## Short Note

# Seasonality and Potential Foraging Grounds of Migratory California Sea Lions from La Paz Bay, Southern Gulf of California, Mexico

Fernando R. Elorriaga-Verplancken,<sup>1</sup> Julieta Sandoval-Sierra,<sup>1</sup> Aurora Paniagua-Mendoza,<sup>2</sup> and Roberto Robles-Hernández<sup>3</sup>

<sup>1</sup>Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional (CICIMAR-IPN),

Departamento de Pesquerías y Biología Marina, Avenida IPN s/n Col. Playa Palo de Santa Rita,

23096, La Paz, Baja California Sur, México

E-mail: felorriaga@ipn.mx

<sup>2</sup>Megafauna Marina, Atención, Rescate, Ecología y Sociedad (MMARES, AC), La Paz, Baja California Sur, México <sup>3</sup>Procuraduría Federal de Protección al Ambiente (PROFEPA),

Blvd. Padre Eusebio Kino s/n Col. Los Olivos, 23040, La Paz, Baja California Sur, México

The Gulf of California (GC), Mexico, is the habitat for a population of 24,000 to 31,000 California sea lions (Zalophus californianus) (CSL) (Szteren et al., 2006). The southernmost breeding site of the species is located near the mouth of the GC on an islet called Los Islotes, where there is a colony of approximately 500 CSLs (Adame et al., 2017). After the breeding season, a large number of adult male CSLs migrate from California and probably Baja California to more northerly latitudes (Peterson & Bartholomew, 1967; Elorriaga-Verplancken et al., 2013). Subadult male CSLs (henceforth, "subadults") also undertake migratory movements. These have been assessed previously in the southern GC, which is their main habitat between autumn and spring (Aurioles-Gamboa et al., 1983). In contrast, movement of adult females is largely constrained to around the rookeries they inhabit as they must alternate between foraging trips and maternal care (García-Aguilar & Aurioles-Gamboa, 2003).

Analyses using stable isotopes of nitrogen ( $\delta^{15}N$ ; indicator of trophic position) and carbon ( $\delta^{13}C$ ; indicator of habitat use) have been used to describe the foraging habits of these animals (e.g., Porras-Peters et al., 2008; Orr et al., 2011; Elorriaga-Verplancken et al., 2013), as well as in assessments of large-scale movements such as between the GC and the northeast Mexican Pacific (Elorriaga-Verplancken et al., 2016a). These analyses are grounded in the observation that, at the base of the trophic webs of the GC, <sup>15</sup>N-enriched is by 2 to 3‰ when compared to the northeast Mexican Pacific. This is mainly because of intense microbial denitrification processes (Altabet et al., 1999), leading to the progressive <sup>15</sup>N-enrichment of all trophic levels up to top predators (Burton & Koch, 1999; Aurioles-Gamboa et al., 2009).

More information is necessary to better understand the movements and habitat use of male CSLs from rookeries in Mexico as robust knowledge is currently scarce. Previous studies have assumed a similar migratory behavior for males from rookeries in California in the United States and from those in Mexico (Elorriaga-Verplancken et al., 2013). This assumption is supported by the presence of a large number of male CSLs on California's Channel Islands during the nonbreeding season (Odell, 1975). This study gathers detailed knowledge for one part of the Mexican CSL distribution using a large, high-resolution time window and direct sampling on individuals.

Abundance of subadults was recorded at Los Islotes (24° 36' N, 110° 24' W), which is part of the Espíritu Santo Archipelago Marine Park in La Paz Bay, southern GC, Mexico (Figure 1). We followed established protocols where animal counts aided with binoculars were made from a boat that circled the rookery (Aurioles-Gamboa & Zavala, 1994; Elorriaga-Verplancken et al., 2015). The main goal was to determine the seasonality of CSL in the region and compare it to that reported nearly four decades earlier (the 1979-1982 study period) when different population conditions prevailed for this species (Le Boeuf et al., 1983). Additionally, a stable isotope ( $\delta^{15}$ N and  $\delta^{13}$ C) analysis was performed on subadults and adult females.

A total of 37 monthly counts was made between August 2012 and May 2016. Subadult males (5 to 8 y of age) are smaller and show less developed neck and sagittal crest compared to adult males;

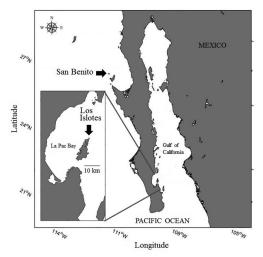


Figure 1. Study area: Los Islotes rookery, located in La Paz Bay. The San Benito Archipelago is also shown in the west region of Baja California, Mexico.

thus, these were identified as intermediate between adult females and adult males in terms of body mass. Subadult males also have a darker coloration than adult females (Lluch-Belda, 1969; Orr et al., 1970) (Figure 2). Fur samples for isotopic analyses ( $\delta^{15}N$  and  $\delta^{13}C$ ) were extracted from nine dead,

stranded subadults at different sites from La Paz Bay between October and March from 2013 to 2016. To have isotopic references for CSLs from the Pacific region (west coast of Baja California) and from La Paz Bay, fur samples were collected from 13 adult females from the San Benito Archipelago (28° 18' N, 115° 34' W) and six adult females from Los Islotes, respectively (June to December, 2013 to 2015). These females were captured and immobilized for their sampling. The CSL diet from these two rookeries has shown similar recent trends in terms of trophic position (Sandoval-Sierra, 2016). No fur samples were collected from subadults from the San Benito Archipelago because of the limited access to this locality in the Mexican Pacific, the logistical challenges of capture due to their larger size (frequently two or more times the size of adult females), and a lack of subadult carcasses. Sampling and counts were undertaken with previous knowledge and authorization by environmental authorities from Procuraduría Federal de Protección Ambiental (PROFEPA) from Baja California Sur or Comisión Nacional de Áreas Naturales Protegidas (CONANP) from Espíritu Santo.

The fur samples from the three groups were processed at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN) in La Paz, Baja California Sur, Mexico. Each sample was homogenized, and ~1 mg was weighed using an



Figure 2. Subadult male California sea lion (Zalophus californianus) (Photo Credit: Fernando R. Elorriaga-Verplancken)

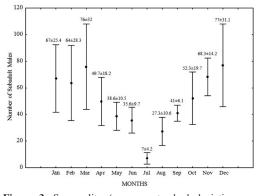


Figure 3. Seasonality (mean  $\pm$  standard deviation per month) of subdult male California sea lions at Los Islotes between August 2012 and March 2016

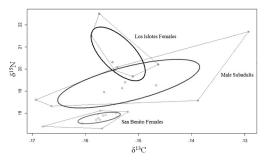


Figure 4. Isotopic niches of California sea lions: subadult males and adult females from Los Islotes and San Benito. Dotted lines correspond to the convex hull (polygons) areas, while subgroups are given by ellipses corrected for small sample sizes (SEAc) that are constructed by the *SIBER* analysis.

analytical microbalance. The samples were placed in capsules and sent to the University of California at Santa Cruz (UCSC) where the isotopic values were obtained via mass spectrometry.

Parametric paired t tests or nonparametric Mann Whitney U-tests (depending on data distributions) between groups (i.e., abundance values of the breeding season vs the nonbreeding season and all possible paired combinations among CSL groups) were performed at a significance level of 0.01. Moreover, the isotopic niches of the three CSL groups were estimated using convex hull areas (polygons) based on the totality of both  $\delta^{15}N$  and  $\delta^{13}C$  data. These were assessed using the SIBER (Stable Isotope Bayesian Ellipses in R) routine in the SIAR (Stable Isotope Analysis for R) package for R software. This analysis provides Bayesian bivariate ( $\delta^{15}N$  and  $\delta^{13}C$ ) standard ellipse areas corrected (SEAc) for small sample sizes (Jackson et al., 2011), reflecting the highest credibility data within each CSL group.

#### Abundance

A marked seasonality was evident in the abundance of subadults at Los Islotes, which remained consistent between 2012 and 2016. The greatest abundance was recorded in winter, particularly in December with an average of  $77 \pm 31.1$  subadults d<sup>-1</sup>, March with  $76 \pm 32$  subadults d<sup>-1</sup>, and November with  $68.3 \pm 14.2$  subadults d<sup>-1</sup>. The lowest abundance was recorded during the breeding season (June-August) with an average of  $25.3 \pm 14.3$  individuals d<sup>-1</sup> per monthly count. This contrasted sharply with the nonbreeding season (January-May and September-December) with an average of  $58.7 \pm 22.7$  subadults d<sup>-1</sup> per monthly count (n = 37, t = -3.9, p < 0.01) (Figure 3).

Stable Isotope Analysis – Foraging Habits-The mean  $\pm$  SD values for  $\delta^{15}$ N were 19.3  $\pm$  1.0% for subadults,  $20.7 \pm 1.1\%$  for adult females from Los Islotes, and  $17.8 \pm 0.2\%$  for adult females from the San Benito Archipelago. Subadults stranded in La Paz Bay showed δ<sup>15</sup>N values significantly higher (n = 22, U = 20, p < 0.01) and lower but not significant (n = 15, U = 5, p = 0.02) than adult females from San Benito and Los Islotes, respectively. Females showed significant differences in  $\delta^{15}$ N between sites (*n* = 19, U = 10, *p* < 0.01). The mean  $\pm$  SD values for  $\delta^{13}$ C were  $-15.2 \pm 1.3\%$  for subadults,  $-15.4 \pm 0.5\%$  for adult females from Los Islotes, and  $-15.7 \pm 0.4\%$  for adult females from the San Benito Archipelago. The  $\delta^{13}$ C for subadults was not significantly different from that for adult females from Los Islotes (n = 15, U = 5, p = 0.68) or San Benito (n = 22, U = 20, p = 0.08). Females from both sites did not show significant differences in  $\delta^{13}$ C (*n* = 19, U = 10, *p* = 0.23). The SIBER analysis revealed a larger isotopic niche area for subadults based on all data (convex hull =  $5.8\%^2$ ) as well as just those with the highest credibility (SEAc =  $3.4\%^2$ ) relative to adult females  $(\text{convex hull} = 0.7 - 1.6\%^2, \text{ SEAc} = 0.3 - 1.5\%^2)$ (Figure 4).

Our study revealed a seasonal presence of subadults in La Paz Bay throughout 2012 to 2016, mainly between October and April. Our monthly effort permitted comparison of our findings to similar data for the same region from 34 to 38 y ago (1979 to 1982), when CSL populations were smaller (Aurioles-Gamboa et al., 1983). These authors addressed the possibility of subadults migrating between colonies in the Pacific Ocean and the southern GC because of the lack of significant differences in their seasonal abundance at other northern sites in the GC.

Our mean number of subadults was  $\sim 30\%$  higher (58.7 vs 43) during the nonbreeding season and  $\sim 40\%$  higher (25 vs 15) during the breeding season (June-August) than the respective abundances reported in the 1979-1982 study. These

differences are due to the population increase reported over the last few decades. For instance, the highest abundance previously reported for the CSL colony at Los Islotes was 209 individuals in August 1979 compared to the 530 CSLs we recorded in August 2014. This difference may be used as a proxy for the population growth which followed the species' near extinction as a result of overexploitation during the 19th and 20th centuries (Gerber & Hilborn, 2001). At the beginning of the 1980s, the abundance was 23,200 in the GC, 66,700 on the west coast of Baja California, and 50,750 in California for a grand total of ca. 140,650 CSLs (Le Boeuf et al., 1983). In contrast, the current abundance estimates range between 24,000 and 31,000 for the GC (Szteren et al., 2006), 58,859 for the west coast of Baja California (Milanés-Salinas, 2012), and 296,750 for California (Carretta et al., 2014) for an overall total of ca. 385,000 CSLs.

Foraging Habits  $-\delta^{15}N$  values for subadults in La Paz Bay were lower ( $\sim 1.4\%$ ) than those for adult females at Los Islotes (GC) and higher  $(\sim 1.5\%)$  than those for adult females from the San Benito Archipelago in the Pacific Ocean. A previous isotopic analysis focusing on dental collagen samples from CSLs from different rookeries in the central and northern GC and on the west coast of Baja California (Santa Margarita Island) reported  $\delta^{15}N$  values ~1% higher for subadults relative to adult females due to the higher trophic position of males as a result of their larger body mass and probable consumption of larger prey (Elorriaga-Verplancken, 2009; Elorriaga-Verplancken et al., 2013). Similar differences have been reported for other sexually dimorphic pinniped species such as the northern fur seal (Callorhinus ursinus; Burton & Koch, 1999), the southern elephant seal (Mirounga leonina; Lewis et al., 2006), the northern elephant seal (Mirounga angustirostris; Velázquez & Elorriaga-Verplancken, 2017), and the Guadalupe fur seal (Arctocephalus philippii townsendi; Juárez et al., Accepted). These consistencies suggest that subadults that were sampled in La Paz Bay showed  $\delta^{15}$ N values that reflect the use of foraging habitats outside of the GC, likely on the west coast of Baja California during summer when they are mostly absent from La Paz Bay and the surrounding areas. In contrast, females from Los Islotes feed on a trophic web that presents the 15N-enriched baseline typical of the GC (Altabet et al., 1999). This results in lower  $\delta^{15}N$  values for subadults relative to adult females from Los Islotes, regardless of their trophic position.

Subadults sampled from January to March (n = 5) showed higher  $\delta^{15}$ N values (19.6%) than those sampled in October and November (n = 4)

(19.0‰), which may be a consequence of a slight <sup>15</sup>N-enrichment after a certain period in the GC. However, since our sample is small, this hypothesis should be considered with caution.

The analysis of nitrogen stable isotopes is an efficient indicator of habitat use (Aurioles-Gamboa et al., 2009). Although  $\delta^{13}$ C values also show a latitudinal baseline gradient (Elorriaga-Verplancken et al., 2016b), they also reflect an inshore-offshore pattern (Burton & Koch, 1999). Thus, subadults showed wide variability in this stable isotope (4‰) relative to adult females from both localities (1.3 to 1.6‰). This may be related to the marked difference in migratory capacity of subadults, including the latitudinal and shore-offshore movements mentioned previously. This finding was supported by the *SIBER* analysis of both the  $\delta^{15}$ N and  $\delta^{13}$ C values, which clearly distinguished different isotopic areas for subadults and adult females.

Since the sample sizes for the stable isotope analysis were small, our results should be considered with caution. Future studies should employ complementary approaches (e.g., telemetry) to determine migratory routes to assess our conclusions. It is not possible to eliminate the possibility that our results are biased because we examined different years (2013 to 2016) and compare dead individuals (subadults) with live ones (females). Moreover, the addition of data from subadults from San Benito would also strengthen our conclusions. However, this study provides valuable insight regarding the seasonal residency of subadults in La Paz Bay in the southern GC. Our study also shows the utility of stable isotope analysis for inferring migrations, thus contributing to our understanding of the ecology of male CSL migrations between different colonies in Mexico.

#### Acknowledgments

Instituto Politécnico Nacional (IPN) provided financial support for these field trips through Projects SIP-20120715, 20130944, 20140277, 20150326, and 20160164. We thank Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) through Dirección General de Vida Silvestre en México (DGVS) for providing Research Permits SGPA/DGVS/01847/12, 11744/13, 00195/15, and DGVS/00050/16, as well as Irma González and the Comisión Nacional de Áreas Naturales Protegidas (CONANP-Parque Nacional Zona Marina del Archipiélago Espíritu Santo). We also thank Procuraduría Federal de Protección Ambiental (PROFEPA) and the Marine Mammal Stranding Network from La Paz, BCS, Mexico. For their support during some of the field trips to Los Islotes, we thank Ecological Project International (EPI), Museo de la Ballena y Ciencias del Mar, AC, Dr. Mario A.

Pardo from Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE-Unidad La Paz), and Marine Biologist Karen Adame-Fernández (Grants-in-Aid of Research Program of the Society for Marine Mammalogy).

### Literature Cited

- Adame, K., Pardo, M. A., Salvadeo, C., Beier, E., & Elorriaga-Verplancken, F. R. (2017). Detectability and categorization of California sea lions using an unmanned aerial vehicle. *Marine Mammal Science*, 33(3), 913-925. https://doi.org/10.1111/mms.12403
- Altabet, M. A., Pilskaln, C., Thunell, R., Pride, C., Sigman, D., Chávez, F., & Francois, R. (1999). The nitrogen isotope biogeochemistry of sinking particles from the margin of the eastern North Pacific. *Deep-Sea Research I*, 46(4), 655-679. https://doi.org/10.1016/S0967-0637(98)00084-3
- Aurioles-Gamboa, D., & Zavala, A. (1994). Algunos factores ecológicos que determinan la distribución del lobo marino Zalophus californianus, en el Golfo de California [Some ecological factors that determine the distribution of the sea lion Zalophus californianus, in the Gulf of California]. Ciencias Marinas, 20, 535-553.
- Aurioles-Gamboa, D., Newsome, S. D., Salazar-Pico, S., & Koch, P. (2009). Stable isotope differences between sea lions (*Zalophus*) from the Gulf of California and Galápagos Islands. *Journal of Mammalogy*, 90(6), 1410-1420. https://doi.org/10.1644/08-MAMM-A-209R2.1
- Aurioles-Gamboa, D., Sinsel, F., Fox, C., Alvarado, E., & Maravilla, O. (1983). Winter migration of subadult male California sea lions (*Zalophus californianus*) in the southern part of Baja California. *Journal of Mammalogy*, 64(3), 513-518. https://doi.org/10.2307/1380369
- Burton, R. K., & Koch, P. (1999). Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. *Oecologia*, 119(4), 578-585. https:// doi.org/10.1007/s004420050822
- Carretta, J. V., Oleson, E., Weller, D. W., Lang, A. R., Forney, K. A., Baker, J., . . . Mattila, D. K. (2014). U.S. Pacific marine mammal stock assessments: 2013 (Technical Memorandum, NMFS-SWFSC-532). Washington, DC: National Oceanic and Atmospheric Administration.
- Elorriaga-Verplancken, F. R. (2009). Variación de  $\delta^{15}$ N y  $\delta^{13}$ C en colágeno dental de lobos marinos del género *Zalophus*: Patrones ontogénicos y geográficos [ $\delta^{15}$ N and  $\delta^{13}$ C variation in dental collagen of *Zalophus* sea lions: Ontogenetic and geographic patterns] (Ph.D. dissertation). Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), La Paz, BCS, México. 163 pp.
- Elorriaga-Verplancken, F. R., Ferretto, G., & Angell, O. C. (2015). Current status of the California sea lion (*Zalophus californianus*) and the northern elephant seal (*Mirounga angustirostris*) at the San Benito Archipelago, Mexico. Ciencias Marinas, 41(4), 269-281. https://doi.org/10.7773/cm.v41i4.2545
- Elorriaga-Verplancken, F. R., Rosales-Nanduca, H., & Robles, R. (2016a). Unprecedented records of Guadalupe

fur seals in La Paz Bay, Southern Gulf of California, Mexico, as a probable result of warm conditions in the northeastern Pacific. *Aquatic Mammals*, 42(3), 261-267. https://doi.org/10.1578/AM.42.3.2016.261

- Elorriaga-Verplancken, F. R., Aurioles-Gamboa, D., Newsome, S. D., & Díaz, S. (2013). δ<sup>15</sup>N and δ<sup>13</sup>C values in dental collagen as a proxy for sex and age variation in foraging strategies of California sea lions. *Marine Biology*, *160*(3), 641-652. https://doi.org/10.1007/ s00227-012-2119-y
- Elorriaga-Verplancken, F. R., Morales-Luna, L., Heckel, G., & Schramm, Y. (2016b). Foraging ecology of harbor seals (*Phoca vitulina*) and northern elephant seals (*Mirounga* angustirostris) from Baja California, Mexico: Inferences from stable isotopes in pups. Journal of Marine Biological Association of the United Kingdom, 96(1), 903-908. https://doi.org/10.1017/S0025315415002143
- García-Aguilar, M. C., & Aurioles-Gamboa, D. (2003). Cuidado materno en el lobo marino de California (Zalophus californianus) de Los Islotes, Golfo de California, México [Maternal care in the California (Zalophus californianus) sea lion from Los Islotes, Gulf of California, Mexico]. Ciencias Marinas, 29(4B), 573-583. https://doi.org/10.7773/cm.v29i42.199
- Gerber, L. R., & Hilborn, R. (2001). Catastrophic events and recovery from low densities in populations of otariids: Implications for risk of extinction. *Mammal Review*, 31(2), 131-150. https://doi.org/10.1046/j.1365-2907.2001.00081.x
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology, 80(3), 595-602. https://doi.org/10.1111/j.1365-2656. 2011.01806.x
- Juárez, A., Elorriaga-Verplancken, F. R., Moreno-Sánchez, X., Aguíñiga, S., Amador-Capitanachi, M. J., & Gálvez, C. (Accepted). Diversification of foraging habits among Guadalupe fur seals from their only well-established breeding colony, Guadalupe Island, Mexico. *Marine Biology*.
- Le Boeuf, B. J., Aurioles-Gamboa, D., Condit, R., Fox, C., Gisiner, R., Romero, R., & Sinsel, F. (1983). Size and distribution of the California sea lion population in Mexico. *Proceedings of the California Academy of Sciences*, 43, 77-85.
- Lewis, R., Connell, T. C. O., Lewis, M., Campagna, C., & Hoelzel, A. R. (2006). Sex specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). Proceedings of the Royal Society B: Biological Sciences, 273, 2901-2907. https:// doi.org/10.1098/rspb.2006.3642
- Lluch-Belda, D. (1969). El lobo marino de California, Zalophus californianus californianus (Lesson, 1828): Observaciones sobre su ecología y explotación [The California sea lion, Zalophus californianus californianus (Lesson, 1828): Observations on its ecology and exploitation]. Mexico City: Instituto Mexicano de Recursos Naturales Renovables.

- Milanés-Salinas, M. A. (2012). Abundancia y distribución del lobo marino de California (Zalophus californianus) en el Pacífico Mexicano (Abundance and distribution of California sea lions (Zalophus californianus) in the Mexican Pacific) (M.Sc. dissertation). Universidad Autónoma de Baja California (UABC), Ensenada, BC, México.
- Odell, D. K. (1975). Breeding biology of the California sea lion, Zalophus californianus. Rapports et Procésverbeaux des Reúnions Conseil International pour l'Exploration de la Mer, 169, 374-378.
- Orr, A. J., VanBlaricom, G. R., DeLong, R. L., Cruz-Escalona, V. H., & Newsome, S. D. (2011). Intraspecific comparison of diet of California sea lions (*Zalophus californianus*) assessed using fecal and stable isotope analyses. *Canadian Journal of Zoology*, 89, 109-122. https://doi.org/10.1139/Z10-101
- Orr, R. T., Schonewald, J., & Kenyon, K. W. (1970). The California sea lion: Skull growth and comparison of two populations. *Proceedings of the California Academy of Sciences*, 37, 381-394.
- Peterson, R. S., & Bartholomew, G. A. (1967). The natural history and behavior of the California sea lion (Special Publication No. 1, pp. 73-76). Lawrence, KS: American Society of Mammalogists. https://doi.org/10.5962/bhl. title.39535
- Porras-Peters, H., Aurioles-Gamboa, D., Cruz-Escalona, V., & Koch, P. (2008). Trophic level and overlap of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. *Marine Mammal Science*, 24(3), 554-576. https://doi.org/10.1111/j.1748-7692.2008.00197.x
- Sandoval-Sierra, J. (2016). Nicho isotópico de dos colonias de lobo marino de California (Zalophus californianus): Análisis de amplitud y de la relación entre crías y adultos [Isotopic niche of two California sea lions (Zalophus californianus) rookeries: Breadth analysis and the relationship between pups and adults] (B.Sc. dissertation). Universidad Autónoma de Baja California Sur (UABCS), La Paz, BCS, México. 60 pp.
- Szteren, D., Aurioles, D., & Gerber, L. R. (2006). Population status and trends of the California sea lion (*Zalophus* californianus californianus) in the Gulf of California, Mexico. In A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, & K. M. Wynne (Eds.), Sea lions of the world (Alaska Sea Grant College Program, AK-SG-06-01, pp. 369-384). https://doi.org/ 10.4027/slw.2006.25
- Velázquez, C. M., & Elorriaga-Verplancken, F. R. (2017). Isotopic evidence for intersexual foraging variation in northern elephant seals from Baja California, Mexico. *Marine Biology*, 164, 168. https://doi.org/10.1007/ s00227-017-3192-z