

Guadalupe fur seal pup production predicted from annual variations of sea surface temperature in the southern California Current Ecosystem

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We evaluated the effects of sea surface temperature anomalies (SST_A) in the southern California Current Ecosystem on the annual Guadalupe fur seal (*Arctocephalus townsendi*) pup production, a species recovering from near extinction. Pup counts from 1991 to 1993 and from 2006 to 2019 were used to estimate deviations from a long-term trend as a proxy for the population's reproductive success. We estimated interannual SST_A as a subtraction from the linear trend spanning 1991–2019 for a 778,000 km² area, which represents the primary foraging range of adult females. The long-term increase in pup production followed an exponential curve ($R_B^2 = 1$), typical of species in a recovery phase. Pup production deviations from this trend responded to SST_A during the gestation period as a cubic polynomial function ($R_B^2 = 0.837$), revealing that SST_A < −0.2°C and between ~0.6 and 1.38°C increased pup production in the subsequent breeding season, whereas normal to slightly warm (−0.17 to 0.6°C) and extreme SST_A (>1.4°C) decreased pup counts, arguably resulting from low prey availability and quality. This model allowed us to estimate pup production for years without observations, needed to understand the environmental variability influence on the recovery process of this species, and therefore constitutes a practical tool for its conservation and management.

Keywords: bottom-up effect, hierarchical Bayesian analyses, oceanic predators, population trends, sea surface temperature effects.

Introduction

The understanding of population growth dynamics has made clear that extrinsic factors, like environmental variability, can explain better the increase or decrease of a population than by using life-history parameters only (Wade, 2018). Changes in sea surface temperature are strongly related to fecundity and survival of several otariid species, due to the cascade effect that modulates the food availability (Forcada *et al.*, 2005). In the California Current Ecosystem (CCE), warm interannual anomalies and warm phases of the Pacific decadal oscillation (Sánchez-Pérez *et al.*, 2021) increase the water column stratification, limiting upward nutrient transport close to the surface and reducing upwelling intensity, making it biologically less efficient (Xiu *et al.*, 2018). As a consequence, coastal and offshore regions experience a shift from a highly productive, diatom-dominated regime to a less productive food-web dominated by small phytoplankton (<5 µm in diameter, e.g. dinoflagellates; St. John, 2001; Xiu *et al.*, 2018). In southern CCE, stratification reduce aerobic habitat generating an expansion of prey distributions, like that of northern an-

chovy (*Engraulis mordax*), offshore and northward (Howard *et al.*, 2020). In response to these changes, top predators such as the California sea lion (*Zalophus californianus*) and the Guadalupe fur seal (*Arctocephalus townsendi*) perform more oceanic foraging trips and expand their trophic niche (Weise *et al.*, 2006; Elorriaga-Verplancken *et al.*, 2016).

The Guadalupe fur seal has oceanic feeding habits and feeds mainly on squid, with <15% of its diet composed of mesopelagic fish (Gallo-Reynoso and Esperón-Rodríguez, 2013). Currently, the Guadalupe fur seal is endemic to the CCE, but historically, it was distributed from Ozette in the northwest Washington coast to the Revillagigedo Archipelago (Figure 1a) in the northeast Pacific Ocean (Fleischer, 1978; Etnier, 2002). However, the intense hunting for its fur from the late 1800s to the early 1900s almost led to its extinction (Townsend, 1924; Hamilton, 1951; Hubbs, 1956). Currently, there is a single reproductive colony on Guadalupe Island (29°01'42"N 118°17'30"W), an oceanic island 260 km off the west coast of Baja California, Mexico; although some births have been documented in the San Benito Archipelago,

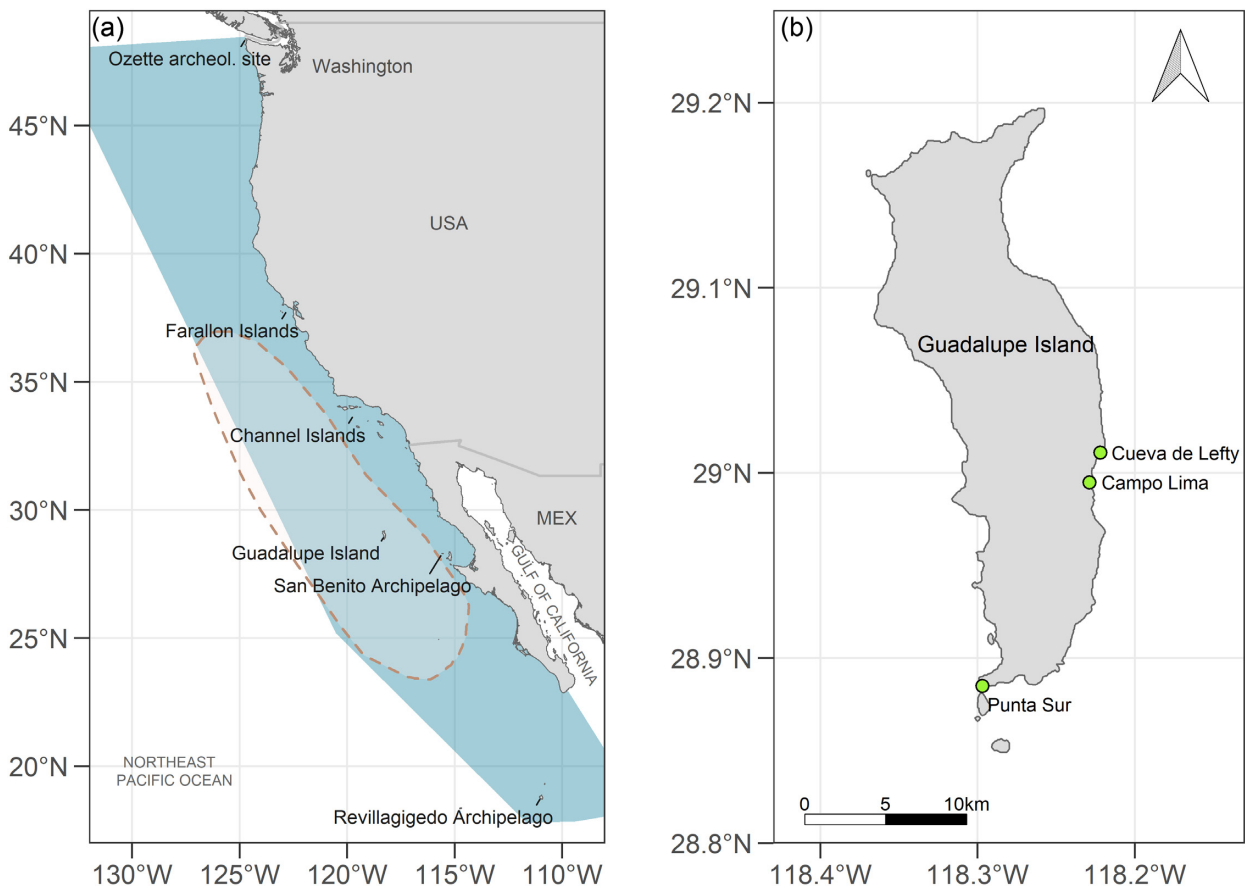


Figure 1. Foraging area and terrestrial habitat of Guadalupe fur seals. (a) Delimitation of the foraging area of Guadalupe fur seal adult females (represented by the dashed line and the pink-shaded area), and the historical distribution of the species proposed by Gallo-Reynoso (1994; blue-shaded area). (b) Guadalupe Island; the green dots indicate the area surveyed on foot (Punta Sur), as well as the two study areas used to analyse the timing of births by Torres-García (1991).

160 km south off the same coast (Maravilla-Chavez and Lowry, 1999), and on the US Channel Islands (Melin & DeLong, 1999). In 2014 and 2019, two new rest haul-out sites of juvenile Guadalupe fur seals were described in the southern Gulf of California (Elorriaga-Verplancken *et al.*, 2021; Gutiérrez-Osuna *et al.*, 2021), which suggests a recent foraging range expansion.

The feeding areas of Guadalupe fur seal females reach 444 ± 151 km northwest and south-southeast of Guadalupe Island (Gallo-Reynoso *et al.*, 2008), but may extend shoreward and northward in response to prey availability (Amador-Capitanachi *et al.*, 2020). Scat analyses have shown interannual variations in the main squid species consumed by Guadalupe fur seals, which incorporate prey of lower trophic levels during anomalous warm years (Amador-Capitanachi *et al.*, 2020). Quantity and/or quality of prey can also decrease depending on the timing, extent (spatial and temporal), and intensity of warm water anomalies, which can cause nutritional stress in female Guadalupe fur seals. Due to the added energetic demands associated with gestation and lactation (Boyd, 1991), warm conditions have resulted in significant decreases in the probability of successful gestation and/or weaning in other otariids species (Pitcher *et al.*, 1998; Trites *et al.*, 2007). Female Guadalupe fur seals give birth to a single pup each pregnancy. Similar to other pinnipeds, gestation lasts 12 months, including a 3-month delayed implantation period (Riedman, 1990). Births occur in the boreal summer and lac-

tation lasts around 9 months, but females can get pregnant again while nursing (Pierson, 1978).

The negative impacts of warm anomalies on pup production (Melin *et al.*, 2012; Laake *et al.*, 2018), weight gain (Elorriaga-Verplancken *et al.*, 2016; Gálvez *et al.*, 2020), and pup survival are well described in several pinnipeds, including Guadalupe fur seals (Melin *et al.*, 2012; McClatchie *et al.*, 2016). However, there is no quantification of these effects on pup production in the context of population growth for this species. Guadalupe fur seal population monitoring efforts have been sparse and sporadic at Guadalupe Island. The most recent abundance estimate for the colony is 34000–44000 individuals in 2013, with an average annual increase rate of 5.9% from 1984 to 2013 (García-Aguilar *et al.*, 2018). However, there is a lack of information on pup production in years with important climate events. For example, no fur seal counts were performed at Guadalupe Island from 1994 to 2005, a 12-year period with extreme warm water events in the CCE, including the 1997–1998 El Niño (Lavaniegos *et al.*, 2003).

Here, we present a hierarchical model that validates the relationship between oceanographic conditions, expressed in terms of interannual sea surface temperature anomalies (SST_A), and fluctuations in the pup production of Guadalupe fur seals at Guadalupe Island. We start from the premise that interannual variations in SST affect the availability and quality of prey for pregnant females, impacting their probability of successful pregnancy. We compiled pup counts on Guadalupe

Island from 1991 to 1993 and from 2006 to 2019 to analyse the pup production trend and deviations from it, as well as to relate it to annual SST_A in the foraging area of Guadalupe fur seal females.

Methods

Pup production estimates and trend analysis

We compiled published (1991–2010) and unpublished (2013–2019) pup counts at Guadalupe Island (Table 1) carried out during the Guadalupe fur seal pupping season (June to August; Peterson *et al.*, 1968), when newborns depend entirely on lactation and their swimming skills are not enough to be in water, except for the incursion in the splash zone and tide pools where they learn to swim (Fleischer, 1978). Currently, the breeding and haul-out sites of this species on the island are located in Punta Sur and along the east coast (Figure 1b). In all surveys, the entire island was circumnavigated in small boats and counts were carried on by at least two observers, one counting and classifying individuals by naked eye or using binoculars if necessary, and the other recording the counts, at a minimum distance of 10 m from the shoreline, at a speed of 2–3 knots. Counts from 1991 to 1993 were carried out entirely by boat, while those from 2006 to 2019 were conducted on foot at Punta Sur and from boat along the remainder of the coast.

Pups may be underestimated from boat-based counts, mainly on platform and boulder cliffs where they tend to hide between rocks or are overlooked due to their dark colour (García-Capitanachi *et al.* 2017). Therefore, it was necessary to correct counts by adding the proportion of pups that were not detected from boat. Based on available simultaneous boat- and land-based counts (García-Capitanachi *et al.* 2017) along the shoreline of Guadalupe Island, we estimated a global correction factor as a proportion (g). This assumes that pups detected from boat (X) come from a binomial distribution of those detected during the land-based counts (F):

$$\begin{aligned} X &\sim \text{Binomial}(g, F), \\ CC_i &= C_i * (1 + g), \end{aligned} \quad (1)$$

where C is the number of pups recorded during the boat-based count in the year i and CC_i is the estimated number of pups present at the time of the count. We corrected all boat-based counts except those from 1991 to 1993 because they already included their own correction factor (Gallo-Reynoso, 1994). A total of 303 pups were added to the 1992 count, which corresponds to the estimated number of dead pups due to Hurricane Darby passing through Guadalupe Island in early July, 5–8 days before the count of that year took place (Gallo-Reynoso, 1994). Finally, after correcting the boat-based counts for the period 2006–2019, we added the counts made on foot in Punta Sur each year.

Since some counts were carried out in early July, when presumably not all the females had given birth, we modeled the timing of births to correct the counts for potentially unborn pups. We used weekly (i) counts (n) of the total pups present in the area between Campo Lima (29°0'00"N 118°13'45"W) and Cueva de Lefty (29°0'42"N 118°13'19"W) (Figure 1b; Torres-García, 1991), carried out during two consecutive breeding seasons, 1987 and 1988. This cumulative pup counts were fitted as a Gompertz sigmoidal function of the day of the year (d) with an asymptote A and random effects of each year (j). We assumed that each observation of cumulative counts

came from a Normal likelihood with means μ and unknown standard deviations:

$$\begin{aligned} n_i &\sim \text{Normal}(\mu_{n_i}, \sigma_{n_i}^2) \\ \mu_{n_i} &= A_i * \exp^{-\alpha_0 * \exp(a_{1,j} * d_i)} \\ A_i &\sim \text{Normal}(\mu_A, \sigma_A^2) \\ \alpha_{1,j} &\sim \text{Normal}(\mu_{\alpha_1}, \sigma_{\alpha_1}^2). \end{aligned} \quad (2)$$

Using the posterior distributions of the hyperparameters of α coefficients in Equation 2, we predicted the expected number of pups born each day of the breeding season (B), and estimated the total pup production (P) for each year (i) as

$$P_i = CC_i * \left[\left| \left(\frac{B}{\mu A} \right) - 1 \right| + 1 \right]. \quad (3)$$

The next model was that of the long-term pup production temporal trend. To account for the uncertainty of corrected pup count estimations from the previous model, we declared this response variable to come from a Normal likelihood with known means (μ_P) and standard deviations (σ_P) extracted from the posterior distributions estimated by the previous model. To test for a possible deceleration on pup production during the last years of the series, we tested for several polynomials in increasing complexity of the logarithmic link of pup production as a function of time in years y , plus an error (ε) term with Normal likelihood of unknown standard deviation and mean at zero:

$$\begin{aligned} P_i &\sim \text{Normal}(\mu_{P_i}, \sigma_{P_i}^2), \\ \log(P_i) &= \beta_0 + \beta_1 * y_i + \beta_2 * y_i^2 + \varepsilon_i. \end{aligned} \quad (4)$$

Therefore, the expected pup production (eP) for each year (i), spanning 1991–2019, was predicted as:

$$eP_i = \exp(\beta_0 + \beta_1 * y_i + \beta_2 * y_i^2). \quad (5)$$

Then, the annual growth rate (r , expressed as percentage) for the entire time series (T) was estimated as (Vandermeer, 2010):

$$r = \left(\frac{eP_t}{eP_1} \right)^{\frac{1}{T}} - 1, \quad (6)$$

where eP_t was the expected pup production in the last year of the time series and eP_1 was that of the first year.

Sea surface temperature

We delimited an area of ~ 778000 km² as the foraging area for Guadalupe fur seal non-pup females (Figure 1a) based on satellite tracking data of 7 individuals during the breeding season (Gallo-Reynoso *et al.*, 2008), and based on the information of the species' distribution core area (McCue *et al.*, 2021) from 15 individuals tagged before the breeding season (Norris and Elorriaga-Verplancken, 2019, 2020) (Figure 1a). SST values within this area were obtained from the Met Office Hadley Centre (<http://hadobs.metoffice.com/>; HadISST model version 1.1) for the period 1990–2019, with a 1° spatial resolution and monthly frequency (Rayner, 2003). The product was provided by the National Oceanic and Atmospheric Administration's Environmental Research Division Data Access Program (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdHadISST.html>). Then, we estimated 1-year SST running means (SST) for each July of the time series for the entire foraging area, since the gestation period of Guadalupe fur seals is ~ 12 months, including an up-to-3-month-delayed

Table 1. Boat (east coast) and land-based (Punta Sur) counts of Guadalupe fur seal (*A. townsendi*) pups on Guadalupe Island, Baja California, and total pup production estimates for the 1991–2019 breeding seasons.

Year	Initial date	Final date	East coast counts	Punta Sur counts	Pup production mean estimates ($\pm SD$)	Counts source
1991	7 July	9 July	1 197*	NA	1 365 (± 38)	Gallo-Reynoso (1994)
1992	11 July	11 July	1 197**	NA	1 310 (± 30)	Gallo-Reynoso (1994)
1993	17 July	27 July	1 852*	NA	1 914 (± 24)	Gallo-Reynoso (1994)
2006	16 August	18 August	1 587	372	2 832 (± 13)	(Hernández-Montoya, 2009)
2010	17 July	26 July	2 499	667	4 699 (± 66)	García-Capitanachi <i>et al.</i> , 2017
2013	11 July	14 July	4 561	1 116	8 861 (± 199)	Hernández & Milanés/GECI ^a
2014	7 July	9 July	2 692	1 293	6 222 (± 174)	Hernández & Milanés/GECI ^a
2015	21 July	23 July	4 631	1 026	8 460 (± 113)	Hernández & Milanés/GECI ^a
2016	6 July	9 July	5 400	917	10 444 (± 282)	Hernández & Milanés/GECI ^a
2017	3 August	6 August	5 721	1 716	10 652 (± 66)	Hernández & Milanés/GECI ^a
2018	26 July	30 July	6 709	1 983	12 577 (± 114)	Hernández & Milanés/GECI ^a
2019	8 August	13 August	8 291	2 527	15 408 (± 74)	CICIMAR-TMMC ^b

* Counts included correction factor.

** Counts included correction factor plus dead pups by a hurricane event.

^aGrupo de Ecología y Conservación de Islas A.C (GECI)/Unpublished material.

^bCentro Interdisciplinario de Ciencias Marinas (CICIMAR), in collaboration with The Marine Mammal Center.

implantation period (Gallo-Reynoso and Figueroa-Carranza, 2010). These means, namely hereafter “pregnancy period SST mean”, represent the environmental conditions during pregnancy each year (i). These SST means were used to estimate the variable’s long-term linear trend during the 29-year period, because we were interested only in the deviations from it, which we defined as interannual anomalies. For this, we assumed that the pregnancy period SST means came from a Normal likelihood with means (μ_{SST}) stated as a linear function of time in Julian days (J), and known standard deviations, which corresponded to those from the 1-year running mean estimations (σ_{SST}):

$$SST_i \sim Normal(\mu_{SST_i}, \sigma_{SST_i}^2), \quad (7)$$

$$\mu_{SST_i} = \gamma_0 + \gamma_1 * J_i.$$

The SST anomalies (SST_{A_i}) for each year (i) were estimated as the difference between the observed SST mean and the value predicted by the linear trend (μ_{SST}):

$$SST_{A_i} = SST_i - \mu_{SST_i}. \quad (8)$$

Finally, SST_A were classified as warm or cold when their means were outside the 95%-credible interval of the predicted linear trend. The rest of the anomalies were considered as normal conditions.

Ecological model

The difference between the expected pup production given the exponential model (eP) and the observed pup production (P) was defined as a pup production anomaly. To make them comparable among years and evaluate the effects of interannual variability, we converted these anomalies into proportions of the expected pup production for a given year (Pa):

$$Pa_i = \left(\frac{P_i}{eP_i} \right) - 1. \quad (9)$$

Then, we stated Pa as a function of SST_A each year (i). After testing for different polynomials in ascending complexity, a cubic polynomial was chosen as the best model, based on the lowest widely applicable information criterion (WAIC) and the evaluation of its posterior predictive check (i.e. Bayesian p -value; Gelman, 2005; Kéry and Schaub, 2012) :

$$Pa_i \sim Normal(\mu_{Pa_i}, \sigma_{Pa_i}^2), \quad (10)$$

$$\mu_{Pa_i} = \zeta_0 + \zeta_1 * SST_A + \zeta_2 * SST_A^2 + \zeta_3 * SST_A^3.$$

We used the posterior distributions of ζ coefficients to predict the pup production proportional anomalies (ePa) of all years (i), including those without observations (1994–2005 and 2007–2012), but with available SST_A :

$$ePa_i = \zeta_0 + \zeta_1 * SST_A + \zeta_2 * SST_A^2 + \zeta_3 * SST_A^3. \quad (11)$$

Finally, we estimated the pup production for those years as:

$$PP_i = eP_i * (Pa_i + 1). \quad (12)$$

We truncated the predictions of maximum pup production within the model based on the maximum potential number of reproductive females for each year. For this, we used available reproductive rate estimations for two similar fur seal species, the Antarctic fur seal (*Arctocephalus gazella*; 0.6) (Lunn *et al.*, 1994) and the Alaska fur seal (*Callorhinus ursinus*; 0.58) (Kunish, 2011). If we assume that the expected pup production (eP) in each year (i) reflects a median reproductive rate (R_μ) of 0.6, then the approximate number of reproductive females (rF) for that year would be:

$$rF_i = \frac{eP_i}{R_\mu}. \quad (13)$$

If the pup production predictions of the model for certain year exceeded this number of females, those predictions were truncated to the 80% of expected females, which is the max-

imum reproductive rate (R_{max}), as:

$$PP_i = \frac{eP_i}{R_\mu} * R_{max}. \quad (14)$$

Modeling approach

We based all our analyses on a series of hierarchical Bayesian regression models (Kéry and Schaub, 2012; Kéry and Royle, 2016) with non-informative priors, connected only by the mean and standard deviations of the posterior distributions of common parameters. The posterior distributions were approximated with a Markov chain Monte Carlo (MCMC) simulation implemented in the JAGS language (Plummer, 2003) within R (R Core Team, 2018). We ran 1 million iterations in five independent chains, retaining one of every 20 values to reduce autocorrelation, and removing the first 20% of the MCMC output as a burn-in period (Kéry and Royle, 2016). We tested polynomials of ascending complexity and different likelihood families. We tracked each log-likelihood evaluated at the posterior simulations of the parameter values and compiled the MCMC results in a single matrix to apply the WAIC and the efficient approximate leave-one-out cross-validation criterion (LOOIC) for Bayesian models, using the `loo` package in R (Vehtari *et al.*, 2017). We also estimated the Pareto smoothed importance sampling (PSIS), which is a measure of the distribution of the importance weights used in the LOOIC estimates. Values of the PSIS tail shape parameter (k) > 0.7 imply impractical convergence rates and unreliable Monte Carlo error estimates (Vehtari *et al.*, 2017), which could result in a model misspecified or overfitted. We used the `loo_compare` function to compare fitted models based on the difference between models of the theoretical expected log pointwise predictive density (ELPD) for a new dataset (`elpd_diff`). Finally, we selected as best model that with lowest WAIC, after the Gelman–Rubin convergence diagnosis criterion (\hat{R}) of each candidate to assure good chain convergence (i.e. \hat{R} close to 1) and the effective number of iterations (N_{eff}), where high values indicate less uncertainty in the parameters' estimation (Gelman and Rubin, 1992). For all models, we estimated the Bayesian R^2 as a measure of the explained variance and model predictability. It was obtained by dividing the predicted variance (σ_{pred}^2) by the sum of the predicted variance plus the variance of the vector of residuals, which corresponds to the difference between the observed values minus the predicted ones (Gelman *et al.*, 2019):

$$R_B^2 = \frac{\sigma_{pred}^2}{\sigma_{pred}^2 + \sigma_{obs-pred}^2}. \quad (15)$$

In order to test for the models' goodness-of-fit, we estimated a Bayesian p -value as a posterior predictive check, based on the discrepancy between the squared residuals of the observed data and those of a new set simulated under the same model. The mean proportion of iterations (Pr) when the squared residuals of the simulated data set (y_{rep}) is more extreme than those of the actual data (y) is named the Bayesian p -value. A proportion close to 0.5 indicates a high goodness of fit (Gelman, 2005; Kéry and Schaub, 2012):

$$B_{p-value} = \Pr(T_{y_{rep}} > T_y). \quad (16)$$

Results

For each parameter estimated, we summarize its results with the median and the 95%-credible interval (range) of the posterior distribution (Tables 2 and 3), as well as the diagnostic statistics for the MCMC simulations and their posterior distributions (Supplementary Figure S2). WAIC, LOOIC, ELPD, and the PSIS tail shape parameter k are shown in Supplementary Table S1 for all models tested.

Guadalupe fur seal pup production estimates and trend analysis

We tested for Normal and Poisson likelihoods for the birth timing sigmoidal model, with years as random effects on the slope. The PSIS tail shape parameters k showed good diagnosis ($k < 0.7$) for the Poisson likelihood in all models tested. However, based on the lowest WAIC, we chose a Normal likelihood, with years as random effect on the slope (Supplementary Table S1). The mean multiplicative correction factor for the proportion of pups that are not detected from boat-based surveys was estimated at 1.546 (range: 1.531–1.56; Table 2). The posterior predictive check showed a good fit of the model (Bayesian p -value = 0.525, Table 2). It exhibited a high explained variance ($R_B^2 = 0.998$, range: 0.9934–0.999; Table 2) and showed a steep increase in births between the second week of June and the second week of July, reaching the asymptote on August 1st (Figure 2). A total of 9 of the 12 counts were made before the end of the birth season (i.e. before the asymptote of the birth timing model). Table 1 summarizes the mean values ($\pm SD$) of pup production estimates corrected for birth timing.

For the pup production model, we tested for an exponential and a second-order polynomial, with and without explicit error terms. Since all models showed k estimates > 0.7 in the 50% of the observations, we discarded the ELPD difference as a reliable method for model selection and used the lowest WAIC instead, which corresponded to the second-order polynomial (Supplementary Table S1). This model allowed us to test for the presence of an asymptote in the pup production long-term trend during 1991–2019. It also exhibited a high explained variance ($R_B^2 = 1$, range: 0.999–1) and high goodness-of-fit (Bayesian p -value = 0.492; Table 3). Over this period, pup production showed a sustained exponential increase (Figure 4a), with an average annual growth rate of 8.4% (range: 8.1–8.84; Table 3). The largest pup production relative to the expected long-term trend was observed in 2013, with 35.9% (range: 23.7–49.6%) more than expected, while the lowest was in 2014, with 16.6% (range: 8.5–23.9%) less than expected. The estimated pup production for 2019 was 15963 (range: 14300–18158).

Sea surface temperature anomalies

For the long-term SST trend, we chose a simple linear model. The PSIS k values were < 0.5 (Supplementary Table S1). For the 1990–2019 period, the annual SST mean in July increased from 17.95°C (range: 17.68–18.21) to 18.12°C (range: 17.87–18.38) (Figure 3). The variance explained by the linear trend model was low ($R_B^2 = 0.009$, range: 0–0.064; Table 3), indicating that it is not the main process of variability in the study area for the period studied. The warmest SST_A was 1.43°C (range: 1.19–1.65) in 2015, followed by 2016 with 1.12°C (range: 0.88–1.35), while the coldest was -1.05°C (range: -1.28 to -0.85) in 2011. During years with pup count

Table 2. Summary of the posterior distributions of the most relevant parameters estimated in birth timing model.

Parameter	Symbol	Equation #	mean	SD	Low 2.50%	50%	High 97.50%	\hat{R}	N_{eff}
Correction factor									
Detectability	g	(1)	0.546	0.007	0.531	0.546	0.560	1	200 000
Number of births by day in the breeding season									
Intercept	α_0	(2)	0.32	0.054	0.223	0.317	0.435	1	38 857
Hypermean first coefficient	$\mu_{\alpha 1}$	(2)	2.22	0.258	1.703	2.217	2.74	1	102 215
Hyper-SD first coefficient	$\sigma_{\alpha 1}$	(2)	0.205	0.162	0.007	0.163	0.562	1	200 000
Mean asymptote	μ_A	(2)	107.433	5.178	97.884	107.214	118.288	1	100 823
SD asymptote	σ_A	(2)	15.758	2.781	11.202	15.435	22.141	1	80 483
Bayesian R-squared	BR^2_{day}	(15)	0.997	0.002	0.993	0.998	0.999	1	200 000
Deviance	DIC		137.481	18.417	102.672	137.229	172.38	1	200 000
Bayesian p -value	p -value	(16)			0.525			1	200 000

The symbols are the same as those used in the equations in the Methods section. \hat{R} = Gelman–Rubin statistic, n_{eff} = number of effective iterations.

Table 3. Summary of the posterior distributions of the most relevant parameters estimated in the hierarchical model of SST_A, pup production trend and the ecological model.

Parameter	Symbol	Equation #	Mean	SD	Low 2.50%	50%	High 97.50%	\hat{R}	N_{eff}
Pup production trend									
Intercept	β_0	(4)	8.269	0.059	8.152	8.269	8.380	1.000	2 465
First coefficient	β_1	(4)	1.122	0.037	1.057	1.120	1.198	1.000	3 331
Second coefficient	β_2	(4)	0.344	0.045	0.260	0.344	0.431	1.000	3 095
Growth rate	r	(6)	0.084	0.002	0.080	0.084	0.088	1.000	4 870
Bayesian R-squared	BR^2_{exp}	(16)	1.000	0.000	0.999	0.999	1.000	1.000	4 852
Bayesian p -value	p -value _{trend}	(16)			0.492			1	5 000
Sea surface temperature anomaly model									
Intercept	γ_0	(8)	18.034	0.108	17.836	18.030	18.248	1.000	4 828
First coefficient	γ_1	(8)	0.052	0.050	-0.046	0.053	0.153	1.000	5 260
Bayesian R-squared	BR^2_{SST}	(15)	0.015	0.017	0.000	0.009	0.064	1.000	4 808
Bayesian p -value	p -value _{SST}	(16)			1.000			1.000	0
Ecological model: SST_A effect on pup production									
Intercept	ζ_0	(10)	-0.107	0.066	-0.228	-0.111	0.036	1.000	4 297
First coefficient	ζ_1	(10)	-0.355	0.330	-1.064	-0.329	0.205	1.000	5 000
Second coefficient	ζ_2	(10)	1.387	0.369	0.737	1.364	2.159	1.000	4 490
Third coefficient	ζ_3	(10)	-0.781	0.159	-1.098	-0.783	-0.466	1.000	4 669
Bayesian R-squared	BR^2_{ecol}	(15)	0.814	0.087	0.576	0.837	0.911	1.000	4 668
Bayesian p -value	p -value _{ecol}	(16)			0.563			1	5 000
Deviance	DIC		1 470.994	7.176	1 458.741	1 470.581	1 486.400	1.000	5 000

The symbols are the same as those used in the equations in the Methods section. \hat{R} = Gelman–Rubin statistic, n_{eff} = number of effective iterations.

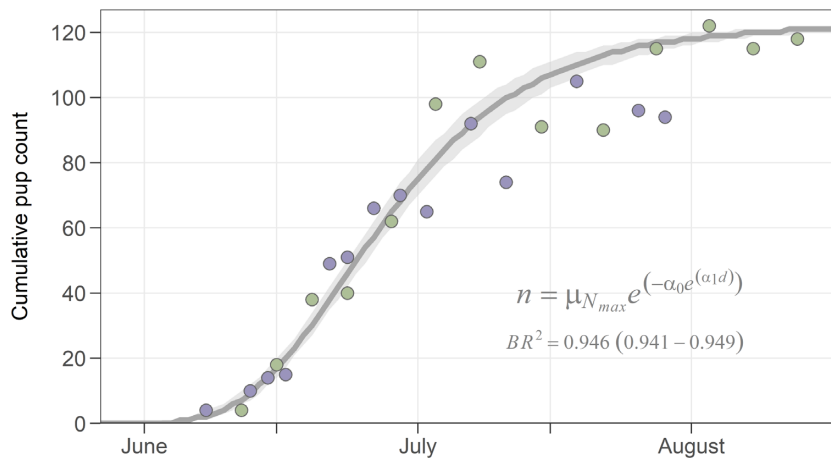


Figure 2. Birth timing model of Guadalupe fur seals based on data from Torres-García (1991). The purple and green dots represent the 1987 and 1988 cumulative pup counts, respectively, the solid line is the median returned by the model, and the shaded area is the 95%-credible interval.

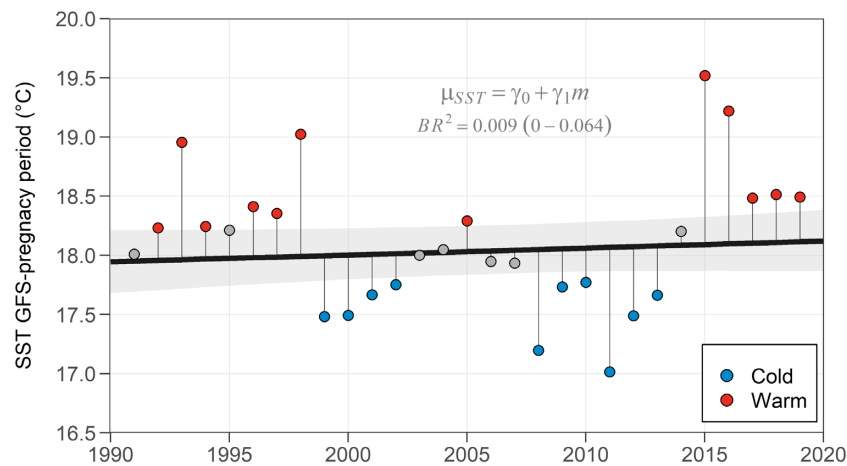


Figure 3. Monthly SST long-term trend within the foraging area of Guadalupe fur seal females spanning 1990–2019. The black line is the median and the shaded area is the 95%-credible interval. Coloured dots represent SST 1-year running means during the pregnancy period (starting in July) for warm (red), cold (blue), and normal (grey) years.

observations, SST_A ranged from -0.42 (range: -0.64 to 0.21) to 1.43°C (range: 1.19 – 1.65). Although warm and normal years were well represented in the data, there were no pup production observations during the coldest years (e.g. 1999, 2000, 2008, 2011, and 2012; Figure 3).

Ecological model

For the ecological model, we tested for a linear model, a second-degree and a third-degree polynomial. For all models we obtained PSIS k values >0.7 , due to a pup production observation made during the extremely warm conditions of 2015. Based on the lowest WAIC, we chose a third-order polynomial with a high explained variance (0.837, range: 0.576–0.911; Table 3), indicating high predictability. The model predicted positive effects on pup production of $SST_A < -0.2^\circ\text{C}$, as well as of warm anomalies between 0.6 and 1.38°C . Conversely, normal to slightly warm conditions (-0.17 to 0.6°C) had negative effects on the pup production proportional anomalies. Under extreme warm conditions ($>1.38^\circ\text{C}$), pup production anomalies were close to zero ($Pa = -0.014$, range: -0.102 to 0.078 ; Figure 4b). The model's Bayesian p -value of 0.563 (Table 3) indicated a good representation of data by the model and coincides with the overlap of the observed pup productions with those estimated from SST_A (Figure 4a). However, for coldest years like 1999, 2000, 2008, 2011, and 2012, the estimated pup productions were truncated by the model based on the maximum possible reproductive females, and exhibited the highest uncertainties (Figure 4a).

Discussion

Data to estimate pup production of Guadalupe fur seals are scarce. Our study period spanned 29 years, but available data came from only 12 breeding seasons, and 75% of the counts were made before the end of the birth season. Nevertheless, our modeling approach of birth timing allowed us to avoid underestimating the pup production in those years. This model was based on data from two pupping seasons in the late 1980s, so we assumed that the seasonal timing of births remained constant over the last three decades. However, since environ-

mental changes and the availability of prey could modify this pattern (Pitcher *et al.*, 2001), it is highly recommended to regularly monitor the timing of births. Our robust estimation of a detectability correction factor for some counts also allowed us to make all the available data comparable. Therefore, we consider that the estimates of pup production made in this study are the most reliable to date, and are useful for further population trend analyses.

Our results showed that the production of Guadalupe fur seal pups has increased exponentially during the last three decades without reaching an asymptote, despite the use of a flexible second-degree polynomial, which suggests that the species is still in a recovery phase (Lotze *et al.*, 2011). This exponential increase in pup production is typical of long-lived mammalian populations that were severely reduced (Sinclair *et al.*, 1996). The annual growth rate of 8.4% (range: 8–8.8) estimated for the 1991–2019 period is higher than the 5.9% estimated for 1984–2013 (García-Aguilar *et al.*, 2018), which indicates a steep increase in pup production in recent years. Nevertheless, it was lower than those estimated for other fur seal species whose numbers decreased due to commercial hunting, such as the Antarctic fur seal (*Arctocephalus gazella*) from Cape Shirreff and the San Telmo Islets (average growth rate of 20%, period 1966–2002; Hucke-Gaete *et al.*, 2004), and the New Zealand fur seal (*Arctocephalus forsteri*) from Kangaroo Island (average growth rate of 10%, period 1988–2013; Shaughnessy and Goldsworthy, 2015). According to our pup production estimates, the population size in 2019 would have been 63850 individuals (range: 57199–72631), assuming a population:pup ratio of 4:1, estimated for the northern fur seal (Johnson, 1975), which is far from reaching the estimated population size prior to commercial exploitation, which was ~ 200000 individuals (Hubbs, 1979).

Pup production depends on life-history parameters, density-dependent effects, as well as extrinsic factors that regulate population dynamics (Wade, 2018). However long-term variability in pup production has been correlated to environmental factors, such as fluctuations in ocean productivity and subsequent prey availability, both strongly influenced by changes in SST (Forcada *et al.*, 2005; Forcada and Hoffman, 2014; Kalberer *et al.*, 2018). Nevertheless, in this study, SST_A effects on pup production were only observable on the pro-

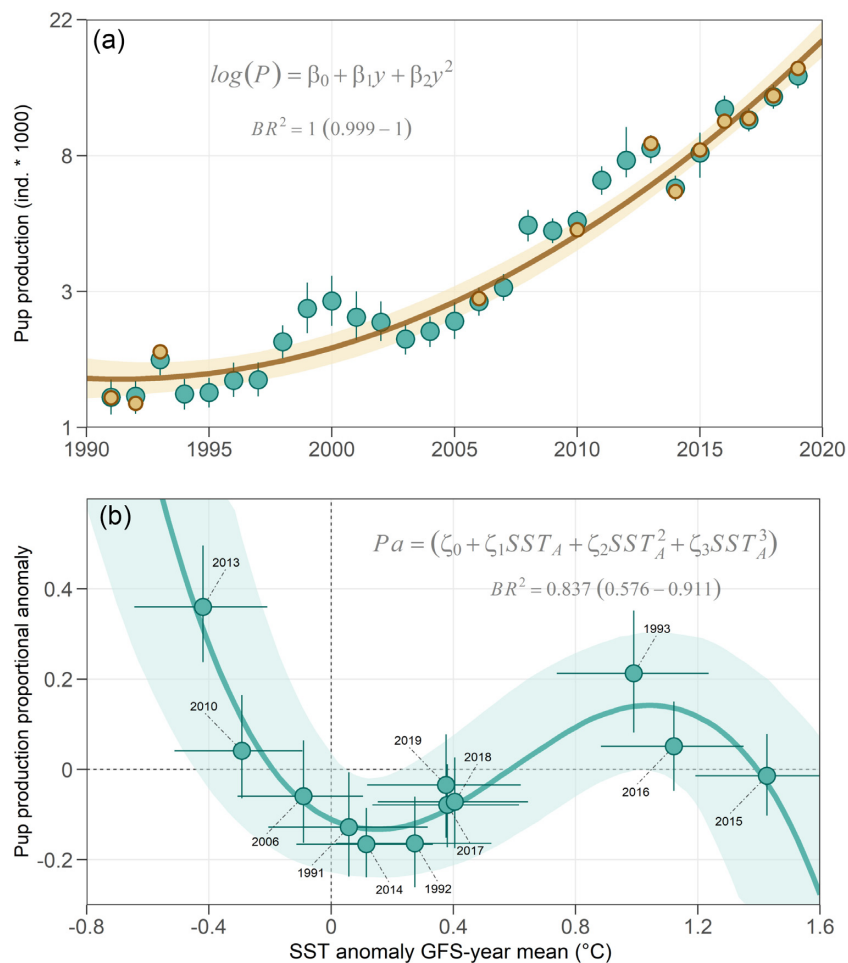


Figure 4. Guadalupe fur seal pup production trend and ecological model. In all panels, solid lines represent the median predictions, and the shaded areas and error bars are the 95%-credible intervals. (a) Long-term pup production trend estimated with an exponential model and observations (brown), and predicted pup production by the ecological model from SST anomalies (green). (b) Ecological model of pup proportional production anomalies as a function of SST_A .

portional anomalies from the exponential growth. Therefore, it is highly uncertain how the pup production would react to long-term changes in the species foraging habitat, or the effects of interannual anomalies when it is close to a density-dependent state (i.e. the recovery), theoretically, with a more stable growth rate (Roux, 1987). In other pinniped species like the California sea lion, long-term environmentally driven forage declines are correlated with lower pup production and population declines (Mcclatchie *et al.*, 2016; Adame *et al.*, 2020).

The performance of the ecological model was highly influenced by the pup production observation at the upper level of SST_A (i.e. 2015). Since most of the available data were collected during normal or warm years, the strong positive effects on pup production suggested by the model results during cold years (i.e. 1999, 2000, 2008, 2011, and 2012) had to be truncated according to the typical reproductive rates for others fur seal species to avoid the overestimation of pup production. During the extremely warm conditions of 2015 ($>1.4^\circ\text{C}$), the predictions of pup production showed high uncertainty and could be underestimated, although these conditions are less common in the CCE compared to cold years. This highlights the need for future monitoring during extreme cold conditions, similar to those of 2008 or 2011 to corrob-

orate their effects. Such cold anomalies have been associated with a higher productivity and enhanced trophic web (Jacox *et al.*, 2015). During the 2011 La Niña, Galapagos sea lions (*Zalophus wollebaeki*) exhibited higher pup production and pupping rate (Kalberer *et al.*, 2018).

The model predicted negative effects on pup production under normal to slightly warm conditions (-0.16 to 0.6°C), $\sim 60\%$ of the pup production observations fall within this range, in which the offshore southern CCE is less productive than its coastal region (Bograd and Lynn, 2003), where forage prey species are constrained to upwelling and high productive cores (Thompson *et al.*, 2019). This includes the squids' distribution (i.e. *Doryteuthis opalescens* and *Dosidicus gigas*), which follows the patches of high aggregation of small pelagic fish (Koslow and Allen, 2011; Field *et al.*, 2013; Van Noord and Dorval, 2017). This typically increases the distance and duration of the females' foraging trips and their energy invest (Amador-Capitanachi *et al.*, 2020). These conditions can also decrease the probability of successful pregnancy and can be associated with the slow population recovery of this species compared to those of other fur seal populations (Costa *et al.*, 2003).

In addition, the model predicted a positive effect of slightly cold years ($<-0.2^\circ\text{C}$) on pup production which reached the

highest peak in 2013. This positive effect could be the consequence of higher availability of prey for pregnant females, since cold and productive waters are dominated by diatoms which impart greater lipid content and essential fatty acids to the food web (Litz *et al.*, 2010), increasing the density of zooplankton (Wells *et al.*, 2008). These positive environmental conditions at birth improve survival and fecundity in the adult phase and can lead to positive lagged responses on population growth (Pigeon *et al.*, 2017). A positive effect of negative SST anomalies was evidenced through heavier Guadalupe fur seal neonates during the cold year 2013 (Gálvez *et al.*, 2020).

The ecological model also predicted a slight positive effect of moderately warm conditions (~ 0.6 up to 1.3°C) on pup production. The potential mechanisms associated with this result are not clear. On the one hand, it is possible that Guadalupe fur seal females could move to feeding areas that remain cold due to local processes like mesoscale eddies, and take advantage of their high prey availability, as the northern fur seals do (Ream *et al.*, 2005). Another mechanism that could explain this positive effect is the displacement of coastal prey species offshore due to the stronger stratification of the water column (Bograd and Lynn, 2003; Howard *et al.*, 2020). However, this response could also be related to the ability of Guadalupe fur seal females to vary their diet according to available prey (Juárez-Ruiz *et al.*, 2018) and/or to an overturn of dominant squid species in favour of the jumbo squid (*Dosidicus gigas*), which typically migrates into the females' foraging habitat during summer (Field *et al.*, 2013). Interannual warming events decrease the jumbo squid's age and size of sexual maturity (Mejía-Rebollo *et al.*, 2008), reducing the overall mantle length to the size range preferred by Guadalupe fur seals, which is no larger than ~ 30 cm, because their relatively small bite lacks the strength to cut larger prey (Franco-Moreno *et al.*, 2020).

Extreme warming with a multi-year duration, such as that induced by the northeast Pacific Marine Heatwave (NPMHW) (Di Lorenzo and Mantua, 2016) during 2014–2016, had a lower effect on Guadalupe fur seal pup production, compared to those exhibited by other otariid species with coastal feeding areas (Elorriaga-Verplancken *et al.*, 2016; Laake *et al.*, 2018). This effect was only observed in 1 year because the presence of the NPMHW was unique in the CCE, with the highest intensity (2.7 times the historical standard deviation) since 1983, and changed the entire ecosystem structure (Jacox *et al.*, 2016). This observation had a high influence on the model's performance, causing an apparent overfit in the upper range of SST_A . However, this trend was expected, since it agrees with that observed in other fur seal species, in which intense warm anomalies and low food availability throughout the year (Forcada *et al.*, 2005) increase nutritional stress, thereby reducing the reproduction success (Guinet *et al.*, 1998; Gibbens *et al.*, 2010). Additionally, females of other pinnipeds, such as the Galapagos sea lion, extend their lactation period up to 2 years during limited prey conditions (Trillmich, 1990), reducing the probability of pupping in the next breeding season (Trillmich and Wolf, 2008). This strategy, which results in an increase in the inter-birth interval and the subsequent reduction of pup production (Kalberer *et al.*, 2018), cannot be totally dismissed for Guadalupe fur seal females under warm conditions.

Based on population viability analyses (Hernández-Camacho and Trites, 2018), the Guadalupe fur seal conservation status according to the IUCN (International Union for

Conservation Nature) Red List is of least concern (Aurioles-Gamboa, 2015). In contrast, Mexican law classifies it as endangered (SEMARNAT, 2010) and the US species' listing as threatened (McCue *et al.*, 2021). Since Guadalupe Island is still the only reproductive colony of the species, and the current abundance (this study) represents $\sim 32\%$ of that before the population's decline in the 1890s (Hubbs, 1956), the effect of climatic events on its recovery should be included as part of its monitoring, management, and conservation plans.

Conclusions

The annual pup production of Guadalupe fur seals exhibited exponential growth without an apparent asymptote until 2019. The difference between the expected number of pups from this trend and the observed counts responds to interannual changes in the oceanic environment within the pregnant females' foraging habitat, indicated by sea surface temperature anomalies. Despite the sparseness of the data available, our modeling approach allowed us to predict the species' pup production from the observed range of SST interannual anomalies. New observations are required to corroborate the pup production predictions for cold years.

Supplementary data

Supplementary material is available at the ICESJMS online.

Author contributions

AJ: conceptualization, data curation, formal analysis, investigation, methodology, model design, writing—original draft, and writing—review and editing. MP: conceptualization, model design, and writing—review and editing. JH: funding acquisition, data collection, and writing—review and editing. FE: funding acquisition, data collection, and writing—review and editing. AM: data collection, and writing—review and editing. TN: funding acquisition, data collection, and writing—review and editing. EB: writing—review and editing. GH: writing—review and editing.

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Data availability statement

The data underlying this article are available in the article and in its online supplementary material. WAIC, ELPD difference, and PSIS k diagnoses for all models tested are available as Table format in Supplementary information S1 as a PDF file. Posterior distributions of the main parameters estimated by the MCMC are available as Supplementary images S2 as a PDF file. JAGS model codes are available in Supplementary text S3 as a PDF file. A data list with all values needed for running the JAGS code are available as a Supplementary RData file S4.

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