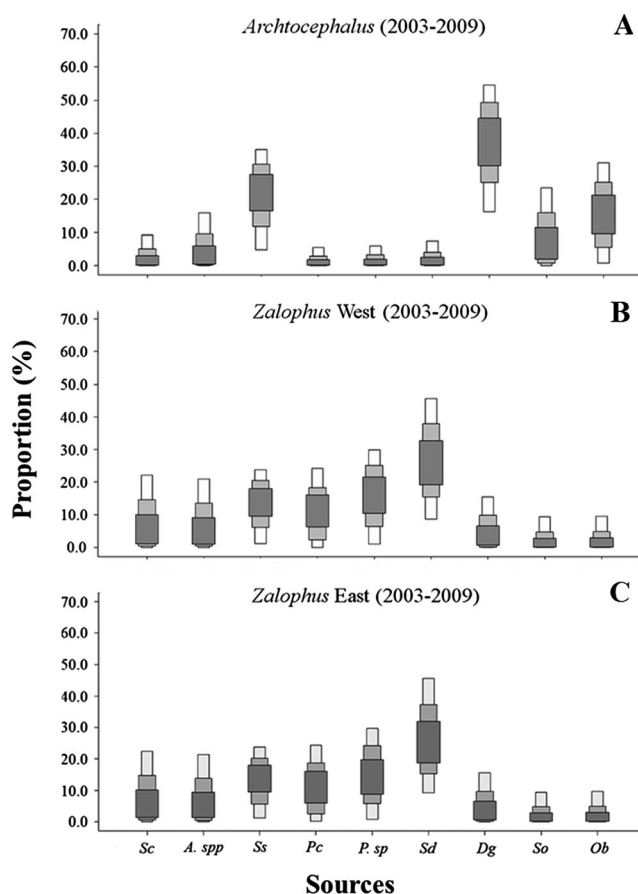


Figure 2. Ranges of species contribution (%) to pinnipeds diet produced by the SIAR model using isotope values from reported preys. Sc: *Selar crumenoptalmus*, Asp: *Anchoa* sp., Ss: *Sardinops sagax*, Pc: *Pontinus clemensi*, Psp: *Paralabrax* sp., Sd: *Semicossyphus darwini*, Dg: *Dosidicus gigas*, So: *Sthenoteuthis oualaniensis*, Ob: *Ommastrephes bartramii*. Gray boxes shows 95%, 75% and 50% credibility intervals.

reaching mean contributions of 14.9% and 16.1%, respectively: ranking second of the percentage contribution of preys in 2004 (Figs. 3(A) and 3(B)).

Niche breadth

The SIBER analysis revealed the highest extension of the trophic niche size for ZwW (1.91), followed by ZwE (0.94) and Ag (0.83) (Fig. 4). SIBER showed differences in the trophic niche between Ag and both populations of Zw (0.999 and 0.667, Ag vs ZwW and ZwE, respectively), although this was not the case for both colonies of Zw because their variability was not significant (0.001, ZwW vs ZwE). Although a significant overlap index was not found for any of the three cases (all comparisons <1), a better coincidence was observed between the ZwW and ZwE groups (0.482; Table 4).

DISCUSSION

The SIAR results demonstrate that the diet of *A. galapagoensis* is primarily composed of squid (*D. gigas* and *Ommastrephes bartramii*), complemented to a lesser extent by other

pelagic species as *S. sagax*. This result suggests a higher degree of specialization in *A. galapagoensis* than in *Z. wollebaeki* for both the west and the east populations (ZwW and ZwE), whose diet contains a more proportional representation of fish corresponding to different environments. These aspects may be associated with a resources distribution at the intra-population level, since the two populations of *Zalophus* showed a diet composed of prey from different environments, such as benthic (*S. darwini*) and pelagic (*S. sagax*) fish.

These aspects coincide with previous reports that refer to the trophic ecology of both species, showing that *A. galapagoensis* exhibited some preference for daily migrating pelagic species, such as squid.^[36] In contrast, the *Z. wollebaeki* populations from the eastern region of the archipelago have been able to develop at least three foraging strategies (epipelagic, mesopelagic, and benthic) as a product of the strong intra-specific competition observed in these colonies.^[3,41]

The western *Z. wollebaeki* population, which is exposed to a strong sympatry with *A. galapagoensis*, exhibited a greater preference towards benthic fish than the eastern population (ZwE), which complemented their diet with pelagic fish. These results could be interpreted as a feeding strategy of ZwW that is focused on allocating resources with Ag to reduce inter-specific competition levels. This trophic niche allocation has been registered for various marine predators that coexist in sympatry, which has been interpreted as an adaptation to reduce the competition for food and facilitate coexistence in certain ecosystems.^[42,43]

Previous studies based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements and sightings at sea of these species have suggested trophic segregation between *A. galapagoensis* and *Z. wollebaeki*.^[42,43] Given that isotopic analysis is based on two variables that are subject to the influence of organic matter sources ($\delta^{13}\text{C}$ values) as well as variations derived from the type of prey and trophic level ($\delta^{15}\text{N}$ values),^[20,28] our results support the hypothesis that these otariids use different feeding areas around the Galapagos Islands, and this, in turn, influence their diet.

There is a similar pattern in other latitudes, specifically in the case of the Otariidae family, where sea lion and fur seal populations, which also coexist in sympatry on the coasts of Mexico (*Zalophus californianus* vs *Arctocephalus townsendii*) and Uruguay (*Otaria flavescens* vs *Arctocephalus australis*), show a differential use of feeding habitat (benthic vs pelagic, respectively) as a result of trophic competition, the species' physiological capabilities, and the available resources at these sites.^[18,44]

Several authors mention that Galapagos sea lions visit the same sites during repeated foraging trips in a season.^[3,42] Even when they display different foraging strategies, they maintain the primary prey on their diet throughout this time.^[3] This suggests that *Z. wollebaeki* repeatedly utilize the same feeding grounds, as also probably occurs in *A. galapagoensis*. However, changes in the foraging zones during anomalous years should not be disregarded as a factor that causes variation in the isotopic values of these species, mainly in *A. galapagoensis*.^[17,34]

Although *A. galapagoensis* exhibits a specific preference towards prey from pelagic environments, such as squid (primarily) and sardines, the contribution of the prey to their

Table 3. Average percentage contribution of prey to the diet of Galapagos fur seal (Ag) and Galapagos sea lions (ZwW and ZW) produced by the SIAR model using isotope values from reported preys, during the years 2003, 2004, 2005, 2008, 2009 and global. Minimum and maximum contribution values for each prey are shown in parentheses. The coefficient of variation (CV) shows the variability in the percentage contribution of preys to the diet of the otariids throughout the years. The mean CV values by population are Ag = 29.1%, ZwW = 16.3, ZW = 9.9%

<i>Arctocephalus galapagoensis</i>							
Preys	2003	2004	2005	2008	2009	CV	Global
<i>S. crumenophthalmus</i>	7.8 (0.0–19.0)	6.7 (0.0–16.7)	5.7 (0.0–14.7)	5.0 (0.0–13.5)	2.9 (0.0–19.0)	32.9	3.4 (0.0–9.1)
<i>Anchoa</i> spp.	12.2 (0.0–25.6)	10.7 (0.0–24.0)	8.6 (0.0–20.3)	8.1 (0.0–20.1)	6.2 (0.0–19.0)	25.5	6.5 (0.0–16.4)
<i>S. sagax</i>	14.9 (1.2–26.9)	16.1 (1.0–30.2)	9.7 (0.0–21.9)	12.2 (0.0–28.0)	8.8 (0.0–19.0)	25.7	20.1 (4.3–34.8)
<i>P. clemensi</i>	4.8 (0.0–12.2)	3.9 (0.0–10.2)	3.4 (0.0–8.9)	3.1 (0.0–8.8)	1.6 (0.0–19.0)	35.0	2.0 (0.0–5.4)
<i>Paralabrax</i> spp.	5.4 (0.0–13.8)	4.4 (0.0–11.4)	3.6 (0.0–9.3)	3.3 (0.0–9.2)	1.9 (0.0–19.0)	35.0	2.3 (0.0–6.2)
<i>S. darwini</i>	6.8 (0.0–16.2)	5.6 (0.0–13.5)	3.4 (0.0–8.9)	3.5 (0.0–9.6)	2.0 (0.0–19.0)	45.0	2.8 (0.0–7.4)
<i>D. gigas</i>	18.4 (3.4–32.4)	23.2 (6.0–42.5)	20.0 (2.1–37.1)	22.3 (0.1–44.5)	22.6 (7.6–38.5)	9.5	35.9 (17.1–54.3)
<i>S. oualaniensis</i>	14.2 (0.3–27.1)	13.4 (0.0–26.7)	21.8 (2.8–39.8)	19.0 (0.0–38.7)	25.5 (5.8–44.2)	27.2	11.4 (0.0–25.0)
<i>O. bartramii</i>	15.6 (0.7–28.5)	15.9 (0.8–29.7)	23.7 (4.0–43.0)	23.3 (1.1–44.2)	28.4 (9.0–47.0)	25.8	15.5 (0.2–31.1)
<i>Zalophus wollebaeki</i> – West							
<i>S. crumenophthalmus</i>	11.8(0.0–22.8)	12.4(0.2–23.5)	11.9(0.0–24.5)	12.2(0.0–25.3)	11.2(0.3–21.0)	3.9	10.2 (0.0–23.1)
<i>Anchoa</i> spp.	10.9(0.0–22.4)	10.7(0.0–21.7)	9.8(0.0–22.0)	10.5(0.0–23.2)	11.4(0.3–21.4)	5.5	9.1 (0.0–21.3)
<i>S. sagax</i>	11.2 (0.0–22.4)	9.4 (0.0–19.3)	9.9(0.0–20.8)	10.5(0.0–23.1)	9.5(0.0–18.6)	7.4	13.1 (1.5–23.7)
<i>P. clemensi</i>	14.1(1.2–25.3)	15.1(2.4–26.6)	16.0(1.0–28.8)	15.2(0.4–28.1)	11.5(0.8–20.8)	12.1	12.0 (0.0–24.1)
<i>Paralabrax</i> spp.	14.7(1.2–26.5)	15.2(1.7–26.9)	16.6(1.4–30.3)	15.1(0.3–28.3)	11.8(0.6–21.4)	12.0	15.5 (0.7–29.9)
<i>S. darwini</i>	17.5(4.0–26.5)	15.9(2.8–28.1)	19.1(3.2–34.2)	16.2(0.6–30.0)	11.4(0.5–20.9)	17.9	26.7 (8.0–45.6)
<i>D. gigas</i>	8.1(0.0–17.7)	7.5(0.0–7.5)	6.5(0.0–15.7)	7.5(0.0–18.3)	10.3(0.2–19.5)	17.8	6.5 (0.0–15.2)
<i>S. oualaniensis</i>	5.8(0.0–14.5)	7.0(0.0–16.4)	5.1(0.0–13.5)	6.4(0.0–16.6)	11.5(0.5–21.2)	35.3	3.3 (0.0–9.2)
<i>O. bartramii</i>	5.9(0.0–14.9)	6.7(0.0–15.7)	5.0(0.0–13.1)	6.2(0.0–16.4)	11.3(0.5–20.9)	35.2	3.5 (0.0–9.5)
<i>Zalophus wollebaeki</i> – East							
<i>S. crumenophthalmus</i>	11.9(0.0–22.8)	11.5(0.2–21.4)	12.0(0.0–25.1)	12.2(0.0–23.5)	12.1(0.2–23.1)	2.3	9.7 (0.0–22.0)
<i>Anchoa</i> spp.	10.8(0.0–21.7)	11.2(0.0–21.5)	9.6(0.0–22.0)	10.8(0.0–22.5)	11.0(0.0–22.0)	5.9	9.6 (0.0–21.9)
<i>S. sagax</i>	9.9 (0.0–20.2)	10.1 (0.0–19.8)	9.2(0.0–20.8)	10.3(0.0–21.5)	9.8(0.0–19.6)	4.2	13.1 (1.3–23.5)
<i>P. clemensi</i>	13.4(0.5–24.2)	12.5(0.6–22.6)	16.5(0.6–30.9)	14.1(0.6–25.6)	14.5(1.4–25.3)	10.5	12.1 (0.0–24.2)
<i>Paralabrax</i> spp.	13.5(0.5–24.8)	13.0(0.7–23.4)	16.1(0.1–31.4)	13.8(0.5–25.4)	14.6(1.2–25.7)	8.5	15.0 (0.4–29.2)
<i>S. darwini</i>	13.8(0.5–25.3)	13.5(0.6–24.6)	17.8(0.2–35.4)	14.0(0.6–25.4)	15.3(2.5–26.9)	11.9	27.6 (9.2–46.5)
<i>D. gigas</i>	8.9(0.0–19.0)	9.5(0.0–18.9)	6.6(0.0–16.9)	8.6(0.0–19.4)	8.3(0.0–18.1)	13.0	6.2 (0.0–14.8)
<i>S. oualaniensis</i>	9.1(0.0–19.6)	9.5(0.0–19.4)	6.2(0.0–16.6)	8.1(0.0–18.5)	7.3(0.0–17.0)	16.7	3.3 (0.0–9.3)
<i>O. bartramii</i>	8.7(0.0–19.1)	9.2(0.0–19.2)	6.0(0.0–16.2)	8.0(0.0–18.4)	7.1(0.0–16.6)	16.4	3.4 (0.0–9.5)

diet has varied over time due to the region's own environmental variability. Generally, the jumbo squid (*D. gigas*) has been the primary prey over time; however, prey such as sardines have complemented this predator's diet during years when El Niño Southern Oscillation ENSO prevailed (2003 and 2004) and displaced other species. During years with normal conditions (2005 and 2009), the diet of Ag was primarily composed of squid.

It is widely known that an increase in ocean temperature reduces the amount of dissolved nutrients, which decreases both the primary productivity^[45] and the abundance and distribution of different species used as prey by top predators.^[46,47] This situation alters the feeding strategies of pinnipeds because, when the biomass of their primary prey decreases, the pinnipeds consume easily accessible secondary prey with a high energy content to satisfy their physiological needs.^[48,49]

Previous studies have noted that there is a decrease in various squid species during the ENSO^[50] due to the physical and productivity changes characteristic of the event. These changes would cause *A. galapagoensis* to select

other prey species or to increase their effort to capture food to obtain the necessary energy content for their survival.^[51]

Given the significant population decrease due to environmental variability and the constant feeding stress to which the populations of *A. galapagoensis* are exposed in the western region of the archipelago,^[8,32] it is expected that the species would adopt new feeding alternatives that provide the necessary energy content to maintain stable colonies.^[33,52]

Niche breadth

Both pinniped species that coexist in the western region of the Galapagos Archipelago exhibited a low degree of trophic overlap due to the different feeding strategies identified for each species.

The isotope values and the ellipses areas demonstrate a higher trophic breadth for the western population of *Z. wollebaeki* (ZwW) than for the other otariid populations. That is because of the differential prey consumption by ZwW, which come from different environments (primarily

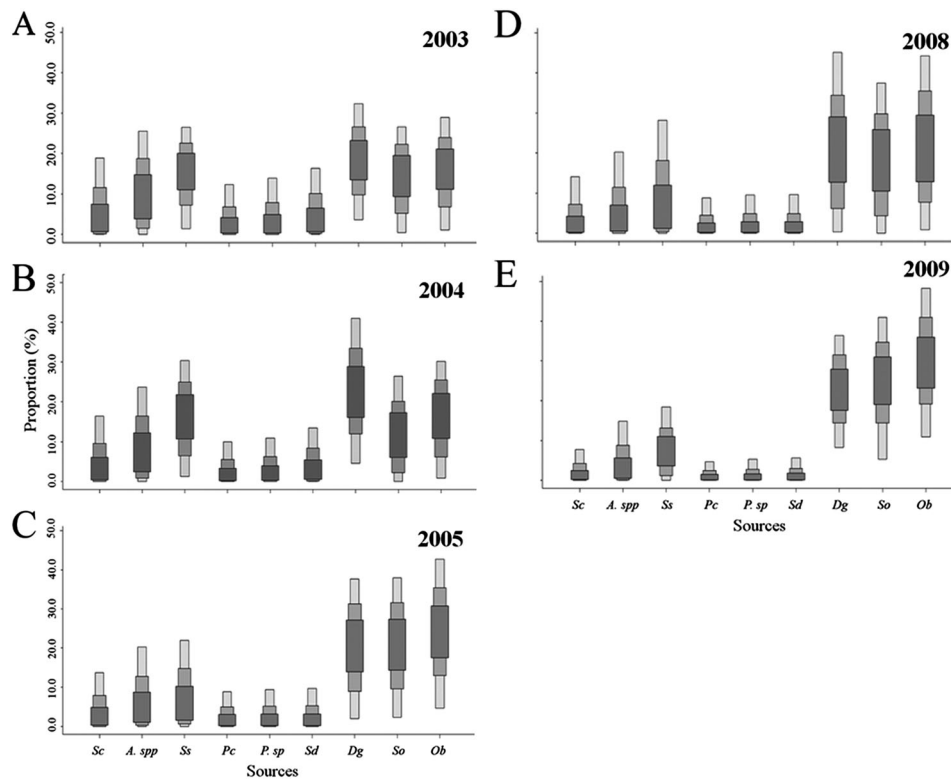


Figure 3. Boxplots of the percentage of preys in the diet of *A. galapagoensis* in different years estimated by SIAR analysis. Sc: *Selar crumenophthalmus*, Asp: *Anchoa* sp., Ss: *Sardinops sagax*, Pc: *Pontinus clemensi*, Psp: *Paralabrax* sp., Sd: *Semicossyphus darwini*, Dg: *Dosidicus gigas*, So: *Sthenoteuthis oualaniensis*, Ob: *Ommastrephes bartramii*. Gray boxes shows 95%, 75% and 50% credibility intervals.

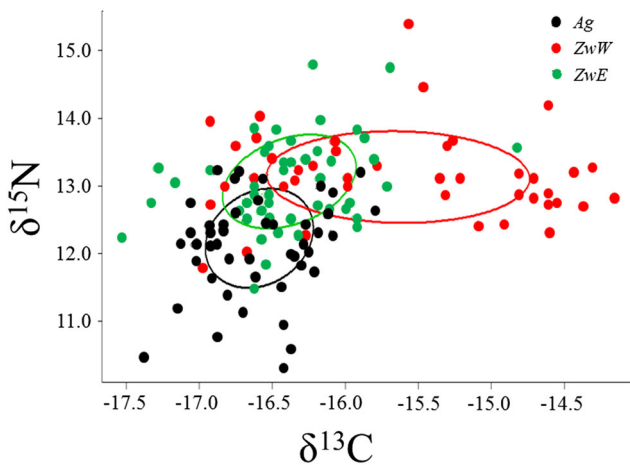


Figure 4. Isotopic niche area ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) for *A. galapagoensis* (Ag) and *Z. wollebaeki* (ZwW and ZwE) estimated by a convex hull areas and the ellipse corrected for the SIBER analysis (Stable Isotope Bayesian Ellipses in R).

benthonic, with the inclusion of pelagic environments to a lesser extent), where a variability in productivity exists across the archipelago.^[12,53] This situation is directly related to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability present from the base of the trophic web to the top levels.^[19,54]

The inter-annual variability in terms of productivity may affect the isotope values and the ellipse area for ZwW, which could be interpreted as generalized behavior. However, these results must be regarded with caution because it is known that the Galapagos sea lion is a specialized predator that presents a degree of plasticity in its feeding behavior, an adaptation that allows it to consume a specific group of prey in a large proportion to avoid inter- and intra-population competition.^[3,33,52]

At the intra-specific level, differences in trophic amplitude were observed in both the eastern and the western populations of *Z. wollebaeki*, where the western population exhibited greater generalist behavior than the eastern population. Previous studies have highlighted the presence of at least three specific feeding strategies in sea lion colonies from the eastern and center Galapagos Islands (San Cristobal and Santa Cruz Islands), suggesting the intra-specific allocation of the trophic niche accompanied by strong specialized behavior in each one of these groups.^[32,41]

In the case of the western colonies of *Z. wollebaeki* (Isabela and Fernandina Islands), the information regarding their feeding behavior is limited. However, satellite telemetry studies suggest the presence of two feeding strategies (pelagic and benthic), which could expand the trophic niche of this species given the region's environmental variability and the competition with other predators.^[49,52] This type of behavior has been related to a strategy by *Z. wollebaeki* to avoid competition with *A. galapagoensis*, primarily during the warmest months of the year when there is less prey available.^[16,52]

Table 4. Ranges of niche breadth and trophic overlap of Galapagos pinnipeds populations calculated by SIBER analysis

Species	SEAc	TA	Ellipses areas: Group differences	Overlap index: Group differences
<i>A. galapagoensis</i> (Ag)	0.832	3.224	1 vs 2 (0.999)	1 vs 2 (0.023)
<i>Z. wollebaeki</i> – West (ZwW)	1.919	6.694	1 vs 3 (0.667)	1 vs 3 (0.255)
<i>Z. wollebaeki</i> – East (ZwE)	0.947	4.850	2 vs 3 (0.001)	2 vs 3 (0.482)

SEAc = standard ellipse area, TA = total area of the polygon.
The last two columns show the statistical differences in the ellipse areas and the overlap index among the population groups.
Group 1: Ag, Group 2: ZwW, Group 3: ZwE

CONCLUSIONS

The results of this study demonstrate a partition of trophic niche among populations of *Z. wollebaeki* (ZwW) and *A. galapagoensis* (Ag) in the west of the archipelago. At the intra-specific level, higher trophic breadth was observed in the western population of *Z. wollebaeki* (ZwW) than in the eastern population (ZwE). This is a strategy adopted by ZwW for dealing with the strong fluctuations in primary productivity that are characteristics of this area, and to decrease the levels of competition with a sympatric predator of similar characteristics.

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