Trophic Variation Between the Two Existing Guadalupe Fur Seal Colonies on Guadalupe Island and the San Benito Archipelago, Mexico

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Abstract

Scat analysis and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) were used to perform a trophic comparison between two existing Guadalupe fur seal (*Arctocephalus philippii townsendi*) colonies on Guadalupe Island (GI) and the San Benito Archipelago (SBA) during the 2013 breeding season. The stable isotope analysis included 67 samples from GI and 36 from the SBA, indicating that this otariid is a teuthophagous specialist. The two colonies showed different trophic levels: (1) 4.5 for GI, for which the most dominant prey was the jumbo squid, and (2) 4.0 for the SBA, for which the main item was the opalescent squid. The stable isotope analysis included 15 fur samples from each site. Both analyses were complementary, identifying prey species from an oceanic habitat, with fur seal $\delta^{13}C$ values that are typically associated to that environment. Although assigned a higher trophic level (scat analysis), GI had lower $\delta^{15}N$ and $\delta^{13}C$ values, suggesting latitudinal segregation. These differences between colonies may be related to their distinct age proportions or a strategy to avoid intrapopulation competition. Our contribution regarding trophic variation is based on a snapshot regarding scat analysis and a time window of ~16 wks prior to collection reflected by stable isotope analysis in fur. Additionally, this species is currently experiencing population growth, which increases the possibility of overlap for resources between both colonies. Therefore, it is important to establish baselines and continue these comparative analyses over time to determine their significance within its recovery.

Introduction

The Guadalupe fur seal (*Arctocephalus philippii townsendi*) (GFS) is recognized as an endangered species under Mexican law (NOM-059-SEMARNAT-2010). The only well-established breeding colony of the species is located on Guadalupe Island (GI), where an estimate of ~17,000 GFSs are found (International Union for Conservation of Nature [IUCN], 2015); meanwhile, the San Benito Archipelago (SBA), 268 km southeast, has a colony of up to 3,700 to 4,500 individuals that is undergoing a process of recolonization since the late 1990s (Maravilla-Chávez & Lowry, 1999; Sierra, 2015) and is mainly composed of juveniles and subadults. Additionally, vagrant GFSs on the islands off California have become more frequent since the 1980s (IUCN, 2015).

Female GFSs make foraging trips that vary from 222 to 589 km and around 14 d in duration (Gallo-Reynoso et al., 2008). Foraging variation may exist between individuals within a given pinniped population because of physiological limitations associated with age (Kuhn et al., 2006) or sex (Weise & Costa, 2007), and may even occur when phenotypes and dispersion capabilities are similar (Van Valen, 1965; Bolnick et al., 2003; Estes et al., 2003) as evidenced via telemetry in Antarctic fur seals (*Arctocephalus gazella*; Staniland & Boyd, 2003) and northern fur seals (*Callorhinus ursinus*; Robson et al., 2004).

Few published studies have examined the GFS diet, which is mostly teuthophagous, with evidence for both spatial and seasonal variation (Gallo-Reynoso & Esperón, 2013). Scat analysis has been applied to determine the diet composition of GFSs and other otariids through the identification of hard structures like fish otoliths and cephalopod beaks (e.g., Porras-Peters et al., 2008; Gallo-Reynoso & Esperón, 2013). Analysis of stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) complements scat analysis. A consumer's δ^{13}C reflects the habitat of their prey as a result of dissolved CO_2 concentration (Rau et al., 1992); the phytoplankton growth rate (France, 1995); and the presence of macrophyte algae in coastal ecosystems, which enriches the ^{13}C baseline value (Michener & Schell, 1994). The δ^{15}N facilitates inferences regarding trophic level and breadth based on the accumulation that occurs between prey and consumer through increments that are relatively predictable within a range from 3 to 5‰ (Minagawa & Wada, 1984; Martínez del Rio et al., 2009). The trophic discrimination factor for δ^{13}C ranges from 0.5 to 2‰ (Post, 2002; Bearhop et al., 2004). Additionally, a latitudinal isotope gradient takes place at the base of the food chain; denitrification processes, which are more intense at middle latitudes, enrich the ^{15}N values from the baseline (Altabet et al., 1999; Voss et al., 2001); and the solubility of CO_2 (^{12}C-enriched) decreases at middle latitudes (Goericke & Fry, 1994; France, 1995). As a result, these factors give a basal isotopic depletion of ~1‰ per +4 to 5° latitude as also observed among predators from distinct regions (Aurioles-Gamboa et al., 2006; Elorriaga-Verplancken et al., 2016a).

Several studies of stable isotopes have inferred the foraging habits of adult female pinnipeds based on values of their offspring. The latter are not independent consumers; rather, their tissues are generated by the catabolism of their mother's fat and muscle when milk is produced, with an isotopic signature corresponding to adult females, emulating the relationship between prey and predator (Habran et al., 2010; Elorriaga-Verplancken et al., 2016b). Otariids are born with a dark coat, which starts developing at around the sixth or seventh month of gestation (Odell, 1972); thus, collected neonate fur must provide an isotopic temporal window of ~16 wks.

The current study was based on this isotopic premise, analyzing newborns' fur. Additionally, a scat analysis was made to perform the first simultaneous comparison of foraging habits between the two existing GFS colonies.

Methods

Sampling of GFS scats and fur was carried out during the 2013 breeding season at GI (29° 00' N, 118° 15' 30" W) from 1 to 15 July, and the SBA (28° 18' N, 115° 32' W) from 1 to 8 July. Both sites are located off the west coast of Baja California, Mexico (Figure 1).

Scat Collection and Processing
All fresh scat present on GI (n = 67) and SBA (n = 36) were stored in labeled plastic bags. At Laboratorio de Ecología de Peces in the Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN, La Paz, Mexico), scat samples were passed through sieves of varying mesh size (2 to 0.7 mm). Otoliths and beaks were removed and stored in vials for identification based on specialized guides (Wolff, 1984; Clarke, 1986; Diaz, 2007). Following other studies (Porras-Peters et al., 2008), we assumed that each scat sample was deposited by a single individual. They were most likely deposited by adult females at GI, which constitutes one of the two most abundant classes in breeding colonies (Gallo-Reynoso, 1994); the other class is pups, but their scats are clearly differentiated because or their small size and liquid appearance. In the SBA, scats were more likely deposited by juveniles or subadults, which are the most common age classes in this archipelago (Sierra, 2015).

Diversity Curves to Determine the Minimum Adequate Sample Size
To determine the representativeness of the number of scat samples analyzed for each location, a cumulative diversity curve (*EstimateS Swin820*) was generated using the Shannon-Wiener (H') diversity index value for each scat sample (Colwell, 2009). The coefficient of variation (CV) was calculated to obtain a number of scat samples (with hard structures) that would be statistically representative of the diet. This number was obtained when the CV ≤ 5% (0.05) (Ferry et al., 1997; Jiménez & Hortal, 2003).

Analysis of Scat Samples
The index of prey importance (IIMP) was calculated following García-Rodríguez & De la Cruz-Agüero (2011):

$$IIMPi = \frac{1}{U} \sum_{j=1}^{u} \frac{xij}{Xj}$$
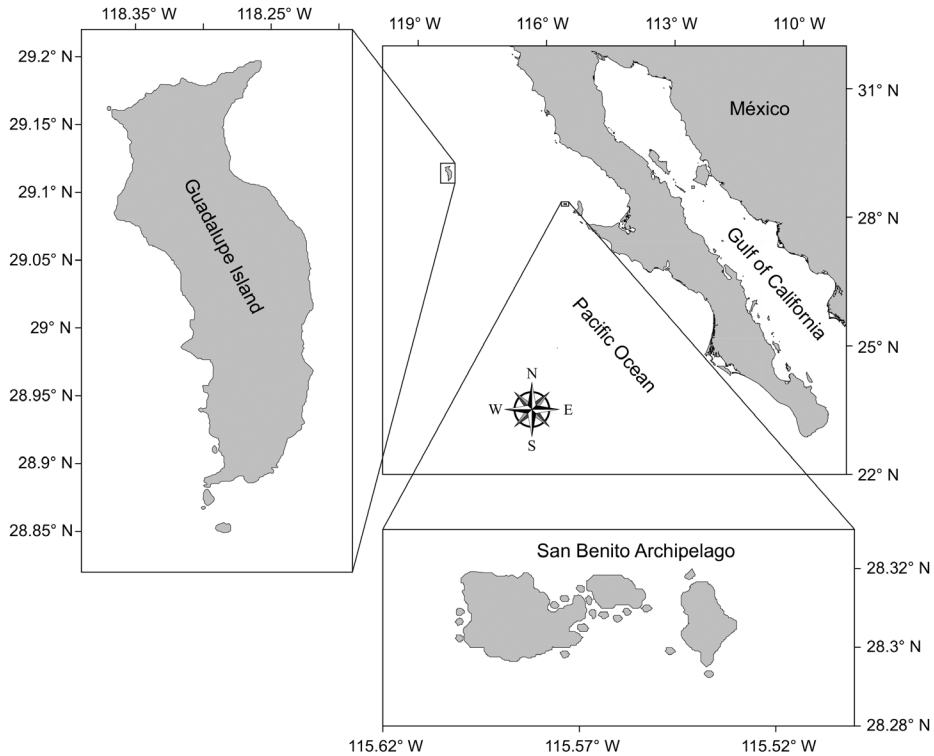
Figure 1. Location of the two Guadalupe fur seal (*Arctocephalus philippii townsendi*) (GFS) colonies on the Guadalupe Island (GI) and the San Benito Archipelago (SBA), Baja California, Mexico

where:

xij = Number of observations of species i in scat sample j

Xj = Total identifiable structures in scat sample j

u = Total number of scat samples where taxon i was identified

U = Total number of scat samples

Levin's standardized index (Hurlbert, 1978) was used to calculate the breadth of the trophic spectrum using the following formula:

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right)$$

where:

B_i = Trophic breadth

p_{ij} = Proportion of prey j in the diet of predator i

n = Total number of prey species in the diet

The values for B_i range from 0 to 1; values closer to 0 reflect specialist predators, whereas values closer to 1 indicate generalist predators (Krebs, 1999).

To interpret the species' foraging strategy and identify individual or population-wide patterns in diet specialization, we used Costello's graphs (Amundsen et al., 1996) of plotting the relative abundance against the proportion of the frequency of occurrence for different prey. These authors distinguished between four distinct strategies: (1) specialization in different types of prey, (2) a more generalized diet with some individual variation in diet breadth, (3) specialization in one type of prey while occasionally consuming other species, and (4) a mixed foraging strategy in which some individuals consume a specialized diet and others employ a more generalized foraging strategy.

The trophic level of each colony was calculated using the equation presented by Christensen & Pauly (1992):

$$TL = 1 + \sum_{j=1}^{n} D_{cij} * TL_j$$

where:

TL = Trophic level being calculated

DC_{ij} = Diet composition (i.e., the proportion of prey j in the diet of predator i)

TL_j = Trophic level of species j

n = Number of prey in the system

The TL of the prey species identified was obtained from Mearns et al. (1981), Froese & Pauly (2009), and Hernández-Montoya (2009). Only the latter one was conducted in our study area. The TL values reported by these sources are not necessarily the exact ones that may apply to our study period or area; however, they were the options available and were taken as a consistent approach for the different items.

Trophic Similarity
Nonmetric multidimensional scaling (NMDS) was used to assess the trophic similarity between the two colonies. The resulting dispersion pattern was examined using one-way analysis of similarity (one-way ANOSIM, 999 permutations; Dale et al., 2011). The resulting statistical *R* (-1 > R < 1) describes the similarity between groups; values closer to 0 indicate no difference, whereas those closer to 1 or -1 reflect a significant separation between the groups analyzed. The values generated by the *R* statistic were considered significant when *p* < 0.05. No units are expressed on the axes because plots are adimensional (Clarke & Warwick, 2001).

Collection and Processing of Fur Samples
On the SBA, we collected fur samples from 15 pups that were within 1 mo old during the 2013 breeding season (July); it was not possible to sample more individuals as there are very few births at SBA (Aurioles-Gamboa et al., 2010; Sierra, 2015). To compare the isotopic information with that from GI, we collected the same number of fur samples from that colony during the same month in 2013. Pups were captured using nets, and each sample was taken from the dorsal area using scissors. The samples were stored in paper envelopes. Pups were analyzed instead of their mothers because the mothers were mostly absent at SBA (pups were usually alone), and this comparison needed to be conducted under the same conditions for both sites.

The samples were washed with a 1:1 chloroform/methanol solution. These were cut into small pieces, using tweezers and scissors, and then homogenized to a fine powder in an agate mortar.

An analytical microbalance (precise to 0.0001 mg) was used to weigh ~1 mg of each sample to be stored in 8 × 5 mm tin capsules. The samples were sent to the University of California–Santa Cruz Stable Isotope Facility for analysis.

The proportion of stable isotopes of N and C is given as delta (δ; DeNiro & Epstein, 1978):

$$\delta^{13}C \; or \; \delta^{15}N = 1{,}000(R_{sample}/R_{standard}) - 1$$

where:

$\delta^{13}C$ or $\delta^{15}N$ = Difference between the ^{13}C or ^{15}N content of the sample and the standard, expressed in parts per thousand (‰)

R_{sample} = Ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) for the sample

$R_{standard}$ = Ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) for the standard

The elemental composition of carbon and nitrogen was estimated based on standards with known values: Vienna Pee Dee Belemnite ($\delta^{13}C = 0.011‰$) for carbon and atmospheric N_2 ($\delta^{15}N = 0.004‰$) for nitrogen. To identify significant differences between the two isotopic groups (GI and SBA), a Mann-Whitney U nonparametric test was performed.

The isotopic niche characteristics of both groups of pups were estimated using the *Stable Isotope Bayesian Ellipses in R* (*SIBER*) routine in *SIAR*, a package in *R* (R Development Core Team, 2008; Jackson et al., 2011). This approach involves the use of Markov-Chain Monte Carlo simulations to construct ellipse parameters. Bivariate ellipses and convex hulls were used to delineate isotopic niche space for each GFS colony.

Results

Scat Analysis
Based on 36 GFS scat samples from the SBA, we identified 911 hard structures present in 29 scat samples. The other seven did not contain structures. The CV for the cumulative diversity curve for this colony identified 35 (scats) as the minimum adequate sample size. All structures belonged to cephalopods. Three species of squid were identified—*Doryteuthis opalescens*, representing the vast majority (90.11% IIMP) of the trophic spectrum; *Onychoteuthis compacta* (5.79%); and *Dosidicus gigas* (1.97%)—and one octopus (*Octopus rubescens*) (Table 1). A total of 26 scat samples included embedded seagrass (*Phyllospadix* spp.).

Of the 67 GFS scat samples collected from GI, 351 hard structures were identified in 43 samples. The diversity curve for this colony determined the minimum adequate sample size to be 36 (scats).

Table 1. Identified prey from the Guadalupe fur seal (*Arctocephalus philippii townsendi*) (GFS) scats of the San Benito Archipelago (SBA); *N* = Number, O = Occurrence, IIMP = Index of importance by prey, P = Pelagic, EP = Epi-pelagic, M = Mesopelagic, and B = Benthic.

| Family	Species	*N*	O	IIMP (%)	Habitat	Trophic level
Loliginidae	Opalescent squid (*Doryteuthis opalescens*)	884	27	90.11	B	3.05
Onychoteuthidae	Hooked squid (*Onychoteuthis compacta*)	10	3	5.79	EP	3.2
Octopodidae	Pacific red octopus (*Octopus rubescens*)	7	5	2.11	B	3.8
Ommastrephidae	Jumbo squid (*Dosidicus gigas*)	10	2	1.97	P	3.91
Total		911	37	100		

Table 2. Identified prey from the GFS scats of the Guadalupe Island (GI); *N* = Number, O = Occurrence, IIMP = Index of importance by prey, and NI = Not identified.

	Family	Species	*N*	O	IIMP (%)	Habitat	Trophic level
Cephalopods	Ommastrephidae	Jumbo squid (*Dosidicus gigas*)	131	32	55.53	P	3.9
		Luminous flying squid (*Eucleoteuthis luminosa*)	4	2	4.06	P	3.7
	Onychoteuthidae	Hooked squid (*Onychoteuthis compacta*)	106	19	22.18	EP/MP	3.2
	Enoploteuthidae	Enope squid (*Abraliopsis felis*)	10	4	5.87	P	3.2
Fishes	Atherinopsidae	Topsmelt (*Atherinops affinis*)	2	2	0.51	P	2.7
	Myctophidae	Dogtooth lampfish (*Ceratoscopelus townsendi*)	14	3	1.69	P	3.5
		Lanternfish (*Symbolophorus californensis*)	70	5	5.63	EP/MP	3.3
		California headlight fish (*Diaphus theta*)	2	2	0.27	EP	3.1
		Otolith NI	2	2	0.66		
	Scorpaenidae	Chilipepper rockfish (*Sebastes goodei*)	3	1	0.36	B	3.8
	Cynoglossidae	California tonguefish (*Symphurus atricauda*)	1	1	0.12	B	3.3
	Paralichthyidae	Pacific sanddab (*Citharichthys sordidus*)	6	2	3.14	B	3.4
Total			351	43	100		

Cephalopod beaks were identified in 41 scat samples, and fish otoliths were recovered from 12 samples (Table 2). Twenty-six scat samples contained embedded seagrass.

A total of 11 prey species were identified for GI, seven of which were fish: *Atherinops affinis*, *Ceratoscopelus townsendi*, *Citharichthys sordidus*, *Diaphus theta*, *Sebastes goodei*, *Symbolophorus californensis*, and *Symphurus atricauda*. Another four prey species were cephalopods: *Abraliopsis felis*, *D. gigas*, *Eucleoteuthis luminosa*, and *O. compacta*. Although more fish
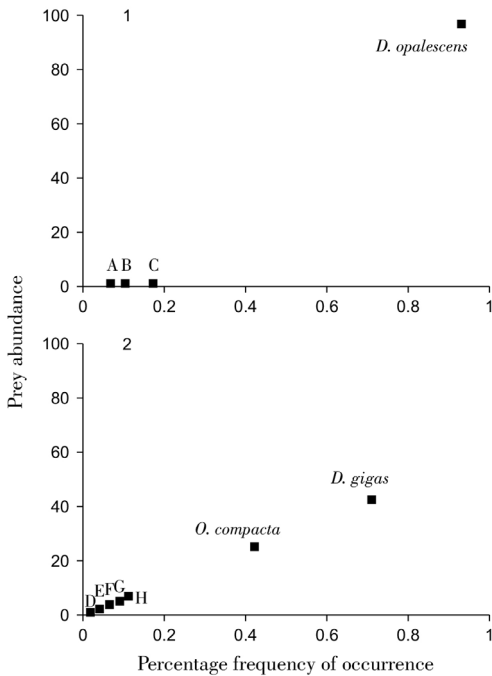
Figure 2. *Costello`s graph:* Numerical abundance of prey species by frequency of occurrence in the GFS diet from (1) SBA and (2) GI: (A) *Onychoteuthis compacta*; (B) *Dosidicus gigas*; (C) *Octopus rubescens*; (D) *Symphurus atricauda* and *Sebastes goodei*; (E) *Citharichthys sordidus*, *Eucleoteuthis luminosa*, *Diaphus theta*, and *Atherinops affinis*; (F) *Ceratoscopelus townsendi*; (G) *Abraliopsis felis*; and (H) *Symbolophorus californensis*.

species were identified by number, the highest IIMP for any given fish species was 5.63% for *S. californensis*. Meanwhile, cephalopods had a higher IIMP, with *D. gigas* having the highest value overall (55.53%), followed by *O. compact*a (22.18%) (Table 2).

Diet Breadth
The Levin's index value for the SBA was 0.02; whereas the index value for GI was 0.24, indicating that GFSs from both colonies were specialist consumers. When comparing the Costello's graphs (Amundsen et al., 1996) for both locations, we observed the same foraging strategy: a main specialization in one (*D. opalescens* for the SBA) or two prey species (*D. gigas* and *O. compacta* for GI; Figure 2).

Trophic Similarity Between Both
Fur Seal Colonies
GFSs from the SBA had a main diet of *D. opalescens* (90.11%); whereas the individuals from the

GI showed a higher frequency for *D. gigas* and *O. compacta* (77.71%). Significant differences were identified in this regard between the two colonies (ANOSIM, R = 0.704; *p* = 0.01; Figure 3). Additionally, the trophic level for GFSs, calculated by the Christensen & Pauly (1992) criteria, was 4.0 for the SBA and 4.5 for GI.

Isotopic Niche of Guadalupe Fur Seals from Guadalupe Island and San Benito Archipelago
The mean (± SD) $\delta^{13}C$ for GFSs from GI was -17.6 ± 0.3‰, with values ranging from -17.9 to -16.6‰. The mean $\delta^{15}N$ at GI was 18.4 ± 0.4 ‰, with a range of 17.7 to 19.5‰.

Individuals on the SBA had a mean $\delta^{13}C$ of -17.1 ± 0.4‰, with values ranging from -17.8 to -16.4‰; meanwhile, the mean $\delta^{15}N$ was 18.8 ± 0.4‰, with values ranging from 18.1 to 19.5‰.

Both stable isotopes were significantly higher for the SBA than those from GI ($\delta^{13}C$: U = 36; g.l. = 28; *p* < 0.05; $\delta^{15}N$: U = 53.5; g.l. = 28; *p* < 0.05).

Based on the *SIBER* analysis, pups from both colonies had similar isotopic niches, with an ellipse area of 0.40 for the SBA and 0.35 for GI. For both colonies, the polygon (convex hull) area was 0.84, with low overlap between the two colonies (0.37; Figure 4).

Discussion

Our scat analysis categorized the GFSs from the SBA and GI as specialist predators that fed almost exclusively on squid; however, no significant trophic similarity was observed between the two colonies. The small time window of scat analysis must be acknowledged; it only represents a snapshot of diet. Its results were supported by the stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis, which reflected segregation in the grounds exploited by the mothers of the pups analyzed during the ~16 wks prior to sample collection. Our findings could be reflecting trophic niche partitioning; however, a more extensive sampling over time is necessary to fully corroborate this hypothesis.

Scat Analysis
Based on the CV for the cumulative diversity curve for prey, the 29 scat samples (with otoliths or beaks) recovered from the SBA were not sufficient as six more scat samples would be required to achieve the minimum sample size. We recognize that this factor should be taken into account; however, consistent results were observed for the SBA, which was strongly dominated by one prey species. For the GI colony, the CV was adequate for minimum sample size as we were able to collect seven additional scat samples beyond the minimum necessary. The CV based its results on
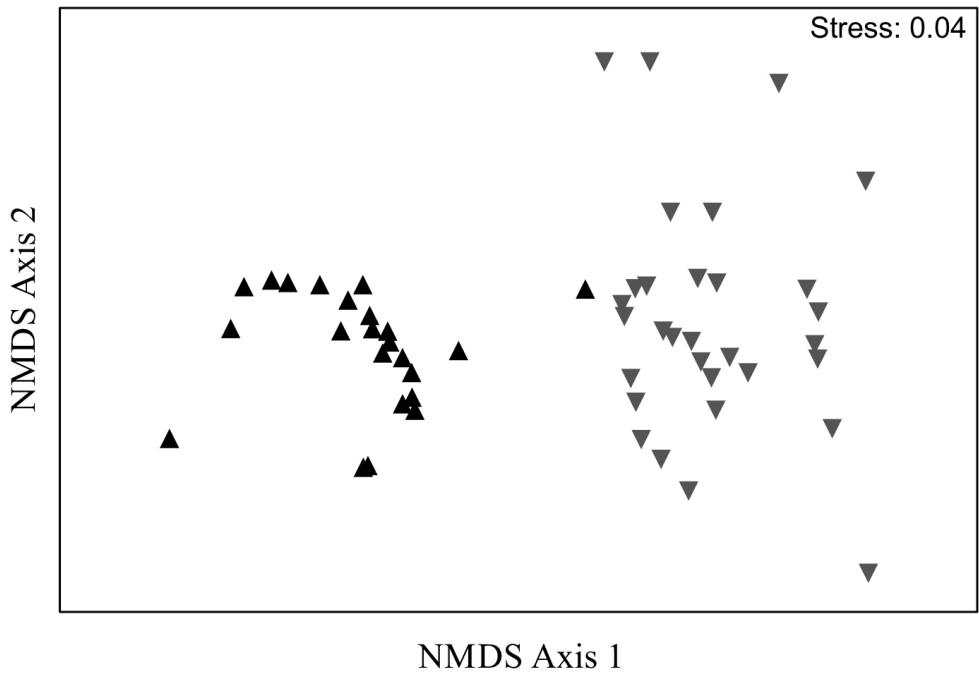
Figure 3. Nonmetric multidimensional scaling analysis (NMDS), based on the scat analysis of GFSs; ▲ = SBA and ▼ = GI.
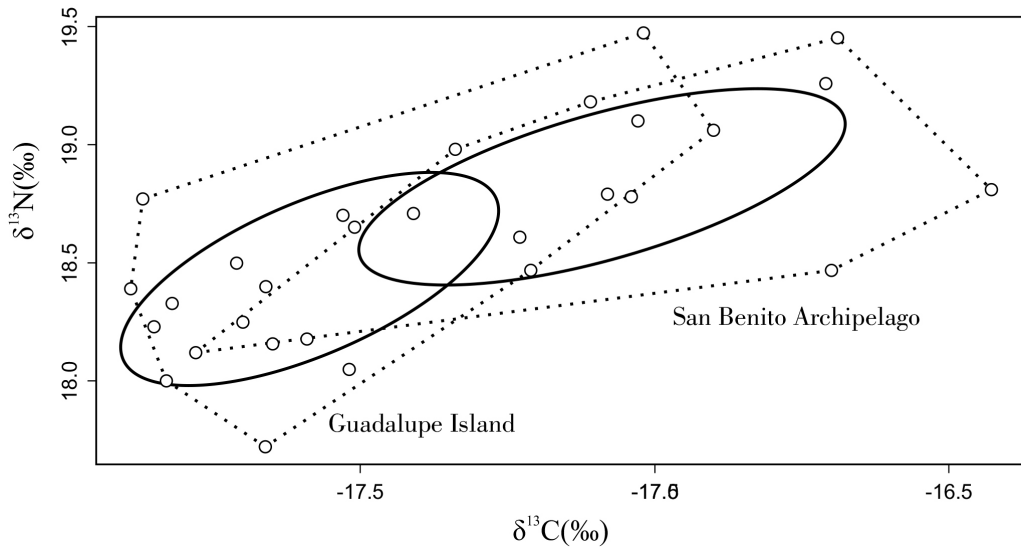
Figure 4. Isotopic niche for GFSs from GI and the SBA, based on the analysis of pups' fur, as proxies for maternal foraging

prey diversity rather than population size of GFSs, which is highly different between colonies.

Other studies have also reported cephalopods as one of the main prey consumed by GFSs (e.g., Gallo-Reynoso & Esperón, 2013). In contrast to other studies like Aurioles-Gamboa & Camacho (2007), for which fish made up 12% of the prey at the SBA, only cephalopod beaks were identified in our study. In this regard, diet reconstruction and differences between studies are likely to

be influenced by the availability of prey in any given season or year (Gallo-Reynoso & Esperón, 2013). No fish were reported here as no otoliths were identified; however, 12 scats included damaged scales or vertebra fragments, so the GFSs from the SBA fed occasionally on fish.

As reported previously, the opalescent squid was the dominant prey in the diet of individuals from the SBA (Aurioles-Gamboa & Camacho, 2007; Gallo-Reynoso & Esperón, 2013). This squid's reproductive season lasts from April to November, during which time they form large aggregations near the coast at depths of 20 to 60 m (Forsythe et al., 2004; Macewicz et al., 2004). The high availability of this cephalopod within the GFS diving range (Gallo-Reynoso et al., 2008) may be one of the reasons the species was important for SBA GFSs. At GI, which is farther from the coast (~270 km), the most important prey was the jumbo squid. In contrast, Hernández-Montoya (2009) reported that opalescent squid was the most important prey at GI (35%), while jumbo squid was a minor component (13%). In other studies, such as Gallo-Reynoso (1994), the jumbo squid was not reported. In March 2006, the year Hernández-Montoya (2009) collected scat samples, the live weight of jumbo squid caught off the coast of Ensenada, Baja California, was 7 tons; in January 2013, the year we collected scat samples, the live weight was 351 tons (CONAPESCA, 2015). Additionally, Waluda et al. (2006) described a recent major population increase for the jumbo squid in the northeastern Pacific, which may explain why the GFS diet at GI was so dominated by this squid during the 2013 breeding season.

The enope squid has not previously been reported in the GFS diet at GI, although species belonging to the same family have been identified. The hook squid was previously reported in the diet of this otariid at GI (Hernández-Montoya, 2009).

The difference in the available prey reported at GI by this and earlier studies may be due to the fact that the diet of otariids living in temperate and tropical regions can vary from year to year due to changes in resource availability, which is influenced by the environment (Gallo-Reynoso & Esperón, 2013). Fluctuations of fisheries support this argument (CONAPESCA, 2015; Juárez-Ruiz, 2015).

Seagrass was found in ~60% of the scat samples from both sites, which is unusual in pinnipeds but has been reported for the GFS in the past (Aurioles-Gamboa & Camacho, 2007; Pablo, 2009). There are two possible explanations in relation to its presence: (1) accidental intake while consuming prey or (2) consumption for use as a purgative, which is common among some terrestrial mammals (Petterson, 1968).

The trophic levels for the GFS colonies on the SBA and at GI were 4.0 and 4.5, respectively, which is within or close to the range of 3.9 to 4.3 reported elsewhere for the GFS (Pauly et al., 1998; Aurioles-Gamboa & Camacho, 2007; Hernández-Montoya, 2009; Pablo, 2009). These trophic-level differences were attributed to the main prey consumed by each colony—the jumbo squid, with a trophic level of 3.9; whereas the opalescent squid had a trophic level of 3.0.

Indicators of overlap reflected trophic segregation between GI and the SBA, which is important considering that even though both sites are located ~270 km apart, the foraging trips undertaken by GFS females can cover distances in excess of ~500 km (Gallo-Reynoso et al., 2008). Censuses at the SBA during summer 2013 indicated that juveniles and subadult males made up the majority (~90%) of the colony (Sierra, 2015) as it is a recolonization site (Aurioles-Gamboa et al., 2010). In contrast, at GI, the majority of the population is composed of adult females and pups (Gallo-Reynoso, 1994; Hernández-Montoya, 2009). This difference in age structure may explain the foraging differences between the two sites. Foraging segregation by age class has been suggested for fur seals before (Kurle & Worthy, 2001). Among otariids, the juvenile stage lasts for 3 to 4 y after pups are weaned, with individuals reaching adult size and sexual maturity by the end of this developmental stage. Juveniles gradually develop capture skills and their physiological capacity for diving (Kuhn et al., 2006; Weise & Costa, 2007). This behavioral distinction has been reported among other otariids, including the California sea lion (*Zalophus californianus*; Orr et al., 2011; Elorriaga-Verplancken et al., 2013) and the Steller sea lion (*Eumetopias jubatus*; Merrick & Loughlin, 1997).

Isotopic Analysis on the Guadalupe Fur Seals from Guadalupe Island and the San Benito Archipelago

Contrary to expectations, higher $\delta^{15}N$ values were obtained at the SBA relative to GI. This contrasts with the results of the scat analysis, which indicated a higher trophic level on GI than on the SBA. The $\delta^{13}C$ for GI was also lower than for the SBA. We provide two hypotheses to explain this: the differences in the base of the food chains at each site are a result of either (1) a latitudinal gradient (lower isotopic values at higher latitudes) between foraging grounds that may be at a greater distance than the one between the two colonies or (2) a horizontal variation between foraging grounds near and away from the coast (lower isotopic values further off coast). The latitudinal effect for both

stable isotopes has been reported for pinnipeds in the past (Burton & Koch, 1999; Aurioles-Gamboa et al., 2006; Elorriaga-Verplancken et al., 2016a). Regarding the second hypothesis, in our study, opalescent squid was the main prey for GFSs from the SBA, showing a high coastal frequency in summer (Forsythe et al., 2004; Macewicz et al., 2004); this is in contrast to the jumbo squid, the main prey at GI, which exhibits a more oceanic occurrence. Due to these differences in habitat, we cannot rule out the possibility that the isotopic differences between both sites may be influenced by individuals from the SBA feeding closer to shore as evidenced in other pinnipeds (Burton & Koch, 1999; Pablo, 2009; Elorriaga-Verplancken et al., 2016c); however, this hypothesis would only explain the differences in $\delta^{13}C$. It should be noted that these hypotheses are not mutually exclusive.

Final Remarks
The analysis of scats and stable isotopes showed complementarity, identifying prey species (mainly squids) from an oceanic habitat and $\delta^{13}C$ values in fur that were low, which are characteristic of that environment (Burton & Koch, 1999; Elorriaga-Verplancken et al., 2016c).

We concluded that the isotopic difference between colonies is due to spatial segregation rather than differences in trophic level. However, a simultaneous determination of baseline isotopic values for each foraging ground is necessary to reduce the uncertainty around this conclusion.

The weaknesses of our study must be acknowledged. We cannot totally discard prey items in the scat analysis that were not identified (scales or bones) or found. Identification of prey DNA in scats could be an alternative technique for building a more accurate diet (Deagle & Tollit, 2007), constituting a valuable tool for future GFS studies. Additionally, our results only include a small time window of summer for scat analysis and ~16 wks prior to fur recollection for stable isotopes. GFS foraging habits could change seasonally (Gallo-Reynoso & Esperón, 2013).

Our contribution regarding trophic variation within the GFS population is based on consistent results, but it is important to continue these and other long-term analyses to evidence a consistent trophic niche partitioning. The species is currently experiencing population recovery, which increases the possibility of overlap for resources between colonies. Moreover, anomalous warm conditions such as the ones recently present in the northeastern Pacific could create trophic uncertainties for this species' success (Elorriaga-Verplancken et al., 2016c).

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