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An individual-based energetics model for
rorqual foraging dives.

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where F_t is the stomach fullness at time t , β is the digestion rate and Δt is the interval between feeding dives. If an animal is replete it does not dive again until stomach fullness declines to:

$$F \leq \varepsilon \phi_{\max} \quad (1.3)$$

This requires the animal to not initiate another feeding dive for an interval given by:

$$\Delta t = \frac{-\log\left(\frac{\varepsilon \phi_{\max}}{F_t}\right)}{\beta} \quad (1.4)$$

where ε is the proportion of fullness remaining before the next feeding dive is undertaken. If after a dive an animal returns to the surface but is not replete then it undertakes another feeding dive after a surface interval $\Delta t = t_s$, where t_s is the inter-dive interval. While at the surface, digestion occurs according to equation 1.3.

Once initiated a feeding dive lasts so long as dive-time $\Delta t \leq t_d$ where t_d is the maximum dive duration, and the number of lunges in the dive $n_\lambda \leq \lambda_{\max}$, but will also be terminated if the animal becomes replete. Thus a feeding dive ends whichever condition attains first. During a dive an animal only makes a feeding lunge if the local krill density is above a threshold value. That threshold is set such that the energy obtained from the food will cover the energetic cost of the lunge, which is calculated as follows:

The food in kg ingested during a single lunge (designated λ) is the krill density (kg.m^{-3}) multiplied by the volume (m^3) of water filtered by the lunge;

$$\phi_\lambda = \rho_k V \quad (1.5)$$

The lunge engulfment volume is given by:

$$V = \nu M_L \quad (1.6)$$

where ν is the (constant) specific lunge volume ($\text{m}^3.\text{kg}^{-1}$) and M_L is the animal's lean mass (kg). Lean mass is accounted for in the individual based energetics model, but for the purposes of the illustrative results presented here it is taken to be:

$$M_L = p_L A L^B \quad (1.7)$$

where $A L^B$ is the commonly used form of mass-length relationship which gives the total body mass of an animal of length L and p_L is the proportion of body mass that is lean mass.

Following the approach of Potvin *et al.* 2012 the energy dissipated (Joules [J]) in one lunge is calculated as:

$$E_\lambda = t_\lambda M (a + bL) \quad (1.8)$$

where:

- t_λ is a scaling factor (units seconds); in effect the nominal lunge duration
- M is total body mass in (kg)
- a is the intercept of the relationship between lunge power and length (W.kg^{-1})
- b is the slope of the relationship between lunge power and length ($\text{W.kg}^{-1}.\text{m}^{-1}$)
- L is the body length (m)

This has the effect that lunge energy is supra-linear with body size as indicated in Potvin *et al.* 2012. To this must be added the energy dissipated due to metabolism:

$$E_M = (t_\lambda + t_i) \eta M^\xi \quad (1.9)$$

where t_i is the inter-lunge interval and η and ξ are the constants of an allometric relationship between body mass and metabolic rate (W). The other energy dissipation is due to locomotion between lunges. The power of locomotion depends the animal's surface area and drag coefficient. The animal's surface area is given by:

$$A_s = 0.08 M^{0.65} \quad (1.10)$$

The force resisting locomotion is

$$f_l = 0.5A_s\rho_w C_D v^2 \quad (1.11)$$

Where ρ_w is the density of seawater, C_D is the drag coefficient and v is the swimming speed between lunges. The food energy expended from swimming is:

$$E_l = \frac{f_l v t_l}{q_l} \quad (1.12)$$

Where q_l is the conversion rate of food energy into work. Thus the energy expended during a lunge is $E_\lambda + E_M + E_l$. The energy gained from food in a lunge is:

$$E_f = \phi_\lambda J_k \theta \quad (1.13)$$

Where J_k is the energy density of krill (J.kg^{-1}) and θ is the proportion of food energy assimilated. Thus the minimum density for a feeding lunge is given by:

$$\rho'_k = \frac{(E_\lambda + E_M + E_l)}{V J_k \theta} \quad (1.14)$$

which is the krill density where the amount of food ingested recovers the energetic cost of the lunge.

There are two types of feeding dives: exploratory and immediate. Provided the conditions for a dive are met, exploratory dives are undertaken at regular intervals to determine the depth of the highest krill density. The animal dives to its maximum depth z_{\max} making a feeding lunge whenever the local krill density exceeds the threshold ρ'_k . The animal remembers the depth at which the maximum krill density was found, and after reaching z_{\max} returns to that depth to continue feeding until the maximum number of lunges, maximum fullness or maximum dive-time is used up. An immediate dive omits the full depth exploration and instead the animal dives immediately to the last known depth of highest krill density and continues to feed. The exploratory dives adjust the animal's foraging to the changes in the density profile of krill with time of day (due to vertical migration and redistribution).

Test krill model

In the examples presented here, krill vertical distribution is modelled as having an expected krill density with depth which is proportional to the probability density of a normal distribution with mode z_t and standard deviation σ_t . The krill distribution profile, obviously, is truncated at the sea-surface. Fig 1 shows an example of such a profile as used in the illustrative examples that follow. The parameters of this distribution vary by time of day. In the examples below σ_t is fixed (at 50m) and z_t is related to the time of day by a double ogive given by:

$$z_t = \frac{-100}{\left(1 + e^{k_r(t-t_{r50})}\right)\left(1 + e^{-k_s(t-t_{s50})}\right)} \quad (1.15)$$

Where k_r and k_s determine the rate of change of modal depth at sunrise and sunset respectively and t_{r50} and t_{s50} are related to the time of sunrise and sunset respectively, but allowing for specific time differences to be applied. Given this modal-density depth profile a specified number of krill layers of random thickness (at a resolution of one metre) are assigned at random depths between the surface and two standard deviations below the mode. In each layer the krill density is set from the relative expected krill density multiplied by a random lognormal variate with an expected value of 1.0 and a specified coefficient of variation. The densities are added together wherever randomly assigned layers overlap. The sum of the krill densities over the set of layers are normalised to have a specified krill density per unit surface area. The densities in each layer are thus densities of krill per unit volume as required in the feeding model. Fig. 2 shows two examples the resulting krill density profiles for two different numbers of krill layers.

A five layer model is used in the examples that follow. The krill density profile is updated each hour and randomly redistributed into layers as described above. Whales make an exploratory dives each hour when the conditions for making a dive are satisfied.

Illustrative results

Fig 3 shows examples of two different feeding profiles of an 8.5m minke whale over a 48 hour period at two krill densities. The relationship between krill density and the amount of food ingested is shown in Fig 4. The

parameter values used in these calculations are shown in table 1. The shape of the food ingested per day reasonably conforms to a type II functional relationship (Holling, ??), but slightly right-shifted to include a threshold non-zero prey density. The calculated values show some bumps. These arise because of the non-continuous nature of diving and lunging behaviour. For example, for a slight increase in krill density, repletion will occur with fewer lunges or with one less dive. However, the total food consumed for the day may not increase roughly in proportion to krill density because fewer dives or lunges fitted into the day. A further increase in krill density will thereafter increase the total food consumed, until the next step down in the numbers of dives or lunges in the day. Fig 5 shows the number of feeding lunges per day as a function of prey density.

A number of these parameters used in these illustrative examples will require further refinement; the values used here are for demonstrating the basic properties of the feeding model. However, the results may not be particularly sensitive to the values of some of the parameters, and this will require further investigation.

References

- de la Mare, W. K. 2014. The relationship between MSY_{Rmat} and MSY_{R1+}, based on energetics modelling. SC/65b/EM04 presented to the IWC Scientific Committee. 17pp.
- Goldbogen, J. A. *et al.* 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J. Exp. Biol.* 214:131-46.
- Potvin, J., Goldbogen, J. A. and Shadwick, R. E. 2012. Metabolic expenditures of lunge feeding rorquals across scale: Implications for the evolution of filter feeding and the limits to maximum body size. *PLOS ONE* 7:9.

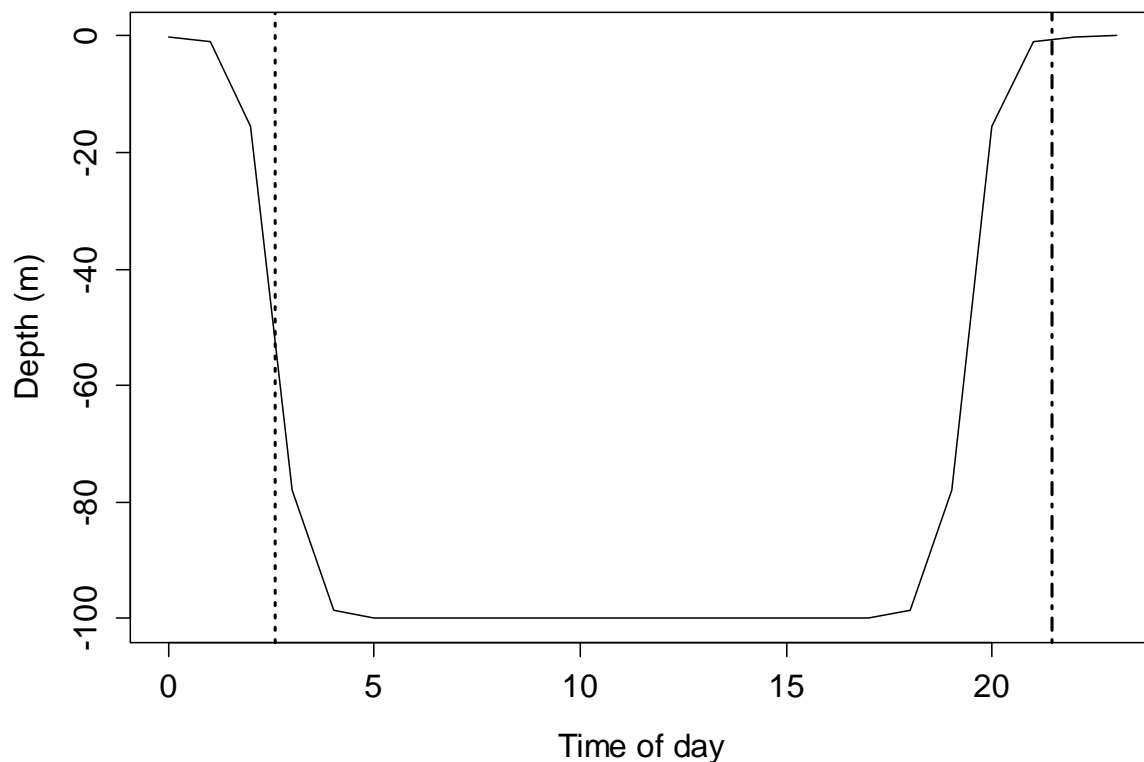


Fig 1. Modal depth of vertical distribution of krill by time of day. The vertical lines show the times of sunrise and sunset. This example is for January 21 at 65°S.

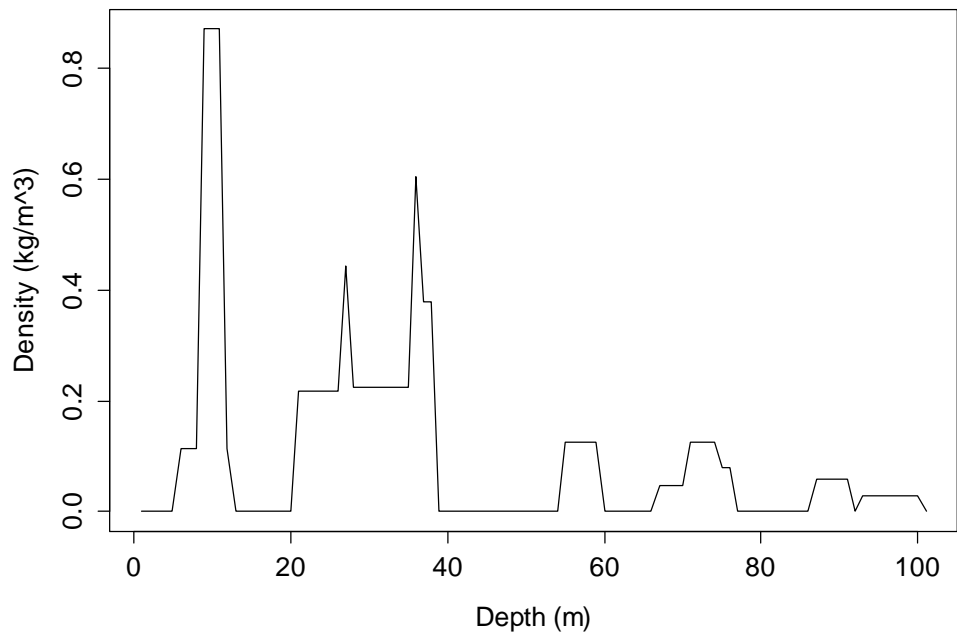
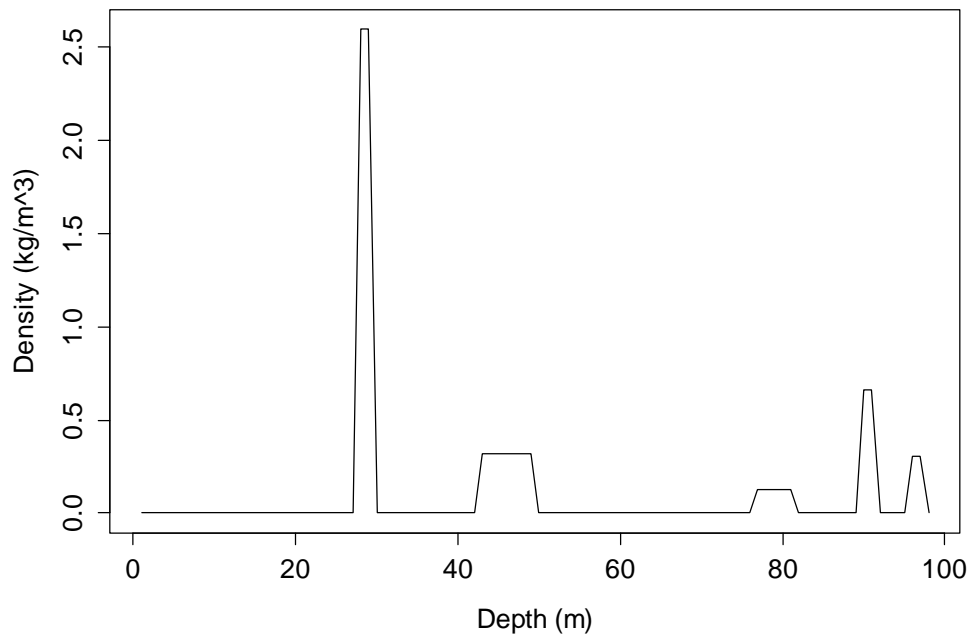


Fig 2. Upper panel is a realisation of the randomised krill density-depth profile with five krill layers. The lower panel has ten krill layers. In both these realisations the standard deviation of the density determining normal distribution (σ_r) is set at 50m and the coefficient of variation of local krill density is 0.5. These examples apply to midnight.

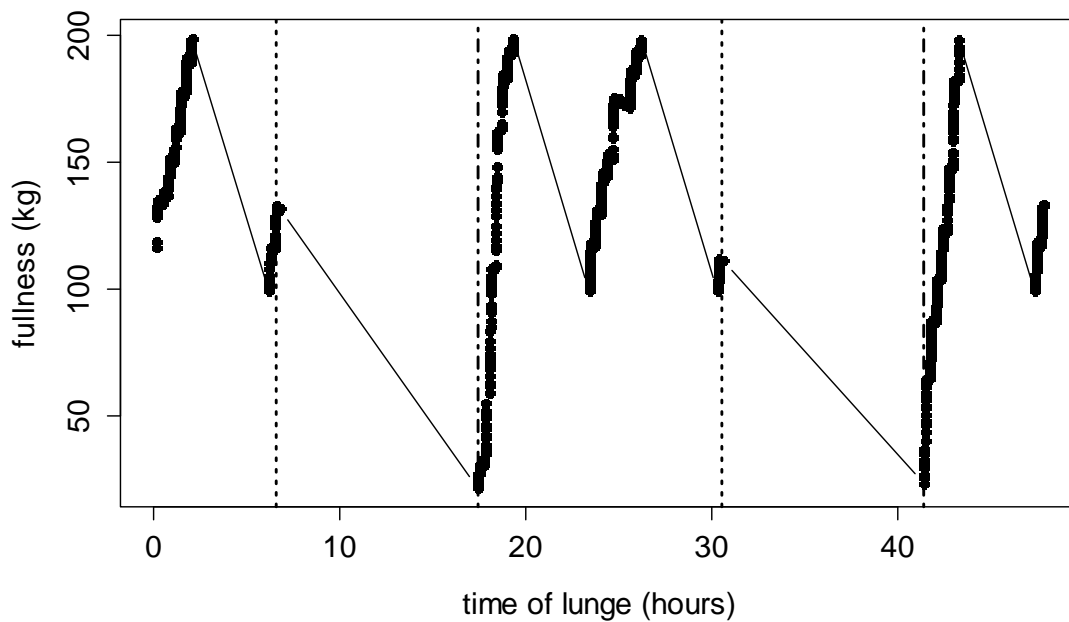
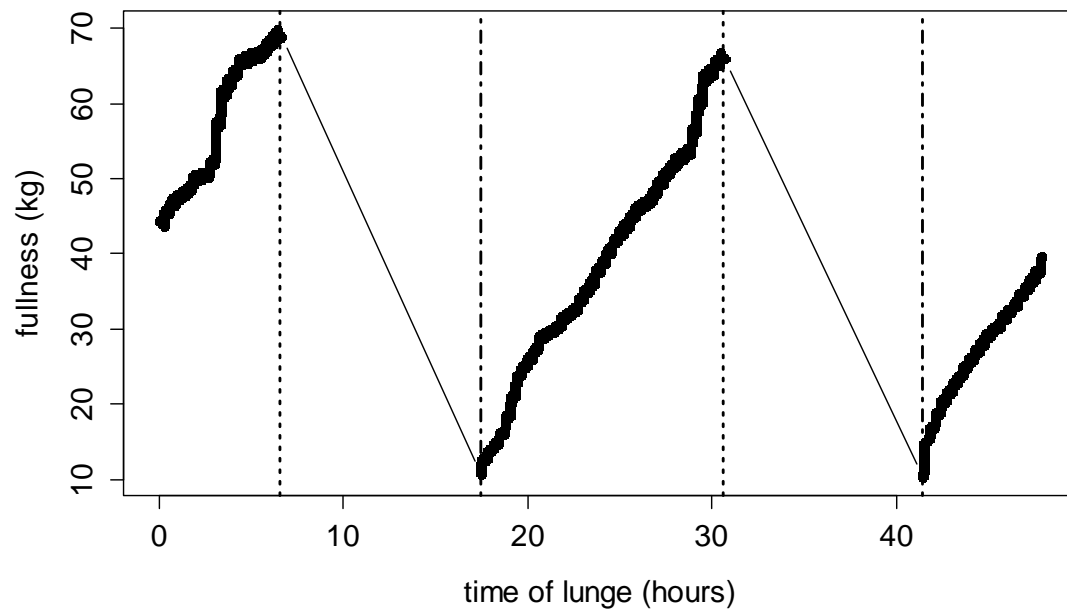


Fig 1. Feeding profiles at different krill densities (upper = $1. \text{ kg.m}^{-2}$, lower = $10. \text{ kg.m}^{-2}$). The dotted and dashed lines show the ends and starts of the feeding day respectively. Each feeding lunge is plotted as a point. The upper panel shows that at this krill density the animal is unable to feed to repletion (which is set here at about 200 kg) during the feeding day, and hence feeds continuously during the feeding day. In the lower panel the animal begins feeding at the start of the feeding day (about hour 18) and by 20 hours it is replete, and so stops feeding until about hour 24 at which time it feeds again until replete at about 27 hours, pauses again until around 30 hours and feeds for a short time until the end of the feeding day.

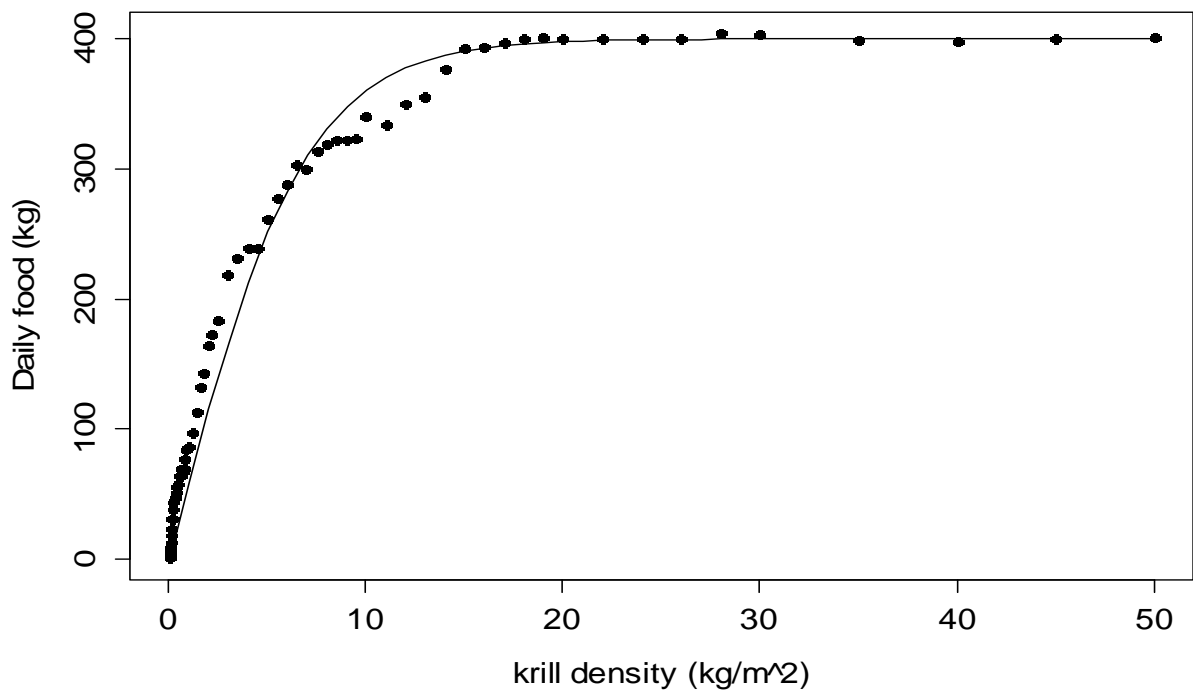


Fig 2. The functional response showing the relationship between krill density and the amount of food eaten.

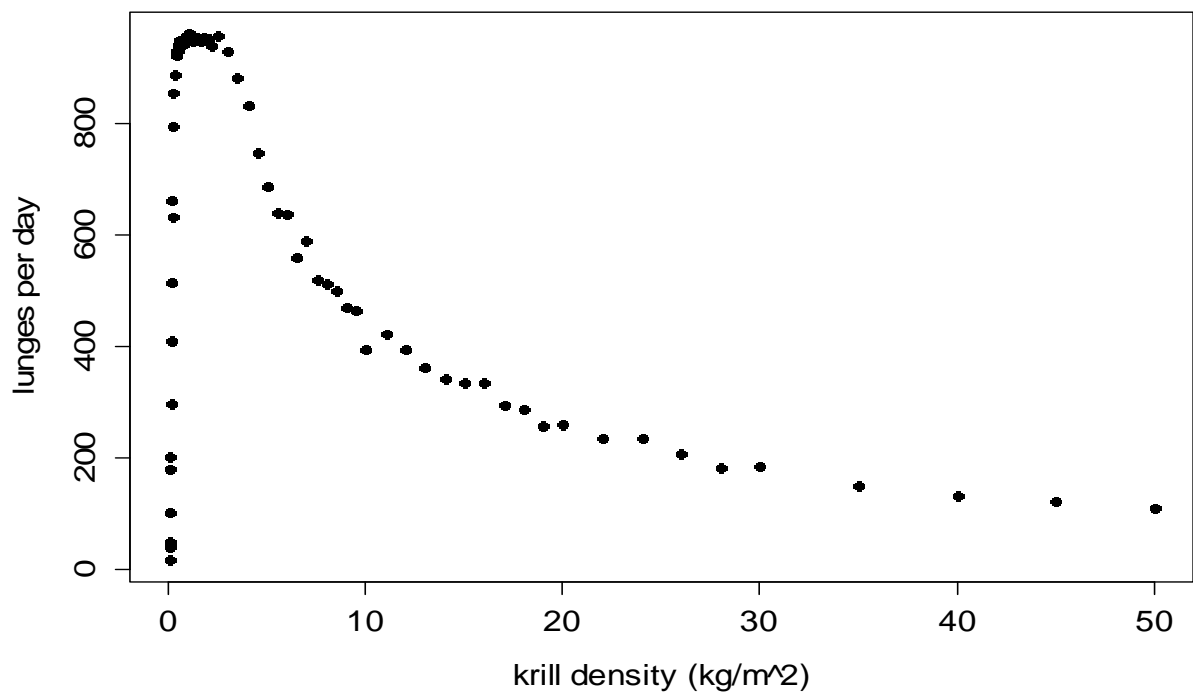


Fig 3. Number of feeding lunges per day for a range of krill densities. At low krill densities the number of lunges is low because feeding lunges only occur when the local krill density is above the breakeven threshold.

Minke whale feeding model coefficients.

Maximum daily ration:	ϕ_{\max}	= 0.05*(body mass) kg
Maximum stomach fullness	γ	= 0.5
Fullness to restart feeding:	ε	= 0.25
Digestion rate	β	= $\ln(0.5)/4 \text{ hr}^{-1}$
Body length:	L	= 8.5 metres
Mass length scaling factor:	A	= 26 (gives mass in kg)
Mass-length exponent:	B	= 2.675
Proportion of lean mass:	p_L	= 0.7
Maximum dive depth	z_{\max}	= 100 m
Nominal lunge duration	t_λ	= 3.35 s
Inter-lunge interval	t_i	= 25 s
Maximum dive time	t_D	= 600 s
Minimum surface time	t_s	= 300 s
Lunge power intercept	a	= 0.4 W.kg ⁻¹
Lunge power slope	b	= 0.2 W.kg ⁻¹ .m ⁻¹
Specific lunge volume	v	= 0.0003393 m ³ .kg ⁻¹
Swimming speed on surface	v_s	= 0.7 m.s ⁻¹
Swimming speed during dive	v	= 2. m.s ⁻¹
Drag coefficient	C_D	= 0.002
Density of seawater	ρ_w	= 1025 kg.m ³
Surface area	A_s	= 0.08M ^{0.65} m ²
Energy gained from prey	J_k	= 4 600 000 J.kg ⁻¹
Metabolic rate	P_M	= 3.4M ^{0.7} W
Convert metabolism to work	q	= 0.2
Night feeding is True		
Inflection in krill descent term	t_{r50}	= sunrise
Rate of krill descent	k_r	= $\ln(19)$
Inflection on krill ascent term	t_{s50}	= sunset - 2
Rate of krill ascent	k_s	= $\ln(19)$

The values d , a and b were manipulated to get ~56 kJ lunge energy for an 8.5 m animal.

These values lead to a break-even requirement for just over 800 lunges per day at a prey density of 0.05 kg.m⁻³.