**Supplementary Information to**

**Combining bioenergetics and movement models to improve understanding of the population consequences of disturbance**



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# Supplementary Information A. Description of the bioenergetic model following the Overview, Design and Details (ODD) protocol.

Below we present a generic description of the bioenergetics models used in this paper following the ODD protocol (Grimm et al. 2020), which was developed for describing agent-based models. The sub-models developed for each species are described in later sections.

At the end of the ODD we present a table with parameter values for the three modelled species. For details on how each submodel was tailored to species-specific processes, see Harwood et al. (2020, 2022).

## Purpose and patterns

The purpose of the bioenergetic models is to investigate how a series of disturbance events, which might for example occur during the installation of foundations for an offshore windfarm, may affect the energy intake and vital rates of three marine mammal species.

To evaluate whether or not the simulations of the bioenergetic models provided realistic outputs, we compared model outputs for an undisturbed population to published values using the pattern-oriented modelling approach. The outputs chosen were: seasonal changes in body condition or weight of females; calf/pup survival; and birth rate (proportion of reproductively mature females giving birth each year).

## Entities, state variables, and scales

The model is not spatially explicit and is composed of one kind of entity: individuals of the modelled species. It follows individual females from an initial age until their death, the time of which is determined at the beginning of each simulation. All offspring of each female are followed from embryonic implantation up to weaning. The model proceeds in discrete time steps of 1 day, and each year consists of 365 days.

Individuals are characterised by the following state variable: age, length, structural (core) mass, reserve mass, life expectancy and energy assimilation (Table A1). These vary over time depending on an individual’s life history stage and the resource densities it encounters.

The life expectancy of each simulated individual is determined by sampling at random from a cumulative curve describing the variation in daily survival with age. We used the approach of Barlow and Boveng (1991) and derived these curves by using the approach developed fitting a 5-parameter Siler model by Barlow and Boveng (1991) to published age- or stage-specific survival data for each species (see SI A for species-specific details). However, simulated individuals are assumed to experience an additional risk of death if their body condition falls below a starvation threshold, which is based on the minimum body condition observed in free-ranging animals (see SI A and B for species-specific details, including parameterisation of this threshold).

Females can be in one of four life history stages: ‘resting’ (i.e. neither pregnant nor lactating, this includes the juvenile period from weaning to first conception); ‘pregnant (but not lactating)’; ‘lactating (but not pregnant)’; and ‘lactating & pregnant’ (Figure A1).

Table A1 provides an overview of the state variables considered in the models.

Table A - State variables and deduced state variables (calculated using other state variables) of the modelled individuals.

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable** | **Code** | **Unit** | **Description** |
| ***For all individuals*** | | | |
| *a* | age | days | Age |
| *L* | L | cm | Structural length |
| *S* | Sa | kg | Structural (core) mass |
| *F* | F | kg | Reserve mass |
| *W* | W | kg | Total body mass (S + F) |
|  | GR | kg/day | Daily growth rate (derived from S) |
| *ρ* | rho | - | Relative body condition (F/W) |
|  | life\_expectancy | days | Life expectancy derived from cumulative survival curve |
| *I* | Ir | MJ/day | Assimilated energy |
| *CM* | Cm | MJ/day | Field metabolic costs |
| ***For pregnant or lactating females and their offspring*** | | | |
| *life history stage* | - | - | One of: resting; pregnant; lactating; pregnant & lactating |
| *Fneonate* | F\_preg, skipping\_point | kg | Threshold for starting or continuing pregnancy |
| *Sfoetus* | S\_foetus | kg | Foetus size |
| *GRfoetus* | GR\_foetus | kg/day | Growth rate of foetus |
| *IMC* | Im\_C | MJ/day | Calf/pup assimilated energy from milk |
| *IC* | Ir\_C | MJ/day | Calf/pup assimilated energy from prey |
| *CL* | CLact | MJ/day | Daily cost of lactation |
| *CMC* | Cm\_C | MJ/day | Field metabolic costs for calf/pup |

## Process overview and scheduling

Figure A1 provides a flow chart outlining the model processes. An individual’s assimilated energy varies with resource density, its body condition, structural mass and life history stage. Pregnancy begins on the day on which the embryo implants, which is determined by the day of the year on which the simulated individual was born. Foetal mass is included in maternal structural mass for the calculation of metabolic and growth costs. At specific point in the pregnancy (the “decision day”), a female can abort the foetus if her reserves are too low. A calf/pup depends entirely on milk provided by its mother until a specified day of lactation (*TN*). Calf/pup demand for milk depends on its body condition and age. The amount of milk provided by the female depends not only on calf/pup demand but also on her body condition. Females abandon lactation if their relative body condition is close to the starvation threshold (see below). At a specified point during the lactation period, the calf/pup starts foraging on its own and its foraging efficiency increases with age. Grey seal and harbour seal pups fast for a period after weaning, and their foraging efficiency is set to zero during this time.

If assimilated energy on a particular day exceeds the combined costs of metabolism, growth and reproduction, the surplus energy is converted to reserve mass. Individual females give priority to lactation. If lactation costs can be met from assimilated energy, a predefined proportion of the remaining assimilated energy is assigned to growth (including growth of the foetus if any). If this is less than the energy required for growth, the growth rate of the female and her foetus is reduced accordingly. The remaining balance of the energy intake is allocated to metabolism. Any unfulfilled energetic costs of lactation and metabolism are met by catabolism of reserve tissue. If the relative body condition of an individual falls below the starvation threshold (*ρS* ), it has an increased chance of death.

The list of parameters used in the model is given in Tables A2 and A4.

Diagram

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Figure A. Flow diagram describing the details of the model. The same set of processes is applied to females and their offspring, but calves/pups are only followed to an age equivalent to the minimum inter-birth interval. Parallelograms indicate model inputs and rectangles indicate calculations or changes of life history stage. Females also change life history stage if their foetus or calf/pup dies but these changes are not illustrated here. A detailed account of all elements of this flow diagram can be found in the submodel descriptions. K is the proportion of daily assimilated energy allocated to growth (see Table A3).

## Design concepts

### Basic principles

This model follows the approach developed by (Hin et al. 2019) for long-finned pilot whales, which uses the basic principles of bioenergetics theory (Kooijman 2010). The model tracks the way in which individual female marine mammals assimilate energy over the course of their lives from age\_day1 to death, and how this energy is allocated to field metabolism, growth, foetal development and lactation. If assimilated energy on a particular day exceeds the energy required for these activities, the surplus energy is stored in a reserve compartment (De Roos et al. 2009, Kooijman 2010), primarily – but not exclusively - as fat tissue around internal organs and as blubber. If energy expenditure exceeds energy assimilation, the balance is provided by catabolizing tissue from this reserve compartment. The model also tracks these energy fluxes up to age\_day1 for every calf/pup that a female produces.

### Emergence

Although individual life-history traits such as growth, non-resource driven survivorship, and maturation time are imposed, others emerge from rules of metabolic organization and are driven by the influence of seasonal differences in resource density and energy balance.

The use of a maximum probability for successful fertilization/implantation above a specified age imposes a cap on the annual birth rate. However, the actual number of pups/calves born and the actual age at first reproduction emerge from the current physiological state (body condition) of females. Age-related and seasonal fluctuations in body condition emerge from variations in the resource density experienced by individuals and seasonal changes in energy demand. Body condition then influences the individual’s probability of reproducing or dying. In this way, it is possible to use the lifetime reproductive output of each simulated female to examine the population consequences of different conditions (including a changing environment and/or the effects of disturbance).

### Objectives

Animals attempt to maximize their fitness by allocating available energy to different life history processes in order of necessity. If processes necessary to survival are not covered by energy intake, energy stored in reserve tissue will be used to cover them. As reserve levels decrease, the animal has an increasing probability of dying.

### Prediction

Females can predict whether they can successfully continue with pregnancy using proxies of their current body condition.

### Sensing

Individuals can sense their storage levels and make decisions specific to their current body condition and life history stage, e.g. abort foetus or use energy derived from reserve tissue.

### Interaction

The only interactions between individuals in the model are between mother and offspring. The foetus and calf/pup are linked to their mother via energy and mass transfer.

### Stochasticity

The following processes can be stochastic: life expectancy of females, their foetuses and pups/calves; successful fertilization/implantation; dates related to reproduction (e.g., calving/pupping date); deaths due to starvation (see *Mortality* section below); and the resource density that an individual encounters on a particular day.

### Collectives

Collective behaviour is not modelled.

### Observation

The values of all state variables for each individual are recorded daily. For model output corroboration, the following variables and follow-up calculations were used: length, structural mass, reserves and body condition, assimilated energy, cause of death, proportion of adult females breeding each year, calf/pup survival till age1, inter birth intervals, and population growth rate.

## Initialization

The model is initialised by creating a number of individuals defined by the user (*sim\_number*), all of which have the same initial age (*age\_day1*) and body condition *ρstart* (Table A2). Initial body condition is determined iteratively from the mean condition of simulated calves/pups at *age\_day1*. Initial reserve level (*Fstart*) is then calculated as:

where *Sstart* is the female’s structural mass at *age\_day1* derived from the growth curve.

Table A. Initial body condition (ρstart) and age for the modelled species

|  |  |  |
| --- | --- | --- |
| **Species** | ***ρstart*** | **Initial age (age\_day1)** |
| Harbour seal | 0.20 | 1 year |
| Grey seal | 0.22 | 1 year |
| Harbour porpoise | 0.1 | 1 year |

Life expectancy of each individual at *age\_day1* is determined by sampling from a cumulative survival curve.

## Input data

The time series of resource densities that will be encountered by an individual during its lifetime is created at the beginning of each simulation.

## Submodels

The original model is cast as a set of differential equations (Table 1 in Hin et al. (2019)), which we have converted to difference equations. Throughout, we use the parameter symbols and names from Tables 1 and Supplementary Information 1 (S1) in Hin et al. (2019) (Table A3).

Table A. Description of parameters used in the model. for all the equations refer to Hin et al. (2019). The values for each of the three modelled species are given at the end of the odd.

| ***Variable, parameter*** | ***Code*** | **Units** | **Description** |
| --- | --- | --- | --- |
| ***Resource density*** | | | |
| *R* | *Rmean* |  | Annual mean resource density |
| *abeta* | a\_beta | - | Shape parameters of beta distribution defining stochasticity in resource density |
| *bbeta* | b\_beta | - |
|  | amplitude | - | Parameter defining the amplitude of seasonal variation in resource density |
|  | offset | - | Parameter determining when during the year *Rmean* has its maximum value |
| ***Timing of life history events*** | | | |
| *min\_age* | min\_age | years | Minimum age for reproduction |
| *mean\_birthday* | mean\_birthday |  | Mean date on which calves/pups are born |
| *TP* | Tp | days | Gestation period |
| *TL* | Tl | days | Age at weaning (duration of lactation) |
| *TR* | Tr | days | Age at which calf’s resource foraging efficiency is 50% |
| *max\_age* | max\_age | years | Maximum age |
|  | max\_age\_calf | days | Maximum modelled age of calf/pup |
| *moult\_duration* | moult\_duration | days | Duration of moult (seals only) |
| ***Reserves*** | | | |
| *ρ* | rho | – | Target body condition for adults |
| *ρc* | rho\_C | – | Target body condition for calves/pups |
| *θF* | Theta\_F |  | Relative cost of maintaining reserves |
| ***Growth*** | | | |
| *L0* | L0 | cm | Length at birth |
| *L∞* | Linf | cm | Female maximum length |
| *k* | K | 1/days | Von Bertalanffy growth function: growth rate parameter |
| *X0* | x0 | days | Von Bertalanffy growth function: length at age zero |
| *ω1* | omega1 | kg/cm | Structural mass-length scaling constant |
| *ω2* | omega2 | – | Structural mass-length scaling exponent |
| ***Energetic rates*** | | | |
| *σM* | Sigma\_M | – | Field metabolic maintenance scalar |
| *σG* | Sigma\_G | MJ/kg | Energetic cost per unit structural mass |
| *ε* | epsi | MJ/kg | Energy density of reserve tissue |
| *ε-* | epsi\_minus | MJ/kg | Catabolic efficiency of reserve conversion |
| *ε+* | epsi\_plus | MJ/kg | Anabolic efficiency of reserve conversion |
| *ε+pups* | epsi\_plus\_pups | MJ/kg | Anabolic efficiency of reserve conversion for pups |
| *η* | eta | – | Steepness of assimilation response |
| *ϒ* | upsilon | – | Shape parameter for effect of age on resource foraging efficiency |
| *K* | Kappa | – | Proportion of the daily assimilated energy allocated to growth |
|  | moult\_reduction | – | Reduction in resource assimilation during moult (seals only) |
|  | moult\_duration | – | Duration of the moult period (seals onlu) |
| ***Pregnancy*** | | | |
| *fert\_success* | fert\_success |  | Probability that implantation will occur |
| *decision\_day* | decision\_day | days of gestation | Day of pregnancy when female decides whether or not to continue |
| ***Lactation*** | | | |
| *φL* | phi\_L | – | Lactation scalar |
| *σL* | Sigma\_L | – | Efficiency of conversion of mother’s reserves to calf/pup tissue |
| *TN* | Tn | days | Calf/pup age at which female begins to reduce milk supply |
| *ξc* | xi\_c |  | Non-linearity in milk assimilation-calf age relation |
|  | lact\_feed | days | Day of lactation when female starts foraging (harbour seals only) |
|  | R\_prop\_lactation | – | Proportion of time female spends foraging during lactation (harbour seals only) |
| *ξM* | xi\_m | – | Non-linearity in female body condition-milk provisioning relation |
|  | pw\_fast | days | Duration of pup’s post-weaning fast (seals only) |
| *pup\_mass\_gain* | pup\_mass\_gain | kg/day | Daily mass increase of pups (seals only) |
| *daily\_pup\_ee* | daily\_pup\_ee | MJ/day | Daily energy expenditure of pups during lactation (seals only) |
| ***Mortality*** | | | |
| *foetal\_mortality* | foetal\_mortality |  | Background foetal mortality rate |
| *α1* | alpha1 | – | Coefficients of age-dependant mortality curve |
| *α2* | alpha2 | – |
| *β1* | beta1 | – |
| *β2* | beta2 | – |
| *ρS* | rho\_s | – | Starvation body condition threshold |
| *μs* | mu\_s | – | Starvation mortality scalar |

### Resource

**Resource density** (*R*) To avoid having to account for differences among prey in energy density, catchability, and digestibility, and differences among individuals in their ability to assimilate energy, the model of Hin et al. (2019) characterises the resources on which a species feeds in terms of the amount of assimilated energy they can provide to a female. Although it would be virtually impossible to measure resource density defined in this way, *R* provides a useful quantitative index of environmental quality, with high resource density indicating high quality environments, and low resource density associated with poor environments. Seasonal variation in *R* is modelled using a sine function, following Hin et al. (2019).

*R* is the most important determinant of lifetime reproductive success (the number of female offspring raised to age\_day1 in a female’s lifetime). It is therefore possible to choose an appropriate value for *R* based on what is known about the status of the population being modelled. For example, if the population is stable, *R* can be tuned so that lifetime reproductive success is 1.0. The seasonal pattern of change in R was varied to reflect the timing of life history events, such as moulting or breeding time, of each modelled species.

### Timing of life history events

**Gestation period** (*TP*) This is usually estimated from a combination of estimates of foetal growth rate and mean length at birth, using the assumption that foetal growth in length is approximately linear (Perrin and Reilly 1984).

**Lactation period/age at weaning** (*TL*) Perrin and Reilly (1984) provide a review of the methods used to determine lactation period and age at weaning. These include estimates of the ratio of lactating to pregnant animals in a sample of mature females, estimates of the age of the largest calf observed associating with a female, stomach content analysis, and behavioural observations.

### Reserves and growth

**Reserve thresholds** (*ρ, ρs*) In the Hin et al. (2019) model the rate of energy assimilation on a particular day is affected by an individual’s current body condition (*ρt*) relative to the **target body condition** (*ρ*). It is tempting to simply set *ρ* to the maximum recorded blubber: total body mass ratio for a particular species. However, captive harbour porpoises show strong seasonal variations in blubber thickness and total mass (Lockyer et al. 2003, Kastelein et al. 2019) which are closely correlated with water temperature and probably reflect a requirement for less insulation in summer. This suggests that in some species *ρ* may vary seasonally and that blubber mass cannot always be equated with reserve mass.

**Relative cost of maintaining reserves** (*ΘF*) According to bioenergetics theory, reserve mass does not require any maintenance (i.e. *ΘF* = 0). However, the large lipid reserves maintained by most marine mammal species probably do incur additional costs in terms of drag and buoyancy. Hin et al. (2019) set *ΘF* to 0.2 in order to account for these costs. We use the same value for all the modelled species.

**Structural length and structural mass** *(K,L0, L∞, ω1, ω2, k, b, xo,)*Most marine mammal bioenergetics models have used a von Bertalanffy growth curve to describe changes in *L0* with age, and then converted length to mass using a simple power function (e.g. *Sa = ω1.Laω2*).

**Modelling growth (***Κ***)** The model developed by Hin et al. (2019) assumes that growth in length and core mass continues unabated, regardless of energy intake. This may be the case for the porpoises but clearly not the case in both seal species (e.g. Hall and McConnell 2007). We therefore assumed that growth in seals may be reduced if energy intake is less than the combined costs of metabolism, growth and reproductive activities (pregnancy and lactation). We assumed that an individual will allocate a proportion of the assimilated energy (*It*) it acquires on a particular day to growth (including growth of the foetus, because this is treated as part of the female’s core mass), up to a maximum of (1-*Κ*)\**It,* where *Κ* is a constant with a value between 0 and 1. If this amount of energy is less than the energy required for growth, the growth rate of the female and any foetus is reduced accordingly. The balance of the energy intake is allocated to metabolism. If this is insufficient to cover all of the costs of metabolism, reserve tissue is catabolised. Values of *Κ* < 0.5 indicate that growth is prioritised over metabolism. Because there is no empirical information that can be used to estimate a value for *K* we explored the implications of a wide range of values for this parameter.

### Energetic rates

**Field metabolic maintenance scalar** (*σM*) The Hin et al. (2019) model assumed that an individual’s Field Metabolic Rate (FMR) is a simple multiple *σM* of the Resting Metabolic Rate (RMR) predicted by the Kleiber (1975) relationship (i.e. *K.Mt0.75*, where *K*= 0.294 MJ·kg–1.day-1). Estimates of *σM* can be obtained from respirometry studies of captive animals (e.g. Worthy and Lavigne 1987, Sparling et al. 2006), or they may simply be assumed. For example, Hin et al. (2019) used a value of 0.75 for *σM.K* based on an assumption that the FMR for pilot whales is 2.5x their RMR (Lockyer 1993).

**Energetic cost per unit structural mass** (*σG*) This is the amount of energy required to produce 1 kg of tissue (i.e. the energetic content of the new tissue and the energetic overheads required to produce it). Hin et al. (2019) obtained an indirect estimate of *σG*= 30 MJ.kg-1 from Brody’s (1968) formula for the heat of gestation and Lockyer’s (1993) estimate of the energy density of pilot whale calf tissue. However, direct measurements of this cost can also be obtained from captive animals (e.g. Noren et al. (2014) for Pacific walrus).

**Catabolic efficiency of reserve conversion** (*ε-*) This is the amount of energy produced by metabolising 1kg of reserve tissue. It can be calculated from measurements of the changes in mass of fasting animals and estimates of their metabolic requirements during that fast (Muelbert and Bowen 1993, Bennett et al. 2007).

**Anabolic efficiency of reserve conversion** (*ε+*) This is the amount of energy required to produce 1kg of reserve tissue. Since anabolism is likely to be less efficient than catabolism, Hin et al. (2019) used a value for *ε+* that was ~40% higher than *ε-*. However, it may be possible to estimate this parameter from measurements of the amount of additional food consumed by captive animals that have experienced fasting. For example, Kastelein et al. (2019) report that fasted, captive harbour porpoises recovered their original body weight within 2 days when they were offered twice the normal amount of food on those days. Estimates of the actual amount of additional energy consumed by these animals could be used to calculate *ε+.*

**Steepness of assimilation response** (*η*) The amount of assimilated energy obtained from feeding each day depends on the resource density, the structural size of the animal to the power 2/3 following Kooijman (2010), and the individual’s body condition (*ρt*). Individuals are assumed to assimilate energy at half of the maximum possible rate when their body condition is at the target body condition (*ρ*) and to increase their energy assimilation progressively if their body condition is reduced below the target value. This relationship also allows animals to compensate for the effect of lost foraging opportunities on their body condition by increasing energy assimilation on subsequent days, provided sufficient resources are available. Energy assimilation (*It*) on day *t* is described by:

Figure A2 shows the effect of body condition relative to the target value (and *η* on energy assimilation with *η* ranging from 5 to 25. The value of 15 used by Hin et al. (2019) is shown in bold. With higher values of *η*, energy assimilation is close to its maximum level over a wide range of value for *ρt*. Lower values of *η* result in a wider range of variation in energy assimilation with *ρt*. Information on how quickly fasting individuals that are in good condition recover the weight lost during the fast (e.g. Kastelein et al. 2019) could provide guidance as to a suitable value for *η*.

A close up of text on a white background

Description automatically generated

Figure A2 - The effect of body condition relative to the target level (and the steepness of the assimilation response (η) on energy assimilation as a proportion of its maximum rate. The relationship for η = 15 is shown in solid black. Curves in green are for values of η = 5 and 10; curves in red are for values of η = 20 and 25.

**Effect of age on resource foraging efficiency** (*Υ*, *TR, pw\_fast*): These parameters take account of the fact that newly weaned pups/calves will not be 100% efficient at foraging and that, for species with long lactation periods, calves may begin feeding during lactation. In addition, harbour and grey seal pups undertake a post-weaning fast, whose duration is set by the parameter *pw\_fast*. The shape of the feeding efficiency relationship is controlled by *TR*, the age at which a calf/pup achieves a foraging efficiency that is 50% of an adult, and a shape parameter (γ) that determines how rapidly foraging efficiency approaches 100%. Figure A3 shows the effects of different values of γ on the shape of the function determining foraging efficiency. The value of γ = 3 used by Hin et al. (2019) is shown in bold. As an example, if *TR*is 1 year, the function predicts that 100% foraging efficiency would be achieved by age 5. Lower values of γ result in higher ages for 100% efficiency and higher values of γ result in lower ages for 100% efficiency. Although it may be possible to determine when pups/calves begin feeding independently from an examination of stomach contents (e.g. Fig. 3 in Muelbert and Bowen 1993), direct estimation of these parameters is unlikely to be feasible. However, γ will affect post-weaning survival and age at first reproduction. Independent information on current values for these demographic characteristics can therefore provide insights into the feasible range for this parameter.

A close up of a map

Description automatically generated

Figure A3 - The effect of the shape parameter γ on the relationship between foraging efficiency and age (shown as a multiple of the age at which a calf/pup achieves 50% foraging efficiency). TR is 1 year. The curve for γ = 3 is shown in solid black. Green curves show the relationship for values of γ <3; red curves represent values >3.

### Pregnancy

**Pregnancy threshold** (*Fneonate*, *decision\_day, skipping\_point*) Hin et al. (2019) assumed that females can only become pregnant when the size of their reserves exceeds *Fneonate*. For pilot whales, they used a value equivalent to the energetic costs of foetal growth and development plus the amount of reserves needed to avoid the onset of starvation related mortality, but other formulations have been used (e.g. for beaked whales - New et al. 2013). This parameter effectively sets a minimum value for the age at first conception, because the absolute size of a female’s reserves are determined by *Sa* and young females are too small to build up sufficient reserves, even if their foraging efficiency has attained its maximum level. Estimates of age at first conception are available from many marine mammal populations and these can be compared with predictions from the bioenergetics model to provide a “reality check” on the appropriateness of the value chosen for *Fneonate*.

Smout et al. (2019) documented a relationship between a female grey seal’s total mass at the end of lactation and the likelihood of giving birth in the following breeding season. The threshold mass that resulted in a 0.5 probability of giving birth was lower if prey abundance was greater than average in the subsequent year. Given that females do not increase their body mass from the end of lactation until implantation (Boyd 1984), this implies that in grey seals the decision to give birth to a pup is made some time during pregnancy, rather than at implantation. However, the exact time at which females should make this decision is not entirely obvious, and the model allows the user to define when this decision is made (*decision\_day*).

### Lactation

**Efficiency of conversion of mother's reserves to calf/pup tissue** (*σL*) This parameter combines the efficiency with which a female converts ingested or reserve energy to milk and the assimilation efficiency of the calf/pup. Lockyer (1993) assumed that efficiency of milk assimilation is 95% and that the efficiency of milk production in the mammary gland is 90%. Combining these estimates yields a value of 0.86, which was used by Hin et al. (2019) and may also be useful for other cetacean species. Direct estimation of this parameter should be possible from studies of energy transfer in lactating pinnipeds (Costa et al. 1986, Lang et al. 2011). For example, Fig. 3 in Costa et al. (1986) implies that conversion efficiency in northern elephant seals is close to 100%. However, it is not possible to calculate a precise value for *σL* from the results presented in this and other pinniped studies.

**Effect of calf/pup age on milk assimilation** (*TC* , *ξC, TC,, lact\_feed, R\_prop\_lactation*) Hin et al. (2019) proposed that females will provide all their calf’s energy demands until the calf is *TC* days old, and after this they will gradually reduce the amount of energy they supply according to the formula:

Where *a* is calf/pup age and *TL* is age at weaning. Figure A4 shows the effect of the value of *ξC* on the shape of this relationship. For capital breeding species, such as many pinnipeds, which provide almost all of their pup’s energy demands up until the age at weaning, *TC* should be close to *TL* and *ξC* will be close to 1. Species, such as bottlenose dolphins, with an extended period of maternal care will have relatively small values of *TC* and *ξC.*

The reproductive strategy of harbour seals is intermediate between capital and income breeding, because females start foraging before the end of lactation. We, therefore, modelled a 10% decrease in milk provisioning by female at Tc and assumed that females start foraging at *lact\_feed* with a foraging efficiency of *R\_prop\_lactation.*

A close up of a map

Description automatically generated

Figure A4 - The effect of the non-linearity parameter *ξc* on the proportion of a calf/pup’s milk demand provided by its mother at different stages of lactation. *TΝ*(the calf/pup age at which the mother begins to reduce the amount of milk she supplies) was set at 60% of the duration of lactation (*TL*). The solid black line shows the relationship for *ξc* = 0.9 (the value used by Hin et al. (2019). Green lines show the relationships for smaller values of *ξc* (0.5 and 0.75). Red lines show the relationship for larger values (0.95 and 0.99).

**Effect of female body condition on milk provisioning** (*ξM*) Hin et al. (2019) assumed that females will reduce the amount of milk they provide to their calf as their own body condition declines. They used the function:

to predict this reduction, where *ρt* is the female’s body condition on day *t*, and *ξM* is described as the “non-linearity in female body condition-milk provisioning relation”. Figure A5 shows how the shape of this relationship varies, depending on the value of *ξM*. Lower values of *ξM* represent a more conservative strategy, with females reducing the amount of milk they supply by 50% if their body condition falls below 60% of *ρ* if *ξM =* 0.5. Larger values reflect a strategy that is more “generous” to the calf/pup. For example, if *ξM =*10, body condition must be reduced close to *ρs* before milk supply is reduced by 50%.

A close up of a mans face

Description automatically generated

Figure A5 - The effect of body condition relative to the target level ( of the female and the non-linearity parameter *ξM*on the proportion of a calf/pup’s milk demand provided by its mother. The solid black line shows the relationship for *ξM* = 2 (the value used by Hin et al. 2019). Green lines show the relationships for larger values of *ξM* (3 and 5). Red lines show the relationship for smaller values (0.5 and 1.0).

**Lactation scalar** (*ΦL, ,pup\_mass\_gain, daily\_pup\_ee, ε, ρpup*) The lactation scalar is analogous to *R*, because the maximum amount of energy a calf/pup can obtain from milk on day *t* is determined by *ΦL*, where *Sc,t* is the structural mass of the calf/pup on day *t*. Hin et al. (2019) estimated *ΦL* for pilot whales on the assumption that the female provides all of her calf’s energy needs up to age *TC*. They calculated the mean amount of energy expended each day by the calf during this period for maintenance and growth, and then divided this by the average structural mass of the calf x 0.5 (on the assumption that the body condition of both mother and calf was equal to *ρ*). Similar calculations can be performed for other species, provided a value for *σG* (the energetic cost per unit structural mass) is available.

### Mortality

**Age-dependent mortality rate** Hin et al. (2019) calculated an age-varying mortality rate for pilot whales based on published estimates of age-specific survival rates. A similar procedure was used to estimate this rate for the three species modelled here from the age-specific survival rates provided in published estimates (Winship 2009, Arso Civil et al. 2019, Sinclair et al. 2020).

The **starvation body condition threshold** *(ρs)* represents the point at which further reduction in body condition is likely to have a negative effect on survival. It can be estimated from the ratio of blubber: total body mass of dead or dying animals that exhibit symptoms of terminal starvation (Kastelein and Van Battum 1990, Koopman et al. 2002).

**Starvation-induced mortality rate** (*μs*) This parameter determines how long an individual is likely to survive if its body condition falls below the starvation body condition threshold (*ρs*). Probability of survival is modelled as:

Higher values of *μs* result in a lower probability of survival (Figure A6). Hin et al. (2019) used a value of 0.2, which implies that 50% of starving individuals will survive for one week if their body condition remains below the threshold.

A screenshot of a cell phone

Description automatically generated

Figure A6 - The effect of the starvation-induced mortality parameter (mu\_s = *μs*) on the probability that an individual whose body condition has fallen to *ρs*/2 will survive for 1 week.

### Modelling disturbance

Users can define the start and end points (*Diststart* and *Distend*) of the period during which disturbance can occur, and the number of days on which disturbance occurs (*Distdur*). Specific days when disturbance occurs are chosen at random within the defined period. During each day of disturbance, the resource density experienced by a simulated individual, and consequently the amount of energy it assimilates, is reduced by *Disteffect*. The effects of this reduction on energy assimilation will depend on the age and life history stage of the affected individuals, and the user can define the age classes that are affected using the parameter *Agedist*. In the current version the disturbances occur in a single year and their effect on vital rates are determined within the same time frame (for example, the survival of calves/pups that are alive at the time of the disturbance or are born shortly after it).

table A4. parameters used in the final simulations for the three studied species. the references are colour coded by species or remain black if they apply to all three species. if there is no reference given, see text in the odd or in the extended version of the odd in harwood et al. (2020, 2022). ‘abc’ refers to the parameters which were parameterised using approximate bayesian computation.

| ***Variable, parameter*** | **Grey seals** | **Harbour seals** | **Harbour porpoise** | **Reference** |
| --- | --- | --- | --- | --- |
| ***Resource density*** | | | | |
| *R* | ABC | ABC | ABC |  |
| *abeta* | 23.65 | 23.65 | - |  |
| *bbeta* | 19.35 | 19.35 | - |  |
| *amplitude* | 0.1 | 0.1 | - |  |
| *offset* | 184 | 184 | - |  |
| ***Timing of life history events*** | | | | |
| *min\_age* | 3 | 4 | 3 | Härkönen and Heide-Jørgensen (1990), Sinclair et al. (2020) |
| *mean\_birthday* | 23rd Nov | 17th Jun | 1st June | Reijnders et al. (2010), Härkönen and Heide-Jørgensen (1990) |
| *TP* | 240 | 240 | 305 | Reijnders et al. (1993), Hall and Russell (2018), Lockyer (2003) |
| *TL* | 18 | 23 | 250 | Muelbert and Bowen (1993), Cordes and Thompson (2013), Hall and Russell (2018), Gaskin (1984), Lockyer (2003) |
| *TR* | ABC | ABC | ABC | Gaskin (1984) |
| *max\_age* | 40 | 30 | 30 | Hall et al. (2019), Hall and Russell (2018) |
| *max\_age\_calf* | 1 | 1 | 1 |  |
| *Moult\_duration* | 20 | 20 | - |  |
| ***Reserves*** | | | | |
| *ρ* | 0.5 | 0.43 | 0.35 | Pomeroy et al. (1999), Lang et al. (2011), Lockyer (2007), McLellan et al. (2002) |
| *ρc* | 0.7 | 0.55 | 0.35 | Pomeroy et al. (1999) |
| *θF* | 0.2 | 0.2 | 0.2 | Hin et al. (2019) |
| ***Growth*** | | | | |
| *L0* | 89.8 | 82.9 | 70 | Hall et al. (2019), Härkönen and Heide-Jørgensen (1990), McLaren (1993), Lockyer (2003) |
| *L∞* | 184 | 140.5 | 160 | Hall et al. (2019), McLaren (1993), Lockyer (2003) |
| *k* | 0.0005 | 0.0012 | 0.0015 | Hall et al. (2019), McLaren (1993) |
| *X0* | -58.04 | 2.02\*365 | - | Hall et al. (2019), McLaren (1993) |
| *b* | 0.27 | - | - | McLaren (1993) |
| *ω1* | 1.5x10-4 | 3.6\*10-5 | 5.9\*10-5 | Härkönen and Heide-Jørgensen (1990), Hauksson (2007), Lockyer and Kinze (2003) |
| *ω2* | 2.575 | 2.86 | 2.67 | Härkönen and Heide-Jørgensen (1990) but see text Hauksson (2007), Lockyer and Kinze (2003) |
| ***Energetic rates*** | | | | |
| *σM* | ABC | ABC | ABC |  |
| *σG* | 30 | 25 | 25 | Derived using the approach of Hin et al. (2019) |
| *ε* | 25.8 | 25.8 | 25.8 | Reilly et al. (1996) |
| *ε-* | 23.2 | 23.2 | 23.2 | Kastelein et al. (2019) |
| *ε+* | 35.5 | 35.5 | 35.5 | Hin et al. (2019) |
| *ε+pups* | 28.5 | 28.5 | - |  |
| *η* | 40 | 20 | 20 |  |
| *ϒ* | ABC | ABC | ABC |  |
| *K* | ABC | ABC | - |  |
| moult\_reduction | 0.5 | 0.5 | - | Paterson et al. (2012) |
| ***Pregnancy*** | | | | |
| *fert\_success* | 1 | 1 | 1 |  |
| *decision\_day* | ABC | ABC | - |  |
| ***Lactation*** | | | | |
| *φL* | 8.85 | 4.02 | 3.55 | Calculated using the approach of Hin et al. (2019) |
| *σL* | 0.86 | 0.86 | 0.86 | Lockyer (1993), Lockyer (1993),Hin et al. (2019), based on data in Lockyer (2003) |
| *TN* | 0.95\*TL | 0.90\*TL |  | Gallagher et al. (2018) |
| *ξc* | - | - | 0.5 | Gallagher et al. (2018) |
| *lact\_feed* | - | 10 | - | Boness et al. (1994), Thompson et al. (1994) |
| *R\_prop\_lactation* | - | ABC | - |  |
| *ξM* | 2 | -2 | -3 | Muelbert and Bowen (1993), Hin et al. (2019) |
| *pw\_fast* | 21 | 15 | - |  |
| *pup\_mass\_gain* | - | 0.55 | - | Bowen et al. (1992), Harding et al. (2005), Jørgensen et al. (2001) |
| *daily\_pup\_ee* | - | 8.3 | - |  |
| ***Mortality*** | | | | |
| *foetal\_mortality* | 0 | 0.1 | 0.2 | Murphy et al. (2015) |
| *α1* | 0.007 | 0.0022 | 10 | Sinclair et al. (2020) and see text, Thomas et al. (2019) |
| *α2* | 1.3 x 10-4 | 0.0019 | 2.2 |  |
| *β1* | 0.01 | 2.1\*10-4 | 24 |  |
| *β2* | 10-7 | 0.3\*10-6 | 8 |  |
| *ρS* | ABC | ABC | ABC |  |
| *μs* | ABC | ABC | ABC |  |

# Supplementary Information B. Parameterisation of the bioenergetics models using Approximation Bayesian Computation (ABC).

## Prior distribution and rejection criteria

table b1. Parameters and their prior distributions used in the ABC analysis. ‘uni’ – uniform distribution

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Parameter** | **Description** | **Prior distribution** | | |
| **Grey seal** | **Harbour seal** | **Harbour porpoise** |
| *K* (Kappa) | Proportion of surplus assimilated energy allocated to growth | Uni(0.6, 0.9) | Uni(0.2, 0.4) | - |
| *ϒ* (upsilon) | Shape parameter for effect of age on resource foraging efficiency | Uni(1.4, 1.75) | Uni(1.7, 1.9) | Uni(3,5) |
| *TR* | Age at which calf’s resource foraging efficiency is 50% | Uni(70, 120) | Uni(60, 90) | Uni(110, 160) |
| *μs* (mu\_s) | Starvation mortality scalar | Uni(0.1, 0.3) | Uni(0.1, 0.3) | Uni(0.1, 0.4) |
| *σM (S*igma\_M) | Field metabolic rate scalar | Uni(2, 3) | Uni(2, 3) | Uni(4.5, 6.5) |
| *R* | Mean resource density | Uni(1.3, 2.4) | Uni(1.4, 2.4) | Uni(2, 4) |
| *decision\_day* | Day of pregnancy when female decides whether or not to continue | Uni(160, 200) | Uni(160, 200) | - |
| *R\_prop\_lactation* | Proportion of time female spends foraging during lactation | - | Uni(0.5, 0.8) | - |
| *ρS* (rho\_s) | Starvation body condition threshold | Uni(0.05, 0.15) | Uni(0.05, 0.15) | - |
| *Tn* | Calf age at which female begins to reduce milk supply | - | - | Uni(90,140) |

table b2. Rejection criteria used in the ABC analysis

|  |  |  |  |
| --- | --- | --- | --- |
| **Pattern** | **Grey seal** | **Harbour seal** | **Harbour porpoise** |
| Annual population growth rate | 0.985 - 1.035\*\* | 0.98 – 1.025\*\* | > = 1\*\* |
| Median birth rate | > 0.8\*\*\* | > 0.8\*\* | > 0.44\* |
| Female starvation mortality rate | < 0.02\*\*\* | < 0.08\*\* | <0.15\*\* |
| Pup/Calf survival rate | 0.14 - 0.22\*\*\*\* | 0.20 – 0.44 \*\* | 0.60 – 0.70\*\* |
| Pup condition at age 1 | - | < 0.43 |  |

\* Harwood and King (2017)

\*\* Sinclair et al. (2020)

\*\*\* Smout et al. (2019)

\*\*\*\* Thomas et al. (2019)

## Results of ABC: Comparison of prior and posterior distributions for the three species

### Grey seal

2987 out of 300.000 (1%) simulations for grey seals fulfilled all the rejection criteria listed in Table B2. Frequency distribution of these results as well as prior and posterior distribution is given in Figures B1-B2.

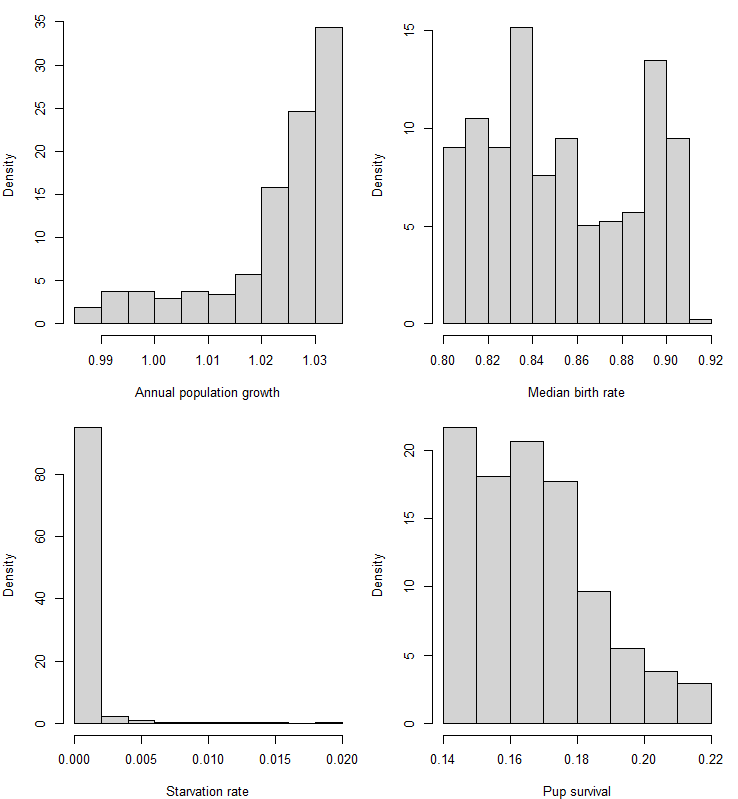


Figure B1. Frequency distributions of the four rejection criteria used for grey seals for the simulations passing these criteria.

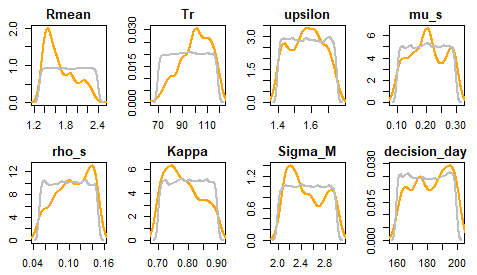


Figure B2. Prior (grey) and posterior (orange) distribution of parameters used in the grey seal model.

### 3.2 Harbour seal

122 100 out of 300 000 (41%) simulations for harbour seals fulfilled all the rejection criteria listed in Table B2. Frequency distribution of these results as well as prior and posterior distribution is given in Figures B3-B4.

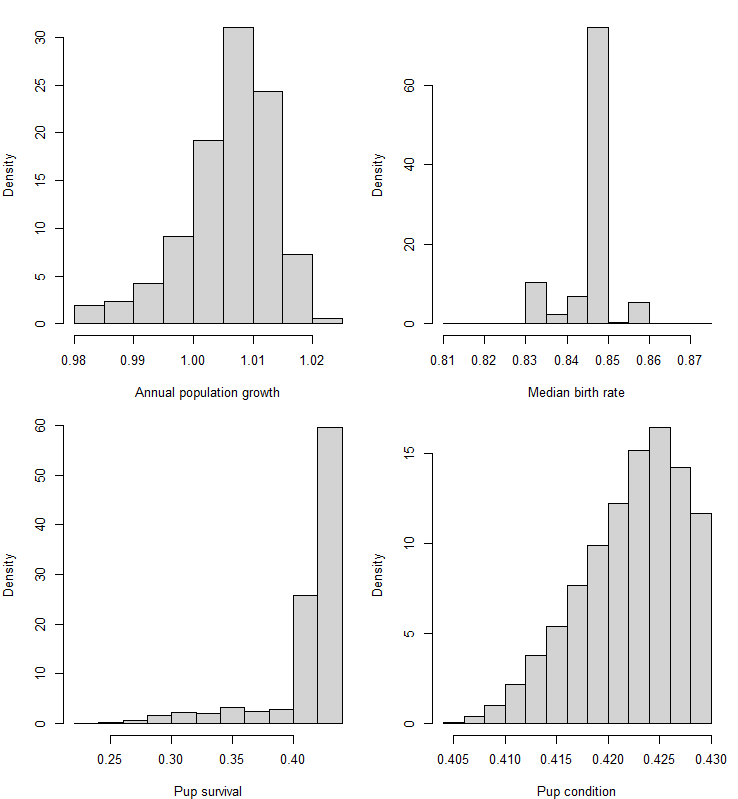


Figure B3. Frequency distributions of the four rejection criteria used for harbour seals for the simulations passing these criteria. Female starvation rate = 0 for all simulations which pass the remaining four criteria.

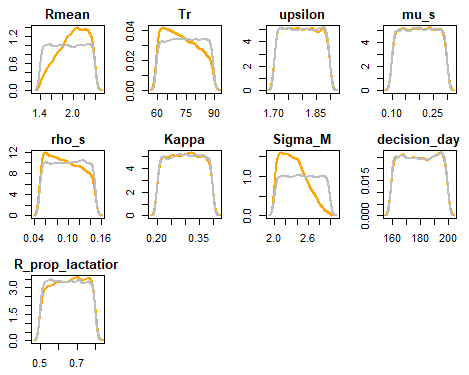


Figure B4. Prior (grey) and posterior (orange) distributions of parameters used in the harbour seal model.

### Harbour porpoise

140 392 out of 300 000 (47%) simulations for harbour porpoises fulfilled all the rejection criteria listed in Table B2. Frequency distribution of these results as well as prior and posterior distribution is given in Figures B5-B6.

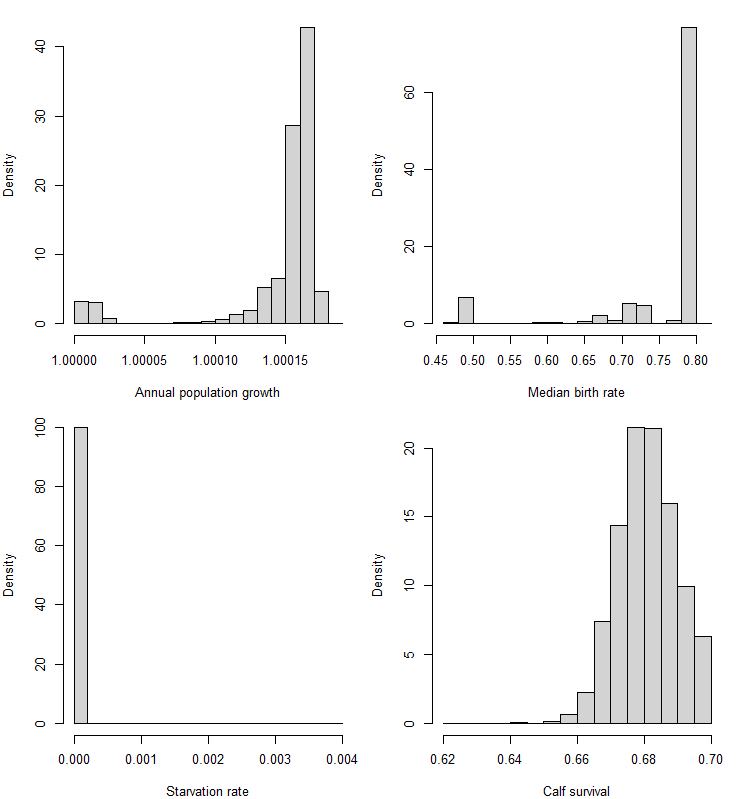


Figure B5. Frequency distributions of the four rejection criteria used for harbour porpoise for the simulations passing these criteria.

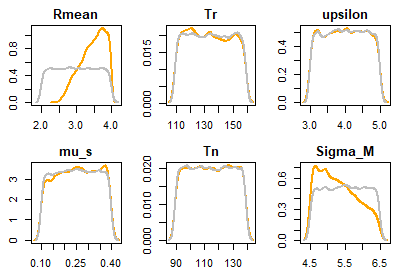


Figure B6. Prior (grey) and posterior (orange) distribution of parameters used in the harbour porpoise model.

# Supplementary Information C. Individual heterogeneity (IH) in the effect of disturbance

Chart

Description automatically generated

Figure C1. Proportion of individual females predicted to experience different disturbance effects.

We assumed that the duration of a disturbance effect would be directly related to perceived sound intensity. The distribution of the individual heterogeneities in disturbance effect was therefore based on the fact that sound intensity/loudness decreases with distance from the sound source, but the area affected by a particular sound intensity increases with distance, potentially exposing more animals (Figure C2). The distribution of disturbance effects used in the simulations is meant as a purely hypothetical example of their likely heterogeneity and is not based on any empirical data.

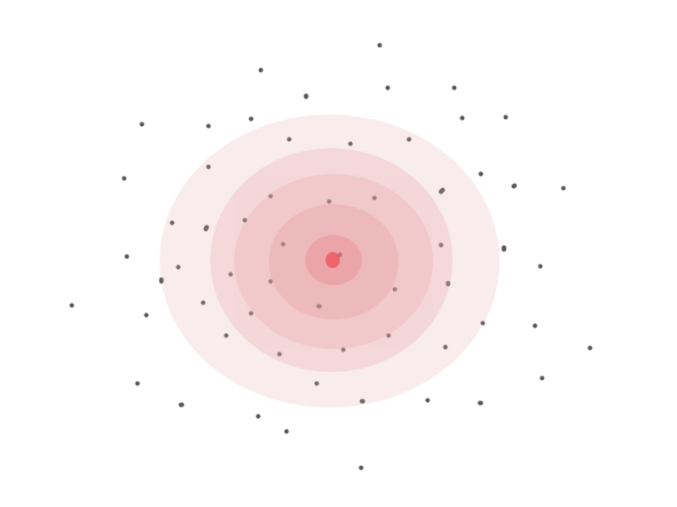
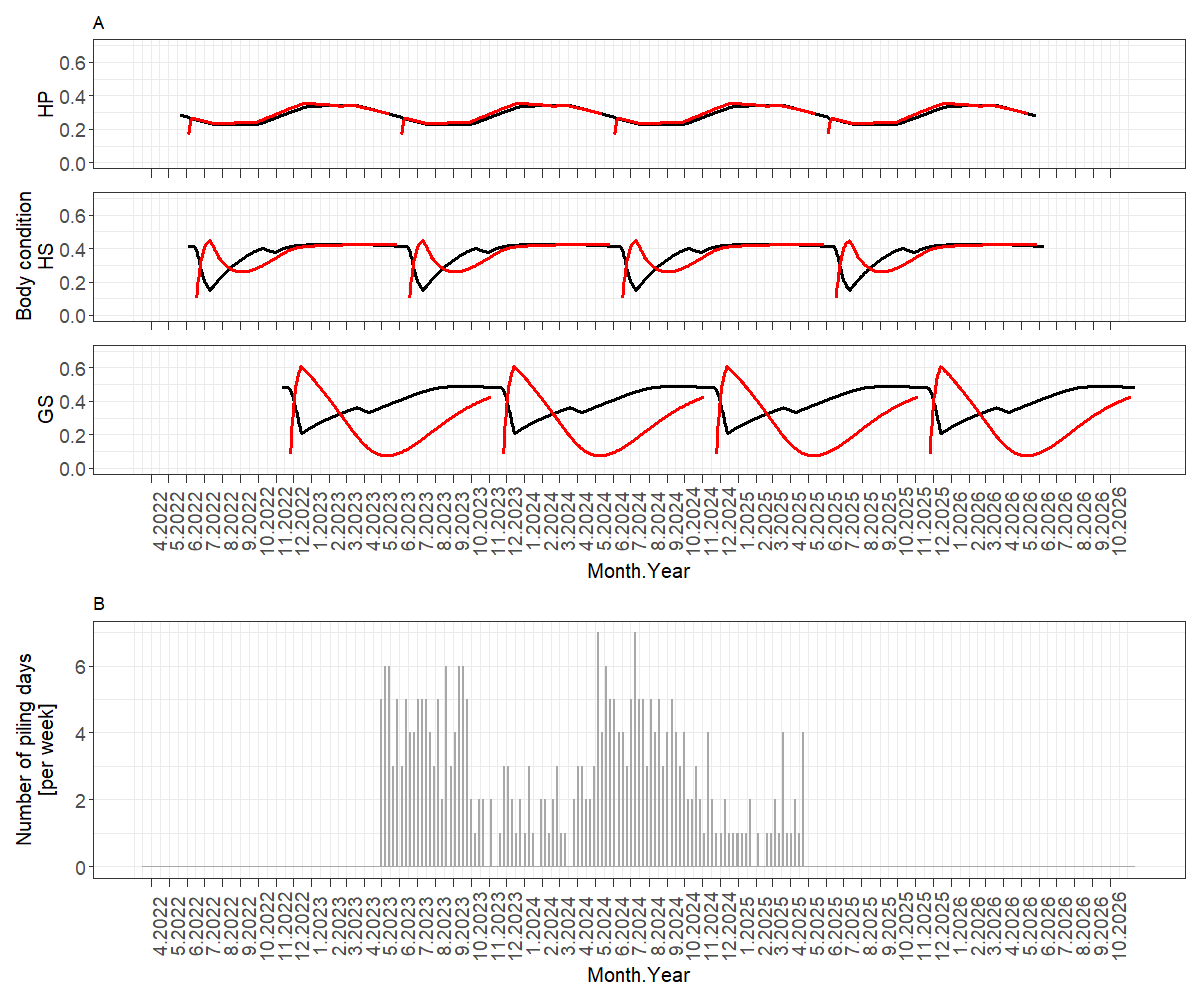


Figure C2. Diagram explaining the basis on which the distribution of IH was created. The darkness of the concentric red circles corresponds to the sound intensity at different distances from the source. Grey dots represent the potential distribution of animals.

# Supplementary Information D. Results of simulations when the disturbance scheme was intensified over summer months.

We also considered a piling schedule in which 100 days of piling occurs in the summer months (i.e. between May and September) each year, and the remaining 50 days of piling are randomly distributed over the winter months (October to April) (Figure D1). Comparison between the two piling schedules is shown on Figure D2 and the results of disturbance simulations are shown in Figures D3 and D4.

Figure D1. (A) Predicted changes in relative body condition of an average female (black lines) of each species (‘GS’ - grey seal, ‘HP’ - harbour porpoise, ‘HS’ - harbour seal) and her offspring (red lines) over the course of four reproductive cycles in an undisturbed environment for the period for which all calculations were done when modelling the effect of disturbance. (B) The bottom panel shows weekly number of piling days over the two years of piling schedule with piling schedule intensified over the summer months. The timespan of the x axis matches the axis in panel A.e

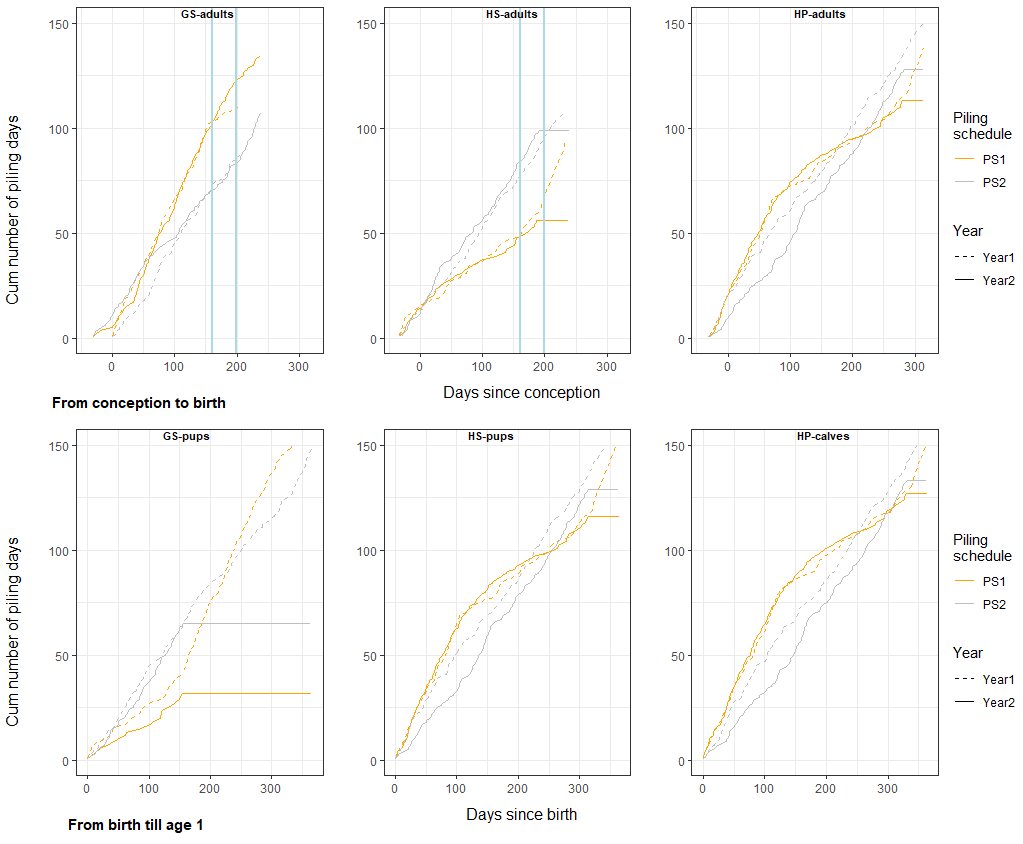


Figure D2. Comparison between cumulation number of piling days for two life periods for all three species (from conception to birth for adult females and from birth to weaning for their offspring) for the two piling schedules: PS1: piling intensified over summer months, PS2: piling uniformly distributed over each year. The species are GS-grey seals, HS-harbour seals, HP-harbour porpoises. The blue vertical lines in the two top panels show periods of ‘decision days’: days when females of seals species ‘decide’ to continue with pregnancy or to abort based on their conditions.

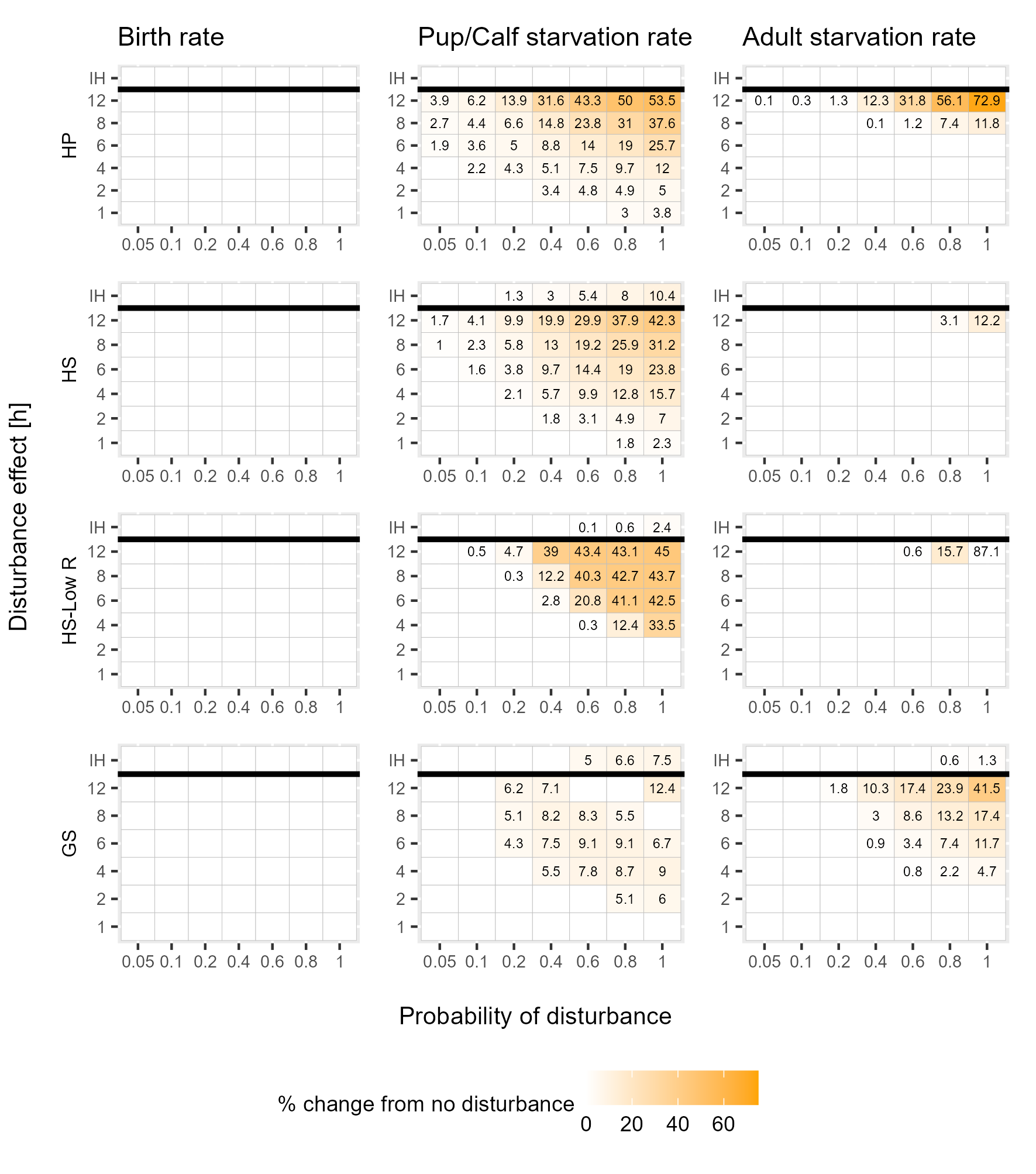
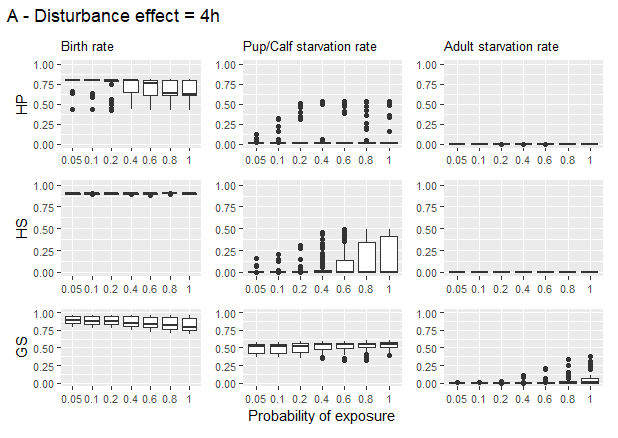


Figure D3. Percentage change from no disturbance in birth rate, pup/calf and adult starvation rate for different combinations of probability of disturbance and disturbance effect for the three studied species: ‘GS’ - grey seal, ‘HP’ - harbour porpoise, ‘HS’ - harbour seal from stable population, ‘HS-Low R’ – harbour seal from a food-limited population for the piling schedule intensified over summer months. The results of the individual heterogeneity (IH) analysis are shown as the top row of each panel. Empty cells indicate that there was no significant change between undisturbed and disturbed simulations for a given combination of probability of disturbance and disturbance effect.



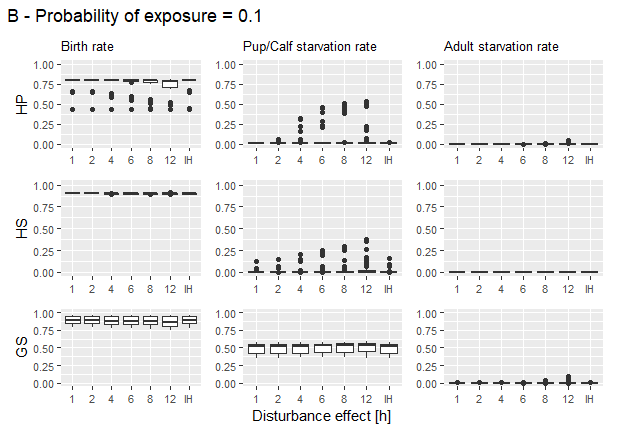
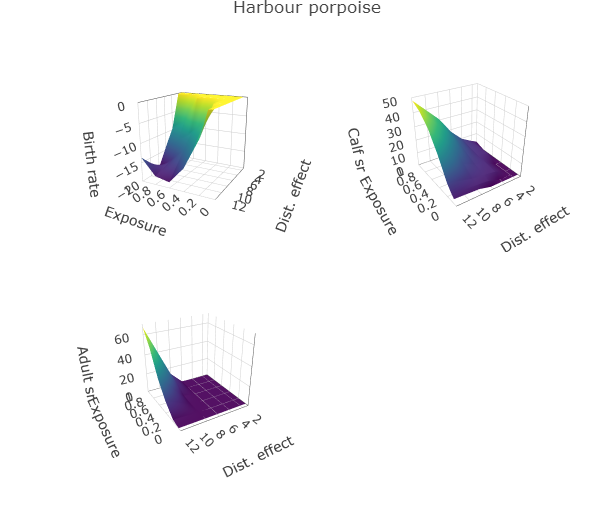


Figure D4. Variation in the effect of disturbance on the three vital rates between 90 parameter combinations for the entire range of probabilities of disturbance and fixed disturbance effect = 4h (Figure D4A) and the entire range of disturbance effect and fixed probability of disturbance = 0.1 (Figure D4B) for the three studied species: ‘GS’ - grey seal, ‘HP’ - harbour porpoise, ‘HS’ - harbour seal from stable population, ‘HS-LowR’ – harbour seal from a food-limited population) for the piling schedule intensified over summer months.

# Supplementary information E: Relationship between probability of disturbance and effect of disturbance



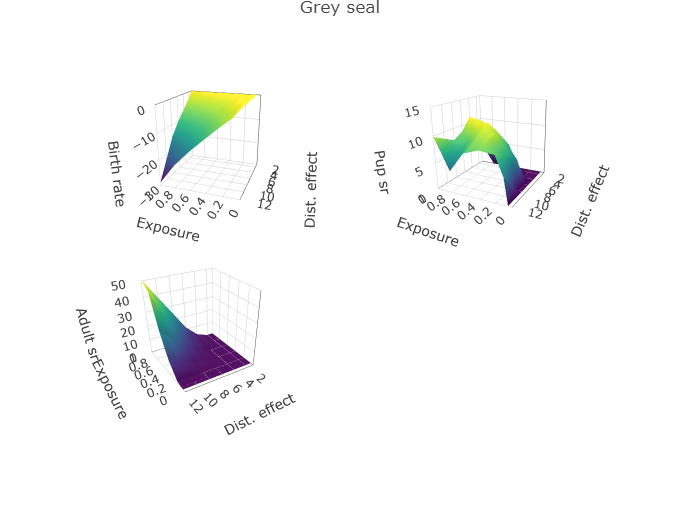


Figure E1. 3D interpretation of Figure 2 from the main text for the two species: harbour porpoise and grey seals depicting the relationship between probability of disturbance (‘Exposure’) and disturbance effect (‘Dist. Effect’) for the three vital rates: percentage change of birth rate from no disturbance (‘Birth rate’), percentage change of pup/calf starvation rate (‘Calf sr’) and percentage change of adult starvation rate (‘Adult sr’). The code and input data to reproduce the graphs is here https://github.com/MagdaChu/Chudzinska-et-al.-Bioenergetic-and-movement.git.

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