Predicting the impacts of anthropogenic disturbances on marine populations - Supporting Information – TRACE document

Method · May 2018

6 authors, including:

Jacob Nabe-Nielsen
Aarhus University
83 PUBLICATIONS   **1,163** CITATIONS

Floris M van Beest
Aarhus University
64 PUBLICATIONS   **796** CITATIONS

Volker Grimm
Helmholtz-Zentrum für Umweltforschung
291 PUBLICATIONS   **15,837** CITATIONS

Richard Sibly
University of Reading
257 PUBLICATIONS   **10,034** CITATIONS

Some of the authors of this publication are also working on these related projects:

The impact of off-shore wind turbines on harbour porpoise behaviour and population dynamics   View project

Spatial modeling of forest fire ecosystems   View project

TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation"), which provides supporting evidence that our model presented in:

> **Nabe-Nielsen J., van Beest F.M., Grimm V., Sibly R.M., Teilmann, J. & Thompson, P.M. (2018). Predicting the impacts of anthropogenic disturbances on marine populations. *Conserv. Lett.***

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

> Schmolke A., Thorbek P., DeAngelis D.L., Grimm V. (2010). Ecological modelling supporting environmental decision making: a strategy for the future. *Trends Ecol. Evol.* 25, 479-486.

and uses the updated standard terminology and document structure in:

> Grimm V., Augusiak J., Focks A., Frank B., Gabsi F., Johnston A.S.A., Liu C., Martin B.T., Meli M., Radchuk V., Thorbek P., Railsback S.F. (2014). Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecol. Modell.* 280, 129–139.

and

> Augusiak J., Van den Brink P.J., Grimm V. (2014). Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecol. Modell.* 280, 117–128.

Contents

1 Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

> **Anthropogenic noise can induce behavioral responses in marine mammals, which may influence the individual animals' foraging success and, ultimately, the dynamics of the population. Pile-driving noise associated with construction of offshore wind farms can have pervasive effects on the harbor porpoise (*Phocoena phocoena*). In this study we present an agent-based model, the DEPONS model, for assessing population consequences of such pile-driving noise on the porpoise population in the North Sea. Population dynamics emerge from the individuals' competition for a dynamically replenishing food resource and from altered movements in the presence of pile-driving noise. Model predictions are influenced by the exact timing and spatial location of individual pile-driving events.**

Marine populations experience increasing levels of noise from offshore renewable energy developments, seismic surveys, military sonars and ship traffic (Tyack 2008; Slabbekoorn et al. 2010; Nowacek et al. 2015). A comprehensive assessment of the effects of human noise on marine populations is increasingly demanded for management of marine ecosystems in Europe and the U.S. (EU Marine Strategy Framework Directive 2008; White House Executive Order 2010). Many types of offshore activities (including wind farm construction) require an environmental impact assessment (EIA) to be conducted prior to development. EIAs are particularly focused at fragile and protected populations, and in European waters the species mentioned on the Habitats Directive (EU 1992) are of concern. Critically, they often require a cumulative assessment of the population level impacts of the primary development in combination with other human activities in the region. The model we present here can be used for conducting spatial planning to ensure that offshore activities affect the population as little as possible and conduct EIAs of planned projects. The model has been developed for the harbor porpoise (*Phocoena phocoena*), a small cetacean listed on the Habitats Directive Annexes II and IV, but the principles behind the model can be applied for any marine species.

Noise can travel over long distances in marine environments and induce behavioral responses of affected individuals (DeRuiter et al. 2013; Miller et al. 2015). This can lead to disruption of natural foraging behavior and habitat displacement, with potential consequences for individual survival and population dynamics. Pile-driving of wind turbine foundations, which is one of the most pervasive sources of noise in many areas, is known to affect harbor porpoise densities at distances >20 km

(Tougaard et al. 2009; Brandt et al. 2011). The modeling framework we present here links the dynamics of harbor porpoise populations directly with the response of individuals to pile-driving noise. Model predictions depend on the exact timing and location of pile-driving events. Population densities and the time it takes the population to recover after pile-driving stops can be measured either locally or for the entire population.

The model takes a data-driven, mechanistic approach to management of marine populations. Population dynamics emerge from the individuals' competition for a dynamically replenishing food resource and from altered movements and foraging success when pile-driving noise is present. The model framework is currently parameterized for assessing effects of wind farm construction on the North Sea harbor porpoise population, but can be parameterized for other populations and other types of impulsive noise. The use of general relationships between population regulation and resource availability (Sinclair 2003; Goss-Custard et al. 2006) is likely to cause the model to generate robust predictions for a wide range of environmental conditions (Grimm & Railsback 2005; Stillman et al. 2015).

Although the model is likely to be robust to variations in environmental conditions, it should be noted that it was developed for the North Sea population. As population dynamics are tightly linked to animal foraging behavior and space use (home ranges), the model can only be extrapolated to areas outside the North Sea if there are empirical data available for re-calibrating the movement patterns. We consistently used the simplest possible implementation of the different processes and behaviors in the model (i.e. the submodels that involved the smallest number of parameters) if there were no data to suggest that particular parameters could play a role for harbor porpoise movement, energetics or population dynamics in nature.

2   Model description

This TRACE element provides supporting information on: The model. Provides a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

> **Here we present the complete description of the DEPONS model for simulating population effects of pile-driving noise (version 1.1). The description follows the updated ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2010). The model extends an existing agent-based model (Nabe-Nielsen et al. 2014). The present documentation includes both elements previously described for the original model, an overview of the underlying fine-scale movement model (Nabe-Nielsen et al. 2013b) and the novel behaviors related to large-scale movement and to changes in movements in the presence of noise. The model, which was implemented in**

TRACE document: Nabe-Nielsen et al. (2018): Disturbances and marine populations

Section contents

2.1   Purpose

The model simulates how harbor porpoise population dynamics are affected by pile-driving noise associated with construction of offshore wind farms. The animals' survival is directly related to their energy levels, and the population dynamics are affected by noise through its impact on the animals' foraging behavior. By ensuring that the animals' movement patterns, space use and reactions to noise are realistic, the population dynamics in the model should have the same causal drivers in the model as in nature.

2.2   Entities, state variables, and scales

The model includes four kinds of entities: porpoises, wind turbines, landscape grid cells and cell groups. The porpoise agents are characterized by their location, speed, movement direction, age, age of maturity, energy level, pregnancy status, lactation

status and preferred dispersal distance. Each porpoise agent is a 'super individual' (Scheffer et al. 1995) representing several real-world female porpoises. The wind turbine agents are characterized by their location, noise source level, the start time and end time for their construction.

Simulations are based on a 835.2 km × 870 km landscape covering the North Sea. The landscape is divided into 2088 × 2175 grid cells, each covering 400 m × 400 m, and into cell groups covering 2 km × 2 km. The choice of cell sizes was arbitrary. Cell groups do not have state variables, but are characterized exclusively by their location. They enable porpoises to navigate back to the places where they experienced the highest energy intake rates. Grid cells are characterized by their coordinates, average water depth, food level, maximum food level, distance to land and by whether they are used as food patches or not. The landscape includes land and bodies of water with unknown food levels (northern part of the North Sea; Figure 1), i.e. areas that are not used by simulated porpoises (42.0% of the grid cells), food patches (0.67%) and water without food (57.3%). Each of the 30549 food patches covers one grid cell. Food level and maximum food level are always zero for grid cells that are not used as food patches. The distribution of the food patches is identical to the one used by Nabe-Nielsen et al. (2013b), i.e. it included on average 1000 food patches per 100 km × 100 km. The number of food patches is arbitrary, but sufficiently large to enable simulated porpoises to develop realistic movement patterns. The only other environmental parameter in the model is the time of year.

2.3 Process overview and scheduling

The model proceeds in time steps of half an hour and simulations typically last for 30 years. At the beginning of each time step porpoises detect noise originating from active pile-driving operations. This permits porpoises within a certain radius from pile-driving operations to know the direction of the noise source and the received sound level. The radius depends on the sound source level.

The animals' fine-scale movements are controlled by a combination of correlated random walk (CRW) behavior (Turchin 1998), their ability to move towards known food patches (directed by a spatial memory) and the extent to which they are deterred by noise. CRW movements predominate as long as energy intake is high, else animals gradually become more directed towards patches where they have previously found food (Nabe-Nielsen et al. 2013b). The animals turn and slow down if there is land ahead. Animals turn away from noise, and the strength of the bias away from the noise source depends on the received sound level. The noise level does not affect the length of their fine-scale moves. Animals can remain deterred for some time after the pile-driving stops, although to a decreasing extent (by default this behavior is turned off). The updating of this 'residual deterrence' takes place at the end of each time step.

The animals' energy levels and mortality are tightly coupled in the model. An animal's energy level (scaled to lie in the range 0–20) increases when it encounters food in a food patch, but decreases with every move. Animals consume a decreasing fraction of the food as their energy levels increase from 10 to 20, assuming that there is a limit to how much energy they can store. Consumption of food causes their energy levels to increase equivalently. Their energy expenditure per time step depends on the season and whether they are lactating. The lower their energy levels, the higher their risk of dying. Animals with lactating calves do not die, but abandon their calves

instead. Individual energy budgets were constructed following established principles of physiological ecology (Sibly et al. 2013). The animals move one at a time in an order that is randomized after each half-hour time step. Animals whose energy levels have been decreasing for some time stop using fine-scale movements, and start dispersing towards more profitable areas (cell groups) instead.

Food is only found in the food patches, which are randomly distributed across the seascape. The maximum amount of food (energy) varies among patches and seasons. It is derived from seasonal maps of the relative porpoise densities in the North Sea (Figure 1; Gilles et al. 2016), assuming that porpoises are only observed in areas with sufficient food. Updating of the food distribution map takes place four times per year. The actual amount of food in the patches changes dynamically: When a porpoise visits a patch, it consumes all or part of the food found there, but afterwards the food (energy) level increases logistically until reaching the maximum level. The updating of patch energy levels, i.e. replenishment of food, takes place at the end of every simulation day, after porpoises have moved and consumed food.

At the end of each day a number of life-history processes take place: Porpoises die if they reach their maximum age. They may mate, depending on the time of the year and their age. If they are already pregnant, they may give birth. If accompanied by a lactating calf they may wean the calf, which results in the creation of a new, independent individual in the model (if the calf is a female). Independent male porpoises are not included in the model, as the number of males was not considered a limiting factor for reproduction. The number of males is therefore not expected to affect population dynamics. Once every year, new mating dates are calculated.

The different variables in the model are updated asynchronously, i.e. immediately after a process has been executed.

2.4 Design concepts

2.4.1 Basic principles: The model builds on the assumption that the porpoise population is food limited, at least in the absence of noise. Noise acts by scaring porpoises away and by causing habitat fragmentation, thereby reducing the animals' foraging efficiency. The animals' foraging efficiency is also influenced by their ability to return to high quality areas they have previously visited, which assumes that they have a spatial memory (see Nabe-Nielsen et al. 2013b). The animals' energy budget is represented using the model presented by Sibly et al. (2013).

2.4.2 Emergence: The equilibrium population size (carrying capacity) emerges from a balance between mortality and reproduction, where mortality is linked to the energy levels of individual animals (i.e. porpoise agents). The energy levels, in turn, emerge from a balance between energy expenditure and food intake. Animals adapt their foraging behavior to increase food intake and fitness when they have not found food in the recent past. The animals' spatial distribution in the landscape emerges from their tendency to disperse towards more profitable parts of the landscape and their age class distribution emerges from their starvation-related mortality.

The rate at which local porpoise densities recover after a pile-driving operation ends emerges from the animals' decision to either return to previously visited food patches

close to the pile-driving area, to utilize food patches in the area they were displaced to, or to start dispersing. Their choice between these three alternatives depends on their energetic state and their success finding food in the area they were displaced to (partially related to chance events and partially to fitness-optimizing behavior).

2.4.3 *Adaptation:* Animals react to decreasing food levels in particular patches by being less attracted to them. They react to decreasing energy levels by dispersing towards parts of the landscape (i.e. cell groups) where they have previously experienced a high energy intake rate.

2.4.4 *Objectives:* Animals attempt to optimize their foraging behavior, and hence maximize their fitness, by returning to previously visited food patches when correlated random walk movements result in a low food acquisition rate. They also attempt to optimize foraging by dispersing towards more profitable areas when fine-scale movements do not enable them to sustain their energy levels.

2.4.5 *Learning:* Animals do not learn from what other animals have experienced. They do remember the location of previously visited food patches for some days (Nabe-Nielsen et al. 2013b), which enables them to adapt their fine-scale movements. They also have a persistent memory of the profitability (i.e. the energy intake rate) of all cell groups they have visited since they were born, so they gradually learn about the quality of different parts of the landscape. This guides their dispersal behavior. The animals learn/inherit their preferred dispersal distance from their mother before entering the model as independent individuals, but they do not inherit their mothers' knowledge of where the most profitable cell groups are.

2.4.6 *Prediction:* Animals base their prediction of how much food they can gather in different areas on their previous visits to those areas.

2.4.7 *Sensing:* Animals are able to sense if there is land in the direction they are about to move, which permits them to turn towards deeper water to avoid the coast. They also sense noise, which causes them to turn away from the noise emitting object(s). The animals know when their energy levels decrease, which causes them to disperse and to be more likely to abandon their lactating calves, or to die.

2.4.8 *Interaction:* The modeled animals only interact indirectly via competition for food.

2.4.9 *Stochasticity:* Fine-scale movement, mating date and mortality involve stochastic events. The probability of surviving increases with increasing energy levels.

2.4.10 *Collectives:* Social structure is not included in the model, but each agent represents several real animals.

2.4.11 Observation: The number of animals, their energy levels and the total amount of food in the landscape are recorded daily. The number of animals in different parts of the landscape can be counted (based on the 'blocks file'), and the movement tracks of a specified number of animals can be recorded to analyze for variations in home range sizes etc. The extent to which animals react to noise (i.e. the length of the deterrence vector, $|\mathbf{V}_D|$, see Eqn. 3) can be recorded for each half-hourly position. The age-class distribution and age specific mortalities are recorded yearly.

2.5 Initialization

The model was initialized by creating 10,000 randomly distributed porpoise agents. Their age-class distribution corresponded to that of stranded and by-caught animals (Lockyer & Kinze 2003), and 68% of the adults in the model were pregnant (corresponding to parameter *h* in Table 1). The energy level, E_p, of each porpoise was initially modeled as a random normal variable with mean 10 and standard deviation one (parameter E_{init}). Mating date was a random normal variable with mean 225 and standard deviation 20. Simulations were set to start on 1 January 1981. They included 3900 piling operations distributed on 65 wind farms that were planned to be built in the period 2011–2020 as part of the European Union 2020 goals (Directive 2009/28/EC, http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32009L0028, summarized in http://www.ewea.org/fileadmin/ewea_documents/documents/publications/reports/Seanergy_2020.pdf). The food levels in the patches were set to the location specific maximum food levels for 1 January.

The model simulations can be initialized and executed through a Graphical User Interface (GUI) or through a batch procedure. The GUI allows for one simulation run at a time where the user can view the porpoise movements and distribution across the landscape, the location and construction period of wind farms, the population size, energy levels of porpoise agents, energy levels in food patches distributed across the landscape, as well as the age class distribution of the population. In the batch procedure the user can initialize multiple simulations that run simultaneously, but the user cannot see the aforementioned components on the screen or obtain information on age class distribution. Once the simulation(s) has completed the model output is automatically written out for both the GUI and batch procedure.
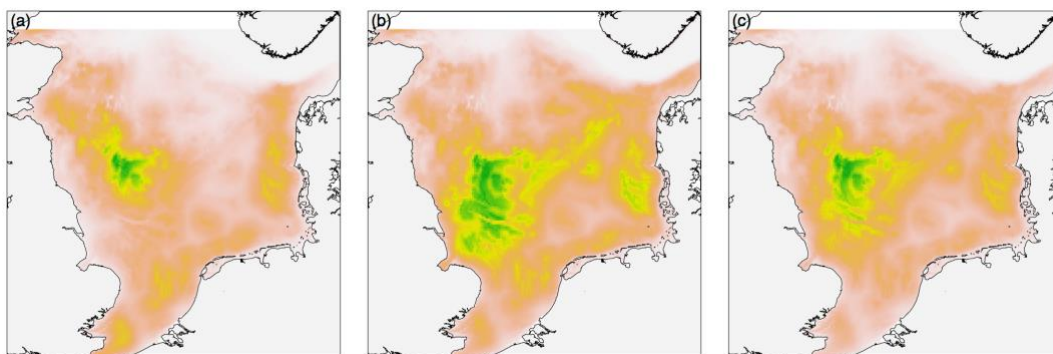

Figure 1. Food distribution maps derived from seasonal maps of porpoise densities in the North Sea for (a) spring, (b) summer, and (c) autumn (Gilles et al. 2016). Green shows areas with high porpoise

densities, grey shows land and white indicates missing data. No porpoise density map was available for the winter, so the map from the autumn was used instead.

2.6   Input data

Eight different background maps are used in the model: The maximum amount of food in each food patch was derived from a map of the porpoise densities in the different parts of the North Sea (see Gilles et al. 2016 for details). These are included as four raster files with a spatial resolution of 400 m × 400 m, one for each season (Figure 1). No food was found outside the food patches. The raster file for the winter season (December–February) is read in from the file 'quarter1.asc' at the start of simulations. The ETRS89 - EPSG:3035 projection is used throughout. As there was no map available for porpoise densities in the winter, the map from the autumn season was used during winter. The raster maps were standardized to have a mean value of 0.3914, corresponding to the mean food level previously used in simulations of the Inner Danish Waters population (Nabe-Nielsen et al. 2014). Four additional raster files with the same extent and resolution are used: a 'patches' file describing the location of the food patches, a 'bathymetry' file that allows animals to avoid water depths $<w_{min}$ (see parameter list), a 'distance-to-coast' file (allowing animals to turn when approaching land) and a 'blocks' file that makes it possible to count the number of porpoises in user defined areas.

The simulations include details about pile-driving events. These are provided in a tab separated 'wind-farms' text file with columns id (identifier), x, y (coordinates), impact (sound source level, dB SEL @1m), start and end (timing of pile-driving, measured in number of half-hour time steps since the beginning of the simulation). Noise is emitted during both the start and the end time step. The sound source level was 234 dB SEL for pile-driving in all scenarios, corresponding to the value calculated for the Gemini wind farm (see below). See the Submodels section for details on how noise from wind turbine agents was represented in the model.
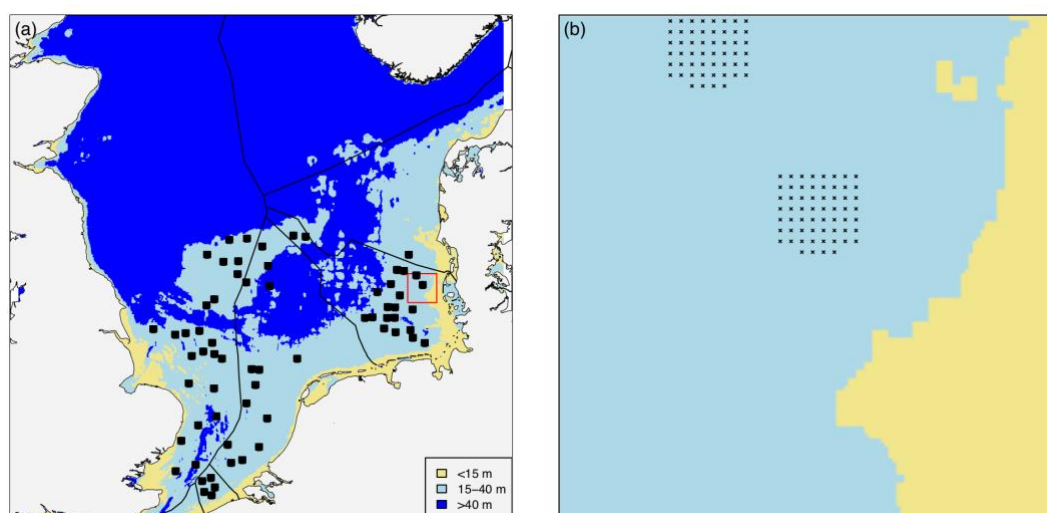

Figure 2. Positions of wind turbines in the three pile-driving scenarios used in this study. The red square on (a) indicates the 50 km × 50 km area shown in greater detail in (b).

Three different scenarios were used for investigating the population effect of wind farm construction in the North Sea. All scenarios included 65 wind farms with the same spatial distribution (Figure 2). A pre-specified number of wind farms were selected per country (Denmark: 1 wind farm; Germany: 21; Netherlands: 14; Belgium: 5; UK: 24), which enabled the individual countries to meet the EU 2020 target for renewable energy development (EU 2009). Wind farms were selected in areas with water depths between 15–40 m and >4 km from any neighboring wind farm. Aside from these rules wind farms were placed at random. Each wind farm included 60 wind turbines distributed in a regular 1078 m x 1078 m grid. 6 MW turbines constructed with monopile foundations was assumed throughout. Turbines were installed using pile-driving, which took two hours for each pile. No noise mitigation or soft start was included in the scenarios. The turbines were constructed in the 10-year period starting 1 January 2011, with 6–7 farms being built per year. In Scenario 1, the parks were constructed in random order, in Scenario 2 the parks in the eastern North Sea were built first, followed by the ones in the western North Sea (starting in the north in each area). In Scenario 3 parks were constructed in the same order as in Scenario 1, but the time between individual pilings within the wind farms was halved (from 48 hours to 24 hours). The start time of the first pilings in the different wind farms were the same in scenarios 1 and 3. In addition to these scenarios, we used a reference scenario without any wind farms to establish the population size in the absence of noise.
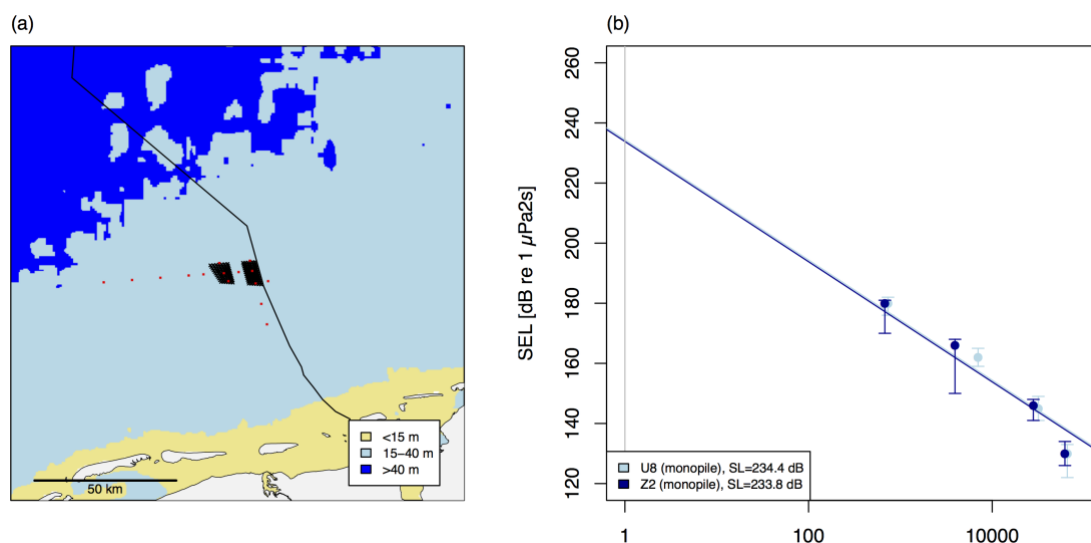
Figure 3. Data from the Gemini wind farm construction site used for calibration of the porpoises' response to noise. (a) Virtual landscape including wind turbine construction sites (black dots) and CPODS (red dots). The black line shows the border to Germany. (b) Received sound levels recorded using hydrophones at different distances [m] from two pilings. Sound source levels (*SL*) and sound transmissions were modeled assuming spherical spreading of the noise.

A different landscape, combined with a different set of pile-driving events, was used for calibration of the parameters *c* and *T* (see parameter list). The landscape was a 400 × 400 cell subset of the North Sea landscape covering the area around the Gemini wind farm construction site in the Netherlands (Figure 3). The landscape included a number of virtual CPODS (i.e. acoustic monitoring stations that detect the presence of porpoises based on the clicks they emit while foraging and navigating) whose

positions corresponded to those of real CPODS deployed during wind farm construction. The 160 pile-driving events had the exact same positions as those of the real pile-driving events. Their sound source levels ('impact'; 234 dB SEL @1m) were calculated based on data from four hydrophones placed near two of the pile-driving locations (Figure 3b). See details on calibration of the porpoises' response to noise in the section 'Data evaluation'.

2.7   Submodels

The different submodels are executed in the order they are listed below (see overview in 'Process overview and scheduling'). Names of variables and parameters are retained from Nabe-Nielsen et al. (2013b, 2014).

2.7.1   Porpoises detect noise

At the beginning of each time step, porpoises register the noise from active pile-driving operations. This is done by letting the wind turbine agents emit noise if they are under construction, thus producing a dynamic soundscape. Noise source levels (SL), positions and timings of pile-driving events are provided as input data. Animals react to noise only up to a certain distance from a pile-driving event. This distance is determined by the response threshold (T) and the extent to which sound is transmitted in water. Here T was determined based on data from the Gemini wind farm using pattern-oriented modeling. The sound level received by the animals (R) was modeled assuming spherical spreading (Figure 4a; Urick 1983), so

$$R = SL - 20 \log_{10}(\text{dist}(p,k)) \qquad\qquad \text{Eqn. A1}$$

where $\text{dist}(p,k)$ is the distance from the porpoise p to the pile-driving event k. Noise emitted by a pile-driving operation only influences animals out to a certain distance, $dist_{max}$, where $R = T$. By rearranging Eqn. 1 we get

$$dist_{max} = 10^{(SL - T) / 20} \qquad\qquad \text{Eqn. A2}$$

Each pile-driving event equips all porpoise within the distance $dist_{max}$ with a deterrence vector that points directly away from the noise source (Figure 4). The length of the deterrence vector $\mathbf{V}_D$ is determined by

$$|\mathbf{V}_D| = c(R - T) \qquad\qquad \text{Eqn. A3}$$

assuming a linear relationship between the received sound level and the strength of reaction. Here c is the deterrence coefficient. Each animal's fine-scale movements are only influenced by the pile-driving event that yields the largest deterrence vector. This is usually without any practical implications, as wind farms are generally constructed by piling one turbine foundation at a time.

Animals can be assumed to sense the distance to anthropogenic noise sources, (as demonstrated by DeRuiter et al. 2013) and to stop being deterred when they are further away from the noise than a certain distance. When $\text{dist}(p,k) > d_{max\_deter}$ the length of the deterrence vector is therefore set to 0. When using the default value of d_{max_deter} (Table 2), this parameter does not affect population dynamics. The parameter is only included to make it possible to assume a maximum deterrence distance in other studies.
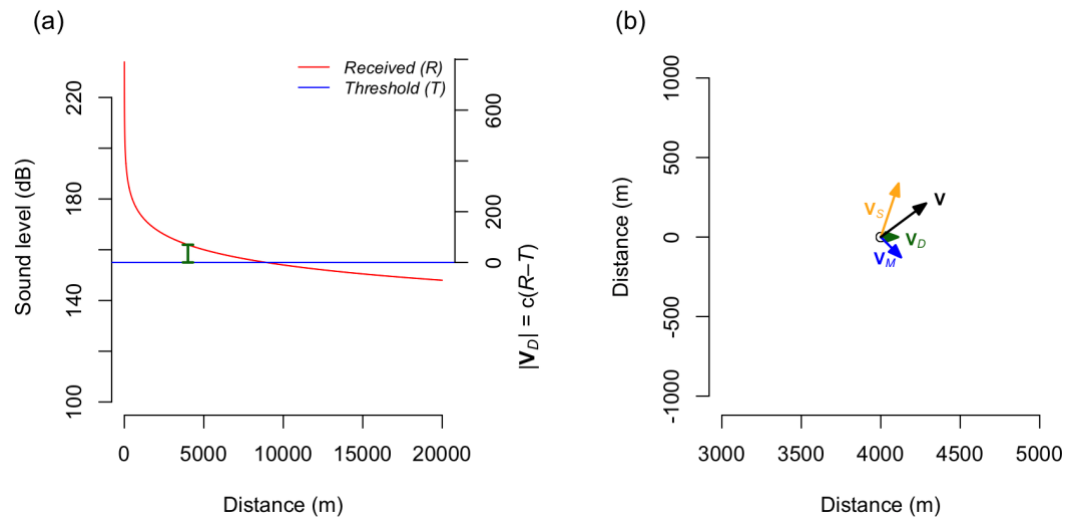
Figure 4. Relationship between received sound level (R) and deterrence behavior in the model. (a) Decrease in R with distance assuming spherical spreading for pile-driving in Gemini, without noise mitigation (SL=234 dB SEL). The green bar shows the length of the deterrence vector for a porpoise located 4 km from the pile-driving, $|\mathbf{V}_D|$, i.e. the bias away from the noise. (b) Vector $\mathbf{V}_S$ represents the correlated random walk during **one** 30-min time step, $\mathbf{V}_M$ represents the spatial memory move and $\mathbf{V}_D$ represents the deterrence from North Sea pile-driving noise. $\mathbf{V}$ is the standardized resultant vector, i.e. the actual move in the presence of noise. Here shown for c=10 (deterrence coefficient; arbitrary value) and Threshold (T)=155 dB SEL. Here $dist_{max}$= 8913 m.

Figure 5. Tracks of 25 free-ranging porpoises equipped with ARGOS satellite tags providing a position every 1–3 days. All animals were tagged at Skagen, northern Denmark (DNK). Each track shows positions from a maximum of 150 days.

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2.7.2   Disperse

We distinguish large-scale movements/dispersal from the fine-scale movements described in section 2.7.3. In each time step each porpoise agent takes either a dispersal step or a fine-scale movement step depending on whether it is in dispersal mode (turned on in the submodel 'Life history processes').
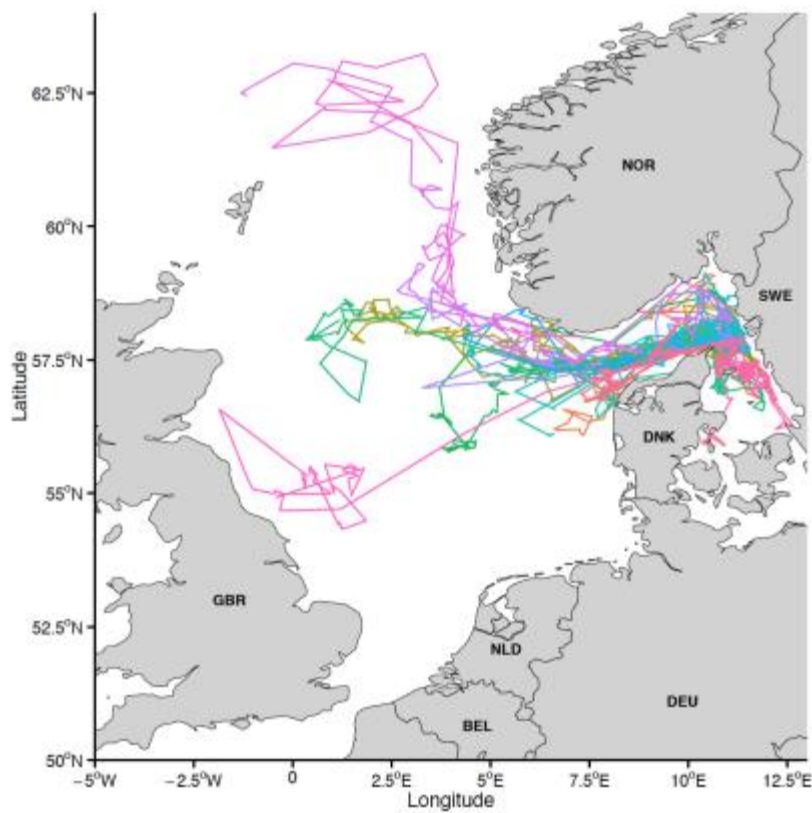
When an animal agent disperses, it is guided by a persistent spatial memory (PSM) of the energy intake rate it has achieved in each of the different parts (cell groups) of the landscape that it has visited since it was born. Fine-scale movements, in contrast, are guided by a gradually decreasing memory of the foraging success in recently visited food patches. The rationale for introducing PSM to guide large-scale movements is that satellite tagged animals tend to return to the same general part of the landscape after having been elsewhere for several weeks or months (Figure 5). Such behavior must be guided by a spatial memory. Often such dispersal moves gradually switch from being relatively directed to becoming increasingly exploratory, which would enable animals to search for new foraging grounds in the vicinity of areas where they previously experienced a high food intake rate. Most animals keep moving back and forth over the same area, thus maintaining a constant dispersal distance.
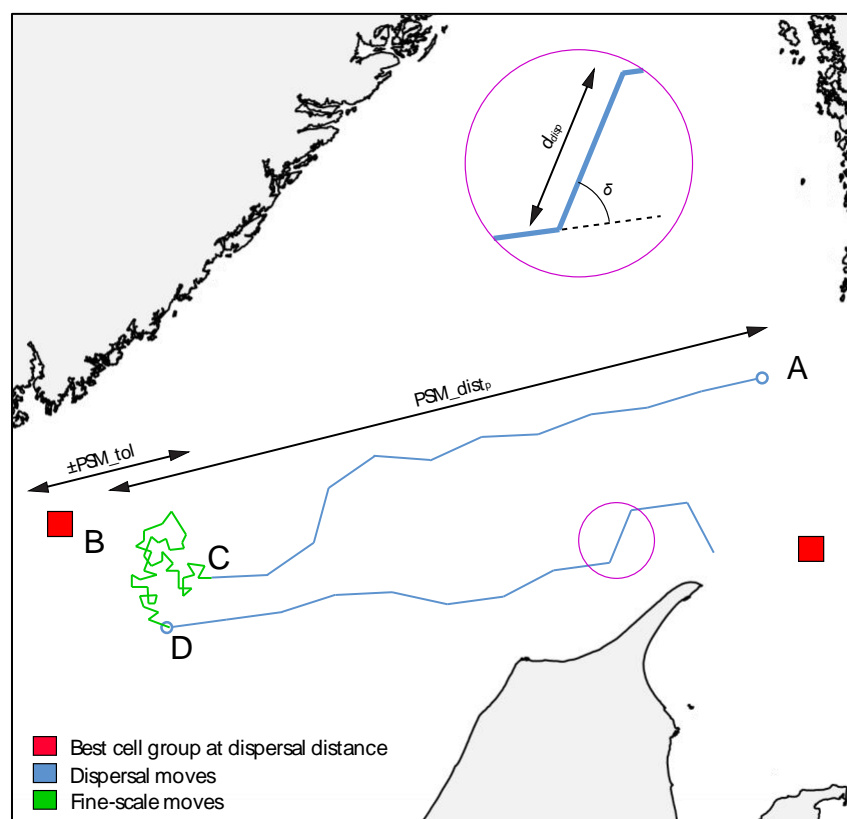
Figure 6. Dispersal behavior. When dispersal starts (A), the porpoise agent starts moving towards the most profitable 2 km × 2 km cell group (B) at its preferred dispersal distance. The distance from A to B is d_{target}. All dispersal steps have the length d_{disp} and the total distance dispersed in a particular dispersal event is d_{cum}. After each dispersal step, the porpoise makes a random turn δ. The turning angle increases the further the porpoise has dispersed. It stops dispersing when $d_{cum}=0.95\ d_{target}$ (at point C), but may start dispersing again at a later point (D).

To incorporate PSM dispersal behavior into the model, the entire landscape was divided into 2 km × 2 km cell groups. Each animal is equipped with a preferred, fixed dispersal distance (PSM_dist_p) at birth. Initially its value is drawn from a normal distribution, PSM_dist, but calves subsequently inherit the preferred dispersal distance from their mothers. Animals whose energy levels have been decreasing for t_{todisp} days stop using fine-scale movements and start dispersing (Figure 6).

Figure 7. Simulated change in turning angle distribution as the porpoise agent approaches the dispersal target. In this example, PSM_angle was set to 40 and each dot represents a dispersal step (1987 steps within 26 distinct dispersal events). Angles are larger for animals that have dispersed a larger proportion of the initial distance to their dispersal targets.

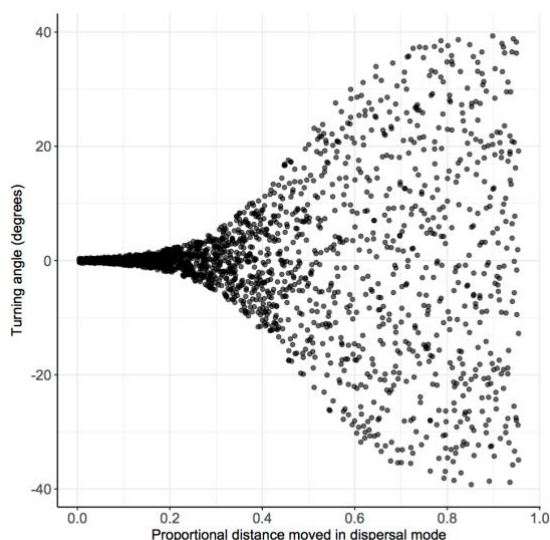When an animal starts dispersing, it turns towards the most profitable cell group at its preferred dispersal distance ($PSM\_dist_p \pm PSM\_tol$, see Table 2), i.e. the group where it has previously obtained the highest energy intake rate (calculated as total amount of food eaten divided time spent in each cell group). The distance to this cell group is d_{target}. Animals that have visited <50 cell groups disperse towards a random cell group at their preferred dispersal distance (burn-in behavior). All dispersal steps have the same length d_{disp}. Turning angles δ between consecutive steps increase logistically,

$$\delta = PSM\_angle\ \omega_2/(1+e^{-z/PSM\_log}) \qquad \text{Eqn. A4}$$

where ω_2 is a random number in the range -1−1 and z is determined by

$$z = (3 \times d_{cum} / d_{target}) - 1.5 \qquad \text{Eqn. A5}$$

Here d_{cum} is the cumulated distance moved using dispersal moves during the current dispersal event, d_{target} is the initial distance to the center of the selected cell group and PSM_log is >0 (see Table 2). Turning angles gradually increase from a value close to 0 (depending on the choice of PSM_log) to a maximum of PSM_angle (see Figure 7). The animals remember the amount of food they encounter while dispersing and the amount of time they spend in different cell groups. This enables them to navigate back towards these cell groups during subsequent dispersal events.

An animal stops dispersing (a) once it has moved $0.95 \times d_{target}$ using dispersal steps, or (b) if the next step would have caused it to move on land (i.e. to an area with water depth$<w_{disp}$) or (c) across the edge of the landscape, or (d) if its daily average energy level increases to a level that is higher than any of the daily energy levels they have experienced over the previous seven days, or (e) if it moves into an area with high noise levels (where $R>T$).

New independent calves inherit their preferred dispersal distance from their mother (but not their knowledge about relative profitability of different parts of the landscape). See Section 3.2.2 for details regarding calibration of dispersal parameters.

2.7.3 Fine-scale movement

All animals that are not dispersing take a fine-scale move in each step.

The length and direction of a fine-scale move is determined by the sum of three vectors: $\mathbf{V}_S$, which describes a correlated random walk (CRW) move (Turchin 1998), $\mathbf{V}_M$, which describes a spatial memory move, and $\mathbf{V}_D$, which describes the deterrence from noise. The CRW behavior introduces a positive correlation between the lengths of consecutive steps and a negative correlation between consecutive turning angles. This corresponds to the behavior described in detail in the appendix of (Nabe-Nielsen et al. 2013b). Here

$$\mathbf{V}_S = \mathbf{x}(k + E) \qquad \text{Eqn. A6}$$

where $\mathbf{x}$ is a vector defining an unweighted CRW move and k is an 'inertia constant' (see list of parameters related to movement, Table 2). E is a measure of the benefit of using an undirected search for food, which is determined by how much food the animal remembers that it has found in the recent past. This is controlled by the actual amount of food encountered and the satiation memory decay rate r_S (see details in Nabe-Nielsen et al. 2013b). As k is small, the length of $\mathbf{V}_S$ is mostly related to E, which is used as a proxy for how much food the animal should expect to find if taking an undirected CRW step. The vector $\mathbf{x}$ allows the autocorrelation in turning angles and in step length, and the variance in these variables, to be controlled through the parameters a, b, m and R_1–R_3. The equations describing these relationships are provided in Nabe-Nielsen et al. (2013b).

Fine-scale movements, in contrast to large-scale dispersal, are guided by a gradually decreasing memory of its foraging success in recently visited food patches. The animals' tendency to move towards previously visited food patches is determined by their memory of where they have found food in the past, and how much. This spatial memory move, $\mathbf{V}_M$, is determined by

$$\mathbf{V}_M = \sum M[c]\, \mathbf{i}[c] \qquad \text{Eqn. A7}$$

where M is a measure of the amount of food that the animal remembers that it has found in patch c, weighed by the costs of going there (i.e. a measure of the benefit of returning to patch c). The animal's memory of previously visited patches decreases logistically with time. The shape of the logistic function is controlled by the reference memory decay rate r_R. $\mathbf{i}$ is a unity vector pointing in the direction of patch c (Nabe-Nielsen et al. 2013b). The calculation of the deterrence vector is explained in Eqn.

A3. The standardized resultant vector, i.e. the fine-scale move taken in the presence of noise, is then determined by

$$\mathbf{V}^* = \frac{\mathbf{V}_M + \mathbf{V}_S + \mathbf{V}_D}{\|\mathbf{V}_M + \mathbf{V}_S + \mathbf{V}_D\|} \times \|\mathbf{V}_S\| \qquad \text{Eqn. A8}$$

This equation is equivalent to Eqn. A2 of Nabe-Nielsen et al. (2014). In Eqn. A8 $\mathbf{V}^*$ has been standardized to have the same length as $\mathbf{V}_S$, so the length of the step is not affected by the noise level.

If the move defined by $\mathbf{V}^*$ would cause the porpoise to move to an area with too shallow water ($<w_{\min}$) it turns in the direction with deepest water (40°, 70°, 120° or 180° as needed).

2.7.4 Update energy level and mortality

Porpoises increase their energy levels E_p when moving through food patches and reduce the amount of food (energy) in the patches equivalently. They never eat more than 99% of the food they encounter in a patch, and always leave at least U_{min} food units (see Table 1) to allow food levels to replenish (see section 2.7.6). Their energy levels are scaled to lie in the range 0–20. The animals consume a smaller proportion of the food as their energy levels increase from 10–20, and animals with an energy level of 20 do not consume any of the food they encounter (Nabe-Nielsen et al. 2014).

Porpoises use a season-dependent amount of energy E_{use} in every step. They spend more energy during the summer ($E_{\text{use}} \times E_{\text{warm}}$ in the months May–September and $E_{\text{use}} \times (0.5 \times (1 - E_{\text{warm}}) + 1)$ in April and October) and when they are lactating ($E_{\text{use}} \times E_{\text{lact}}$).

The porpoises' risk of dying increases as their energy levels decrease. The yearly survival probability s_y (Figure 8) is calculated as

$$s_y = 1 - e^{-\beta E_p} \qquad \text{Eqn. A9}$$

which is subsequently converted to a per-step survival probability

$$s_s = e^{\log(s_y)/(360 \times 48)} \qquad \text{Eqn. A10}$$

If ω_1 is a random number in the range 0–1 and the animal is lactating, the calf is abandoned if $\omega_1 > s_s$ (calves do not appear as independent individuals in the model). If $\omega_1 > s_s$ and the animal is not lactating, it dies (following the principles described by Sibly et al. 2013).

These processes take place in every time step.

2.7.5 Update food distribution map

Every 3rd month (on simulation day 60, 150, 240 and 300), a new seasonal food distribution map is loaded. The map is used for determining the maximum amount of food that can be present in food patches in different parts of the landscape (Figure 1). The spatial distribution of the patches remains constant.

2.7.6 Update patch energy level

Takes place every day.

$$E_k[t+1] = E_k[t] + r_U \times E_k[t] \, (1 - E_k[t] / M_k[t]) \qquad \text{Eqn. A11}$$

where r_U is the food replenishment rate, $E_k[t]$ is the food level in patch k at time t and $M_k[t]$ is the maximum amount of food in each patch (derived from season-specific map of porpoise densities in the different parts of the North Sea; Gilles et al. 2016). This is equivalent to Eqn. A4 of Nabe-Nielsen et al. (2014).
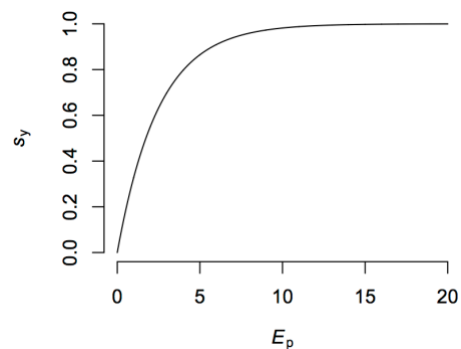

Figure 8. Relationship between energy level and yearly mortality for β=0.4.

2.7.7 Calculate mating dates

Takes place every year, on 1 January. Each porpoise's mating date, t_{mating}, is drawn from a normal distribution.

2.7.8 Life-history processes

This submodel is executed at the end of every day, i.e. every 48th time step.

Update the animals' dispersal status based on their daily average energy level. Animals start dispersing when their energy levels decrease for t_{todisp} consecutive days.

Die of old age: Animals older than t_{maxage} years are removed from the simulation.

Mate and become pregnant: If the simulation date is t_{mating} the animals that are not already pregnant mate and become pregnant with a probability h.

Give birth: Animals that have been pregnant for t_{gest} days give birth to a calf and start lactating.

Wean calf: Lactating animals stop nursing their calves after t_{nurs} days. This results in the creation of a new independent individual in the model with probability 0.5 (assuming equal sex ratios). From the time of weaning male porpoises are omitted from the model.

See Table 1 for list of parameters related to animal life history.

2.7.9 Update residual deterrence

Animals may keep being deterred by a noise source for some time after the noise stops. This is termed 'residual deterrence'. At the end of each step their movements become less biased by these noises that they are no longer exposed to. The decrease in residual deterrence is controlled by ψ_{deter}, so

$$|\mathbf{V}_D|_{t+1} = |\mathbf{V}_D|_t \, (100 - \psi_{deter})/100 \qquad \text{Eqn. A12}$$

After t_{deter} time steps animals are assumed to stop being deterred by noise sources that no longer emit noise. By default t_{deter} is set to 0 (see Table 2).

(Go to process overview).

3   Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

There is a total of 45 parameters in the DEPONS model, all of which can be specified by the user. Thirteen are related to animal life history and energetics, 23 are related to animal movement and reactions to noise, and 9 are related to general model behavior (specification of input and output files etc.). Seven of the parameters related to animal movement and reactions to noise are not currently used, but maintained to increase model flexibility and facilitate easy re-parameterization for other applications. The 36 parameters related to animal life history, energetics and movement are region-specific. Values are obtained from the literature for six parameters; four parameters controlling the animals' response to noise and dispersal movements were calibrated following a pattern-oriented modeling approach.

Section contents

3.1   Parameters and data related to animal life history and energetics

The processes and parameter names of the DEPONS model related to birth and death of animals and to how animal survival is related to their energetic status are identical to the ones in the model described in Nabe-Nielsen et al. (2014).

Seven of the 13 parameters related to life history and energetics were obtained from the literature (Table 1). The parameter values for h and t_{mature} were based on data collected in the northwest Atlantic, off the coast of Maine (United States). The parameters are inherently hard to estimate due to difficulties studying harbor porpoises in the wild, and may vary among regions and among years. The parameters t_{gest} and t_{nurs} are based on a Danish study of captive animals and on studies of harbor porpoises in Danish waters. There are no data on how much the parameters vary among populations. The parameter t_{maxage} is an upper limit for how old porpoises are likely to get, based on records of stranded animals in Denmark. The parameter t_{mating} may vary among populations and years, but again this is difficult to assess due to the limited number of studies of porpoises in the wild. The parameter E_{warm} was obtained from a study of captive animals, based on their food consumption. It is difficult to assess to what extent the parameter varies among animals and depending on the size and health of the animals.

Six parameters related to energetics were either obtained from unpublished studies or calibrated based on general considerations regarding animal energetics (Sibly et al. 2013). The parameter E_{lact} was obtained from a study of Danish captive animals. This is unlikely to vary much among populations due to energetic constraints related to animal energy consumption, but is likely to vary depending on the age of the lactating calf. The parameter U_{min} is the minimum amount of food in a patch. The unit is scalable to kJ and other measures of energy content (hence we use the term 'relative unit' for energy-related variables). U_{min} influences how fast food recovers in a patch after being nearly depleted. E_{use} was calibrated to ensure that the population reached a dynamic equilibrium size, assuming that food recovered after approximately 2 days. This is based on the observation that satellite tagged porpoises in the inner Danish waters often return to the same area after approximately two days (J Nabe-Nielsen, unpubl. data). As porpoises have a high energetic demand (Wisniewska et al. 2016), we take such repeated returns to the same area as an indication that food has recovered. Details of the calibration procedure are provided in the appendix of Nabe-Nielsen et al. (2014). When letting the maximum amount of food in a patch be 1 during winter in the Inner Danish Waters simulations, the average food level in the patches was 0.3914 (Nabe-Nielsen et al. 2014). In the current study, the average food level in the patches was scaled to be the same (see input data), i.e. the average food level was assumed to be the same in the North Sea and the inner Danish waters. One unit of food in a patch is equivalent to one unit of energy available for the porpoise agents, and it is assumed that no energy is lost when food is consumed. The value of β determines the relationship between the animals' energetic status and their risk of dying (Eqn. A9). The value used in this study was obtained through calibration (see details in Nabe-Nielsen et al. 2014). The relationship between the animals' energetic status and mortality is likely to vary among populations, but the use of a slightly different value of β has a very small impact on population dynamics and carrying capacity (appendix of Nabe-Nielsen et al. 2014 and sensitivity analyses in chapter 7). The value of r_U was calibrated to ensure that the population reached a stable population size (Nabe-Nielsen et al. 2013a, 2014). Unfortunately, there are no field studies that allow us to determine how r_U varies among geographic regions.

Parameter	Standard value	Code name	Description [units] (reference)
h	0.68	h	Probability that adult females become pregnant (Read & Hohn 1995).
t_{gest}	300	tgest	Gestation time [days] (Lockyer et al. 2003).
t_{nurs}	240	tnurs	Nursing time [days] (Lockyer 2003; Lockyer & Kinze 2003).
t_{maxage}	30	tmaxage	Maximum age of porpoises [years] (Lockyer & Kinze 2003).
t_{mature}	3.44	mage	Age of maturity [years] (Read 1990).
t_{mating}	N(225, 20)	randomMatingDayNormal	Mating day [day of year] (peaking in August; Lockyer 2003).
E_{lact}	1.4	Elact	Energy use multiplier for lactating mammals [unitless] (Magnus Wahlberg, unpubl. data).
E_{warm}	1.3	Ewarm	Energy use multiplier in warm water [unitless] (Lockyer 2003).
E_{use}	4.5	Euse	Energy use per half-hour step in May–September [relative unit] (calibrated, Nabe-Nielsen et al. 2014).
E_{init}	N(10, 1)	porpInitEnergyNormal	Initial energy level for porpoises [relative unit] (arbitrary).
r_U	0.1	rU	Food replenishment rate; the rate that food recovers after being eaten [unitless] (calibrated, Nabe-Nielsen et al. 2014).
U_{min}	0.001	regrowthFoodQualifier	Minimum food level in a patch; the starting value for logistic replenishment of the food [relative unit] (arbitrary).
β	0.4	beta	Survival probability constant [unitless] (calibrated, Nabe-Nielsen et al. 2014).

Table 1. Model parameters related to life history and energetics. The parameter names and parameter values are the same as used in Nabe-Nielsen et al. (2013b, 2014). The 'code names' are the names used in the Repast Java code in the current version of the model. Standard values of parameters written as N(x,y) indicate random values drawn from a Gaussian distribution with mean x and standard deviation y. In the input parameter files x and y are separated by ';'. The units of the parameters E_{use}, E_{init} and U_{min} are scaled by the same factor relative to Joule, hence the term 'relative unit'.

3.2 Parameters and data related to animal movements and response to noise

3.2.1 Parameters related to fine-scale movements

The parts of the DEPONS model related to simulation of fine-scale movements are identical to the model described by Nabe-Nielsen et al. (2013b, 2014), except that the model has now been ported from NetLogo to the Repast framework to increase simulation speed. Fine-scale movements are influenced by the first 10 parameters in Table 2. Parameter names are kept the same as in Nabe-Nielsen et al. (2013b).

Fine-scale movements are simulated using a mixture of correlated random walk (CRW) behavior and spatial memory moves. The parameterization of the fine-scale movement model was done after $\log_{10}$ transforming the distance moved per 30-minutes step, as step lengths were approximately log-normally distributed in the movement data that was used for parameterization. The CRW is specified using the parameters a, b, m, R_1, R_2, and R_3, where R_x, provide mean and variation in distance moved per step, turning angles and in the relationship between turning angle and distance moved. The spatial memory behavior is controlled by the parameters r_S, r_R, and k. All parameters were calibrated to ensure realistic fine-scale movement behavior (see Nabe-Nielsen et al. 2013b).

Parameter	Standard value	Code name	Description [units] (reference)
r_S	0.2	rS	Satiation memory decay rate [unitless] (Nabe-Nielsen et al. 2013b). Value used in (Nabe-Nielsen et al. 2014).
r_R	0.1	rR	Reference memory decay rate [unitless] (Nabe-Nielsen et al. 2013b). Value used in (Nabe-Nielsen et al. 2014).
k	0.001	k	Inertia constant; the animal's tendency to keep moving using CRW irrespective of foraging success [unitless] (arbitrary).
a	0.94	a	Autocorrelation constant for $\log_{10}(d/100)$, where d is distance moved per time step [unitless] (Nabe-Nielsen et al. 2013b).
b	0.26	b	Autocorrelation constant for turning angles in CRW [unitless] (Nabe-Nielsen et al. 2013b).
m	0.74	m	Value of $\log_{10}(d/100)$ where turning angles stop decreasing with speed. d is distance moved per time step [m] (Nabe-Nielsen et al. 2013b).
R_1	N(0.42, 0.48)	r1	$\log_{10}(d/100)$, where d is distance moved per time step [m] (Nabe-Nielsen et al. 2013b).

Parameter	Standard value	Code name	Description [units] (reference)
R_2	N(0, 38)	r2	Turning angle between steps [degrees] (Nabe-Nielsen et al. 2013b).
R_3	N(96, 28)	r3	Relationship between turning angle and $\log_{10}$ step length [unitless] (Nabe-Nielsen et al. 2013b).
$d_{maxmove}$	1.18	dmax_mov	Maximum value of $\log_{10}(d/100)$ while using fine-scale moves. Here d is distance moved per time step [m].
d_{disp}	1.25	ddisp	Dispersal distance per time step [km] (calibrated in current study).
t_{todisp}	3	tdisp	Time before onset of dispersal [days]. Standard value based on the observations that captive porpoises appear to starve after not eating for three days (Magnus Wahlberg, unpubl. data).
PSM_angle	20	psmType2RandomAngle	Maximum absolute turning angle after each persistent spatial memory (PSM) dispersal step [degrees] (calibrated in current study).
PSM_dist	N(210, 50)	psmDistancePreference, psmDistanceStddev	Preferred distance to dispersal target. [km] (calibrated in current study).
PSM_log	0.3	psmLogDecrease	Parameter controlling logistic increase in turning angle during dispersal [unitless] (calibrated in current study).
PSM_tol	5	psmDistancePreferenceTolerance	Tolerance band within which the dispersal cell is selected (PSM dist±PSM tol) [km] (calibrated in current study).
w_{disp}	4	wdisp	Minimum water depth when dispersing [m] (Nabe-Nielsen et al. 2014).
w_{min}	1	wmin	Minimum water depth [m] required by porpoises (J. Tougaard, pers. obs).
T	155	drespthreshold	Response threshold; received sound level above which porpoises start getting deterred [dB] (calibrated in current study).
c	0.07	c	Deterrence coefficient [unitless] (calibrated in current study).

Parameter	Standard value	Code name	Description [units] (reference)
d_{max_deter}	1000	dmax_deter	Maximum deterrence distance [km]. Animals that are more than this far from the noise source should stop being deterred (worst-case scenario based on Brandt et al. 2012).
t_{deter}	0	tdeter	Residual deterrence time; number of time steps the deterrence effect lasts when the animal is no longer exposed to noise [time steps] (arbitrary).
ψ_{deter}	50	ddecay	Deterrence decay constant; decrease in deterrence per time step after noise has stopped [percent] (arbitrary).

Table 2. Model parameters related to animal movements and response to noise. Parameter names and parameter values are the same as used in Nabe-Nielsen et al. (2013b, 2014), except for parameters that were introduced and calibrated in the current study. The 'code names' are the names used in the Repast computer code. Standard values of parameters written as N(x,y) indicate random values drawn from a Gaussian distribution with mean x and standard deviation y. In the input parameter files x and y are separated by ';'. The three last parameters in the table are not used (i.e. they are turned off) in the current study.

The CRW movement behavior of real porpoises, i.e. the animals' tendency to zig-zag and their speed while doing so, is likely to vary among animals and to depend on local environmental conditions. In the DEPONS model (version 1.1) the CRW behavior was calibrated based on data from a single animal equipped with a dead reckoning tag[†] in the inner Danish waters (Figure 9; J. Teilmann, unpublished data). Its movements are unlikely to be representative for all animals in all parts of the North Sea, but these were the only data available at the time the model was parameterized.

The spatial memory allows animals to navigate back to patches where they have found food in the past, which enables them to remain in the same area for several days or weeks. The behavior is controlled by the parameters r_S (satiation memory decay rate, controlling whether animals keep using a correlated random walk), r_R (reference memory decay rate, controlling animals' ability to navigate back to previously visited patches), k and w_{min}. Here k is a constant that only influences animal movements in the rare cases where they do not have any memory of previously visited food patches (e.g. in the beginning of simulations). w_{min}, which determines the minimum water depth required by porpoises, influences animal movements in the vicinity of the coast only. r_S and r_R were calibrated using pattern-oriented modeling (POM; Grimm et al. 2005; Kramer-Schadt et al. 2007) to ensure that animals developed movement tracks that closely resembled those observed for satellite-tracked animals in the inner Danish

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[†] Dead reckoning provides a means for calculating animal movements by integrating the speeds and headings for consecutive small segments of a movement path to construct the entire path, see (Wilson et al. 2007) for details.

waters, i.e. with the same home range sizes, mean residence times and displacement distances (Nabe-Nielsen et al. 2013b). Again, these movements are unlikely to be representative for animals in all parts of the North Sea. The spatial memory behavior may therefore be improved by obtaining values of r_S and r_R that enable simulated animals to move similarly to North Sea animals equipped with satellite tags.
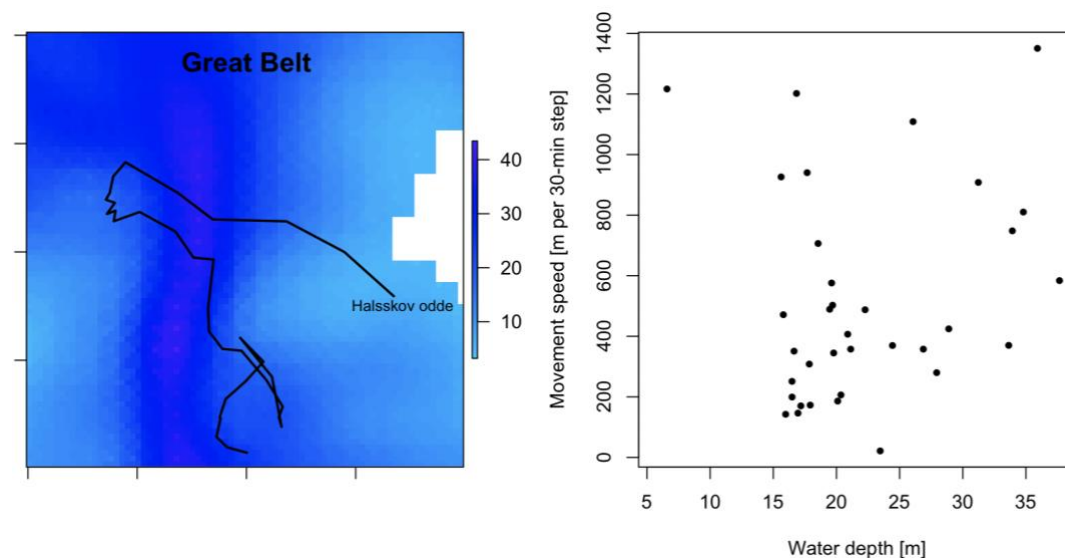

Figure 9. Movement track used for calibration of fine-scale movements (from animal equipped with Dead Reckoning tag). Each line segment shows a 30-min step. The legend shows the bathymetry in the area. The distance moved per step was weakly correlated with bathymetry ($r=0.17$). The same was the case for absolute turning angles ($r=-0.23$).

The fine-scale movements are not only influenced by the movement-related parameters themselves, but also by the spatial distribution of food patches and the average food levels in the patches. On the average, the food levels were the same in the current study as those used in the inner Danish waters (Nabe-Nielsen et al. 2013b, 2014) and the animals' fine-scale movements are therefore, on the average, the same as those previously documented for the inner Danish waters. The food levels were derived from maps of the spatial distribution of porpoises in the North Sea (see Figure 1). Further refinements of these maps can be expected to make fine-scale movements even more realistic for North Sea conditions. In order to use the model in other regions of the world similar maps must be produced for the entire area used by the population of interest.

3.2.2 Parameters related to dispersal

Dispersal behavior was modeled based on a persistent spatial memory (PSM) movement behavior that enabled animals to navigate back to the 2 km × 2 km cell group where they had previously obtained the highest energy intake rate and that was located at their preferred dispersal distance. The seven parameters used for controlling dispersal are listed in Table 2.

To find the optimal values of the parameters d_{disp} (distance moved per dispersal step), *PSM_angle* (maximum turning angle after each step) and *PSM_dist* (preferred dispersal distance) we simulated animal movement tracks based on a range of

parameter values. The aim was to enable the model to produce tracks similar to those observed for 25 satellite-tracked porpoises (Figure 5). For d_{disp} we considered the range 0.3–0.9 km 30 min^{-1} (with 0.2 km 30 min^{-1} increments), for *PSM_angle* we considered the values 20°, 40° and 60°, and for *PSM_dist* we considered mean values in the range 50–300 km (with 50 km increments). The standard deviation in *PSM_dist*, which controlled the variation in preferred dispersal distances among porpoise agents, was calibrated visually. The selected value allowed the variation in home range size of simulated animals to resemble that of satellite-tracked animals (Figures 5 and 11). All possible combinations of d_{disp}, *PSM_angle* and *PSM_dist* were tested. For each combination we recorded the movements of 25 porpoise agents over a 3-year period. All agents were initialized at Skagen (northern Denmark), which was where the satellite-tracked animals were tagged. We discarded the tracks for the first 2 simulation years, which was the time it took the agents to develop their spatial memory.

We compared the tracks of simulated animals with those of satellite-tracked animals based on three statistics: home range size, home range length and cumulative distance moved. The different statistics were calculated for day 150 of each track. The median value for the 25 satellite-tracked animals was compared to the corresponding median value for 25 simulated animals for each statistic. The procedures for calculating the different statistics are provided in TRACE Appendix A.
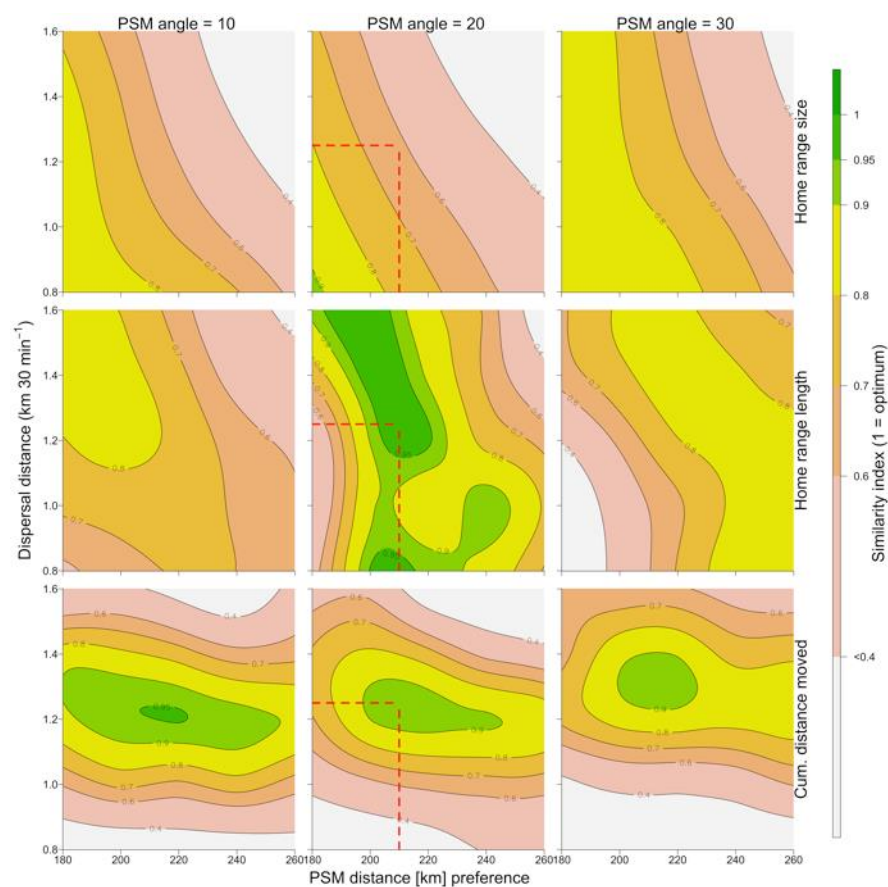

Figure 10. Calibration of the dispersal parameters *PSM_dist*, d_{disp} and *PSM_angle* using pattern-oriented modeling. Each row in the figure represents one of the patterns observed for 25 satellite-tracked animals. Green regions indicate parameter values that enabled the simulation model to produce

patterns similar to those observed for free-ranging animals. The similarity index is calculated as $1-(\mathrm{abs}(x_{nature}-x_{simulated})/\max(x_{nature}, x_{simulated}))$, where x is one of the three patterns. The axes values at the dashed red lines provided the highest similarity with those observed in the field and are therefore used in all simulations.

Two of the remaining parameters used for controlling dispersal behavior (*PSM_log* and *PSM_tol*) were calibrated visually to make the simulated tracks resemble those of satellite-tracked animals as closely as possible. This was done both before and after calibrating d_{disp}, *PSM_angle*, and *PSM_dist*. For *PSM_log*, a simple one-parameter logistic function (Eqn. A4) was used to enable animals to gradually become less directed the longer they dispersed. The movement statistics were relatively insensitive to the choice of *PSM_log*. *PSM_tol* defined the tolerance band within which a porpoise agent should find the most profitable PSM-cell when starting to disperse.

The parameter t_{todisp} determines the number of days with decreasing average energy levels before the animal starts dispersing. The default value is based on the observations that captive porpoises lose weight after not eating for three days, which in nature would probably cause them to disperse to more profitable foraging areas. The parameter w_{disp} determines the minimum depth at which porpoises were allowed to disperse. The value was visually assessed based on satellite-tracking data.
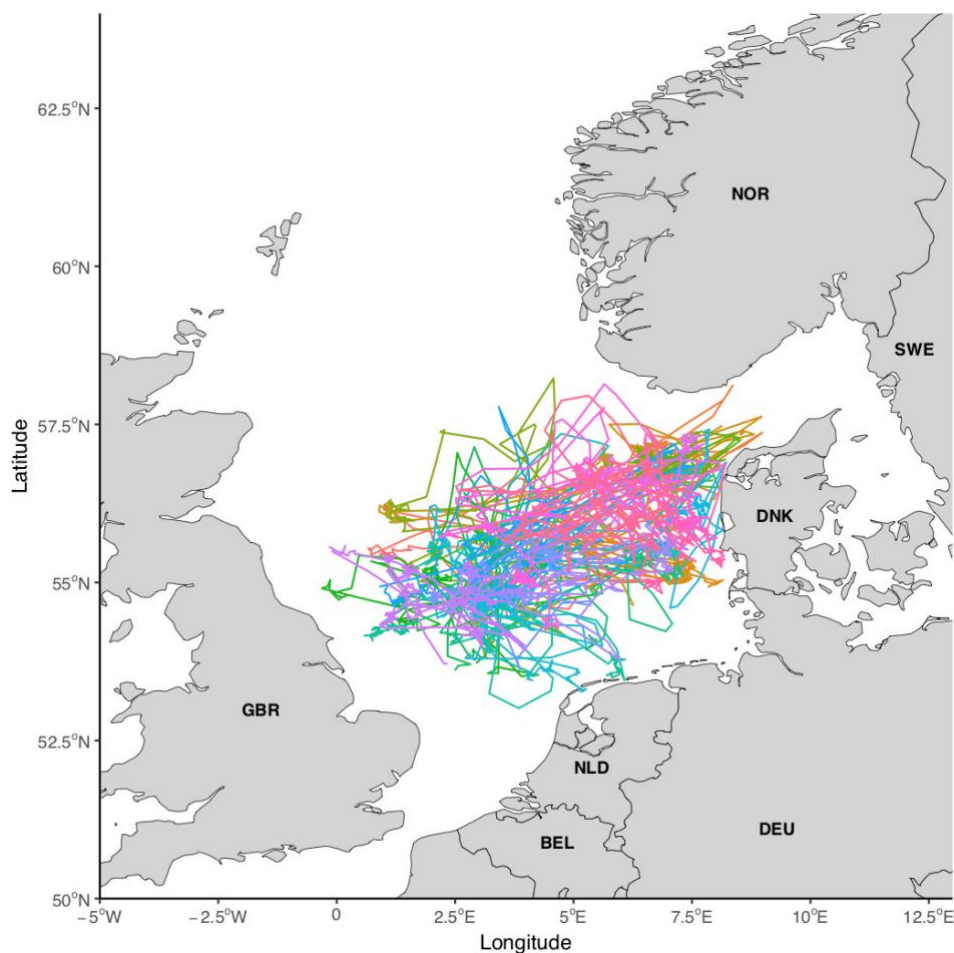
Figure 11. Daily movements of 25 simulated porpoises using values of d_{disp}, *PSM_angle*, and *PSM_dist* that caused their median home range length and cumulated distance moved after 150 days to closely match those of satellite tracked animals.

The dispersal tracks produced by the calibrated model resembled those of free-ranging animals in several respects. Animals developed home ranges with the same length (measured at day 150 of the tracking period), and with the same cumulated distance moved, as satellite-tracked animals (Figure 10). Their movement speeds also matched those observed in nature (see TRACE Appendix A – Calibration of dispersal behavior). Simulated home ranges were, however, more rounded, and therefore larger, than those observed in nature. Examples of tracks generated with the calibrated model (with parameters as in Table 2) are shown in Figure 11.

The parameters used for defining dispersal movements in this study are not necessarily suitable for other geographic regions. The majority of the parameters were obtained through inverse parameterization (using pattern-oriented modelling; Grimm et al. 2005; Kramer-Schadt et al. 2007; Grimm & Railsback 2012) based on animal tracks observed in the north-eastern part of the North Sea. The shapes of these tracks are influenced by the food distribution (defined as background maps; see Input data) and by proximity to land. As many of the simulated animals moved into the central part of the North Sea, their movements were less constrained by land than those of the satellite-tracked animals tagged by Skagen. This enabled them to develop more rounded, and therefore larger, home ranges than the ones observed for free-ranging animals (Figure 10). Animals may also be influenced by other environmental conditions than proximity to land, which could cause them to disperse differently in other parts of the North Sea and elsewhere (other prey species, presence of predators etc.). Unpublished data for satellite-tracked porpoises reveal larger dispersal distances for animals in South Greenland waters (N. Nielsen, pers. comm.), suggesting that it may be important to re-parameterize the model based on local movement data when using it for populations outside the North Sea. The differences between the tracks of simulated and free-ranging animals are discussed further in the section 'Assumptions regarding dispersal'.

3.2.3 Parameters related to response to noise

The porpoise agents' response to noise is controlled by the parameters T, c, d_{max_deter}, t_{deter}, and ψ_{deter} (Table 2). The first two parameters determine the length of the deterrence vector ($\mathbf{V}_D$ in Figure 4). T determines the maximum distance at which porpoise movements are influenced by noise for a given sound source level, whereas c determines the strength of their response at close ranges. The other parameters determine the maximum distance at which porpoises can be influenced by noise and the 'residual deterrence', i.e. the animals' tendency to move away from an area for some time after the noise has stopped.
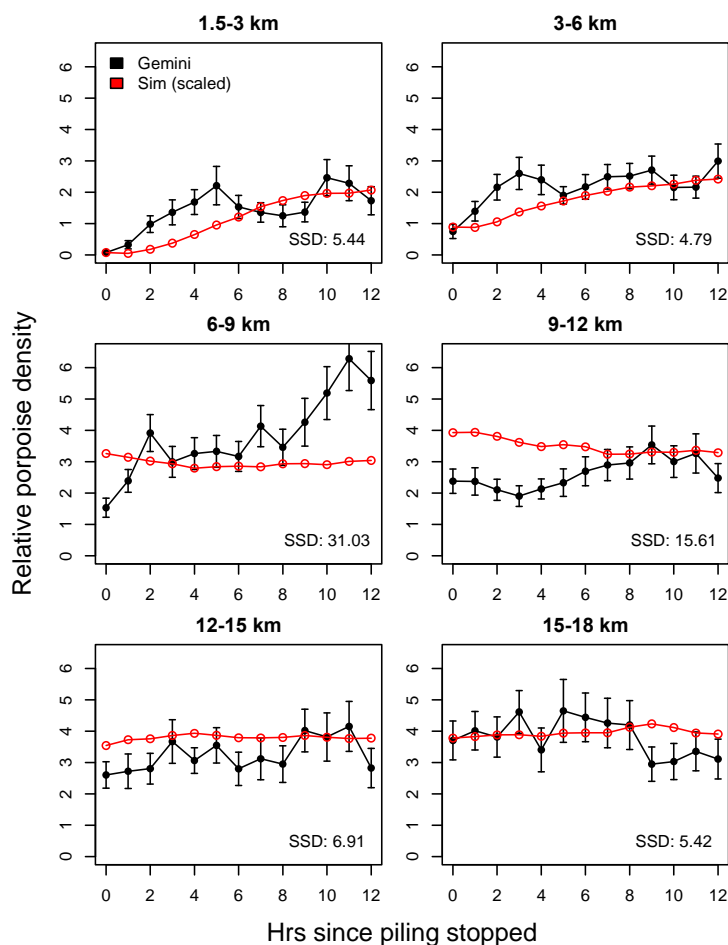
Figure 12. Recovery of porpoise densities after end of pile-driving. Black lines show changes in porpoise densities (mean % porpoise positive minutes±1SE) at different distances from closest pile-driving in the Gemini wind farm. The red lines show the corresponding relative number of porpoises in simulations based on c=0.07 and T=155 dB.

The parameters T and c were calibrated to make recovery of simulated porpoise densities resemble those observed during construction of the Gemini wind farm (Figure 12; Luuk Folkerts, unpubl. data). In the field, the relative porpoise densities were measured using CPODS that recorded the clicks emitted by echo-locating porpoises. Sound source levels were calculated based on noise data collected at different distances from two of the pile-driving sites using hydrophones (Figure 3). This was done using linear regressions, assuming spherical spreading of noise (Eqn. A1). Simulations were based on a landscape that included virtual CPODS (each covering 2×2 cells) placed in the exact same positions as those used in the field. The simulations included pile-driving events with the same timings and sound source levels as the real ones (Figure 3). Due to the limited size of the landscape, dispersal was turned off. We ran simulations using a range of parameter combinations (c in the range 0.00–0.15 and T in the range 151–158 dB SEL). The simulated porpoise densities were standardized to obtain the same overall mean and variance as observed around Gemini. The aim was to find the values of c and T that simultaneously minimized the squared difference between field and simulated data across a range of

different distances from the nearest pile-driving. The optimal values of c and T were therefore the ones that yielded the smallest value of ε in

$$\epsilon(c,T) = \sum_{d,t}(n_{d,t}(c,T) - p_{d,t})^2 = \sum_{d}SSD_d$$

Eqn. A13

Here n is the number of simulated porpoises observed at a particular distance interval d from a virtual CPOD and p is the number of porpoises observed at the same distance interval from a pile-driving at Gemini and t is time since end of pile-driving. We used the distance intervals d shown in Figure 12.

The smallest value of ε was obtained for T=155 dB SEL and c=0.07 (Figure 13). In Figure 13, ε is referred to as 'Sum of Squared Deviation'.

The parameter d_{max_deter} defines an upper boundary for the distance at which porpoises can react to noise. It is only influencing model behavior if sound source levels (SL) are so high that they would otherwise have caused animals to react at very long distances. The reason for introducing the parameter d_{max_deter} is, that a study of Cuvier's beaked whale suggests that the way cetaceans respond to noise may depend on the distance to the noise source rather than on the received sound level (DeRuiter et al. 2013), at least for relatively low received levels. The parameter d_{max_deter} makes it possible to ensure that simulated animals are only deterred out to a certain distance, irrespective of the noise level. When d_{max_deter} is set to 1000 km (default), the parameter has no impact on the animals' response to noise, as this is far beyond the area where $R > T$ (see Figure 4).
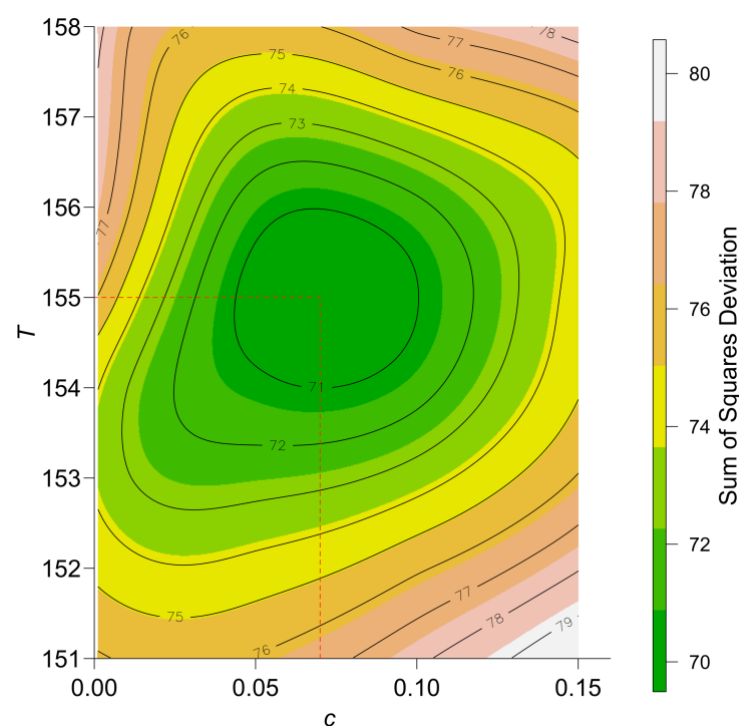

Figure 13. Calibration of c and T using pattern-oriented modeling. The target was to find values of c and T that enabled the model to produce porpoise recovery rates that resembled those observed at different distances from real pile-driving. This was obtained for c=0.07 and T=155 (red dotted line).

The parameters t_{deter} and ψ_{deter} determine how long porpoises keep moving away after the sound that deterred them has stopped, i.e. their 'residual deterrence' behavior. t_{deter} determines the number of 30-minute time steps that porpoises remain deterred and ψ_{deter} determines the reduction in deterrence after each time step (in percent, i.e. a reduction relative to the deterrence that remained prior to the step). Our knowledge of how free-ranging porpoises respond to loud noises is limited to one study (van Beest et al. 2018 subm.). Here some porpoises appeared to remain slightly deterred up to ca. 10 hours after being exposed to loud impulsive noises, whereas others did not respond. As there is limited evidence that animals remain deterred when they are no longer exposed to noise, we use a default value of t_{deter}=0 (i.e. no residual deterrence).

The parameters related to the animals' response to noise are likely to be site-specific. The way porpoises and other cetaceans respond to noise may depend on their condition, on whether the area where the disturbance takes place is an important foraging ground and on whether they have become habituated to noise (Richardson & Würsig 1997; Bejder et al. 2006). These factors are likely to cause the optimal values of c and T to vary among different wind farm construction sites. In Gemini porpoises only respond to noise out to a distance of 6–9 km (Figure 11), which is less than reported in most studies. Diederichs et al. (2009) found reduced porpoise numbers at 14–18 km from active pilings during construction of the Alpha Ventus wind farm, and Tougaard et al. found animals to respond at distances >20 km from Horns Reef I (Tougaard et al. 2009) in the eastern North Sea. Brandt et al. (2011) reported negative effects out to a distance of 17.8 km from the Horns Reef II wind farm, but no effect at 22 km. This suggests that T values that would cause animals to respond approximately 20 from the piling zone might be more representative for simulating population effects of pile-driving in the North Sea.

3.3   Parameters controlling general model behavior

The DEPONS model can run simulations using any landscape provided by the user, or one of the four built-in landscapes (parameter: 'landscape'). It requires eight different background maps to run simulations with any given landscape (see input data). The default landscape is the North Sea (Figure 1). This landscape was used for assessing the impact of pile-driving noise on the porpoise population. The Gemini landscape was created for parameterizing the animals' response to noise (see section Parameters related to response to noise). Simulations can also be run in the DanTysk landscape, in a Homogeneous landscape, which has no land/coast line, and where habitat quality and bathymetry are constant, or in a user defined landscape.

Although DEPONS simulations use realistic landscapes, agents that hit the edge of a landscape are unable to exit or disappear. It is sometimes (e.g. during model development and testing) useful to allow the landscape to wrap (i.e. using a non-bounded landscape). Wrapping of landscape borders is only possible in the Homogeneous landscape (parameter: 'wrapBorderHomo').

The DEPONS model can run a wide variety of wind farm construction scenarios (parameter: 'turbines'), including the three North Sea scenarios used in this study (Figure 2), the Gemini scenario (Figure 3) and the DanTysk scenario (not shown). It is possible to run simulations with alternative scenarios by selecting the 'User-def' turbines file after modifying the accompanying file (see input data). The default option is to run simulations without construction (with 'turbines' set to 'off').

The number of simulation years is set with the parameter "simYears". The default value is 50 simulation years, which allows for a 20 year burn in period, a 10 year period at carrying capacity prior to wind farm construction, a 10 year period with pile-driving noise, and a 10 year recovery period post wind-farm construction.

The number of porpoise agents to be created at the start of a simulation is set with the parameter 'porpoiseCount'. The default value of 10 000 will produce a stable population size in the North Sea landscape within the first 20 years of simulation.

Movement data of porpoise agents can be recorded by specifying how many porpoises to track using the parameter 'trackedPorpoiseCount'. Two options are available to track movements of porpoise agents. First, the user can record movement data for an unlimited number of agents from the very start of the simulation. To do so, the user must provide the starting position (x, y coordinates), and heading of the first step for each porpoise agent to track in a comma separated text file (trackedporpoise.txt; file without headers) stored in the data/landscape directory. If the file is empty, the tracked porpoise agents will have random starting locations. The second option to track movements of porpoise agents allows the user to set a delay in the start of the recording (i.e. starting from a specified time step during the simulation). This is done by writing a single line, in a semicolon separated .txt file (trackedporpoise.txt; file without headers) stored in the data/landscape directory, starting with the text delayedSelection; followed by the time step when recording should initiate; followed by the starting position (x, y coordinates). Here only one starting position can be specified, and movements of porpoise agents closest to the specified starting location are recorded. The two options of tracking the movements of porpoise agents cannot be combined.

The harbor porpoise population is subject to multiple anthropogenic disturbances and stressors, including by-catch in commercial gillnet fisheries (Read et al. 2006; van Beest et al. 2017). Although by-catch was not considered in the current study, it is possible to assess the impact of by-catch on the population in the DEPONS model (parameter: 'bycatchProb'). The parameter was first introduced by Nabe-Nielsen et al. (2014) and ported directly into the DEPONS model (as part of the one-to-one conversion from NetLogo to Repast).

Two different parameters are used for code testing. The parameter 'randomSeed' makes it possible to repeatedly reproduce the exact same simulation (when not set to 'random'). This option should not be selected when investigating population effects of pile-driving noise. A range of built-in testing options were included to test model output under various conditions (parameter 'debug', see details in the section 'Implementation verification').

Parameter	Standard value	Code name	Description [units]
Landscape	NorthSea	landscape	The landscape that is used in a simulation. Can take the values "NothSea", "Homogeneous", "Gemini", "DanTysk" or "UserDefined".
Turbines	off	turbines	The wind farm construction scenario that is used in a simulation. It reads in the

Parameter	Standard value	Code name	Description [units]
			selected text file that defines the turbine locations and period of activity etc. Can take the values "off", "DanTysk-construction", "Gemini-construction", "NorthSea_scenario1", "NorthSea_scenario2", "NorthSea_scenario3", and "User-def".
simYears	50	simYears	Number of simulation years.
porpoiseCount	10000	porpoiseCount	Number of porpoise agents in the simulation when initiated.
trackedPorpoise Count	1	trackedPorpoiseCount	Number of porpoise agents for which to track the xy coordinates (to monitor their movements).
bycatchProb	0	bycatchProb	Randomly selected proportion of the population to remove each year. Can take any value in range 0–1. [unitless]
wrapBorderHomo	true	wrapBorderHomo	Whether the border of the landscape should wrap. Can take the values "false" or "true". The landscape is without borders when "wrapBorderHomo"="true" and "landscape"="Homogeneous".
randomSeed	random	randomSeed	Allows the user to reproduce simulation output of earlier model runs by using the same random seed as previously used. Can take any integer value.
debug	0	debug	Built-in code testing parameter (values 0–5). When set to 0 no code testing/debugging occurs (see details in section 'Implementation verification').

Table 3. Model parameters controlling general model behavior and output types. The 'code names' are the names used in the Repast code in the current version of the model.

4 Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The DEPONS model builds on an existing model that simulates harbor porpoise movements and population dynamics in the inner Danish waters. We discuss the simplifying assumptions underlying the submodels that control animal movement, energetics and responses to noise in the existing model. We further discuss the assumptions underlying the dispersal behavior that was introduced when extending the model to become suitable for simulating effects of pile-driving noise in the North Sea. The rationale for the design and choice of simplifying assumptions are discussed.

4.1 Assumptions regarding fine-scale movements

The fine-scale movement behavior builds on the assumption that animals attempt to optimize their foraging when not exposed to noise. Although fine-scale movements are influenced by the animals' energetic status and proximity to places where they have previously found food, it is unaffected by social behavior, animal age and whether they are nursing. The movements were parameterized based on data collected for one animal (Nabe-Nielsen et al. 2013b). At the time when the model was parameterized, the available fine-scale movement data (i.e. data on a 30-min resolution or finer) did not suggest that the distance moved per 30-minutes or turning angles between steps were strongly related to environmental variation (Figure 9), fine-scale movements are therefore assumed to be independent of environmental variability in DEPONS model version 1.1.

The values of r_R and r_S, estimated for animals in the inner Danish waters, were assumed to be representative for North Sea animals. These parameters controlled the animals' ability to return to previously visited food patches based on a spatial memory (Nabe-Nielsen et al. 2013b).

4.2 Assumptions regarding effects of noise

Noise from pile-driving operations is assumed to influence the fine-scale movements of harbor porpoises by introducing a bias to their moves (Figure 4). This type of response to noise enables the model to reproduce the decline in population densities often observed in the vicinity of pile-driving (Brandt et al. 2011; Dähne et al. 2013), but the results of the only study where wild porpoises were exposed to noise did not yield a clear indication that noise introduces a consistent noise-level dependent bias to the fine-scale movements in wild animals (van Beest et al. 2018 subm.). As such, there might be considerable variation in how individual porpoises respond to noise in terms of their tendency to move away from noise. Such variation was not incorporated in DEPONS model version 1.1.

In the DEPONS model the parameters c and T were assumed to be constant. This may not be the case for wild animals, where habituation to noise may cause either c to decrease or T to increase in the habituated animals. Such habituation to noise may be prevalent in cetaceans (Richardson & Würsig 1997; Nowacek et al. 2007). The way wild animals react to noise may also depend on their energetic status and the quality of the area where the noise exposure takes place (Bejder et al. 2006). This is to some extent accounted for in the DEPONS model: animals that get disturbed in an unfavorable area are more likely to get permanently displaced than the animals that get disturbed in a favorable area. This results from the simulated animals' tendency to return to places where they have previously found food when they have not been able to find food for some time.

4.3   Use of constant vital rates

The animals' probability of becoming pregnant, the gestation time, nursing time and mating day are all assumed to be constant. In reality, they may be influenced by the animals' health, which in turn depends on a number of environmental parameters, and they may also be influenced by the age structure of the population. The choice of using temporally constant parameter values was based on a lack of empirical data indicating otherwise.

4.4   Assumptions regarding energetics

Population dynamics are directly linked to the balance between individuals' energy expenditure and their ability to replenish their energy reserves by finding patches with food. Assumptions regarding the animals' energy balance and availability of food in the landscape are therefore crucial to the behavior of the model.

The energy balance of individual animals depends on their energy use, which is assumed to be constant (except for increases associated with lactation and with high water temperatures in the summer months). This is likely to be realistic, as animals must maintain a fairly constant speed to forage enough to meet their high energy requirements (Kastelein et al. 1997; Wisniewska et al. 2016).

The dynamics of the food patches is influenced by how fast food replenishes after being consumed. This is influenced by the food growth rate (r_U) and by how much food that is left in a patch when it is nearly depleted (U_{min}). The selected value of r_U (which allowed food to replenish after approx. two days with the selected value of U_{min}) was based on the observation that satellite-tracked animals in the inner Danish waters often returned to the same place several times over a period of a few weeks. As the porpoise depends on a continuously high food intake (Kastelein et al. 1997) this was thought to indicate that food had replenished in the areas visited.

Both the animals' food intake rates and the amount of time they spend within a confined area depend on the spatial distribution of the food patches. There is currently no data on the spatial distribution of the fish that porpoises forage on in the North Sea (or in the inner Danish waters). The only indication that the spatial distribution of food patches used in our simulations is sensible comes from the similarity of the simulated movement tracks and those of satellite-tracked animals (Nabe-Nielsen et al. 2013b). When using landscapes with a low patch density in the simulations, animals return to the same area less often than they do in nature, causing them to develop larger home ranges than they do in nature (whereas animals maintained realistic home ranges in our simulations).

4.5   Assumptions regarding dispersal

The dispersal behavior included in the DEPONS model is based on the assumption that animals have a persistent memory of places they have previously visited. Although it has not been demonstrated that harbor porpoises have a persistent spatial memory (PSM), the ability to repeatedly return to the same area is common across a wide range of animal species (Berger-Tal & Bar-David 2015). The satellite tracks for porpoises tagged by Skagen in northern Denmark suggest that porpoises also have the ability to navigate back to places they have not visited for weeks or months (Figure 5). These tracks suggest that North Sea porpoises prefer to forage in particular areas, although it is unclear if they move over long distances in order to reach areas where they can maximize their food intake rate. The dispersal behavior implemented in the model assumes that animals disperse towards the area where they have previously obtained the highest energy intake rate, i.e. they are assumed to attempt to forage optimally, but to not take the costs of travelling to a new area into account when deciding where to go. Similar optimal foraging behavior has been demonstrated for several other species (e.g. Austin et al. 2004; Fagan et al. 2013). The dispersal behavior also builds on the assumption that animals gradually drift away from the route that would take them straight to the place where they previously experienced the highest energy intake rate. This allows them to gradually become more exploratory when approaching a region with high food availability.

The calibration of dispersal behavior is based on the assumption that home ranges of simulated animals and free-ranging animals are influenced in the same way by environmental variations. This is not always the case. Some of the satellite-tracked animals moved out of the area used in the simulation model, and as their movements were not constrained by the presence of a landscape border, their home ranges were potentially larger than those of simulated animals. The satellite-tracked animals also remained in the easternmost part of the landscape longer than the simulated animals, presumably due to the presence of local high-quality food patches that were not included in the simulation landscape. The simulated animals often moved out of this area and into the central parts of the North Sea. This enabled their home ranges to become more rounded and larger than those of the satellite-tracked animals (Figure 5 vs. Figure 11).

5   Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code for implementing the model has been thoroughly tested for programming errors and (2) whether the implemented model performs as indicated by the model description.

Summary:
> **The computer code was continually tested during model development to ensure that each consecutive step in development was only initiated after the model had passed a wide range of visual and statistical tests. Visual inspection of movement tracks was continuously carried out using the NetLogo and Repast graphical user interfaces (GUIs). The majority of the program code was initially developed and tested in NetLogo and**

> **subsequently scrutinized and re-implemented in Repast by independent programmers. Only the animals' response to noise and dispersal behavior was not part of this first version of the model.**

5.1 Testing the fine-scale movement model and reactions to noise

The fine-scale movement model was the first component of the DEPONS model to be developed. The structure of this submodel is described in the section 'Fine-scale movement'. All aspects of the model (including default parameter values) were kept exactly as described in the original publication (Nabe-Nielsen et al. 2013b), which described how a spatial memory could enable animals to stay in the same area for several weeks. The landscapes used during development of this model included food patches, but no other types of environmental variation. The simulated tracks were inspected visually in the homogeneous landscape as well as in landscapes including land (Figure 14). A wide range of movement statistics were calculated based on simulations in a homogeneous landscape (Nabe-Nielsen et al. 2013b). After porting the model to Repast, it was tested that the new version of the model produced movement tracks identical to those of the original NetLogo model. This was done by comparing the coordinates, spatial memory variables and energy levels of simulated animals that had been initiated on the same location in the two versions of the models (using fixed randomSeed parameter values).
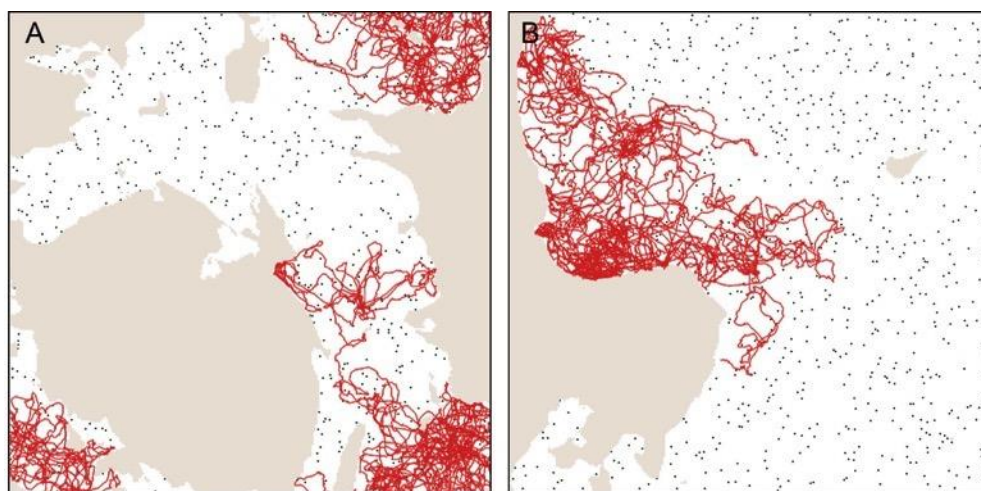

Figure 14. Tracks simulated with fine-scale movement model in landscapes with land and identical, randomly distributed food patches, but no other types of environmental variation. The tracks were produced using the porpoise movement model developed in NetLogo (doi: 10.5281/zenodo.53149). The spatial distribution of the patches was retained in the DEPONS model version 1.1.

Dedicated code was developed for testing the different submodels in the fine-scale movement model (controlled with the parameter 'debug'). This was used for developing the NetLogo version of the code (DOI:10.5281/zenodo.53097). The debug value 1 was used for developing and testing the porpoises' behavior when approaching land and to develop code that enabled them to back-track in rare situations where they got trapped by land. When setting the debug parameter to 2, the porpoises' behavior when approaching land was tested to ensure that animals turned as little as possible, while still avoiding land (distance to land, positions and turning

angles were written to the console for a subset of the simulated animals). Debug value 3 was used for debugging turning angles related to CRW behavior. Debug value 4 enabled inspection of the length of the porpoises' attraction to previously visited food patches by writing the perceived/remembered value of the patch and the direction of the attraction vector to the console. Debug value 5 was used for writing out the position of the porpoise and the length of the contribution of the CRW and spatial memory moves to the console (Eqns. A5 and A6), allowing a close inspection of whether turning angles and the direction of the vector that characterized fine-scale movement were related to food availability and proximity to the visited patch as expected. This dedicated debugging code was used in combination with stress tests, where simulations were run with extreme parameter values, to identify errors that would be difficult to detect with the default/realistic parameter values.

The reaction to noise was verified by checking that the length of the deterrence vector $\mathbf{V}_D$ was exactly as specified in Figure 4 and the ODD. We used a visual inspection of the simulation to double-check that simulated porpoises reacted to noise out to the distance specified in Eqn. A1 in the submodel 'Porpoises detect noise' (see also Figure 15).
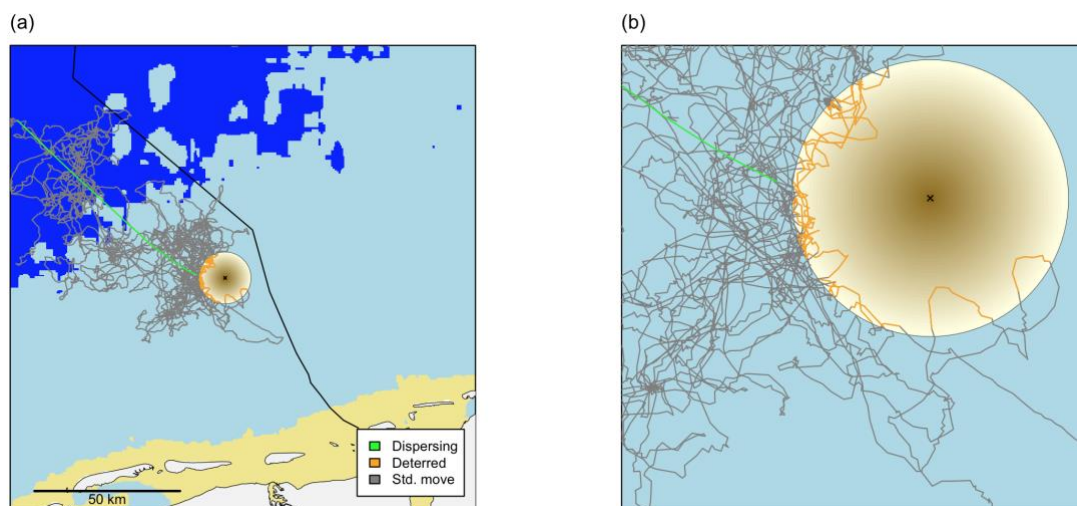

Figure 15. Porpoise movement tracks in the presence of continuous pile-driving noise. The yellow circle indicates the area where porpoises react to noise when the model is parameterized based on data from the Gemini wind farm.

5.2   Testing the dispersal model

The persistent spatial memory (PSM) dispersal behavior was developed exclusively in Repast/Java. It differs from the dispersal model described by Nabe-Nielsen et al. (2014), which was specific to the inner Danish waters. We tested that the dispersal model produced the desired output by plotting and analyzing the movement tracks for dispersing porpoise agents. This was done using the parameter "trackedPorpoiseCount" and the trackedporpoise.txt file that records movements (coordinates) of random agents after each time step. We plotted how the turning angles following each dispersal step changed as the simulated animals approached their dispersal targets (Figure 7) and by monitoring variations in step lengths and energy levels. Further, we conducted stress tests of the PSM dispersal by analyzing

simulated tracks for extreme values of d_{disp}, *PSM_angle, PSM_dist, PSM_log* and *PSM_tol*.

5.3   Testing population dynamics

The population model (Nabe-Nielsen et al. 2014) was tested by inspecting how porpoise agent movements were influenced by their energetic status and by analyzing relationships between their average energetic status of porpoises and food patches. The inspection of individual porpoise agents was done using the built-in inspector in NetLogo as well as custom made code for writing out the track, food consumption, energy use and fate of individual porpoises. Population dynamics were inspected using the built-in functionality for creating dynamic plots in NetLogo and by close inspection of generated output.

6   Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

> **The DEPONS model was able to reproduce the fine-scale movement patterns and dispersal patterns observed for porpoises in nature. It was also able to reproduce the relative animal densities observed at different distances from a wind farm during construction. These three types of output were parameterized using pattern-oriented modeling. Emergent patterns related to variations in population size could not be compared to observations due to lack of field data.**

6.1   Types of model output

The DEPONS model writes out three data files after each simulation. (1) The first file (.csv) reports the change in population size over time. By default it produces one line of output per 30-min time step, but the reporting interval can be changed in the graphical user interface (GUI). (2) Data on the distribution of porpoise agents (.csv) among 'blocks' in the simulation landscape (defined in a raster file, see the section 'Input data'), which is by default recorded for each 30-min step. (3) Data on the movements (.csv) of individual porpoise agents during the simulation, measured and recorded by default for each 30-min step. By default, one porpoise is tracked, but multiple agents can be tracked using the parameter trackedPorpoiseCount.

In the GUI version of the model an additional data set is written out: Data on number of animals per age class in the population and number of animals that have died in the preceding year in that age class. When running simulations in batch mode only the first three files are produced, but in addition the associated parameter input values used during the simulation are written to a separate file. The data files are written out to the working directory when simulations are run in the GUI while output from the

batch procedure is written out to the output folder within the working directory. Each output file has a date and time stamp in the title, which reflects when the simulation finished.

6.2   Comparison of model output and observations

Only animal movement patterns and recovery of local population densities after pile-driving could be compared to corresponding field data recorded in the North Sea. The emergent population dynamics could not be compared to field data, as the available data on variations in population densities are either unavailable for the North Sea, or available on a very rough temporal and spatial resolution (Hammond et al. 2013). In the inner Danish waters, the predecessor of the DEPONS model was, however, capable of reproducing the spatial distribution observed for porpoises using acoustic survey data (Figure 7 in Nabe-Nielsen et al. 2011). The age class distribution observed for simulated animals that died each year corresponded to the one observed for stranded animals along the Danish shores (Nabe-Nielsen et al. 2014).

The fine-scale movement model enabled animals to develop a range of track characteristics observed for animals in the inner Danish waters (Nabe-Nielsen et al. 2013b). In version 1.1 of the DEPONS model, the correlated random walk component of the fine-scale movement model was calibrated to ensure a close match with field data (by iteratively calibrating the parameters a, b, m, R_1, R_2 and R_3 as described in the appendix of Nabe-Nielsen et al. 2013b; see Table 2 for description of parameters). Subsequently the parameters r_R and r_S were calibrated using pattern-oriented modeling (POM) to ensure that animal home range sizes and residence times (Barraquand & Benhamou 2008) closely resembled those observed for satellite-tracked animals (see details on POM). Here residence time is a measure of how long animals have spent in the neighborhood of each position in a track, which is often interpreted as a measure of how suitable the area is for foraging. Although fine-scale movements may depend on various types of environmental variation in nature (e.g. bathymetry, salinity and distance to coast), these did not have a direct impact on the distance animals moved per step or on turning angles in DEPONS model version 1.1. The reason was that there was no data available to parameterize such variations. We consistently used the simplest possible model (i.e. the model that involved the smallest number of parameters) if there was no data to support the use of a more complex relationship in the model.

The recovery of relative porpoise densities after the pile-driving ended resembled those observed at different distances from the Gemini wind farm during construction (Figure 12). The recovery resulted from the simulated animals' tendency to move back to known food patches after deterrence stops.

The simulated dispersal patterns matched those observed for satellite-tracked animals in the north-eastern part of the North Sea after calibrating parameters related to persistent spatial memory (see details on POM).

7   Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

A sensitivity analysis was performed to explore how the equilibrium population size changed in response to variations in each of the parameters in the model. The emergent equilibrium population size was most sensitive to variations in food replenishment rate and to parameters related to animal energetics, but relatively insensitive to changes in the parameters related to animal movements. It is discussed to what extent the realism of the patterns that emerge from the model have been tested against field data.

7.1   Sensitivity analysis

7.1.1   Sensitivity – parameters related to general porpoise behavior

We conducted a sensitivity analysis to explore how the equilibrium population size changed when varying parameters related to life history, energetics, fine-scale movements and dispersal in simulations without noise (Figure 16). Parameters were changed one at a time to produce a local sensitivity analysis (cf. Bar Massada & Carmel 2008). In this study parameters were increased or decreased by 20% relative to their default values and the corresponding impact on equilibrium population size was calculated as the mean daily population size for 8 replicate simulations. For the sensitivity analyses we used 40-year simulations, but calculated the equilibrium population size based on the last 20 years only (a 20-year burn-in period was always sufficient to ensure that the population had stabilized).

The equilibrium population size was most sensitive to variations in parameters related to energetics (2nd group of parameters in Figure 16), and variations in the food replenishment rate, r_U were particularly important. The default value for this parameter caused food to replenish after approximately 48 hours (see appendix of Nabe-Nielsen *et al.* 2013b). When increasing r_U by 20% relative to its default value (see Table 1) food replenished faster, leading to generally higher food availability and a larger population size. The equilibrium population size is nearly equally sensitive to parameters that influence the individual animals' energy consumption per time step, E_{use}, their increased energy use while lactating, E_{lact}, and increased energy use in periods with warm water, E_{warm}. It is, however, insensitive to variations in the survival probability constant β, which determines the exact relationship between the animals' energetic status and their survival probability.

Equilibrium population size was less sensitive to variations in parameters related to animal life history (1st group in Figure 16), fine-scale movement (3rd group) and dispersal (4th group). One exception is the maximum distance moved during a fine-scale move, $d_{maxmove}$. When decreasing this parameter by 20% relative to its default

value (provided in Table 2) it caused the mean population size to decrease by 16.5%, suggesting that the distance animals move while using fine-scale movements is important for their ability to rapidly return to previously visited patches when they do not find much food using a correlated random walk. For R_1 and R_3, which control distance moved and turning angles during fine-scale movements, respectively, only the parameter means were varied (standard deviation components were kept constant).
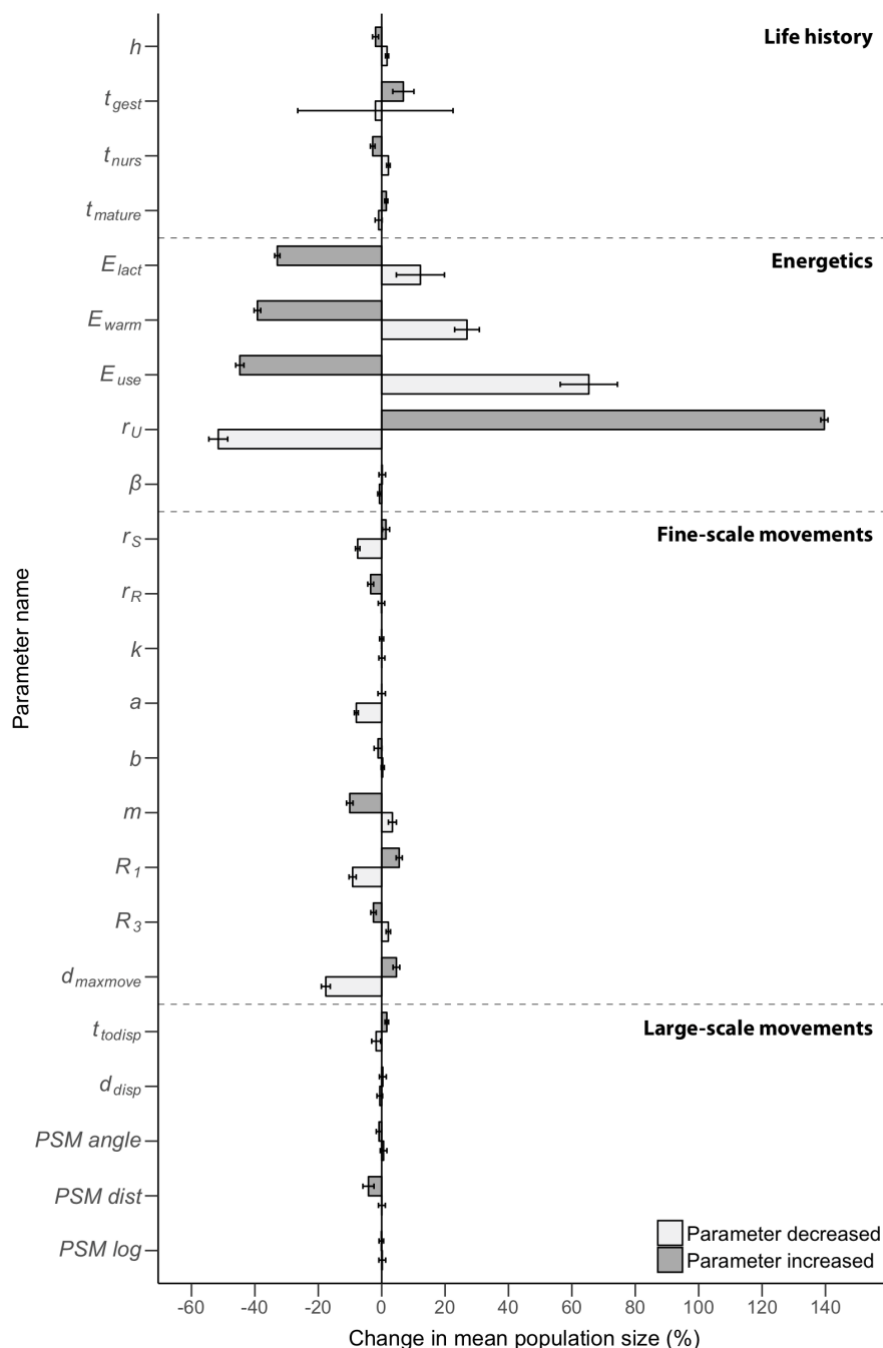

Figure 16. Sensitivity analysis for parameters related to animal life history, energetics, fine-scale movements and large-scale movements/dispersal. Bars show changes in equilibrium population size when increasing or decreasing each parameter by 20% relative to its default value. Error bars show confidence intervals based on 8 replicate simulations.

The relatively low sensitivity for most parameters related to animal movements, as compared to parameters related to energetics, does not indicate that population dynamics are unaffected by animal movements. Inclusion of, e.g., novel types of dispersal might result in changes in the equilibrium population size that exceed those observed with the current dispersal model for any parameter combinations.

Only parameters that could potentially influence the behavior of all animals, and where an adjustment of ±20% made sense, were included in the sensitivity analysis. The sensitivity to the life history/energetics parameters t_{maxage}, E_{init}, t_{mating}, U_{min} was not studied. The t_{maxage} only influenced the few, old animals. E_{init} was only important during the burn-in period. For t_{mating} it did not make sense adjusting by ±20%. The same was the case for R_2 (turning angle between consecutive fine-scale moves), which had a mean of 0. U_{min} affects the time it takes food in patches to replenish, which could be adequately analyzed by adjusting r_U. PSM_tol presumably mostly affected animals while they gathered information about potential areas to disperse to (i.e. during the burn-in phase). The parameters w_{disp}, w_{min} influenced only the relatively few animals that were close to land, and varying these parameters by ±20% therefore inevitably has small impact on overall population dynamics.
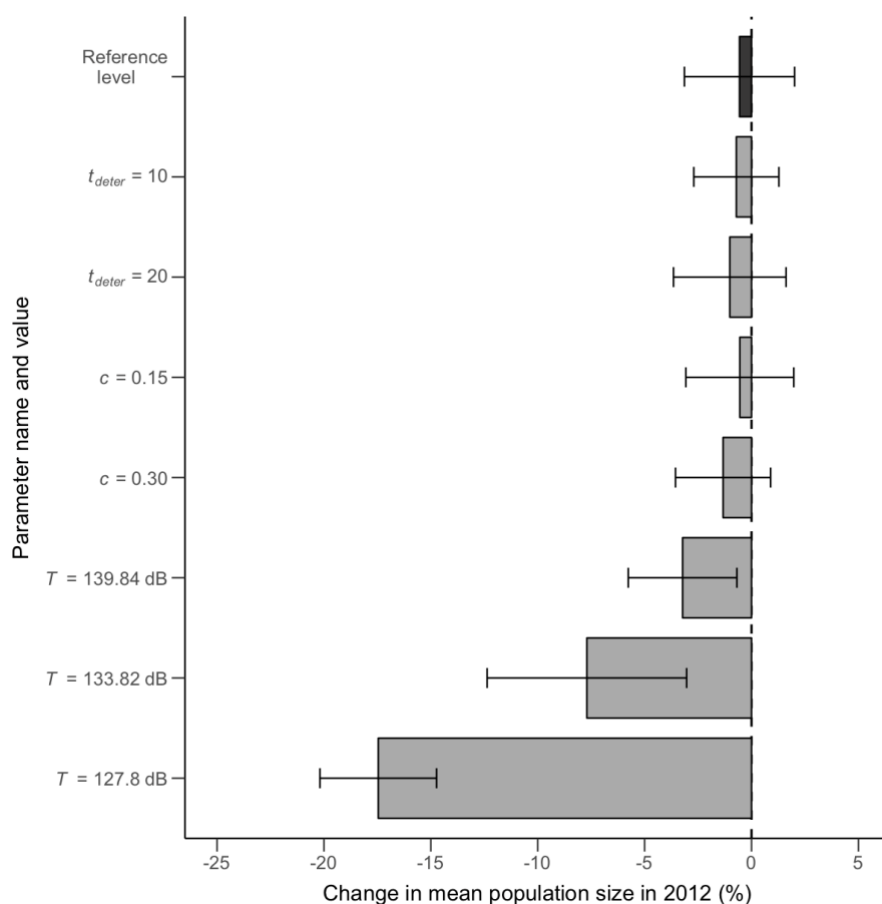

Figure 17. Sensitivity analysis for parameters related to noise, i.e. residual deterrence time t_{deter}, deterrence coefficient c, and response threshold T. T equal to 139.8 dB, 133.8 dB and 127.8 dB cause simulated animals to respond to distances of 51.3 km, 102 km and 204 km, respectively. Error bars show 95% confidence intervals based on 8 simulations.

7.1.2   Sensitivity – parameters related to impacts of noise

To assess the model's sensitivity to variations in parameters influencing individual animals' response to noise, we measured the population size in the year where it was most affected by noise. This happened in the second year of the 10-y wind farm construction period in Scenario 1 (i.e. in year 2012 in the 'Random, slow' scenario; Figure 3 in main text). The population effect of noise was measured after increasing or decreasing the noise parameters by 20%, one at a time, and recording the corresponding mean population size in eight replicate simulations. The same was done for the default parameter values, which yielded the 'reference level', where animals responded up to 8.9 km from the noise source.

When decreasing the noise parameter T to 139.8 dB, 133.8 dB and 127.8 dB (causing simulated animals to react to noise out to distances of 51.3 km, 102 km and 204 km from the noise source, respectively) it resulted in a much larger decrease in the mean population size than the one observed when using default parameter values (Figure 17). There was, however, a large variation in mean population size among simulations. When increasing c to either 0.15 or 0.30, which caused individual animals to respond much more strongly to noise than observed during construction of the Gemini wind farm (Figure 13), it did not significantly influence the population impact of noise, i.e. the confidence intervals overlapped with the reference level. Increasing the residual deterrence time, t_{deter}, to either 10 or 20 did not cause the population impact to differ from the reference level either. Here 20 corresponds to a residual deterrence of 10 hours, which is the highest likely value of t_{deter} as based on field data; van Beest et al. (2018). The sensitivity of ψ_{deter} was not investigated as it was closely related to t_{deter}, and that of d_{max_deter} was not relevant with the default parameter settings. The simulated population effect of noise was therefore only influenced by decreasing T, which also caused the population size to drop below the equilibrium level.

7.1.3   Sensitivity – impact of energetics parameters on response to noise

To test if the population impact of noise was sensitive to the choice of energetics parameters, which were the parameters with the largest influence on equilibrium population size (Figure 16), we increased or decreased these parameters one at a time in simulations including noise. This is equivalent to testing for interactions between T and each of the energetics parameters. The reference population size was obtained as the daily mean population size during the second year of the 10-y wind farm construction period in scenario 1 (i.e. in 2012; mean of 8 simulations). It was based on default parameter values, except that T was decreased to 127.8 dB SEL (causing animals to react up to 204 km from the pilings). The population impact of noise was considered sensitive to an energetics parameter when either increasing or decreasing the parameter by 20% resulted in a change in the population size relative to the reference population size.

The population impact of noise was sensitive to E_{lact}, E_{warm} and r_U, as changing either of these parameters caused the population size during the second year of the wind farm construction period to differ from the reference population size (i.e. the confidence intervals did not overlap with the reference value; Figure 18). When reducing E_{lact} or E_{warm} by 20%, wind farm construction noise no longer had a significant impact on the population, even when letting animals be deterred up to 204 km from the piling. The population impact of noise was not sensitive to changes in

E_{use} or β, but a 20% decrease in E_{use} caused the impact of noise to be non-significant. Only an increase in E_{warm} caused noise to have a larger impact on the population, but only slightly so. Although improved estimates of the noise parameters could potentially result in more accurate estimates of the population impacts of noise, it is unlikely that larger population effects would be predicted with moderately altered energetics parameters.
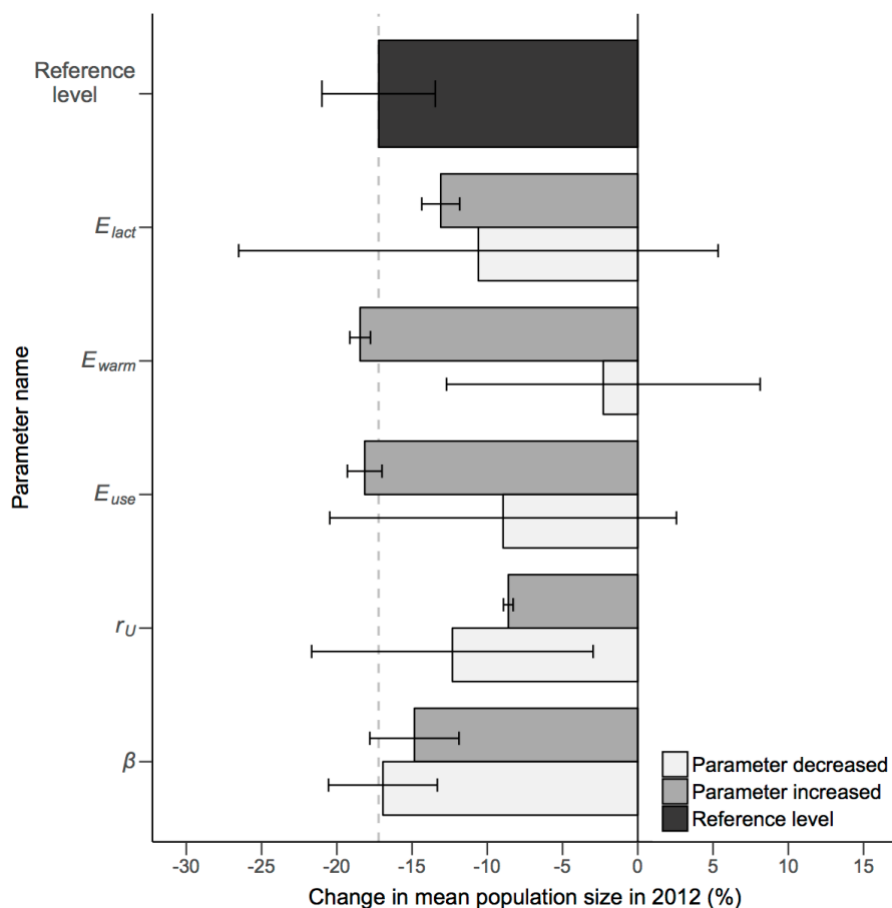

Figure 18. Sensitivity of population effect of noise to parameters related to energetics. Bars show mean population sizes during the second year of the wind farm construction period, when increasing or decreasing parameters by 20% relative to their default values. Error bars show 95% confidence intervals. Simulations were based on T=127 dB, assuming that animals reacted up to 204 km from pilings.

7.2 Tests of emergence

The model produces four different emergent patterns: (1) population size, (2) spatial distribution of animals, (3) their age class distribution, and (4) local recovery of populations after exposure to pile-driving noise (see 'Design concepts'). All four patterns emerge from ubiquitously valid mechanisms derived from 'first principles' (Nathan et al. 2008; Sibly et al. 2013), including use of energy for maintenance and movement and acquisition of food by actively searching for optimal foraging areas. Such models where population and community-level patterns emerge from adaptive traits related to general evolutionary and physiological principles are more likely to

maintain their predictive power across a wide range of environmental conditions than other models (Stillman et al. 2015).
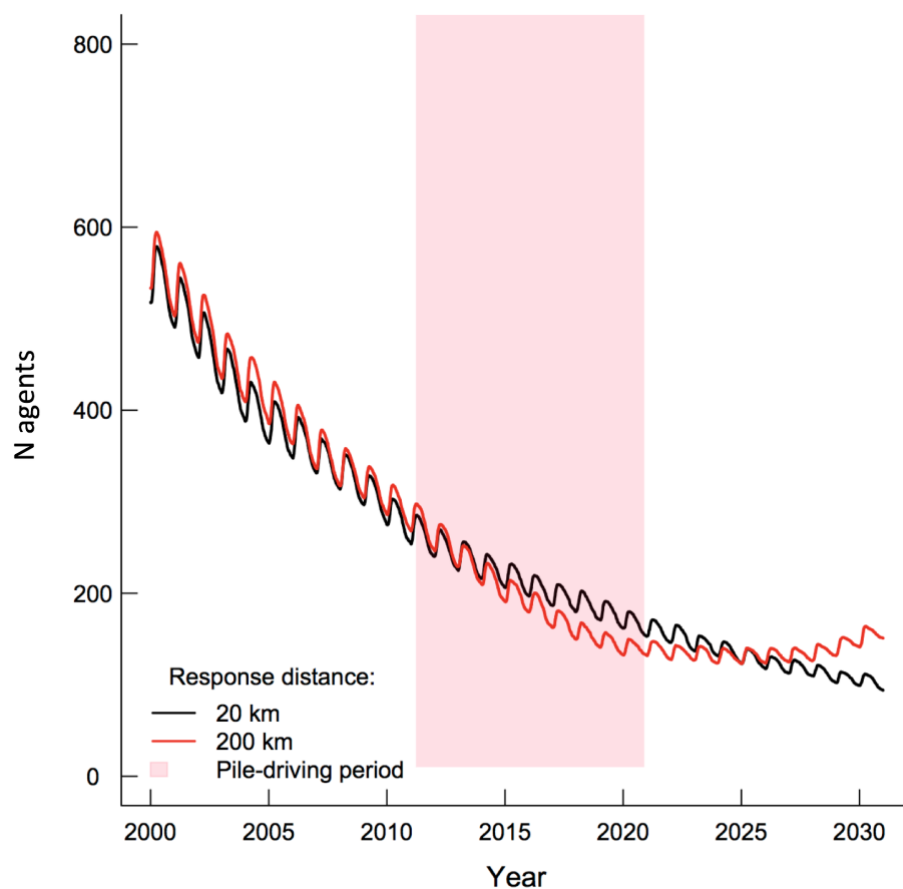

Figure 19. Population dynamics in model without dispersal. Impacts of noise are illustrated for the 'Random, slow' scenario.

In order to test which elements of the model were responsible for the observed emergent patterns, we gradually refined the model until reaching the level of complexity present in the current version of the DEPONS model. While increasing model complexity we monitored the changes in population size and spatial distribution of animals and in the animal movement patterns. The simplest model, where animal movements were simulated using a correlated random walk model without spatial memory of previously visited patches did not allow realistic fine scale space-use patterns to emerge. This suggested that the model was too simple to represent real animals (see Table A1 in Nabe-Nielsen et al. 2013b for details on the relationship between animal space use and spatial memory). Inclusion of a mechanism that allowed animals to return to previously visited food patches (see 'Fine-scale movement') allowed simulated animals to develop space-use patterns that closely resembled those of satellite-tracked animals by balancing their tendency to move at random (i.e. following a correlated random walk) and their tendency to return to previously visited food patches (Nabe-Nielsen et al. 2013b). This also enabled simulated animals to forage optimally, thereby facilitating fitness-maximization. Although this suggested that the inclusion of spatial memory in the model was

required to faithfully simulate the movements and energetics of real animals, it did not permit the simulated animals to develop long-term home ranges that resembled those observed for satellite-tracked animals. It is essential that simulated animals have home ranges of a realistic size in order to ensure that they have access to the same amount of food resources as real animals have. Only in that case will the decreased food intake that they experience when being scared away from a wind-farm construction site result in a realistic decrease in in the population size. The model was only able to simulate home ranges that resembled those of satellite-tracked animals after including a dispersal mechanism that allowed individuals to return to the area where they had previously experienced the highest energy intake rate (Figure 10 illustrates how animals that disperse less, i.e. with smaller *PSM_dist*, have unrealistically small home ranges). The inclusion of this dispersal mechanism in the model caused the equilibrium population size to increase (relative to a model without dispersal; Figure 19). It also resulted in the emergence of realistic movement patterns at multiple spatial and temporal scales (see TRACE Appendix A), and in the emergence of realistic local population densities. This suggests that the mechanisms that control animal foraging and food acquisition in the current version of the DEPONS model are sufficiently realistic for the purpose of the model. It also suggests that the model cannot be simplified without compromising its realism.

8   Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence, which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

> **The model's ability to faithfully predict population effects of wind farm construction noise cannot be corroborated using independent data, as harbor porpoise population estimates based on field data are scarce and inherently imprecise. The simulated effects of noise on local population densities have not been compared with independent data due to the scarcity of data from comparable wind farm construction sites.**

Only some of the model predictions can be directly compared to independent data due to the scarcity of harbor porpoise survey data from the North Sea and due to the large variability associated with such data. Four different patterns emerged from the model: (1) variations in total population size in time; (2) spatial distribution of animals, (3) their age class distribution, and (4) local recovery of populations after exposure to pile-driving noise (see 'Design concepts'). In the following we discuss to what extent each of these patterns can be corroborated using independent data and which types of

independent data that should be collected to further evaluate the realism of the model predictions.

A direct comparison of the predicted porpoise population size with population estimates based on survey data (e.g. those collected during SCANS surveys; SCANS II 2008) is unlikely to be informative for two reasons: (i) The North Sea population estimates based on SCANS data are associated with considerable variation, making it relatively easy for the simulation model to produce population estimates within the confidence limits of these estimates. (ii) The SCANS surveys are conducted relatively infrequently, making them unsuited for validation of the fine-scale temporal population dynamics produced by the DEPONS model. The robustness of the model predictions regarding variations in population sizes in space and time is therefore only ensured by the generality of the mechanisms responsible for producing this emergent pattern.

The predicted spatial distribution of animals could, in principle, be compared to independent data, but although alternative porpoise distribution maps exist (e.g. Reid et al. 2003) they are partly based on the same underlying data as the study by Gilles et al. (2016), so they are not truly independent. The spatial distribution patterns produced by the predecessor of the DEPONS model in the inner Danish waters, did, however, closely match those obtained from acoustic survey data that were not used for designing or calibrating the model (see page 23 in Nabe-Nielsen et al. 2011; monthly average densities per 40 km x 40 km block). These simulations of the inner Danish waters population did not include wind-farm construction scenarios. The model's ability to reproduce the porpoise distributions observed in nature is reassuring, as this causes a realistic proportion of the simulated porpoises to get exposed to noise during wind farm construction scenarios.

The age class distribution of the simulated animals can be directly compared to the age class distribution of stranded and by-caught animals. This comparison has already been conducted in the inner Danish waters (Nabe-Nielsen et al. 2014). Here the age class distribution that emerged from the model corresponded closely to that in the field data.

Recovery of local population densities following the construction of individual wind turbine foundations was studied in the Gemini wind farm during construction. This data set was the only one available providing both noise measurements and relative porpoise population densities at different distances from the mono-pile pilings, and where no noise mitigation was used. This data set was used for simultaneously calibrating deterrence and local population recovery (Figures 11 and 12). As the only available data set was used for model calibration, there are no data available for model output corroboration.

In addition to using already collected data for model output corroboration, the collection of local population densities around other wind farm construction sites would help us obtaining a better understanding of the structural realism of the DEPONS model and of the generality of the model predictions. This would also make it possible to verify that the sound propagation model employed is realistic for the sound frequencies that porpoises react to. In such field studies it is essential to measure how porpoise densities change during and after pile-driving at large distances from the wind farm construction sites in order to determine whether model predictions are realistic at these distances.

It is possible that the animals' tendency to return to areas they have been deterred from depends on the food availability in that area, in nature as well as in the model. Animals are more likely to return to profitable areas. The model's ability to faithfully simulate local population recovery in areas with different levels of food availability could be corroborated using long-term data collected with CPODS in areas where wind farms are constructed. This would provide an independent measure of local food availability as well as local population recovery.

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TRACE Appendix A – Calibration of dispersal behavior

This appendix provides supporting information on: How porpoise movement tracks were analyzed to make it possible to calibrate animal dispersal using pattern-oriented modeling. The appendix is not part of the standard TRACE documentation.

Summary:

> **This appendix provides information on the procedure used for calibrate the simulated porpoises' dispersal behavior using pattern-oriented modeling. The animal dispersal patterns obtained from animals equipped with Argos satellite tags and from the DEPONS model were analyzed using non-linear mixed effects models. This yielded estimates of the asymptotic home range sizes for each movement track. We here demonstrate that the median asymptotic values for simulated animals resembled those of satellite-tracked animals.**

Analysis of porpoise dispersal patterns

To ensure that the simulated dispersal movements resembled those of satellite-tracked animals as closely as possible, we calibrated the parameters controlling dispersal, i.e. d_{disp} (distance moved per dispersal step), *PSM_angle* (maximum turning angle after each step) and *PSM_dist* (see section 3.2.2 for details). To do so we used three different statistics for comparing simulated tracks to those of satellite-tracked animals: (1) home range size (km^2), (2) home range length (km) and (3) cumulative distance moved. These statistics characterize complementary aspects of the animals' space use. As all three statistics are sensitive to the number of positions in the movement track, i.e. the number of days from the beginning till the end of the track, we decided to compare the statistics for day 150 of each tracks. All tracks were based on 3-year simulations with 2-years burn in period. Not all tracks lasted 150 days (because the satellite tags stopped working), so the first step in the analysis was to fit a function that enabled us to extract the values for day 150 of the tracks.

The temporal change in home range size and length was modeled using non-linear mixed models for both simulated and satellite-tracked animals. These were fitted using a negative exponential function (i.e. asymptotic regression function through the origin)

$$x = Asym \times (1 - \exp(-\exp(lrc) \times t) \qquad \text{Eqn. A14}$$

where *x* is the track statistic, *Asym* is the horizontal asymptote, *lrc* is the rate constant and *t* is time since the start of the track (unit: days) (Pinheiro et al. 2016). Both *Asym* and *lrc* were fitted as fixed and random effects to capture individual variation in the large-scale movements. Temporal autocorrelation in the residuals was reduced by fitting a continuous autocorrelation structure to *t* (corCAR1 class). Homogeneity of residuals was ensured by incorporating a power variance weights structure to *t*.
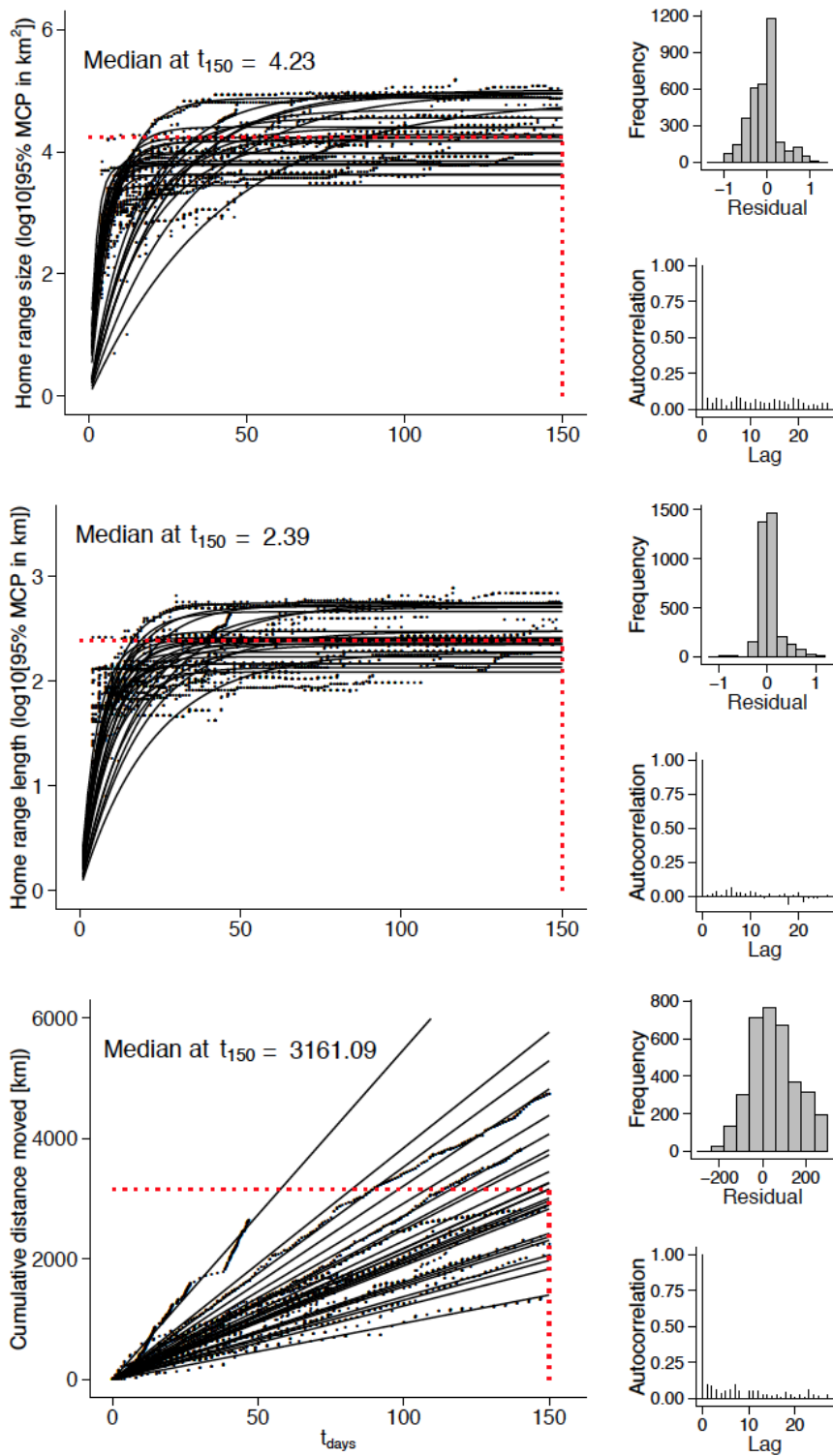
Figure 20. Median home range size, home range length and distance moved after 150 days for 25 free-ranging porpoises equipped with satellite tags.
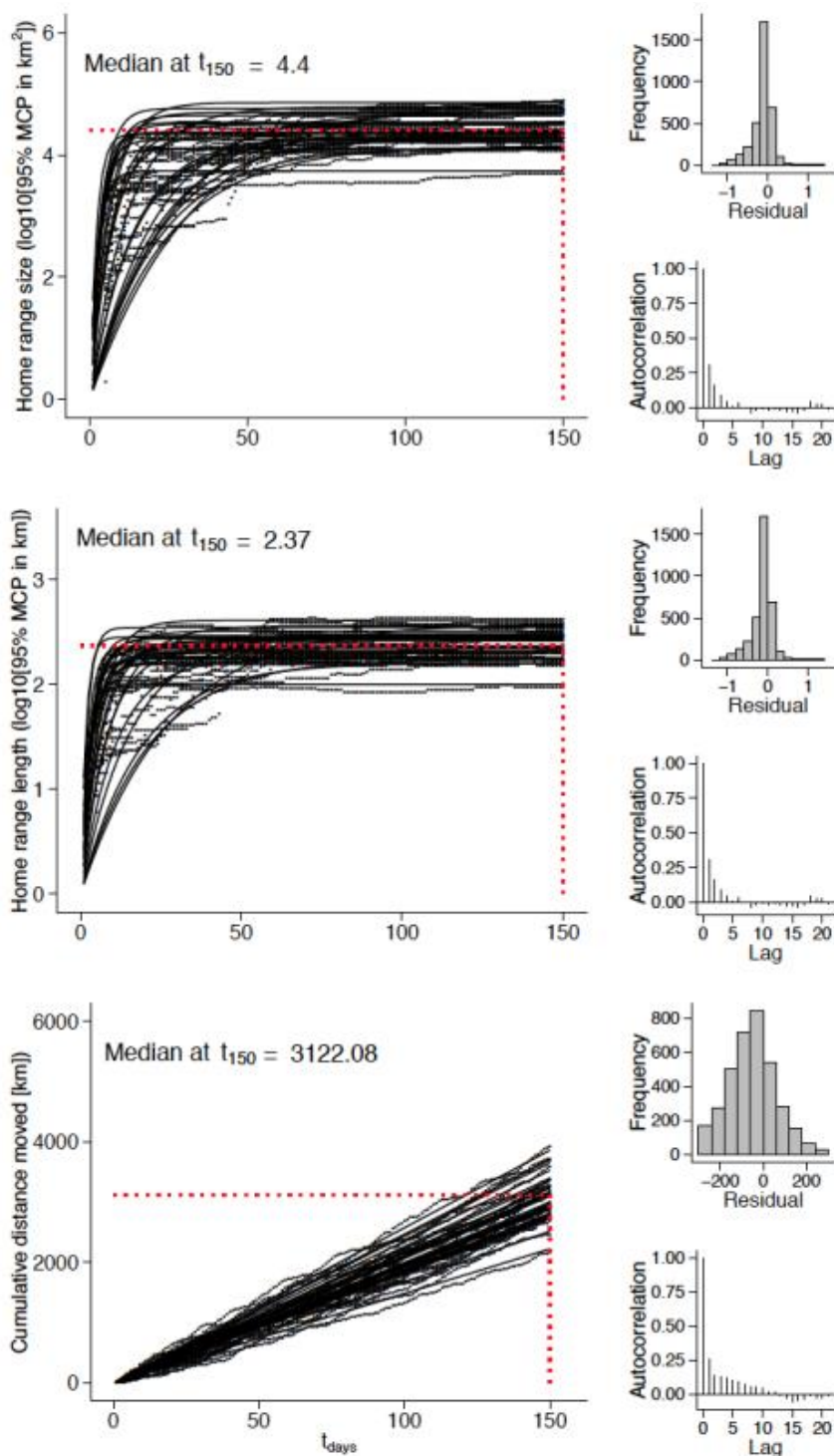
Figure 21. Median home range size, home range length and distance moved after 150 days for 25 porpoise agents. Simulations were based on parameter values provided in Table 2.

Cumulative distance moved over time was quantified with a linear mixed model forced through the origin. Here t was both a fixed and random effect and porpoise ID was included as an additional random effect. Again, we included the corCAR1 autocorrelation function and the power variance weights structure to t_d to ensure the

validity of the model residuals. All statistical analyses were performed in the package nlme (Pinheiro et al. 2016) within R (R Development Core Team 2016).

For each of the three statistical models, we extracted the median predicted value at day 150 (t_{150}; Figure 20), which were set as the target values in the POM procedure. This procedure consisted on running simulations corresponding to all different combinations of the parameters d_{disp}, *PSM_angle* and *PSM_dist* and calculating home range size, home range length and distance moved after day 150 for each combination. Figure 21 shows the value of these statistics for the best fitting combination of the three parameters (correspondence between statistic based on simulated and satellite-tracked animals shown in Figure 10).

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