

Managed culls mean extinction for a marine mammal population when combined with extreme climate impacts

Katrina J Davis^{*}

Department of Biology, University of Oxford, 11a Mansfield Road, Oxford, OX1 3SZ, United Kingdom

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ABSTRACT

Human actions led to the worldwide decline of marine mammal populations in the 18th–19th centuries. Global adoption of protective legislation during the 20th century has recently allowed many marine mammal populations to recover. This positive trend is particularly true of pinnipeds (e.g., seals and sea lions), whose recovering populations are increasingly in conflict with fisheries. Fisheries organisations have called for managed culls of sea lion populations to reduce competition for target fish species as well as damage to catch and fishing gear through operational interactions. However, despite widespread perceptions that sea lion populations are generally increasing, to-date, culls have often been considered or implemented without quantitative evidence of their impacts on seal lion population viability. This knowledge gap is particularly concerning given the expected increase in extreme climate conditions, such as extreme El Niño events, which together with culls could push sea lion populations in some parts of the world into the extinction vortex. Here, I develop stochastic matrix population models of the South American sea lion (*Otaria flavescens*) parameterised through a combination of species-specific field data and phylogenetic imputation using data from related species in the COMADRE animal matrix database. Using these models, I project the impact of (1) three cull scenarios with different intensity and temporal frequency targeting adult females, (2) extreme El Niño events whose frequency is modelled using a Markovian transition matrix, and (3) the interaction of culls and extreme climate events on population dynamics. I focus on the Chilean population of *O. flavescens*, where recent increases in sea lion numbers have triggered widespread conflict with small-scale fisheries, and where sea lion populations will increasingly be affected by extreme El Niño conditions. I find that sea lion populations decline below minimum viable population sizes within 16–28 years under all scenarios involving culls and extreme climate events. This research explicitly incorporates parameter uncertainty into population projections—in so doing, it illustrates the need for future research to collect stage-specific, annual population data to reduce uncertainty regarding marine mammal vital rates.

1. Introduction

Human actions, notably hunting, led to the worldwide decline of marine mammal populations in the 18th–19th centuries (Gerber and Hilborn, 2001). Fortunately, the global adoption of protective legislation during the 20th century has allowed many populations to bounce back (Magera et al., 2013). This is particularly true of pinnipeds, including sea lions (Milano et al., 2020), whose recovering populations are now increasingly in conflict with fisheries (Cook et al., 2015; Scordino, 2010). The exact economic impacts of conflict between fisheries and sea lion populations are unknown. Regardless, the perception that

these impacts are large and increasing has led many fisheries organisations to call for managed culls of sea lion populations. The expectation is that reducing sea lion numbers will reduce competition for target species (i.e., biological or predatory interactions (Beverton, 1985)), and damage to catch and fishing gear (i.e., operational interactions (Beverton, 1985)). However, before managers can sanction population culls, it is essential to understand the projected impacts of these culls on the viability of natural populations. For a population to be viable, it must be able to withstand stochastic perturbations, e.g., environmental stochasticity or natural catastrophes, in the long-term given its specific biogeographic setting (Shaffer, 1981). Thus, a robust population

Abbreviations: MPM, Matrix population model.

^{*} Corresponding author.

E-mail address: Katrina.davis@biology.ox.ac.uk.

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viability assessment of sea lions must incorporate the impact of future climate change, which may have profound consequences for these animals (de Oliveira et al., 2012; Kovacs et al., 2012).

To-date, most pinniped demographic research has had a methodological focus—with the objective of developing population models when demographic data are limited. This includes work by Kauhala et al. (2012), who estimated demographic structure and mortality rates of the Baltic grey seal population based on the age structure present in hunted grey seals (*Halichoerus grypus*), and Wielgus et al. (2008) who used inverse methods to estimate demographic rates and asymptotic population growth rates for the California sea lion (*Zalophus californianus*). Other analyses have focused on assessing the impact of site selection and data aggregation decisions on estimates of population survival in grey seals (Engbo et al., 2020). Recently, Rossi et al. (2021) used an integrated population model to assess the impact of sustainable harvest on grey seal populations in Canada—with the ultimate goal of reducing seal predation of key fish stocks while maintaining a viable grey seal population size in line with conservation goals. Finally, Silva et al. (2021) have assessed the viability of harbor seal (*Phoca vitulina*) populations in Sweden and Denmark under different hunting levels, disease threat from epizootic outbreaks, and reduction in fecundity due to xenobiotics. By contrast, the contribution of the current analysis is to assess the impact of managed culls in combination with extreme climate events—as well as to explicitly incorporate uncertainty regarding vital rates into the model architecture. This analysis therefore provides a first step towards understanding the potential impact of managed culls and extreme climate events on the population dynamics of a marine mammal species whose demographic parameters are highly uncertain.

Here, I overcome limitations in the availability of demographic data by building a stochastic demographic model that incorporates parameter uncertainty in a species that is at the center of much human-wildlife conflict: the South American sea lion (*Otaria flavescens*, (Cappozzo and Perrin, 2009)). Specifically, I explore the potential impacts of managed culls and projected climate change impacts on the population dynamics of *O. flavescens* in Chile. Recovery of this species (*O. flavescens*) has led to widespread conflict with small-scale fisheries (Davis et al., 2021), particularly along the coast of Chile. Although Chile does not currently cull sea lion populations, a moratorium on sea lion harvest expires in 2021 (Decreto Exento N° 31 2016 (CL)), thus creating a legal loophole for which quantitative evidence is urgently missing. Culls of sea lion populations are widely demanded by fishing communities in this region (Davis et al., 2021), and hence there is a need to assess their potential impacts on the species. However, this region is also affected by extreme El Niño conditions, which have previously had large negative impacts on pinniped populations in the north of Chile and also in neighbouring Peru (de Oliveira et al., 2012; Sepúlveda et al., 2015). Extreme El Niño events are characterised by sea surface temperatures exceeding 28 °C (Cai et al., 2014). These conditions lead to large decreases in prey availability—causing decreases in fecundity and increases in juvenile and adult sea lion mortality (de Oliveira et al., 2012).

To assess the impact of managed culls and extreme climate events on the Chilean population of *O. flavescens*, I combine known and phylogenetically imputed vital rates (i.e., stage-specific survival (σ), maturation (γ), and reproduction (ϕ)) for *O. flavescens* to parameterise stochastic matrix population models. I then project the *O. flavescens* population under a range of scenarios and impacts. Scenarios include a base case scenario—absent of any cull or extreme climate impacts, as well as three cull scenarios with different intensity and temporal frequency targeting adult females, and an extreme climate scenario where extreme El Niño conditions impact sea lion vital rates at frequencies expected for the coming century. Finally, I assess the combined impact of culls and extreme climate events on sea lion population size through time. I hypothesise that the impact of managed culls or extreme climate events in isolation will not adversely affect the viability of this population. However, I expect that the population will decrease below a minimum viable population size, thus become functionally extinct (*sensu* Shaffer,

1981), under managed culls in combination with projected frequencies of extreme El Niño conditions. The findings of this research will provide quantitatively-based recommendations for the management of human-wildlife conflict between pinnipeds and fisheries.

2. Methods

In what follows, I provide an overview of the modelling framework, followed by detailed information on the study species, and of the demographic and climate modelling approaches. To assess the impact of managed culls and extreme climate conditions on the population dynamics of a marine mammal on the west coast of South America, I parameterised a stochastic matrix population model (MPM, hereafter) for the South American sea lion (*Otaria flavescens*). MPMs combine information about the rates of survival (σ), maturation (γ), and reproduction (ϕ) (i.e., vital rates) experienced by individuals in discrete time within discrete stages (e.g., juvenile, adult) in a population to produce a model describing the dynamics of the whole population (Caswell, 2001). Though initially MPMs only considered age (Leslie, 1945), now these models often include other predictors of vital rates, such as developmental stage, and/or size (Crone et al., 2011), allowing for a wider range of life cycles to be assessed, e.g., species with shrinkage (Salguero-Gómez and Casper, 2010). MPMs are a flexible tool that have been used in applications as diverse as assessing the impact of temporal environmental autocorrelation on population viability (Paniw et al., 2018), or to develop optimal harvesting strategies (Gamelon et al., 2012). Because of their relative ease of construction, analysis, and interpretation (Griffith et al., 2016), MPMs have been developed for thousands of species (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016b), including other pinniped species, such as the endangered Kuril harbour seal (*P. vitulina stejnegeri*) in Japan (Kobayashi et al., 2014), and New Zealand sea lion (*Phocartos hookeri*) in the Southern Pacific Ocean (Meyer et al., 2015). In this analysis, I parameterised a MPM for *O. flavescens* based on species-specific vital rate data, and vital rates imputed using phylogenetic comparative methods from other closely-related pinniped species. The resulting variance in these imputed vital rate estimates informed a distribution of matrix population models. Using a population vector of stage-specific population estimates, I then projected the population under different management and climate scenarios. To assess the impacts of culls and extreme climate events on *O. flavescens* population viability, I conducted eight separate analyses of the population dynamics of *O. flavescens* over a 30-year time horizon. First, I assessed a base case condition (I), without managed culls and in the absence of extreme climate impacts. Then, I assessed the impact of three population cull scenarios: (II) 15% of adult females in year one, (III) 10% of adult females every year, and (IV) 30% of adult females every five years. These cull scenarios describe trade-offs in culling-effort (and population impact) through time, as well as mimicking a range of harvest conditions previously considered in Chile (Sepúlveda et al., 2006). Next, I assessed the impact of extreme climate events (V), represented by extreme El Niño conditions whose frequency I modelled using a Markovian transition matrix and whose impacts on vital rates were informed by observations from previous extreme El Niño years (Sielfeld and Guzmán, 2002; Soto et al., 2004). Finally, I assessed the combined impacts of the same three cull scenarios in combination with extreme climate events (VI–VIII) (Fig. 1). Below, I describe each of these steps in more detail.

2.1. Study species

The South American sea lion (*O. flavescens*) is found along the South American coast, from Peru to Brazil, with a global population of ~400,000 individuals. Of these, 50% are found in Chile (Dans et al., 2004; Oliva et al., 2020). The species has been described as having plastic trophic habits, with diet determined by local prey abundance (Hückstädt and Antezana, 2006). In Chile, prey species include anchovy

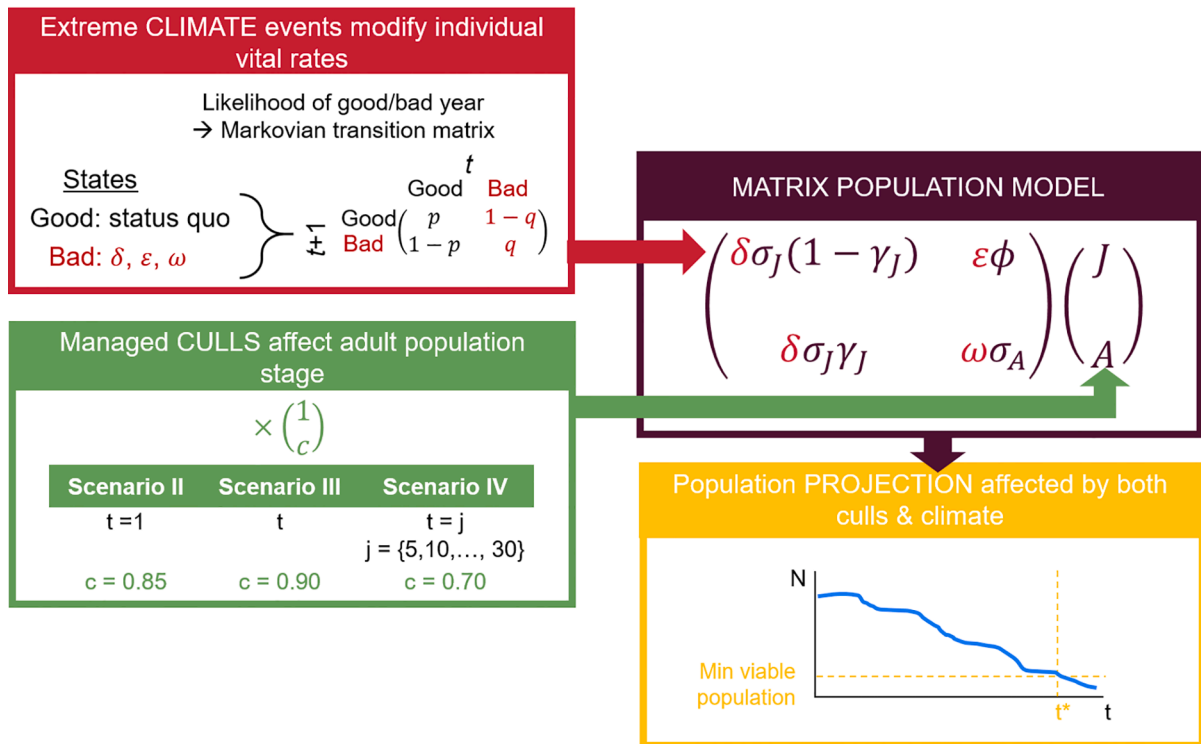


Fig. 1. Overview of methodological pipeline to project the population dynamics of the South American sea lion (*Otaria flavescens*) using a matrix population model (dark purple panel) under the separate and combined impacts of managed culls (green panel) and extreme climate impacts (red panel). The vital rates of the matrix population model are: σ = survival; γ = maturation; and ϕ = fecundity; representing juvenile females and adult females. Stage-specific managed culls remove adults from the population with different intensities (c = moderator describing population remaining after culling) and frequencies (t = year). Extreme climate events, here extreme El Niño events, will alter vital rates by the terms δ (impacts on juvenile survival), ω (impact on adult survival), and ε (impact on fecundity). The frequency with which extreme climate events will occur is controlled through a Markovian transition matrix, where p = probability of climate remaining good, e.g., the absence of extreme climate conditions, and q = probability of extreme climate conditions. The population (N) of *O. flavescens* is projected over time (yellow panel) and assessed with relation to the year (t^*) in which the population drops below a minimum viable population size (dashed yellow lines).

(*Engraulis ringens*), elephant fish (*Callorhynchus callorhynchus*), and hake (*Merluccius gayi*) (Hückstädt and Antezana, 2006). *O. flavescens* is one of the largest and most sexually dimorphic otariids (family Otariidae, describing pinnipeds with ears), with adult males reaching 3 m in length and 300–350 kg, and adult females reaching 2 m in length and weighing up to 150 kg (Cappozzo and Perrin, 2009). The species is polygynous, with males attempting to mate with as many females as possible (Cappozzo and Perrin, 2009). In Chile, the ratio of adult males to females in 2019 was ~1:11 (Oliva et al., 2020). Adult females typically produce one pup each year (Soto et al., 2004), and the sex ratio at birth is 1:1 (Cappozzo and Perrin, 2009). In this analysis, I adopted a simplified female-only life cycle with pup and juvenile stages collapsed into a single ‘juvenile’ stage. This approach is consistent with several other studies that focused on female population dynamics (e.g., Barlow and Boveng, 1991; Hadley et al., 2006; Lalas and Bradshaw, 2003), and allowed me to better accommodate the emergent uncertainty from the available field data than more complex life-cycle models.

2.1.1. Vital rate estimation

I combined species-specific and imputed vital rates to parameterise stochastic MPMs for *O. flavescens*. Some information on vital rates for *O. flavescens* was available from Sepúlveda et al. (2006). Specifically, these authors estimated juvenile-adult maturation and adult fecundity for *O. flavescens* populations in the central regions of Chile. Other vital rates (juvenile and adult survival) needed to be imputed due to the lack of available field information. Following recent findings regarding the robustness of phylogenetic methods to impute vital rates and life history traits (James et al., 2020; Johnson et al., 2021; Penone et al., 2014), I imputed juvenile survival and adult female survival using the

Rphylopars package (Goolsby et al., 2017) in R (R Core Team, 2021). This method imputes missing data across a set of phylogenetically-related species (11 pinniped species in this case, including the target species) using a phylogeny and sparse trait matrix to simultaneously estimate phylogenetic and phenotypic trait covariance. Previous literature has shown that imputation methods based on traits and phylogeny are generally superior (Penone et al., 2014), hence this approach was followed. I sourced vital rates for 10 pinniped species from the COMADRE Animal Matrix Database v.4.20.11.0 (Jones et al., 2021). COMADRE houses 3321 MPMs for 415 animals worldwide. In the case of pinnipeds, six of the 10 species contained >1 MPM, while four species were represented by only 1 MPM. Available matrices described unmanipulated populations (i.e., no experimental treatments).

For the variable number of stages in the 11 pinniped species to be consistent with my 2-stage life cycle (Fig. 2A), I collapsed available matrices to 2×2 stages (juveniles and adults) following methods by Salguero-Gomez and Plotkin (2010), using the R package Rage (Jones et al., 2021). Also using Rage, I estimated stage-specific vital rates (mean and standard deviation) for each species. For the six pinniped species with multiple MPM available, I sampled 1000 estimates of each vital rate using the mean and standard deviation across the available MPMs, drawing from a truncated normal distribution (0–1 for survival and maturation, and 0– ∞ for fecundity). I sourced a phylogenetic tree for mammals from Vertlife (Upham et al., 2019), which I pruned to the 11 pinniped species with MPM data from COMADRE and *O. flavescens* using R package ape (Paradis and Schliep, 2019). Using Rphylopars (Goolsby et al., 2017), I imputed missing vital rates for *O. flavescens* for each combination of the 1000 estimates of vital rates for females of related species. I then parameterised MPMs for each of these 1000 estimated

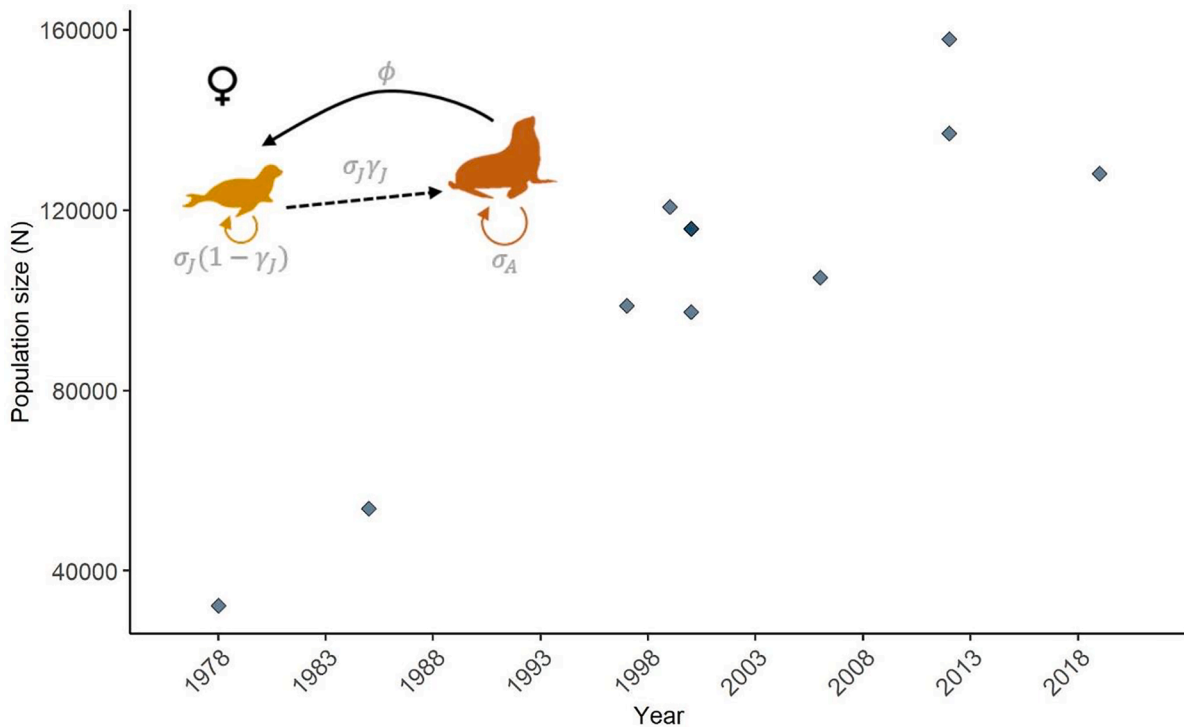


Fig. 2. Reported estimates of the total population size of *Otaria flavescens* (South American sea lion) along the coast of Chile through time with insert of the life cycle of female sea lions. Stages: J = juvenile female (< 4 years), A = adult female (≥ 4 years); Vital rates: σ = survival; γ = maturation; ϕ = fecundity. Data sourced from Contreras et al. (2014); MMA (2012); Oliva et al. (2003); Sepúlveda et al. (2006); Sielfeld (1999); Torres et al. (2000a) Oliva et al. (2020).

vital rate values. An evaluation of the imputation method is provided in the Supplementary Materials. This evaluation shows that known vital rates can be successfully imputed, but that estimates are better when only single vital rates are ‘missing’ compared to pairs of vital rates. Previous findings have also shown that phylogenetic imputation performs well for vertebrates (Di Marco et al., 2021; James et al., 2020; Penone et al., 2014).

2.1.2. Population data

I combined a vector of stage-specific population data with the MPMs to project the population through time. Changes in the abundance of the Chilean population of *O. flavescens*, as reported in government censuses and the published literature (see caption for citations), are shown in Fig. 2. Stage-specific population estimates for *O. flavescens* from a post-breeding census were available for 2019 from Oliva et al. (2020). In this most recent census (2019) for Chile, there were an estimated 78,709 adult females (SD estimated in current study = 1050), 7,126 juveniles (SD = 223), and 29,827 pups (SD = 992). Based on final reported values from Oliva et al. (2020), and assuming a sex ratio of 1:1 in pups and juveniles, I calculated a combined pup and juvenile estimate for females (hereafter referred to simply as ‘juvenile’) of 18,477. These data provided a two-stage population vector for 2019 of 78,709 adult females and 18,477 juvenile females for the entire Chilean population (Fig. 2).

To understand the base case dynamics of *O. flavescens* (scenario I), I projected the population of juvenile and adult females over 30 years (2019 – 2049) without any impacts of cull or extreme climate impacts. To do so, at time $t + 1$, I sampled a single MPM from the 1000 estimated MPMs, and multiplied this matrix by the population vector in time t . I iterated this process 1000 times.

$$\begin{pmatrix} \sigma_J(1 - \gamma_J) & \phi \\ \sigma_J\gamma_J & \sigma_A \end{pmatrix} \times \begin{pmatrix} J \\ A \end{pmatrix} \quad (1)$$

The top left-hand term of the matrix describes the probability that a juvenile female (J) survives (σ_J) but remains a juvenile in year $t + 1$. The

bottom left-hand term of the matrix describes the probability that a juvenile female survives and matures (γ_J) into an adult (A) in year $t + 1$. The bottom right-hand term of the matrix describes the probability an adult female survives (σ_A) to year $t + 1$. Finally, the top right-hand term of the matrix describes the number of juvenile females that an average adult female contributes to the population each year (ϕ). The two-element vector (J, A) describes the population size of juvenile females and adult females in year t .

To evaluate whether the population of *O. flavescens* will become functionally extinct during the modelled time horizon, I assessed whether and at what point in time the projected population drops below a minimum viable population size (MVP, *sensu* Shaffer, 1981). I used a MVP value of 5000 breeding adults, thought to be sufficient to ensure long-term population persistence and to avoid evolutionary decay across a broad range of taxonomic groups (Traill et al., 2010). Based on the sex ratio observed in the Chilean population (1:11.45 adult males to females), this criterion implies an MVP for adult females of 4,598 individuals. I quantified the time that quasi-extinction was reached as the year when >95% of 1000 simulated projections produced a population size (N) below the MVP value (Morris and Doak, 2002).

2.2. Cull simulations

I assessed the impact of three different cull scenarios on the population of *O. flavescens* in Chile over 30 years. The three scenarios I considered were:

- Scenario II. Cull 15% of adult females in year 1 only.
- Scenario III. Cull 10% of adult females every year; or
- Scenario IV. Cull 30% of adult females every 5 years.

These cull levels mimic a range of harvest conditions previously considered in Chile (Sepúlveda et al., 2006). I simulated these culls on adult females rather than juveniles as culling in pinnipeds has historically targeted adults due to their better accessibility relative to juveniles,

particularly during the breeding season when adult females come to shore to pup. To estimate the impact of managed culls, I assessed the population dynamics of *O. flavescens* as described previously, but with the relevant proportion of the adult female population removed from the population vector at the appropriate time step, e.g., year 1 in scenario II, and every five years for scenario IV.

2.3. Climate conditions

In scenario V, I assessed the impact of extreme climate events on the population of *O. flavescens* in Chile. To model transitions between ‘normal’ and extreme climate years, I used a Markovian transition matrix. At each time step t (i.e., each year), climate is probabilistically assigned as normal or as an extreme climate year. If t is a normal year, then the MPM used to estimate the population in $t + 1$ is drawn from the base case distribution. If t is an extreme climate year, the MPM is drawn from an extreme climate distribution, here indicating a year with an extreme El Niño event (Cai et al., 2014), an event for which austral summer rainfall is greater than 5 mm per day. These extreme El Niño events, which included the 1982/83 and 1997/98 El Niño events, are characterised by exceptional warming, with sea surface temperatures exceeding 28 °C extending into the eastern equatorial Pacific (Cai et al., 2014). These conditions lead to large decreases in prey availability (de Oliveira et al., 2012) and cause widespread environmental disruptions in the Pacific and beyond. Previous research in Peru, which neighbours Chile to the north, describes a 100% mortality of juveniles and 60% mortality of adults during the 1997/98 El Niño (Soto et al., 2004). Decreases in fecundity of 95% were also observed during this period (Soto et al., 2004). Siefert and Guzmán (2002) estimated similar levels of pup and juvenile mortality for populations in northern Chile. To represent these effects in my simulations, I modified each of the 1000 previously estimated MPMs as below.

$$\begin{pmatrix} \delta\sigma_J(1 - \gamma_J) & \varepsilon\phi \\ \delta\sigma_J\gamma_J & \omega\sigma_A \end{pmatrix} \quad (2)$$

Where δ indicates the impact of extreme climate events on juvenile survival, ω indicates the impact on adult survival, and ε indicates the impact on fecundity. I parameterised these elements according to previous estimations as a 100%, 60%, and 95% decrease in the respective vital rates (Soto et al., 2004). This approach provided a distribution of matrix population models for extreme climate years. The population projection was as previously described, but this time, a Markovian transition matrix determined whether the population vector in $t + 1$ was multiplied by a matrix from the base case (e.g., ‘normal’ climate years) or extreme climate distribution of MPMs.

El Niño events typically last 12–18 months (National Oceanic and Atmospheric Administration 2022), and the frequency of extreme El Niño events is predicted to increase under global warming (Cai et al., 2018). Relative to a ‘control’ period (1891–1990), when the frequency of extreme El Niño conditions was estimated at one event every 20 years, under current and future climate conditions (1991–2090), extreme events are predicted to occur once every ten years (Cai et al., 2014). I used this prediction to parameterise the Markovian transition matrix. When climate was ‘normal’ for the population in time t , the probability of climate transitioning to an extreme climate scenario in $t + 1$ was 0.1 ($1 - p$, Fig. 1, red panel). When extreme climate conditions were prevalent in time t , the probability of climate transitioning to good in $t + 1$ was 0.5 ($1 - q$, Fig. 1, red panel). This transition is consistent with NOAA observations of El Niño durations (12–18 months).

2.4. Culls and climate

In scenarios VI–VIII, the previously described processes: culls and extreme climate conditions, were combined. These separate stressors impact the population in a multiplicative fashion: at $t = i$, culling

removes a given proportion of adult females; if the Markovian transition matrix defines climate as extreme in this time period, then the revised vector of juvenile and adult population size is multiplied by a MPM drawn from the extreme climate distribution, which incorporates extreme climate impacts on population vital rates. This approach allows me to assess impacts that are expressed at the individual level—culls, which remove individuals from the population—with impacts observed at the broader population level—the impact of extreme climate events on vital rates. I assessed the same three cull scenarios (II–IV), and in each of these scenarios I incorporated extreme climate conditions as previously described in scenario V.

2.5. Transient dynamics

Transient dynamics, the short-term dynamics of a population perturbed from a stationary stable population structure, provide further insight into the impact of different cull and extreme climate scenarios on the *O. flavescens* populations (Capdevila et al., 2020; Stott et al., 2011). Specifically, by assessing demographic amplification and demographic attenuation—respectively, how a population increases in size after disturbance or alternatively, decreases in size after disturbance (Capdevila et al., 2020)—we can understand how far a disturbance perturbs a population away from its stationary equilibrium. In this sense, it is important to note that a population that fails to resist a disturbance will show a high value of attenuation, and vice versa (Capdevila et al., 2020). I assessed the largest and smallest population size (e.g., maximum amplification and attenuation values), as well as the 5th and 95th percentile population size, observed across all scenario iterations 10 years into the projection. I then assessed the percentage of model iterations that amplify or attenuate relative to the average base case (scenario I) population size at year 10 for all scenarios. At that time point, populations in all scenarios have been subject to disturbance, either through culls, extreme climate, or both, but importantly have not converged back to stationary equilibrium conditions.

2.6. Sensitivity analysis

To identify how the population viability of *O. flavescens* is affected by extreme El Niño conditions, I assessed the sensitivity of results to different extreme El Niño impacts on vital rates. For each of the vital rates: (i) juvenile survival, (ii) juvenile maturation, (iv) adult survival, and (v) fecundity, I assessed a range of possible impacts varying from no impact, to a 100% decrease in each vital rate. I discretised this range of impacts into five levels: 0%, 20%, 40%, 60% and 100%. For each of the 1000 combinations of vital rates previously estimated, I modified the relevant vital rate by each level of the discretisation and conducted the population projection as previously described for the extreme climate scenario (scenario V).

3. Results

Vital rates (mean and 95% CI) for female *O. flavescens* from available field data (juvenile maturation γ , and adult reproduction ϕ) and

Table 1
Vital rates from field data^a and estimated through phylogenetic imputation.

Vital rate	Source	Mean	Lower CI	Upper CI
Juvenile survival (σ_J)	Phylogenetic imputation	0.743	0.737	0.749
Juvenile maturation (γ_J)	Field data	0.333	0.333	0.333
Adult survival (σ_A)	Phylogenetic imputation	0.802	0.793	0.811
Adult reproduction (ϕ)	Field data	0.100	0.100	0.100

^a Reported in Sepúlveda et al. (2006).

estimated through phylogenetic imputation (juvenile survival σ_J , and adult survival σ_A) are shown in Table 1. Note that female adult reproduction (ϕ) indicates reproduction of female pups only. The population projections of Scenarios I–IV are exclusively derived from these vital rate estimates. The population projections of Scenarios V–VIII are derived from these estimates in combination with the distribution of vital rates corresponding to extreme climate events (see Table 3).

Based on these vital rates, the average MPM (95% CI in square brackets) estimated for *O. flavescens* in Chile is:

$$\begin{pmatrix} 0.495[0.491, 0.499] & 0.100[0.100, 0.100] \\ 0.248[0.246, 0.250] & 0.802[0.793, 0.811] \end{pmatrix}$$

This MPM describes a juvenile female as having a 50% chance of surviving and remaining a juvenile, and a 25% chance of surviving and maturing to an adult. Adult females have an 80% chance of survival and contribute 0.1 juvenile females to the population each year. Based on this MPM, the average long-term growth rate for the female *O. flavescens* population is 0.876 (95% confidence interval: 0.869, 0.884), which suggests that the population will decrease over time. The stage-specific vital rate with the largest impact on the per-capita population growth rate (λ) is adult survival (Table 2). A small proportional positive change of 0.001 in this vital rate will increase λ by 75.8%. By contrast, there is little impact on λ of perturbations to juvenile survival, juvenile maturation, or adult reproduction.

Based on the estimated distribution of MPMs, the Chilean population of *O. flavescens* is projected to decline over the assessed 30-year time horizon. Specifically, under the base case scenario (I), and based on the initial population vector of 78,709 adult females and 18,477 juvenile females, the population projection for *O. flavescens* in Chile describes a population decline over the 30-year assessment period (Fig. 3.I). This result is consistent with the estimated value of $\lambda < 1$. Within this assessed time horizon (30 years) the population falls below the MVP size of 4598 adult females (assessed as >95% of iterations meeting this criteria). This suggests that the population will not persist or avoid evolutionary decay within this time period.

The *O. flavescens* population in Chile is also projected to decrease below an MVP under all of the assessed cull scenarios (scenarios II–IV, Fig. 3). Specifically, the MVP threshold is reached in year 28 when 15% of adult females are culled in year 1 only (scenario II), in year 17 when 10% of adult females are culled every year (scenario III), and in year 20 when 30% of adult females are culled every five years (scenario IV). Culling 10% of adult females each year therefore has the most extreme impact on the population viability of female *O. flavescens* in Chile. By contrast, a population cull of 15% of adult females in year one (scenario II) has negligible impacts on the population relative to the base case scenario (scenario I). Under the projected frequencies of extreme climate events (scenario V), 14.7% of model iterations decline to <100 adult females within 15 years (Fig. 3.V). However, the population is not assessed as quasi-extinct until year 22.

An estimation of the vital rates (mean and 95% CI) that correspond with extreme climate conditions are shown in Table 3. These are the base case estimates for juvenile survival (σ_J), adult survival (σ_A), and adult reproduction (ϕ) modified by δ , ω , and ε (see Fig. 1). Note that no observations are available for the impacts of extreme climate conditions on juvenile maturation, however, as this term is multiplied by

0 (juvenile survival) in the matrix population model this has no impact on extreme climate projections.

The average MPM (95% CI in square brackets) for female *O. flavescens* in Chile derived from these extreme climate vital rates is:

$$\begin{pmatrix} 0[0, 0] & 0.005[0.005, 0.005] \\ 0[0, 0] & 0.321[0.317, 0.325] \end{pmatrix}$$

This MPM is estimated from the distribution of vital rates underlying Table 3 e.g., vital rates that correspond with extreme climate conditions. Based on this MPM, the average long-term growth rate for the female *O. flavescens* population under extreme climate conditions is 0.321 (95% confidence interval: 0.317, 0.325). The combined impact of culls and extreme climate events is to speed up the population decline of *O. flavescens*. When the population of *O. flavescens* is subjected to culls and extreme climate events (scenarios VI–VIII), the population reaches quasi-extinction under all assessed cull regimes and declines much faster than in cull scenarios without extreme climate events (Fig. 3, II–IV compared to VI–VIII). Under an initial cull of 15% of adult females in year one (scenario VI), extreme climate impacts lead to the population reaching quasi-extinction in year 21—7 years earlier than in the cull-only scenario (II). Quasi-extinction is hastened by 1 year in the case of an annual cull of 10% of adult females (to year 16, Fig. 3.VII), and by 3 years in the case of a 30% cull of adult females every five years (year 17, Fig. 3.VIII). An annual cull of 10% of adult females (scenario VII) remains the cull regime with the largest impact on population viability over the assessed time horizon when combined with extreme climate impacts. It should also be noted that the proportion of simulated populations declining to very low numbers (<100 adult females in the first 15 years) increases in all cull scenarios with the combined impact of extreme climate events. Across scenarios VI–VIII, between 14.7% and 29.3% of all iterations fall below 100 adult females within the first 15 years, compared to <1% across scenarios I–IV.

Based on these results, it is clear that the separate impacts of managed culls or extreme climate events would adversely affect the population of *O. flavescens* in Chile. In all assessed scenarios, the population declines below an MVP threshold over a 30 year time horizon when subject to culls (scenarios II–IV) or extreme climate events (scenario V). Under the combined impacts of managed culls and extreme climate events, the speed at which the population will become functionally extinct increases. Under all combined scenarios (VI–VIII) the population of *O. flavescens* in Chile falls below an MVP within 16–21 years.

An analysis of the transient dynamics observed in each of the eight scenarios indicates how far populations would be perturbed away from their stationary stable population structures by culls and/or El Niño climatic extremes. The scenario where the greatest demographic amplification (i.e., ability of the population to increase in size following a disturbance) is observed in year 10 of the projected time horizon, i.e., after all scenarios have experienced perturbation, is scenario V (Table 4). This finding suggests that the female population of *O. flavescens* will amplify most strongly after extreme climate events when there are no population culls. The scenario where the highest attenuation (i.e., decrease in population size) is observed in year 10 is scenario VII. This suggests that the female population of *O. flavescens* would attenuate most strongly when subject to extreme climate events and a cull of 10% of adult females each year. A similar result is demonstrated in an analysis of the percentage of model iterations that amplify or attenuate in year 10 relative to the average base case (scenario I) population (Table 5)—amplification is highest in scenario II, where there are no climate impacts and a single cull of 15% of adult females in year 1. Attenuation was greatest in scenarios III and VII, where 10% of adult females were culled each year without and with extreme climate events.

In keeping with the analysis of the elasticity of the per-capita population growth rate (λ), a sensitivity analysis of the impact of extreme

Table 2

Elasticity of the long-term population growth rate (λ) of the female Chilean *Otaria flavescens* population to a positive proportional perturbation of 0.001 in stage-specific vital rates.

Vital rate	Mean	Lower CI	Upper CI
Juvenile survival (σ_J)	0.177	0.168	0.185
Juvenile maturation (γ_J)	0.010	0.007	0.013
Adult survival (σ_A)	0.758	0.749	0.768
Adult reproduction (ϕ)	0.065	0.064	0.067

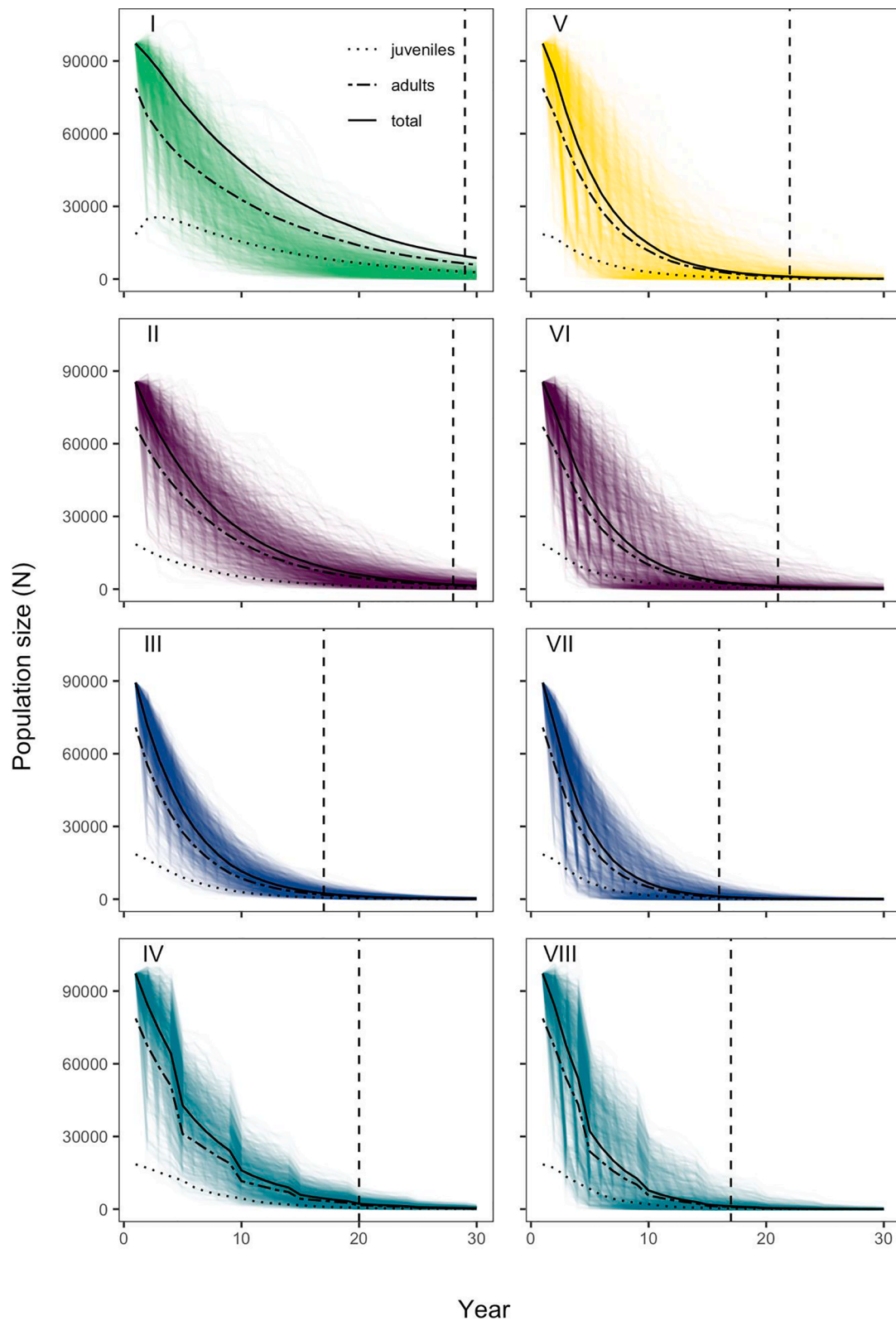


Fig. 3. Population projections of combined adult and juvenile females of *O. flavescens* in Chile, where each line represents a model iteration ($n = 1000$). Time horizon is 30 years with an initial population vector of 78,709 adult females and 18,477 juvenile females. Solid and dashed horizontally orientated lines show stage-specific average values across all iterations. Vertical dashed line indicates year where probability of all iterations dropping below the quasi-extinction threshold (4,598 adult females) is $> 95\%$. I: Base case scenario. II: Cull 15% of adult females in year 1. III: Cull 10% of adult females every year. IV: Cull 30% of adult females every 5 years. V: Extreme climate impacts. VI: Cull 15% of adult females in year 1 and extreme climate impacts. VII: Cull 10% of adult females every year and extreme climate impacts. VIII: Cull 30% of adult females every 5 years and extreme climate impacts.

Table 3

Vital rates consistent with extreme climate events.

Vital rate	Mean	Lower CI	Upper CI
Juvenile survival (σ_J)	0	0	0
Adult survival (σ_A)	0.321	0.317	0.325
Adult reproduction (ϕ)	0.005	.	.

Table 4Maximum and minimum population values for the Chilean *Otaria flavescens* population observed across 1000 model iterations under 8 scenarios indicating cull and/or extreme climate impacts.

Scenario	1 st percentile	5 th percentile	Mean	95 th percentile	100 th percentile
I	2,080	7,046	27,288	49,201	74,241
II	1,798	7,010	24,162	42,985	64,041
III	1,074	3,467	11,464	20,740	32,080
IV	1,290	4,650	16,000	29,147	40,119
V	4	240	14,533	44,081	74,987
VI	8	191	12,563	37,017	56,481
VII	0	81	6,551	19,349	29,021
VIII	2	88	7,706	24,653	36,592

Notes: I: Base case scenario. II: Cull 15% of adult females in year 1. III: Cull 10% of adult females every year. IV: Cull 30% of adult females every 5 years. V: Extreme climate impacts. VI: Cull 15% of adult females in year 1 and extreme climate impacts. VII: Cull 10% of adult females every year and extreme climate impacts. VIII: Cull 30% of adult females every 5 years and extreme climate impacts.

Table 5

Percentage of model iterations that amplify (increase) or attenuate (decrease) relative to mean base case population size in year 10.

Scenario	Amplification (%)	Attenuation (%)
I	.	.
II	37.5	62.5
III	0.2	99.8
IV	7.6	92.4
V	21	79
VI	17.1	82.9
VII	0.2	99.8
VIII	3.1	96.9

climate events on vital rates (Table 6) shows the greatest change in quasi-extinction occurs when adult survival is impacted by climate. Specifically, time to quasi-extinction is increased to 25 or 26 years (relative to 22 in scenario V) when extreme climate events do not affect adult survival, or only reduce adult survival by 20%. Table 3 shows the different levels of extreme climate event impacts that were assessed. These range from no impact (0% decrease) to a 100% decrease in the relevant vital rate value. Note that in this analysis, non-target vital rates were maintained at levels observed during extreme climate events (see

Table 6Time to quasi-extinction (years) of the Chilean population of *Otaria flavescens* under different simulated impacts on vital rates of extreme El Niño events.

Decrease in vital rate (%)	Juvenile survival (σ_J)	Juvenile maturation (γ_J)	Adult survival (σ_A)	Fecundity (ϕ)
100	23	22	22	22
80	22	22	22	21
60	23	22	23	22
40	22	22	23	22
20	22	22	25	23
0	22	23	26	22

Notes: Year of quasi-extinction implies that for >95% of the 1000 model iterations, the population is below the minimum viable population size of 4598 adult females.

Table 3). For vital rates other than adult survival, there is little difference in the speed with which populations decrease below the MVP threshold irrespective of the assumed impacts of extreme climate events on each vital rate.

4. Discussion

Using stochastic matrix population models (MPMs), in this mathematical exercise I show that the Chilean population of the South American sea lion (*Otaria flavescens*) could decline well below a minimum viable population (MVP, Shaffer, 1981) threshold over a 30 year time horizon. Based on the stochastic MPMs, I estimate a long-term population growth rate for the Chilean population of this species of 0.88, indicating a population decline of 12% every year—in the absence of managed culs or extreme climate conditions. This key finding contrasts with historically observed increases in the population from ~1978 to 2012. One can speculate that legal protection from hunting allowed the *O. flavescens* population to increase rapidly from the 1970's (e.g., from <40,000 individuals (Torres et al., 2000b)) to the 2010's (~158,000 individuals) (Oliva et al., 2020). In a closed population, the only way a population can increase is via reproduction overcompensating deaths. We can therefore surmise that adult reproduction was high during this period. However, the recent decade has seen a slowing or even decline in this growth (currently ~130,000 individuals (Oliva et al., 2020)). In the current modelling exercise, stochastic MPMs were developed from available field data and phylogenetically imputed vital rates. As adult reproduction was one of the vital rates available from field data, we can deduce that this vital rate has decreased in recent years—which is why the Chilean population is no longer increasing. To understand how the *O. flavescens* population will respond to management culs and extreme climate events in the short term, the long-term population growth rate is insufficient—we must use short-term (transient) metrics. The current analysis showed that the Chilean *O. flavescens* population attenuates (e.g., decreases in population size) when perturbed by either managed culs, extreme climate conditions or a combination of the two. In combination, the long-term population growth rate and transient metrics provide a more comprehensive perspective regarding how populations will respond over different time horizons and environmental conditions. This understanding helps us plan management actions accordingly—either for population control or protection.

This research shows that the speed of *O. flavescens* population decline is expected to accelerate under managed culs and/or expected frequencies of future extreme El Niño events. When managed culs and extreme El Niño impacts are combined, model simulations indicate populations will decrease below an MVP between 1 and 7 years faster than under managed culs alone. Based on these results, the Chilean population of *O. flavescens* is unlikely to support a managed cull—particularly given current expectations about the frequency of extreme climate events, including El Niño conditions. A similar conclusion was reached by Silva et al. (2021). These authors found that harbor seal populations (*P. vitulina*) in Sweden and Denmark could sustain modest hunting and infrequent epizootic events, but that external stressors that reduced fecundity (e.g., exposure to endocrine disruptors) would leave seal populations vulnerable to rapid population decline. In keeping with these results, management efforts to reduce conflicts with fisheries in Chile should avoid managed culs. Management of fisheries conflict with seals in Scotland similarly switched focus from population reduction to targeting of individual seals found to be frequenting rivers and netting stations (Butler et al., 2011). The new management approach reduced seal shooting by 60% and was considered a successful conflict management policy by the Scottish Government. Other alternative conflict-management options may include capacity building schemes, financial compensation or growth in eco-tourism enterprises (Davis et al., 2021). For example, pinniped tourism has experienced strong growth in recent decades (Birtles et al.,

2001). Public engagement with pinnipeds through tourism activities likely increases appreciation and desire to conserve these animals. However, it is worth noting that tourism can also have detrimental impacts on the animals involved (Páez-Rosas and Guevara, 2017)—which must be minimised through appropriate guidelines and regulation (Kirkwood et al., 2003).

This analysis demonstrates that extreme climate events are expected to hasten the decline of *O. flavescens* below an MVP value. This finding indicates that the precautionary principle, i.e. precautionary action despite scientific uncertainty (Resnik, 2003), may need to be exercised when managing the population of *O. flavescens* on the west coast of South America—larger populations will be required to allow the population to buffer against extreme climate events. A similar conclusion was reached by de Oliveira et al. (2012) in an assessment of the effective population size of *O. flavescens* in Peru, which explicitly considered the impacts of the mating system and demographic variations caused by the 1998–98 extreme El Niño event. In this work, the authors recommended a population of 7715 individuals to ensure the population was large enough to avoid inbreeding and retain sufficient adaptive genetic variation to survive future El Niño events.

Demographic simulations in the current analysis show considerable variation in the assessed population projections through time. After 10 years, the maximum and minimum population sizes observed across model iterations under all scenarios vary by at least one order of magnitude. These fluctuations are due to the transient dynamics that originate when disturbances impact stage-structured populations (Capdevila et al., 2020; Stott et al., 2010). Disturbances can change the total size of a population, but also the relative number of individuals in each stage therein (i.e., its population structure) because the disturbance may kill more individuals in a given life cycle stage relative to other stages. These changes in population structure can then lead to increased (amplified) or decreased (attenuated) growth in the short-term as part of its transient dynamics (Caswell, 2001; Stott et al., 2011). The population may recover its stationary equilibrium if and when the relative number of individuals in each life cycle stage returns to its pre-disturbance (i.e., asymptotic) state. In this context, it is important to note that *O. flavescens*, similarly to other pinniped species, is a “slow” species (Gaillard et al., 1989; Salguero-Gómez et al., 2016; Stearns, 1992), meaning that it is long-lived, has long generation times, and low reproductive output. Such “slow” species tend to have longer recovery times, greater ability to resist disturbances (i.e., lower attenuation), and lower ability to amplify (increase) after a disturbance (Capdevila et al., 2021; Stott et al., 2011). A recent assessment of how life history traits can predict a species intrinsic resilience (Capdevila et al., 2021) found that species with longer generation times require longer recovery times post-disturbance. The authors also found generation time to be negatively correlated with resistance (the inverse of how far populations attenuate after disturbance). These findings can help explain why *O. flavescens* populations in this analysis attenuate (decrease) so strongly after disturbance and show long recovery times.

A sensitivity analysis of the effects of extreme El Niño events on *O. flavescens* vital rates demonstrates that these events will be most damaging to sea lion populations when they decrease adult survival. By contrast, if adult survival can be buffered from extreme climate impacts—perhaps through policies to reduce mortality through fisheries bycatch (Breen et al., 2003), or reduce fishing pressure on prey species (Hennen, 2006; Sepúlveda et al., 2011)—then negative impacts on population viability will be reduced. Results showed that quasi extinction risk for the Chilean *O. flavescens* population is relatively insensitive to changes in the magnitude of extreme climate impacts on juvenile survival, juvenile maturation, and fecundity. In this sensitivity analysis, as in Scenarios V–VIII, extreme climate events do not occur every year—hence even when extreme climate events have large negative impacts on sea lion vital rates (e.g., 100% adult mortality), this will not necessarily lead to an immediate population decline below the MVP size. It is worth noting that the impact of extreme El Niño events on vital rates

was parameterised from northern populations in Chile (e.g., de Oliveira et al., 2012; Soto et al., 2004). It is unlikely that these impacts would be as severe for southern populations in Chile. However, southerly populations of *O. flavescens* may experience similar extreme population declines due to epizootic outbreaks (Silva et al., 2021) or other stressors. For example, populations on the Argentinian coast decreased by 93% between 1938 and 1975 due to unknown causes (Gerber and Hilborn, 2001).

The large historical increases in population size of Chilean *O. flavescens* without doubt contribute to the widespread perceptions of fishers in Chile that sea lion populations are currently too large and that they are rapidly increasing (Davis et al., 2021). This dichotomy may be explained by a shifting baseline syndrome (Pauly, 1995), i.e., fishers use the prevailing sea lion population size when they began fishing as their ‘baseline’, irrespective of the status of the population relative to historical levels at that point. Although many sea lion populations around the world, and in Chile, have not yet recovered to historical population abundance (i.e., levels observed before widespread sealing in the 18th – 19th centuries) (Lotze et al., 2011; Magera et al., 2013), many fishers began their careers in the years when sea lion populations were still small. For example, in Chile, over a third of fishers surveyed in a recent assessment of conflict with sea lions (Davis et al., 2021) began fishing over 40 years ago—when sea lion populations in Chile were approximately a quarter of the size they are now (Fig. 2). Hence, current increases in pinniped populations may be seen as unprecedented growth rather than a recovery towards historical levels.

The present study is one of the few existing demographic analyses to incorporate uncertainty in vital rates into population projections (e.g., see Paniw et al., 2017) and, to my knowledge, the first one to do so in pinnipeds. However, results clearly point to the need for more annual stage-based field data, which would allow species-specific vital rates to be estimated through inverse methods (Wielgus et al., 2008)—assuming that individual-based records were not feasible. Note that despite the current modelling approach estimating a very narrow confidence interval around the long-term growth rate (mean = 0.876, 95% CI = 0.869 and 0.884), this precision can be interpreted as certainty in the estimation (i.e., due to large number of model iterations, $n = 1000$), rather than certainty in the approximation of the modelled estimate to the ‘true’ long-term growth rate. This approximation will be improved by the addition of further annual stage-based field data. In particular, more exact estimates of vital rates would allow a more complex life cycle to be assessed, including a two-sex model. As male animals interact more often with fisheries (Kauhala et al., 2012), a two-sex model would permit more nuanced modelling of cull or population control measures. In Chile, some level of illegal harvest of sea lions also occurs (Davis et al., 2021)—the impact of this mortality is not incorporated in the current analysis, as reliable data for these activities remain elusive. Data on illegal-mortality levels would allow a better estimate of vital rates and of the long-term population growth rate.

Conflict between marine mammals—including sea lions—and fisheries remains a highly contentious management issue (Davis et al., 2021; Ramos et al., 2020). The present research provides quantitative evidence that this conflict may be best resolved independent of management culls, a historically implemented approach in this context (Galatius et al., 2020; Mancilla González, 2018). Perceptions of increases in sea lion populations may be an artefact of shifting baselines (Pauly, 1995), or the saliency of short-term (transient) population dynamics (Stott et al., 2010). Increases in the frequency of extreme climate events will leave sea lion populations vulnerable to extinction—requiring larger populations to remain viable over time. This precautionary, but necessary, approach is likely to exacerbate conflict with fisheries, highlighting an urgent need to develop and test alternative conflict-management solutions.

Author contributions

All aspects of this work were conceptualised, analysed, and written by the author, KJD.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2022.110122](https://doi.org/10.1016/j.ecolmodel.2022.110122).

References

- Barlow, J., Boveng, P., 1991. Modeling age-specific mortality for marine mammal populations. *Mar. Mamm. Sci.* 7, 50–65.
- Beverton, R., 1985. Analysis of marine mammal-fisheries interactions. Beddington, J.R., Beverton, R., Lavigne, D.M. (Eds.). *Marine Mammals and Fisheries*. George Allen & Unwin, London, pp. 3–33.
- Birtles, A., Valentine, P.S., Curnock, M., 2001. Tourism based on free-ranging marine wildlife: opportunities and responsibilities.
- Breen, P.A., Hilborn, R., Maunders, M.N., Kim, S.W., 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocartos hookeri*). *Can. J. Fish. Aquatic Sci.* 60, 527–541.
- Butler, J.R.A., Middlemas, S.J., Graham, I.M., Harris, R.N., 2011. Perceptions and costs of seal impacts on Atlantic salmon fisheries in the Moray Firth, Scotland: implications for the adaptive co-management of seal-fishery conflict. *Mar. Policy* 35, 317–323.
- Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L., England, M.H., Wang, G., Guilyardi, E., Jin, F.-F., 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Change* 4, 111–116.
- Cai, W., Wang, G., Dewitte, B., Wu, L., Santoso, A., Takahashi, K., Yang, Y., Carréric, A., McPhaden, M.J., 2018. Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature* 564, 201–206.
- Capdevila, P., Stott, I., Beger, M., Salguero-Gómez, R., 2020. Towards a comparative framework of demographic resilience. *Trends Ecol. Evol. (Amst.)* 35, 776–786.
- Capdevila, P., Stott, I., Cant, J., Beger, M., Rowlands, G., Grace, M., Salguero-Gómez, R., 2021. Life history mediates the trade-offs among different components of demographic resilience. *BioRxiv*, 450480, 20212006.2030.
- Capozzo, H.L., Perrin, W.F., 2009. South American sea lion: *Otaria flavescens*. Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.). *Encyclopedia of Marine Mammals*, 2nd Edition. Academic Press, London, pp. 1076–1079.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Sunderland.
- Contreras, F., Bartheld, J., Montecinos, M., Moreno, F., Torres, J., 2014. Cuantificación poblacional de lobo marino común (*Otaria flavescens*) en el litoral de la XV, I y II Regiones. Subsecretaría de Pesca. Informe Final Proyecto 2012-6-FAP-1, 86 pp + Anexos. Chile. Available electronically from Research Gate: https://www.researchgate.net/publication/278713906_Cuantificacion_poblacional_del_lobo_marino_comun_Otaria_flavescens_en_el_litoral_de_la_XV_I_y_II_Regiones_2012#.
- Cook, T.C., James, K., Bearzi, M., 2015. Angler perceptions of California sea lion (*Zalophus californianus*) depredation and marine policy in Southern California. *Mar. Policy* 51, 573–583.
- Crone, E.E., Menges, E.S., Ellis, M.M., Bell, T., Bierzychudek, P., Ehrhén, J., Kaye, T.N., Knight, T.M., Lesica, P., Morris, W.F., Oostermeijer, G., Quintana-Ascencio, P.F., Stanley, A., Ticktin, T., Valverde, T., Williams, J.L., 2011. How do plant ecologists use matrix population models? *Ecol. Lett.* 14, 1–8.
- Dans, S.L., Crespo, E.A., Pedraza, S.N., Alonso, M.K., 2004. Recovery of the South American sea lion (*Otaria flavescens*) population in northern Patagonia. *Can. J. Fish. Aquatic Sci.* 61, 1681–1690.
- Davis, K.J., Alfaro-Shigueto, J., Arlidge, W.N.S., Burton, M., Mangel, J.C., Mills, M., Milner-Gulland, E.J., Palma Duque, J., Romero-de-Diego, C., Gelcich, S., 2021. Local Disconnects in Global Discourses - The Unintended Consequences of Marine Mammal Protection on Small-Scale Fishers. *Conservation Letters*, p. e12835.
- de Oliveira, L.R., Fraga, L.D., Majluf, P., 2012. Effective population size for South American sea lions along the Peruvian coast: the survivors of the strongest El Niño event in history. *J. Mar. Biol. Assoc. United Kingdom* 92, 1835–1841.
- Di Marco, M., Pacifici, M., Maiorano, L., Rondinini, C., 2021. Drivers of change in the realised climatic niche of terrestrial mammals. *Ecography* 44, 1180–1190.
- Engbo, S., Bull, J.C., Börger, L., Stringell, T.B., Lock, K., Morgan, L., Jones, O.R., 2020. Census data aggregation decisions can affect population-level inference in heterogeneous populations. *Ecol. Evol.* 10, 7487–7496.
- Gaillard, J.-M., Pontier, D., Allaine, D., Lebreton, J., Trouvilliez, J., Clobert, J., 1989. An Analysis of Demographic Tactics in Birds and Mammals. *Oikos*, pp. 59–76.
- Galatius, A., Teilmann, J., Dähne, M., Ahola, M., Westphal, L., Kyhn, L.A., Pawliczka, I., Olsen, M.T., Dietz, R., 2020. Grey seal *Halichoerus grypus* recolonisation of the southern Baltic Sea, Danish Straits and Kattegat. *Wildlife Biol.* 2020.
- Gamelon, M., Gaillard, J.M., Servanty, S., Gimenez, O., Toigo, C., Baubet, E., Klein, F., Lebreton, J.D., 2012. Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. *J. Appl. Ecol.* 49, 833–841.
- Gerber, L.R., Hilborn, R., 2001. Catastrophic events and recovery from low densities in populations of Otariids: implications for risk of extinction. *Mamm. Rev.* 31, 131–150.
- Goolsby, E.W., Bruggeman, J., Ané, C., 2017. Rphylopar: fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods Ecol. Evol.* 8, 22–27.
- Griffith, A.B., Salguero-Gómez, R., Merow, C., McMahon, S., 2016. Demography beyond the population. *J. Ecol.* 104, 271–280.
- Hadley, G.L., Rotella, J.J., Garrott, R.A., Nichols, J.D., 2006. Variation in probability of first reproduction of Weddell seals. *J. Anim. Ecol.* 75, 1058–1070.
- Hennen, D., 2006. Associations between the Alaska Steller sea lion decline and commercial fisheries. *Ecol. Appl.* 16, 704–717.
- Hückstädt, L., Antezana, T., 2006. The Diet of *Otaria Flavescens* in Chile: What Do We Know? Alaska Sea Grant College Program, Fairbanks, pp. 83–102.
- James, T.D., Salguero-Gómez, R., Jones, O.R., Childs, D.Z., Beckerman, A.P., 2020. Bridging gaps in demographic analysis with phylogenetic imputation. *Conserv. Biol.*
- Johnson, T.F., Isaac, N.J.B., Paviolo, A., González-Suárez, M., 2021. Handling missing values in trait data. *Glob. Ecol. Biogeogr.* 30, 51–62.
- Jones, O.R., Barks, P., Stott, I.M., James, T.D., Levin, S.C., Petry, W.K., Capdevila, P., Che-Castaldo, J., Jackson, J., Römer, G., Schuette, C., Thomas, C.C., Salguero-Gómez, R., 2021. Rcompadre and Rage - two R packages to facilitate the use the COMPADRE and COMADRE databases and calculation of life history traits from matrix population models.
- Kauhala, K., Ahola, M.P., Kunasranta, M., 2012. Demographic structure and mortality rate of a Baltic grey seal population at different stages of population change, judged on the basis of the hunting bag in Finland. *Ann. Zool. Fenn.* 49, 287–305.
- Kirkwood, R., Boren, L., Shaughnessy, P., Sztren, D., Mawson, P., Hückstädt, L.A., Hofmeyr, G., Oosthuizen, H., Schiavini, A., Campagna, C., Berris, M. (Eds.) 2003. Pinniped-focused tourism in the southern hemisphere: a review of the industry 257 pp.
- Kobayashi, Y., Kariya, T., Chishima, J., Fujii, K., Wada, K., Baba, S., Ito, T., Nakaoka, T., Kawashima, M., Saito, S., 2014. Population trends of the Kuril harbour seal *Phoca vitulina stejnegeri* from 1974 to 2010 in southeastern Hokkaido, Japan. *Endanger. Species Res.* 24, 61–72.
- Kovacs, K.M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., Gelatt, T., Goldsworthy, S.D., Goodman, S.J., Hofmeyr, G.J.G., Härkönen, T., Lowry, L., Lydersen, C., Schipper, J., Sipilä, T., Southwell, C., Stuart, S., Thompson, D., Trillmich, F., 2012. Global threats to pinnipeds. *Mar. Mamm. Sci.* 28, 414–436.
- Lalas, C., Bradshaw, C.J.A., 2003. Expectations for population growth at new breeding locations for the vulnerable New Zealand sea lion (*Phocartos hookeri*) using a simulation model. *Biol. Conserv.* 114, 67–78.
- Leslie, P.H., 1945. On the use of matrices in certain population mathematics. *Biometrika* 33, 183–212.
- Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C., Airoldi, L., 2011. Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol. (Amst.)* 26, 595–605.
- Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B., Lotze, H.K., 2013. Recovery trends in marine mammal populations. *PLoS ONE* 8, e77908.
- Mancilla González, P., 2018. Federico Albert: Apreciaciones sobre La Caza y Pesca De Los Lobos Marinos En Los Territorios Australes De Chile, 1901. *Sophia Austral*, pp. 71–87.
- Meyer, S., Robertson, B.C., Chilvers, B.L., Krkošek, M., 2015. Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocartos hookeri*. *Mar. Biol.* 162, 1587–1596.
- Milano, V.N., Grandi, M.F., Schiavini, A.C.M., Crespo, E.A., 2020. Sea lions (*Otaria flavescens*) from the end of the world: insights of a recovery. *Polar Biol.* 43, 695–706.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology*. Sinauer Associates Inc., Massachusetts, USA.
- National Oceanic and Atmospheric Administration, 2022. Pacific Marine Environmental Laboratory El Niño Theme Page. n.d. NOAA. Laboratory, P.M.E. (Ed.).
- Páez-Rosas, D., Guevara, N., 2017. Management strategies and conservation status of Galapagos sea lion populations at San Cristóbal Island, Galapagos, Ecuador. *Tropical Pinnipeds: Bio-Ecology, Threats and Conservation*, 159–175.
- Oliva, D., Durán, L.R., Sepúlveda, M., Cárcamo, D., Pizarro, M., Anguita, C., Santos, M., Canto, A., Herrera, P., Muñoz, L., Orellana, M., Vázquez, P., 2020. Estimación poblacional de lobos marinos e impacto de la captura incidental. Pre-informe Final Proyecto FIP 2018-54, 190 pp + Anexos. Valparaíso, Chile.

- Oliva, D., Sielfeld, W., Durán, L.R., Sepúlveda, M., Pérez, M.J., Rodríguez, L., Stotz, W., Araos, V., 2003. Interferencia de mamíferos marinos con actividades pesqueras y de acuicultura. Subsecretaría de Pesca. FIP 2003-32. Chile. Available from: https://www.subpesca.cl/fipa/613/articles-89037_informe_final.pdf.
- Paniw, M., Ozgul, A., Salguero-Gómez, R., 2018. Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecol. Lett.* 21, 275–286.
- Paniw, M., Quintana-Ascencio, P.F., Ojeda, F., Salguero-Gómez, R., 2017. Accounting for uncertainty in dormant life stages in stochastic demographic models. *Oikos* 126, 900–909.
- Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528.
- Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol. (Amst.)* 10, 430.
- Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., Rondinini, C., Brooks, T.M., Young, B.E., Graham, C.H., Costa, G.C., 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.* 5, 961–970.
- R Core Team, 2021. R: A Language and Environment For Statistical Computing. Vienna, Austria. Computing, R.F.f.S. (Ed.).
- Ramos, K., Machado, R., Schiavetti, A., 2020. Operational interactions between sea lion species (Otariidae) and commercial fisheries. *Ethnobiol. Conserv.* 9.
- Resnik, D.B., 2003. Is the precautionary principle unscientific? *Studies in history and philosophy of science part c: studies in history and philosophy of biological and biomedical sciences* 34, 329–344.
- Rossi, S.P., Cox, S.P., Hammill, M.O., den Heyer, C.E., Swain, D.P., Mosnier, A., Benoît, H.P., 2021. Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. *ICES J. Mar. Sci.* 78, 1804–1814.
- Salguero-Gómez, R., Casper, B.B., 2010. Keeping plant shrinkage in the demographic loop. *J. Ecol.* 98, 312–323.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., 2016b. COMADRE: a global data base of animal demography. *J. Anim. Ecol.* 85, 371–384.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D.A., Brinks, E., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., Wille, J., Zeh, S., Davison, R., Viereg, D., Baudisch, A., Altwegg, R., Colchero, F., Dong, M., de Kroon, H., Lebreton, J.-D., Metcalf, C.J.E., Neel, M.M., Parker, I.M., Takada, T., Valverde, T., Vélez-Espino, L.A., Wardle, G.M., Franco, M., Vaupel, J.W., 2015. The compadre plant matrix database: an open online repository for plant demography. *J. Ecol.* 103, 202–218.
- Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., de Kroon, H., Buckley, Y.M., 2016a. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. In: *Proceedings of the National Academy of Sciences*, 113, pp. 230–235.
- Salguero-Gomez, R., Plotkin, J.B., 2010. Matrix dimensions bias demographic inferences: implications for comparative plant demography. *Am. Nat.* 176, 710–722.
- Scordino, J., 2010. West coast pinniped program investigations on California sea lion and Pacific Harbor seal impacts on salmonids and other fishery resources. Pacific states marine fisheries commission Portland.
- Sepúlveda, M., Oliva, D., Sielfeld, W., José Perez, M., Moraga, R., Schrader, D., Urrea, A., Díaz, H., 2006. Cuantificación Poblacional de Lobos Marinos en el Litoral de la V a IX Region. Subsecretaría de Pesca. Proyecto F.I.P. No 2006-49. Valparaíso, Chile.
- Sepúlveda, M., Oliva, D., Urrea, A., Pérez-Álvarez, M.J., Moraga, R., Schrader, D., Inostroza, P., Melo, Á., Díaz, H., Sielfeld, W., 2011. Distribution and abundance of the South American sea lion *Otaria flavescens* (Carnivora: Otariidae) along the central coast off Chile. *Rev. Chil. Hist. Nat.* 84, 97–106.
- Sepúlveda, M., Santos, M., Veas, R., Muñoz, L., Olea, D., Moraga, R., Sielfeld, W., 2015. Annual, seasonal and daily variation in the abundance of the South American sea lion *Otaria flavescens* in two breeding colonies in northern Chile. *Rev. Biol. Mar. Ocean.* 50, 205–220.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *Bioscience* 31, 131–134.
- Sielfeld, W., 1999. The knowledge and conservation status of *Otaria flavescens* (Shaw, 1800) and *Arctocephalus australis* (Zimmermann, 1783) at the Chilean coasts. *Estudios Oceanol.* 18, 81–96.
- Sielfeld, W., Guzmán, A., 2002. Effect of El Niño 1997/98 on a population of the southern sea lion (*Otaria flavescens* Shaw) from Punta Patache/Punta Negra (Iquique, Chile). *Investigaciones marinas* 30, 158–160.
- Silva, W.T., Bottagisio, E., Härkönen, T., Galatius, A., Olsen, M.T., Harding, K.C., 2021. Risk for overexploiting a seemingly stable seal population: influence of multiple stressors and hunting. *Ecosphere* 12, e03343.
- Soto, K.H., Trites, A.W., Arias-Schreiber, M., 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *J. Zool.* 264, 419–428.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, USA, p. 264 pp.
- Stott, I., Franco, M., Carslake, D., Townley, S., Hodgson, D., 2010. Boom or bust? A comparative analysis of transient population dynamics in plants. *J. Ecol.* 98, 302–311.
- Stott, I., Townley, S., Hodgson, D.J., 2011. A framework for studying transient dynamics of population projection matrix models. *Ecol. Lett.* 14, 959–970.
- Torres, D., Aguayo-Lobo, A., Acevedo, J., 2000a. Mamíferos marinos de Chile. II. Carnívora. *Ser. Cient. INACH* 50, 25–103.
- Torres, D., Lobo, A., Acevedo, J., 2000b. Los Mamíferos marinos de Chile: II. Carnívora. *Ser. Cient. INACH* 50, 25–103.
- Traill, L.W., Brook, B.W., Frankham, R.R., Bradshaw, C.J.A., 2010. Pragmatic population viability targets in a rapidly changing world. *Biol. Conserv.* 143, 28–34.
- Upham, N.S., Esselstyn, J.A., Jetz, W., 2019. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* 17, e3000494.
- Wielgus, J., Gonzalez-Suarez, M., Auriolles-Gamboa, D., Gerber, L.R., 2008. A noninvasive demographic assessment of sea lions based on stage-specific abundances. *Ecol. Appl.* 18, 1287–1296.