Population viability analysis of Guadalupe fur seals *Arctocephalus townsendi*

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ABSTRACT: The Guadalupe fur seal *Arctocephalus townsendi* was intensively hunted and considered extinct by the end of the 1800s. However, small numbers (<20 seals) were reported on Guadalupe Island (Mexico) in the mid-1950s and were observed at a second location (San Benito Islands, Mexico) in the late 1990s. Sporadic counts at these 2 sites have followed a relatively rapid increase in numbers, but considerable uncertainty remains about the long-term viability of this recovering species. We performed a population viability analysis using historic seal counts from Guadalupe Island and the San Benito Islands to predict the probability of each colony (and both colonies combined) going extinct under 3 critical population threshold scenarios (100, 500, and 1000 seals). Using a diffusion approximation model, we found that the growth rates of the 2 colonies were similar (10–11% yr^{-1}) and that the population totaled ~41000 individuals in 2017 ($\overline{x}$ = 40614, 95% CI = 35779–46877). Guadalupe fur seals appear to be vulnerable to extreme climatic events. Of the 2 fur seal colonies, the San Benito Islands colony is less secure and is Endangered to Critically Endangered, depending on the quasi-extinction value used under the quantitative listing criteria established by the IUCN. In contrast, the Guadalupe Island colony and the 2 colonies combined meet the quantitative analysis criteria of Least Concern. Population viability analysis is an important component of assessing the status of wildlife populations and assisting nations and organizations in assigning appropriate categories of protection.

KEY WORDS: Guadalupe fur seal · Population viability analysis · PVA · Probability of extinction · Endangered species · Population trend · Pinnipeds

INTRODUCTION

The Guadalupe fur seal *Arctocephalus townsendi* is endemic to the Pacific Ocean and currently only breeds in Mexico (Aurioles-Gamboa et al. 2010). It was thought to have gone extinct by the end of the 1800s because of the commercial fur trade. However, a small number of Guadalupe fur seals (<20) were discovered breeding on Guadalupe Island in 1950 (Hubbs 1956b). The population grew slowly and began hauling out at a second location (San Benito Islands) over 270 km southeast in the late 1990s (Fig. 1) (Maravilla-Chavez & Lowry 1999).

As with Guadalupe Island, the San Benito Islands were also an important breeding site in the 19th century. However, the animals that have recolonized the San Benito Islands are mainly juveniles, adult females, and subadult males. Less than 1% of the seals on the San Benito Islands are pups, which is notably lower than the 24% of the population that are pups on Guadalupe Island—the only recognized reproductive colony (see Table 1). Thus, the San Benito Islands population is considered an extension of the Guadalupe Island population and not a reproductive colony (Aurioles-Gamboa et al. 2010).

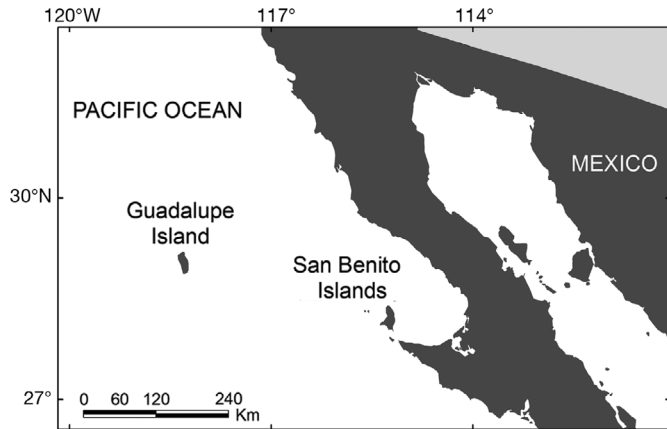*Corresponding author: cjhernandez78@gmail.com

Fig. 1. Location of Guadalupe Island and the San Benito Islands (Mexico), used by Guadalupe fur seals *Arctocephalus townsendi* to breed and rest

In 2010, the minimum population size of Guadalupe fur seals during the breeding season was estimated to be 2503 seals at the San Benito Islands and 13 327 at Guadalupe Island (García-Capitanachi 2011). At that time, the San Benito population was experiencing a 30% annual growth rate (1997−2014), and the Guadalupe population was increasing 10.3% per year (1955−2015) (Sierra-Rodríguez 2015, Carretta et al. 2017). All of these positive changes boded well for the recovery of Guadalupe fur seals. However, unusual numbers of fur seals of different age and sex classes stranded in recent years throughout parts of their former distribution and beyond (i.e. central California, Pacific coast of Mexico, Gulf of California, and Vancouver Island in British Columbia, Canada) (Villegas-Zurita et al. 2015, Elorriaga-Verplancken et al. 2016a, Aurioles-Gamboa et al. 2017, Carretta et al. 2017). Equally troublesome are the recent numbers of young seals that have stranded and died along the coasts of California and Baja California, as well as the dead adult and subadult fur seals that have washed ashore (Aurioles-Gamboa et al. 2017, Carretta et al. 2017).

The young stranded animals along the coast of California showed signs of malnutrition with bacterial and parasitic infections (https://www.fisheries.noaa.gov/national/marine-life-distress/2015-2018-guadalupe-fur-seal-unusual-mortality-event-california). This unusual mortality event was associated with the large-scale warming of the Pacific Ocean caused by the 2015 El Niño event (Elorriaga-Verplancken et al. 2016b) and the 'Blob', which reached the waters of the west coast of the Baja California peninsula in 2014 and 2015 (Cavole et al. 2016). The Blob was a patch of anomalously warm water formed in the northeastern

Pacific during the winter of 2013 to 2014. It extended to the Baja California peninsula and affected organisms at all levels of the food web (Kintisch 2015). The adult and subadult male fur seals that stranded on the Baja California peninsula during the post-breeding migration were possibly using a new feeding ground in the Gulf of Ulloa (Aurioles-Gamboa et al. 2017).

The future of Guadalupe fur seals is uncertain in light of the recent strandings and the increasing frequencies of extreme ocean climate events (Elorriaga-Verplancken et al. 2016b). One means of assessing the probability that Guadalupe fur seals may go extinct is by conducting a population viability analysis (PVA) (Shaffer 1978, 1981). This quantitative technique is commonly used in conservation biology to assess the probability of a population going extinct within a given number of years — and is one of the classification criteria used by the IUCN and other organizations to assess whether wildlife populations are endangered, threatened, vulnerable, or not at risk (IUCN 2012). However, a PVA has never been conducted to determine the viability of the Guadalupe fur seal population.

We developed 3 count-based PVAs for the Guadalupe fur seal occurring on (1) Guadalupe Island, (2) the San Benito Islands, and (3) the 2 colonies combined (Morris & Doak 2003). Count-based PVAs are based on systematic counts and estimates of the total number of individuals in the population to define the average growth trend and its variance (Dennis et al. 1991). We used the models to determine the probability of Guadalupe fur seals going extinct (IUCN 2012) and estimated the average total population size of Guadalupe fur seals in 2017 using stochastic lambda values (λ).

MATERIALS AND METHODS

Model approach

We performed a count-based PVA using a simple stochastic diffusion approximation model. The diffusion approximation model uses linear regression parameters to estimate λ. The model also provides measures of uncertainty, such as median time to extinction and the probability of the population declining to threshold abundances (i.e. the cumulative probability of quasi-extinction) (Dennis et al. 1991). We developed a PVA for each colony of fur seals and for both colonies combined. For the latter, we combined data from the 2 sets of islands starting in 1997, when Guadalupe fur seals were first re-

ported on the San Benito Islands. Considering that population counts were not made in the same years in both colonies, we fit a deterministic exponential growth model on observed population counts to estimate missing counts for each colony.

We evaluated 3 scenarios of quasi-extinction thresholds occurring when the populations fall below 100, 500, and 1000 individuals. This parameter is generally difficult to define for any imperiled species because empirical data are limited. We chose those 3 scenarios based on the historical reports of Guadalupe fur seals during the first half of the 19th century. Although it is unknown how many animals survived hunting, the first reports of Guadalupe fur seals at Guadalupe Island put numbers at <20 individuals (Hubbs 1956b). However, we suspect the actual number was more likely closer to 100 because some individuals would have been at sea during the surveys. This is also the minimum number of individuals (100) recommended to account for demographic stochasticity (see Assumption 2 in the next subsection).

We determined the probability of the Guadalupe fur seal going extinct in 10, 20, and 100 yr from the unconditional cumulative probability of extinction and its bootstrapped 95% CI (Morris & Doak 2003). In this way, we assessed whether the Guadalupe fur seal population met the IUCN quantitative analysis criteria for being Critically Endangered (i.e. if the probability of extinction is at least 50% within 10 yr or 3 generations, whichever is longer), Endangered (if the probability of extinction is at least 20% within 20 yr or 5 generations, whichever is longer), or Vulnerable (if the probability of extinction is at least 10% within 100 yr or 5 generations, whichever is longer) (IUCN 2012). Generation time is the average age of parents in the population. It is 10 yr for a related species, the northern fur seal *Callorhinus ursinus* (COSEWIC 2010), and was presumed to be the same for Guadalupe fur seals.

We estimated the unconditional instead of the conditional cumulative probability of extinction because the latter only considers those simulated populations that will eventually fall below the quasi-extinction threshold. However, when the growth rate is greater than zero (as in our case), not all trajectories hit the threshold. Thus, using the conditional extinction time for Guadalupe fur seals would be overly pessimistic (W. F. Morris & D. F. Doak pers. comm.).

The unconditional cumulative probability of extinction (Morris & Doak 2003) was estimated as:

$$G(T \mid d, \mu, \sigma^2) = \phi\left(\frac{-d - \mu T}{\sqrt{\sigma^2 T}}\right) + \exp\left(\frac{-2\mu d}{\sigma^2}\right) \times \phi\left(\frac{-d + \mu T}{\sqrt{\sigma^2 T}}\right)$$

$$(1)$$

where G is the inverse Gaussian distribution, T is the future time of interest, d is the difference between the natural logarithm of the current population size N_c and the natural logarithm of the quasi-extinction threshold N_q, μ is the slope of the linear regression (x vs. y; see Eqs. 2 & 3), σ^2 is the mean square residual (x vs. y), and ϕ is the standard normal cumulative distribution function:

$$x_i = \sqrt{t_{i+1} + t_i} \qquad (2)$$

$$Y_i = \frac{\ln(N_{i+1})/N_i}{x_i} \qquad (3)$$

Finally, we estimated the average total size of the Guadalupe fur seal population in 2017 using the stochastic growth rate (λ) for both colonies combined. All analyses were performed using the popbio library (Stubben & Milligan 2007) within R (R Core Team 2018). The graphic representation of unconditional cumulative probability of extinction was done using the ggplot2 library in R (Wickham 2016).

We based our analysis on historical population counts from Guadalupe Island and the San Benito Islands (Table 1) made during the breeding season (June–July), when most animals of all age and sex classes are present at the rookery (including newborn pups). Historic and current counts were made from a boat. In some cases, counts from boats were complemented by counts made during walking surveys on the islands (Gallo-Reynoso et al. 2005).

Previous studies that estimated population size of the Guadalupe fur seal population on Guadalupe Island (Table 1) derived different correction factors to account for animals onshore that they failed to see because of substrate or other factors. For example, García-Capitanachi (2011) corrected for adult males, adult females, and pups breeding on different substrate types (12 different correction factors in total). In contrast, Gallo-Reynoso (1994) and Gallo-Reynoso et al. (2005) applied 3 different correction factors to single surveys by (1) taking the percent difference between boat counts and shore counts as a correction factor and (2) applying counts made for portions of the rookery to areas not counted. They also (3) added an adult female for each dead or weaned pup found at the colony. Other surveys based their correction factors on the difference between counts made from a boat and those made on land (Fleischer 1978, Seagars 1984, Torres 1991, Hernández-Montoya 2009).

Because of the heterogeneity of the correction factors and the difficulty of applying them to the raw counts, we calculated a mean correction factor (23% ± 15) based on the differences between the observed and estimated number of individuals for each year in

which both counts were available (Table 1). Thus, we used the corrected data for our PVA when both raw and corrected counts were available. When only raw counts were available, we applied the estimated mean correction factor. We call these values the minimum corrected population. Studies reporting the size of the San Benito Islands colony did not use any correction factor; thus, we applied the same mean correction factor to those counts as well.

Applying the correction factors to animals counted onshore yields a minimum estimate of population size. However, they do not account for the number of animals at sea during a survey. Another approach for estimating total population size is to use the number of newborn pups as an index of population size (multiplicative factor) because pups do not leave the colony during their first few weeks of life (Berkson & DeMaster 1985, Loughlin et al. 1994, Trites & Larkin 1996). The relationship between the number of pups and the total population depends on a population's age structure and vital rates (Berkson & DeMaster 1985).

The multipliers to estimate population size from pup counts vary depending on life history parameters (e.g. longevity, age-specific mortality rates) and population tendency (Taylor et al. 1995). Thus, for the Guadalupe fur seal, we obtained a mean value (4.5) from the multipliers available for 2 fur seal species with increasing populations: the Australian fur seal *Arctocephalus pusillus doriferus* (4.5; Kirkwood et al. 2010) and the New Zealand fur seal *A. fosteri* (4.2, 4.9; Taylor et al. 1995). These values fall

Table 1. Historical abundance of Guadalupe fur seals on Guadalupe Island and the San Benito Islands, Mexico, beginning with the first census in 1955 after being presumed extinct in 1928. Age and sex categories counted include males (breeding age adult males), subadults (young non-breeding adult males), females (breeding age females), juveniles (sexually immature individuals of both sexes >1 yr old), pups (nursing young of both sexes), and unknown or undetermined ages (Gallo-Reynoso 1994). Also shown are the total number of fur seals observed (T_o) during the survey, the total corrected (T_c) for animals at the colony not seen during the survey, and the total population (T_p) estimated by multiplying the number of pups by 4.5. Blanks: no data available

Year	Month	Males	Subadults	Females	Juveniles	Pups	Unknown	T_o	T_c	T_p	Source
Guadalupe											
1955	Jun							35	46	49	Hubbs (1956a)
1956	Jun							92	120	130	Hubbs (1956a)
1968	Jun							314	410	443	Brownell et al. (1974)
1977	Jun–Jul							591	1073	1159	Fleischer (1978)
1983	Jun	374	60	642	134	24	62	1296	1879	2029	Gallo-Reynoso (1994)
1984	Aug					649		1597	1600	1728	Seagars (1984)
1988	Jun–Jul	468	78	1134	472	998	109	3259	3531	3813	Torres (1991)
1991	Jul	1349	198	1707	895	1197	78	5424	6361	6870	Gallo-Reynoso (1994)
1992	Jul	1907	362	2036	419	894	134	5752	7348	7936	Gallo-Reynoso (1994)
1993	Jul	1366	263	2594	347	1852	21	6443	7408	8001	Gallo-Reynoso (1994)
1995	Aug							2381	7858	8487	Gallo-Reynoso et al. (2005)
2000	Jun							5644	9346	10094	Gallo-Reynoso et al. (2005)
2003	Jul							7648	12176	13150	Gallo-Reynoso et al. (2005)
2006	Aug							7265	11625	12555	Hernández-Montoya (2009)
2009	Jun–Jul	2763[a]		1567	300	2298	3104	10032	11046	11930	García-Capitanachi (2011)
2010	Jun–Jul	3980[a]		3855	26	3183	2283	13327	17581	18987	García-Capitanachi (2011)
San Benito											
1997	Aug	0	0	0	0	9	247	256	334		Maravilla-Chavez & Lowry (1999)
2000	Jun	21	57	375	51	0	78	582	760		Aurioles-Gamboa et al. (2010)
2007	Jul	17	96	540	292	7	614	1566	2045		Aurioles-Gamboa et al. (2010)
2008	Jul	26	266	494	615	8	704	2113	2759		Aurioles-Gamboa et al. (2010)
2009	Jun–Jul	438[a]		63	633	7	4130	5271	6883		García-Capitanachi (2011)
2010	Jun–Jul	683[a]		538	296	8	978	2503	3268		García-Capitanachi (2011)
2012	Jul					6		4572	5970		Sierra-Rodríguez (2015)
2013	Jul					19		1969	2571		Sierra-Rodríguez (2015)
2014	Jul	2		6	3674[b]	28	0	3710	4844		Sierra-Rodríguez (2015)
2015	Jul	5		13	1460[b]	16	0	1494	1951		Elorriaga-Verplancken et al. (2016b)

[a]Males and subadults
[b]Juveniles and subadults

within the estimated range (3.5–4.5) for other polygynous pinnipeds with increasing populations (Harwood & Prime 1978). We multiplied the number of pups (obtained from the minimum corrected population) by 4.5 to estimate the total Guadalupe fur seal population.

Guadalupe fur seal pups make up an estimated 24 ± 3.4 % of the total population (Gallo-Reynoso 1994, Hernández-Montoya 2009). We therefore applied this percentage to the minimum corrected population estimates to obtain the number of pups born when this value was not available (Table 1). Since the San Benito Islands site is not a reproductive colony, we could not estimate the total population based on the number of pups; thus, we only corrected the non-pup counts for this colony.

The population counts represent the period from the first year animals were reported to have recolonized the 2 islands to the most recent published count (1955–2010 for Guadalupe Island and 1997–2015 on the San Benito Islands). However, counts were made at irregular intervals, and count data are missing for both colonies for some years (Table 1).

Model assumptions

Our model assumed that (1) all individuals are identical, and the count data represent the true number of individuals in a population (i.e. observation error is minimal); (2) the patterns of population growth and fluctuations will be the same in the future (i.e. the mean and variance of the population growth remain constant); (3) environmental conditions are uncorrelated from one year to the next; and (4) there are no catastrophes or bonanzas (Dennis et al. 1991, Morris & Doak 2003). The validity of this type of model has been questioned by some because of the difficulty of projecting the distant future when conditions are challenging to predict (Boyce 1992, Ludwig 1999). However, such uncertainty does not mean that PVA predictions are meaningless given that they contribute to evaluating the potential outcomes of different scenarios — and biologists using their predictions acknowledge the model limitations and are conservative when drawing conclusions and making interpretations (Gerber & González-Suárez 2010).

We evaluated whether these assumptions (except no occurrence of catastrophes and bonanzas) were met to determine if our analysis was valid and, more importantly, to assess whether the violation of any of these assumptions was likely to render our estimates of the probability of extinction optimistic or pessimistic. We did not have enough data to determine whether catastrophes or bonanzas occurred and with what frequency. Thus, our estimates of the extinction risk would be underestimated if one or the other should occur.

Assumption 1: Individuals are identical, and the counts represent the true number of individuals in a population. Observation error results in the failure to count the true number of animals during a survey and will lead to pessimistic measures of viability (Morris & Doak 2003). We accounted for observation error (undercounts) by applying 2 correction factors to the minimum population size estimates, as detailed in the previous subsection. The Guadalupe fur seal counts are not estimates of total population size but rather estimates of the minimum number of animals at a colony. There are 2 main sources of uncertainty regarding the number of fur seals not counted during a survey. The first is that the number of animals counted may be affected by weather, tides, visibility from the boat, observer experience, etc. The second source of uncertainty is due to an unknown number of animals being at sea during any given survey. In our study, we accounted for both sources of uncertainty.

Several methods (models) have been used to account for observation error under different sampling scenarios and for a variety of species (Morris & Doak 2003). However, in our case, applying correction factors previously used by other researchers working with the same or related species was a biologically more informed way to account for the major issue of observation error (undercounts) than trying to fit a model that attempts to estimate these errors (D. F. Doak pers. comm.).

Assumption 2: Mean and variance of population growth do not change over time. After eliminating the observation error from our estimates, it would be reasonable to assume that any variation in the estimated growth rates was due to environmental stochasticity. However, density dependence, demographic stochasticity, and temporal environmental trends may cause growth rates to vary from year to year, violating Assumption 2, and lead to inaccurate estimates of extinction risk.

We tested whether negative density dependence (decline in growth rate at high density) existed in our populations (at each colony and at both colonies combined) by assessing the correlation between $\ln(N_{i+1}/N_i)$ versus N_i. Since the census interval was >1 yr in some cases, we accounted for the time interval as

$$\frac{\ln(N_{i+1})/N_i}{x_i} \qquad (4)$$

where i is year, N_i is population size at time i, N_{i+1} is population size at time $i+1$ and x_i is Eq. (2). If the correlation is significant and positive slope values are present at low population sizes, or negative values are present at larger ones, then the population growth rate is density dependent (Pollard et al. 1987, Morris & Doak 2003).

Demographic stochasticity is the random variation around mean birth and death rates that will cause the growth rate of small populations to vary even in a constant environment with no change at all in mean vital rates (Foley 1994, Mills 2012). The most convenient way to account for demographic stochasticity is to set the quasi-extinction threshold (lower limit population size below which a population goes extinct) at >100 individuals or sufficiently high that demographic stochasticity is minimized (Morris & Doak 2003, Mills 2012). Thus, as we previously described, we assessed the quasi-extinction threshold scenario wherein the population was reduced to 100, 500, and 1000 individuals.

Environmental stochasticity produces random changes in the mean (μ) and variance (σ²) of the population growth rate; the effect can be either positive or negative and will violate the assumption of constant parameters. All populations are inevitably exposed to some degree to environmental stochasticity and will experience good and bad years. There are 2 types of changes in μ and σ². The first one is an abrupt change following an unusual event, with μ and σ² having one value before and another value after that event. The second and most common type of change is an ongoing trend in μ and σ² over a specific number of years, which represents a greater violation of the assumption of constant parameters than the first type. Thus, we explored whether there was a significant linear change in μ by regressing $\ln(N_{i+1}/N_i)$ against year. Finding a significant positive or negative slope would indicate a temporal trend (Mills 2012).

Assumption 3: Environmental conditions are uncorrelated from one year to the next. The count-based PVA assumes all μ values at different time intervals are independent. Where an autocorrelation exists between μ values, the effect may be positive or negative. A positive autocorrelation means that a good year is followed by another good year or that a bad year is followed by another bad year. If μ is density independent, a positive correlation would mean a higher risk of extinction because the events that cause a population to decrease occur in a series. On the other hand, a negative autocorrelation would delay extinction because bad years tend to be followed by good years, leading to an increase in the population (Morris & Doak 2003).

We used the Durbin-Watson d statistic and the autocorrelation coefficient to test the strength of the autocorrelation in the regression residuals (Dennis et al. 1991). We compared the d (positive correlation) and $4 - d$ (negative correlation) with the lower and upper critical values d_L and d_U at a significance level of $\alpha = 0.05$. Finding $d < d_L$ or $4 - d < d_L$ means the residuals are significantly autocorrelated, whereas $d > d_U$ or $4 - d > d_U$ means the residuals are not significantly correlated; otherwise, the test is inconclusive (Kutner et al. 2005).

RESULTS

Model assumptions

We accounted for observation error (undercounts) by applying 2 correction factors to the minimum population size estimates. The μ indicates that no significant density dependence occurred on Guadalupe Island (r = 0.4, p = 0.07) or at both colonies combined (r = 0.3, p = 0.14) over the range of population sizes from 1952 to 2015. However, there does appear to be a density-dependent response in numbers of seals using the San Benito Islands colony over all the years analyzed (r = 0.75, p = 0.007).

Regarding temporal environmental variation, there was no linear change in the rate of increase of the San Benito Islands colony (r = 0.4, p = 0.12) or of both colonies combined (r = 0.4, p = 0.10). However, there was a linear change in the population growth rate in numbers of seals breeding at Guadalupe Island (r = 0.7, p < 0.001). This linear trend may be a function of the significant gaps in the time series count — particularly during the first 4 census counts when the interval between counts was quite wide (e.g. 12, 9, and 6 yr) relative to the rest of the data set (1–5 yr). Such gaps in annual counts make it difficult to identify seasonal tendencies. We confirmed this by carrying out the analysis using data starting in 1983, from which point the time interval was similar between abundance data sets. It showed no evidence of a linear tendency in rates of increase between census count (Guadalupe Island p = 0.61; San Benito Islands p = 0.12; both colonies combined p = 0.87).

Finally, we found no autocorrelation in the population growth rates (μ values) at the San Benito Islands colony ($d = 3.0$, $4 - d = 1$, r = 0.2, p = 0.52, df = 10) or at the Guadalupe Island colony ($d = 1.4$, $4 - d = 2.6$, r = 0.60, p = 0.01, df = 14). For both colonies combined, there was a negative autocorrelation ($d = 2.6$, $4 - d = 1.4$, r = 0.3, p = 0.09, df = 21), although the $4 -$

d value was nearly equal to the d_U (1.5). Thus, the d value leads to a result falling between inconclusive and no significant autocorrelation. Moreover, the first-order autocorrelation of the residuals has a non-significant p-value.

PVA

Guadalupe fur seals have increased at an annual growth rate of 11% on Guadalupe Island and 10% at the San Benito Islands (Table 2, Fig. 2). Both colonies appear to have similar growth rates. However, the lower bound of the 95% CI on these rates also encapsulates a rate of decline at the San Benito Islands of 2%. The higher range of the CI for the San Benito colony is due to the high variability in the recent annual counts (Table 2, Fig. 2). Combining counts

from both islands indicates an overall annual growth rate of 11% and yields an average minimum total population size in 2017 of ~41000 individuals ($\bar{x}$ = 40614, 95% CI = 35778–46877). This represents an increase of 55% over 7 yr from the last population size reported for the species in 2010.

The San Benito population is the less secure of the 2 Guadalupe fur seal colonies and meets the IUCN's quantitative criteria for being Endangered if the quasi-extinction threshold is 100 or 500 seals and Critically Endangered if the threshold is set at 1000 seals (Fig. 3, Table 2). In contrast, the larger population breeding on Guadalupe Island is secure and viable. Treating both colonies as a single population also leads to the same conclusion that the Guadalupe fur seal is not close to the IUCN quantitative analysis criteria for being considered Critically Endangered, Endangered, or Vulnerable (IUCN 2012) and is thus
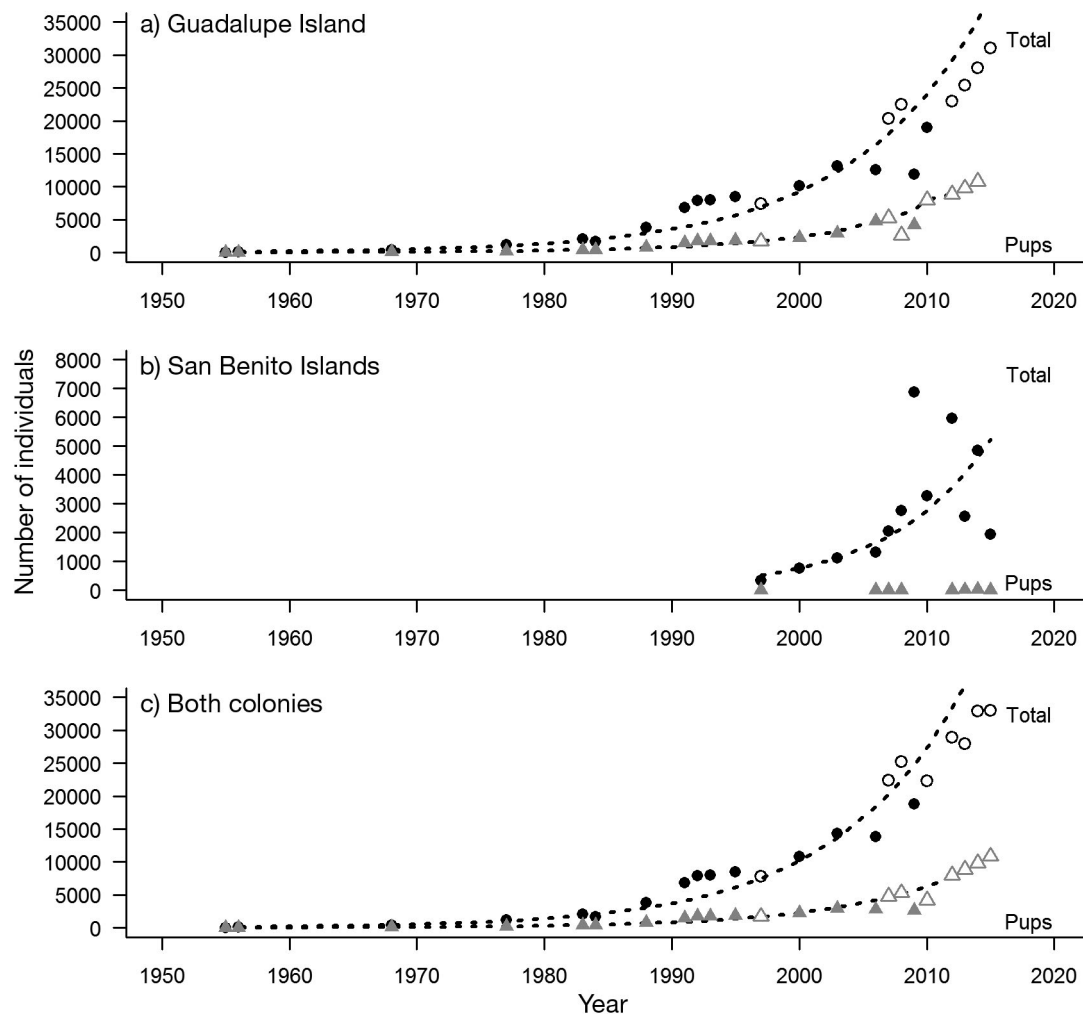

Fig. 2. Corrected numbers of pups born (triangles) and estimated total population size (including newborns) (circles) for Guadalupe fur seals on (a) Guadalupe Island, (b) the San Benito Islands, and (c) both colonies combined. Open circles and triangles represent estimated values for the missing counts for each colony

Table 2. Results of the count-based population viability analysis for Guadalupe fur seals at the Guadalupe Island colony (GI), the San Benito Islands colony (SBI), and both colonies combined showing the stochastic rate of colony increase (λ) and the probability of extinction with 95% CIs occurring in 10, 20, 30, 50, and 100 yr for 3 quasi-extinction levels (N_q; 100, 500, and 1000 seals). Also shown are the IUCN criteria that are met (in **bold**) to be classified as Critically Endangered (CE), Endangered (E), or Vulnerable (V). Note that the mathematical (engineering, E) notation was used for space reasons. (−) not at risk

Colony	λ (95% CI)	N_q	Probability of extinction (95% CI) 10	20	30	50	100	IUCN
GI	1.11 (1.03–1.21)	100	3.8E-12 (4.1E-21 to 6.9E-7)	2.1E-8 (4.8E-19 to 2.3E-3)	1.3E-7 (4.9E-20 to 8.2E-3)	6.1E-7 (4.2E-20 to 5.4E-2)	1.0E-6 (1.4E-18 to **4.2E-1**)	V
		500	2.7E-7 (9.3E-14 to 7.3E-4)	1.2E-5 (1.5E-12 to 2.6E-2)	3.4E-5 (3.6E-13 to 1.1E-1)	6.8E-5 (3.5E-13 to **3.0E-1**)	6.9E-5 (1.8E-12 to **6.8E-1**)	E
		1000	1.3E-5 (3.1E-10 to 6.7E-3)	1.5E-4 (1.9E-9 to 7.3E-2)	2.9E-4 (4.7E-10 to **2.3E-1**)	4.0E-4 (4.7E-10 to **4.7E-1**)	**7.7E-1** (2.1E-9 to **6.9 E-1**)	E
SBI	1.1 (0.99–1.23)	100	7.3E-2 (1.2E-5 to **7.1E-1**[b])	1.4 E-1 (1.0E-5 to **9.6E-1**[b])	1.7E-1 (1.9E-5 to **9.0E-1**[b])	2.1E-1[a] (1.9E-5 to **9.0E-1**[b])	2.4E-1[a] (1.0E-5 to **9.9E-1**[b])	E, CE
		500	**3.0E-1**[a] (1.0E-2 to **9.4E-1**[b])	**4.4E-1**[a] (1.0E-2 to **9.9E-1**[b])	**4.7E-1**[a] (5.5E-3 to **9.9E-1**[b])	**5.0E-1**[a] (5.5E-3 to **9.9E-1**[b])	**5.3E-1**[a] (1.0E-2 to **1.0**[b])	E, CE
		1000	**6.2E-1** (1.0E-1 to **9.7E-1**)	**6.8E-1** (1.0E-1 to **9.9E-1**)	**7.0E-1** (1.0E-1 to **9.9E-1**)	**7.2E-1** (1.0E-1 to **9.9E-1**)	**7.3E-1** (1.0E-1 to **1.0**)	CE
Both	1.11 (1.04–1.19)	100	3.6E-18 (1.4E-30 to 5.1E-11)	2.2E-12 (3.3E-24 to 2.2E-6)	1.2E-10 (5.6E-22 to 2.1E-4)	1.1E-9 (9.4E-22 to 3.4E-3)	2.3E-9 (9.6E-23 to 3.1E-2)	–
		500	4.5E-11 (1.9E-18 to 4.0E-6)	2.9E-8 (7.1E-16 to 8.4E-4)	1.7E-7 (2.2E-16 to 3.3E-3)	4.7E-7 (2.3E-16 to 1.7E-2)	5.8E-7 (1.4E-15 to 8.3E-2)	–
		1000	1.2E-8 (1.3E-15 to 1.8E-4)	9.8E-7 (5.8E-14 to 6.9E-3)	3.1E-6 (1.4E-12 to 1.2E-2)	5.6E-6 (1.5E-12 to 5.0E-2)	6.2E-6 (8.1E-14 to **1.2E-1**)	V

[a]Endangered; [b]Critically Endangered

of Least Concern. However, the probability of extinction at the upper confidence limit meets the IUCN's quantitative criteria for being Vulnerable if the threshold is 1000 seals.

DISCUSSION

A count-based PVA is a useful quantitative technique for determining the probability of Guadalupe fur seals going extinct. While it is impossible to make precise predictions about extinction times for a species, the technique provides insight into a range of likely fates for the 2 colonies of Guadalupe fur seals and the species as a whole.

In contrast to count-based PVAs, demographic PVAs offer more informative predictions for species (e.g. identifying the most vulnerable life history age and sex class, estimating the probability of extinction under different management scenarios). However, better predictions are possible only if age- and sex-specific vital rates are available for the study species. When these data are lacking, it is common to parameterize demographic PVA models with surrogate data based on the assumption that the life history traits and the ecological conditions experienced by the target population are similar to the surrogate population (Caro et al. 2005).

Although the life history parameters for organisms of similar species share general patterns, there are likely major regional differences due to site-specific environmental and demographic conditions specific to each population as well as the anthropogenic disturbances unique to each region. Thus, it may be unrealistic to assume that the demography of one species can serve as a proxy for another species (Nilsen et al. 2009, Murphy et al. 2011). For example, using demographic data from one colony of California sea lions *Zalophus californianus* in the Gulf of California to make predictions for another colony led to erroneous conclusions — which were particularly pronounced when colonies had different population trends (Hernández Camacho et al. 2015).

For the Guadalupe fur seal, we lacked nearly all parameters needed to undertake a demographic PVA. As an exercise, we tried running a model in Vortex (Lacy & Pollack 2014) using surrogate data from northern fur seals. Northern fur seals inhabit the North Pacific Ocean and share habitat in the northern limits of the Guadalupe fur seal population range. Unfortunately, we were unable to run the model because of a lack of data on genetics (e.g. inbreeding depression), status variables (e.g. habitat
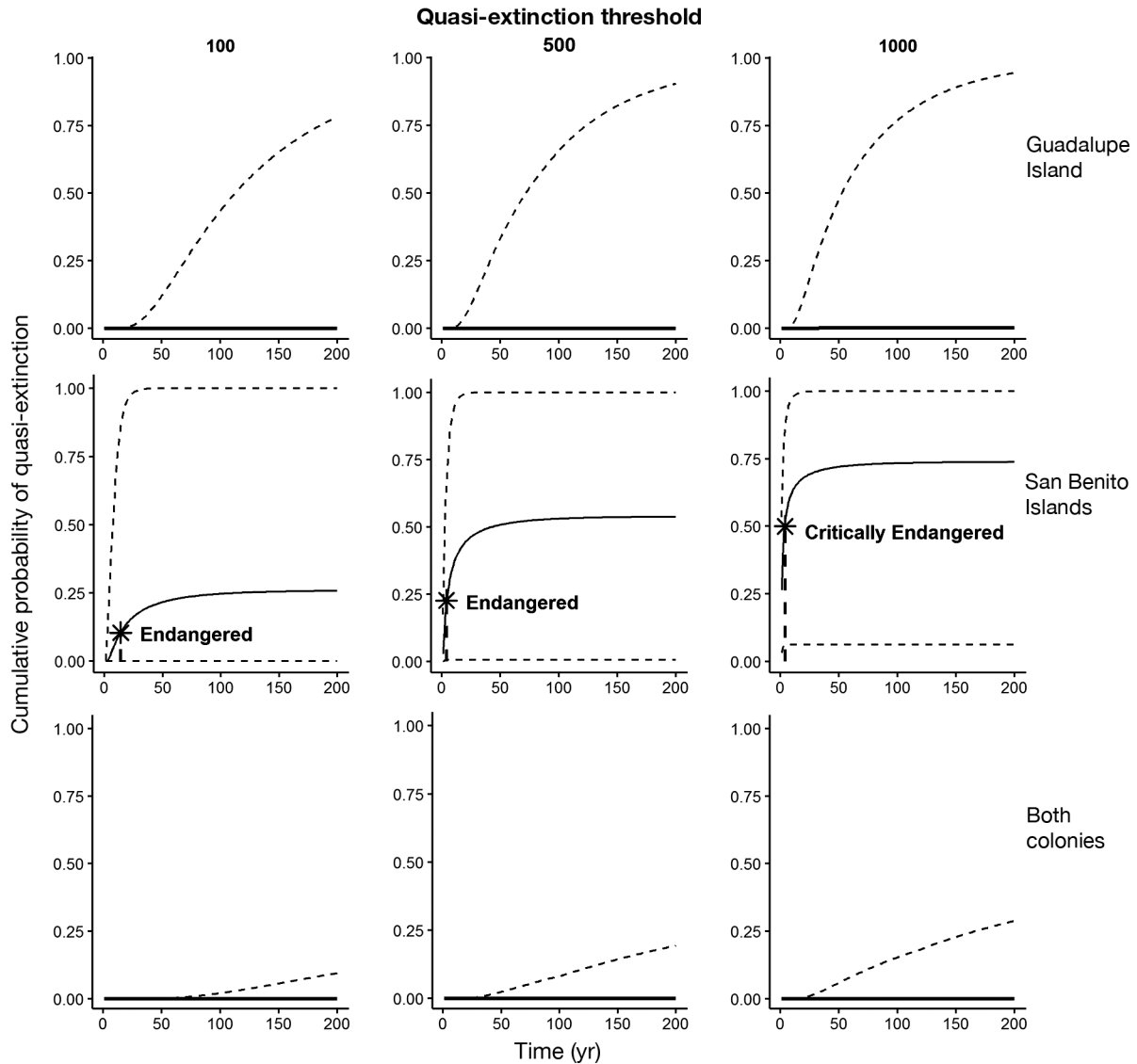
Quasi-extinction threshold

Fig. 3. Unconditional cumulative probability of Guadalupe fur seal numbers falling below the quasi-extinction thresholds of $N_e = 100$, 500, and 1000 seals over time (from 2017 to 200 yr in the future) at the Guadalupe Island colony (top panels), the San Benito Islands colony (middle panels), and both colonies combined (bottom panels). The solid line is the cumulative probability of quasi-extinction (based on the best estimates of mean, μ, and variance, σ^2), and the dashed lines delineate an approximate 95% CI determined by bootstrapping. Stars indicate when the probability of extinction in the wild is at least 50% (Critically Endangered when occurring within 10 yr or 3 generations, i.e. 30 yr), 20% (Endangered when within 20 yr or 5 generations, i.e. 50 yr), and 10% (Vulnerable when within 100 yr or 5 generations) (IUCN quantitative analysis criteria)

characteristics), dispersion between colonies, and catastrophes (e.g. survival frequency and survival effect).

Model assumptions

A count-based PVA model can provide reasonable assessments of extinction probabilities as long as the assumptions of the model are met (Boyce 1992).

Specifically, violating the density independence assumption can lead to inaccurate results (Morris & Doak 2003). In our study, the density independence assumption was not met for the San Benito Islands colony. However, PVA models can still provide an accurate assessment of the extinction probability as long as the population does not increase or decrease drastically over the study time horizon (Sabo et al. 2004). Meeting the model assumption of density independence was only met when San Benito was

combined with Guadalupe Island to treat both colonies as a single population.

The rate of increase in fur seal numbers between census counts at Guadalupe Island was linear over time but not at the San Benito Islands colony or at both colonies combined. The linear increase in growth rates at Guadalupe Island violates the PVA model assumption that mean growth rates are constant. However, we suspect that the linear trend at Guadalupe Island is an artifact of the paucity of census counts at the beginning of the time series—and not because the growth rate changed significantly.

Although there was a negative autocorrelation in the growth rate (μ) values for both colonies combined, it was a very weak correlation (the d value of the Durbin-Watson test fell between inconclusive and no significant autocorrelation). A negative autocorrelation will cause viability results to be overly optimistic (delaying extinction) (Morris & Doak 2003). However, in our case, the effect was negligible.

We were unable to determine if catastrophes or bonanzas occurred over the years we analyzed. However, we observed notable variability in counts in recent years, especially at the San Benito Islands, which coincided with the 2015 El Niño event (Elorriaga-Verplancken et al. 2016b) and the Blob, which reached the waters of the west coast of the Baja California peninsula in 2014 and 2015 (Cavole et al. 2016). These 2 events occurred simultaneously and affected organisms at all levels of the food web (Kintisch 2015).

In addition to the assumptions tested, genetic factors may also influence population viability. Very small populations have certain genetic disadvantages (e.g. low genetic diversity) that increase the risk of extinction because of environmental and demographic stochasticity (Mills & Smouse 1994, Armbruster & Reed 2005). To evaluate such scenarios, the effective population size (i.e. the size of an ideal population that experiences genetic drift at the same rate as the population in question) can be used to estimate the rate of inbreeding and the genetic variation in wildlife (Frankham 1995, Charlesworth 2009, Husemann et al. 2016).

The Guadalupe fur seal population went through 2 bottlenecks—and is now increasing. Although this species has still not returned to its original population size (estimated at ca. 200 000 individuals) (Hubbs 1956a), the population is considered genetically robust (Bernardi et al. 1998, Weber et al. 2004). The effective population size (N_e) for the Guadalupe fur seal during the 2015 breeding season was 13 627 individuals for both colonies, and its harmonic mean (average N_e) was 283 individuals (Frankham 1995). We calculated the effective population size as $N_e = 4N_{ef}N_{em}/N_{ef} + N_{em}$,

where N_{ef} is the corrected number of breeding females, and N_{em} is the number of breeding males — with adult males assumed to comprise 15% of the total population and adult females 33% (data from Hernández-Montoya 2009). The estimated effective population size for the Guadalupe fur seal is significantly higher than that reported for the South American fur seal *Arctocephalus australis* in Peru (N_e = 2153 individuals), which is in danger of extinction and has decreased significantly (de Oliveira et al. 2006). Genetic drift may thus have a greater impact on the South American fur seal population than on the Guadalupe fur seals.

The Guadalupe fur seal counts covered only a few years and were made at irregular intervals, with some missing years for both colonies. Despite these shortcomings, we met most of the model assumptions, including that the growth rate be density independent (which could have led to inaccurate estimates of extinction risk). We also ruled out genetic factors affecting the PVA.

Even if some assumptions of our PVA had been violated, count-based models are still very useful (Morris & Doak 2003). They provide, for example, relative measurements of extinction risk, facilitating comparison of the extinction risks of different species or populations.

A greater concern than violating assumptions is that limited count data sets can compromise the reliability of viability measurements. The minimum number of counts recommended to obtain reliable estimates of extinction is 10 (Morris & Doak 2003). In our case, we had 16 for Guadalupe Island and 10 for the San Benito Islands.

Thus, both count-based as well as demographic PVA models are useful for estimating the probability that a population will persist. Researchers must consider the available data and the specific goals of their research when selecting the most appropriate model for a given study (Coulson et al. 2001, Gerber & González-Suárez 2010).

PVA

The San Benito Islands colony is a recolonization of a former breeding site and appears to be well established after 2 decades of occupation (1997–2017; Fig. 2). However, variability in colony size from one year to the next has been extremely high during the past decade (ranging from 6883 seals in 2009 to just 1951 seals in 2015; Fig. 2). In addition, the San Benito colony is not yet a distinct breeding population because so few pups are currently born here (pups

represent <1% of the total San Benito population). Thus, most of the changes in numbers at the San Benito Islands reflect immigration of individuals from Guadalupe Island rather than reproduction.

The San Benito Islands colony can be considered the 'bedroom community' of the Guadalupe Island colony. It is essentially a resting place where large numbers of non-breeding animals born on Guadalupe Island stay between feeding trips (Aurioles-Gamboa et al. 2017). A small number of pups are born here (<30 pups; Table 1), but it is not yet large enough to be considered a breeding site. For some species, such as Steller sea lions (Pitcher et al. 2007), numbers of pups born need to exceed 100 before a haulout is reclassified as a rookery. Should births continue to increase at the San Benito Islands, there is every reason to expect it will become large enough to be recognized as a second breeding location for Guadalupe fur seals.

The relationship between the 2 island colonies means their numbers should be totaled and treated as a single population to assess the conservation status of Guadalupe fur seals. Combining the 2 sets of counts showed an overall annual growth rate of 11% and a world population totaling ~41000 Guadalupe fur seals in 2017 ($\bar{x}$ = 40614, 95% CI = 35778−46877; Fig. 2c). While these positive changes bode well for the future of Guadalupe fur seals, notable drops in numbers from one year to the next and the volatile variability in counts in recent years at the San Benito Islands suggest they may be particularly vulnerable to shifts in the availability of prey caused by extreme climatic events such as occurred in 2014 (the Blob) and 2015 (El Niño) (Cavole et al. 2016, Elorriaga-Verplancken et al. 2016b, Aurioles-Gamboa et al. 2017).

The impact of extreme climatic events on Guadalupe fur seals will be reflected in their vital rates in the coming years. Unfortunately, birth and death rates have never been estimated for this species. Obtaining age- and sex-specific vital rates would provide better monitoring and allow more complex models to be developed to assess the sensitivity of annual population growth rate to changes in vital rates. Such models could also be used to incorporate factors such as density dependency and environmental and demographic stochasticity (Caswell 2001).

There is considerable concern about the population status of pinniped species around the world (Kovacs et al. 2012). Like the Guadalupe fur seal, other otariids (eared seals, sea lions, and fur seals) were historically hunted to the point that their populations were significantly reduced. Most of these species are increasing, and their populations appear to be thriving (e.g. Guadalupe fur seal, Juan Fernandez fur seal, Australian fur seal, Antarctic fur seal). However, in many cases seal populations have not recovered to their pre-exploitation numbers. Half of the sea lion species (3 species) and 1 fur seal species (Galapagos fur seals) have declining populations and are classified as Endangered on the IUCN Red List (Kovacs et al. 2012). The causes of these population declines include direct and indirect fisheries interactions, low food availability, changes in the prey base associated with El Niño events, and changes due to ecosystem shifts (Gerber & Hilborn 2001, Kovacs et al. 2012).

PVA models are key for assessing the population status and effectiveness of different management recommendations. However, it has only been possible to run these models on some species because the necessary vital rates data are lacking (Steller sea lion *Eumetopias jubatus*, New Zealand sea lion *Phocarctos hookeri*, California sea lion *Z. californianus*) (Gerber & VanBlaricom 2001, Maunder 2004, Szteren et al. 2006, Winship & Trites 2006, Chilvers 2012).

Our finding that the Guadalupe fur seal meets the IUCN quantitative analysis criteria for being listed as Least Concern concurs with its current status on the IUCN Red List (IUCN 2012). We recognize that a PVA is only one of a number of criteria used to assess population status and that conservation decisions are based on multiple criteria that address geographic range, habitat requirements, and demographics (generation time, population size, population structure, age at maturity) and identify threats (COSEWIC 2013, IUCN 2017). However, PVA is an extremely important component of wildlife assessment (Beissinger & McCullough 2002) and has become a valuable tool to predict the conservation status of marine mammal species (e.g. Gerber & VanBlaricom 2001, Shelden et al. 2001, Szteren et al. 2006, Winship & Trites 2006, National Marine Fisheries Service 2008, Chilvers 2012).

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