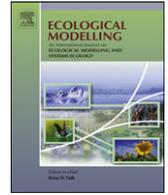




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Exploring the effects of reductions in krill biomass in the Southern Ocean on blue whales using a state-dependent foraging model

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ABSTRACT

Many species of baleen whales were hunted to near extinction in the Southern Hemisphere. The recovery of these populations will be affected by the availability of krill, a major dietary component, in the Southern Ocean. We combine a novel energetics model for baleen whales with a state dependent foraging model to explore the impacts of an expanding krill fishery on baleen whales. We parameterize the model for blue whales, but with simple modifications it could be applied to most baleen whales. We predict that an expanding fishery will have a small but significant impact on the blue whale population through decreased birth rates. However, spreading the catch limit throughout the range of krill can reduce these effects. In addition, whales may be able to reduce these impacts through adaptive changes in foraging behavior. The relationship between krill abundance and blue whale foraging and reproductive success is nonlinear, such that larger reductions in krill biomass, potentially following a loss of sea ice due to climate change, could have a much larger negative impact on the recovery of blue whales.

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1. Introduction

Between 1904 and 1986, roughly 1.6 million rorqual whales (belonging to the Family Balaenopteridae) were harvested in the Southern Ocean, resulting in the decimation of the Southern Hemisphere populations of blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*), and humpback (*Megaptera novaeangliae*) whales (Mackintosh, 1965; Ballance et al., 2006; Mori and Butterworth, 2006). The International Whaling Commission (IWC) enacted a moratorium on all commercial whaling in 1986, although bans on whaling had been enacted earlier for blue, fin and humpback whales (Mori and Butterworth, 2006). Population trends for fin and sei whales are unknown, but for both blue and humpback whales, which have not been harvested in the Southern Ocean since 1972 (when illegal Soviet operations stopped; Yablokov, 1994), the trend is increasing. For humpback populations where data are available, steady increases have been documented (Bannister, 1994;

Paterson et al., 1994; Ward et al., 2006). In fact, humpbacks are listed as a species of least concern by the IUCN, while blue, fin and sei whales remain endangered (Reilly et al., 2009). For blue whales, Branch et al. (2004) estimate that the population has grown by roughly 7% year⁻¹, but the population was so depleted that it is still less than 1% of the pre-exploitation level.

The continued recovery of rorquals in the Southern Hemisphere will depend in part on the availability of their prey. Most rorqual species feed seasonally in the Southern Ocean, then migrate long distances to temperate or tropical latitudes to mate and reproduce (Mackintosh, 1965). During the breeding period, it is believed that whales live primarily off energy reserves accumulated during the shortened feeding season because whales that were caught leaving the feeding grounds typically contained large amounts of blubber, while those caught entering the feeding grounds were considerably leaner (Lockyer, 2007). In addition, stomach analysis of whales caught outside the Southern Ocean often showed little or no food in their stomachs (Lockyer, 1981). Therefore, survival and successful reproduction during the overwinter breeding period will be affected by the level of energy reserves acquired during the feeding season in the Southern Ocean, which will be affected by the availability of prey. In fact, it has been shown that for southern right whales (*Eubalaena australis*) that breed off Argentina, calving

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success is positively correlated with a proxy for prey abundance in an important summer feeding area around the island of South Georgia in the Southern Ocean (Leaper et al., 2006).

Baleen whales that feed in the Southern Ocean eat predominantly Antarctic krill, *Euphausia superba* (henceforth krill; Kawamura, 1980), and there is concern that a changing ecosystem in response to global warming, combined with an expanding krill fishery may result in a considerable reduction in the biomass of krill available to predators (Nicol and Foster, 2003). Many studies have demonstrated a link between krill recruitment and seasonal sea-ice extent off the west Antarctic Peninsula (Siegel and Loeb, 1995; Quetin and Ross, 2003; Wiedenmann et al., 2009). These studies suggest that a decline in sea ice in this region may result in poor recruitment events, reducing biomass both locally and in downstream regions like the Scotia Sea. Warmer sea temperatures may also affect krill biomass, since krill growth is temperature-dependent (Wiedenmann et al., 2008).

While the effects of a loss of sea ice and a warming Southern Ocean on krill cannot be directly managed, the impacts may be mitigated by adaptive changes in the management of the krill fishery. The Southern Ocean krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which has adopted an ecosystem-based, precautionary approach towards the krill fishery (Constable, 2004). Annual catch limits are currently set at roughly 10% of the estimated biomass in the Atlantic, Pacific and Indian Ocean sectors of the Southern Ocean (Croxall and Nicol, 2004; more details at www.ccamlr.org). The intention of such catch limits is to limit the potential for ecosystem-wide depletion of the krill, but there remains the potential for local depletion. There is also some concern that recent advances in harvesting technology allow krill to be continuously pumped from the water (Kawaguchi and Nicol, 2007), greatly increasing the likelihood of severe local depletion.

CCAMLR has recognized the need to subdivide the precautionary catch limit in the south Atlantic sector of the Southern Ocean into small-scale management units (SSMUs) to minimize the impact that the krill fishery has on krill predators (Hewitt et al., 2004). There are currently five scenarios being explored for the allocation of catches among SSMUs. The first four are static, with catch in a single SSMU proportional to (1) historical catch in that SSMU, (2) predator demand, (3) total krill biomass, or (4) proportional to krill biomass less predator demand. The fifth scenario is dynamic, accounting for the potential variation of krill biomass from year to year among SSMUs, and would be proportional to some ecosystem index yet to be determined (Hewitt et al., 2004). These scenarios are being explored via modelling, and no scenario has been implemented to date (Hill et al., 2006).

Here, we explore how changes in krill biomass and patchiness may affect blue whales in the Southern Ocean. Specifically, we ask what happens if the whales have evolved to exploit a particular landscape of krill, but an expanding krill fishery changes this landscape? Although we develop the model specifically for blue whales, with simple modifications it could be applied to other whale species.

We focus on blue whales for two reasons. First, despite evidence for population growth, the population size is still at critically low levels (Branch et al., 2004). Second, blue whales have incredibly high energetic demands, forcing them to feed on incredibly dense krill aggregations (Croll et al., 2005). The commercial krill fishery also targets the densest aggregations of krill to maximize profits (Kawaguchi and Nicol, 2007; Kawaguchi and Candy, 2009), setting up the potential for competition between blue whales and the fishery.

We use state dependent life history theory, implemented by stochastic dynamic programming (SDP; Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000) to answer

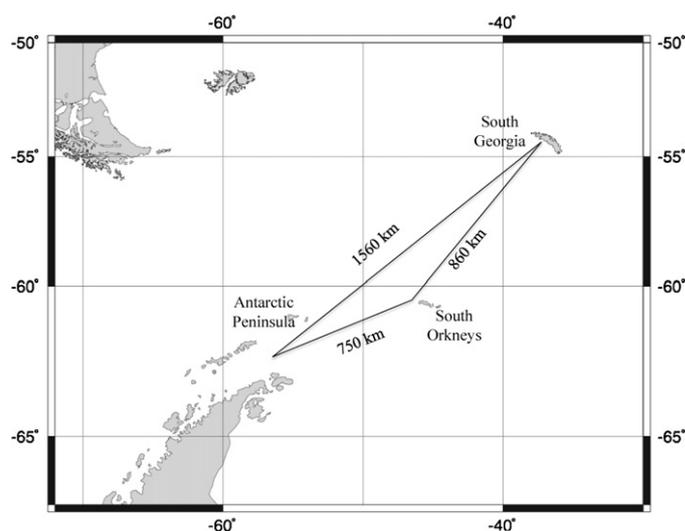


Fig. 1. Map of the South Atlantic sector of the Southern Ocean, with locations and approximate distances between the assumed patches used in the model.

this question. SDP models have already been used to address ecological questions in the Southern Ocean, such as the effects of changes in krill abundance and patchiness on the foraging and breeding success of penguins (Cresswell et al., 2008), and the effects of predation on krill behavior and life-history (e.g. Alonzo and Mangel, 2001; Willis, 2007).

2. Methods

Our model has three components; (1) the krill landscape, (2) the physiological model for blue whales, and (3) the foraging model for blue whales. In determining the level of biological detail for each model component we consider the tradeoff between detail (i.e. complexity) and model tractability and understandability (Hilborn and Mangel, 1997).

2.1. The krill landscape

There is a large amount of information on the characteristics of individual krill swarms (e.g. size, density), and their distribution in space and time (Miller and Hampton, 1989; Sprong and Schalk, 1992; Cox et al., 2009; Tarling et al., 2009; Klevjer et al., 2010). Our goal in this paper is to present a framework for exploring changes in krill abundance and patchiness on the foraging success of blue whales. Therefore, incorporating all the complexities of krill aggregations and their spatial distribution is beyond the scope of this paper. Instead, we create a simplified model of krill in the South Atlantic sector of the Southern Ocean. We select this area because it is both the region of highest krill abundance (Atkinson et al., 2008) and the region where the fishery currently operates (Kawaguchi and Nicol, 2007). We model krill swarms (dense aggregations of individual krill) within areas of consistently above average swarm frequency, called patches (Siegel and Kalinowski, 1994). Although there are many areas where krill swarms concentrate, we only consider three patches; one off the Antarctic Peninsula, one off the South Orkney Islands, and one off the island of South Georgia (Fig. 1). We select these areas because they represent areas of high krill density (Siegel, 2005) and also because the fishery consistently operates in these areas on an annual basis (Kawaguchi and Nicol, 2007) within the South Atlantic sector of the Southern Ocean. In Appendix A we describe the details for constructing patches within the model and justification for the patch parameters, but provide a brief description here. Each patch is divided into a number of

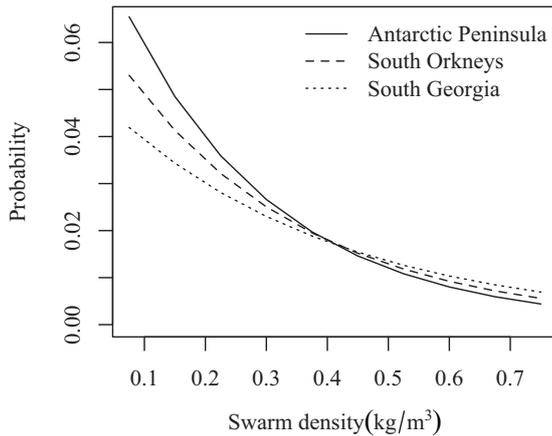


Fig. 2. Probability distribution for the swarm densities (kg m^{-3}) found in each patch (i.e. the probability of finding a swarm with a particular density, or $p(c_j|t)$). See Appendix A for more details.

grids, or cells. Each cell within patch c will contain a swarm with time-dependent probability $p(c|t)$, and the probability that a cell will have a swarm with the j th density (in kg m^{-3}) is denoted by $p(c_j|t)$ (Fig. 2).

2.2. The physiological model

We are interested in the foraging behavior of a whale throughout the feeding season, and how these behaviors vary with physiological state. For simplicity, we assume that energy is stored only as blubber, and that during periods of starvation, the whale meets its energy requirements by breaking down stored blubber, and not other tissues such as muscle (Brodie, 1975; Noren and Mangel, 2004). Although there are lipid reserves in other parts of the body (Lockyer et al., 1985), assuming energy is only stored as blubber makes calculations straightforward. To generate a range of different energy stores for a whale of length L (in m), we estimate the average mass \bar{W} (in kg) at that length (Lockyer, 1976)

$$\bar{W}(L) = 4.6L^{3.05} \quad (1)$$

According to Lockyer (1976), an average blue whale is made up primarily of muscle (39%), blubber (27%), bone (17%) and viscera (12%), leaving 5% of unclassified tissue. To generate a range of energy reserves for a whale of a given length, we assume that as a whale's blubber mass changes, the mass of its other tissues remains constant. Therefore, a blue whale of length L will have on average $0.73\bar{W}(L)$ kg of non-blubber tissue. If 1 kg of blubber contains u kJ of utilizable energy, a whale with X kJ of energy stored will have a blubber mass of $W_b = X/u$, and a total mass $W(X, L) = W_b + 0.73\bar{W}(L)$. For each length, we explore a range of X such that the percent of body mass comprised of blubber is between 2 and 35%. This range extends lower than that reported by Lockyer (1976; 21–33%), but it allows us to explore the effects of extreme leanness in whales. We model lengths between, 20 and 30 m, assuming that whales mature at 23 m (Lockyer, 1981).

No direct metabolic estimates have been made for blue whales. Therefore, we must extrapolate the allometric relationships for mammalian metabolic costs well beyond the body masses used to generate them. We rely on the allometric relationships relating mass, W (in kg) to basal metabolic rate (BMR) and the cost of transport (COT). The relationship between BMR (in kJ day^{-1}) and W

$$BMR = 293.1W^{0.75} \quad (2)$$

was developed by Kleiber (1975) using data on terrestrial mammals. There is currently debate over whether the value of this

exponent is 0.75 (Sieg et al., 2009; White et al., 2009), but without specific estimates for marine mammals we use 0.75. Additionally, there is debate over whether or not marine mammals have a higher BMR than terrestrial mammals for a given mass. Leaper and Lavigne (2007) reviewed the available evidence and concluded that there is no statistical support for marine mammal BMR being higher than that of terrestrial mammals. We therefore estimate BMR from Eq. (2), but explore the sensitivity of model results to higher values.

Williams (1999) provides a means for estimating the mass-specific cost of transport (in $\text{kJ kg}^{-1} \text{ km}^{-1}$), COT . This analysis includes data from a variety of marine mammals, all much smaller than blue whales. COT includes maintenance costs, and is calculated with

$$COT = 7.79W^{-0.29} \quad (3)$$

Eqs. (2) and (3) allow us to calculate the costs of various activities of a whale. Within day t , a whale can engage in three distinct activities: traveling, feeding, and resting. We define traveling as any directed lateral movement within a patch or between patches, and assume that if a whale moves to an area that contains a swarm, it immediately finds the swarm (i.e. there is no additional time spent searching). Feeding involves diving to the swarm, lunging at the swarm and engulfing krill (done multiple times during a single dive), followed by a return to the surface where the whale remains for a short period recovering from the prolonged period of oxygen deprivation. Resting is considered as any period where the whale is not traveling or feeding.

To illustrate how we calculate the energetic costs, consider a whale on some day t during some length of time Δ (we discuss below the specifics about the behavioral decisions and how Δ is determined). During this period, the whale spends some time (in hours) moving (τ_m), feeding (τ_f), and resting (τ_r). The total metabolic cost for the whale during this period is the sum of the costs of these different activities. If a whale moves distance d (in km), the cost of moving, $C_m(d)$ (in kJ) is

$$C_m(d) = COT \cdot W \cdot d \quad (4)$$

Blue whales travel at different speeds depending on their behavior, moving slower when searching for food than when long-distance transiting (Bailey et al., 2010). We therefore set two different speeds for movement within a patch, s_c , and between patches, s_l (Table 1). Given a particular s , $\tau_m = d/s$. After moving d km, if the whale encounters a swarm of type j and feeds, it will have a maximum of $\Delta - \tau_m$ hours to feed. The cost of feeding depends on the number of lunges a whale makes during this period, which depends on the volume that a whale can engulf in a single lunge, swarm density, and the amount of time available for feeding. Lunge feeding is energetically costly (Goldbogen et al., 2007). We calculate the energetic cost of engulfment during a single lunge C_g (in kJ) using an unsteady hydrodynamic model (Potvin et al., 2009, 2010), with engulfment simulated for different sized whales, integrating morphological and kinematic data (Goldbogen et al., 2007, 2008, 2011). The energetic cost of engulfment scales allometrically with body length as

$$C_g(L) = 0.00784L^{3.4} \quad (5)$$

The cost of engulfment does not include maintenance costs, nor does it include the acceleration phase prior to engulfment. Potvin et al. (2009) suggest that a reasonable approximation for the energetic cost of acceleration and engulfment is $2C_g(L)$. Therefore, assuming a whale makes ω lunges per hour, and spends τ_f hours feeding, the cost of foraging C_f is

$$C_f(j, L, W, \tau_f) = \tau_f \cdot \omega \cdot 2 \cdot C_g + \frac{\tau_f}{24} \alpha_f \cdot BMR \quad (6)$$

Table 1

Model parameters, values used in the model, descriptions, and sources where they exist. The distance to the breeding grounds (D_B) is a rough approximation of the distance from the Scotia Sea to the hypothesized breeding area off southwest Africa (Branch et al., 2007). The movement speed is inflated from the maximum values reported in Mate et al. (1999), as such estimates are likely biased low due to the temporal resolution of the data.

Parameter	Value	Description	Source
T	120	Days on the feeding grounds	Lockyer (1981)
D_B	5000	Distance (km) to breeding grounds	
v	3200	Swarm volume (m ³)	Tarling et al. (2009)
z	0.9	Parameter controlling krill patchiness	
s_c	7	Movement speed within a patch (km h ⁻¹)	Mate et al. (1999)
s_c	10	Movement speed to a new patch (km h ⁻¹)	Mate et al. (1999)
α_f	2.5	Feeding cost as a multiple of BMR	
α_r	2	Resting cost as a multiple of BMR	
τ_c	4	Clearance rate (h) of the forestomach	Vikingsson (1997)
C_D	9.29×10^6	Cost of calf development (kJ)	Lockyer (1981)
C_L	3.27×10^8	Lactation costs from birth to re-entering the feeding grounds	Lockyer (1981)
η	2.88	Exponent relating forestomach capacity to length	Modified from Vikingsson (1997)
A	0.8	Assimilation efficiency	Costa and Williams (2000)
u	31,798	Utilizable energy (kJ kg ⁻¹) in blubber	Lockyer (1981)
w	6276	Energy content of non-blubber tissue (kJ kg ⁻¹)	Lockyer (1981)
ρ	4184	Energy content of krill (kJ kg ⁻¹)	Lockyer (1981)
ω	20	Lunges made per hour during the overwinter period	Croll et al. (2001)
λ	0.002	Proportion of body mass consumed daily during the overwinter period	

where α_f scales BMR to account for increased activity (Table 1). We delay discussion of the calculation of τ_f until the discussion of food intake. Given τ_m and τ_f , we estimate τ_r with $\Lambda - \tau_m - \tau_f$, and estimate the cost of resting, C_r ,

$$C_r(W, \tau_r) = \frac{\tau_r}{24} \cdot \alpha_r \cdot BMR \quad (7)$$

where α_r scales BMR to account for additional energy expenditure, such as digestion, as BMR is estimated for fasting animals (Table 1). In addition, BMR is estimated for thermo-neutral animals, so this parameter could also be used to account for thermoregulation in cold waters (Kshatriya and Blake, 1988). However, there is evidence that large marine mammals do not need to increase metabolic activity to maintain homeothermy in polar waters (Watts et al., 1993), so we do not account for thermoregulation separately here. The total cost a whale experiences during this period $C_{tot}(j, L, W, d, \tau_f, \tau_r)$ is then

$$C_{tot}(j, L, d, \tau_f, \tau_r) = C_m(d, W) + C_f(j, L, W, \tau_f) + C_r(W, \tau_r) \quad (8)$$

Estimating the daily food intake of large whales remains a challenge (see Reilly et al., 2004; Leaper and Lavigne, 2007 for reviews). Most approaches (e.g. Innes et al., 1986; Croll et al., 2006; Barlow et al., 2008) produce an estimate of the average daily intake, which is not suitable for our purposes. Presumably, whales consume as much as they can during an encounter to account for periods where no food is found, so we are interested in the maximum daily intake for a whale of a particular size. Baleen whales have a forestomach that is believed to be used for mechanical grinding and storage of large quantities of food. Food is initially stored in the forestomach and gradually passed to the digestive stomach chamber (Vikingsson, 1997). Therefore, the storage capacity of the forestomach and the rate at which it is emptied limit the maximum daily intake of baleen whales. Vikingsson (1997) relates forestomach capacity, $\psi(L)$ (in kg) to length in fin whales by

$$\psi(L) = 0.47L^{2.36} \quad (9)$$

The value of the exponent is similar to the exponent in the length-mass relationship for fin whales (2.53; estimated by Lockyer, 1976). Fin whales are leaner than blue whales for a given length, so it is likely that the estimate is higher for blue whales. We therefore adjust $\eta = 2.88$ to account for the difference between the length-weight exponents for blue and fin whales. The clearance rate of the forestomach is estimated to be between 3 and 6 h, and Vikingsson (1997) notes that shorter rates are more likely. We select a clearance rate, τ_c , of 4 h, but explore the effects of different

values on the results. The amount of time it takes a whale to fill up the forestomach depends on the swarm density, $\delta(j)$ (kg m⁻³) and the volume of water that can be engulfed in a single lunge, β (Goldbogen et al., 2009) and is

$$\beta(L) = 0.0011L^{3.56} \quad (10)$$

By itself, swarming is an antipredatory behavior (Hamilton, 1971), but individual krill within a swarm exhibit evasive behaviors in response to predators causing changes in swarm number, shape and density (Hamner and Hamner, 2000; Cox et al., 2009). However, the net effect that a particular predator (e.g. a batch-feeding whale compared to a penguin that targets individual krill) has on swarm density and shape, and how such changes affect capture success is unclear. We assume that as a whale feeds the density of the swarm remains the same but the total swarm biomass decreases by $\delta(j) \cdot \beta(L)$ (i.e. krill do not scatter or concentrate). Therefore, the time required to fill up the forestomach is

$$\tau_\psi(L) = \frac{\psi_L}{20 \cdot \delta(j) \cdot \beta(L)} \quad (11)$$

For a maximum foraging period of Λ , then the total number of times the forestomach can be filled, n_ψ is

$$n_\psi \begin{cases} \frac{\Lambda}{\tau_\psi} & \tau_\psi \geq \tau_c \\ \frac{\Lambda}{\tau_c} & \tau_\psi < \tau_c \end{cases} \quad (12)$$

If the whale is feeding on a low density patch such that the clearance rate equals or exceeds the intake rate, then it can feed continuously, and $\tau_f = \Lambda$. Alternatively, a whale feeding on a high density swarm will fill the forestomach faster than it can clear it, and will spend $\tau_f = n_\psi \tau_\psi$ hours actively foraging, and the remaining time will be spent resting (digesting). If krill contain ρ kJ kg⁻¹, the total energy gained G during a feeding bout is

$$G(j, L, \tau_f) = n_\psi \psi(L) A \rho \quad (13)$$

where $A (<1)$ is the assimilation efficiency (Table 1). Thus, a whale that expends $C_{tot}(j, L, W, d, \tau_f, \tau_r)$ while gaining $G(j, L, \tau_f)$ will have a change in blubber mass, ΔW_b of

$$\Delta W_b = \frac{G(j, L, \tau_f) - C_{tot}(j, L, W, \tau_f, \tau_r)}{u} \quad (14)$$

2.3. The behavioral model

Lockyer (1981) suggests that on average baleen whales spend approximately 120 days on the feeding ground. We therefore assume that the number of days spent on the feeding grounds, T , is 120 (entering in early December and leaving in late March; Lockyer, 1981; Brown and Lockyer, 1984). At the start of day $T = 120$, the whale leaves the feeding ground and migrates some distance D_B to the breeding grounds. The future survival and reproductive success depends on accumulated reserves. The amount of energy needed to survive the breeding period depends on a number of factors, including the distance to the breeding grounds, the amount of feeding that occurs during the overwinter period, and whether or not the whale is pregnant. In Appendix B we describe how we estimate the total energetic costs during the overwinter period, denoted $C_w(I)$, where I is an indicator function that is 1 if the whale is pregnant and 0 otherwise.

Predation may be an important source of mortality for baleen whales, especially for calves (Corkeron and Connor, 1999), but we found no estimates of the predation rate (or mortality rates from other sources), so we only consider mortality resulting from starvation. The future expected survival and reproductive success for a whale with reserves $X(T) = x$, denoted $\phi(x)$, is

$$\phi(x) \begin{cases} 0 & x < C_w(I) \\ 1 & x \geq C_w(I) \\ 1 + I & x \geq C_w(I) \end{cases} \quad (15)$$

Here, $x \geq C_w(I)$ accounts for cases when a pregnant female does not have enough energy to successfully nurse a calf, but can survive if the calf is abandoned. In such a case we assume the calf is abandoned.

We model the hourly foraging decisions of a whale, and an outline of all of the sequential decisions made can be found in Fig. 3. It is currently unknown how much feeding occurs at night. Although blue whales have been observed feeding at night (Doniol-Valcroze et al., 2011), other studies suggest little or no feeding at night (Calambokidis et al., 2007; Oleson et al., 2007). For simplicity we assume that blue whales only feed during daylight hours, and model the foraging decisions between dawn ($h = 1$) and dusk ($h = H(t)$). The length of daylight varies by day and latitude, and we compute the patch-specific day length (in hours) using the equation of Forsythe et al. (1995), assuming that $t = 1$ and $T = 120$ corresponds to December 1st and March 31st, respectively, and assuming a fixed latitude for each patch (63°S for the Antarctic Peninsula, 61° for the South Orkneys, and 55°S for South Georgia).

A whale that is located in cell i within patch c at the start of hour h on day t moves some distance d in search of krill. The distance traveled can either be within the current patch, d_c , or some distance d_c' to another patch. For simplicity, we assume that whales know the locations of the other patches, but not the locations of individual swarms within a patch. If the whale remains in the current patch, it travels d_c in search of a swarm. If the whale moves d_c and encounters a swarm of type j , with probability $p(j|i, c, d_c, t)$, it can reject the swarm and wait until the next time period to search for a different swarm. The next time period refers to the new hour, h' , and possibly new day, t' depending on when the whale started to search for krill and the time it took to travel d_c (methods for calculating t' and h' are shown in Table 2). If the whale feeds on the swarm, it will continue to feed for the remainder of the day or until the swarm is depleted, whichever comes first.

For days previous to T we define $F(x, l, i, c, h, t)$ as the maximum expected value of $\phi(X(T))$ for a whale in location i within patch c on hour h of day t with reserves $X(t) = x$ and length $L(t) = l$ (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000). We refer to $F(x, l, i, c, h, t)$ as the fitness of a whale, and we maximize it over the behavioral decisions

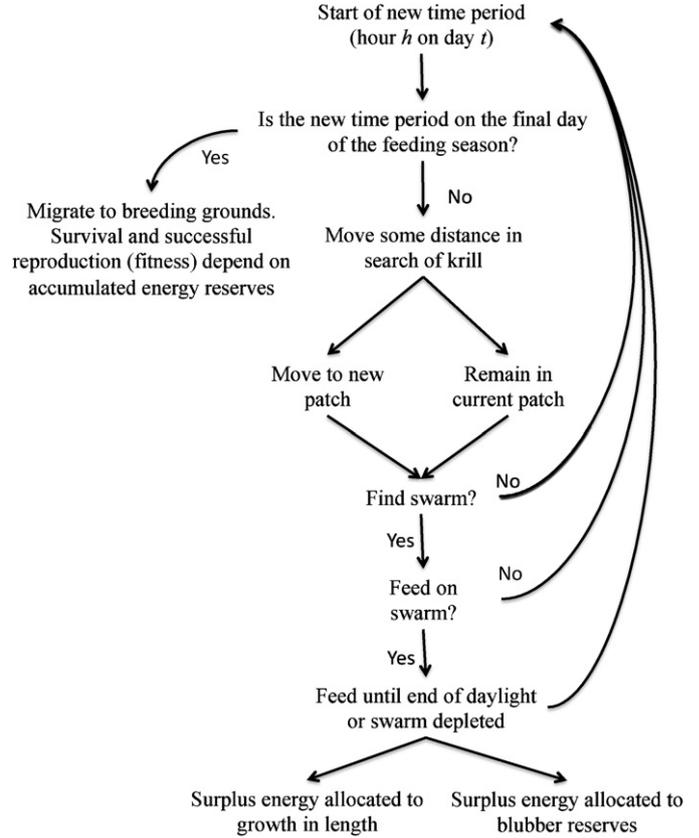


Fig. 3. Progression of decisions made in the model.

and physiological constraints detailed above. We let $V_c(x, l, i, c, d_c, h, t)$ denote the fitness value of staying in patch c and traveling d_c in search of food, and $V_c'(x, l, i, c, d_c', h, t)$ the fitness value of leaving the patch and traveling some distance d_c' to another patch. Then

$$F(x, l, i, c, h, t) = \max[V_c(x, l, i, c, d_c, h, t), V_c'(x, l, i, c, d_c', h, t)] \quad (16)$$

Regardless of the decision to remain in or leave a patch, a whale may encounter a swarm at the end of its journey, and it either feeds or ignores the swarm and searches for another one. We first consider the fitness value of accepting (V_A) and rejecting swarms (V_R) for a whale that remains in the current patch, then describe the modifications for a whale that leaves the patch. At the start of hour h on day t , a whale in patch c moves d_c km, and finds a swarm of type j with probability $p(j|i, c, d_c, t)$. If it rejects the swarm, then it will be in cell of type j with a new level of reserves x' , and a new time $h' (>h)$ and $t' (\geq t; \text{Table 2})$. The value of rejecting the patch is

$$V_R(x, l, i, c, d_c, h, t) = F(x', l, i, c, h', t') \quad (17)$$

where change in energy reserves, x' , is

$$x' = x - C_{tot}(j, L, W, d, \tau_r) \quad (18)$$

If the whale feeds on the patch, surplus energy will either be instantaneously allocated to energy reserves (and the whale will have new reserves of x''), or it will be allocated to growth in length (and the whale will have a new length of l'') where x'' is

$$x'' = x - C_{tot}(j, L, W, d, \tau_f, \tau_r) + G(j, L, \tau_f) \quad (19)$$

The change in mass is calculated using Eq (14), replacing the cost of blubber production (u) with the cost of producing non-blubber

Table 2

Example calculations of the new hour and day (h') and (t') and the daylight remaining (Δ) for a whale starting on hour h of day t that travels τ_m hours in search of krill. The calculations are only shown for travel times that result in the journey ending during daylight the next day ($t+1$). These equations can be easily extended to account for long distance journeys that take days to complete. The notation $[h + \tau_m]$ indicates the rounding up of $h + \tau_m$ to the nearest integer.

Description	Equations	h'	t'	Δ
Journey ends during daylight of current day	$h + \tau_m < H(t)$	$[h + \tau_m]$	t	$H(t) - h'$
Journey ends at night of current day	$H(t) \leq h + \tau_m < 24$	1	$t+1$	0
Journey ends during daylight of next day	$24 \leq h + \tau_m < H(t+1) + 24$	$[h + \tau_m - 24]$	$t+1$	$H(t+1) - h'$

tissue (w ; Table 1), and the new length is calculated by rearranging Eq. (1)

$$l'' = \left(\frac{W + \Delta w_b}{4.6} \right)^{1/3.05} \quad (20)$$

The value of accepting a swarm that is encountered is therefore

$$V_A(x, l, i, c, d_c, h, t) = \max[F(x', l, i, c, h', t'), F(x, l'', i, c, h', t')] \quad (21)$$

Given the values for accepting and rejecting patches, the value of staying in a patch is

$$V_C(x, l, i, c, d_c, h, t) = \max_{d_c} \sum_{j=1}^{j_{\max}} p(j|i, c, d_c, t) [V_A(x, l, i, c, d_c, h, t), V_R(x, l, i, c, d_c, h, t)] \quad (22)$$

Calculating the value of leaving the current patch is very similar to that of staying, except we maximize it over the different patches and not travel distance, and the probability of finding food is independent of the starting location and the distance traveled ($p(c' | j | t)$). In addition, calculating V_A and V_R is nearly identical to Eqs. (17) and (21), but now the whale is located in patch c' instead of c . Thus, the value of leaving the current patch is

$$V_{C'}(x, l, i, c, d_{c'}, h, t) = \max_{c'} \sum_{j=1}^{j_{\max}} p(c' | j | t) [V_A(x, l, i, c', d_{c'}, h, t), V_R(x, l, i, c', d_{c'}, h, t)] \quad (23)$$

The optimal behaviors (how far to travel, which patch to occupy, whether or not to accept an encountered swarm, and whether to allocate surplus energy to growth in length or reserves; Fig. 3) are determined by iterating backwards through time (from $t = T$ to $t = 0$) and solving for the suite of behaviors that maximize the fitness given for the different states of the whale. This process is called the backwards iteration.

2.4. Exploring the impacts of fishing

To explore the impacts of fishing-induced reductions in krill on whales we use the forward iteration; a Monte Carlo simulation in which individual whales are projected throughout the entire feeding season, with daily behaviors determined by the optimal behavior determined in the backwards iteration for the whale's current state (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000).

In the forward iteration, we model 900 pregnant whales (where individuals are indexed by k) with random starting

length ($L(k, t=0)$) that is uniformly distributed between 23 m and 30 m and energy reserves, $X(k, 0)$ are a truncated normal with mean μ_x and standard deviation σ_x and where the distribution for $X(k, 0)$ bounded by $X_{\min}(L)$ and $X_{\max}(L)$, with $\mu_x = 0.15 X_{\max}(L)$ and $\sigma_x = 0.25 \mu_x$ ($X_{\min}(L)$ and $X_{\max}(L)$ correspond to the energy reserves for a whale of length L with 2 and 35% of total mass comprised of blubber). We incorporate fishing by generating krill distributions and randomly removing swarms from the patches until the catch limit is met, then re-estimating the encounter probabilities. Because the catch limit set by CCAMLR is approximately 10% of the estimated biomass, we set the total catch limit in the model to 10% of the unfished biomass, and explore 4 fishing scenarios. In the first scenario, the catch is distributed evenly among the patches, while in the other scenarios (2–4) the entire catch is removed from a single patch (Table 3). These scenarios are run for different levels of krill patchiness (Appendix A) to explore the possibility of the fishery making krill swarms more clumped through the removal of entire swarms.

The fishing scenarios assume the whales apply fixed behaviors (based on the environmental conditions specified in the backwards iteration) to a changing environment. However, it is possible that whales may respond to a changing environment either through gradual changes in behavior across generations (evolution), or by individual changes in behavior throughout a feeding season (learning). We therefore explored an additional scenario in which the whales adapt to the changing environment. We accomplish this by solving the backwards iteration using the probabilities for the fishing scenarios shown in Table 3, such that the optimal behaviors are solved for an environment with less krill. This model run can be considered a “best case” in response to change, as the whales have evolved the optimal response to that particular landscape. The actual situation must be between these two limits of no learning and immediately learning about krill biomass.

For all scenarios explored, we run the forward simulation 1000 times, and tabulate the number of successful births and adult deaths that result in each iteration.

3. Results

The following results are for a clumped distribution of krill and for the parameter values in Table 1. A calculation of COT for an entire day of traveling at an assumed speed of 7.5 km h^{-1} using Eq. (3) reveals that the cost of traveling (which includes maintenance costs) is less than $3 \times \text{BMR}$. We therefore constrain α_r (the ratio of resting to basal metabolic costs) below the minimum values shown in Fig. 4.

Table 3

The initial and ending probabilities of finding a swarm in each patch ($p(c|0)$ and $p(c|T)$, respectively) under the different scenarios explored in the backwards and forward iterations (with and without fishing and climate change).

	Starting probability	End probability No fishing	End probability Fishing in all patches	End probability Fishing in one patch
Antarctic Peninsula	0.24	0.2	0.176	0.128
South Orkneys	0.22	0.18	0.158	0.114
South Georgia	0.2	0.16	0.14	0.1

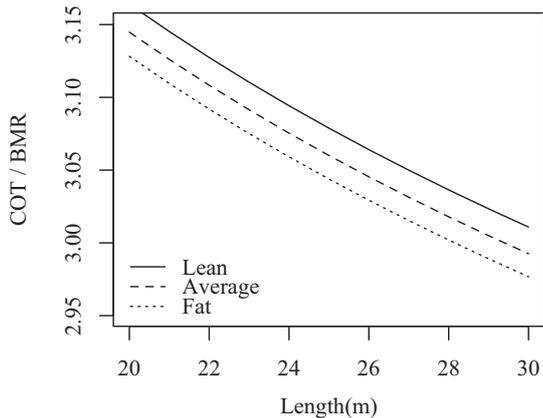


Fig. 4. The ratio of daily COT to BMR in relations to length for whales with different levels of energy reserves (and therefore mass). Daily COT is calculated assuming whales travel at a speed of 7 km h⁻¹.

3.1. Optimal behaviors

The behavioral decisions affect the energy reserves of a whale, which determines the survival and reproductive success of the whale during the overwinter period. The level of reserves needed to survive and reproduce depend on how far the whale must migrate to the breeding grounds, and also how much food is ingested there. Both factors have a large effect on the critical level of reserves needed, as increasing the migration distance and decreasing the overwinter food intake result in more reserves needed when exiting the feeding grounds to survive and reproduce (Fig. 5). For the

calculation of critical energy reserves, we relaxed the assumption that whales mature at a length of 23 m, and explored a wider range of reserve levels to determine if it is even possible for whales smaller than this threshold to have enough energy to survive the overwinter period. Because mass increases with length to the power 3.05 (Lockyer, 1976), smaller whales have much less mass than larger whales. Therefore, the energy necessary to survive or reproduce takes up a much greater proportion of overall mass in smaller whales. The reserve threshold varies with the migration distance and overwinter food intake, but whales below the maturity size require between 35 and 45% of their total body mass to consist of blubber. Such amounts are beyond those reported by Lockyer (1976) and may be too taxing physiologically for whales. For a 23 m whale, the range is between approximately 28 and 40%. Values at the lower end of this range are consistent with observed levels of blubber, so the results suggest that the maturity threshold makes sense for females in terms of plausible values of energy storage.

Whether or not a swarm of particular density is accepted or rejected depends on a number of factors. Over the range of densities in our model (0.075–0.75 kg m⁻³), the mean rejection density threshold is 0.11 kg m⁻³. In Fig. 6 we show the mean rejection thresholds in relation to day (*t*), hour (*h*), and the proportion of body mass comprised of blubber. We predict:

- (a) The rejection threshold density is dome-shaped with respect to day within the feeding season, with higher density swarms rejected more often in the middle of the season.
- (b) Within a particular day, whales are more likely to feed on lower swarm densities later in the day, as there is less time to search for new swarms.

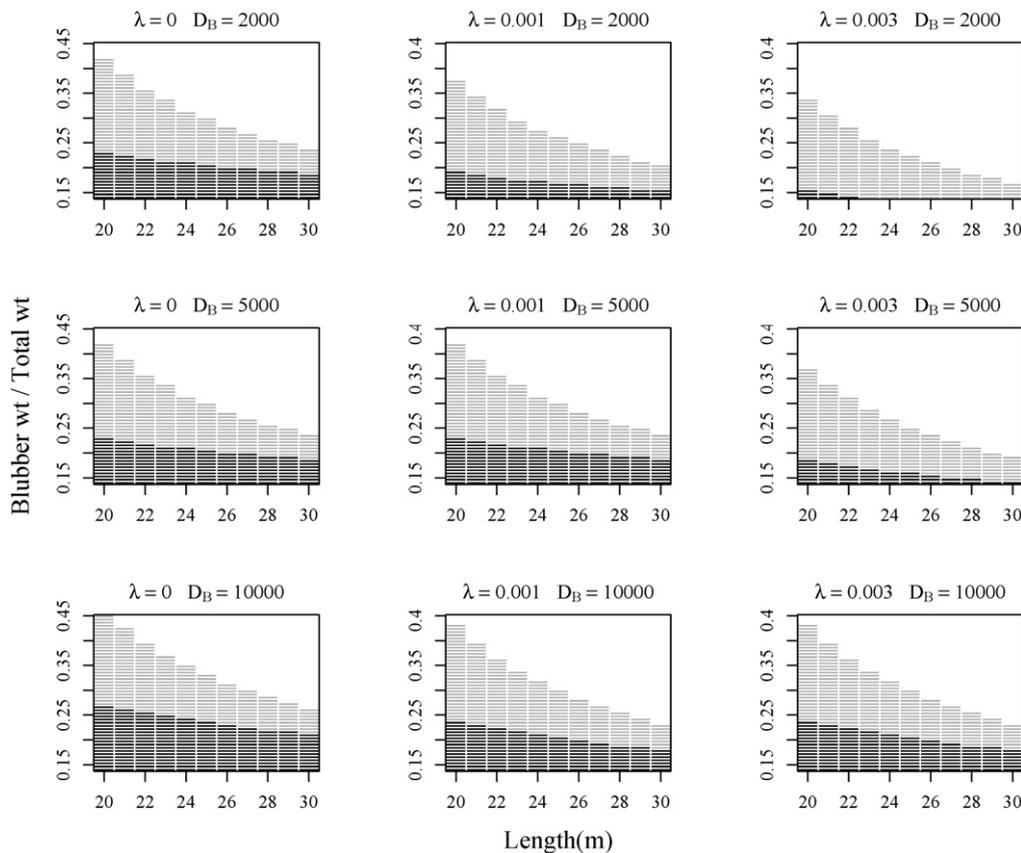


Fig. 5. Surface plots showing if whales of a certain length (m) and energy reserves (the proportion of body mass comprised of blubber) have enough energy to successfully reproduce (white region), survive (gray), or if they die during the overwinter period (black). The plots are created for three different distances to the breeding grounds ($D_B = 2000, 5000$ and $10,000$ km) and daily food intake on the breeding grounds ($\lambda = 0, 0.001, 0.003$).

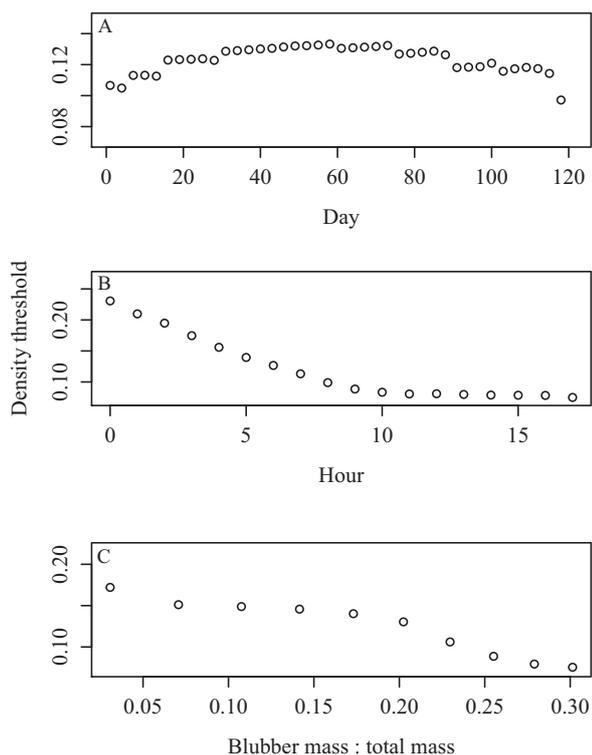


Fig. 6. Mean swarm rejection threshold density (kg m^{-3}) as a function of (A) day (t), (B) hour within a day (h), and (C) the proportion of body mass made of blubber. For a given state variable, the mean threshold density is calculated as the average over all other state variables.

(c) The threshold density decreases with respect to energy reserves, as lean whales must gain more energy throughout the feeding season and therefore select for higher density swarms.

The surplus energy from feeding on a swarm may be either allocated to growth in length or to increase existing reserves. Under the current model, there is no value in growing in length under any condition. The level of energy reserves determines fitness, so whales must accrue sufficient energy to survive and reproduce. Because the time period of the model is only 1 year, there is no incentive (future fitness) for immature whales to reach the maturity size of 23 m. To explore when a whale is predicted to grow in length, we modified the model to allow whales smaller than 23 m to become pregnant, but required that successful reproduction could only occur at lengths ≥ 23 m. Under this modification, a whale smaller than the maturity threshold is predicted to grow earlier in the feeding season, but only if it has sufficient reserves. The transition to switch from growing in length to building energy reserves is knife-edged, with the transition occurring later in the feeding season for larger whales (in length) and for higher levels of energy reserves (Fig. 7). For a given length and energy reserves, there reaches a point in the season where the whale must begin to fatten. Given that reserve allocation towards growth in length in the model is all or nothing (Eq. (21)), it makes sense that the transition to grow in length is knife-edged.

Because swarms are clumped, if a whale finds a swarm, it has a high probability of finding another swarm in an adjacent cell. Therefore, regardless of the patch, if a whale has found a swarm and is in search of another (due to depleting the swarm or rejecting it), the optimal behavior is to remain in the patch and move to an adjacent cell ($d_c = 1$). When whales are not in a cell that contains a swarm, they will either move some distance within the patch, or move to the new patch. In Fig. 8 we show the mean optimal distance moved

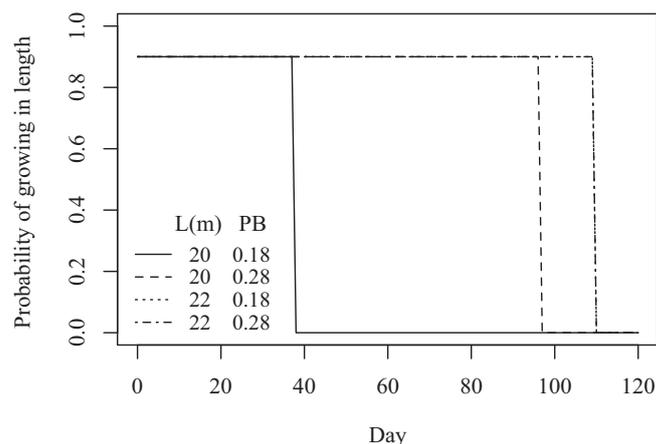


Fig. 7. The decision to grow in length in relation to length and the proportion of body mass made of blubber (denoted PB). The probability of growing in length is calculated as the proportion of instances where the optimal allocation strategy is to grow in length.

(in Fig. 8A–C the distance is averaged over movements within and between patches whereas in Fig. 8D–F the distance is averaged over only within patch movements) as a function of day, length, and energy reserves. A similar dome-shaped pattern appears for day, although the location of the peak is different (Fig. 8A and D). We predict that smaller whales are more likely to make the long distance movements between patches (Fig. 8B), but within a patch, we predict no difference between lengths (Fig. 8E). Whales with extreme levels of energy reserves (both low and high) are more likely to make long distance movements (Fig. 8C). Within a patch, however, we predict that fat whales make shorter trips (Fig. 8F).

3.2. Daily food intake and energy expenditure

In the forward iteration we calculate the average daily food intake, energy expenditure and distance traveled in search of food. Energy expenditure and intake quantities are widely used in models attempting to estimate annual food intake. The metrics commonly used are the average daily food intake as a percentage of mass, and the average daily metabolic rate as a multiple of BMR (e.g. Reilly et al., 2004; Leaper and Lavigne, 2007). In the model, whales expend between 2.07 and 3.1 times the daily estimate of BMR (with a mean value of 2.29). Average daily consumption is 3.3% of total body mass, with a range between 2.2 and 4.7%. These values are daily averages, and include days when no feeding occurs. Including only days when feeding occurs in the calculation results in the daily intake of krill ranging between 1 and 6.6% of total body mass. The relationship between food intake and swarm density is a saturating function with swarm density (Fig. 9). This relationship is a Type II functional response (Holling, 1959). Under the base model run, the daily food intake is such that whales increase in mass by 20.6 mt on average during the feeding season (Fig. 10), and this increase represents a 26.2% increase in initial mass (range 5–48%).

3.3. Impacts of fishing

To explore the impacts of fishing on whales, we compare the number of successful births that occur per 900 pregnant whales and the number of adult deaths. As before, if the whale does not have enough reserves to nurse a calf, we assume the calf is abandoned; the mother may survive (if she has enough reserves) but the calf will not. Under the scenario with no fishing (and for the parameter values in Table 1), there is a median success rate of 0.9 births per pregnant whale (95% CI 0.88–0.92). All of the fish-

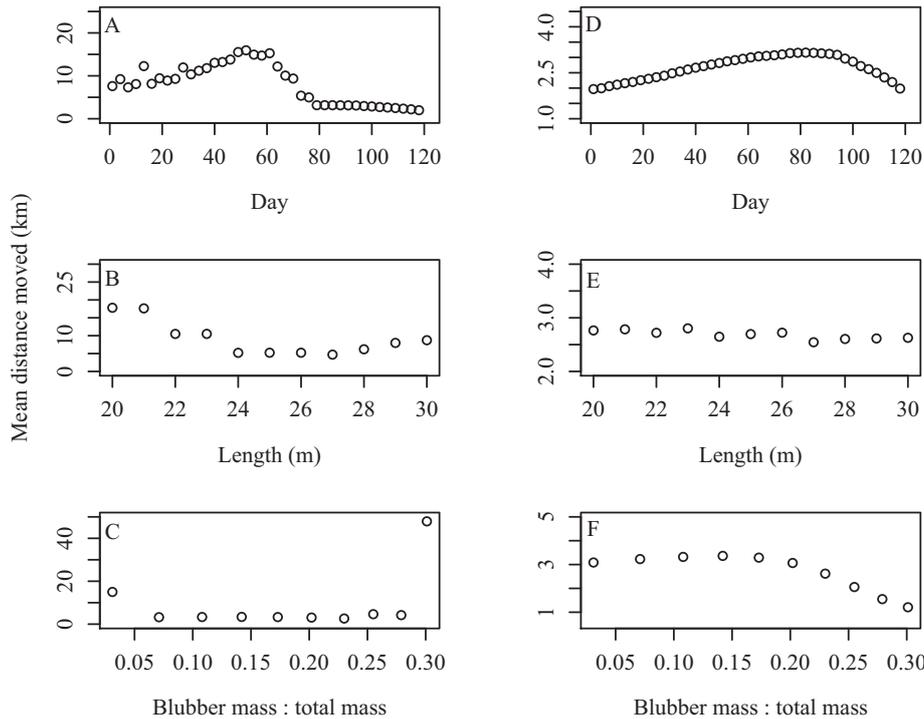


Fig. 8. The mean optimal distance moved (d^*) as a function of day (t), length (L), and the proportion of body mass made of blubber. The mean is calculated across all movements (both within a patch and between A and C) and only for movements within a patch (D–F).

ing scenarios explored had a significant, negative impact on birth rate (non-overlapping confidence intervals; Table 4). However, the negative impact was due to the reduction in krill biomass alone, as increasing the patchiness of krill swarms did not have an additional effect on birth rates. The smallest decline in birth rates occurs when fishing is evenly dispersed across patches, while the largest declines result from the entire catch limit being removed from either the Antarctic Peninsula or South Georgia (Table 4). Fishing only in these patches has a larger effect on birth rates because more whales occupy them throughout the feeding season. In each simulation the number of whales in each patch starts out the same, but there is an initial migration of whales to the Antarctic Peninsula, followed by a migration to South Georgia (Fig. 11). Therefore, fishing in either one of these patches causes a larger decline in birth

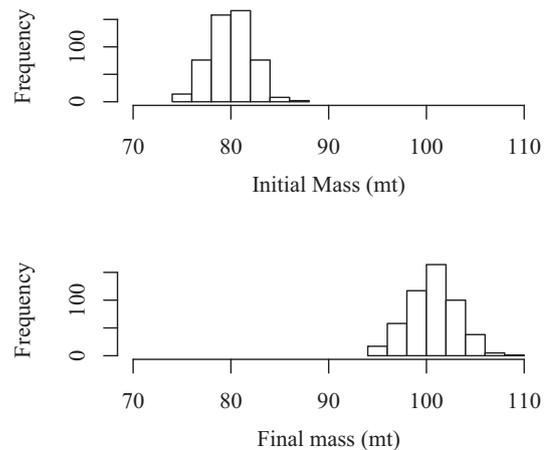


Fig. 10. The mean initial and final mass of whales (mt) during the feeding season calculated in the forward simulations.

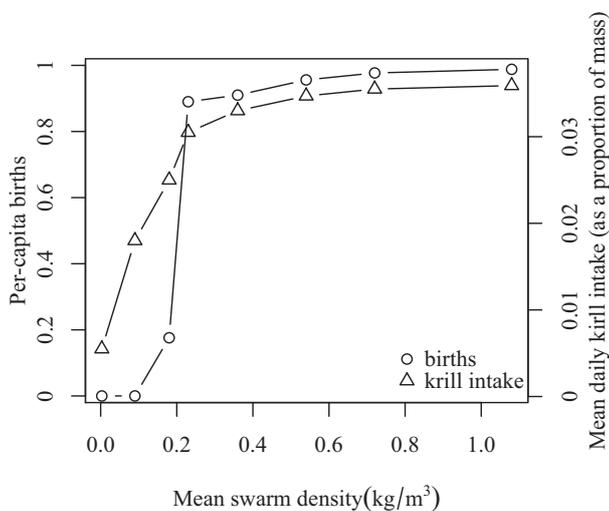


Fig. 9. The average daily consumption of krill (as a proportion of body mass) and per-capita births with respect to the mean density of krill available.

Table 4
Impacts of fishing on whale birth and death rates under different scenarios incorporating fishing. The upper and lower values correspond to the bounds of the 95% confidence intervals. AP refers to the Antarctic Peninsula, SO refers to the South Orkneys, and SG refers to South Georgia. In the adapted scenario, we solved the backwards iteration with fishing only in AP as fishing in this patch produced the largest effect on birth rates.

Fishing scenario	Birth rate			Death rate		
	Lower	Median	Upper	Lower	Median	Upper
No fishing	0.88	0.9	0.92	0	0	0
Fishing in all	0.82	0.85	0.87	0	0	0
Fishing in AP only	0.75	0.78	0.792	0	0	0.004
Fishing in SO only	0.82	0.83	0.85	0	0	0
Fishing in SG only	0.77	0.8	0.81	0	0	0.003
Adapted	0.86	0.88	0.9	0	0	0

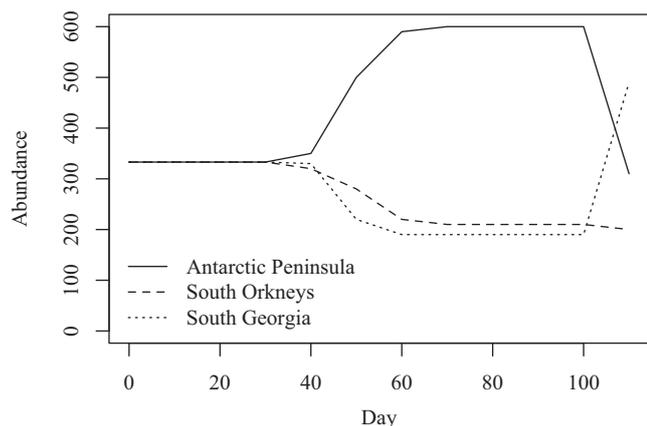


Fig. 11. Abundance of whales in each patch throughout the feeding season, averaged across all simulations in the forward iteration.

Table 5

Sensitivity in the model estimate of birth rate (under the base case without fishing or climate) to change in parameter values. All parameters were changed in the direction that results in a decline in birth rates. Changes marked by a * are significant (95% confidence intervals for birth rates do not overlap).

Parameter	Change in parameter (%)	Change in birth rate (%)
Mean swarm density ($\delta(j)$)	-50	-80*
Initial probability of finding a swarm ($p(c,j 0)$)	-50	-100*
Patchiness parameter (z)	-50	-3.7
Overwinter food intake (λ)	-50	-13*
Distance to breeding grounds (D_B)	+50	-10*
Initial energy reserves ($X(k,0)$)	-50	-47*
Feeding cost multiplier (α_f)	+50	-1
Resting cost multiplier (α_r)	+50	-65*
Hours to clear the forestomach (τ_c)	+50	-91*
Assimilation efficiency (A)	-25	-82*

rates than fishing in the South Orkneys. When whales are allowed to adapt to fishing-induced reductions in krill, birth rates do not change significantly from the base run (Table 4).

3.4. Sensitivity analysis

The model contains a large number of parameters, and many of the values used are rough approximations. We therefore explore the sensitivity of model results to changes in parameter values. In Fig. 9, we show the per-capita birth rate in relation to the mean density of swarms. This relationship is sigmoid-shaped, and is a Type III functional response (Holling, 1959). In Table 5, we show the % decrease in birth rate that results from changing the parameters. The parameters that have the largest influence on birth rate are the mean swarm density (δ), the initial encounter probability ($p(c|t=0)$), resting metabolic costs (α_r), forestomach clearance rate (τ_c), the energy reserves upon entering the feeding grounds ($X(k,0)$) and the assimilation efficiency (A). The distance to the breeding grounds (D_B) and the overwinter food intake (λ) also had small but significant effects on birth rates, while the parameter controlling the patchiness of krill swarms (z) had a negligible effect on birth rates (Table 5).

4. Discussion

We have developed a framework for exploring the effects of reductions in krill biomass and changes in swarm patchiness on blue whale foraging and reproductive success. Although the model is parameterized for blue whales, our novel energetics model could

be applied to other baleen whales. By combining the energetics model with state dependent behavioral theory, we are able to explore the impacts of an expanding krill fishery in the Southern Ocean on blue whales. We predict that an expanding fishery, may have a small, negative impact on the population through decreased birth rates, and that spreading the catch limit throughout the range of krill can reduce these effects. These effects are predicted to result from declining krill biomass only, and not from fishery-induced changes in the patchiness of krill swarms.

The relationships between krill density and predator consumption and reproductive success are important inputs for models used in ecosystem-based management to determine the impacts of fishing on krill predators in the Southern Ocean (Hill et al., 2007). Our model predicts nonlinear relationships, with Types II and III functional responses between krill density and food intake, and reproductive success, respectively (Fig. 9). However, in our model we only included very dense swarms, as these are what are relevant blue whales (Appendix A), such that mean swarm densities shown in Fig. 9 cannot be used directly in ecosystem models, which typically use a spatial average of krill biomass (calculated using swarms of all densities). Our model could be modified to include a broader range of swarm densities to better inform the management models (we discuss potential model modifications below). Nevertheless, knowledge of the relative shape of these functional responses can better inform management models. Larger declines in krill biomass, potentially from a loss of sea ice, are predicted to have much larger impacts on the population vital rates, and thus the recovery, of blue whales.

The relationship between krill recruitment and sea ice has only been identified for one region in the Southern Ocean (Siegel and Loeb, 1995; Quetin and Ross, 2003; Wiedenmann et al., 2009), and trends in ice extent are not consistent throughout the Southern Ocean (Zwally et al., 2002; Stammerjohn et al., 2008). Thus decreased krill recruitment in one area could be mitigated by increases in other areas, so whales could respond to poor local conditions by making long migrations to a new area. In our model run where whales are able to adapt to the decreases in krill abundance in a particular patch, the net effect on population vital rates was negligible. Therefore if whales change their foraging behaviors in response to changes in local environmental conditions, they may be able to reduce the impacts of declines in krill abundance. In the California Current there is some evidence to suggest that blue whales exploit different feeding areas depending on the large-scale abundance of their prey, since whales tend to concentrate in a few productive areas when coast-wide prey abundance is low (during El Nino years, for example; Benson et al., 2002; Bailey et al., 2010). Adaptive foraging behavior, coupled with the ability to migrate great distances within a single feeding season (Bailey et al., 2010) suggests that blue whales may be better able to cope with a changing environment than species with a more restricted foraging area.

The Southern Ocean is considered a high-nutrient, low chlorophyll region, in that phytoplankton do not utilize all the available macronutrients (nitrate and phosphate). Iron, a micronutrient, is limiting in these waters, such that increased supply of iron into surface waters results in increased primary productivity (Boyd et al., 2007). Krill contain large amounts of iron in their tissue, and Nicol et al. (2010) estimate that krill may contain 24% of the total iron in the surface Southern Ocean. Baleen whales may be important for recycling this iron, since their feces, which is diffuse and typically remains in surface waters, is high in iron. Nicol et al. (2010) hypothesize that a positive feedback loop exists whereby a high abundance of baleen whales in the Southern Ocean results in increased productivity of the ocean as a whole. If such a positive feedback loop exists, even small changes in whale birth and death rates could have a larger effect on the entire Southern Ocean ecosystem.

The large number of parameters and assumptions in the model makes it essential to compare model output with observations to determine the fidelity of the parameters and assumptions. On the feeding grounds, blue whales in the model are predicted to consume 3.3% of their total mass on average, although this value includes days spent not eating. In reviews of studies estimating cetacean consumption rates, both Reilly et al. (2004) and Leaper and Lavigne (2007) indicate that daily average consumption rates above 3.5% of body mass are likely too high, and Reilly et al. (2004) suggest that between 2 and 3% of total mass is a reasonable estimate. When food is encountered, whales in the model consume between 1 and 6.6% of their mass daily. This range is consistent with the range reported by Tamura and Konishi (2006) (between 1.5 and 7%), who examined the stomach contents of thousands of minke whales. The level of feeding combined with the energetic costs in the model result in a mass increase of approximately 26% during the feeding season (range between 5 and 48%). The upper values in this range are very close to the increase of 49% reported by Lockyer (1981).

Determining plausible food intake rates can be accomplished through refining estimates of metabolic expenditures. It is commonly assumed that the daily metabolic expenditure in cetaceans is some multiple of *BMR* (Eq. (2)). Leaper and Lavigne (2007) note that values between 2 and 5 are widely used in modeling approaches, but that values <1 are possible and those >4 are unlikely. The median model estimate of 2.29 is within the range reported by Leaper and Lavigne (2007), but largely depends on the estimate of resting metabolic rate (determined by the parameter α_r , set to 2 in the model). Increasing the cost of resting above $2 \times BMR$ results in a dramatic drop in birth rates (α_r increased by 50%; Table 4), and would require similar increases in food intake (discussed below). The fact that a day spent traveling is $\sim 3 \times BMR$ based on the calculation using *COT* suggests that daily expenditures greater than $3 \times BMR$ are unlikely. Our results do not provide any insight on the lower bound of the range of daily energy expenditure.

On average, blue whales in our model are predicted to reject swarms below 0.11 kg m^{-3} , very similar to the value of 0.1 kg m^{-3} calculated by Goldbogen et al. (2011) using a different approach. In the field, however, it is difficult to estimate the threshold swarm density. Friedlaender et al. (2009) found a difference in the mean krill densities in areas with and without minke and humpbacks in the Southern Ocean. The mean spatial density in areas without whales was between $1/3$ and $1/2$ of the density in areas with whale present. Our model-predicted thresholds are higher than the value reported by Friedlaender et al. (2009), but their densities are spatial averages (including areas without krill), and are not necessarily representative of the densities of individuals swarms being consumed.

We predict that a whale will grow in length early in the season, but only if it has sufficient energy reserves (Fig. 7). Therefore, lean whales that enter the feeding ground are predicted to first allocate surplus energy towards blubber reserves, then towards growth. Lockyer (1981) notes that the ratio of blubber thickness to length in many species often decreases between December and February, suggesting that this decline may be result of late-arriving whales to the feeding grounds. It is possible though that the decline in this ratio is due to an increase in length, and not from a surge in the number of lean whales on the feeding ground.

Leaper and Lavigne (2007) point out that many of the parameter values used in cetacean energetics models are often “based on little more than guess work.” Thus model sensitivity analysis as we have done here can be used as a guide to focus future research on parameters that have the largest effect on model results. For example, the amount of food that is consumed during the overwinter period is incredibly difficult to estimate, but it does not have a large impact

on model results, suggesting that determining this quantity is not as important as other model inputs (Table 5). As already noted, resolving the debate over basal metabolic costs is very important. The assimilation efficiency and forestomach clearance rate also have proportionally large effects on model results, and such quantities could potentially be refined through studies on captive animals.

The existing model framework can be modified in a variety of ways. For example, the model could be expanded to explore the effects of krill reductions over a broader range of whale lengths and over multiple years. Doing so would likely result in more pessimistic predictions on survival and birth rates, as smaller whales need to allocate much of the surplus energy consumed towards growth in length during the feeding season, potentially reducing total energy stores needed for the overwinter period.

The krill spatial model could also be modified to account for different swarm characteristics and distributions. For example, a broader range of swarm sizes and densities might be used, or swarms could be distributed in relation to environmental features known to influence krill aggregation (e.g. distance from land masses or the ice edge). While a wide range of krill landscapes could be implemented into the current framework, it likely requires adding more state variables into the behavioral model (e.g. the optimal decision would also depend on where the whale is in relation to such features). Increasing the environmental complexity in this model (and in all models) requires weighing the trade-offs between the information gained and computational power required. Experiences in SDP modeling suggest that increasing environmental complexity often affects only the quantitative and not the qualitative results (Mangel and Clark, 1988; Clark and Mangel, 2000).

This model framework could also be used to explore different questions regarding observed whale behaviors. For example, a flexible final time period (*T*) could allow for the testing of observed migration patterns in some species, as Dawbin (1966) found an orderly progression based on sex and reproductive status in humpbacks. In addition, one could test the hypothesis of Corkeron and Connor (1999), who suggest that baleen whales migrate to reduce calf predation in polar waters. By adding calf-mortality in the model and not allowing whales to migrate, one could quantify the level of calf mortality that results in a fitness advantage to the long-distance migration.

In summary, we predict that the recovery of blue whales will be negatively impacted by future reductions in krill biomass resulting from an expanding fishery, although adaptive foraging behavior may be able to mitigate against such reductions. In addition, catch limit allocation strategies that allocate catches among areas in proportion to biomass as preferable to concentrating catches in a single area, as such strategies are predicted to have a smaller effect on blue whales. Our model shows a nonlinear relationship between krill abundance and blue whale foraging and reproductive success, suggesting that larger reductions in krill biomass (potentially from a loss of sea ice) will have a more negative impact on the recovery of blue whales.

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Appendix A. The krill spatial model

There is a considerable amount of information on the factors affecting the spatial distribution of krill swarms in the Southern Ocean. In addition, swarm characteristics (i.e. density, area, size composition of krill) are also known to vary within particular areas. For example, Lascara et al. (1999) found across-shelf gradients in krill abundance and size composition off the west Antarctic Peninsula, with more dense swarms with smaller individuals being found more inshore. Similarly, in the Scotia Sea Klevjer et al. (2010) found swarms with greater biomass closer to shore, but there were a greater number of swarms in the more offshore areas. Krill have also been found to aggregate in dense, narrow bands just south of the ice edge during the summer months (Brierley et al., 2002). Within a particular area the density and size of individual swarms may also vary on short temporal scales, as Tarling et al. (2009) found different swarm characteristics depending on the amount of light, surface fluorescence, and also the size and maturity of krill within the swarms.

While it is possible to model such complex dynamics within this framework, doing so greatly increases the computation time of the model, and such complexity is beyond the scope of this paper. We therefore create a simplified landscape of krill swarms distributed between patches three patches, indexed by c . These patches are located near the Antarctic Peninsula, the South Orkney Islands, and South Georgia (Fig. 1). The patches last for the duration of the feeding season, and the same size: a square grid $100 \text{ km} \times 100 \text{ km}$. Patch size is based on the foraging radius reported for blue whales in the California Current (Fig. 6 of Bailey et al., 2010). Each patch therefore has $N = 10,000$ 1 km^2 cells.

Tarling et al. (2009) provide information on swarm characteristics in the South Atlantic sector of the Southern Ocean, and we use some of this information to create a distribution of swarms within each patch. We only consider the information on the densest category of swarms observed by Tarling et al. (2009), as Goldbogen et al. (2011) estimate that only very dense swarms ($>0.1 \text{ kg m}^{-3}$) are profitable for blue whales. Based on the frequency of swarms observed in the regions we are modeling, we assume that the time-dependent probability of finding a swarm, denoted $p(c|t)$ is highest around the Antarctic Peninsula and lowest around South Georgia. The probability that a swarm in each patch will have the j th density is denoted $p(c,j|t)$. Swarms around South Georgia contain larger krill, while swarms around the Antarctic Peninsula contain smaller krill (Tarling et al., 2009), such that we assume higher density swarms are more common around South Georgia and less common around the Antarctic Peninsula (Fig. 2).

Swarms in our model have the same volume, v , and differ in density, $\delta(j)$ (kg m^{-3}) only. The mean densities reported by Tarling et al. (2009) and Klevjer et al. (2010) are well below the profitable density reported by Goldbogen et al. (2011). We therefore only consider high-density swarms, as these are the swarms that are likely relevant to blue whales (Fig. 2).

The arrangement of krill swarms within a patch is determined by a spatial structure parameter z which determines how spatially clumped swarms are (modified from Travis and Palmer, 2005). For the c th patch, the placement of swarms within a patch is done as follows.

- (1) Pick a random location within the grid, and place the lowest density swarm ($j=1$) in it.
- (2) Draw a random variable $z^* \sim \text{Unif}[0,1]$.
- (3) If $z^* \leq z$, place the next swarm ($j=1$) in an adjacent cell, go to step 2.
- (4) If $z^* > z$, go to step 1.

- (5) Continue filling cells of type $j=1$ by repeating 1–4 until $p(c,1|t=0)N$ cells are filled, then do the same (starting at step 2) for the remaining types of swarm ($j=2,3, \dots, j_{\max}$).

Note that this algorithm does not fill all cells with swarms. If the overall probability of finding a swarm $p(c|t)$ is 0.2, there will be $0.8N$ empty cells. In the placement of swarms, if all adjacent cells are filled during step 3, the swarm is placed 2 cells away (i.e. adjacent to the filled cells).

For a given patch, we generate thousands of krill arrangements (for a fixed z and $p(c,j|t)$) and estimate the probability of finding a swarm of type j , given the whale is currently in a cell that contained a swarm of type i in patch c by moving d km away, $p(j|i,c,d,t)$. We set $j_{\max} = 10$ for each patch, with $\delta(j) = 1, 2, \dots, 10$ corresponding to densities of $0.075, 0.15, \dots, 0.75 \text{ kg m}^{-3}$.

The above algorithm ignores all environmental characteristics that might affect the distribution of krill within a patch. With $z=0$, krill are placed completely at random within the patch. However, as z is increased swarms are more likely to be found close together. The algorithm allocates swarms in steps by their density, such that swarms of similar densities are more likely to be found in close proximity to one another. As a result, even though we ignore the environmental factors affecting swarm distribution and characteristics, running the model with a high z can at least mimic some of the broad-scale patterns observed (i.e. that swarms of similar characteristics are often found close to one another in similar strata).

For the base model run we use $z=0.9$, but also the sensitivity of results to this parameter. When exploring the effect increased patchiness (resulting from fishing), we set $z=0.95$.

Appendix B. The energetic costs of the overwinter period

To calculate the total amount of energy needed to survive the overwinter period, we model the energetic costs during the overwinter period using a daily timestep (denoted t_w), accounting for changes in mass that occur as the whale depletes its reserves during this period of reduced feeding. The total costs expended during the overwinter period C_w depends on numerous factors, including the whale's size, reproductive status, distance to the breeding grounds, D_B , and the amount of food consumed during the overwinter period. The cost of reproducing, C_R , is a function of the costs of calf development, C_K and lactation, C_L . Estimates of C_K and C_L are taken from Lockyer (1981; Table 1). For simplicity, if the whale is pregnant we assume the whale gives birth as soon as it reaches the breeding grounds. The number of days to reach the breeding grounds, t_m is

$$t_m = \frac{D_B}{24s_m} \quad (\text{B1})$$

where s_m is the migration speed to the breeding grounds (Table 1). The daily cost of migrating north to the breeding grounds is

$$C_N(t_w) = COT \cdot W(t_w) \cdot D_B \cdot 24 + I \frac{C_K}{t_m} \quad (\text{B2})$$

where I is an indicator function that takes a value of 1 if the whale is pregnant, and 0 otherwise, accounting for the additional metabolic costs of pregnancy. If a whale spends T days on the feeding grounds, then the number of days spent on the breeding grounds, $t_B = 365 - (T + 2t_m)$, and during this period, activity is likely greatly reduced. The daily cost on the breeding grounds, $C_B(t_w)$ is

$$C_g(t_w) = \alpha_r \cdot BMR + I \frac{C_L}{t_B} \quad (\text{B3})$$

The daily cost of migrating south to the feeding grounds, $C_s(t_w)$, is

$$C_s(t_w) = COT \cdot W(t_w) \cdot \frac{D_B}{t_m} + I \frac{C_L}{t_m} \quad (\text{B4})$$

While on the breeding grounds, whales may do some feeding, but the amount consumed is likely far less than the amount consumed on the feeding grounds. We assume that on average, whales consume some fraction, λ of \bar{W} on the breeding grounds. The total cost of the overwinter period, $C_w(I)$, is therefore

$$C_w(I) = \sum_{t_w=T}^{T+t_m} C_N(t_w) + \sum_{t_w=T+t_m+1}^{t_w=T+t_m+t_B} (C_B(t_w) - \lambda \cdot \bar{W}(L) \cdot \rho \cdot A) + \sum_{t_w=T+t_m+t_B}^{365-T} C_S(t_w) \quad (B5)$$

For a pregnant whale, this equation accounts for the nursing costs until the mother and calf re-enter the feeding grounds. Situations may arise where the mother does not have enough energy to produce sufficient milk for the duration of the overwinter period. Under such circumstances, we assume following the birth of the calf, the mother abandons the calf, and denote this situation with l' . The total cost in this situation, $C_w(l')$ is calculated using Eq. (B5), with $C_N(t_w)$ calculated with $l = 1$ (Eq. (B2)) and $C_B(t_w)$ and $C_S(t_w)$ are calculated with $l = 0$ (Eqs. (B3) and (B4)).

References

- Alonzo, S.H., Mangel, M., 2001. Survival strategies and growth of krill: avoiding predators in space and time. *Mar. Ecol. Prog. Ser.* 209, 203–217.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.H., 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.* 362, 1–23.
- Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bogard, S.J., Costa, D.P., 2010. Behavioral estimation of blue whale movements from state-space model analysis of satellite track movements. *Endang. Species Res.* 10, 93–106.
- Bannister, J.L., 1994. Continued increase in humpback whales off Western Australia. *Rep. Int. Whal. Commn.* 44, 309–310.
- Ballance, L., Pitman, R.L., Hewitt, R.P., Siniff, D.B., Trivelpiece, W.Z., Clapham, P.J., Brownell Jr., R.L., 2006. The removal of large whales from the Southern Ocean: evidence for long-term ecosystem effect? In: Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell Jr., R.L. (Eds.), *Whales Whaling Ocean Ecosystems*. University of California Press.
- Benson, S.R., Croll, D.A., Marinovic, B.B., Chavez, F.P., Harvey, J.T., 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. *Prog. Oceanogr.* 54, 279–291.
- Barlow, J., Kahru, M., Mitchell, B.G., 2008. Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem. *Mar. Ecol. Prog. Ser.* 371, 285–295.
- Boyd, P.W., Jickells, T., Law, C.S., Blain, S., Boyle, E.A., Buesseler, K.O., Coale, K.H., Cullen, J.J., de Baar, H.J.W., Follows, M., Harvey, M., Lancelot, C., Levasseur, M., Owens, N.P.J., Pollard, R., Rivkin, R.B., Sarmiento, J., Schoemann, V., Smetacek, V., Takeda, S., Tsuda, A., Turner, S., Watson, A.J., 2007. Mesoscale iron enrichment experiments 1993–2005: synthesis and future directions. *Science* 315, 612–617.
- Branch, T.A., Matsuoka, K., Miyashita, T., 2004. Evidence for increases in Antarctic blue whales based on Bayesian Modelling. *Mar. Mammal Sci.* 20, 726–754.
- Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Galletti Vernazzani, B., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.-N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsari, P., Brownell Jr., R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilan-gakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughn, B., McCauley, R.D., McKay, S., Norris, T.F., Oman whale and dolphin research group, Rankin, S., Samarán, F., Thiele, D., Van Waerebeek, K., Warneke, R.M., 2007. Past and present distribution, densities and movements of blue whale *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. *Mammal Rev.* 37, 116–175.
- Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G., Griffiths, G., 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. *Science* 295, 1890–1892.
- Brodie, P.F., 1975. Cetacean energetics, an overview of intraspecific size variation. *Ecology* 56, 152–161.
- Brown, S.G., Lockyer, C.H., 1984. Whales. In: Laws, R.M. (Ed.), *Antarctic Ecology*, vol. 2. Academic Press, London.
- Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshal, G., Oleson, E.M., Gendron, D., Robertson, K., 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (CRITTERCAM). *Mar. Technol. Soc. J.* 41, 19–29.
- Clark, C.W., Mangel, M., 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, Oxford.
- Constable, A., 2004. Managing fisheries effects on marine food webs in Antarctica: trade-offs among harvest strategies, monitoring, and assessment in achieving conservation objectives. *B. Mar. Sci.* 74, 583–605.
- Corker, P.J., Connor, R.C., 1999. Why do baleen whales migrate? *Mar. Mammal Sci.* 15, 1228–1245.
- Costa, D.P., Williams, T.M., 2000. Marine mammal energetics. In: Reynolds, J., Twiss, J. (Eds.), *The Biology of Marine Mammals*. The Smithsonian Institution Press, Washington D.C.
- Cox, M.J., Demer, D.A., Warren, J.D., Cutter, G.R., Brierley, A.S., 2009. Multibeam echosounder observations reveal interactions between Antarctic krill and air-breathing predators. *Mar. Ecol. Prog. Ser.* 378, 199–209.
- Cresswell, K., Wiedenmann, J., Mangel, M., 2008. Can macaroni penguins keep up with climate and fishing induced changes in krill? *Polar Biol.* 31, 641–649.
- Croll, D.A., Acevedo-Guitierrez, A., Tershy, B.R., Urban-Ramirez, J., 2001. The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comp. Biochem. Phys. A* 129, 797–809.
- Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R., Tershy, B.R., 2005. From wind to whales: trophic links in a coastal upwelling system. *Mar. Ecol. Prog. Ser.* 289, 117–130.
- Croll, D.A., Kudela, R., Tershy, B.R., 2006. Ecosystem impact of the decline of large whales in the North Pacific. In: Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.E., Brownell Jr., R.L. (Eds.), *Whales Whaling Ocean Ecosystems*. University of California Press.
- Croxall, J.P., Nicol, S., 2004. Management of Southern Ocean fisheries: global forces and future sustainability. *Antarct. Sci.* 16, 569–584.
- Dawbin, W.H., 1966. The seasonal migratory cycle of humpback whales. In: Norris, K.S. (Ed.), *Whales, Dolphins and Porpoises*. University of California Press, Berkeley.
- Doniol-Valcroze, T., Lesage, V., Giard, J., Michaud, R., 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav. Ecol.* 22, 880–888.
- Forsythe, W.C., Rykiel Jr., E.J., Stahl, R.S., Wu, H., Schoolfield, R.M., 1995. A model comparison for daylength as a function of latitude and day of year. *Ecol. Model.* 80, 87–95.
- Friedlaender, A.S., Lawson, G.L., Halpin, P.N., 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar. Mammal Sci.* 25, 402–415.
- Goldbogen, J.A., Pyenson, N.D., Shadwick, R.E., 2007. Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* 349, 289–301.
- Goldbogen, J.A., Calambokidis, J., Croll, D., Harvey, J., Newton, K., Oleson, E., Schorr, G., Shadwick, R.E., 2008. Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *J. Exp. Biol.* 211, 3712–3719.
- Goldbogen, J.A., Potvin, J., Shadwick, R.E., 2009. Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proc. R. Soc. B* 277, 861–868.
- Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G., Shadwick, R.E., 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J. Exp. Biol.* 214, 131–146.
- Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31, 295–311.
- Hamner, W.M., Hamner, P.P., 2000. Behavior of Antarctic krill (*Euphausia superba*); schooling, foraging, and antipredatory behavior. *Can. J. Fish. Aquat. Sci.* 57, 192–202.
- Hewitt, R.P., Watters, G., Trathan, P.N., Croxall, J.P., Goebel, M.E., Ramm, D., Reid, K., Trivelpiece, W.Z., Watkins, J.L., 2004. Options for allocating the precautionary catch limit of krill among the small-scale management units in the Scotia Sea. *CCAMLR Sci.* 11, 81–97.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton.
- Hill, S.L., Murphy, E.J., Reid, K., Trathan, P.N., Constable, A.J., 2006. Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. *Biol. Rev.* 81, 581–608.
- Hill, S.L., Watters, G.M., Punt, A.E., McAllister, M.K., Le Quere, C., Turner, J., 2007. Model uncertainty in the ecosystem approach to fisheries. *Fish. Fish.* 8, 315–336.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Houston, A.I., McNamara, J.M., 1999. *Models of Adaptive Behaviour: An Approach Based on State*. Cambridge University Press.
- Innes, S., Lavigne, D.M., Earle, W.M., Kovacs, K.M., 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Mar. Mammal Sci.* 2, 227–229.
- Kawaguchi, S., Nicol, S., 2007. Learning about Antarctic krill from the fishery. *Antarct. Sci.* 19, 219–230.
- Kawaguchi, S., Candy, S.G., 2009. Quantifying movement behaviour of vessels in the Antarctic krill fishery. *CCAMLR Sci.* 16, 131–148.
- Kawamura, A., 1980. A review of food of balaenopterid whales. *Sci. Rep. Whales Res. Inst.* 32, 155–197.
- Kleiber, M., 1975. *The Fire of Life. An Introduction to Animal Energetics*. R.E. Kreiger Publishing Co., Huntington, NY.
- Klevjer, T.A., Tarling, G.A., Fielding, S., 2010. Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea. *Mar. Ecol. Prog. Ser.* 409, 157–170.
- Kshatriya, M., Blake, R.W., 1988. Theoretical model of migration energetics in the blue whale, *Balaenoptera musculus*. *J. Theor. Biol.* 133, 479–498.
- Lascara, C.M., Hofmann, E.E., Ross, R.M., Quetin, L.B., 1999. Seasonal variability in the distribution of Antarctic krill *Euphausia superba*, west of the Antarctic Peninsula. *Deep-Sea Res.* 46, 951–984.

- Leeper, R., Cooke, J., Trathan, P., Reid, K., Rowntree, V., Payne, R., 2006. Global climate drives southern right whale (*Eubalaena glacialis*) population dynamics. *Biol. Lett.* 2, 289–292.
- Leeper, R.L., Lavigne, D., 2007. How much do large whales eat? *J. Cetacean Res. Manage.* 9, 179–188.
- Lockyer, C., 1976. Body weights of some species of large whales. *J. Cons. Int. Explor. Mer.* 36, 259–273.
- Lockyer, C., 1981. Growth and energy budgets of large baleen whales from the Southern Hemisphere. In: *Mammals in the Seas. Vol. III, General Papers and Large Cetaceans*, FAO Fisheries Series, vol. 5, pp. 379–487.
- Lockyer, C., 2007. All creatures great and smaller: a study in cetacean life history energetics. *J. Mar. Biol. Assoc. U.K.* 87, 1035–1045.
- Lockyer, C.H., McConnell, L.C., Waters, T.D., 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. *Can. J. Zool.* 63, 2328–2338.
- Mackintosh, N.A., 1965. *The Stocks of Whales*. Fishing News (Books) Ltd., London.
- Mangel, M., Clark, C.W., 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton.
- Mangel, M., Ludwig, D., 1992. Definition and evaluation of the fitness of behavioral and developmental programs. *Annu. Rev. Ecol. Syst.* 23, 507–536.
- Mate, B.R., Lagerquist, B.A., Calambokidis, J., 1999. Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Mar. Mammal Sci.* 15, 1246–1257.
- Miller, D.G.M., Hampton, I., 1989. Krill aggregation characteristics: spatial distribution patterns from hydroacoustic observations. *Polar Biol.* 10, 125–134.
- Mori, M., Butterworth, D.S., 2006. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Sci.* 13, 217–277.
- Nicol, S., Foster, I., 2003. Recent trends in the fishery for Antarctic krill. *Aquat. Living Res.* 16, 42–45.
- Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K., van der Merwe, P., 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish Fish.* 11, 203–209.
- Noren, D.P., Mangel, M., 2004. Energy reserve allocation in fasting Northern Elephant Seals: inter-relationships between body condition and fasting duration. *Funct. Ecol.* 18, 233–244.
- Oleson, E.M., Calambokidis, J., Burgess, W.C., McDonald, M.A., LeDuc, C.A., Hildebrand, J.A., 2007. Behavioral context of call production by eastern North Pacific blue whales. *Mar. Ecol. Prog. Ser.* 330, 269–284.
- Paterson, R., Paterson, P., Cato, D.H., 1994. The status of humpback whales *Megaptera novaeangliae* in east Australia thirty years after whaling. *Biol. Conser.* 70, 135–142.
- Potvin, J., Goldbogen, J.A., Shadwick, R.E., 2009. Passive versus active engulfment: verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *J. R. Soc. Interface*, doi:10.1098/rsif.2008.0492.
- Potvin, J., Goldbogen, J.A., Shadwick, R.E., 2010. Scaling of lunge feeding in rorqual whales: an integrated model of engulfment duration. *J. Theor. Biol.* 267, 437–453.
- Quetin, L.B., Ross, R.M., 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in Palmer LTER study region. *Mar. Ecol. Prog. Ser.* 259, 185–200.
- Reilly, S.B., Hedley, S., Borberg, J., Hewitt, R., Thiele, D., Watkins, J., Naganobu, M., 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51, 1397–1409.
- Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell Jr., R.L., Butterworth, D.S., Clapham, P.J., Cooke, J., Donovan, G.P., Urbán, J., Zerbini, A.N., 2009. IUCN Red List of Threatened Species Version 2009.1, www.iucnredlist.org. Downloaded on 23 September 2009.
- Sieg, A.E., O'Connor, M.P., McNair, J.N., Grant, B.W., Agosta, S.J., Dunham, A.E., 2009. Mammalian metabolic allometry: do intraspecific variation, phylogeny, and regression models matter? *Am. Nat.* 174, 720–733.
- Siegel, V., Kalinowski, J., 1994. Krill demography and small scale processes. In: El-Sayed, S.Z. (Ed.), *Southern Ocean Ecology: The BIOMASS Perspective*. Cambridge University Press, Cambridge.
- Siegel, V., Loeb, V., 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* 123, 45–56.
- Siegel, V., 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biol.* 29, 1–22.
- Sprong, I., Schalk, P.H., 1992. Acoustic observations on krill spring-summer migration and patchiness in the northern Weddell Sea. *Polar Biol.* 12, 261–268.
- Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X., Rind, D., 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño-southern oscillation and southern annular mode variability. *J. Geophys. Res.* 113, C03S90, doi:10.1029/2007JC004269.
- Tamura, T., Konishi, K., 2006. Food habit and prey consumption of Antarctic minke whale *Balaenoptera bonaerensis* in JARPA research area. Paper SC/D06/J18 presented to the JARPA Review Workshop, Tokyo.
- Tarling, G.A., Klevjer, T., Fielding, S., Watkins, J., Atkinson, A., Murphy, E., Korb, R., Whitehouse, M., Leaper, R., 2009. Variability and predictability of Antarctic krill swarm structure. *Deep-Sea Res.* 156, 1994–2012.
- Travis, J.M.J., Palmer, S.C.F., 2005. Spatial processes can determine the relationship between prey encounter rate and prey density. *Biol. Lett.* 1, 136–138.
- Vikingsson, G.A., 1997. Feeding of fin whales (*Balaenoptera physalus*) off Iceland – diurnal and seasonal variation and possible rates. *J. Northwest Atl. Fish. Sci.* 22, 77–89.
- Ward, E., Zerbini, A.N., Kinas, P.G., Engel, M.H., Andriolo, A., 2006. Estimates of population growth rates of humpback whales (*Megaptera novaeangliae*) in the wintering grounds off the coast of Brazil (Breeding Stock A). Paper SC/58/SH14 submitted to the IWC.
- Watts, P., Hansen, S., Lavigne, D.M., 1993. Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. *J. Theor. Biol.* 163, 505–525.
- Wiedenmann, J., Cresswell, K.A., Mangel, M., 2008. Temperature dependent growth of Antarctic krill: predictions for a changing climate from a cohort model. *Mar. Ecol. Prog. Ser.* 358, 191–202.
- Wiedenmann, J., Cresswell, K.A., Mangel, M., 2009. Connecting krill recruitment and sea ice. *Limnol. Oceanogr.* 54, 799–811.
- White, C.R., Blackburn, T.M., Seymour, R.S., 2009. Phylogenetically informed analysis of the allometry of mammalian metabolic rate supports neither geometric nor quarter-power scaling. *Evolution* 63, 2658–2667.
- Williams, T.M., 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philos. Trans. R. Soc. Lond. B* 354, 193–201.
- Willis, J., 2007. Could whales have maintained a high abundance of krill? *Evol. Ecol. Res.* 9, 1–12.
- Yablokov, A.V., 1994. Validity of whaling data. *Nature* 367, 108.
- Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J., Gloerson, P., 2002. Variability of Antarctic sea ice 1979–1998. *J. Geophys. Res.* 107, 3041, doi:10.1029/2000JC000733.