## **Short Note**

## Northernmost Habitat Range of Guadalupe Fur Seals (*Arctocephalus townsendi*) in the Gulf of California, México

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Marine megafauna breeding sites are key for the survival and conservation of populations; therefore, there is a wide range of knowledge on the subject (e.g., Hooker & Gerber, 2004). For marine mammals such as pinnipeds, unisexual haul-out sites are relevant places related to foraging activities and rest after the breeding season (Sullivan, 1980); however, the dynamics are not well defined for some sea lion and fur seal species (Giardino et al., 2016; Baylis et al., 2017), including the Guadalupe fur seal (Arctocephalus townsendi) (GFS). This species is an oceanic predator with an important dispersal capacity according to sightings and strandings from the west coast of the United States (California, Oregon, and Washington) (Hanni et al., 1997; D'Agnese et al., 2020) to the Central (Jalisco and Colima; Ortega-Ortiz et al., 2019) and South Pacific Ocean in México (Villegas-Zurita et al., 2015) and the Galapagos Islands in Ecuador (Páez-Rosas et al., 2020). Guadalupe Island, located in the western region of the Baja California Peninsula, México, is recognized as the only GFS breeding colony worldwide (García-Aguilar et al., 2018), although a few births have been reported in San Miguel Island (Melin & DeLong, 1999), California, and in the San Benito Archipelago (Maravilla-Chávez & Lowry, 1999). GFS males arrive at Guadalupe Island beginning in May to start the breeding season (June to August), which concludes with the post-breeding migration and arrival to haulout sites (September to April) until the next breeding season (Gallo-Reynoso, 1994). Currently, the GFS is classified as endangered by Mexican law (NOM-059-SEMARNAT-2010) and as threatened under the U.S. Endangered Species Act of 1973.

The limited geographical reproduction of the GFS is the result of overexploitation by the fur industry during the 18th and 19th centuries (Bartholomew, 1950), which reduced its population from approximately ~200,000 individuals (Hubbs, 1979) from the Washington coast (Etnier, 2002) and Monterey Bay, California (Starks, 1922), to the Revillagigedo Archipelago (Socorro Island) in Colima, México (Townsend, 1924; Hamilton, 1951), to < 20 GFSs at Guadalupe Island (Hubbs, 1956). It is suggested that at least 52,000 individuals were killed during this period (Townsend, 1916), which led to the first apparent GFS extinction and genetic bottleneck (Weber et al., 2004). However, after Guadalupe Island was protected by the Mexican government in 1922 (Bezaury-Creel, 2005), approximately 600 GFSs were observed on the island during the 1960s (Rice et al., 1965). Recently (2013), the GFS population has reached 34,000 to 44,000 individuals at an annual growth rate of 5.9% (range: 4.1 to 7.7%) (García-Aguilar et al., 2018). Interestingly, an increase of GFS sightings, especially of young individuals (e.g., weaners) along the California coast (D'Agnese et al., 2020), has coincided with the historical range of the GFS according to archaeological data collected from northwestern Washington (Etnier, 2002) to California (e.g., Point Conception), where ancient GFS rookeries have been identified (Rick et al., 2009). Moreover, recent records have been made off Central México, close to or in old occupation sites like Revillagigedo Islands, México (Ortega-Ortiz et al., 2019; Hoyos-Padilla et al., 2021). However, the historical identification of GFS bull (reproductive male) haul-out sites is widely unknown.

Therefore, based on the newly reemerging GFS population in the Pacific Northwest of the U.S. (D'Agnese et al., 2020), this study aims to contribute to modern pinniped demographic data regarding this species' habitat expansion range along the

Gulf of California, involving the potential establishment of a GFS bull haul-out site at San Pedro Mártir Island (SPMI). Nonetheless, there is solid evidence that GFSs were not registered at SPMI between 1994 and 2010 (Tadd Pfister, pers. comm. data). However, some anthropogenic threats are reported (Enríquez-Andrade et al., 2005) that could have an impact on this establishment, such as fishery interactions (e.g., entanglements and overfishing), pollution (e.g., pesticides), and harmful algal blooms (Zavala-Gonzalez & Mellink, 1997; Páez-Osuna et al., 2017). These findings should be an important contribution to knowledge regarding recent population dynamics with important conservation implications in México.

SPMI is a volcanic and isolated isle with an area of 302 km² that is part of the Midriff Islands Region. It is located in the northern faunal region of the Gulf of California, 61 km from Kino Bay, Sonora. This island has several national and international protection and conservation distinctions, such as a Marine Protected Area (Biosphere Reserve), by the Mexican government (Comisión Nacional de Áreas Naturales Protegidas—Secretaría del Medio Ambiente y Recursos Naturales [CONANP-SEMARNAT], 2007; Figure 1).

This region is an important upwelling zone supported by its characteristic oceanography and topography, which promote strong mixing processes by tidal and wind currents that result in a supply of nutrients. As a result, it is one of the most productive regions within the Gulf of California (Paden et al., 1991), with important abundance and diversity of macrofauna (Brusca et al., 2005). Moreover, there is a colony of approximately 700 California sea lions (Zalophus californianus) on SPMI (Adame et al., 2020). Although SPMI is considered one of the most oceanic islands in the Gulf of California, it is an area of special interest for artisanal, industrial, and sport fishing boats, mainly from Sonora and Baja Peninsula. The increase in tourism, as well as fishing activities, represent the main threats that most likely cause a loss of the island's marine ecosystem (CONANP-SEMARNAT, 2007).

Records of GFSs on SPMI were obtained from nonsystematic surveys between 2009 and 2021, which were part of the cetacean monitoring and photo-identification project of the Marine Mammal Program of the Prescott College Kino Bay Center for Cultural and Ecological Studies in the region. Surveys around SPMI were carried out aboard an approximately 7-m-long skiff boat with a 115-hp outboard motor. At least two observers were present in each survey, performing continuous scans along the periphery of the island with the naked eye and/or with 8 × 42 mm Vortex binoculars (Vortex Optics, Barneveld, WI, USA). There were no surveys during

May, July, August, or September (2012 to 2021) due to the influence of strong storms (poor weather conditions) and logistical limitations. The GFS observation activity spanned between 40 to 50 min at an approximate speed of 4 to 5 kts. When a GFS sighting was recorded, the speed of the boat was reduced, and a slow approach was made, keeping approximately 10 m in a parallel and non-invasive way to avoid any disturbance. Each sighting was recorded in a field data sheet, which included the number of animals, geographical position with a Garmin GPS (Global Positioning System; Garmin Ltd., Olathe, KS, USA), date (month and year), and the general behavior (e.g., resting, swimming, grooming). Photographs of the animals were taken with a digital camera (Canon EOS 7D, with 75-300 mm ultrasonic lens; Canon, Ota City, Tokyo, Japan) for age and sex classification. Individuals were counted manually, and those not properly observed for description (e.g., behind rocks, in caves, or at sea) were recorded as undetermined.

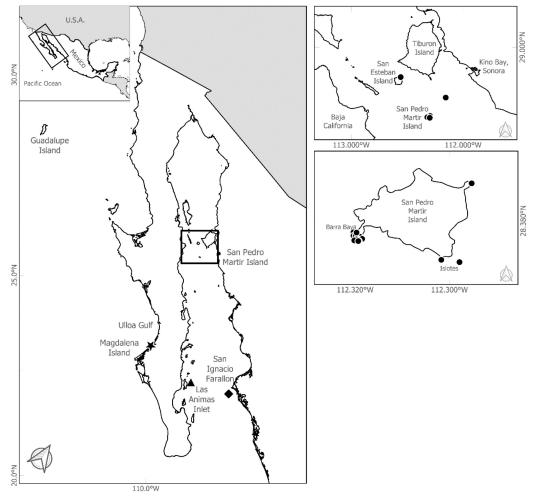
Morphology of the GFS was used to distinguish them from California sea lions at the island. They are characterized by a pointed narrow snout slightly downcurved at the tip, with a long and narrow muzzle (Reeves et al., 2002; Allen et al., 2011). Similar to other fur seals, GFSs have dense fur due to the presence of guard hairs and underfur, which is easily recognized as light stripes (Riedman, 1990). GFS age class classification was established as follows:

- Adult male Biggest body size and fully developed muscular neck, shoulders, and chest. Body colors vary from brown, to reddish, to dusky black. Mane and head crown colors are silvery gray, yellow, or blonde to reddish, extending until the shoulders. Individuals have a grizzled appearance when they are dry. Whiskers are light to cream.
- Subadult male Nose as large as adult males, mane not well developed as in adults, muscular but slimmer neck and shoulders, and chest not as gross as adults. Body colors are brown, to reddish, to dusky black. Mane and head crown colors are not as light as adults but vary from silvery gray to blonde or reddish, extending until the shoulders. Whiskers are light to cream.
- Juvenile Smallest body size among males, with a short mane and gross neck. Shoulders and chest are not as well developed as they are in subadults and adults. Body colors are brownish, and whiskers have a patchy black and light to cream color appearance. (Reeves et al., 2002; Allen et al., 2011)

Data were tested for normality with a Kolmogorov-Smirnov-Lilliefors test, followed by a Levene's test for homoscedasticity. The results were not normal, and a lack of homoscedasticity was identified; therefore, a nonparametric statistic was applied. Since the survey efforts by years and months were not similar, a Kruskal-Wallis test (Zar, 1999) was performed to identify differences among years (2009 to 2021) regarding total individual sightings at SPMI. Results were considered significant when p < 0.05. The location of each GFS sighting was mapped using *QGIS*, Version 3.12.0, to visualize the sightings distribution and to recognize specific occurrence sites along the

SPMI. In this regard, frequency (percentage) by age classes was described among years (2011 to 2021) to establish a structure. From 2009 to 2021 (except 2016), a total of 292 GFSs were counted in 33 surveys at SPMI (Table 1; Figure 1). In order to compare abundance by seasons due to lack of surveys during the same months (2009 to 2021) at SPMI, the GFS males' migratory cycle was considered as breeding (June to August) and postbreeding seasons, which were divided into two periods: (1) early (September to December) and (2) late (January to April).

Although there was not a homogenous survey effort during these periods, and there was a lack



**Figure 1.** Localization of Guadalupe fur seal (*Arctocephalus townsendi*) male individuals (black dots) sighted at the San Pedro Mártir Island (SPMI) and surroundings in the central region of the Gulf of California, México, during the surveys (2012-2015/2017-2021) by Prescott College Kino Bay Center for Cultural and Ecological Studies. Localizations of Magdalena Island (star), Las Animas Islet (triangle), and San Ignacio Farallon (diamond) are indicated where GFSs have been previously registered by other authors.

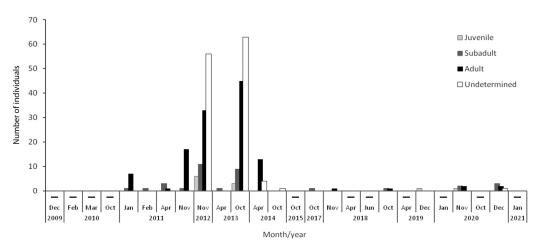
of data within some months of the study due to poor weather conditions and logistical limitations, interannual differences in the total number of individuals were observed at SPMI among years (Kruskall-Wallis test, p = < 0.005; Table 1). The highest GFS abundances were recorded in 2012 (n = 106) and 2013 (n = 121), while the lowest abundances were registered in 2017 (n = 1), 2018 (n = 3), and 2019 (n = 1). No GFSs were observed during the 2015 and 2021 surveys. The highest number of GFS individuals in SPMI was estimated during the post-breeding period, particularly in the early season, followed by the late season, with no records available during the breeding period (Table 1; Figure 2).

The SPMI site with the highest GFS abundance (65%) was Barra Baya, located in the southwest portion of the island, while 25% of the records took place in Los Islotes and 10% around SPMI (Figure 1). GFSs classified as undetermined (e.g.,

behind rocks, in caves, or at sea) were considered as potential males. The urogenital opening was an important characteristic to corroborate sex in juveniles, as well as the absence of pups in the case of adult females. Identified GFS age classes (n = 292) were represented by male adults (42%, n = 122), male subadults (11%, n = 34), juveniles (4%, n = 11), and undetermined individuals (43%)n = 125) (Figures 2 & 3); physical characteristics were similar to GFS males observed during the breeding season at Guadalupe Island (2013 to 2015; Figure 4). During surveys at SPMI (2013) to 2021), GFS males were found resting (43.5%, n = 127), moving around (8%, n = 23), scratching (3.5%, n = 10), vocalizing (3%, n = 8), and grooming (2%, n = 6), as well as swimming (40%, n = 6)n = 118), exhibiting thermoregulatory behavior (29%, n = 86), and diving (11%, n = 32). Based on the current study, GFS males have been present at SPMI since 2012.

**Table 1.** Guadalupe fur seal (*Arctocephalus townsendi*) records at San Pedro Mártir Island and surroundings from 2009 to 2015 and 2017 to 2021

Year	Month	No. of surveys	Total no. of individuals
2009	December	1	0
2010	February	1	0
	March	2	0
	October	1	0
2011	January	2	8
	February	1	1
	April	1	4
	November	1	18
2012	November	1	106
2013	April	1	1
	October	1	120
2014	April	2	17
	October	1	1
2015	October	1	0
2017	October	1	1
2018	April	1	0
	June	1	0
	October	2	2
	November	1	1
2019	April	1	0
	December	1	1
2020	January	2	0
	October	2	0
	November	1	5
	December	2	6
2021	January	1	0



**Figure 2.** Male Guadalupe fur seals sighted at SPMI in the Central Gulf of California by year, month, and age class (2011 to 2021); the horizontal black bars indicate surveys at SPMI with no GFS records.



Figure 3. Male Guadalupe fur seals at SPMI: (a) juvenile, (b) subadult, (c) adult, and (d) group of resting reddish adult males (*Photo credit:* Héctor Pérez Puig)



Figure 4. Male Guadalupe fur seals at Guadalupe Island, Baja California, México, during the 2013 to 2015 breeding seasons (June through August): (a) juvenile, (b) subadult, and (c & d) adults (*Photo credit:* Casandra Gálvez)

In otariids, sexual and age segregation is common after the breeding season when males migrate to haul-out sites located near or far away from reproductive colonies (Sullivan, 1980; Beentjes, 1989; Grandi et al., 2008). This is related to specific agesex foraging behavior (Dobson, 1982) and physiological constraints (e.g., oxygen stores; Weise & Costa, 2007). The GFSs prey on squids (Gallo-Reynoso & Esperón-Rodríguez, 2013; Amador-Capitanachi et al., 2020) and exhibit an important dispersal capacity since records of young GFSs have been registered in northern latitudes in the U.S. (Oregon and Washington; D'Agnese et al., 2020) and in central/southern México (Oaxaca and Colima; Villegas-Zurita et al., 2015; Ortega-Ortiz et al., 2019), including two new colonies in the southwest and southeast Gulf of California composed mostly of juveniles related to population expansion (Elorriaga-Verplancken et al., 2021; Gutiérrez-Osuna et al., 2021). The present study involves the northernmost record of a GFS haul-out site in the Gulf of California, mainly composed of

bulls, reflecting an apparent increase in the species' habitat range.

Sightings of different GFS age classes during October and November from 2011 to 2013 at SPMI suggest that some males move south from Guadalupe Island into the Gulf of California and arrive in SPMI after the breeding season. This male post-breeding route hypothesis is supported by the carcasses of juveniles, subadults, and adults found in Magdalena Island in the Gulf of Ulloa (west coast of the Baja California Peninsula) during August and September through December (2003) to 2015), coinciding also with the post-breeding migration period (Aurioles-Gamboa et al., 2017). Moreover, there is an absence of adult males at SPMI during the breeding season in Guadalupe Island, reflecting the potential relevance of sites like SPMI as a haul-out site during GFS males' post-breeding season (early and late).

The absence of GFSs at SPMI in 2015 and low numbers in 2011, 2014, 2017, and 2018 coincided with high numbers of GFS carcasses in the Gulf

of Ulloa from August to January in 2011, 2014, and 2015. Factors related to the latter may be the northeast Pacific warming (~+2.5°C) related to the marine heatwave that took place from 2014 to 2016 (Di Lorenzo & Mantua, 2016) in that region, as well as important ecological shifts that occurred as a consequence, including at the Baja California Peninsula and the southern and central Gulf of California (2014 to 2016) (Cavole et al., 2016; García-Morales et al., 2017; Sánchez-Velasco et al., 2017; Dorantes-Gilardi & Rivas, 2019). Unfortunately, there is scarce knowledge regarding GFS males' post-breeding migration behavior and foraging habits (Esperón-Rodríguez & Gallo-Reynoso, 2013; Aurioles-Gamboa & Szteren, 2020) to determine long-term consequences in bulls' presence and abundance at SPMI. Nonetheless, overall changes in GFS foraging grounds, body weight, and diet have been related to the northeast Pacific warming among individuals at Guadalupe Island and San Benito Archipelago (Elorriaga-Verplancken et al., 2016; Amador-Capitanachi et al., 2020; Gálvez et al., 2020), coinciding with the GFSs' ongoing unusual mortality event (UME) in the U.S. (2015 to 2021) along the coasts of California, Oregon, and Washington (D'Agnese et al., 2020), associated with an important environmental stressor (National Oceanic and Atmospheric Administration [NOAA], 2021). Therefore, considering that prey availability is one of the main drivers in foraging ecology among otariids, including interindividual preferences (Knox et al., 2017) related to post-breeding migration behavior (Kernaléguen et al., 2012), it is plausible that the warm ocean conditions in the northeast Pacific (e.g., northern heatwaves or El Niño) and foraging shifts across the GFS range could have an impact on the bulls' frequency and abundance at post-breeding haul-out sites.

In otariids, habitat selection is associated with intrinsic factors, such as morphology and behavior (Carter et al., 2017), as well as extrinsic characteristics, such as habitat and prey availability (Wolf et al., 2005; Grandi et al., 2008). However, haul-out site selection and its establishment are still poorly understood for GFS males. The Gulf of California exhibits an elevated primary productivity yearround, with a seasonal peak in winter and spring, especially along the central east coast and the northern area, where the Midriff Islands are located (including SPMI) (Alvarez-Borrego & Lara-Lara, 1991). This favors the mating, spawning, and early development of (juvenile) giant squids (Dosidicus gigas; Gilly et al., 2006). California sea lions from SPMI have a diet based on different species, such as cephalopods (e.g., giant squid) and fish (jack mackerel [Trachurus symmetricus]; García-Rodríguez & Aurioles-Gamboa, 2004). The GFS

is an opportunistic predator with preferences for squid (Juárez-Ruiz et al., 2018), including the giant squid, opalescent squid (Doryteuthis opalescens), and hooked squid (Onychoteuthis banksi), as well as fish species such as the jack mackerel (Aurioles-Gamboa & Camacho-Ríos, 2007). Moreover, GFS males may exhibit oceanic and coastal foraging habits (Esperón-Rodríguez & Gallo-Reynoso, 2013; Aurioles-Gamboa & Szteren, 2020). It is possible that prey diversity and availability along the Gulf of California could be triggering GFS sightings around SPMI, especially during stable environmental conditions (2011 to 2013). In consequence, it is important to perform scat analyses to establish the prey spectrum of the GFSs from SPMI and its relationship with its abundance, especially in the absence of a clear pattern from 2011 to 2021.

The highest GFS density at SPMI was recorded in the southern area along rocky platforms and boulders, probably related to waves and high tide protection, as well as shade, coinciding with overall species preferences (Arias-del-Razo et al., 2016). Isolation and minimal disturbance in SPMI could favor the occurrence of GFS males, making it an important place to rest, feed, and recover after the breeding season at Guadalupe Island. More studies are necessary to determine higher resolution of habitat preferences and behavior, and to assess the effects of this potential GFS haul-out site on resident California sea lions, which have declined since the 1990s-not only in SPMI but also along the Gulf of California (Adame et al., 2020).

Data regarding modern demography of otariids are limited, particularly during extreme environmental conditions and when secondary consequences are involved such as changes in foraging behavior and fishery interactions, which are catalogued as threats for the survival of otariids (Simmonds & Isaac, 2007; Kovacs et al., 2012). In the present study, we highlight the relevance of the increased spatial and temporal efforts of the monitoring of GFSs in SPMI to determine the establishment of a unisexual haul-out site in a region where important anthropogenic activities are performed (e.g., fisheries; Zavala-Gonzalez & Mellink, 1997), representing a potential risk for GFS bulls' welfare and their survival along the Gulf of California.

By using opportunistic surveys of GFS at SPMI over a multitude of years, our sightings provide evidence of an expansion of the species' habitat range into the Gulf of California as part of the current population's recovery process. This scenario offers a unique opportunity to keep studying potential suitable habitats for GFSs in new ecosystems. In this regard, it is important to start with GFS demographic and behavioral studies

on individuals at SPMI during the non-breeding season (September through April) to improve our understanding of species' age class-foraging behavior in relation to environmental factors (e.g., prey availability) to elucidate its influence on current demographic processes (e.g., colonization) and the males' migration period, habitat preferences, abundance, survival rates, and threats, preferably via low-impact techniques (e.g., drones).

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## **Literature Cited**

- Adame, F. K., Elorriaga-Verplancken, F. R., Beier, E., Acevedo-Whitehouse, K., & Pardo, M. (2020). The demographic decline of a sea lion population followed multi-decadal sea surface warming. *Scientific Reports*, 10, 10499. https://doi.org/10.1038/s41598-020-67534-0
- Allen, S. G., Mortenson, J., & Webb, S. (2011). Field guide to marine mammals of the Pacific coast. University of California Press. https://doi.org/10.1525/9780520947313
- Álvarez-Borrego, S., & Lara-Lara, J. R. (1991). The physical environment and primary productivity of the Gulf of California. In J. P. Dauphin & B. R. T. Simoneit (Eds.), *The gulf and peninsular province of the Californias* (Chapter 26). American Association of Petroleum Geologists. https://doi.org/10.1306/M47542C26
- Amador-Capitanachi, M. J., Moreno-Sánchez, X. G., Ventura-Domínguez, P. D., Juárez-Ruiz, A., González-Rodríguez, E., Gálvez, C., Norris, T., & Elorriaga-Verplancken, F. R. (2020). Ecological implications of unprecedented warm water anomalies on interannual prey preferences and foraging areas of Guadalupe fur seals. *Marine Mammal Science*, 36(4), 1254-1270. https://doi. org/10.1111/mms.12718
- Arias-del-Razo, A., Heckel, G., Schramm, Y., & Pardo, M. A. (2016). Terrestrial habitat preferences and segregation of four pinniped species on the islands off the western coast of the Baja California Peninsula, México.

- Marine Mammal Science, 32(4), 1416-1432. https://doi.org/10.1111/mms.12339
- Aurioles-Gamboa, D., Pablo-Rodríguez, N., Rosas-Hernández, M. P., & Hernández-Camacho, C. J. (2017). Guadalupe fur seal population expansion and its postbreeding male migration to the Gulf of Ulloa, México. In J. J. Alava (Ed.), Tropical pinnipeds: Bio-ecology, threats and conservation (pp. 105-133). CRC Press. https://doi. org/10.1201/9781315151588
- Aurioles-Gamboa, D., & Szteren, D. (2020). Lifetime coastal and oceanic foraging patterns of male Guadalupe fur seals and California sea lions. *Marine Mammal Science*, *36*(1), 246-259. https://doi.org/10.1111/mms.12649
- Aurioles-Gamboa, D., Pablo-Rodríguez, N., Rosas-Hernández, M. P., & Hernández-Camacho, C. J. (2007). Guadalupe fur seal population expansion and its postbreeding male migration to the Gulf of Ulloa, México. In J. J. Alava (Ed.), *Tropical pinnipeds: Bio-ecology,* threats and conservation (pp. 105-133). CRC Press. https://doi.org/10.1201/9781315151588
- Bartholomew, G. A. (1950). A male Guadalupe fur seal on San Nicolas Island, California. *Journal of Mammalogy*, 31(2), 175-180. https://doi.org/10.2307/1375513
- Baylis, A. M., Orben, R. A., Costa, D. P., Tierney, M., Brickle, P., & Staniland, I. J. (2017). Habitat use and spatial fidelity of male South American sea lions during the nonbreeding period. *Ecology and Evolution*, 11, 3992-4002. https://doi.org/10.1002/ece3.2972
- Beentjes, M. P. (1989). Haul-out patterns, site fidelity and activity budgets of male Hooker's sea lions (*Phocarctos hookeri*) on the New Zealand mainland. *Marine Mammal Science*, 5(3), 281-297. https://doi.org/10.1111/j.1748-7692.1989.tb00341.x
- Bezaury-Creel, J. E. (2005). Protected areas and coastal and ocean management in México. *Ocean & Coastal Management*, 48(11-12), 1016-1046. https://doi.org/10.1016/j.ocecoaman.2005.03.004
- Brusca, R. C., Findley, L. T., Hastings, P. A., Hendrickx, M. E., Cosio, J. T., & van der Heiden, A. M. (2005). Macrofaunal diversity in the Gulf of California. In J. L. Cartron, G. Ceballos, & R. S. Felger (Eds.), Biodiversity, ecosystems, and conservation in northern México (pp. 179-203). Oxford University Press.
- Carter, M. I., Russell, D. J., Embling, C. B., Blight, C. J., Thompson, D., Hosegood, P. J., & Bennett, K. A. (2017). Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behavior in a marine top predator. *Scientific Reports*, 7(1), 1-14. https://doi.org/10.1038/ s41598-017-15859-8
- Cavole, L. M., Demko, A. M., Diner, R. E., Giddings, A., Koester, I., Pagniello, C. M., Paulsen, M-L., Ramirez-Valdez, A., Schwenck, S. M., Yen, N. K., Zill, M. E., & Franks, P. J. S. (2016). Biological impacts of the 2013-2015 warm-water anomaly in the northeast Pacific: Winners, losers, and the future. *Oceanography*, 29(2), 273-285. https://doi.org/10.5670/oceanog.2016.32
- Comisión Nacional de Áreas Naturales Protegidas—Secretaría del Medio Ambiente y Recursos Naturales (CONANP-

- SEMARNAT). (2007). Programa de conservación y manejo Reserva de la Biosfera Isla San Pedro Mártir [Conservation and management program of San Pedro Mártir Biosphere Reserve]. CONANP-SEMARNAT. 218 pp. https://simec.conanp.gob.mx/pdf\_libro\_pm/25\_libro\_pm.pdf
- D'Agnese, E., Lambourn, D., Rice, J., Duffield, D., Huggins, J., Spraker, T., & Smith, W. (2020). Reemergence of Guadalupe fur seals in the U.S. Pacific Northwest: The epidemiology of stranding events during 2005-2016. *Marine Mammal Science*, 36(3), 828-845. https://doi.org/10.1111/mms.12678
- Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change, 6(11), 1042-1047. https://doi.org/10.1038/nclimate3082
- Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, 30(4), 1183-1192. https://doi.org/10.1016/ S0003-3472(82)80209-1
- Dorantes-Gilardi, M., & Rivas, D. (2019). Effects of the 2013-2016 northeast Pacific warm anomaly on physical and biogeochemical variables off northwestern Baja California, derived from a numerical NPZD ocean model. Deep Sea Research Part II: Topical Studies in Oceanography, 169, 104668. https://doi.org/10.1016/j. dsr2.2019.104668
- Elorriaga-Verplancken, F. R., Sierra-Rodríguez, G. E., Rosales-Nanduca, H., Acevedo-Whitehouse, K., & Sandoval-Sierra, J. (2016). Impact of the 2015 El Niño– Southern Oscillation on the abundance and foraging habits of Guadalupe fur seals and California sea lions from the San Benito Archipelago, México. PLOS ONE, 11(5), e0155034. https://doi.org/10.1371/journal. pone.0155034
- Elorriaga-Verplancken, F. R., Paniagua-Mendoza, A., Hernández-Camacho, C. J., Webber, M. A., Cruz-Vallejo, R., Nevels, C. R., & González-López, I. (2021). A new Guadalupe fur seal colony in the Gulf of California? Ecological and conservation implications. Aquatic Mammals, 47(1), 1-9. https://doi.org/10.1578/ AM.47.1.2021.1
- Enríquez-Andrade, R., Anaya-Reyna, G., Barrera-Guevara, J. C., Carvajal-Moreno, M. A., Martínez-Delgado, M. E., Vaca-Rodríguez, J., & Valdés-Casillas, C. (2005). An analysis of critical areas for biodiversity conservation in the Gulf of California region. *Ocean & Coastal Management*, 48(1), 31-50. https://doi.org/10.1016/j.ocecoaman.2004.11.002
- Esperón-Rodríguez, M., & Gallo-Reynoso, J. P. (2013). Juvenile and subadult feeding preferences of the Guadalupe fur seal (*Arctocephalus townsendi*) at San Benito Archipelago, México. *Aquatic Mammals*, 39(2), 125-131. https://doi.org/10.1578/AM.39.2.2013.125
- Etnier, M. A. (2002). Occurrences of Guadalupe fur seals (Arctocephalus townsendi) on the Washington coast over the past 500 years. Marine Mammal Science, 18(2), 551-557. https://doi.org/10.1111/j.1748-7692.2002.tb01056.x

- Gallo-Reynoso, J. P. (1994). Factors affecting the population status of Guadalupe fur seal, Arctocephalus townsendi (Merriam, 1897) at Isla de Guadalupe, Baja California, México (Doctoral dissertation). University of California, Santa Cruz.
- Gallo-Reynoso, J. P., & Esperón-Rodríguez, M. (2013). Diet composition of the Guadalupe fur seal (Arctocephalus townsendi). Where and what do they eat? Marine and Freshwater Behaviour and Physiology, 46(6), 455-467. https://doi.org/10.1080/10236244.2013.849400
- Gálvez, C., Pardo, M. A., & Elorriaga-Verplancken, F. R. (2020). Impacts of extreme ocean warming on the early development of a marine top predator: The Guadalupe fur seal. *Progress in Oceanography*, 180, 102220. https://doi.org/10.1016/j.pocean.2019.102220
- García-Aguilar, M. C., Elorriaga-Verplancken, F. R., Rosales-Nanduca, H., & Schramm, Y. (2018). Population status of the Guadalupe fur seal (Arctocephalus townsendi). Journal of Mammalogy, 99(6), 1522-1528. https://doi.org/10.1093/jmammal/gyy132
- García-Morales, R., López-Martínez, J., Valdez-Holguin, J. E., Herrera-Cervantes, H., & Espinosa-Chaurand, L. D. (2017). Environmental variability and oceanographic dynamics of the central and southern coastal zone of Sonora in the Gulf of California. *Remote* Sensing, 9(9), 925. https://doi.org/10.3390/rs9090925
- García-Rodríguez, F. J., & Aurioles-Gamboa, D. (2004). Spatial and temporal variation in the diet of the California sea lion (*Zalophus californianus*) in the Gulf of California, México. *Fishery Bulletin*, 102(1), 47-62. http://fishbull.noaa.gov/1021/garcia.pdf
- Giardino, G. V., Mandiola, M. A., Bastida, J., Denuncio, P. E., Bastida, R. O., & Rodríguez, D. H. (2016). Travel for sex: Long-range breeding dispersal and winter haulout fidelity in southern sea lion males. *Mammalian Biology*, 81(1), 89-95. https://doi.org/10.1016/j.mambio.2014.12.003
- Gilly, W. F., Elliger, C. A., Salinas, C. A., Camarilla-Coop, S., Bazzino, G., & Beman, M. (2006). Spawning by jumbo squid *Dosidicus gigas* in San Pedro Mártir Basin, Gulf of California, México. *Marine Ecology Progress Series*, 313, 125-133. https://doi.org/10.3354/ meps313125
- Grandi, M. F., Dans, S. L., & Crespo, E. A. (2008). Social composition and spatial distribution of colonies in an expanding population of South American sea lions. *Journal of Mammalogy*, 89(5), 1218-1228. https://doi. org/10.1644/08-MAMM-A-088.1
- Gutiérrez-Osuna, M. C., Díaz-Gaxiola, J. M., Trites, A. W., & Hernández-Camacho, C. J. (2021). New colony of Guadalupe fur seals (Arctocephalus townsendi) discovered on El Farallón de San Ignacio Island, Gulf of California. Marine Mammal Science, 1-9. https://doi. org/10.1111/mms.12844
- Hamilton, A. (1951). Is the Guadalupe fur seal returning? Natural History, 60, 90-96.
- Hanni, K. D., Long, D. J., Jones, R. E., Pyle, P., & Morgan, L. E. (1997). Sightings and strandings of Guadalupe fur seals in central and northern California, 1988-1995.

Journal of Mammalogy, 78(2), 684-690. https://doi.org/10.2307/1382920

- Hooker, S. K., & Gerber, L. R. (2004). Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. *Bioscience*, 54(1), 27-39. https://doi.org/10.1641/0006-3568(2004)054[0027:MRA ATF]2.0.CO;2
- Hoyos-Padilla, E. M., Gallo-Reynoso, J. P., & Barba-Acuña, I. D. (2021). Presence of Guadalupe fur seals (Arctocephalus philippii townsendi) at Isla Roca Partida, Revillagigedo Archipelago, México. Aquatic Mammals, 47(6),612-617. https://doi.org/10.1578/AM.47.6.2021.612
- Hubbs, C. L. (1956). Back from oblivion. Guadalupe fur seal: Still a living species. *Pacific Discovery*, 9, 14-21.
- Hubbs, C. L. (1979). Guadalupe fur seal. *Mammals in the Seas*, 2, 24-27.
- Joh, Y., & Di Lorenzo, E. (2017). Increasing coupling between NPGO and PDO leads to prolonged marine heatwaves in the northeast Pacific. *Geophysical Research Letters*, 44(22), 11,663-11,671. https://doi.org/10.1002/2017GL075930
- Juárez-Ruiz, A., Elorriaga-Verplancken, F. R., Moreno-Sánchez, X. G., Aguíniga-García, S., Amador-Capitanachi, M. J., & Gálvez, C. (2018). Diversification of foraging habits among Guadalupe fur seals from their only well-established breeding colony, Guadalupe Island, México. *Marine Biology*, 165(5), 1-12. https://doi.org/10.1007/s00227-018-3339-6
- Kernaléguen, L., Cazelles, B., Arnould, J. P., Richard, P., Guinet, C., & Cherel, Y. (2012). Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PLOS ONE*, 7(3), e32916. https://doi.org/10.1371/journal.pone.0032916
- Knox, T. C., Baylis, A. M., & Arnould, J. P. (2017). Habitat use and diving behavior of male Australian fur seals. *Marine Ecology Progress Series*, 566, 243-256. https://doi.org/10.3354/meps12027
- Kovacs, K. M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., & Trillmich, F. (2012). Global threats to pinnipeds. *Marine Mammal Science*, 28(2), 414-436. https://doi.org/10.1111/j.1748-7692.2011.00479.x
- Maravilla-Chávez, M. O., & Lowry, M. S. (1999).
  Incipient breeding colony of Guadalupe fur seals at Isla Benito del Este, Baja California, México.
  Marine Mammal Science, 15(1), 239-241. https://doi.org/10.1111/j.1748-7692.1999.tb00796.x
- Melin, S. R., & DeLong, R. L. (1999). Observations of a Guadalupe fur seal (Arctocephalus townsendi) female and pup at San Miguel Island, California. Marine Mammal Science, 15(3), 885-888. https://doi. org/10.1111/j.1748-7692.1999.tb00854.x
- National Oceanic and Atmospheric Administration (NOAA). (2021). 2015-2021 Guadalupe fur seal unusual mortality event in California, Oregon and Washington. https://www.fisheries.noaa.gov/national/marine-life-distress/2015-2021-guadalupe-fur-seal-unusual-mortality-event-california
- Ortega-Ortiz, C. D., Vargas-Bravo, M. H., Olivos-Ortiz, A., Zapata, M. G. V., & Elorriaga-Verplancken, F. R.

- (2019). Guadalupe fur seal encounters in the Mexican Central Pacific during 2010-2015: Dispersion related to the species recovery? *Aquatic Mammals*, 45(2), 246-254. https://doi.org/10.1578/AM.45.2.2019.246
- Paden, C. A., Abbott, M. R., & Winant, C. D. (1991). Tidal and atmospheric forcing of the upper ocean in the Gulf of California: 1. Sea surface temperature variability. *Geophysical Research: Oceans*, 96(C10), 18337-18359. https://doi.org/10.1029/91JC01597
- Páez-Osuna, F., Álvarez-Borrego, S., Ruiz-Fernández, A. C., García-Hernández, J., Jara-Marini, M. E., Bergés-Tiznado, M. E., & Sánchez-Cabeza, J. A. (2017). Environmental status of the Gulf of California: A pollution review. *Earth-Science Reviews*, 166, 181-205. https://doi.org/10.1016/j.earscirev.2017.01.014
- Páez-Rosas, D., Pazmiño, A. D., & Riofrío-Lazo, M. (2020). Unprecedented records of Guadalupe and Juan Fernández fur seals in the Galapagos Archipelago. *Aquatic Mammals*, 46(6),549-555. https://doi.org/10.1578/AM.46.6.2020.549
- Reeves, R. R., Stewart, B. S., Clapham, P. J., Powell, J. A., & Folkens, P. A. (2002). National Audubon Society guide to marine mammals of the world. Chanticleer Press. 527 pp. ISBN 0375411410 9780375411410
- Rice, D. W., Kenyon, K. W., & Lluch, B. D. (1965). Pinniped populations at Islas Guadalupe, San Benito, and Cedros, Baja California, in 1965. Transactions of the San Diego Society of Natural History, 14(7), 73-84.
- Rick, T. C., DeLong, R. L., Erlandson, J. M., Braje, T. J., Jones, T. L., Kennett, D. J., Wake, T. A., & Walker, P. L. (2009). A trans-Holocene archaeological record of Guadalupe fur seals (*Arctocephalus townsendi*) on the California coast. *Marine Mammal Science*, 25(2), 487-502. https://doi.org/10.1111/j.1748-7692.2008.00273.x
- Riedman, M. (1990). The pinnipeds: Seals, sea lions, and walruses (Vol. 12). University of California Press. https://doi.org/10.1525/9780520320086
- Sánchez-Velasco, L., Beier, E., Godínez, V. M., Barton, E. D., Santamaría-del-Ángel, E., Jiménez-Rosemberg, S. P. A., & Marinone, S. G. (2017). Hydrographic and fish larvae distribution during the "Godzilla El Niño 2015-2016" in the northern end of the shallow oxygen minimum zone of the Eastern Tropical Pacific Ocean. Geophysical Research: Oceans, 122(3), 2156-2170. https://doi.org/10.1002/2016JC012622
- Simmonds, M. P., & Isaac, S. J. (2007). The impacts of climate change on marine mammals: Early signs of significant problems. Oryx, 41(1), 19-26. https://doi.org/10.1017/S0030605307001524
- Starks, E. C. (1922). Records of the capture of fur seals on land in California. *California Fish and Game*, 8, 155-160.
- Sullivan, R. M. (1980). Seasonal occurrence and haulout use in pinnipeds along Humboldt County, California. *Mammalogy*, 61(4), 754-760. https://doi. org/10.2307/1380334
- Townsend, C. H. (1916). The Guadalupe fur seal: A contribution to its history. *Bulletin of the New York Zoological Society*, 19, 1330-1331.

- Townsend, C. H. (1924). The northern elephant seal and the Guadalupe fur seal. *Natural History*, 24(5), 567-577.
- Villegas-Zurita, F., Castillejos-Moguel, F., & Elorriaga-Verplancken, F. R. (2015). Southernmost presence of the Guadalupe fur seal (Arctocephalus townsendi) in the Mexican South Pacific. Revista Mexicana de Biodiversidad, 86(4), 1107-1109. https://doi.org/10.1016/j. rmb.2015.09.011
- Weber, D. S., Stewart, B. S., & Lehman, N. (2004). Genetic consequences of a severe population bottleneck in the Guadalupe fur seal (*Arctocephalus townsendi*). *Journal of Heredity*, 95(2), 144-153. https://doi.org/10.1093/jhered/esh018
- Weise, M. J., & Costa, D. P. (2007). Total body oxygen stores and physiological diving capacity of California sea lions as a function of sex and age. *Journal of Experimental Biology*, 210(2), 278-289. https://doi.org/10.1242/jeb.02643
- Wolf, J. B., Kauermann, G., & Trillmich, F. (2005). Males in the shade: Habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). *Behavioral Ecology and Sociobiology*, 59(2), 293-302. https://doi.org/10.1007/s00265-005-0042-7
- Zar, J. (1999). Biostatistical analysis (4th ed.). Prentice-Hall.
- Zavala-González, A., & Mellink, E. (1997). Entanglement of California sea lions, Zalophus californianus californianus, in fishing gear in the central-northern part of the Gulf of California, México. Fishery Bulletin, 95(1), 180-184.