EFFECTS OF WIND FARMS ON HARBOUR PORPOISE BEHAVIOUR AND POPULATION DYNAMICS

Report commissioned by The Environmental Group under the Danish Environmental Monitoring Programme

Scientific Report from Danish Centre for Environment and Energy no. 1 2011

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Data sheet

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Abstract: We developed an individual-based simulation model in order to study the cumulative impacts of wind farms and ship traffic on the long-term survival and population dynamics of the harbour porpoise (*Phocoena phocoena*) in Kattegat and the Belt Seas. The model is based on knowledge of the porpoises' fine-scale foraging behaviour, dispersal between areas where porpoises are commonly observed in nature and their reproductive patterns. It assumes that individual porpoises turn away more steeply from objects the more noisy they are, and that they react to the noise emitted from large ships at distances >1 km. Our simulations suggest that operating wind farms and wind farms under construction do not affect the size or dynamics of the harbour porpoise population in Kattegat. Ship traffic may, in contrast, cause the population size to decrease.

Keywords:	agent-based model; cumulative effects; disturbances; harbour porpoise; individual-based model; management model; movement ecology; *Phocoena phocoena*; ship noise; simulation model; wind turbines; wind farms.
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Contents

Summary

The harbour porpoise (*Phocoena phocoena*) is the smallest of the whale species that inhabit European waters. Over the recent years it has experienced dramatic population declines in many parts of its range, and it has therefore become increasingly important understanding how fluctuations in its abundance might be linked to various anthropogenic factors. Here we use an individual-based model (Porpoise-POP) to investigate how possible disturbances by wind farms and ship traffic affect the porpoise population in Kattegat. The model simulates both the detailed movement behaviour that has been observed in nature using dead-reckoning instruments, long distance dispersal between areas where porpoises are often observed, and reproductive patterns reported in the literature. Disturbances are simulated by letting virtual porpoises turn away more steeply from objects the more noisy they are. The results do not suggest that the existing wind farms affect the size of the porpoise population and its long-term survival. Construction of new wind-farms at Kriegers Flak and Store Middelgrund is not predicted to affect its dynamics either, whereas the existing ship traffic is likely to cause a reduction in the population size, assuming that porpoises react to noise from ships by turning away. The results suggest that the Kattegat porpoise population is capable of recovering after being reduced to levels far below its potential carrying capacity.

Dansk resumé

Marsvinet (*Phocoena phocoena*) er den mindste af de hvalarter, der optræder i europæiske farvande. Gennem de senere år er der sket en dramatisk reduktion i dens populationsstørrelse mange af de steder hvor arten forekommer, og det er derfor blevet vigtigere og vigtigere at forstå, hvordan variationer i antallet af marsvin kan sammenkædes med forskellige antropogene effekter. I denne undersøgelse benytter vi en individbaseret model (Porpoise-POP) til at belyse, hvordan mulige forstyrrelser forårsaget af havvindmøller og skibsfart påvirker marsvinepopulationen i Kattegat. Modellen er i stand til at simulere de detaljerede bevægelsesmønstre, som er blevet observeret vha. bestiksnavigationsinstrumenter, samt langdistancespredningen mellem områder hvor marsvin ofte bliver observeret og de reproduktionsmønstre som er beskrevet i litteraturen. Forstyrrelser bliver simuleret ved at lade virtuelle marsvin have større tendens til at dreje væk fra objekter jo mere de støjer. Resultaterne tyder ikke på at de eksisterende vindmølleparker medfører en reduktion i marsvinenes populationsstørrelse eller at de påvirker deres chancer for at overleve på længere sigt. Konstruktionen af nye vindmølleparker ved Kriegers Flag og Store Middelgrund forudses heller ikke at påvirke populationens dynamik, hvorimod den eksisterende skibstrafik sandsynligvis medfører en reduktion af populationsstørrelsen, forudsat at marsvin reagerer på den hørbare skibs-støj ved at dreje væk. Vores resultater tyder på at Kattegat-populationen er i stand til at komme sig efter at være blevet reduceret til et niveau langt under dens potentielle bærekapacitet.

1 Introduction

The aim of the project 'Effects of wind farms on harbour porpoise behaviour and population dynamics' is to assess the combined effect of noise emission from wind farms and ships on the movements and population dynamics of harbour porpoises (*Phocoena phocoena*) using an individual based model (IBM)[1], the Porpoise-POP model. One of the great advantages of using an IBM for this kind of analyses is that it facilitates a direct study of the population level effects of altered movement patterns. The reason for this is that the population size is exclusively a product of the individuals' responses to variations in their environment, their memory of things that occurred in the past and their interactions with each other. The behaviour of the simulated animals is also affected by stochastic events and decisions, just like in the real world. The dynamics of the population is therefore a so called 'emergent property' of the model, which means that it is not directly related to the parameters that are used to characterize the movement patterns of the individuals (Auyang 1998, Grimm et al. 2005). An IBM therefore resembles the real world in many ways, as the dynamics of real populations also emerge from the complex interactions among autonomous organisms. This is one of the reasons why IBMs often produce more realistic population patterns than other kinds of models (Stephens et al. 2002, DeAngelis and Mooij 2005). The simulated population dynamics yields information about how much the population size can be expected to fluctuate under natural environmental conditions, but the model can also be used as a 'virtual laboratory' where the population-level consequences of e.g. reductions in by-catch or of constructing a wind farms in a particular area can be studied.

When considering the implications of a management action, resource extraction, construction of new bridges or wind farms, etc. in marine environments, it is important to bear in mind that that the status and long-term survival of each of the species living there is likely to be affected by the cumulative impact of a multitude of environmental factors (Masden et al. 2010). The need to carry out cumulative impact assessments is formalized in the Environmental Impact Assessment (EIA) Directive (85/337/EEC) of the European Community. The role of cumulative impact studies is to inform the management of developments so resultant impacts on the population level do not exceed some pre-specified threshold level. Given the large number of wind farms that are planned in Danish and German waters (Wollny-Goerke and Eskildsen 2008, Klima- og Energiministeriet 2011), combined with the possible construction of new bridges in e.g. Kattegat and Fehmarn Belt and fluctuating impacts of fisheries on different marine populations, such cumulative impact studies become increasingly important. Because many different stakeholders have overlapping and conflicting interests in the marine environment, an overall strategic area planning is required. Such a strategic planning should balance the interests of all stakeholders in order to identify locations suitable for offshore wind power development while at the same time minimising environmental and socioeconomic impact. Although studies of cumulative impacts are thus in high demand, very few

[1] We do not distinguish between individual-based and agent-based models. The latter term is often used for IBMs in economics, engineering etc.

tools are available that facilitate them. The current study is based on one of the first spatially explicit models that use a mechanistic approach to investigate the cumulative effect of multiple actions in a marine environment.

One of the most important prerequisites for producing realistic population predictions with an IBM is, that the factors that affect the individuals' fitness are explicitly incorporated in the model and of course that the model structure reflects the mechanisms that govern the individuals' behaviour, reproduction and survival in nature. One of the factors that may affect the behaviour of harbour porpoises in nature is disturbance from ships and wind farms(Tougaard et al. 2009). If something is keeping a porpoise away from a particular area it may cause a decrease in the amount of food that is accessible to the porpoise, or alternatively it may result in the creation of a barrier between different areas that are essential to the animal at different times (e.g. at different seasons or at different life-history stages). It is therefore essential that the natural movement patterns of harbour porpoises are simulated as realistically as possible. This is of paramount importance for the choice of two basic parameters in the model: the temporal resolution of the model and the size of the simulated landscape (the model 'resolution' and 'extent', respectively). If the temporal resolution of the model is too coarse it enables animals to 'skip over' areas with environmental conditions that they should have responded to, because it only explicitly considers the positions where the animal is located at the beginning and the end of each time step. The extent of a landscape is particularly important for animals that move over large areas and that are strongly influenced by temporal variations in the distribution of their food items and other resources.

One of the most challenging aspects of developing an IBM is the procurement of data regarding the factors that influence the animals' behaviour in nature. The parameters that control the movements of the individuals in an IBM fall in two categories: if the relationship between animal behaviour and some environmental parameter is known very exactly, it is possible to include the parameter in the model using a direct parameterization (Grimm and Railsback 2005). We do, for example, know a lot about the variations in porpoise gestation times and this information can therefore be directly incorporated in the model. In other cases we know very little about the effect of some parameter that we wish to include in the model. In that case we can only include it by calibrating (or 'tuning') the model. In the case of porpoises we have only limited knowledge about the connection between the animals' energy balance and their risk of dying. This parameter must therefore be obtained through calibration of the model, and adjusted until several emergent patterns in the model predictions resemble the corresponding patterns in the real world. In some cases it is impossible to obtain such a resemblance, which suggests that the structure of the model must be improved. This process, where the model structure is iteratively improved and re-calibrated, is called pattern-oriented modelling (POM) (Grimm et al. 2005). The next step in the model development process is to validate the model by comparing the predicted population distribution and dynamics with independent observations of the corresponding patterns in nature. In order to be independent, it is important that these patterns, or the datasets they are derived from, have not been used in the previous steps of the model development.

In the remainder of this report we describe the different components in the porpoise model. The main focus will be on our choice of model parameters and we will discuss how the choice of temporal and spatial resolution and extent of the model makes it possible to study the connection between disturbances from e.g. wind farms and the over-all population dynamics of the population. We provide examples of model predictions based on different scenarios for the distribution of wind farms and for ship traffic intensity. Finally we explain in detail how to conduct an experiment with the model. A detailed description of the structure of the model is provided in the ODD documentation in Appendix 1.

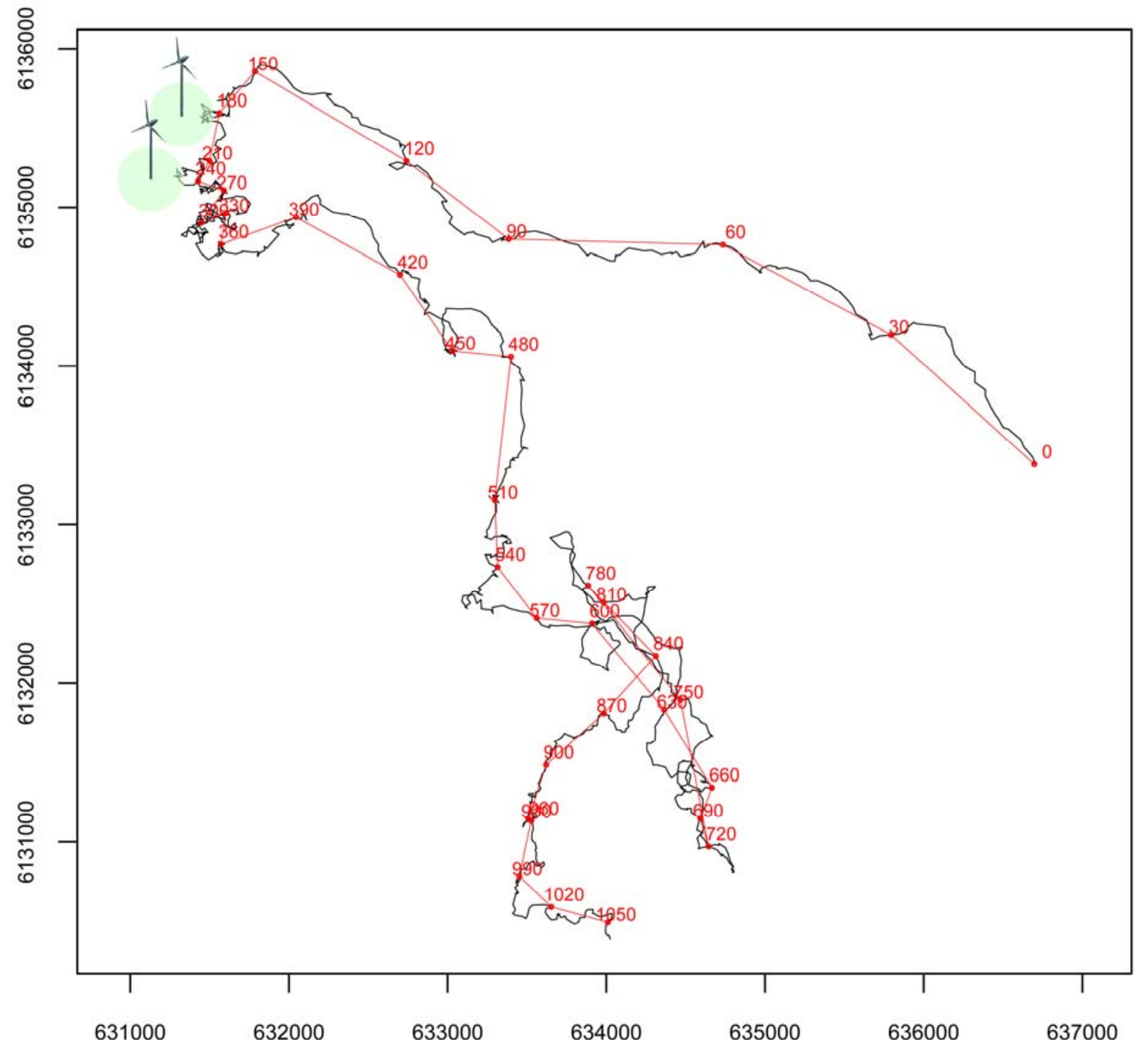


Figure 1. The route taken by a porpoise that was equipped with a dead-reckoning sensor. The animal was tracked for 1056 minutes (17.6 hours) in the eastern part of The Great Belt, Denmark. Two hypothetical wind turbines with 200-m impact zones (green circles) are included to illustrate how we expect porpoises to react to noise. The black movement track is drawn on basis of one position per minute and the red one on basis of one position per 30-minutes. The numbers in the margin are UTM coordinates.

2 Methods

2.1 Simulation of detailed movement patterns in porpoises

In order to describe how changes in the individuals' movement patterns (due to e.g. disturbances) affect the dynamics of the porpoise population, the simulation model must be able to reproduce their natural movement patterns. We have therefore put a strong emphasis on the part of the model that controls the detailed movement patterns of the porpoises. We conducted an extensive validation of the movement model in order to build the population model on a solid foundation. The details of the movement model are described in detail in a separate publication (Nabe-Nielsen et al. submitted).

Our knowledge of the detailed movement patterns for harbour porpoises originates from two different kinds of observations: (1) Data from 64 porpoises equipped with satellite transmitters yields information on the differences in their movement in different seasons and in different geographical area (Sveegaard et al. 2011b). This provides data with a relatively low temporal resolution (typically one daily position). (2) Data from a single porpoise that was equipped with dead-reckoning instruments (a speed sensor and a 3D compass) gives us information about the detailed porpoise movements over an 18-hour period (Figure 1).

The detailed movement patterns in the model are based on data from both satellite-tracked animals and from the animal that was equipped with dead-reckoning instruments. At an early point in the development process we decided to use a temporal resolution of 30-minutes in order to guarantee that simulated porpoises rarely skip over features in the landscape that they should have reacted to. Porpoises move approximately 500 m per 30-minute interval (Figure 2). We used a correlated random walk (CRW) model to simulate turning angles at the end of each 30-minute step and the distances moved. The drawback of CRW models is that the simulated animals gradually move further and further away from their starting point, which does not correspond to the patterns we observed for satellite tracked porpoises. In many cases the satellite tracked animals stayed within a limited area, or home range, for several weeks (see Nabe-Nielsen et al. 2010b). In order to mimic this behaviour we equipped the animals with a memory of where they had previously been. This enables them to return to areas where they have previously found food if they have not been able to find food using the CRW behaviour for some time. The combination of CRW behaviour and a memory based behaviour enables the model to simulate home ranges that are stable for the same length of time and that cover areas of same size as the satellite-tracked animals (se description of parameter choice etc. in Nabe-Nielsen et al. submitted). We validated the movement model by comparing the dispersal patterns for the simulated and the satellite-tracked animals.

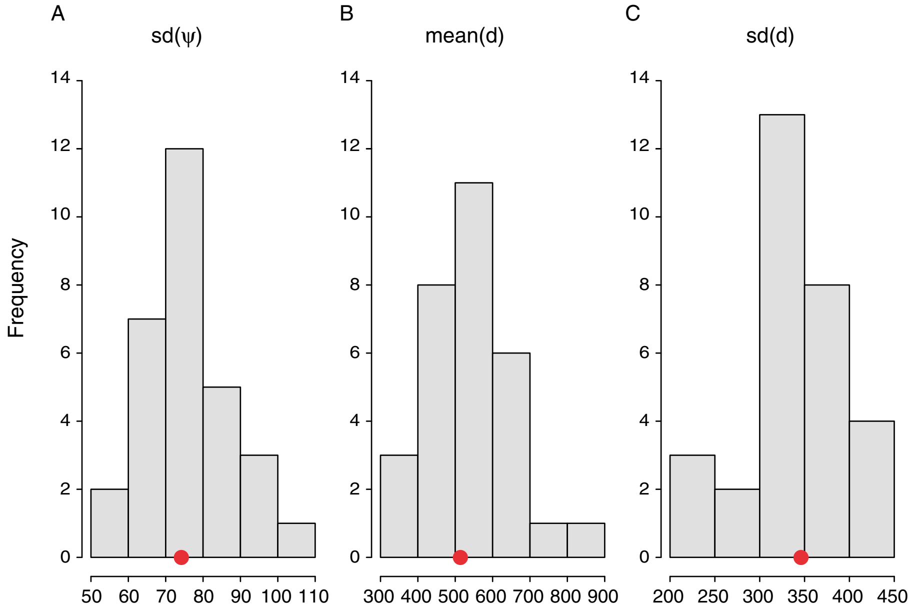


Figure 2. Calibration of the detailed movement patterns in the model. The red dots indicate values calculated on basis of dead-reckoning data for A: standard deviation of the turning angle after each 30-minute interval, B: the mean and C: the standard deviation in how far the observed porpoise moved (m per 30-minutes). The histograms show the distribution of the same parameters for a single porpoise in the calibrated movement model. The figure is from Nabe-Nielsen et al. (submitted).

2.2 Modelling the resource dynamics in food patches

The model builds on the assumption that the food items that porpoises utilize are distributed in small patches that are randomly scattered over the landscape. As several of the food items that porpoises consume (especially herring, cod and gobies, see Sveegaard et al. in prep.) occur in schools or can be expected to be associated with particular environmental conditions, this assumption appears reasonable. Studies of the satellite-tracked porpoises has, however, shown that they are often associated with areas with particular environmental conditions (Edrén et al. 2010), suggesting that the amount of food that is available is not the same in different parts of the landscape. Further, the distribution of the porpoises changes over the year. In these models the predicted porpoise densities were calculated using Maxent models where environmental conditions in areas with high porpoise densities were used to predict which parts of the landscape that should be able to sustain large porpoise densities.

The Porpoise-POP IBM uses the season-specific Maxent-values as estimates of the amount of food that can be found in patches in different parts of the landscape. Detailed descriptions of the dynamics in this system are available in Appendix 1 and in Nabe-Nielsen et al. (submitted).

2.3 Calibrating the individuals' energy requirements

The distribution of the satellite-tracked porpoises gives us a clear indication of which environmental conditions they prefer. These are presumably also areas with high food availability. We do not, however, have any data on the absolute amount of food in the different parts of the landscape and we therefore decided to measure the amount of food per patch on an arbitrary scale. In order to ensure that the simulated porpoises could in principle reach an energetic equilibrium, we calibrated the porpoises' energy use per 30-min step so that a population of 200 super-individuals maintained a nearly constant mean energy level through time. For the purpose of this calibration we prevented animals from dying or giving birth and did not require their energy level to remain in the range 0–20 as we did elsewhere (see below).

2.4 Simulating dispersal behaviour

Even though a porpoise often stays within a limited area for a long time, it sometimes moves to an entirely different part of the population's range. Our knowledge about the mechanisms that trigger these dispersal events is extremely limited and we have not been able to find any connection between where each porpoise disperses to and variations in the environmental parameters that we expected to be of importance for the distribution of their prey (see Nabe-Nielsen et al. 2010b). Their dispersal patterns are presumably related to their memory of where resources are likely to be abundant. This assumption forms the basis of the model that determines their dispersal behaviour.

In the Porpoise-POP IBM the dispersal behaviour is controlled by two different mechanisms: (1) An individual that experiences a decreasing energy level for three consecutive days tends to move towards one of the areas with highest Maxent values. Mean Maxent values were calculated for all 40 × 40 km blocks in the landscape in order to facilitate their choice of dispersal target. On their way towards the selected area they tend to stay in deep water. (2) When an animal approaches its dispersal target, or if it finds itself on low water, it changes dispersal strategy and starts moving away from the areas that it just visited, while tending to stay at a fixed distance from the coast. If its energy level continues to decrease, it turns around and moves towards the area where it was three days earlier. If it finds so much food that the energy level increases, it stops dispersing (see Appendix 1 for details). This dispersal model can reproduce most of the dispersal patterns that have been observed in the satellite-tracked porpoises.

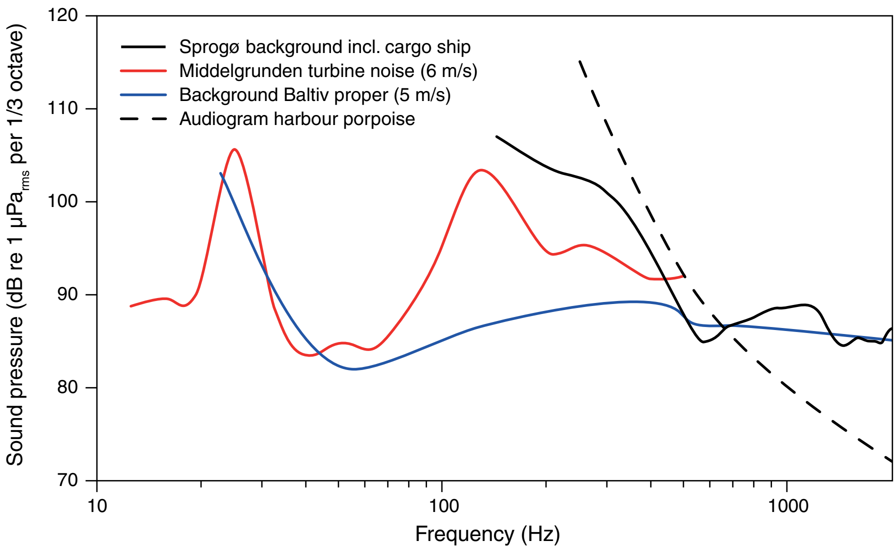
2.5 Simulating disturbance

Little is known about how porpoises react to disturbances (Sveegaard et al. 2008, Tougaard et al. 2009), but the most likely response is probably a tendency to turn away from the objects that disturb them, as illustrated in Figure 1. Adverse reactions has been documented numerous times to both low frequency noise (Koschinski et al. 2003, Tougaard et al. 2011) and high frequency noise (Koschinski and Culik 1997, Teilmann et al. 2006, Kastelein et al. 2007, Carlström et al. 2009). Already at a distance of 20 m from wind turbines the porpoises can more easily hear the noise emitted from a distant cargo ship than the noise from a wind turbine, at least in calm weather (Figure 3). Porpoises have been observed to react to playback of turbine noise at a distance of 200 m (Koschinski et al. 2003, in Madsen et al. 2006). Although there were technical issues with the experiment, making it unclear whether the porpoises really reacted to the turbine noise or rather to elevated noise from the recording, 200 m is an upper estimate of the reaction distance (see further discussion in Tougaard 2009). The sound pressure level decreases with the distance to the foundation of the wind turbine in different ways depending on the water depth and the type of the substrate. In shallow water areas with hard bottom the sound pressure can be expected to decrease linearly with the distance to the source (cylindrical spreading Urick 1983) and on other substrate types it decreases even more rapidly.

In the IBM individuals react to noise by turning away from it. We implement this behaviour using a biased random walk model (Börger et al. 2008). The strength of their tendency to move away is proportional to the sound pressure level, and the direction they move in when they get disturbed is determined by the sum of a vector pointing away from the object that disturbs them and the vector pointing in the direction that they would have moved in if they had not been disturbed. The movement speed is unaffected by the disturbance. We modelled the deterrence behaviour to persist for five 30-minute time steps, but let the strength of the deterrence be halved in each step. If a porpoise is located 290 m from an object that it can hear at distances up to 300 m, it therefore turns very slightly away from it. If it was previously moving nearly straight towards the object at full speed, it will actually continue getting closer to the object, as it is only slightly deterred by it. If the porpoise, on the other hand, moves out of the zone where it can hear the object, its tendency to turn away becomes half as large in the following time step, and this bias may well be unimportant compared by the random walk turning angle.

In order to calibrate the disturbance behaviour near wind farms in the model we adjusted the maximum distance where wind turbines could affect porpoises (the 'deterrence distance') and the strength of the disturbance effect for a typical turbine (the 'deterrence coefficient'). Typical wind farms are assigned with an impact factor of 1. We calibrated the disturbance behaviour by a wide range of possible combinations of these two parameters and selecting the combination that yielded porpoise densities similar to the ones observed for real animals by the Nysted Offshore wind farm (Tougaard et al. 2006), i.e. a slightly reduced density in the distances 100–200 m from the wind farm. The simulations were carried out in a landscape with a long line of wind turbines located 100 m apart, but without other landscape features. The artificial turbines were placed close together in order to ensure that the porpoises actually encountered the turbines, so that the reaction we observed was not a result of the porpoises moving between the turbines. These simulations included 300 animals that were monitored for 287 time steps.

Figure 3. Sound pressure in water for different frequency bands, each 1/3 octave wide. The red curve shows measurements 20 m from a wind turbine, blue shows normal background noise and the black curve shows background noise including the noise emitted from a distant cargo ship. The dashed line indicates the noise threshold for porpoises in different frequency bands (only the noise above the line is audible). The figure is from Sveegaard et al. (2008).



Effects of constructing new wind farms were investigated in a similar fashion. The potential wind farms were located in one group at Store Middelgrund and in four groups at Kriegers Flak. We included 60 wind turbines in each group. These were arranged like the ones in the Rødsand wind farm. The porpoises' tendency to turn away from areas where turbines were simulated in the same way as deterrence during the post-construction phase, but with a deterrence distance of 20 km. This means that the deterrence closer to the turbine was very strong during the pile driving phase. The construction of each wind turbine was set to last two days, and in the population simulations the construction period was repeated in the simulation years 1, 10, 20, 30 and 40.

We included three different sources of disturbance in the model: (1) Disturbance from existing wind farms. A list of the included wind farms and their coordinates is provided in Appendix 3. (2) The noise from new potential wind farms during construction or the post-construction phase. (3) The noise from existing ships was included in the model based on AIS data from the Baltic in 2010. The average number of large ships passing reference points at Skagens Gren, Great Belt Bridge, Drogden and north of Bornholm was extracted from the HELCOM database (www.helcom.dk). These ships include all commercial ships above 300 tons and all fast ferries (all required to have an AIS transmitter), as well as some smaller ships voluntarily using AIS, but excludes fishing vessels and navy ships. Based on a simplifying assumption that all ships entering or leaving the study area follows the designated traffic routes either through the Great Belt or through the Sound, the average daily ship traffic along these routes were calculated. Average ship traffic through the Great Belt was set at 49 ships/day and through the Sound at 121 ships/day (18,000 and 44,000 ships/year, respectively). Ships were then added individually to the model, each assigned an individual average speed. The speed was randomly selected from a normal distribution with mean 30 km/h and standard deviation 5 km/h. Next to nothing is known about reactions of porpoises to ship noise. Noise levels from ships are, however, generally higher than from wind turbines, and they are at least 10 times as noisy as the most noisy turbines. We therefore let the impact depend linearly on the speed of the ships, so that ships that sailed 20 km/h had an impact of 5 and one that sailed twice as fast had an impact that was 10 times as high as that of a standard wind turbine.

In addition to regular ship traffic a ferry route with high-speed ferries was also added. The ferries operate on the route Odden-Aarhus and sail at speeds up to 70 km/h. Average density of ferries corresponded to the sail plan, but was evenly distributed across day and night, i.e. ignoring that the real ferries only sail between 7:00 and 23:00. Relative impact of fast ferries was assumed to be greater than for cargo ships, due to expected higher noise levels and higher speed of approach, and was set to 15 times that of an individual wind turbine in a basic ship traffic scenario.

In addition to the basic scenarios we ran a scenario where the ships were assumed to disturb half as much as in the basic scenario.

A number of scenarios were run in order to analyze the effects of disturbance on porpoise population dynamic (Table 1). Each scenario was replicated five times, and each simulation included 40-years of simulated data. In the scenarios that analyse the effect of noise from wind farms after the construction phase the disturbance intensity of the turbines was set to 1 as the existing Danish wind turbines are approximately equally noisy (Madsen et al. 2006, Tougaard et al. 2009). In the scenarios that analyse the effect of ships, all large ships from the routes Aarhus-Odden, Kattegat T-Route and the route through The Sound were included. Planned wind farms included the ones at Kriegers Flak and Store Middelgrund (see Figure 15).

Table 1. Description of the simulation scenarios.

	Scenario					
	1	2	3	4	5	6
Constant low bycatch rate	x	x	x	x	x	x
Post-construction noise from existing wind farms		x		x		
Noise from large ships			x	x		
Post-construction noise from planned wind farms					x	
Construction noise from planned wind farms						x

2.6 Simulating reproduction and mortality

The dynamics of animal populations are determined by the balance between reproduction and the animals' risk of dying. Disturbances by wind farms and ships therefore only affect the dynamics of the porpoise population in Kattegat if they lead to a reduction in the amount of food available to them, or if they result in barrier effects that separate a sub-population from the main population. A sub-population that has been cut off from the main population in this fashion is more likely to disappear as a result of local variations in the amount of available food and due to stochastic mortality.

In the Porpoise-POP IBM both the survival and the probability of successfully rearing an offspring are affected by the energy level of the individuals (Figure 4), which in turn results from the balance between energy use and food consumption. Data from captive animals suggest that porpoises spend energy at a constant rate, although the rate increases for lactating animals and when the water temperature drops (Magnus Wahlberg, unpubl. data). This is likely also to be the case for wild porpoises that are constantly moving and use resources for maintaining a constant body temperature. We therefore take the same approach and model the amount of energy spent per 30-minute interval as being independent of the distance moved, but let it vary among seasons. In the model the animals' energy intake is determined by the amount of food they find in the randomly distributed food patches. As there is no data on how porpoise foraging rates vary among areas, we use the standardized Maxent levels as an indicator of the maximum amount of food available in a patch. The standardization is done in order to keep the total amount of food constant among seasons. As high Maxent values are only obtained in areas where satellite-tracked porpoises are frequently found, which is also the places where they stay for extended periods of time, they must be good indicators of food availability. As adult mortality the probability of abandoning a lactating calf are controlled by food availability, which is in turn determined by the number of porpoises, the amount of food available to the porpoises reaches a dynamic equilibrium when the population level approaches carrying capacity.

Every day each of the individuals in the model are confronted with a number of choices that affect their reproduction and survival (Figure 5). The choices they make – whether it is time to mate, die or wean a calf – depend on the time of year and often also on their energetic status and age. The parts of the model that affect movement and energetic status are updated every 30 minutes. The survival of both adults and lactating juveniles are modelled as energy dependent (see Figure 4) and in top of the natural mortality we have added a constant by-catch rate corresponding to the maximum safe by-catch rate recommended by (ASCOBANS 2000). The likelihood of becoming pregnant is determined by their age and the time of the year (only females are modelled explicitly and each 'individual' in the model is a so-called super-individual (Scheffer et al. 1995) that represents a large number of adult females in the real world). We parameterized the model using the pregnancy rates observed in the Gulf of Maine population (Read and Hohn 1995), which has a life history that closely resembles the one in Kattegat (Sørensen and Kinze 1994). Age of sexual maturity was obtained from a study from Bay of Fundy (Read 1990). The parameters that control when animals mate and how long they are pregnant were obtained from literature (see details in Appendix 1). The calves do not appear as independent individuals in the model till after they stop lactating, which happens eight months after they are born (Lockyer 2003). Adult females are able to mate even when they are lactating.

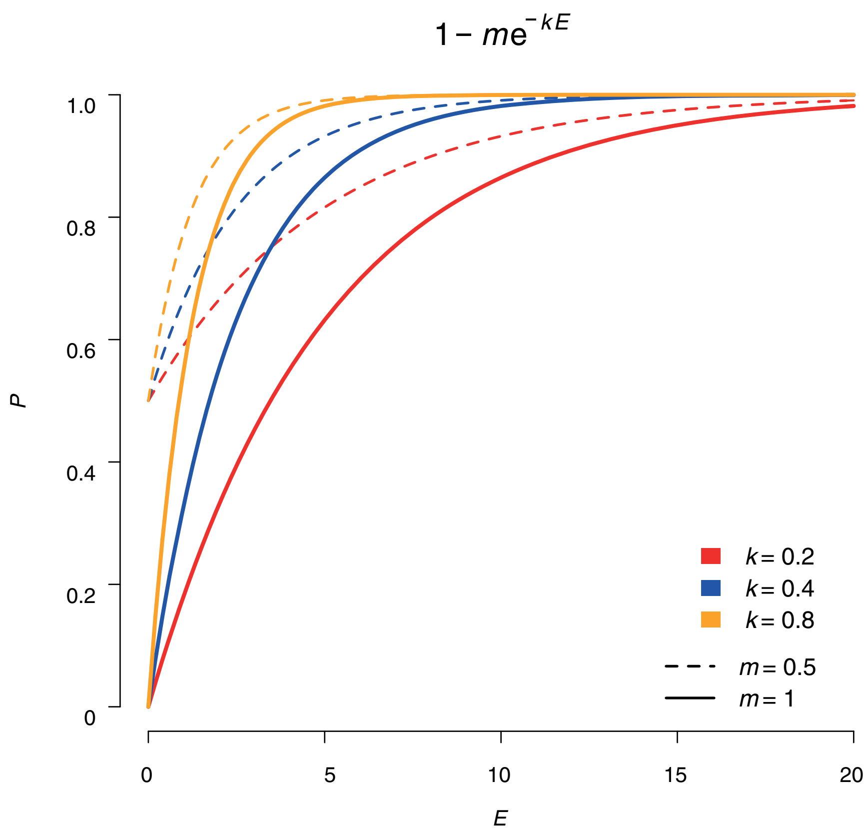


Figure 4. Modelling the yearly survival probability (P) for adult porpoises and lactating juveniles as a negative exponential function of the energy level (E), which is standardized to lie in the range 0–20. The constants k and m determine the shape of the survival curve.

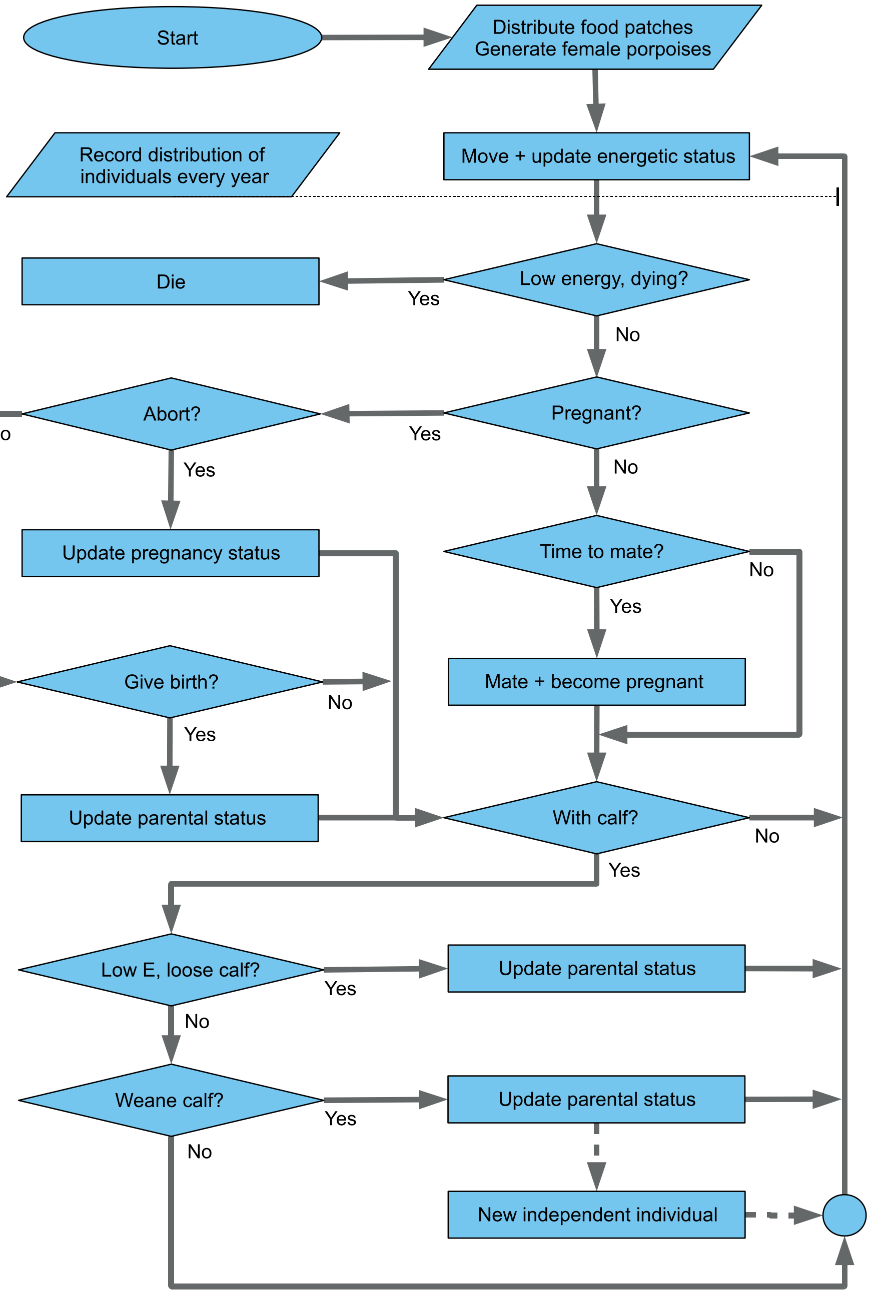


Figure 5. Flow diagram describing the details of the population part of the Porpoise-POP IBM. Only females are modelled explicitly and each 'individual' in the model represents a large number of real females. Diamond shaped symbols indicate decisions taken by porpoises, parallelograms indicate model input/output and rectangles indicate calculations.

3 Using the simulation model

3.1 Description of the user interface

The Porpoise-POP IBM is built using the application NetLogo 4.2.1, which can be downloaded from http://ccl.northwestern.edu/netlogo/. NetLogo must be installed on the computer in order to run the Porpoise-POP IBM.

The first thing the user sees when opening the Porpoise-POP IBM is a window with three tabs called Interface, Information and Procedures. When clicking on the Interface tab a window resembling Figure 6 appears. The different buttons and monitors allow the user to initiate the model and to monitor the simulation as it runs. The model documentation from Appendix 1 can also be accessed by clicking on the Information tab. The code that controls the program flow can be accessed by clicking on the Procedures tab.

3.2 Initiating the model

In order to start a simulation the user must set up the model using various sliders and buttons (Figure 6A). First the number of model animals must be selected. We have chosen only to simulate groups of adult females. If the slider 'n-porps' is set to 200 the population is close to carrying capacity causing the simulation output to stabilize more rapidly. Next the user selects which area to model (Kattegat or a homogeneous area) and whether the reaction to wind farms and ships should be included in the model. Three ship routes are included automatically when the reaction to ships is investigated: the fast ferries between Aarhus and Odden, the T-Route through Kattegat and the Great Belt, and the shipping route through Kattegat and The Sound. The speed and impact of each of the modelled ships is adjusted in the input text files located in the 'ships' directory that must be present together with the porpoise model. The directory must contain the files 'Aarhus-Odden.txt', 'Great-Belt.txt' and 'Kattegat-Sound.txt' and each line in the files represents a ship. A file containing just the header does not include any ships. The wind farms are included in a similar fashion and the 'wind-farms' directory must be present together with the porpoise model. Here the user can select which wind farms to include and it is also possible to specify if wind farms are more noisy than standard wind farms, as is the case for the wind farm in Utgrunden (Madsen et al. 2006, Sveegaard et al. 2008). The format of the wind farm input file is shown in Figure 7. Finally the user must select whether to save the positions for all porpoise individuals every year (on 1 January), on the 1st of every month, or daily for a single porpoise (called 'porp 0'). The output is stored in the 'output' directory using the name selected in the 'output-name' field.

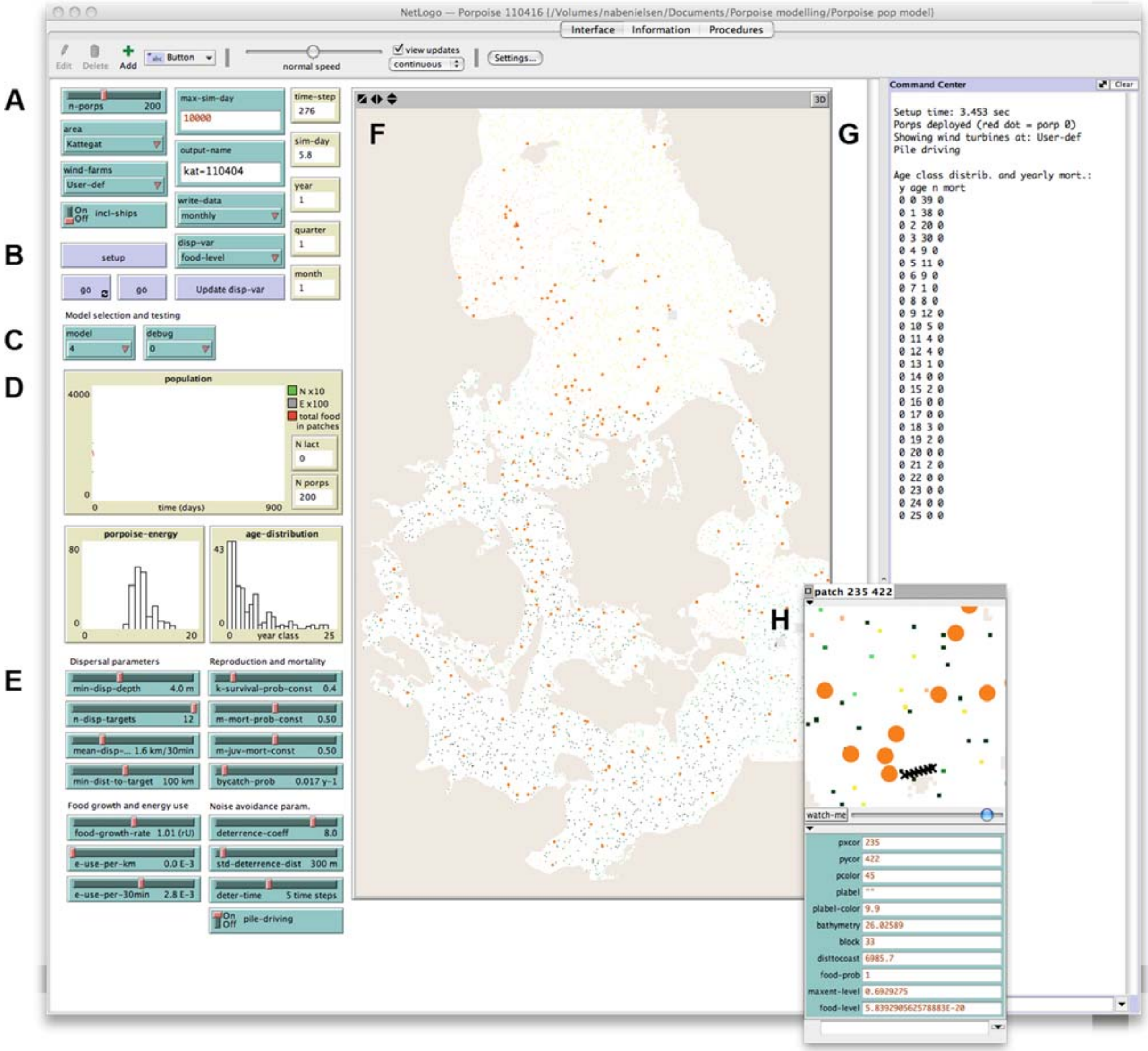
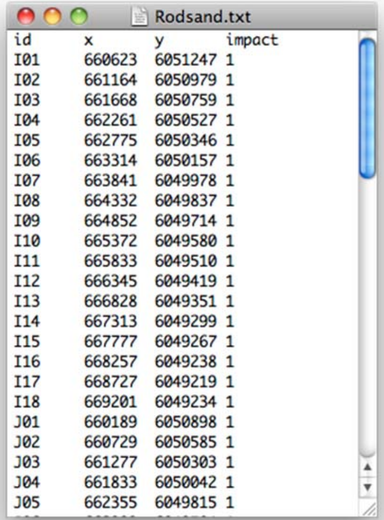


Figure 6. The user interface of the Porpoise IBM. The green buttons and sliders on the left side of the window allow the user to modify the settings. The orange dots in the central plot show the porpoise super-individuals as the model runs and the pane on the right hand side is designated for model output. The number of porpoises per age class and the age-specific mortality is printed in the output pane by default (when 'debug' is set to 0). See text for details on the different panels in the figure.

In order to run a population model with the simplest possible output, the user must select 'model' to be 4 and 'debug' to be 0 (Figure 6C). Models of type 1–3 simulate only movement, or population behaviour without reproduction (see details in top of the model code, on the Procedures tab). Now the model can be run by first pressing 'setup' and then 'go' (Figure 6B).

The display type can be updated while the model runs by picking a 'disp-var' and clicking the 'Update disp-var' button. The different display types are: (1) bathymetry, indicating the water depth, (2) Maxent, (3) food-prob, which shows the locations of the food patches, (4) food-level, which shows the amount of food available en the food patches and (5) blocks, which shows the 40 × 40 km blocks that the landscape is divided in when performing some kinds of statistical tests.

A number of parameters that control dispersal, noise-avoidance behaviour, reproduction, food availability and energy use etc. can be adjusted in the model (Figure 6E). As the standard settings result from a careful calibration of the model any modification of the model may, however, have unexpected results. The standard settings are shown in Appendix 2.


Rodsand.txt

id	x	y	impact
I01	660623	6051247	1
I02	661164	6050979	1
I03	661668	6050759	1
I04	662261	6050527	1
I05	662775	6050346	1
I06	663314	6050157	1
I07	663841	6049978	1
I08	664332	6049837	1
I09	664852	6049714	1
I10	665372	6049580	1
I11	665833	6049510	1
I12	666345	6049419	1
I13	666828	6049351	1
I14	667313	6049299	1
I15	667777	6049267	1
I16	668257	6049238	1
I17	668727	6049219	1
I18	669201	6049234	1
J01	660189	6050898	1
J02	660729	6050585	1
J03	661277	6050303	1
J04	661833	6050042	1
J05	662355	6049815	1

Figure 7. One of the text files that is used for storing UTM-positions and expected impact of the individual turbines in a wind farm. The numbers in the impact column makes it possible for the user to simulate effects of particularly noisy wind farms.

3.3 Inspecting the model output

While the model runs the behaviour of the individuals can be monitored on the map in the central part of the window (Figure 6F). The detailed behaviour of an individual or a cell in the landscape can be monitored by right-clicking on it and selecting 'inspect', as shown in Figure 6H. When the food level of the patches is displayed (selected using 'disp-var'), the amount of food in the food patches initially reflects the Maxent value for the area (see the section 'Modelling the resource dynamics in food patches'). High-quality food patches are black. When a porpoise visits a patch it eats the food that it finds there, causing the patch to turn yellow. After a while the food is replenished, causing the patch to turn orange, green and finally black (if in an area with a high Maxent value). Porpoises that have a high energy level only consume part of the food they encounter, causing a smaller change in the colour of the food patch.

While the model runs the three graphs on the left side of the model window (Figure 6D) gives real-time information about the population dynamics, the energetic status of the porpoises and about their age distribution. The population dynamics graph shows the current population size, the mean energy level of the porpoises and the total amount of food available in the landscape. The histogram that illustrates the energetic status of the porpoises allows the user to assess the mortality risk of the different parts of the population, as the mortality increases with decreasing energy reserves for both adults and lactating juveniles (Figure 4).

4 Results

The results fall in two parts. The first part is related to the detailed movement patterns of each porpoise individual, both when these are only influenced by their foraging behaviour and when they are also influenced by dispersal behaviour and disturbances. The second part is related to the dynamics of the porpoise population, i.e. how the population size changes through time in response to variations in food availability and in the way individuals react to noise emitted from ships and wind farms.

4.1 Validating the detailed movement model

Our ultimate goal is to investigate whether noise from ships and wind turbines can result in altered population dynamics and long-term survival of the porpoises by causing them to change movement behaviour. The part of our model that simulates fine-scale animal movements is a modified Correlated Random Walk (CRW) model, where the animals have the ability to use a spatial memory to find their way back to areas where they have previously found food. It has been calibrated by adjusting their short-term and long-term memory of their foraging success until they stay within well-defined home ranges to the same extent as porpoises do in nature(se details in Nabe-Nielsen et al. submitted). The residence time, i.e. the time they spend within a particular area, is not directly related to how far they move away from their starting point over time, and the detailed movement patterns can therefore be validated by comparing this emergent property of the model with the corresponding pattern for real world porpoises (Figure 8).

The detailed movement patterns of the simulated porpoises closely resemble the ones of real-world porpoises. The time they spend within their home ranges are similar to what we observe in the real world (Nabe-Nielsen et al. submitted), and Figure 8 illustrates that the distance moved during a specific period is also similar in simulated and real-world porpoises. The simulated porpoises mainly differ from real-world porpoises by rarely moving back to the place where they started at time zero. The reason for this pattern is that simulated porpoises move in an open system, where the population is not confined to stay within certain boundaries. In nature all porpoises in the Kattegat population eventually return to the central locations in the population range. The displacement distances of real-world porpoises also change slightly more steeply than the ones for simulated animals. This is caused by the dispersal behaviour that is frequently observed, but that not incorporated in the model that simulates the fine-scale porpoise behaviour.

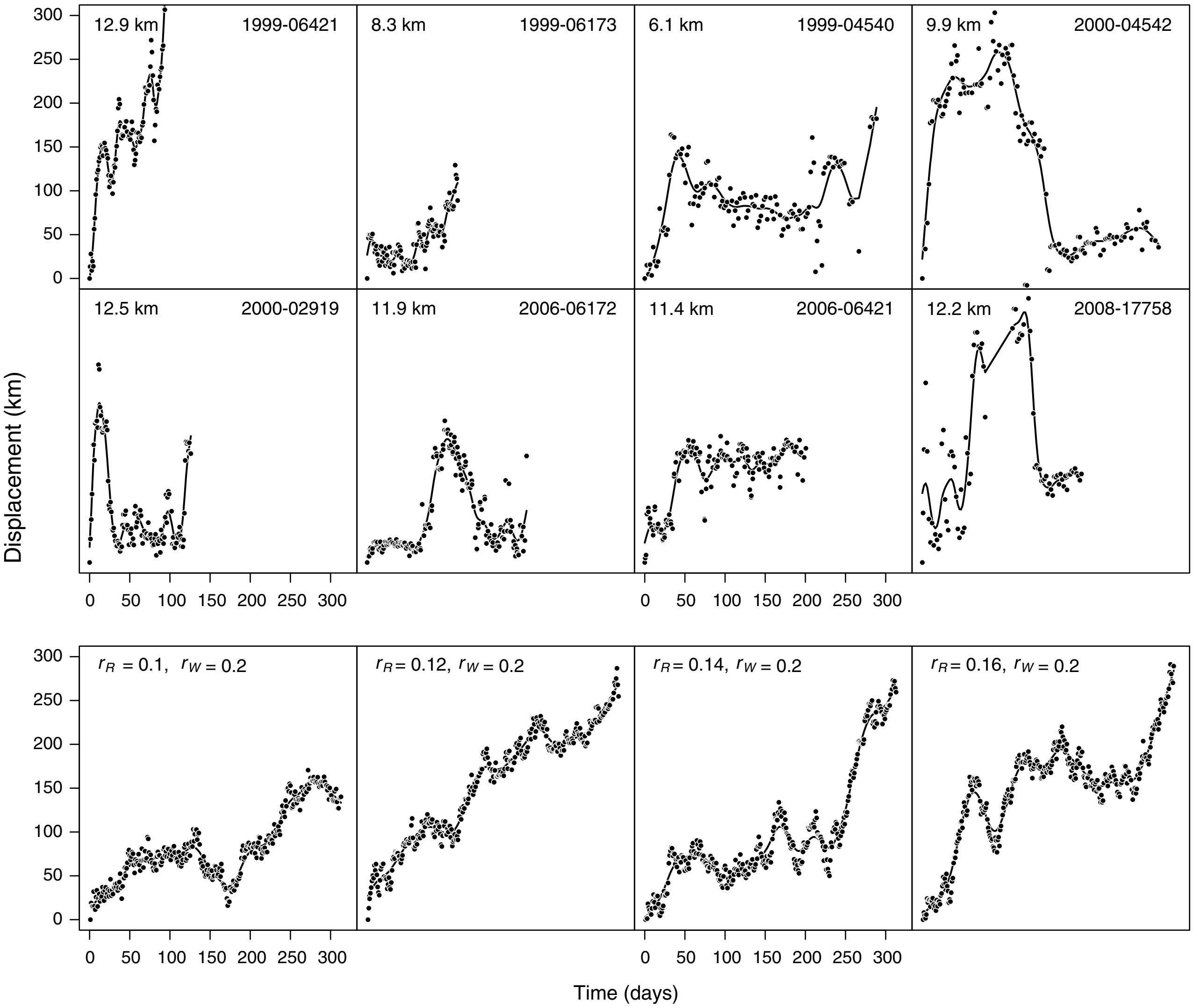


Figure 8. Distance to the location visited at time zero for eight satellite-tracked porpoises (top) and four simulated porpoises with suitable combinations of long-term (r_R) and short-term memory (r_W) of the positions they previously visited. Only satellite-tracked proposes that were on the average >6 km from land were used. The figure is from Nabe-Nielsen et al. (submitted).

4.2 Effects of including long-distance dispersal in the model

We introduced long-distance dispersal in the Porpoise-POP IBM by letting animals move towards favourable areas whenever their energy level had dropped for three consecutive days. These areas were selected at random among the twelve 40 × 40 km blocks that had the highest Maxent-value at that particular season. The number of potential dispersal targets had to be set to at least 12 in order to ensure that animals sometimes dispersed to northern Kattegat, but much larger numbers resulted in less directed dispersal patterns. The average dispersal distance per 30 minutes was set to 1.6 km, which resulted in dispersal patterns and daily dispersal distances that were similar to the ones commonly observed for satellite-tracked animals (J. Teilmann et al., unpubl. data).

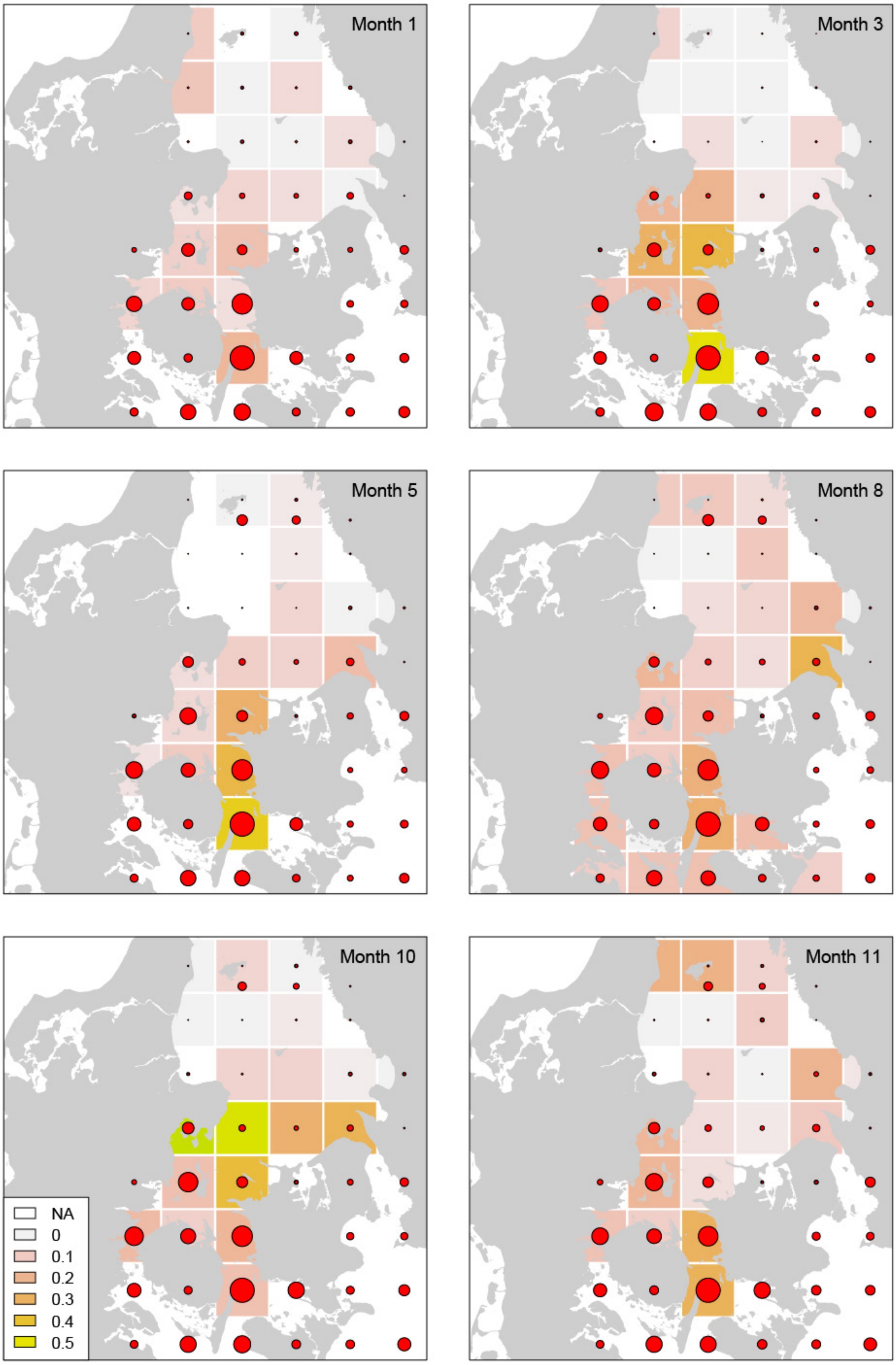


Figure 9. Validating the model simulations by comparing the spatial distribution of simulated porpoises to porpoises observed in six acoustic surveys in 2007 (Sveegaard et al. 2011a). The colours of the 40 × 40 km blocks indicate the number of porpoises observed per km sailed in surveys. White indicates areas that were not visited. The areas of the red circles are proportional to the average number of simulated porpoises per block over a 40-year simulation period.

In the Porpoise-POP IBM the dispersal direction is controlled by the magnitude of the Maxent values in the different 40 × 40 km blocks. These are high in areas that are similar to the places where the satellite-tracked individuals were most frequently found, in particular where the distance to the coast and the bottom salinity are similar (Edrén et al. 2010). We tested how the distribution of simulated animals was related to the spatial distribution of porpoises in nature using an independent data set, where the number of porpoises were recorded using a towed hydrophone array in Kattegat and the Belt Seas during six surveys in 2007 (Sveegaard et al. 2011a). Overall there was good agreement between the number of simulated animals in the different 40 × 40 km blocks and the porpoise densities observed in the acoustic surveys (Figure 9). Both simulated and real animals reached far higher densities in the Belt Seas than in the northern parts of Kattegat for all census periods and there was little variation among the different survey periods. Some of the apparent differences between the blocks in the different surveys, such as the high-density areas by Djursland in October, are caused by a small sample size (a relatively large number of porpoises recorded over a very short sailing route inside the block). Unfortunately survey data from the areas south of Sealand and Funen were scarce and a direct validation of the model's performance in this area could not be performed.

4.3 Effects of wind turbines and ships on porpoise movement

Noise from ships and wind turbines affect animal movement in the Porpoise IBM. The animals' response to disturbances were calibrated in order to obtain slightly lower porpoise densities at distances up to 200 m from wind turbines than in areas further away. This was obtained using a deterrence coefficient of 8 and a deterrence distance of 300 m (Figure 10). The reason why the deterrence distance had to be 300 m in the model in order to observe a reduced number of individuals in the interval 0–200 m from the turbines is that the simulated animals only react to noise they experience at the beginning and the end of a 30-minute time step. As both the sound pressure and the impact of noise on animal behaviour was assumed to decrease linearly with the distance to the disturbing object, a ship that was twice as noisy as a standard wind turbine (i.e. with impact = 2) was modelled to affect porpoise movement up to distances twice as large.

Although the deterrence parameters we use may result in a realistic decrease in the number of porpoises that are observed in the vicinity of wind farms, they do not prevent simulated animals from moving between the wind turbines. Animals that move full speed towards a gap between two wind turbines tend to continue straight ahead and to be only slightly affected by the turbines. The simulated porpoise movement is therefore largely governed by the distribution of food patches and by stochastic movements, even close to a wind farm (Figure 11).

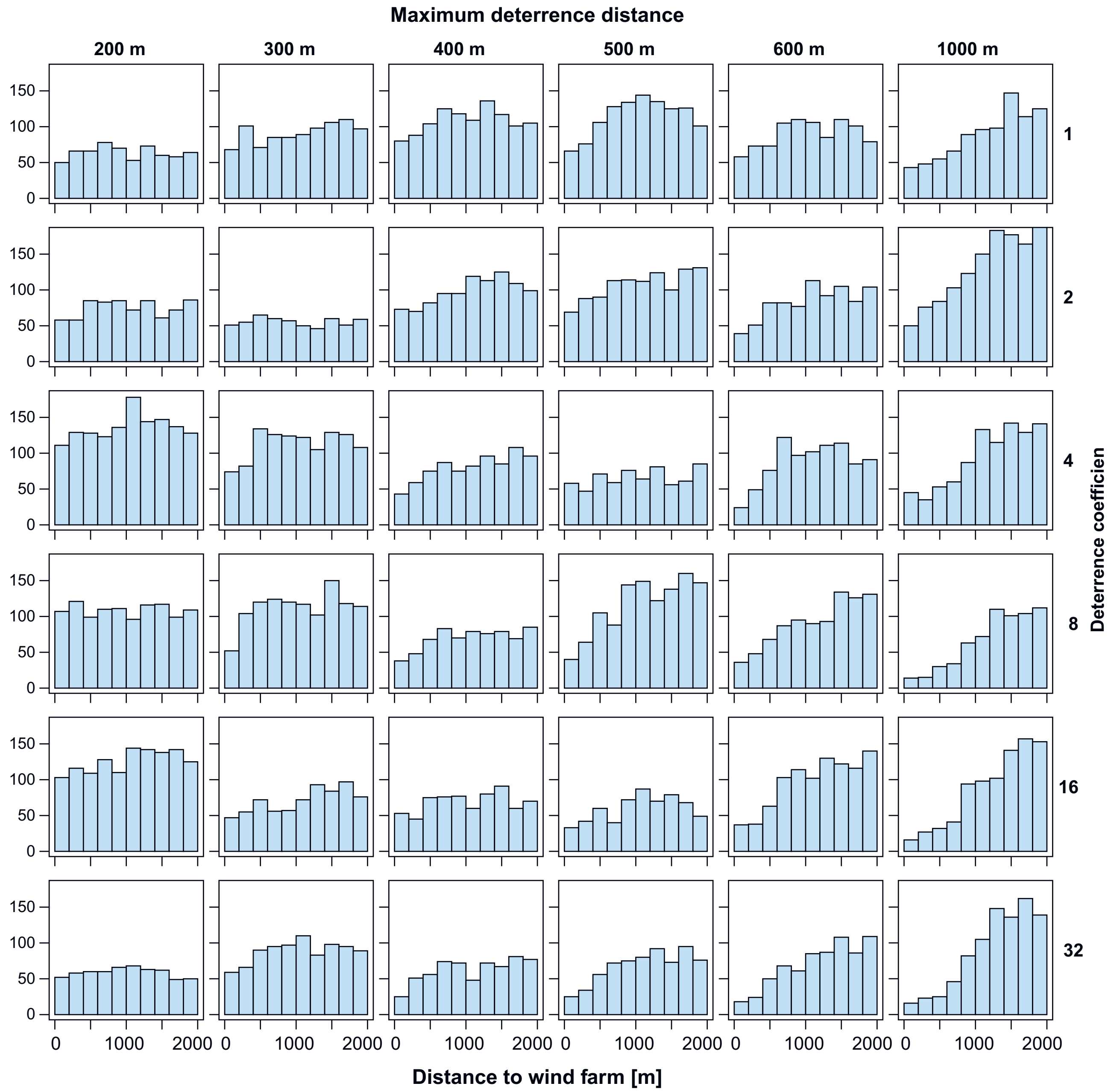


Figure 10. Effects of noise emission on porpoise densities near simulated wind turbines. Each panel shows the number of porpoises observed at different distances from wind turbines for a particular deterrence coefficient ('deter') and a particular maximum deterrence distance, beyond which there is no effect of the noise emitted from the turbine.

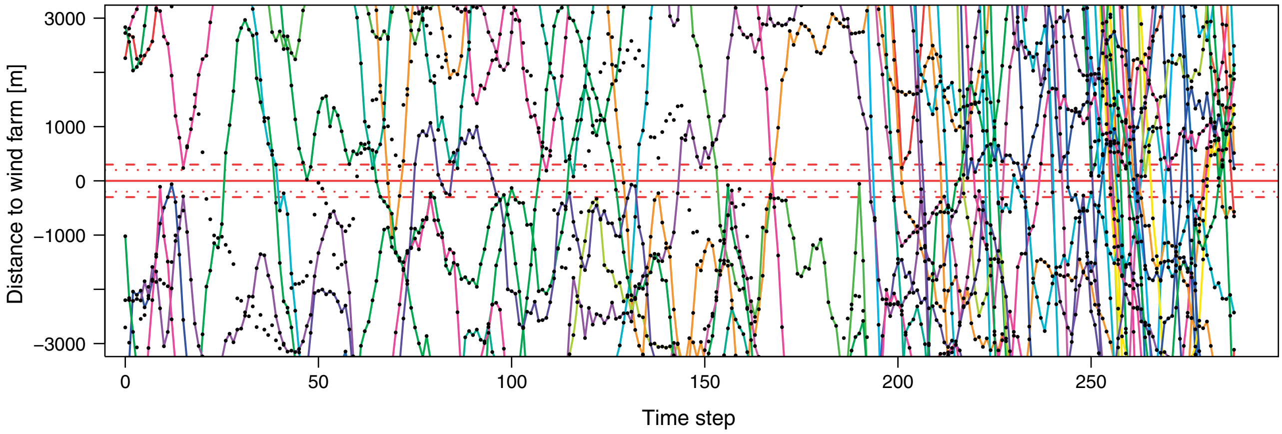


Figure 11. Movements of simulated animals in the vicinity of wind turbines placed in a long line. The simulation used standard disturbance parameters (deterrence coefficient = 8, deterrence distance = 300 m). Each colour represents an individual track. Note that some porpoises cross through the wind farm (0-m line) while others stay on one side and return to where they came from.

4.4 Food availability and population dynamics

The dynamics of the simulated population is closely linked to the amount of available food in the landscape (Figure 12). When food is abundant, most individuals are able to attain high energy levels, which lead to high survival probabilities of both adult females and lactating juveniles. One of the characteristic features of the simulated population is that its size gradually increases over a period of many years before it abruptly decreases again. This abrupt decrease in population size results from a decrease in the porpoises' energy levels.

The abruptness of the population decline is strongly affected by the relationship between the porpoises' energetic status and their probability of surviving (Figure 4). When even animals with low energy levels have a high probability of surviving, as is the case when the survival parameter k is large, the population size keeps increasing until all resources have been exploited, followed by a rapid decrease.

This also results in an age structure that differs from the one observed for stranded ani by having a relatively high proportion of old animals (cf. Lockyer and Kinze 2003), except immediately after the rapid population decline. The other extreme, where animals with intermediate energy levels have a low probability of surviving, results in a population that gradually goes extinct. This is the case when k is small. We therefore calibrated the model by adjusting k and m until the age class distribution was the same as observed for stranded animals along Danish coasts (Figure 13). The parameter m was adjusted to ensure that animals with high energy levels (E>10) maintained a very low mortality. Juvenile individuals are likely to be over-represented in stranded animals as young animals are likely to drown in gillnets more frequently than older animals and to subsequently drift ashore. As this bias is not included in our model, we tried to obtain a slightly lower juvenile mortality than observed in nature (for stranded animals).

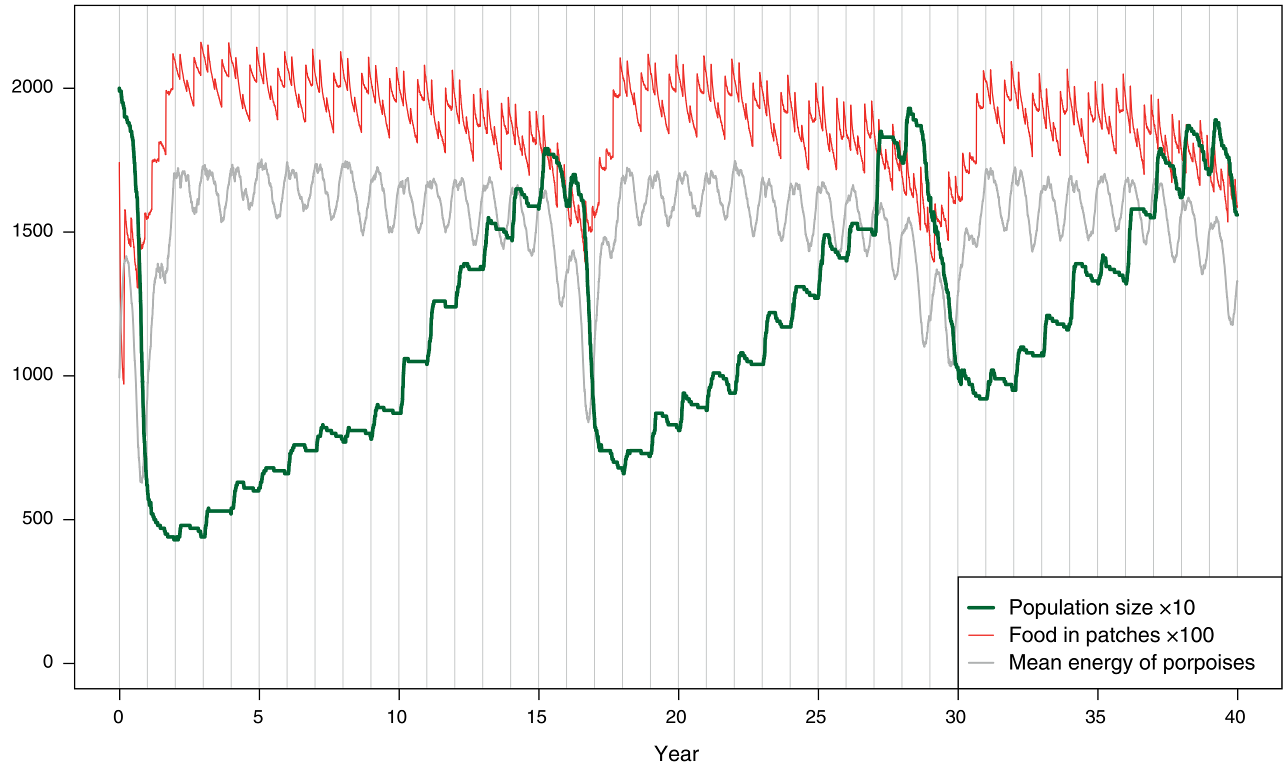
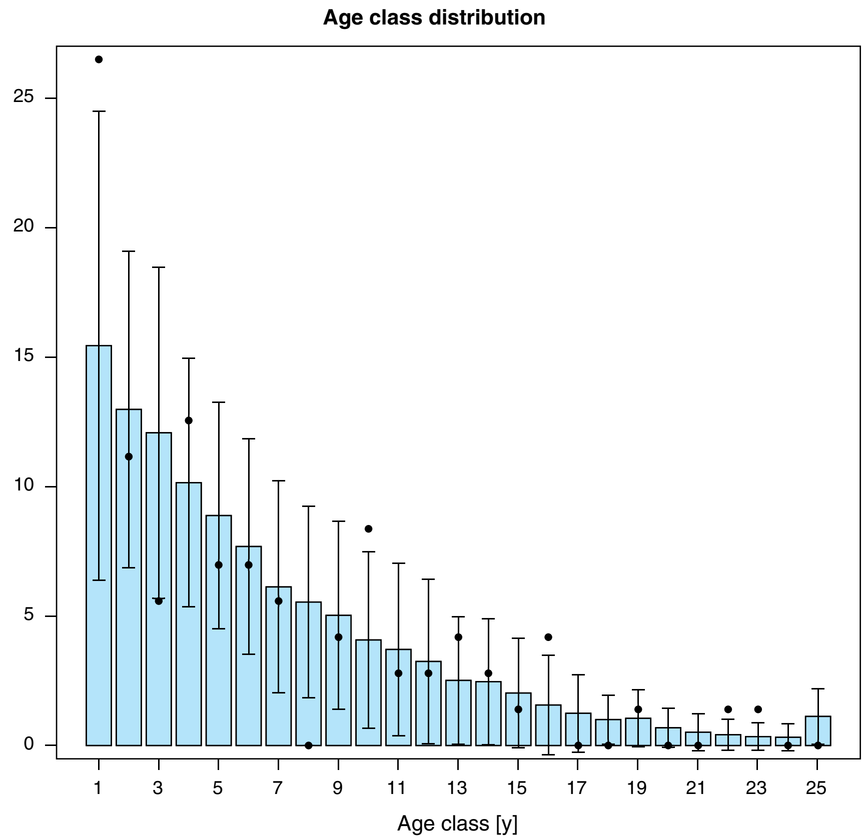


Figure 12. Simulated population dynamics based on standard parameters. The population size is counted in number of super-individuals, each representing 30 adult female porpoises.

Figure 13. Mean age-class distribution in the simulated porpoise population ±1SD using survival parameters *m*=0.5 and *k*=0.4 (cf. Appendix 2). Values for animals stranded in Danish waters are shown with black dots (Data from Lockyer 2003). The plot is based on the same reference data set as Figure 12. The data for stranded animals was standardized in order to obtain the same sample size as for simulated animals.



4.5 Effects of wind farms and ships on the porpoise population

The population dynamics of the undisturbed reference population strongly resembled the ones where porpoises were disturbed by wind farms (Figure 14).

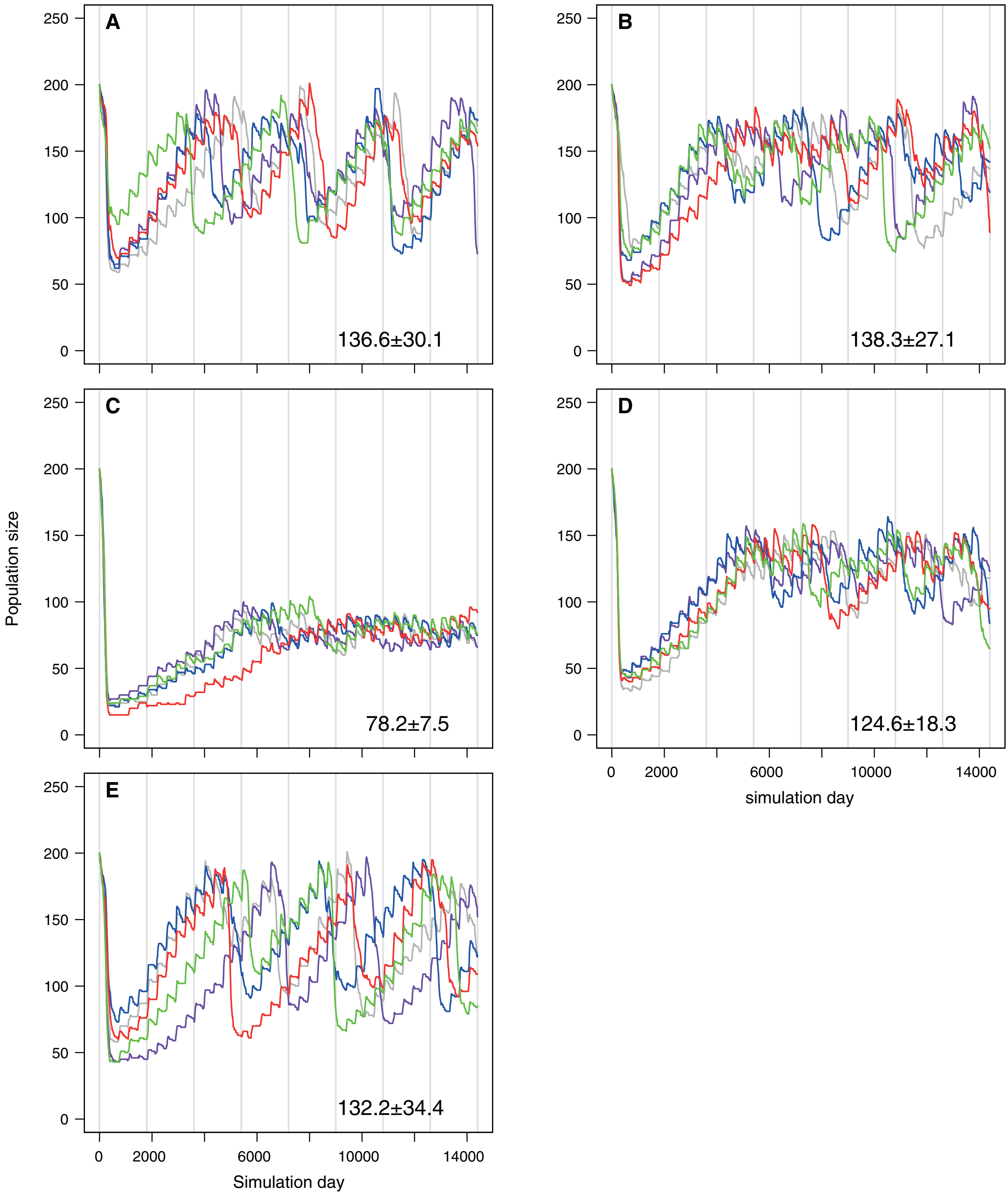


Figure 14. Porpoise population dynamics under different disturbance scenarios, with five replicate runs for each scenario. A: Reference scenario without wind farms and ships, B: with existing wind farms, C: with ships (full impact), D: with ships, half impact, E: construction of wind farms at Kriegers Flak and Store Middelgrund (see details in Table 1). Vertical lines indicate five simulation years and numbers on the y-axis show number of porpoise super-individuals. Values in the lower right of the plots show mean population sizes ±SD for the last 20 years of the simulations.

The reference scenario, the one that included post-construction disturbance from all existing wind farms and the one that investigated potential effect of constructing new wind farms at Kriegers Flak and Store Middelgrund (Figures 14E and 15) all predicted population sizes of between 100 and 200 super-individuals. In the scenario investigating the construction of wind farms the population growth was unaltered in the years where noise from pile driving was included in the model, i.e. in simulation years 1, 10, 20 and 30. The average population sizes were approximately equal in all scenarios, and all populations appeared to be cyclic, with a periodicity of approximately 6–15 years.

In contrast to wind farms, disturbance by ships may have a substantial impact on the porpoise population. We investigated the effects of ship traffic in two different scenarios, both including a number of large ships corresponding to the number of ships currently passing through Kattegat on the main shipping routes. In the scenario that assumed a relatively benign disturbance by ships (half impact; Figure 14D), the long-term mean number of simulated porpoises was reduced to 125, and the maximum number of porpoises was substantially below the 200 that were observed in the reference simulation. In this scenario the average impact for the ships was 3.71±0.59 (mean ± 1 SD), which may cause porpoises to react to them at distances up to 1.1 km. In the scenario that assumed a strong effect of ships on porpoise movement (full impact; Figure 14C) the mean number of simulated porpoises was reduced to 78 and the maximum population size was reduced to approximately 100.

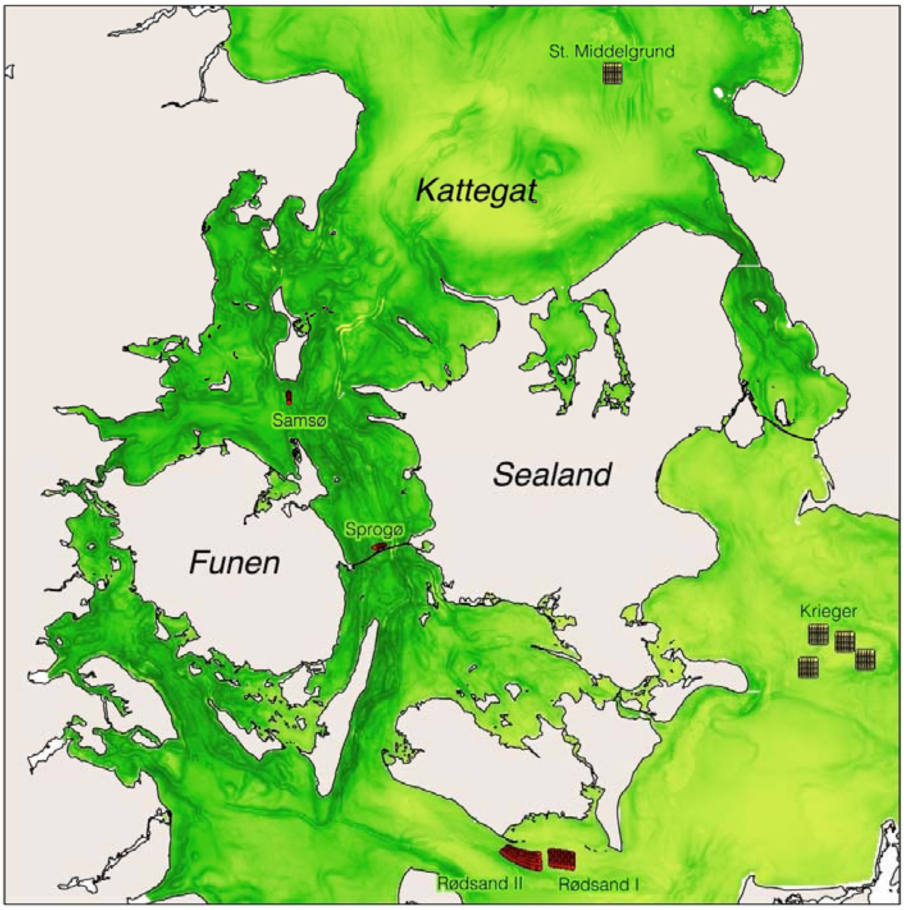


Figure 15. Positions of existing wind farms (red) and potential wind farms (yellow). The dark background colours indicate areas with high probability of encountering porpoises in season 3 (June–August) based on Maxent-values (Edrén*et al.* 2010).

5 Discussion

5.1 Natural dynamics of the Kattegat porpoise population

Our study demonstrates how a structurally realistic model, where the dynamics of the porpoise population ultimately results from foraging behaviour in a complex landscape, can produce population dynamics that is not related to the input parameters in a trivial manner (Figures 12 and 14). The model is a big improvement over earlier models of porpoise population dynamics, where the population growth rates were treated as unrelated to the population size (Caswell et al. 1998). In our model the population tends to grow beyond the long-term carrying capacity, which results in over-exploitation of the resources and a steep decrease in the population size.

The time it takes the population to reach carrying capacity after a severe reduction is closely related to the porpoises' reproductive patterns. These are relatively well known (Read 1990, Read and Hohn 1995, Lockyer 2003) and we therefore believe that the rates of population increase predicted by the model can be considered to be relatively robust. As long as the population size does not fall below a critical level where the individuals can no longer find each other and mate (the so-called Allee effect, Stephens et al. 1999) it is likely to be able to recover from even quite severe reductions in population size over a period of 5–20 years. Such population recovery is, however, less likely to occur if the population is exposed to repeated severe disturbances(Nabe-Nielsen et al. 2010a) as might be the case if the population is exposed to high levels of bycatch every year.

Several different mechanisms may cause the population to decline less abruptly in nature than it does in our model. First of all, the individuals in our model are identical. They have the same knowledge of which areas to disperse to in order to have a high likelihood of finding food, and they are all equally likely to die. In nature some individuals are weak, possibly because they are parasitized, infected or because they do not know about the best foraging sites. These individuals are likely to die relatively early when food becomes scarcer, which prevents the population from exceeding the long-term carrying capacity and also the subsequent rapid population decline. The population may also be prevented from growing beyond its carrying capacity by fluctuations in local food availability: some animals may experience high food levels, for example if they have encountered a school of herrings, while others are starving. This can result in a differentiated mortality and cause the population growth to level off before the total amount of food starts decreasing. The real porpoise population in Kattegat may therefore fluctuate less than predicted by our model, but there is no data available that allows us to investigate this.

Interestingly, the dynamics of the population also affects its spatial distribution. When the population is small the competition for food is less intense in the most favourable areas. This causes the porpoises' energy levels to keep increasing, and the decreasing energy levels that trigger dispersal therefore never occur. This could potentially influence our estimates of the population-level effects of disturbances by ships and wind-farms. If a wind farm is placed in a sub-optimal porpoise habitat, it may potentially still scare some animals away when the population size is at its maximum. When the population size is at its minimum the animals most likely stay in more favourable areas, and the wind farm will therefore not affect them. This suggests that even if wind farms etc. scare porpoises away from an area it does not necessarily have a strong impact on the population dynamics as long as they are placed in areas of low quality. These areas may be little used by porpoises when the population size is small and relatively vulnerable.

5.2 The relative impact of ships and wind farms on porpoise dynamics

The simulations based on the Porpoise IBM do not suggest that the existing wind farms have any impact on porpoise population dynamics, or that construction of new wind farms at Kriegers Flak or Store Middelgrund will cause any changes in the long-term dynamics of the population. The simulations of the post-construction effects of wind farms assume that noise from wind turbines result in substantially reduced porpoise densities up to 200 m from the turbines (deter. coeff. = 8 and deter. dist. = 300 m; Figure 10), which is probably a relatively conservative estimate[2]. The apparent lack of an effect of wind farms may have several different explanations. First of all the area where porpoises are potentially disturbed by wind farms is small in comparison to the range of the population, so even if the existing wind farms scared porpoises away entirely, they would only cause a minor reduction in the total amount of food available. Further, the existing wind farms are located outside the areas where porpoises most frequently occur (cf. Edrén et al. 2010) and away from areas used for dispersal between different porpoise hot spots. Thus, future large scale wind farms placed inside important porpoise areas may have a much stronger effect on the population than seen in this study. Beside the possible negative effects of wind turbines that are included in the model, they may have several positive effects that have not been included. The turbine foundations may, for example, act as artificial reefs, which could result in increased food availability in the vicinity of the wind farms. This, together with a possible reduction in the fishing intensity in wind farm areas and a gradual habituation to noise from turbines may potentially cause wind farms to have a positive net effect on the porpoise population.

The ship traffic may, in contrast to the wind farms, have a substantial negative impact on the porpoise population. If we assume that the 'half impact' scenario of how strongly porpoises are scared away from ships is correct, our model predicts that the porpoise population could increase by 10 % if the noise from the existing large ships could somehow be removed. We suspect that porpoises are less likely to become accustomed to noise from ships than from stationary wind turbines, except maybe in the vicinity of harbours, and the effects of ships on porpoise movement and population dynamics is therefore likely to persist. Porpoises are in-

[2]Conservative in the sense that the assumed effect of noise is likely to be overestimated, cf. Madsen et al. (2006) and Tougaard et al (2009).

cluded in the EU Habitats Directive Annexes II and IV (EU 1992), and it is therefore necessary to consider how an alteration of the shipping routes through Kattegat may affect the porpoise population. Our results suggest that intense ship traffic may cause a substantial reduction in the population size, and it may therefore be necessary to avoid new shipping routes that go through porpoise high-density areas.

In the current scenarios of the effect of ships we assume that porpoises react to them by turning away, and that their memory of having been scared by a ship decreases rapidly during the 2.5 hours after encountering the ship. We know that noise emitted by ships is audible to porpoises at long distances, but have no knowledge about how the individuals react to the noise, how persistent the reaction is, how it is related to the size and speed of the ships and to environmental variation. Such information, which can currently only be obtained using dead-reckoning loggers, is essential for predicting the exact consequences of e.g. new shipping routes.

5.3 Limitations of the model predictions

It is important to bear in mind that although the Porpoise IBM can predict the relative impact of various kinds of disturbances and management actions, it cannot be expected to produce reliable predictions about the future porpoise population sizes in Kattegat. In many cases the dynamics of real populations are strongly influenced by events that cannot be predicted, and that therefore cannot be included in a simulation model (c.f. discussion by Taleb 2007). Examples of events that may have a strong impact on the Kattegat porpoise population, but are difficult to predict, include oil spills, new diseases that appear in Denmark due to a climate changes and increased by-catch caused by the introduction of new fishing gear.

The predictions of the model may be influenced by variations in the porpoises’ fine-scale behaviour. At the moment our knowledge of their fine-scale behaviour is based on data from a single animal. If the porpoises’ intrinsic behaviour (which we simulate using a correlated random walk) is affected by environmental variation, it may affect the way they search for food in other habitat types. This may, for example, cause them to turn less steeply after consecutive half-hour steps when swimming in deep water. This could at the same time affect the relative importance of the intrinsic behaviour and the effect of deterrence by disturbing object, although the exact effect is unclear.

The predictions of the model are strongly affected by how we simulate the porpoises’ response to disturbances. In the case of wind farms we calibrated the model to generate realistic, but relatively conservative, porpoise density estimates in different distances from the turbines (decreased densities <200 m from the turbine, based on Figure 10). In the case of large ships (the ones required to have an AIS transmitter), we do not have similar density estimates, and the predictions of the mode therefore assume that the porpoises react to noise emitted by ships in the same way as they do to noise emitted by wind turbines. It is possible that porpoises become habituated to ship-noise, or that the effect of noise emitted by ships varies geographically or depending on whether the porpoise have calves or not. This may affect the predicted impact of ships on porpoise population dynamics, and the effect of ship-noise on porpoise behaviour therefore deserves to be studied further.

5.4 Future developments of the model

The model is currently limited to predicting effects of disturbances and by-catch in Kattegat and the Belt Seas. It would be extremely interesting to also investigate the effects of establishing marine protected areas (MPAs) or new wind farms in different areas of the North Sea. In order to do so three different kinds of data are needed: (1) it is necessary to investigate the geographical delimitation of the population that is found in the area under consideration for establishment of an MPA or wind farm. Populations that are limited to a small geographical region, as might for example be the case for the Belt Sea population, are more fragile than populations that cover large areas. This delimitation of the population can take place using Argos satellite telemetry or genetic methods. The range of the population should determine the extent of the landscape used in the simulation model. (2) It is necessary to identify the porpoise hot spots within the population's geographical range, i.e. areas with environmental conditions that permit particularly high porpoise densities. This could be done statistically, for example using the Maxent method mentioned previously. Instead of basing the analysis of porpoise abundance on satellite-tracked animals it would be possible to use data from acoustic surveys. (3) It is necessary to include information on the fine-scale movements of porpoises in the place that the simulation should cover. Porpoises in the North Sea are less affected by proximity to land, may eat other kinds of food and have a diving behaviour that differs from the only animal we have data for, which is from the Great Belt. It is therefore not necessarily recommendable to incorporate the dead-reckoning data from the Inner Danish Waters in a model for the North Sea populations.

6 Literature

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Appendix 1 – Detailed model documentation

The model documentation presented here follows a standard that is recommended for describing the structure of individual-based simulation models (Grimm et al. 2006). Appendix 1 complements the main text of the report by going into details on parts of the model that have not been discussed in the main text, but does not discuss the calibration process, scenarios or results.

Odd for the harbour porpoise population model

Purpose

The purpose of the model is to investigate the relative impact of wind farms and ship traffic on the dynamics of Danish harbour porpoise populations. The noise from wind farms and ships may scare porpoises away and thereby cause habitat fragmentation and reduced amounts of available food, which is likely to affect porpoise population sizes.

State variables and scales

Individuals are characterised by the state variables: age, energetic status, pregnancy status and lactating. Each individual in the model represent 30 female porpoises. Animals in the age class 8 months to 3.44 years are independent juveniles (cf. Read 1990 and Lockyer and Kinze. 2003). Younger animals (calves) are not included as independent individuals. The pregnancy status of independent animals can be pregnant/not pregnant, or infertile. Individuals are assumed not to interact except through their consumption of a common resource.

Anthropogenic objects (AOs) are characterised by the state variables: type and noise level. Two types of AO are modelled: wind turbines and boats (that are able to move).

Simulations are based on a 240 km wide and 400 km tall non-wrapped landscape divided into 400 x 400 m cells (i.e. 600x1000 cells in total) and sixty 40 x 40 km blocks. The landscape represents Kattegat and the waters between Denmark and Germany. It includes three kinds of environment: land (52.1%), water without food, and 1-cell large food patches. The amount of food in a patch is characterised by a variable food level.

Process overview and scheduling

The model runs in half-hour steps, and individuals respond to land and AOs by turning after each step. Fine-scale animal movement is modelled to result from a mixture of correlated random walk (CRW) behaviour and a memory-based ability to return to areas where individuals found food previously (see Nabe-Nielsen et al., submitted).

The animal energy level *E* is updated after each time step. The individuals' energy consumption per half-hour step is modelled to reflect basic metabolic costs, which are higher when the water is cold (approx. 15% increase in April and October and 30% in May–September; Lockyer et al. [2003]) and to increase when animals lactate (40% increase, M. Wahlberg, pers. comm.). The individuals' energy E level is scaled to lie in the range 0–20 in the model. When their energy level is higher than 10 they build up energy reserves, causing them to consume a smaller proportion of the food they encounter. This proportion is modelled to decrease linearly as the energy level increases from 10 to 20. The amount of food in the food patches is adjusted accordingly. Afterwards the food level increases logistically up to a maximum level; see details under Input.

Animal mortality is modelled to depend on their energetic status, with a yearly survival probability equal to $1 - \exp(-k \times E)$, where k is a positive constant. Animals risk dying each time step after updating their energetic status, and also die when reaching 30 years. Lactating animals abandon their offspring rather instead of dying, unless their energy level is ≤0. Further, the model includes an age and energy independent by-catch rate of 1.7% (the Ascobans safety limit for by-catch).

Animal reproduction is divided in three phases: mating, gestation and nursing. Mating peaks in August (Lockyer 2003), and in our model each individual has a mating day that is selected as a random normal variable with mean 7.5 x 30 and a standard deviation of 20. Individuals that are sexually mature, i.e. at least 3.44 years old (Read 1990) they are modelled to become pregnant with a probability of 0.68, following Read &Hohn (1995). After 10 months they give birth to a calf (Lockyer 2003). After a lactation period of eight months the calf gives rise to a new, independent individual with a probability of 0.5 (assuming equal sex ratio). Abortions of unborn calves is not taken into account.

Long-distance dispersal results from two different processes in the model: (1) if the average daily energy level decreases for three consecutive days, porpoises turn towards a 40 x 40 km block selected at random among the 12 blocks with highest expected quality (based on average Maxent value for the blocks each quarter; see Edrén et al. 2010) >40 km away. Afterwards they turn ≤20° in the direction with deepest water, provided that there is no land further away (8x disp-dist) in that direction. Finally they turn ≤30° to get as far away from land as possible if water depth <min-disp-dept or if <2 km from the coast. (2) When approaching the target block or if they are unable to get to an area with deep water (>min-disp-dept) the porpoises start moving away from the areas they visited the previous day. They attempt to stay at a constant distance from land if 1-4 km from land, else they try to get there. If the average energy level was higher 6–9 days ago than for the last three days the porpoise turns towards the place where it were three days ago. Finally the dispersing porpoises move disp-dist forward. The porpoises stop dispersing when they get trapped in areas with low water or when the current energy level is higher than at any time during the previous week. The target blocks are not selected entirely at random for animals that start dispersing immediately north of Djursland and Funen or E of Sealand, as these do not use directed dispersal.

Deterrence behaviour, i.e. the porpoises' reaction to wind turbines and ships, is related to the distance to the disturbing object (DO), to how much the object disturbs (its impact on the porpoise, IP) and to the maximum deterrence distance for a standard wind turbine, MD. Standard wind turbines (e.g. Rødsand II turbines) have IP=1. Whenever a porpoise gets closer than MD * IP from a ship or wind turbine, its movement direction in the next step is calculated as the sum of a deterrence vector and the vector defining the normal fine-scale movement. The deterrence vector is calculated as j * DC*(IP * MD - DO), where j is a unity vector pointing away from the disturbing object and DC is a constant deterrence coefficient that controls the balance between the standard fine-scale move and the deterrence effect throughout. The step length is not affected by the strength of the deterrence. The length of the deterrence vector therefore decreases linearly with distance to the disturbing object. This is similar to sound in water under some circumstances. At the end of each time step the length of the deterrence vector is halved, and after deter-time = 5 time steps it is set to zero (i.e. the porpoise only moves away from the disturbing object for deter-time time steps).

Variables describing the state of the food patches and of the individuals (except movement and energetic status) are updated daily in the following order: (1) increase food level in patches, (2) start dispersing if energy level drops, (3) die due to age-specific background mortality and loose unborn or lactating offspring (related to energetic status), (4) update pregnancy status: mate, give birth and weane lactating calves depending on time of year. Movement and energetic status of the individuals is updated in every time step.

See separate flowchart of animal-related processes in the model.

Design concepts

Emergence: Population dynamics emerge from the behaviour of the individuals and the balance between their energy expenditure (related to time, water temperature and lactation) and to their food acquisition rate.

Adaptation: Individuals' responses to land and AOs is fixed, and adaptation is not modelled explicitly.

Fitness: Shifts between two different types of movement behaviour is modelled to result from optimal foraging based on an evaluation of the amount of food acquired in the past.

Sensing: Individuals are modelled to respond to the presence of land and AOs by adjusting their movement behaviour, but the response is assumed to be independent of their state.

Interaction: Interactions among individuals are modelled implicitly through their competition for food.

Stochasticity: Both movement (direction and distance moved when moving locally), mortality, mating date and dispersal behaviour (which area to disperse to) depend on stochastic processes.

Collectives (groups of individuals): Animals do not interact in the model, except that juveniles are inextricably linked to their mother till they finish lactating.

Observation (collecting data from the IBM): The positions of the individuals are sampled monthly and compared to an independent dataset. The age-class distribution and age specific mortality is sampled yearly and compared to independent datasets.

Initialisation

The model is initialised by creating 300 porpoises and 9600 randomly distributed food patches. The initial energy level of the porpoises is modelled as a random normal variable with mean 10 and standard deviation one. Each patch has a size of one cell. Both the patch size and the number of patches (on the average 1000 per 100 x 100 km) correspond to the numbers used in the movement model. The patch locations remain constant among model runs. Patches that happen to be on land are subsequently removed so only 4572 food patches are retained. The simulation is initiated on 1 January, which affects the food replenishment rate.

Input

The food level in the randomly distributed food patches increases logistically after being eaten. The maximum food level is calculated as the season-specific Maxent value for the patch divided by the mean season-specific Maxent value for the entire landscape. Maxent values fall in the range 0–1, with high values in areas with environmental conditions resembling the ones found in areas with a high porpoise density (Edrén et al. 2010). The first season covers the months December–February. The rate of increase in the amount of food is kept constant (r_U) = 0.2). See details in Nabe-Nielsen et al. (submitted).

Appendix 2 – Standard settings

Parameter name	Value	Description
"e-use-per-30min"	2.8	
"k-survival-prob-const"	0.4	See Figure 4
"m-juv-mort-const"	0.5	See Figure 4
"m-mort-prob-const"	0.5	See Figure 4
"deter-time"	5	
"n-disp-targets"	12	Number of possible dispersal targets
"food-growth-rate"	1.01	Logistic growth parameter
"debug"	0	Various debugging options
"mean-disp-dist"	1.6	
"wind-farms"	"off"	
"bycatch-prob"	0.017	
"deterrence-coeff"	8	See Figure 10
"std-deterrence-dist"	300	See Figure 10
"min-dist-to-target"	100	Dispersal parameter
"min-disp-depth"	4	Dispersal parameter
"e-use-per-km"	0	Energy use related to time only
"n-porps"	200	Initial population size
"max-sim-day"	10000	When to stop
"model"	4	Models <4 do not include pop. dyn.
"pile-driving"	false	Wind farms under construction
“Umax”	1	Maximum patch utility (when notlimited by low Maxent value)

Appendix 3 – Wind turbines used in the analyzed scenarios

The list includes the UTM-coordinates of all wind turbines that were included in scenarios investigating the effects of existing wind farms. The impact was modelled as identical for all turbines.

Rødsand I			Rødsand II			Potential St. Middelgrund		
id	x	y	id	x	y	id	x	y
A1	672418	6050159	I01	660623	6051247	S1-1	687675	6264664
A2	672424	6049680	I02	661164	6050979	S1-2	687675	6265164
A3	672455	6049202	I03	661668	6050759	S1-3	687675	6265664
A4	672473	6048713	I04	662261	6050527	S1-4	687675	6266164
A5	672491	6048234	I05	662775	6050346	S1-5	687675	6266664
A6	672510	6047756	I06	663314	6050157	S1-6	687675	6267164
A7	672528	6047266	I07	663841	6049978	S1-7	687675	6267664
A8	672546	6046788	I08	664332	6049837	S1-8	687675	6268164
A9	672564	6046310	I09	664852	6049714	S1-9	687675	6268664
B1	673277	6050046	I10	665372	6049580	S1-10	687675	6269164
B2	673296	6049557	I11	665833	6049510	S1-11	688475	6264664
B3	673314	6049079	I12	666345	6049419	S1-12	688475	6265164
B4	673332	6048600	I13	666828	6049351	S1-13	688475	6265664
B5	673350	6048122	I14	667313	6049299	S1-14	688475	6266164
B6	673369	6047633	I15	667777	6049267	S1-15	688475	6266664
B7	673387	6047154	I16	668257	6049238	S1-16	688475	6267164
B8	673406	6046676	I17	668727	6049219	S1-17	688475	6267664
B9	673424	6046187	I18	669201	6049234	S1-18	688475	6268164
C1	674136	6049923	J01	660189	6050898	S1-19	688475	6268664
C2	674154	6049445	J02	660729	6050585	S1-20	688475	6269164
C3	674173	6048967	J03	661277	6050303	S1-21	689275	6264664
C4	674191	6048477	J04	661833	6050042	S1-22	689275	6265164
C5	674210	6047999	J05	662355	6049815	S1-23	689275	6265664
C6	674228	6047521	J06	662909	6049584	S1-24	689275	6266164
C7	674246	6047042	J07	663455	6049362	S1-25	689275	6266664
C8	674265	6046553	J08	663971	6049178	S1-26	689275	6267164
C9	674284	6046075	J09	664417	6049043	S1-27	689275	6267664
D1	674995	6049811	J10	665069	6048838	S1-28	689275	6268164
D2	675010	6049422	J11	665567	6048727	S1-29	689275	6268664
D3	675032	6048844	J12	666116	6048599	S1-30	689275	6269164
D4	675057	6048362	J13	666645	6048494	S1-31	690075	6264664
D5	675069	6047887	J14	667170	6048409	S1-32	690075	6265164
D6	675088	6047398	J15	667685	6048346	S1-33	690075	6265664
D7	675106	6046919	J16	668217	6048287	S1-34	690075	6266164
D8	675125	6046441	J17	668741	6048242	S1-35	690075	6266664
D9	675143	6045963	J18	669269	6048235	S1-36	690075	6267164
E1	675854	6049689	K01	659755	6050549	S1-37	690075	6267664
E2	675872	6049210	K02	660293	6050192	S1-38	690075	6268164
E3	675891	6048732	K03	660841	6049867	S1-39	690075	6268664
E4	675910	6048254	K04	661405	6049557	S1-40	690075	6269164

E5	675928	6047764
E6	675947	6047286
E7	675965	6046808
E8	675984	6046318
E9	676003	6045840
F1	676713	6049577
F2	676731	6049099
F3	676750	6048609
F4	676769	6048131
F5	676788	6047653
F6	676807	6047164
F7	676825	6046685
F8	676844	6046207
F9	676862	6045729
G1	677572	6049455
G2	677591	6048976
G3	677609	6048498
G4	677628	6048020
G5	677647	6047530
G6	677666	6047052
G7	677685	6046574
G8	677704	6046085
G9	677722	6045606
H1	678431	6049344
H2	678450	6048865
H3	678469	6048376
H4	678478	6047897
H5	678497	6047419
H6	678516	6046930
H7	678535	6046451
H8	678554	6045973
H9	678572	6045495

Sprogø

id	**x**	**y**
S1	626063	6135250
S2	625627	6135140
S3	625190	6135030
S4	624754	6134920
S5	624318	6134810
S6	623882	6134700
S7	623445	6134590

K05	661934	6049285
K06	662505	6049010
K07	663070	6048746
K08	663610	6048519
K09	664182	6048312
K10	664766	6048095
K11	665301	6047944
K12	665935	6047766
K13	666463	6047636
K14	667027	6047519
K15	667592	6047424
K16	668177	6047336
K17	668756	6047266
K18	669337	6047235
L01	659321	6050200
L02	659858	6049798
L03	660404	6049431
L04	660977	6049072
L05	661514	6048754
L06	662100	6048437
L07	662684	6048130
L08	663249	6047859
L09	663847	6047612
L10	664463	6047353
L11	665036	6047162
L12	665657	6046959
L13	666280	6046779
L14	666884	6046629
L15	667500	6046502
L16	668137	6046386
L17	668821	6046289
L18	669405	6046236
M01	658887	6049851
M02	659422	6049405
M03	659968	6048995
M04	660549	6048587
M05	661093	6048224
M06	661696	6047863
M07	662298	6047514
M08	662888	6047200
M09	663512	6046911
M10	664160	6046611
M11	664770	6046379
M12	665428	6046139
M13	666097	6045922
M14	666741	6045739
M15	667407	6045580
M16	668097	6045435
M17	668786	6045313
M18	669354	6045250

S1-41	690875	6264664
S1-42	690875	6265164
S1-43	690875	6265664
S1-44	690875	6266164
S1-45	690875	6266664
S1-46	690875	6267164
S1-47	690875	6267664
S1-48	690875	6268164
S1-49	690875	6268664
S1-50	690875	6269164
S1-51	691675	6264664
S1-52	691675	6265164
S1-53	691675	6265664
S1-54	691675	6266164
S1-55	691675	6266664
S1-56	691675	6267164
S1-57	691675	6267664
S1-58	691675	6268164
S1-59	691675	6268664
S1-60	691675	6269164

Samsø

id	**x**	**y**
sa1	599514	6177761
sa2	599514	6177463
sa3	599514	6177156
sa4	599530	6176850
sa5	599538	6176252
sa6	599538	6176252
sa7	599561	6175655
sa8	599561	6175655
sa9	599569	6175357
sa10	599569	6175050

Potential Krieger

id	x	y	id	x	y
K1-1	742272	6098863	K3-1	752366	6106045
K1-2	742272	6099363	K3-2	752366	6106545
K1-3	742272	6099863	K3-3	752366	6107045
K1-4	742272	6100363	K3-4	752366	6107545
K1-5	742272	6100863	K3-5	752366	6108045
K1-6	742272	6101363	K3-6	752366	6108545
K1-7	742272	6101863	K3-7	752366	6109045
K1-8	742272	6102363	K3-8	752366	6109545
K1-9	742272	6102863	K3-9	752366	6110045
K1-10	742272	6103363	K3-10	752366	6110545
K1-11	743072	6098863	K3-11	753166	6106045
K1-12	743072	6099363	K3-12	753166	6106545
K1-13	743072	6099863	K3-13	753166	6107045
K1-14	743072	6100363	K3-14	753166	6107545
K1-15	743072	6100863	K3-15	753166	6108045
K1-16	743072	6101363	K3-16	753166	6108545
K1-17	743072	6101863	K3-17	753166	6109045
K1-18	743072	6102363	K3-18	753166	6109545
K1-19	743072	6102863	K3-19	753166	6110045
K1-20	743072	6103363	K3-20	753166	6110545
K1-21	743872	6098863	K3-21	753966	6106045
K1-22	743872	6099363	K3-22	753966	6106545
K1-23	743872	6099863	K3-23	753966	6107045
K1-24	743872	6100363	K3-24	753966	6107545
K1-25	743872	6100863	K3-25	753966	6108045
K1-26	743872	6101363	K3-26	753966	6108545
K1-27	743872	6101863	K3-27	753966	6109045
K1-28	743872	6102363	K3-28	753966	6109545
K1-29	743872	6102863	K3-29	753966	6110045
K1-30	743872	6103363	K3-30	753966	6110545
K1-31	744672	6098863	K3-31	754766	6106045
K1-32	744672	6099363	K3-32	754766	6106545
K1-33	744672	6099863	K3-33	754766	6107045
K1-34	744672	6100363	K3-34	754766	6107545
K1-35	744672	6100863	K3-35	754766	6108045
K1-36	744672	6101363	K3-36	754766	6108545
K1-37	744672	6101863	K3-37	754766	6109045
K1-38	744672	6102363	K3-38	754766	6109545
K1-39	744672	6102863	K3-39	754766	6110045
K1-40	744672	6103363	K3-40	754766	6110545
K1-41	745472	6098863	K3-41	755566	6106045
K1-42	745472	6099363	K3-42	755566	6106545
K1-43	745472	6099863	K3-43	755566	6107045
K1-44	745472	6100363	K3-44	755566	6107545
K1-45	745472	6100863	K3-45	755566	6108045
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K1-48	745472	6102363	K3-48	755566	6109545
K1-49	745472	6102863	K3-49	755566	6110045
K1-50	745472	6103363	K3-50	755566	6110545

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K1-52	746272	6099363	K3-52	756366	6106545
K1-53	746272	6099863	K3-53	756366	6107045
K1-54	746272	6100363	K3-54	756366	6107545
K1-55	746272	6100863	K3-55	756366	6108045
K1-56	746272	6101363	K3-56	756366	6108545
K1-57	746272	6101863	K3-57	756366	6109045
K1-58	746272	6102363	K3-58	756366	6109545
K1-59	746272	6102863	K3-59	756366	6110045
K1-60	746272	6103363	K3-60	756366	6110545
K2-1	745054	6108181	K4-1	757996	6101127
K2-2	745054	6108681	K4-2	757996	6101627
K2-3	745054	6109181	K4-3	757996	6102127
K2-4	745054	6109681	K4-4	757996	6102627
K2-5	745054	6110181	K4-5	757996	6103127
K2-6	745054	6110681	K4-6	757996	6103627
K2-7	745054	6111181	K4-7	757996	6104127
K2-8	745054	6111681	K4-8	757996	6104627
K2-9	745054	6112181	K4-9	757996	6105127
K2-10	745054	6112681	K4-10	757996	6105627
K2-11	745854	6108181	K4-11	758796	6101127
K2-12	745854	6108681	K4-12	758796	6101627
K2-13	745854	6109181	K4-13	758796	6102127
K2-14	745854	6109681	K4-14	758796	6102627
K2-15	745854	6110181	K4-15	758796	6103127
K2-16	745854	6110681	K4-16	758796	6103627
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K2-18	745854	6111681	K4-18	758796	6104627
K2-19	745854	6112181	K4-19	758796	6105127
K2-20	745854	6112681	K4-20	758796	6105627
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K2-22	746654	6108681	K4-22	759596	6101627
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K2-25	746654	6110181	K4-25	759596	6103127
K2-26	746654	6110681	K4-26	759596	6103627
K2-27	746654	6111181	K4-27	759596	6104127
K2-28	746654	6111681	K4-28	759596	6104627
K2-29	746654	6112181	K4-29	759596	6105127
K2-30	746654	6112681	K4-30	759596	6105627
K2-31	747454	6108181	K4-31	760396	6101127
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K2-33	747454	6109181	K4-33	760396	6102127
K2-34	747454	6109681	K4-34	760396	6102627
K2-35	747454	6110181	K4-35	760396	6103127
K2-36	747454	6110681	K4-36	760396	6103627
K2-37	747454	6111181	K4-37	760396	6104127
K2-38	747454	6111681	K4-38	760396	6104627
K2-39	747454	6112181	K4-39	760396	6105127
K2-40	747454	6112681	K4-40	760396	6105627
K2-41	748254	6108181	K4-41	761196	6101127
K2-42	748254	6108681	K4-42	761196	6101627
K2-43	748254	6109181	K4-43	761196	6102127

K2-44	748254	6109681	K4-44	761196	6102627
K2-45	748254	6110181	K4-45	761196	6103127
K2-46	748254	6110681	K4-46	761196	6103627
K2-47	748254	6111181	K4-47	761196	6104127
K2-48	748254	6111681	K4-48	761196	6104627
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K2-50	748254	6112681	K4-50	761196	6105627
K2-51	749054	6108181	K4-51	761996	6101127
K2-52	749054	6108681	K4-52	761996	6101627
K2-53	749054	6109181	K4-53	761996	6102127
K2-54	749054	6109681	K4-54	761996	6102627
K2-55	749054	6110181	K4-55	761996	6103127
K2-56	749054	6110681	K4-56	761996	6103627
K2-57	749054	6111181	K4-57	761996	6104127
K2-58	749054	6111681	K4-58	761996	6104627
K2-59	749054	6112181	K4-59	761996	6105127
K2-60	749054	6112681	K4-60	761996	6105627

EFFECTS OF WIND FARMS ON HARBOUR PORPOISE BEHAVIOUR AND POPULATION DYNAMICS

Report commissioned by The Environmental Group under the Danish Environmental Monitoring Programme

We developed an individual-based simulation model in order to study the cumulative impacts of wind farms and ship traffic on the long-term survival and population dynamics of the harbour porpoise *(Phocoena phocoena)* in Kattegat and the Belt Seas. The model is based on knowledge of the porpoises' fine-scale foraging behaviour, dispersal between areas where porpoises are commonly observed in nature and their reproductive patterns. It assumes that individual porpoises turn away more steeply from objects the more noisy they are, and that they react to the noise emitted from large ships at distances >1 km. Our simulations suggest that operating wind farms and wind farms under construction do not affect the size or dynamics of the harbour porpoise population in Kattegat. Ship traffic may, in contrast, cause the population size to decrease.

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