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A state-dependent model for assessing the population consequences of disturbance on income-breeding mammals

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ABSTRACT

Human activities continue to expand in marine and terrestrial environments, leading to increased interactions with wildlife that can have negative impacts on population dynamics. Approaches for quantifying how these interactions translate to population-level effects are therefore crucial for effective management practices and balancing human-wildlife tradeoffs. We developed a method using state-dependent behavioral theory implemented via Stochastic Dynamic Programming (SDP) for predicting the population consequences of disturbance on the physiology and reproductive behavior of an income-breeding mammal, using California sea lions (*Zalophus californianus*) as a motivating species. Emergent properties of the model included reproductive characteristics associated with long-lived species, such as variation in the age at first reproduction, early termination of pregnancy, and skipped breeding. In undisturbed model simulations, reproductive rates and the average wean date were consistent with empirically-derived estimates from sea lions and other marine mammals, highlighting the utility of this model for quantifying fecundity estimates of data-deficient species and addressing fundamental ecological processes. In disturbed model simulations, exposure to prolonged, repetitive disturbances negatively impacted population growth; in addition, short, infrequent disturbances had the potential for adverse effects depending on the behavioral response of sea lions and the probability of being disturbed. The adverse effect of disturbance on population dynamics was due to a combination of reduced pup recruitment (survival to age one) resulting from a lower wean mass and increased abortion rates that led to skipped reproductive years, both of which have been documented for marine mammal populations experiencing natural fluctuations in prey availability. The derivation of state- and time-dependent reproductive decisions using an SDP model is an effective approach that links behavioral and energetic effects at the individual level to changes at the population level, and one that serves a dual purpose in the ability to quantify basic biological parameters and address ecological questions irrespective of disturbance.

1. Introduction

Wildlife populations face increasing pressure from human activities that can result in direct mortality or indirect effects, including behavioral changes or disruption of life histories (Knowlton and Kraus, 2001; Shannon et al., 2016; Smith et al., 2015; Stankowich, 2008). A growing human footprint in the marine environment has led to increased interactions between humans and marine mammals, resulting in concern about the impact of these activities on populations that already face a myriad of other threats (Davidson et al., 2012). Exposure to disturbance from naval exercises and vessel traffic associated with ecotourism results in short-term disruptions of natural behavior (Castellote et al., 2012; DeRuiter et al., 2013; Goldbogen et al., 2013; Melcón et al., 2012; Pirotta et al., 2015; Williams et al., 2006), but these disruptions do not necessarily translate to biologically meaningful effects on population dynamics (Gill et al., 2001). Despite the growing need to understand the consequences of disturbance on marine mammal populations, there have been comparatively few studies that have attempted to quantify the potential long-term effects of disturbance for this taxonomic group (Christiansen and Lusseau, 2015; King et al., 2015; New et al., 2014, 2013; Villegas-Amtmann et al., 2017, 2015).

Early efforts towards understanding the population-level effects of acoustic disturbance led to the development of the Population Consequences of Acoustic Disturbance (PCAD) framework by a US National Research Council committee in 2005 (Wartzok et al., 2005).

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Further development of these ideas led to the Population Consequences of Disturbance (PCoD) framework, which conceptualizes how disturbance translates from the individual to the population level through a series of transfer functions that link a behavioral or physiological response by an individual (often modeled as a change in energy) with changes in health, vital rates, and population dynamics (New et al., 2014). Applications of the PCoD framework have been limited (Costa et al., 2016; Nabe-Nielsen et al., 2018; New et al., 2014) due to the combination of a lack of basic life history data for many species and the challenges of quantifying some of these transfer functions for species that are long-lived and often wide-ranging and elusive.

McHuron et al., (2017a) proposed that state-dependent behavioral theory implemented via Stochastic Dynamic Programming (SDP; Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000) is a viable method for quantifying the functions that link behavior with vital rates, thereby enabling implementation of the PCoD framework. SDP models have been applied across a broad range of taxonomic groups for quantifying the effects of natural environmental disturbance (Bull et al., 1996; Denis et al., 2012; Satterthwaite and Mangel, 2012; Tenhumberg et al., 2000), but until recently had not been applied in the context of anthropogenic disturbance (McHuron et al., 2017a; Pirotta et al., 2018). This approach originates from the tenant that behavior is an evolutionary trait and allows for different behavioral responses to disturbance conditioned on the environment and an individual's physiological state.

Initial efforts to model the effects of disturbance on marine mammals using SDP models focused on the impact of disturbance on expected reproductive success within a single year and did not explicitly model transitions between reproductive states. Individuals either remained in a fixed reproductive state throughout that time period (McHuron et al., 2017a) or transitioned between two reproductive states (pregnant or not pregnant) based on a simple threshold value (Pirotta et al., 2018). The incorporation of reproductive transitions into SDP models is an important next step that will facilitate species-specific applications, particularly for income-breeding species that have the potential for simultaneous gestation and lactation, necessitating an approach that can capture transitions among reproductive states (i.e. early weaning and abortion) in a way that is more akin to how these transitions likely occur in nature. Income breeding is a reproductive strategy used by many mammalian (and non-mammalian) species (Bonnet et al., 1998; Costa, 1991; Jönsson, 1997; Oftedal, 1997; Schulz and Bowen, 2004) that may increase the susceptibility of individuals and populations to energetic disruptions (Costa et al., 2016; McHuron et al., 2017a). This reproductive strategy complicates PCoD models because, as females rely on energy gained throughout lactation to support offspring growth, the timing of disturbance becomes a more complicated subject and requires an approach that goes beyond bioenergetic models (Costa et al., 2016; Villegas-Amtmann et al., 2017, 2015). SDP models represent a natural framework in which to address these issues, however, as will be seen below, modeling the transitions among multiple reproductive states is not a trivial addition.

We present an SDP model expanding on McHuron et al., (2017a) that includes many of the biologically relevant extensions that would be desired to model the population consequences of disturbance for an income-breeding marine mammal. We illustrate these extensions using California sea lions (*Zalophus californianus*) as a case study because their physiology, behavior, and demographics have been well-studied compared with many other marine mammals. In addition to describing the derivation of the SDP equations, we simulated a variety of hypothetical disturbance scenarios to examine how variability in (1) an individual's response to exposure, (2) the timing of exposure within the year, (3) the duration of exposure, and (4) the repetitiveness of the exposure affected pup recruitment and population growth rates. We focus on highlighting the utility of this approach in implementing the PCoD framework and how it can be used to identify and prioritize research needs, but also discuss its application in addressing key ecological questions and processes irrespective of disturbance.

2. Methods

SDP models involve two primary components, a backward iteration where optimal behavioral decisions are identified assuming individuals act to maximize some metric of Darwinian fitness, and an individual-based forward simulation where the state dynamics and behavioral decisions of a population are simulated. Anthropogenic disturbance can be introduced in the forward simulation under the assumption that it is not in the evolutionary history of the organism, and thus does not influence the behavioral decisions generated in the backward iteration (Clark and Mangel, 2000; Mangel and Clark, 1988; McHuron et al., 2017a). The backward iteration consists of (1) identification of a time horizon, (2) characterization of physiological state variables and how they change in response to the environment and behavior, (3) definition of a function that links the state variables(s) to a measure of Darwinian fitness (referred to as the terminal fitness function), and (4) derivation of the SDP equations that predict the behavior of individuals based on state and time. The sections below follow this progression. A conceptual diagram of the backward iteration and forward simulation as described below is shown in Fig. 1.

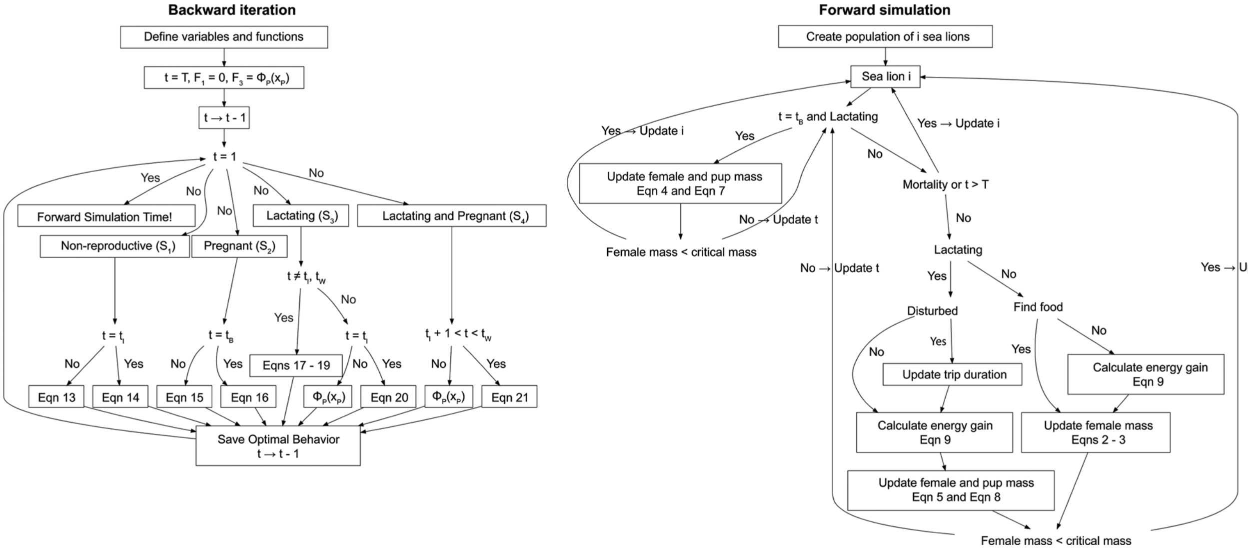

Fig. 1. Conceptual diagram of the model consisting of a backward iteration (left) and a forward simulation (right) as described in the text.

2.1. Life cycle

California sea lions typically give birth to a single pup annually in late May through June (Peterson and Bartholomew, 1967). The majority of the US population breeds in the Channel Islands in southern California on one of two islands, San Miguel and San Nicolas Islands. Breeding occurs ~6 weeks after birth in July and August (Peterson and Bartholomew, 1967), but implantation of the embryo is delayed for several months (Greig et al., 2007). Female sea lions are income breeders and central-place foragers during the 10–11 month lactation period (Harris, 2016; Melin et al., 2000). During this time, they alternate foraging trips to sea (2 to 7+ days) with short periods onshore nursing their pup (1–2 days), supporting their metabolic needs and those of their pup using energy gained on each foraging trip (Costa et al., 1991; McHuron et al., 2016; Melin et al., 2000). Weaning can be initiated by either the female or the pup. After weaning, females may continue to frequent the rookery or leave the area for more productive foraging areas before returning to give birth (Melin et al., 2000). In contrast to nursing females, juvenile sea lions and non-lactating females are not tied to a central place and may forage throughout the California Current System (McHuron et al., 2018; Melin et al., 2000; Orr et al., 2012). Pregnancy and reproductive failure rates of California sea lions are unknown, but age-specific birth and survival rates (the probability of a female surviving and being seen with a pup the following year) provide evidence of reproductive senescence in this species (Hernández-Camacho et al., 2008a; Melin et al., 2012).

2.2. Model timeline

In nature, there is variability in the timing of life history events, but for simplicity we assumed either a fixed date (birth, implantation, death) or a maximum fixed date (weaning) for each of these events. Pups were born on day t_B, which we set to be calendar date June 15 and model day $t = 1$, 365, etc. We assumed that implantation occurred on day t_I, which we set to be calendar date October 15 and model date $t = 125$, 490, etc. Pups were weaned on or before day t_W, which we set to be calendar date May 15 in the year following birth and model date $t = 335$, 700, etc. Once weaned, surviving pups recruited into the population as juveniles on calendar date June 15 in the year following their birth. We set the age (in years) of juvenile sea lions as $a = 1, 2\ldots a_m$ or the age of first possible implantation, and the age (in years) of an adult female sea lion as $a = a_m + n$ where $n = 1, 2, 3\ldots N$ is the number of years a female can be reproductively active. Thus, reproductive senescence occurs at age $a_m + N$ years. We set the age of death (in years) at 25 ($t = T$) and model date $t = 9489$ (a female died just before she turned 26).

The timing of each life history event for a pup born in year y to a female in her n^{th} reproductive year can be calculated as

$$\begin{aligned} t_B(y) &= (a_m + n)365 \\ t_I(y) &= 125 + t_B(y) \\ t_W(y+1) &= 335 + t_B(y) \end{aligned} \tag{1}$$

Based on data, we set $a_m = 4$ years and $N = 17$ years so that a female was 21 years old when she weaned her last pup (Hernández-Camacho et al., 2008a; Melin et al., 2012).

There are four reproductive states possible for adult females and one reproductive state possible for juveniles (Fig. 2): non-reproductive (State 1), pregnant (State 2), lactating (State 3), and lactating and pregnant (State 4). In the year of reproductive senescence, a female can only be in State 1 or State 3, and after weaning is continually in a non-reproductive state until the time of her death (a_d). The transition from State 2 to State 3 can only occur at t_B and transitions from either State 1 to State 2 or State 3 to State 4 can only occur at t_I. In contrast, transitions from a higher to a lower reproductive state can occur between transition periods due to aborting a pregnancy or early weaning of the pup (Fig. 2).

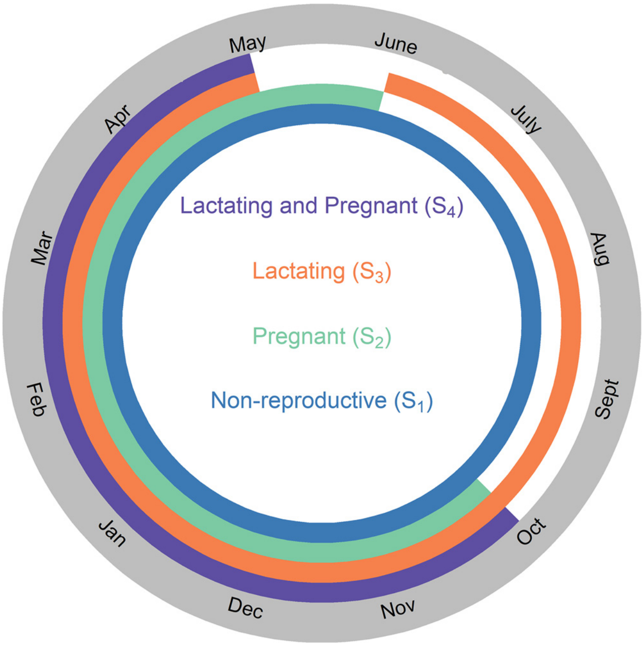

Fig. 2. The reproductive timeline and potential reproductive states of an adult female California sea lion not in her last year of reproduction. For simplicity, we assume that birth, implantation, and weaning occur at specific times within the season (Eq. (1)).

2.3. Physiological dynamics

We characterized non-reproductive and pregnant females (States 1 and 2) by a single physiological state, mass in kg $X_F(t)$ at time t within a period of total time T. A female's mass was bounded by a maximum value $x_{\max,F}$ and a minimum value $x_{\min,F}$, such that she died if she fell below this critical level. We chose 120 kg for $x_{\max,F}$ based on data from the age-specific morphometric study by Laake et al., (2016); we used a single value for all age classes because the primary purpose of this bound is to operationalize the model. Because we modeled sea lions throughout their life (i.e. at varying ages and masses), we calculated $x_{\min,F}$ as a function of age (Figs. S1, S3, Supp. Text). Adult females in States 3 (lactating) and 4 (lactating and pregnant) were characterized by an additional physiological state, $X_P(t)$, the mass in kg of their dependent pup. The pup's mass was also bounded by $x_{\max,P}$ (36 kg) and $x_{\min,P}$, which was again an age-specific value (Figs. S2 – S3, Supp. Text)

The energy requirements of a sea lion at each time step consist of energy needed for maintenance, digestion, thermoregulation, and locomotion (collectively referred to as field metabolic rate or FMR), and reproduction (where applicable). Growth costs were not explicitly included in the energy budget but were instead addressed when estimating the energy gain from foraging (Supp. Text). We calculated mass-specific FMRs based on metabolic measurements collected from free-ranging and captive adult female California sea lions (McHuron et al., 2017b; Williams et al., 2007; Table 1). We did not have similar data for juveniles, but a comparison of data from free-ranging juvenile and adult Australian sea lions (*Neophoca cinerea*) revealed that the mean mass-specific at-sea FMR of juveniles was 1.4 times the value for adult females during the same time of year (Costa and Gales, 2003; Fowler et al., 2007). Thus, we assumed that the mass-specific FMR of juvenile sea lions was 1.4 times adult rates. The cost of lactation was calculated using data from Oftedal et al., (1987), a study that measured milk energy intake and mass changes of sea lion pups during the first two months of lactation. We used the values from McHuron et al., (2017b) to calculate the daily cost of gestation (α_g). In Table 1, we show values used in the calculation of the physiological dynamics.

The time step across which energy requirements and mass dynamics

Table 1
Parameters used to calculate the physiological dynamics and estimate the foraging environment of California sea lions in the SDP model. Reproductive states are as follows: Non-reproductive (State 1), Pregnant (State 2), Lactating (State 3), and Lactating and Pregnant (State 4). Parameter citations provided in text. Early corresponds to the first three months of lactation and late corresponds to the remaining seven to eight months of lactation.

Parameter	Description	Adults			Juveniles
		States 3, 4		States 1, 2	State 1
		Early	Late		
FMR	Field metabolic rate (MJ day^{-1} kg$^{-0.75}$)	n/a	n/a	0.96	1.35
At-sea		1.38	1.38	n/a	n/a
On land		0.6	0.6	n/a	n/a
Lactation[a]	Daily energy intake by pup (MJ day^{-1})	7.65–22.34		n/a	n/a
Gestation	Daily gestation cost (MJ day^{-1})	n/a	0.80–2.40	0.80–2.40 (State 2)	n/a
P_{ME}	Proportion of energy from prey available for metabolism	0.86	0.86	0.86	0.86
$\bar{d}_{sea}$	Average trip duration	5.4	5.4	n/a	n/a
$\bar{\tau}$	Average travel duration	0.5	0.5	n/a	n/a
$\bar{s}$	Average days of successful foraging	2.4	2	n/a	n/a
$\bar{k}$	Average days of unsuccessful foraging	2	2.4	n/a	n/a
$\bar{d}_{land}$	Average time on land	2.7	1.4	n/a	n/a
$\bar{d}_{MC}$	Average duration of maternal cycle	8.1	6.8	n/a	n/a
$\bar{\lambda}_r$	Probability of finding prey	0.54	0.45	0.6	0.55
$Y_{r,t}$	Profitability of finding prey	1.15	1.15	1.7	1.72

[a] Daily milk energy required by pups (8–36 kg) to grow at 0.085 kg day^{-1}.

were assessed differed between females that were non-lactating (States 1 and 2) and lactating (States 3 and 4). We assumed a time step = 1 day for non-lactating females, which contrasts with the natural behavior of sea lions (and the approach used for lactating females) that consists of alternating foraging trips at sea with periods resting onshore. We chose not to model this additional complexity for these two reproductive states because unlike lactating females, non-lactating females can 1) use multiple haul-outs that may in fact be close or far from foraging grounds, making it difficult to predict the duration of foraging trips, and 2) exploit the most profitable foraging grounds, moving considerable distances to find new foraging patches if they have poor foraging success on any given day. Additionally, there are very few empirical data on trip and haul-out durations for juvenile and non-lactating California sea lions, and there is no apparent fitness implication associated with this assumption, as the length of the foraging trip primarily affects pup but not female condition (Costa et al., 1989). The time step for lactating females varied as a function of foraging trip length, which was determined using a negative binomial (NB) foraging model (see *NB Foraging Model*).

The mass dynamics for non-lactating females (States 1 and 2) were as follows. If a female did not find prey on any given day, which happened with probability $1 - \lambda_{1 \text{ or } 2}$, her mass declined as a function of mass-specific FMR (MJ day^{-1} kg$^{-0.75}$; Kleiber, 1961) and daily gestation costs (when applicable, α_g)

$$X_F(t+1) = X_F(t) - \frac{FMR_{land/sea}X_F(t)^{0.75} + \alpha_g}{33} \tag{2}$$

where 33 MJ kg^{-1} is the energy density of blubber (Kuhnleini and Soueida, 1992) assuming that all mass changes occur through the deposition or metabolism of blubber at no additional cost. If a female did find prey on any given day, which happened with probability $\lambda_{1 \text{ or } 2}$, mass was added after accounting for the costs of maintenance and gestation

$$X_F(t+1) = X_F(t) - \frac{FMR_{land/sea}X_F(t)^{0.75} + \alpha_g}{33} + \frac{E_{Prey_{X_F}}P_{ME}}{33} \tag{3}$$

where $E_{Prey_{X_F}}$ is the energy gain from foraging in MJ day^{-1} for a female of mass X_F (see *Foraging environment*), and P_{ME} is the proportion of energy available for metabolism (Costa, 1986).

The state dynamics for lactating females (States 3 and 4) were as follows. After birth, females spent an extended duration ashore with the pup (termed the perinatal period) before they undertook their first foraging trip to sea. We used a fixed duration for the time spent ashore during this period (d_{PN} = 8days) based on data from Heath et al., (1991), and assumed that a female lost 2% of her body mass for each day of fasting (Costa and Trillmich, 1988). Thus, the mass dynamics for a lactating female during the perinatal period were

$$X_F(t_B(a_m+n)+d_{PN}) = X_F(t_B(a_m+n)) - 0.02X_F(t_B(a_m+n))d_{PN} \tag{4}$$

The mass dynamics for a lactating female during the rest of lactation were similar to Eq. (3), although maintenance costs were divided into sea and land periods and there was an added cost associated with providing energy to the pup

$$X_F(t+d_{MC}) = X_F(t) - \frac{((FMR_{sea}d_{sea} + FMR_{land}d_{land})X_F(t)^{0.75} + E_{Pup} + \alpha_g d_{MC})}{33} + \frac{E_{Prey_{X_F,X_P}}P_{ME}}{33} \tag{5}$$

where d_{sea} and d_{land} are the number of days spent at sea and ashore and the duration of the maternal cycle (d_{MC}) is the sum of those two values, E_{Pup} is the energy allocated to the pup in MJ trip^{-1} (see below), and $E_{Prey_{X_F,X_P}}$ is the energy gained from foraging in MJ trip^{-1}.

We calculated the energy required by the pup to grow at an average mass gain of 0.085 kg day^{-1} (McClatchie et al., 2016a; Oftedal et al., 1987) based on mass-specific estimates of daily gross energy intake ($\bar{E}_{Milk}$) and the average duration of the maternal cycle ($\bar{d}_{MC}$).

$$\bar{E}_{Pup} = \bar{E}_{Milk}\bar{d}_{MC} \tag{6}$$

We calculated $\bar{E}_{Milk}$ by solving the equation from Fig. 2B in Oftedal et al., (1987b) that describes daily mass gain as a function of daily gross energy intake. For example, to grow at a rate of 0.085 kg day^{-1}, a 15 kg pup would require 11.7 MJ day^{-1} ($\bar{E}_{Milk}$) or 94.8 (early) or 79.6 (late) MJ trip^{-1} ($\bar{E}_{Pup}$), assuming the trip was of average duration. The resulting value of $\bar{E}_{Milk}$ was used in conjunction with a series of milk allocation rules (Fig. S4, Supp. Text) to calculate E_{Milk} and thus E_{Pup} based on the actual length of the maternal cycle. For example, when a foraging trip was one day longer than expected, a female would need to allocate an additional 11.7 MJ to the pup to maintain pup growth at 0.085 kg day^{-1}; the milk energy allocation rules (Supp. Text) dictated how much energy a female delivered to her pup, and the resulting growth rate, when her foraging trip was shorter/longer than expected. These rules account for that fact that in nature pups do not always grow at the average rate, particularly during periods of above average or reduced prey availability (McClatchie et al., 2016b).

During the perinatal period, we assumed that the pup gained a fixed rate of 0.1 kg day^{-1} (Ono et al., 1987) so that

$$X_P(t_B(a_m + n) + d_{PN}) = X_P(t_B(a_m + n)) + 0.1d_{PN} \tag{7}$$

During the rest of lactation, the pup mass dynamics were

$$X_P(t + d_{MC}) = X_P(t) + \frac{E_{Pup_g}}{1000} \tag{8}$$

where E_{Pup_g} represents the conversion of E_{Pup} from MJ trip^{-1} to kcal kg$^{-0.83}$ day^{-1} so that daily mass gain (in g) could be calculated using the equation in Fig. 2B in Oftedal et al., (1987b) and then rescaled back to the entire trip (g trip^{-1}).

2.4. Foraging environment

The foraging environment for each reproductive state r was characterized by the long-term probability of finding prey on any given day ($\overline{\lambda}_r$), the energy gain from foraging (E_{Prey}), and the daily age-specific risk of mortality (β_a). The fine-scale temporal and spatial dynamics of sea lion prey are not well characterized, making it difficult to parameterize $\overline{\lambda}_r$ and E_{Prey} using empirical data. Instead, for non-lactating females where the time step was one day, we assumed that $\overline{\lambda}_r$ was 0.55 (juveniles) and 0.6 (adults), and used satellite tracking and diving data to estimate $\overline{\lambda}_r$ for lactating females (States 3 and 4; see *NB Foraging Model*, Table 1). We calculated E_{Prey} following McHuron et al., (2017b)

$$E_{Prey} = \overline{E}_{X_F,X_P}\,\overline{Y}_{r,t} \tag{9}$$

where $\overline{E}_{X_F,X_P}$ is the average gross energy requirement for a female given her mass and the mass of her pup (when applicable), and $\overline{Y}_{r,t}$ is the profitability associated with foraging ($\overline{Y}_{r,t} > 1$; Table 1, Supp. Text). Thus, the energy gained from successful foraging was a fixed multiple of a female's gross energy requirements. For a non-lactating female this always resulted in a net mass gain when she found prey (dictated by $\overline{\lambda}_r$) because the time step was always a single day and she had no dependent pup. In contrast, the magnitude and direction of mass changes for a lactating female depended on whether the length of her foraging trip was shorter, longer, or equivalent to the average duration (Supp. Text). We used the annual survival estimates from Hernández-Camacho et al., (2008b) for different age classes to calculate age-specific daily mortality β_a (Fig. S5, Supp. Text), which likely already includes some level of anthropogenic disturbance. Our effects of disturbance are thus in addition to these baseline values.

2.5. The negative binomial (NB) foraging model for lactating females

In the case of lactating females (States 3 and 4), we used the NB model described in McHuron et al., (2017b) to calculate $\overline{\lambda}_r$ and determine the time steps in the backward iteration and the duration of each foraging trip in the forward simulation. The NB distribution describes the probability of waiting for a fixed number of successes; in this scenario, it describes the probability distribution of the number of days at sea needed before a female has s days of successful foraging. The remaining days spent at sea are comprised of travel time to a foraging patch (τ) and unsuccessful days of foraging (k) such that the average trip duration is

$$\overline{d}_{sea} = \overline{s} + \overline{k} + 2\overline{\tau} \tag{10}$$

The average number of successful foraging days ($\overline{s}$) is determined by $\overline{\lambda}_r$ (McHuron et al., 2017b)

$$\overline{\lambda}_r = \frac{\overline{s}}{\overline{d}_{sea} - 2\overline{\tau}} \tag{11}$$

We used existing tracking and diving data of lactating adult females collected during early and late lactation to estimate $\overline{s}$,$\overline{\tau}$, $\overline{d}_{sea}$, and$\overline{d}_{land}$ and calculated $\overline{\lambda}_r$ from these values (Table 1). We assumed that $\overline{d}_{sea}$and$\overline{\tau}$ during early lactation were the same as measured during late lactation based on satellite telemetry of a limited number of sea lions tracked in both periods (S. Melin, unpublished data). We also assumed that the behavior of lactating females was equivalent.

2.6. Stochastic Dynamic Programming equations

When solving the SDP equations, we assume that individuals act in such a way to maximize their lifetime reproductive fitness. The fitness of females in all states is defined as the expected maximum accumulated pup recruitment taken over stochastic events of mortality and finding prey. Pup recruitment is defined as survival to age one. The output of the SDP equations is both fitness and the optimal behavioral decision for each reproductive state ($d_1^*(x_F, t)$, $d_2^*(x_F, t)$, $d_3^*(x_F, x_P, t)$, $d_4^*(x_F, x_P, t)$); we generically denote these by d^*.

At the time of weaning in the year of reproductive senescence, T, there are two possible reproductive states. The terminal fitness of a non-pregnant female (States 1 and 3) is

$$\begin{aligned} F_1(x_F, T) &= 0 \\ F_3(x_F, x_P, T) &= \Phi_P(x_P) \end{aligned} \tag{12}$$

where $\Phi_P(x_P)$ describes the probability of pup recruitment into the population at age one as a function of mass at weaning (Fig. S6, Supp. Text). After T, the future fitness of all females is 0 (i.e. we ignore any grandparental effects) and all females transition to State 1 until death. The fitness and optimal decisions for each reproductive state for $t < T$ were calculated moving backwards through time, and are described in detail below. If at any time a female's mass fell below $x_{\min,F}$ she was presumed dead and all future fitness goes to zero. Similarly, a female with a pup whose mass fell below $x_{\min,P}$ did not receive any credit for that pup because the probability of pup recruitment was zero. For all fitness comparisons, we assumed that if the fitness values of two different states were equivalent, a female transitioned to the less energetically expensive state. For example, if a female in State 3 had a pup that fell below $x_{\min,P}$, she would have a future expected fitness value equal to a female in State 1, thus transitioning between the two states.

2.6.1. Reproductive state 1 (juveniles or non-pregnant, non-lactating adults)

For times less than T, the fitness of females in State 1 is

$$F_1(x_F, \mathrm{t}) = e^{-\beta_a}[\overset{\text{Find food}}{\lambda_1 F_1(x'_F, t + 1)} + \overset{\text{Does not find food}}{(1 - \lambda_1)F_1(x'_F, t + 1)}]$$

where x'_F is the future expected mass calculated using Eq. (2) (for the second term on the right-hand side of Eq. (13)) and Eq. (3) (for the first term on the right-hand side of Eq. (13)). To simplify notation, we denote the right-hand side of Eq. (13) as $<F_1(x'_F, t + 1)>_{\{\lambda_1,\beta_a,Y_1\}}$ in future equations.

At the time of the next possible implantation, a female either implants, in which case she moves to State 2, or remains in a non-reproductive state. This decision depends on a comparison of fitness values in these two states

$$F_1(x_F, t_I(a_m + \mathrm{n})) = \max\{\overset{\text{Remain non-reproductive}}{<F_1(x'_F, t_I(a_m + n) + 1) >_{\{\lambda_1,\beta_a,Y_1\}}}, \overset{\text{Implant}}{<F_2(\mathrm{x}'_F, t_I(a_m + \mathrm{n}) + 1) >_{\{\lambda_2,\beta_a,Y_2\}}\ n) + 1)>_{\{\lambda_2,\beta_a,Y_2\}}}\} \tag{14}$$

2.6.2. Reproductive state 2 (pregnant)

A pregnant female may abort the fetus at any time between the day after implantation and the day before birth, returning to State 1 so that

$$F_2(x_F,\mathrm{t}) = \max\ \{\overset{\text{Remain pregnant}}{<F_2(x'_F, t+1)>_{\{\lambda_2,\beta_a,Y_2\}}}\ ,\ \overset{\text{Abort fetus}}{<F_1(\mathrm{x}'_F, \mathrm{t}+1)>_{\{\lambda_1,\beta_a,Y_1\}}}\ \} \tag{15}$$

At the time of birth, a female returns to the rookery and moves to State 3, remaining onshore for the duration of the perinatal period. Thus, her expected future fitness the day before birth is

$$F_2(x_F, t_b(a_m+\mathrm{n})-1)=\ e^{-\beta_a}[\overset{\text{Find food}}{\lambda_2 F_3(x'_F, x'_P, t_b(a_m+n))}+\ \overset{\text{Does not find food}}{(1-\lambda_2)F_3(x'_F, x'_P, t_b(a_m+n))}] \tag{16}$$

We used a value of $x'_P = 9\mathrm{kg}$ in Eq. (16).

2.6.3. Reproductive state 3 (lactating)

The expected fitness of a female at the time of birth (of her pup) is

$$F_3(x_F x_P, t_b(a_m+n)) = F_3(x'_F, x'_P, t_b(a_m+n)+d_{PN}) \tag{17}$$

where x'_F and x'_P are calculated as described in Eqs. (4) and (7), respectively. Between the end of the perinatal period and the time step before weaning, the NB foraging model applies so that fitness depends on the probability distribution of the number of unsuccessful foraging days (k) given the probability of finding prey ($p(k|\lambda_{3_t})$) and a binomial variable $s'(k_i, x_F) = 0\mathrm{or}1$ describing whether a female would fall below $x_{\mathrm{min,F}}$ if all unsuccessful foraging days occurred at the beginning of the trip. Thus,

$$F_3(x_F, x_P, t) = \sum_{k=0}^{K_{\max}} p(k_i|\lambda_{3_t})s'(k_i, x_F)(e^{-\beta_a d_{sea}}F_3(x'_F, x'_P, t')) \tag{18}$$

where x'_F and x'_P are calculated using Eqs. (5) and (8), respectively. When $x'_P < x_{\mathrm{min},P}$ we set $F_3(x_F, x_P, t) = F_1(x_F, t)$ because the female loses the pup. As above, we use $<F_3(x'_F, x'_P, t')>_{\lambda_{3_t},\beta_a,Y_{3_t}}$ to denote the right-hand side of Eq. (18).

Between the end of the perinatal period until the day before implantation (or the day after implantation to the day before weaning), a female could continue nursing her pup, or choose to wean the pup early

$$F_3(x_F, x_P, \mathrm{t})=\ \max\{\overset{\text{Continue lactating}}{<F_3(x'_F, x'_P, t')>_{\{\lambda_{3_t},\beta_a,Y_{3_t}\}}}\ ,\ \overset{\text{Wean pup}}{<F_1(x'_F, t+1)>_{\{\lambda_1,\beta_a,Y_1\}} + \Phi_P(x_p)}\} \tag{19}$$

If the time step spanned the time of implantation $t < t_I(a_m + n)\mathrm{and}t' > t_I(a_m+n)$, we set $F_3(x_F, x_P, t) = F_3(x'_F, x'_P, t_I(a_m+n))$. At the time of implantation, a female in State 3 could transition to any of the reproductive states since she could wean and implant on the same day so that

$$F_3(x_F, x_P, t_I(a_m+\mathrm{n})) = \max\left\{\begin{array}{cc} \text{Continue lactating} & \text{Wean pup} \\ <F_3(x'_F, x'_P, t_I(a_m+n)+1)>_{\{\lambda_{3_t},\beta_a,Y_{3_t}\}}\ , & <F_1(x'_F, x'_P, t_I(a_m+n)+1)>_{\{\lambda_1,\beta_a,Y_1\}} + \Phi_P(x_p) \\ \text{Implant, Wean pup} & \text{Continue lactating, Implant} \\ <F_2(x'_F, x'_P, t_I(a_m+n)+1)>_{\{\lambda_2,\beta_a,Y_2\}} + \Phi_P(x_p), & <F_4(x'_F, x'_P, t_I(a_m+n)+1)>_{\{\lambda_{4_t},\beta_a,Y_{4_t}\}} \end{array}\right\} \tag{20}$$

At the time of weaning, the increment in fitness of a female in State 3 was assessed based on pup mass, and she transitioned to State 1.

2.6.4. Reproductive state 4 (lactating and pregnant)

Between the day after implantation and the day before weaning, a female could transition to any of the reproductive states, so that

$$F_4(x_F, x_P, \mathrm{t}) = \max\left\{\begin{array}{cc} \text{Continue lactating, Pregnant} & \text{Abort fetus, Wean pup} \\ <F_4(\mathrm{x}'_F, \mathrm{x}'_P, \mathrm{t}')>_{\{\lambda_{4_t},\beta_a,Y_{4_t}\}}\ , & <F_1(\mathrm{x}'_F, \mathrm{x}'_P, \mathrm{t}+1)>_{\{\lambda_1,\beta_a,Y_1\}} + \Phi_P(x_p) \\ \text{Pregnant, Wean pup} & \text{Continue lactating, Abort fetus} \\ <F_2(\mathrm{x}'_F, \mathrm{x}'_P, \mathrm{t}+1)>_{\{\lambda_2,\beta_a,Y_2\}} + \Phi_P(x_p), & <F_3(\mathrm{x}'_F, \mathrm{x}'_P, \mathrm{t}')>_{\{\lambda_{3_t},\beta_a,Y_{3_t}\}} \end{array}\right\} \tag{21}$$

At the time of weaning, the increment in fitness of a female in State 4 was assessed based on pup mass, and she transitioned to State 2.

2.7. Individual-based forward simulation and disturbance exposure scenarios

We assessed the fitness and population consequences of disturbance by simulating a population of California sea lions (initial size $n = 250$ non-pups) across 15 years under different disturbance exposure scenarios, assuming that individuals followed the optimal decisions based on Eqs. (12)–(21). We initialized the simulations with a stable age structure representing a well-established population (Figs. S7–S8, Supp. Text). We used data from Melin et al., (2012) that described the probability that a female of a given age range would survive and give birth the following year to assign a reproductive state to all reproductive-aged females at the start of each simulation. At the first time step in the simulation, all pregnant females gave birth; thus, the initial population size was > 250. We assigned initial masses to each individual from a normal distribution with mean and standard deviation based on their age calculated from von Bertalanffy parameters in Table 4 of Laake et al., (2016).

For simplicity, we replaced $e^{-\beta_a}$ by its Taylor expansion in the forward simulation. At the beginning of each time step, we compared β_a to a random number drawn from a uniform distribution (i.e. $\tilde{U} \sim (0,1)$) to determine if a female survived that time step (she survived if $\tilde{U} \geq \beta_a$). A similar approach was used to determine if non-lactating females (States 1 and 2) found food on any given day (she found food if $\tilde{U} \leq \lambda$). The appropriate equations (Eqs. (2)–(5),(7) and (8)) were used to calculate x_F and x_P (when applicable) at the next time step, and reproductive state determined from the optimal decision. At the time of birth, which was the first time step in the simulation, pups were assigned a mass based on a normal distribution using the mean and standard deviation from Table 4 in Ono et al., (1987) with a 50:50 sex ratio. For lactating females, we randomly drew the duration of a foraging trip from a distribution of values based on the probabilities from the NB model (Fig. S9). In addition to early weaning determined from the SDP model, we assumed that early weaning was initiated if a female had such a long foraging trip that she delivered no milk energy to her pup. Female pups recruited into the population on June 15th in the year following birth at their wean mass if $\tilde{U} \leq \Phi_P(x_P)$. For each year of the simulation, we calculated the probability of pup recruitment (i.e. the number of female pups that survived divided by the number of female pups born) and the population size at the start of each year, based on the number of adult and juvenile females alive plus the number of male and female pups born. This allowed us to determine the mean pup recruitment across all years and the population growth rate, which was calculated based on the initial and final population size. We replicated each simulation 100 times to calculate a mean pup recruitment and population growth rate for each disturbance exposure scenario.

We simulated a total of 60 scenarios to determine how the (1) response of individuals to exposure, (2) timing of exposure (early vs. late lactation), (3) duration of exposure (1, 3, or 6 months), and (4) frequency of exposure (the first year of the simulation *vs.* all years of the simulation) affected pup recruitment and population growth rates. We assumed that when exposed to a disturbance on any given day, an individual female responded by increasing her foraging trip duration, either because foraging was disrupted or because she left the area to forage in a new location. We modeled four fixed responses, where all sea lions increased their trip duration by 0 (undisturbed scenario), 1, 4, or 12 h for each day they were exposed, and one variable response where the increase in foraging trip duration for each day of exposure was drawn from a truncated normal distribution from 0 h (no response) to 1 day (strong response) with a mean and standard deviation of 12 h. The daily probability of exposure (E_{dist}) was arbitrarily set at 0.3; a sea lion was disturbed on a given foraging day if $\tilde{U} < E_{dist}$. We chose not to model disturbance for non-lactating females because if exposed to a potential disturbance, these individuals have the flexibility to forage outside of the disturbed area for extended periods of time.

We used Cohen's *d* to determine the impact of exposure to disturbance on pup recruitment and population growth rates, which is the difference between two means scaled by their pooled standard deviation (Cohen, 1992; McHuron et al., 2017a; White et al., 2014). We computed mean values by averaging the mean pup recruitment and population growth rates across simulation replicates. We compared mean values from each scenario to values obtained with no disturbance. The resulting values for Cohen's *d* are a measure of the reduction in pup recruitment or population growth rate that can be attributed to disturbance in multiples of the common standard deviation. In addition to the actual values, we used values of 0.2 (small effect), 0.5 (moderate effect), and 0.8 (large effect) to qualitatively assess the impact of exposure to disturbance (Cohen, 1992, 1977). Because the probability of disturbance was arbitrarily chosen, we examined how changes in this parameter affected Cohen's *d* by altering it by ± 50% for two scenarios that resulted in either a small or large effect of disturbance, as determined using Cohen's *d*. We implemented the model using R version 3.4.1 (R Core Development Team, 2017).

3. Results

The model captured many of the complexities of the sea lion reproductive cycle, including variability in the timing of life history events (Fig. 3). Juveniles were more likely to die than adults from both starvation and other sources of mortality, with an average age at death of 3.2 years. For sea lions that survived to reproductive age, the majority of females first gave birth at ages 5 or 6, but some delayed reproduction up to 12 years of age. Pregnancy rates were high within any given year, with an average of 92% of mature females becoming pregnant; however, many of these pregnancies were aborted, as only 68% of mature females gave birth to a pup the following year. When faced with periods of poor foraging success that resulted in loss of mass, sea lions in State 4 (lactating and pregnant) generally aborted their fetus before weaning their current pup (Fig. 3). The average wean date was April 8th, 37 days before the weaning deadline of May 15th, with female pups weaning at an average mass of 32.4 kg and a minimum mass of 9.1 kg. On average, 70% of pups weaned before the deadline, largely because the pup had reached or was very close to $x_{\max,P}$ (70% of early weaning events) with the remaining 30% of early weaning due to the combination of female and pup mass.

In the absence of disturbance, the average pup recruitment was 0.70 ± 0.09, with values ranging from 0.37 to 0.82 for individual replicates. The mean population size in the last simulation year was 871 ± 48, resulting in a mean population growth rate of 0.05 ± 0.04, with values ranging from 58 to 1885 and −0.12 to 0.11 for individual replicates, respectively. In the presence of disturbance, mean values for each scenario ranged from 0.48 to 0.72 (pup recruitment), 402 to 926 (population size in last year), and −0.09 to 0.05 (population growth rate). Mean values for individual replicates in the presence of disturbance were 0.18 to 0.82 (pup recruitment) and −0.05 to 0.11 (population growth), with a minimum population size at the last time period (across all scenarios and replicates) of 2 sea lions. Disturbance that was recurrent in each year resulted in reductions in pup recruitment and population sizes, even when sea lions had relatively mild behavioral responses to the disturbance (> 1 h) or when the disturbance occurred for a relatively short duration (> 1 month) (Fig. 4; Table S3 – S4). The effect of a recurrent disturbance on population growth trajectories was not apparent for several years under less severe disturbance conditions (Fig. 5A). The effect of disturbance on population size and growth rate was driven not only by changes in pup recruitment resulting from an earlier wean date and a lighter wean mass (Figs. 4C and 5B), but also from changes in pregnancy rates, birth rates, and the inter-pup birth interval (Fig. 5B). There was a slight trend towards increased age at first reproduction with disturbance severity, but the magnitude of the change was relatively small compared with the other parameters (Fig. 5B).

Disturbance had a similar effect on pup recruitment and population growth rates, with Cohen's *d* values for individual scenarios ranging from −0.3 to 2.8 and mean values across all disturbance scenarios of 0.39 for both variables. Changes in the duration, frequency, and behavioral response of sea lions to disturbance all had a strong effect on Cohen's *d*, whereas changes in the timing of disturbance during the year had relatively little effect on Cohen's *d* (Fig. S10, Table S3 – S4). For example, there was an 11% increase in Cohen's *d* for population growth rate when a disturbance occurred in late *vs.* early lactation, but a 700+% increase when it occurred in every year *vs.* just the first year of the model. There was a relatively small effect of disturbance on pup recruitment or population growth when the behavioral response and duration of disturbance was short (< 4 h and ≤ 3 months) regardless of the frequency of the disturbance (Cohen's $d < 0.5$), although the probability of disturbance had a large effect on absolute values of Cohen's *d* (Table S5). When the effect of disturbance, as measured by Cohen's *d*, was relatively small, changes in the probability of disturbance had a larger impact on the percentage change in Cohen's *d* than when the effect of disturbance was large. For example, a 50% decrease in the probability of disturbance resulted in a 62% or 58% reduction in Cohen's *d* with respect to population growth, whereas a 50% increase resulted in a 123% or 30% increase in the value of Cohen's *d*.

4. Discussion

Our model captured many of the reproductive complexities of a long-lived income-breeder, using California sea lions as a motivating species. These complexities, which were emergent properties of the model, included variation in the age at first reproduction, termination of pregnancy and skipped breeding years, and variation in the timing of weaning. This ability to capture variation in reproductive behaviors is crucial for ecological models because changes in reproductive success are a primary driver of population dynamics. While no model can capture all of the intricacies of a natural population, the fecundity estimates from undisturbed scenarios were generally consistent with empirically-derived data for California sea lions and other pinnipeds (Hammill and Gosselin, 1995; Hernández-Camacho et al., 2008a; Lima and Paez, 1995; McKenzie et al., 2005; Pitcher and Calkins, 1981; Shero et al., 2018). We calculated that on average 92% of mature females were pregnant in any given year, with an annual abortion rate around 25%, which is within the range of birth rate estimates of California sea lions from the Gulf of Mexico (Hernández-Camacho et al., 2008a). Similarly, studies on Steller sea lions (*Eumetopias jubatus*) and New Zealand fur seals (*Arctocephalus forsteri*) found pregnancy rates as high as 96%, with an average of 32% of these pregnancies ending in early termination (McKenzie et al., 2005; Pitcher and Calkins, 1981). Once pups were "born" in the forward simulation, some females nursed up until the weaning deadline, but the average length of lactation was approximately 10 months with 59% of pups weaned before May 1st.

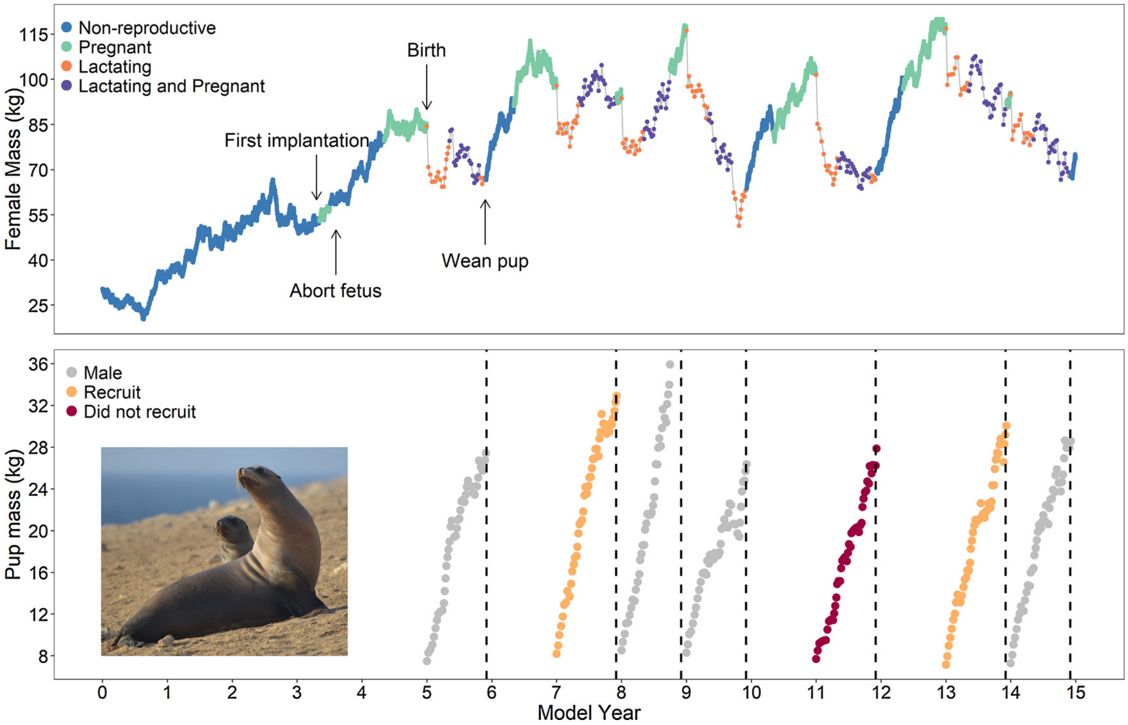

Fig. 3. Example output from the forward simulation for a female that was one year old at the start of the simulation, showing changes in her mass and reproductive state (top) and each of her pup's masses (bottom) with time. Colors correspond to reproductive state (top), or the sex and recruitment status of the pup (bottom). In the bottom panel, the dashed line indicates the weaning deadline (May 15th) in each year that a pup was born. Photo showing an adult female sea lion and her pup by S. Peterson.

These findings are similar to a mark-recapture study of branded California sea lion pups that found a minimum of 40% of pups were still nursing by the end of April, with the majority of weaning occurring during a one month period starting at the end of April (Harris, 2016). The earlier time of weaning estimated from our model compared with estimates from Harris (2016) may have been due to differences in energy availability (i.e. greater energy return to females from foraging in our model) or energy allocation to pups (i.e. greater energy allocated to pups in our model). This could represent inaccuracies in our model, but it also may simply reflect that we simulated better foraging conditions than the actual conditions experienced by the mothers of pups resighted in Harris (2016).

Measurements of reproductive characteristics, such as reproductive rates and weaning dates, are important for understanding population dynamics and in quantifying population responses to environmental variability. Empirical measurements can however be difficult to obtain as they typically require time intensive resighting effort of marked individuals, which is particularly challenging for species that have extended periods of maternal care and reproduce in remote areas. The similarities between the model output from the forward simulations and empirically-derived estimates suggests that the state transitions derived from the backward iteration are consistent with the behavioral decisions of sea lions in nature. Thus, while our primary goal was to highlight the use of SDP models in the context of anthropogenic disturbance, the model we developed here could be used to estimate these variables, as well as address fundamental ecological processes and the mechanisms that give rise to these processes (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel and Clark, 1988). For example, several otariid species including California sea lions can exhibit extended lactation durations > 1 year (Higgins and Gass, 1993; Trillmich and Wolf, 2008), and a modified version of our model could be used to investigate the environmental conditions that give rise to this phenomena. These modifications include a relaxation or elimination of the weaning deadline, as well as the inclusion of an additional reproductive state(s) to allow a female to nurse a juvenile.

Practical application of our approach requires knowledge of the disturbance and dose-response curve, which are exogenous to the behavioral and life history modeling. Lacking those for California sea lions, we were still able to quantify the consequences of a general anthropogenic disturbance on pup recruitment and population dynamics via analysis of a wide range of scenarios. We modelled the behavioral response of sea lions to disturbance as an increase in foraging trip duration; as such, the results from our disturbance scenarios are comparable with natural environmental fluctuations because female otariids often alter their foraging trip duration in response to changes in prey availability and distribution (Costa, 2008). In our model, disturbance had a negative impact on population dynamics primarily through reproductive changes and not adult mortality, which is in accordance with life history theory (Roff, 1993; Stearns, 1992). While reduced pup recruitment due to a lower mass at weaning was an important driver of negative impacts of disturbance on population dynamics, alterations in other reproductive characteristics also contributed to this trend. Pregnancy rates declined slightly, but there were much larger changes in birth rates and the inter-pup interval, indicating that disturbance increased abortion rates and led to skipped reproductive years. Pups that weaned at a lower mass were more likely to delay reproduction, but the magnitude of this change compared with undisturbed scenarios was relatively ssmall. These results are consistent with the response of otariid populations to El Niño events and other time periods of prey depletion (Lunn et al., 1994; Soto et al., 2004; Trillmich et al., 1991), further validating that our model captured some of the reproductive complexity of California sea lions.

Our focus was largely on model development and the disturbance scenarios should not be interpreted as representative of a specific disturbance situation. We do however show the utility of using SDP models to fully implement the PCoD framework by using a range of disturbance scenarios. In the undisturbed case, combining backward iteration and forward simulation allows us to both simulate the trajectories of populations and compute the entries for a stage-or age-structured matrix model of population dynamics. When anthropogenic disturbance not in

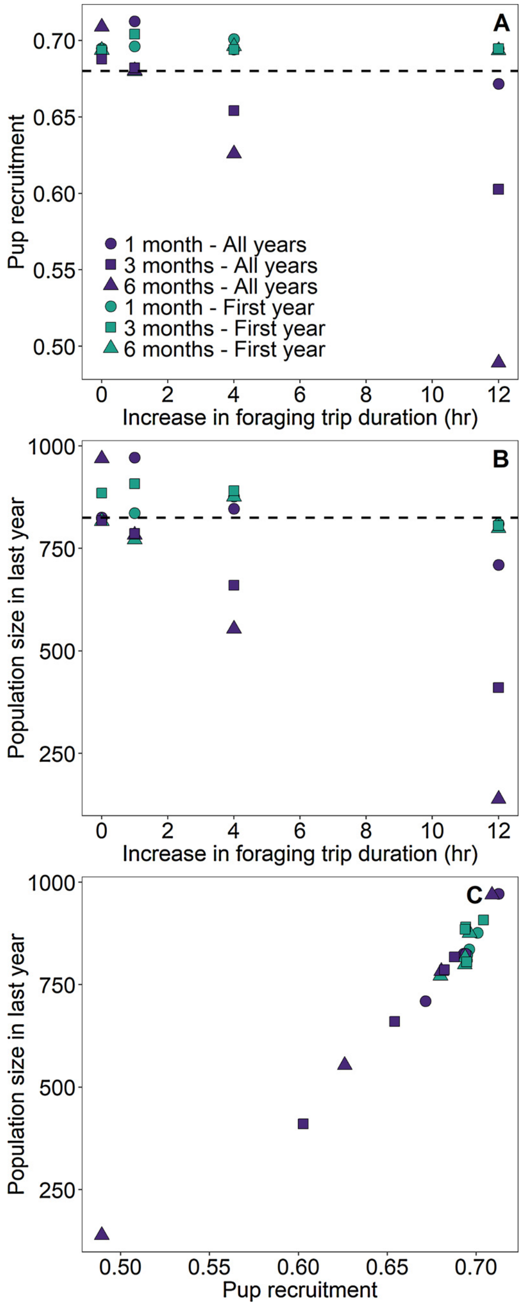

Fig. 4. The influence of disturbance on pup recruitment (A) and population size in the last year of the forward simulation (B), and the relationship between population size in the last year and pup recruitment (C). In each plot, points represent the mean value for a disturbance scenario averaged across 100 replicates (and all years within a replicate for pup recruitment), with shape representing the duration of the disturbance and color the frequency of the disturbance. In A and B, the x-axis represents the behavioral response of sea lions to a disturbance, modelled as a daily increase in foraging trip duration for each day disturbed. The behavioral response scenario where an individual's response was drawn from a distribution of 12 h is not shown but was similar to the 12-hour scenario. Points below the dashed line correspond to scenarios where Cohen's *d* was > 0.2, indicating an effect of disturbance on either pup recruitment (A) or end population size, hence growth rate (B). Only scenarios where disturbance began in late lactation are shown.

the evolutionary history of the animals is added, forward simulation becomes essential because we do not know *a priori* how disturbance will affect them. For marine mammals, approaches for determining the effects of disturbance on vital rates and population dynamics have largely focused on bioenergetic models, which are primarily limited to capital-breeding species (Costa et al., 2016; Villegas-Amtmann et al., 2017, 2015), or individual-based models solely comprised of a forward simulation (King et al., 2015; Nabe-Nielsen et al., 2018; New et al., 2014). Our approach is also individual based and uses forward simulation, however, it is the combination of backward iteration with the SDP model and forward simulation that makes it so powerful. The backward iteration links environment and reproductive success through physiology and leads to state- and time-dependent behavioral decisions. By implementing those rules in the forward simulation, we are able to obtain estimates of annual reproductive success and survival in the absence and presence of disturbance. It is those estimates that allow us to reach the objective of population consequences – the trajectory in Fig. 5. Pirotta et al., (2018) provides another example of the power of the backward iteration and forward simulation, particularly as it relates to differential responses to natural environmental fluctuations that are in the evolutionary history of a species and an anthropogenic or other environmental disturbance that is not.

Using Cohen's *d* allowed us to assess the relative influence of disturbance scenario parameters, which can help prioritize future data collection efforts and provide insight into planning activities that create disturbance. For example, characteristics of the disturbance such as how often and how long the disturbance occurred had a relatively strong impact on whether disturbance affected vital rates and population dynamics. Repetitive disturbances had the largest impact on pup recruitment even when the behavioral response of sea lions to disturbance was relatively mild or the duration of the disturbance was relatively short. While our disturbance scenarios were not meant to represent a disturbance specific to sea lions, potential repetitive disturbances that may be experienced by wild populations across the durations we simulated include ecotourism, seismic surveys, road and vessel noise, annual Naval exercises, and development of renewable energy sources (e.g. wind or tidal turbines). For the probability of disturbance that we simulated, disturbance scenarios that only occurred in the first year of the simulation generally did not affect pup recruitment or population growth; however, the animals' sensitivity to disturbance (probability of being disturbed and behavioral response) also had a strong impact on the effect of disturbance on these parameters. This suggests that income- breeding populations may be vulnerable to even short, infrequent disturbances, such as sonar or construction (Nabe-Nielsen et al., 2018), although the results from our model indicated that it may take several years after the initial disturbance to detect its effect on population growth rates. This lag is likely due to the delay between recruitment and reproductive maturity, as it took a minimum of three years for sea lions that were pups at the time of the initial disturbance to reach reproductive maturity. On the other hand, the timing of disturbance during lactation had a relatively small influence on Cohen's *d*; however, it is important to consider that this may not be a general characteristic across species if there are significant temporal changes in prey availability that co-occur with an anthropogenic disturbance. While not included here, temporal changes in prey availability are straightforward to incorporate into SDP models (Pirotta et al., 2018). In addition to characteristics of the disturbance itself, the behavioral response of an individual to disturbance was influential, highlighting the importance of short-term behavioral response studies that attempt to measure just this. Collectively, these results suggest that caution should be applied in making blanket conclusions about the robustness of income-breeding species to anthropogenic disturbance, since types of disturbance (e.g. naval sonar, seismic surveys) may differ in their characteristics and individuals may not exhibit the same behavioral response to all types of anthropogenic disturbance.

As the human footprint continues to expand in the natural world, the ability to assess the consequences of anthropogenic disturbance by linking behavioral and energetic effects at the individual to the population level becomes essential for accurate prediction of population trajectories. The challenges raised by human-wildlife interactions are a

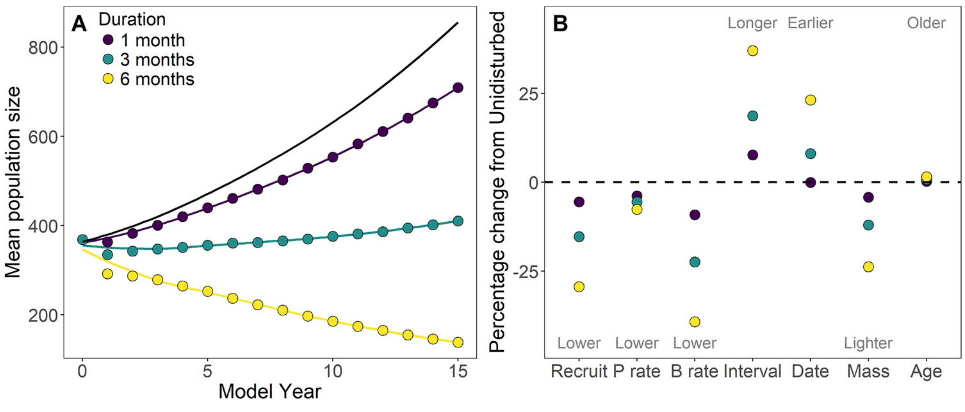

Fig. 5. Population trajectories for three disturbance scenarios occurring during late lactation in all years of the simulation (A), and differences in pup and reproductive characteristics as a percentage change from the undisturbed scenario (dashed line) for the same three scenarios (B). In A, the undisturbed trajectory is represented by the black line and colors represent variation in the duration of the disturbance. In B, characteristics are as follows: Recruit = Probability of pup recruitment, P rate = Pregnancy rate, B rate = Birth rate, Interval = Interval between pups, Date = Wean date, Mass = Wean mass, and Age = age at primiparity. The text description represents the direction of the change in each variable under disturbed conditions. In both plots, values are averaged across all 100 replicates per scenario.

global problem common to both terrestrial and marine environments and understanding the population effects of human-related disturbances on wildlife has been identified as a conservation priority (Francis and Barber, 2013). The methods we have developed here, and illustrated with California sea lions, are a natural framework for studying the linkages between disturbance and population consequences. We have shown that characteristics of the disturbance itself and animal behavior are both important components of understanding when a disturbance results in biologically meaningful effects, which underscores the importance of research efforts to understand the short-term behavioral responses of species to a disturbance and more general ecological studies that quantify animal movements and habitat use. Our results indicate that while prolonged, repetitive exposures are more likely to have an effect, even relatively short, infrequent disturbances can adversely affect population dynamics of an income-breeding species. The derivation of state- and time-dependent reproductive decisions using an SDP model captures many of the important aspects of an income-breeders life history strategy, and while parameterized for California sea lions, could be adapted to model reproductive decisions in a wide range of mammalian species. The structure of SDP models is also flexible, allowing for the incorporation of additional state variables or biological parameters that may be of interest for specific applications, such as density-dependent effects, age-specific reproductive rates, and desensitization of individuals that are repetitively disturbed. In addition to reproductive decisions, foraging location is likely to be an important state variable for anthropogenic applications, and this model serves as a stepping stone towards the development of these more complex models that incorporate reproductive and foraging decisions.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.07.016.

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