Incorporating an individual based energetics model into the RMP trials software

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Abstract
This note outlines the incorporation of an individual-based energetic model to the RMP testing software. There are no technical difficulties in calling the individual based model software from the existing FORTRAN control program. A set of appropriate functions for incorporating the energetic model into the RMP framework have been written and tested successfully using a mixed language framework provided by the open-source "GNU compiler collection" (GCC).

At last year's Scientific Committee (SC65a) de la Mare undertook to develop software to allow the use of an individual-based energetic model (IBEM) (de la Mare, 2013) in the RMP trials software. This note reports on progress to date.

The conventional simulation testing framework used for RMP trials uses population models based on stock recruitment relationships derived from a Pella-Tomlinson model. Mortality rates were assumed density independent. A comparison between the properties of this class of model and an IBEM is presented in de la Mare (this meeting). This note describes the incorporation of the IBEM into the RMP trials software.

The IBEM uses individual animal models with a detailed energy budget to determine reproductive success and mortality in an environment where food has a stochastic and 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 Maximum Sustainable Yield (MSY) rates in the IBEM are determined by manipulating the amount of food available. Setting the amount of food to obtain a given $MSYR_{1+}$ is obtained by trial and error. First, a separate program ("IndividualWhales") is used to "spin up" the model to bring it to an unexploited state. This is population is then depleted to a low level using the same program to obtain a required rate of increase from a low population size. A separate program "IndividualR0" is used to estimate the rate of increase from the low population level to determine $MSYR_{1+}$. The amount of food is adjusted and the two programs re-run until the required $MSYR_{1+}$ is achieved. The state of the unexploited population is saved so that it can be used to initialise the IBEM from within the trials program so that the "spin up" does not have to be repeated for each trial. This setup exercise has to be conducted only once for each trial scenario.

Adding the model to the trials software is straightforward because it already configured to deal with models with different structures and parameters. This is brought about through calls to functions to (1): initialise the model, which is done once at the beginning of a series of trial runs, (2): reset the model to the initial management year in each trial, and (3): update the model each year under RMP management within each trial. The functions use the parameters set for each test and set the population values used in generating simulated survey data and other reporting values used in the RMP control program MANTST.

However, because the IBEM is stochastic the facility offered by the deterministic models of knowing carrying capacity (K) in each year for calculating depletion statistics is not available. The solution included in this first version of the software is to include two copies of the IBEM so that depletion statistics can be derived as the ratio of the abundance in the exploited copy of the model to that from the unexploited version. In each model the amount of food available at the beginning of each season is driven by the same set of random numbers, so that the differences in the exploited and unexploited populations derive only from exploitation. However, the depletion statistic will be affected by demographic stochasticity because the numbers of animals are different in each population. Also the foraging movements of animals between patches are stochastic, which will also contribute to random differences between the exploited and unexploited versions. While the random variations in food at the beginning of each feeding season can be kept identical, the random fluctuations in births and deaths and foraging patterns in each year cannot be kept aligned.

A new model option has been added to the MANTST program (OPTMOD = 6). During initialisation an IBEM initialisation function EINIT is called. This function reads the parameters required for the energetic model from a data file and reads a copy of the unexploited population from the spin-up program. This function also calculates the harvest rate required to drive the unexploited population to the required pre-management abundance in each trial. This is only approximate because each stochastic realisation of the model will have a different pre-management depletion.

The function EMRESET is called at the start of each trial to advance the population from the start date of historic whaling to the first year of management under the RMP. This period results in the population being driven to the degree of depletion specified in the trial by applying the pre-management harvest rate calculated in EINIT to the exploited population. The unexploited population is advanced to the first year of management.

The third function that completes the population modelling is STKUPDE, which advances both the exploited and unexploited populations one year at a time. Catches set by the RMP are removed from the exploited population over about 2 months of the feeding season. This is to ensure that catches are taken from age classes in proportion to their abundance. The linked list of animals stores them in natural age order and if the catches were not spread over a season a disproportionate number of younger animals might be taken.

The standard output file has the last column re-assigned to the unexploited abundance. Some minor changes will be needed to the programs used for the analysis and presentation of the results.

The software is now mixed language with slightly modified original FORTRAN code calling C++ functions for the population simulations. The changes to the FORTRAN code are very minor, merely setting up a new model type and the set of function calls for the new model option. The FORTRAN and C++ compilers are in the open-source GNU compiler collection (OSF, 2013), with the open-source" Netbeans" (Oracle Corporation, 2013) being used as the development environment (no software cost implications). This also makes the software easily portable between Windows and Linux operating systems. Unsurprisingly, the IBEM simulations are much slower (100 trials took about 2 weeks on a single processor) than the deterministic models, and so trials benefit from being run on multiple processors, with a small number of trials on each, with the results being re-assembled for the standard analysis software.

Test Results

I did not have time to produce a full set of results, but to illustrate that the model is working reasonably as expected I completed one set of 100 trials for an MSYR ~ 4% case with nominal initial depletion of 0.99. Fig 1 shows the results from a single trial. Fig 2 shows a summary from all 100 trials.

References

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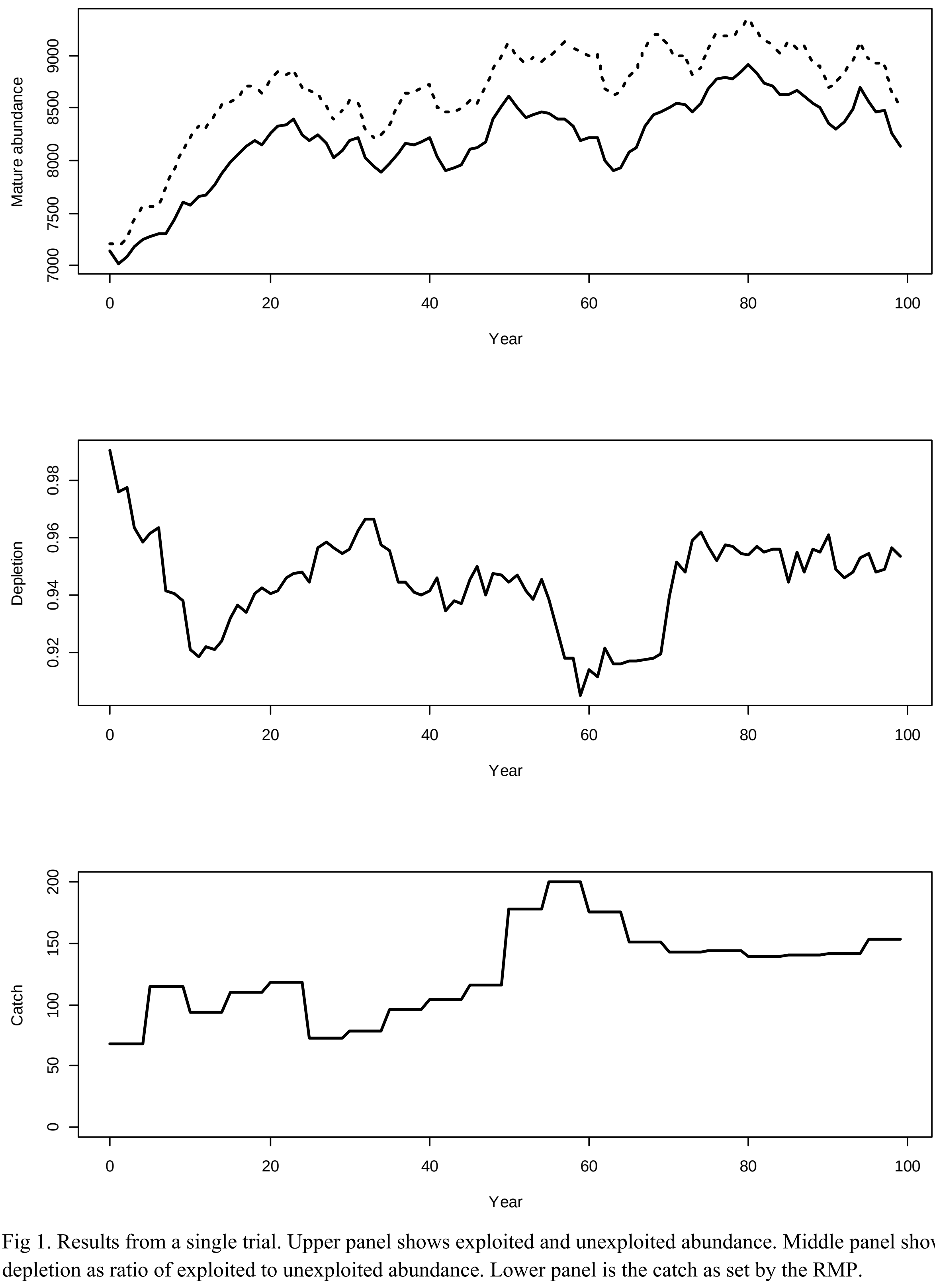

Fig 1. Results from a single trial. Upper panel shows exploited and unexploited abundance. Middle panel shows depletion as ratio of exploited to unexploited abundance. Lower panel is the catch as set by the RMP.

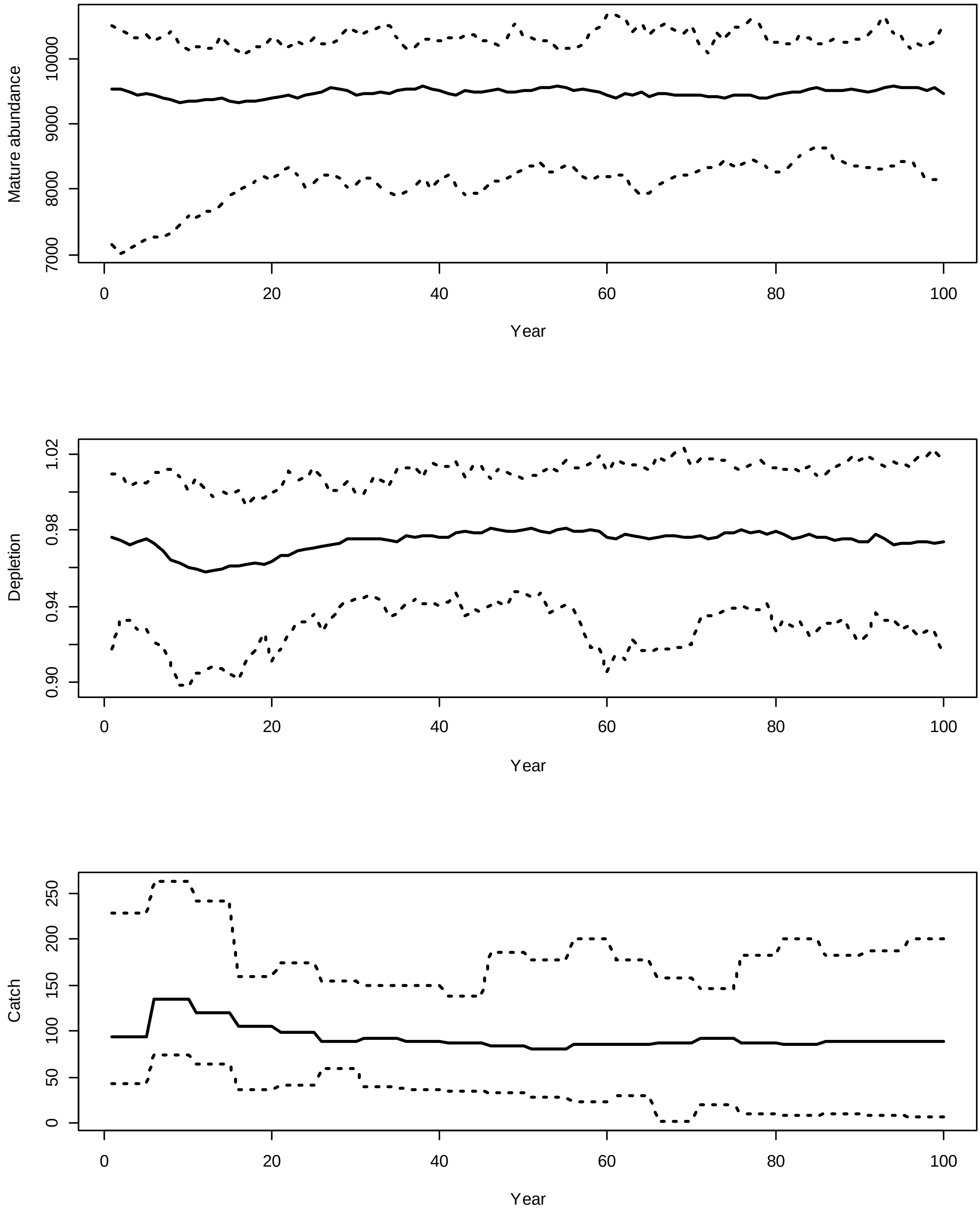

Fig 2. Summary results from 100 trials. The traces in each plot show the median and range of each variable for each year in the trials. Upper panel shows exploited and unexploited abundance. Middle panel shows depletion as ratio of exploited to unexploited abundance. Lower panel is the catch as set by the RMP.

APPENDIX

The animal state variables are

Age	a	years
day of year	n_d	
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	λ	decimal degrees
Longitude	φ	decimal degrees
Speed	v	$m.s^{-1}$
Direction	θ	decimal degrees
Pregnant (1 = pregnant)	P	
Maximum foetal growth rate	τ	$m.day^{-1}$
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 at places visited) (year, day, latitude, longitude, food density)

$H_{t,1...j}$

Migration state (function of day of year)

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

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 (with some random variation)

von Bertalanffy growth parameters

$L_{\infty S}$, k_S, t_{0S}

Mass length	A	$tonnes.m^{-1/B}$
Mass length	B	
Calving Interval	t_c	years
Foetal growth rate	g_f	$m.day^{-1}$
Length sexual maturity	L_m	m

Fixed demographic parameters

Female minimum mortality at age a	$M_{f,a;} = f(a, \beta_{f,1} \ldots \beta_{f,5})$	$year^{-1}$
Male minimum mortality at age a	$M_{m,a} = f(a, \beta_{m,1} \ldots \beta_{m,5})$	$year^{-1}$

Additional mortality hazard parameters (which is a function of body condition)		
Maximum value	M	year^{-1}
Body condition at M50	c_{M50}	
Rate parameter	g_M	
Female proportional length sexual maturity	ψ_f	
Male proportional length at sexual maturity	ψ_m	
Maximum age at sexual maturity	a_{max}	years
Sex ratio at birth	ρ	
Minimum viable calf length	L_{min}	m

Energetics parameters

Energy content of fat	E_f	J.kg^{-1}
Energy content of non-fat tissues	E_n	J.kg^{-1}
Energy content of milk	E_m	J.kg^{-1}
Energy content of prey	E_p	J.kg^{-1}
Maximum body condition	c_{max}	
Minimum body condition to conceive	c_{min}	
Daily feeding rate per unit body mass	κ	kg.tonne^{-1}
Assimilation efficiency	q	
Milk assimilation efficiency	q_m	
Growth efficiency	γ	
Proportion of lean mass (in m-L relation)	R	
Body condition at birth	ν	
Male breeding FMR/BMR	ξ	
Drag coefficient	C_D	
Density of seawater	$\rho_{seawater}$	kg.m^{-3}
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 abundance)		
Prey abundance range	$f_{f\,range}$	
Prey abundance at food intake inflection	f_{f50}	tonnes
Rate parameter	h_f	tonnes^{-1}
Feeding parameters for males (a function of prey abundance)		
Prey abundance at 50% food intake	f_{m50}	tonnes
Rate parameter	h_m	tonnes^{-1}
Growth as a function of body condition		
Maximum relative growth	$g_{\max}$	
Body condition at 50% point	c_{L50}	
Rate parameter	ε	
Foetal growth as a function of body condition		
body condition at 50% point	$c_{\tau 50}$	
Rate parameter	η	
Milk production as a function of body condition		
Body condition at 50%	l_{50}	

Rate parameter d

Milk production as a function of calf size

Minimum production	l_{min}	kg day^{-1}
Increase per unit calf mass	u	kg.(day.tonne)$^{-1}$

Common demographic parameters

Probability of conception for calving interval and time since last birth

$p(I, a - a_B)$

Calving interval probabilities

Mean of calving interval distribution	$I_{1...4}$	
Std. dev. of calving interval distribution	$\sigma_{1...4}$	
Birth mass under good food conditions	w_G	tonnes
Coefficient of change with birth mass	G	
Fat ratio at birth	Φ	

Timing parameters (day of year)

Birthday	t_0
Conception	t_c
Arrive on breeding grounds	$t_{b...}$
Migration towards feeding grounds	$t_{1...}$
Arrive on breeding grounds	$t_{2...}$
Migration towards breeding grounds	$t_{3...}$

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 daily survival probability	S_p
Prey maximum daily recruitment	r_p

Relations

Length and growth

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

To allow for food dependence, growth is modelled incrementally;

$$L_{t+n} = L_t + \frac{n}{365}L_{\infty\bullet}k'\exp\left(-k'\left(\Omega a+\frac{n_d+0.5n}{365}-t_{0\bullet}\right)\right) \quad \text{A - (2)}$$

where n is the number of days elapsed and k' is the growth constant adjusted for body condition given by:

$$k' = \frac{k_{\bullet} g_{\max}}{\Omega\left(1+\exp\left(-\varepsilon\left(c-c_{L50}\right)\right)\right)} \quad \text{A - (3)}$$

As a consequence, the specified growth curve represents the sizes animals reach when they can feed to satiation. Otherwise, under worsening food conditions animals will grow more slowly. If $g_{\max}$ is greater than unity 'catch up' growth can occur when energetically feasible but this is truncated so that an animal cannot exceed the size at age on its individual growth curve. 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):

$$L_{\infty} = L_{\infty,Q}\sqrt{\inf\left(\left\{\frac{L_B}{L'_B},1\right\}\right)} + \text{Norm}\left(0,0.2\right) \quad \text{A - (4)}$$

where:

$$L'_B = \sqrt[B]{\frac{w_G}{A}} \quad \text{A - (5)}$$

and

$$k = k_Q + \text{Norm}(0.,0.01) \quad \text{A - (6)}$$

where Norm(.) is a random variable. L_{∞} and k are perfectly positively correlated. The value of t_0 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)

$$\Delta w_l = RA\left(L_{t+n}{}^B - L_t{}^B\right) \quad \text{A - (7)}$$

Hence energy used in growth is

$$e_g = \Delta w_l \frac{E_n}{\gamma} \quad \text{A - (8)}$$

Foetal growth

Foetal growth rate is assumed to be constant in terms of length, but dependent on the body condition of the mother.

$$L_{F,t+n} = L_{F,t} + \frac{n}{365}\left(\frac{\tau}{1+\exp\left(-\eta\left(c-c_{\tau 50}\right)\right)}\right) \quad \text{A - (9)}$$

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

$$\Delta w_F = A\left(L_{F,t+n}{}^B - L_{F,t}{}^B\right) \quad \text{A - (10)}$$

Energy used in foetal growth is:

$$e_F = \Delta w_F \frac{(1-\Phi)E_n + \Phi E_f}{\gamma} \quad \text{A - (11)}$$

The partitioning of foetal growth to fat tissue (Φ) 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:

$$M_{\bullet,a} = \beta_{\bullet,1} \exp(-\beta_{\bullet,2} a) + \beta_{\bullet,3} + \exp(\beta_{\bullet,4}(a - \beta_{\bullet,5})) \quad \text{A - (12)}$$

The hazard of death is given by:

$$z = M_{\bullet,a} + \frac{M}{1 + \exp(-g_M(c - c_{M50}))} \quad \text{A - (13)}$$

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:

$$\text{p}(\text{death}) = 1 - \exp\left(\frac{-zn}{365}\right) \quad \text{A - (14)}$$

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 inter-calving interval.
- A probability of becoming pregnant that is different for each inter-calving interval class, which 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.

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

$$P|a, t_c = \text{B}(p_{t_c, a-a_B}) \quad \text{A - (15)}$$

The inter-calving interval is a phenotypical character that is expressed at birth depending on an animal's birth-weight and the inter-calving interval of the mother ($t_c[Q]$);

$$t_c|t_c[Q] = \text{N}(i + 0.5; I_{t_c[Q]} + G_{t_c[Q]}(w_G - w_B), \sigma_{t_c[Q]}) - \text{N}(i - 0.5; I_{t_c[Q]} + G_{t_c[Q]}(w_G - w_B), \sigma_{t_c[Q]}) \quad \text{A - (16)}$$

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

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:

$$e_f = \frac{nE_p\left(w_f + w_l\right)\kappa}{q}\left(f_{\bullet\min} + \frac{f_{\bullet range}}{1+\exp\left(-h_\bullet\left(f - f_{\bullet 50}\right)\right)}\right) \quad \text{A - (17)}$$

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

$$e_f = lq_m E_m \quad \text{A - (18)}$$

Lactation

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

$$l = n\left(\frac{l_{\min} + u\left(w_l + w_f\right)}{1+\exp\left(-d\left(c - l_{50}\right)\right)}\right) \quad \text{A - (19)}$$

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:

$$e_l = lE_m \quad \text{A - (20)}$$

Basal metabolic rate (Watts)

$$W_B = 0.034\left(1000\left(w_l + w_f\right)\right)^{0.75} \quad \text{A - (21)}$$

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:

$$A_s = 0.08\left(1000\left(w_l + w_f\right)\right)^{0.65} \quad \text{A - (22)}$$

The force resisting locomotion is

$$F_r = 0.5\times\rho_{seawater}C_D A_s v^2 \quad \text{A - (23)}$$

and hence power:

$$W_m = \frac{F_r v}{q_m} \qquad \text{A - (24)}$$

Energy expended basal plus activity (FMR)

$$e_a = 86400 \times n\left(W_B + W_m\right) \qquad \text{A - (25)}$$

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.

$$e_B = e_a\left(\alpha_{\min} + \frac{\alpha_{range}}{1+\exp\left(-\zeta\left(\alpha - \alpha_{50}\right)\right)} - 1\right) \qquad \text{A - (26)}$$

where α is the current sex ratio of the mature population as males per female.

Net energy

An animal's net energy budget is:

$$e_{net} = e_f - e_a - e_B - e_g - e_F - e_l \qquad \text{A - (27)}$$

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 into growth after the lean mass has been restored. Any surplus is converted to fat.

Annual cycle and migration

The animals have a typical baleen whale migratory cycle from breeding to feeding grounds. 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 ENVIRONMENT

The animals move around an environment described by a grid in the form of a "ragged" array. 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.

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

$$B_{p,t+n} = \left(B_{p,t} - \sum_{whales} qe_f \right) S_p^{\ n} + B_{p,t} \left(1 - S_p^{\ n} \right) \left(1 + r_p \left(1 - \frac{B_{p,t}}{K_{p,t}} \right) \right) \qquad \text{A - (28)}$$

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 no prey diffusion or advection between cells. A diagram of a grid showing the carrying capacity is shown in Fig x. 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° to 110° or 250° – 290° 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 around 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

Calves accompany their mothers during the feeding season, and so their first set of memories of good feeding grounds is 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}.

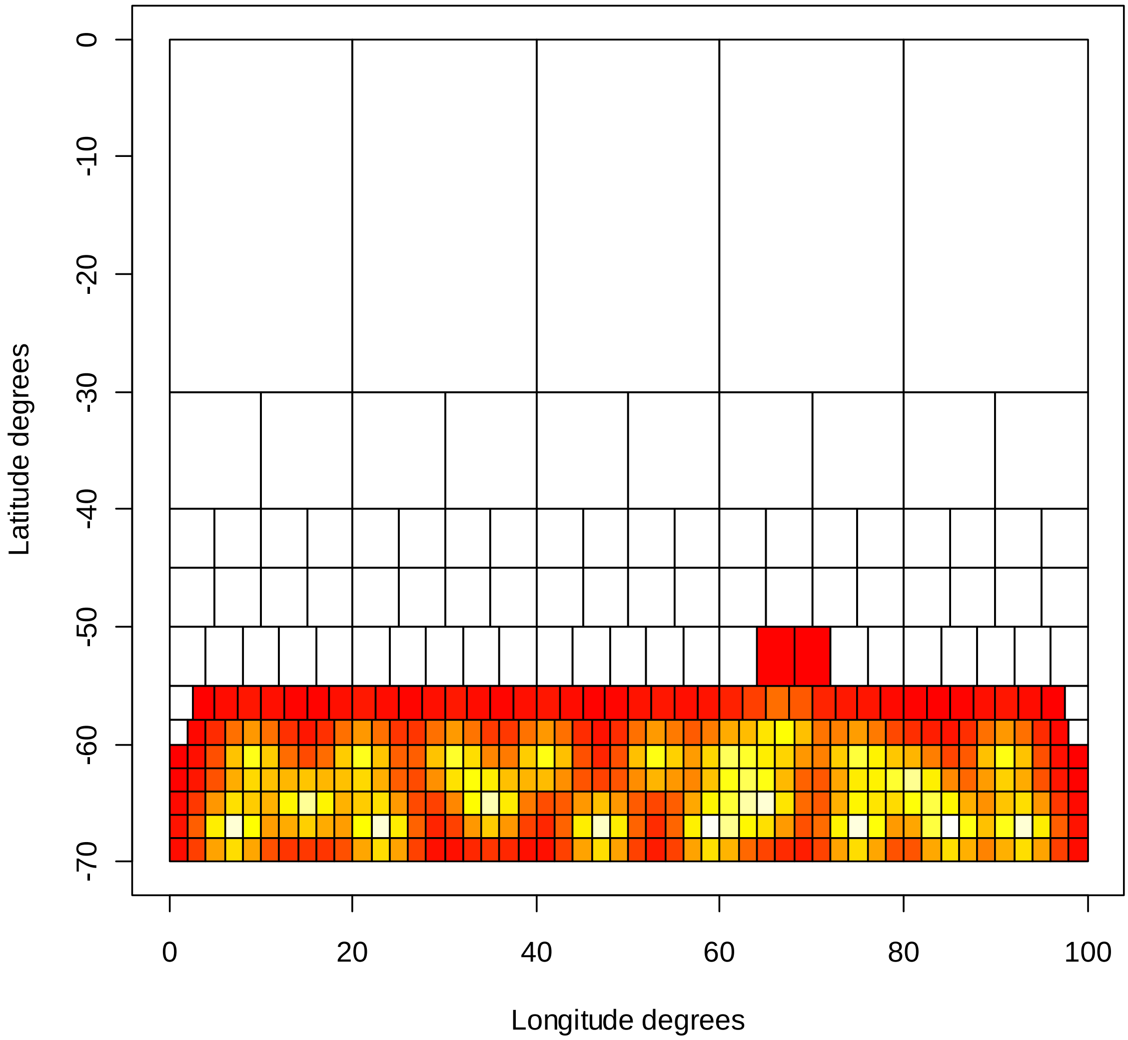

Fig 116. Grid plot of prey carrying capacity. The colours indicate where prey is not abundant as red and is more abundant yellow to white regions. The white cells outside the red region are devoid of prey.

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
Arrive Breeding Ground	301	341	341	301