Guadalupe Fur Seal Population Census and Tagging in Support of Marine Mammal Monitoring Across Multiple Navy Training Areas in the Pacific Ocean, 2019-2020

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Guadalupe Fur Seal Population Census and Tagging in Support of Marine Mammal Monitoring Across Multiple Navy Training Areas in the Pacific Ocean, 2019-2020

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Cover photo

Four Guadalupe fur seals on a rocky outcrop at the north end of Guadalupe Island, México. Photo credit: J. Bredvik, NAVFAC SW, Environmental Core. Permit #: SERMARNAT SGPA/DGVS/01643/19, CONANP F00.DRPBCPN.RBIG.0242/2019, and SEMAR 368/19.

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Abstract

As the population of Guadalupe fur seals (*Arctocephalus townsendi* or *A. philippii townsendi*) continues to recover, this species, which is listed as threatened in the U.S. and endangered in México, is increasingly common in their historical range extending from central México to Washington State. Relatively little is known about this species compared with other pinnipeds that occur in the California Current System. Accurate and current population estimates are lacking because censuses at the only rookery have been sparse and sporadic, and there is a paucity of data on at-sea movements because few individuals have been tracked using telemetry instruments. Therefore, the goal of this multiyear study was to better understand Guadalupe fur seal abundance, behavior, distribution, and habitat use, and to determine the degree to which this recovering population uses U.S. Navy training and testing ranges in the Northeast Pacific. During the second year of this study, censuses were performed at Guadalupe Island, México and San Benito Archipelago, México in summer 2019. Satellite tags were subsequently deployed on adult females ($n = 15$), juvenile females ($n = 10$), juvenile males ($n = 10$), and pups ($n = 30$) at Guadalupe Island in March 2020. These census and telemetry data were compared to data collected during the first project period (2018-2019). At San Benito Archipelago, twice as many animals were counted in 2019 (1,113 individuals) relative to 2018 (539 individuals), but only approximately 20 mother-pup pairs were observed at this site during both years. In contrast, at Guadalupe Island, approximately the same number of animals were observed in 2018 (26,217 individuals) and 2019 (26,369 individuals), but there were ~2,800 more adult females and ~2,500 fewer pups in 2019 compared with 2018. In spring and summer 2020, Guadalupe fur seals broadly used waters off the west coast of North America but traveled farther offshore and north (21-51°N, 108-140°W) than the animals tracked November 2018 through April 2019 (20-42°N, 112-130°W). The majority of animals traveled north of Guadalupe Island during all or part of both tracking periods. Adult females were distributed farther offshore in 2020 (<1,400 km from shore) than in 2018-2019 (<800 km from shore). In 2020, juvenile females also used more offshore areas to a greater extent, and a greater proportion of juvenile males used habitat south of Guadalupe Island. Only pups, which were not tracked in 2018-2019, traveled north of 41°N in 2020, and this was the only group that had substantial home range overlap with the U.S. Navy Northwest Training and Testing (NWTT) Study Area (31% overlap). Overall, there was greater home range overlap with the Point Mugu Sea Range (PMSR; ≥61% for each group), and group home range overlap with the Southern California (SOCAL) Range Complex was 18-50%. With the pelagic distribution of this species, the nearshore portions of each Navy range with water depths <2,000 m were used to a lesser extent (<38% overlap) relative to the entire area of each range, and the Southern California Anti-submarine Warfare Range (SOAR) was used by only one juvenile male each year. Most adults and juveniles dove to shallow depths during the night, primarily <60 m, with minimal daytime diving. Large numbers of dives >8 m occurred nightly, which likely indicates foraging activity, along portions of tracks with directed, relatively straight travel over long distances that often are interpreted as transiting rather than foraging areas. Most notably, foraging behavior was observed throughout the offshore area (>2,000 m water depth) of the SOCAL Range Complex that previously appeared to be primarily a transit corridor to and from Guadalupe Island. These results improve our understanding of Guadalupe fur seal abundance, behavior, and use of U.S. Navy training and testing ranges in the Northeast Pacific across seasons and years, but additional census and telemetry data collected in subsequent years will further elucidate population trends and interannual and seasonal variability in habitat use and movement patterns.

Introduction

The Guadalupe fur seal (*Arctocephalus townsendi* or *A. philippii townsendi*) population has been steadily increasing since the 1950s, but this is still the only pinniped species inhabiting the California Current System that is protected under the U.S. Endangered Species Act (ESA) as "threatened" and catalogued as "endangered" by Mexican law (Norma Oficial Mexicana Secretaría de Medio Ambiente y Recursos Naturales 2010). As the population continues to recover, these animals are increasingly common in their historical range extending from central México to Washington State (Aurioles-Gamboa et al. 1999, Hanni et al. 1997, Lambourn et al. 2012, Ortega-Ortiz et al. 2019, Seagars 1984, Stewart 1981). In recent years, unprecedented numbers of Guadalupe fur seals have been stranding, or coming ashore sick and/or injured, along the U.S. West Coast and in the southern Gulf of California (Elorriaga-Verplancken et al. 2016a, NOAA Fisheries 2020). Most animals (~97%) that have stranded in the U.S. have been pups and yearlings, whereas those that strand in México typically are juvenile and subadult males (*e.g.*, Villegas-Zurita et al. 2015). Beginning in 2015, increased numbers of stranded Guadalupe fur seals primarily occurred in California; and in 2019-2020, there also were greater numbers of young fur seals stranding in Oregon and Washington State (Figure 1). The majority of animals have been emaciated, and reduced prey availability likely is the primary cause of the increased number of strandings.

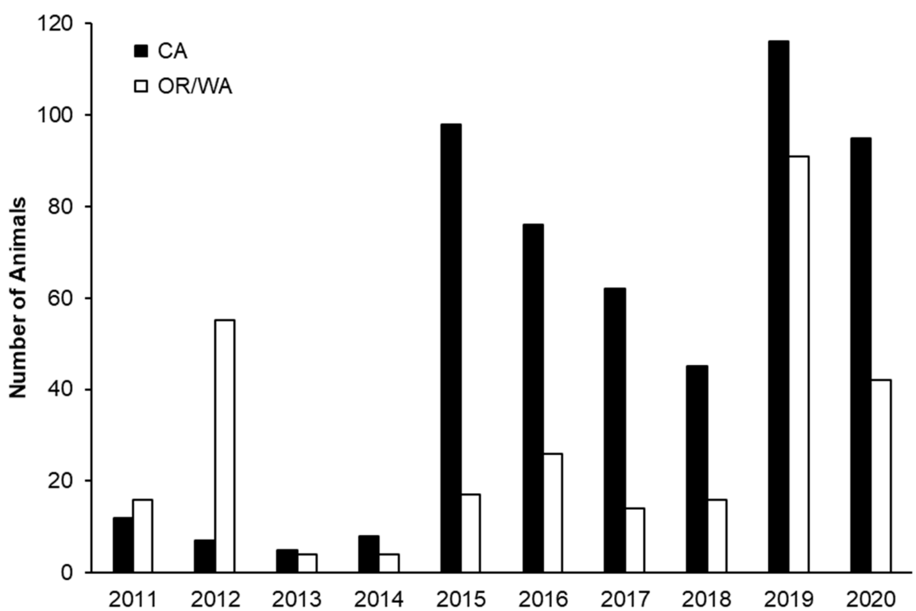

Figure 1. Annual number of Guadalupe fur seals that stranded along the coast of California and Oregon/Washington over the last 10 years (NOAA Fisheries 2020 and unpublished data).

During and preceding the 2015-2020 increase in Guadalupe fur seal strandings, anomalously warm waters persisted across the Northeast Pacific Ocean (Di Lorenzo & Mantua 2016, Jacox et al. 2016, Leising et al. 2015) and caused unprecedented ecosystem-level effects, including dramatic shifts in species distribution and abundance as well as mass strandings and mortalities related to prey limitation for many species (Cavole et al. 2016, McClatchie et al. 2016, Morgan et. al 2019, Peterson et al. 2017, Sanford et al. 2019). In the California Current region, the most severe marine heatwaves (*i.e.,* periods of extremely warm sea surface temperatures for days or months), in terms of spatial extent, persistence, and intensity, were in 2014-2016 and 2019-2020 (Leising & Bogard 2020). These extreme ocean warming events likely explain the increase in Guadalupe fur seal strandings in recent years, but we do not know if this was related to northward and/or onshore shifts in abundance and distribution because prior to 2015 only 12 Guadalupe fur seals had been tracked using satellite telemetry devices, nine of which were stranded animals released after rehabilitation (Gallo-Reynoso et al. 2008, Lander et al. 2000, Norris et al. 2015). Additionally, as a shallow-diving, pelagic species that primarily feeds on squid (Amador-Capitanachi et al. 2017), Guadalupe fur seals may be more vulnerable to marine heatwaves, especially those that remain farther offshore, as was the case in 2019-2020 (Leising & Bogard 2020).

As these marine heatwaves increase in frequency, duration, and intensity (Oliver et al. 2018), it is increasingly important to study the occurrence, abundance, and distribution of Guadalupe fur seals across multiple seasons and years to better understand the impacts of climate change and multiple other stressors, including those caused by human activity, on this imperiled species. Specifically, this species, which is ESA-listed and covered under the Marine Mammal Protection Act (MMPA) where it occurs in U.S. waters, may use multiple U.S. Navy training and testing areas in the California Current System more extensively than previously thought (U.S. Department of the Navy 2015). For example, many young fur seals released after rehabilitation in central California with satellite tracking devices from 2015-2017 (n = 28) traveled north into the Northwest Training and Testing (NWTT) Study Area that extends from northern California to Washington State (Norris et al. 2017a), and Guadalupe fur seals primarily breed on an offshore volcanic island immediately south of the Southern California (SOCAL) Range Complex (see Figure 5 for range locations). The goal of this study, therefore, was to improve our understanding of Guadalupe fur seal abundance, behavior, distribution, and habitat use and determine the degree to which this recovering population uses U.S. Navy training and testing ranges in the Northeast Pacific.

Methods

Population Surveys

Study Sites and Timing of Surveys

Guadalupe fur seals primarily use two terrestrial sites: Guadalupe Island and San Benito Archipelago, México (Figure 2). Guadalupe Island is the only established breeding site and San Benito Archipelago is the main recolonization site for this species (Aurioles-Gamboa et al. 2010, Elorriaga-Verplancken et al. 2016b, García-Aguilar et al. 2018, García-Capitanachi et al. 2017, Maravilla-Chavez & Lowry 1999, Sierra-Rodríguez 2015).

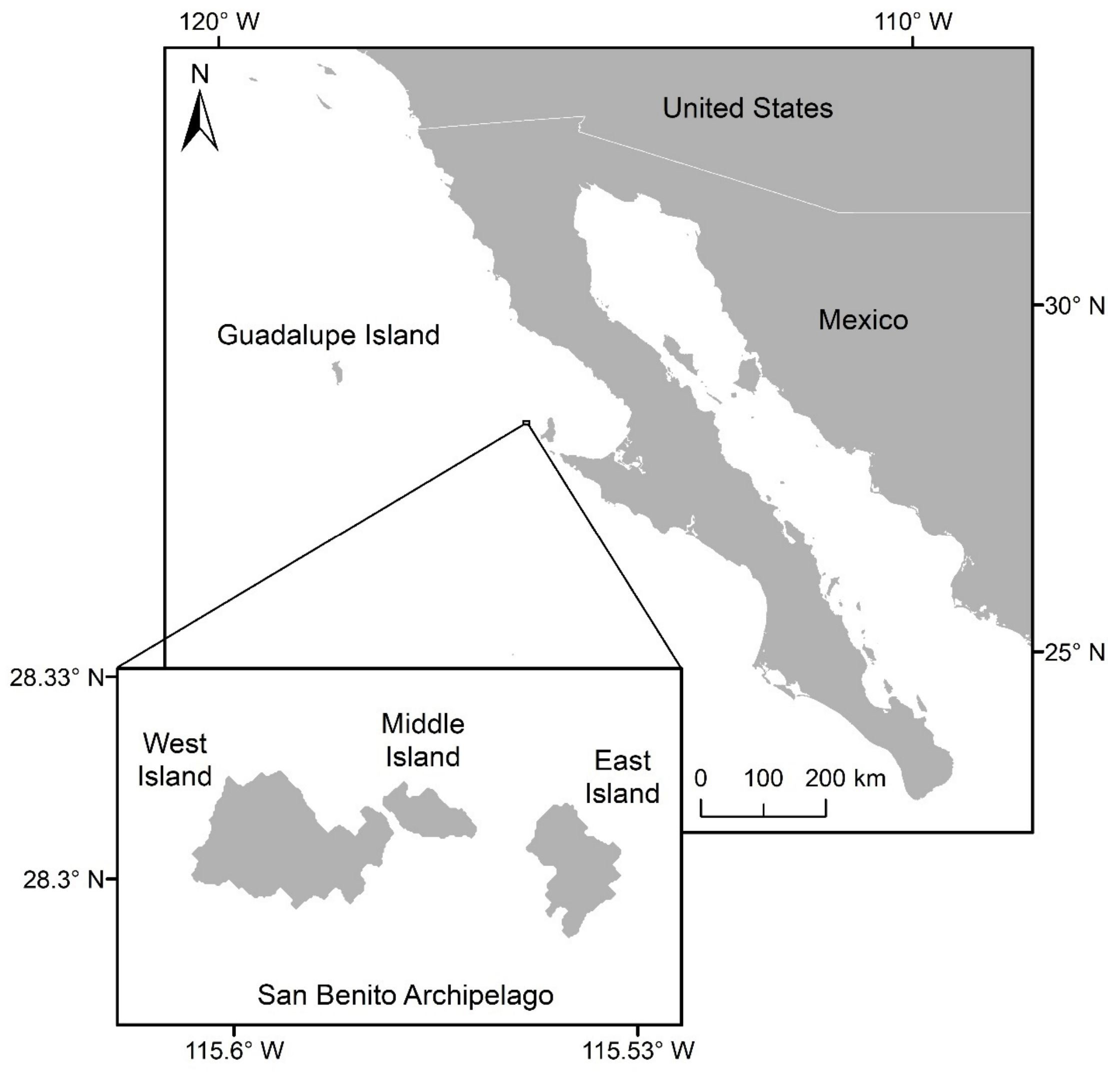

Figure 2. Map of the two study sites, Guadalupe Island and San Benito Archipelago, offshore of the Baja California Peninsula, México.

We conducted Guadalupe fur seal population monitoring surveys at San Benito Archipelago 23-29 July 2019 and at Guadalupe Island 8-13 August 2019 because the greatest number of animals are found on land during the summer breeding season (Gallo-Reynoso 1994). Most adult males already had departed the rookery by late July-early August and are underrepresented in our census data. However, because population estimates for otariids frequently are extrapolated from pup counts (Berkson & DeMaster 1985), the surveys were timed to follow peak pupping season, with the majority of pups born by late July. To count as many pups across the two sites as possible, San Benito Archipelago was surveyed first because few pups are born at this site. The time between the surveys at the two sites was as short as was logistically possible and coincided closely with the timing of previous surveys (11-14 July 2018 at San Benito Archipelago and 30 July-4 August 2018 at Guadalupe Island). Migration from San Benito Archipelago to Guadalupe Island during the period between surveys at the two sites, which would have resulted in double counting individuals, likely was negligible. This is because almost all fur seals at San Benito Archipelago are juveniles that may have been displaced from Guadalupe Island during the breeding season (Aurioles-Gamboa et al. 2010, Elorriaga-Verplancken et al. 2016b) or born at this site, and fur seals often have high natal site fidelity (*e.g.*, Baker et al. 1995). Additionally, no fur seals tracked previously during the summer used both terrestrial sites (Norris et al. 2017a).

Direct Counts

Across both sites and years, Guadalupe fur seals were classified into six demographic groups based on morphology and behavior: adult males, subadult males, adult females, juveniles (both sexes), pups (both sexes), and an unknown category for individuals that could not be identified (Gallo-Reynoso 1994).

At San Benito Archipelago, land-based surveys (walked inland of the animals) were used for all areas of the coastline accessible by foot (all of Middle Island and most of West Island; Figure 2). Surveys from a small boat <50 m from shore were used when land-based surveys were not possible (all of East Island and a small section of West Island). All counts and demographic group assignments were performed by the same individual that previously collected Guadalupe fur seal census data at San Benito Archipelago. These methodologies are the same as those used in previous studies and in 2018 as part of this project (Elorriaga-Verplancken et al. 2016b, Norris & Elorriaga-Verplancken 2019).

Similar to past survey efforts at Guadalupe Island, land-based survey methods (walked through colony) were conducted at Punta Sur (southernmost point) and boat-based surveys were used for the entire east side and three nearby islets south of the island (Norris & Elorriaga-Verplancken 2019). However, because of high northwest winds and swell, we were unable to survey the west side of Guadalupe Island in 2019. All non-pups were counted and classified by the individual that performed the counts at San Benito Archipelago and has the most experience assigning Guadalupe fur seals to demographic groups during visual surveys. Pups were counted by two other observers, one of whom counted pups at Guadalupe Island in 2018 and 2019. Similar to 2018, these two observers counted pups along sections of the coast demarcated by visual features in 2019, and the highest pup count from the two observers for each section was used. Because of weather conditions, pup counts were not repeated or averaged when there were significant differences between the two counters in 2019 as was done in 2018.

At Guadalupe Island, we recorded substrate type (boulder, high platform, low platform, pebble beach, and wall) during the boat-based surveys that were similar to those used by García-Capitanachi and colleagues (2017). For our surveys, we defined boulders as piles of jagged, loose rocks with diameters >0.5 m, with some larger than 10 m in diameter, and this was the dominant substrate type. Relatively flat, horizontal rock surfaces elevated above sea level were defined as platforms. Platform substrate that observers could not see the top of were called high platforms, and low platforms were those that observers could see over. Both types of platforms often had tidepools of varying sizes. Pebble beaches had loose rocks <0.5 m in diameter, and walls were flat, vertical rock surfaces. These five substrate types were collapsed into two categories: high- and low-visibility substrate. Fur seals on low platforms, pebble beaches, and walls were easily detected during boat-based surveys, and these three substrate types were grouped together as high-visibility substrate. It is possible that some animals using high-visibility substrate, especially pups on low platforms with large tidepools, still went undetected during our surveys. The low-visibility substrate grouping included boulders and high-platforms because many fur seals using these two substrates likely went undetected. Fur seals in the water were counted separately during boat-based surveys. Substrate type was not recorded at San Benito Archipelago because only a small portion of the three small islands at this site were surveyed by boat, and the substrate in areas where fur seals occur is more homogenous. This is in contrast to Guadalupe Island, which is a large island that was surveyed primarily by boat and has more variable substrate.

These 2018 and 2019 survey methods differed from other Guadalupe fur seal census efforts at Guadalupe Island because we had two individuals counting pups and traveled more slowly during our boat-based surveys (Borjes Flores pers. comm.). Because of differences in survey methods, we did not apply previously developed substrate-based correction factors (García-Capitanachi et al. 2017). Instead, only adult female counts were corrected to match the number of observed pups on both islands when the number of pups was larger than the number of females observed. This correction was only applied to total counts at each site because females can move to another area of the island and may have been counted on different substrate, including in nearshore water, than their pups. This correction also assumes that each female has a single pup. Additionally, without correcting for animals that went undetected during the surveys, both those hidden on-land and on at-sea foraging trips, all census results presented here represent minimum abundance estimates.

Telemetry Data Collection and Analyses

Animal Handling and Selection

From 12-20 March 2020, 65 Guadalupe fur seals (15 adult females, 10 juvenile females, 9 juvenile males, 1 subadult male, 14 female pups, and 16 male pups) were captured at Punta Sur, Guadalupe Island for satellite tagging. This location was selected because it has the greatest density of fur seals and is the most accessible to researchers. Juvenile and adult females were differentiated between using pregnancy status (palpable ~5-month-old fetus in March) and nursing/lactation status. Guadalupe fur seal pups are weaned at 8-9 months of age between February and April and were captured along with their mothers for tagging whenever possible. For all analyses, the single subadult male, a younger subadult based on his body size and morphology, was grouped with juvenile males.

Once captured using a modified hoop net, animals were manually restrained in the net until a cone was placed over the head to administer isoflurane gas anesthesia. Anesthesia averaged 31 min (range: 21-48 min) across all animals and was performed by a veterinarian with pinniped anesthesia experience. A satellite-linked time-depth recorder (SPLASH10-F-297A-02 tag, 132 g, 86×55×28 mm; Wildlife Computers, Redmond, WA) was attached to each non-pup (adults, subadult, and juveniles), and a satellite location-only transmitter (SPOT6-275E tag, 40 g, 86×17×20 mm; Wildlife Computers, Redmond, WA) was attached to each pup. All tags weighed <0.5% of animal body mass and were glued to the dorsal pelage, midline behind the scapula, using 10-min epoxy resin (ITW Devcon, Danvers, MA; Figure 3). Plastic identification tags were attached to the trailing edge of both fore-flippers of each animal (same number on both flippers). Mass, morphometric measurements, blood, fur, one vibrissa, and swabs (nasal and rectal) also were collected from all satellite-tagged animals for health and trophic ecology studies not further reported here.

Figure 3. Photograph of an adult female (right) and her ~9-month-old pup (left) following capture and satellite instrument attachment.
(Permit #: Secretaría de Medio Ambiente y Recursos Naturales SGPA/DGVS/11794/19, Secretaría de Gobernacion UG/211/00186/2020 SATI/PC/060/20, Comisión Nacional de Areas Naturales Protegidas F00.DRPBCPN.RBIG.0048/2020; Photo credit: Jeff Harris)

Satellite Instrument Programming

The SPLASH10-F tags were programmed to collect and transmit Argos and Fastloc™ global positioning system (GPS) locations, as well as dive depth histogram data. GPS locations were attempted at 6-h intervals with a maximum of one successful (signal received by ≥4 satellites) and six failed transmissions per hour (maximum of 24 attempts and 4 successful transmissions per day). These tags also collected dive data every 1 s for dives >2 m in depth and >20 s in duration, with transmitted dive depth data binned into 14 frequency histograms (upper bin limits: 4, 8, 12, 16, 20, 25, 30, 40, 60, 80, 100, 150, 200, and >200 m) for four 6-h periods (start times: 01:00, 07:00, 13:00, and 19:00 Greenwich Mean Time; GMT). Animal movements spanned multiple local time zones (GMT-7 to GMT-9); thus, all times are reported in GMT, but these histogram period start times roughly correspond with dusk, midnight, dawn, and mid-day, respectively. The tags transmitted messages up to 300 times per day during periods with the greatest satellite coverage for the area we expected this species to use (02:00-05:59, 14:00-14:59, and 16:00-18:59 GMT). Transmissions were attempted every ~45 s during seal surfacings (at-sea mode) and every ~90 s after the tag wet/dry sensor was dry for ≥5 min (haul-out mode). Tags returned to at-sea mode after the wet/dry sensor was wet for 30 s in 1 min. To conserve battery power, transmissions paused when the tag was dry for ≥48 h. GPS locations (high priority) and dive histogram messages (low priority) collected over the previous two days were transmitted.

The smaller SPOT6 tags deployed on pups transmit Argos locations only but provide greater control over transmission parameters than SPLASH tags. Most notably, the at-sea mode could be split into multiple periods to better distribute Argos transmissions across more hours of the day. Two roughly equal periods (11 and 12 h) was determined to be optimal given the satellite coverage for the area we expected this species to use, based on previous studies (Norris et al. 2017a). An 11-h and 12-h period allows the start time for each transmission day to change by 1 hour, which further distributes transmissions across more hours through time. Tags were programmed to transmit up to 126 messages per 11-h period and 137 messages per 12-h period (approximately 275 transmissions per day) while in at-sea mode (transmissions attempted every ~45 s during seal surfacings). During haul-out mode (transmissions attempted every ~90 s), SPOT6 tags transmitted up to 40 messages per 2-h period then turned off (0 transmissions) for 48 h. Haul-out mode was entered when the wet/dry sensor was 75% dry for each of 5 consecutive minutes and exited when the wet/dry sensor was 50% wet for each of 5 consecutive minutes. The SPOT6 tags transmitted data during the same periods as the SPLASH10-F tags (02:00-05:59, 14:00-14:59, and 16:00-18:59 GMT).

Spatial Use and Navy Range Overlap Analyses

Individual non-pup and pup tracks were filtered to remove GPS and/or Argos locations that likely were erroneous based on manufacturer location quality parameters, swim speed between consecutive locations, and path tortuosity (Argos 2016, Dujon et al. 2014, Freitas et al. 2008, McConnell et al. 1992, Norris et al. 2017b). For non-pup tracks, GPS locations with residuals >35 and that exceeded a maximum swim speed of 2.5 m/s, if locations were <5 km apart, were removed (>98.9% of GPS locations retained per individual). Argos locations categorized as invalid (Location Class Z) or extremely inaccurate (>4 deviations from the mean), and those that were >100 m inland of the North American coastline, excluding all islands, were removed before combining these with the filtered GPS locations. The combined (GPS + Argos) track was filtered to remove Argos locations only based on swim speed (>2.5 m/s, if locations were <5 km apart, and >6 m/s, regardless of distance between locations) and both location types, with Argos locations preferentially removed over GPS locations, based on path tortuosity (removed locations with turn angle >155º, if incoming and outgoing path was >5 km, or >165º, if incoming and outgoing path was >2.5 km). For pup tracks, the same Argos location filtering steps were applied with removal of locations with: Location Class Z; >4 deviations from the mean; >100 m inland of the North American coastline, excluding all islands; swim speeds >2.5 m/s between consecutive location, if locations were <5 km apart, and >6 m/s, regardless of distance between locations; and turn angle >155º, if incoming and outgoing path was >5 km, or >165º, if incoming and outgoing path was >2.5 km. On average, 15% of Argos locations exceeded the speed/distance thresholds, and 3% of locations exceeded the turn angle/distance thresholds.

Filtered tracks were interpolated using the hermite spline method on a 3-h interval, based on an average interval between filtered locations of 3.3 ± 0.1 h, to obtain an equal sampling interval (Tremblay et al. 2006). These tracks were used to calculate foraging trip statistics, with interpolated locations ≤200 m of Guadalupe Island considered on-land. For non-pups, trips were separated into departures from Guadalupe Island that were <2 d and ≥2 d in duration. Pup tracks were separated into an on-island period, during which pups remained on or close to Guadalupe Island and repeatedly returned to it, and a single post-weaning migration trip where the pup did not return to the island during the tracking period as has been observed in other fur seals (*e.g.*, Baker 2007) .

Various foraging trip metrics were determined for non-pup trips lasting ≥2 d and the single trip for pups (Call et al. 2008, Norris & Elorriaga-Verplancken 2019). These included: (1) maximum trip distance, calculated as the great-circle path from where the incoming or outgoing path, whichever resulted in the shortest distance estimate, intersected with the 200-m island buffer to the farthest location for each trip; (2) total trip distance, calculated as the sum of straight-line distances between consecutive locations for each trip, starting and ending at the 200-m buffer; (3) relative search index (RSI), defined as the total trip distance divided by maximum trip distance with values closer to 1 indicating less search effort; (4) trip duration, calculated as the time elapsed between the last on-land location and last at-sea location for each trip; and (5) travel rate, calculated as total trip distance divided by trip duration. Additionally, duration ashore was calculated as the time between trips ≥2 d that included time on land, and on short <2-d duration trips for non-pups, and as the total on-island period before the single trip for pups. Mean trip statistics were calculated for each individual then averaged for each group to account for unequal number of trips among individuals. Only complete roundtrips (*i.e.,* returned to the island) were used to determine individual and group means; unless an individual made only one trip, then the single trip was included.

Additionally, to determine the seafloor depth associated with each interpolated location, we used nearest neighbor interpolation of the NOAA National Centers for Environmental Information (NCEI) ETOPO1 bedrock 1 arc-minute Global Relief Model (cell-registered; NOAA 2009). Mean seafloor depth for at-sea interpolated locations (≥200 m from Guadalupe Island) for each individual were calculated then averaged for the four groups of seals: adult females, juvenile females, juvenile males, and pups.

At-sea horizontal spatial use was examined using the grid cell method because it is transparent and allows for more precise utilization distributions (UDs) than other similar methods (*e.g.,* kernel density estimators; Kie et al. 2010; Maxwell et al. 2011, 2013; Rosenbaum et al. 2014). These UDs represent relative frequency of occurrence with 10% isopleths containing an increasing proportion of locations (Keating & Cherry 2009). A grid cell size of 0.25°×0.25° was used, similar to Maxwell and colleagues (2013) that covered a similar geographic area, as the optimal balance between making grid cells as small as possible to examine fine-scale movements and large enough to produce smooth contours that minimized gaps between used cells (Maxwell et al. 2011). Additionally, grid cells were positioned by dividing Guadalupe Island in half with two cells latitudinally and centering these two cells on the island longitudinally to minimize the number of cells with land. For each individual, the number of 3-h interpolated locations per grid cell was normalized to proportions using total number of interpolated at-sea locations, excluding locations ≤200 m of Guadalupe Island. These proportions were sorted from largest to smallest and converted to cumulative proportions, with all cells with the same proportions summed together. Group UDs (adult female, juvenile female, juvenile male, pups, non-pups, and all animals) were generated by averaging proportions per individual and converting these to cumulative proportions.

These individual and group UDs were overlaid with the U.S. Navy NWTT Study Area, SOCAL Range Complex, Southern California Anti-submarine Warfare Range (SOAR), and Point Mugu Sea Range (PMSR; see Figure 5 for range locations). All ranges, except SOAR, were divided into two areas by the 2,000-m depth contour that approximately represents range areas with greater (<2,000 m water depth; continental slope) and lesser (>2,000 m water depth) Navy activity. SOAR represents one of many ranges around San Clemente Island, California, and the entire area of this range was categorized as having greater Navy activity (in water depth <2,000 m). Total home range area, defined as the 100% UD isopleth, and percentage overlap between the fur seal group home ranges and each Navy range was determined. Percentage overlap was calculated by dividing the entire area of each Navy range by the animal group home ranges for adult females, juvenile females, juvenile males, pups, and all seals combined. The percentage of this overlap within the area classified as having greater Navy activity (<2,000 m water depth) also was calculated (total area of the Navy range divided by the animal home range area in each Navy range with <2,000 m water depth). At least two grid cell vertices had to be present within the Navy range for a cell to be considered overlapping.

Residence time within the entire area of each Navy range, and each range area classified as having greater Navy activity (<2,000 m water depth), were determined by summing the number of 3-h interpolated locations in each area by individual. Group mean residence times then were determined by averaging across individual residence times for only those animals that used each range area.

Five tags deployed on pups stopped transmitting before or shortly after (<5 days) the animal left Guadalupe Island, and data from these individuals was excluded from all analyses. Each tag attached to a non-pup transmitted for longer durations, and data from all non-pups were included in the analyses. The 2020 non-pup telemetry data were compared to the data collected from 35 non-pup Guadalupe fur seals (15 adult females, 10 juvenile females, and 10 juvenile males) tracked from November 2018 to April 2019 (Norris & Elorriaga-Verplancken 2019). For both tracking periods, identical analyses were performed for all results presented here, but seafloor depths associated with the at-sea interpolated locations and residence times were not determined for the non-pups tracked in 2018-2019.

All telemetry data processing and analyses were conducted in MATLAB 9.6 using custom-written and built-in codes. Geospatial data were analyzed and displayed using the Mercator projection and

World Geodetic System (WGS) 1984 reference ellipsoid in MATLAB's Mapping Toolbox 4.8. For all results, means are reported along with standard error (SE).

Dive Behavior Analyses

Dive depth histogram data was collected for non-pups only. The 14 dive depth frequency histograms were condensed into eight bins (upper bin limits: 4, 8, 12, 16, 20, 30, 60, and >60 m) to simplify interpretation without losing the resolution necessary to investigate among-group differences in diving activity. Number of dives to each of the eight pooled bins, as well as the number of messages with zero dives (*i.e.*, on land or no diving exceeded the dive definition thresholds), were calculated for each 6-h period by individual. Proportion of dives per pooled bin was calculated for each message, excluding periods with no dives, to standardize for differences in number of messages transmitted across individuals. Mean depth frequency histograms were compared qualitatively among the three groups (adult females, juvenile females, and juvenile males) and for all non-pups combined.

Because fur seals were tracked during the spring and summer in 2020, versus in the winter and spring in 2018-2019 (Norris & Elorriaga-Verplancken 2019), there were more daylight hours across the 2020 tracking period. Therefore, two of the periods, spanning dusk and dawn, contained different amounts of daytime and nighttime hours across the two tracking periods. As a result, only 2020 results broken out into 6-h periods are presented here and are not directly comparable to the 2018-2019 results.

Dive data collected in 2020 also were linked to the 3-h interpolated tracks with each 6-hour histogram period assigned to two interpolated locations (histogram period start time and midpoint time). Many locations had no associated dive data, and dive histogram messages were not evenly distributed along tracks because animal behavior impacts transmission of these messages. For interpolated locations with corresponding dive data, the number of dives to depths >8 m was summed for each 6-h histogram period for each non-pup. This depth was used to define dives that were more likely linked to foraging behavior and was selected based on the diving behavior of fur seals tracked in 2018-2019 and 2020, as well as the nighttime dive depth of various squid species in the California Current System (rarely <10 m; Bazzino et. 2010, Gilly et al. 2006). Therefore, a large number of dives >8 m (*e.g.*, >50 dives during a 6-h period) was used as a proxy for foraging activity regardless of path tortuosity, which sometimes is used to differentiate between foraging (decreased travel rate and/or increased turning frequency and angle) and transiting (faster travel and infrequent and small turning angles) behaviors (*e.g.*, Jonsen et al. 2007, Turchin 1991).

Results

Population Estimate and Trends

Overall, at San Benito Archipelago, twice as many Guadalupe fur seals were counted in 2019 relative to 2018 (Table 1). Approximately the same number of animals were observed at Guadalupe Island in 2018 and 2019 (Table 2). In 2018, only ~300 fur seals were counted on the west side of Guadalupe Island, and with higher northwest winds and swells in 2019, fewer animals likely were using this side of the island during our surveys. Thus, not surveying the west side of Guadalupe Island in 2019 likely did not significantly change our counts.

Table 1. Number of Guadalupe fur seals observed at San Benito Archipelago during summer 2018 and 2019. Direct counts of adult females were corrected using the number of pups when more pups were counted than adult females, and corrected total numbers are in parentheses.

Year	Island	Adult Males	Subadult Males	Adult Females	Juveniles	Pups	Total
2018	Middle Island	0	1	2	1	5	9
	East Island	0	6	0	51	0	57
	West Island	0	48	4	403	18	473
	Total	**0**	**55**	**6**	**455**	**23**	**539 (556)**
2019	Middle Island	0	1	1	1	2	5
	East Island	0	9	1	175	0	185
	West Island	3	53	7	842	18	923
	Total	**3**	**63**	**9**	**1,018**	**20**	**1,113 (1,124)**

Table 2. Number of Guadalupe fur seals observed at Guadalupe Island during summer 2018 and 2019. For boat-based surveys, animals were found on high- or low-visibility substrate (VS) or in the water. Land-based walkthrough surveys were only possible at Punta Sur. Direct counts of adult females were corrected using the number of pups when more pups were counted than adult females, and corrected total numbers are in parentheses.

Year	Survey Type	Adult Males	Subadult Males	Adult Females	Juveniles	Pups	Unknown	Total
2018	Boat-based, high VS	2	19	257	137	719	0	1,134
	Boat-based, low VS	162	343	7,510	1,219	10,614	98	19,946
	Boat-based, in water	11	69	1,885	81	6	120	2,172
	Land, walkthrough	7	26	741	133	2,045	13	2,965
	Total	**182**	**457**	**10,393**	**1,570**	**13,384**	**231**	**26,217 (29,208)**
2019	Boat-based, high VS	3	17	435	137	521	8	1,121
	Boat-based, low VS	44	332	8,147	1,324	7,771	182	17,800
	Boat-based, in water	0	35	3,668	28	0	38	3,769
	Land, walkthrough	3	45	927	142	2,528	34	3,679
	Total	**50**	**429**	**13,177**	**1,631**	**10,820**	**262**	**26,369**

The majority of the animals at San Benito Archipelago were juveniles in 2019 (91%) and 2018 (82%; Table 1). Approximately the same proportion of animals were counted on each island during both surveys with >80% of animals found on West Island. Less than 30 mother-pup pairs were observed at San Benito Archipelago in both years. It is unlikely that the timing of these surveys in mid- to late-July resulted in missing too many mother-pup pairs because few animals large enough to be reproductively active have been observed at this site in recent years, even with year-round monitoring (Elorriaga-Verplancken et al. 2016b).

In contrast, greater than 90% of the fur seals on Guadalupe Island were adult females and pups, with pups comprising only 41% of the animals counted in 2019 compared with 46% in 2018 (Table 2). Despite conducting the 2019 census at Guadalupe Island nine days later than in 2018, approximately 2,500 fewer pups were observed in 2019 compared with 2018. Very few (<10) dead pups were found at Punta Sur during each survey. In contrast to the decreased number of pups, there were approximately 2,800 more adult females at Guadalupe Island in 2019, most of which were in the water (3,668 females in 2019 versus 1,885 females in 2018). This resulted in an adult female to pup ratio of 1:0.82 in 2019, whereas the adult female to pup ratio in 2018 was 1:1.29. During boat-based surveys, >75% of fur seals counted in 2018 were found on low-visibility substrate (boulders and high platforms) compared with 68% in 2019 (Table 2). This difference primarily resulted from ~3,000 fewer pups being counted on low-visibility substrate along the east side of the island in 2019. Conversely, a greater proportion of fur seals, primarily mother-pup pairs, were counted at Punta Sur in 2019 (14%) than 2018 (11%). Fewer adult males were observed at the island in 2019 relative to 2018, likely because the surveys were conducted slightly later after the peak breeding season, but numbers of juveniles, subadult males, and fur seals of unknown age class and sex were almost identical between years.

Correcting adult female numbers using the number of pups counted (1:1 ratio) across the two sites, resulted in a *minimum* Guadalupe fur seal population estimate of 29,764 individuals in 2018 and 27,493 individuals in 2019.

Foraging Behavior, Habitat Use, and Navy Range Overlap

Animal and Tracking Overview

Adult female fur seals captured for satellite tagging in 2018 and 2020 had similar body sizes and were larger than juvenile males and females (Tables 3-5). In contrast, juvenile males captured for this study were on average 13 kg heavier and 17 cm longer in 2020 than 2018, but juvenile females captured during each year were similarly sized. We also recaptured and re-instrumented one juvenile female in March 2020 that we had previously tracked from November 2018 to February 2019. This female was the same weight and had the same axillary girth in 2018 and 2020 but was 9 cm longer in 2020 versus 2018.

Table 3. Tagging summary for 35 non-pup Guadalupe fur seals captured at Guadalupe Island in March 2020. Three age classes were captured: adult (A), subadult (S), and juvenile (J). Transmission duration was the number of days from the tagging date to last transmission date. The number of global positioning system (GPS) and combined GPS and Argos locations retained after transit speed (TS) and turn angle (TA) filtering included at-sea and on-land locations. Unique platform transmitting terminal (PTT) numbers were assigned for each satellite tag.

PTT	Tagging Date	Age class	Sex	Mass (kg)	Length (cm)	Axillary Girth (cm)	Last transmission date	Transmission duration (d)	# locations retained	
									GPS (TS)	Combined (TS/TA)
198322	03/12/20	A	F	58.2	148.0	97.5	05/12/20	61	62	416
198323	03/12/20	J*	F	36.0	139.0	78.5	06/13/20	94	132	778
198324	03/12/20	A	F	48.6	151.0	81.5	08/19/20	161	247	1,275
198325	03/12/20	A	F	78.9	156.0	105.0	07/18/20	129	185	1,223
198326	03/12/20	J	F	26.6	123.5	69.0	07/25/20	135	201	1,062
198327	03/13/20	A	F	39.8	135.5	78.5	08/01/20	141	143	974
198328	03/13/20	A	F	61.9	152.0	98.0	06/27/20	107	196	927
198329	03/13/20	A	F	44.1	151.0	83.5	05/24/20	72	111	623
198330	03/13/20	A	F	59.1	151.0	100.0	06/14/20	93	121	813
198331	03/13/20	J	M	23.8	119.0	65.5	06/01/20	80	159	830
198332	03/13/20	A^	F	39.4	136.0	79.5	08/14/20	155	265	1,481
198333	03/14/20	A	F	47.4	143.0	87.0	07/06/20	114	181	1,158
198334	03/14/20	A	F	48.3	146.0	86.5	05/02/20	49	57	320
198335	03/14/20	J	F	24.1	117.0	70.0	05/27/20	74	128	584
198336	03/14/20	J	M	31.5	127.0	74.0	06/11/20	90	131	856
198337	03/14/20	J	M	28.7	117.5	77.0	06/26/20	104	191	903
198338	03/14/20	A	F	35.3	130.0	78.0	07/13/20	121	123	845
198339	03/15/20	J	F	31.0	132.0	74.0	06/21/20	99	244	1,000
198340	03/15/20	J	F	29.1	118.0	74.0	07/21/20	128	115	692
198341	03/15/20	J	F	25.6	119.0	73.0	06/22/20	99	185	766
198342	03/15/20	J	M	44.8	141.0	88.0	07/22/20	129	317	1,553
198343	03/16/20	J	M	31.3	125.5	78.0	06/17/20	94	170	860
198344	03/15/20	J	F	27.7	125.0	75.5	05/30/20	77	92	589
198345	03/16/20	J	M	36.1	131.5	80.0	07/02/20	109	237	1,231
198346	03/16/20	A	F	58.7	149.0	91.0	06/26/20	102	131	796
198347	03/16/20	A	F	41.9	143.0	81.5	06/05/20	82	44	480
198348	03/16/20	J	F	23.0	117.0	86.5	05/11/20	56	85	489
198349	03/16/20	J	M	45.7	137.0	87.5	06/16/20	93	164	951
198350	03/17/20	J	F	30.8	119.0	78.0	06/10/20	85	121	601
198351	03/17/20	J	M	37.6	139.0	80.0	06/18/20	93	133	737
198352	03/17/20	A^	F	33.4	132.0	72.5	07/02/20	107	110	669
198353	03/17/20	J	F	30.8	122.0	76.0	06/05/20	81	115	594
198354	03/17/20	J	M	38.6	132.0	78.5	07/20/20	125	247	1,157
198355	03/18/20	S	M	75.3	161.0	100.5	07/28/20	133	274	1,351
198356	03/20/20	A	F	45.6	149.0	81.0	06/22/20	94	113	623

* Previously captured in November 2018 (PTT 177386)

^ Adult female not sighted with a nursing pup

Table 4. Tagging summary for 30 Guadalupe fur seal pups captured at Guadalupe Island in March 2020. Transmission duration was the number of days from the tagging date to last transmission date. The number of Argos locations retained after transit speed and turn angle filtering included at-sea and on-land locations. Five satellite tags stopped transmitting before or soon after (<5 d) these pups left the island, and these individuals were excluded from all analyses (no data for number of Argos locations retained). Unique platform transmitting terminal (PTT) numbers were assigned for each satellite tag.

PTT	Tagging Date	Sex	Mass (kg)	Length (cm)	Axillary Girth (cm)	Last transmission date	Transmission duration (d)	# Argos locations retained
198292	03/12/20	M	24.5	96.0	78.0	05/26/20	75	462
198293	03/12/20	F	12.4	85.5	57.0	04/28/20	47	350
198294	03/12/20	M	20.6	98.0	73.0	05/17/20	66	389
198295	03/13/20	M	18.0	95.0	86.5	05/14/20	62	422
198296	03/13/20	F	18.5	96.0	71.0	03/28/20	15	--
198297	03/13/20	M	12.5	85.0	59.5	05/16/20	64	296
198298	03/13/20	M	20.9	96.0	70.5	04/22/20	40	--
198299	03/14/20	M	15.9	89.5	63.3	05/28/20	75	462
198300	03/14/20	M	16.6	94.0	65.5	05/09/20	56	353
198301	03/15/20	F	14.9	90.0	61.0	05/21/20	67	358
198302	03/16/20	F	18.6	93.0	67.5	05/22/20	67	515
198303	03/16/20	F	15.5	89.0	63.5	05/22/20	67	437
198304	03/18/20	M	29.8	111.0	82.0	05/07/20	50	371
198305	03/18/20	M	22.6	98.0	74.5	06/06/20	80	396
198306	03/19/20	F	19.6	90.0	74.5	05/10/20	52	403
198307	03/19/20	F	16.9	87.0	68.0	04/01/20	13	--
198308	03/19/20	F	15.8	89.0	64.0	05/27/20	69	448
198309	03/19/20	M	19.6	91.0	73.0	05/28/20	70	506
198310	03/19/20	F	17.0	94.0	68.0	05/12/20	54	296
198311	03/19/20	M	30.8	110.0	84.5	05/01/20	43	--
198312	03/19/20	F	17.6	88.0	68.0	05/18/20	60	401
198313	03/19/20	M	17.8	96.0	69.0	06/04/20	77	446
198314	03/19/20	F	20.1	93.0	72.5	04/01/20	13	--
198315	03/20/20	F	22.0	93.0	75.0	05/26/20	67	408
198316	03/20/20	M	18.4	92.0	70.0	05/20/20	61	444
198317	03/20/20	M	19.9	99.0	70.0	05/18/20	59	413
198318	03/20/20	M	27.1	104.0	82.5	05/25/20	66	339
198319	03/20/20	F	16.0	89.0	67.5	07/14/20	116	846
198320	03/20/20	M	15.3	91.5	67.0	05/21/20	62	387
198321	03/20/20	F	16.0	87.0	67.5	05/31/20	72	494

Table 5. Mean body sizes of adult female, juvenile female, and juvenile male Guadalupe fur seals satellite tagged in November 2018 and March 2020.

Year	Group	Mass (kg)	Length (cm)	Girth (cm)
2018	Adult Females	49.8 ± 2.3	144.1 ± 1.3	89.7 ± 2.0
	Juvenile Females	26.7 ± 1.6	118.7 ± 2.3	70.5 ± 1.4
	Juvenile Males	27.3 ± 1.3	116.5 ± 2.1	71.7 ± 1.4
2020	Adult Females	49.4 ± 3.1	144.8 ± 2.1	86.7 ± 2.5
	Juvenile Females	28.5 ± 1.2	123.2 ± 2.3	75.5 ± 1.6
	Juvenile Males	39.3 ± 4.5	133.1 ± 4.0	80.9 ± 3.0

In 2020, all of the adult females were pregnant, and 13 of these females were nursing an ~9-month-old pup, at the time of tagging. Twelve pups (7 females and 5 males) were captured prior to weaning and satellite tagged along with their mothers (Table 6). There was no correlation between the body sizes of the mothers and their pups, but nursing pups captured with their mothers were smaller (mass = 17.0 ± 0.9 kg, length = 91.7 ± 1.0 cm, girth = 67.5 ± 2.1 cm) than the pups captured without their mothers (9 males and 9 females; mass = 20.4 ± 1.1 kg, length = 94.9 ± 1.7 cm, girth = 72.4 ± 1.3 cm) that were located in peripheral areas of the rookery and likely had weaned already. In addition, for all 30 pups, females were smaller (mass = 17.2 ± 0.7 kg, length = 90.3 ± 0.8 cm, girth = 67.5 ± 1.3 cm) than males (mass = 20.6 ± 1.3 kg, length = 96.6 ± 1.7 cm, girth = 73.1 ± 2.0 cm).

Table 6. Mass of 12 mother-pup pairs that were satellite tagged in March 2020. Platform transmitting terminal (PTT) numbers are unique to each satellite transmitter with more information provided in Tables 3-4 for these animals.

PTT		Mass (kg)	
Dam	**Pup**	**Dam**	**Pup**
198324	198292	48.6	24.5
198325	198293	78.9	12.4
198327	198295	39.8	18.0
198328	198296	61.9	18.5
198329	198297	44.1	12.5
198330	198298	59.1	20.9
198333	198299	47.4	15.9
198334	198300	48.3	16.6
198338	198301	35.3	14.9
198346	198302	58.7	18.6
198347	198303	41.9	15.5
198356	198320	45.6	15.3

Satellite transmissions were received March through August 2020, and tracking durations ranged from 49-161 d (101.9 ± 4.5 d) for non-pups and 47-116 d (66.4 ± 2.7 d) for pups (Tables 3-4, Figure 4). After filtering, there were approximately eight locations per day across non-pups (range: 2-12 filtered locations/d) and six locations per day across pups (range: 5-8 filtered locations/d). Typically, one to two GPS locations were successfully transmitted daily from the tags attached to non-pups. Many Argos locations for non-pups (75.0 ± 1.0%) and pups (49.1 ± 1.4%) were Location Class A and B, for which location accuracy estimations are not generated because <4 messages are received per satellite pass. Locations also were more concentrated between 02:00-05:59 GMT for non-pups (65.7 ± 0.9%) but were fairly evenly distributed across transmission hours for pups (56.2 ± 0.9% between 02:00-05:59 GMT).

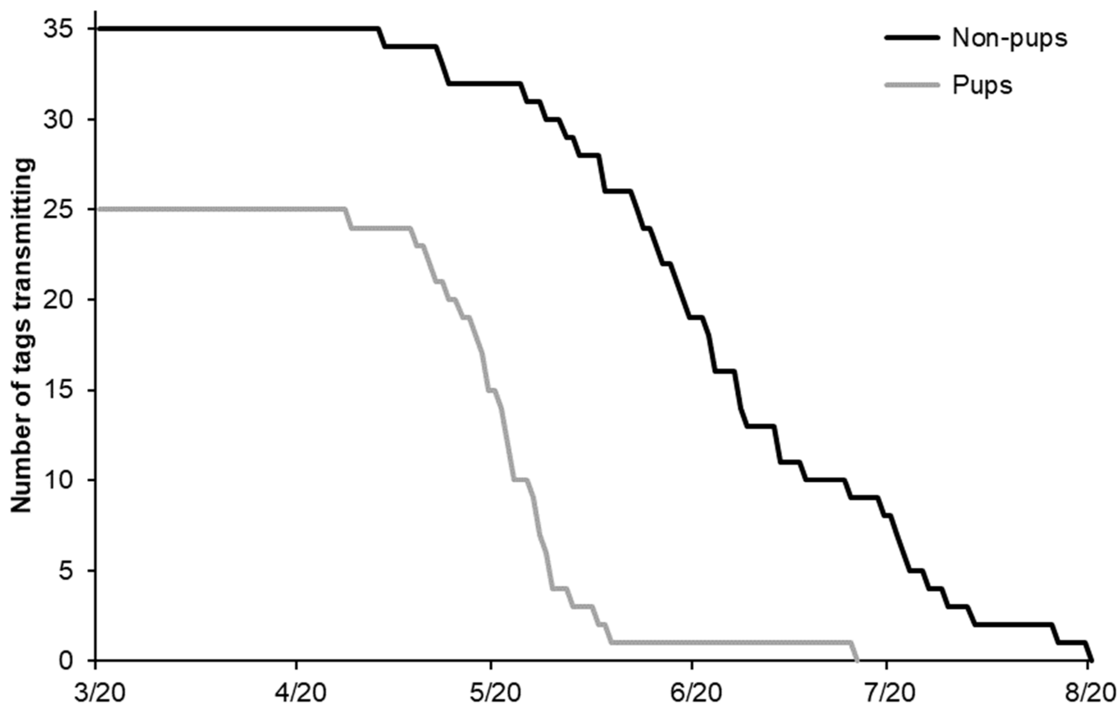

Figure 4. Number of satellite tags attached to non-pups and pups transmitting each day from March to August 2020.

Horizontal Spatial Use

In spring and summer 2020, Guadalupe fur seals broadly used waters off the west coast of North America from Vancouver Island, British Columbia, to the southern tip of the Baja California Peninsula, México, but traveled farther offshore and north (21-51°N, 108-140°W) than the animals tracked November 2018 through April 2019 (20-42°N, 112-130°W; Figure 5). The majority of animals (n = 51, or 85% of tagged animals) traveled north of Guadalupe Island during all or part of the 2020 tracking period, compared with 77% in 2018-2019.

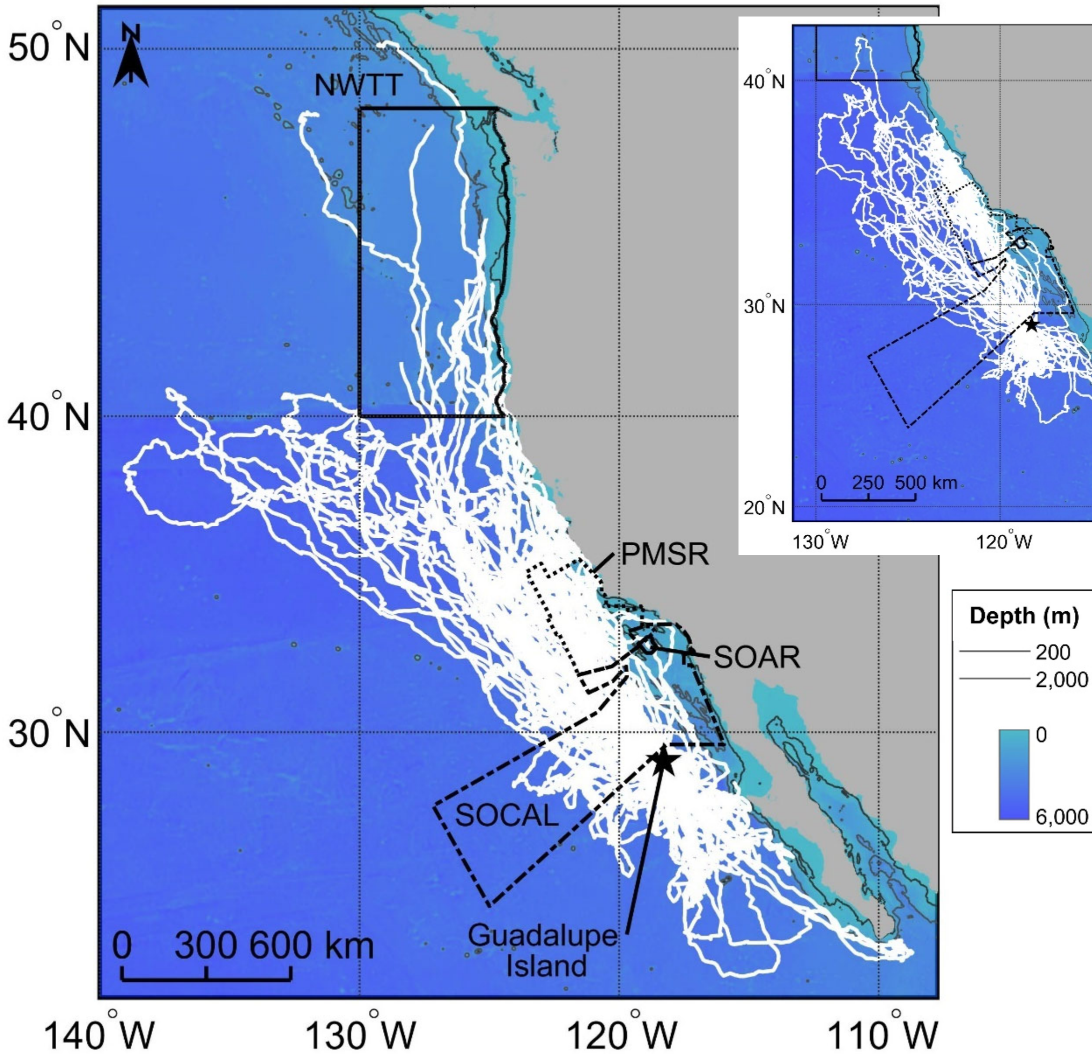

Figure 5. Three-hour interpolated tracks for 60 Guadalupe fur seals with satellite tags that transmitted March to August 2020. Inset shows 3-hour interpolated tracks for 35 non-pups with tags that transmitted November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

Adult females were distributed farther offshore in 2020 (up to 1,400 km from the coast) compared with 2018-2019 (up to 800 km from the coast; Figure 6). In 2020, six females traveled west of 130°W offshore of central and northern California. During each tracking period, two adult females (13%) exclusively used habitats south and east of Guadalupe Island. Adult females made up to five trips lasting ≥2 d in 2020 that were longer in duration and had greater maximum and total trip distances and RSI, than the 2018-2019 adult female trips (≤6 trips per individual; Table 7).

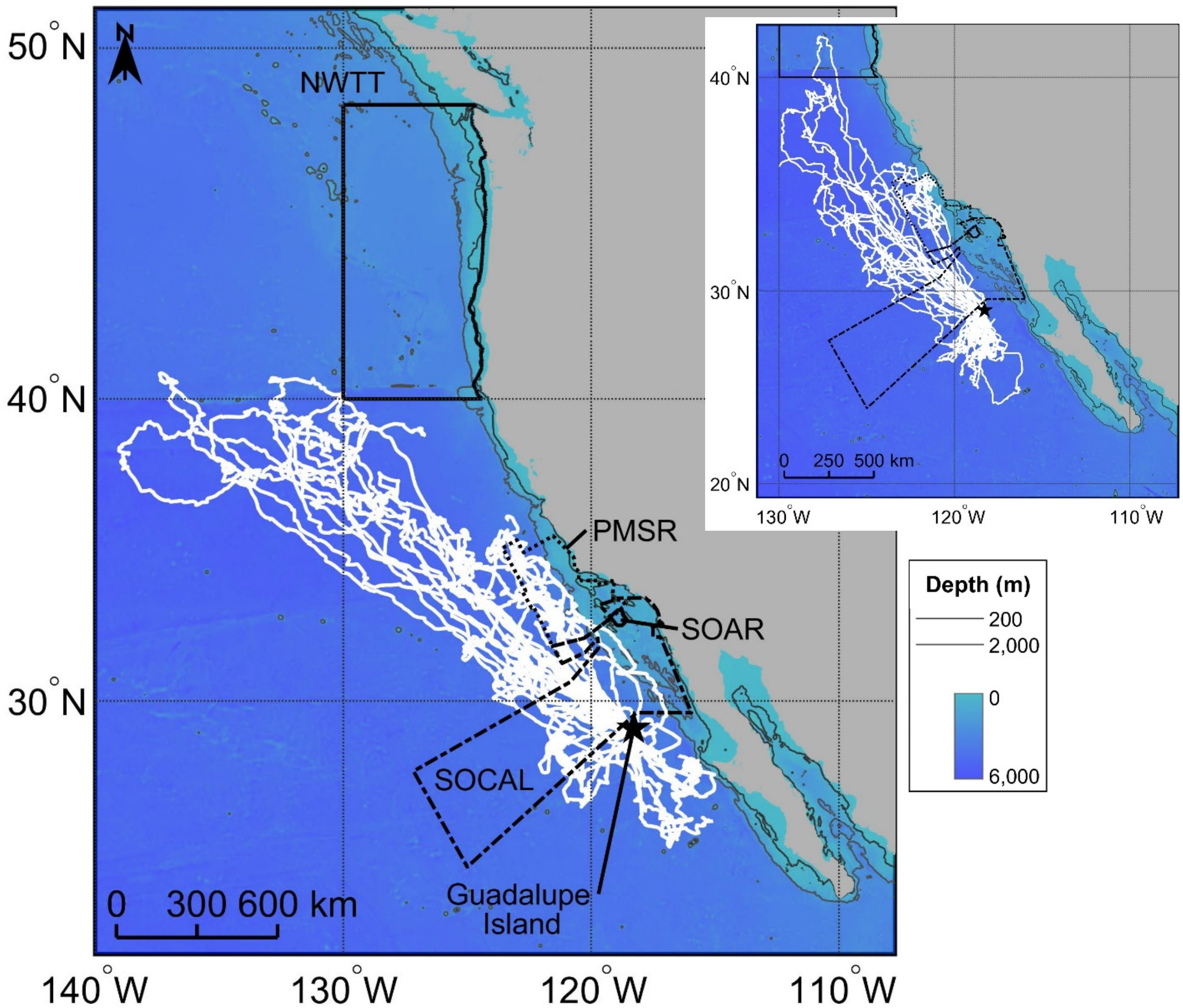

Figure 6. Three-hour interpolated tracks for 15 adult female Guadalupe fur seals with satellite tags that transmitted March to August 2020. Inset shows 3-hour interpolated tracks for 15 adult females with tags that transmitted November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

Similar to adult females, juvenile females primarily traveled north in 2020 (n = 8) and 2018-2019 (n = 8) but remained closer to shore (<800 km of the coast) than adult females (Figure 7). Most juvenile females tracked in 2020 were found farther from shore than those tracked in 2018-2019, which primarily were found along the continental shelf break <250 km offshore of central California. Foraging trip durations, distances, and RSI values were similar for juvenile females across both tracking periods (Table 7).

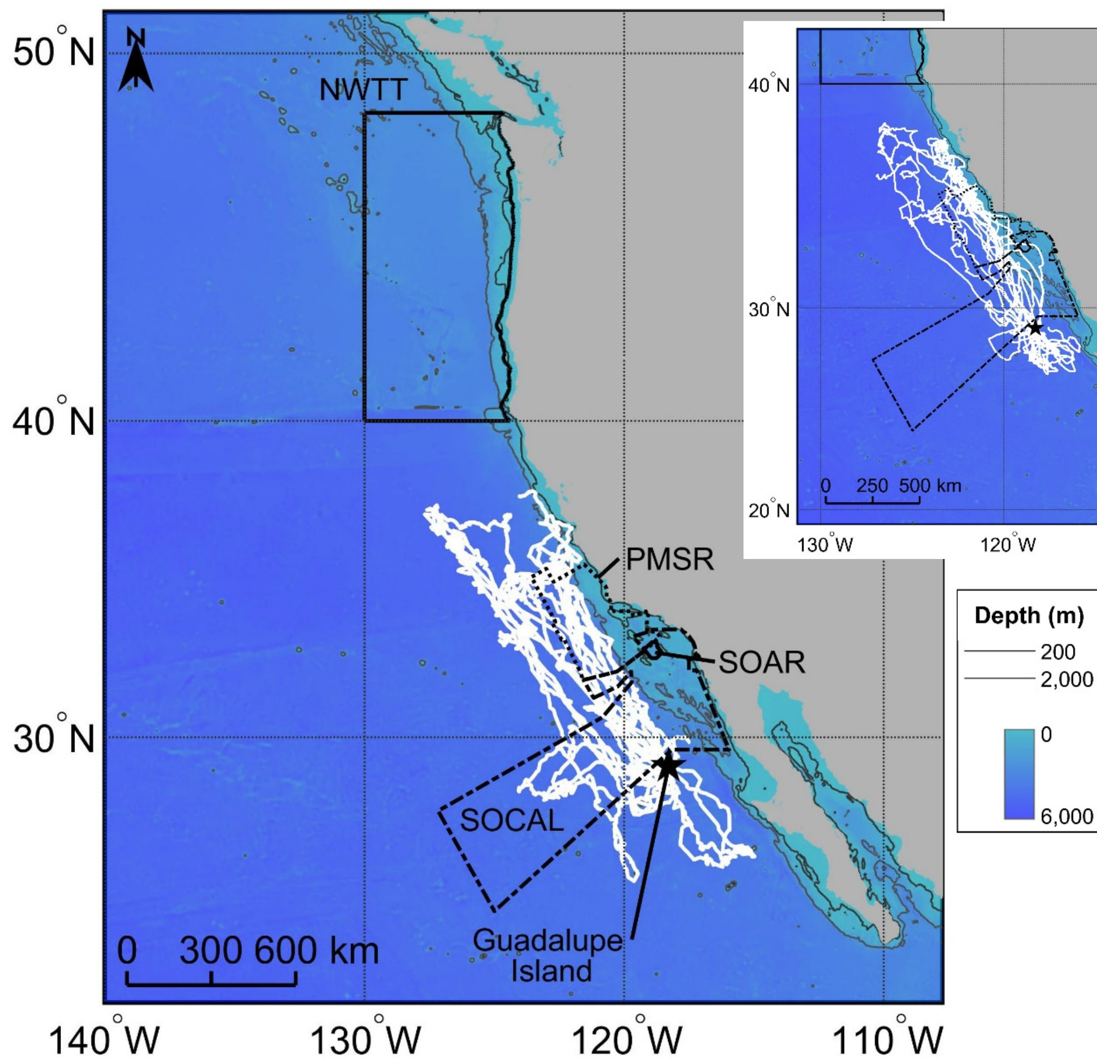

Figure 7. Three-hour interpolated tracks for 10 juvenile female Guadalupe fur seals with satellite tags that transmitted March to August 2020. Inset shows 3-hour interpolated tracks for 10 juvenile females with tags that transmitted November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

A greater number of juvenile males, seven individuals in 2020 and four individuals in 2018-2019, were found south of the island over all or most of the tracking periods compared with adult and juvenile females (Figure 8). In 2020, two males used waters off the southern tip of the Baja California Peninsula, and one of these individuals was the first fur seal tagged at Guadalupe Island that hauled out at San Benito Archipelago, arriving at this site on 2 July 2020. Juvenile males also remained within 500 km of the coast of North America during both tracking periods and exhibited more resident behavior, with a greater number of shorter distance and duration trips, in 2020 (≤7 trips) than in 2018-2019 (≤2 trips; Table 7).

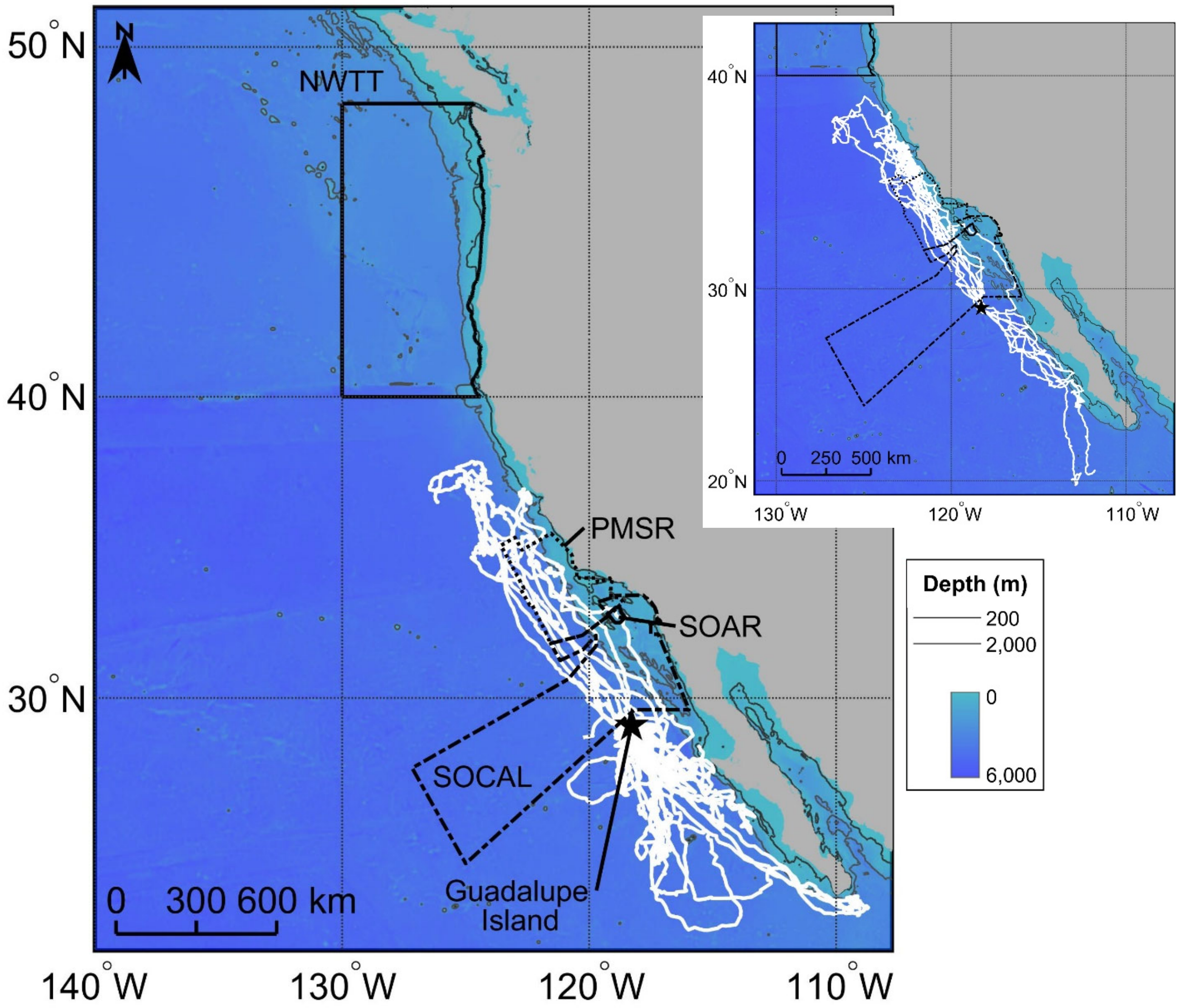

Figure 8. Three-hour interpolated tracks for 10 juvenile male Guadalupe fur seals with satellite tags that transmitted March to August 2020. Inset shows 3-hour interpolated tracks for 10 juvenile males with tags that transmitted November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

All weaned pups traveled north of Guadalupe Island, with only one pup briefly spending time south of the island, and pups were the only animals that traveled north of 41°N in 2020 (Figure 9). The smallest pup, captured with the largest female, left the island first on March 26th, and the last pup (not captured with a female) left the island on May 10th. In contrast to non-pups, many of the tags attached to pups (n = 10) stopped transmitting between 37-48°N while these animals were still traveling northward on nearly linear paths and at approximately the same transit speeds, suggesting they may have traveled farther north than their tracks indicated, regardless of the reason transmissions ceased (*i.e.*, animal mortality, tag loss, or tag failure). Pups remained within 600 km of the coast with many using nearshore areas over the continental shelf (water depths <200 m).

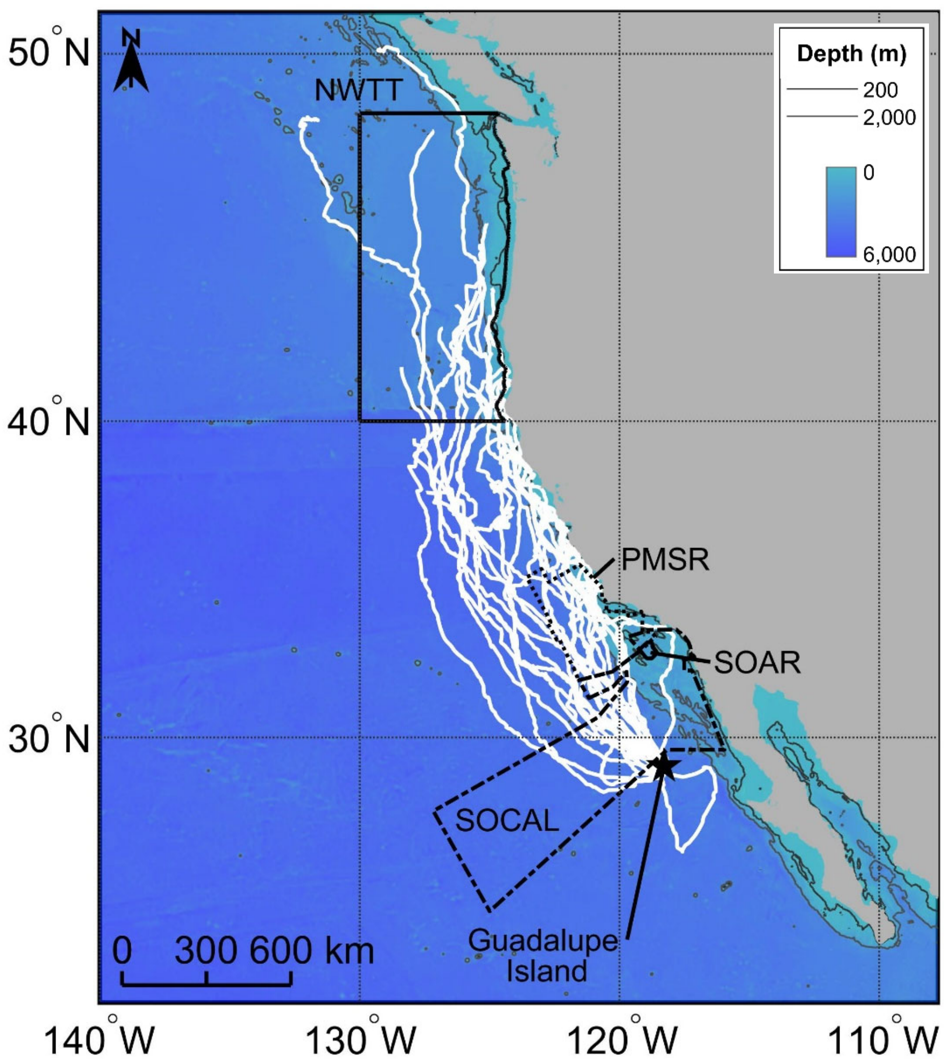

Figure 9. Three-hour interpolated tracks for 25 weaned Guadalupe fur seal pups with satellite tags that transmitted March to August 2020. Four U.S. Navy ranges are indicated by black outlines. No pups were tracked in 2018-2019 because they were still nursing at the time of tagging in November.

On average, for non-pups, adult females tracked in spring and summer 2020 had the greatest trip durations and maximum and total trip distances, whereas the fastest travel rates were recorded by adult females tracked in winter 2018 and spring 2019 (Table 7). Pups remained on or close to the island for 28.5 ± 1.9 d (range: 10.2-50.5 d) before traveling 1,509 ± 103 km (range: 564-2,536 km) north of the island (Table 7). As indicated by the RSI values closer to one, pup travel was more directed (*i.e.,* less path tortuosity; RSI = 1.5 ± 0.1) than non-pups (group mean RSI ~3).

During both tracking periods, 80% of adult females were found exclusively in deep-water habitat (seafloor depth >2,000 m). A greater number of juvenile fur seals, eight females (80%) and four males (40%), only used deep-water habitat in 2020, compared with 40% for juvenile females and 10% for juvenile males in 2018-2019. However, only four pups (16%) remained in deep-water habitat throughout the tracking period. As a result, the seafloor depths associated with the 3-h interpolated locations were deepest for adult females and shallowest for pups (Table 8).

Table 7. Foraging trip statistics for each group. Means were calculated for each individual for complete (*i.e.,* returned to the island) trips ≥2 d, unless the individual did not return to the island during the tracking period (i.e., single "incomplete" trip ≥2 d was included), then across individuals within a group, along with standard error, for: trip duration, duration ashore, maximum and total trip distance, and relative search index (RSI). Travel rate was similarly calculated, but across all (complete and incomplete) trips ≥2 d. The total distance traveled across complete and incomplete trips ≥2 d also was summed (sum distance) for each individual then the mean was calculated across individuals within a group. For each group, the maximum for each metric across all individuals is in parentheses, with complete trips included for each as is described for means.

Year	Group	Duration (d)		Distance (km)			RSI	Travel Rate (km/d)
		Trip	Ashore	Maximum	Total	Sum		
2018	Adult Females	31.2 ± 4.3 (49.1)	6.1 ± 1.0 (9.7)	795 ± 114 (1,667)	2,070 ± 295 (4,134)	3,951 ± 412 (6,657)	2.9 ± 0.2 (5.2)	63.2 ± 4.2 (101.9)
	Juvenile Females	42.8 ± 6.5 (61.4)	8.7 ± 1.8 (21.2)	771 ± 126 (1,273)	2,325 ± 373 (3,833)	3,514 ± 297 (4,877)	3.1 ± 0.2 (4.7)	55.7 ± 4.2 (96.9)
	Juvenile Males	53.2 ± 8.1 (75.0)	12.1 ± 1.2 (20.4)	944 ± 96 (1,260)	2,681 ± 416 (4,090)	3,155 ± 559 (7,300)	2.8 ± 0.3 (3.2)	51.5 ± 1.9 (65.9)
2020	Adult Females	56.1 ± 8.1 (109.0)	4.4 ± 0.6 (20.0)	992 ± 162 (2,190)	3,141 ± 473 (6,463)	5,070 ± 354 (6,493)	3.3 ± 0.3 (7.0)	56.0 ± 2.3 (99.7)
	Juvenile Females	48.4 ± 6.5 (103.4)	7.0 ± 1.0 (17.3)	764 ± 125 (1,275)	2,588 ± 356 (5,658)	4,029 ± 369 (5,821)	3.4 ± 0.2 (6.0)	54.7 ± 2.8 (66.9)
	Juvenile Males	34.7 ± 7.3 (74.9)	7.0 ± 2.2 (25.1)	620 ± 118 (1,205)	2,018 ± 407 (3,960)	4,770 ± 343 (6,378)	3.2 ± 0.2 (4.5)	55.1 ± 2.4 (83.2)
	Pups	36.3 ± 2.6 (89.9)	28.5 ± 1.9 (50.5)	1,509 ± 103 (2,536)	2,083 ± 117 (3,639)	2,083 ± 117 (3,639)	1.5 ± 0.1 (2.7)	59.0 ± 2.4 (78.8)

Table 8. Seafloor depth associated with the 3-h interpolated locations for each group. Means were calculated for each individual then across individuals within a group along with standard error.

	Adult Females	Juvenile Females	Juvenile Males	Pups
Depth (m)	4,069 ± 96	3,766 ± 114	3,390 ± 121	2,834 ± 187

The areas used most intensely by Guadalupe fur seals in spring and summer 2020 were slightly different than those that were primarily used in winter and spring 2018-2019 (Figure 10). In contrast to 2018-2019, the areas south of Guadalupe Island (≤300 km) and offshore of central California, along the continental shelf break, were not used as much in 2020. Instead, an area extending northwest from Guadalupe Island to the San Francisco Bay Area and extending up to 500 km from shore primarily was used in 2020. The total home range area also was greater in 2020 (1.55×10^6 km^2) than 2018-2019 (0.94×10^6 km^2; Table 9).

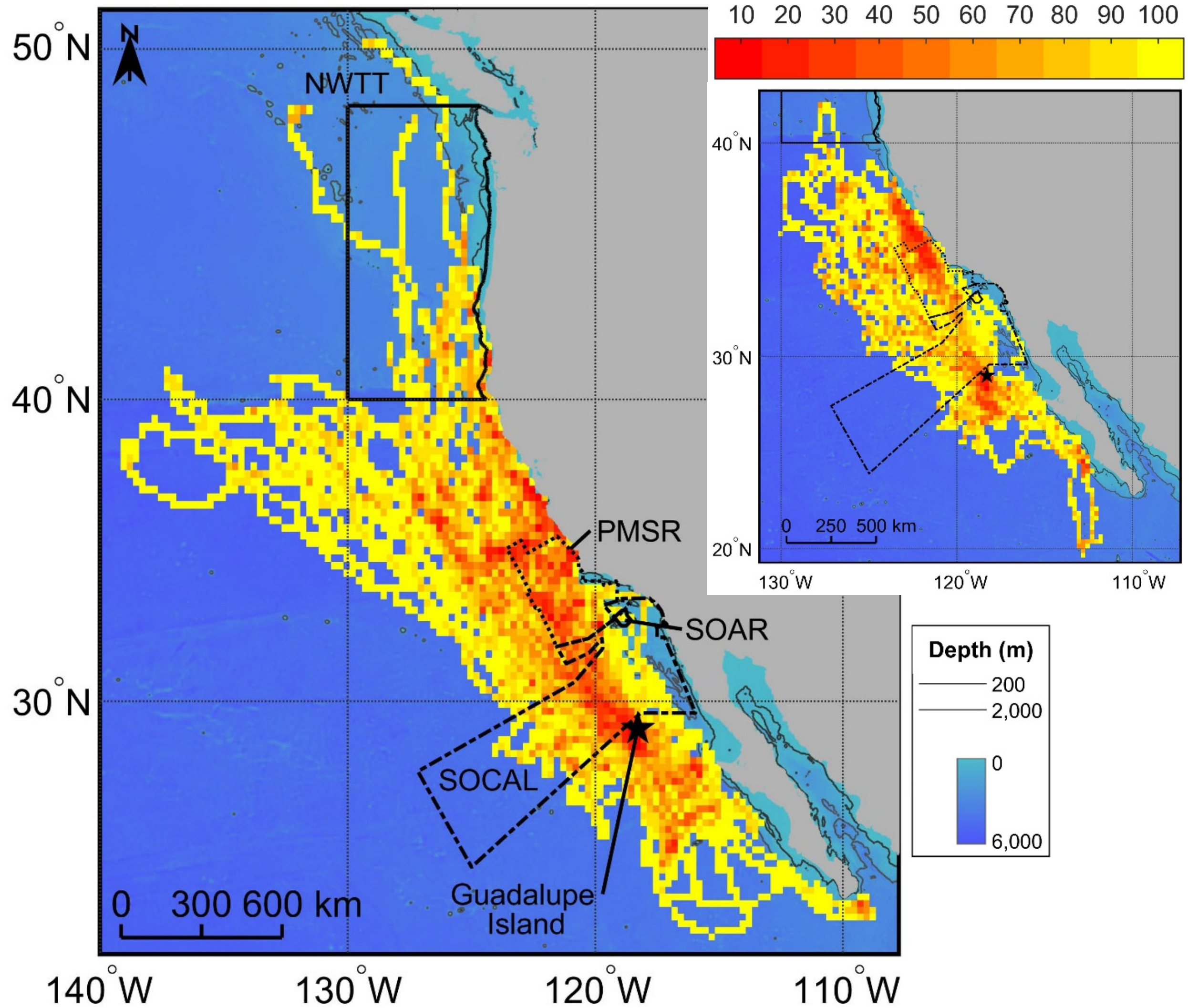

Figure 10. Utilization distribution (UD), in 10% increments, for 60 Guadalupe fur seals tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Inset shows the UD for 35 Guadalupe fur seals, all non-pups, tracked from November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

These differences between the two tracking periods were driven in part by the spatial distribution of pups, which were tracked in 2020 but not 2018-2019. With pups excluded from the UD analyses, non-pups used areas farther offshore to a greater extent and had less concentrated use along the continental shelf break offshore of central California in 2020 compared with 2018-2019 (Figure 11). The home range area for non-pups in 2020 (1.26×10^6 km^2) was still larger than the 2018-2019 home range area for all non-pups (Table 9).

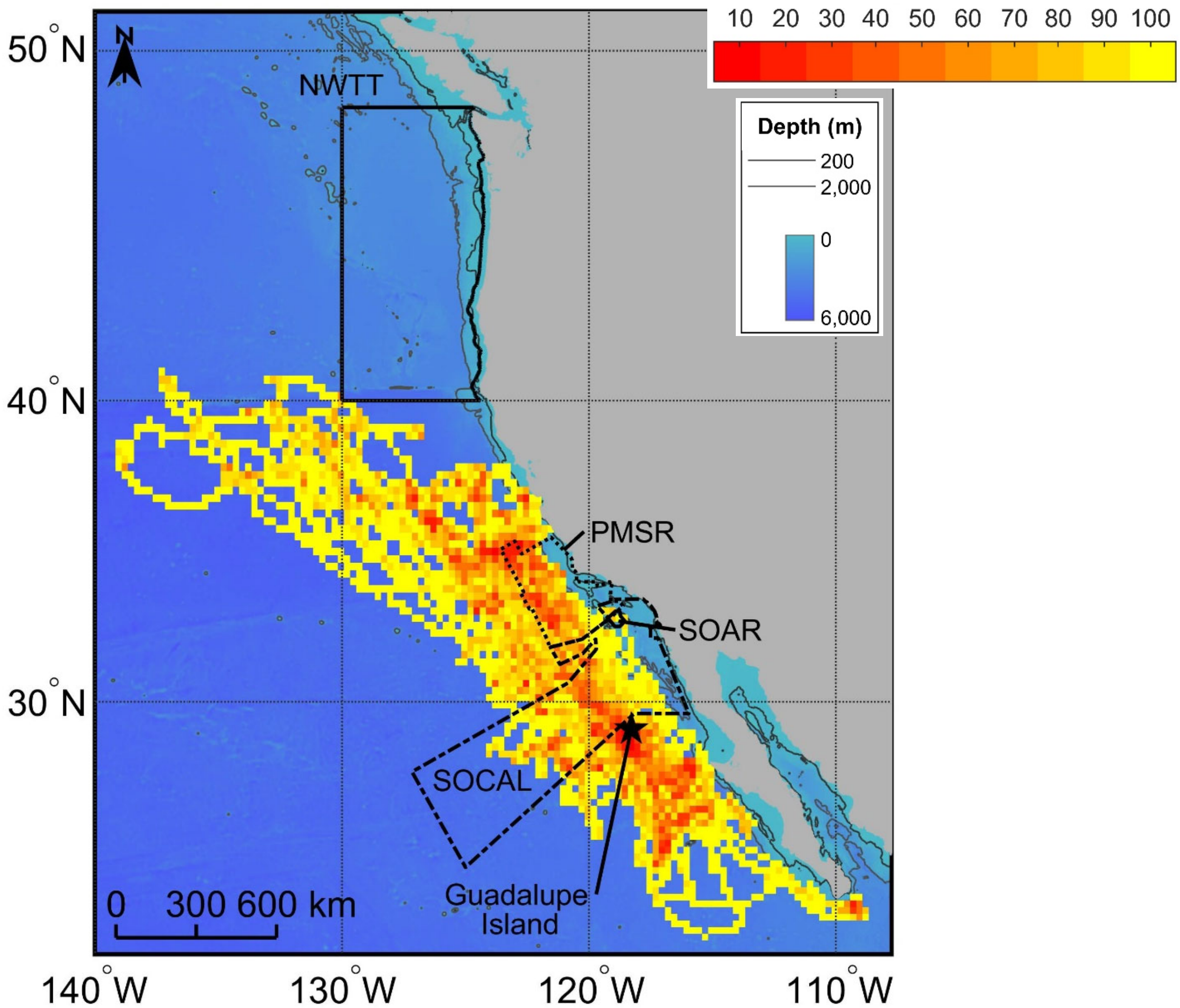

Figure 11. Utilization distribution (UD), in 10% increments, for 35 non-pup Guadalupe fur seals tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Four U.S. Navy ranges are indicated by black outlines.

Table 9. Home range areas (km^2) for each group and all seals combined for Guadalupe fur seals satellite tagged in November 2018 and March 2020.

	Adult Females	Juvenile Females	Juvenile Males	Pups	All
2018	617,566	404,274	379,792	n/a	944,689
2020	881,489	455,322	569,294	704,171	1,552,450

Similar to 2018-2019, there was spatial segregation among adult females in 2020, with many females concentrated in areas that were not used by other females (Figure 12). As a result, the areas used more intensely by adult females were dispersed across much of their home range (*i.e.,* many areas with UD isopleths <70%), and adult female home ranges were larger than the home ranges of the other groups across both tracking periods (Table 9). Adult females rarely used the area immediately south of Guadalupe Island in 2020, and the home range of adult females was larger in 2020 (8.8×10^5 km^2) than 2018-2019 (6.2×10^5 km^2).

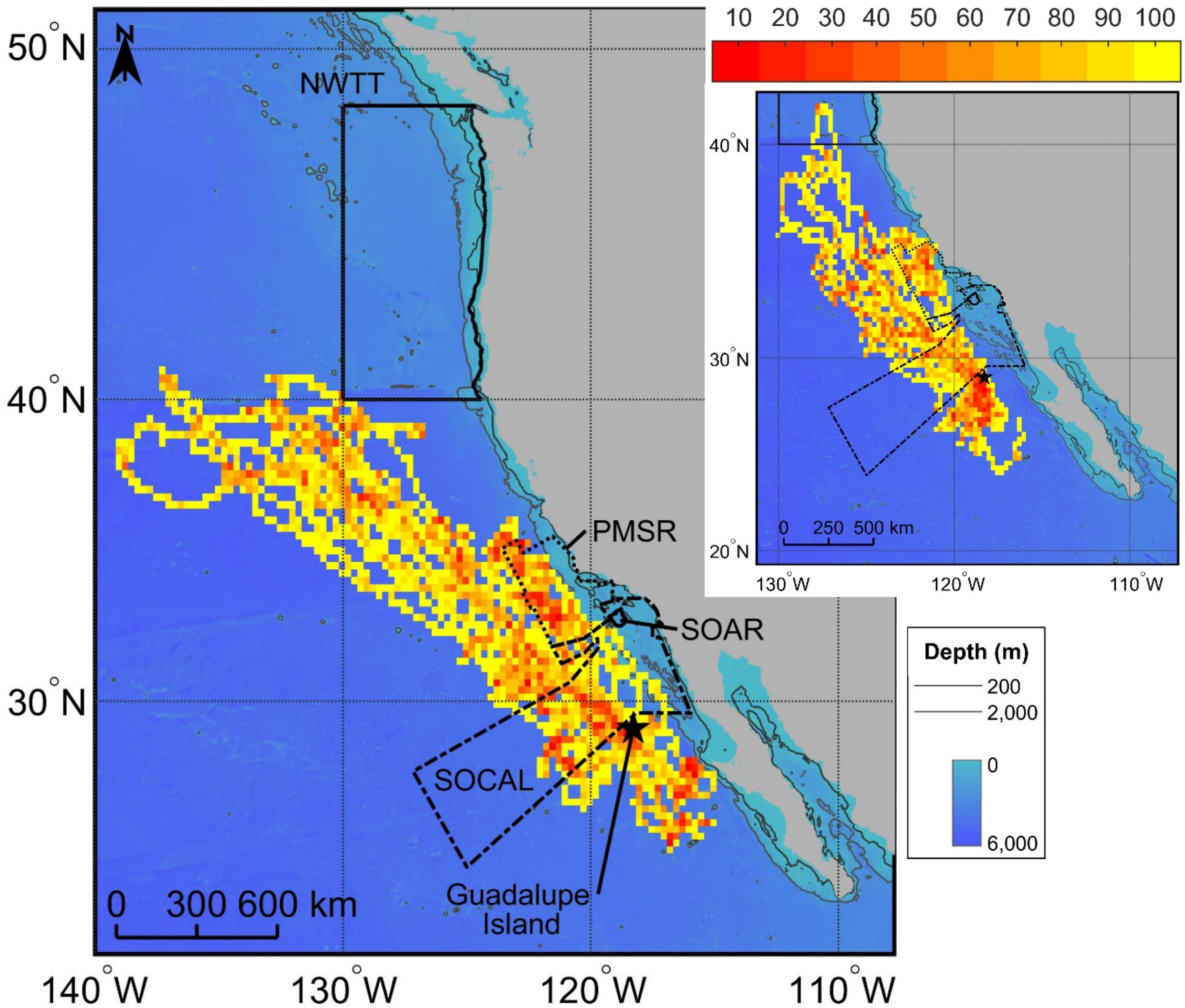

Figure 12. Utilization distribution (UD), in 10% increments, for 15 adult female Guadalupe fur seals tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Inset shows the UD for 15 adult females tracked from November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

Juvenile females and males primarily used an area 50-250 km offshore of central California, extending from Point Conception to San Francisco Bay, in 2018-2019 (Figures 13-14). In 2020, juvenile habitat use was concentrated farther offshore of central California. Additionally, juvenile males intensely used an area ≤600 km south-southeast of Guadalupe Island in 2020, which was an area that was not used by this group in 2018-2019. Similar habitat (≤400 km south-southeast of Guadalupe Island) also was extensively used in 2018-2019, and to a lesser extent in 2020, by juvenile females. The home range area of juvenile females was similar between the two tracking periods (4.0-4.6×10^5 km^2), whereas the 2020 juvenile male home range area was much larger in 2020 (5.7×10^5 km^2) than 2018-2019 (3.8×10^5 km^2; Table 9).

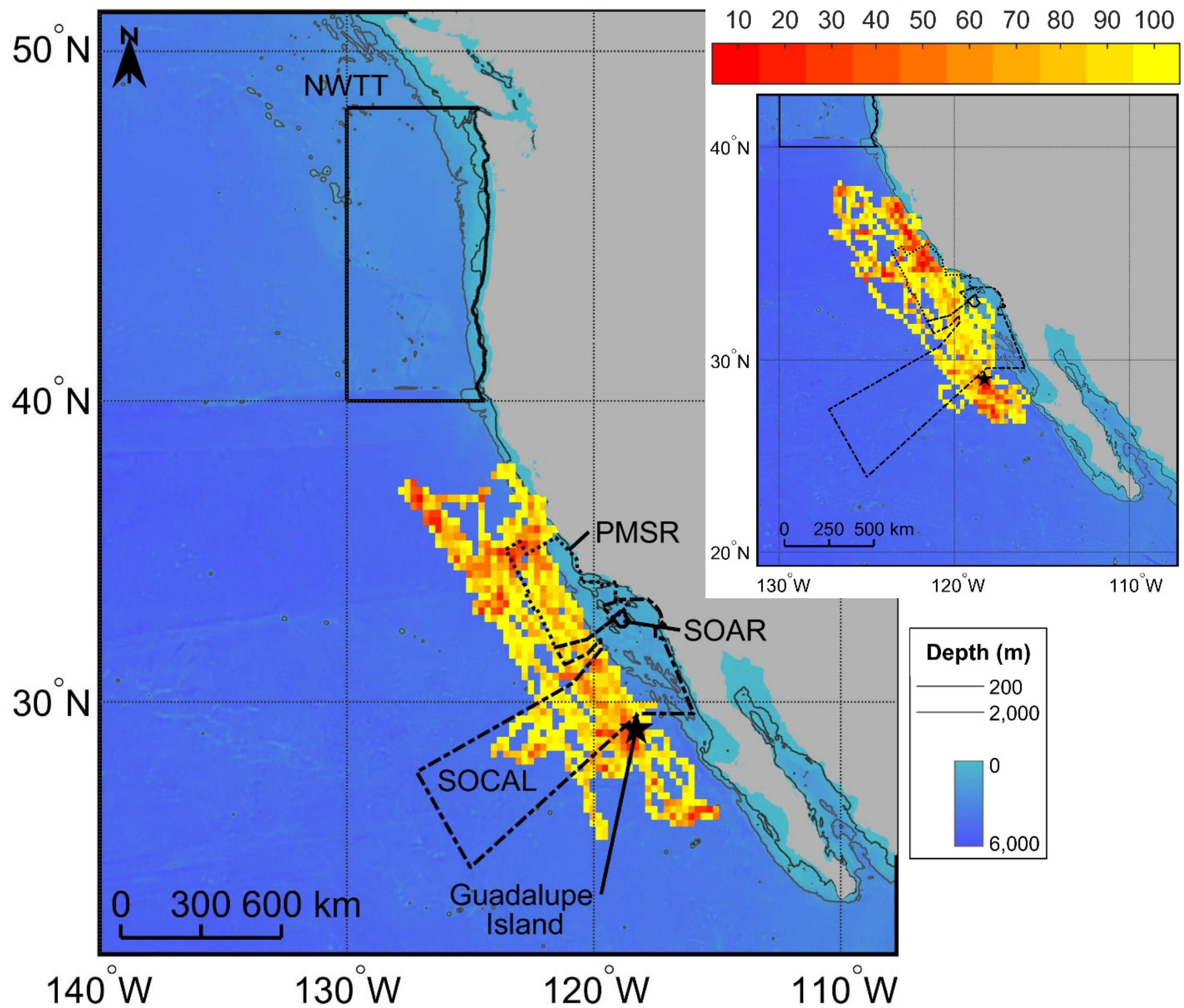

Figure 13. Utilization distribution (UD), in 10% increments, for 10 juvenile female Guadalupe fur seals tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Inset shows the UD for 10 juvenile females tracked from November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

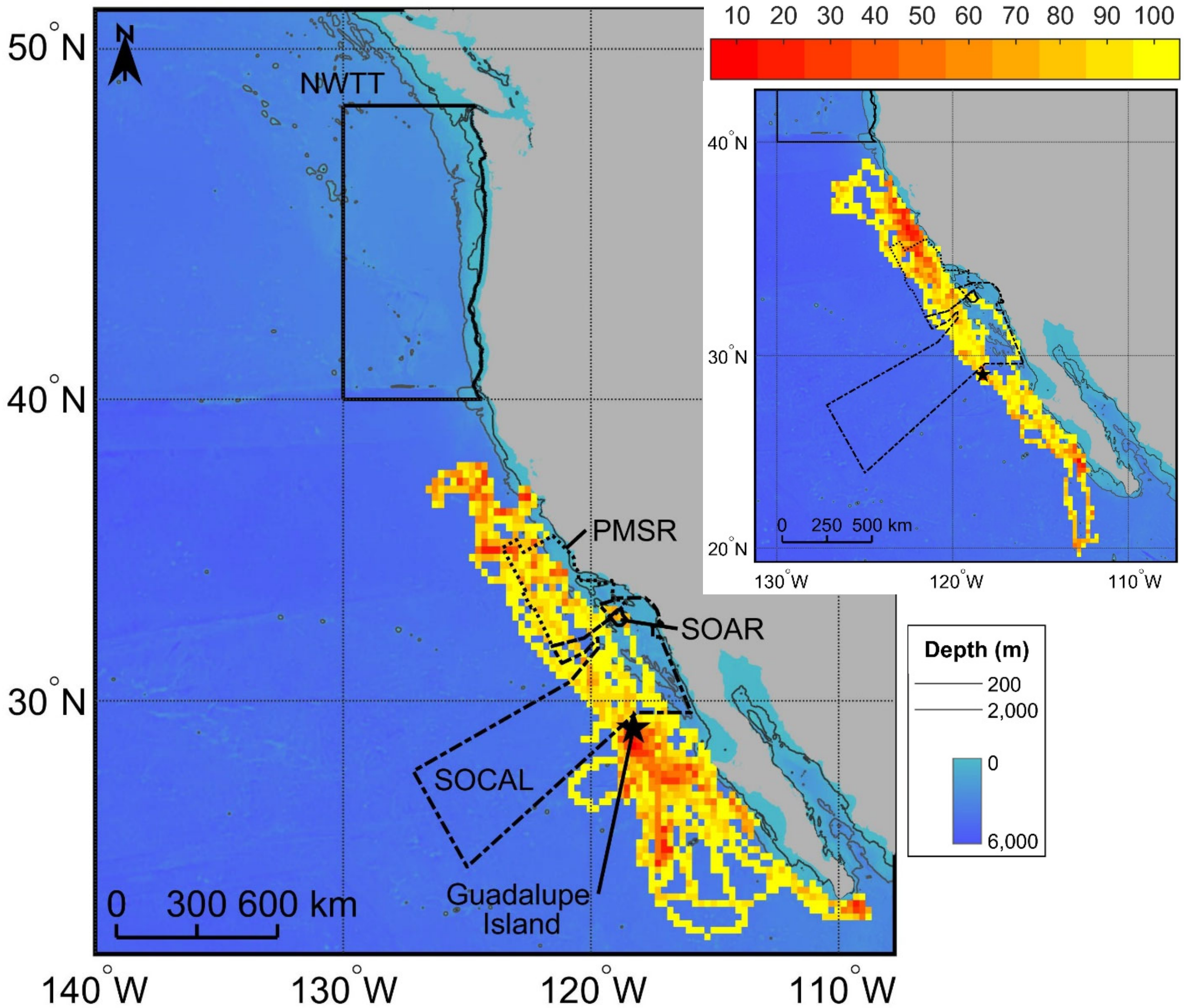

Figure 14. Utilization distribution (UD), in 10% increments, for 10 juvenile male Guadalupe fur seals tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Inset shows the UD for 10 juvenile males tracked from November 2018 to April 2019, with the same four U.S. Navy ranges indicated (black outlines) in both maps.

Weaned pups used several nearshore areas along the coast of central and northern California and central Oregon (<200 km from shore) the most intensely after their initial departure from Guadalupe Island (Figure 15). The home range for these 25 pups (7.0×10^5 km^2) was larger than the home range areas of juveniles (10 females and 10 males, for both tracking periods) and adult females in 2018-2019 (n = 15), but smaller than the adult female home range area in 2020 (n = 15, Table 9).

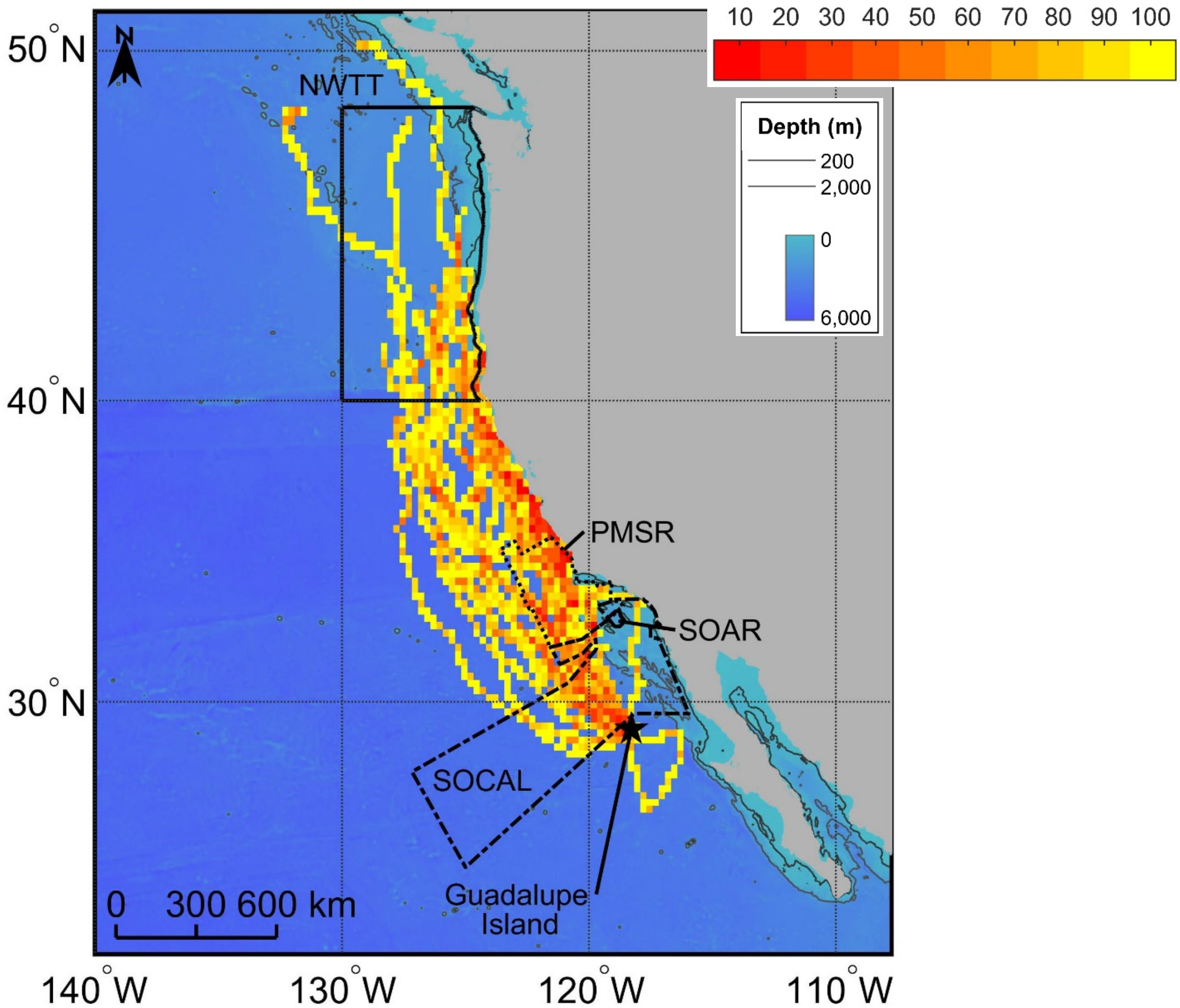

Figure 15. Utilization distribution (UD), in 10% increments, for 25 weaned Guadalupe fur seal pups tracked from March to August 2020. Red to yellow shading represents more to less intensely used areas. Four U.S. Navy ranges are indicated by black outlines. No pups were tracked in 2018-2019 because they were still nursing at the time of tagging in November.

Overlap with Navy Ranges

Twenty percent of non-pups tracked in spring and summer 2020 almost exclusively used habitat south of Guadalupe Island and had little or no spatial overlap with U.S. Navy training and testing areas, compared with 17% in winter and spring 2018-2019. The other non-pups (both years) and 25 pups (2020 only) used the Navy ranges offshore of the U.S. west coast to varying degrees.

The NWTT Area was briefly used by one non-pup, an adult female, during both tracking periods. In 2020, only the southwest corner of this area was used, resulting in <1% home range overlap for adult females and all non-pups with the NWTT Area compared with 3% overlap in 2018-2019 (Table 10). Additionally, between March and August 2020, this single female spent <1 d within the NWTT Area (Table 11).

Table 10. Percentage overlap between four U.S. Navy training and testing areas and the home ranges of each group of Guadalupe fur seals, and all seals combined. This was calculated as the area of each Navy range divided by the home range area within each range. The percentage of the NWTT Area, PMSR, and SOCAL Range Complex over seafloor depths <2,000 m (continental slope) used by fur seals was calculated separately (home range area in water depths <2,000 m divided by entire range area). No pups were tagged in 2018, and SOAR is entirely over the slope.

	Adult Females		**Juvenile Females**		**Juvenile Males**		**Pups**	**All**	
	2018	**2020**	**2018**	**2020**	**2018**	**2020**	**2020**	**2018**	**2020**
NWTT, all	3	<1	0	0	0	0	31	3	31
NWTT, slope	0	0	0	0	0	0	7	0	7
PMSR, all	67	65	85	61	80	71	90	99	100
PMSR, slope	16	7	33	2	30	16	34	38	38
SOCAL, all	25	34	28	32	18	21	28	42	50
SOCAL, slope	0	4	7	0	6	4	4	10	8
SOAR	0	0	29	0	87	58	0	87	58

Table 11. Residence times for Guadalupe fur seals in four U.S. Navy training and testing areas in 2020. Means were calculated by including only individuals that used each area for each group, and all seals combined. The residence times in the NWTT Area, PMSR, and SOCAL Range Complex over seafloor depths <2,000 m (continental slope) were calculated separately. SOAR is entirely over the slope.

	Adult Females		**Juvenile Females**		**Juvenile Males**		**Pups**		**All**
	Mean	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**
NWTT, all	0.9	0.9	0.0	0.0	0.0	0.0	8.2	19.0	7.7
NWTT, slope	0.0	0.0	0.0	0.0	0.0	0.0	2.2	5.4	2.2
PMSR, all	24.8	62.6	15.1	36.0	15.2	29.0	7.8	23.0	12.9
PMSR, slope	1.5	1.9	0.6	1.0	4.9	12.5	6.6	17.6	5.1
SOCAL, all	17.2	64.6	16.4	57.3	9.8	14.8	5.2	11.4	10.7
SOCAL, slope	8.0	8.0	0.0	0.0	3.8	9.1	2.3	6.1	3.6
SOAR	0.0	0.0	0.0	0.0	3.4	3.4	0.0	0.0	3.4

In contrast to non-pups, 14 pups (56%) traveled north of 40°N into the NWTT Area, and the movements of ten of these pups overlapped with the range area associated with greater Navy activity (<2,000 m water depth; Figure 16). This resulted in the pups' home range overlapping with 31% of the NWTT Area, with 7% of this overlap within the continental slope region (Table 10). Pups arrived in the NWTT Area in late April, approximately 25 d after leaving Guadalupe Island, and remained in this Navy range until at least early June, when their tags stopped transmitting (Table 12). Residence times were ≤19 d and ≤5 d for individual pups within the NWTT Areas (entire area and slope area, respectively). On average, pups were within the NWTT Area for 8 d, with only 2 d spent in water depths <2,000 m (Table 11).

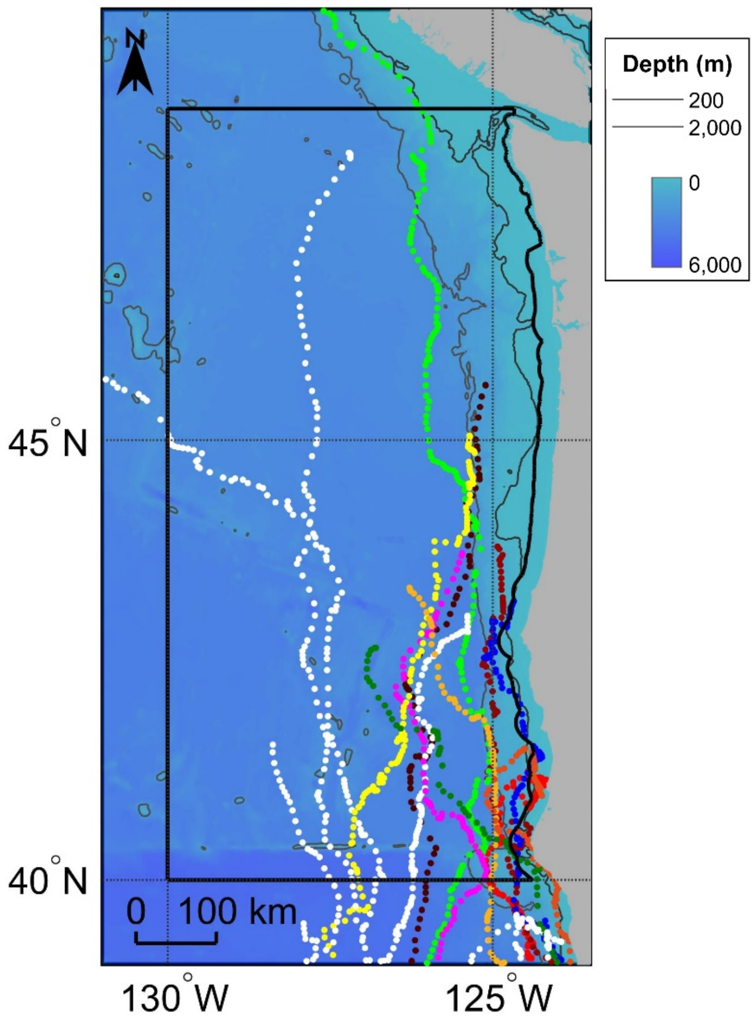

Figure 16. Three-hour interpolated locations for pups tracked in 2020 within and adjacent to the NWTT Area (solid black line). Locations for each of the 10 pups that used the NWTT Area with water depths <2,000 m are color-coded by individual, and locations for individuals that only used range areas farther offshore of the continental slope (>2,000 m water depth) or south of the NWTT Area are white. Most of the tags stopped transmitting while these pups were offshore of northern California and Oregon.

Table 12. Date of arrival in the NWTT Area and travel duration to this Navy range from Guadalupe Island for 14 pups that traveled north of 40°N.

Date Arrived at NWTT Area	Travel Duration to NWTT Area (d)
04/21/20	26
04/27/20	24
04/27/20	26
04/30/20	31
05/07/20	23
05/08/20	24
05/08/20	23
05/11/20	22
05/12/20	23
05/14/20	22
05/14/20	31
05/19/20	32
05/21/20	22
05/23/20	21

There was substantial and similar Guadalupe fur seal home range overlap with PMSR across all groups in 2020 and 2018-2019 (61-100%), but reduced percentage overlap with the continental slope region of the range in 2020 for non-pups, especially for juvenile females (33% in 2018-2019 vs. 2% in 2020; Table 10). For all groups, except juvenile males, there were high concentrations of locations (UD isopleths <70%) within this range, indicating there was a greater likelihood of this species being found within PMSR in spring and summer 2020 than winter 2018 and spring 2019. This difference between tracking periods was driven in part by the pup home range overlap of 90% with PMSR. Residence times within PMSR in 2020 were greatest for adult females (mean = 25 d, max = 63 d) with similar residence times for juvenile females (mean = 15 d, max = 36 d) and males (mean = 15 d, max = 29 d; Table 11). Pups had reduced residence times within PMSR (mean = 8 d, max = 23 d) compared with non-pups but greater residence times over the continental slope region (water depths <2,000 m) of this range (mean = 7 d, max = 18 d) than juvenile males (mean = 5 d, max = 13 d) and adult and juvenile females (mean and max <2 d).

During both tracking periods, Guadalupe fur seals primarily used the SOCAL Range Complex offshore of the continental slope but did not use the portion of this range >800 km from the North American coast. There was slightly greater use of the SOCAL Range in 2020 (50%) compared with 2018-2019 (42%) across groups (Table 10). The home ranges of adult and juvenile females overlapped with the SOCAL Range (34% and 32%, respectively) more than that of juvenile males (21%) and pups (28%) in 2020, with ≤10% of this over the continental slope region. Therefore, residence times in the SOCAL Range Complex were greater for adult females (mean = 17 d, max = 65 d) and juvenile females (mean = 16 d, max = 57 d) relative to pups and juvenile males (Table 11). Across groups, residence times were relatively short (<10 d for each individual) in the continental slope region (seafloor depth <2,000 m) of the SOCAL Range. Additionally, SOAR was used to a lesser extent in 2020 compared with 2018-2019, with 58% home range overlap (87% in 2018-2019) and a residence time of 3.4 d in SOAR (Tables 10-11).

In 2020, only two adult females, one juvenile female, and three juvenile males used habitats with water depths <2,000 m in one or more of the Navy ranges off the California coast (Figures 17-19). One juvenile male spent more time inshore of the 2,000 m depth contour within PMSR, SOCAL Range Complex, and SOAR than the others and may have briefly hauled out on San Clemente Island (Figure 19). Eleven pups used the continental slope region of PMSR with only four of these pups also using the continental slope of the SOCAL Range Complex (Figure 20).

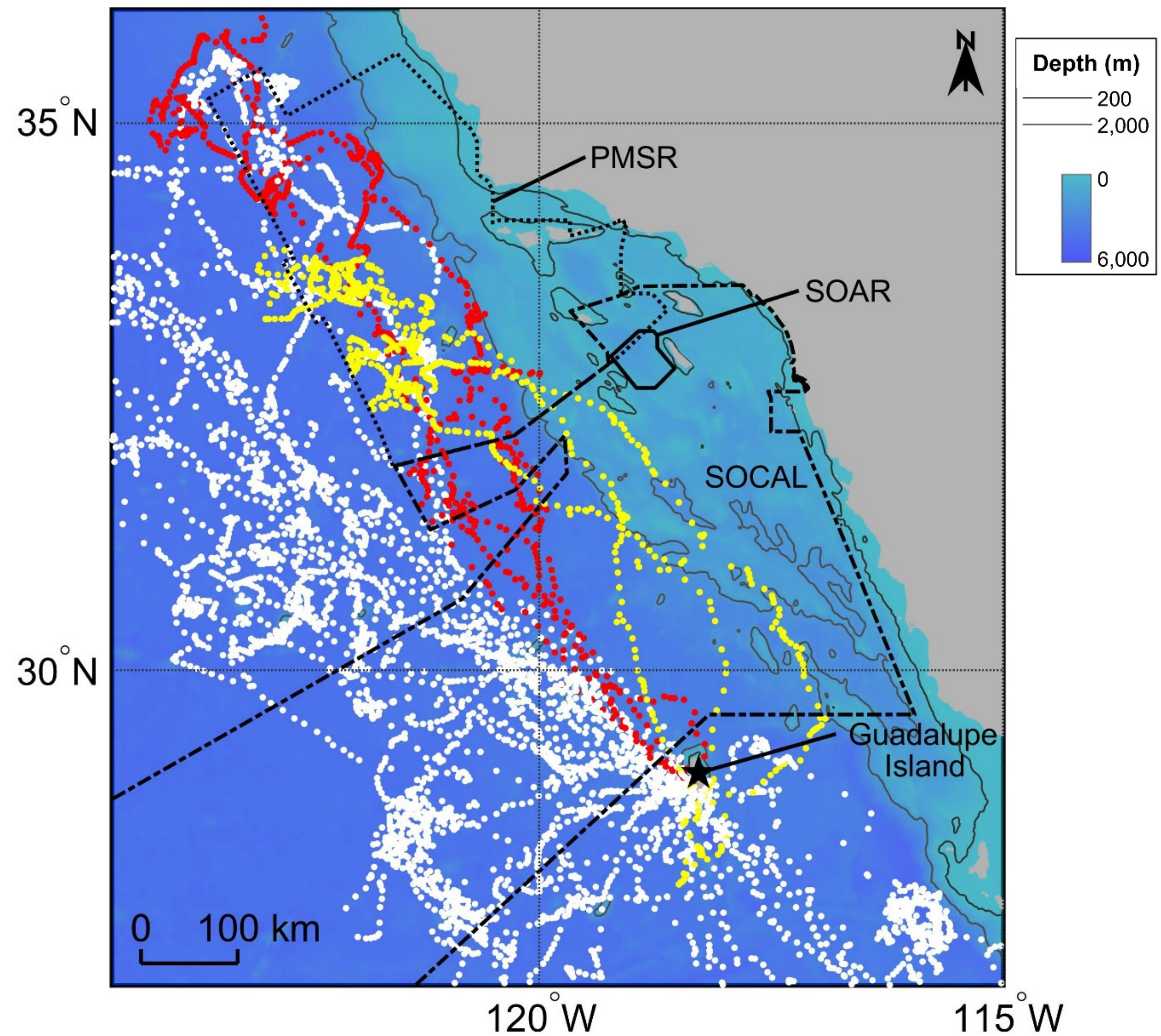

Figure 17. Three-hour interpolated locations for adult females tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations for the two females that used water depths <2,000 m within one or more of these Navy ranges are red and yellow for each of these seals, and locations for individuals that only used range areas farther offshore of the continental slope (>2,000 m water depth) or south of these ranges are white.

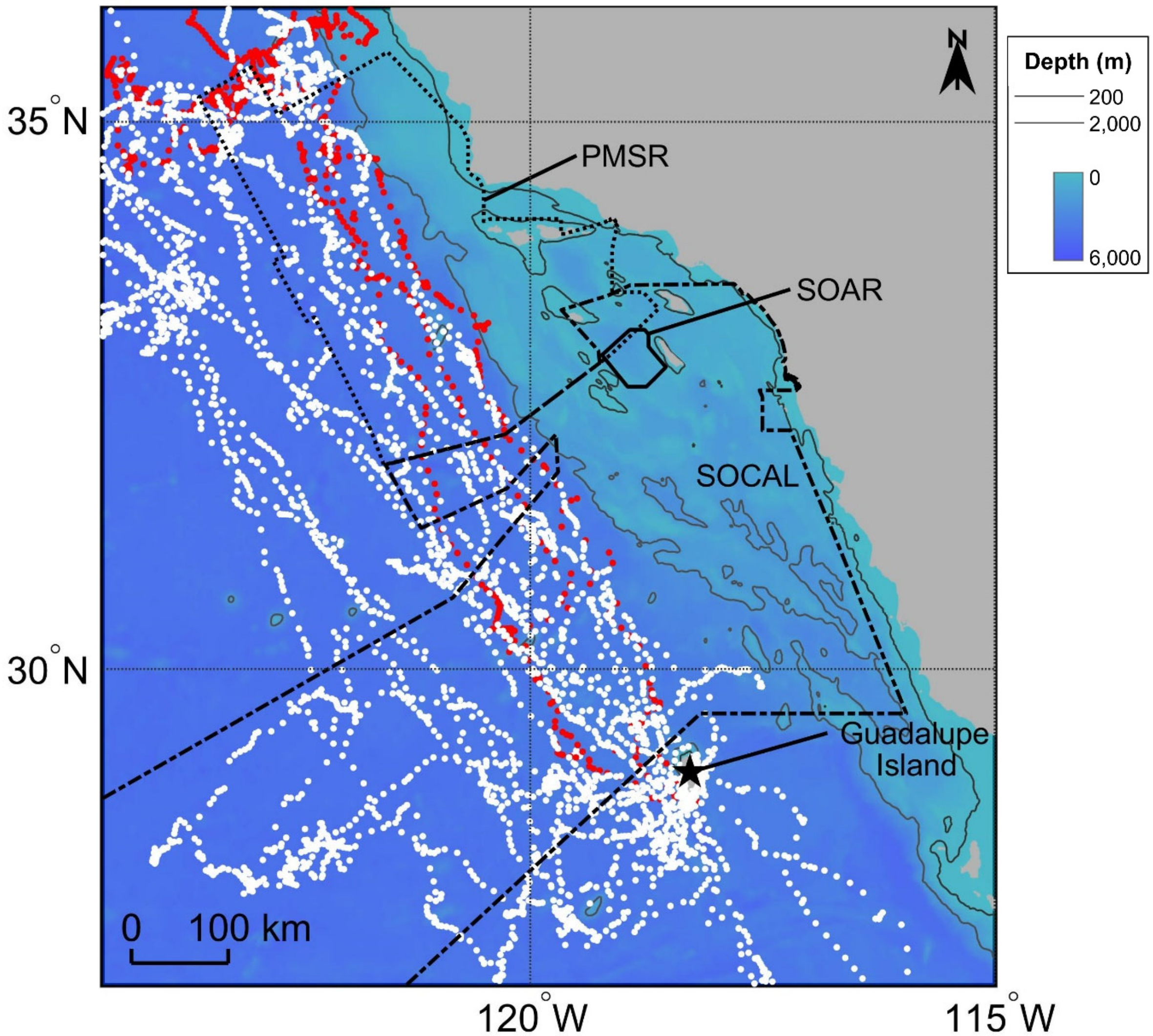

Figure 18. Three-hour interpolated locations for juvenile females tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations for the female that briefly used water depths <2,000 m within the PMSR are red, and locations for individuals that only used range areas farther offshore of the continental slope (>2,000 m water depth) or south of these ranges are white.

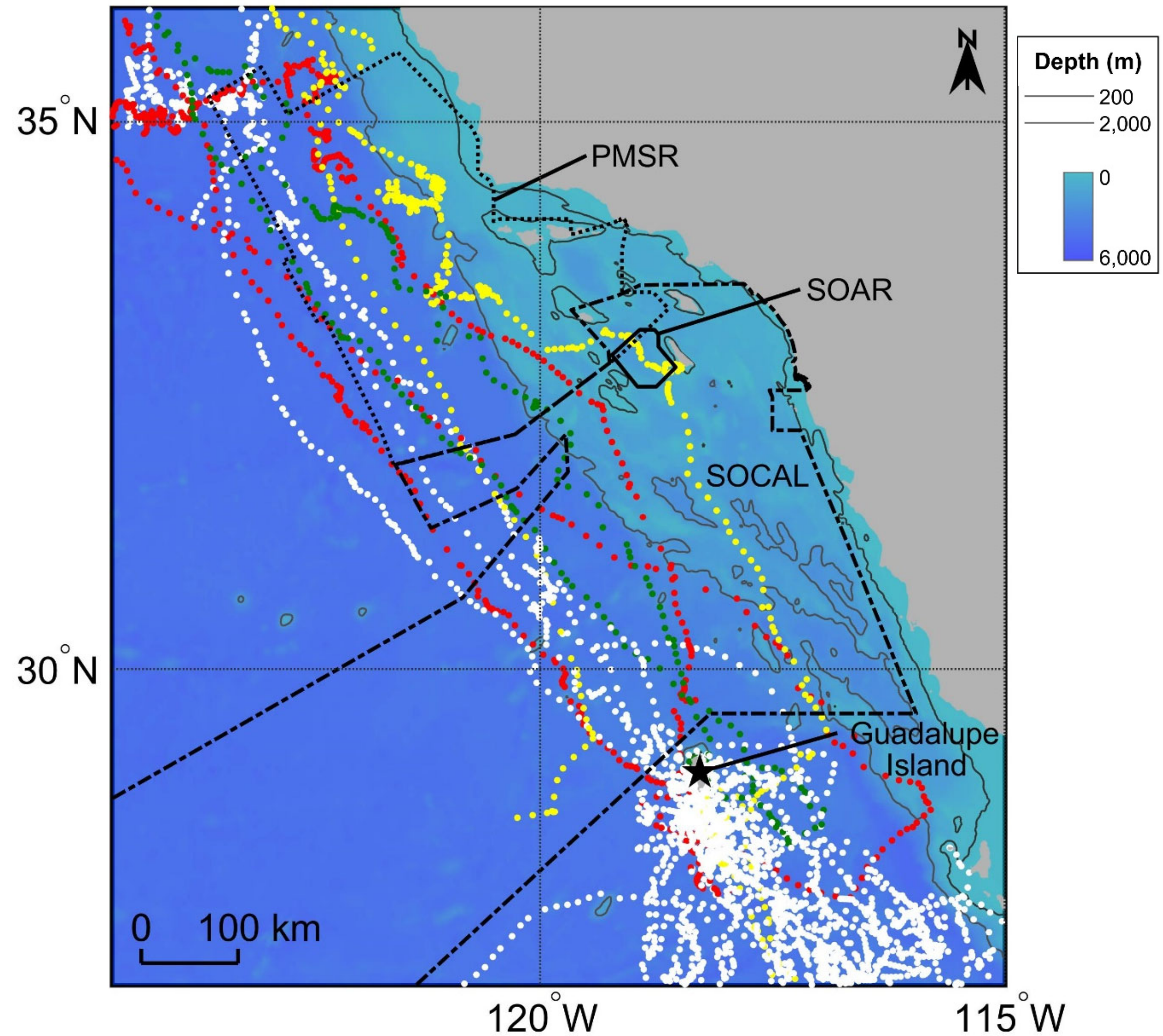

Figure 19. Three-hour interpolated locations for juvenile males tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations for the three males that used water depths <2,000 m within one or more of these Navy ranges are red, yellow, and green for each of these seals, and locations for individuals that only used range areas farther offshore of the continental slope (>2,000 m water depth) or south of these ranges are white.

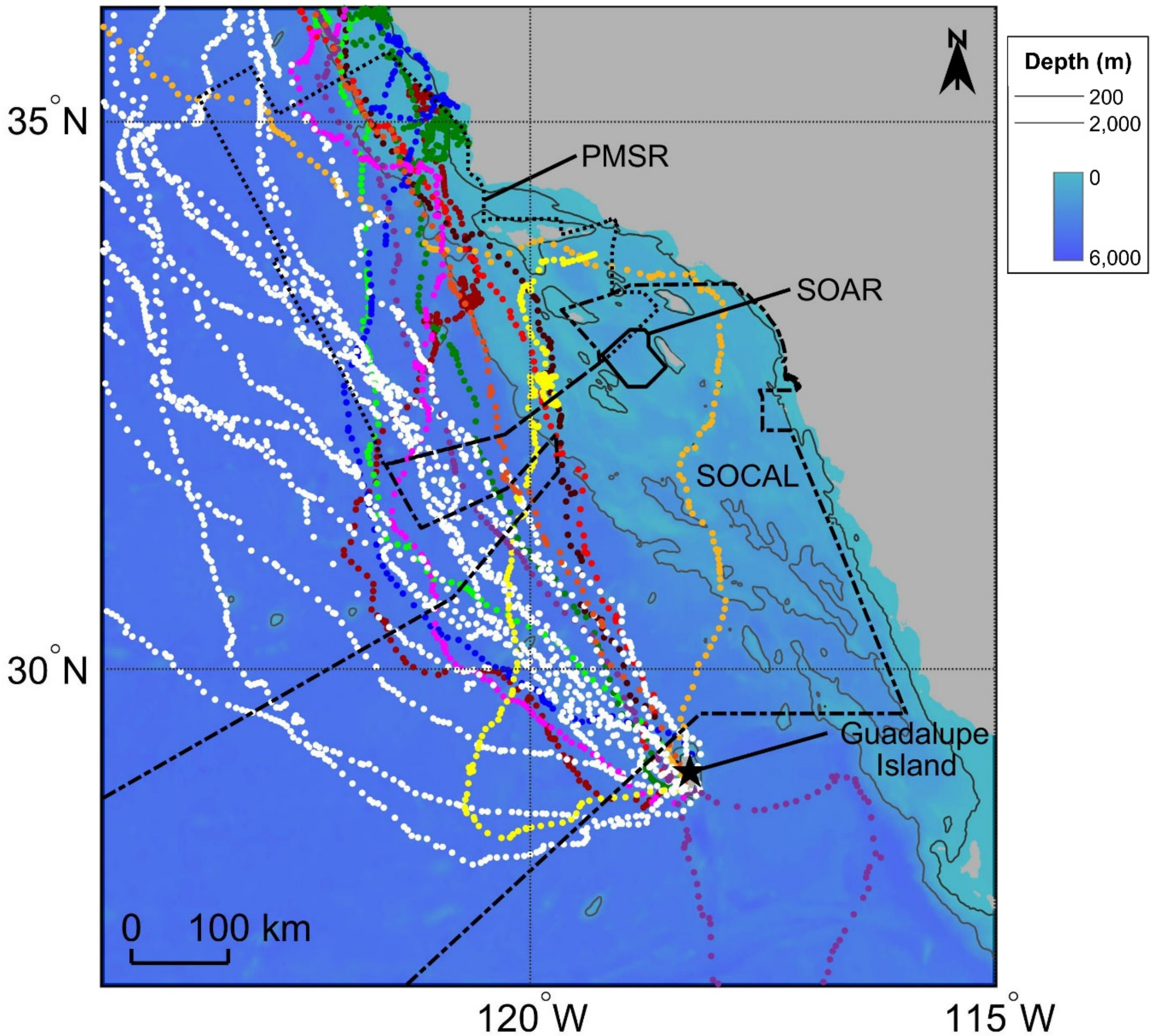

Figure 20. Three-hour interpolated locations for pups tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations for the 11 pups that used water depths <2,000 m within one or more of these Navy ranges are color-coded by individual, and locations for individuals that only used range areas farther offshore of the continental slope (>2,000 m water depth) are white.

Diving Behavior

There was a strong diel pattern in diving activity for all non-pups during both tracking periods, both in terms of the number of dives and depth of those dives (Figures 21-24). At least 90% of diving activity occurred during the night in 2020. In addition, 62% of dive messages from daytime hours contained no dives (*i.e.,* for the entire period, no dives exceeded 2 m in depth and 20 s in duration or the individual was on-land), although 15-24% of dives occurred during the day for six females (five adults and one juvenile).

Non-pups dove to similar depths across the two tracking periods, but there was slightly deeper diving in 2020 compared with 2018-2019, especially among juvenile seals. The majority of dives across all periods and individuals were <60 m (8.9 ± 1.3% of dives deeper than 60 m in 2020 and <8% of dives in 2018-2019). Also similar to 2018-2019, adult females more frequently dove deeper than juvenile fur seals in 2020. Approximately 30% of dives in the afternoon period were between 4-8 m for adult and juvenile females (Figures 22-23). Across all other periods, adult females most frequently dove to 20-30 m (28-32% of dives), whereas juvenile female diving was concentrated over a greater range of depths (11-21% of dives to each bin between 4-60 m) with slightly more diving to 20-60 m at night (17-19% of dives to each bin; Figures 22-23). Juvenile males most frequently dove to 4-8 m during both daytime periods (21% and 34% of dives). Similar to juvenile females, the diving of juvenile males was distributed across a broad range of depths at night (12-20% of dives to each bin between 4-60 m; Figure 24). Three adult females and one juvenile female logged 21-33% of dives >60 m, and three adult females and one juvenile male recorded dives >200 m.

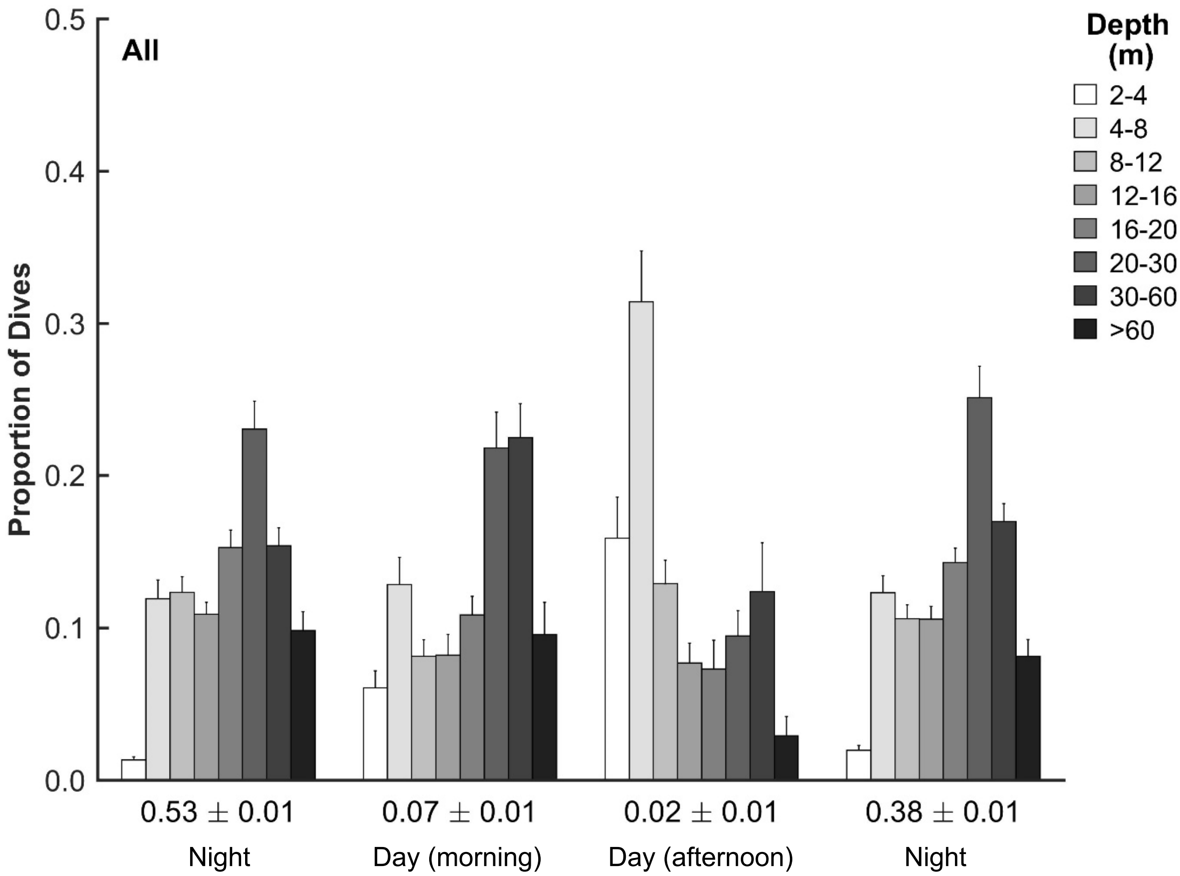

Figure 21. Proportion of dives to each depth bin across four 6-h periods for 35 adult and juvenile Guadalupe fur seals tracked in 2020. Mean ± SE proportion of dives per period provided along the x-axis.

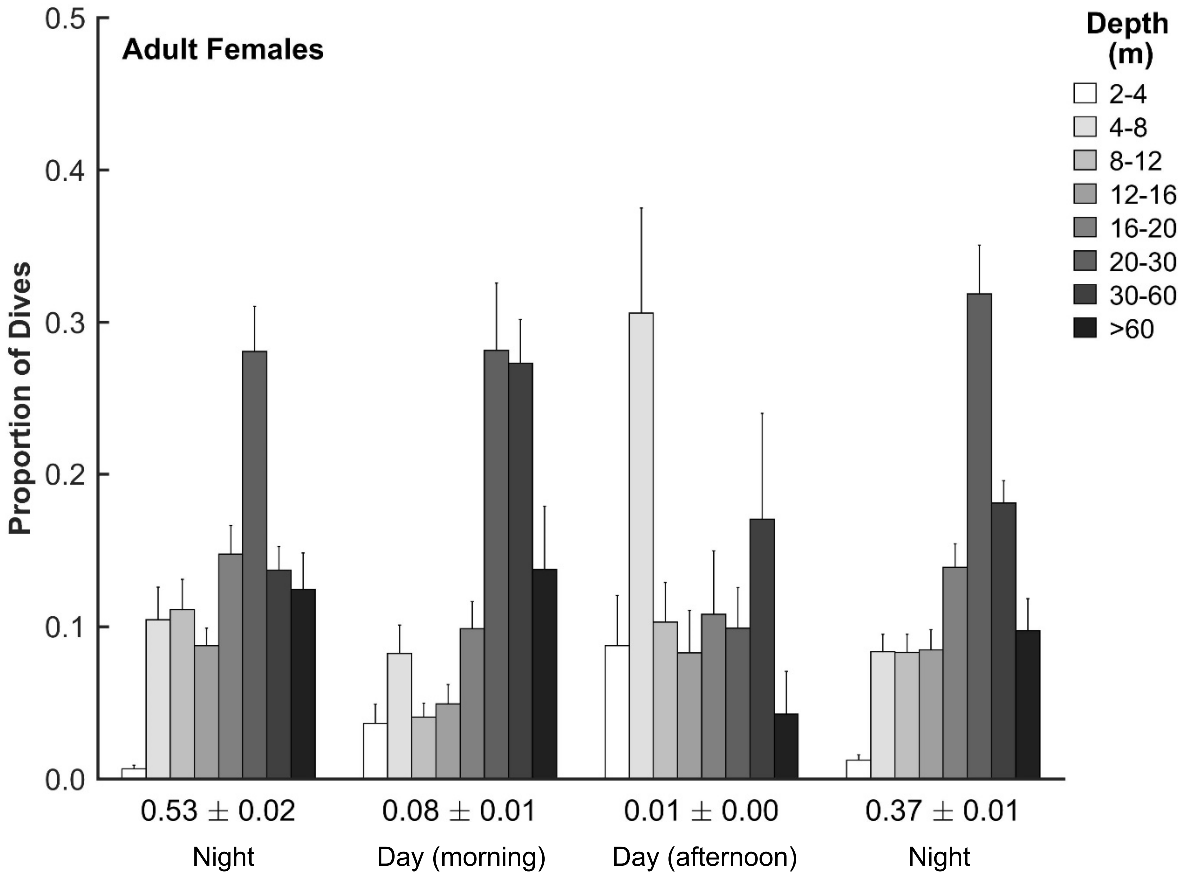

Figure 22. Proportion of dives to each depth bin across four 6-h periods for 15 adult female Guadalupe fur seals tracked in 2020. Mean ± SE proportion of dives per period provided along the x-axis.

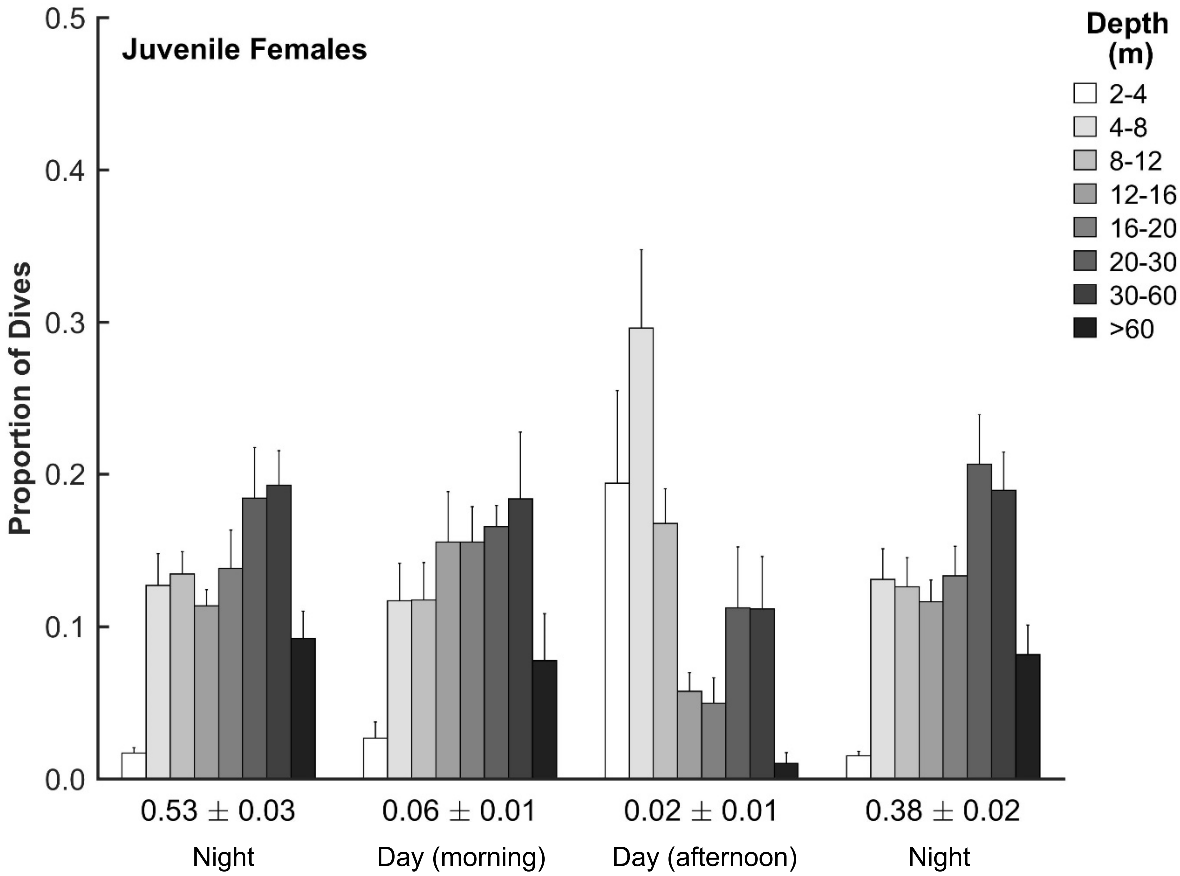

Figure 23. Proportion of dives to each depth bin across four 6-h periods for 10 juvenile female Guadalupe fur seals tracked in 2020. Mean ± SE proportion of dives per period provided along the x-axis.

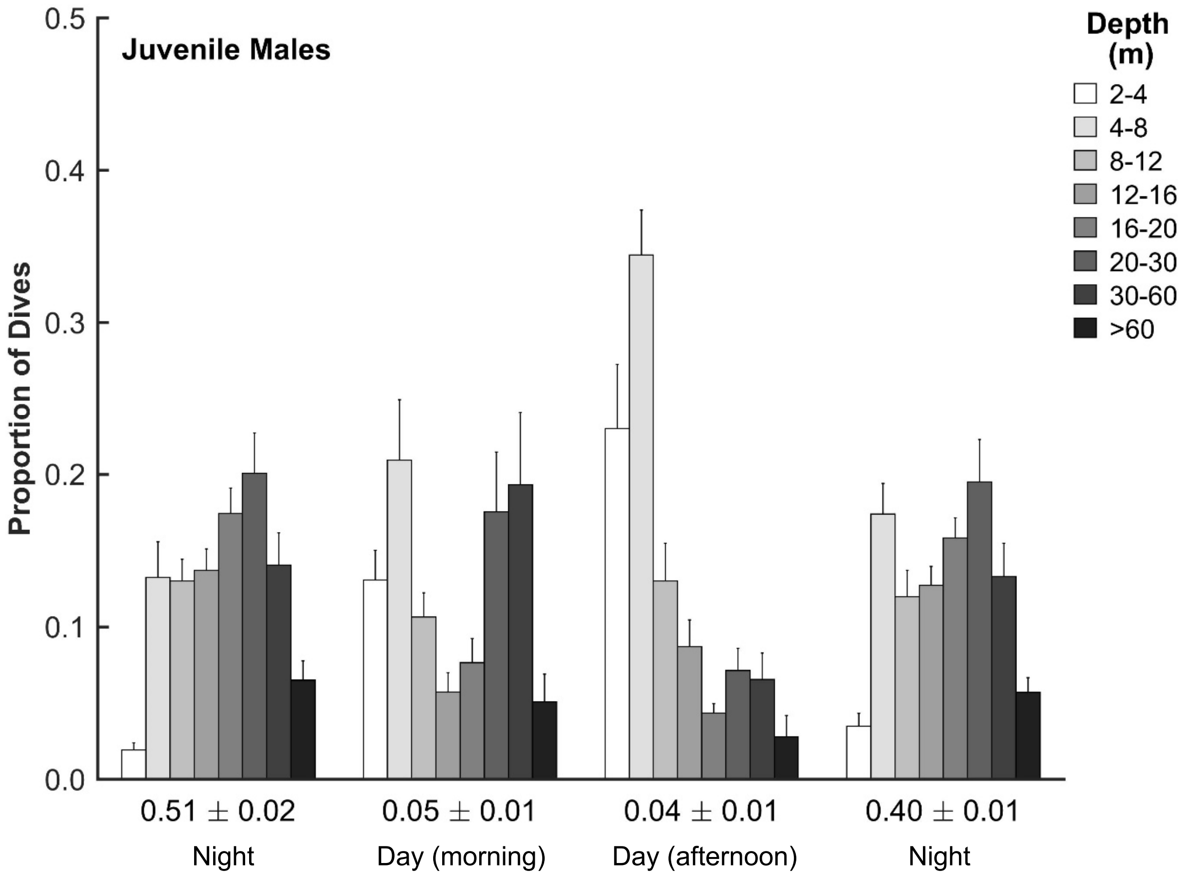

Figure 24. Proportion of dives to each depth bin across four 6-h periods for 10 juvenile male Guadalupe fur seals tracked in 2020. Mean ± SE proportion of dives per period provided along the x-axis.

Combining histogram dive data with the 3-h interpolated tracks highlighted that diving occurred along most portions of the individual tracks, which could be assessed when dive messages were received in series (Figures 25-29). Diving was not restricted to areas with greater use as indicated by the UDs, and many portions of the tracks categorized as having diving appeared to be periods where the animal was transiting based on the lack of directional changes along the path (*i.e.,* straight path over long distances; Figures 28-29). This was because diving activity was observed almost every night with few dives logged during the day. Most notably, although many non-pups appeared to primarily transit through the offshore area (>2,000 m water depth) of the SOCAL Range Complex, large numbers of dives to depths >8 m at night were observed along this transit corridor (Figures 25-29).

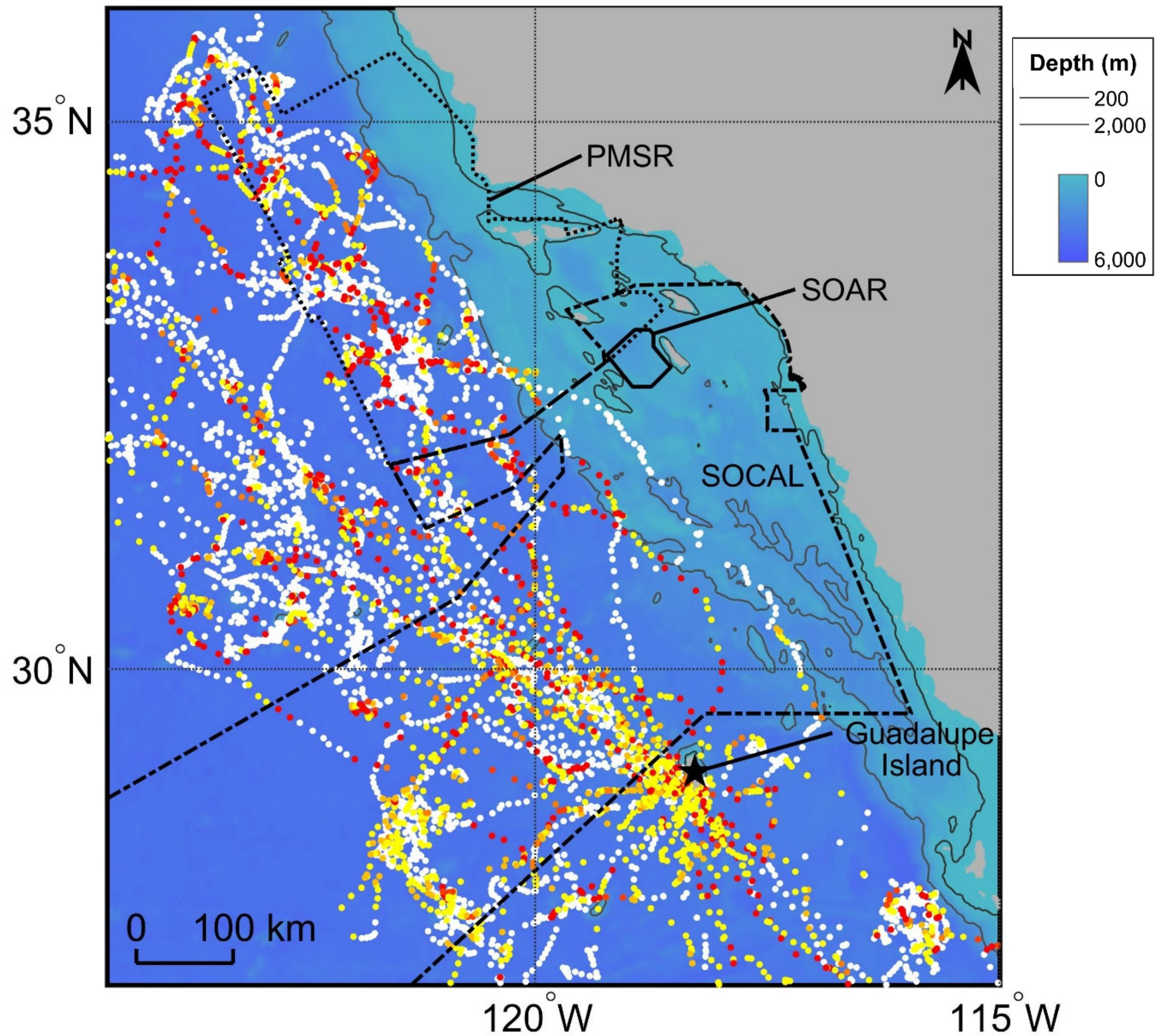

Figure 25. Dive histogram data integrated with 3-h interpolated locations for 15 adult females tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations with no associated dive data are white, and those with dive data are color coded from red to yellow. Locations with ≥50 dives to depths >8 m in a 6-h histogram period are red, and yellow locations had ≤10 dives >8 m in a 6-h histogram period (maximum of 332 dives in a 6-h period for all non-pups).

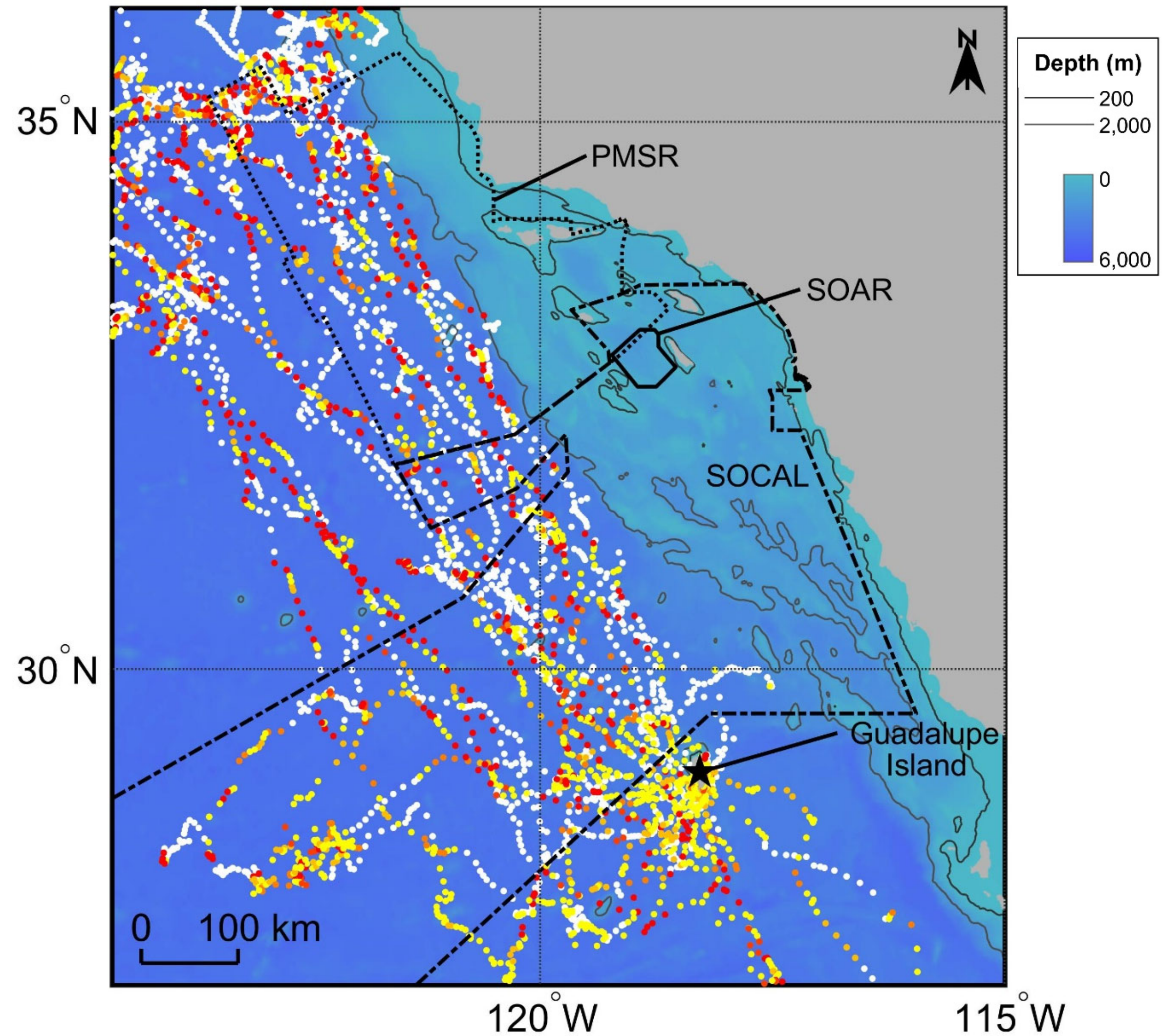

Figure 26. Dive histogram data integrated with 3-h interpolated locations for 10 juvenile females tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations with no associated dive data are white, and those with dive data are color coded from red to yellow. Locations with ≥50 dives to depths >8 m in a 6-h histogram period are red, and yellow locations had ≤10 dives >8 m in a 6-h histogram period (maximum of 332 dives in a 6-h period for all non-pups).

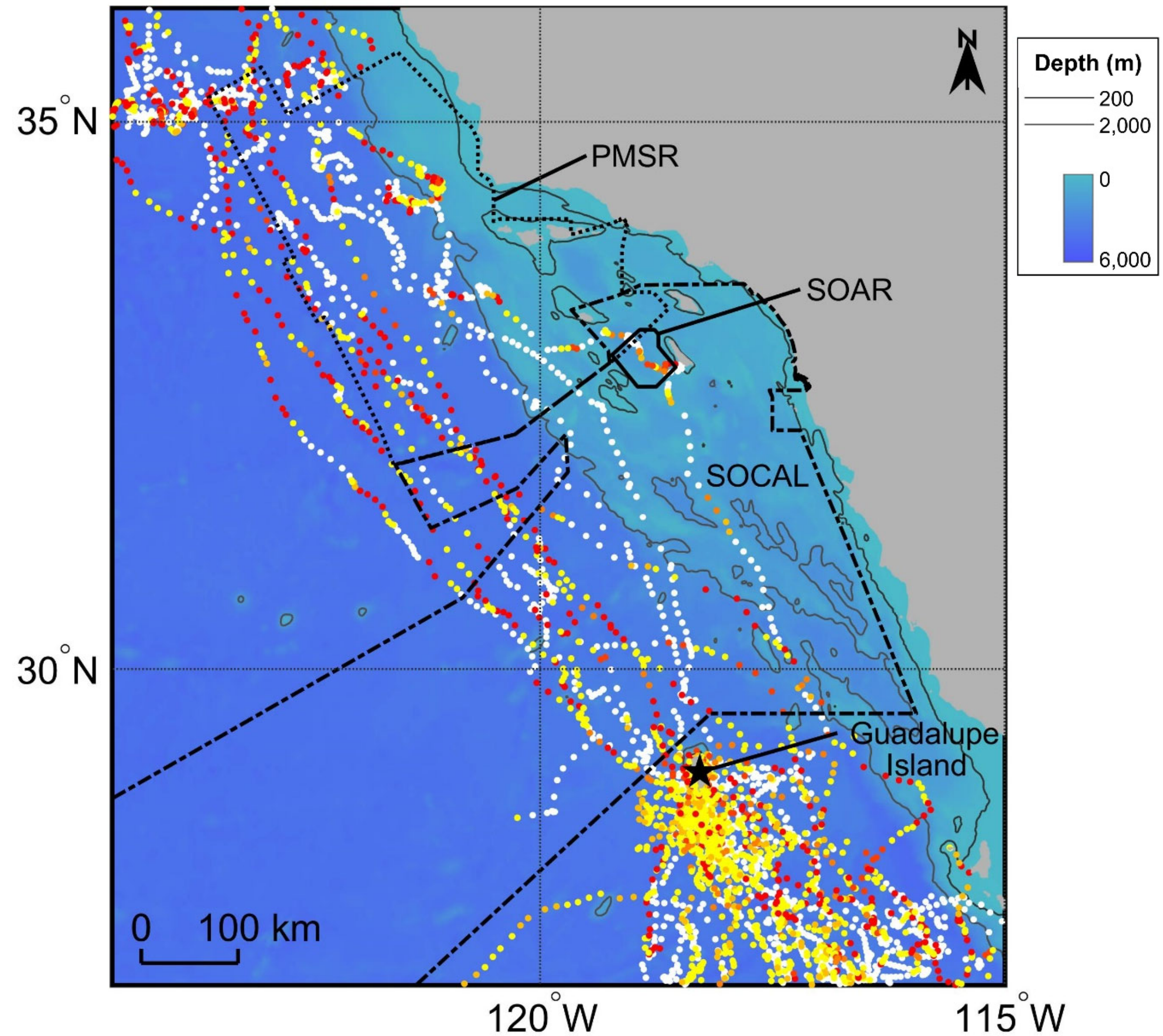

Figure 27. Dive histogram data integrated with 3-h interpolated locations for 10 juvenile males tracked in 2020 within and adjacent to three U.S. Navy ranges (black outlines). Locations with no associated dive data are white, and those with dive data are color coded from red to yellow. Locations with ≥50 dives to depths >8 m in a 6-h histogram period are red, and yellow locations had ≤10 dives >8 m in a 6-h histogram period (maximum of 332 dives in a 6-h period for all non-pups).

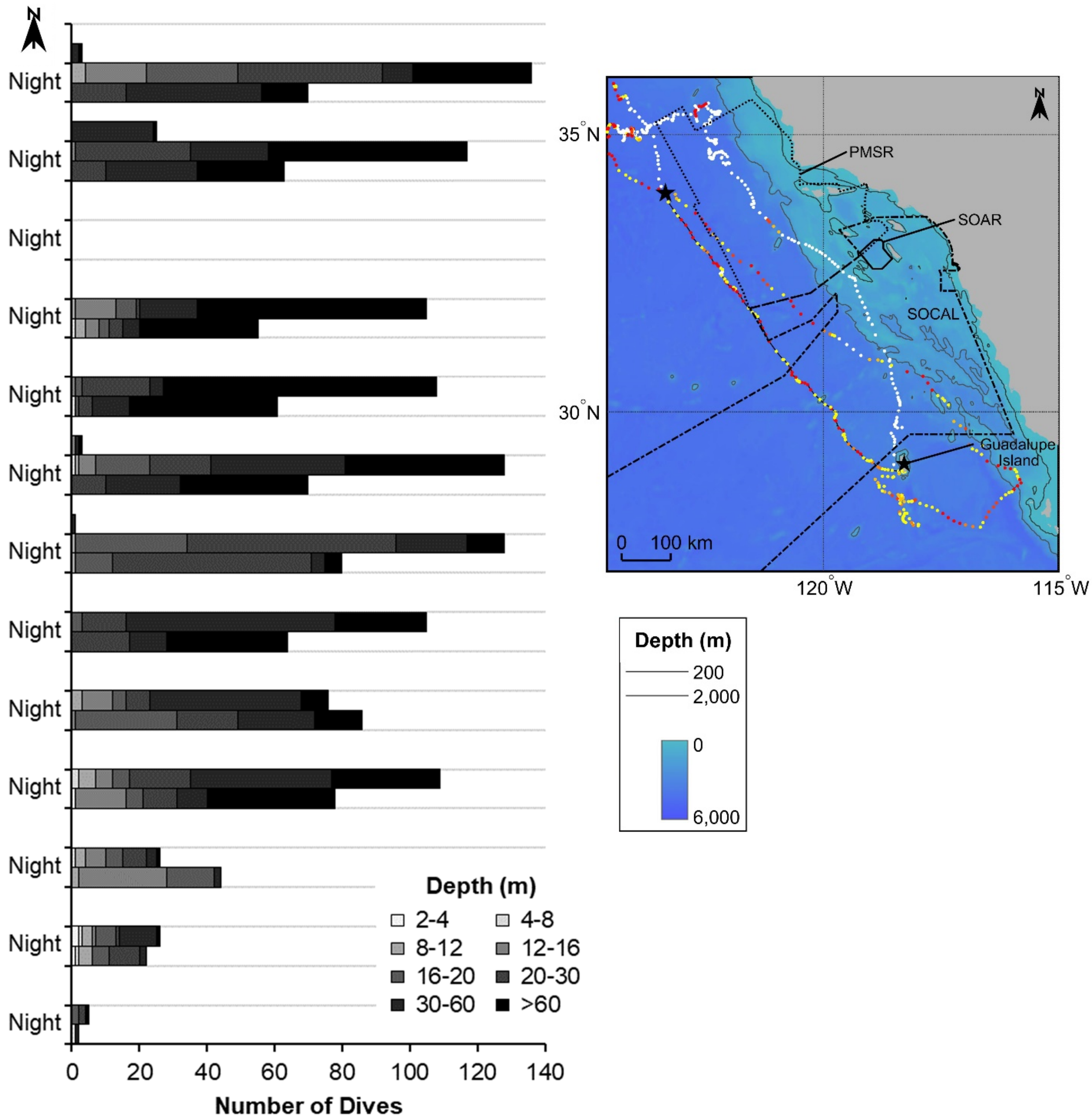

Figure 28. Example of the diel diving activity along a section of the 3-h interpolated track with directed, relatively straight travel for a juvenile male. Dive histograms are shown for the track section between the two black stars in the map, with top to bottom for the histograms corresponding to north to south for this track section that started on May 27th and ended on June 8th. Each stacked histogram represents the number of dives to each depth bin per 6-h period. Dive messages were received for all but three 6-h periods (two night periods with zero dives and an adjacent day period). Locations with no associated dive data are white, and those with dive data are color coded from red to yellow within and adjacent to three U.S. Navy ranges (black outlines in the map). Locations with ≥50 dives to depths >8 m in a 6-h histogram period are red, and yellow locations had ≤10 dives >8 m in a 6-h histogram period.

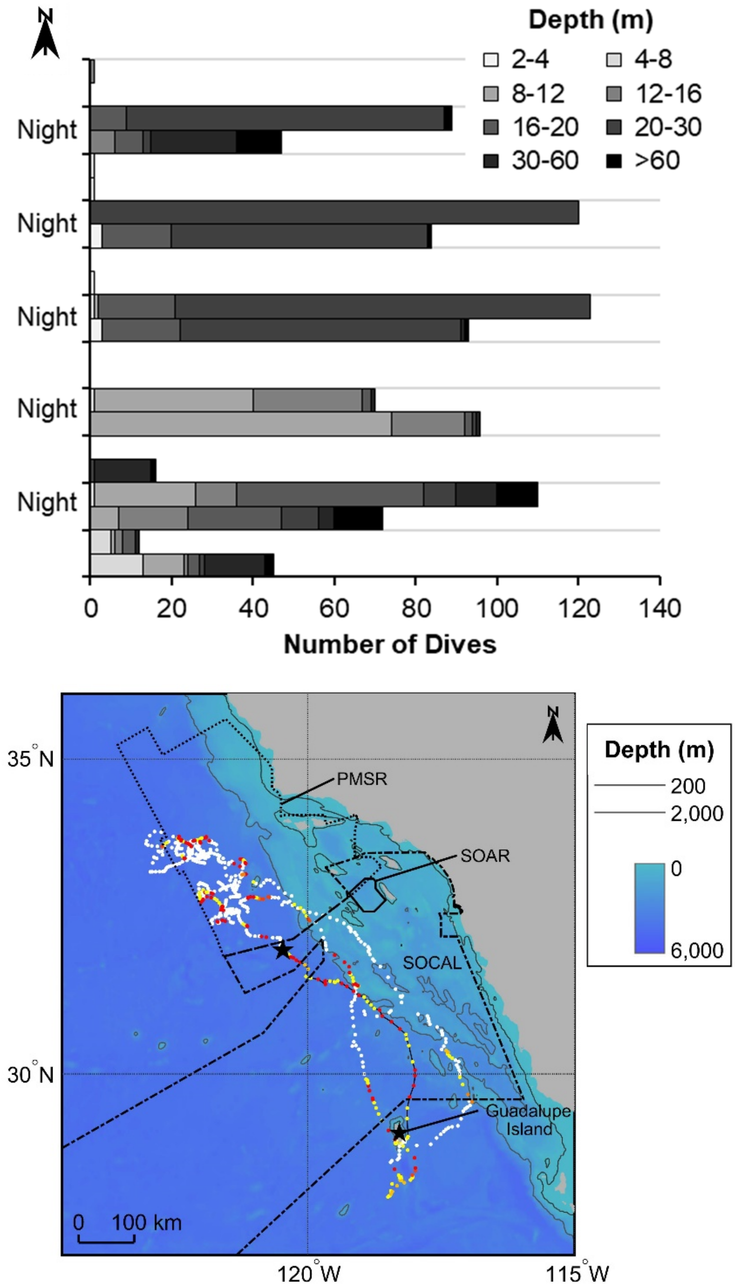

Figure 29. Example of the diel diving activity along a section of the 3-h interpolated track with directed, relatively straight travel for an adult female. Dive histograms are shown for the track section between the two black stars in the map, with top to bottom for the histograms corresponding to north to south for this track section that started on June 2nd and ended on June 7th. Each stacked histogram represents the number of dives to each depth bin per 6-h period. Dive messages were received for all 6-h periods. Locations with no associated dive data are white, and those with dive data are color coded from red to yellow within and adjacent to three U.S. Navy ranges (black outlines in the map). Locations with ≥50 dives to depths >8 m in a 6-h histogram period are red, and yellow locations had ≤10 dives >8 m in a 6-h histogram period.

Discussion and Conclusions

Population Trends

Similar to every other Guadalupe fur seal population monitoring survey at San Benito Archipelago since fur seals were rediscovered at this site in 1997, less than 30 mother-pup pairs were observed here in summer 2018 and 2019 (Aurioles-Gamboa et al. 2010, Elorriaga-Verplancken et al. 2016b, Maravilla-Chavez & Lowry 1999, Sierra-Rodríguez 2015). Therefore, San Benito Archipelago still is considered a recolonization site, and Guadalupe Island remains the only established rookery (breeding site) for the Guadalupe fur seal population, making this species particularly vulnerable to localized environmental perturbations, such as hurricanes. Emigration of animals from Guadalupe Island to San Benito Archipelago that occurred during the first phase of recolonization (Aurioles-Gamboa et al. 2010) may still occur with juveniles displaced to San Benito Archipelago from Guadalupe Island during the breeding season. However, only one individual juvenile male out of 40 juveniles tracked during the summer of 2017 and 2020 used both terrestrial sites (Norris et al. 2017a). The current exchange of Guadalupe fur seals between these two sites remains unknown as does the population-level impact of the recent decrease in abundance at San Benito Archipelago after 2009 when 5,271 individuals were observed at this site, especially because most animals at San Benito Archipelago are juvenile males.

In terms of overall abundance, population estimates for otariids frequently are extrapolated from pup counts (Berkson & DeMaster 1985). Greater than 99% of Guadalupe fur seal pups are born at Guadalupe Island. Prior to 2018, the last pup count was in 2013 when 4,924 pups were observed (García-Aguilar et al. 2018). This four-year data gap between 2014 and 2017 coincided with a period of persistent, widespread anomalously warm waters across the Northeast Pacific Ocean that caused unprecedented ecosystem-level effects (Cavole et al. 2016, McClatchie et al. 2016, Morgan et. al 2019, Sanford et al. 2019). Guadalupe fur seals were impacted by the 2014-2016 marine heatwave in ways that likely imply widespread population-level effects. These included increased strandings in California beginning in 2015, unprecedented records of emaciated individuals in the southern Gulf of California in 2015-2016, significantly decreased neonate weights and survival in 2015, and increased foraging effort of lactating females in 2015 (Amador-Capitanachi et al. 2020; Elorriaga-Verplancken et al. 2016a, 2016b; Gálvez et al. 2020; NOAA Fisheries 2020). Fur seal pups that stranded in 2015, the first year of the ongoing Guadalupe fur seal Unusual Mortality Event along the west coast of the U.S. (NOAA Fisheries 2020), were born in 2014, and many pinniped females first reproduce at an age of ~5 years old. Therefore, increased pup mortality in 2014-2015 would lead to an approximately five-year delay in decreased recruitment of breeding females and a corresponding decrease in the number of pups born in 2019. A 19.2% decrease in the number of pups counted at Guadalupe Island from 2018 to 2019 was observed during this study, but more adult females were sighted in 2019 relative to 2018. This decrease in pup counts did not appear to be related to increased neonate mortality because few dead pups were observed on the island in 2018 and 2019.

There were, however, changes in the distribution of fur seal density at Guadalupe Island in 2018 versus 2019 with ~2,800 fewer pups observed on low-visibility substrate along the east side of Guadalupe Island. It is possible that more pups were not detected on low-visibility substrate during boat-based surveys in 2019, possibly related to the windier and rougher sea conditions that forced the survey to occur slightly farther from shore and at faster speeds along sections of the coast in 2019. Approximately 2,800 more adult females were counted at Guadalupe Island in 2019, many of which were in the water (~1,800 more females in the water in 2019 compared with 2018), indicating that these females either had not given birth in 2019 or they had <1-month-old pups on land that possibly went undetected during the survey. With only two consecutive years of Guadalupe fur seal population monitoring, it is unknown if these 2018-2019 census data reflect possible unavoidable differences in methodologies, interannual fluctuations, and/or longer term abundance trends. Therefore, ongoing annual censuses are necessary to generate accurate and current population estimates and trends, especially given the anomalously warm waters that continue to persist in the Northeast Pacific (Leising & Bogard 2020).

Foraging Behavior, Habitat Use, and Navy Range Overlap

The foraging behavior and distribution of marine predators, such as the Guadalupe fur seal, change in response to intra- and inter-annual variations in prey resources (*e.g.*, Amador-Capitanachi et al 2020). Newly weaned individuals transitioning to independent foraging are particularly vulnerable to oceanographic conditions that decrease prey availability, including anomalously warm waters or marine heatwaves. During this study, all 25 fur seal pups, weaned in March or April 2020 and tracked until July 2020, traveled north into waters offshore of the U.S. west coast and southern Canada. These movements were similar to those of recently weaned free-ranging pups tracked March-May 2017 (n = 13) and those released after rehabilitation with a satellite tracking device at 11-15 months of age in 2015-2017 (n = 28; Norris et al. 2017a). However, as was the case for young, rehabilitated fur seals tracked in summer 2015, the pups tracked in 2020 as part of this study traveled farther north and remained closer to shore than the free-ranging and rehabilitated animals tracked in 2016 and 2017. Three of the largest marine heatwaves in the Northeast Pacific Ocean since 1982 were documented in these two years (2015 and 2020), as well as in 2019 (Gentemann et al. 2017, Leising & Bogard 2020). In 2019 and 2020, anomalously warm waters were concentrated farther offshore and mostly north of California compared with the 2014-2016 marine heatwave (Leising & Bogard 2020), which likely explains the greater number of Guadalupe fur seals that stranded in 2019-2020, especially in Oregon and Washington State. Therefore, these extreme warm water events in the Northeast Pacific may push young fur seals farther north and closer to shore into areas that are more heavily used by the U.S. Navy. Differences between free-ranging and rehabilitated animals, as well as short tracking periods for the 2017 free-ranging pups (36 ± 17 d), also may explain some of these interannual differences in pup distribution and habitat use. Because of these factors and the increasing frequency of severe marine heatwaves, additional tracking of newly weaned pups in subsequent years is needed to better understand their distribution and habitat use, especially in the NWTT Study Area. The pups' use of the NWTT Area likely was underestimated in 2020 given that most tags stopped transmitting while pups were in this Navy range, or before they reached this range and were still traveling north.

In contrast to the distribution of pups, adult female and juvenile fur seals rarely traveled north of Cape Mendocino (~40°N) during this study or in 2017 (Norris et al. 2017a). As a result, non-pups rarely used the NWTT Study Area in winter-spring (2018-2019) and spring-summer (2020; ≤3% overlap). However, adult female and juvenile Guadalupe fur seals have stranded along the coast of Oregon and Washington State, and there may be greater use of this Navy range, especially in different times of year, than indicated by the 85 non-pups tracked using telemetry instruments in 2017-2020. Adult females also were not nursing pups during most of the 2020 tracking period, from approximately April when most pups have weaned to July when females return to the island to give birth and breed. As a result, adult females did not have to return to Guadalupe Island for 3-4 months and traveled farther from the island for longer durations in 2020 compared with most adult females tracked in 2018-2019, which were nursing four- to nine-month-old pups throughout the tracking period. Additionally, many adult females traveled farther offshore (west of 130°W) in 2020 and may have utilized the North Pacific Transition Zone, a highly productive frontal zone spanning the North Pacific basin that migrates seasonally north to south between 30°N and 45°N (farther north in the summer) and is used by many marine predators (Polovina et al. 2001). This frontal zone did not appear to be used by adult females in 2018-2019 or juvenile animals during either tracking period but may be an important foraging area for adult females after their pups wean, as well as possibly at other times of the year and/or for other groups.

Across both tracking periods and all groups of seals, Guadalupe fur seal used 61-90% of PMSR and 18-34% of the SOCAL Range Complex. Although individual animals spent up to 63 d in PMSR and 65 d in the SOCAL Range Complex in 2020, mean residence times in each of these ranges were much shorter (<25 d) across all groups. Additionally, the more offshore distribution of adult and juvenile females in 2020, as well as a greater number of juvenile males traveling south of Guadalupe Island, resulted in reduced use of the portion of these ranges associated with greater Navy activity (water depths <2,000 m) in 2020 compared with 2018-2019. Nearshore areas of the SOCAL Range with water depths <2,000 m appear to be minimally used by Guadalupe fur seals, likely because these animals primarily travel from Guadalupe Island, an oceanic island ~240 km offshore of the west coast of the Baja California Peninsula, to areas north of Point Conception, and the Southern California Bight is less frequently used by this species. However, these results are from tracking across a single season each year, during periods with anomalously warm waters. Because marine predator at-sea distribution and movement patterns vary seasonally and interannually, especially with the increasing frequency of marine heatwaves, additional satellite tracking is necessary to better understand Guadalupe fur seal spatial use patterns and overlap with U.S. Navy ranges in the Northeast Pacific Ocean.

In 2018-2019 and 2020, non-pups almost exclusively used surface waters (≤2 m) during daytime hours with shallow diving, primarily <60 m, at night as this species feeds on squid and other prey that migrate vertically (Amador-Capitanachi et al. 2017, 2020; Gallo-Reynoso & Esperón-Rodríguez 2013; Juárez-Ruiz et al. 2018). There were relatively high concentrations of locations within some portions of the Navy ranges offshore of California, such as the SOCAL Range Complex northwest of Guadalupe Island, that appeared to be primarily linked to transiting to and from the island based on path straightness through the range, compared to greater path tortuosity and more intense spatial use farther north. However, there was diel diving activity, with almost all dives >8 m occurring at night, within this area, indicating these animals may be frequently engaging in foraging activity along this SOCAL Range Complex transit corridor and in other regions with directed, relatively straight travel over long distances. Therefore, a greater portion of the areas used by Guadalupe fur seals that overlap with U.S. Navy activity may be important for foraging. Further analyses are needed to determine the factors, such as mesoscale oceanographic features (*e.g.,* fronts and eddies), that influence the vertical and horizontal behavior and habitat use of Guadalupe fur seals across the California Current System.

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Literature Cited

Amador-Capitanachi, M. J., Moreno-Sánchez, X. G., Ventura-Domínguez, P. D., Juárez-Ruiz, A., González, 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.

Amador-Capitanachi, M. J., Moreno-Sánchez, X. G., Juárez-Ruiz, A., Ferretto, G., & Elorriaga-Verplancken, F. R. (2017). Trophic Variation Between the Two Existing Guadalupe Fur Seal Colonies on Guadalupe Island and the San Benito Archipelago, Mexico. *Aquatic Mammals*, *43*(1).

Argos, C. L. S. (2016). Argos user's manual: worldwide tracking and environmental monitoring by satellite. Retrieved from: http://www.argos-system.org/wp-content/uploads/2016/08/r363_9_argos_users_manual-v1.6.6.pdf.

Aurioles-Gamboa, D., Elorriaga-Verplancken, F. R., & Hernández-Camacho, C. J. (2010). The current population status of Guadalupe fur seal (*Arctocephalus townsendi*) on the San Benito Archipelago, Mexico. *Marine Mammal Science, 26(2)*, 402-408.

Aurioles-Gamboa, D., Hernández-Camacho, C. J., & Rodríguez-Krebs, E. (1999). Notes on the southernmost records of the Guadalupe fur seal, *Arctocephalus townsendi*, in Mexico. *Marine Mammal Science, 15*(2), 581-583.

Baker, J. D. (2007). Post-weaning migration of northern fur seal *Callorhinus ursinus* pups from the Pribilof Islands, Alaska. *Marine Ecology Progress Series*, *341*, 243-255.

Baker, J. D., Antonelis, G. A., Fowler, C. W., & York, A. E. (1995). Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour*, *50*(1), 237-247.

Bazzino, G., Gilly, W. F., Markaida, U., Salinas-Zavala, C. A., & Ramos-Castillejos, J. (2010). Horizontal movements, vertical-habitat utilization and diet of the jumbo squid (*Dosidicus gigas*) in the Pacific Ocean off Baja California Sur, Mexico. *Progress in Oceanography*, *86*(1-2), 59-71.

Berkson, J. M., & DeMaster, D. P. (1985). Use of pup counts in indexing population changes in pinnipeds. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(5), 873-879.

Call, K. A., Ream, R. R., Johnson, D., Sterling, J. T., & Towell, R. G. (2008). Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(16-17), 1883-1896.

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. (2016). Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: Winners, losers, and the future. *Oceanography*, *29*(2), 273-285.

Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, *6*(11), 1042-1047.

Dujon, A. M., Lindstrom, R. T., & Hays, G. C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods in Ecology and Evolution*, *5*, 1162-1169.

Elorriaga-Verplancken, F. R., Rosales-Nanduca, H., & Robles-Hernández, R. (2016a). Unprecedented records of Guadalupe fur seals in La Paz Bay, southern Gulf of California, Mexico, as a possible result of warming conditions in the Northeastern Pacific. *Aquatic Mammals*, *42*(3), 261-267.

Elorriaga-Verplancken, F. R., Sierra-Rodríguez, G. E., Rosales-Nanduca, H., Acevedo-Whitehouse, K., & Sandoval-Sierra, J. (2016b). 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, Mexico. *PloS One*, *11*(5), e0155034.

Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science, 24*(2), 315-325.

Gallo-Reynoso, J. P. (1994). Factors affecting the population status of Guadalupe fur seal, *Arctocephalus townsendi* (Merriam, 1897), at Isla de Guadalupe, Baja California, Mexico. Doctoral dissertation, University of California, Santa Cruz. Santa Cruz, CA.

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.

Gallo-Reynoso, J. P., Figueroa-Carranza, A. L., & Le Boeuf, B. J. (2008). Foraging behavior of lactating Guadalupe fur seal females. Avances en el Estudio de los Mamíferos de México, C. Lorenzo, E. Espinoza and J. Ortega (eds.). *Publicaciones Especiales, 2*, 595-614.

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*, 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.

García-Capitanachi, B., Schramm, Y., & Heckel, G. (2017). Population fluctuations of Guadalupe fur seals (*Arctocephalus philippii townsendi*) between the San Benito Islands and Guadalupe Island, Mexico, during 2009 and 2010. *Aquatic Mammals, 43*(2), 492-500.

Gentemann, C. L., Fewings, M. R., & García-Reyes, M. (2017). Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophysical Research Letters*, *44*(1), 312-319.

Gilly, W. F., Markaida, U., Baxter, C. H., Block, B. A., Boustany, A., Zeidberg, L., Reisenbichler, K., Robison, B., Bazzino, G., & Salinas, C. (2006). Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series*, *324*, 1-17.

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.

Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., & Bograd, S. J. (2016). Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters*, *43*(13), 7072-7080.

Jonsen, I. D., Myers, R. A., & James, M. C. (2007). Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, *337*, 255-264.

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, Mexico. *Marine Biology*, *165*(5), 86.

Keating, K. A., & Cherry, S. (2009). Modeling utilization distributions in space and time. *Ecology*, *90*(7), 1971-1980.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J.M., & Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2221-2231.

Lambourn, D. M., Jefferies, S. J., Wilkinson, K., Huggins, J., Rice, J., Duffield, D., & Raverty, S. A. (2012). *2007-2009 Pacific Northwest Guadalupe fur seal (Arctocephalus townsendi) Unusual Mortality Event (UME) summary repor*t. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Lander, M. E., Gulland, F. M., & DeLong, R. L. (2000). Satellite tracking a rehabilitated Guadalupe fur seal (*Arctocephalus townsendi*). *Aquatic Mammals, 26*(2), 137-142.

Leising, A. & Bograd, S. (2020). The California Current marine heatwave tracker – an experimental tool for tracking marine heatwaves. Retrieved from: https://www.integratedecosystemassessment.noaa.gov/regions/california-current/cc-projects-blobtracker

Leising, A. W., Schroeder, I. D., Bograd, S. J., Abell, J., Durazo, R., Gaxiola-Castro, G., Bjorkstedt, E. P., Field, J., Sakuma, K., Robertson, R. R., & Goericke, R. (2015). State of the California Current 2014-15: Impacts of the Warm-Water" Blob". *California Cooperative Oceanic Fisheries Investigations Reports*, *56*.

Maravilla-Chavez, M. O., & Lowry, M. S. (1999). Incipient breeding colony of Guadalupe fur seals at Isla Benito del Este, Baja California, Mexico. *Marine Mammal Science*, *15*(1), 239-241.

Maxwell, S. M., Breed, G. A., Nickel, B. A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell, R. J., Formia, A., Ngouessono, S., Godley, B. J., Costa, D. P., Witt, M. J., & Coyne, M. S. (2011). Using satellite tracking to optimize protection of long-lived marine species: olive ridley sea turtle conservation in Central Africa. *PLoS One, 6*(5), e19905.

Maxwell, S. M., Hazen, E. L., Bogard, S. J., Halpern, B. S., Breed, G. A., Nickel, B., Teutschel, N. M., Crowder, L. B., Benson, S., Dutton, P. H., Bailey, H., Kappes, M. A., Kuhn, C. E., Weise, M. J., Mate, B., Shaffer, S. A., Hassrick, J. L., Henry, R. W., Irvine, L., McDonald, B. I., Robinson, R. W., Block, B. A., & Costa, D. P. (2013). Cumulative human impacts on marine predators. *Nature Communications,* 4, 2688.

McClatchie, S., Field, J., Thompson, A. R., Gerrodette, T., Lowry, M., Fiedler, P. C., Watson, W., Nieto, K. M., & Vetter, R. D. (2016). Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science*, *3*(3), 150628.

McConnell, B. J., Chambers, C., & Fedak, M. A. (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science, 4*(4), 393-398.

Morgan, C. A., Beckman, B. R., Weitkamp, L. A., & Fresh, K. L. (2019). Recent ecosystem disturbance in the Northern California Current. *Fisheries*, *44*(10), 465-474.

NOAA Fisheries. (2020). 2015-2020 Guadalupe fur seal Unusual Mortality Event in California, Oregon, and Washington. Retrieved from: https://www.fisheries.noaa.gov/national/marine-life-distress/2015-2020-guadalupe-fur-seal-unusual-mortality-event-california

NOAA National Geophysical Data Center. (2009). ETOPO1 1 Arc-Minute Global Relief Model. NOAA National Centers for Environmental Information. doi:10.7289/V5C8276M

Norma Oficial Mexicana Secretaría de Medio Ambiente y Recursos Naturales. (2010). *Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión cambio.* Lista de especies en riesgo. Diario Oficial de la Federación; NOM-059-SEMARNAT-2010.

Norris, T., DeRango, G., DiGiovanni, R., & Field, C. (2015). Distribution of and threats to Guadalupe fur seals off the California coast. Paper presented at the 21st Biennial Conference on the Biology of Marine Mammals, San Francisco, CA.

Norris, T. A., & Elorriaga-Verplancken, F. R. (2019). Guadalupe Fur Seal Population Census and Tagging in Support of Marine Mammal Monitoring Across Multiple Navy Training Areas in the Pacific Ocean, 2018-2019. Technical Report. Prepared for Commander, Pacific Fleet, Environmental Readiness Division. Submitted to Naval Facilities Engineering Command (NAVFAC) Southwest, Environmental Corp, San Diego, CA 9213, under Contract No. N62473-18-2-004.

Norris, T., Fauquier, D., Field, C., Whoriskey, S., Gálvez, C., Rowles, T., Viezbicke, J., & Elorriaga-Verplancken, F. R. (2017a). At-sea distribution and habitat use of free-ranging and rehabilitated Guadalupe fur seals. Paper presented at the 6th International Bio-logging Science Symposium, Konstanz, Germany.

Norris, T. A., Littnan, C. L., Gulland, F. M., Baker, J. D., & Harvey, J. T. (2017b). An integrated approach for assessing translocation as an effective conservation tool for Hawaiian monk seals. *Endangered Species Research, 32*, 103-115.

Oliver, E. C., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Gupta, A. S., Hobday, A. J., & Holbrook, N. J. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*(1), 1-12.

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.

Peterson, W. T., Fisher, J. L., Strub, P. T., Du, X., Risien, C., Peterson, J., & Shaw, C. T. (2017). The pelagic ecosystem in the Northern California Current off Oregon during the 2014–2016 warm anomalies within the context of the past 20 years. *Journal of Geophysical Research: Oceans*, *122*(9), 7267-7290.

Polovina, J. J., Howell, E., Kobayashi, D. R., & Seki, M. P. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography*, *49*(1-4), 469-483.

Rosenbaum, H. C., Maxwell, S. M., Kershaw, F., & Mate, B. (2014). Long-Range Movement of Humpback Whales and Their Overlap with Anthropogenic Activity in the South Atlantic Ocean. *Conservation Biology, 28*(2), 604-615.

Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H., & Largier, J. L. (2019). Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports*, *9*(1), 4216.

Seagars, D. J. (1984). *The Guadalupe fur seal: a status review*. National Marine Fisheries Service, Southwest Region. Administrative Report. SWR-84-6.

Sierra-Rodríguez G.E. (2015). Recolonización y hábitos alimentarios maternos del lobo fino de Guadalupe (*Arctocephalus philippii townsendi*) del Archipiélago San Benito, BC, México.

MSc thesis, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, BCS.
Stewart, B. (1981). The Guadalupe fur seal (*Arctocephalus townsendi*) on San Nicolas Island, California. *Bulletin of the Southern California Academy of Sciences, 80*(3), 134-136.
Tremblay, Y., Shaffer, S. A., Fowler, S. L., Kuhn, C. E., McDonald, B. I., Weise, M. J., Bost, C. A., Weimerskirch, H., Crocker, D. E., Goebel, M. E., & Costa, D. P. (2006). Interpolation of animal tracking data in a fluid environment. *Journal of Experimental Biology, 209*(1), 128-140.
Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology*, *72*(4), 1253-1266.
U.S. Department of the Navy. (2015). *Commander Task Force 3rd and 7th Fleet Navy Marine Species Density Database.* NAVFAC Pacific Technical Report. Naval Facilities Engineering Command Pacific, Pearl Harbor, HI.
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.