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.

Key Words: Bioenergetics, pinnipeds, agent-based model, climate change, fishing pressure

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 formation 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 fisheries (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 (National Research Council, 2005, 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 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 models 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. However, 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*) (Figure 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 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-minute 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 model. 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 (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. 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.

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

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 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 (Figure 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 (Figure S2). Then a random number generator (0 to 1) was used to predict the seals’ behavior, 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 (Figure 1). Net energy at each timestep depended on foraging success and situational energy demand:

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

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 Equation 1) and converted to a resting metabolic rate using a scalar of 2 (Table S1 Equation 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 (77.84S, 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-hour 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 Equation 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 Equation 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 Equation 5) summed forced convection from the upper surface of the animal to air, conduction from the lower portion of the animal to the surface, radiative heat flux from the upper surface of the animal, and respiratory evaporative water loss (Table S1 Equations 6-11) (Ling 1970). Heat loss in water (Table S1 Equation 12) was due to forced convection (Table S1 Equations 13). Heat was gained from resting metabolic rate and the inefficiencies of gestation, lactation, and growth in air (Table S1 Equation 14) and activity inefficiency in water (Table S1 Equation 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 Equations 16 and 17). Since heat flux is partially determined by 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 Equation 8). The thermoregulation calculations described above required an extensive set of functions that are represented in Table S1 Equations 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 Equation 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, Wheatley et al. 2008). The metabolic cost of thrust forces required to swim at that velocity was then calculated using Table S2 Equations 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 Equation 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 Equation 42 which is based on Bernstein et al. (1997). The cost of producing the fetus was then calculated (Table S1 Equation 43) based on the energy stored in added mass (lipid and lean) and the efficiency of gestation (Ofstedal 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 Equation 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, Ofstedal et al. 1993, Pinkerton et al. 2007)(Table 2, Table S1 Equation 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 Equations 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 Equation 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 Equations 48-51) multiplied by the amount of hair needed to cover the animals surface area (Table S1 Equation 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 Equation 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 Equations 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 to 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 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 55 input parameters (10 specific to Weddell seals, 23 from pinniped literature and 21 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 (Figure 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 (Figure 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.

Figure 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.

Figure 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.

3.2. Activity Selection Submodel

Free-ranging animals that were instrumented with time-depth recorders spent 16.86 ± 3.26 hours/day during winter and 10.64 ± 1.74 hours /day during summer foraging. The time-activity budgets of simulated seals aligned relatively well with empirical time-activity budgets derived from real animals (Figure 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.

Figure 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.

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 6,159 and 6,771 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 modelled 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 (Figure 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). 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 (Figure 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 (Figure 3).

3.3.4. Reproduction Energetics

The total costs of gestation and lactation were high for the simulated seals ($2,634 \pm 423 \text{ MJ}$ and $4,386 \pm 183 \text{ MJ}$, 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 reduction in swimming activity (Figure 3). Molt costs amounted to <1% of total annual energy requirements (Figure 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 $1.85 \text{ MJ timestep}^{-1}$ and $1.30 \text{ MJ timestep}^{-1}$, respectively) so net energy was generally positive (Figure 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 (Figure 2). These energy expenditure and consumption values resulted in marked mass changes during critical life history events (Figure 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.

Figure 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.

3.5. Energy Allocation Submodel

Mass changes followed the expected seasonal patterns (Figure 5). The simulated seals' masses were generally highest at parturition (range 354.5 to 399.7, mean $\pm$ SD 375.4 ± 13.8 kg) and lowest at weaning (range 264.5 to 303.3, mean $\pm$ SD 281.6 ± 11.3 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 kilograms per day during days 110-150) but

then declined as active gestation became a prominent source of energy expenditure (Figure 6, bottom panel). Specifically, the simulated seals regained ~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 kilograms 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).

Figure 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).

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 ($t_9=-4.2$, $p<0.0001$, $d=-2.80$) across 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 (Figure 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 (Figure 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-minute 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, Pirodda 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 7,020 MJ for both gestation and lactation. Reproductive costs have been estimated for several other phocid species, including bearded seals (5,283 MJ), grey seals (1,847 MJ), harp seals (1,350 MJ), hooded seals (1,879 MJ), and ringed seals (1,075 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, modelled 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 modelling 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 $\sim 17^{\circ}\text{C}$ (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 $11 \pm 7^{\circ}\text{C}$ (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 modelled, 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 begin 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 (Pirotta 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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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=.326, SD=0.05	(Burns, in prep)
Target Percent Lipid	%	Fat_target	Uniform, Min=0.337, Max=.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)

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 obtained solely from Weddell seal literature are denoted. 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, Wheatley et al. 2008)
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	0.0003854952	-	(Beltran 2015)
Uptake	W	Prey Availability Summer	kg	I_kg_summer	Value	0.000751722	-	(Beltran 2015)
Molt	M	Energetic Density of Hair	MJ kg ⁻¹	ED_hair	Normal	0.02348795	0.000226	(McCullough and Ullrey 1983)
Molt	M	Energetic Density of Skin	MJ g ⁻¹	ED_skin	Normal	0.0239485	0.001034	(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, Boily 1995)
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	(Ofstedal 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	41.05555556	14.93438	(Tedman and Green 1987)
Reproduction	P	Efficiency of Gestation	%	Eff_gestation	Value	0.133	-	(Ofteidal 1985)
Reproduction	P	Proportion of Gestational Costs Associated with Conceptus	%	ConceptusProp	Value	0.8	-	(Ofteidal 1985)
Reproduction	W	Efficiency of Conversion: Milk to Storage	%	Eff_milk	Normal	0.521	0.077	(Tedman and Green 1987)
Reproduction		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, Øristland and Markussen 1990)
Thermoregulation	M	Emmisivity of Animal	Unitless	Emiss_a	Value	0.98	-	(Hammel 1956)
Thermoregulation	M	Emmisivity 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 ⁻²	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)
T	P	Respiratory Evaporative Water Loss Multiplier	%	REWL	Value	1.1	-	(Yallop and Hohenkerk 1985)

T	M	Stefan-Boltzmann Constant	$\text{W m}^{-2} \text{K}^{-1}$	SB	Value	5.67E-08	-	(Erdsack et al. 2012)
T	P	Core Temperature	C	T_core	Value	37	-	(Malavear 2002)
T	P	Core-Blubber Interface Temperature	C	T_coreblubber	Value	37	-	(Malavear 2002)
T	P	Temperature of Ground Snow	C	T_ice	Normal	-5.1	4.3	(Mellish et al. 2015)

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 %

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 (Winship et al. 2002).

<i>Input</i>	<i>Treatment</i>	<i>Parameter Value</i>	<i>Output – Body Mass (kg)</i>	<i>Relative Sensitivity Value</i>
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

Literature Cited

- Ainley, D. G., and G. Ballard. 2012. Trophic interactions and population trends of killer whales (*Orcinus orca*) in the Southern Ross Sea. *Aquatic Mammals* **38**:153-160.
- Ainley, D. G., and D. B. Siniff. 2009. The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. *Antarctic Science* **21**:317-327.
- Arrigo, K. R., D. H. Robinson, D. L. Worthen, R. B. Dunbar, G. R. DiTullio, M. VanWoert, and M. P. Lizotte. 1999. Phytoplankton community structure and the drawdown of nutrients and CO₂ in the Southern Ocean. *Science* **283**:365-367.
- Atkinson, S. 1997. Reproductive biology of seals. *Reviews of Reproduction* **2**:175-194.
- Barboza, P. S., K. L. Parker, and I. D. Hume. 2008. Integrative wildlife nutrition. Springer Science & Business Media.
- Beauplet, G., C. Guinet, and J. P. Arnould. 2003. Body composition changes, metabolic fuel use, and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiological and Biochemical Zoology* **76**:262-270.
- Becher, M. A., V. Grimm, P. Thorbek, J. Horn, P. J. Kennedy, and J. L. Osborne. 2014. BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. *Journal of Applied Ecology* **51**:470-482.
- Beck, C. A., W. D. Bowen, J. I. McMillan, and S. J. Iverson. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour* **66**:777-789.
- Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Kruetzen. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* **20**:1791-1798.
- Beltran, R. 2015. An agent-based bioenergetics model for predicting impacts of environmental change on Weddell seals (*Leptonychotes weddellii*). University of Alaska Anchorage.
- Bernstein, I. M., M. I. Goran, S. B. Amini, and P. M. Catalano. 1997. Differential growth of fetal tissues during the second half of pregnancy. *American Journal of Obstetrics and Gynecology* **176**:28-32.
- Blaxter, K. L. 1989. Energy metabolism in animals and man. CUP Archive.
- Board, O. S. 2005. Marine Mammal Populations and Ocean Noise:: Determining When Noise Causes Biologically Significant Effects. National Academies Press.
- Boily, P. 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology* **172**:235-244.
- Bowen, W. 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series* **158**:267-274.
- Boyd, I., and A. Murray. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology* **70**:747-760.
- Brody, S. 1945. Bioenergetics and growth; with special reference to the efficiency complex in domestic animals.
- Burek, K. A., F. M. Gulland, and T. M. O'Hara. 2008. Effects of climate change on Arctic marine mammal health. *Ecological Applications* **18**:S126-S134.
- Castellini, M. A., G. L. Kooyman, and P. Ponganis. 1992. Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *Journal of Experimental Biology* **165**:181-194.

- CCAMLR. 2013. Exploratory fishery for *Dissostichus* spp. in Subareas 88.1 and 88.2. Fishery Report 2013.
- Chambert, T., J. J. Rotella, and R. A. Garrott. 2014. An evolutionary perspective on reproductive individual heterogeneity in a marine vertebrate. *J Anim Ecol.* **83**:1158-168.
- Chappell, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. *Journal of Mammalogy* **61**:278-291.
- Costa, D., B. Le Boeuf, A. Huntley, and C. Ortiz. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology* **209**:21-33.
- Costa, D. P. 2012. A bioenergetics approach to developing a population consequences of acoustic disturbance model. *Adv Exp Med Biol* **730**:423-426.
- Costa, D. P., J. P. Croxall, and C. D. Duck. 1989. Foraging energetics of antarctic fur seals in relation to changes in prey availability. *Ecology*:596-606.
- Costa, D. P., L. A. Huckstadt, D. E. Crocker, B. I. McDonald, M. E. Goebel, and M. A. Fedak. 2010. Approaches to studying climatic change and its role on the habitat selection of antarctic pinnipeds. *Integr Comp Biol* **50**:1018-1030.
- Croxall, J., T. McCann, P. Prince, and P. Rothery. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. Pages 261-285 *Antarctic Ocean and resources variability*. Springer.
- DeAngelis, D. L., and W. M. Mooij. 2005. Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics* **36**:147-168.
- Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44**:163-176.
- Dunkin, R. C. 2012. From tissues to landscapes: how thermal physiology, water use, and climate influence patterns of landscape use in elephants. Dissertation. University of California Santa Cruz.
- Durant, J. M., D. Ø. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research (CR)* **33**:271-283.
- Eisert, R., O. T. Oftedal, and G. K. Barrell. 2013a. Milk composition in the Weddell seal *Leptonychotes weddellii*: evidence for a functional role of milk carbohydrates in pinnipeds. *Physiol Biochem Zool* **86**:159-175.
- Eisert, R., M. Pinkerton, S. Newsome, and O. Oftedal. 2013b. A critical re-examination of the evidence for a possible dependence of Weddell seals (*Leptonychotes weddellii*) on Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. **CCAMLR Document WG EMM 13**:1-30.
- Erdsack, N., F. D. Hanke, G. Dehnhardt, and W. Hanke. 2012. Control and amount of heat dissipation through thermal windows in harbor seals (*Phoca vitulina*). *Journal of Thermal Biology* **37**:537-544.
- Fedak, M., and S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the Grey seal (*Halichoerus grypus*). *Journal of Zoology, Lond.* **198**:473-479.
- Feldkamp, S. D. 1987. Swimming in the California sea lion: morphometrics, drag and energetics. *Journal of Experimental Biology* **131**:117-135.

- Feltz, E. T., and F. H. Fay. 1966. Thermal requirements in vitro of epidermal cells from seals. *Cryobiology* **3**:261-264.
- Field, I. C., C. J. Bradshaw, H. R. Burton, and M. A. Hindell. 2005. Juvenile southern elephant seals exhibit seasonal differences in energetic requirements and use of lipids and protein stores. *Physiological and Biochemical Zoology* **78**:491-504.
- Folkow, L. P., and A. S. Blix. 1987. Nasal heat and water exchange in gray seals. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* **253**:R883-R889.
- Forcada, J., P. N. Trathan, P. L. Boveng, I. L. Boyd, J. M. Burns, D. P. Costa, M. Fedak, T. L. Rogers, and C. J. Southwell. 2012. Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biological Conservation* **149**:40-50.
- Forcada, J., P. N. Trathan, and E. J. Murphy. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*. **14**: 2473-2488.
- Fraser, W. R., and E. E. Hofmann. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem. *Marine Ecology Progress Series* **265**:1-15.
- Fregosi, S., H. Klinck, M. Horning, D. P. Costa, D. Mann, K. Sexton, L. A. Hückstädt, D. K. Mellinger, and B. L. Southall. 2016. An animal-borne active acoustic tag for minimally invasive behavioral response studies on marine mammals. *Animal Biotelemetry* **4**:1.
- Fuiman, L. A., K. M. Madden, T. M. Williams, and R. W. Davis. 2007. Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. *Deep Sea Research Part II: Topical Studies in Oceanography* **54**:270-289.
- Gales, N., and H. Burton. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leonina*. *Australian Journal of Zoology* **35**:207-217.
- Gales, R., D. Renouf, and E. Noseworthy. 1994. Body composition of harp seals. *Canadian journal of zoology* **72**:545-551.
- Gittleman, J. L., and S. D. Thompson. 1988. Energy allocation in mammalian reproduction. *American Zoologist* **28**:863-875.
- Goldbogen, J., J. Calambokidis, E. Oleson, J. Potvin, N. Pyenson, G. Schorr, and R. Shadwick. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *Journal of Experimental Biology* **214**:131-146.
- Goundie, E. T., D. A. Rosen, and A. W. Trites. 2015. Low prey abundance leads to less efficient foraging behavior in Steller sea lions. *Journal of Experimental Marine Biology and Ecology* **470**:70-77.
- Grav, H. J., and A. S. Blix. 1976. Brown adipose tissue-a factor in the survival of harp seal pups. *Canadian Journal of Physiology and Pharmacology* **54**:409-412.
- Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: a review and first update. *Ecological modelling* **221**:2760-2768.
- Hadley, G. L., J. J. Rotella, and R. A. Garrott. 2007. Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology* **76**:448-458.
- Hamby, D. 1994. A review of techniques for parameter sensitivity analysis of environmental models. *Environmental monitoring and assessment* **32**:135-154.
- Hammel, H. 1956. Infrared emissivities of some arctic fauna. *Journal of Mammalogy*:375-378.

- Hansen, S., and D. M. Lavigne. 1997. Ontogeny of the thermal limits in the harbor seal (*Phoca vitulina*). *Physiological Zoology*:85-92.
- Harwood, J., and J. P. Croxall. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Science* **4**:13-33.
- Hazen, E. L., S. Jorgensen, R. R. Rykaczewski, S. J. Bograd, D. G. Foley, I. D. Jonsen, S. A. Shaffer, J. P. Dunne, D. P. Costa, and L. B. Crowder. 2013. Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change* **3**:234-238.
- Hedd, A., R. Gales, and D. Renouf. 1997. Inter-annual consistency in the fluctuating energy requirements of captive harp seals *Phoca groenlandica*. *Polar Biology* **18**:311-318.
- Hind, A., and W. Gurney. 1997. The metabolic cost of swimming in marine homeotherms. *Journal of Experimental Biology* **200**:531-542.
- Hindell, M. A., R. Harcourt, J. R. Waas, and D. Thompson. 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* **242**:275-284.
- Hückstädt, L. A., J. M. Burns, P. L. Koch, B. I. McDonald, D. E. Crocker, and D. P. Costa. 2012. Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. *Marine Ecology Progress Series* **455**:287-301.
- Innes, S., G. Worthy, D. Lavigne, and K. Ronald. 1990. Surface areas of phocid seals. *Canadian journal of zoology* **68**:2531-2538.
- Iverson, S. J., C. E. Sparling, T. M. Williams, L. Shelley, I. Boyd, W. Bowen, and S. Iverson. 2010. Measurement of individual and population energetics of marine mammals. *Marine mammal ecology and conservation: a handbook of techniques* (IL Boyd, WD Bowen, and SJ Iverson, eds.). Oxford University Press, New York:165-189.
- Jay, C. V., M. S. Udevitz, R. Kwok, A. S. Fischbach, and D. C. Douglas. 2010. Divergent movements of walrus and sea ice in the northern Bering Sea. *Marine Ecology Progress Series* **407**: 293-302.
- Johnston, A. S. A., M. E. Hodson, P. Thorbek, T. Alvarez, and R. M. Sibly. 2014. An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides. *Ecological Modelling* **280**:5-17.
- Kawaguchi, S., S. Nicol, and A. J. Press. 2009. Direct effects of climate change on the Antarctic krill fishery. *Fisheries Management and Ecology* **16**:424-427.
- Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten. 2012. RNCEP: global weather and climate data at your fingertips. *Methods in Ecology and Evolution* **3**:65-70.
- Kooyman, G. L. 1981. Weddell seal—*Leptonychotes weddelli*. *Handbook of Marine Mammals* **2**:275-296.
- Kovacs, K. M., C. Lydersen, J. E. Overland, and S. E. Moore. 2010. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* **41**:181-194.
- Kvadsheim, P. H., A. R. Gotaas, L. P. Folkow, and A. S. Blix. 1997. An experimental validation of heat loss models for marine mammals. *Journal of Theoretical Biology*. **184**:15-23.
- Lake, S., H. Burton, R. Barker, and M. Hindell. 2008. Annual reproductive rates of Weddell seals in eastern Antarctica from 1973 to 2000. *Marine Ecology Progress Series* **366**:259-270.
- Lake, S., H. Burton, and M. Hindell. 1997. Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. *Polar Biology* **18**:319-324.

- Lavigne, D., W. Barchard, S. Innes, and N. Øritsland. 1976. Pinniped bioenergetics. Fisheries Dept. Advisory Committee on Marine Resources Research. Scientific Consultation on Marine Mammals. Bergen (Norway).
- Ling, J. K. 1970. Pelage and molting in wild mammals with special reference to aquatic forms. *Quarterly Review of Biology*:16-54.
- Lusseau, D., and L. Bejder. 2007. The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment. *International Journal of Comparative Psychology* **20**:228-236.
- Lydersen, C., and K. M. Kovacs. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series* **187**:265-281.
- MacIntyre, K., K. Stafford, C. Berchok, and P. Boveng. 2013. Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008–2010. *Polar Biology* **36**:1161-1173.
- Malavear, M. Y. G. 2002. Modeling the energetics of Steller sea lions (*Eumetopias jubatus*) along the Oregon coast. Master's Thesis. University of British Columbia.
- McCafferty, D. J., C. Gilbert, A.-M. Thierry, J. Currie, Y. Le Maho, and A. Ancel. 2013. Emperor penguin body surfaces cool below air temperature. *Biology letters* **9**:1-4.
- McCullough, D. R., and D. E. Ullrey. 1983. Proximate mineral and gross energy composition of white-tailed deer. *The Journal of Wildlife Management*:430-441.
- Mellish, J.-A., A. Hindle, J. Skinner, and M. Horning. 2015. Heat loss in air of an Antarctic marine mammal, the Weddell seal. *Journal of Comparative Physiology B* **185**:143-152.
- Mellish, J. A., A. G. Hindle, and M. Horning. 2011. Health and condition in the adult Weddell seal of McMurdo Sound, Antarctica. *Zoology* **114**:177-183.
- Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* **78**:505-521.
- New, L. F., J. S. Clark, D. P. Costa, E. Fleishman, M. A. Hindell, T. Klanjšček, D. Lusseau, S. Kraus, C. R. McMahon, P. W. Robinson, R. S. Schick, L. K. Schwarz, S. E. Simmons, L. Thomas, P. Tyack, and J. Harwood. 2014. Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series* **496**:99-108.
- Nicol, S., J. Foster, and S. Kawaguchi. 2012. The fishery for Antarctic krill - recent developments. *Fish and Fisheries* **13**:30-40.
- Noren, S. R., M. S. Udevitz, and C. V. Jay. 2012. Bioenergetics model for estimating food requirements of female Pacific walruses *Odobenus rosmarus divergens*. *Marine Ecology Progress Series* **460**:261-275.
- Oftedal, O. 1985. Pregnancy and lactation. *Bioenergetics of wild herbivores* **10**:215-238.
- Oftedal, O. T., W. D. Bowen, and D. J. Boness. 1993. Energy transfer by lactating hooded seals and nutrient deposition in their pups during the four days from birth to weaning. *Physiological Zoology*:412-436.
- Øritsland, N., and N. Markussen. 1990. Outline of a physiologically based model for population energetics. *Ecological Modelling* **52**:267-288.
- Paine, R. T. 1971. The measurement and application of the calorie to ecological problems. *Annual Review of Ecology and Systematics*:145-164.
- Parkinson, C. L. 2004. Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. *Antarctic Science* **16**:387-400.

- Paterson, W., C. E. Sparling, D. Thompson, P. P. Pomeroy, J. I. Currie, and D. J. McCafferty. 2012. Seals like it hot: Changes in surface temperature of harbour seals (*Phoca vitulina*) from late pregnancy to moult. *Journal of Thermal Biology* **37**:454-461.
- Pearson, L. E., H. E. Liwanag, M. O. Hammill, and J. M. Burns. 2014a. Shifts in thermoregulatory strategy during ontogeny in harp seals (*Pagophilus groenlandicus*). *Journal of Thermal Biology* **44**:93-102.
- Pearson, L. E., H. E. Liwanag, M. O. Hammill, and J. M. Burns. 2014b. To each its own: thermoregulatory strategy varies among neonatal polar phocids. *Comp Biochem Physiol A Mol Integr Physiol* **178**:59-67.
- Pianka, E. 1981. Resource acquisition and allocation among animals. Pages 300-314 *Physiological ecology: an evolutionary approach to resource use*. Blackwell Scientific Publishers, Oxford, UK.
- Pinkerton, M., S. Hanchet, and J. Bradford-Grieve. 2007. Finding the role of Antarctic toothfish in the Ross Sea ecosystem. *Water and Atmosphere* **15**:20-21.
- Piou, C., M. H. Taylor, J. Papaix, and E. Prévost. 2015. Modelling the interactive effects of selective fishing and environmental change on Atlantic salmon demogenetics. *Journal of Applied Ecology*. **52**: 1629-1637.
- Pirotta, E., J. Harwood, P. M. Thompson, L. New, B. Cheney, M. Arso, P. S. Hammond, C. Donovan, and D. Lusseau. 2015. Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences. *Proc. R. Soc. B. The Royal Society*.
- Pirotta, E., L. New, J. Harwood, and D. Lusseau. 2014. Activities, motivations and disturbance: An agent-based model of bottlenose dolphin behavioral dynamics and interactions with tourism in Doubtful Sound, New Zealand. *Ecological Modelling* **282**:44-58.
- Ponganis, P., and T. Stockard. 2007. Short Note: The Antarctic toothfish: how common a prey for Weddell seals? *Antarctic Science* **19**:441-442.
- Rea, L., D. Rosen, and A. Trites. 2007. Utilization of stored energy reserves during fasting varies by age and season in Steller sea lions. *Canadian Journal of Zoology* **85**:190-200.
- Rechsteiner, E. U., D. A. S. Rosen, and A. W. Trites. 2013. Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. *Journal of Mammalogy* **94**:820-832.
- Reid, K., and J. P. Croxall. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**:377-384.
- Reiter, J., N. L. Stinson, and B. J. Le Boeuf. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology* **3**:337-367.
- Ronald, K., K. Keiver, F. Beamish, and R. Frank. 1984. Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). *Canadian Journal of Zoology* **62**:1101-1105.
- Rosen, D. A., and A. Trites. 2000. Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. *Canadian Journal of Zoology* **78**:234-239.
- Rosen, D. A., and A. W. Trites. 1997. Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comparative Biochemistry and Physiology Part A: Physiology* **118**:877-881.

- Sato, K., Y. Mitani, M. F. Cameron, D. B. Siniff, Y. Watanabe, and Y. Naito. 2002. Deep foraging dives in relation to the energy depletion of Weddell seal (*Leptonychotes weddellii*) mothers during lactation. *Polar Biology* **25**:696-702.
- Shelton, P. A., W. G. Warren, G. B. Stenson, and J. W. Lawson. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part II: Uncertainty in consumption estimates associated with population size, residency, energy requirement and diet. *Journal of Northwest Atlantic Fishery Science* **22**:303-315.
- Shero, M. R., R. T. Krotz, D. P. Costa, J. P. Avery, and J. M. Burns. 2015. How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? *Functional Ecology* **29**: 1278-1291.
- Simpkins, M., L. Hiruki-Raring, G. Sheffield, J. Grebmeier, and J. Bengtson. 2003. Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. *Polar Biology* **26**:577-586.
- Siniff, D. B., R. A. Garrott, J. J. Rotella, W. R. Fraser, and D. G. Ainley. 2008. Opinion: Projecting the effects of environmental change on Antarctic seals. *Antarctic Science* **20**: 425-435.
- Speakman, J., and J. McQueenie. 1996. Limits to sustained metabolic rate: the link between food intake, basal metabolic rate, and morphology in reproducing mice, *Mus musculus*. *Physiological Zoology*:746-769.
- Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research* **113**.
- Stewart, R., and D. Lavigne. 1984. Energy transfer and female condition in nursing harp seals *Phoca groenlandica*. *Ecography* **7**:182-194.
- Tedman, R., and B. Green. 1987. Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (*Leptonychotes weddellii*). *Journal of Zoology* **212**:29-42.
- Testa, J. W., K. J. Mock, C. Taylor, H. Koyuk, J. R. Coyle, and R. Waggoner. 2012. Agent-based modeling of the dynamics of mammal-eating killer whales and their prey. *Marine Ecology Progress Series* **466**:275-291.
- Thorson, P. H., and B. Le Boeuf. 1994. Developmental aspects of diving in northern elephant seal pups. Pages 271-289 *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley.
- Trites, A. W., V. Christensen, and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science* **22**:173-187.
- Villegas-Amtmann, S., L. Schwarz, J. Sumich, and D. Costa. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* **6**:1-19.
- Watts, P., S. Hansen, and D. Lavigne. 1993. Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. *Journal of Theoretical Biology*. **163**:505-525.
- Wheatley, K. E., C. J. Bradshaw, L. S. Davis, R. G. Harcourt, and M. A. Hindell. 2006. Influence of maternal mass and condition on energy transfer in Weddell seals. *J Anim Ecol* **75**:724-733.

- Wheatley, K. E., C. J. Bradshaw, R. G. Harcourt, and M. A. Hindell. 2008. Feast or famine: evidence for mixed capital–income breeding strategies in Weddell seals. *Oecologia* **155**:11-20.
- Wiedenmann, J., K. A. Cresswell, J. Goldbogen, J. Potvin, and M. Mangel. 2011. Exploring the effects of reductions in krill biomass in the Southern Ocean on blue whales using a state-dependent foraging model. *Ecological Modelling* **222**:3366-3379.
- Williams, T., and G. Kooyman. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology*:576-589.
- Williams, T. M. 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *Journal of Experimental Biology* **207**:973-982.
- Williams, T. M., S. R. Noren, and M. Glenn. 2011. Extreme physiological adaptations as predictors of climate-change sensitivity in the narwhal, *Monodon monoceros*. *Marine Mammal Science* **27**:334-349.
- Winship, A. J. 2000. Growth and bioenergetic models for Steller sea lions (*Eumetopias jubatus*) in Alaska. Dissertation. University of British Columbia.
- Winship, A. J., A. W. Trites, and D. A. S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology Progress Series* **229**:291-312.
- Wood, K. A., R. A. Stillman, and J. D. Goss-Custard. 2015. Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. *Journal of Applied Ecology* **52**:810-815.
- Worthy, G., P. Morris, D. Costa, and B. Le Boeuf. 1992. Moulting energetics of the northern elephant seal (*Mirounga angustirostris*). *Journal of Zoology* **227**:257-265.
- Yallop, B., and C. Hohenkerk. 1985. Compact data for navigation and astronomy for the years 1986-1990. Stationery Office Books, London, England.
- Yunker, G., M. Hammill, J.-F. Gosselin, D. Dion, and J. Schreer. 2005. Foetal growth in north-west Atlantic grey seals (*Halichoerus grypus*). *Journal of Zoology* **265**:411-419.