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Research article

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

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We developed dynamic bioenergetics models to investigate how behavioural responses to anthropogenic disturbance events might affect the population dynamics of three marine mammal species (harbour porpoise, grey seal and harbour seal) with contrasting life-history traits (capital versus income breeders) and movement behaviour (resident versus nomadic). We used these models to analyse how individual vital rates were affected by differences in the probability of disturbance and the duration of any behavioural response, while taking account of uncertainty in the model parameters and heterogeneity in behaviour. The outputs of individual movement models and telemetry data were then used to determine how the probability of exposure might vary among species, individuals, and geographical locations. We then demonstrate how these estimated probabilities of exposure can be translated into probabilities of disturbance. For illustrative purposes, we modelled the potential effects of a temporary decrease in energy assimilation associated with a series of disturbance events that might realistically occur during the construction of an offshore windfarm. Offspring starvation mortality was the vital rate that was most affected by these disturbance events. Monitoring of rate should be considered as standard practice so that populations responses can be detected as early as possible. Predicted effects on individual vital rates depended on the species' movement behaviour and the likely density of animals where the modelled construction activity was assumed to take place. The magnitude of these effects also depended critically on the assumed duration of the reduction in energy assimilation. No direct estimates of this variable are currently available, but we suggest some ways in which it could be estimated. The described approach could be extended to other species and activities, given sufficient information to parameterise the component models. However, we emphasise the need to account for among-individual heterogeneities and uncertainties in the values of the many model parameters.

Keywords: capital and income breeder, disturbance, dynamic bioenergetics models, exposure, grey seal, harbour porpoise, harbour seal, highly-mobile species, movement, offshore construction, resident species, stressor



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Introduction

There is increasing concern over how stressors (i.e. physical, chemical or biotic entities that can move a biological system out of its normal operating range, Segner et al. 2014) associated with human activities may affect the behaviour of individuals of many species from a wide range of taxa. Environmental management would be more effective if we better understand the ways in which these behavioural changes may affect individual vital rates (e.g. survival or reproduction) and population characteristics (Sutherland 1996, Gill et al. 2001, Beale and Monaghan 2004, Ames et al. 2020).

Stressors in the marine environment include changes in prey resources, ocean acidification, fishing gear (e.g. bycatch), marine plastics and other contaminants, and anthropogenic noise, including construction of offshore windfarms (Davies et al. 2009, Poloczanska et al. 2016). Anthropogenic noise is likely to be particularly important for species, such as marine mammals, that use sound for key life functions (Stanley et al. 2012, Hawkins and Popper 2017). Although observed behavioural responses to anthropogenic noise may increase predation risk and reduce the probability of finding a mate (Southall et al. 2010), one of the most commonly considered pathways along which anthropogenic noise can affect marine mammal involves its effect on an individual's energy budget. Energy intake may be reduced as a result of disrupted foraging and energetic costs may be increased if there is a flight response. Consequential changes in health, often mediated by a change in body condition, may increase an individual's risk of death or reduce its ability to reproduce.

Keen et al. (2021) suggested that the vulnerability of a marine mammal species to human activities that may affect their behaviour (henceforth referred to as 'disturbance') is likely to depend on the species' movement ecology, reproductive strategy and body size. A species' movement ecology will affect the aggregate exposure of individuals (i.e. the total duration and intensity of exposure to a given stressor, sensu Jones-Todd et al. 2022) to disturbance from a particular activity. Keen et al. (2021) described three broad categories of movement in marine mammals (resident, nomadic and migratory) that result in different probabilities of exposure to a localised source of disturbance (Fig. 2 in Keen et al. 2021). Resident species (e.g. sea otters) show strong site fidelity with limited movement in a defined area. However, because individuals use different defined areas, some individuals may be frequently exposed to a particular disturbance whereas others may never be exposed. Individuals of nomadic species (e.g. oceanic dolphins) may travel over the entire range occupied by a population and show limited or no site fidelity. Such individuals are likely to be exposed only infrequently to a particular disturbance. Migratory species (e.g. baleen whales and some phocid seals) move seasonally between discrete areas within the species' range. For these species, individual exposure will depend critically on when, where and at what scale disturbance-inducing activity occurs.

Marine mammal reproductive strategies lie along a spectrum from pure income breeding (where the costs of lactation

are fuelled by a concurrent increase in energy intake e.g. harbour porpoises) to pure capital breeding (where the lactation costs are entirely met by metabolising accumulated energy reserves e.g. grey seals). Disturbance during lactation can have an immediate effect on the provision of energy to the dependent calves or pups of income breeders. Underwater noise or other anthropogenic at-sea stressors will not affect the energy budget of capital breeders during lactation if, like many seal species, they raise their young on land. However, disturbance outside this period may have a negative effect on the size of the energy reserves individual capital breeders can accumulate and their rate of recovery from the effects of lactation.

Body size affects the absolute size of an individual's energy reserves and therefore the length of time it can survive an extended period of negative energy balance. In addition, among homeotherms, smaller individuals expend more energy per unit mass than larger ones and therefore require a relatively higher resource acquisition rate to meet their metabolic requirements (Keen et al. 2021).

Finally, the current status of a population may also affect how individuals are affected by disturbance. Individuals from populations that are not food limited or are below carrying-capacity may be able to compensate for a reduction in energy intake as a result of disturbance by increasing their subsequent feeding activity. However, this may not be possible if the population is food limited.

The short-term changes in health that may be caused by disturbance are difficult to document in the field, and most studies of their potential effects on marine mammal populations have relied on dynamic bioenergetics models (McHuron et al. 2017, Abrahms et al. 2019, Pirodda 2022). These models track changes in the energy acquisition and expenditure of individuals over time and infer how the resulting change in health (usually represented by body condition) may affect their vital rates (specifically survival and probability of giving birth). Here, we use models of this type to investigate how repeated disturbance events may affect the energy intake and vital rates of three marine mammal species (harbour porpoise, *Phocoena phocoena*, grey seal *Halichoerus grypus* and harbour seal *Phoca vitulina*) with contrasting life-history strategies. Dynamic bioenergetics models normally require large numbers of parameters whose values may be empirically derived, borrowed from the literature, 'guestimated' or based on expert opinion (Pirodda 2022). We describe how the uncertainty associated with these values can be quantified and investigate how it affects our model predictions.

Harbour porpoises are nomadic, pure income breeders with a generalist diet. Grey seals are central place foragers and pure capital breeders that use terrestrial breeding sites. Outside the breeding season they range widely (75–100 km day⁻¹, McConnell et al. 1999, Jones et al. 2015) from a variety of different haul out sites. Harbour seals are also central place foragers but show greater fidelity to specific haul out sites and rarely travel as far offshore as grey seals (< 50 km day⁻¹, Cunningham et al. 2009, Jones et al. 2015). Lactating females begin to forage before their calves are weaned and

they therefore have a life history strategy that is intermediate between capital and income breeding.

We used our models 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 the three focal marine mammal species. The aggregate effect of these events on an individual will depend on the probability that it is exposed to each of the events in the series, the probability that it will respond if it is exposed and the duration of any resulting response. We carried out a systematic exploration of the effects of different values of these parameters. We then used outputs from individual-based movement models (Chudzinska et al. 2021, Nabe-Nielsen et al. 2014) and telemetry data (Carter et al. 2022) to determine how the probability of exposure to these events might vary among individuals of the three species.

Our analysis is not intended as an assessment of the potential effects of wind farm construction on the dynamics of specific populations of these three species. Rather, our aim is to demonstrate how the outputs from bioenergetics and movement models can be combined to perform such an assessment and to illustrate how the effects of disturbance are influenced by a species' life history strategy and movement ecology.

Material and methods

We adapted the individual-based, dynamic bioenergetics model developed by Hin et al. (2019) for long-finned pilot whales so that it could be applied to three case study species, with different reproductive strategies and movement ecology: harbour seal (HS), grey seal (GS) and harbour porpoise (HP). We then ran a range of simulations with these models in which we systematically varied the probability of disturbance and the duration of disturbance (in terms of lost foraging). A full description of the bioenergetic models using the overview, design concepts, and details (ODD) protocol, a standardised format for documenting individual-based models (Grimm et al. 2020), together with detailed information on the way in which model parameters were derived can be found in the Supporting information. Below we provide a shorter, general description of the bioenergetic models, and the way in which uncertainty around model parameter values was addressed.

A full description of the individual-based movement models using the ODD are provided in Nabe-Nielsen et al. (2018) and Chudzinska et al. (2021). A shorter description of these two models, as well as information on animal tracking is presented below.

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

Only individual females and their offspring are modelled. Individuals are characterised by the following state variables: age, stage, length, structural (core) mass, reserve mass, energy assimilation and life expectancy. These vary over time depending on an individual's age and the resource densities it encounters. Females are tracked in discrete time steps of one day from age one year until death. Their offspring are tracked from birth until they die or reach age one.

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 fitting a five-parameter Siler model to published age- or stage-specific survival data for each species (Supporting information).

Process overview and scheduling

A simulated individual's daily assimilated energy varies with resource density, its structural mass, its state (e.g. pregnant, lactating, moulting) and its relative body condition (defined as the ratio of reserve mass to total mass). Individuals are assumed to have a target body condition (which is based on the maximum body condition observed in free-living animals – Supporting information). Following Hin et al. (2019), we assumed that animals assimilate energy at half of the maximum possible rate when their body condition is at the target level and increase their energy assimilation progressively if their body condition is reduced below this value.

If assimilated energy on a particular day exceeds the combined costs of metabolism, growth and reproduction, the surplus energy is converted to reserve tissue. If the combined costs cannot be covered by assimilated energy, a predefined proportion (which may be zero, depending on the species reproductive strategy) of the assimilated energy is assigned to growth (including growth of any foetus). If this is less than the energy required for growth, the growth rate of the female and her foetus is reduced accordingly. The daily costs of maintenance and lactation are always met in full by a combination of the assimilated energy remaining after realized growth costs have been subtracted and catabolism of reserve tissue. In these circumstances, a female's relative body condition will be reduced on the next day.

We assume that individuals 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 (Supporting information).

We assume that all females above a certain age can become pregnant every year. However, the actual age at first successful reproduction and the total number of offspring produced by a female depend on her body condition and life expectancy. The metabolic and growth costs of pregnancy are calculated by including foetal mass in maternal structural mass. Following New et al. (2013) and Hin et al. (2019), we assume that a female may choose to terminate a pregnancy at a pre-defined time, which may be the day of ovulation (in HP) or later (HS and GS) depending on her reproductive strategy, if her reserve mass is below a threshold value (Supporting information).

Offspring are entirely dependent on milk provided by their mother until they start foraging on their own. As for adults, their demand for milk depends on their structural mass and body condition. However, following Hin et al. (2019), we assumed that females will reduce the amount of milk they actually provide to their calf as their own body condition declines (Supporting information). Independent foraging is assumed to begin during lactation for HP and HS, but after the end of lactation in GS, whose pups fast for a period after weaning. Offspring foraging efficiency is assumed to increase with age until it attains the adult value.

Age-related and seasonal fluctuations in body condition are therefore the result of variations in the resource density experienced by individuals and in their energy demands. Figure 1A shows the predicted changes in body condition of a typical female of each species and her offspring over the course of four reproductive cycles in an undisturbed environment.

We determined the fitness of each simulated female from her lifetime reproductive success. Combining the mean lifetime reproductive success of all simulated females with their mean longevity provided an estimate of the long-term growth rate of a population with the underlying population characteristics of the simulation.

With one exception, we assumed that the simulated populations were food limited. We therefore used age- and species-specific survival rates from Sinclair et al. (2020) for populations of the three species that were increasing. We then adjusted resource density until the long-term growth rate of all the simulated populations was 1.0 as a result of increased starvation mortality and a reduced birth rate. Some HS populations appear to be limited by factors other than food (Matthiopoulos et al. 2014). We therefore developed an alternative model for this species using stage-specific survival rates for a stable population. These simulated populations achieved a growth rate of 1.0 with a higher resource density than the food-limited HS population, which we refer to as HS-Low R.

Birth and death are stochastic processes and growth varies among individuals, depending on the resources they encounter. It was therefore necessary to simulate a large number of females in order to obtain reliable estimates of mean lifetime reproductive success for a particular combination of parameter values. We found that a minimum of 1000 females was required to obtain consistent estimates and we chose to simulate 2000 females.

A flow chart of all the processes happening in the bioenergetic models at each time step is shown in the Supporting information.

Modelling the pattern of disturbance events

The species modelled in this study occur in regions of increasing offshore wind farm development. We reviewed construction approaches undertaken by offshore wind farm developers to determine the scale and duration of potential disturbance-inducing activities. We then created a piling schedule that approximated the most intensive pattern of monopile construction as a worst-case scenario. This involved 300 days of piling over a two year period. The simulated piling was scheduled to start on 1 May, with 150 days of piling randomly distributed throughout each year (Fig. 1B). To understand how sensitive the results are to the distribution of piling days across the piling duration, we also simulated a piling schedule where 100 days of piling occurred between May and September each year, and the remaining 50 days of piling were randomly distributed over the winter months (October–April). The results obtained using this piling schedule are presented in the Supporting information.

Estimating the effect of disturbance on individual energy balance

The effect of a particular disturbance-inducing activity on an individual's energy balance will depend on the probability that it is exposed to noise associated with that activity (which we refer to as 'probability of exposure'), the probability that it will respond to that exposure ('probability of response') and how long that individual ceases to feed as a result of its response (which we refer to as the 'disturbance effect'). Within the bioenergetic model, the product of the probability of exposure and the probability of response acts as a single parameter, which we refer to as 'probability of disturbance'. We evaluated the effects of the piling schedules on all three species by systematically varying the probability of disturbance and the disturbance effect. On each day of piling, we determined whether a simulated individual would be disturbed by conducting a binomial trial using the chosen probability of disturbance. If it was disturbed, we reduced its total assimilated energy on that day by the duration of the chosen disturbance effect expressed as a proportion of the day (e.g. a disturbance effect of 1 h resulted in a 1/24 reduction in assimilated energy). As there are no empirical data on how long individuals of each of these three species stop foraging after being exposed to disturbance from pile-driving noise, we used values of 1, 2, 4, 6, 8 and 12 h day⁻¹. The same process was followed for each of the 2000 simulated females. For most simulations, we assumed that each disturbance event resulted in the same reduction in assimilated energy for each modelled individual. However, we also considered a scenario in which the disturbance effect varied among events (referred to as individual heterogeneity, IH). Such variation could arise because of differences in the location of individuals relative to the sound source at the time piling commenced. We modelled this by sampling on each piling day, for each individual, from the hypothetical frequency distribution of disturbance effects shown in the Supporting information.

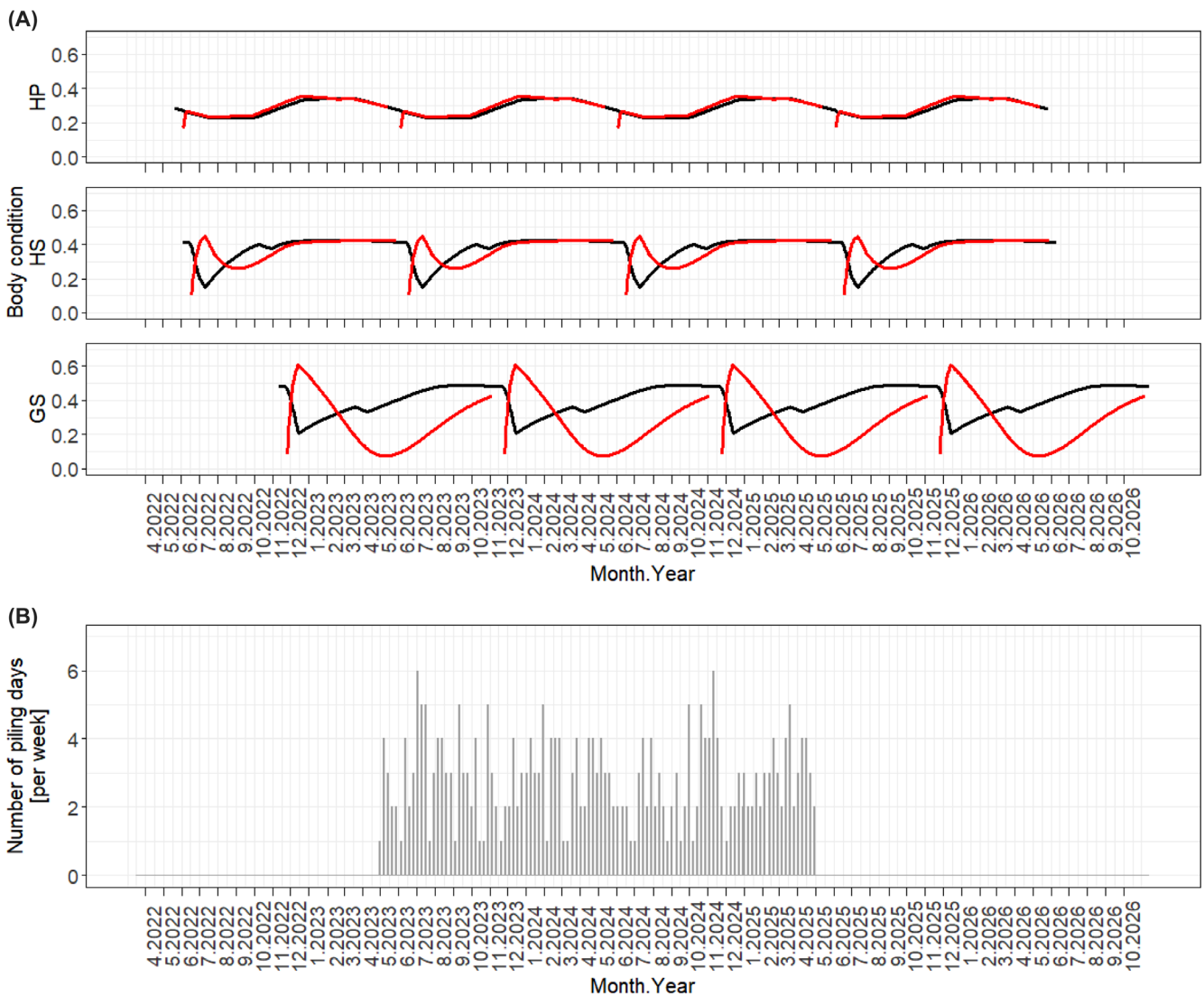


Figure 1. (A) Predicted changes in relative body condition of an average female (black lines) of each species ('HP' – harbour porpoise, 'HS' – harbour seal, 'GS' – grey seal,) and her offspring (red lines) over the course of four reproductive cycles in an undisturbed environment for the period for which all calculations were done when modelling the effect of disturbance. (B) Weekly number of piling days over the 2 years of piling schedule (A).

We assumed that both seal species were unaffected by any piling that occurred while they were ashore, or close to shore, during their lactation period. This encompassed the entire lactation period for GS. However, HS females are known to resume foraging towards the end of lactation and we assumed that they could be disturbed if piling occurred at that time. The two seal species also spend more time ashore during the moult and we reduced their energy assimilation by 50% at this time. This effectively reduced the response duration by the same amount.

Estimating individual probabilities of exposure and disturbance

In order to determine a range of plausible values for the probability of exposure we used already published individual-based

movement models and telemetry data to estimate how the probability of exposure might vary among individuals of all three species in an area of potential off-shore development. The actual probability of disturbance will be less than the probability of exposure because the probability of response to a particular disturbance event is likely to be < 1.0 . We discuss how to deal with this in the Results section.

For each species, we identified two areas, each of 30 km radius, in regions where intensive development of offshore wind farms is planned or has occurred (4C_Offshore 2023, Fig. 2A). One area was at a location where high densities of animals are expected to occur and the other where low density are expected. Thirty km is the likely limit of disturbance effects for a typical piling event (Graham et al. 2019, Whyte et al. 2020). For HP, these areas were located in inner Danish water; for HS and GS they were off the east coast of Scotland (Fig. 2A).

For HP, we used DEPONS (Nabe-Nielsen et al. 2014), which was developed to model long term movement of the entire population of HP in Inner Danish Water, to simulate the movements of 150 individuals over five years. For HS, we used AgentSeal (Chudzinska et al. 2021) to simulate the movements of 350 adult seals off the east coast of Scotland over six months. AgentSeal models the movements of adult HS outside their breeding season and is, therefore, not suitable for simulations of long-term movement. Both models were parameterised to reproduce movement characteristics (e.g. turning angles, step length, seasonal movement) observed for real animals based on tracking data.

We also used satellite tracking data from 12 adult HS and 19 adult GS that were tagged on the east coast of Scotland between 2008 and 2013 (see Carter et al. 2020 for details on tagging and data processing). The duration of deployment was 10–160 days (mean 85 days) for HS and 14–230 days (mean 85 days) for GS. For each simulated or tagged individual.

The models and telemetry data provided time series of x- and y-coordinates for each individual. AgentSeal provides locations every 15 min, whereas DEPONS outputs porpoise position every 30 min. The seal telemetry data have a temporal resolution of 1 h. We used these coordinates and the location of the 30 km radius areas of high- and low-density (Fig. 2) to calculate what proportion of each modelled or tracked day each individual spent within those areas. Haul-out time was included in the calculations for seals. Carter et al. (2020) describe how haul-out time was identified in the telemetry data. Figure 2B illustrates the proportions of each modelled or tagged day each individual spent in each of the defined areas. These were used as estimates of the probability of exposure to disturbance for each individual. The code and input data for estimating these probabilities are provided in the Dryad data repository (Chudzinska et al. 2023).

The telemetry data and the data used to construct the movement models were collected before any offshore wind farm construction took place and represent the movements of individuals that were not exposed to disturbance.

Quantifying uncertainty around model parameter values in the bioenergetic models

The bioenergetics models require values for more than 50 parameters (see full list in the Supporting information), some of which are not directly observable, and it is important to try to quantify the uncertainties that are associated with the values used for these parameters. We used rejection Approximate Bayesian Computation (ABC –, Wiegand et al. 2003, Lagarrigues et al. 2015) to establish plausible statistical distributions for the unobservable parameters, and for other parameters whose reported values showed large variations.

The ABC approach involves: 1) defining a set of rejection criteria based on empirical information that can be used to evaluate the plausibility of outputs from a model with a particular set of parameter values; 2) simulating the model a large number of times with values drawn from prior distributions for the parameters under investigation; 3) comparing

the simulation outputs to the rejection criteria; and 4) retaining only those combinations of parameter values that produce outputs that fall within the plausible range. This process generates a joint posterior distribution for the parameters under investigation.

The parameters chosen for ABC and their prior distributions are listed in the Supporting information. They were: proportion of assimilated energy allocated to growth (HS and GS only), effect of age on foraging efficiency, age of offspring when foraging efficiency was 50% of the adult level, starvation threshold and starvation mortality, field metabolic rate scalar, resource density, day of pregnancy when female ‘decides’ whether to continue with pregnancy (HS and GS only) and calf age at which female begins to reduce milk supply (HP only).

We ran 300 000 simulations for 2000 females each, in the absence of disturbance, with parameters drawn from a prior distribution (Supporting information).

We developed rejection criteria based on the following population characteristics: population growth rate; proportion of females giving birth each year; female starvation mortality; offspring survival rate; and seasonal changes in the body condition of offspring (HS only) (Supporting information).

The joint posterior distribution of parameter value combinations that fulfilled the rejection criteria for each species are shown in the Supporting information. This distribution was then sampled at random to provide parameter values for the simulations.

Final simulation schedule and calculation of vital rates

For each species we run combinations of seven probabilities of disturbance: 0.05, 0.1, 0.2, 0.4, 0.6, 0.8 and 1 and seven disturbance effects: 1, 2, 4, 6, 8, 12 h and IH.

To account for parameter uncertainty, we drew 90 combinations of values from the joint posterior distribution derived from the ABC analysis and used these to simulate the effect of each permutation of probability of disturbance and disturbance effect values on females that were seven years old when piling commenced. We chose this age because younger (i.e. seven years) females are expected to be most vulnerable to the effects of disturbance (Hin et al. 2019).

For each simulation, we documented three vital rates: adult starvation rate, calf/pup starvation rate, and birth rate (percentage of females alive at the start of the breeding season that gave birth). Birth rate and calf/pup starvation rate were calculated for each year from the breeding season before piling commenced to the breeding season after piling ended (Fig. 1A–B). In order to identify significant differences between these rates and those calculated when there was no disturbance, we applied Welsh’s unequal variance t-test to pairs of values that used the same combination of parameter values from the ABC analysis. If a significant difference was detected, we expressed this as a percentage change from the value observed in a scenario with no disturbance.

The code to run the bioenergetic models for the three studied species, the movement data and the reports describing the

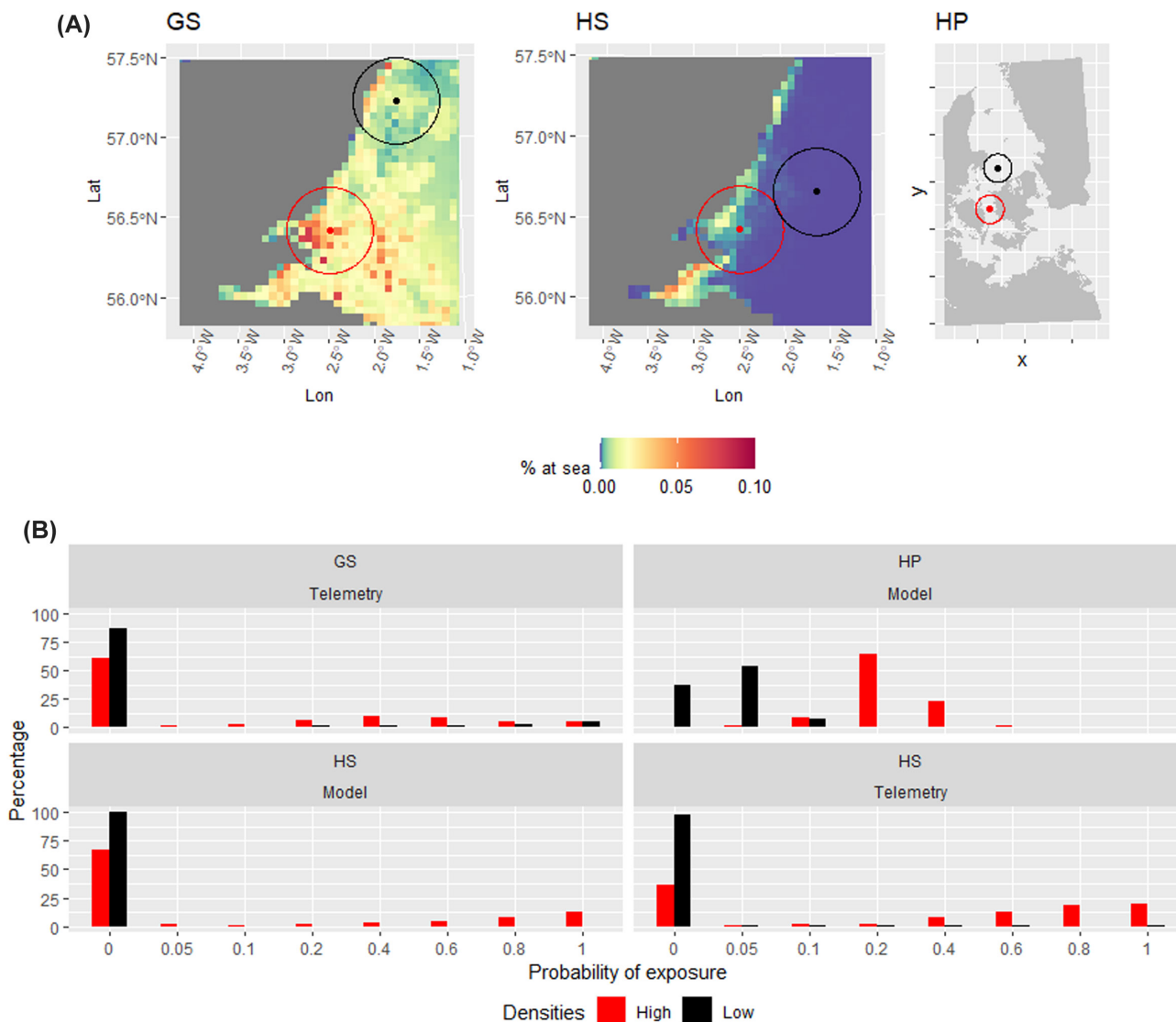


Figure 2. (A) At sea distribution (a proxy for animal density) of the two seal species on the east coast of Scotland (Carter et al. 2020) and the 30 km radius areas of low and high densities are shown on the two left maps. The locations of the low- and high-density areas for harbour porpoise in the Inner Danish water are shown in the right-hand map. For depictions of the observed densities of this species see Edrén et al. (2010). (B) The histograms show the proportion of tracked (“Telemetry”) or modelled (“Model”) days individuals of the three species (‘GS’ –grey seal, ‘HP’ – harbour porpoise, ‘HS’ – harbour seal) spent in the areas of high (red bars and red circles on the maps) and low (black bars and black circles on the maps) densities.

previous versions of the bioenergetic models are provided in the Dryad repository (Chudzinska et al. 2023).

Results

Effect of disturbance on the three modelled species

For all three species, most combinations of disturbance effect and probability of disturbance resulted in an increase in the calf/pup starvation rate (Fig. 3), with an almost linear increase in the effect on this vital rate with increasing probability of disturbance (Supporting information). The exception appears to be GS, where there was no relationship between pup starvation rate and either of the two disturbance

variables (Supporting information). This is because the total pup mortality in the undisturbed GS population is around 90% (Thomas et al. 2019), so even small increases in starvation rate as a result of disturbance can result in the death of all the surviving pups in a cohort. This sets an upper limit on the potential increase in mortality caused by disturbance. For HP and GS increases in disturbance effect and probability of disturbance were also predicted to result in a reduction in birth rate and an increase in the starvation rate of adults.

Disturbance had a greater effect on pup and adult starvation rates for the food limited HS population (HS Low – R in Fig. 3) than for the HS population that was not food-limited (HS in Fig. 3). This is because resource density was higher for the latter population, allowing disturbed

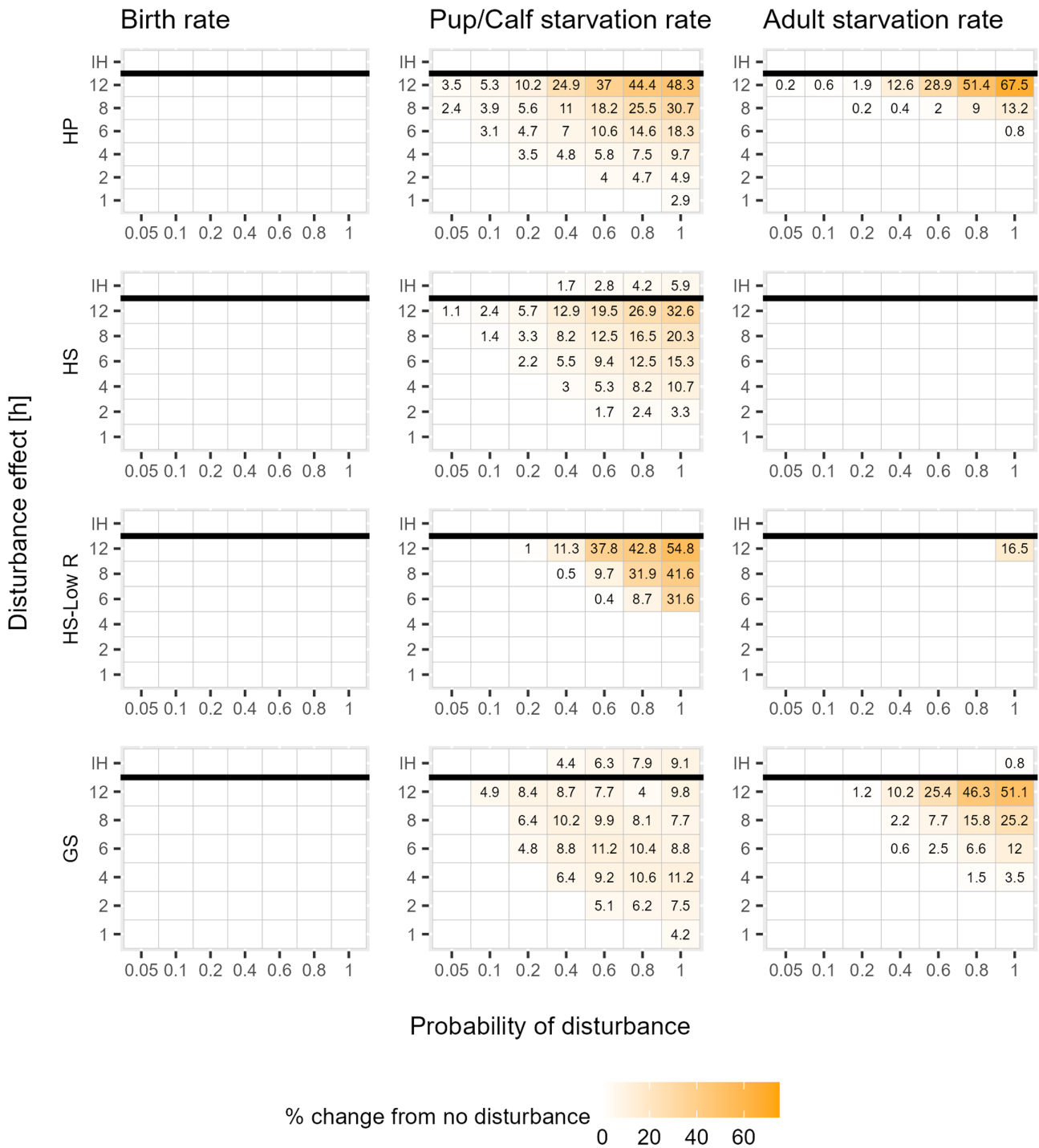


Figure 3. Percentage change from no disturbance in birth rate, pup/calf and adult starvation rate for different combinations of probability of disturbance and disturbance effect for the three studied species: ‘HP’ – harbour porpoise, ‘HS’ – harbour seal, ‘HS-Low R’ – harbour seal from a food-limited population, ‘GS’ –grey seal. 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.

individuals to compensate more easily for temporary reductions in daily energy assimilation. Simulations using a disturbance effect that varied among individuals (IH in Fig. 3) resulted in smaller changes in vital rates than those observed

in simulations with a disturbance effect that was the same as the mean of the IH values (2.64 h). Figure 2 illustrates the among-individual variation in probability of exposure to disturbance events in low- and

high-density areas derived from movement models and analysis of telemetry data. The actual probability of disturbance will also depend on the probability that an individual will respond when it is exposed to these events (the probability of response). This probability is likely to vary with the individual's distance from the source of disturbance at the moment of exposure (Graham et al. 2019). For illustrative purposes, we calculated a mean probability of response of 0.23 for HP within 30 km of the piling activity associated with the construction of the Beatrice Offshore Windfarm (Scotland) from the dose–response relationships shown in Fig. 6 of Graham et al. (2019) using the approach described by Tyack and Thomas (2019). We used this value to convert the probabilities of exposure shown in Fig. 2 to probabilities of disturbance for HP. Unfortunately, similar data were not available for HS and GS.

The low-density areas were rarely visited by any individuals, so that the vast majority had a probability of exposure, and hence a probability of disturbance, close to zero. These individuals would not be affected by any anthropogenic disturbance generated in the low-density areas, regardless of the value for disturbance effect. However, approximately 10% of the simulated HP had a probability of exposure of 0.1 (equivalent to a probability of disturbance of 0.023) in the low-density area. Figure 3 shows that these individuals might experience a small reduction (< 5%) increase in calf starvation rate and an even smaller (< 0.2%) increase in adult starvation rate if the disturbance effect lasted 12 h.

In contrast, most of the simulated HP spent some time in the high-density area, with 75% having exposure probabilities in the range 0.15–0.35. Disturbance in this area is therefore predicted to have a temporary effect on the vital rates of a large number of individuals if the disturbance effect exceeds 4 h (Fig. 3). To illustrate how the potential population-level effects of these changes might be calculated, we multiplied the individual probabilities of exposure for HP by 0.23 to obtain probabilities of disturbance. We then calculated a mean effect of disturbance for each vital rate using the proportions of simulated individuals that experienced probabilities of disturbance of 0, 0.05, 0.1, 0.2, 0.4, 0.6 as weights. The mean effects on HP birth rate and adult survival in the high-density area were close to zero. However, the overall reduction in calf survival was predicted to be 2.7% if the response duration was 8 h and 0.8% if it was 6 h. The equivalent values calculated using the mean probability of exposure for all individuals (0.24×0.23) were 2.4 and 0% respectively.

For HS, the distribution of exposure probabilities in the high-density area is bimodal, with most individuals not visiting the area, and therefore not being affected by the disturbance. These results are consistent whether the probability of exposure is obtained from the movement model or from the telemetry data. However, 30% of the tagged individuals and 20% of the simulated individuals had an exposure probability > 0.80. Disturbance in this area would result in a substantial increase in pup starvation mortality if the disturbance effect is greater than 6 h (Fig. 3) and there is a high probability of response.

The distribution of exposure probabilities for GS was similar in both the low- and high-density areas. Most individuals (approx. 90% in the case of the low-density area) did not visit either area and would therefore be unaffected by the disturbance events. However, 37% of the tagged individuals did spend some time in the high-density area and may be affected.

Piling that was more intense in the summer months had a larger effect on the three vital rates for HP and HS (Supporting information), with adult starvation rate in HS also affected by the highest values of disturbance effect. For GS, this piling schedule resulted in larger changes in birth rate but smaller changes in pup and adult starvation rate than when piling was randomly distributed over the year.

Uncertainty around model parameter values

For all three species, the largest difference between the prior and posterior distribution in the ABC analysis was determined by the available resources and the field metabolic rate scalar (Supporting information). For both seal species, there were large differences between prior and posterior distributions for two other parameters. These were the age at which a pup's resource foraging efficiency is 50% of the adult level, and the body condition threshold for the onset of starvation mortality (Supporting information).

The uncertainty associated with the relationships between the three vital rates and the two variables (disturbance effect and probability of disturbance) is illustrated in the box plots of Fig. 4. For all vital rates, variation increased with increased disturbance effects. Comparing the three vital rates, the variations in adult starvation rates were lowest regardless of the species and the effect that was varied. The largest variations around the mean were observed for birth rate in HP and birth rate and pup starvation rate in GS. HS and HP showed little variation around the mean in pup/calf starvation but there were a large number of outliers for this vital rate.

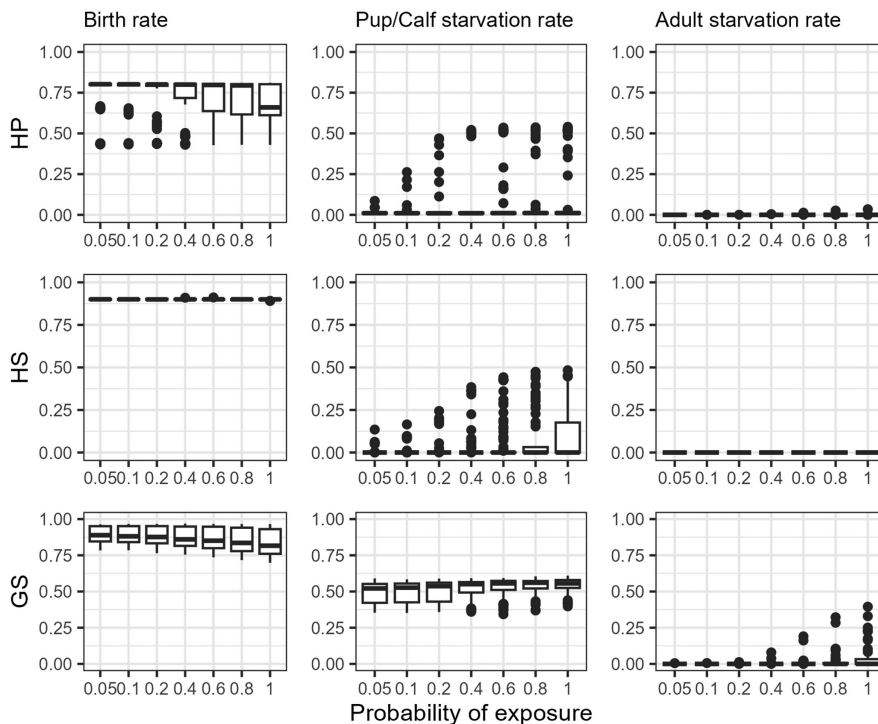
Discussion

We have shown how individual-based bioenergetics and movement models can be used to quantify the potential effects of disturbance on individual vital rates of species with different reproductive strategies and movement ecology.

The modelled piling schedule was predicted to have a similar effect on the vital rates of HP (physically small, pure income breeders) and GS (physically larger, pure capital breeders), despite their different reproductive strategies. This was probably because piling occurred year-round and therefore some disturbance events were bound to coincide with critical periods in the life cycle of each species, when their relative body condition was close to the threshold for starvation mortality (Harwood et al. 2022, Fig. 1A).

This conclusion is further supported by the results from the simulations in which there was increased piling activity during

(A) Disturbance effect = 4h



(B) Probability of exposure = 0.1

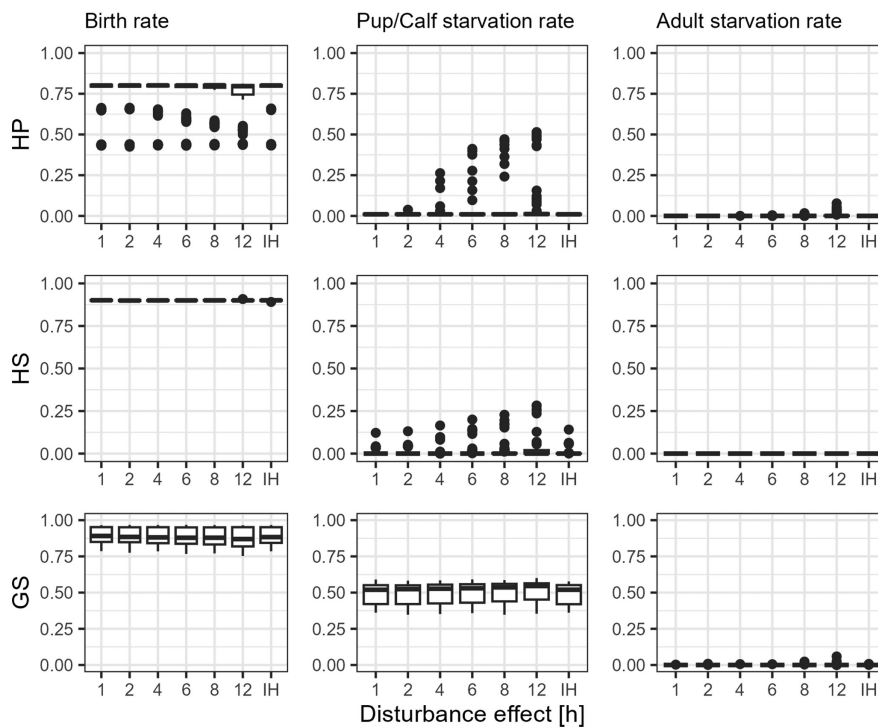


Figure 4. Variation in the effect of disturbance on the three vital rates between 90 parameter combinations for the entire range of probabilities of disturbance and fixed disturbance effect = 4 h (A) and the entire range of disturbance effect and fixed probability of disturbance = 0.1 (B) for the three studied species: ‘HP’ –harbour porpoise, ‘HS’ – harbour seal, ‘GS’ – grey seal.

the summer months (Supporting information). This schedule resulted in a further reduction in the birth rate for HP and GS, because there was more disturbance around the assumed day when females 'decide' whether or not to continue with the pregnancy. It also resulted in an increase in calf starvation mortality for HP (Supporting information), as also demonstrated by Gallagher et al. (2021), and HS. However, the body condition of adult HP is closest to the starvation threshold in winter (Gallagher et al. 2021, Fig. 1). As a result, adult starvation mortality was lower when piling was intensified during the summer.

The value used for the probability of disturbance in the bioenergetic models had a large effect on the predicted consequences. We were able to gain some insight into how this probability might vary among individuals by investigating how the probability of exposure (which is a key component in the calculation of probability of disturbance) was affected by a species' movement ecology and by among-individual variation. We did not investigate the effect of heterogeneity in the probability of response, which will vary depending on the precise location of each individual when construction work starts. Using the mean probability of response for all individuals, as we did, may underestimate the number of individuals that are disturbed a large number of times by a particular disturbance scenario. But it will also underestimate the number of individuals that are never disturbed by the same scenario. Further analysis is required to determine the net effect of these underestimates on predicted changes in vital rates.

We also assumed that the daily probability of disturbance for a particular individual is temporally independent, i.e. it is unaffected by that individual's movement history. Relevant data to test this assumption is limited, but Elmgaard et al. (2023) that tagged HP exposed to noise from an Acoustic Harassment Device moved away at speeds of 1.4–1.9 m s⁻¹ (5.0–6.8 km h⁻¹). If HP show the same reaction to pile driving noise they would exit the 30 km radius area around that disturbance event within 6 h.

Our results support Keen et al.'s (2021) suggestion about the role of movement ecology in determining the distribution of exposure probabilities. The two resident species (HS and GS) had a distribution that was skewed to the right, with many individuals experiencing an exposure probability of zero but a small number of individuals experiencing high probabilities. The vital rates of the latter individuals could be significantly affected by disturbance events, although the magnitude of this effect will depend on the duration of their response to the disturbance. Nomadic HP had a more symmetrical distribution, with most individuals experiencing similar exposure probabilities.

This analysis was only possible because of the availability of appropriate movement models or telemetry data for our study species. However, telemetry data are usually only available from a small number of individuals that have not been exposed to disturbance. Their behaviour may not, therefore, be representative of the entire population or of disturbed animals. For example, if individuals avoid areas in which they have been disturbed, telemetry data (and movement models derived from those data) will underestimate their probability of exposure to subsequent disturbance events at the same locations.

There is an additional problem with the use of the GS telemetry data. We assumed that GS offspring had the same probability of exposure to piling-related noise as their mother. However, GS pups appear to disperse more widely than adults (Carter et al. 2017, 2020, Peschko et al. 2020). They are therefore likely to have a lower mean probability of disturbance at a particular location. Unfortunately, the spatial resolution of the available telemetry data from pups is too coarse to allow the estimation of probabilities of exposure on the scale we used.

The effects of disturbance on adult survival may have been over-estimated in the simulations, particularly for GS. The total body weight of adult female GS in the North Sea is lowest at the end of lactation and does not begin to increase until 3–4 months later (Boyd 1984, Fig. 1). During this time their body condition is close to the threshold we have used for starvation mortality. However, such mortality is rarely if ever recorded in undisturbed adult GS. This suggests that, like many other mammals (Millar and Hickling 1990, Worthy et al. 1992, Kastelein et al. 2019), they have physiological mechanisms for coping with any harmful effects of extended periods of low energy intake. Such mechanisms are not included in the model.

Reduced energy assimilation did not appear to have any effect on the birth rate of HS. However, this should not be taken as evidence that HS are immune from such effects because we had to use data from GS to parameterise the relationship between body condition and birth rate. The GS model is based on a comprehensive analysis of this relationship performed by Smout et al. (2020). However, there are no equivalent data for HS and we therefore assumed that the pregnancy threshold and decision day for this species were determined by the same rules as in GS. The values of these parameters determine which vital rates (pup survival or birth rate) are affected by reduced energy intake. This is clearly an area where more research is needed. Unfortunately, the rejection criteria used for this species in the ABC provided little insight into the most appropriate values for these parameters, producing a posterior distribution that was virtually identical to the prior (Supporting information).

We found that the predicted effect of disturbance on individual vital rates depends critically on the assumed duration of the disturbance effect. Unfortunately, there are very few studies that provide any information on this variable for the species in this study.

The best information on seals comes from Russell et al.'s (2016) analysis of the response to actual piling events of HS tagged with satellite-relay transmitters. They found that usage of the area around the piling site returned to pre-disturbance levels within 2 h of the cessation of piling. The average piling duration was 6 h, which implies a displacement duration of 8 h. However, the effect of this displacement on energy intake is unclear because the tags provided no information on the displaced seals' behaviour.

There are similar issues with the available information on the duration of the disturbance effect in HP. Dähne et al. (2017) and Benhemma-Le Gall et al. (2021) used passive acoustic data from arrays of hydrophones to demonstrate a decline in HP vocal activity during construction

of an offshore windfarm using pile-driving. [Benhemma-Le Gall et al. \(2021\)](#) also recorded a decline in the buzzing activity that is associated with foraging. In both studies, vocalisation rates returned to baseline levels soon after construction ended. These results were based on the changes in population density that occurred in response to the disturbance events. However, the vocalisations recorded by these arrays cannot be assigned to individual animals and so they cannot be used to quantify individual behavioural responses.

Data on foraging behaviour have been collected from a number of marine mammal species using specialised telemetry devices capable of detecting prey capture attempts. These have provided insights into typical foraging rates and/or consumption rates in pinnipeds ([Iwata et al. 2012](#), [Ydesen et al. 2014](#), [Volpov et al. 2015](#), [Cole et al. 2021](#), [Vance et al. 2021](#)) and cetaceans ([Johnson et al. 2006](#), [Aguilar Soto et al. 2008](#), [Wisniewska et al. 2014](#), [Malinka et al. 2021](#)). Although such tags have been used to identify the onset of changes in foraging behaviour following exposure to a disturbance event they have only rarely provided information on the duration of that change. Further analysis of data from these experiments could therefore provide greater insight into the likely magnitude of the disturbance effect in different marine mammal species.

The duration of the disturbance effect is likely to vary among individuals, and to be affected by each individuals' precise location (which determines the received sound level) and behaviour when noise production commences. We used simple assumptions to explore the effect of this individual heterogeneity (IH). In the example we chose, the effect of a particular combination of disturbance effect and probability of disturbance was increased when we included IH. However, more work is needed to quantify the effects of different forms of IH.

It is important to highlight that the combination of a high probability of exposure disturbance and the largest reductions in intake do not always result in the largest predicted effects in all species (Supporting information). Such instances highlight the need for a better understanding of the intricacies of such models, particularly if they are to be used for conservation and management purposes.

Management implications and future studies

We have used a concrete example of a specific activity that is likely to generate underwater noise that could potentially disturb large number of marine mammals. This was done to illustrate how the approach we have developed could be used to estimate the consequences at the population level. However, it is not intended as a quantitative analysis of the risks to marine mammals likely to be associated with wind farm construction at any of the six locations we have used as examples of low- and high-density areas. That process would require an extension of the bioenergetic modelling to consider the effect of reduced energy assimilation on all the age classes in each population, not just younger females.

It would also require a more extensive analysis of each species' movement ecology to ensure that reliable estimates of the frequency distributions describing among-individual variation in probability of exposure at a particular location were obtained.

Our results indicate that disturbance-inducing activities are most likely to impact vital rates if they are carried out in an area with a high density of animals and at a time of year when individuals are likely to be in poor condition. In line with other studies ([McHuron et al. 2018](#), [Hin et al. 2019](#), [Silva et al. 2020](#)), we found that pup/calf survival is the vital rate that is most likely to be affected by disturbance, regardless of when the disturbance-inducing activities occur. Pre- and post-construction monitoring of pup/calf survival should, therefore, be considered as standard practice so that populations responses to these activities can be detected as early as possible.

The approach we describe here could readily be extended to other activities that result in a decrease in energy intake (e.g. redistribution of animals to areas of low prey availability), and to other species, provided there is sufficient information to parameterise the component models. However, we emphasise the need to account for among-individual heterogeneities and uncertainties in the values of the many model parameters. It is of particular concern that there is currently little published information on the duration of the response of individual marine mammals to disturbance because this has a large effect on predicted changes in vital rates. More research in this area is urgently needed.

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Author contributions

Magda Chudzińska: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Project administration (equal); Writing – original draft (lead); Writing – review and editing (lead). **Katarína Klementisová:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Cormac Booth:** Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **John Harwood:** Conceptualization (equal); Formal analysis (lead); Funding acquisition (supporting); Methodology (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are provided in the Dryad repository, <https://doi.org/10.5061/dryad.v41ns1s35> ([Chudzińska et al. 2023](#)).

Supporting information

The Supporting information associated with this article is available with the online version.

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