COMPARISON OF THE IPCOD AND DEPONS MODELS FOR MODELLING POPULATION CONSEQUENCES OF NOISE ON HARBOUR PORPOISES

Scientific Report from DCE – Danish Centre for Environment and Energy No. 186 2016

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Abstract: Two different frameworks have been developed to assess the potential effects of noise associated with offshore renewable energy developments on harbour porpoise populations: The Interim Population Consequences of Disturbance (iPCoD) and Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS). Although both models simulate population dynamics based on the birth and survival rates of individual animals, they model survival in a different way. iPCoD uses average survival rates derived from data from North Sea animals. In the DEPONS model, survival emerges from the individuals' ability to continuously find food. In this report we compare the structure of the two models, and describe the data they require and the kinds of output they provide. We then identify key differences between the approaches and discuss how their outputs can be compared.

Keywords: anthropogenic disturbances; DEPONS; harbour porpoise; iPCoD; management models; offshore renewable energy; *Phocoena phocoena*, population models; wind farm construction

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Summary

The Interim Population Consequences of Disturbance (iPCoD) and Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS) frameworks were both developed to assess the potential effects of noise associated with offshore renewable energy developments on harbour porpoise populations. Although both models simulate population dynamics based on the birth and survival rates of individual animals, they model survival in a different way. iPCoD uses average survival rates derived from data from North Sea animals. In the DEPONS model, survival emerges from the individuals' ability to continuously find food. The models also differ in the way they model the consequences of exposure to noise and the kinds of output they can provide.

The DEPONS approach is based on a more realistic model of porpoise biology than iPCoD, and it can provide detailed predictions of the short-term effects of disturbance that are likely to be valuable for spatio-temporal planning and mitigation. However, iPCoD runs faster than the DEPONS model, making it possible to compare a larger number of different scenarios and to take account of a wider range of uncertainties. The structural differences between the two modelling frameworks make each model better suited to answer a different set of questions. These differences between the two models are likely to result in different predictions of the population effects of particular development scenarios, and a direct comparison of model predictions is only likely to be informative if input parameters are aligned and model outputs are carefully analysed.

Sammenfatning

Der findes to forskellige modelleringsværktøjer til vurdering af, hvordan støj fra konstruktion af havvindmøller kan påvirke marsvin: iPCoD (Interim Population Consequences of Disturbance) og DEPONS (Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea) modellerne. Selv om begge modeller simulerer marsvinenes populationsdynamik på baggrund af fødselsrater og de enkelte individers overlevelse bliver deres overlevelse beregnet forskelligt i de to modeller. iPCoD benytter de gennemsnitlige overlevelses-rater for dyr i Nordsøen. I DEPONS-modellen bliver de enkelte individers overlevelse bestemt af, hvor gode de er til hele tiden at finde føde. I denne rapport sammenligner vi strukturen af de to modeller og beskriver hvilke data, der skal til for at parametrisere dem, samt hvilke typer output de kan generere. Derefter beskriver vi de vigtigste forskelle mellem de to modeller og diskuterer hvordan outputtet fra de to modeller kan sammenlignes.

1 Introduction

There is increasing evidence that loud noise generated by activities such as sonar operations, pile driving, and seismic surveys can affect the behaviour of marine mammals. Southall *et al.* (2007) reviewed the historical evidence for this, and more recent examples include Tougaard *et al.* (2012), DeRuiter *et al.* (2013), and Goldbogen *et al.* (2013). Behavioural disturbance may result in animals being displaced temporarily from preferred, and potentially critical, habitats. This could have an indirect effect on survival and reproduction if they are displaced into an area where prey is less abundant or more difficult to capture, thus reducing their energy intake. There is substantial evidence that harbour porpoises are particularly sensitive to anthropogenic noise (Lucke *et al.* 2009; Tougaard, Henriksen & Miller 2009; Brandt *et al.* 2011; Thompson *et al.* 2013; Dähne *et al.* 2013; Kastelein *et al.* 2013). There is concern about the potential effects of noise associated with the construction of planned offshore renewable energy facilities on populations of harbour porpoises, particularly in the North Sea where a large number of offshore wind farms are planned.

Two different approaches have been developed to investigate these potential effects. The Interim Population Consequences of Disturbance (iPCoD) uses independent estimates of the number of porpoises that may be disturbed by a particular activity together with the results from an expert elicitation process (Donovan *et al.* 2016) as inputs into a model that simulates the effects of differential exposure to noise on a harbour porpoise population (Harwood *et al.* 2014; King *et al.* 2015). The approach is considered to be 'interim', because the values provided by experts should be replaced with empirically derived values as soon as they become available. The Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS) model builds on the work of Nabe-Nielsen *et al.* (2014), who developed an individual-based model of harbour porpoise movements and foraging behaviour in inner Danish waters and used this to investigate the potential effects of wind farm operational noise and ship noise. In this report, we compare the structure of these two models, and describe the data they require and the kinds of output they provide. We then identify key differences between the approaches and discuss how their outputs can be compared once the DEPONS model is fully tested.

2 Structure of the iPCoD and DEPONS models

At their core, both iPCoD and DEPONS use age and stage specific survival and birth rates to model harbour porpoise population dynamics. iPCoD is a stage-based matrix model (Caswell 2001) whereas the DEPONS model is an individual-based model (Grimm & Railsback 2005). Only females are modelled explicitly in both models, although total population size can be readily calculated using an estimate of the population sex ratio. In iPCoD, the population is divided into three stages (calf, juvenile, and adult), with the calf stage having a duration of exactly 1 year. In the DEPONS model, animals are characterized as either juvenile, adult with calf, or adult without calf. The survival of individual animals is determined by their energetic status. The last category is referred to as "adult" or "normal adult" from now on. Calves are modelled as independent individuals after they have stayed with their mother for 240 days (the length of the lactation period reported in the literature). In both models juveniles are defined by their age, and they are assumed to become adult at the same age. Adult age is not modelled explicitly in iPCoD but it is in DEPONS. Maximum longevity is constrained to be 30 years in the DEPONS model, although users can change this value. This value exceeds the maximum age observed by Lockyer and Kinze (2003), but the simulated age-class distribution matches the one observed for stranded animals in Danish waters (Nabe-Nielsen *et al.* 2014).

The DEPONS model operates on a time step of 30 minutes, and the movements, exposure to noise and energetic status of each animal is updated after each step (30 minutes). The iPCoD population model operates on a time step of 1 year, but exposure to noise is modelled with a time step of 1 day. The structure of the two models is shown as a series of life cycle graphs (Caswell 2001) in Figures 1–3.

2.1 Modelling population dynamics in the absence of disturbance

In the DEPONS model, only juveniles and adults are considered outside the lactation period, which extends from a mean value of day 160 in one year to approximately day 40 of the subsequent year ('Winter'; Figure 1). The probability of survival for each individual in a particular time step is determined by the current value of its energy level (shown as $EJ_{i,t}$ for juveniles and $EA_{i,t}$ for adults in Figure 1) and the assumed relationship between energy level and survival (Nabe-Nielsen *et al.* 2014). Any juveniles that have reached the age at maturity (3.44 yrs) become adult. On the first day of the lactation period, a proportion of the adults become "adults with calves" (Figure 1). This proportion is determined by the birth rate (user specified, but with a default value of 0.68 as estimated by Read and Hohn (1995) for harbour porpoises in the Northwest Atlantic). During the entire lactation period, the number of juveniles and adults surviving in each time step is determined by their energetic status, as described above. The survival of each calf in a particular time step is determined by the energy level of its mother ($EAwc_{i,j}$ in Figure 1). If her calf dies, the mother returns to become a normal adult. On the last day of lactation, the number of juveniles is increased by half the number of "adults with calves" alive on that day, and all "adults with calves" become normal adults. The individual animals' energy levels and survival depend on their foraging efficiency (Figure 2). All simulations start on 1 January.

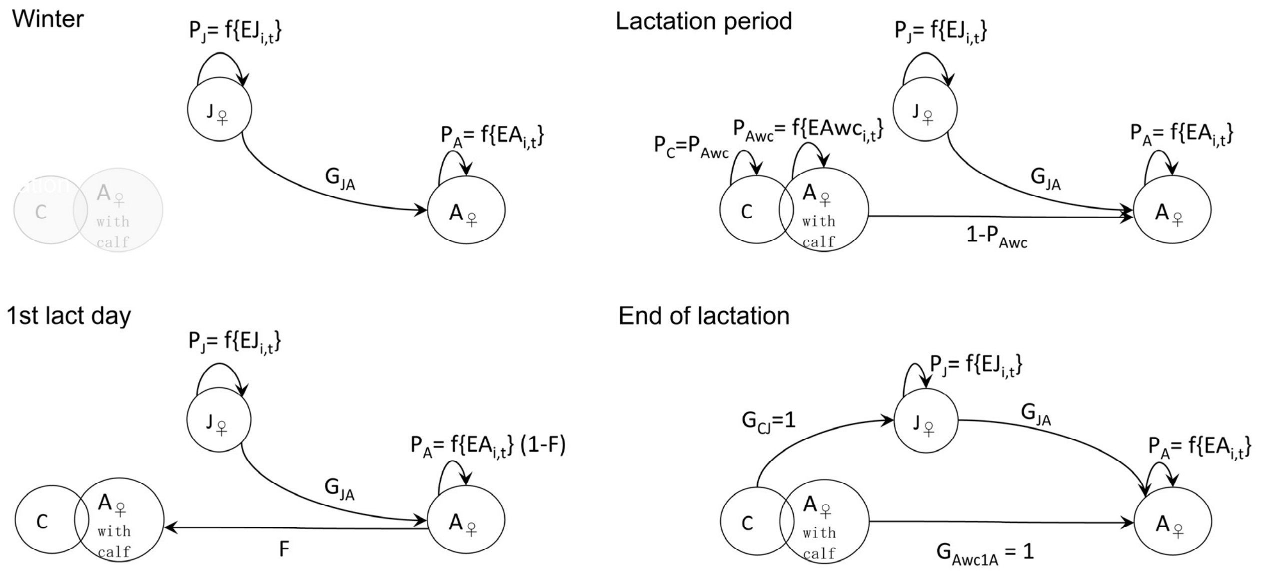
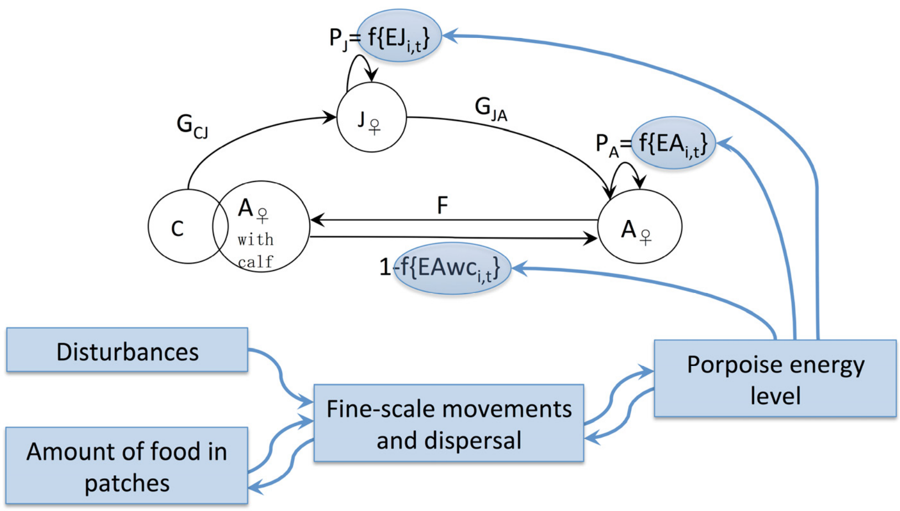


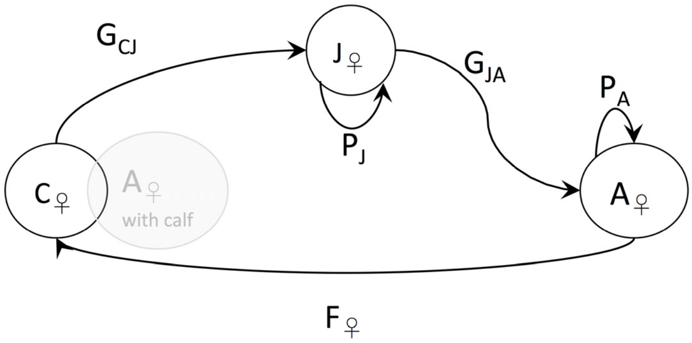
Figure 1. Life cycle diagram for the DEPONS model at different times of the year. C: calf (modelled as an attribute of the lactating mother), J: juvenile, A: adult. Only females are modelled. G_{XY}: probability an animal will transition from class X to class Y the next time step, P_X: probability an animal will still be in class X in next time step, F: probability that an adult will give birth to a female calf. $EA_{i,t}$ and $EJ_{i,t}$ represent the energy level of adults *i* and juveniles *i*, respectively, at time step *t*.

Figure 2. Mechanisms responsible for half-hourly changes in vital rates in the DEPONS model (blue arrows). Not all transitions in the life cycle diagram (black arrows) apply at all times of the year. C: calf (modelled as an attribute of the lactating mother), J: juvenile, A: adult. Only females are modelled.



iPCoD models the dynamics of the population in the absence of disturbance using a simple Leslie/Levkovitch matrix approach (Caswell 2001). The corresponding life-cycle diagram is shown in Figure 3. At the start of the modelled year (which is equivalent to the first day of the lactation period in DEPONS), the number of calves is determined using the birth rate, which is specified by the user using an appropriate value from the literature (e.g. Winship and Hammond 2006, for harbour porpoises in the North Sea). The number of surviving juveniles and adults is then calculated. No further mortality occurs until the start of the next simulated year. Survival and birth rates are allowed to vary from year to year around a mean value, using parameters obtained by expert elicitation (King *et al.* 2015), to mimic the effects of environmental variation.

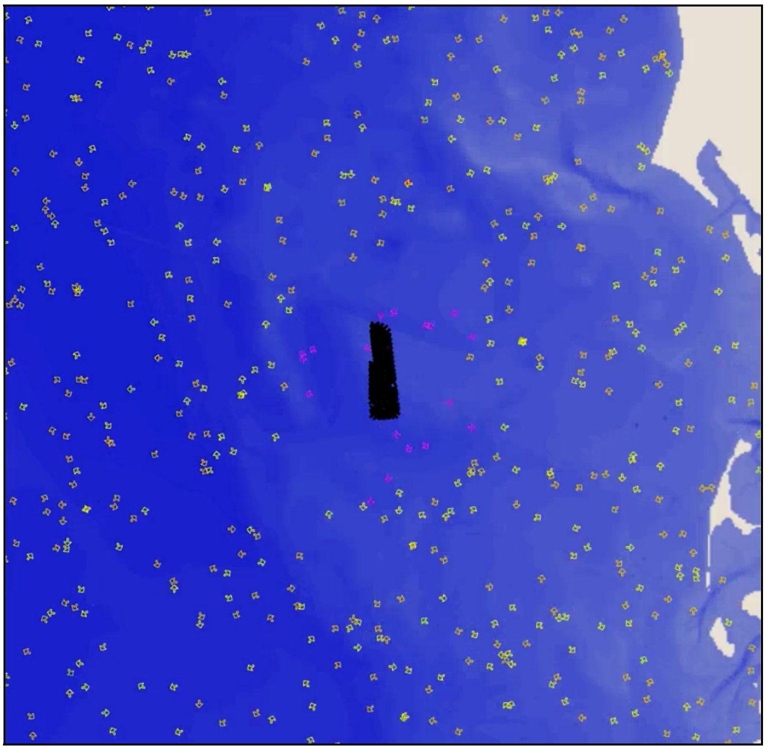
Figure 3. Yearly life cycle diagram for the iPCoD model. C: calf, J: juvenile, A: adult. Only females are modelled. G_{XY}: probability an animal will transition from class X to class Y the next year, P_X: probability an animal will still be in class X in next year, $F_♀$: probability that an adult will give birth to a female calf. For simplicity, we have represented the juvenile age-classes by a single juvenile stage.



2.2 Modelling population dynamics in the presence of disturbance

In DEPONS, the probability that an individual is exposed to disturbance activities depends on the spatial and temporal patterning of disturbances. The spatial distribution of animals depends on their movement patterns, which are calibrated to resemble those of real animals (Nabe-Nielsen *et al.* 2013). Individuals that encounter noise from an activity move away from the noise source (Figure 4). The extent to which they change their heading depends on the calculated received level of noise (Nabe-Nielsen *et al.* 2014), so that the response to noise is progressive. This response affects the individuals' energy levels because they spend more time travelling through the landscape without encountering food patches than is the case for undisturbed animals. These changes in energy level determine the effects of disturbance on the population.

Figure 4. Screenshot from a DEPONS simulation where animals are being scared by pile-driving noise during construction of the DanTysk wind farm. The black area includes a large number of individual turbines, pink dots show porpoises that are being scared and move away from the turbines, orange, yellow and green dots represent porpoises with poor to good energetic status.



In iPCoD the temporal patterning of disturbances is used to determine the number of simulated animals to be disturbed each day. The probability that an individual is disturbed by a particular event is calculated from the ratio of the estimated number of animals likely to be disturbed on each day of the activity to the size of the population or sub-population. The estimates of the number of animals likely to be disturbed on one day of each activity is provided by the user, and is not calculated within iPCoD. It may be obtained from a calculation of the number of animals likely to be within a particular distance of the activity (e.g. King *et al.* 2015; Heinis et al., 2015), by combining a dose-response relationship and telemetry data (e.g. Thompson *et al.* 2013), or from a simulation model of animal movement similar to that used in DEPONS (e.g. Donovan *et al.* 2012).

The user can specify that all individuals in a population are equally likely to be exposed to disturbance from a particular activity. However, it is also possible to specify that only a sub-set of the population (referred to as the vulnerable sub-population) is exposed to noise from that activity. For example, the user can specify that different vulnerable sub-populations are affected by each wind farm development (see King et al. 2015).

At the end of the year, simulated individuals are classified into three disturbance classes (undisturbed, moderately disturbed, or severely disturbed, Figure 5) based on the total number of days of disturbance they have experienced. These are then translated into effects on vital rates using results from an expert elicitation process. New survival and birth rates are calculated for each disturbance class and stage. The survival and birth rates for undisturbed animals are unaffected, but the rates for severely disturbed animals are reduced by multiplying the undisturbed rate by the value of A in Figure 6. For moderately disturbed animals, the mean number of days of disturbance experienced by all the animals in this category is calculated and their survival or birth rate is reduced, using the appropriate value from Figure 6 for that mean number of days. All surviving individuals are then assumed to transition into the relevant undisturbed category (i.e. they have no memory of the disturbance they experienced in the previous year). In the DEPONS model animals have a memory of their foraging success in different areas, which is, in turn, influenced by the amount of disturbance they have experienced in those areas.

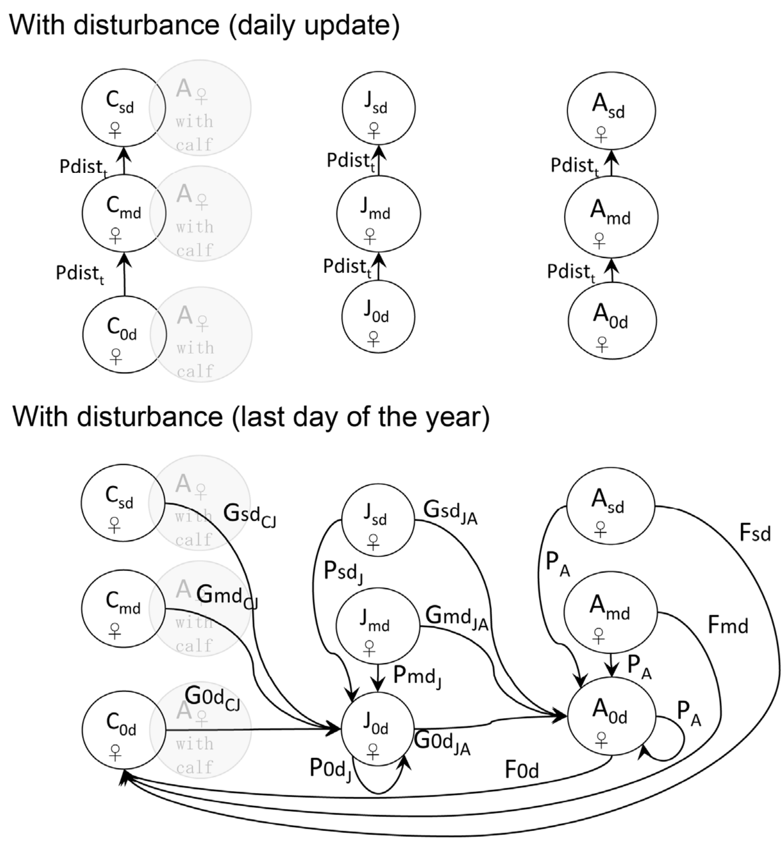


Figure 5. Modelling the effects of disturbance in iPCoD. C: calf, J: juvenile, A: adult. Only females are modelled. Animals in each stage are categorized as undisturbed (0d), moderately disturbed (md) or severely disturbed (sd). G_{XY} = probability an animal will transition from stage X to stage Y in next year. P_X = probability an animal will still be in stage X in next time step. $F_♀$ = probability that an adult will give birth to a female calf. $Pdist_t$ = probability that an individual is disturbed on day t.

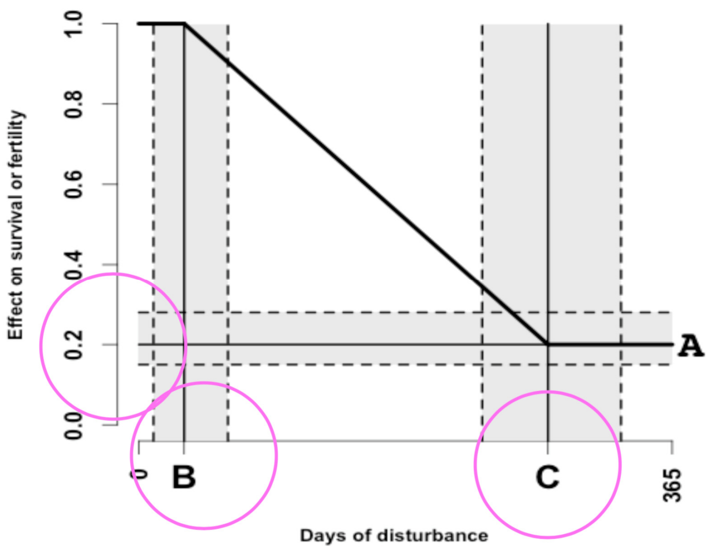


Figure 6. The hypothetical relationship used in iPCoD relating the number of days of disturbance experienced by an individual porpoise in one year to its effect on survival or birth rate. Experts were asked to provide input on the quantities A, B and C. The shaded areas represent the experts' opinion of the likely range for each quantity. B is the number of days below which there is no effect of disturbance. Animals that are disturbed for more than B days, but less than C are considered to be moderately disturbed, and animals that are disturbed for more than C days per year are categorized as severely disturbed. Modified from Fig. 2 of King et al. 2015.

2.3 Data required to parameterise the models

DEPONS:

1. Basic life-history parameters (birth rate, start date for lactation, lactation duration, age of maturity, relationship between energy status and survival).
2. Spatial distribution of activities likely to cause disturbance, their timing and source strength.

3. Fine and coarse scale movement data to calibrate the 17 different parameters of the movement model.
4. Values for modelling response to noise exposure (5 parameters).
5. Energy consumption in relation to water temperature/season and whether lactating or not (3 parameters).
6. A map of relative food availability in different parts of the landscape, and values for the 3 parameters that determine changes in food availability over time.

iPCoD:
1. Basic life-history parameters (birth rate, calf survival, juvenile survival, adult survival, age of maturity).
2. Spatial distribution of activities likely to cause disturbance and their timing.
3. An estimate of the number of animals predicted to be disturbed by 1 day of activity for each of the developments being modelled.
4. Uncertainty associated with density estimates used to predict the number of animals disturbed by 1 day of activity. Modelled using a log-normally distributed scalar with mean 1.
5. Population size (not required if output is in the form of percentage changes in abundance).
6. Values for the parameters determining the relationship between the number of days of disturbance experienced by an individual and its survival or birth rate (obtained by expert elicitation)
7. Expected inter-annual variation in juvenile survival, adult survival and birth rate as a result of environmental variation (3 parameters, obtained by expert elicitation).

It is important to recognize that some of the apparently different data requirements of the two approaches may actually be provided by the same data source. For example, the map of relative food availability used by DEPONS is derived from maps of porpoise density based on survey data. Exactly the same kind of information (e.g. Heinis *et al.* 2015, Paxton et al. 2016) is required to calculate the number of animals predicted to be disturbed by 1 day of activity used in iPCoD.

The list above is intended to illustrate similarities in parameter requirements between the two modelling frameworks. A full list of parameters and data input requirements in the DEPONS framework will be published together with a full documentation of the model in the near future (Nabe-Nielsen *et al.*, in prep.). A full documentation of the iPCoD model, including a list of parameters and the computer code required to run the model is available at http://www.gov.scot/Topics/marine/science/MSInteractive/Themes/pcod

2.4 Representativeness of data used for parameterising the models

DEPONS requires detailed data on the fine-scale movements of individual animals in order to calibrate its underlying movement model. Currently, the only movement data for North Sea porpoises comes from animals caught along the Danish coast. It is unlikely that porpoises from the western North Sea will have identical movement patterns. Although it is possible to evaluate the population consequences of variations in movement patterns in the DEPONS model, it is difficult to evaluate which parameter values are most representative for the western North Sea. A related problem is the need for data on long-range movements of porpoises over periods of weeks and months, which is also only available for animals tagged along the Danish coast. The lack of such data for the entire North Sea is also an issue for iPCoD, because its predictions are sensitive to assumptions about the size of vulnerable sub-populations. The actual size of these sub-populations will be determined by the frequency with which porpoises make long-range movements and how far they travel.

iPCoD includes a facility for the user to specify how long the behaviour of an individual is affected by a disturbance event (the number of days of 'residual' disturbance). The duration of this response seems to vary with location and piling method. For example, at a location where 2.6 m monopiles were vibrated into position and then piled using 500 kJ hammer energy, Dähne *et al.* (2013) found that harbour porpoise densities returned to pre-disturbance levels within 1 day. However, Brandt et al. (2011) found that the effects of piling 3.9 m monopiles with a hammer energy of 900 kJ lasted for up to 3 days. Varying the amount of 'residual' disturbance has a substantial effect on the predictions of iPCoD (King *et al.* 2015). The equivalent parameters in DEPONS are the deterrence decay constant, which defines how much the deterrence behaviour is reduced in each time step, and the residual deterrence time. Both can be specified by the user. The population consequences of varying these parameters is also minor in the DEPONS model (Nabe-Nielsen *et al.*, in prep.).

DEPONS by default uses birth rate and age of maturity values obtained from studies of harbour porpoises in the Northwest Atlantic, whereas most of the life history parameters values used by iPCoD come from studies of North Sea harbour porpoises. Sensitivity analysis of the iPCoD model indicates that its predictions are not particularly sensitive to the choice of life history parameters. The same is true for the DEPONS model (Nabe-Nielsen *et al.*, in prep.). A complete sensitivity analysis is currently being conducted for the DEPONS model in order to assess how the equilibrium population size changes when modifying each of the model parameters.

2.5 Kinds of output that can be obtained from the two models

Both models simulate changes in population size over time. iPCoD produces them on a yearly basis, whereas the DEPONS model is capable of producing population numbers on a daily basis. The iPCoD model runs very fast (5–15 mins for 500 replicate simulations of one scenario), and can therefore be used for evaluating the implications of uncertainty in the inputs provided. This is much more time consuming when using the DEPONS model (5–8 days for 10 replicate simulations of one scenario).

Both models can be used to provide outputs that may be useful for the development of monitoring programmes, such as expected changes in abundance and population age structure as a result of disturbance. However, DEPONS can provide a wider range of predictions than iPCoD. For example, it can be used to predict how the spatial distribution of porpoises in the North Sea may change in relation to the sources of noise, and how average energetic status and age class distribution of porpoises may vary over time and space.

3 Key differences between models and their consequences

As we have shown in the preceding section, the two models resemble each other in simulating population dynamics based on the birth and survival rates of individual animals. However, there are substantial differences in the way in which exposure to noise and the effects of noise on vital rates are modelled. In this section we list these differences and discuss when the differences can be expected to cause the two models to predict different population effects of noise.

3.1 Differences between iPCoD and DEPONS

1. **Probability of noise exposure**. In the DEPONS model the probability that an individual animal is exposed to noise is largely determined by the way the sound field associated with the activity is modelled and the threshold received sound level below which there is no behavioural response. Currently the sound field is modelled assuming spherical spreading. In iPCoD, the probability of exposure to noise is calculated using independent estimates of the number of animals that are likely to be disturbed during each day of construction and the total number of animals in the (sub) population.

2. **Quantifying level of noise exposure**. In the DEPONS model the effects of exposure increase progressively with noise level. The effects are modelled explicitly and calibrated to reproduce the relative porpoise densities observed at different distances from a wind farm during construction. In iPCoD the response to noise exposure is categorical (either disturbed or not disturbed on a particular day).

3. **Consequences of noise exposure for individual survival and birth rate**. In the DEPONS model, noise influences survival through its effects on foraging efficiency, which affects the energetic status of individuals. Survival probabilities of adults, juveniles and calves are related to their energetic status by a negative exponential function (see details in Nabe-Nielsen *et al.* 2014). iPCoD uses a set of relationships (Figure 6), parameterised using expert elicitation, that relate the number of days of disturbance experienced by an individual over the course of one year to its birth rate (adults), or its survival (juveniles and calves).

4. **Spatial distribution of noise**. The DEPONS model is spatially explicit. This prevents individual animals from being exposed to noise sources in different parts of the landscape shortly after each other, but causes them to be exposed to noise from the same source for an extended period unless they move away from it. The iPCoD model is not spatially explicit, but it is possible to specify that only a proportion of the population (the vulnerable sub-population) is likely to be disturbed by a particular noise source. Members of that vulnerable sub-population are only exposed to noise from specified operations.

5. **Density dependence**. The DEPONS model includes density dependent regulation of mortality rates. Food is depleted more rapidly when the population is larger, causing the animals' energy levels to decrease and

their mortality to increase. This density dependence causes a population carrying capacity to emerge even in the presence of noise. It also allows the population to recover after noise exposure ceases, unless noise causes the population to go extinct. iPCoD does not currently include density dependent population regulation. However, it can be extended to model density dependence in situations where data on the form of density dependence experienced by a population are available (e.g. for the Moray Firth population of harbour seals - Thompson et al. 2013).

6. **Environmental stochasticity**. The DEPONS model does not include environmental stochasticity. iPCoD models environmental stochasticity by allowing survival and birth rates to vary from year to year using variance estimates obtained by expert elicitation, as described in the previous sections.

7. **Accounting for uncertainty**. In the DEPONS model uncertainty in the number of animals disturbed at a given time is accounted for by repeatedly running the same disturbance scenarios. In iPCoD the uncertainty in number of animals disturbed per day and population size are modelled by resampling from log normal distributions. Uncertainty in experts' opinions is modelled in iPCoD by resampling from a density surface (King *et al.* 2015).

3.2 Implications of the differences between the two models

In the iPCoD model the predicted population consequences of disturbances are largely determined by the number of animals that are disturbed and the number of days on which an activity that might cause disturbance occurs. In the DEPONS model the consequences of disturbances are determined by the behavioural reactions of the animals that are exposed to noise, which in turn depends on the received sound level. The animals that are far from the sound source are less deterred than the ones that are close to the source. This is modelled in half-hourly time steps. Both frameworks model variations in the timing and distribution of construction events. However, the predictions of iPCoD are less affected by the spatial distribution of these events because no account is taken of the location of the different construction activities within the boundaries of a vulnerable sub-population. In the DEPONS model, the effects of the construction schedules and the precise locations of the construction activities are modelled explicitly. As a result, differences in construction schedules among sites may have a greater effect on model predictions. This capability means that DEPONS is particularly suited to investigations of the population effects of different piling schedules for wind farm construction within a year.

Disturbances influence different life history parameters in the two models, which may result in differences in model predictions. The iPCoD model does not model any effects that disturbance may have on adult survival, and DEPONS does not model any effects that disturbance may have on birth rate. The implications of this difference for the predictions of the two models are not clear.

The spatial distribution of noise also influences the predictions of both models. However, in iPCoD these effects are only modelled implicitly, through the developers' estimates of the number of porpoises that may be disturbed by a particular activity and the choice of boundaries for any vulnerable subpopulations. iPCOD does not account for long-distance movements, and treats each sub-population as a closed unit. As a result, it is likely that more animals will be predicted to experience severe levels of disturbance when iPCoD is used with the assumption of a small vulnerable sub-population than when all individuals are considered to be equally vulnerable to disturbance. The DEPONS model is likely to predict smaller population effects than those of the iPCoD when assuming small vulnerable sub-populations with exactly the same schedule of disturbance activities, because animals are allowed to move away from the disturbed area.

iPCoD does not currently include density dependent population regulation. As a result, a population that is reduced in size as result of a disturbance activity will only be predicted to recover when the disturbance activity ceases if the population was increasing in size before the disturbance. This limitation means that iPCoD is most suitable for predicting the population level effects of acute disturbance associated with particular events (e.g. wind farm construction) over a relatively short (~10 year) period, rather than chronic disturbance (e.g., shipping noise, wind farm operation) The DEPONS model, in contrast, does include density dependence, which is a direct consequence of the individuals' competition for food. This makes it possible to evaluate how long it takes the population to recover after being reduced by disturbances. It could also make it possible to develop a wind farm construction scenario with a relatively small impact on the population, provided that there are sufficiently long noise-free periods during the construction phase.

Both models account for demographic stochasticity in a similar way, but currently it is only iPCoD that incorporates environmental stochasticity (i.e. variations in vital rates from year to year, informed by expert elicitation). iPCoD also accounts for more sources of uncertainty than DEPONS, such as uncertainty in estimates of the number of animals disturbed by a particular source (due to uncertainty in the choice of sound propagation model and in the threshold received level at which animals respond to noise), and potential variation in the effect of disturbance on vital rates. As a result, iPCoD produces a wide range of population-level predictions. Although the DEPONS model can also be used to investigate how uncertainty in the threshold level affects population estimates it is very time consuming. Because the iPCoD computer code runs quickly it is possible to quantify the effects of this uncertainty and present the model predictions as a risk statistic (e.g. the probability that the population will decline by more than 1% per annum, rather than a simple statement that "the population is predicted to decline by 1% per annum") based on the proportion of many 100s of simulations in which a particular effect is observed. Although an analysis of the sensitivity of the predictions of DEPONS to model parameter values is currently underway it is impracticable to run hundreds of simulations (as is the case with iPCoD) for every disturbance activity scenario. Instead, predictions are usually based on the average of ten model runs for each scenario.

4 Future development of the two models

4.1 Extension to other harbour porpoise populations

iPCoD can easily be extended to other harbour porpoise populations by conducting new expert elicitations. A version of DEPONS that is suitable for another harbour porpoise population could be developed if suitable data on individual movement and maps of food availability are available for that population.

4.2 Inter-calibration and harmonization of the two models

Once the final version of the DEPONS model is available it will be possible to generate outputs which can be used to compare the predictions of the two model frameworks. As we have noted above, a simple comparison of the population-level predictions from the two models for the same development scenario is unlikely to be particularly informative, because we expect these predictions to be different for a number of reasons. Parameters in the two models would have to be carefully aligned before results can be compared in a meaningful way. As we have noted above, the iPCoD framework produces a wide range of predictions because it takes account of uncertainties about the effects of disturbance on vital rates and the amount of 'residual' disturbance. Here we suggest how outputs from DEPONS can be used to identify changes that could be made to the iPCoD framework so that its predictions can be more easily compared with those from DEPONS.

1. It is possible to extract information from the outputs of the DEPONS model that can be compared to the expert opinions used for parameterizing the iPCoD model. This would involve investigating the relationship between the number of times during a year that each simulated porpoise is exposed to a noise level sufficient to cause deterrence and its subsequent survival. The analysis would be applied separately to adults with calves, and juveniles. The resulting relationships could then be compared with the heat maps shown in Fig. 3 of King et al. (2015) that represent the degree of support among experts for different relationships. In addition, iPCoD could then be run using the relationships derived from DEPONS and the population-level predictions from the two frameworks could be compared.

2. The length of time that the behaviour of an individual is affected by a disturbance event (the number of days of 'residual' disturbance) is a critical parameter in iPCoD. The equivalent parameters (the deterrence decay constant and residual deterrence time) are also incorporated in the DEPONS model. Although it is difficult to measure the decay and duration of the disturbance response for individual animals in the field, it has been done for a limited number of animals exposed to airgun noise. These measurements were used for parameterizing the DEPONS model (van Beest *et al.*, subm.). Examination of the predicted changes in the energy levels of these simulated animals would allow an evaluation of the realism of the assumption in iPCoD that 1 day of 'residual' disturbance has the same effect on survival or birth rate as 1 day of actual disturbance. iPCoD could then be run with the more realistic values for 'residual' disturbance.

3. The predictions of iPCoD are also sensitive to the assumed size of the vulnerable sub-population(s). Outputs from DEPONS could be used to identify an appropriate size for a vulnerable sub-population in the North Sea that could be used in iPCoD. This could be done by investigating how the proportion of time that simulated animals are predicted to spend in a particular part of the North Sea varies with the size of that area.

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COMPARISON OF THE IPCOD AND DEPONS MODELS FOR MODELLING POPULATION CONSEQUENCES OF NOISE ON HARBOUR PORPOISES

Two different frameworks have been developed to assess the potential effects of noise associated with offshore renewable energy developments on harbour porpoise populations: The Interim Population Consequences of Disturbance (iPCoD) and Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS). Although both models simulate population dynamics based on the birth and survival rates of individual animals, they model survival in a different way. iPCoD uses average survival rates derived from data from North Sea animals. In the DEPONS model, survival emerges from the individuals' ability to continuously find food. In this report we compare the structure of the two models, and describe the data they require and the kinds of output they provide. We then identify key differences between the approaches and discuss how their outputs can be compared.

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