

Effects of noise and by-catch on a Danish harbour porpoise population



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ABSTRACT

Ships and wind turbines generate noise, which can have a negative impact on marine mammal populations by scaring animals away. Effective modelling of how this affects the populations has to take account of the location and timing of disturbances. Here we construct an individual-based model of harbour porpoises in the Inner Danish Waters. Individuals have their own energy budgets constructed using established principles of physiological ecology. Data are lacking on the spatial distribution of food which is instead inferred from knowledge of time-varying porpoise distributions. The model produces plausible patterns of population dynamics and matches well the age distribution of porpoises caught in by-catch. It estimates the effect of existing wind farms as a 10% reduction in population size when food recovers fast (after two days). Proposed new wind farms and ships do not result in further population declines. The population is however sensitive to variations in mortality resulting from by-catch and to the speed at which food recovers after being depleted. If food recovers slowly the effect of wind turbines becomes negligible, whereas ships are estimated to have a significant negative impact on the population. Annual by-catch rates $\geq 10\%$ lead to monotonously decreasing populations and to extinction, and even the estimated by-catch rate from the adjacent area (approximately 4.1%) has a strong impact on the population. This suggests that conservation efforts should be more focused on reducing by-catch in commercial gill-net fisheries than on limiting the amount of anthropogenic noise. Individual-based models are unique in their ability to take account of the location and timing of disturbances and to show their likely effects on populations. The models also identify deficiencies in the existing database and can be used to set priorities for future field research.

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1. Introduction

Disturbances can affect animal foraging and dispersal with large effects on individual fitness and population survival (Kerley et al., 2002; Tuomainen and Candolin, 2011). Their effects on fitness are partly caused by the exclusion of animals from high-quality foraging areas (Baveco et al., 2011; Gill et al., 1996) and partly by the net energy losses associated with fleeing from disturbances (Rodríguez-Prieto and Fernández-Juricic, 2005). Disturbances contribute to the fragmentation of landscapes and can have particularly

large effects on population dynamics in fragmented landscapes where local subpopulations recover more slowly (Altermatt et al., 2011; Nabe-Nielsen et al., 2010). As the impacts of anthropogenic disturbances to a large extent arise from their effect on animal movements, effective conservation of species in disturbed habitats must be built on a better understanding of the link between animal movement and population dynamics. Although this it is widely recognised (Buchholz, 2007; Caro, 2007; Gonzalez-Suarez and Gerber, 2008) the effects of disturbances on animal behaviour are rarely taken into account when managing populations.

Animals in natural environments are exposed to a wide range of factors that influence their fitness, including multiple types of disturbance, predation, competition and variations in food availability. These factors may influence fitness directly, e.g. by increasing the animals' probability of dying, or indirectly by influencing their energy balance. As the influence of the different factors varies in both space and time, their cumulative impact on the fate of the population is most appropriately studied using spatially explicit models such as behaviour-based individual-based models (IBMs;

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sometimes referred to as agent-based models) (Bennett et al., 2009; Davidson et al., 2012). One advantage of IBMs is that they make it possible to study the population-level consequences of altered animal movements, for example changed foraging behaviour in disturbed areas, while at the same time allowing the incorporation of direct mortality events.

The study of cumulative effects is particularly challenging in marine environments where it is often difficult to quantify the spatial and temporal distribution of resources, disturbances and other factors that affect the organisms living there. Nevertheless there is an increasing demand for such studies in order to evaluate the potential effects of different management options (Crain et al., 2008; Korpinen et al., 2012). When multiple stressors interact synergistically, as would be the case if additional sources of noise prevent animals from moving through the last remaining corridor to important foraging areas, it may have large effects on the population. Perhaps the largest challenge is to quantify the distribution of resources. For many marine organisms, including most marine mammals, little is known about the distribution of the prey they depend on. For species with low energy storage capacities the spatial distribution of food may instead be assessed indirectly by assuming that the habitat types where animals spend most time are also the ones where their food is abundant. In this study we demonstrate how this approach can be used for modelling the prey distribution in an IBM for the harbour porpoise (*Phocoena phocoena*) population in the Inner Danish Waters (IDW).

The potential carrying capacity for the modelled porpoise population, that is, the equilibrium population size in the absence of human activities, would presumably be determined by the amount of available food as is generally the case for mammals (Sinclair, 1989). The size of the population has, however, most likely been reduced by by-catch in commercial fisheries (Berggren et al., 2002; Fock, 2011) as well as by anthropogenic disturbances. Noise from large ships and operational noise from wind turbines may, for example, affect porpoises in large parts of their range. The relative importance of different kinds of disturbances and by-catch for the population is, however, not known. In this paper we investigate the cumulative effects of noise and by-catch on the harbour porpoise population in the IDW. We examine their relative impacts on equilibrium population size and population resilience and consider whether effects are additive, synergistic or antagonistic (Crain et al., 2008).

2. Methods

2.1. Study species

The harbour porpoise is a small cetacean that is wide spread along the coasts of Europe and North America. The porpoises in the IDW constitute a distinct population (Andersen et al., 1997; Wiemann et al., 2010) that predominately preys on cod (*Gadus morhua*) and pelagic herring (*Clupea harengus*), but also on gobies (Gobiidae) and a number of other benthic species (Aarefjord et al., 1995; Börjesson et al., 2003). Many of these species have a patchy distribution, either because they occur in schools or because they are associated with particular microhabitats. The porpoise population is particularly dense in the areas around Funen and north of Sealand (Edrén et al., 2010; Sveegaard et al., 2011) where food is presumably abundant. The animals often stay within a limited area for weeks, although they are capable of dispersing between different parts of their range at speeds of up to at least 30–40 km per day for several days (J. Teilmann unpubl. data). Porpoises only occasionally collaborate in catching prey, although they sometimes occur in small groups (SCANS II, 2008).

Reproduction is a major determinant of the porpoises' population dynamics. Female porpoises on the average become sexually mature when 3.4 years old (Read, 1990). After the mating season, which peaks in August (Lockyer, 2003), 68% of the adult females are pregnant (Read and Hohn, 1995). After ten months they give birth to a single calf that stays together with them for approximately eight months while lactating (Lockyer, 2003; Lockyer and Kinze, 2003). Adult females are able to mate even when they are lactating.

The natural mortality of porpoises is presumably related to their energy levels, as is the case for a wide range of animal species (Sibly et al., 2013). Data from captive animals suggest that they spend energy at a constant rate, which increases up to about 30% when the water temperature drops during winter (Lockyer et al., 2003) and up to 40% when animals lactate (Magnus Wahlberg, pers. comm.). In addition to the natural mortality porpoises are frequently bycaught in gillnet fisheries. In the North Sea an estimated 5900 animals were bycaught annually in 1987–2001 just by the Danish gillnet fleet (Vinter and Larsen, 2004). No estimate of the bycatch rate exists for the IDW. This incidental bycatch in gillnet fisheries is considered a significant threat to harbour porpoises in European waters (Carlström et al., 2009; Kock and Benke, 1996).

There is evidence that porpoises react to disturbances by being scared away. During the construction of offshore wind farms harbour porpoise densities are reduced up to 20 km away from the construction site (Brandt et al., 2011; Carstensen et al., 2006), and in at least one case (the Nysted Offshore Wind Farm) the porpoise densities remained low after several years of normal wind farm operation (Teilmann and Carstensen, 2012). In two studies from the North Sea porpoise densities were not reduced near the wind farm during normal operation (Scheidat et al., 2011; Tougaard et al., 2006). Little is known about how porpoises react to other kinds of disturbances, although they have been reported to avoid boats (Polacheck and Thorpe, 1990).

2.2. Model description

The model description follows the updated ODD (Overview, Design concepts, Details) protocol suggested by Grimm et al., 2006, 2010.

2.2.1. Purpose

The model simulates how harbour porpoise population dynamics are affected by by-catch and noise emitted from wind turbines and large ships. The animals' survival is related to their energy levels, and the population dynamics are affected by noise through its effect on the animals' foraging behaviour.

2.2.2. Entities, state variables, and scales

The model includes three kinds of agents: porpoises, wind turbines and ships. The porpoise agents are characterised by their location, speed, movement direction, age, age of maturity, energy level, pregnancy status and lactation status. Their energy levels are scaled to lie in the range 0–20. Each porpoise agent is a 'super individual' (Scheffer et al., 1995) representing several real-world female porpoises. The wind turbines are characterised by their location and noise level. Ships are characterised by location, speed, movement direction and noise level. Simulations are based on a 240 km × 400 km landscape covering the IDW around the islands Funen and Sealand (Fig. 1). The landscape is divided into 600 × 1000 grid cells, each covering 400 m × 400 m. The grid cells are characterised by their location, average water depth, distance to land, food level and maximum food level. The landscape includes land (52.1%), 4572 randomly distributed food patches with a size of 1 cell (0.76%) and water without food (47.1%). The distribution of the patches is the same as used by Nabe-Nielsen et al. (2013), i.e. it included on the average 1000 food patches per 100 km × 100 km. The

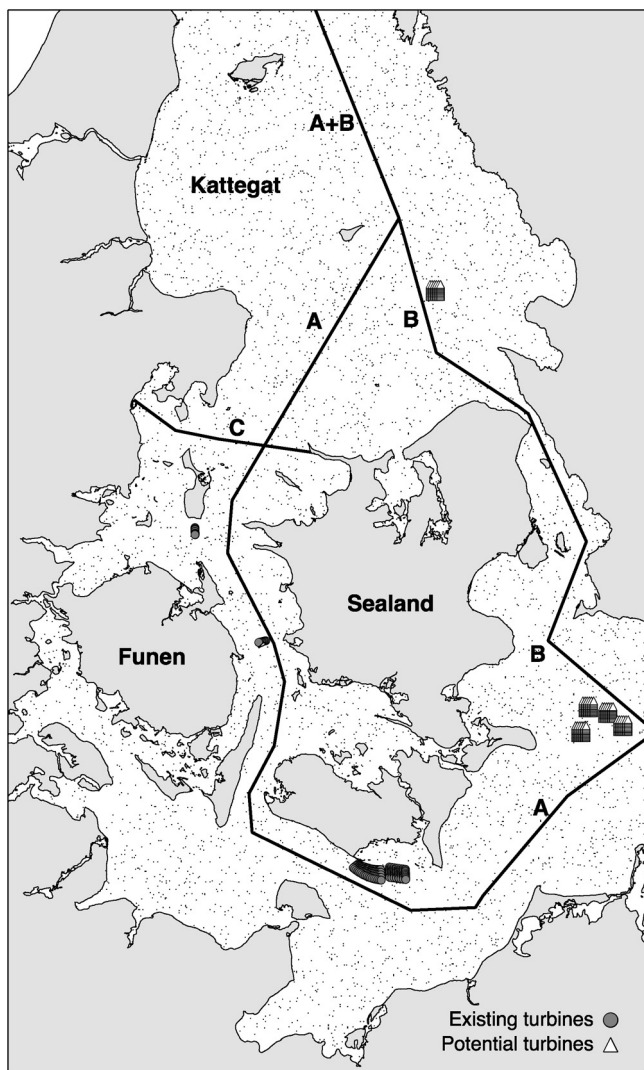


Fig. 1. Map of the study area in Denmark. Existing wind turbines are shown as grey circles and planned turbines are shown as white triangles. The 'existing wind turbines' do not encompass all turbines that are currently in operation in the Inner Danish Waters. Major ship routes are shown as black lines ((A) route through Great Belt between Funen and Sealand, (B) route through The Sound east of Sealand and (C) the Aarhus-Odden fast ferry route). Food patches are shown as small black dots.

average maximum food level was calculated for the patches in each $40 \text{ km} \times 40 \text{ km}$ square in the landscape (hereafter called 'potential food level'). The only other environmental parameter in the model is the time of year. Each simulation was allowed to run for 40 years using half-hour time steps.

2.2.3. Process overview and scheduling

In each time step all porpoises move and consume the food they encounter on their way, although they consume a decreasing fraction of the food as their energy levels increase from 10 to 20 (see details in Appendix A). Individual energy budgets were constructed following established principles of physiological ecology (Sibly et al., 2013). Consumption of food causes their energy levels to increase equivalently. They spend a fixed, but season dependent, amount of energy per time step. The animals' fine scale movements are controlled by a combination of correlated random walk (CRW) behaviour (Turchin, 1998) and a tendency to move towards patches where they previously found food. Nabe-Nielsen et al. (2013) provided a detailed description of the model that has been used for simulating the porpoises' fine scale movements in

the current paper. The contribution of the CRW behaviour is controlled by the amount of food found in the recent past. If the fine scale movements do not allow them to sustain their energy level they disperse towards squares with high potential food levels. The dispersal speeds and routes resemble those in satellite-tracked animals (Sveegaard et al., 2011). Porpoises whose energy levels were higher in the previous week turn back to where they then foraged. Turns are also made if there is land ahead or if ships or wind turbines are close, particularly if these have high noise levels (that is, the porpoises get scared by noise). The porpoises remain scared by the ships for 2.5 h, but the extent to which they are scared is halved at every time step. The animals move one at a time in an order that is randomised after each half-hour time step.

Once every day the porpoises may die, mate or become pregnant with a certain probability that depends on their energy levels and the time of the year (Fig. 2). 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), or they may lose it. Independent male porpoises were not included in the model.

The wind turbines in the model correspond to established and planned turbines in the IDW (Fig. 1). Ships move along the major Danish shipping routes at constant speeds. Noise levels are constant for both ships and wind turbines.

The food levels in the patches are dynamically changing. When a patch is visited by a porpoise its food level drops corresponding to the amount consumed by the porpoise, but afterwards it increases logarithmically in daily steps until reaching the maximum food level for the patch (see Appendix A). Whereas the logistic food growth rate is kept constant, the maximum food level in a patch depends on the time of the year and on where it is located. The season-specific maximum food level was obtained from maximum entropy (Maxent) estimates of where porpoises are most likely to occur (Edrén et al., 2010). These were calculated from the number of observations of satellite-tracked animals in areas with different environmental conditions.

2.2.4. Design concepts

Basic principles: The model builds on the assumption that the porpoise population is food limited, at least in the absence of anthropogenic effects. Whereas by-catch has a direct effect on population size, by causing a number of randomly selected animals to be removed from the population, noise acts by scaring porpoises away from areas with abundant resources, or by causing habitat fragmentation.

Emergence: Population size emerges from a balance between mortality and reproduction, where mortality is influenced by individual animals' energy levels. The spatial distribution of animals emerges from their tendency to disperse if their energy levels decrease and from their ability to return if necessary to patches where they previously found food. Age class distributions emerge from animals' energy-related mortality rates.

Adaptation: Animals react to decreasing food levels in particular patches by being less attracted to them and to decreasing energy levels by dispersing towards squares with high potential food levels.

Objectives: Animals attempt to optimise their foraging behaviour, and hence maximise their fitness, by returning to previously visited food patches when random walk movements result in a low food acquisition rate. Further, an animal starts dispersing towards a square with a high potential food level when its energy level continues to decrease.

Learning: Animals do not learn from what other animals have experienced. They do remember the location of previously visited food patches for some days (see details in Nabe-Nielsen et al., 2013).

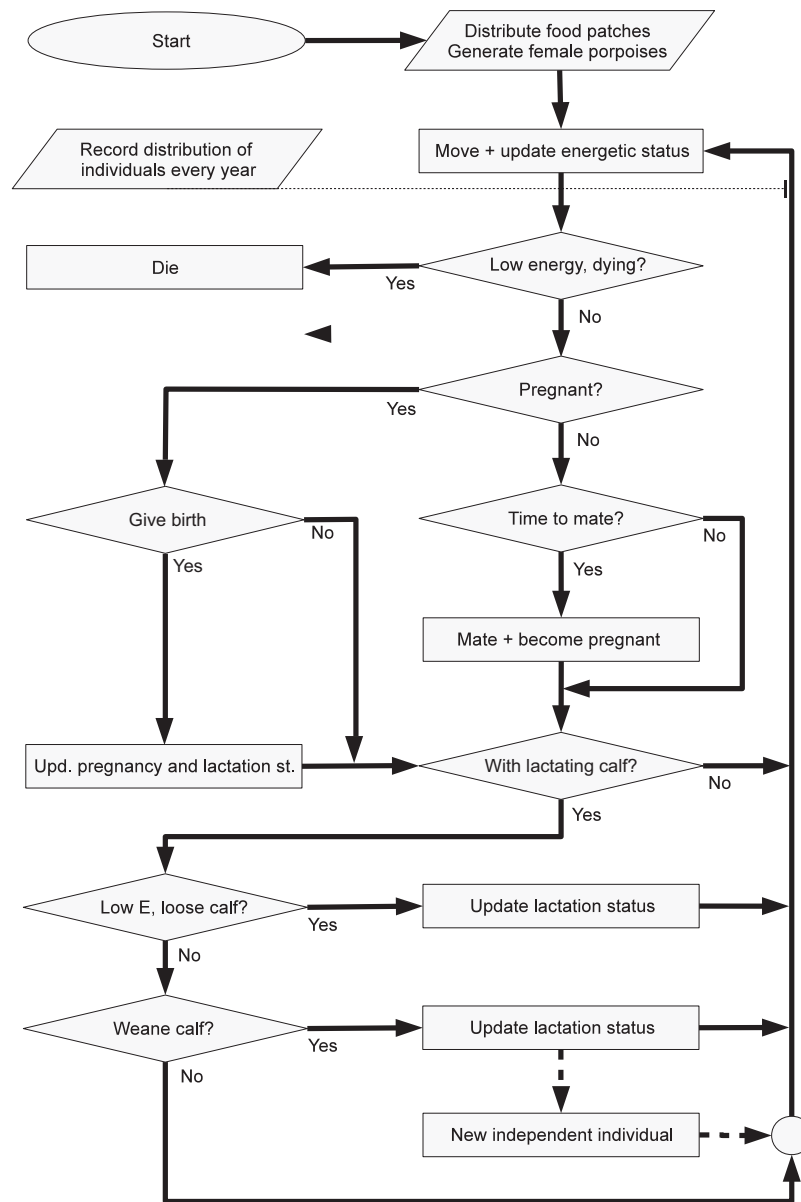


Fig. 2. Flow diagram describing the details of the population part of the model. Only adult females are modelled explicitly. Diamond-shaped symbols indicate decisions made by porpoises, parallelograms indicate model input/output and rectangles indicate calculations.

Prediction: Animals are assumed to have knowledge about where food levels are high at different times of the year. This permits them to disperse to one of the 40 km × 40 km squares with the highest potential food level.

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 objects. The animals know when their energy levels decrease, which causes them to disperse and to be more likely to die and to abandon lactating calves.

Interaction: The modelled animals only interact indirectly via their competition for food.

Stochasticity: Fine-scale movement, mating date, dispersal behaviour (which square to disperse to) and mortality are stochastic events. The probability of surviving increases with increasing energy levels (Fig. A1 in Appendix A).

Collectives: Social structure or groupings are not included in the model.

Observation: The number of animals, their energy levels and the total amount of food in the landscape are recorded daily. The age-class distribution and age specific mortalities are recorded yearly.

2.2.5. Initialisation

The model was initialised by creating 200 randomly distributed porpoise agents. Their age-class distribution corresponded to that of stranded and by-caught animals (Lockyer and Kinze, 2003), and 68% of the adults in the model were pregnant. The energy level, E_p , of each porpoise was initially modelled as a random normal variable with mean 10 and standard deviation one. Mating date was a random normal variable with mean 225 and standard deviation 20 (ensuring that most mating takes place in August, cf. Lockyer, 2003). The initial number of ships was 50 on the Great Belt route (route A in Fig. 1), 80 on the route through the Sound (route B) and 2 on the Aarhus-Odden fast ferry route (route C). Ship speeds were drawn from a normal distribution with mean 30 km h⁻¹ and standard deviation 5 for routes A and B, and set to 70 km h⁻¹ for route C. Ship

densities and speeds corresponded to the ones observed on these routes in 2010 (www.helcom.dk). The model included 179 existing and 300 planned wind turbines distributed in six wind farms (Fig. 1). The simulations were initiated on 1 January, and the food levels in the patches were set to the location specific maximum food levels for that date.

2.2.6. Input data

The maximum food levels in the food patches were obtained from Maxent estimates of porpoise incidence (Edrén et al., 2010). New Maxent values were loaded every third month and rescaled across the landscape in order to ensure that the potential total amount of food in the landscape stayed constant.

2.2.7. Sub-models

A description of the sub-models corresponding to the processes listed in 'Process overview and scheduling' is presented in Appendix A.

The model was implemented in NetLogo 4.0.5 (Wilensky, 1999). The model is available upon request.

2.3. Model parameterisation

2.3.1. Calibration of mortality and energy requirements

Porpoises are assumed to have higher mortality when their energy levels are low, which in turn depends on the balance between food intake and energy use. As there is no data on the spatial and temporal variation in the animals' food consumption, we used the rescaled Maxent values as estimates of the amount of food that they could potentially find in different areas. The amount of food that was actually available in a patch also depended on how fast food replenished after being eaten, r_U . When keeping these values constant the animals' energy level, E_p , depended on the amount of energy they used per half-hour interval, E_{use} . We modelled their survival probability, s_p , as a negative exponential function of their energy levels, so $s_p = 1 - \exp(-\beta E_p)$, where β is a constant (Fig. 1A in Appendix A). In order to obtain an equilibrium population size of approximately 200 super individuals and at the same time ensure that only animals with relatively low energy levels ($E_p < 10$) had a high mortality, we simultaneously calibrated β and E_{use} . The targets were reached for $E_{use} = 4.5$ and $\beta = 0.4$ (Fig. A2) when food was allowed to replenish after approximately two days ($r_U = 0.10$). These values of E_{use} and β were used in subsequent simulations. The value $r_U = 0.10$ was used because it seemed realistic and because it resulted in realistic home ranges for the simulated individuals (Nabe-Nielsen et al., 2013).

2.3.2. Calibration of the individuals' reactions to noise

Although there is evidence that porpoises react to noise (Koschinski et al., 2003; Tougaard et al., 2011), precise details of their behavioural response are lacking. Here we assume that they react by turning away from noisy objects, and that their tendency to turn increases linearly with the amount of noise they receive (Fig. 3). Underwater noise levels generally decrease linearly with distance from the noise-emitting object (Urlick, 1983).

The simulated animals' tendency to turn away from noisy objects was calibrated in order to obtain a realistic decrease in the number of porpoises at different distances from wind turbines. This was achieved by adjusting to what extent the turbines deterred the animals when they were close to them (determined by a deterrence coefficient, c) and how far from the turbines they reacted to them (deterrence distance, d_{deter}). Turbine noise is only likely to be audible to porpoises at distances up to a few hundred metres (Madsen et al., 2006), but the discrete time steps used in the model made it necessary to calibrate d_{deter} to get realistic population densities around the simulated turbines. For each combination of $d_{deter} \in$

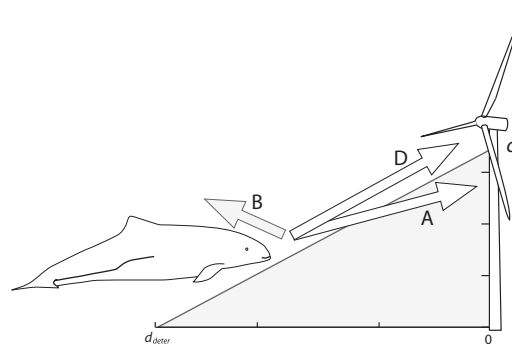


Fig. 3. Effects of noise on porpoise movement in the model. The vector **A** shows the move as it should be in the absence of noise (calculated from a mixture of correlated random walk and directed food search behaviour); **B** is the step that the porpoise should take if it was determined exclusively by its reaction to the wind turbine. The length of **B** is proportional to the noise level, which decreases linearly with distance from the turbine (shaded grey area). d_{deter} is the maximum distance at which standard turbines deter porpoises, c is the deterrence coefficient and **D** is the standardised resultant movement vector, the step that the porpoise actually takes in the presence of noise.

[200, 300, 400, 500, . . . , 1000] and $c \in [1, 2, 4, 8, 16, 32]$ (56 different combinations) we measured the simulated number of animals at different distances from a line of wind turbines. In the simulations presented in the main text we used a parameter combination ($c = 8$ and $d_{deter} = 300$) that caused the population density to be approximately halved in the area 100–200 m from wind turbines, which corresponded to the reduction observed by the Nysted Offshore Wind Farm (Tougaard et al., 2006). This also ensured that porpoises only rarely moved close to turbines (Fig. A3). In Appendix A we studied the population consequences of using shorter deterrence distances ($d_{deter} \in [100, 200]$).

The simulated porpoises responded to ships like they did to noise from wind turbines, but their tendency to move away from ships was proportional to the logarithm of the noise power they emitted (i.e. linear with the sound pressure level, expressed in decibel). The noise power of standard ships that sailed 30 km h^{-1} , and therefore also the porpoises' reaction to them, was set at 10 times (+10 dB) that of a standard turbine ($n_k = 10$; see Appendix A for details). This is most likely an underestimation, as broadband source levels of wind turbines are below 150 dB re. $1 \mu\text{Pa}$ (Tougaard et al., 2009) while small commercial ships typically have broadband source levels of 170 dB or above (Richardson et al., 1995). For simplicity the simulated noise of ships (expressed as sound pressure level) was set to increase linearly with their speed. This seems to have general support (McKenna et al., 2012), although it may not be true for all ships.

2.4. Model analysis

2.4.1. Estimating effect sizes and testing for additivity

The effects of disturbances were estimated based on simulations that included one or more types of noise: from existing wind turbines [e], from planned wind turbines [p] and from large ships [s] (see Fig. 1). The scenarios included yearly by-catch probabilities [b] of 0.00, 0.01, 0.02, 0.05, 0.10, 0.15, 0.20, and 0.25. The population dynamics stabilised less than 10 years after initiating a simulation for $b \leq 0.05$ and we therefore assessed changes in population size (measured on day 180 every year) for these scenarios based on the simulation years 11–40. This yielded a mean population size for each of the five replicate simulations for each scenario. Initial experimentation with the model suggested that five replicates was sufficient to provide a good estimate of the variations in the population dynamics. The replicate simulations were compared to the

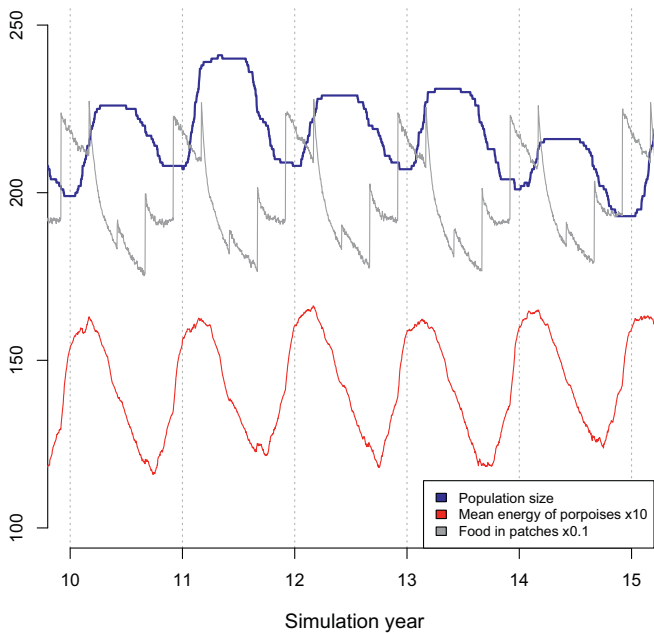


Fig. 4. Simulated population dynamics based on standard parameters ($\beta=0.4$ and $E_{use}=4.5$) in a landscape without ships and wind turbines (blue line). The red line shows the mean energy level of the porpoises and the grey line shows the total amount of food available in the landscape. The population size is counted in number of super-individuals, each representing several adult female porpoises.

population sizes obtained from reference simulations [ref] without wind turbines, ships or by-catch.

In order to test whether the effects of by-catch (b) and disturbances from existing wind turbines (e) were additive (i.e. whether $[b+e]=[b]+[e]$) we used a factorial design for annual by-catch probabilities of 0.01, 0.02 and 0.05. Here a significant interaction term indicated deviation from the null hypothesis of additivity (Crain et al., 2008). The analyses were performed with R 1.15 (R Development Core Team, 2012).

2.4.2. Model sensitivity to changes in r_U

The sensitivity of the model to changes in the food growth rate was estimated by re-calculating the equilibrium population size for $r_U \in [0.06, 0.08, 0.09, 0.10]$ based on the yearly population sizes for the simulation years 11–40. Mean population sizes (± 1 SD) were calculated for the reference scenario, the scenario with expected and planned wind farms [e + p] and the one that also included ships [e + p + s].

2.4.3. Population resilience

We evaluated the population’s ability to recover from disasters by removing 90% of the population in the beginning of year 6. This was done for the reference scenario as well as the scenarios [e + p] and [e + p + s]. The resilience of the population was quantified by observing how fast the population recovered to 50% of population size that was reached by year 40.

3. Results

3.1. Dynamics of the porpoise population

The population size increased in January–April every year when calves that were born eight months earlier became independent of their mothers (Fig. 4). The increasing population sizes were accompanied by a depletion of the food and decreasing energy levels for the simulated porpoises. By the end of the summer all the lactating calves had been weaned and no more independent animals

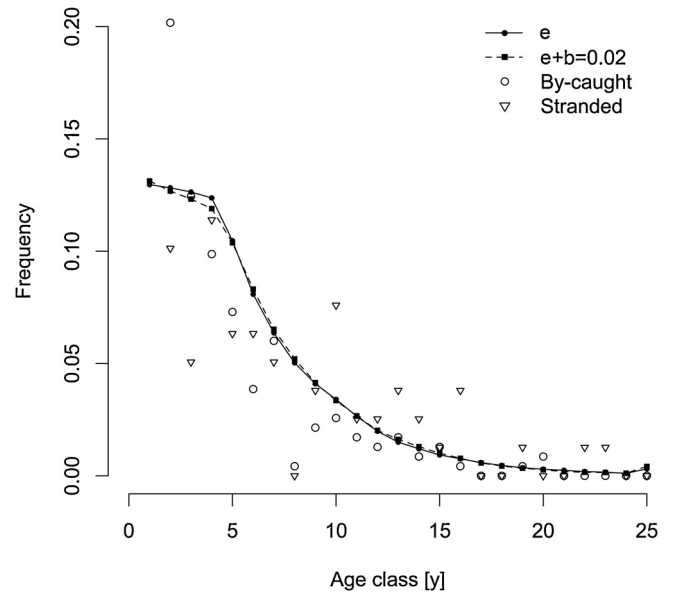


Fig. 5. Age class distribution in by-caught and stranded animals (Lockyer and Kinze, 2003) and in simulations including existing wind turbines [e] or both existing wind turbines and a by-catch rate of 0.02 y^{-1} [e + b]. The simulations used $r_U=0.10$. Only simulated data from years 11–40 are shown.

entered the population. At this time of year the large population size resulted in strong competition for food, which caused the individuals’ energy levels to decrease further. This was accompanied by increased mortality and decreasing population size. The abrupt changes in food availability that occurred four times every year were related to shifts in the spatial distribution of food. After each such shift it took the porpoises some time to find the patches where the food levels had increased and to once more reduce the food.

The age-class distribution of the animals that died in the model was very similar to the one observed for both by-caught animals and for animals that had stranded on Danish shores (Fig. 5). The distribution was similar in simulations with and without a yearly by-catch rate of 0.02. The age class distribution was not analysed for other by-catch rates.

3.2. Effects of disturbances and by-catch

The mean population size was slightly higher in the reference scenario than in any of the scenarios that included wind turbines, ships or by-catch (Fig. 6), although there was a large variation in

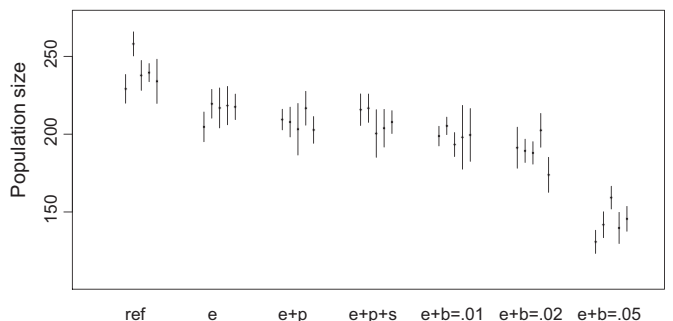


Fig. 6. Effects of by-catch [b] and noise emitted by ships [s], existing [e] and planned [p] wind turbines on the equilibrium population size. The mean population sizes (± 1 SD) were calculated from one yearly population count (from day 180) for the last 30 years of each simulation. The reference scenario [ref] did not include any anthropogenic noise. Yearly by-catch probabilities were 0.01, 0.02 or 0.05. All scenarios used $r_U=0.10$. Five replicates were produced for each scenario.

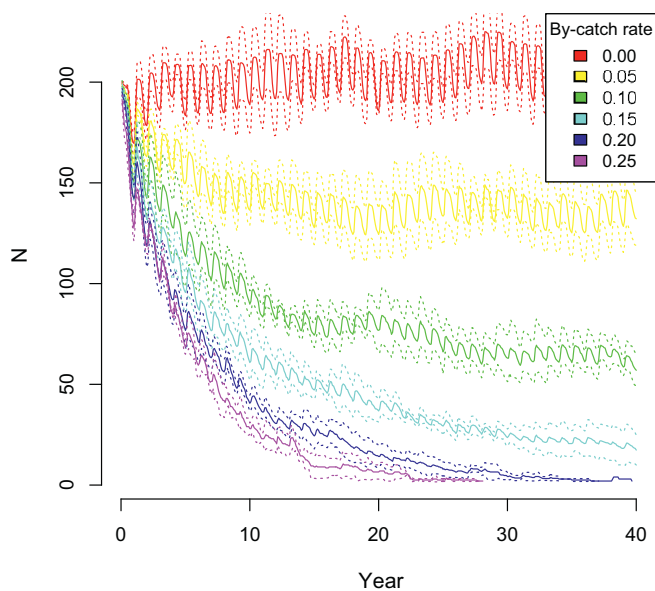


Fig. 7. Effects of variations in annual by-catch rates on the mean population size in five replicate runs. Dotted lines indicate ± 1 SD.

population sizes among replicate simulations and among years within each simulation. Inclusion of existing wind turbines resulted in a 10.4% decrease in the mean population size relative to the reference scenario ($F_{1,8} = 18.68$, $P = 0.003$, $R^2 = 0.75$; one-way ANOVA). The inclusion of planned wind turbines did not cause the population size to decrease further ($F_{1,8} = 4.0$, $P < 0.08$) and neither did the inclusion of both ships and planned wind turbines ($F_{1,8} = 2.4$, $P < 0.16$). Noise from ships and existing wind turbines had a smaller impact on the population size when the deterrence distance was reduced, and when set to 100 m the combined effect of ships and turbines was almost negligible (Fig. A4 in Appendix A).

The inclusion of a by-catch rate of 0.01 y^{-1} caused the mean population size to drop 7.4% relative to the scenario with existing wind turbines ($F_{1,8} = 24.4$, $P = 0.001$, $R^2 = 0.75$), a rate of 0.02 y^{-1} caused a decline of 12.3%, and a rate of 0.05 y^{-1} caused a decline of 33.4%. An increase of the by-catch rates to $\geq 0.10 \text{ y}^{-1}$ resulted in continuous population declines (Fig. 7), and a rate of 0.25 y^{-1} invariably resulted in extinction (i.e. $N = 0$) in < 30 years. The population effects were even larger when increasing the by-catch rate more. There was no indication that the population effects of by-catch and wind turbines were non-additive ($F_{2,24} = 0.01$, $P = 0.99$).

3.3. Resilience to perturbations

The time it took the population to recover to half of its carrying capacity after being reduced by 90% did not differ between the reference scenario, the scenario that included both established and planned wind turbines and the one that also included ships ($P = 0.30$, $F_{2,12} = 1.34$; ANOVA). On the average it took the population between 21.4 and 23.1 years to reach half of its carrying capacity.

3.4. Sensitivity to variations in the food replenishment rate

Equilibrium population sizes are shown for four food replenishment rates in the panels of Fig. 8. The population sizes were lower when food replenished more slowly. When the food replenishment time (the time it took food to recover to 95% of the maximum food level) increased from 1.6 to 2.7 days (corresponding to $r_U = 0.10$ and $r_U = 0.06$, respectively) the population size decreased by more than 75%. The relative impact of wind turbines and ships also depended on the food replenishment rate. For $r_U = 0.06$ wind turbines no

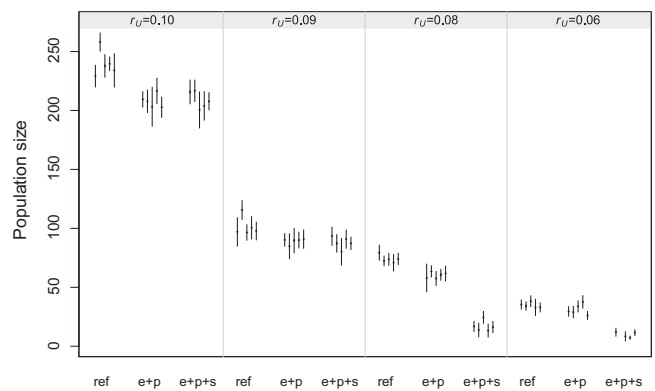


Fig. 8. Effects of variations in the food replenishment rate (r_U) on the mean equilibrium population sizes. The values of r_U are given at the top of each panel. The scenarios are: without ships, wind turbines or by-catch [ref], with existing and planned turbines [e + p] and with turbines and ships [e + p + s].

longer had a significant effect on the porpoise population size ($F_{1,8} = 2.4$, $P < 0.16$) whereas the inclusion of ships [e + p + s] reduced the mean population size from 35 to 10 individuals ($F_{1,8} = 280.7$, $P < 0.0001$, $R^2 = 0.98$).

4. Discussion

There is a growing demand for management models that allow us to predict how human activities affect the dynamics and long-term survival of wild animal populations (Crain et al., 2008; Korpinen et al., 2012). The model we present here allows us to assess the relative impact of different types of activities on harbour porpoise population dynamics. The activities include disturbances that affect population dynamics through their impact on animal movement as well as by-catch, which has a direct influence on animal survival. The model builds on energetic principles for the relation between movement, foraging and mortality, and can therefore be generalised to most animal species (Sibly et al., 2013). This, combined with the model's ability to incorporate spatially realistic management scenarios, distinguishes it from others that have previously been used for assessing the population consequences of human activities in marine environments (e.g. Caswell et al., 1998; Gerber et al., 2003; Korpinen et al., 2012).

The simulations revealed that both disturbances and by-catch may affect the size of the harbour porpoise population in the IDW, and that annual by-catch rates $\geq 10\%$ most likely leads to population extinction. None of the considered scenarios suggested that post-construction noise from wind turbines or ships had any influence on the long-term survival or the resilience of the population. The most surprising result is the 10% drop in the equilibrium porpoise population that took place when including existing wind turbines in the simulations (Fig. 6), especially when considering that the wind turbines and the 300 m zone where they can affect the porpoises cover $< 0.1\%$ of the total foraging area available to them in the model. There are at least two different explanations for this pattern. The first reason is that the porpoises in the model remain scared by disturbances for 2.5 h, although with a decreasing intensity, causing the effective influence zone around wind turbines to be larger than 300 m. The other and slightly less obvious reason is related to the mechanisms that control the animals' fine-scale movements in the model. An animal that finds food close to a wind turbine or some other disturbing object will get scared and start moving away. Their movements will therefore, for some time, follow a biased correlated random walk (see Nabe-Nielsen et al., 2013 for details). Due to the low density of food patches in the model the probability that they encounter food elsewhere is, however, small, and they will

therefore often start moving back towards the last patch where they found food. These excursions into areas with scarce food take more time than they would in the absence of disturbances, sometimes causing their energy levels to decrease for days. This increases their probability of dying, and also the chance that they start dispersing towards one of the areas they know to have high potential food levels. If the local population in this area has already reached its carrying capacity, the risk that the dispersing animal dies remains high after dispersing, and the scaring effects of disturbances can thereby have a much larger effect than would be anticipated on basis of the area they cover.

The apparently non-intuitive results of these simulations illustrate one of the strengths of explicitly taking movement into account in population models. In many cases this may considerably improve our estimates of population survival (Gonzalez-Suarez and Gerber, 2008). It also illustrates how sensitive population models can be to slight changes in the assumptions about what causes animals to alter the way they move, and how much. It is therefore important to stress that the simulated effects of noise from wind turbines are based on a worst-case scenario, where it is assumed that turbines are capable of permanently scaring approximately half of the animals away. This resembles the reduction in porpoise densities observed by the Nysted Offshore Wind Farm (Teilmann and Carstensen, 2012), although it is questionable whether the decreased densities were caused by noise from wind turbines. On Horns Rev in the North Sea porpoise densities were not reduced close to the wind farm (Tougaard et al., 2006), and in a study from the Dutch part of the North Sea the densities were higher inside than outside the wind farm (Scheidat et al., 2011), suggesting that deterrence distances (d_{deter}) of 100–200 m might be more realistic. For $d_{deter} = 100$ the population size was nearly the same in the reference scenario and the scenario that included both ships and turbines. Further, the effects of noise from non-moving objects may also decrease with time. Although porpoises have been demonstrated to sometimes react to noise (Brandt et al., 2011; Richardson and Würsig, 1997) they are often found in high densities in areas with heavy traffic (Sveegaard et al., 2011), suggesting that they are capable of acclimating to noise. Both the inclusion of a constant reaction to noise and conservative d_{deter} values contribute to producing conservative estimates of the population effects of noise.

The simulated population size emerges from the balance between food replenishment and the amount of food eaten by the porpoises. When food is scarce they experience an increased risk of dying, causing the population to decline. The population size is therefore under density dependent regulation, as is generally the case in mammals (Begon et al., 2006; Sibly and Hone, 2002; Sinclair, 1989). The relatively high lipid reserves observed in porpoises in the IDW in winter appear to suggest that the population is not food limited. However if the winter population is made up of individuals who survived a period of population decline in the fall it is likely that these individuals are more skilful in finding food and so in better condition than those who died earlier possibly of starvation. For some species predation contributes to controlling the population carrying capacity (Sinclair, 1989), but as no predation has been reported for porpoises in the IDW this mechanism is unlikely to be important for the studied population.

The lack of data on the distribution and abundance of prey makes it particularly challenging to produce a simulation model where population dynamics are related to food availability. This problem is tackled here by distributing food patches at random and assuming that mortality is related to the balance between food consumption and energy use, measured in relative terms. The validity of these simplifying assumptions is supported by the model's ability to produce several emergent patterns that resemble those observed in the real world (Grimm et al., 2005; Wiegand et al., 2003). The simulated animals' ability to stay within home ranges, and the size of

these home ranges, closely correspond to those observed in nature (Nabe-Nielsen et al., 2013). The same is the case for the age class distribution observed in the simulation (Fig. 5, Lockyer and Kinze, 2003). It is, however, likely that the age class distribution for simulation years 11–40 would have corresponded less closely to the one observed in nature if the model had not been initialised with animals with an age-class distribution resembling the one observed in stranded and by-caught animals. For relatively long-lived animals it can take more than 10 years for the age class distribution to stabilise. In spite of the apparent realism of the model it is important to bear in mind that the predicted effects of disturbances depend on the animals' ability to forage efficiently, and that this in turn depends on both the spatial and temporal distribution of the food as well as the mechanisms that induce dispersal behaviour. Future research should therefore be directed towards acquiring more information about these parameters in order to get a better understanding of the mechanisms that control porpoise population dynamics in nature.

It is interesting that even quite high by-catch rates do not lead to fast population extinction (Fig. 7). ASCOBANS (2000) suggested that it would be necessary to keep the by-catch below 1.7% annually in order to maintain the population at 80% or more of carrying capacity. Our results indicate that even a 2% by-catch rate enables the population to stay at 87.7% of carrying capacity. Although an annual by-catch rate of 5% would lead to population declines that exceed the ASCOBANS (2000) goals, our results do not suggest that it would lead to population extinction. Only higher by-catch rates appear to cause uninterrupted population declines. Although the by-catch rate is not known for the study area, our results can be compared to approximate values from adjacent waters. Vinther & Larsen (2004) estimated that around 7500 porpoises were caught annually in the Danish North Sea set-net fisheries alone in the period 1994–1998. As the population size in this area was approximately 185,000 in 1994 (strata L, F, G, H and Y, Hammond et al., 2002) this corresponds to a by-catch rate of roughly 4.1%. This rate leads to substantial population reductions according to our model, whereas annual by-catch rates $\geq 10\%$ leads to monotonously decreasing population sizes and in many cases to extinction.

It is important to notice that several factors that might influence the dynamics of the porpoise population were not considered in this model, and that some of them might increase the risk of population extinction if the population is already decimated due to high by-catch rates. Stochastic variations in mortality, which could be caused by e.g. diseases or fluctuating parasite loads, would be one example. The negative effects of such stochasticity could be exacerbated through positive density dependent effects caused by a decreasing likelihood of reproducing if the population size is small. Further, the animals may be influenced by other types of anthropogenic disturbances including noise from wind farms under construction. Our results suggest that the cumulative impacts of disturbances are additive, and the inclusion of other types of disturbances in the model would therefore be expected to further reduce the population size. Future studies should address the implications of including stochastic variability and other types of disturbances in the model.

Ecological models generally produce more realistic predictions when they incorporate the mechanisms that are responsible for generating the pattern of interest (Grimm and Railsback, 2012). Models that build on fundamental ecological principles such as competition and fitness maximisation, including the model we present here, are also more likely to maintain their predictive power under changed environmental conditions than models that build on empirical relationships observed in historical data (Goss-Custard and Sutherland, 1997; Stillman and Goss-Custard, 2010). This kind of models has previously been used for fish (e.g. Huse et al., 1999; Railsback et al., 2002) and coastal birds (Stillman and

Goss-Custard, 2010), but the present study is the first to use a mechanistic model for simulating population dynamics in a marine mammal species. The study illustrates how we may take advantage of predictive, spatially explicit models to improve the way we manage populations in marine environments in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.09.025>.

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