Movement and Seasonal Energetics Mediate Vulnerability to Disturbance in Marine Mammal Populations

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Submitted June 15, 2020; Accepted November 16, 2020; Electronically published February 5, 2021

Online enhancements: supplemental PDF. Dryad data: https://doi.org/10.5061/dryad.80gb5mkpn.

Abstract: In marine environments, noise from human activities is increasing dramatically, causing animals to alter their behavior and forage less efficiently. These alterations incur energetic costs that can result in reproductive failure and death and may ultimately influence population viability, yet the link between population dynamics and individual energetics is poorly understood. We present an energy budget model for simulating effects of acoustic disturbance on populations. It accounts for environmental variability and individual state, while incorporating realistic animal movements. Using harbor porpoises (Phocoena phocoena) as a case study, we evaluated population consequences of disturbance from seismic surveys and investigated underlying drivers of vulnerability. The framework reproduced empirical estimates of population structure and seasonal variations in energetics. The largest effects predicted for seismic surveys were in late summer and fall and were unrelated to local abundance, but instead were related to lactation costs, water temperature, and body fat. Our results demonstrate that consideration of temporal variation in individual energetics and their link to costs associated with disturbances is imperative when predicting disturbance impacts. These mechanisms are general to animal species, and the framework presented here can be used for gaining new insights into the spatiotemporal variability of animal movements and energetics that control population dynamics.

Keywords: agent-based model, energy budget, harbor porpoise, marine mammals, anthropogenic disturbances, bioenergetics.

Introduction

Marine environments are increasingly threatened with degradation and destruction by accelerating and cumulative human disturbances (Halpern et al. 2015; Nowacek et al. 2015), resulting in increased risk of population extinction for even common species (Ceballos et al. 2017). Human disturbances affect individuals directly through mortality or indirectly through changes in animal behavior, morphology, or physiology (Werner and Peacor 2003). These indirect or nonconsumptive effects are a topic of wide interest, as they may outweigh lethal effects (Preisser et al. 2005) and can be difficult to quantify (MacLeod et al. 2018). Perhaps the most widespread nonconsumptive effects are behavioral changes that occur when animals get disturbed, which can effectively reduce food availability by displacing them from important foraging grounds (Gill et al. 1996; Pirotta et al. 2014). Behavioral responses may differ across timescales, with discrete exposures causing temporary avoidance behavior and prolonged disturbance causing area abandonment (Lusseau and Bejder 2007). These deviations from normal behavior can result in increased mortality and suppressed reproduction (MacLeod et al. 2018; DeWitt et al. 2019). A primary goal in conservation is to establish a link between individual behavioral responses and population-level consequences to predict and mitigate the effects of future disturbance events (Pirotta et al. 2018).

However, individuals respond differently to disturbances, and responses are likely influenced by local resource availability and the individuals’ energetic status (Beale and Monaghan 2004a; Lusseau and Bejder 2007; Ellison et al. 2012; van Beest et al. 2018). Models that link responses to population effects should therefore account for spatiotemporal variation in resources and individual energetics. This can be accomplished using agent-based models (ABMs) where population dynamics emerge from...
interactions between autonomous individuals and their responses to environmental variations (van der Vaart et al. 2016; Railsback and Grimm 2019). Additionally, ABMs that build on first principles likely maintain predictive power in novel environments (Zurell et al. 2015).

To link food availability to population reproductive and mortality rates, energy budgets (EBs) can be integrated into ABMs (Sibly et al. 2013). Energy budgets use general equations based on first principles and species-specific parameters to calculate individual energetics (Hind and Gurney 1997; Sibly et al. 2013). These models rely on insight from physiological and evolutionary theory to dictate how animals allocate energy to maximize Darwinian fitness, prioritizing survival over nonessential processes like growth and reproduction (Sibly et al. 2013). The flexibility and dynamic nature of EB-ABMs make them powerful predictors of the fate of disturbed populations (Boyles and Brack 2009; Boult et al. 2019) and, because of their spatial explicitness, they are ideal for spatial planning focused on mitigating the impact of disturbance on populations (Nabe-Nielsen et al. 2018). Using EB-ABMs, simulated populations and their environments can be concurrently monitored in space and time to investigate drivers of disturbance impact severity, allowing not only for prediction of impacts but also an understanding of mechanisms influencing population vulnerability.

Anthropogenic disturbances can be particularly detrimental for animals with high energy requirements. Harbor porpoises (*Phocoena phocoena*), a cetacean species known for its exceptionally high metabolic rates (Kanwisher and Sundnes 1965; Hoekendijk et al. 2018; Rojano-Donáté et al. 2018), are dependent on sound for navigation, foraging, and communication (Olesiuk et al. 2002; Lucke et al. 2009; Tougaard et al. 2009; Thompson et al. 2013; Dyndo et al. 2015). This places porpoises at a high risk of nutritional stress in areas with elevated disturbance levels (Wisniewska et al. 2016, 2018; Hoekendijk et al. 2018), including areas where seismic surveys, which produce intense pulses of sound, are conducted for offshore development and exploration (Nowacek et al. 2015). Seismic surveys can cause such behavioral responses in porpoises as short-term displacement (Thompson et al. 2013), reduced rates of foraging buzzes (Pirotta et al. 2014), or altered movement patterns (Kastelein et al. 2013; Pirotta et al. 2014; van Beest et al. 2018). Their high sensitivity to noise and energetic constraints makes porpoise populations particularly vulnerable to seismic survey disturbance.

We present a process-based spatiotemporally explicit framework to model marine mammal population dynamics and demonstrate its use for mitigation of acoustic disturbance. The framework extends the ABMs in Nabe-Nielsen et al. (2014, 2018) by including a process-based energy budget for individual animals in the existing movement-based population model. We first aimed to develop a general framework to assess population consequences of disturbance while accounting for animal energetics, movements, and spatiotemporal variability of resources. We informed the framework using empirical data for harbor porpoises in the inner Danish waters. Second, we used the model to investigate the underlying drivers of the population’s vulnerability to seismic survey disturbance, particularly whether effects were related to local abundance or seasonal energetic status of affected animals. We used the framework to demonstrate the importance of accounting for temporal variability in energy requirements when assessing the population effects of disturbances.

**Material and Methods**

We constructed a model to simulate animal energetics for predicting spatiotemporal effects of disturbances on population dynamics in realistic landscapes. The model is composed of two submodels, the previously published “movement and population” model (Nabe-Nielsen et al. 2013, 2014) and a newly developed “energy budget” model based on first principles. In the following we present a summary description of the model. The TRACE document (Schmolke et al. 2010; Grimm et al. 2014) in the supplemental PDF (available online) includes a detailed model description following the overview, design concepts, details (ODD) protocol (Grimm et al. 2006, 2020) and presents additional evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

Three entity types are represented: female porpoises, ship agents, and grid cells. Porpoises are characterized by their location, speed, movement direction, age, age of maternity, pregnancy status, and lactation status (supplemental PDF, sec. 1, table 2.1). We also included state variables for spatial memory, length, mass, blubber mass, and storage level (percentage of body mass comprised of blubber). Porpoises are “super-individuals” (Scheffer et al. 1995), hereafter referred to as “individuals,” that represent 100 females. Ships are represented by their location, speed, movement direction, and noise level. The simulated landscape covers a 240 × 400-km area of the inner Danish waters and is composed of 600 × 1,000 grid cells, each covering 400 × 400 m. About half of these cells represent water. Of the water cells, only about 4,500 randomly distributed cells are assumed to contain food and are referred to as food patches. Maximum food levels were obtained from estimates of porpoise abundance (Edrén et al. 2010). All water cells are characterized by a suite of physical variables, such as temperature.
and salinity (supplemental PDF, sec. 1, table 2.2), which affect the porpoises’ movement and energy budget. Physical variables are updated monthly.

Simulation time steps proceed as follows: (1) ships move and emit noise, (2) animals move and respond to noise, and, as they move, assimilate energy from food patches, (3) animals then calculate their energetic costs and assimilated energy is expended on fulfilling costs in order of priority to survival (fig. 1).

Movement and Population Model

Movements are modeled on fine and large scales as shown in Nabe-Nielsen et al. (2013, 2014).

Fine-Scale Movements. Fine-scale movements follow a combination of correlated random walk (CRW), spatial memory, and deterrence. While animals encounter new food patches using CRW behavior, they use spatial memory return to patches where food was previously found. Animals gradually switch from using CRW to spatial memory behavior when they have been unsuccessful at finding food for some time. Together, CRW and spatial memory behaviors have effectively replicated fine-scale movements and home ranges of satellite-tracked porpoises (Nabe-Nielsen et al. 2013).

Responses to Noise. The effect of anthropogenic noise on movements is modeled as in the DEPONS model (Nabe-Nielsen et al. 2018), where animals are deterred by noise exceeding a threshold level representing the minimum sound exposure level where a behavioral reaction occurs. The deterrence severity is proportional to excess noise above the threshold and is based on the distance from the sound source, source level, and transmission loss (Nabe-Nielsen et al. 2018). See “Noise Models” below for parameter values used. In the presence of noise, fine-scale movements are therefore a combination of CRW, spatial memory, and deterrence behavior, allowing simulated animals to dynamically adjust their movements depending on the food levels and noise they encounter.

Large-Scale Movements. Modeled animals transition into large-scale movements if their energy storage levels decrease over three consecutive days (Nabe-Nielsen et al. 2014, 2018). Individuals are equipped with seasonally specific knowledge on the regions (40 × 40-km squares) where food levels are high, allowing animals to move toward the region with the highest potential overall food level. Large-scale movement speeds and routes resemble those of porpoises tagged with satellite transmitters in inner Danish waters (Nabe-Nielsen et al. 2014).

Animal Life History. Population dynamics are determined by the balance between reproduction and storage-dependent mortality. The pregnancy rate of porpoises was set to 67% (Sørensen and Kinze 1994), but pregnant animals with low storage levels stop allocating energy to reproduction, resulting in pregnancy termination. For lactating animals, low energy intake can cause reduced calf growth or calf death. The maximum life span is set at 30 years.

Energy Budget Model

Calculation of Metabolic Costs. The EB model is based on fundamental physical and physiological principles and serves to extend the equation-based model in Gallagher et al. (2018) within an ABM framework. Our novel approach allows costs incurred by animals to relate to body size and shape, storage level, swimming speed, reproductive state, and environmental conditions. This framework builds on similar approaches, such as that in Beltran et al. (2017), by additionally considering age-specific costs throughout the lifetime of animals and linking thermal and activity costs directly to adaptive and realistic movements.

![Figure 1](https://example.com/figure1.png)

*Figure 1*: Schematic representation of the energy acquisition and allocation processes in the energy budget model. Each modeled individual follows this procedure once per time step. Processes irrelevant for specific individuals are ignored.
Maintenance rates are modeled to scale with body mass following principles of physiological ecology (Sibly et al. 2013). Thermoregulation and locomotion costs depend on animal morphometrics, swimming speed, and thermophysical properties of their environment (Hind and Gurney 1997). Pregnancy costs are calculated as the combined costs of fetal tissue investment and reproductive tissue maintenance (Brody 1968). Lactation costs include calf maintenance, thermoregulation, growth, and storage. Pregnancy and lactation periods are assumed to be 300 and 240 days, respectively (Lockyer 2003; Lockyer and Kinze 2003). As harbor porpoises can begin weaning their calves early in the lactation period (around 3 months; Ofstedal 1997; Camphuysen and Krop 2011), modeled calves are considered 100% dependent up to 3 months, and then dependency decreases linearly to 0% by day 240. Growth costs are calculated assuming von Bertalanffy growth curves based on the current and maximal structural masses in a time step (Sibly et al. 2013). Any available excess energy is stored as blubber, and storage levels are updated. Once per day, blubber depth is updated and used for calculating heat loss. For a full description of metabolic calculations, see TRACE/ODD in the supplemental PDF.

Energy Acquisition and Allocation. While moving through resource patches, animals ingest food that they encounter. Assimilated energy is allocated to costs in the order that follows: maintenance, thermoregulation, locomotion, reproduction, and, finally, growth and storage (fig. 1). This prioritizes processes that are essential for survival (maintenance, thermoregulation, and locomotion) over those that can be forgone in periods of low energy intake (reproduction and growth; Sibly et al. 2013). Due to blubber’s importance for marine mammals (Ryg et al. 1993), growth and storage are equally prioritized, meaning assimilated energy that remains after fulfilling other costs is split equally between them. If energy allocated to growth is in excess of costs, the difference is also diverted to storage. When assimilated energy is insufficient to cover demands, animals first mobilize blubber to cover vital costs. Animals with sufficient stores will also mobilize blubber to cover reproduction and growth costs. As stores become increasingly depleted, the probability of calf loss, and eventually also adult mortality, increases.

Environment

We assumed that maximum food levels are higher in areas where porpoises were abundant in nature. After being depleted, food levels increase logistically in daily steps until reaching a maximum level (Nabe-Nielsen et al. 2014). Water temperature and salinity are updated monthly to use in thermoregulation and locomotion calculations and correspond to monthly averages from the Baltic Sea physical reanalysis product in the Copernicus database for 2007–2016 (http://marine.copernicus.eu). Additional thermophysical properties of seawater (density, conductivity, specific heat capacity, coefficient of thermal expansion, dynamic and kinematic viscosity, and Prandtl number) used in locomotion and thermoregulation calculations are then updated for each grid cell (details in TRACE sec. 3.3). To simulate disturbance, seismic survey vessels traveling along realistic survey routes are represented (see “Simulation Scenarios” below).

Model Calibration

While most model parameters were obtained directly from data or literature values, four parameters (ratio of active to passive drag, $\lambda$; maintenance normalization constant, $B_m$; ingested food to energy conversion factor, $IR(EA)$; and survival probability constant, $\beta_s$), required calibration using pattern-oriented modeling (Railsback and Grimm 2019). The parameters used for calibrating $\lambda$ and $B_m$ were empirical data on porpoise energetics (Otani et al. 2001; Rojano-Donâte et al. 2018), swimming speed-dependent oxygen consumption rates (Otani et al. 2001), and the relationship between body mass and field metabolic rate (FM; Rojano-Donâte et al. 2018). The parameters $IR(EA)$ and $\beta_s$ were simultaneously calibrated using two patterns: (1) an equilibrium population size corresponding to empirical inner Danish waters estimates and (2) a low probability of mortality at average storage levels. Calibration runs were executed using NetLogo’s BehaviorSpace feature (Shargel and Wilensky 2002). Output fits were established through global ranking (Chion et al. 2011), using ranks calculated for each pattern as the deviation of model outputs from pattern values. The parameter combination yielding the tightest fit to patterns, that is, the lowest ranking value, was selected. The calibrated model was subjected to a global sensitivity analysis in which model sensitivity to parameter values was determined. For sensitivity analysis details and results, see TRACE (SI) section 7.

Comparison of Model Outputs with Independent Data

To evaluate the model’s ability to predict key features of porpoise populations that were not used or addressed while developing or parameterizing the model, we compared model outputs with additional patterns of harbor porpoise morphometrics, energetics, and population structure (Read 1990; McLellan et al. 2002; Lockyer and Kinze 2003; Rojano-Donâte et al. 2018; A. Galatius and C. C. Kinze, unpublished data). Patterns used for model evaluation were blubber masses of four age and reproductive
classes, mass-length relationship, age-class distribution, seasonal trends in blubber thickness, and both average and seasonal trends in FMR and energy intake (see TRACE sec. 8).

Simulation Scenarios

Simulation Specifications. To investigate whether disturbance impact severity varied seasonally, we simulated seismic survey exposures occurring in the different months of the year. Each simulated survey lasted 30 days, was 510 km long, and resembled a past seismic survey conducted in the inner Danish waters. Surveys occurred in three locations: Omø, Sejerø Bay, and Samsø. Each simulation began January 1 and covered 20 years, with exposure occurring in a specific month in year 15. Twelve scenarios were constructed, one per month, during which surveys were conducted simultaneously in the three locations. Each exposure scenario was repeated 100 times (totaling 1,200 simulations). One hundred control simulations were also run for each scenario (an additional 1,200 simulations) where surveys occurred but no noise was produced.

Noise Models. Noise source levels (NSLs) of survey vessels and the threshold level for behavioral reactions, $T$, were 262 and 165 dB re 1 µPa peak-peak, respectively (Thompson et al. 2013; Kyhn et al. 2019). Transmission loss was modeled as $\text{NSL} = \beta \log(r) + \alpha r$, where $r$ is the distance from the sound source in meters (Urick 1983; TRACE sec. 2.7.1). Empirical values were available for $\beta$ and $\alpha$ for Omø and Sejerø Bay (NIRAS et al. 2015; Barham 2016) but unavailable for the Samsø site, so here averages of other site values were used. Because the deterrence coefficient, $c$, for porpoises exposed to seismic surveys is unknown, we used the value for pile driving disturbance in Nabe-Nielsen et al. (2018).

Model Output Metrics and Analysis. For each simulation, we recorded five metrics daily to assess impact severity: population size, total calf loss (abortions and dependent calf death), storage level, calf mass, and juvenile mass. The last three metrics were recorded as averages for all animals within 40 km of a survey ship. Additionally, the number of juvenile and adult porpoises within this 40-km region was monitored to measure local abundance. For each scenario, all control simulation outputs were averaged per time step. We then computed the deviation at each time step between (1) the averaged controls and each of the corresponding exposure simulations and (2) the averaged controls and each of the corresponding individual control simulations (as a measure of variance within controls) and recorded the maximum deviation value found. Maximum deviation values for each exposure scenario were divided at random into five groups of 20 runs, and group averages and standard deviations were computed to estimate variability in calculated effect sizes. For control scenarios, the average and standard deviation of all maximum deviation values were calculated. Using Hedges’ $g$ effect size estimator and established rules of thumb (Hedges 1981; Cohen 1988), we compared the averages and standard deviations of exposure and control scenarios to evaluate disturbance impact severity.

Results

Realistic Simulations of Porpoise Energy Budgets

The calibrated model outputs closely resembled data for wild and captive animals (fig. 2). Oxygen consumption increased with swimming speed in the same way in simulated and real porpoises, indicating that costs of locomotion were realistic. Likewise, FMR increased with animal mass similarly for simulated and real porpoises.

Without further calibration, the model successfully reproduced independent patterns of porpoise morphometrics, energetics, and population structure observed empirically (see details in TRACE sec. 8). The model predicted that blubber mass increased with age, that total mass of porpoises increased exponentially with length, and that the population was composed primarily of young animals, patterns that were observed for wild porpoises (Read 1990; McLellan et al. 2002; Lockyer and Kinze 2003; Rojano-Donáte et al. 2018). Blubber depth varied seasonally and was thinnest in late summer and thickest in late winter (fig. 3a). Mean daily energy use followed similar trends, with the lowest costs experienced in months with the warmest water temperatures and the highest costs during cold months (fig. 3b). The FMRs of nonlactating animals were, on average, 15.9 ± 3.5 MJ per day (mean ± 1 SD), while average daily intake rates were 19.2 ± 8.8 MJ per day. Porpoise ingestion rates also displayed seasonal patterns, with animals ingesting less energy in spring and summer and more in fall and winter (fig. 3c).

Seasonal Variations in Animal Energetics and Noise Impacts

In the survey region, water temperature, porpoise storage levels, energy balance, and local population size varied seasonally (fig. 4). Seasonal variation in animal storage levels (fig. 4b) mirrored water temperature (fig. 4a). From September to February, animals maintained a positive energy balance, ingesting more energy than they used (fig. 4c), while energy balance was negative from April
to July. The highest local abundances were observed in June–August (fig. 4d).

Seismic survey exposures resulted in reduced mass for porpoises (fig. 5a). This reduction in storage level caused abortions for some pregnant animals (fig. 5a) and reduced body condition for dependent calves (fig. 5b). Animals exposed to noise biased their movements away from survey vessels, sometimes moving to regions with lower food availability (fig. 5d).

The severity of population impacts resulting from seismic survey disturbances varied temporally (fig. 6). The largest impact severity occurred in August–November for all five measured metrics, which did not coincide with the period of highest local abundance (fig. 4d). Large effect sizes were found for the three metrics related to morphometrics, storage levels, calf mass, and juvenile mass, where maximums ranged between 1.74 and 3.17. For the two mortality metrics, total calf loss and population size, maximum effect sizes were 1.44 and 2.17, respectively. When evaluating the results of all measures, a strong seasonal trend appeared, with the largest impacts occurring in August–October and the lowest impacts occurring in March–May.

Discussion

To predict population vulnerability to anthropogenic stressors in a changing world, it is essential to link individual responses to disturbance to resulting population-level impacts (Pirotta et al. 2018). We established this link by integrating a process-based energy budget into an ABM incorporating movement responses to disturbance.

ABMs with detailed individual-level representation of mammalian energetics are being increasingly developed for both marine and terrestrial systems (Beltran et al. 2017; Boult et al. 2018; McHuron et al. 2018; Chimienti et al. 2020; Pirotta et al. 2020). To understand the effects of disturbance on populations, we extended these approaches to consider the link between energy use and adaptive movement behavior in dynamic landscapes. When parameterized for harbor porpoises, the model reproduced empirical observations of the study species, successfully made independent predictions for evaluation, and allowed for investigation of underlying drivers of population vulnerability to disturbance. By exposing the population to theoretical disturbance scenarios, we demonstrated that impact severity was not influenced by any single driver, but rather by seasonally variable and interacting physiological and environmental conditions experienced by the population.

While the model is general and can be used, after recalibration, for other marine mammal species, we focused on harbor porpoises because of their high energetic constraints and potentially elevated sensitivity to disturbance (Wisniewska et al. 2016; Rojano-Donáte et al. 2018). Energy intake is reported to vary seasonally in this species, with porpoises ingesting more energy in fall and winter (Kastelein et al. 2018; Rojano-Donáte et al. 2018). Seasonal fluctuations in the FMRs of porpoises have not been documented; however, their respiration rates, which can be linked to energy expenditure, show seasonal variation (Kastelein et al. 2018; Rojano-Donáte et al. 2018). In the model, maximum energy intake varies temporally depending on animal mass, reproductive status, and local

Figure 2: Fits of the model to empirical data used for calibrating harbor porpoise energetics. a, Oxygen consumption for porpoises swimming at different speeds. b, Relationship between field metabolic rate (FMR) and animal mass. Error bars show ±1 SD. The width of the red lines represents the range of outputs for the best-fitting 100 simulations.
water temperature, which then, based on their energy balance, influences animal body condition and FMR. The model reproduced independent empirical seasonal trends in porpoise energy intake, FMR, and blubber thickness. The overall intake rates predicted by the model (19.2 ± 8.8 MJ per day; mean ± 1 SD) were in good agreement with values from captive settings (15.5–31.3 MJ per day, Rojano-Donâte et al. 2018; 18 MJ per day, Kastelein et al. 2018) and were highest in fall and winter and lowest in spring and summer. Similar to empirical trends for respiration rates, FMRs of modeled porpoises were higher in winter and lower in summer. The model also reproduced independent empirical patterns of class-specific blubber masses, mass-length relationship, and age-class distribution. Models such as this, in which empirical patterns are reproduced by low-level mechanisms, are more likely to yield realistic predictions about future disturbance scenarios (Stillman et al. 2015).

Reproductive rates, such as the abortion and recruitment rate, are emergent properties of the model that are mediated by female body condition and energy balance. These rates provide insight into mechanisms through which environmental variability affects population dynamics. However, for cetaceans, little is known about reproductive processes and relevant data are scarce, although the model was not sensitive to these parameters (TRACE sec. 7). Despite this, the model produced rates consistent with findings for several marine mammals (Read and Hohn 1995; Guinet et al. 1998; Testa and Adams 1998; Lockyer and Kinze 2003; Stolen and Barlow 2003; McKenzie et al. 2005; Gibbens et al. 2010; Henderson et al. 2014; Wells et al. 2014), suggesting that model processes capture aspects of natural reproductive dynamics. Simulated individuals become pregnant at rates consistent with inner Danish waters porpoises (Sørensen and Kinze 1994), but not all pregnancies were successful (74.9% ± 5.3%; mean ± 1 SD). This success rate is consistent with Read and Hohn (1995), who reported high porpoise lactation rates. The abortion rate (25.1%) was higher than recorded in bottlenose dolphins, *Tursiops truncatus* (17%, Wells et al. 2014), but less than estimates for two fur seal species, *Arctocephalus pusillus* and *Arctocephalus forsteri* (31%, Gibbens et al. 2010; 35%, McKenzie et al. 2005). Once calves were born, calf death occurred if females experienced extended periods of negative energy balance with 20.5% ± 4.9% (mean ± 1 SD) of calves dying prior to weaning, falling within the range of first-year mortality rates reported for cetaceans (e.g., bottlenose dolphins; 33%, Henderson et al. 2014; 16.4%, Stolen and Barlow 2003). Both the probability of successful weaning and birth of calves increased with mother’s storage level, as has been documented in several mammals (Guinet et al. 1998; Testa and Adams 1998). Similar to estimates for porpoises in the inner Danish waters (Lockyer and Kinze 2003), modeled females gave birth to 3.2 ± 2.3 (mean ± 1 SD) calves over their lifetimes. The model shown here linked reproductive success to food availability, energy balance, and body condition, which has been long supported in marine mammals empirically (Pitcher et al. 1998; Seyboth et al. 2016).

Figure 3: Comparison of harbor porpoise energetics for simulated (red) and real (blue) animals showing seasonal variation in blubber depth (*a*), field metabolic rate (*b*), and energy intake (*c*). Red shading shows the mean ± 1 SD for all animals in 100 simulations of year 15; blue shading shows averages (*a* and *b*) and 95% confidence interval range (*c*) for animals from inner Danish waters (*a*, *n* above violin plots; *b*, *n* = 16; *c*, *n* = 3).
This link allows for investigation of mechanisms by which reproduction is suppressed under disturbance in wild populations and prediction of reproductive impacts on population size and stability.

By explicitly and realistically representing movement and energetics, the ABM enabled simulation of a seismic survey impact assessment to answer questions and elucidate underlying mechanisms useful for spatial planning and management. When exposed to noise, the model predicted that the abundance of animals in the survey area (<40 km from survey ships) was reduced (~16.3% to 20.4%; minimum in February, maximum in June). This displacement decreased animals’ storage levels, causing slowed growth, abortions, loss of dependent calves, and death. The impact on calf loss (1.5%–36.6%; minimum in July, maximum in September) was higher than for juvenile and adult mortality (0.4%–2.4% population reduction; minimum in April, maximum in October). It has been

![Figure 4](image-url)
suspected that disturbed animals experiencing periods of low energy intake are less likely to be deterred from quality foraging grounds (Beale and Monaghan 2004; Bejder et al. 2009), and the model here simulates such effects. Variability in the movements of simulated animals exposed to identical noise levels (TRACE sec. 5) emerged from the energetic status of animals and recent encounters with survey vessels and agreed with observations of responses of cetaceans in nature (van Beest et al. 2018).

Recent studies of porpoise responses to seismic surveys have found variation in movements (van Beest et al. 2018), presence, and foraging behaviors (Pirotta et al.

**Figure 5:** Simulation output for an individual female porpoise observed in an area exposed to survey noise in September. 

- **a,** Structural and total mass; line color shows reproductive status. 
- **b,** Structural and total mass of the female’s calf; line color corresponds to legend in **a**. 
- **c,** Received noise level for the same porpoise. 
- **d,** Seismic survey routes (in black); background colors show potential food availability (food proxy), with darker colors representing higher levels of potential food availability. 
- **e,** The animal’s movement path during the survey period, showing one position every 3 days with point color indicating whether the received sound level (RL) exceeded the behavioral threshold (T).
Our model predicted that disturbance impact severity did not directly correlate with local population size. However, current environmental impact assessments base predictions on, and create policy decisions using primarily local abundance, that is, the number of animals potentially exposed (Goodale and Milman 2019). Model findings suggest that context related to energetics and movement of animals should also be considered when making these assessments.

A benefit of our approach, which relies on low-level processes, is that it can elucidate how various environmental and physiological drivers relate to disturbance impact.
severity to better understand how populations are affected by disturbances in space and time. Temporal variability in energetic requirements, prey availability, and abiotic conditions can all influence the severity of disturbance impacts. This occurs because seasonality in reproduction and body fat stores leads to temporal variations in energy needs of and buffer available to individuals facing disturbance. In the model, the local abundance around simulated survey ships varied seasonally as animals moved to exploit shifting resources. However, disturbance impact severity did not directly relate to seasonal trends in local abundance. For instance, while May and September had similar numbers of animals around exposure zones (fig. 4), the overall population effect was more than seven times greater in September than in May (fig. 6). This could be attributed to differences in the energy balance and storage of animals during these periods. In May, animals have greater stores, making them less vulnerable to nutritional stress, and in September, animals seek a positive energy balance to increase body fat to survive cold winter months. Reproductive seasonality may also influence the population response to disturbance effects, as most animals in May have already weaned their calves or have yet to give birth, whereas in September, animals with calves are nearing the costliest period for lactation and are also potentially pregnant. Our findings suggest that population vulnerability to disturbance arises from interactions between disturbance effects and naturally occurring temporally variable aspects of the energetics and movement of populations and their environment.

Our model successfully made independent predictions based on ubiquitous and low-level mechanisms; still, several simplifying assumptions were made in model development when data were lacking or for maintaining model tractability. When using the body mass and FMR relationship (Rojano-Donâte et al. 2018) to calibrate the maintenance normalization constant, specifics on the storage levels and thermal environments experienced by animals were unknown, so we assumed that animals were not expending energy on thermoregulation. Any thermal costs actually incurred by observed animals would therefore be attributed to the estimation of maintenance costs, resulting in modeled thermal costs being present only when rates of heat loss exceed those of the observed animals. To model growth and reproductive investment, we assume that these processes were suppressed when energy intake was low. This is supported by empirical findings that growth and reproduction are reduced under periods of predation risk (MacLeod et al. 2018; DeWitt et al. 2019), which is thought to elicit responses similar to those resulting from nonconsumptive human disturbance (Beale and Monaghan 2004b). We additionally assume that reproductive investment is linked to storage level. While this is generally supported both by theory (Sibly et al. 2013) and empirical evidence (Persson 2005; Christiansen et al. 2014), data for parameterizing reproductive decision values are lacking. However, the model was not found to be very sensitive to this parameter (TRACE sec. 7), and if it were to deviate considerably from reality, we would not expect the model to reproduce several patterns used for evaluation—for example, blubber and overall mass of young individuals and population age structure. When modeling responses to noise, animal habituation was not included. Although this would likely influence behavioral reactions (Bejder et al. 2009), it is not known whether animals habituate to seismic survey noise. Prey resource maps in the model are based on season-specific porpoise distributions and therefore empirical and modeled population distributions are similar. However, it is possible that site fidelity differs among seasons and reproductive states and that, for example, females with calves prefer certain areas (Koschinski 2001; Loos et al. 2010), but little is known with regard to special nursing areas for harbor porpoises. This could lead to differences in the population effects of disturbance depending on the location of the disturbance event, with disproportionately large impacts for animals with high energetic costs (lactating females). To model landscapes, we represented prey as a general resource and calibrated its energy density, although more specific prey fields could be incorporated with accompanying energy contents for the assessment of different prey types or qualities. The flexibility of the model design allows for specific proposed disturbances to be evaluated. Being so, we caution that results found here for disturbance scenarios do not necessarily represent overall predictable trends for disturbances in general. Instead, we advocate that the model be used as a tool to test specific disturbances and investigate the underlying mechanisms contributing to predicted effects.

In this study, we focused on harbor porpoises and seismic surveys as an example; however, the generality of the model makes it widely applicable for testing the effects of disturbances on marine mammals. This generality also means that it is straightforward to adapt the model for other systems or to include other stressors or environmental scenarios, making the model useful for predicting impacts under cumulative disturbance (e.g., Galic et al. 2018) or shifts in food resources, such as those predicted with climate change (e.g., Beltran et al. 2017). Our framework takes a novel and detailed approach by explicitly modeling animal energetics, movements, and spatial distribution of resources for investigating disturbances and mechanisms mediating energetics. When applying our model, we showed that physiological and environmental drivers of population vulnerability to disturbance vary temporally and interact to produce seasonally variable impact severity.
Animal population regulation in space and time is governed by the interplay between biotic and abiotic processes (Lundberg et al. 2000), and disturbances can interact with these natural mechanisms unexpectedly to produce variations in impact severity that may be missed when focusing on single drivers. In the future, when predicting the effects of disturbance, we must consider how the energetics, movements, and fitness of animals are affected by disturbances in space and time, and we must use modeling approaches that can explicitly consider these low-level processes for better predictability of the effects of humans on marine populations.

Acknowledgments

This study was a part of C.A.G.’s PhD project funded by Aarhus University. We thank Jürgen Groeneveld and Steve Railsback for their help and advice on a draft of the overview, design concepts, details (ODD) model. We also thank the GenomeDK cluster team for allowing us access to their cluster, which allowed for speedy simulations. This study is part of the DEPONS project (http://www.depons.au.dk) funded by the offshore wind developers Vattenfall, Forewind, ENECO Luchterduinen, Ørsted, and Scottish Power Renewables. We also thank an anonymous reviewer and Karin C. Harding for their constructive comments on the manuscript.

Statement of Authorship

C.A.G. and J.N.N. designed the study. C.A.G. performed the modeling work and analysis. V.G. assisted with developing the model documentation. C.C.K. provided porpoise data used for informing and evaluating the model. L.A.K. assisted in designing seismic survey scenarios. C.A.G. led the writing of the manuscript with input from all authors.

Data and Code Availability

Full model code, associated run files, input data, and scripts used to produce article figures have been deposited in the Dryad Digital Depository (https://doi.org/10.5061/dryad.80gb5mkpn; Gallagher et al. 2020).

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