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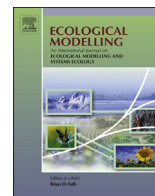
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An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal



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ABSTRACT

One of the crucial scientific challenges of this century is characterizing the vulnerability of ecosystems to climate change. Bioenergetics models can provide a theoretical construct for addressing specific physiological and ecological hypotheses about how individuals may respond; however, many models fail to link energy deficiencies with reproductive consequences, and thus cannot be used to predict population-level impacts. Here, we present an agent-based, ecophysiological model that simulates the energy balance of adult, female Weddell seals (*Leptonychotes weddellii*). The input parameters include physiological values and population-wide ranges for the duration and phenology of life history events. Energy intake depends on foraging effort and stochastic prey availability, whereas energy expenditure is calculated from time- and behavior-specific demands. The simulated seal selects an activity (forage, nurse pup, molt, rest) based on body condition and life history constraints. At the end of each timestep, the energy budget is balanced, and catabolism or anabolism occurs. Following model development and validation with empirical data, simulations were run to study the responses of individuals to: (1) baseline conditions; and (2) reduced prey availability. As expected, the model replicated the known fluctuations in energetic requirements associated with reproduction and molt. A 10% reduction in prey availability resulted in seals foraging more and resting less. At the end of the year-long simulations, animals in the baseline simulation had significantly higher body masses than animals in the perturbation simulation. The model was successfully used to explore decision-based energy allocation strategies that occur under different energetic stressors and to elucidate how extrinsic conditions can impact individual fitness. Identifying the temporal sensitivities of Weddell seals to predicted anthropogenic changes is a valuable contribution to the study of global change biology and can inform management decisions in polar regions.

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1. Introduction

The rapid environmental change that is occurring in polar regions (Parkinson 2004; Stammerjohn et al., 2008; Forcada et al., 2012) has energetic implications for top predators (Fraser and Hofmann 2003; Forcada et al., 2008). For pinnipeds, loss of ice platforms increases the distance between predator haul-outs and prey concentrations (Jay et al., 2010) and reduces suitable habitat used for resting, breeding, and predator avoidance (Siniff et al., 2008; Costa et al., 2010; Kovacs et al., 2010). Further, the delayed for-

mation of sea ice in the fall and winter can alter breeding and molting phenology of ice-obligate species that embark upon foraging trips in conjunction with the seasonal advance and retreat of sea ice (Simpkins et al., 2003; MacIntyre et al., 2013). Lastly, reductions or changes in the timing of ice coverage can indirectly impact predators by interrupting typical primary productivity regimes and decreasing prey availability (Durant et al., 2007; Kovacs et al., 2010).

Reductions in the abundance or quality of prey can increase baseline energetic costs as animals are forced to increase their foraging effort to obtain the same energetic return (Trites et al., 1997; Goundie et al., 2015). Overfishing of high-energy prey items can lead to reduced prey availability or a dietary shift to low-energy prey items (Hückstädt et al., 2012). In the Antarctic, the existing competition between commercial fisheries and pinnipeds (Ainley and Siniff 2009) will likely worsen as demands for fish increase and sea ice reductions promote the expansion of commercial fish-

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eries (Kawaguchi et al., 2009; Nicol et al., 2012). To fully understand how environmental perturbations, such as climate change and fishing pressure, might impact seal populations, it is first important to determine the physiological mechanisms that mediate those impacts (Bejder et al., 2006; Wiedenmann et al., 2011; Costa 2012).

Knowledge of bioenergetics mechanisms and physiological requirements can allow for fine-scale predictions about how energy balance can mediate the links between disturbances and population-level consequences (DeAngelis and Mooij, 2005; New et al., 2014). Quantifying the delicate balance between energy acquisition and expenditure in animals is important for several reasons. First, it helps researchers understand the evolution of behaviors and life history traits by predicting the costs of different critical life history events (Bowen, 1997; Simpkins et al., 2003) under different environmental conditions. Second, knowledge of the baseline energy and prey requirements for apex predators is required to evaluate their top-down effects on marine ecosystems (Boyd and Murray, 2001), and to identify periods when increased energetic requirements may temporarily deplete localized prey. Perhaps most importantly, changes in mass and body condition of top predators relative to baseline values can be used to indicate ecosystem health, since their body composition reflects the difference between energetic requirements and prey availability (Costa et al., 1989; Atkinson, 1997; Boyd and Murray, 2001; Reid and Croxall, 2001; Derocher et al., 2004; Burek et al., 2008). If changes in body composition result in compromised insulative abilities, it can cause feedback loops between reduced energetic reserves and increased energetic costs (Pearson et al., 2014b).

In many species, it is logistically challenging to conduct high resolution physiological, ecological, and behavioral studies throughout the entire year due to difficulty accessing animals in their wild habitat. Therefore, our understanding of energy balance during certain times of the annual cycle, such as when seals are at sea, is poorly known in many species. To fill these gaps, bioenergetic modeling can be used to estimate year-round prey consumption by combining daily energy requirements for individuals with empirically measured diets and population estimates (Lavigne et al., 1976). These models range in complexity from parsimonious equations with few parameters to detailed energy budgets with numerous parameters. Unfortunately, bioenergetics models seldom address the sensitivity of these energetic demands to changing environmental conditions and often cannot account for many sources of natural variability and/or behavioral responses to changing conditions. Further, many bioenergetic models are static in that the parameters used are discrete fixed values that rarely incorporate uncertainty and are independent of variations in other parameters. Many of the existing models also fail to consider energetic costs on a daily level, and as such, are insufficient to address costs associated with changes in phenology or variations in foraging success (Moen et al., 1997; Winship et al., 2002; Iverson et al., 2010; Rechsteiner et al., 2013). Additionally, models typically assume that animals remain within their thermoneutral zones (Watts et al., 1993; Winship, 2000) and do not include feedbacks between body condition and insulation capacity or consider thermoregulatory tradeoffs during the annual molt (Paterson et al., 2012). Finally, many models do not allow for simulated animals to increase their foraging effort in response to negative energy balance or starvation.

Dynamic, agent-based bioenergetic models that include feedback loops between different energetic components (Piou et al., 2015) offer the advantage of being able to identify potential shifts in energy allocation to those components under environmental stressors (Becher et al., 2014). In addition, by adding uncertainty to parameters using Monte Carlo simulations, these types of models can more accurately represent the ranges of parameters noted in free-ranging animals. Dynamic, agent-based bioenergetic mod-

els have been developed and utilized in recent years (Lusseau and Bejder, 2007; Rechsteiner et al., 2013; Johnston et al., 2014; Pirotta et al., 2014; Pirotta et al., 2015; Villegas-Amtmann et al., 2015) to calculate individual or population energy requirements for several species so that practitioners can make informed management decisions (Wood et al., 2015). Despite recent advances in agent-based modeling, there remain shortcomings that preclude the use of models to predict the impacts of environmental change on top predator populations. Many of these models fail to account for life history events, such as gestation and molt, and do not allow for animals to alter behavior in the face of changing extrinsic conditions.

Weddell seals are an ideal species for the development of a dynamic, agent-based model that includes behavioral plasticity because they have been the focus of a myriad of experiments and observational studies (Castellini et al., 1992; Hindell et al., 2002; Williams 2004; Wheatley et al., 2006; Fuiman et al., 2007; Hadley et al., 2007; Lake et al., 2008; Mellish et al., 2011; Eisert et al., 2013a; Chambert et al., 2014; Shero et al., 2015) that provide data for empirical validation of a predictive model. After pupping around mid-October, Weddell seals nurse their pups for around 6 weeks, during which they can lose up to 40% of their body mass (Wheatley et al., 2006). The seals employ a modified capital breeding strategy in which they supplement energy from lipid stores gained overwinter with intermittent foraging during the lactation period (Wheatley et al., 2008). Starting in late summer, Weddell seals undergo the annual molt, during which they are thought to increase the amount of time hauled out so that they can perfuse the skin to maintain a warm skin temperature and promote hair regrowth (Feltz and Fay 1966). Following the initiation of active gestation and seasonal molt, they begin the winter foraging period and, if pregnant, undergo active gestation (Shero et al., 2015). Time-depth recorders deployed on Weddell seals indicate that reproductive females spend 40–80% of each day during the winter period foraging to regain body condition (Shero et al., 2015), effort which far exceeds that of spring and summer (Beltran, *in prep*). These large fluctuations in activity patterns and energy intake buffer the animals against seasonal periods when they cannot forage (Wheatley et al., 2008).

The aim of this research was to develop a general model that describes Weddell seal energy requirements as a function of physiological and environmental variables and to investigate how that balance might respond to prey reduction. The dynamic model provides a decision-based matrix of internal energy allocation using species-specific input parameters as well as empirical data on environmental parameters. Following model development and validation, model runs were simulated to elucidate potential responses to changing environmental conditions. The potential impacts of different environmental scenarios can be evaluated so that appropriate management decisions can be made to optimize marine resource conservation (Lavigne et al., 1976).

2. Material and methods

The model description follows the ODD (Overview, Design concepts, and Details) protocol for describing agent-based models (Grimm et al., 2010). Model code is available upon request.

2.1. Model description

We used an ecophysiological modeling approach to represent the dynamic, interactive links between physiological processes in adult, female Weddell seals (*Leptonychotes weddellii*) (Fig. 1). The model was developed and implemented in R 3.1.1 (R Development Core Team 2011). Model input values included ranges of physiological parameters and duration estimates for the length of the

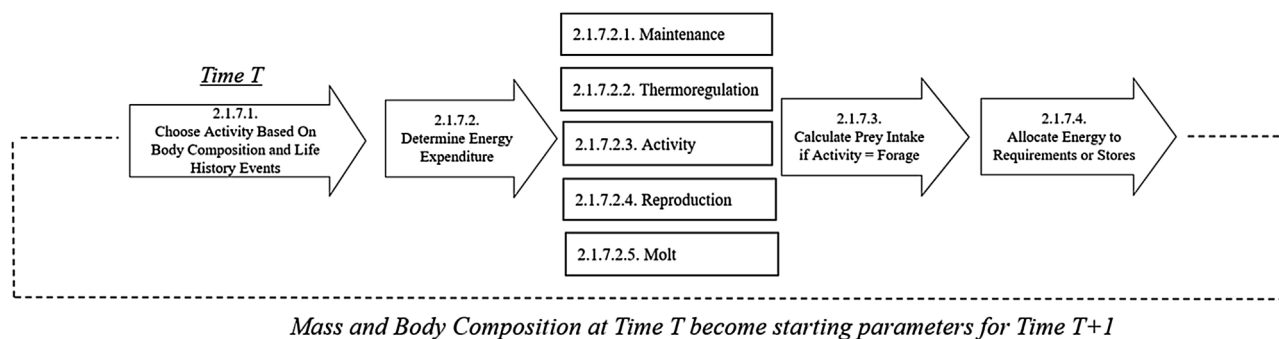


Fig. 1. Conceptual energetics model for one timestep (15-min duration) in the baseline simulation, where arrows represent submodels and boxes represent calculations. The model subheading numbers are included for reference.

molt and lactation periods. Values were obtained from the literature and from ongoing field studies. At the beginning of each timestep, the simulated animal selected an activity (forage, haul out to molt, nurse pup, or rest). The energy budget for the timestep was calculated by subtracting metabolic costs (maintenance, thermoregulation, activity, reproduction, and molt) from caloric intake. At the end of each timestep, energy allocation (mass loss or gain) occurred and females that were of adequate mass and body composition could survive and (if pregnant or lactating) continue to support their offspring.

2.1.1. Purpose

The purpose of the model was to simulate the energy balance, survival probabilities, and reproduction probabilities of free-ranging adult female Weddell seals (*Leptonychotes weddellii*) and to investigate how that balance could change under prey reduction scenarios.

2.1.2. Entities, state variables and scales

The model is comprised of the number of individual Weddell seals specified by the user with state variables including mass, percent fat, and activity at each timestep.

2.1.3. Process overview and scheduling

Each modeled Weddell seal has its own energy uptake and expenditure functions that interact based on fundamental physiological principles. After choosing an activity based on their current body condition and seasonal life history constraints (gestation, lactation or molt), individual seals assimilate energy from ingested food and allocate available energy to fulfill requirements in the order of importance to survival (Pianka, 1981): maintenance, thermoregulation, activity, reproduction, and molt.

2.1.4. Design concepts

2.1.4.1. Basic principles. The model relies on the processes involved in strategic decisions that must occur under trade-offs and constraints. Thus, model functions determine how energy intake and output direct behavior in response to baseline and prey reduction scenarios.

2.1.4.2. Emergence. The activity budget of each simulated individual is considered an emergent property, as it results primarily from mechanistic representations of behavior rather than imposed rules that force the model to produce a certain result.

2.1.4.3. Stochasticity. Monte Carlo simulations were used to generate a stochastic input value for each model component based on the mathematical distributions and values specified for each parameter (Hamby, 1994). In a similar manner, each component of the model was stochastically assigned a value at each timestep, such

that every run of the model accounted for parameter uncertainties and the model outputs reflected the variability characteristic in natural processes and the uncertainty in parameter estimates.

2.1.4.4. Observation. Outputs include survival rates (proportion of individuals that survive the 365-day simulation), reproductive rates (number of pups produced divided by the number of individuals surviving to the end of the simulation), average adult female mass, average adult female lipid percent (body composition), average proportion of time spent foraging, and average pup weaning mass.

2.1.5. Initialization

For the modeling exercise described in this paper, 10 individual Weddell seals were simulated in 15-min increments for 365 days. Simulations began on Jan 01, 2013 and continued through Dec 31, 2013. Seals were hauled out and pregnant at the start of the simulation. There was no spatial landscape for the model. Data and parameters are presented as mean \pm standard deviation.

2.1.6. Input data

Initial animal properties (Table 1) and parameters for energetic processes (Table 2) were derived from literature sources. Parameters were assigned one of the following distributions based on literature values: (1) Normal, defined by a mean and standard deviation; or (2) Uniform, defined by a lower limit and upper limit, with every value having an equal probability of being sampled. All equations are provided in Supplemental Table 1. Baseline model configurations are specified in Supplemental Table 2.

2.1.7. Submodels

The energy budget model is divided into several submodels. Each submodel, including the components, starting parameters, and assumptions necessary for model development, is presented in the following sections.

2.1.7.1. Activity selection submodel. Based on body condition (% lipid) and life history constraints operating at each timestep, each animal 'decides' whether to forage, haul out to molt, nurse their pup, or rest. The initiation dates (e.g. parturition date, molt start date) of the molt and lactation periods were randomly assigned to each simulated animal based on empirically-measured distributions of start dates. Both the duration of these events and the expected daily rate of progress through molt or lactation were fixed (Table 1). Seals lactated or molted only when hauled out, and if seals spent less time hauled out, they could fall behind the expected lactation and molt completion trajectories. If at a given timestep, the seal's molt or lactation progress was below the expected progress, the seal performed that activity in the next timestep, provided that

Table 1

Baseline parameter values for each simulated individual, with reference to literature sources. Stochastic parameters (i.e. those with normal distributions) were randomly assigned a value within the given distribution and range at the beginning of the simulation. Parameters were assigned one of the following distributions based on literature values: (1) Normal, defined by a mean and standard deviation; (2) Uniform, defined by a lower and upper limit; (3) Value, a single value; or (4) Equation. Abbreviation corresponds to the name of the parameter that was used in the R code. These functions were used to assign basic animal properties (such as surface area, body condition, and the phenology and duration of life history events such as lactation and molt) at the beginning of the simulation based on input parameters.

Parameter	Unit	Abbreviation	Distribution, Value	Reference
Date of Parturition (Since Jan 01)	Julian date	Date.parturition	Normal, Mean = 301, SD = 7	(Rotella, pers. comm.)
Length of Lactation	Days	Length.lactation	Uniform, Min = 42, Max = 49	Wheatley et al. (2006), Eisert et al. (2013a)
Date of Weaning (Since Jan 01)	Julian date	Date.weaning	Date.parturition + Length.lactation	–
Date of Molt Start (Since Jan 01)	Julian date	Date.molt.start	Normal, Mean = 33.817, SD = 6.77	(Beltran, in prep)
Date of Molt End (Since Jan 01)	Julian date	Date.molt.end	Date.molt.start + Length.molt	–
Length of Molt	Julian date	Length.molt	Value, 60	(Beltran, in prep)
Body Length	m	L	Normal, Mean = 2.47, SD = 0.11	(Burns, in prep)
Starting Percent Lipid	%	Fat.start	Normal, Mean = 0.326, SD = 0.05	(Burns, in prep)
Target Percent Lipid	%	Fat.target	Uniform, Min = 0.337, Max = 0.394	Shero et al. (2015)
Minimum Percent Lipid for Survival	%	Fat.min	Value, 0.05	Malavear (2002)
Target Mass	kg	Mass.target	Normal, Mean = 433.6, SD = 16.4	Shero et al. (2015)
Starting Mass (on Jan 01)	kg	Mass.start	Normal, Mean = 292.93, SD = 30.36	(Burns, in prep)
Axillary Girth	m	axgirth	Normal, Mean = 1.75, SD = 0.155	(Burns, in prep)
Axillary Blubber Thickness	m	axblubthick	$((14.787 * \text{PercBodyFat}) - 0.7412)^* .01$	(Burns, in prep)
Radius of Body at Axillary	m	radius.body	$(\text{axgirth} / (2 * \pi))^2$	Malavear (2002)
Radius of Inner Core	m	radius.lean	$\text{radius.body} - (\text{axblubthick})$	Malavear (2002)

their body condition was twice the minimum value for survival (Table 1).

Alternatively, if an animal was on target or ahead of expected lactation or molt progress, the seal could either remain hauled out or initiate foraging activities in the next time step. The probability of ending a period of haulout and starting to forage was determined based on activity budget data from free-ranging Weddell seals in winter (February–October, $n = 16$) or summer (November–January, $n = 36$) months (Shero, unpublished and Beltran, unpublished). The mean and standard deviation of time hauled out each day was calculated from data obtained from wild seals, and the resulting cumulative probability distribution function used to determine the probability of initiating foraging given the seasonally appropriate amount of time already spent hauled out (Fig. S1). This value was then scaled to account for the seals' current energy balance, such that seals in poor condition were more likely to initiate foraging following a shorter haulout period, and seals in good condition switched behaviors at the rate expected based on the empirical data (Fig. S2). Then a random number generator (0–1) was used to produce a value, and if the value fell above the scaled probability for the cumulative time spent hauled out, the animal began foraging. The same approach was used to determine whether seals that were foraging continued to forage or initiated a haul out, with the exception that foraging time was not scaled based on energy balance.

2.1.7.2. Energy expenditure submodel. The energy budget and body composition of each modeled seal varied through time based on the animal's activity, reproduction and molt status, external conditions, and foraging success (Fig. 1). Net energy at each timestep depended on foraging success and situational energy demand:

$$\text{Net} = \text{Prey} - (\text{Maintenance} + \text{Thermoregulation} + \text{Activity} + \text{Reproduction} + \text{Molt}) \quad (1)$$

where *Net* is the net energy balance at each timestep, *Prey* is the energy brought in through feeding, and *Maintenance*, *Thermoregulation*, *Activity*, *Reproduction*, and *Molt* are the metabolic costs. Mass and body composition changes reflected net energy.

2.1.7.2.1. Maintenance energy costs (resting metabolic rate). The size and body composition of each seal at the beginning of the simulation was randomly assigned to animals based on empirical measurements with known distributions (Table 1). Basal metabolic rate was estimated using Kleiber's equation (Table S1 Eq. 1) and converted to a resting metabolic rate using a scalar of 2 (Table

S1 Eq. 2) that was independent of the animal's reproductive status or activity (Speakman and McQueenie 1996; Hedd et al., 1997; Winship et al., 2002). Additional costs for thermoregulation, activity, and reproduction were calculated as described below and added to the baseline resting metabolic rate.

2.1.7.2.2. Thermoregulatory costs. A comprehensive heat loss model was used to calculate heat budget at each timestep for any given animal activity, air temperature, and water temperature (Boily 1995). The functions and parameters chosen for these calculations are described in detail in McCafferty et al. (2013). The weather conditions were extracted for the temporal and spatial scale specified in the model inputs (see Section 2.1) at McMurdo Station, Antarctica (S77.84, E166.68). The weekly mean water temperatures were obtained from the NOAA Optimum Interpolated Sea Surface Temperature V2, and the ambient conditions (air temperature, wind, relative humidity, and cloud cover) were derived from the National Centers for Environmental Prediction/National Center for Atmospheric Research Reanalysis II dataset at a 6-h resolution using the RNCEP package in R (Kemp et al., 2012). When hauled out, skin temperature in air was calculated from a regression that predicts skin temperature based on air temperature (Table S1 Eq. 3; Mellish et al. (2015)) and the proportion of the animal's surface area that touched the ice was assumed to be $32 \pm 1.5\%$ (Mellish et al., 2015). When in water, skin temperature was assumed to be that of the water (Table S1 Eq. 4) (Erdsack et al., 2012). In both air and water, the skin temperature was bound at a lower limit of -2°C (Kvadsheim et al., 1997) except for the molt, when the lower limit was 17°C based on the thermal requirements for epidermal growth reported in Feltz and Fay (1966). Heat loss in air (Table S1 Eq. 5) summed forced convection from the upper surface of the animal to air, conduction from the lower portion of the animal to the ice surface, radiative heat flux from the upper surface of the animal, and respiratory evaporative water loss (Table S1 Eqs. 6–11) (Ling 1970). Heat loss in water (Table S1 Eq. 12) was due to forced convection (Table S1 Eq. 13). Heat was gained from resting metabolic rate and the inefficiencies of gestation, lactation, and growth in air (Table S1 Eq. 14) and activity inefficiency in water (Table S1 Eq. 15). If heat production exceeded heat loss to the environment, we assumed that heat would be released into the environment (Erdsack et al., 2012) and heat balance therefore became neutral. On the other hand, if heat production was less than heat loss to the environment, there was an additional energetic cost for thermoregulation equivalent to the amount of the deficit (Table S1 Eqs. 16 and 17). Since heat flux is partially determined by

Table 2
Baseline parameter values for the energetic process model with references to literature sources. Submodel denotes the part of the model populated by each parameter. Taxa indicates whether the parameters were obtained from literature specific to mammals (M), pinnipeds (P) or Weddell seals (W). Parameters were assigned one of the following distributions based on literature values: (1) Normal, defined by a mean (value 1) and standard deviation (value 2); or (2) Uniform, defined by a lower limit (value 1) and upper limit (value 2), with every value having an equal probability of being sampled.

Submodel	Taxa	Parameter	Unit	Abbrev	Distr	Value1	Value2	Citation
Swimming	P	Swimming Coefficient of Drag	Unitless	CD	Value	0.0056	–	Feldkamp (1987)
Swimming	P	Ratio of Drag – Active:Passive Swimmer	%	dragratio	Uniform	0.508	0.98	Williams and Kooyman (1985)
Swimming	P	Swimming Propeller Efficiency	%	EP	Uniform	0.8	0.85	Malavear (2002)
Swimming	P	Swimming Velocity	m s ⁻¹	vwater	Uniform	1.5	2.2	Feldkamp (1987), Ponganis and Stockard (2007)
Uptake	P	Fecal Digestive Efficiency	%	DE.fecal	Uniform	0.9	0.96	Ronald et al. (1984), Rosen and Trites (2000)
Uptake	P	Urinary Digestive Efficiency	%	DE.urinary	Uniform	0.905	0.931	Ronald et al. (1984), CCAMLR (2013)
Uptake	P	Efficiency of Heat Increment of Feeding	%	E.HIF	Uniform	0.83	0.953	Grav and Blix (1976), Kooyman (1981), Rosen and Trites (1997)
Uptake	W	Energetic Density of Diet	MJ kg ⁻¹	ED.diet	Normal	5.5	1.0	Eisert et al. (2013b)
Uptake	W	Prey Availability Winter	%	I.kg_winter	Value	0.000	–	Beltran (2015)
Uptake	W	Prey Availability Summer	kg	I.kg_summer	Value	0.001	–	Beltran (2015)
Molt	M	Energetic Density of Hair	MJ kg ⁻¹	ED_hair	Normal	0.023	0.000	McCullough and Ullrey (1983)
Molt	M	Energetic Density of Skin	MJ g ⁻¹	ED_skin	Normal	0.023	0.001	McCullough and Ullrey (1983)
Molt	W	Pelage Thickness	mm	HairThickness	Uniform	12	14	(Kirkham, in prep)
Molt	P	Mass of Dermis	g	MassDermis	Normal	8700	800	Worthy et al. (1992)
Molt	P	Skin Thickness	mm	SkinThickness	Uniform	0.15	0.5	Ling 1970
Allocation	P	Percent of Catabolism – Lipid Breakdown	%	CatBodyFat	Uniform	0.53	0.6	Beauplet et al. (2003), Field et al. (2005), Rea et al. (2007)
Allocation	M	Deposition Efficiency of Lipid	%	DE.lip	Value	0.74	0.90	Malavear (2002)
Allocation	M	Deposition Efficiency of Protein	%	DE.pro	Value	0.38	0.56	Malavear (2002)
Allocation	M	Energetic Density of Lipid	MJ kg ⁻¹	ED_lip	Value	39.30	39.54	Blaxter (1989)
Allocation	M	Energetic Density of Milk	MJ kg ⁻¹	ED_milk	Value	20.8	–	Blaxter (1989)
Allocation	M	Energetic Density of Protein	MJ kg ⁻¹	ED_pro	Uniform	17.9	23.8	Paine (1971), Bejder et al. (2006)
Allocation	P	Proportion of Blubber That Is Lipid	%	P.lip	Value	0.744	0.9	Gales et al. (1994), Board (2005), Ainley and Ballard (2012)
Allocation	P	Proportion of Lean Mass That Is Water	%	P.w	Uniform	0.717	0.729	Oftedal et al. (1993), Board (2005)
Allocation	P	Proportion of Seal In Contact With Air	%	psi	Normal	0.68	0.015	Boily (1995); Mellish et al. (2015)
Reproduction	P	Shaping Parameter	Unitless	b	Normal	136.4	49.82	Yunker et al. (2005)
Reproduction	W	Biomass of Milk Produced Per Day	KG day ⁻¹	Biomass.milk	Normal	3.54	0.87	Tedman and Green (1987)
Reproduction	W	Pup Birth Mass	KG	BM	Normal	41.056	14.934	Tedman and Green (1987)
Reproduction	P	Efficiency of Gestation	%	Eff.gestation	Value	0.133	–	Oftedal (1985)
Reproduction	P	Proportion of Gestational Costs Associated with Conceptus	%	ConceptusProp	Value	0.8	–	Oftedal (1985)
Reproduction	W	Efficiency of Conversion: Milk to Storage	%	Eff.milk	Normal	0.521	0.077	Tedman and Green (1987)
Reproduction	P	Shaping Parameter	Unitless	k	Normal	0.016	0.00153	Yunker et al. (2005)
Reproduction	W	Proportion of Pup Lean Mass that is Water	%	P.w.pup	Value	0.725	–	Tedman and Green (1987)
Reproduction	W	Proportion of Pup Body That Is Lipid	%	PercBodyFat.pup	Normal	0.086	0.0245	Wheatley et al. (2006)
Reproduction	W	Weaning Mass for Pup	KG	WeanMass	Normal	96.8	11.15	Wheatley et al. (2006)
Thermoregulation	M	Specific Heat Capacity of Air	J kg ⁻¹ K ⁻¹	cp.air	Value	1006	–	McCafferty et al. (2013)
Thermoregulation	M	Specific Heat Capacity of Water	J kg ⁻¹ K ⁻¹	cp.water	Value	4219	–	McCafferty et al. (2013)
Thermoregulation	M	Density of Air	kg m ⁻³	density.air	Value	1.276	–	McCafferty et al. (2013)
Thermoregulation	M	Density of Water	kg m ⁻³	density.water	Value	1027	1028	Arrigo et al. (1999)
Thermoregulation	P	Blubber Density	kg m ⁻³	DF	Value	930	950	Gales and Burton (1987), Ørstrand and Markussen (1990)
Thermoregulation	M	Emmissivity of Animal	Unitless	Emiss.a	Value	0.98	–	Hammel (1956)
Thermoregulation	M	Emmissivity of Ground	Unitless	Emiss.g	Value	0.97	–	Hammel (1956)
Thermoregulation	M	Dynamic Viscosity of Air	kg m ⁻¹ sec ⁻¹	eta.air	Value	17.218	–	McCafferty et al. (2013)
Thermoregulation	M	Gravity	m sec ⁻¹	gravity	Value	9.8	–	NA
Thermoregulation	M	Thermal Resistance of Hair in Water	m ² C w ⁻¹	iprime	Value	0.00368	–	Boily (1995)
Thermoregulation	M	Thermal Conductivity of Air	W m ⁻¹ C ⁻¹	lambda.air	Value	0.0225	–	McCafferty et al. (2013)
Thermoregulation	P	Thermal Conductivity of Blubber	W m ⁻¹ C ⁻¹	lambda.blubber	Uniform	0.17	0.2	Arrigo et al. (1999), Hazen et al. (2013), Pearson et al. (2014a)
Thermoregulation	M	Thermal Conductivity of Fur	W m ⁻¹ C ⁻¹	lambda.fur	Uniform	0.08	0.40	Reiter et al. (1978), Hind and Gurney (1997), Pearson et al. (2014b)
Thermoregulation	M	Thermal Conductivity of Skin	W m ⁻¹ K ⁻¹	lambda.skin	Value	0.2	–	Thorson and Le Boeuf (1994)
Thermoregulation	M	Thermal Conductivity of Water	W m ⁻¹ K ⁻¹	lambda.water	Value	0.562	–	McCafferty et al. (2013)
Thermoregulation	P	Meeh Constant	m ² kg ^{-0.67}	Meeh	Normal	0.08	0.011	Innes et al. (1990)
Thermoregulation	P	Respiratory Evaporative Water Loss Multiplier	%	REWL	Value	1.1	–	Yallop and Hohenkerk (1985)
Thermoregulation	M	Stefan-Boltzmann Constant	W m ⁻² k ⁻¹	SB	Value	5.67E-08	–	Erdsack et al. (2012)
Thermoregulation	P	Core Temperature	C	T.core	Value	37	–	Malavear (2002)
Thermoregulation	P	Core-Blubber Interface Temperature	C	T.coreblubber	Value	37	–	Malavear (2002)
Thermoregulation	P	Temperature of Ground Snow	C	T.ice	Normal	-5.1	4.3	Mellish et al. (2015)

the thickness of the insulative blubber layer, and blubber thickness declines with decreasing body condition (Mellish et al., 2015), blubber thickness was estimated for each seal at each timestep based on the relationship between empirically determined blubber thickness and body condition (Table 1 *axblubthick*) (Kirkham, in prep). The resulting blubber thickness values become inputs for the free convection equation (Table S1 Eq. 8). The thermoregulation calculations described above required an extensive set of functions that are represented in Table S1 Eqs. 18–35.

2.1.7.2.3. Swimming energetics. Since adult female Weddell seals exhibit limited mobility when on land (Lake et al., 1997), the model only included activity costs for timesteps in which the simulated animal was foraging. The propulsive force that an animal must exert to move through water at a given velocity and coefficient of drag was calculated for the entire body (Table S1 Eq. 36). The velocity was stochastically determined at each timestep based on the published distribution of possible swim speeds (Table 2 *vwater*) (Feldkamp 1987; Ponganis and Stockard 2007). The metabolic cost of thrust forces required to swim at that velocity was then calculated using Table S2 Eqs. 36–40 (Feldkamp 1987).

2.1.7.2.4. Reproductive energetics. All seals were pregnant at the beginning of the simulation, and if a simulated seal's body condition did not drop below critical levels (see Section 2.1.7.4), it produced and successfully weaned a pup. An approximation of the energy required for gestation was obtained by combining a Gompertz fetal growth curve (Table S1 Eq. 41) with tissue energy densities (Brody 1945; Stewart and Lavigne 1984; Yunker et al., 2005). The change in fetus body composition between each timestep was calculated using Table S1 Eq. 42 which is based on Bernstein et al. (1997). The cost of producing the fetus was then calculated (Table S1 Eq. 43) based on the energy stored in added mass (lipid and lean) and the efficiency of gestation (Oftedal 1985). Finally, the BMR of the fetus was calculated based on the assumption that fetal BMR was equivalent to that of the mother (Gittleman and Thompson 1988) for fetus mass added to maternal mass (Table S1 Eq. 1). Because the circumstances which cause abortion of the fetus have yet to be defined, we assumed that if during gestation the female did not have sufficient energy to allocate to the fetus for long enough that fetal body condition dropped below 50% that expected based on its gestational age, abortion occurred.

Females that successfully carried a pup to term gave birth within the average parturition date for free-ranging Weddell seals (Rotella, pers. comm). The cost of lactation was calculated from proximate composition of milk, the rate of milk production, and the efficiency with which milk was produced (Blaxter 1989; Oftedal et al., 1993; Pinkerton et al., 2007) (Table 2, Table S1 Eq. 44). In order to calculate the maximum amount of milk produced per timestep (and therefore constrain the model such that simulated seals spent an appropriate amount of time attending to their pup during the lactation period), Table S1 Eqs. 45 and 46 were used to incorporate the total milk biomass given to the pup per day with the average amount of time free-ranging seals spend nursing per day (Hindell et al., 2002; Wheatley et al., 2006; Eisert et al., 2013a).

Pup mass was tracked throughout the lactation period by subtracting an estimate of pup's field metabolic rate (FMR) from the milk energy provided by the mother. To approximate pup energy requirements without overly complicating the model, we assumed that pup FMR was three times the mass-specific basal metabolic rate of that predicted for adult animals of similar size to account for growth requirements and costs associated with activity and thermoregulation (Table S1 Eq. 47; Winship et al. (2002)). The mass of the fetus and the associated placenta, fluids and tissues were tracked separately from the adult female's body mass or surface area (i.e. at parturition, the female does not lose mass equivalent to pup mass).

2.1.7.2.5. Molting energetics. The energetic cost of hair replacement was calculated from the energy density of seal hair (Table S1 Eq. 48–51) multiplied by the amount of hair needed to cover the animals surface area (Table S1 Eq. 18) (Innes et al., 1990). The efficiency of hair production was assumed to approximate the efficiency of protein deposition (Table 2 *DE.pro*) (Malavear 2002). The rate of hair regrowth was assumed to be linear throughout the molt, which was determined based on empirical measurements in free ranging seals (Beltran, unpublished). Thus, the simulated seals needed a certain number of timesteps molting to successfully complete the molt. Molt progression was only allowed to occur when the animal was hauled out on the ice, as previous studies have suggested that seals are unlikely to molt in the water (Boily 1995).

2.1.7.3. Energy uptake submodel. Due to the lack of data on quantitative relationships between foraging effort and mass gain, previous bioenergetics models have tuned the prey availability values to fit the model (Malavear 2002). Here, realistic prey density and capture probability values were calculated by combining empirical time-activity budget data with mass gain data from free-ranging Weddell seals. Briefly, nine adult, female Weddell seals were instrumented with flipper tag time-depth recorders (TDRs) during the Nov/Dec breeding season as part of a concurrent study and tags were recovered during the Jan/Feb molting season. A second set of ten seals was instrumented with TDRs during Jan/Feb and tags were removed in Oct/Nov (Shero et al., 2015). Seals were weighed during both procedures. Between-season mass changes were converted to prey ingestion estimates using published distributions of mixed diet energetic density (Table 2 *ED.diet*) (Eisert et al., 2013b) and digestive efficiency (Table 2 *DE.pro* and *DE.lip*) (Malavear 2002). Using Monte Carlo simulations, we combined time-activity budgets with caloric intake values to back-calculate average prey abundance per foraging effort (Table S1 Eq. 52). Detailed methods and results are available in Beltran (2015). For each simulated seal, the efficiency with which prey energy is conserved throughout the digestive processes (including fecal inefficiency (Ronald et al., 1984) and urinary inefficiency (Lavigne et al., 1976)), and the inefficiencies associated with deposition/catabolism of fat and protein were calculated using Table S2 Eqs. 53 and 33, respectively. The average energy density of the diet was obtained from Eisert et al. (2013b).

2.1.7.4. Energy allocation submodel. At the end of each time step, positive energy balance was allocated to fulfill requirements in order of their importance to survival: first maintenance, then thermoregulation, activity, reproduction, molt, and finally new tissue production (Pianka 1981). Excess energy was deposited as lipid or lean mass, with deposition efficiency values of 38–56% for protein and 74–90% for lipid (Table 2 *DE.pro* and *DE.lip*) (Malavear 2002). Conversely, if the energy obtained from prey could not satisfy baseline requirements, the animal catabolized tissues with 80% efficiency (Barboza et al., 2008) to satisfy energy requirements. Energy deficits were met by catabolizing a mixture of protein (40–47%) and lipid (53–60%) (Table 2 *CatBodyFat*) (Beauplet et al., 2003; Field et al., 2005; Rea et al., 2007). If lipid stores were reduced by catabolism to less than 5% of body mass (Malavear 2002) the seal died. At critically low body condition levels (below 10%), simulated seals have the option of aborting their fetus or prioritizing foraging over lactating, which could result in a lower pup birth mass or weaning mass (i.e. pup abandonment) for lactating females. Such abandonment resulted in negative energy balance of the fetus or pup as the metabolic rate exceeded the energy given to the fetus/pup from the adult female. Similar to the adult female, fetal loss or pup death occur when the percent lipid of the fetus or pup

Table 3

The quantitative model outputs to baseline and 10% prey reduction scenarios. The asterisk (*) denotes a significant difference (*t*-test) in output variables at the end of the simulations between animals (*n* = 10) in the baseline treatment and decreased prey treatment.

Output Parameter	Simulation Type	
	Baseline	Prey Decrease
Adult Mass	306 ± 15 kg*	262 ± 12 kg*
Adult% Fat	38 ± 5%	36 ± 7%
Time Foraging	48 ± 6%*	60 ± 8%*
Pup Wean Mass	96 ± 12 kg	95 ± 10 kg
Adult Reproduction	100.0 ± 0.0%	100.0 ± 0.0%
Adult Survival	100.0 ± 0.0%	100.0 ± 0.0%

drop below 50% or 5%, respectively, of expected mass given Julian date (Malavear 2002).

2.2. Validation

Following initial model development and parameterization, we tested the ability of the model to replicate expected energetics parameters given published input parameters. The model was considered an accurate representation of the system if the simulation results fell within the range or one standard deviation of published values, dependent upon what was available in the literature. In addition, the activity budgets of simulated animals were compared visually to those of free-ranging animals.

2.3. Sensitivity analysis

After subjectively evaluating the model to verify that it generated realistic parameter estimates, a local sensitivity analysis was performed to test the sensitivity of one model output (body mass) to uncertainty in parameter values. Stochasticity in parameters not being tested was removed from the simulation to ensure that results from subsequent runs would be equivalent (i.e. while one parameter was varied across runs to test the sensitivity of body mass to it, the remaining parameters were assigned one value at the beginning of the simulation and not re-assigned values during subsequent runs). The baseline input parameters (*P*), output values for baseline input parameters (*C*₀), and output values for ten percent decreases in the targeted input parameters (*C*₋) were calculated. The sensitivity (*S*₋) of output parameters *C*₋ to decreases in input parameters *P* were then calculated as $S_{-} = (C_{-} - C_{0}) / (0.1/P)$. Likewise, the sensitivity (*S*₊) of output parameters *C*₊ to increases in input parameters *P* were calculated as $S_{+} = (C_{+} - C_{0}) / (0.1/P)$. The model was run systematically with the parameter values outlined in Table 4, with values obtained from the literature, and again with parameter values increased (*C*₊) or decreased (*C*₋) one at a time by 10% with mean values determined from runs using 15 individuals (Johnston et al., 2014). All other parameters were held constant at their mean/median values (Winship et al., 2002). Changes in the means and standard deviations of body mass were calculated. The sensitivities of those outputs to baseline values are presented as the changes in mean output variables to the 10% increases or decreases in input parameter values.

2.4. Perturbation simulations

Following model development and validation, experimental simulations were run to study the vital rates (survival and reproduction) of seals under baseline conditions, and in response to a 10% reduction in absolute prey availability (Table 2 *I.kg.winter* and *I.kg.summer*) (Beltran 2015). Starting body mass were compared between baseline and perturbation simulations using a Student's *t*-test to ensure that they were not significantly different. Outputs

of the perturbation simulations were compared to the baseline simulations results using a Student's *t*-test for significance and Cohen's *d* metric for effect size.

3. Results

3.1. Model description

In total, the model required 49 input parameters (10 specific to Weddell seals, 19 from pinniped literature and 20 from mammal literature) and 53 input functions that were each carefully selected from published literature and combined using over 1200 lines of R code. The bioenergetics model was then used to simulate the energy balance of adult, female Weddell seals. In general, the structure of the activity selection submodel caused simulated animals to switch behaviors appropriately (Fig. 2). The baseline model also replicated the large fluctuations in total energetic requirements known to result from seasonal life history events such as gestation, lactation, and molt (Fig. 3). Baseline model outputs were not significantly different than the validation parameters (Table S3), and thus, the model was used to run perturbation simulations and make predictions about physiological and behavioral responses to predicted environmental changes.

3.2. Activity selection submodel

Free-ranging animals that were instrumented with time-depth recorders spent 16.86 ± 3.26 h/day during winter and 10.64 ± 1.74 h/day during summer foraging. The time-activity budgets of simulated seals aligned relatively well with empirical time-activity budgets derived from real animals (Fig. 4). At the beginning of a year, from January to February, the simulated animals actively foraged to regain condition lost during the lactation period. During the molting and lactation periods, simulated animals spent between 80 and 100% of their time hauled out, which was slightly more than seen in free-ranging seals, likely due to model constraints of expected progress for those life history events. The winter period was characterized by heavy foraging (<40% of the time hauled out) for both the simulated and the free-ranging seals.

3.3. Energy expenditure submodel

The annual energetic expenditure of these reproductive Weddell seals was $35,136 \pm 999$ MJ year⁻¹ (range 33,872 to 37,243). Assuming an average diet energy density of 5.5 MJ kg⁻¹ as reported for Weddell seals by Eisert et al. (2013b), these energetic requirements would require animals to consume between 6159 and 6771 kg of fish per year (17–19 kg fish per day, or 4.3–7.3% of body mass per day based on average body weight for the year). Results from each portion of the energy expenditure submodel are described in detail below.

3.3.1. Maintenance energy costs (Resting metabolic rate)

The mean resting metabolic rate of modeled seals was 0.489 ± 0.019 MJ timestep⁻¹ (0.0000943 ± 0.000004 MJ kg⁻¹ min⁻¹), which corresponds with values presented in Williams (2004). The resting metabolic rate changed with seasonal variations in mass, but remained relatively consistent across the year. These maintenance costs accounted for an average of 49% of total metabolic costs throughout the year (Fig. 3).

3.3.2. Thermoregulatory costs

The average modeled temperature of the skin, given environmental conditions, was 7.26 ± 6.29 °C, which falls within the range of 13.9 ± 11.2 °C presented by Mellish et al. (2015).

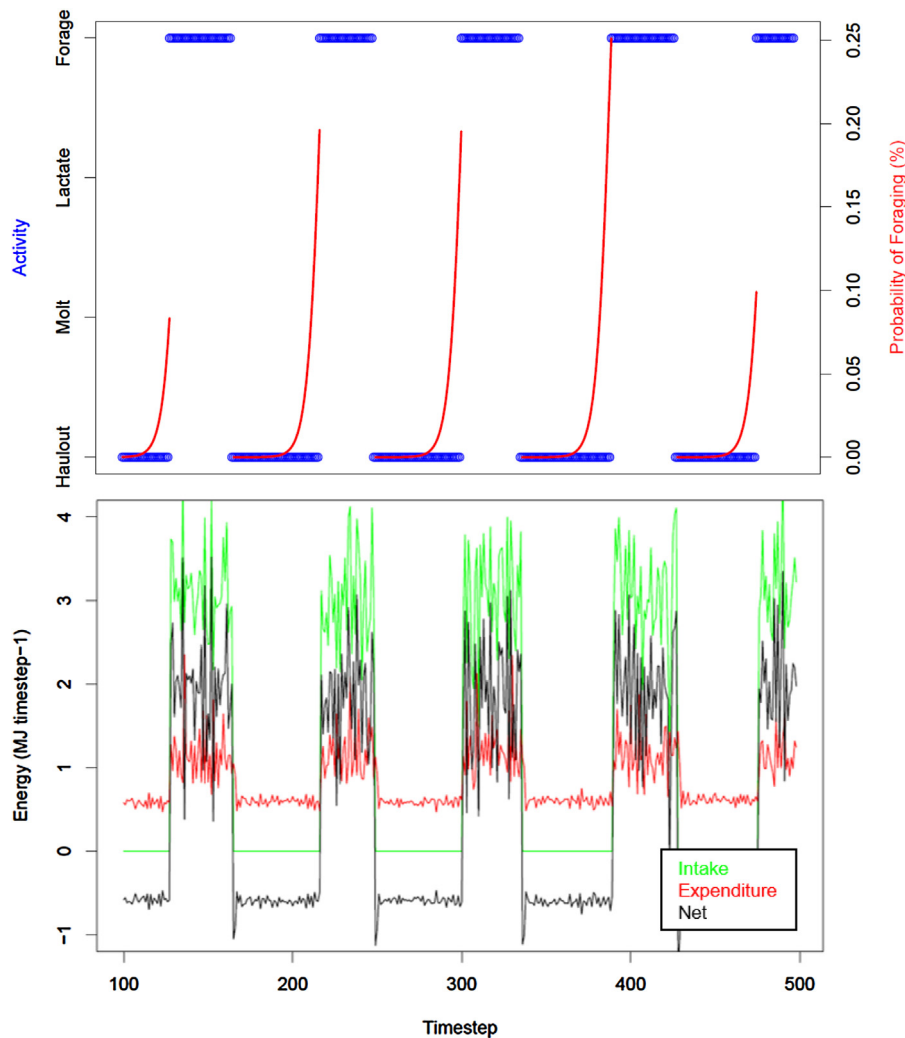


Fig. 2. Example of a behavioral time series (top panel) and the resulting energy intake and expenditure of each timestep (bottom panel) from one representative, simulated animal across 500 timesteps (5.2 days). Because these timesteps occurred during the fall when the animal was not molting or lactating, animal behavior shown here is limited to either hauling out or foraging. Probability of foraging was calculated as a function of time spent hauled out and body condition as described in Section 2.1.7.1. A random number was chosen at each timestep, and if that number fell below the probability of hauling out, the animal would haul out, whereas if the random number fell above the probability of hauling out, the animal would continue foraging. When the animal was hauled out, as in timesteps 100–140, net energy balance was negative because energy expenditure exceeded energy intake. Conversely, when the animal was foraging, as in timesteps 140–180, net energy balance was generally positive because energy expenditure was less than energy intake.

The average energy lost (as heat) to radiation, conduction, and convection were $0.220 \text{ MJ timestep}^{-1}$, $0.064 \text{ MJ timestep}^{-1}$, and $0.044 \text{ MJ timestep}^{-1}$, respectively. The conduction from the lower surface of the simulated seal to ice were low ($0.0065 \pm 0.0009 \text{ MJ timestep}^{-1}$) because skin temperature approximated the ambient water or ice temperature (respectively) and the temperature gradient between the animal and the environment was generally low, except during extremely cold ice surface temperatures. Because of the seasonal weather patterns, negative thermal balance occurred most frequently during the winter, although changes in wind speed, relative humidity, and cloud cover across all seasons lead to high variation in heat flux. Over the year, thermoregulation costs accounted for <1% of total metabolic costs.

3.3.3. Swimming energetics

The cost of activity ranged from $0 \text{ MJ timestep}^{-1}$ during haul out periods to $1.88 \text{ MJ timestep}^{-1}$ during periods of heavy foraging activity. During the molting and reproductive periods, activity was reduced (Fig. 4) due to the rule-based life history decisions that constrain the model. For instance, successful and timely pup

weaning required less maternal foraging and more nursing, so simulated animals spent a larger proportion of time hauled out during the lactation period. On average, activity costs amounted to 30% of total metabolic costs (Fig. 3).

3.3.4. Reproduction energetics

The total costs of gestation and lactation were high for the simulated seals ($2634 \pm 423 \text{ MJ}$ and $4386 \pm 183 \text{ MJ}$, respectively). Given the longer duration of gestation relative to lactation, the daily costs of gestation were much less than those of lactation. The milk energy given to the pup each day was $68 \pm 10 \text{ MJ}$ (145% of female's RMR). Given these parameters, pups gained an average of 1.6 kg day^{-1} . The annual energy expenditure of reproductive females, including both gestation and lactation, was $125 \pm 2\%$ that of non-reproductive seals.

3.3.5. Molting energetics

The total cost of the molt ranged from 224 to 352 MJ during the baseline simulation. This range was due to the differences in surface area between small and large seals. There was a $57 \pm 12\%$ decrease in daily energy expenditure during the molt due to a significant

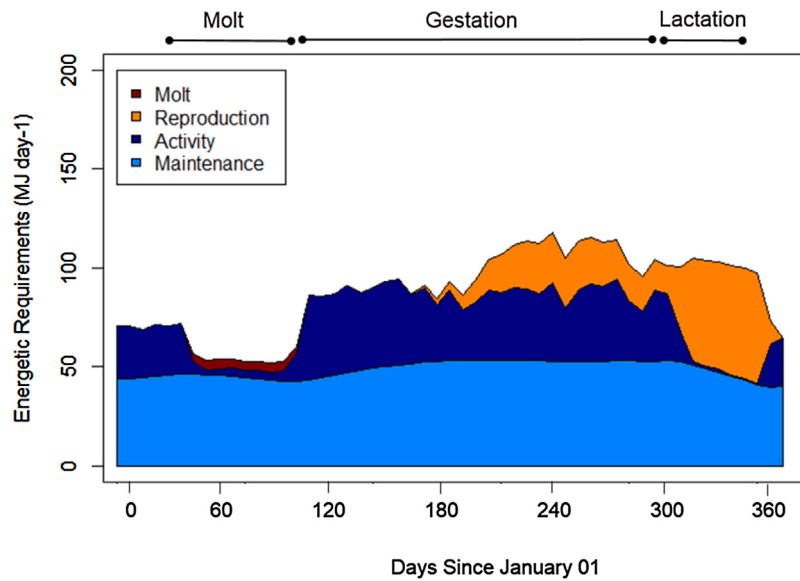


Fig. 3. Energy requirements compartmentalized by category throughout the calendar year for one simulated seal. Energy requirements were highest during the third trimester of gestation (weeks 35–40) and throughout the lactation period. Daily energetic expenditure was not higher during lactation than gestation because foraging costs were low.

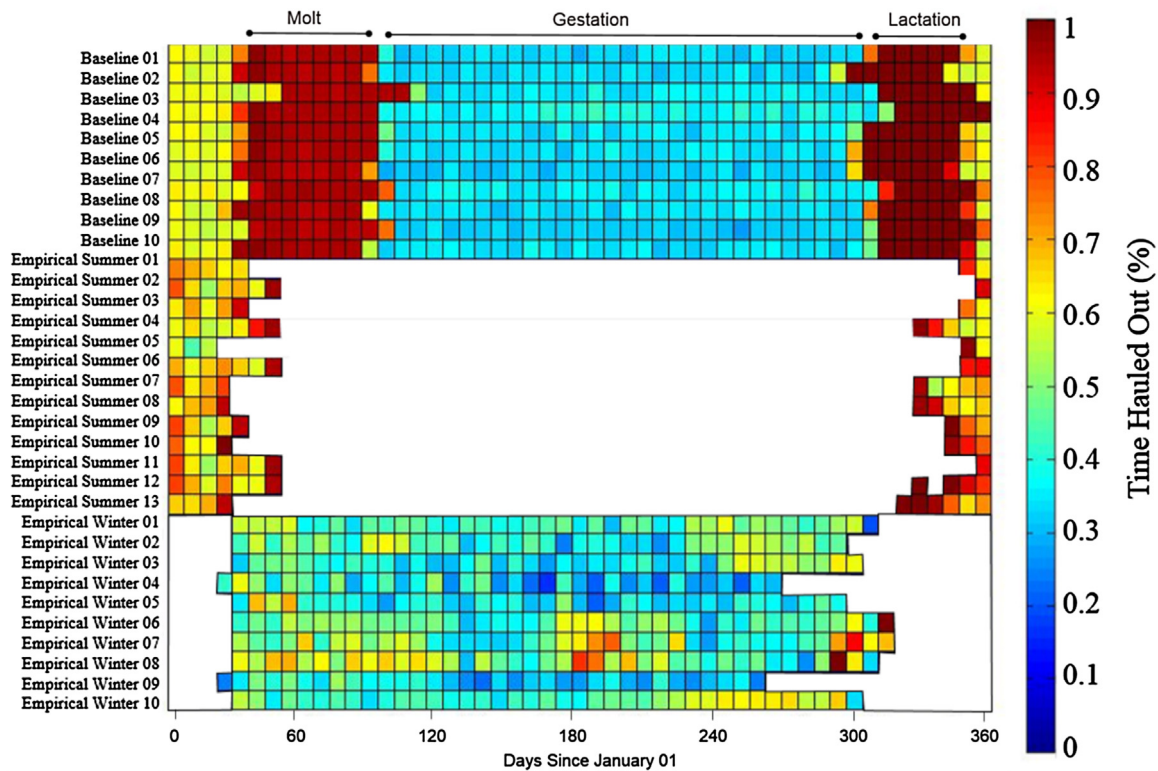


Fig. 4. Time-activity budgets of free-ranging (Empirical) seals, derived from telemetry deployments, and simulated (Baseline) seals, derived from model predictions. Each column represents one week, each row represents an individual seal, and each box is color coded by the activity budget. Due to logistical constraints, Empirical animals have only been instrumented during two separate times of the year: summer seals were instrumented after the lactation period and prior to the molt (Julian days 320–60) and winter seals were instrumented after the molt and prior to the lactation period (Julian days 40–290). Thus, Empirical seal activity budgets do not include the molt or lactation periods, whereas the simulated Baseline seals do.

reduction in swimming activity (Fig. 3). Molt costs amounted to <1% of total annual energy requirements (Fig. 3), suggesting that the metabolic costs of molt are more related to lost opportunities to gain mass and thermoregulatory consequences of increasing perfusion to the skin, than the cost of producing new fur.

3.4. Energy uptake submodel

The energy budget and body composition of each modeled seal varied through time as the animal changed its activity or underwent seasonal life history events. During foraging periods, both energy intake and expenditure were relatively high (mean 1.85 MJ timestep⁻¹ and 1.30 MJ timestep⁻¹, respectively) so net

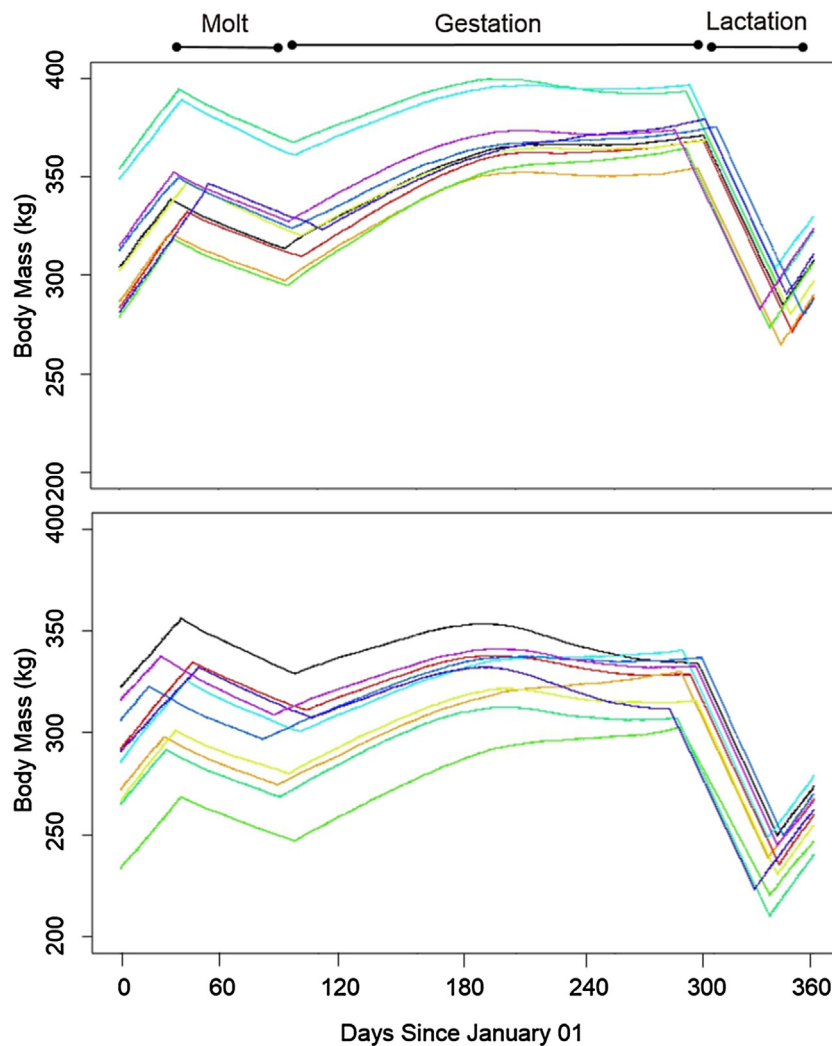


Fig. 5. Body mass as a function of time for 10 simulated seals. Simulations occurred under two scenarios: 1) Baseline conditions (top panel); and 2) 10% reduction in prey availability (bottom panel). Mass dynamics were similar across the two scenarios, with animals losing mass across the lactation and molt periods, and gaining mass during the late summer and overwinter.

energy was generally positive (Fig. 2). During resting periods the energy intake was zero so moderate energy expenditure on maintenance (mean $0.25 \text{ MJ timestep}^{-1}$) resulted in a negative net energy balance (Fig. 2). These energy expenditure and consumption values resulted in marked mass changes during critical life history events (Fig. 5, top panel). For instance, during the molting period, Weddell seals reduced their activity and thus low prey consumption was offset by minimal energy expenditure during haulout. Conversely, during the lactation period, animals were not very active, but because the metabolic demands of lactation were high, this was a period of rapid mass loss.

3.5. Energy allocation submodel

Mass changes followed the expected seasonal patterns (Fig. 5). The simulated seals' masses were generally highest at parturition (range 354.5–399.7, mean \pm SD $375.4 \pm 13.8 \text{ kg}$) and lowest at weaning (range 264.5–303.3, mean \pm SD $281.6 \pm 11.3 \text{ kg}$) and their adipose percentages fluctuated from 21.4 to 43.4%. In the model, mass increases were relatively high during the beginning of the winter period (+1 to +2 kg per day during days 110–150) but then declined as active gestation became a prominent source of energy expenditure (Fig. 6, bottom panel). Specifically, the simulated seals regained $\sim 15\%$ of their mass throughout the first half of the winter

period, although that rate of mass gain slowed prior to lactation (-1 to $+1 \text{ kg per day}$ during Julian days 200–300) due to the increased gestational costs during this time. Mass gain was highest during the over-summer period due to the lack of life history constraints (i.e. no dependent pup, active gestation, or molt).

3.6. Sensitivity analysis

Output and relative sensitivity values from the baseline model are provided in Table 4. Adult mass was highly sensitive to changes in the energy density of the diet. In general, changes of 10% in input variables led to a maximum of 12% changes in body mass. All output variables were most sensitive to changes in the energy density of the diet and the efficiency of digestion. Positive changes in digestive efficiency resulted in a twofold increase in body mass change relative to negative changes in digestive efficiency. For the other two input parameters, body mass outputs were relatively similar between the positive and negative input changes.

3.7. Perturbation simulations

When the prey availability or abundance was decreased by 10%, the ten simulated animals spent significantly more time foraging and less time resting ($t_0 = -4.2$, $p < 0.0001$, $d = -2.80$) across

Table 4
Relative sensitivity of output variables to ten percent changes in input parameters. Relative sensitivity of output variables to ten percent changes in input parameters. The model was run systematically with the parameter values outlined in Table 4, with values obtained from the literature, and again with parameter values increased (C₊) or decreased (C₋) one at a time by 10% with mean values determined from runs using 15 individuals. All other parameters were held constant at their mean/median values (·).

Input	Treatment	Parameter Value	Output – Body Mass (kg)	Relative Sensitivity Value
Diet Energy Density	0	5.50	–	–
	–	4.95	– 12.7%	2144.7
	+	6.05	+ 11.8%	1993.4
Digestive Efficiency	0	0.93	–	–
	–	0.84	– 5.9%	155.1
	+	1.02	+ 12.0%	315.2
Lipid Deposition Efficiency	0	0.825	–	–
	–	0.743	– 2.0%	–44.6
	+	0.908	+ 0.8%	–18.9

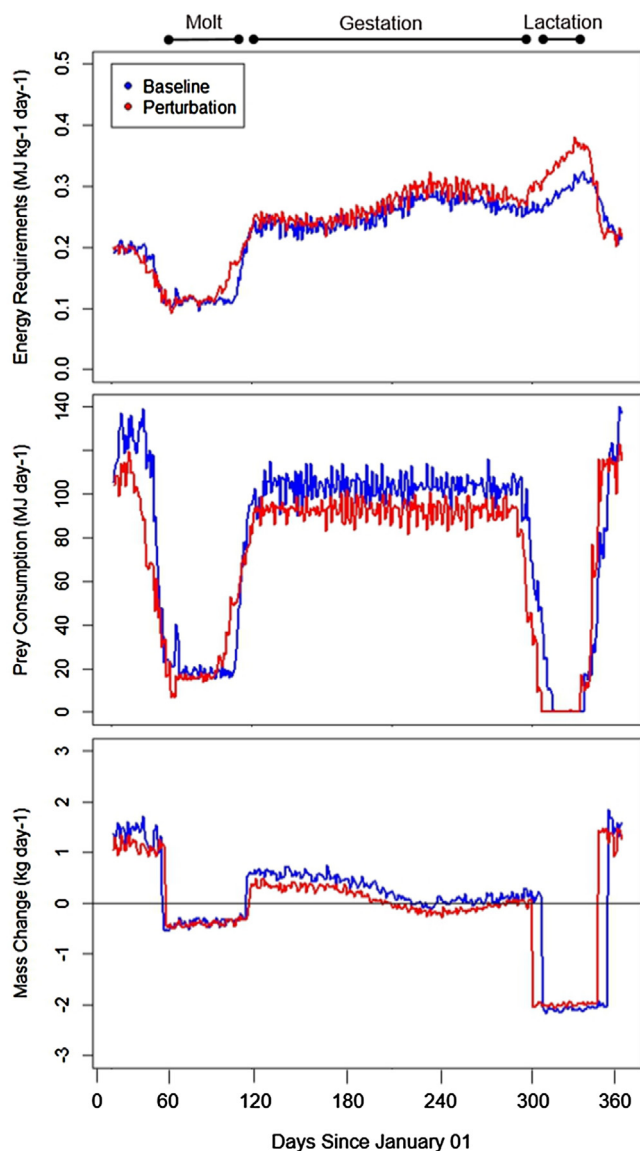


Fig. 6. Daily energy expenditure (top), prey consumption (middle), and mass change values (bottom) for the baseline simulations, pictured in dark blue, and the perturbation simulations, pictured in red. Mass changes reflect the seasonal fluctuations in energy intake and expenditure values. Note that the mass of the fetus and the associated placenta, fluids and tissues were tracked separately from the adult female's body mass or surface area (i.e. at parturition, the female does not lose mass equivalent to pup mass). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

all months (Table 3). At the end of the year-long simulations, the ten seals in the perturbation simulation were in slightly worse condition as compared to the ten baseline seals ($36 \pm 7\%$ lipid vs $38 \pm 5\%$; $t_9 = -0.1$, $p = 0.87$, $d = 0.65$) (Table 3) and had significantly lower masses ($t_9 = -52.5$, $p < 0.0001$, $d = 3.20$) relative to seals in the baseline simulation (Fig. 5). This was a direct result of decreased foraging efficiency (prey ingested per unit foraging effort) because the energy expenditure of the perturbation and baseline simulation seals was nearly identical (Fig. 6). The increase in foraging effort (i.e. % time foraging) was not sufficient to compensate for the decrease in foraging efficiency, and the resulting body mass was less at the end of the simulation than in baseline simulations. There were no significant differences in survival or reproductive rates between seals in baseline and perturbation simulations.

4. Discussion

Here, we simulated the annual energy balance of adult, female Weddell seals using an agent-based modeling approach. In each 15-min timestep, the simulated animal selected an activity and the energy budget was balanced by subtracting metabolic costs (maintenance, thermoregulation, activity, reproduction, and molt) from prey intake. Baseline and reproductive energetic requirements were calculated and revealed potential energy allocation strategies for this species. While similar models have been developed for other marine mammal species and have explicitly manipulated parameters to predict how behavioral and physiological metrics could change under climate change or perturbation scenarios (Testa et al., 2012; Pirota et al., 2014; Villegas-Amtmann et al., 2015), our model explicitly represented the complex feedback loops between physiological processes such as reproduction and molt. In addition, we assessed the ability of seals to survive and reproduce under a 10% reduction in prey availability, and found that simulated animals spent significantly more time foraging when the prey availability or abundance was decreased by 10%. By incorporating both extrinsic (empirical weather data, prey abundance) and intrinsic (physiology and behavior) factors, our mechanistic model contributes to increased understanding of the potential behavioral shifts available to wild animals when they are facing environmental perturbations. Identifying the importance of seasonal foraging activities to annual mass gain and reproductive success will enable management agencies to better understand the biological consequences of extrinsic changes.

The emergent properties of the model such as mass and activity budgets corresponded well with published values and suggested that the model accurately represented the system. For example, the total costs of lactation and gestation matched those predicted by Eisert et al. (2013b) and the milk energy given to the pup each day aligned with Tedman and Green (1987). Overall, the detailed dynamics represented by the model allowed a fine

scale examination of reproductive costs in Weddell seals including mean requirements of 7020 MJ for both gestation and lactation. Reproductive costs have been estimated for several other phocid species, including bearded seals (5283 MJ), grey seals (1847 MJ), harp seals (1350 MJ), hooded seals (1879 MJ), and ringed seals (1075 MJ) (for review see Lydersen and Kovacs (1999)). These costs vary as a function of lactation duration, maternal parturition mass, energy storage capabilities, and maternal activity budgets (Lydersen and Kovacs 1999); however, the daily costs of lactation in our model (average 121 MJ day⁻¹) align well with those published on grey seals (125 MJ day⁻¹) (Fedak and Anderson 1982) and northern elephant seals (163 MJ day⁻¹) (Costa et al., 1986). After adding reproductive costs to the energetic cost of swimming, total energetic expenditure during lactation was not higher than gestation because foraging costs were low.

Despite general agreement, there were some minor inconsistencies and omissions between the model and empirical data. Field studies have demonstrated that lactating Weddell seals spend up to 25% (Hindell et al., 2002) of their time underwater, with the percent time foraging increasing as lactation progresses (Hindell et al., 2002; Sato et al., 2002). In contrast, modeled seals foraged for <10% of the time during the lactation period. The foraging efforts of simulated Weddell seals were more like grey seals and elephant seals, which forage up to 10% and 0% of the lactation period, respectively (Costa et al., 1986; Beck et al., 2003). These species accumulate more than 50% of the energy needed for lactation during gestation, so fasting constraints are less strict than in Weddell seals, which only gain 40% of the required lactation energy during gestation and must forage (Shero et al., 2015). This discrepancy likely results from the strict rule-based energy allocation decisions, wherein simulated seals prioritized nursing over feeding, so long as energy stores were above threshold mortality levels. Such minor differences are expected given that the model is a simplified representation of a complicated and only partially understood system, and are comparable to the differences reported in Pirotta et al. (2014) for their agent-based model of bottlenose dolphins. For parsimony, the model did not include memory or learning by the simulated seals. Rather than incorporating intrinsic motivations (e.g. hunger, fear, inclination to socialize; (Pirotta et al., 2014)), decisions were driven by timestep-specific energy balance and life history constraints (Malavear 2002). Therefore, there exists less inherent inter-individual variability in behavioral decisions than in models that include such motivations. Further, the decisions are more short term than under a stochastic dynamic programming approach with backwards iterations (Dunkin 2012). Free-ranging animals with knowledge and memory might be more flexible under changing conditions; thus, researchers hoping to predict animal behavior under experimental scenarios should carefully evaluate the influence of these factors before applying the model.

Modelled thermoregulation processes suggest that it may be appropriate to assume that adult animals are within their thermal neutral zones, as has been done in other pinniped bioenergetic modeling efforts (Watts et al., 1993; Winship et al., 2002). Based on calculations of heat production (i.e. thermogenesis) and heat flux to the environment (i.e. conduction, convection, and/or radiation), simulated individuals were almost always within their thermoneutral zone (Boily 1995) and rarely needed to produce additional heat through increased metabolic rates. The two scenarios that caused animals to expend excess energy on thermoregulation were high wind (i.e. >12 m sec⁻¹) and/or low air temperature conditions (i.e. <-25 °C) that resulted in skin temperatures declining to the minimum values allowed (Feltz and Fay 1966). Given the proposed lower critical temperature threshold limits of phocid seals (-7 °C from (Hansen and Lavigne 1997) and -11 °C from Folkow and Blix (1987)), the extremely low thermoregulation costs predicted by our model are not surprising. Studies of terrestrial

mammals have found that even in small mammals during arctic winters, thermoregulatory costs are likely to be minimal (Chappell 1980). Of note are the uncertainties surrounding the contributions of metabolic inefficiencies (e.g. heat increment of feeding, inefficiency of catabolism) to the differences between resting and basal metabolic rate.

By manipulating body mass, body condition, air temperature, and wind, the model can be used experimentally to predict lower critical temperature under different scenarios. Unfortunately, there are still many aspects of thermoregulation and molt that are poorly understood due to the challenge of determining stages of hair loss/regrowth and measuring heat flux in free-ranging animals. In the model, we assumed that follicular growth required a minimum skin temperature of ~17 °C (Feltz and Fay 1966). In a concurrent study, the average skin temperature of 40 recently molted Weddell seals (i.e. active follicular growth in the past 30 days) was 11 ± 7 °C (Burns, unpublished). These skin temperature values suggest that follicular growth may be able to occur under slightly lower ambient temperature conditions than those measured in temperate species by Feltz and Fay (1966). While we expected elevated skin temperatures to lead to greater heat loss during the molting period (Paterson et al., 2012), the model did not indicate such an effect. In most cases, heat production still exceeded heat loss to the environment and therefore additional thermoregulatory costs were not incurred. By adding heat produced during inefficiencies (lactation, gestation, growth, and activity) to resting metabolic rate rather than basal metabolic rate, it is possible that our model overestimates total heat production and thus underestimates overall thermoregulatory costs.

The results from our perturbation experiment suggest that a 10% reduction in prey availability results in seals increasing the amount of time spent foraging by approximately 12%. This increase was evident throughout the year, including during the lactation and molt periods. Despite the shift in activity budget, small changes in food availability caused body mass declines. The mass changes were temporally centered on heavy foraging seasons (e.g. the winter foraging period) rather than during critical life history events. Despite the increases in swimming frequency, the lower body mass of seals in the perturbation simulation resulted in lower energy expenditure relative to seals in the baseline simulation. This was due to lower maintenance costs and lower costs of transport due to the relatively smaller body masses and surface areas. These results coincide with empirical studies showing that sea ice reductions and prey shortages increase foraging effort and decrease maternal body mass in pinnipeds (Croxall et al., 1988; Costa et al., 1989). Other authors have hypothesized that reduced sea ice conditions or prey reductions will cause increased foraging efforts, and have implemented their models accordingly (Malavear 2002; Noren et al., 2012). In our perturbation experiment, there were no significant differences in survival or reproductive rates between seals in baseline and perturbation simulations, which could indicate the demographic resilience of this large mammal to relatively small energetic perturbations. However, we did not assess the cumulative effects of reduced prey availability if those conditions persist beyond a single year.

While we have not yet done so, future model simulations could predict the magnitude of prey decline that would impact different components of seal behavior and demography. Additional processes such as diving limitations, predator avoidance behaviors, or social dynamics could be added into the model. Likewise, changes in environmental conditions can also be modeled, and their impact (in combination with prey reductions) can be assessed using the framework developed here. Finally, a sensitivity analysis with manipulations greater than or less than 10% could be used to assess parameter-specific sensitivity. For parameters in which greater than 10% uncertainty is possible, our sensitivity analysis

could have underestimated the relevant sensitivity of body mass to the uncertainty in that parameter. Conversely, for parameters with less uncertainty, our sensitivity analysis could have overestimated the relative sensitivity of body mass to uncertainty in that parameter.

5. Conclusions

Our model produces an estimate of annual energetic expenditure in adult, female Weddell seals and evaluates the energetic impacts of reduced prey abundance. By assigning a caloric value to the energetic costs associated with baseline and seasonal behaviors and linking energetic balance to vital rates, this model will allow researchers to evaluate the effects of changing environmental conditions on pinniped energetics (Harwood and Croxall 1988; Shelton et al., 1997). For example, experimentally manipulating prey availability could elucidate how extrinsic changes might incur population-level consequences, and how physiological processes and behavioral choices could mediate those effects. The model was designed to be extremely flexible and can be easily tuned with species specific variables so that researchers can apply it to poorly understood species with similar life history characteristics (e.g. Arctic ice seals). It can also be used to examine the interaction effects between multiple perturbations, such as the simultaneous reduction of prey abundance and prey quality, as would occur with commercial fisheries that preferentially extract high density prey items (Trites et al., 1997), or changes in prey availability and climate. Further, modifying the model to include a spatial component would allow explicit testing of the animal movement and feeding efficiency changes known to occur with the presence of boats (Pirootta et al., 2014), ocean noise (Fregosi et al., 2016), and prey density (Goldbogen et al., 2011). In addition, model outputs could serve as inputs to population projection models (Iverson et al., 2010; Testa et al., 2012). This would provide valuable insight into past and present population regulation and could help to understand the effects of natural or human influences on long-term ecosystem trends. Such a framework can play an important role in management and conservation of seals and other marine mammals by identifying and quantifying the underlying mechanisms of population-level vulnerability. Given the recent increase in commercial fishing and the forecasted change in ice cover, understanding the adaptive capacity of marine mammals is a time-sensitive scientific priority (Williams et al., 2011).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.02.002>.

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