

TRACE document

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

DEPONS 2.0

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

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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.....	3
2	Model description.....	4
2.1	Purpose.....	5
2.2	Entities, state variables, and scales	6
2.3	Process overview and scheduling.....	6
2.4	Design concepts	7
2.5	Initialization	9
2.6	Input data.....	10
2.7	Submodels	12
3	Data evaluation.....	20
3.1	Parameters and data related to animal life history and energetics	21
3.2	Parameters and data related to animal movements and response to noise	23
3.3	Parameters controlling general model behavior.....	36
4	Conceptual model evaluation.....	39
4.1	Assumptions regarding fine-scale movements.....	39
4.2	Assumptions regarding effects of noise	40
4.3	Use of constant vital rates	40
4.4	Assumptions regarding energetics	40
4.5	Assumptions regarding large-scale movements.....	41
5	Implementation verification.....	41
5.1	Testing the fine-scale movement model and reactions to noise.....	42
5.2	Testing the large-scale movement model.....	43
5.3	Testing population dynamics	43
6	Model output verification.....	45
6.1	Types of model output	45
6.2	Comparison of model output and observations.....	46
7	Model analysis	46
7.1	Sensitivity analysis.....	47
7.2	Tests of emergence.....	50
8	Model output corroboration	51
9	Literature cited.....	53
	List of figures.....	58
	Changes in DEPONS version 2.0	59

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 version 2.0 of an agent-based model, the DEPONS model, and demonstrate how it can be used 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 anthropogenic disturbances on marine populations is therefore 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, also 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 such EIAs of the cumulative impacts of human activities and for spatial planning to ensure that offshore activities affect populations as little as possible.

The model, termed DEPONS, links the dynamics of marine populations directly to the individuals' response to noise. Noise travels 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. In the model, population dynamics emerge from the individuals' competition for a dynamically replenishing food resource and from

altered movements and reduced foraging success when noise is present. The model was calibrated to assess the impacts of noise from pile-driving of wind turbine foundations on harbor porpoises (*Phocoena phocoena*) in the North Sea. The species is listed on the EU Habitats Directive Annexes II and IV, and as pile-driving noise has been observed to affect porpoises at distances >20 km (Tougaard et al. 2009; Brandt et al. 2011) it is critical to understand this type of noise will influence the population. Population densities and the time it takes the population to recover after pile-driving ends can be measured either locally or for the entire population.

The model takes a data-driven, mechanistic approach to management of marine populations. Although it is currently parameterized for assessing effects of wind farm construction on the North Sea harbor porpoise population it is based on general principles of population regulation and resource availability (Sinclair 2003; Goss-Custard et al. 2006). This is likely to cause the model to generate robust predictions for a wide range of environmental conditions (Grimm & Railsback 2005; Stillman et al. 2015), and to make it suitable for other populations and species.

Although the model is likely to be robust to variations in environmental conditions, it should be noted that it was parameterized for the North Sea harbor porpoise 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.

DEPONS version 2.0 differs from the previous version (version 1.1; used by Nabe-Nielsen et al. 2018) in several ways: (1) fine-scale movement patterns are calibrated based on harbor porpoise tracking data collected in the North Sea, (2) the animals' response to noise have been re-calibrated after updating their fine-scale movements, and (3) a their large-scale movement behavior has re-calibrated to ensure that home ranges and movement tracks still resembled those of real animals.

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 DEPONS 2.0. The model extends previous models for simulating impacts of anthropogenic disturbances on harbor porpoise populations (Nabe-Nielsen et al. 2014, 2018). The model description follows the updated ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2010). It includes an overview of the underlying fine-scale movement model, a description of how simulated animals respond to noise and a description of the mechanisms that control

their large-scale movements. The model, which was implemented in Repast Symphony 2.5 (<http://repast.sourceforge.net>), is open-source and published under the [GNU General Public License v2](#). It can be downloaded from <https://doi.org/10.5281/zenodo.2544525>.

Section contents

2.1 Purpose	5
2.2 Entities, state variables, and scales	6
2.3 Process overview and scheduling	6
2.4 Design concepts	7
2.4.1 Basic principles	7
2.4.2 Emergence	8
2.4.3 Adaptation	8
2.4.4 Objectives	8
2.4.5 Learning	8
2.4.6 Prediction	8
2.4.7 Sensing	8
2.4.8 Interaction	9
2.4.9 Stochasticity	9
2.4.10 Collectives	9
2.4.11 Observation	9
2.5 Initialization	9
2.6 Input data	10
2.7 Submodels	12
2.7.1 Porpoises detect noise	12
2.7.2 Large-scale movements	14
2.7.3 Fine-scale movements	17
2.7.4 Update energy level and mortality	18
2.7.5 Update food distribution map	19
2.7.6 Update salinity map	19
Every month a new sea surface salinity map is loaded. The map enables fine-scale movements to depend on local salinity conditions (Figure 1).	19
2.7.7 Update patch energy level	19
2.7.8 Calculate mating dates	19
2.7.9 Daily tasks	20
2.7.10 Update residual deterrence	20

2.1 Purpose

The model simulates how harbor porpoise population dynamics are affected by pile-driving noise emitted during 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 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 movement mode. Each porpoise agent is a ‘super individual’ (Scheffer et al. 1995) representing several real-world female porpoises. Wind turbine agents are characterized by their location, noise source level, start time and end time for their construction.

Simulations are by default based on an $835.2 \text{ km} \times 870 \text{ km}$ landscape covering the North Sea. The landscape is divided into 2088×2175 grid cells, each covering $400 \text{ m} \times 400 \text{ m}$, and into cell groups covering $2 \text{ km} \times 2 \text{ km}$. 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 areas where they have been before when using large-scale movements. Grid cells are characterized by their coordinates, water depth, sea surface salinity, food level, maximum food level, distance to land and by whether they are used as food patches or not. The default 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. The food level is 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, 2014), i.e. it included on average 1000 food patches per $100 \text{ km} \times 100 \text{ km}$. 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 half-hour time steps and simulations typically cover 50 years. At the beginning of each time step [porpoises detect noise](#) originating from active pile-driving operations. This permits animals 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 and a threshold sound level below which they do not react to noise.

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 are deterred by 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 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 using [large-scale movements](#) to move towards more profitable areas (cell groups).

Food is only found in the food patches, which are randomly distributed across the landscape. 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 level increases logarithmically 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 the food they encountered.

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 food distribution map (Figure 1) is updated at the end of each season, i.e. on day 60, 150, 240 and 330 (the model assumes 30 days per month).

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. 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 (Nabe-Nielsen et al. 2013b). The animals' energy budgets are 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 fine-scale movement behavior to increase food intake and fitness when they have not found food in the recent past. The size of the animals' home ranges emerges from their experience of the profitability of different parts of the landscape, which guides their large-scale movements. The animals' spatial distribution emerges from their tendency to move towards more profitable parts of the landscape when using large-scale movements and from elevated mortality in unprofitable areas. Their age class distribution emerges from their starvation-related mortality.

The rate at which local porpoise densities recover after a pile-driving operations end emerge 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 using large-scale movements. Their choice between these three alternatives depends on their energetic state and their success finding food in the area they were displaced to.

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 moving 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 moving towards more profitable areas using large-scale movements when the fine-scale movements do not enable them to sustain their energy levels.

2.4.5 Learning: Animals do not learn from what other individuals 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 energy intake rate experienced in all cell groups they have visited since they were born, so they gradually learn about the profitability of different parts of the landscape. This guides their large-scale movement behavior. The animals learn/inherit a map of the profitability and location of previously visited cell groups from their mother before entering the model as independent individuals.

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 sense when their energy levels decrease, which causes them to start using large-scale movements and to be more likely to abandon their lactating calves or 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 porpoise 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 (corresponding to areas defined in 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 is by default initialized by creating 10,000 randomly distributed porpoise agents. Their age-class distribution corresponds to that of stranded and by-caught animals (Lockyer & Kinze 2003), and 68% of the adults in the model are pregnant (parameter h in [Table 1](#)). The initial values for the animals’ energy levels, E_p , are drawn from a normal distribution with mean 10 and standard deviation one (parameter E_{init}). Mating date (t_{mating}) is a random normal variable with mean 225 and standard deviation 20. Simulations start on 1 January 1981. The North Sea wind-farm construction scenarios include 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/Sea_ergy_2020.pdf). The food levels in the patches are initially set to the location specific maximum food levels for 1 January.

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 and enables the user to 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.

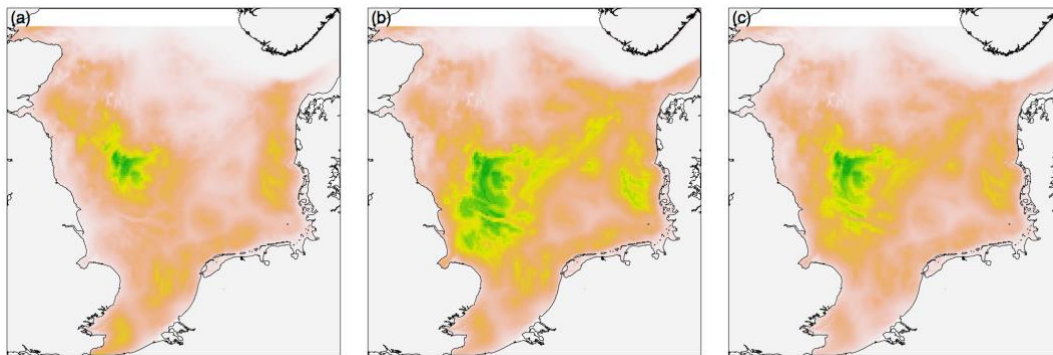


Figure 1. Food distribution maps derived from seasonal maps of porpoise densities in the North Sea for (a) spring, (b) summer, and (c) autumn (Gilles et al. 2016). Green shows areas with high porpoise densities, grey shows land and white indicates missing data. No porpoise density map was available for the winter, so the map from the autumn was used instead.

2.6 Input data

Six different kinds of background maps are used in the model: The maximum amount of food in each food patch was derived from maps 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 $400\text{ m} \times 400\text{ m}$, one for each season (Figure 1). There is no food 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 data on porpoise densities for the winter season, the map from the autumn season is used instead. 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). Five additional types of raster data 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), a ‘blocks’ file that makes it possible to count the number of porpoises in user defined areas, and twelve different ‘salinity’ files, one for each month. The salinity data were derived from the Forecasting Ocean Assimilation Model 7 km Atlantic Margin model (FOAM AMM7) as part of the Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu>).

Simulations include details about pile-driving events. These are provided in a tab separated ‘wind-farms’ text file with columns id (identifier; missing values allowed), 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, only integer values accepted). Noise is emitted during both the start and the end time step. The sound source level is 234 dB SEL in the default North Sea pile-driving scenarios, corresponding to the value calculated for the Gemini wind farm (see the [Submodels](#) section for details on calculation of noise source levels and how noise from wind turbine agents was represented in the model).

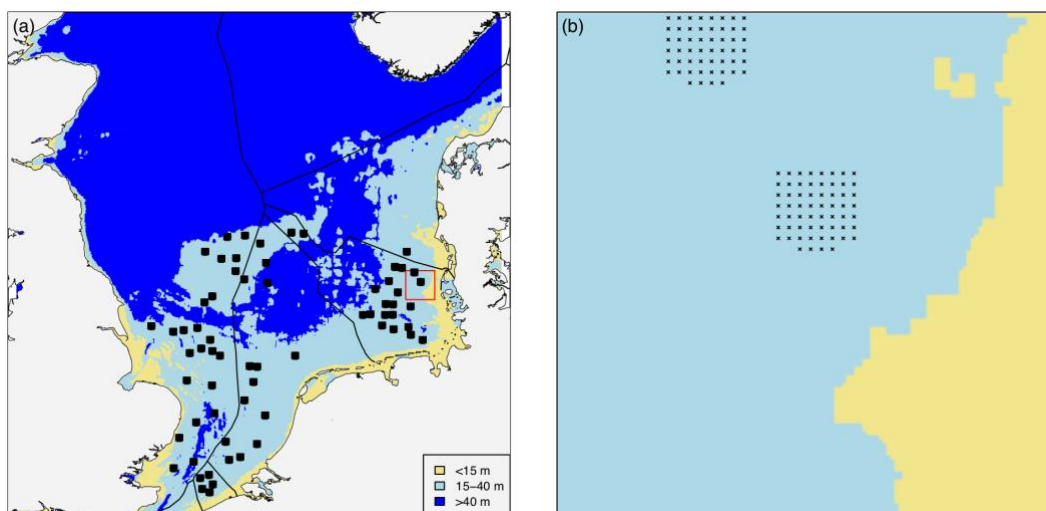


Figure 2. Positions of wind turbines in the three pile-driving scenarios used in this study. The red square on (a) indicates the 50 km × 50 km area shown in greater detail in (b).

Three different scenarios are included to allow users to investigate population effects of wind farm construction in the North Sea. These were the scenarios used by Nabe-Nielsen et al. (2018). All scenarios include 65 wind farms with the same spatial distribution (Figure 2). The number of wind farms per country is the same in all scenarios (Denmark: 1 wind farm; Germany: 21; Netherlands: 14; Belgium: 5; UK: 24), which is the number of wind farms that would enable 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, at the same locations in all North Sea scenarios. Each wind farm includes 60 wind turbines distributed in a regular 1078 m x 1078 m grid. 6 MW turbines constructed with monopile foundations was assumed throughout. Turbines are installed using pile-driving, and installation of a single foundation takes two hours. No noise mitigation or soft start is included in the scenarios. The turbines are constructed in the 10-year period starting 1 January 2011, with 6–7 farms being built per year. In Scenario 1 (called “Random, slow” in Nabe-Nielsen et al. 2018), the parks are constructed in random order, in Scenario 2 (“Ordered, slow”) the parks in the eastern North Sea are built first, followed by the ones in the western North Sea (starting in the north in each area). In Scenario 3 (“Random, fast”) parks are constructed in the same order as in Scenario 1, but the time between individual pilings within the wind farms is halved (from 48 hours to 24 hours). The start time of the first pilings in the different wind farms is the same in scenarios 1 and 3.

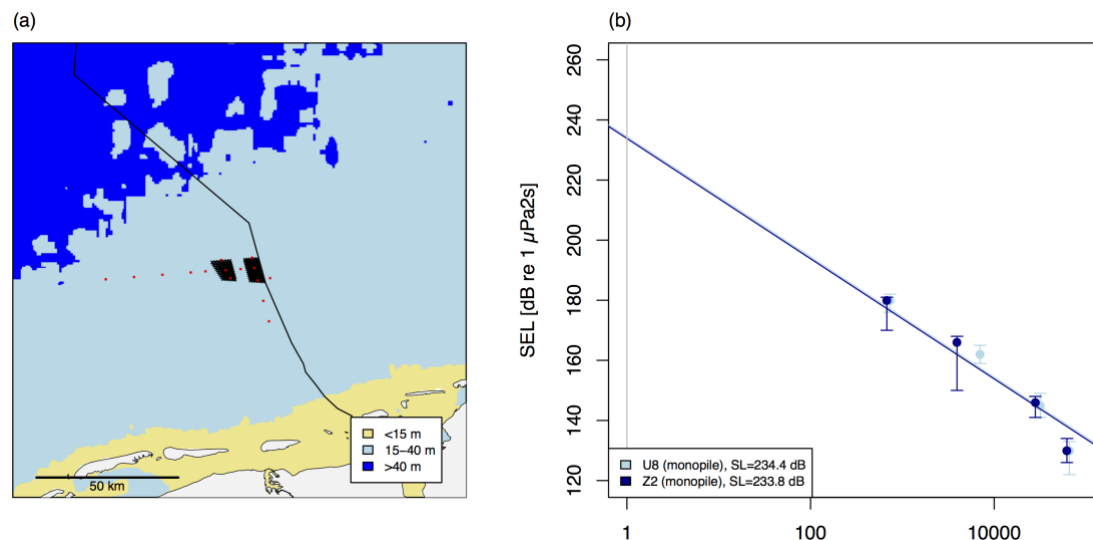


Figure 3. Data from the Gemini wind farm construction site used for calibration of the porpoises' response to noise. (a) Virtual landscape including wind turbine construction sites (black dots) and CPODs (red dots). The black line shows the border to Germany. (b) Received sound levels recorded using hydrophones at different distances [m] from two pilings. Sound source levels (SL) and sound transmissions were calculated assuming spherical spreading of sound.

A different landscape, combined with a different set of simulated 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). SEL provides a measure of the energy transmitted by one single blow expressed as a level. The energy is normalized to a time of one second. 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, 2018).

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

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

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

$$\text{dist}_{\max} = 10^{(SL - T) / 20} \quad \text{Eqn. A2}$$

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

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

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.

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.

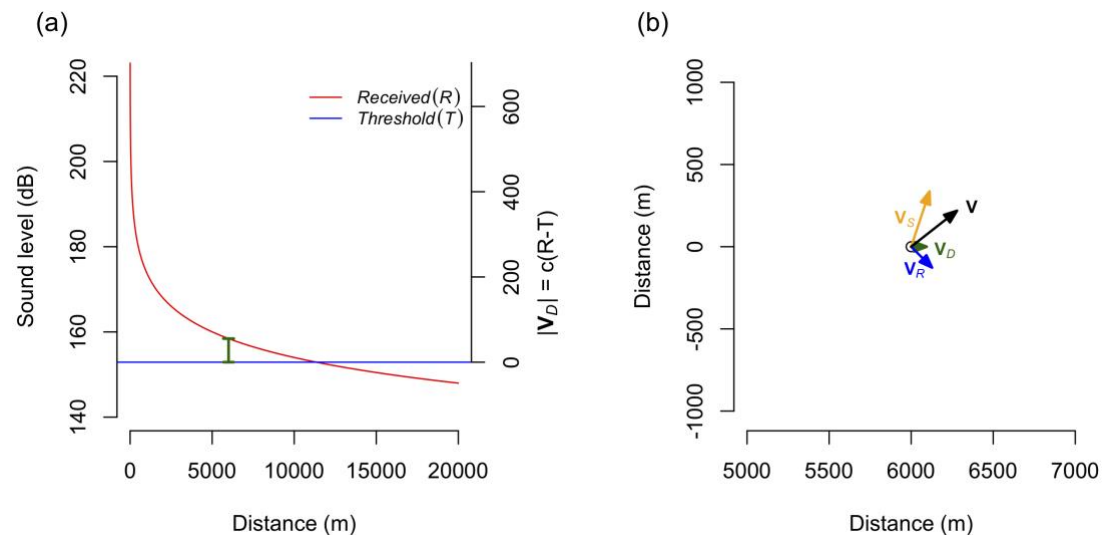


Figure 4. Relationship between received sound level (R) and deterrence behavior in the model. (a) Decrease in R with distance assuming spherical spreading of pile-driving noise and source levels as observed in Gemini (wind farm constructed without noise mitigation; $SL=234$ dB SEL). The green bar shows 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. Here $\text{dist}_{\max}=11350$ m. (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 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)=152.9 dB SEL.

2.7.2 Large-scale movements

We distinguish large-scale movements from the fine-scale movements described in section 2.7.3. In each time step porpoises take either a large-scale movement step or a fine-scale movement step depending on their movement mode (updated in the submodel '[Life history processes](#)').

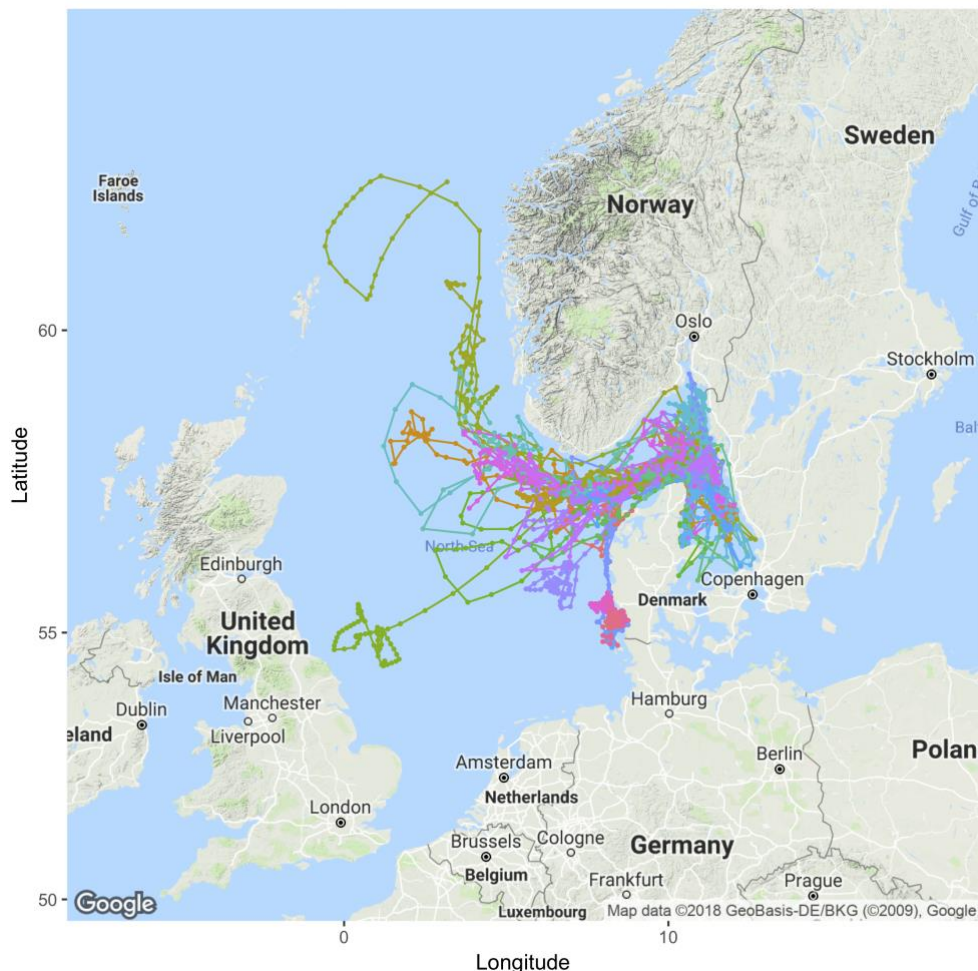


Figure 5. Tracks of 34 free-ranging porpoises equipped with ARGOS satellite tags. Six animals were tagged by Rømø (southern Denmark), the rest were tagged by Skagen (northern Denmark). Tracks were interpolated to one position per day using a state-space model. Each track includes 100 positions.

Animals that use large-scale movements are guided by a persistent spatial memory (PSM) of the energy intake rates they have achieved in each of the different parts (cell groups) of the landscape they have visited since they were 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 large-scale

movements 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.

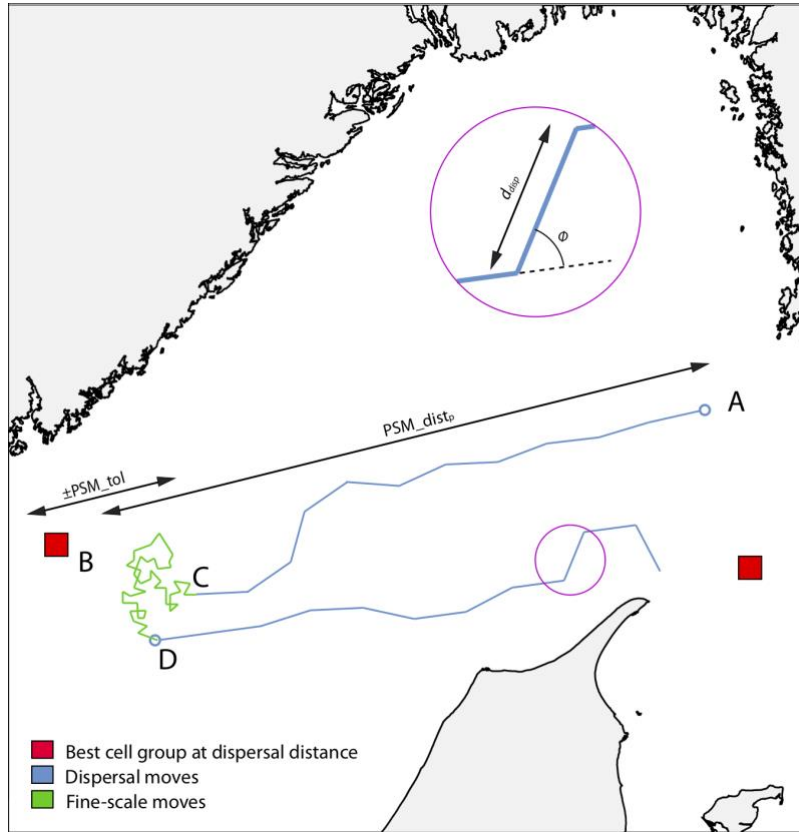


Figure 6. Memory-based large-scale movement behavior used in DEPONS 2.0. (A) When starting to use this behavior, porpoises move towards the most profitable $2 \text{ km} \times 2 \text{ km}$ cell group (B) in the preferred distance (PSM_dist_p). The distance from A to B is d_{target} . All large-scale moves have the length d_{disp} and the total distance moved in a particular large-scale movement event is d_{cum} . After each large-scale move, the porpoise makes a random turn Φ . The turning angle increases the further the porpoise has moved from the starting point. The animal switches to using fine-scale moves when $d_{cum} = 0.95 \times d_{target}$ (at point C), but it may start using large-scale movements again at a later point (D).

2.7.2.1 PSM-Type2

The PSM large-scale movement behavior used in DEPONS 1.1 and 2.0 is labeled PSM-Type2. Animals switch from using fine-scale to large-scale movements when their energy levels have been decreasing for t_{todisp} days (following Nabe-Nielsen et al. 2014). All large-scale moves have the length d_{disp} (Figure 6).

To enable animals to use PSM movements, the entire landscape is divided into $2 \text{ km} \times 2 \text{ km}$ cell groups. When animals start using PSM-Type2 large-scale movements, they turn towards the center of the most profitable cell group at the preferred distance ($PSM_dist_p \pm PSM_tol$, see Table 2), i.e. the group where they have previously obtained the highest energy intake rates (calculated as total amount of food eaten divided time spent in each cell group). The distance to the center of this cell group is d_{target} . Initially, PSM_dist_p is drawn from a normal distribution for each animal, but calves subsequently inherit the preferred distance from their mothers. Animals that

have visited <50 cell groups move towards a random cell group at the preferred distance (burn-in behavior). Turning angles Φ between consecutive steps increase logistically,

$$\Phi = PSM_angle \cdot \omega_2 / (1 + e^{-z/PSM_log}) \quad \text{Eqn. A4}$$

where ω_2 is a random number in the range $[-1; 1]$ and z is determined by

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

Here d_{cum} is the cumulated distance moved using in the current large-scale movement event, 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).

Animals stop using large-scale movements (a) once the cumulated distance moved is $0.95 \times d_{target}$, (b) if the next step would have caused them to move to an area with water depth $< w_{disp}$ or (c) across the border of the landscape, or (d) if their daily average energy levels increase to a level that is higher than any of the daily energy levels they have experienced over the previous seven days, or (e) if they move into an area with high noise levels (where $R > T$).

New independent calves inherit their mothers' preferred large-scale movement distances (PSM_dist), as well as the knowledge about the relative profitability of different parts of the landscape. See [Section 3.2.4](#) for details regarding calibration of parameters.

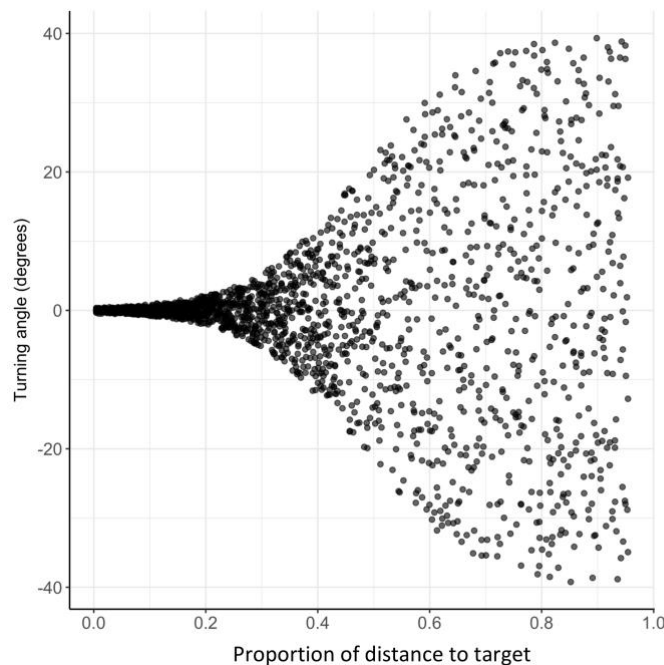


Figure 7. Simulated change in turning angle distribution as porpoise agents approach the target cell group while using PSM-Type2 large-scale movements. In this example, PSM_angle was set to 40 and PSM_log to 0.5. Each dot represents a large-scale move (1987 steps within 26 distinct large-scale movement events). Angles are larger for animals that have moved a larger proportion of the initial distance to their targets.

2.7.2.2 Undirected movements

DEPONS 2.0 also includes a simple large-scale movement behavior, where each step is of length d_{disp} and turning angles between subsequent steps are drawn at random in the range $[-\text{PSM_angle}/2; \text{PSM_angle}/2]$. The first step is taken in a random direction. This movement behavior cannot be calibrated to produce home ranges that resemble those of North Sea animals, but has been included as a simple null model. Conditions for turning this behavior on and off are the same as for PSM-Type2.

2.7.3 Fine-scale movements

All animals that are not using large-scale movements take a fine-scale move in each time step. This usually causes animals to move straight through the food patches they encounter.

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 (Figure 4b). The CRW behavior introduces a positive correlation between the lengths of consecutive steps and a negative correlation between consecutive turning angles. Here the CRW component of the fine-scale move is

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

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 (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 length of vector \mathbf{x} depends on the length of the previous step, water depth, and salinity,

$$\delta_t = R_1 + a_0 \delta_{t-1} + a_1 w_{t-1} + a_2 s_{t-1} \quad \text{Eqn. A7}$$

where the length of $\mathbf{x} = 100 \times 10^\delta$ and R_1 is a random normal variable, following Nabe-Nielsen et al. (2013b), and w_{t-1} and s_{t-1} are water depth and sea surface salinity at the end of the previous time step, respectively. The dependence of δ on salinity and water depth was introduced in DEPONS 2.0 to reproduce the fine-scale movements observed for free-ranging animals in the North Sea (van Beest et al. 2018a).

The vector \mathbf{x} also allows turning angles to depend on the turning angle at the end of the previous step, bathymetry and salinity. This is done in two steps, where the autocorrelation in turning angles Φ is calculated first

$$\Phi_t^* = R_2 + b_0 \Phi_{t-1} \quad \text{Eqn. A8}$$

and their dependence on bathymetry and salinity is calculated in a second step,

$$\Phi_t = \Phi_t^* (b_1 w_{t-1} + b_2 s_{t-1} + b_3) \quad \text{Eqn. A9}$$

The parameters $a_0, a_1, a_2, b_0, b_1, b_2$ and b_3 are new to DEPONS 2.0 (see [Table 2](#)).

Fine-scale movements, in contrast to large-scale movements, are guided by a gradually decreasing memory of the 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

$$\mathbf{V}_M = \sum M[c] \mathbf{i}[c] \quad \text{Eqn. A10}$$

where M is a measure of the amount of food that an 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 animals' memory of previously visited patches decrease 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 \mathbf{V}_D 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

$$\mathbf{V}^* = \frac{\mathbf{V}_M + \mathbf{V}_S + \mathbf{V}_D}{\|\mathbf{V}_M + \mathbf{V}_S + \mathbf{V}_D\|} \times \|\mathbf{V}_S\| \quad \text{Eqn. A11}$$

This equation is equivalent to Eqn. A2 of Nabe-Nielsen et al. (2014). In Eqn. A11 \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 ($40^\circ, 70^\circ, 120^\circ$ 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

$$s_y = 1 - e^{-\beta E_p} \quad \text{Eqn. A12}$$

which is subsequently converted to a per-step survival probability

$$s_s = e^{\log(s_y)/(360 \times 48)} \quad \text{Eqn. A13}$$

If ω_1 is a random number in the range 0–1 and the animal is lactating, the calf is abandoned if $\omega_1 > s_s$ (lactating calves do not appear as independent individuals in the model). If $\omega_1 > s_s$ and the animal is not lactating, it dies (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 330), 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). This is derived from season-specific maps of porpoise densities in the North Sea (Gilles et al. 2016). The spatial distribution of food patches remains constant.

2.7.6 Update salinity map

Every month a new sea surface salinity map is loaded. The map enables fine-scale movements to depend on local salinity conditions (Figure 1).

2.7.7 Update patch energy level

Takes place every day.

$$E_c[t+1] = E_c[t] + r_U \times E_c[t] (1 - E_c[t] / M_c[t]) \quad \text{Eqn. A14}$$

where r_U is the food replenishment rate, $E_c[t]$ is the food level in patch c at time t and $M_c[t]$ is the maximum amount of food in each patch. The equation is equivalent to Eqn. 3 of Nabe-Nielsen et al. (2013).

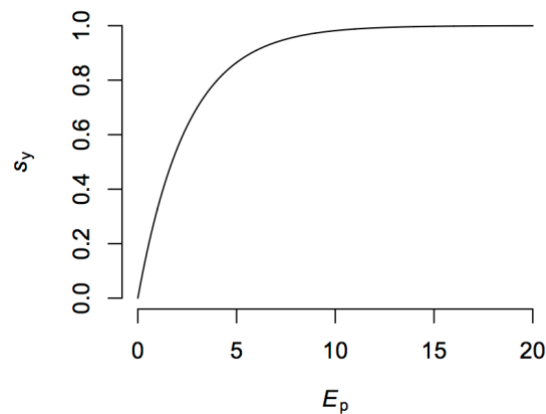


Figure 8. Relationship between energy level and yearly mortality for $\beta=0.4$.

2.7.8 Calculate mating dates

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

2.7.9 Daily tasks

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

Update each animal's movement mode based on its daily average energy level. Animals start using large-scale movements when their energy levels have decreased for t_{disp} 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.

2.7.10 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

$$|\mathbf{V}_D|_{t+1} = |\mathbf{V}_D|_t (100 - \psi_{deter}) / 100 \quad \text{Eqn. A15}$$

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 back 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 are 49 parameters in version 2.0 of DEPONS, all of which can be specified by the user. Thirteen are related to animal life history and energetics, 26 are related to animal movement and reactions to noise, and 10 are related to general model behavior (specification of input and output files etc.). Three of the parameters related to animal movement

and reactions to noise are not used by default, but maintained to increase model flexibility and facilitate easy re-parameterization for other applications. The 39 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 large-scale movements were calibrated following a pattern-oriented modeling approach.

Section contents

3.1 Parameters and data related to animal life history and energetics	21
3.2 Parameters and data related to animal movements and response to noise	23
3.2.1 Parameters related to fine-scale movements	23
3.2.2 CRW component of fine-scale movements	25
3.2.3 Spatial memory component of fine-scale movements	28
3.2.4 Parameters related to large-scale movements	30
3.2.5 Parameters related to response to noise	33
3.3 Parameters controlling general model behavior	36

3.1 Parameters and data related to animal life history and energetics

The processes and parameters related to birth and death of animals and to how animal survival is determined by energetic status are identical to the ones in the models described in Nabe-Nielsen et al. (2014, 2018).

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 whether it depends 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. A12](#)). 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). The value of r_U was calibrated to ensure that the population reached a stable 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	tmature	Age of maturity [years] (Read 1990).
t_{mating}	N(225, 20)	tmating	Mating day [day of year] (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]

Parameter	Standard value	Code name	Description [units] (reference)
			(calibrated, Nabe-Nielsen et al. 2014).
E_{init}	N(10, 1)	Einit	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	Umin	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 DEPONS 2.0 related to simulation of fine-scale movements extend the model described by Nabe-Nielsen et al. (2013b, 2014, 2018) by allowing turning angles and step lengths to depend on bathymetry and salinity, which are the main environmental drivers of fine scale movements of porpoises in the North Sea (van Beest et al 2018a; see [Section 2.7.3 for details](#)). Fine-scale movements are influenced by the first 13 parameters in Table 2.

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 (van Beest et al. 2018a). The CRW is specified using the parameters a_x , b_x , R_1 , and R_2 , where R_x provide mean and standard deviation in distance moved per step and in turning angles. 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.

Parameter	Standard value	Code name	Description [units] (reference)
r_S	0.04	rS	Satiation memory decay rate [unitless] (defined in Nabe-Nielsen et al. 2013b; re-calibrated in this study).
r_R	0.04	rR	Reference memory decay rate [unitless] (defined in Nabe-Nielsen et al. 2013b; re-calibrated in this study).
k	0.001	k	Inertia constant; the animal's tendency to keep moving using CRW irrespective of foraging success [unitless] (arbitrary).
a_0	0.35	a	Autoregressive coefficient for $\log_{10}(d/100)$, where d is distance per CRW move [unitless] (calibrated based on van Beest et al. 2018a).
a_1	0.0005		Coefficient indicating effect of water depth on $\log_{10}(d/100)$ [unitless] (van Beest et al. 2018a).
a_2	-0.02		Coefficient indicating effect of salinity on $\log_{10}(d/100)$ [unitless] (van Beest et al. 2018a).
b_0	-0.024	b	Autoregressive coefficient for turning angles in CRW [unitless] (van Beest et al. 2018a).
b_1	-0.008		Coefficient indicating effect of water depth on turning angles in CRW [unitless] (van Beest et al. 2018a).
b_2	0.93		Coefficient indicating effect of salinity on turning angles in CRW [unitless] (van Beest et al. 2018a).
b_3	-14		Intercept from regression of turning angle on salinity and bathymetry [unitless] (van Beest et al. 2018a).
R_1	N(1.25, 0.15)	R1	Mean and standard deviation in $\log_{10}(d/100)$, where d is distance moved per time step [m] (van Beest et al. 2018a).
R_2	N(0, 4)	R2	Variation in turning angle between steps [degrees] (van Beest et al. 2018a).
$d_{maxmove}$	1.73	dmax_mov	Maximum value of $\log_{10}(d/100)$ while using fine-scale moves. Here d is distance moved per time step [m] (van Beest et al. 2018a).
d_{disp}	1.05	ddisp	Distance moved per time step while using large-scale movements [km] (from Argos data; this study).
t_{10disp}	3	tdisp	Time before onset of large-scale movement [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	PSM_angle	Maximum absolute turning angle after each persistent spatial memory (PSM) large-scale move [degrees] (calibrated as part of this TRACE document).
PSM_dist	N(300, 100)	PSM_dist	Distance to target when initiating PSM moves [km] (calibrated in Nabe-Nielsen et al. 2018).
PSM_log	0.6	PSM_log	Parameter controlling logistic increase in turning angle

Parameter	Standard value	Code name	Description [units] (reference)
			during large-scale movement [unitless] (arbitrary).
PSM_{tol}	5	PSM_tol	Tolerance band within which the target cell group is selected ($PSM_{dist} \pm PSM_{tol}$) [km] when initializing PSM behavior (Nabe-Nielsen et al. 2018).
w_{disp}	4	wdisp	Minimum water depth while using large-scale movement [m] (Nabe-Nielsen et al. 2014).
w_{min}	1	wmin	Minimum water depth [m] required by porpoises (J. Tougaard, pers. obs).
T	152.9	RT	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).
d_{max_deter}	1000	dmax_deter	Maximum deterrence distance [km]. Enables user to introduce distance limit for response to noise.
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	Psi_deter	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, 2018), 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 do not influence simulations when default values are used.

3.2.2 CRW component of fine-scale movements

Real porpoises’ tendency to zig-zag and their speed while doing so can be influenced by local environmental conditions. In DEPONS this behavior is simulated using CRW movements. In DEPONS 2.0 the animals’ CRW movements have been calibrated based on data from a six animals equipped with V-tags in two areas of the Danish North Sea (van Beest et al. 2018a). The animals were observed in a wide range of environments, spanning from shallow near-shore areas to some of the deepest parts of the North Sea (Figure 9a). Their movements are therefore likely to be representative for animals in other parts of the North Sea as well, although a larger sample size is needed to fully understand how porpoise movements are related to environmental conditions in different parts of the North Sea.

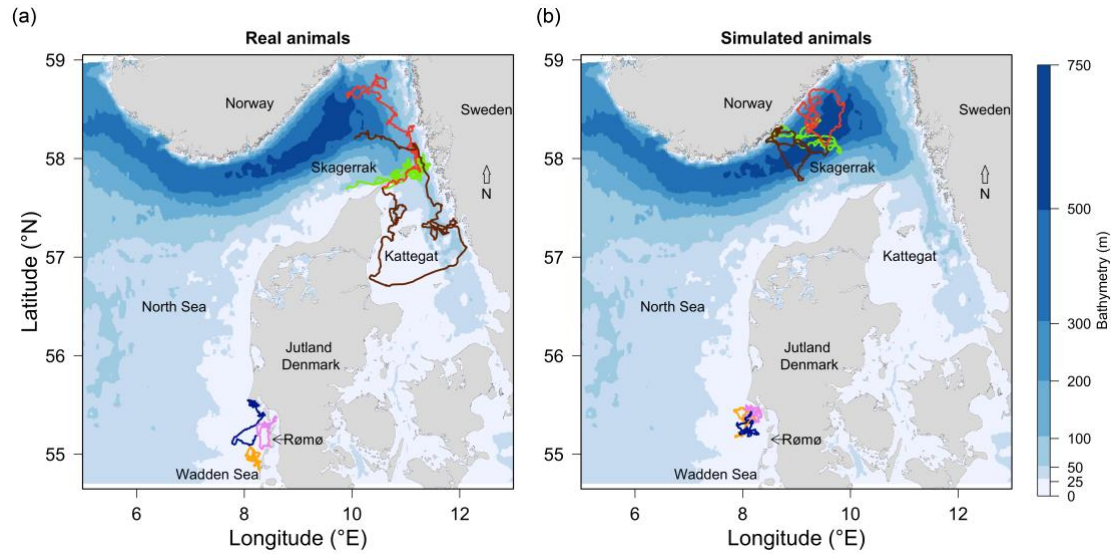


Figure 9. Movement tracks of 2 weeks used for calibration of fine-scale movements (a) from six animals equipped with V-tags and (b) tracks from six simulated animals released in the areas where the real animals were tagged. Differences in background color indicate water depth [m].

Speed and absolute turning angles between consecutive 30-minute steps are mostly related to variations in salinity and bathymetry for real porpoises in the eastern part of the North Sea (van Beest et al. 2018a). The CRW movements of the simulated animals were therefore allowed to be influenced by these two variables in DEPONS 2.0 to ensure that simulated animals could respond to environmental variation in the same way as North Sea animals (Eqns. A7–A9). To do so we used pattern-oriented modeling (POM; Grimm et al. 2005; Kramer-Schadt et al. 2007; Hartig et al. 2011) to calibrate CRW movements to reproduce the speed and turning angle distributions observed for real porpoises (Figure 10), as well as the dependence of these variables on salinity and bathymetry (Figures 11–12). During the POM process we simulated multiple movement tracks where parameters controlling fine-scale movements ($a_0, a_1, a_2, b_0, b_1, b_2, b_3, R_2$) were changed step-by-step and iteratively until we found the optimal parameter value combination. Fine-scale movement parameters R_1 and $d_{maxmove}$ were not calibrated but taken directly from van Beest et al. (2018a). All simulations were run in the North Sea landscape using a population size of 100 and a simulation period of one year. In each simulation we tracked the movements of six simulated animals that had the same starting positions as the real animals. Simulated animals were only allowed to use CRW behavior (large-scale movements and spatial memory behavior were turned off; the latter was done by setting r_s to 0.02 and r_R to 1). For each simulated movement dataset, we calculated speed and absolute turning angles between consecutive locations using the R-package *adehabitatLT* (Calenge 2006). Simulated movement data were analyzed exactly as in van Beest et al (2018a) using generalized least square linear regression (GLS) models constructed in the R package “nlme” (Pinheiro et al. 2015). The beta coefficients and autoregressive coefficients from each GLS on simulated data were compared to those obtained from GLS analyses on empirical data. We iteratively adjusted the parameter values until the simulated movement tracks (Figure 9), frequency distributions (Figure 10), and all GLS coefficients and autocorrelation values for both speed and turning angle analyses

(Figures 11 and 12) were nearly identical to the corresponding values for wild animals (up to 2 decimals behind the comma).

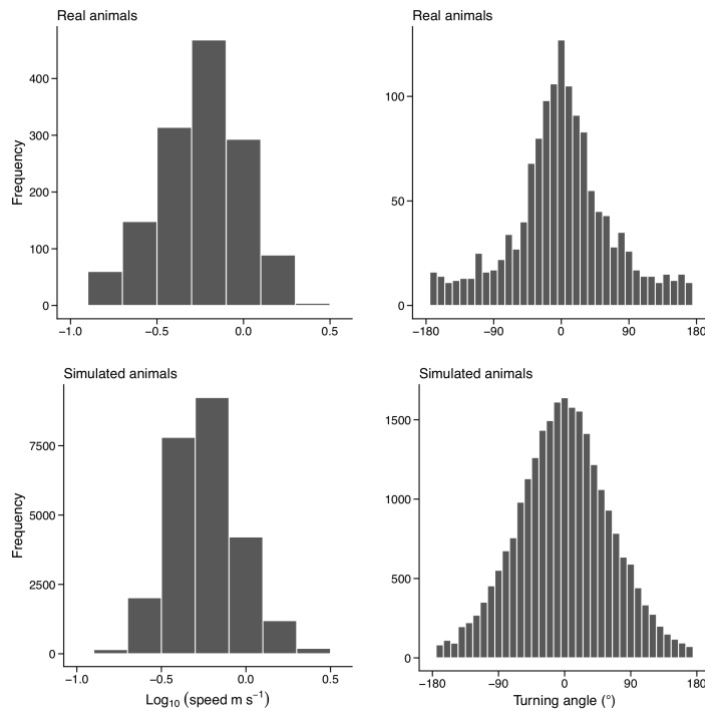


Figure 10. Histograms of $\log_{10}(\text{speed m s}^{-1})$ and turning angles ($^{\circ}$) between consecutive locations taken at 30-minute intervals for six real and six simulated animals. Histograms for simulated animals were produced after calibration of the CRW movement parameters, with spatial memory turned off.

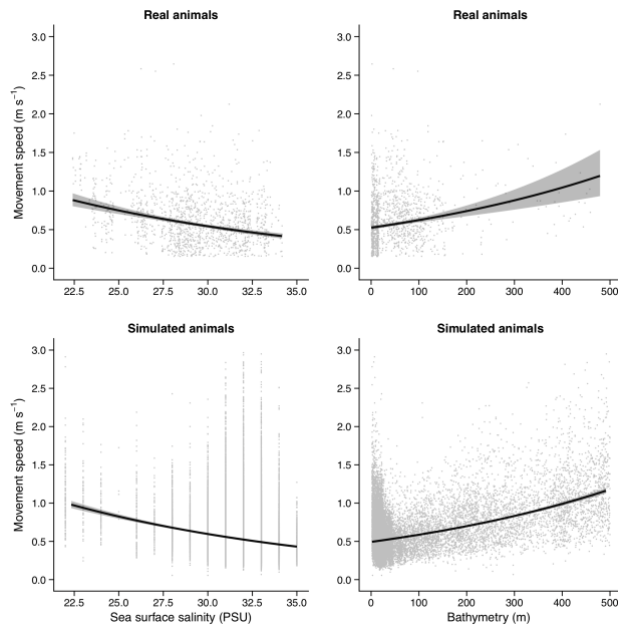


Figure 11. Effects of salinity and bathymetry on movement speed (m s^{-1}) between consecutive locations taken at 30-minute intervals for real and simulated animals. Black lines show the back-transformed (from \log_{10} scale) marginal (population-level) effects as predicted by generalized least square linear regressions; shaded areas indicate 95% CIs.

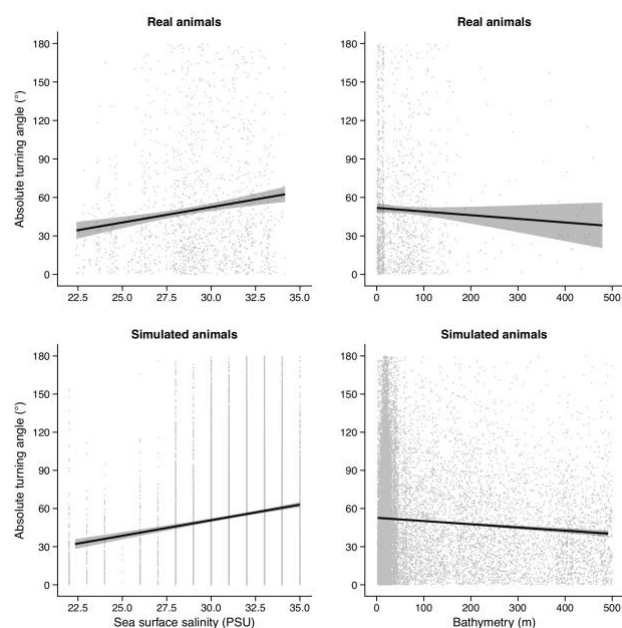


Figure 12. Effects of salinity and bathymetry on absolute turning angles ($^{\circ}$) between consecutive locations taken at 30-minute intervals for real and simulated animals. Black lines show the marginal (population-level) effect as predicted by generalized least square linear regression; shaded areas indicate 95% CIs.

3.2.3 Spatial memory component of fine-scale movements

Real animals tend to stay in the same area for several days or weeks. To enable simulated animals' to produce similar area-concentrated fine-scale movements, they were equipped with a spatial memory of where they have found food in the past. 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.

In DEPONS 2.0 the parameters r_S and r_R were re-calibrated using POM to ensure that simulated animals developed movement tracks that resembled those of 34 satellite-tracked porpoises from Skagerrak and the North Sea (Figure 5) and that they had the same home range size, net squared displacement and residence times (Figure 13). The V-tag data that were used for calibration of fine-scale movements could not be used for calibrating r_S and r_R as V-tags are unable to store data from a sufficient number of days to enable spatial memory movements to emerge. Movement data for the satellite-tagged porpoises included one location per day for 30 days, and the parts of the track that could be characterized as large-scale movements were removed prior to analyses. To do so, large scale-movements were identified using a Bayesian state-space switching model (SSSM) specifically developed to detect switches in movement modes (i.e. fine vs. large-scale movements, also termed area-restricted search and transient behaviour) while accounting for uncertainty in the Argos positional estimates (sensu Jonsen et al. 2005). We fitted the Bayesian SSSM using the R

package “bsam” (Jonsen 2016). With this approach two chains (movement modes) are fitted in parallel and estimated jointly for all individuals based on variation in speed and turning angles. We allowed a burn-in of 60 000 samples per chain and generated 40 000 samples thinned by every 20th sample to remove autocorrelation. Using only fine-scale movement data as identified through the SSSM, i.e. the parts of the tracks where animals did not use large-scale movements, we calculated the kernel home range size (km^2) for each 30-day satellite-track using the *href* smoothing method in the R package *adehabitatHR* (Calenge 2006). The net squared displacement was calculated by taking the mean of the squared distance moved between each location and its starting location (km^2), and residence time (days) was calculated by taking the mean time spent in a circle with radius of 5 km across all locations in a 30 day period (Barraquand & Benhamou 2008; Nabe-Nielsen et al. 2013b).

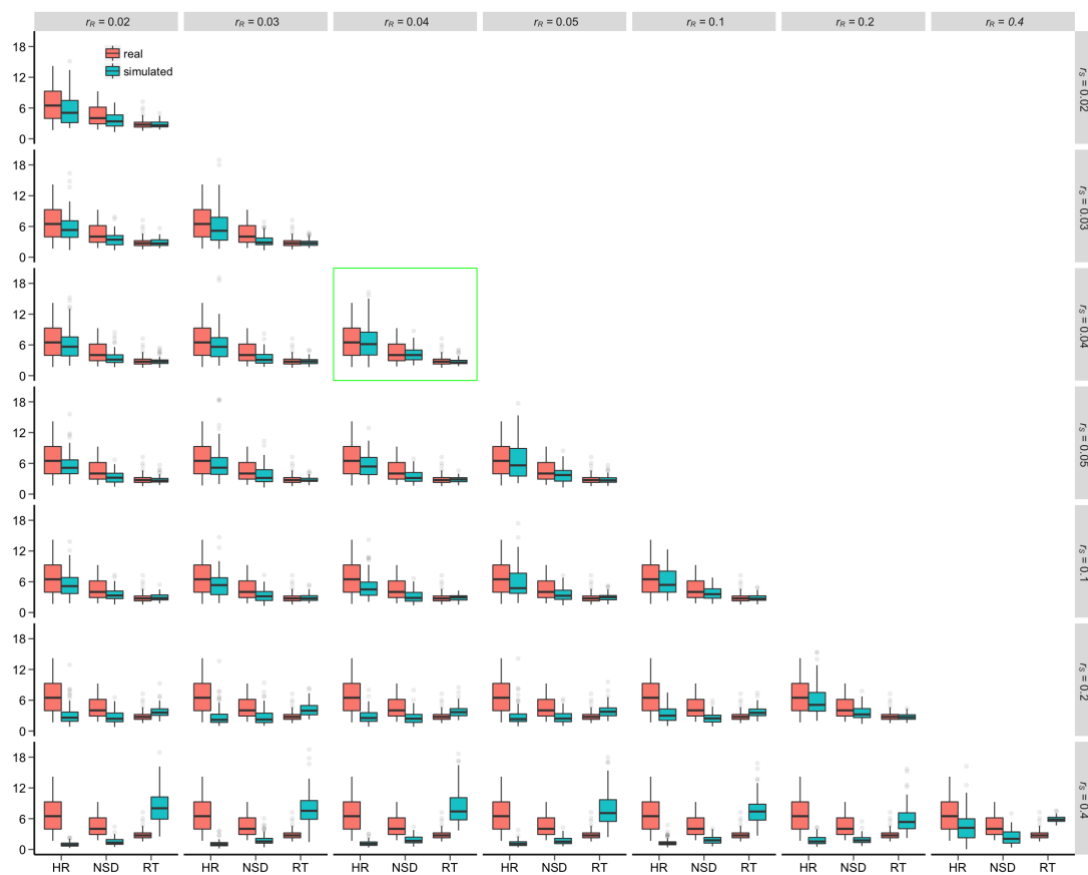


Figure 13. Parameterization of spatial memory component of fine-scale movements, i.e. the parameters r_S and r_R . The y-axis shows home range size (HR; $\text{km}^2 / 1000$), net squared displacement (NSD; $\text{km}^2 / 10$) and residence times (RT; days) for real and simulated animals ($N = 34$ for each group). The panel outlined in green highlights the combination of r_S and r_R values (both 0.04) that produced patterns (mean and variance) that best resembled those based on real animals.

To calibrate the animals’ spatial memory parameters, we simulated multiple movement tracks using a range of values for r_S and r_R to find the parameter value combination that caused home range size, net squared displacement and residence times to simultaneously resemble those of real animals. All simulations were run in the North Sea landscape, with a population size of 10 000 and for a 6-year period,

using the first 5 years as a burn in period to allow simulated animals to develop a spatial memory of profitable patches and to aggregate in areas with sufficient food. We tracked the movements of 34 simulated animals that had the same starting positions as the real animals tracked in the North Sea. Large-scale movements for simulated animals were allowed (using default large-scale movement from DEPONS 1.1) and the parameters controlling CRW movements were set to their default values as calibrated based on North Sea animals (Table 2). Each simulated movement track was subsampled to have one location per day (at noon) for 30 days (as for the satellite-tracked porpoises), and we removed all locations where agents were in large-scale movement mode. We then calculated home range size, net squared displacement and residence times exactly as we did for the real animals, based on the parts of the tracks where animals did not use large-scale movements. Visual inspection of the results revealed that a value of 0.04 for both r_s and r_R resulted in home range sizes, net squared displacement and residence times that corresponded most closely to those observed for real animals (Figure 13).

The animals' fine-scale movements are not only influenced by the movement-related parameters but also by the spatial distribution of food patches and the amount of food in these patches. In the current study the maximum amount of food in the patches was modeled based on porpoise survey data from the North Sea (Gilles et al. 2016), which suggested high food availability in the western-central part of the North Sea (see [Figure 1](#)). The spatial distribution of the patches, i.e. the size of the patches and the distance between them, was random (following Nabe-Nielsen et al. 2013b, 2018). 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 the fine scale movements should be calibrated based on realistic food distribution maps to enable realistic variations in the simulated animals' fine scale movements.

3.2.4 Parameters related to large-scale movements

Large-scale movements are by default modeled based on a persistent spatial memory (PSM) behavior that enables animals to navigate back to the $2 \text{ km} \times 2 \text{ km}$ cell group where they have previously obtained the highest energy intake rate and that is located at their preferred large-scale movement distance. The six parameters used for controlling large-scale movements are listed in [Table 2](#). In DEPONS 2.0, large-scale movements have been re-calibrated after calibrating the animals' fine-scale movements to resemble those of North Sea animals.

The value of the parameter d_{disp} (distance moved per large-scale move) has been obtained directly from the movements of the 34 satellite-tracked porpoises that were also used for calibrating the spatial memory component of fine-scale movements (see section 3.2.3). After classifying different portions of these tracks as either fine-scale or large-scale movements using an SSSM, d_{disp} was obtained as the average distance moved per 30 min for animals using large-scale moves. To find the optimal values of the parameters PSM_angle (maximum turning angle after each large-scale move) and PSM_dist (preferred large-scale movement distance) we simulated animal movements based on a range of parameter values. The aim was to make simulated tracks resemble those of the satellite-tracked porpoises as closely as possible, after resampling both datasets to one position per day for 100 days. For PSM_angle we evaluated the resemblance for the values 20° , 40° and 60° , and for PSM_dist we considered mean

values in the range 150–350 km (in increments of 50 km). For standard deviation in *PSM_dist* a random value of 100 was selected (arbitrary value). All possible combinations of *PSM_angle* and *PSM_dist* were tested. For each combination we recorded the movements of 34 porpoise agents over an 11-year period. All simulations were run in the North Sea landscape, with a population size of 10 000 and for a 11-year period, using the first 10 years as a burn in period to allow simulated animals to develop a spatial memory of profitable cell groups. All agents were initialized at Skagen (northern Denmark), which was where the satellite-tracked animals were tagged.

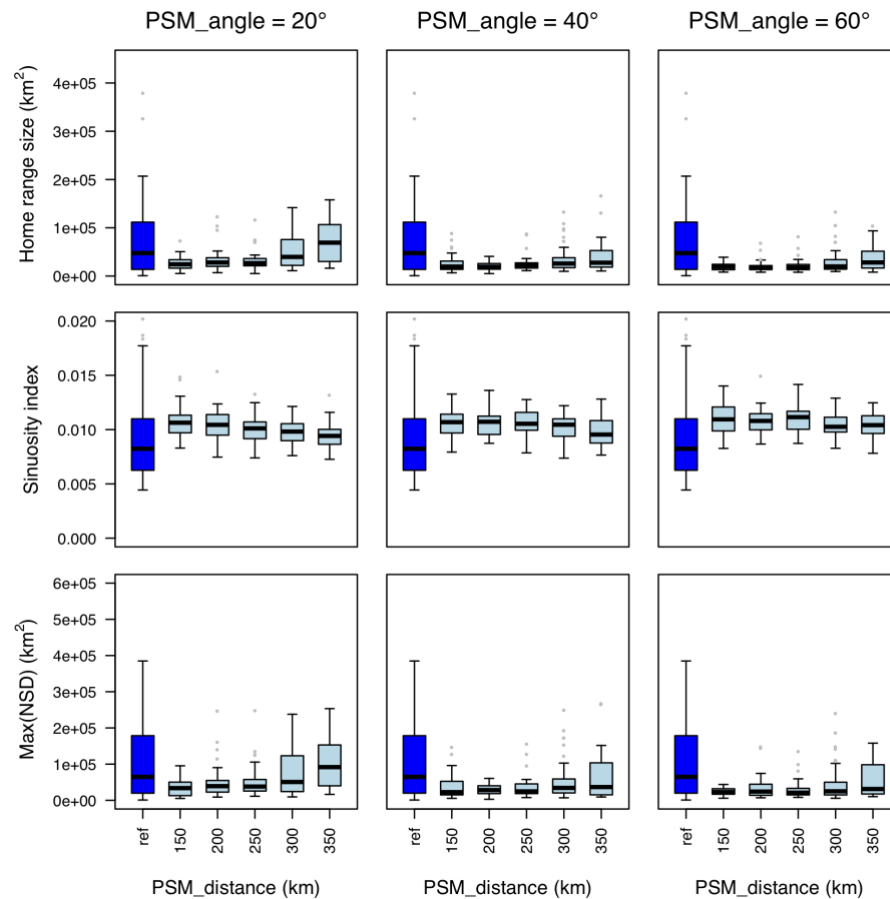


Figure 14. Parameterization of *PSM_dist* and *PSM_angle* in the PSM-Type2 long-distance movement behavior. Track statistics calculated based on satellite-tracked animals are labeled ‘ref’. *PSM_dist* is composed of a mean and a standard deviation that jointly determine the distance that animals prefer to move when using PSM_Type2; the figure is based on tracks simulated with *PSM_dist* standard deviation set to 100. NSD means net squared displacement. The best correspondence between tracks of simulated and wild animals was obtained for a *PSM_dist* of 300 km and *SPM_angle* of 20°.

We compared the tracks of simulated animals with those of satellite-tracked animals based on three statistics: home range sizes, maximum net squared displacement (Max(NSD)) and track tortuosity (as measured using the sinuosity index; Benhamou 2004). The three statistics were calculated based on the first 100 daily positions for each track, irrespective of the animals’ movement mode. We calculated the kernel home range size (km²) for each 100-day satellite-track based on both fine-scale and large-scale movement data, using the *href* smoothing method in the R package

adehabitatHR (Calenge 2006). Max(NSD) was calculated as the maximum distance between the different positions in the track and the start of the track, squared. For each track statistic the median values for the 34 satellite-tracked animals were compared to the corresponding median values for 34 simulated animals.

The track statistics of simulated animals corresponded closely to those of satellite-tracked porpoises for a PSM_dist value of 300 km, combined with a PSM_angle value of 20° (Figure 14). The movement tracks of simulated animals (Figure 15) also resemble those of satellite-tracked porpoises (Figure 5) relatively closely, although the satellite-tracked animals appear to occasionally disperse very far, into areas that are not included in the simulation landscape.

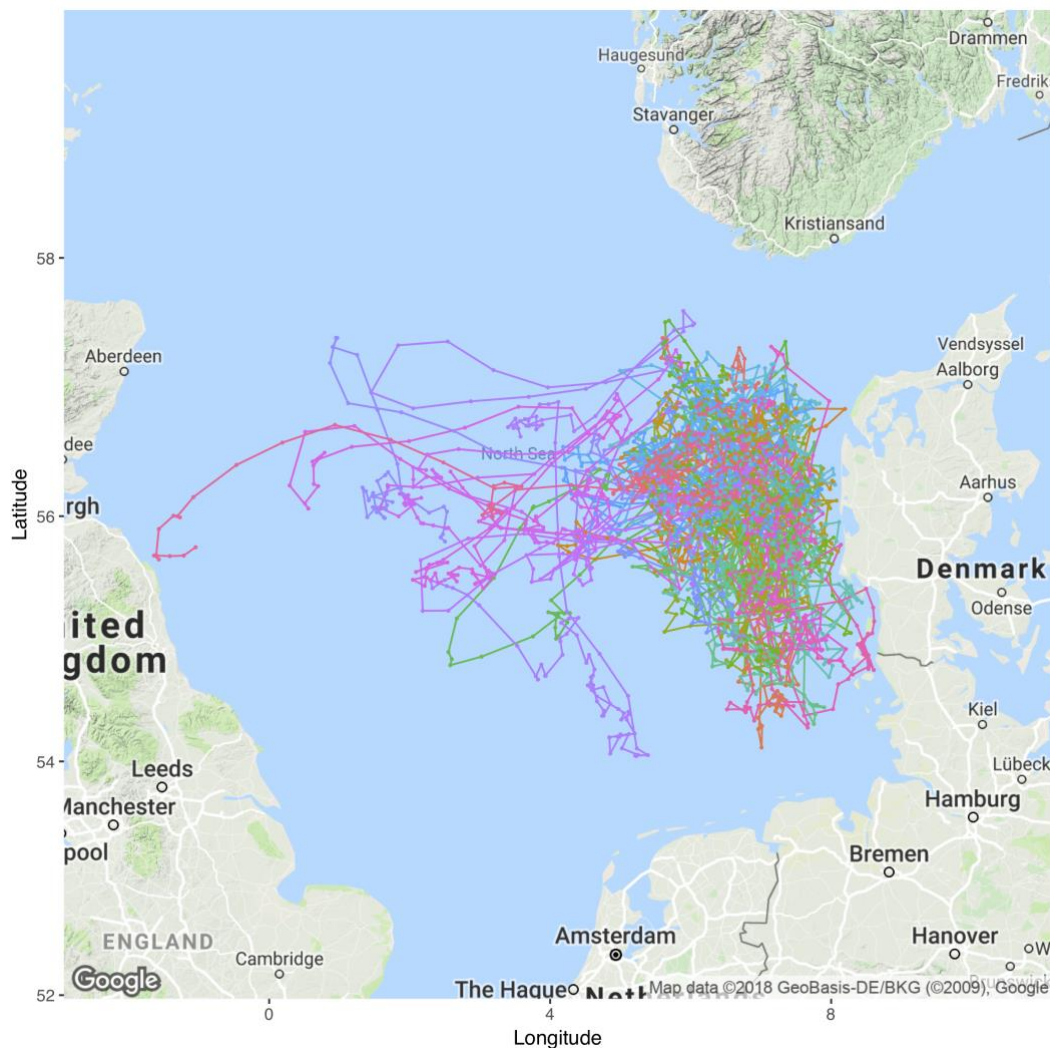


Figure 15. Daily movements of 34 simulated porpoises using the values of PSM_dist and PSM_angle that best enabled them to produce home range sizes, track tortuosity and net squared displacements that best resembled real animals.

The parameter PSM_tol , which defines the tolerance band within which a porpoise agent should find the most profitable PSM-cell when starting to use large-scale movements, was 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 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 closer they were to their target. For this parameter an arbitrary value was used, but visual inspection of the tracks suggested that these were not strongly influenced by the choice of PSM_{log} . The movement statistics were also relatively insensitive to the choice of PSM_{log} .

The parameter t_{todisp} determines the number of days with decreasing average energy levels before the animal starts using large-scale movements. 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 move towards more profitable foraging areas. The parameter w_{disp} determines the minimum depth at which porpoises were allowed to use large-scale movements. The value was visually assessed based on satellite-tracking data.

The parameters used for defining large-scale movements in this study are not necessarily suitable for other geographic regions. Two of the parameters were obtained through inverse parameterization (using POM) 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 home ranges than the ones observed for free-ranging animals. Animals may also be influenced by other environmental conditions than proximity to land, which could cause them to move differently in other parts of the North Sea and elsewhere (other prey species, presence of predators etc.). Unpublished data for satellite-tracked porpoises reveal that porpoises move over larger distances 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 large-scale movements](#)'.

3.2.5 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. d_{max_deter} determines the maximum distance at which porpoises can be influenced by noise (irrespective of noise level), t_{deter} and ψ_{deter} jointly determine the 'residual deterrence', i.e. the animals' tendency to move away from an area for some time after the noise has stopped.

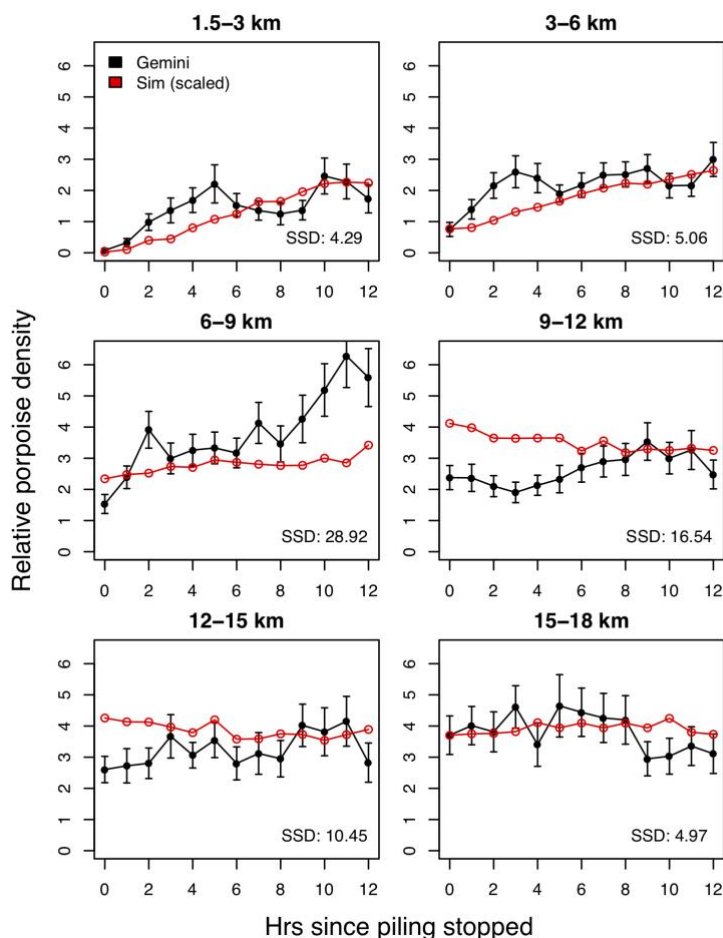


Figure 16. Recovery of porpoise densities after end of pile-driving. Black lines show changes in porpoise densities (mean % porpoise positive minutes \pm 1 SE) at different distances from closest pile-driving in the Gemini wind farm. The red lines show the corresponding relative number of porpoises in simulations based on $c=0.07$ and $T=152.9$ 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 16; 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, large-scale movements were turned off. We ran simulations using a range of parameter combinations (c in the range 0.00–0.15 and T in the range 151–156 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 minimized the sum of the squared differences 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

$$\epsilon(c, T) = \sum_{d,t} (n_{d,t}(c, T) - p_{d,t})^2 = \sum_d SSD_d \quad \text{Eqn. A16}$$

where 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 16.

The smallest value of ε was obtained for $T=152.9$ dB SEL and $c=0.07$ (Figure 17). In Figure 17, ε is referred to as ‘Sum of Squares Deviation’.

The parameter $d_{\text{max_deter}}$ 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 $d_{\text{max_deter}}$ 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 $d_{\text{max_deter}}$ makes it possible to ensure that simulated animals are only deterred out to a certain distance, irrespective of the noise level. When $d_{\text{max_deter}}$ is set to 1000 km (default), the parameter has no impact on the simulated animals’ response to noise, as this is far beyond the area where $R > T$ (see Figure 4).

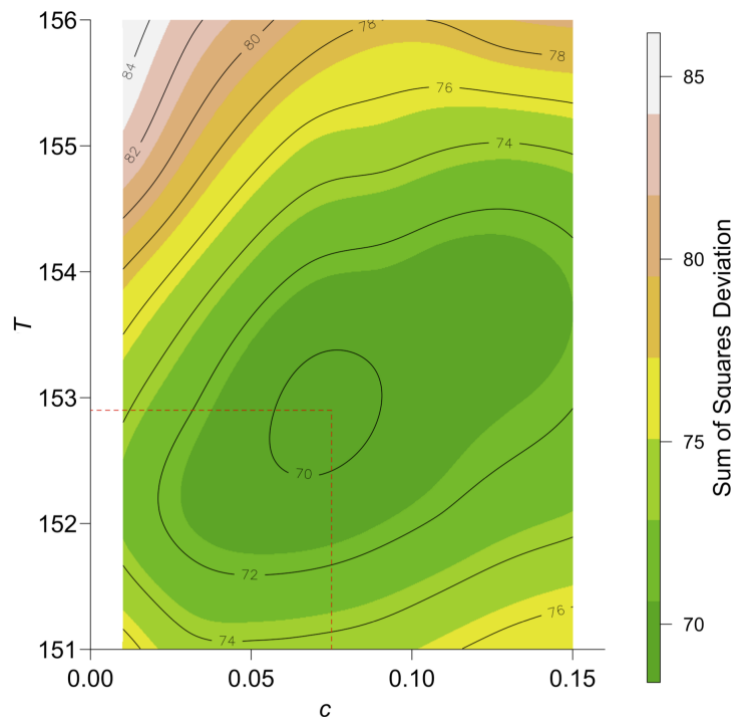


Figure 17. Calibration of c and T using pattern-oriented modeling. The target was to find values of c and T that enabled the model to produce porpoise recovery rates that resembled those observed at different distances from real pile-driving. This was obtained for $c=0.07$ and $T=152.9$ (red dotted line).

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. 2018b). 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 6–12 km (Figure 16), 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. (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, or using 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 10 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".

Parameter	Standard value	Code name	Description [units]
Turbines	off	turbines	The wind farm construction scenario that is used in a simulation. It reads in the 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”.
PSM-Type	PSM-Type2	psmType	Controls the type of large-scale movements used by porpoises. Can take the values “off”, “PSM-Type2” and “Undirected”
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’).
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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 a model developed for simulating 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. We further discuss the assumptions related to large-scale movement behavior and reactions to noise that were introduced when extending the model 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. Fine-scale movements are influenced by the animals’ energetic status and proximity to places where they have previously found food, but they are unaffected by social behavior, animal age and whether animals are nursing or not. The movements were parameterized based on fine-scale movement data collected for six animals in two areas in the North Sea (van Beest et al. 2018a). Van Beest et al. tested whether distance moved per 30-minutes or turning angles between steps were related to a wide range of environmental variables, and found salinity and bathymetry to be most important (Figures 10 and 11). Fine-scale movements are therefore assumed only to be influenced by these two kinds of environmental variability in DEPONS 2.0[†].

[†] This contrasts with DEPONS 1.1, where fine-scale movements were assumed to be independent of environmental variability.

The values of r_R and r_S , which control the animals' short-term spatial memory, were re-calibrated based on satellite tracking data from 25 animals tagged in the eastern part of the North Sea. These are assumed to be representative for North Sea animals.

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, 2018; Dähne et al. 2013), but the only study where wild porpoises were exposed to noise did not indicate that it introduces a consistent bias to their fine-scale movements (van Beest et al. 2018b). This suggests that there is considerable variation in how porpoises respond to noise. DEPONS does not include such variability, which is hence assumed to be unimportant for population impacts of noise.

In DEPONS the parameters c and T , which control the strength of the animals' tendency to move away from noise, 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. 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 noise exposure takes place (Bejder et al. 2006). This is to some extent accounted for in DEPONS, as animals that get disturbed in an unfavorable area are more likely to get permanently displaced than 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 using a random search.

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 energetic status of individual animals, which is in turn determined by the individuals' ability to replenish energy reserves by foraging in patches with high food levels. 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 during 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; Andreassen et al. 2017).

The dynamics of the food patches is influenced by how fast food replenishes after being consumed. This is determined 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 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 DEPONS is sensible comes from the similarity of the simulated movement tracks and those of satellite-tracked animals (Nabe-Nielsen et al. 2013b). If the patch density had been too low, animals would return to the same area too rarely, causing them to develop larger home ranges than they do in nature.

4.5 Assumptions regarding large-scale movements

The large-scale movement behaviors included in DEPONS assume that animals have a persistent spatial memory (PSM) of places they have previously visited. This is supported by the satellite tracks for animals tagged by Skagen in northern Denmark, that show that porpoises have the ability to navigate back to places they have not visited for weeks or months (Figure 5). This is usually considered an indication of a spatial memory (Berger-Tal & Bar-David 2015). The tracks of the animals tagged by Skagen also suggest that North Sea porpoises move far to forage in particular areas, although it is unclear if this results from an attempt to maximize food intake. The large-scale movements that are implemented in the model assume that animals move towards the area where they have previously obtained the highest energy intake rates and that are not too far away, which could enable them to optimize their foraging behavior. Similar optimal foraging behavior has been demonstrated for several other species (e.g. Austin et al. 2004; Fagan et al. 2013). The large-scale movement behaviors in the model also build 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 the large-scale movement behavior assumes that home range sizes are influenced by the same environmental factors for simulated and free-ranging animals. This is, however, 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 ([Figure 5](#) vs. [Figure 15](#)).

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 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, the CRW component of the fine-scale behavior and the large-scale movement behaviors were not part of the NetLogo 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 movements](#)'. All aspects of the model were kept exactly as described in the original publication (Nabe-Nielsen et al. 2013b), except that the random-walk component was allowed to be influenced by salinity and bathymetry in DEPONS 2.0 (Eqns. A7–A9).

During development of the NetLogo version of the fine-scale movement model, dedicated code was used for testing the different submodels (controlled with the parameter 'debug' in the NetLogo code, see [DOI:10.5281/zenodo.53097](https://doi.org/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 (i.e. the relative contribution of V_S [Eqn. A6] and V_M [Eqn. A10]), 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 updated version of the fine-scale movement model, where turning angles and movement speed were allowed to be influenced by salinity and bathymetry, was tested and calibrated based on the North Sea landscape. Simulated tracks were inspected visually (Figure 9b) and using a wide range of movement statistics (Figures 10–12) to ensure that simulated animals behaved like real animals. In DEPONS 2.0 the part of the code controlling the animals' spatial memory while using fine-scale movements was kept as in the NetLogo version of the model.

The animals' behavioral reaction to noise was verified by checking that the length of the deterrence vector 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 18).

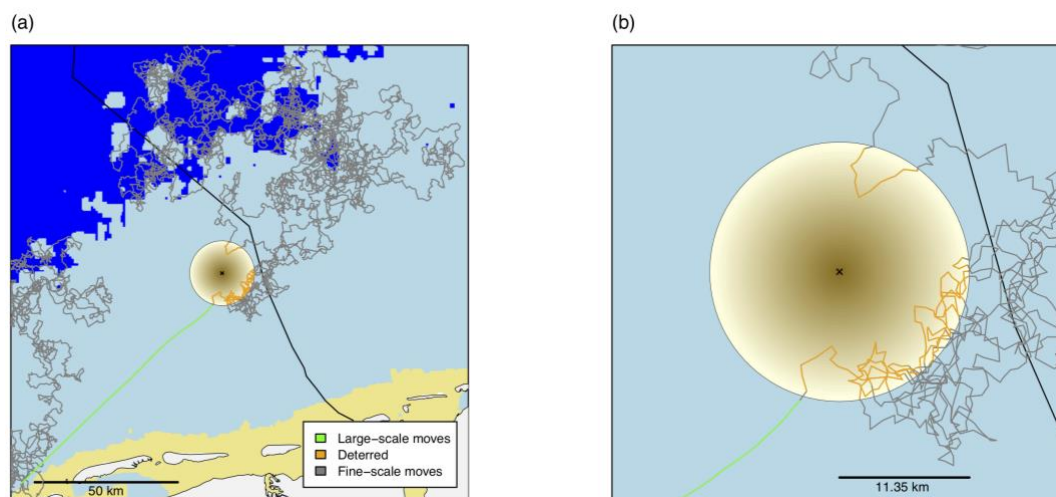


Figure 18. Porpoise movement tracks in the presence of continuous pile-driving noise. The yellow circle indicates the area where porpoises react to noise when the model is parameterized based on data from the Gemini wind farm.

5.2 Testing the large-scale movement model

The persistent spatial memory behavior (PSM-Type2), which is the default large-scale movement behavior in DEPONS 1.1 and 2.0, was developed exclusively in Repast/Java. We tested that the model produced the desired output by plotting and analyzing the movement tracks for animals using large-scale movements. 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 large-scale movement step changed as the simulated animals approached their targets while using large-scale movements (Figure 7) and by monitoring variations in step lengths and energy levels. We developed a dedicated unit test to ensure that energy intake and amount of time that porpoises spend in different 2×2 km cell groups is correct. Further, we conducted stress tests of PSM-Type3 by analyzing simulated tracks for extreme values of d_{disp} , PSM_angle , and PSM_log .

5.3 Testing population dynamics

Population dynamics were tested by inspecting how porpoise agent movements and survival were influenced by their energetic status and by analyzing relationships between the 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.

In order to test if population dynamics were fundamentally different in DEPONS 2.0 as compared to DEPONS 1.1, we ran the three North Sea wind-farm construction scenarios (see [Input data](#)) using DEPONS 2.0. In these simulations we used an unrealistically low response threshold of 127.98 dB SEL, corresponding to a response distance of 200 km, to amplify the impacts of noise and more easily observe the effect of altering the pile-driving schedule.

The results of these simulations are very similar to those obtained using DEPONS 1.1 (see Figure 3 in Nabe-Nielsen et al. 2018). When simulating the population impact of noise using a response threshold of 152.9 dB, which caused animals to change behavior up to 1.135 km from the pilings, population dynamics were indistinguishable from those in the baseline scenario (results not shown). But when using a response threshold of 127.98 dB, the population size was reduced during the 10-y wind-farm construction period. The results were qualitatively the same as those obtained using DEPONS 1.1, i.e. the impact of noise was smaller in the ‘Random, slow’ scenario than in the two other scenarios, and the population was heavily affected by noise in 2014 in the “Ordered, slow” scenario. The impacts of pile-driving were, however, slightly larger in DEPONS 2.0 than in DEPONS 1.1 for all scenarios. For example, the population was reduced by approximately 20 % in the “Random, slow” scenario in 2012 when using DEPONS 1.1, but approximately 30 % when using DEPONS 2.0.

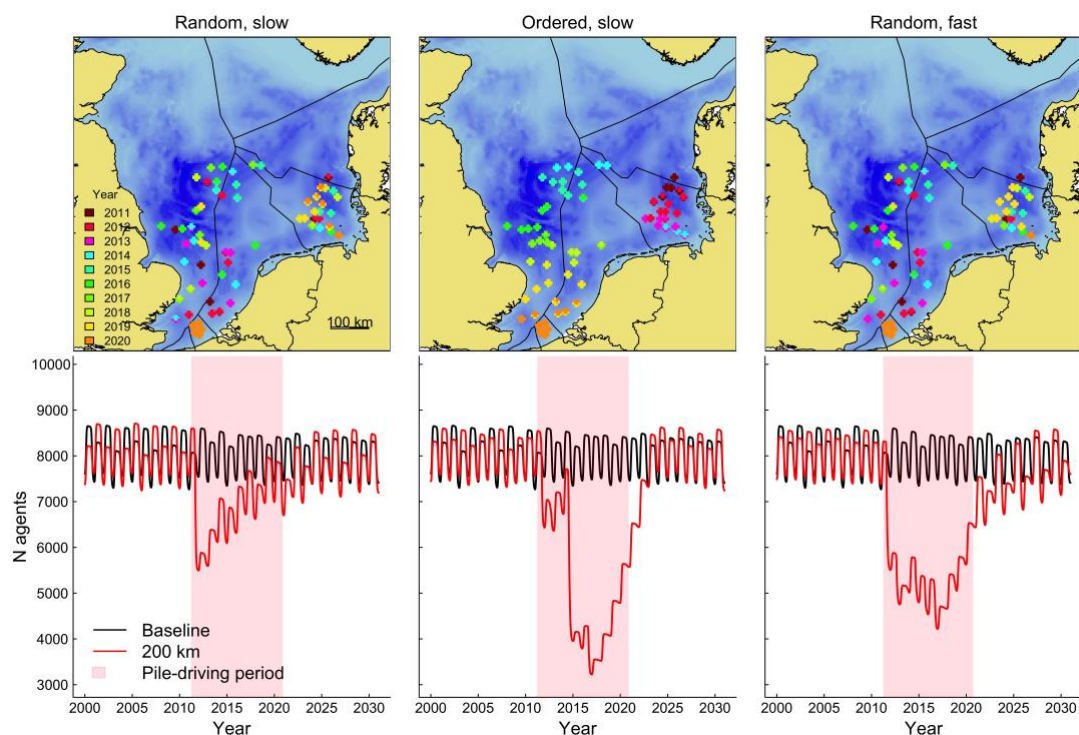


Figure 19. Population impacts of alternative wind farm construction schedules in scenarios with a response distance of 200 km, simulated using DEPONS 2.0. The number of simulated porpoises was counted in the entire North Sea landscape. Fast construction means using a short break (1 hour) between consecutive pilings. Colored dots indicate wind farms with 60 turbines each; dark blue indicates areas with high food levels. In simulations with a response distance of 1.135 km (as in the Gemini wind farm), population dynamics were indistinguishable from the baseline scenario.

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:

DEPONS is able to reproduce the fine-scale and large-scale movement patterns observed for porpoises in nature. It is 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 landscape-scale variations in population size could not be compared to field observations due to lack of data.

6.1 Types of model output

The DEPONS model writes out four 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 for each 30-min step. By default, one porpoise is tracked, but multiple agents can be tracked using the parameter `trackedPorpoiseCount`. Tracked porpoises also store their energy level, deterrence level, and position in each time step, and tracking can be delayed to omit data from the first simulation years. (4) Life-time reproductive output is saved for each porpoise agent when it dies. The age of the animal is recorded when it dies, along with the tick count at the time of death, number of calves born (both males and females), number of calves weaned (only females; males are removed from the simulation when they are weaned, assuming that 50% are males) and the type of large-scale movement used.

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 only available on a relatively rough temporal and spatial resolution for the North Sea (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 North Sea (Figures 10–12). In version 2.0 of DEPONS, the correlated random walk component of the fine-scale movement model was calibrated to ensure a close match with field data collected in the North Sea (by iteratively calibrating the parameters a_x , b_x , m , R_1 and R_2 as described in the section 3.2.1; 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, net squared displacement and residence times 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 (Barraquand & Benhamou 2008). Fine-scale movements are related to bathymetry and salinity in the North Sea (van Beest et al. 2018a), and these variables were therefore allowed to have a direct impact on the distance animals moved per step and on turning angles in DEPONS 2.0.

The recovery of relative porpoise densities after pile-driving ended resembled those observed at different distances from the Gemini wind farm during construction (Figure 16). The recovery resulted from the simulated animals' tendency to move back to known food patches after deterrence stops.

The simulated large-scale movement 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](#) for large-scale movements).

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. The analysis was conducted based on DEPONS 1.1, with fine-scale movement parameters calibrated based on data from the inner Danish waters. 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 large-scale movements in simulations without noise (Figure 20). 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 analysis was conducted based on DEPONS 1.1, with fine-scale movement parameters calibrated based on data from the inner Danish waters and PSM-Type2 large-scale movements parameterized based on North Sea animals. The results may therefore not be valid for DEPONS 2.0.

The equilibrium population size was most sensitive to variations in parameters related to energetics (2nd group of parameters in Figure 20), 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.

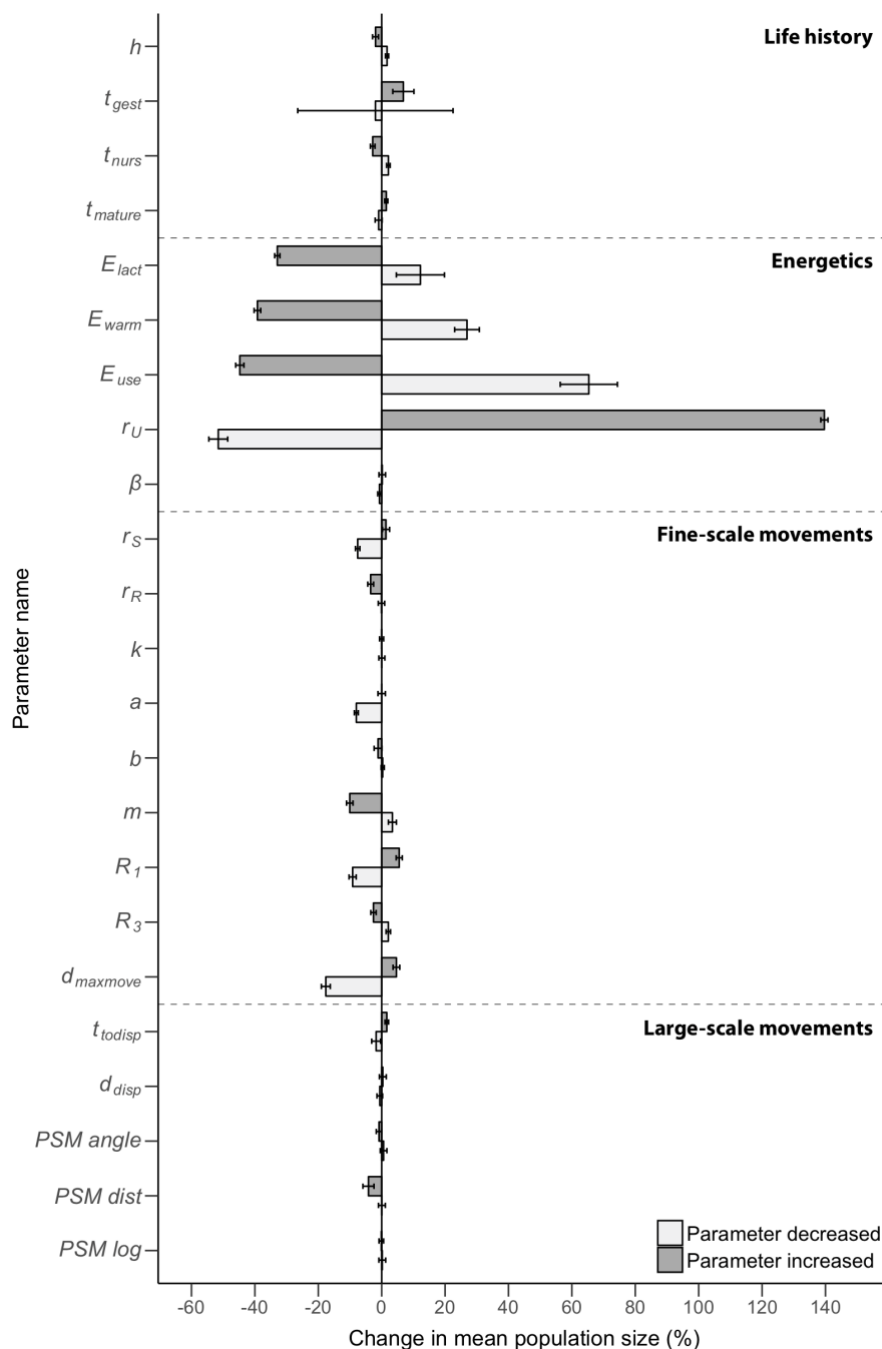


Figure 20. Sensitivity analysis for parameters related to animal life history, energetics, fine-scale movements and large-scale movements. Bars show changes in equilibrium population size when increasing or decreasing each parameter by 20% relative to its default value. Error bars show confidence intervals based on 8 replicate simulations. The analysis was based on DEPONS 1.1, which used fine-scale movements calibrated based on data from the inner Danish waters and a different large-scale movement behavior than DEPONS 2.0.

Equilibrium population size was less sensitive to variations in parameters related to animal life history (1st group in Figure 20), fine-scale movement (3rd group) and large-scale movement (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 moving at random. For R_1 and R_3 , which control distance moved and relationship between turning angle and speed during fine-scale movements, respectively (see Nabe-Nielsen et al. 2013b), only the parameter means were varied (standard deviation components were kept constant). The parameter R_3 was not included in DEPONS 2.0.

Only parameters that could potentially influence the behavior of all animals, and where an adjustment of $\pm 20\%$ 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 $\pm 20\%$. 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 move towards using large-scale movements (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 $\pm 20\%$ therefore inevitably has small impact on overall population dynamics.

7.1.2 Sensitivity – parameters related to impacts of noise

To assess the model's sensitivity for parameters related to responses 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 Nabe-Nielsen et al. 2018). 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. The results of this analysis are shown in the TRACE document for DEPONS 1.1 (Nabe-Nielsen et al. 2018).

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 20), we increased or decreased these parameters one at a time in simulations including noise (Supporting Information (SI) for Nabe-Nielsen et al. 2018). This is equivalent to testing for interactions between T and each of the energetics parameters. This analysis was conducted based on DEPONS 1.1 and fine-scale movements calibrated based on data from the inner Danish waters.

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; see SI for Nabe-Nielsen et al. 2018). 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.

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).

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 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 the population size. The model was only able to simulate home ranges that resembled those of satellite-tracked animals after including a large-scale movement behavior that allowed individuals to return to the area where they had previously experienced the highest energy intake rate. The inclusion of this large-scale movement behavior in the model resulted in the emergence of realistic movement patterns at multiple spatial and temporal scales (see Figure 14) 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 could, in principle, be corroborated using independent data, but due to the scarcity of such data from comparable wind farm construction sites this has not been done.

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 (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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List of figures

Figure 1. Food distribution maps derived from seasonal maps of porpoise densities in the North Sea.....	10
Figure 2. Positions of wind turbines in the three pile-driving scenarios used in this study	11
Figure 3. Data from the Gemini wind farm construction site used for calibration of the porpoises' response to noise	12
Figure 4. Relationship between received sound level (R) and deterrence behavior in the model.....	13
Figure 5. Tracks of 34 free-ranging porpoises equipped with ARGOS satellite tags.	14
Figure 6. Memory-based large-scale movement behavior used in DEPONS 2.0.....	15
Figure 7. Simulated change in turning angle distribution as porpoise agents approach the target cell group while using PSM-Type2 large-scale movements	16
Figure 8. Relationship between energy level and yearly mortality.....	19
Figure 9. Movement tracks of 2 weeks used for calibration of fine-scale movements	26
Figure 10. Histograms of $\log_{10}(\text{speed m s}^{-1})$ and turning angles ($^{\circ}$)	27
Figure 11. Effects of salinity and bathymetry on movement speed (m s^{-1})	27
Figure 12. Effects of salinity and bathymetry on absolute turning angles.....	28
Figure 13. Parameterization of spatial memory component of fine-scale movements	29
Figure 14. Parameterization of PSM_dist and PSM_angle in the PSM-Type2 long-distance movement behavior	31
. Track statistics calculated based on satellite-tracked animals are labeled 'ref'. PSM_dist is composed of a mean and a standard deviation that jointly determine the distance that animals prefer to move when using PSM_Type2; the figure is based on tracks simulated with PSM_dist standard deviation set to 100. NSD means net squared displacement. The best correspondence between tracks of simulated and wild animals was obtained for a PSM_dist of 300 km and SPM_angle of 20°	31
Figure 15. Daily movements of 34 simulated porpoises.....	32
Figure 16. Recovery of porpoise densities after end of pile-driving.	34
Figure 17. Calibration of c and T using pattern-oriented modeling.....	35
Figure 18. Porpoise movement tracks in the presence of continuous pile-driving noise.	43
Figure 19. Population impacts of alternative wind farm construction schedules in scenarios with a response distances of 200 km, simulated using DEPONS 2.0.....	44
Figure 20. Sensitivity analysis for parameters related to animal life history, energetics, fine-scale movements and large-scale movements.....	48

Changes in DEPONS version 2.0

The documentation for DEPONS 1.1 was presented in the online Supporting Information for 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. [Conservation Letters e12563](#). Below we outline the changes implemented in code, parameter settings and documentation since then.

Problem formulation updated to reflect changes made in 2.0.....	3
The model has now been updated to run in RePast 2.5	4
The term "dispersal" has been changed to "large-scale movement" throughout.	
Grid cells are now also characterized by sea surface salinity	6
In DEPONS 1.1 animals turned less steeply when moving fast. This undocumented aspect of the fine-scale movement behavior has been removed in DEPONS 2.0.	
Animals now inherit a map of the profitability of different cell groups from their mother (used in PSM-Type2 large-scale movement behavior)	8
Turning angles no longer depend on speed when animals use fine-scale movements, as there was no evidence that this was the case for North Sea animals	17
Fine-scale movements (i.e. both parameters controlling CRW movements and those controlling spatial memory behavior) have now been re-parameterized based on GPS tracking data collected in the North Sea.....	23
Fine-scale movements now depend on local salinity and bathymetry	17 and 25
The large-scale movement behavior PSM-Type2 has been re-calibrated based on data from 34 satellite-tracked North Sea porpoises after re-calibrating the fine-scale movements based on GPS-tagged North Sea animals. This is now done using a pattern oriented modeling process that resembles to one used for calibrating fine-scale movements.....	30
The parameters controlling animals' response to noise (c and T) were re-parameterized after updating fine-scale movement parameters.....	33
Tracked porpoises now also store information about their energy level, deterrence level, and position in each time step	45
Reproductive output for each simulated porpoise is now written to a separate output file	45
In the DEPONS 1.1 distribution on GitHub, the file ‘.../wind-farms/NorthSea_scenario3.txt’ did not correspond to scenario 3 as described in Nabe-Nielsen et al. (2018). This has been corrected in DEPONS 2.0.	