

SC/67B/EM/07

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Further development of individual base  
energetic models including the effects of  
feeding during migration

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INTERNATIONAL  
WHALING COMMISSION

## Further development of individual base energetic models including the effects of feeding during migration.

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### Abstract

A number of enhancements have been made to the Individual based energetics models for baleen whales to include options allowing for diving and prey school based foraging behaviour, as well as an improved foraging model that allows for longer term memory of feeding grounds. The model allows for feeding to occur during migration between the feeding and breeding grounds. The spatial characteristics of prey can now be modelled in regions that are recursively defined, that is that any spatial region can contain subregions on a finer scale, and within any region prey can be modelled at the level of schools. Some early results from the enhanced model shows that carrying capacity and the characteristics of yield curves including MSYR and MSYL depend on quantity of food consumed by animals during migration. This has implications for the geographic and temporal scales required in the development of ecosystem models.

### Introduction

This paper describes several changes and enhancements that have been made to the individual based energetics model for baleen whales previously described in de la Mare (2015). These include:

- An improved growth model that better links food consumption and growth. The allocation of energy to growth is controlled to ensure that fat storage is maintained.
- An improved model for determining density dependence in the inter-calving interval
- Prey consumption can be scaled to be consistent with the functional relationships based on prey density given in de la Mare et al. (2018).
- An option to use the diving and searching models described in de la Mare et al. (2018) and de la Mare (2018)
- Feeding can occur during migration
- Animals can now accumulate long-term memories about locations where they fed to advantage at specific times over multiple seasons, but with a forgetting coefficient to discount older memories. Complete forgetting occurs when the discounted memory falls below a threshold.
- An improved environment spatial grid structure that allows flexible modelling of spatial characteristics of prey through recursion, i.e. a cell on any level of a spatial grid can itself contain a finer scale grid. Each cell can have an arbitrary number of data values and parameters. A cell address is fully specified by its latitude and longitude, and the smallest cell containing a given latitude and longitude is automatically selected
- A version to allow simultaneous modelling of different whale species on the same feeding grounds is currently being tested

The revised specifications for the model are given in the Appendix and the diving and searching models are described de la Mare et al. (2018) and de la Mare (2018).

### Effects of feeding during migration

The energetics of Antarctic minke whales indicate that they do not ingest sufficient food during the summer feeding season to meet energetic demands for the remainder of the year for migration and reproduction (Leaper and Lavigne, 2007, de la Mare et al. 2017). Consequently the density dependent response of a population will depend on the relative magnitude of feeding on migration, and this is likely to affect the parameters of yield curves. This issue is explored with the energetics model by calculating yield curves with different densities of food available on migration while maintaining nearly constant the characteristics of prey populations encountered during the summer feeding season. It is assumed in these explorations that the abundance of whales has no appreciable effect on the density of migration food.

The results from five runs of the model with different levels of migration food availability (given in Table 1) show that abundance and maximum sustainable yield rate (MSYR) can be highly dependent on migration feeding and maximum sustainable yield level (MSYL) is also affected. Fig 1 demonstrates the effect of the different migration food on the shape of the yield curve, in this case moving the peak of the curve further towards carrying capacity ( $K$ ) as the amount of food available on migration is reduced. Interestingly there is not much difference in these examples of the numerical value of MSY attained from exploiting either the mature or total 1+ population.

Figs 2 and 3 show the contributions of summer and migration feeding to the annual food consumption by age for models 1 (high MSYR model) and 4 (low MSYR model). As would be expected, the growth of younger animals is enhanced by increases in food availability as a population is depleted, but perhaps less obvious is that the size of the effect depends on the amount of feeding migration. There is a positive feedback effect shown in Fig 2 migration food because faster growth increases the food consumed at a given age in younger animals, and consequently the population is larger because of enhanced juvenile survival. Also, and perhaps less intuitive, is that the amount of food consumed by older animals declines with reduced population abundance. This is

because the effect of more food per capita is to reduce the energetic costs of feeding, and so animals are able to meet their energy needs with less food. These effects are less pronounced for the lower level of feeding during migration.

The individual energetics model captures the complex interplay between foraging, food consumption, growth and survival. This interplay is not explicitly programmed into the model, but it is an emergent property deriving from behavioural rules for foraging and feeding interacting with different prey environments. The results imply that the density dependence in juvenile growth and survival in this examples are the dominant effects the arising from better feeding on migration that leads to the threefold difference in MSYR between the two migration feeding regimes. Consequently, the development of ecosystem models that concentrate only on the summer feeding grounds risk overlooking some of the critical mechanisms that affect the magnitude of density dependence and hence the dynamics of the whale populations.

### References

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- de la Mare, W. K. 2018. The contribution of prey spatial distribution to baleen whale functional responses. SC/67B/EM..
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Table 1. Characteristics of yield curves calculated for different levels of food availability on migration. The column headed 'Male 95% food' applies to the functional response of males on the feeding ground, and is shown because this parameter requires some minor adjustment to maintain the modelled sex ratio at around 50%. Swarm density is the proportion of a given region that contains krill swarms available to the particular whale species, which also requires some adjustment to achieve similar population sizes and to help the models to 'spin up' from sub-optimal starting parameters.

Model	Male 95% food (kg.m <sup>-2</sup> )	Migration food (kg.m <sup>-2</sup> )	Swarm density	Food variability	1+				Mature			
					K	MSY	MSYR	MSYL	K	MSY	MSYR	MSYL
1	6.6	1.0	0.00005	0.	37310	805	0.033	0.664	21858	775	0.055	0.651
2	6.6	1.0	0.00005	0.3	35836	731	0.032	0.635	20902	705	0.054	0.619
3	6.4	0.7	0.00005	0.3	23788	268	0.018	0.640	13891	256	0.028	0.655
4	6.2	0.63	0.00004	0.3	22487	175	0.010	0.766	13205	177	0.018	0.729
5	6.2	0.5	0.00004	0.3	19502	107	0.008	0.714	11551	106	0.012	0.760

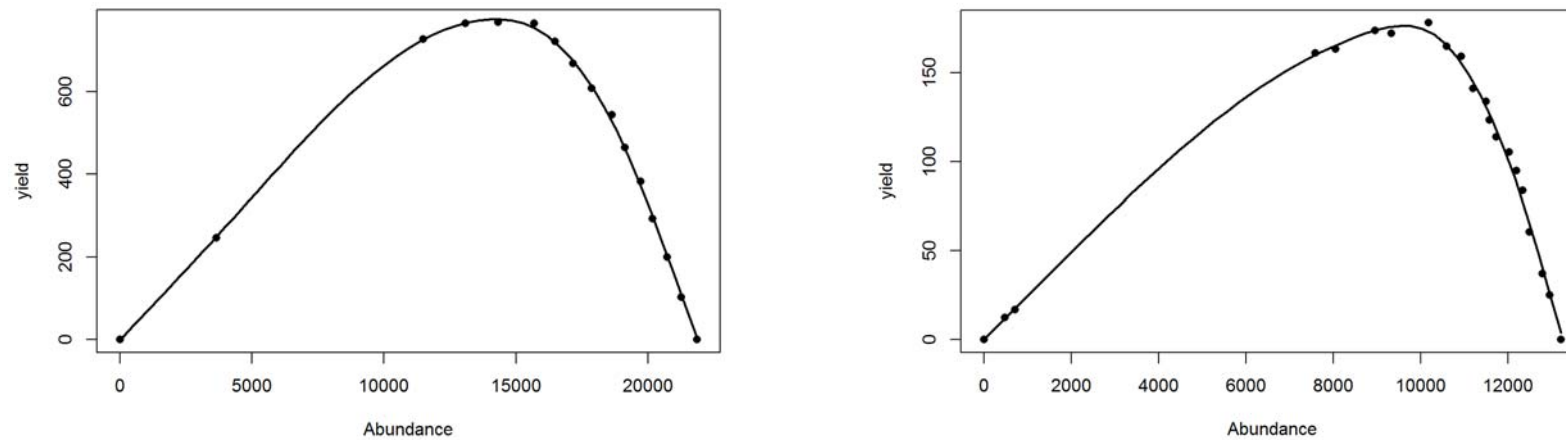


Fig 1. Yield curves for the mature population from models 1 (left) and 4 in table 1.

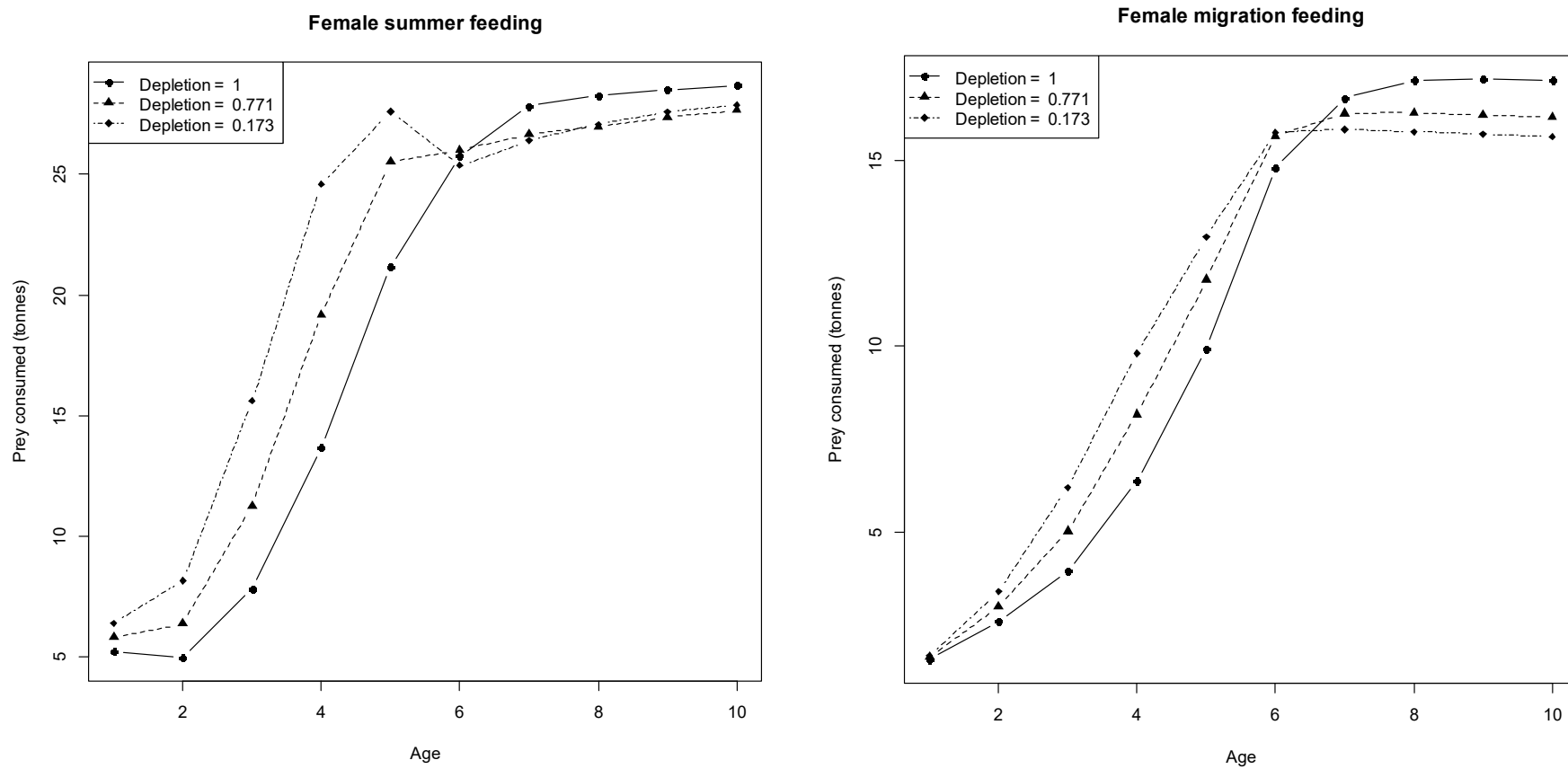


Fig.2. Mean annual prey consumption by age for females from model 1 at three levels of stock depletion for summer (left) and migration feeding. Migration food patch density =  $1 \text{ kg.m}^{-2}$

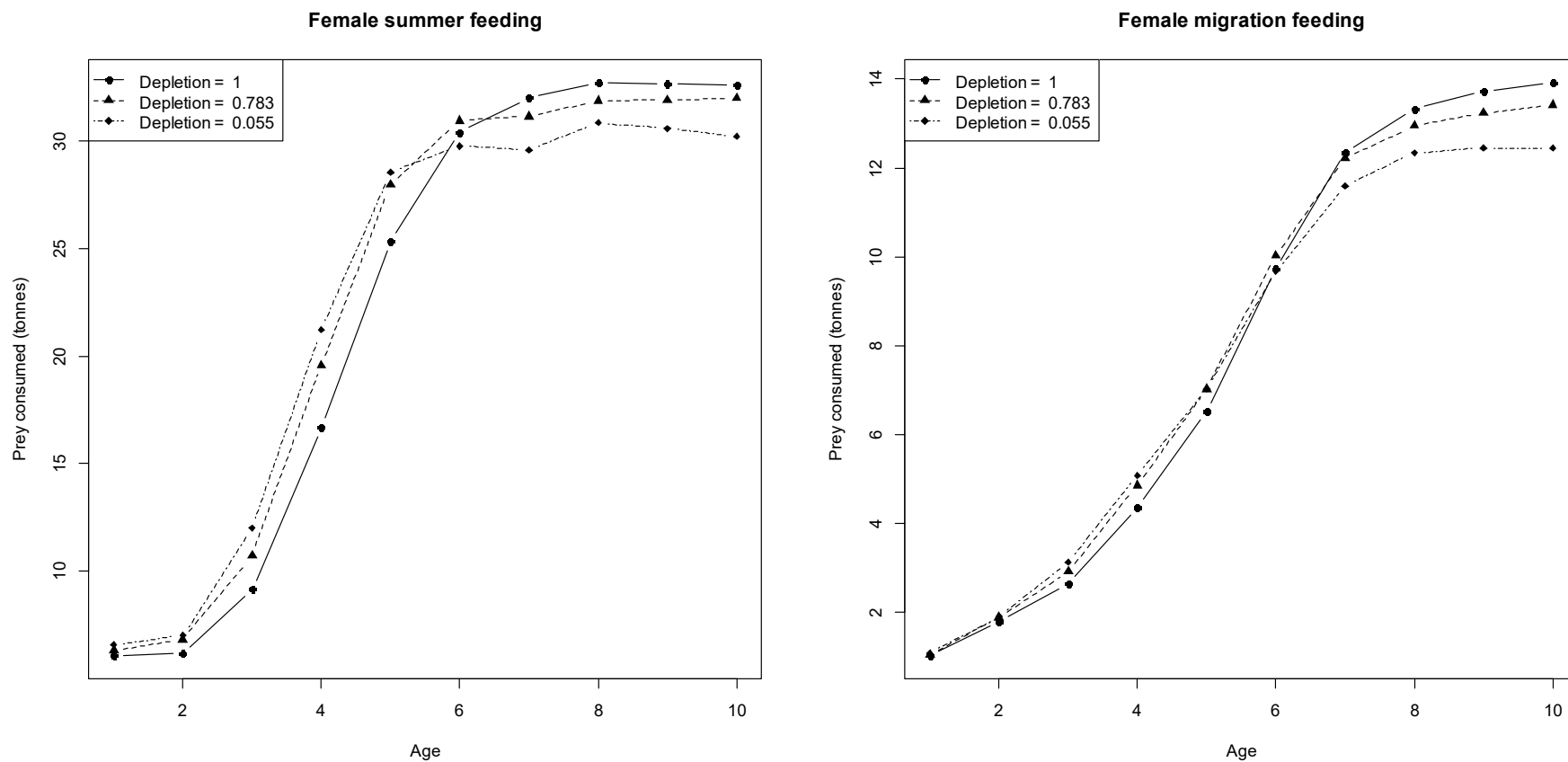


Fig.3. Mean annual prey consumption by age for females from model 4 at three levels of stock depletion for summer (left) and migration feeding. Migration food patch density = 0.63 kg.m<sup>-2</sup>

## Appendix

Population dynamics models for marine mammals are typically deterministic age-structured cohort models with specified forms of stock recruitment relationship. A typical example is the Baleen II model (de la Mare and Cooke, 1994) used in the International Whaling Commission (IWC). In such models density dependence is often determined entirely by the stock-recruitment relationship and effects such as density dependence in growth and natural mortality are not modelled. These deterministic aggregated models treat populations simply in terms of the numbers of animals at each age and so ignore the differences between the individuals. The usual cohort models do not explicitly model the prey field or the animal's foraging strategy, but instead rely on simplifying assumptions about carrying capacity and usually no explicit structure for the distribution and abundance of prey and the extent to which these factors are subject to random variability. In particular the usual age-structured models do not readily allow for an environment to shape a population so that it consists of those animals possessing particular characteristics and behaviours that are more successful in that environment. Witting (2001) demonstrated that the dynamics of a population recovering from depletion can depend on structural details of the population life history other than simple abundance (density).

A class of model for the exploration of the population effects of the interactions of individuals with their environment are individually-based energetic models. The model developed here allows for population density dependence to be shaped by epigenetic effects and heritable traits that improve the fit of the population to a given prey environment. It will be shown that such mechanisms are important for those marine mammals that are "capital breeders", such as the typical mysticete, that inhabit stochastic environments.

The model uses individual animal models with a detailed energy budget to determine reproductive success and mortality in an environment where food has a patchy spatial distribution. All the major processes of the animal's seasonal activities are modelled including migration, breeding and feeding. Animals have to search for food and look for new food patches when local food abundance falls due to the effects of local intra-specific competition. Details of the model are given in Appendix 1.

### The animal state variables are

Age	$a$	years
day of year	$n_d$	1 = animal's nominal birthday
Length	$L$	m
Sex (0 = female, 1 = male)	$S$	
Sexual Maturity	$S'$	
Lean mass	$w_l$	tonnes
Fat mass	$w_f$	tonnes
Mass at birth	$w_B$	tonnes
Latitude	$\lambda$	decimal degrees
Longitude	$\varphi$	decimal degrees
Speed	$v$	$\text{m.s}^{-1}$
Direction	$\theta$	decimal degrees
Pregnant (1 = pregnant)	$P$	
Maximum foetal growth rate	$\tau$	$\text{m.day}^{-1}$
Foetal length	$L_F$	m
Mother identity	$Q$	
Calf identity	$O$	
Suckling (1 = suckling)	$s$	
Age at last parturition	$a_B$	years

Feeding history (food density at places visited) (year, day, latitude, longitude)  $H_{t,l...j}$

Migration state (function of day of year)

Breeding	$\Gamma(t, \dots) = 0$
Migrating to food	$\Gamma(t, \dots) = 1$
Feeding	$\Gamma(t, \dots) = 2$
Migrating to breeding	$\Gamma(t, \dots) = 3$

**Frequently used derived state variable**

The ratio of fat to lean mass  $c = w_f \div w_l$

**Demographic parameters with individual values**

Individual parameter values are heritable as the weighted average of the individual and population values of the parameters (with some random variation)

von Bertalanffy growth parameters, where • represents either male or female:  $L_{\infty\bullet}$ ,  $k_{\bullet}$ ,  $t_{0\bullet}$ .

Mass length	$A$	tonnes.m <sup>-1/B</sup>
Mass length	$B$	
Calving Interval	$t_c$	years
Foetal growth rate	$g_f$	m.day <sup>-1</sup>
Length at birth	$L_0$	m
Length sexual maturity	$L_m$	m

**Fixed demographic parameters**

Population nominal von Bertalanffy growth parameters,

where • represents either male or female:  $\bar{L}_{\infty\bullet}$ ,  $\bar{k}_{\bullet}$ ,  $\bar{t}_{0\bullet}$ .

Heritability of growth characteristics	$H_g$	
Heritability of inter-calving interval	$H_c$	
Female minimum mortality at age $a$	$M_{f,a} = f(a, \beta_{f,1} \dots \beta_{f,5})$	year <sup>-1</sup>
Male minimum mortality at age $a$	$M_{m,a} = f(a, \beta_{m,1} \dots \beta_{m,5})$	year <sup>-1</sup>

Additional mortality hazard parameters (additional mortality is a function of body condition)

Maximum value	$M$	year <sup>-1</sup>
Body condition at $M50$	$c_{M50}$	
Rate parameter	$g_M$	
Female proportional length sexual maturity	$\psi_f$	
Male proportional length at sexual maturity	$\psi_m$	
Maximum age at sexual maturity	$a_{max}$	years
Sex ratio at birth	$\rho$	
Minimum viable calf length	$L_{min}$	m

**Energetics parameters**

Energy content of fat	$E_f$	J.kg <sup>-1</sup>
Energy content of non-fat tissues	$E_n$	J.kg <sup>-1</sup>
Energy content of milk	$E_m$	J.kg <sup>-1</sup>
Energy content of prey	$E_p$	J.kg <sup>-1</sup>
Maximum body condition	$c_{max}$	
Minimum body condition to conceive	$c_{min}$	
Daily feeding rate per unit body mass	$\kappa$	kg.tonne <sup>-1</sup>
Assimilation efficiency	$q$	
Milk assimilation efficiency	$q_m$	
Growth efficiency	$\gamma$	
Proportion of lean mass (in m-L relation)	$R$	
Body condition at birth	$v$	
Fat ratio at birth	$\Phi$	
Male breeding FMR/BMR	$\xi$	
Drag coefficient	$C_D$	
Density of seawater	$\rho_{seawater}$	kg.m <sup>-3</sup>



Nominal number of days in feeding period	$n_e$	
Proportion of year spent growing	$\Omega = n_e \div 365$	
Feeding parameters for females (a function of prey density)		
Prey density range	$f_{f\text{range}}$	
Prey density at food intake inflection	$f_{f50}$	kg.m <sup>-2</sup>
Rate parameter	$h_f$	m <sup>2</sup> .kg <sup>-1</sup>
Feeding parameters for males (a function of prey abundance)		
Prey abundance at 50% food intake	$f_{m50}$	kg.m-2
Rate parameter	$h_m$	m2.kg-1
Remembered food density time-lat-lon ( $t, \theta, \phi$ ) $R_{t,\theta,\phi}$		
Food memory retention coefficient	$\zeta$ ,	$0 \leq \zeta < 1$
Growth as a function of body condition		
Maximum proportion of energy for growth	$g_{\max}$	
Body condition at 50% point	$c_{L50}$	
Rate parameter	$\varepsilon$	
Foetal growth as a function of body condition		
body condition at 50% point	$c_{\tau50}$	
Rate parameter	$\eta$	
Milk production as a function of body condition		
Body condition at 50% production	$l_{50}$	
Rate parameter	$d$	
Milk production as a function of calf size		
Minimum production	$l_{\min}$	kg day <sup>-1</sup>
Increase per unit calf mass	$u$	kg.(day.tonne) <sup>-1</sup>
<b>Common demographic parameters</b>		
Calving interval determining parameters		
Expected calving interval at carrying capacity	$I_K$	years
Maximum nominal calving interval	$I_{\max}$	years
Minimum nominal calving interval	$I_{\min}$	years
Std. dev. of calving interval distribution	$\sigma_c$	years
Offset parameter	$g_c$	
Birth mass under good food conditions	$w_G$	tonnes
Birth mass at carrying capacity	$w_K$	tonnes
<b>Timing parameters (day of year)</b>		
Birthday	$t_0$	
Conception	$t_c$	
Weaning	$t_w$	
Arrive on breeding grounds	$t_{b\dots}$	
Migration towards feeding grounds	$t_{1\dots}$	
Arrive on feeding grounds	$t_{2\dots}$	
Migration towards breeding grounds	$t_{3\dots}$	

The dots indicate timings that depend on sex and reproductive state

## Prey dynamics

Prey carrying capacity at time $t$	$K_{p,t}$
Prey biomass at time $t$	$B_{p,t}$
Prey density at time $t$ at lat-lon $(\theta, \phi)$	$\mathcal{G}_{t,\theta,\phi} = \frac{B_{t,\theta,\phi}}{\Xi_{\theta,\phi}} \Upsilon \text{ kg.m}^2$
Area of cell containing prey	$\Xi_{\theta,\phi} \text{ m}^2$
Proportion of cell containing available prey	$\Upsilon$
Prey daily survival probability	$S_p$
Prey maximum daily recruitment	$r_p$

## RELATIONS

### Length and growth

An animal's growth is controlled by a 'programmed' growth curve unique to each individual, acquired at birth with sex specific values for  $k$  and  $L_{\infty}$ , which are partially inherited from the mother (as a weighted average of the mother's parameters and the population mean values – but re-scaled appropriately for males). This growth curve describes the upper limit of the length of the animal on each birthday and is given by a conventional von Bertalanffy equation (shown as the dotted line in Fig A1):

$$L = L_{\infty} \left( 1 - \exp \left( -k \cdot \left( a + \frac{n_d}{365} - t_{0\bullet} \right) \right) \right) \quad \text{A - (1)}$$

Animals will grow on a realised growth curve that lies below the programmed curve when food availability is low. Moreover, growth is only possible when food has been ingested. Given that feeding is concentrated into a feeding season after migration, the growth curve is transformed into a piece-wise curve as shown by the solid line in Fig A1. This curve is made from segments derived from:

$$L = L_{\infty} \left( 1 - \exp \left( -\frac{k_{\bullet}}{\Omega} \left( \Omega a + \frac{n_d}{365} - t'_{0\bullet} \right) \right) \right) \quad \text{A - (2)}$$

where

$$\Omega = \frac{n_e}{365} \quad \text{A - (3)}$$

and

$$t'_{0\bullet} = \frac{\log \left( 1 - \frac{L_0}{L_{\infty\bullet}} \right) \Omega}{k_{\bullet}} + \frac{t_2}{365} \quad \text{A - (4)}$$

However, during the first year of life the growth period includes suckling from birth and so the first step on the growth curve has different parameters. There are two cases: 1; there is some independent feeding when weaning occurs before the end of the feeding-season, and 2; suckling can continue past the end of the feeding season.

For case 1, the following expressions redefines  $\Omega$  in equation A – (2):

$$\Omega = \frac{t_3}{365} \quad \text{A - (5)}$$

In case 2

$$\Omega = \frac{t_w}{365} \quad \text{A - (6)}$$

In both cases  $t'_{0\bullet}$  is redefined as

$$t'_{0\bullet} = \frac{\log\left(1 - \frac{L_0}{L_{\infty\bullet}}\right)\Omega}{k_{\bullet}} \quad \text{A - (7)}$$

where  $\Omega$  takes the value appropriate for the case.

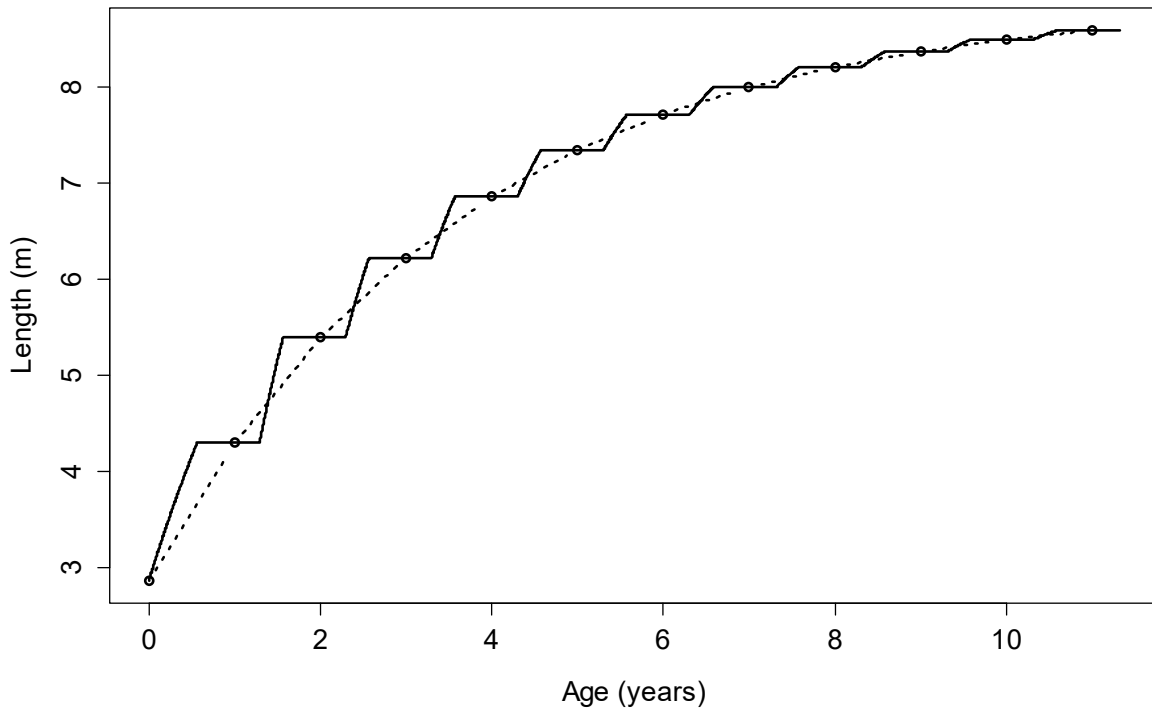


Fig. A1 Incremental programmed growth curve (solid line). Growth occurs during the annual feeding season but nominally stops between feeding seasons. The dotted line is the annualised growth curve referred to age at each birthday (shown as a point).

The programmed growth curve represents the sizes animals reach when they can feed to satiation. Otherwise, under worsening food conditions animals will grow more slowly. ‘Catch up’ growth can occur when energetically feasible but this is through an incremental approach so that an animal cannot exceed the size at age on its individual programmed growth curve. Nominal growth increments are dependent on body condition, so that more energy is diverted to fat storage when body condition is poor. There is also a limit on the amount of energy that can be used for growth and the maximum size of the growth increment is determined by the energy available. If the maximum allowed increment exceeds the nominal growth increment then the nominated growth occurs, otherwise only the maximum energetically allowable growth occurs. The following section clarifies the details.

To allow for food dependence, growth is modelled incrementally, the first step being to find the maximum growth increment needed to progress from current length to the length on the programmed growth curve; this is given by;

$$\Delta L_{prog} = L_{\infty} \left( 1 - \exp\left( -\frac{k_{\bullet}}{\Omega} \left( \Omega a + \frac{n_d + 0.5n}{365} - t'_{0\bullet} \right) \right) \right) - L \quad \text{A - (8)}$$

where  $n$  is the number of days elapsed, and  $L$  is state variable of the actual length of the animal prior to the current time step. This growth increment is reduced by a proportion that depends on current body condition to become the nominal growth increment and added to  $L$  to give the next nominal length:

$$L' = L + \frac{\Delta L_{prog}}{1 + \exp(-\varepsilon(c - c_{L50}))} \quad A - (9)$$

However,  $L'$  may not be reachable given the amount of food recently ingested. Calculating the maximum increase in length given the amount of food ingested is derived from the increase in lean mass available from the feeding energy intake ( $e_f$ ). This potential increase in lean mass is given by:

$$\Delta W_{max} = \frac{g_{max} e_f \gamma}{E_N} \quad A - (10)$$

Using the mass-length relationship this gives the maximum achievable length as:

$$L_{max} = \left( \frac{\Delta W_{max}}{RA} + L^\beta \right)^{\frac{1}{\beta}} \quad A - (11)$$

This is approximate because it assumes that the ratio of lean mass to total mass is at the standard value ( $R$ ) (as is the case for all the calculations that use the mass-length relationship). The realised new length is given by:

$$L = \inf(L', L_{max}) \quad A - (12)$$

These mechanisms ensure that an animal partitions energy into maintaining sufficient body condition while growing, and in particular, does not allow fat stores to be drawn down to provide energy for growth. Survival and reaching maturity depend on a trade-off between somatic growth and fat-storage.

#### *Growth heritability*

Each animal has a unique set of growth parameters, partly inherited from their mother and weakly dependent on its length at birth if undersized (although in the current version the term dependent on birth-length is not used, i.e.  $\beta' = 1$ ). For females the individual's asymptotic length is:

$$L'_{\mathcal{O}f} = \beta' \left( (1-H) \bar{L}_{\mathcal{O}f} + H L_{\mathcal{O}f, \mathcal{Q}} + \text{Norm}(0, \sigma_{L_{\mathcal{O}f}}) \right) \quad A - (13)$$

Where  $H$  (with a value in the range [0:1]) is the heritability, which leads to the individual characteristic being a weighted mean of the mother's and population's values. For males:

$$L'_{\mathcal{O}m} = L'_{\mathcal{O}f} - \bar{L}_{\mathcal{O}f} + \bar{L}_{\mathcal{O}m} \quad A - (14)$$

For females the rate parameter is:

$$k'_f = \beta' \left( (1-H) \bar{k}_f + H k_{f, \mathcal{Q}} + \text{Norm}(0, \sigma_k) \right) \quad A - (15)$$

and for males:

$$k'_m = k'_f - \bar{k}_f + \bar{k}_m \quad A - (16)$$

where  $\beta'$  is the effect of mass at birth given by:

$$\beta' = \inf \left( 1 + \frac{0.1(w'_B - w_B^*)}{w_B^*}, 1.1 \right)$$

where  $\text{Norm}(\mu, \sigma)$  is a random number from a normal distribution with the specified mean  $\mu$  and standard deviation  $\sigma$  and  $w_b^*$  is the population average birth mass under good conditions.  $L_{\mathcal{O}b}$  and  $k_b$  are perfectly

positively correlated. The value of  $t_{0\bullet}$  is set so that an animal's length given by its individual growth curve on its day of birth is equal to the length of the foetus as delivered by its mother.

The energy used for growth is derived from the increase in mass (it is assumed that growth in length is reflected only in lean mass)

$$\Delta w_l = RA(L_{t+n}^B - L_t^B) \quad A - (17)$$

Hence energy used in growth is

$$e_g = \Delta w_l \frac{E_n}{\gamma} \quad A - (18)$$

### *Foetal growth*

Growth rate of a foetus in a female is an individual characteristic partially inherited from its mother as a weighted average of the individual and population values in a similar way to the other growth terms above (equation A – (15)). The value is capped so that there is a maximum size for calves at birth.

The growth of an individual foetus in length is linear with time, but actual growth is dependent on the body condition of the mother.

$$L_{F,t+n} = L_{F,t} + \frac{n}{365} \left( \frac{\tau}{1 + \exp(-\eta(c - c_{t50}))} \right) \quad A - (19)$$

The maternal energy invested in growth is derived from the increase in foetal mass given by:

$$\Delta w_F = A(L_{F,t+n}^B - L_{F,t}^B) \quad A - (20)$$

Energy used in foetal growth is:

$$e_F = \Delta w_F \frac{(1-\Phi)E_n + \Phi E_f}{\gamma} \quad A - (21)$$

The partitioning of foetal growth to fat tissue ( $\Phi$ ) is assumed to be 30%.

### *Natural mortality*

Natural mortality is dependent both on age and on body condition and can be different for males and females. The age dependent mortality is given by a Siler type of function:

$$M_{\bullet,a} = \beta_{\bullet,1} \exp(-\beta_{\bullet,2}a) + \beta_{\bullet,3} + \exp(\beta_{\bullet,4}(a - \beta_{\bullet,5})) \quad A - (22)$$

The hazard of death is given by:

$$z = M_{\bullet,a} + \frac{M}{1 + \exp(-g_M(c - c_{M50}))} \quad A - (23)$$

The rate parameter  $g_M$  is negative and so the hazard of death increases with declining body condition. Death is a Bernoulli trial with the probability of death in an  $n$  day period given by:

$$p(\text{death}) = 1 - \exp\left(\frac{-zn}{365}\right) \quad A - (24)$$

Death by starvation is an additional form of mortality, and this is assumed to occur when the lean body mass has declined to less than 30% of the body mass given by the mass-length relationship. In the case of suckling calves,

the death of the mother also results in the death of the calf. There is also a minimum viable size at birth for calves, below which they are considered to die at birth.

### Pregnancy rate

There are three controls on pregnancy rate:

- An individual and partly heritable inter-calving interval which is fixed at birth depending on the animal's birth-mass as well as the mother's.
- A probability of becoming pregnant that increases with the number of years elapsed since the animal last gave birth.
- A minimum level of body condition – below which pregnancy will not occur.

Animals become sexually mature when of sufficient size and body condition:

$$L \geq \psi \cdot L_{\omega} \cap c \geq c_{\min} \quad \text{A - (25)}$$

The inter-calving interval is a phenotypical character that is expressed at birth depending on an animal's birth-mass, modulated by inheritance from its mother. The calving interval is an expected value in as much as it is not an integer but a continuous number used in the calculation of the probability that an animal will become pregnant given the time elapsed since it last gave birth. This number is determined from the weighted average of a calf's mass at birth and the mother's mass at birth. Thus, animals of low birth mass have longer inter-calving intervals than animals with high birth mass. Animals with low birth mass from mothers that also had low birth mass will have even longer inter-calving intervals. Both sexes are assigned a calving interval to allow for adding paternal inheritance in further development of the model. The weighted average is given by:

$$\bar{w} = H_c w_{\Omega} + (1 - H_c) w \quad \text{A - (26)}$$

Where  $w_{\Omega}$  is the mother's mass birth at birth and  $w$  is that of the calf. The inter-calving interval is given by:

$$I_c = \frac{(I_{\max} - I_{\min})}{1 + \exp(\vartheta(\bar{w} - w_G))} + I_{\min} + \text{Norm}(0, \sigma_I) \quad \text{A - (27)}$$

where  $\text{Norm}(\mu, \sigma)$  is a random deviate from a normal distribution with mean  $\mu$  and standard deviation  $\sigma$ , which allows for some variability, for example derived from paternal or even older intergenerational inheritance. It is required that  $\vartheta > 0$  and it is derived from reference inter-calving intervals and birth-masses:

$$\vartheta = \frac{\log\left(\frac{I_{\max} - I_{\min}}{I_K - I_{\min}} - 1\right)}{w_K - w_G} \quad \text{A - (28)}$$

Females that attain maturity become pregnant in the next breeding season. Becoming pregnant at age  $a$  for a female with a given inter-calving interval is a Bernoulli random variable;

$$P|a, I_c = \text{B}(p_{I_c, a-a_B}) \quad \text{A - (29)}$$

$$p_{I_c, a-a_B} = \text{N}(a - a_B + g_c \sigma_c, I_c, \sigma_c) \quad \text{A - (30)}$$

where  $\text{N}(x; \mu, \sigma)$  is a cumulative normal distribution with mean  $\mu$  and standard deviation  $\sigma$ .

### Feeding

The amount of food eaten per day by an animal is proportional to its body mass and depends on the amount of food available in its location on the feeding grounds and can be different for each sex, thus allowing for a crude form of "contest competition" between sexes. Otherwise, intra-specific competition is the form of "scramble competition". In terms of energy the intake is over a period of  $n$  days given by:

$$e_f = \frac{nE_p (w_f + w_l) \kappa}{q} \left( f_{\min} + \frac{f_{\text{range}}}{1 + \exp(-h_c (f - f_{50}))} \right) \quad \text{A - (31)}$$

For suckling calves the amount of energy acquired is directly proportional to the amount of milk produced by the mother, so that:

$$e_f = l q_m E_m \quad \text{A - (32)}$$

### Lactation

The amount of milk produced by a mother depends on her body condition and on the mass of the calf.

$$l = n \left( \frac{l_{\min} + u (w_l + w_f)}{1 + \exp(-d (c - l_{50}))} \right) \quad \text{A - (33)}$$

where  $w_l$  and  $w_f$  refer to the calf and  $c$  is the body condition of the mother. The energy expended by the mother is:

$$e_l = l E_m \quad \text{A - (34)}$$

### Basal metabolic rate (Watts)

$$W_B = 0.034 \left( 1000 (w_l + w_f) \right)^{0.75} \quad \text{A - (35)}$$

### Power required for locomotion (Watts)

The power of locomotion depends the animal's surface area and drag coefficient. The animal's surface area is given by:

$$A_s = 0.08 \left( 1000 (w_l + w_f) \right)^{0.65} \quad \text{A - (36)}$$

### The force resisting locomotion is

$$F_r = 0.5 \times \rho_{\text{seawater}} C_D A_s v^2 \quad \text{A - (37)}$$

and hence power:

$$W_m = \frac{F_r v}{q_m} \quad \text{A - (38)}$$

### Energy expended basal plus activity (FMR)

$$e_a = 86400 \times n (W_B + W_m) \quad \text{A - (39)}$$

### Male energy expenditure in the breeding season

It is assumed that mature males use additional energy in the breeding season while competing for females, with the cost of competition increasing as the proportion of males rises above 50%. This term helps to keep the sex ratio balanced near 50%. The energy expended is a multiplicative adjustment to the usual energy of activity.

$$e_B = e_a \left( \alpha_{\min} + \frac{\alpha_{\text{range}}}{1 + \exp(-\zeta (\alpha - \alpha_{50}))} - 1 \right) \quad \text{A - (40)}$$

where  $\alpha$  is the current sex ratio of the mature population as males per female.

### Net energy

An animal's net energy budget is:

$$e_{net} = e_f - e_a - e_B - e_g - e_F - e_l \quad \text{A - (41)}$$

If the net energy budget is negative, growth does not occur and the energy shortfall is made up by drawing on fat. If fat is depleted, any further shortfall is made up by catabolising lean mass. If lean mass loss falls below a threshold (30% of the mass given by the mass-length relationship) the animal dies from starvation.

When the energy budget is positive, food energy is converted first to replacing any lean mass previously catabolised and partitioned into growth and fat storage after the lean mass has been restored. Any surplus not used for growth is converted to fat.

### Annual cycle and migration

The animals have a typical baleen whale migratory cycle from breeding to feeding grounds and return. The beginning of the annual cycle is the nominal birthday of animals (day 1). Animals in the various reproductive classes have their own dates for migration to and from the feeding grounds. Table y shows the dates for the transitions between breeding and feeding times for the various classes of animals.

## THE POPULATION

The population is the collection of living animals stored in a doubly linked list. Animals are added at the end of the list at birth and removed at death. The state of each animal is updated for a specified number of days working through the list in order. By adding calves at the end of the list, the state of their mothers have already been updated before the calf is updated, thus allowing for the energetics of suckling to be based on the mother's current state.

## THE ENVIRONMENT

The animals move around an environment described by a grid in the form of a mapped array indexed by latitude and longitude. The size of the grid cells are large on the breeding grounds and migration latitudes, which are devoid of prey. In the feeding grounds the grid cells are much smaller so as to better capture the interactions between whales and prey. Any grid cell can be subdivided into smaller cells. Any position in terms of latitude and longitude is mapped to a single cell at the smallest scale that contains it.

The prey dynamics in each grid cell has a simple logistic model.

$$B_{p,t+n} = \left( B_{p,t} - \sum_{whales} qe_f \right) S_p^n + B_{p,t} (1 - S_p^n) \left( 1 + r_p \left( 1 - \frac{B_{p,t}}{K_{p,t}} \right) \right) \quad \text{A - (42)}$$

The carrying capacity for prey in each grid cell and the prey biomass are both set from the same mixture of bivariate normal distributions at the beginning of each season. There is currently no prey diffusion or advection between cells. A diagram of a grid showing the carrying capacity is shown in Fig 1. Within each season the carrying capacities ( $K_{p,t}$ ) are adjusted multiplicatively by a sine function to give a seasonal signature to production.

## FORAGING STRATEGY

Each whale remembers where it fed at each date during the last feeding season and the abundance of prey at each location. On setting off at the start of the next feeding season each animal heads towards the best location experienced last season (but with some random variation in speed and direction). Once on the feeding grounds foraging occurs according to the following strategy.

if the available food in the current cell (location) allows at least 95% of maximum food intake the animal does not relocate (food intake has a stochastic term so that different animals will experience different food intakes in the same location, so that not all animals necessarily relocate in the same time step).

Otherwise, the animal relocates:

if there is a local gradient of increasing prey abundance the animal follows the gradient and so moves to the adjacent cell with the greatest prey abundance



if there is no favourable gradient but the animal remembers a different location visited at around the same date last year with an adequate food supply, then the animal heads in that direction

otherwise, the animal sets off on a random bearing either east or west, in the range  $70^\circ$  to  $110^\circ$  or  $250^\circ$  –  $290^\circ$  respectively, at a speed of around 2 m.s-1. Animals are reflected at the outer grid boundaries, and hence there is no emigration.

if during the days spent relocating the animal enters a grid cell with prey abundance that allows it to feed at least one half of the maximum food intake it feeds there until the next time step. This means that an animal while relocating does not pass up the opportunity to follow a food gradient

At the end of each year, for each location and date where an animal fed the prey density it found is added to any previous memory it has of that location and date:

$$R_{t+1,\theta,\phi} = \mathcal{G}_{t,\theta,\phi} + \zeta R_{t,\theta,\phi} \quad \text{A - (43)}$$

If there is no previous memory at that date and location then a new memory is established:

$$R_{t+1,\theta,\phi} = \frac{\mathcal{G}_{t,\theta,\phi}}{1-\zeta} \quad \text{A - (44)}$$

The division by  $1-\zeta$  ensures that new locations and previously remembered locations are scaled consistently. Memories of feeding times and locations are expunged when:

$$R_{t,\theta,\phi}(1-\zeta) < f_{.50} \quad \text{A - (45)}$$

Thus, if an animal does not return to a place and time or the place and time no longer contain sufficient food it is eventually forgotten.

In species where calves accompany their mothers during the feeding season their first set of memories of good feeding grounds are set during this season. Thus yearlings visit the feeding grounds used by their mothers.

Animals do not feed whenever their body condition exceeds  $c_{max}$ .

**Table y. Whale year to calendar dates**

Date	Day	Date	Day	Date	Day	Date	Day
15/7	1	1/11	108	1/3	228	1/7	351
1/8	16	1/12	138	1/4	258	14/7	365
1/9	47	1/1	169	1/5	289	15/7	1
1/10	77	1/2	200	1/6	320		

#### Migration dates

Event	Class			
	Males	Pregnant	With calf	Resting
Leave Breeding Ground	46	46	76	46
Arrive Feeding Ground	106	106	131	106
Leave Feeding Ground	211	226	256	211
<b>Arrive Breeding Ground</b>	<b>301</b>	<b>341</b>	<b>341</b>	<b>301</b>

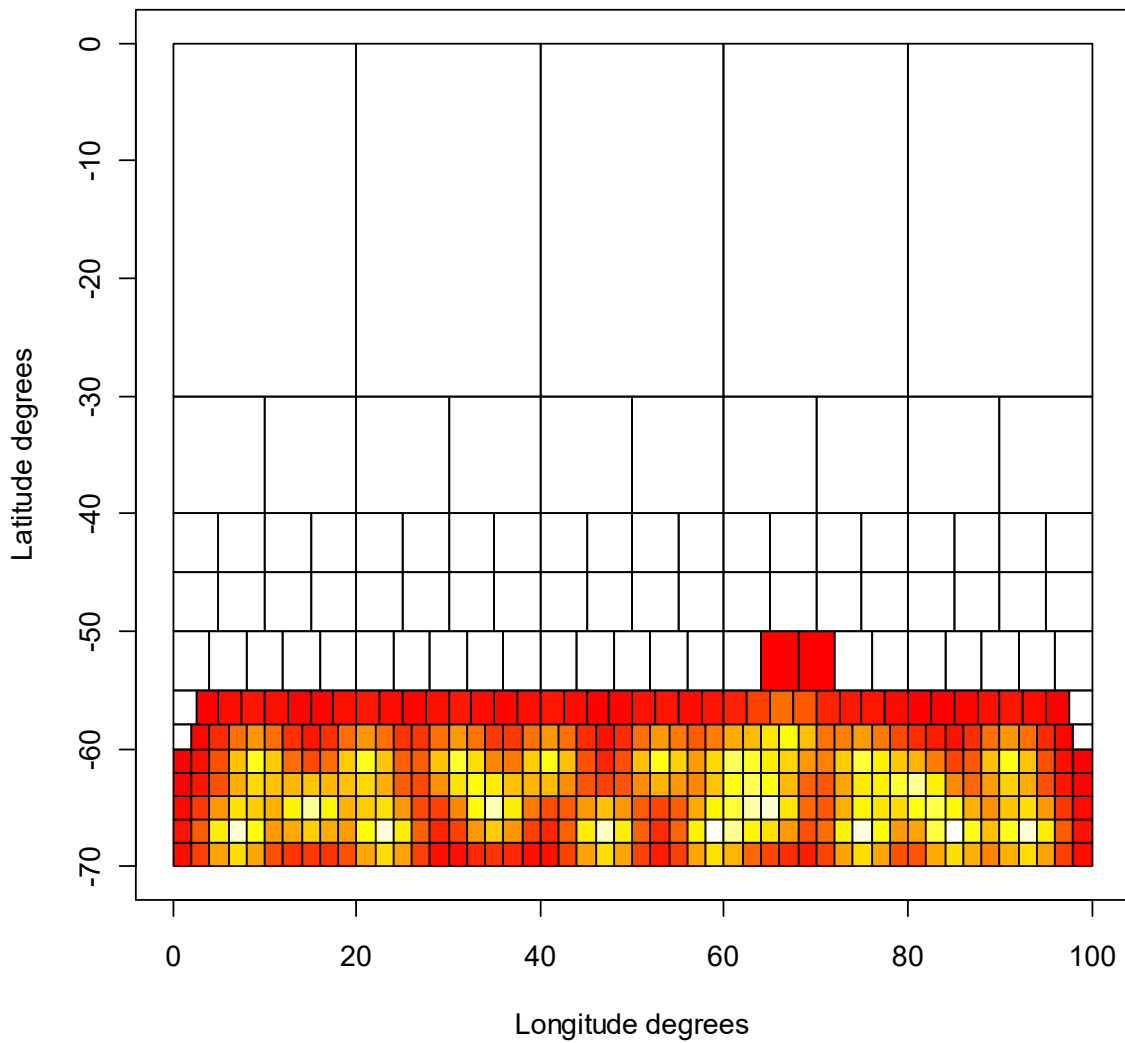


Fig A2. Grid plot of prey carrying capacity. The colours indicate where prey is not abundant as red and is more abundant yellow to white regions. The white cells outside the red region are devoid of prey.