Adapting the iPCoD Framework for Harbour Porpoises to Utilise a Dynamic Energy Budget Model in Modelling the Effects of Disturbance – Final Report

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Adapting the iPCoD Framework for Harbour Porpoises to Utilise a Dynamic Energy Budget Model in Modelling the Effects of Disturbance – Final Report

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1 Glossary of Terms, Acronyms and Abbreviations

Term	**Description**
ABC	Approximate Bayesian Computation
DEB	Dynamic Energy Budget
EE	Expert Elicitation
iPCoD	Interim Population Consequences of Disturbance
PCoD	Population Consequences of Disturbance
PTS	Permanent Threshold Shift
iPCoD version 5.2	The last version of iPCoD using expert elicitation for disturbance transfer functions
iPCoD+DEB version 1.0	The model of iPCoD which includes DEB and is the main subject of this report

2 Introduction

2.1 Background

The potential risk of injury and/or disturbance to marine mammals during construction of offshore renewable energy developments has been identified as a key consenting risk for projects in UK waters. Possible consequences of exposure to underwater noise from piling include disturbance that could cause marine mammals to either move away or change behaviour or suffer temporary and permanent hearing damage.

2.1.1 The iPCoD Framework

To address this, the Marine Directorate (formerly Marine Scotland Science) and Offshore Wind Directorate of Scottish Government and other UK partners have supported the development of the Interim Population Consequences of Disturbance framework (iPCoD). This development has been carried out by a team of researchers at the University of St Andrews, led by Prof. John Harwood (Harwood et al. 2014, King et al. 2015) (Figure 1). The original model framework was developed in the computing language R and released in 2013.

The model is primarily designed to help assess the impacts of disturbance and auditory injury in the form of permanent threshold shift (PTS) on marine mammal populations. The inputs include information about the management unit (MU) (for a given species and population) and the developments that could impact them (e.g. a calendar of days of activity, the numbers of animals impacted etc. – which come from external sources, such as impact assessments). The outputs provide the forecast of the population trajectory with and without the simulated disturbance and PTS.

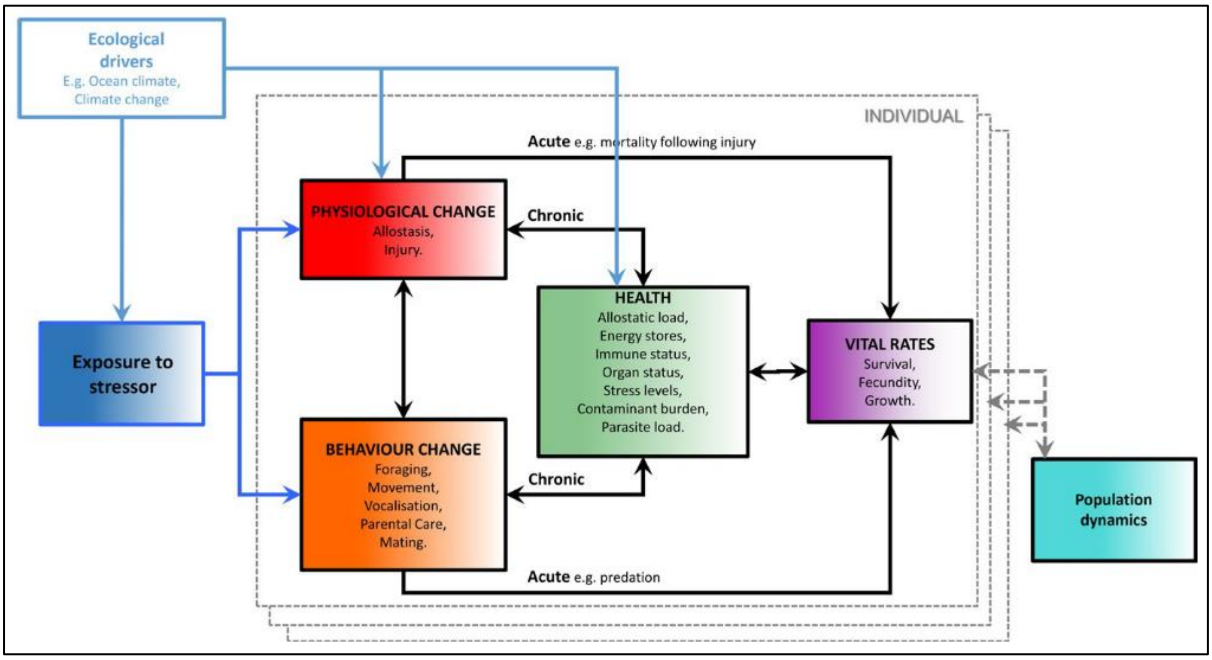

Figure 1. The Population Consequences of Disturbance (PCoD) conceptual framework, representing the effects of exposure to a stressor and a range of ecological drivers on the vital rates of an individual animal (which are then integrated across all individuals in the population to project effects on population's dynamics). From Pirotta et al. (2018).

One of the key areas that the scientific community working on PCoD has focussed on in recent years is the relationships between the amount of disturbance experienced by an individual and its vital rates (survival and the probability of giving birth). These relationships are often referred to as **transfer functions**. In iPCoD, expert elicitations were used to parameterize transfer functions with the form shown in Figure 2. Experts were asked to estimate the number of days of disturbance an animal can tolerate before a vital rate is affected, the number of days of disturbance required to cause the maximum effect of disturbance, and the confidence that had in the values they had provided.

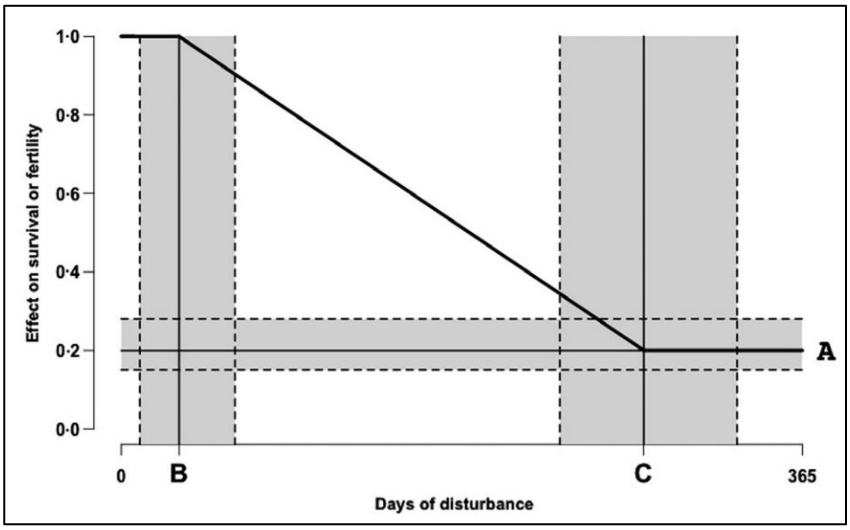

Figure 2. Hypothetical relationship between the number of days of disturbance experienced by an individual during 1 year, and its effect on survival or fertility. A– the maximum effect of disturbance (in this case, the actual probability of surviving or giving birth will be the population rate multiplied by 0.2), B – the number of days of disturbance an individual can tolerate before survival or fertility is affected, C – the number of days of disturbance required to cause A. Shaded areas indicate likely ranges around the best estimates of A, B and C provided by each expert.

In recent years, we have overseen a number of updates of the iPCoD , including new elicitations for the effect of disturbance on porpoise and seal species and auditory injury for all species, except minke whales (e.g. Booth and Heinis 2018, Booth et al. 2019). For any pathway or species not updated, the original elicitation outputs from 2012-2013 are used. The most recent expert elicitations in 2018 resulted in version 5.2 of the iPCoD model code, which is publicly available via SMRU Consulting[1]. We refer to this model as iPCoD v5.2 throughout this report.

2.1.2 Use of energetics in iPCoD

Disturbance can cause behavioural, physiological and health changes which can have subsequent effects on an individual's vital rates. In most cases, the effect of disturbance is mediated by the state of the individual (e.g. life history stage, exposure history, body condition), and the environment that the individual is in (e.g. resource availability). Dynamic

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[1] Population Consequences of Disturbance (PCoD) by SMRU Consulting

bioenergetic models can be used to predict the changes in individual body condition (used as a proxy for overall health) that may occur in response to disturbance and infer how these changes may affect that individual's vital rates. The consequential demographic effects of disturbance can then be predicted by modelling multiple individuals (Pirotta et al. 2018). These bioenergetics models also consider the variation in an individual's energetic requirements during different life history stages and take into account the state of the environment the individual is in (e.g., resource density, presence of predators). Marine mammal species show a variety of life history strategies along a spectrum that extends from pure capital breeding (e.g., humpback whale, grey seal) through to the pure income breeding (e.g. harbour porpoise). The energetic consequences of disturbance will depend on the reproductive strategy adopted by a species and the life history stage of each individual in a population (i.e., the context in which disturbance occurs). For example, a lactating female in a resource poor environment would likely respond very differently to disturbance than a non-lactating female in a resource-rich environment (Hin et al. 2019). Bioenergetic models of this kind have been widely used to investigate the potential impacts of both natural and anthropogenic disturbance on marine mammals at both the individual and population level (see Pirotta et al. 2018, 2023 for reviews).

Between 2020 and 2022 SMRU Consulting developed Dynamic Energy Budget (DEB) models for the five iPCoD species (Harwood et al. 2020, Harwood et al. 2022). These reports describe the parameters that are used in the DEB model and provided suggested values for harbour seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*), bottlenose dolphin (*Tursiops truncatus*), minke whale (*Balaenoptera acutorostrata*) and harbour porpoise (*Phocoena phocoena*) in the UK. For each species, the reports differentiate between parameter values that were obtained from the literature and those that were based on expert judgement. Harwood et al. (2022) also developed an approach to quantify the uncertainties associated with predictions of the effects of disturbance derived from DEB models and applied this to the harbour seal model. Chudzińska et al. (2024) extended this approach to the grey seal and harbour porpoise DEB models and used it to evaluate the potential population-level consequences of exposure to a number of hypothetical piling scenarios. We will use their approach in this project.

It should be recognised that predictions of the effects of disturbance based on the DEB approach are subject to three important “health warnings”. First, this approach only evaluates the effect of changes in energy intake on vital rates. Disturbance may affect the same vital rates in other ways that are not accounted for by the DEB approach (i.e. see other pathways listed in the ‘Health’ box of Figure 1. Second, DEB models require values for a large number of parameters, but there is insufficient empirical information to estimate all of these values for any marine mammal species. Instead, most values are sourced from across the marine mammal and energetics literature on the assumption that they will be appropriate for all species. Finally, the models, as for iPCoD v5.2, require an estimate of the amount of foraging time that will be lost as a result of each day of disturbance. Chudzińska et al. (2024) demonstrate that predictions of the population-level effect of disturbance are strongly influenced by the magnitude of this value, however there are few direct estimates of the duration of disturbance for any marine mammal species. We, therefore, conducted a detailed consultation and literature search to obtain a plausible range of values for this parameter for the harbour porpoise and this is described in detail in section 5.2 4.2.

3 DEB Integration Scope of Work

3.1 Objectives

The main objectives of this work were as follows:

- Outline methodology for DEB use with iPCoD and roadmap for further improvements to iPCoD, along with the advantages / limitations of the approach.
- Integration of harbour porpoise DEB transfer functions into iPCoD which results into a new model which we refer to as iPCoD+DEB v1.0
- Provide an updated iPCoD tool (iPCoD+DEB v1.0) for harbour porpoise (upgrading on Interim Population Consequences of Disturbance (iPCoD) Code Update Version 5.2 by Marine Scotland) with new parameter values and underlying calculations to determine outputs. This tool would be linked on the Scottish Government website and hosted by SMRU Consulting and available for public use.
- Produce detailed guidance to inform iPCoD users how to use iPCoD+DEB v1.0.

3.2 Tasks

Task 1: Incorporating the DEB model into iPCoD (iPCoD+DEB v1.0)

- Simulating exposure histories
- Calculating the effects of exposure

Task 2: Accounting for uncertainty in the iPCoD+DEB v1.0 model

- Uncertainty associated with the values of DEB parameters
- Estimating the ‘effect of disturbance’

Task 3: Incorporating density dependence into iPCoD+DEB v1.0

Task 4: Comparison of iPCoD v5.2 and iPCoD+DEB v1.0, reporting and updates to iPCoD helpfile

4 Task 1: Incorporating the DEB model into iPCoD (iPCoD+DEB v1.0)

As noted above, the iPCoD v5.2 has been widely used as part of assessments of the impact of disturbance on UK cetacean populations. We have therefore ensured that the iPCoD+DEB v1.0 closely resembles the current version which was informed by expert elicitation. This should allow users to run both versions of iPCoD with no additional training and with almost identical sets of input values.

4.1 Simulating exposure histories

Chudzińska et al. (2024) found that the probability an individual is exposed to a particular disturbance event has a substantial effect on DEB-based model predictions of the effects of that disturbance on vital rates. They used individual-based movement models to determine this probability for a hypothetical piling schedule at a specific location, and to generate a history of exposure for each individual they simulated.

Unfortunately, movement models of the kind used by Chudzińska et al. (2024) are not available for harbour porpoises in all UK waters. Instead, we have used the methodology that forms part of iPCoD v5.2 to generate exposure histories for the iPCoD+DEB v1.0. This methodology calculates two different probabilities of disturbance (which is the product of the probability of exposure and the probability of being disturbed as a result of exposure) using assumptions that, in theory, should encompass the range of plausible values for this parameter. The first value is based on the assumption that all individuals in a population are equally likely to spend some time in the area around a particular disturbance-inducing activity. The probability of disturbance on a given day is then calculated as the ratio of the number of individuals that the developer has predicted (as part of their impact assessment) will be disturbed on that day to the total size of the marine mammal population.

The second value is based on the assumption that there is a local population whose members are highly likely to spend time in the impacted area and that all other members of the population are unlikely to use that area. Probability of disturbance is then calculated as the ratio of the predicted number of animals disturbed per day to the size of the local population (which is specified by the user). The first assumption is likely to result in large numbers of simulated individuals experiencing a relatively small number of days of disturbance. The second assumption is likely to result in a smaller number of individuals experiencing a larger number of days of disturbance. The population-level consequences of these two different assumptions depend on the relationship between the number of days of disturbance experienced by an individual and its vital rates. These exposure probabilities and the piling schedules provided by the developer are then used to generate exposure histories (essentially the days of the year on which an individual is likely to be disturbed) for thousands of simulated individuals whose ages reflect the age-structure of the population.

4.2 Calculating the effects of exposure

In the iPCoD v5.2 the effect of a particular exposure history on the vital rates of each simulated individual is determined using a set of transfer functions of the form shown in Figure 1. These values are then averaged across all individuals in each age class to determine their effect at the population level.

In theory, the DEB model for harbour porpoises developed by Harwood et al. (2020) can be used to generate a similar set of transfer functions that would replace those obtained through expert elicitation. However, those EE-derived transfer functions are based on the assumption that one day of disturbance has the same effect on vital rates regardless of when during the year (and hence during an individual’s life cycle) that disturbance occurs. Analyses in Harwood et al. (2020) demonstrate clearly that this is unlikely to be the case, and that disturbance at times of the year when individuals are in particularly poor body condition, for example because they have just finished breeding or because resource levels are at a seasonal low level, has a much greater effect than disturbance at other times of year. This could have been addressed by dividing each year into time periods that reflect the seasonal variations in body condition predicted by the DEB models and generating a set of transfer functions for each time period. However, not only would this process be unwieldy, but it also requires the unrealistic assumption that the effects of disturbance in each time period are independent. In addition, this approach would fail to make use of one of the greatest assets of the DEB approach: the ability to predict the potential effect of specific sequences of disturbance events.

Instead, we have adapted the R code documented in Chudzińska et al. (2024) to assess the potential effect of particular piling schedules using the DEB approach and incorporated this into iPCoD to replace the EE-based calculations.

4.3 Model amendments in Task 1

4.3.1 Introduction

The code used by Chudzińska et al. (2024) has been modified so that it can be used in iPCoD+DEB v1.0. The original code implements a “cradle to grave” bioenergetics model developed by Hin et al. (2019) for long-finned pilot whales. It models the energy acquisition and expenditure of individual females over their lifetimes, and the effects of any disturbance that results in a reduction in feeding. The long-term growth rate of the modelled population is calculated from the mean lifetime reproductive success of the simulated females. This model can be used to generate relationships between the number of days of disturbance experienced by an individual and its vital rates. In principle, the mean changes in vital rates that occur as a result of a particular disturbance scenario could then be incorporated into the simple matrix model of population dynamics that underpins the iPCoD v5.2.

However, we realised that this approach is cumbersome and inflexible. We therefore revised the code used in Chudzińska et al. (2024) so that it models the dynamics of the population rather than just the lifetime reproductive success of individual females. This model replaces both the transfer function derived from expert elicitation and the simple matrix population model that are used in the iPCoD v5.2. It can be used to forecast changes in population size during the period of disturbance and in the period when disturbance activities end. An additional advantage of using a model structure of this kind is that it is possible to incorporate density-dependent effects, as discussed in section 6.4.

4.3.2 Basic Population Dynamics

As noted above, the original harbour porpoise DEB model (Harwood et al. 2020) simulates the life history of individual females, each of whose life expectancy is determined by random sampling from a cumulative survival curve, as described in Hin et al. (2019). The mean reproductive success (the total number of female offspring that survive to the initial age of their simulated mother) can be used to estimate the long-term growth rate of a population with the same demographic rates. However, it cannot be used to model the short-term population dynamics that are simulated in iPCoD v5.2. In order to model these dynamics, the existing DEB model had to be completely restructured so that the initial ages of the simulated animals reflect the stable age structure (rather than all simulated animals having the same initial age) and the life histories of all offspring produced by these individuals can be documented.

In the original version of the DEB model and the version adapted for use with iPCoD (iPCoD+DEB v1.0) the user specifies age-specific survival rates that result in a long-term population growth rate when resource density is high that is close to the maximum observed for the species being modelled. In this scenario, many adult harbour porpoises can successfully raise a calf every year. As resource density is reduced, some females switch to a biennial reproductive cycle and the mean birth rate in the population declines. Further reductions in resource density result in an increase in calf mortality as a result of starvation during the period when calves transition to independence and a further reduction in mean birth rate. At equilibrium, when the population is neither increasing nor decreasing, approximately 50% of mature females become pregnant each year, compared to 90% when food is plentiful.

4.3.3 Harmonization with iPCoD v5.2

We parameterised the iPCoD+DEB v1.0 model so that the predicted dynamics for an undisturbed population were as close as possible to those predicted by iPCoD v5.2.

iPCoD v5.2 uses a stage-structured model of population dynamics with nine age-classes and a final stage-class for adults ten years and older. Demographic rates can be set by the user, but Sinclair et al. (2020). recommended that the following values, based on data in Winship et al. (2008) and Murphy et al. (2015), are for used harbour porpoises: a calf survival of 0.8455, a juvenile survival rate of 0.85, an adult survival rate of 0.925 and a fertility rate of 0.34. We tried to ensure that the iPCoD+DEB v1.0 replicated the dynamics of the iPCoD v5.2. as closely as possible. However, the iPCoD+DEB v1.0 sets an upper limit on the life expectancy of a simulated individual, whereas there is no upper limit in iPCoD v5.2. We therefore raised the adult survival rate to 0.93 so that, with a maximum life expectancy of 40 years, approximately the same number of adult females die each year as in the iPCoD v5.2 model.

The fertility rate used in iPCoD is the probability that a mature female who is alive at the start of the calving season will give birth, whereas the pregnancy rate documented by Murphy et al. (2015) is based on females that were collected throughout the time of year when pregnancies can be detected. Within the DEB model, it is possible to calculate the maximum pregnancy rate (which occurs just after fertilization) and the actual birth rate (which corresponds to the fertility rate used in iPCoD v5.2). At equilibrium, these two values are around 0.45 and 0.35, respectively. These are very close to the range of rates observed by Murphy et al. (2015).

In iPCoD v5.2, survival and fertility rates vary from year to year to reflect the effects of environmental variation. It is not possible to model this variation in the same way in the iPCoD+DEB v1.0 . However, we allowed the daily energy intake of each simulated individual to vary from day to day, which resulted in a similar variation in vital rates among individuals. Following Harwood et al. (2020), these variations were modelled using a beta distribution whose parameters were set to ensure that on most days energy intake was within 15% of the mean value but it could be as low as 30% or as high as 200% of that value.

4.3.4 The effect of Permanent Threshold Shift (PTS) in hearing on vital rates

In the absence of any empirical information on the likely effects of acquiring PTS on an individual's energy budget, iPCoD+DEB v1.0 relies on the same expert opinions as iPCoD v5.2 (i.e., the outputs from the expert elicitation documented in Booth and Heinis (2018)) to evaluate these effects. We assume that individuals can only acquire PTS once and that this has a permanent effect on their vital rates. We also assume that the calves of females that acquire PTS will also be affected by PTS, provided they are still receiving milk from their mothers at that time.

4.3.5 Features of iPCoD v5.2 not included in the iPCoD+DEB v1.0

We have tried to make the user interface for the iPCoD+DEB v1.0 as close as possible to the one used for iPCoD v5.2. In the iPCoD v5.2, all parameter values are set in a file named config_ver5f.R and the user provides the name of an .csv file that contains the piling schedules whose effect is to be evaluated. The iPCoD+DEB v1.0 is run in an almost identical way (see Helpfile provided as a separate file for details).

There are a number of options that iPCoD v5.2 users can specify within the config file thatare unnecessary in the iPCoD+DEB v1.0, as explained below.

- Specifying threshold for demographic stochasticity – demographic stochasticity is always modelled in the iPCoD+DEB v1.0.
- Specifying demographic rates (survival rate, fertility, age at independence (age1), age at maturity(age2)) – this is unnecessary in the iPCoD+DEB v1.0 because, as explained in section 3.3.3, many of these values emerge within the DEB model.
- Specifying the number of days of residual disturbance – this is unnecessary, because we assume that the effect of disturbance for harbour porpoises does not extend beyond 1 day.
- Modelling avoidance during the period of residual disturbance (Avoid set to TRUE or FALSE) – this is unnecessary, because there is no residual effect of disturbance.

5 Task 2: Accounting for uncertainty in the iPCoD+DEB v1.0

iPCoD v5.2 accounts for uncertainty about the form of the transfer function relating the number of days of disturbance experienced by an individual to its vital rates by sampling from the statistical distributions associated with the parameters A, B and C in Figure 2 and using these samples to generate the “opinions” of thousands of “virtual” experts. Each simulation run of iPCoD v5.2 then uses a different “opinion”. We are using a different approach to account for uncertainty in the iPCoD+DEB v1.0 because of the large number of parameters in the model.

5.1 Uncertainty associated with the values of DEB parameters.

The harbour porpoise DEB model requires values for more than 50 parameters (see full list in Harwood et al. 2020, 2022), some of which are not directly observable. Nevertheless, it is important to try to quantify the uncertainties that are associated with the values used for these parameters. Chudzińska et al. (2024) used rejection Approximate Bayesian computation (ABC; Lagarrigues et al. 2015) to establish plausible statistical distributions for the unobservable parameters, and for other parameters whose reported values showed large variations. The parameters chosen for ABC were: effect of age on foraging efficiency (upsilon), age when calf’s foraging efficiency is 50% of the adult level (Tr), starvation mortality scalar (mu_s), field metabolic rate scalar (Sigma_M), mean resource density (Rmean), and calf age at which female begins to reduce milk supply (Tn).

The ABC approach involves: (i) defining a set of rejection criteria based on empirical information that can be used to evaluate the plausibility of outputs from a model with a particular set of parameter values; (ii) simulating the model a large number of times with values drawn from prior distributions for the parameters under investigation; (iii) comparing the simulation outputs to the rejection criteria; and (iv) retaining only those combinations of parameter values that produce outputs that fall within the plausible range. This process generates a joint posterior distribution for the parameter under investigation, which can then be sampled to capture the uncertainty associated with the parameter.

Chudzińska et al. (2024) developed rejection criteria based on the following population characteristics: population growth rate; proportion of females giving birth each year; female starvation mortality; and calf survival rate. Figure 3 shows the joint posterior distribution of parameter value combinations that fulfilled the rejection criteria for harbour porpoises. The ABC analysis was able to refine the prior distributions for two of the parameters (Rmean and Sigma_M), but there was little difference between the prior and posterior distributions for the other four parameters. This suggests that the rejection criteria they used provided only limited information on the appropriate values for these parameters.

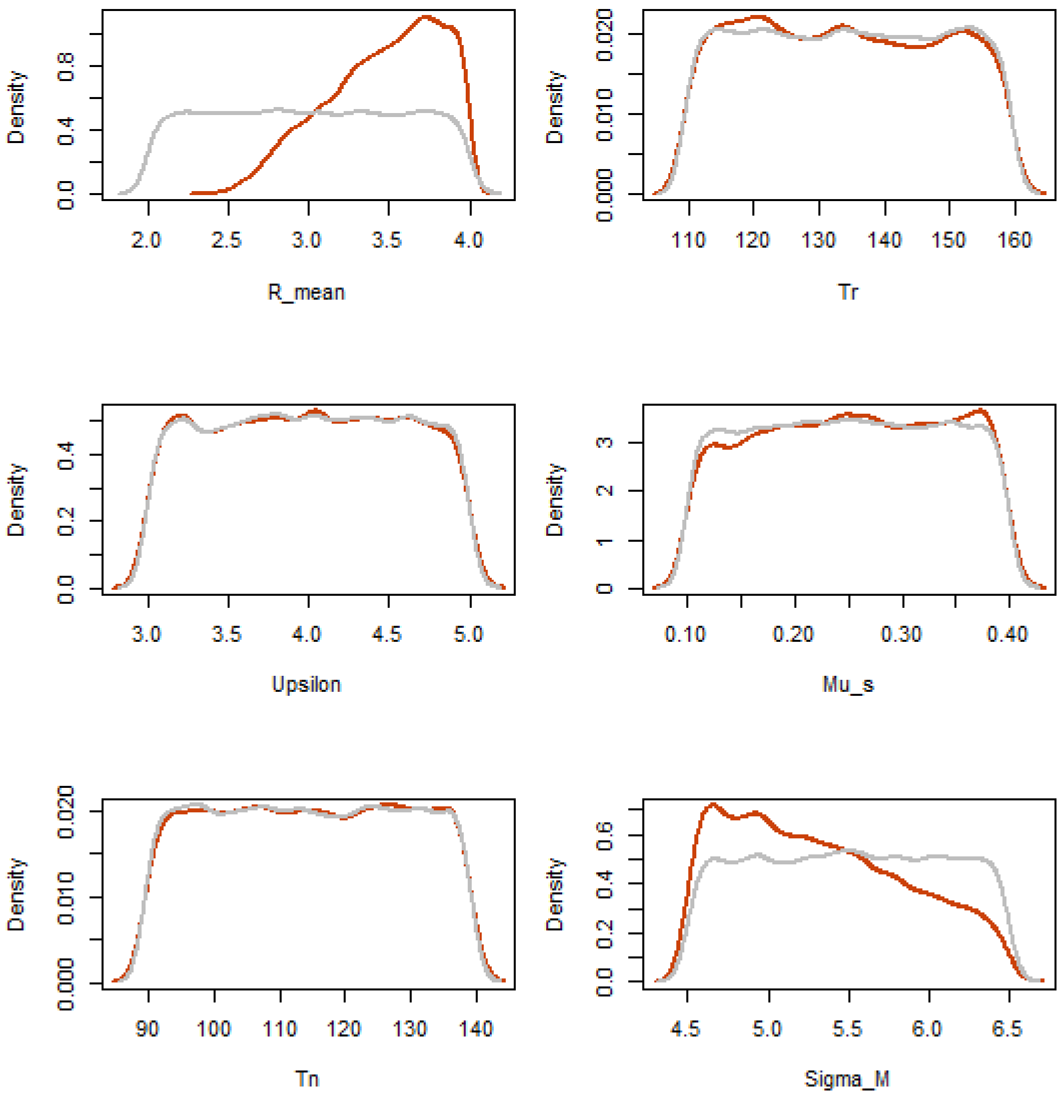

Figure 3. Prior (grey) and posterior (dark orange) distributions from ABC analysis for harbour porpoise as presented in Chudzinska et al. (2024). Rmean = mean resource density, Tr = age when calf's foraging efficiency is 50% of the adult level, upsilon = effect of age on foraging efficiency, mu_s = starvation mortality

scalar, Tn = calf age at which female begins to reduce milk supply, and Sigma_M = field metabolic rate scalar.

5.1.1 Uncertainty

We repeated the ABC analysis presented in Chudzinska et al. (2024) with the prior distributions shown in Table 1 and the rejection criteria in Table 2. For all simulations we assume no disturbance taking place and no effect of density dependence. Each simulation was run for 1500 females (sim_number, see Helpfile for details) and lasted 20 years. We run simulations for the two scenarios: with fixed resource availability (10 000 simulations) and with resources varying stochastically (20 000 simulations). Each simulation outputted two summaries: annual population growth, and median birth rate.

Table 1. Prior distribution of the five parameters used in ABC.

Parameter	Prior distribution
Rmean	uniform()
Tr	uniform(110, 160)
mu_s	uniform(0.1, 0.4)
Sigma_M	uniform(4, 6)
upsilon	uniform(3-5)
Tn	Uniform(90-140)

Table 2. Rejection criteria used in ABC.

Summary	Rejection criteria
Annual population growth	> 0.99 & < 1.01
Median birth rate	> 0.3 & < 0.5

The results are presented in Figure 4 and Figure 5 for simulations excluding and including stochastic resource variability respectively. For both sets of simulations, the prior and posterior distribution was comparable apart from Rmean indicating that the latter parameter needs to be set to a narrow set of values in order to reproduce annual population growth and median birth rate as observed.

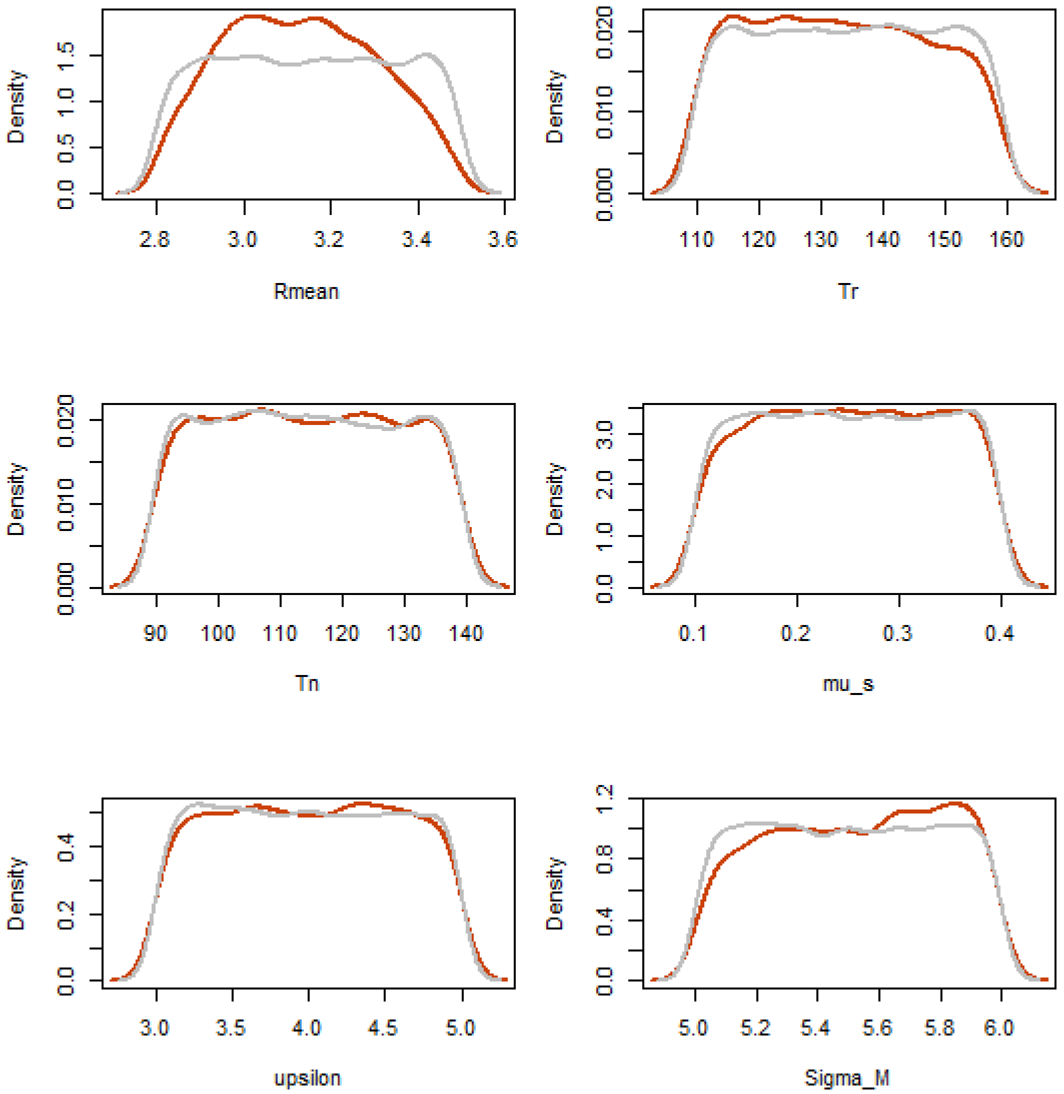

Figure 4. Prior (grey) and posterior (dark orange) distribution of the six parameters used in ABC for simulations without stochastic resource variability.

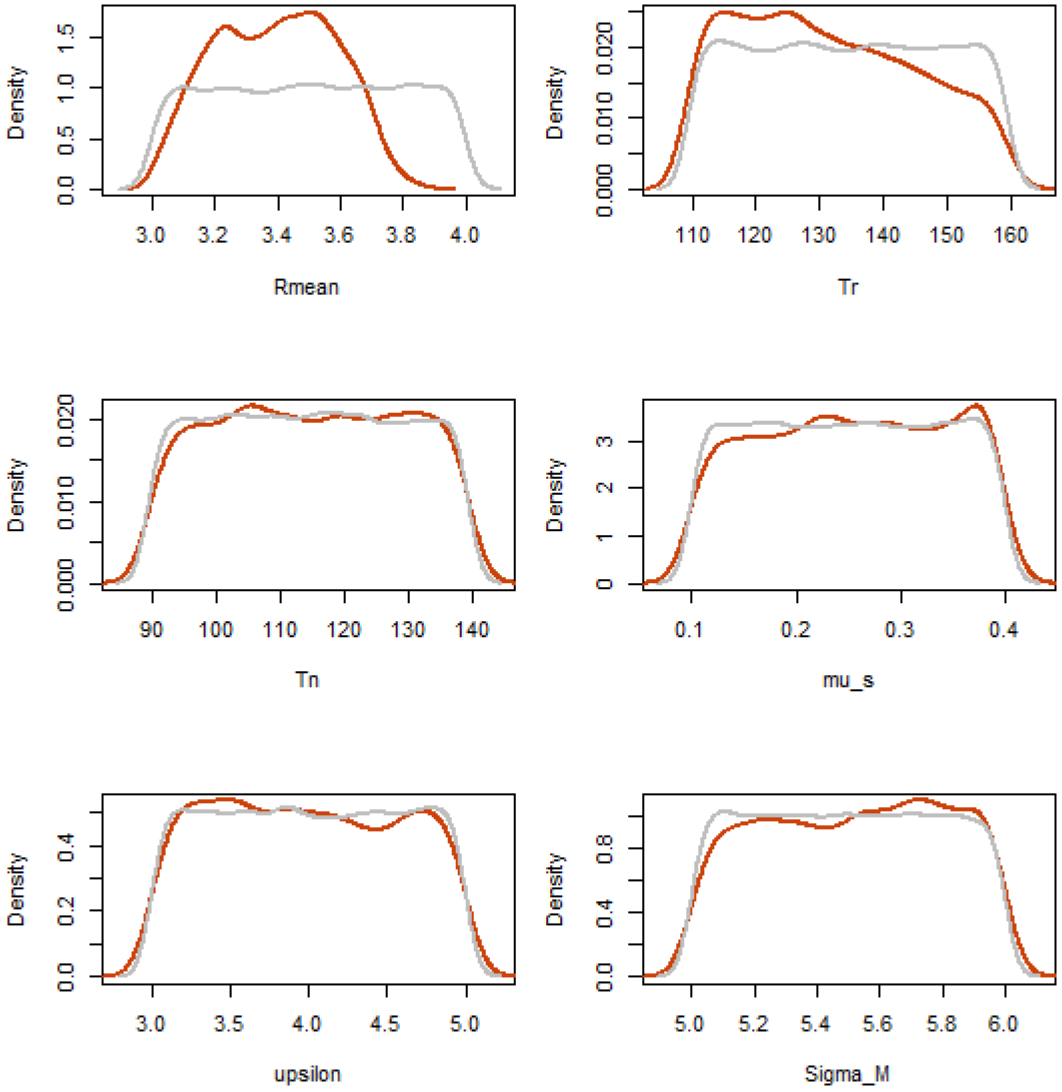

Figure 5. Prior (grey) and posterior (dark orange) distribution of the six parameters used in ABC for simulations with stochastic resource variability.

5.2 Uncertainty associated with the duration of the effect of disturbance

As noted in section 2.1, Chudzińska et al. (2024) demonstrated that predictions of the effect of disturbance on individual vital rates from DEB models are strongly influenced by the assumed amount of foraging time that is lost on each day of disturbance (referred to as the **effect of disturbance)**, which is assumed to result in an equivalent reduction in energy intake.

5.2.1 Estimating the ‘effect of disturbance’

The iPCoD v5.2 relies on transfer functions derived from an expert elicitation in which experts were asked to assume that the effect of disturbance was a 6-hour cessation of foraging (i.e., a 25% reduction in energy intake). This was assumed to apply to every instance when an animal was disturbed (i.e., a uniform response across all disturbed animals).

We intended to quantify uncertainty in the duration of the effect of disturbance on harbour porpoises by fitting a hidden process model to data derived from Benhemma-Le Gall et al.’s (2021) analysis of PAM records collected during the construction of the Beatrice windfarm in the Moray Firth. This model aims to predict the amount of time required for an individual to swim across the zone around the noise source within which porpoise detection rates are reduced.

We also considered performing two new analyses of passive acoustic data collected during wind farm construction in the Moray Firth:

1. Fit a new dose-response relationship to the data used in Graham et al. (2019) with a different response variable. Graham et al. (2019) used a simple binary response: whether or not there was a significant reduction in Detection Positive Hours (DPH) in the 12 hours following commencement of piling. We will use the actual observed reduction in DPH as the response variable because we need to know how the probability that a response will occur varies with distance from the source of disturbance.
2. Fit simple hidden process models to the data used in Benhemma-Le Gall et al. (2021) in order to determine a plausible range of values for the length of time disturbed individuals cease clicking (presumably because they are moving away) and the length of time they cease buzzing (presumably because they are not feeding) The process models are likely to involve three parameters: mean speed of movement away from the sound source, threshold distance or received level at which movement away ceases or buzzing resumes, and the variance in this threshold.

To determine whether or not such analyses were feasible, we created timeseries videos of the data that displayed the piling locations and PAM stations associated with the construction of the Beatrice wind farm on a map. These videos changed colour over time according to harbour porpoise detection rates and piling stage (pre-, during and post-piling). We analysed these videos to see if there was a notable reduction in harbour porpoise detections during and following piling activities, or an increase in harbour porpoise detections which propagated away from the piling location following the start of piling activity. Both of these were predicted from trial runs of the hidden process model. However, neither pattern was clearly observable in the CPOD data. We therefore concluded that, given the number of model parameters that would need to be estimated from the data, further analysis was unlikely to yield useable results for this purpose.

The analysis was probably impeded by the large number of confounding variables at play. For example, it is difficult to isolate disturbance from one single piling event from the effects of the arrival of vessels on site prior to construction, the general increase in vessel traffic throughout the construction period, and the varying intervals between physical piling events – either between different piles or within installation of a single pile. As a result, many harbour porpoises may have already moved away from the area prior to the start of piling for any specific turbine or pile. In addition, harbour porpoise distribution is inextricably linked to site-specific factors such as topography and prey distribution and this will affect their pattern of dispersal. For example, we observed that there were frequently higher detection rates to the southwest of the windfarm, but it is unclear whether this is the result of displacement or other ecological factors.

One approach to estimating the effect of disturbance directly is to combine measurements of harbour porpoise swimming speeds with information on the distance over which animals are observed to move following a disturbance event. Current UK guidance assumes that harbour porpoises within 26 km from any impulsive noise source are likely to be displaced (JNCC and Natural England 2019). However, disturbance is suggested to be limited to the area within 15 km of smaller diameter piles, such as pin piles (JNCC and Natural England 2019). Various studies (summarised in Brandt et al. 2018, Southall et al. 2019, Brown et al. 2023) have described changes in the occurrence or detection rate of harbour porpoises at distances of 2.2 – 33 km from piling operations.

To help estimate the effect of disturbance, representing this variety of effect ranges, we used radii of 6 km, 12 km and 36 km (calculated as the maximum observed effect plus a 3 km buffer) and calculated the time it would take for a harbour porpoise to swim from its starting location to a distance at which no response is detected, and foraging can resume. Three different swim speeds (1.2, 2.0 and 3.0 ms^{-1}) were selected from the literature (Verfuß et al. 2009, Kastelein et al. 2018). These including both travelling and fleeing speeds (see Appendix 1).

Because of these issues highlighted above, we chose to use the hidden process model originally developed for the Moray Firth data in combination with published data on the movement behaviour of harbour porpoises to generate a statistical distribution of plausible values for the effect of disturbance.

We based the hidden process model on data collected by Elmegaard et al. (2023), who exposed six harbour porpoises fitted with suction-cup-attached DTAGs to the output of an Acoustic Harassment Device normally used to deter marine mammals from fish farms, for 15 minutes. Five of these animals moved directly away from the sound source at speeds varying from 1.4-1.9 $m.s^{-1}$, reduced their clicking rate and ceased buzzing (an indicator of feeding activity). These behavioural changes continued for 16-42 minutes after the disturbance event ceased. We therefore hypothesized that harbour porpoises disturbed by noise associated with piling activity would respond in a similar way and swim away from the sound source until they were no longer affected by it. Graham et al. (2019) noted that studies of harbour porpoise response to pile-driving during wind farm construction indicate that “animals may be disturbed at distances of up to 26 km”. We assumed that this was the distance at which fleeing animals would no longer be affected by the noise associated with piling. The length of time a disturbed animal will take to reach the boundary of the affected area will depend on its distance from the sound source when piling started and its swimming speed. The number of animals that are likely to be disturbed increases linearly with distance from the sound source but the proportion of those animals that are disturbed decreases with distance, depending on form of the species’ dose-response relationship (Tyack & Thomas, 2019). We were unable to find a published relationship between the probability that an individual porpoise will be disturbed by a sound source and its distance from that source, so we used the dose-response relationship derived by Graham et al.

(2019) as a proxy. That relationship predicts the probability of a significant reduction in porpoise detection at a PAM station to the distance of that station from the sound source. We used the relationships for the probability of a significant reduction in detections 12 and 24 hr after pile-driving ceased (Table 1 and Figure 7 in Graham et al. 2019) to predict how many porpoises would be disturbed at different distances from the pile-driving activity and calculated how far they would have to swim to be 26 km from that activity. We then assembled five measurements of harbour porpoise swimming speed (1.4,1.8,1.9,1.97 and 3.0 $m.s^{-1}$) from Verfuß et al. (2009), Kastelein et al. (2018) and Elmegaard et al. (2023). We sampled at random from the predicted swimming distances for 10,000 animals and divided each distance by a randomly sampled swimming speed (converted to $km.hr^{-1}$). The resulting estimates of time taken to leave the affected area had a mean of 1.5 hr and a range of 0 – 5 hr.

The minimum piling duration reported by Graham et al. (2019) was 3.27 hr. Ninety-three percent of the estimated times to exit the affected area were less than this, suggesting that almost all disturbed animals would have left the area in which they might be affected before pile-driving ceased. We therefore assumed that disturbed animals would exhibit the same behaviour observed by Elmegaard et al. (2023) and begin feeding 16-42 minutes after they were outside the affected area.

In order to generate a statistical distribution for the “effect of disturbance” we sampled at random from the predicted swimming distances for 10,000 animals, divided each distance by a randomly-sampled swimming speed (converted to $km.hr^{-1}$) and added a “recovery time” sampled at random from the five observation of the length of time after sound exposure before disturbed animals began to produce feeding buzzes reported by Elmegaard et al. (2023). The resulting distribution of effect times is shown in Figure 6. The mean effect of disturbance is 2 hr with a range from 0.25 hr to 5.6 hr. This distribution is closely approximated by an Erlang distribution with mean 2.0 and shape parameter 3, shown in blue in Figure 6. The Erlang distribution is a special case of the Gamma distribution with the shape parameter constrained to be a positive integer. It is commonly used to model waiting times and Hin et al. (2023) used it to simulate among individual and among exposure variation in the effect of disturbance from military sonar on beaked whales. We chose to use this distribution for the effect of disturbance in the iPCoD+DEB v1.0 rather than the empirically generated one because this will allow the user to explore the population consequences of using different mean values for the “effect of disturbance”.

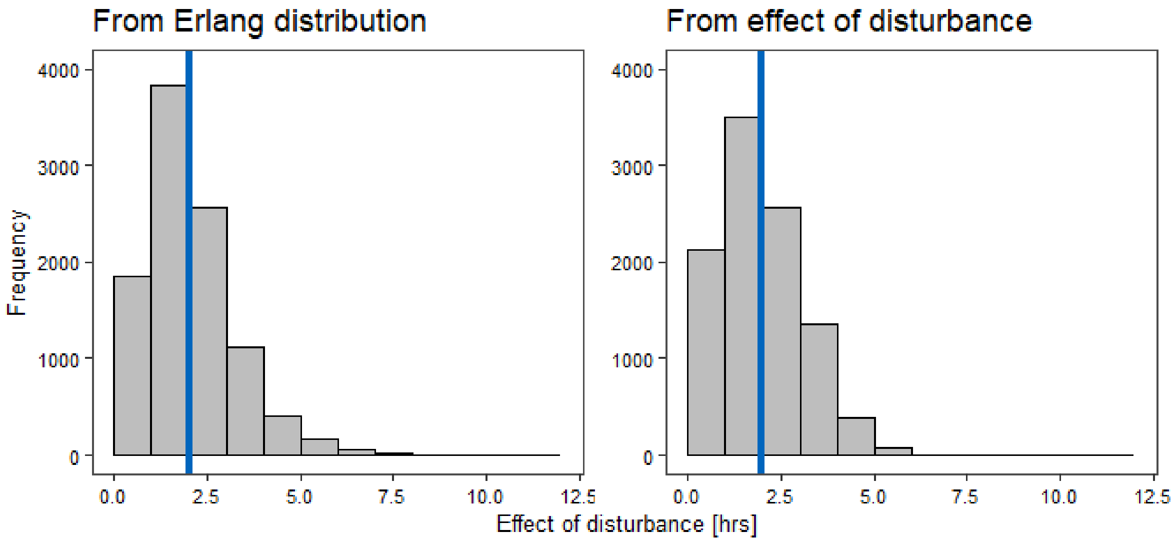

Figure 6. Left panel: The histogram shows the distribution of 10,000 random samples from an Erlang distribution with a shape parameter (k) of 3. The mean (2 hrs) is shown by the blue line. Right panel: The histogram shows the distribution of 10,000 values for the “Effect of disturbance” parameter calculated using randomly selected combinations of observed swimming speeds, likely distances from the sound source on exposure and observed duration of “recovery period”. The mean (2 hrs) is shown by the blue line.

6 Task 3: Incorporating density dependence into the iPCoD+DEB v1.0

Recently, Rijkwaterstaat (RWS) in the Netherlands requested updates to the iPCoD v5.2 to support their cumulative impact assessment for government planning of OWF. The process is called ‘Kader Ecologie en Cumulatie’ (KEC), and was last completed in 2021 (Heinis et al. 2022). RWS offered support to advance the capabilities of the iPCoD+DEB v1.0 more such that density dependence could be incorporated.

Vincent Hin from Wageningen Marine Research (WMR) was asked by Rijkswaterstaat (RWS) to develop a bioenergetics population model for harbour porpoise and, using this model, quantify the relationship between prey availability and porpoise population abundance for use in the iPCoD+DEB v1.0. The below sections are reproduced from the brief delivered RWS by co-author V. Hin as a separate document. It has been amended below to fit the format of this report.

6.1 Material and methods

6.1.1 Model description and the relationship between porpoise abundance and prey density.

To derive a relationship between prey density and porpoise population abundance requires a model that tracks a population of porpoises across multiple generations. In such a model, individuals born during the simulation become independent agents and are tracked until death, instead of weaning. Furthermore, prey density is not fixed, but changes in response to the feeding of all simulated porpoises and autonomous production of new prey. Consequently, the growing whale population will deplete prey density until prey density stabilizes at a level that does not allow any further growth of the porpoise population. Modelled porpoises and their prey have now reached a stationary (equilibrium) state, also referred to as “carrying capacity level.”

An individual-based model (IBM) that tracks multiple-generations of whales was developed for long-finned pilot whales (Hin et al. 2021) and two species of beaked whales (Hin et al. 2021, Hin et al. 2023). The IBM for long-finned pilot whales (Hin et al. 2021) uses the exact same representation of individual-level bioenergetics as the original single-female model of Hin et al. (2019). However, in the IBM, the amount of prey available to porpoises is not fixed, but follows from a dynamic equation (ordinary differential equation) that models autonomous prey growth and prey depletion (Hin et al. 2021, 2023):

$$\frac{dR(t)}{dt} = \delta(R_{max} - R(t)) - V^{-1} \sum_{i=1}^{N} I_R^i(t,\mathbf{x}) \qquad \text{Eq. 1}$$

In Eq. 1, $R(t)$ is the prey density at time t and N is porpoise population abundance. The function $I_R^i(t)$ gives the prey feeding rate of porpoise individual i, which is a function of time t and a vector of individual state variables ($\mathbf{x}$) such as age, length and energy reserves. The total feeding rate is calculated by summing the feeding rates of all porpoises. Prey increase (productivity) is assumed to follow semi-chemostat dynamics, which models prey productivity as a linearly declining function of the amount of prey present. In this function, the prey turn-over rate δ determines how fast prey is replenished and parameter R_{max} controls the prey density in absence of feeding by porpoises (maximum prey density).

Parameter V is a volume conversion scalar that is used for numerical convenience and does not affect population dynamics.

For the current assignment, the long-finned pilot whale IBM was adapted for harbour porpoise using the parameters from Harwood et al. (2020) and Chudzińska et al. (2024), see Table 7 in Appendix 2. We furthermore assume stochastic fluctuations in the maximum prey density (R_{max}) according to a beta distribution with mean 0.25 and standard deviation of 0.055. This harbour porpoise IBM can then be used to derive the required relationship between porpoise abundance and prey density.

The harbour porpoise IBM was used to estimate the relationship between scaled harbour porpoise population abundance as independent variable and scaled prey density as dependent variable, where both are scaled to their values at stationary state. Each single simulation of the harbour porpoise IBM was initialized with a single female at day 142 of the year, which corresponds to the day before modelled females give birth. A simulation lasted 400 simulated years and generally simulations reached a stationary population after 100 simulated years. Although the model was executed using discrete daily time steps (365 steps per year), the population was censused yearly at day 142. This resulted in a single estimate of population abundance per year. The last 200 years (= 200 values) were used to derive stationary values of prey density and porpoise population abundance ('carrying capacity level') that were used for scaling.

To study the amount of variability and sensitivity of the relationship between prey density (P) and porpoise abundance (N) to various model parameters requires running many (replicate) simulations. Therefore, the following protocol, or algorithm, was developed to derive the desired relationship from the model output in a standardized fashion that could easily be applied to the model output:

- Derive the carrying capacity level K as the median population abundance at census day 142 for the last 200 simulated years (200 values in total).
- Define t_{end} as the earliest time (yrs) in the simulation with N > K
- Define t_{start} as the earliest time (yrs) in the simulation with more than 100 females
- Define N_{start} as the population abundance at t_{start}, divided by K
- Define P_{q50} as the median prey density at census day 142 for the last 200 simulated years (200 values in total)
- Define P_{start} as the prey density at t_{start}, divided by P_{q50}
- Derive the population growth rate as $\left(\frac{1}{N_{start}}\right)^{\left(\frac{1}{t_{end}-t_{start}}\right)}$.

- Derive the slope between scaled abundance and scaled prey density as $\frac{P_{start}-1}{N_{start}-1}$
- Derive the intercept between scaled abundance and scaled prey density as 1 – slope.

This protocol assumes a linear relationship with scaled porpoise abundance as independent variable and scaled prey density as dependent variable. This relationship passed through the point (1;1), which reflects the stationary state with prey density and porpoise abundance fluctuating around an equilibrium value.

6.1.2 Variability and sensitivity

The harbour porpoise IBM contains several stochastic processes. Consequently, the outcome of two replicate simulations will vary, even when using exactly the same set of parameters. To assess the amount of variability in the relationship between population abundance (N) and prey density (P) we ran 120 replicate simulations of the harbour porpoise IBM, and for each replicate simulation we applied the protocol described in section 6.1.1.

As part of a sensitivity analysis, we used three values for parameter δ (0.01, 0.05 and 0.1), which is the prey turn-over rate in the autonomous prey productivity function (Eq. 1). For each value other than the default value (0.05) we ran 20 replicates. In addition, the effect of using a census day right after the birth pulse at day 163 on the prey-abundance relationship was investigated using 20 replicate simulations as well.

Several other parameters included in iPCoD+DEB could not be estimated from data. These include R_{mean}, T_R, T_N, γ, μ_s and σ_M (see Table 7 in Appendix 2 for a description of these parameters). To assess the effect of uncertainty in these parameters for the iPCoD+DEB model, an ABC analysis was performed. This analysis filters parameter combinations that result in realistic model outcomes based on several selection criteria (see Chudzińska et al. 2024 for more details). The outcome is a joint posterior distribution for the selected parameters. In total, the ABC analysis used for the iPCoD+DEB model resulted in 1,576 plausible combinations of values of R_{mean}, T_R, T_N, γ, μ_s and σ_M. For each parameter combination we ran 10 replicate simulations of the harbour porpoise IBM. The parameter that represents mean prey density (R_{mean}) was not used, because prey density in the harbour porpoise IBM is an outcome of population dynamics, instead of a fixed (parameter) input. A mean prey – abundance relationship and population growth rate was calculated per ABC parameter combination. In addition, an overall mean values were calculated across all 15,760 simulations. By using the outcome of the ABC analysis, we assess parameter uncertainty in the prey-abundance relationship in an identical manner as parameter uncertainty was assessed for the iPCoD+DEB model. The description of parameters and their range as used in ABC analysis are shown in Table 3.

Table 3. Parameters used in Approximate Bayesian Computation (ABC) analysis.

Parameter	Description	Default	Range
T_R	Age at which prey feeding efficiency is 50%	130	110 - 159
T_N	Calf age at which female begins to reduce milk supply	120	90 - 139
γ	Shape parameter for effect of age on resource foraging efficiency	4	3.0 – 5.0
μ_S	Starvation mortality scalar	0.2	0.1 – 0.4
σ_M	Field metabolic maintenance scalar	5.5	5.0 – 6.0

6.2 Results

6.2.1 Single simulation

For the baseline parameters (Appendix 2) the simulated porpoise population grows exponentially until it reaches a carrying capacity level of around 11,500 simulated individuals at around 100 simulated years (Figure 7). During the same time period the prey density declined from 10 to an average value of 4.3.

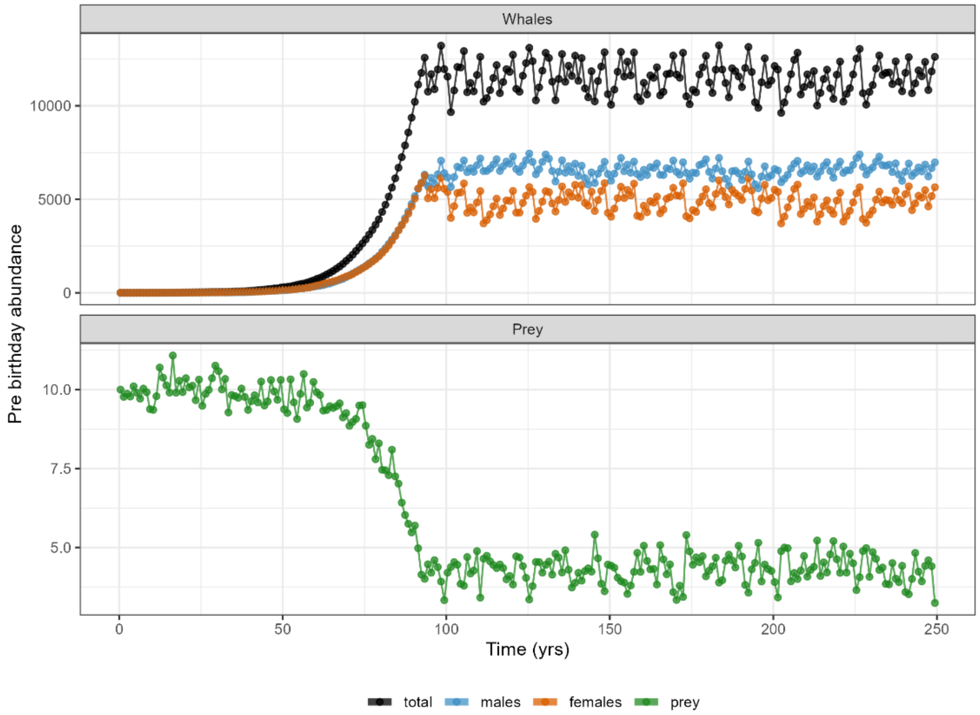

Figure 7. Harbour porpoise population abundance (top panel) simulated from the bioenergetic individual-based population model starting with a single female at t = 0. Maximum prey density of 10 and all other parameters at default value (Appendix 2). The exponential growth phase occurs between years 50 and 100. Prey density (bottom panel) declines as a result of increasing number of porpoises.

Applying the protocol described in section 6.1.1 to the simulation in Figure 7 leads to a t_{start} value of 46 years and a carrying capacity that was reached at t_{end} = 92 years. In between t_{start} and t_{end} mean annual population growth was 1.09 (range: 1.03 – 1.13). The relationship between scaled prey density and scaled abundance was approximately linear with a slope of -1.408 and an intercept of 2.408 (Figure 8, right panel).

6.2.2 Sensitivity analysis

The mean slope across 120 replicates for the default parameter values was equal to -1.338 (range: -1.592 – -1.065) and the mean population growth rate was equal to 1.090 (range: 1.084 – 1.101). The growth rate during the phase of exponential population growth was comparable between the different versions and varied between 8% and 10% per annum (Figure 9 and Table 8 in Appendix 2). The slope of prey-abundance relationship showed stronger differences between versions, and especially for low prey turn-over rate (δ = 0.01), the slope was considerably lower (Figure 9 and in Appendix 2). For this version, the carrying capacity level was around 2,500 individuals and the estimated population growth rate showed more variation between replicates than the other versions.

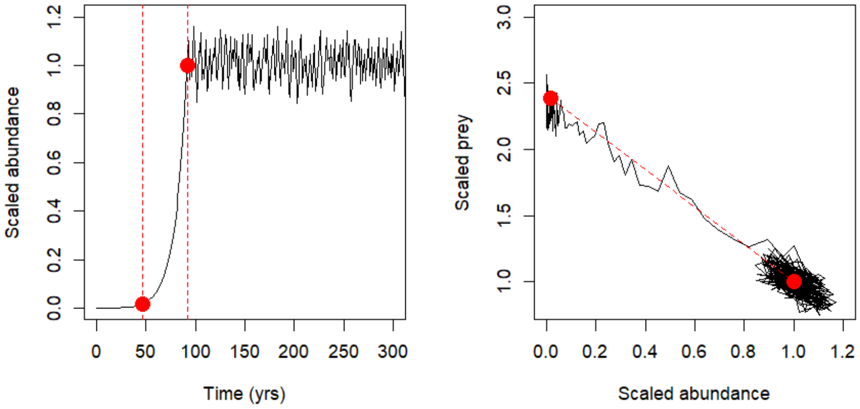

Figure 8. left: scaled porpoise abundance at census day 142 during 300 simulated years with vertical lines tstart = 46 years and tend = 92 years and Nstart = 0.0184. Right: relationship between scaled porpoise abundance (horizontal axis) and scaled prey density (vertical axis) with Pstart = 2.382. The population growth rate equals 1.09, prey slope equals -1.408 and prey intercept equals 2.408. All parameters at default values and Rmax = 10.

6.2.3 ABC analysis

Of the 15,760 simulations performed for the ABC analysis, there were 47 simulations (0.3%) in which the simulated harbour porpoise population went extinct before reaching 400 years. Extinction was solely a result of the stochastic processes in the model and occurred by chance. In most simulations that went extinct, many male offspring were produced, or female offspring with a low life expectancy. All extinctions happened during the first 100 simulated years and there were no parameter combinations for which more than 1 simulation went extinct. Simulations that went extinct were excluded from further analysis. In all other simulations carrying capacity was reached before 200 simulated years, with a maximum value of t_{end} of 178 yrs.

The mean population growth rate per ABC parameter combination ranged between 1.086 and 1.093, with an overall mean of 1.090. Similarly, the mean prey-abundance slope ranged between -1.537 and -1.169 with an overall mean slope equal to -1.313 (Figure 10). Plotting the population growth rate as a function of each of the five ABC-parameters revealed no clear parameter effect on the population growth rate (Figure 17). The partial effect of the ABC parameters on the slope varied per parameter. The slope increased with parameters

μ_s, σ_M and T_R, decreased with parameter γ and remained approximately constant for parameter T_N (Figure 18).

Three different parametric distributions were fitted to the mean estimates per ABC parameter combination (1,576 values in total). In order to fit gamma and beta distributions, mean values were transformed by adding 1.8. This ensured that all values fell within the zero to one range. Parametric density distributions were fitted using maximizing loglikelihood using the R function `fitdist` (package `fitdistrplus`). Goodness-of-fit was compared between distributions using loglikelihood values. The highest loglikelihood was achieved by a normal distribution on the untransformed values with a mean value of -1.314 and a standard deviation of 0.1035 (Table 4).

Table 4. Parameters of parametric distributions fitted using maximum likelihood estimation to the mean values of the prey-abundance slope from the ABC analysis.

Fitted distribution	**Transformation**	**Loglikelihood**	**AIC**
normal(-1.314, 0.1035)	NA	13341	-26678
beta(10.73, 11.31)	+1.8	13270	-26537
gamma(19.83, 40.69)	+1.8	12736	-25468

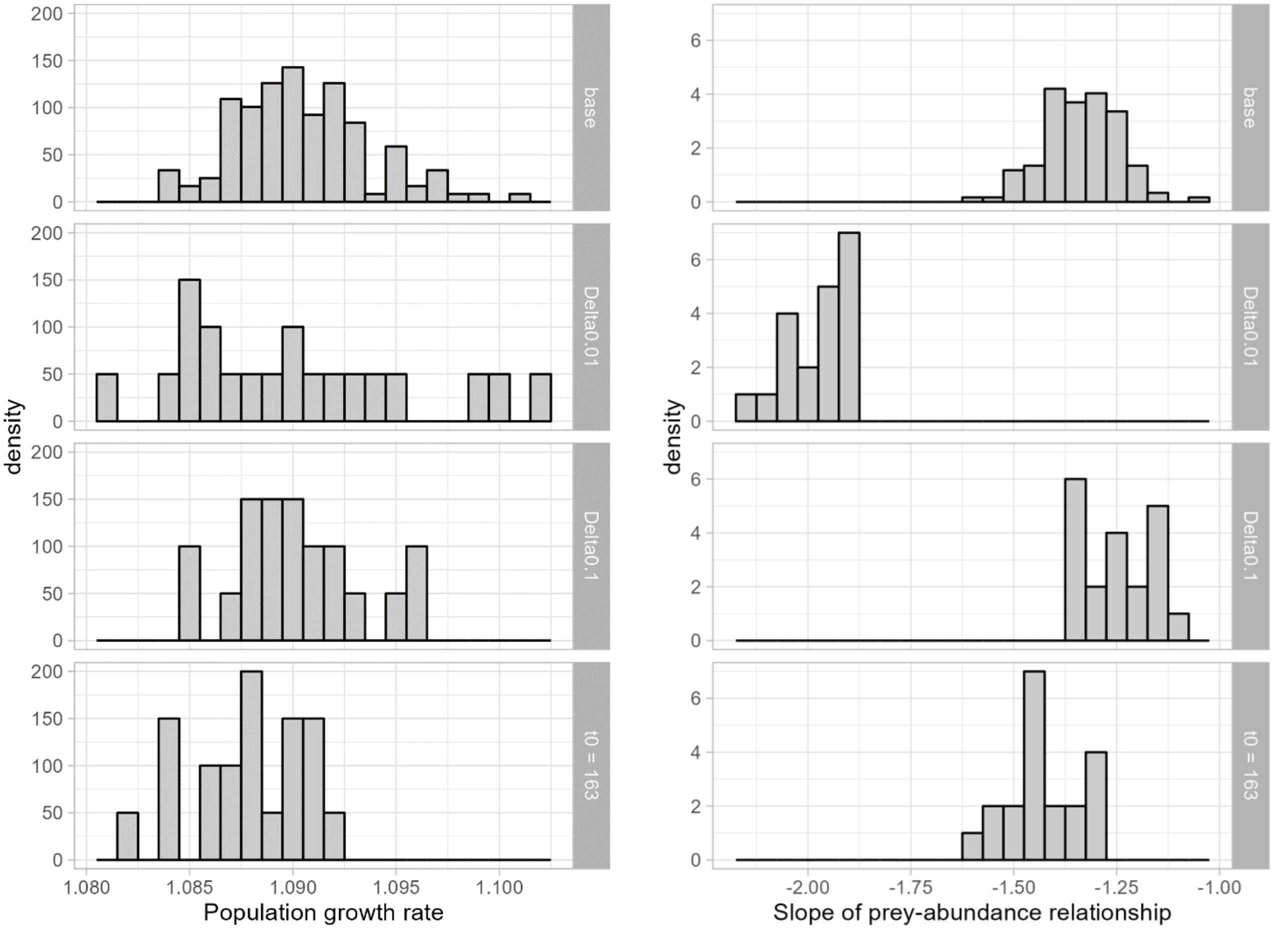

Figure 9. Distribution of population growth rate (left) and slope of prey-abundance relationship (right) for different versions (columns). Base version corresponds to default parameters with $\delta = 0.05$. Version 't0 = 163' corresponds to population census after the yearly birth pulse at day of the year 163. Base version is based on 120 replicate simulations, while the three other versions have 20 replicate simulations each.

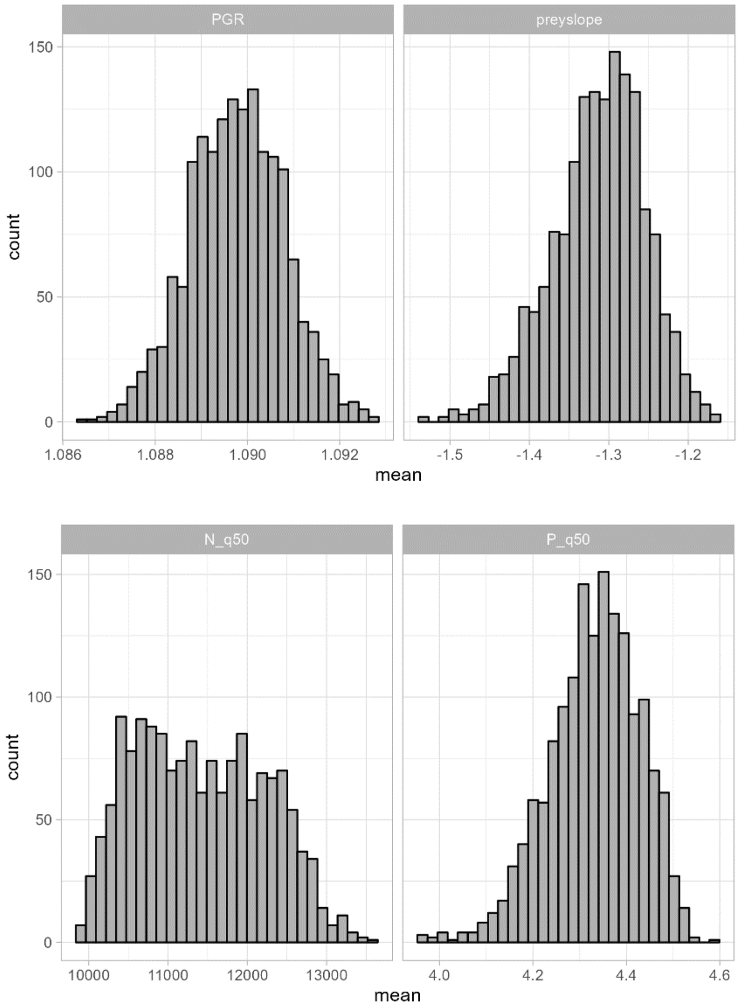

Figure 10. Distribution of mean per ABC parameter combination of population growth rate (‘PGR’: top left panel), mean slope of prey-abundance relationship (top right panel), mean carrying capacity level (‘N_q50’: bottom left) and mean stationary prey density (‘P_q50’: bottom right panel).

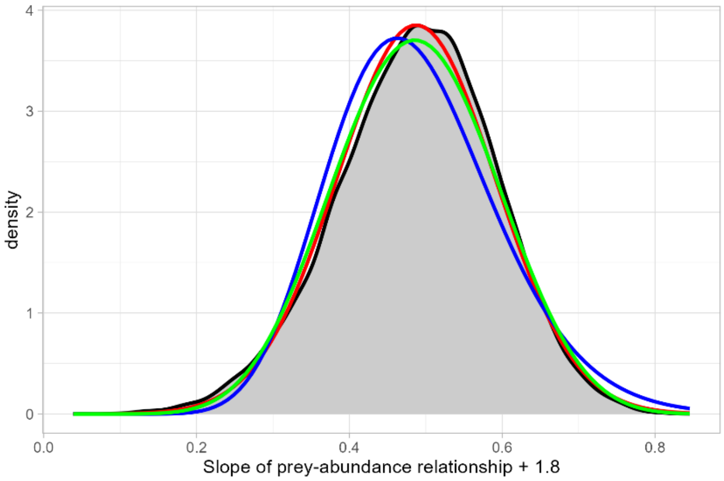

Figure 11. The transformed density distribution of the slope of the prey-abundance relationship (grey shading and black line) with superimposed three parametric distribution fitted using loglikelihood maximization. Normal distribution in red, gamma distribution in blue and beta distribution in green.

6.3 Conclusions

An individual-based model of a harbour porpoise population was used to derive a relationship between scaled prey density and scaled porpoise abundance for use in the iPCoD+DEB v1.0. This relationship was derived from the phase of exponential growth, in which the modelled porpoise population was growing with an annual growth factor of 9% per year (discrete growth rate of 1.09). The resulting slope of the prey-abundance relationship of -1.338 for the default parameters of the harbour porpoise population model (Table 7). The results of an ABC analysis were used to account for uncertainty in parameters that could not be derived empirically. This resulted in a posterior distribution of the slope of the prey-abundance relationship that, after transformation, could be well approximated using a parametric normal distribution with a mean of -1.314 and a standard deviation of 0.1035.

A sensitivity analysis that looked into the effect of the prey turn-over rate (δ) revealed that a low prey turn-over rate leads to more steep (negative) prey-abundance relationships. However, low values of δ also substantially reduce the modelled porpoise population, which might affect the representativeness of the resulting slope estimates. Furthermore, the use of less steep slope estimates represents a more worst-case scenario of density dependence, because it results in a smaller increase in population growth rate with declining population abundance.

6.4 Incorporating density dependence into iPCoD+DEB v1.0

In iPCoD+DEB v1.0, fertility (the probability that a female will become pregnant in a particular year) and calf survival are both affected by the density of prey that each female encounters. This prey density is initially set to a constant mean value that results in a stable population. We hypothesise that a reduction in population size might result in an increase in resource density and a consequential increase in calf survival and fertility. To determine the potential form of this relationship, we used the relationship between prey density and porpoise abundance from an individual-based model for harbour porpoises as described in section 5.1. This generated a relationship between prey density and porpoise abundance relative to equilibrium population size that can be used in iPCoD+DEB v1.0. The statistical distributions established during uncertainty analysis are sampled each time iPCoD+DEB v1.0 is run. This form of density dependence assumes that any increase in prey density that results from a reduction in harbour porpoise numbers will be available to all the individuals in the population. However, there are many other generalist predators in the North Sea that consume similar prey species and prey sizes to harbour porpoises and it is therefore unlikely that all of the “surplus production” of prey will be available to the harbour porpoise population. As a result, this modelling approach will probably over-estimate the speed with which a disturbed population will return to its equilibrium level. We therefore encouraged to run simulations of each scenario with density dependence turned off and turned on because this should capture the full range of potential responses.

7 Task 4: Comparison of iPCoD+DEB v1.0 with iPCoD v5.2, reporting and updates to iPCoD v5.2 helpfile

7.1 Comparison of the two models

To compare the predictions of iPCoD v5.2 with the iPCoD+DEB v1.0, we ran multiple scenarios looking at population dynamics of harbour porpoises affected by piling operations. We chose an already published scenario which results in 6.88 % of population decline over 10 years when modelled with iPCoD v5.2. The detailed description of the scenario is given in Brown et al. (2023), here we provide a short description. The scenario of piling at Celtic and

Irish Sea Management Units (referred to as CISCUM26 in Brown et al. (2023)) includes multiple piling events per season (winter and summer) which were designed to cover noise generated from wind farm installation. An effective detection ranges approach was applied to encompass both unabated monopile installation (26 km, four piling events, two in each season) and abated / pin-pile installation (15 km, five piling events, two in winter, three in summer) (see Table 17 and Figure 19 in Brown et al. (2023)). Activities were modelled for a 10-year disturbance period and in each year, a seasonal average of 10% of the combined, four Special Area of Conservation (SAC) area were disturbed. The SACs are: West Wales Marine, North Anglesey, North Channel and Bristol Channel Approaches. Disturbance did not happen at constant 10% per day throughout the year, as this was considered unlikely to be realistic (in terms of actual distribution of daily disturbance levels). Instead, daily values in 5% increments were applied (from 0-20% which averaged per season to 10%) to more accurately reflect the real-life patterns observed in impulsive noise activity record.

The above-described disturbance scenario was compared with exactly the same scenario run with four scenarios using the extended iPCoD+DEB v1.0:

- iPCoD+DEB v1.0 including density dependence and variable duration of disturbance drawn from Erland distribution (‘DD, Erlang disturbance’, Figure 6);
- iPCoD+DEB v1.0 including density dependence and fixed, 6 hr of disturbance for the disturbed animals (‘DD, fixed disturbance’);
- iPCoD+DEB v1.0
- iPCoD+DEB v1.0 excluding density dependence and fixed, 6 hr of disturbance for the disturbed animals (‘no DD, fixed disturbance’);

We ran 100 simulations for each of the four above-listed scenarios of iPCoD and output population size during 10 years of disturbance and 25 years post-disturbance. The iPCod v5.2 CISCUM26 scenario was only run for 15 years post-disturbance. We also present results of 35 (iPCoD+DEB) and 25 (iPCoD v5.2) years of simulation of undisturbed populations for the five scenarios.

Figure 13 shows the comparison of all scenarios of iPCoD (four extended scenarios and iPCoD v5.2) for undisturbed and disturbed populations under CISCUM26 scenario. The confidence intervals for the extended versions of iPCoD were much smaller than for iPCoD v5.2 predictions but all predictions under the extended versions fall within confidence intervals of the predictions from iPCoD v5.2. The mean population trajectory under iPCoD v5.2 resulted in larger population decline than any of the iPCoD+DEB versions. The decline projected by iPCoD v5.2 was closest to predictions under iPCoD excluding density dependence and assuming fixed duration of disturbance (‘no DD, fixed disturbance’).

Focusing on the results of only the iPCoD+DEB v1.0 scenarios (Figure 13) shows largest population decline in the first few years of disturbance for scenarios excluding density dependence and for the scenario excluding density dependence but assuming variable duration of disturbance. These three scenarios resulted in relatively quick population recovery already in the 10 years when disturbance occurred, whereas scenarios assuming no density dependence and fixed duration of disturbance resulted in population recovery only after disturbance stopped.

All scenarios of the iPCoD+DEB v1.0 model resulted in stable populations in the undisturbed scenario, although larger variabilities were observed for predictions including density dependence (Figure 12, Figure 13).

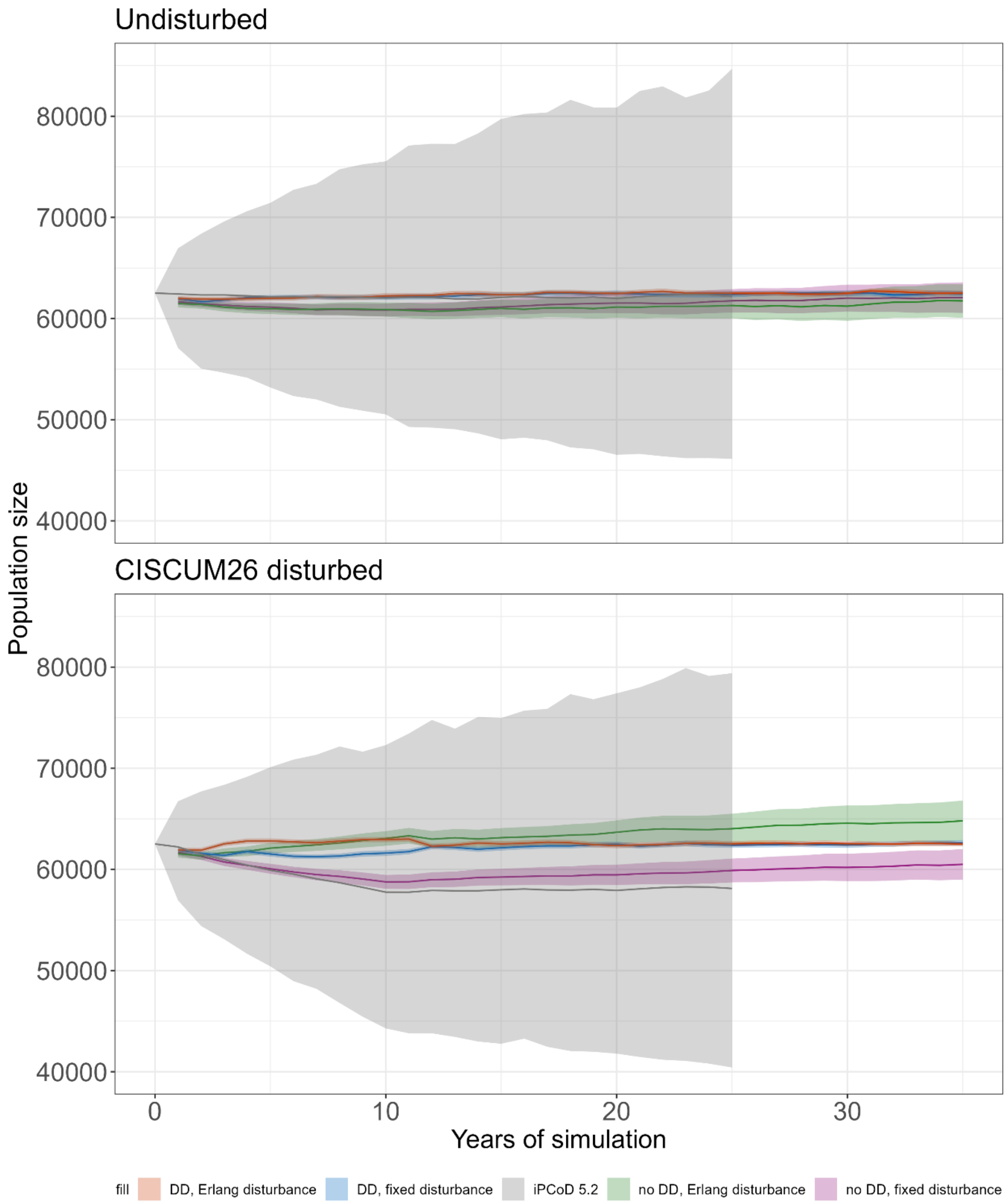

Figure 12. Changes in population size the four scenarios using iPCoD+DEB v1.0 and iPCoD v5.2 for CISCUM 26 disturbance scenario. Solid lines show mean predictions and semi-transparent ribbon of corresponding colours 95% confidence intervals. For simulations assuming disturbance, the first 10 years of simulations assume occurrence of disturbance, followed by 25 years of no-disturbance simulation to track population recovery (if present).

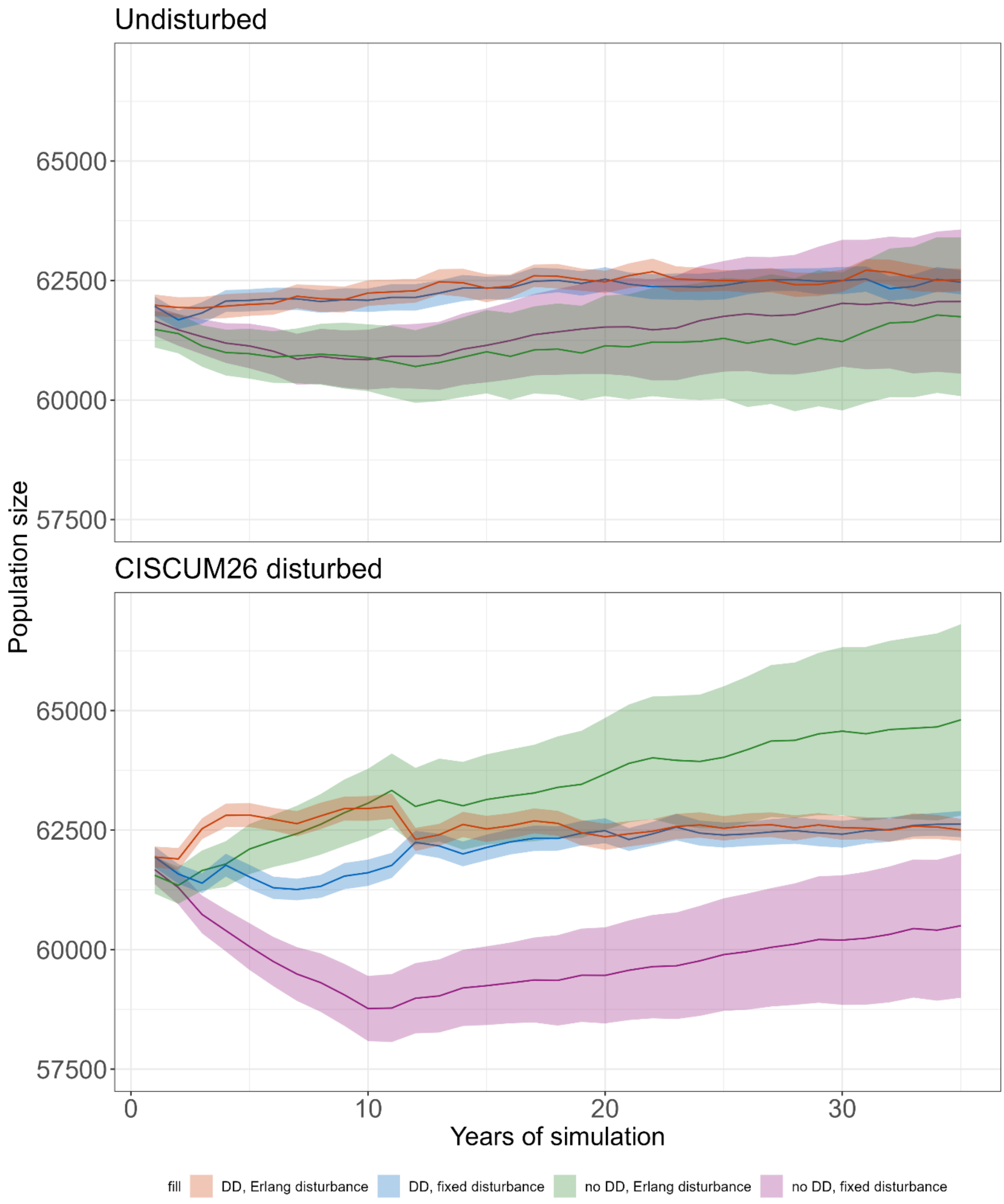

Figure 13. Changes in population size the four extended scenarios using iPCoD+DEB v1.0 for the CISCUM 26 disturbance scenario. Solid lines show mean predictions and semi-transparent ribbon of corresponding colours 95% confidence intervals.

7.2 Updates to the helpfile

A modification of Helpfile for iPCoD v5.2 has been provided as a separate document. It includes detailed description of how to use the iPCoD+DEB v1.0 model and in which sections/functionalities it differs from iPCoD v5.2.

8 Roadmap for iPCoD v5.2 and iPCoD+DEB v1.0 model developments

Whilst the iPCoD v5.2 model is well developed, there are a number of elements of the model that could be improved to better support decision making in the face of uncertainty. In the sections below we discuss each of the elements that can be improved, both within the iPCoD model and - because the model relies on estimates provided by the user (typically from environmental impact assessments) - the inputs to the model.

A disproportionate focus on the development of the model in the past decade has been on the harbour porpoise. As regulatory needs change, it is important to ensure that the model is also sufficiently developed for the other species in the model framework. In the absence of such development, the model in most cases results in highly conservative estimates.

The iPCoD v5.2 model represents an update from the earliest versions of the model that relied on an expert elicitation carried out in 2012. For some species the elicitations were updated using improved elicitation techniques (Booth and Heinis 2018, Booth et al. 2019).

For harbour porpoise and the two seal species, the disturbance transfer function elicitation was updated in 2018 (Booth et al. 2019) and resulted in significantly smaller predicted impacts than those made using the 2012 elicited transfer functions. However, due to time limitations it was not possible to update the transfer functions for minke whales or bottlenose dolphins. As a result, the iPCoD model for both these species rely on the original 2012 elicitation that, based on the improvement in transfer functions for the species that were elicited, is likely to be heavily precautionary.

The auditory injury transfer functions (i.e., the effect of Permanent Threshold Shift (PTS) on vital rates) were also elicited in 2012 (Harwood et al. 2014) and updated for some species in 2018 (Booth and Heinis 2018). Due to time limitations, the focus of the elicitation was on harbour porpoise, although updates for seal species and bottlenose dolphins were achieved. No update was made to the minke whale transfer functions.

8.1 Estimating the probability of exposure

Currently, iPCoD models require the user to input estimates of the numbers of animals of the species under consideration that may be disturbed. The model assumes that all individuals in a population are equally likely to be exposed to disturbance from a particular activity, or that only the members of a user-defined vulnerable local population are likely to be exposed. The real-world situation is likely to be somewhere between these two extremes (see Keen et al. 2021). One way to address this is to use outputs from individual-based movement models, such as DEPONS (Nabe-Nielsen et al. 2018) or AgentSeal (Chudzińska et al. 2020), to generate statistical distributions for the probability that individuals will be exposed to disturbance from each of the disturbance-inducing activities being investigated. Chudzińska et al. (2024) illustrates how this can be done. The code to implement iPCoD+DEB v1.0 has been written so that it could take advantage of such information as it becomes available.

8.2 Other key sensitivities

There are a number of other areas which are important to note, but are challenging to provide a roadmap for given the scale of investment required, the likelihood of useful outputs to support consenting.

The iPCoD v5.2 and iPCoD+DEB v1.0 models, like all models, are sensitive to the quality of the input parameters. The main input parameters to both models include the size of the management unit (or population considered affected), the density of animals (which underpins estimates of disturbed and injured animals), the thresholds at which animals respond and the type of response. This could be addressed via a large sensitivity analysis using iPCoD standardising inputs to understand the relative contributions. However, the value of this must be considered in the context of the other uncertainties highlighted above.

Impact assessments do not directly assess the impact of reduced foraging, rather they assess the impact range and duration of disturbance, informed by studies which show a reduction in detected vocalisations from baseline levels. Key to this is the fact that it is unknown if a reduction in vocalisation means a displacement of animals out of the area, or a change in vocal behaviour in response to the disturbance impact, neither of which directly informs us of a change in foraging. This is challenging to assess but could be addressed via further tagging of harbour porpoises with DTAGs or other acoustic tags to better understand this topic area and help quantify key parameters.

Additionally, as highlighted above, the general iPCoD framework considers many different pathways by which acute and chronic disruption can impact on vital rates such as survival and reproduction. The other pathways (considered in expert elicitation, but not in an energetic model) include allostatic load, immune status, organ status, stress physiology, contaminant burden and parasite load. This is a very challenging area to advance as it involves many different pathways (which may interact). We have not estimated a cost to advance this topic.

8.3 Speeding up the model.

The iPCoD+DEB v1.0 is currently taking several minutes to run one simulation. The speed of the analysis is positively correlated with number of simulated females (see Helpfile for sim_number), number of tested piling operation and number of specified vulnerable population (see Helpfile for vulnmean). The current code is designed to perform all operations on a single core.

The speed of the simulations can be increased if operations, which are not dependant on each other, can be performed on multiple cores. This way each simulated piling operation and each simulated vulnerable population can be simulated on a separate core so the results of any of these simulations (like the results for one operation) does not affect the results of other simulations. Different simulated females, on the other hand, cannot be simulated separately as for simulations including density dependence, there is a dependency between simulated individuals.

9 Appendix 1 – Effect of disturbance review

9.1 Estimating the 'effect of disturbance'

It is necessary to specify an appropriate 'effect of disturbance'.

Here we explored the grey and published literature and available data to help guide estimates of this parameter. Three approaches were taken to explore methods of systematically estimating the effect of disturbance on the iPCoD species, in order to compare the effect of lost foraging hours on model results. For this analysis, we used harbour porpoise as the model species and consequently, data are drawn from the available literature on harbour porpoise.

Version v5.2 of the iPCoD model relies on transfer functions where the effect of disturbance is defined as a 6-hour cessation of foraging (i.e., a 25% reduction in energy intake). This applies to every animal disturbance, and this occurs irrespective of the animal's location relative to the noise stressor (i.e., a uniform response is used across disturbed animals).

Given the state of knowledge on behavioural responses in marine mammals, it is highly probable that some form of relationship follows those observed from controlled exposure experiments, in which the probability of response increases with increasing proximity or received level from the source (e.g. summarised by Harris et al. 2018). As such, in a population of uniformly distributed animals, a greater number of individuals will be subject to lower disturbance effects, while fewer individuals located close to the noise source will experience high disturbance effects (Chudzińska et al. 2024) (Figure 14).

To explore this in a systematic manner, using the best available knowledge, a simple disturbance framework was developed, consisting of six disturbance effect levels, corresponding to 2.5%, 5%, 7.5%, 13%, 25% and 47% of the exposed animals, respectively, from animals closest to the noise source (2.5%) to those furthest away (47%), based on this uniform distribution (Figure 14). It is assumed that there will be unexposed animals outside the impact zone. These percentages were arbitrarily chosen to capture the cascading pattern of effect with increasing range from the source as observed in dose response functions in porpoises (e.g. Benhemma Le Gall, et al 2021).

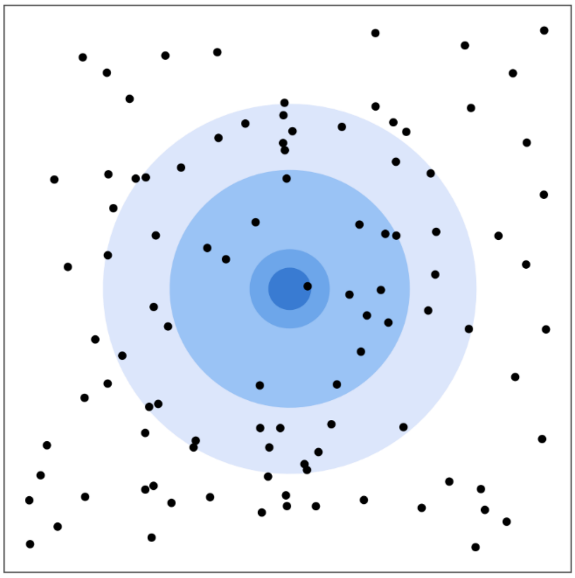

Figure 14. Diagram explaining the basis of individual disturbance effects. The darkness of the concentric blue circles corresponds to the sound intensity at different distances from the source and black dots represent a uniform distribution of animals. The greatest number of animals is located in the outermost ring and will be subject to the lowest disturbance effect. Animals in the darkest circle in the centre will experience the highest disturbance effect.

Three approaches have been used to quantify how harbour porpoises foraging might be affected by noise disturbance.

The first approach was a product of the estimated baseline daily foraging duration and change in foraging probability following disturbance. Few studies provide robust estimates of daily foraging duration in harbour porpoises; however, Wisniewska et al. (2016) suggest that they may forage almost continuously over a 24-hour period. However, it is unlikely that harbour porpoises are able to sustain such high levels of foraging in the long term (Hoekendijk et al. 2018). To adopt a conservative approach, we used 24 hours as the upper limit of baseline foraging duration in our calculations of disturbance effects. Further estimates of baseline foraging duration in harbour porpoises were obtained from the results from Wisniewska et al. (2018). We utilised those published minimum, mean and maximum buzz-positive minutes from this paper as a percentage of recording duration (day and night) and calculated the resulting daily foraging duration by scaling to day length. This resulted in baseline foraging estimates of 4.3, 12.6 and 18.2 hrs in scenarios where the animals are considered not to be disturbed.

To calculate potential effects of disturbance from these baseline estimates, we then used predicted change in probability of foraging with distance from a piling vessel from the Beatrice offshore wind farm (Figure 15) (published in Benhemma-Le Gall et al. 2021).

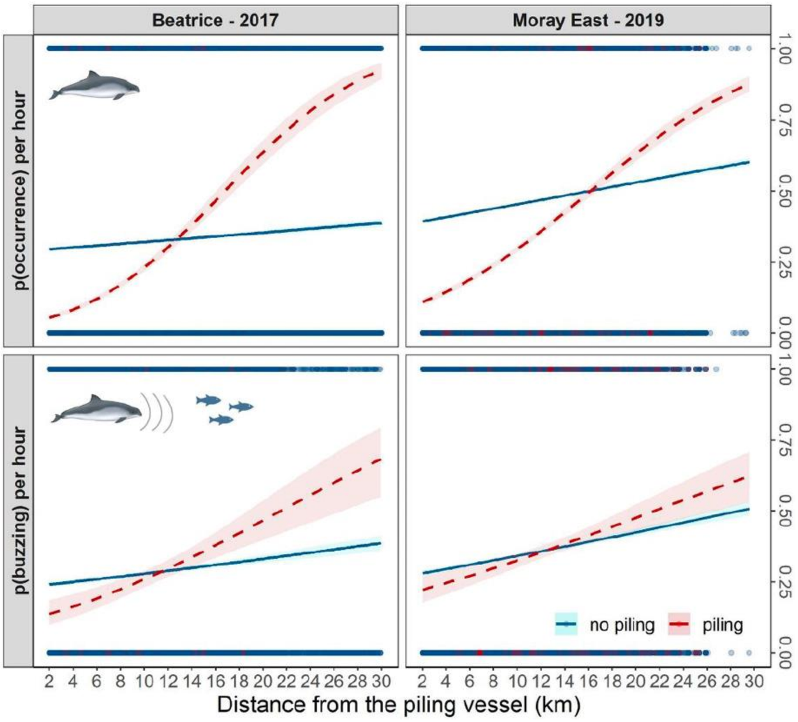

Figure 15. The probability of harbour porpoise occurrence (top) and buzzing (a foraging proxy) activity (bottom) per hour during pile driving hours (red dashed line) and when no piling was occurring (blue solid line) with respect to distance from the piling vessel. Plots are shown for two offshore wind farms – Beatrice in 2017 (left) and Moray East in 2019 (right) (published from Benhemma-Le Gall et al. 2021).

Based on an animal's location at the onset of disturbance, the distance at which there is no reduction in foraging probability between piling and non-piling scenarios was between 11 and 12 km (Figure 15 above) (published in Benhemma-Le Gall et al. 2021). As such, the distances chosen to evaluate reduction in foraging probability were 1, 2, 4, 6, 8 and 10 km. These produced reductions in foraging probability during piling scenarios of 0.11, 0.10, 0.09, 0.07, 0.05 and 0.02, respectively. Effect of disturbance was then calculated by baseline foraging duration multiplied by the reduction in foraging probability (Table 5 and Figure 16C).

Table 5. Effect of disturbance (number of foraging hours lost) as a function of baseline foraging duration (Wisniewska et al. 2018) and reduction in foraging probability during piling activities (Benhemma-Le Gall et al. 2021). Distance from the source refers to the distance of an animal to the piling vessel at the start of piling and refers to the range of foraging probabilities extracted from Benhemma-Le Gall et al. (2021).

		Baseline foraging duration (hours)			
		24	18.2	12.6	4.3
Hypothetical distance from source (km)	Reduction in foraging probability	Effect of disturbance (hours)			
1	0.11	2.66	2.02	1.40	0.47
2	0.10	2.45	1.86	1.29	0.44
4	0.09	2.11	1.60	1.11	0.38
6	0.07	1.61	1.22	0.85	0.29
8	0.05	1.10	0.84	0.58	0.20
10	0.02	0.50	0.38	0.27	0.09

The second method of estimating the effect of disturbance was based on harbour porpoise swim speeds and the distance at which there is no detrimental effect on foraging from the disturbance source. Current UK guidance is based on a maximum displacement distance of 26 km from any impulsive noise source for harbour porpoises (JNCC and Natural England 2019). However, evidence suggested that area avoidance is limited to 15 km for smaller diameter piles, such as pin piles (JNCC and Natural England 2019). Various studies present spatial harbour porpoise response (where effect is a change in occurrence or detection rate – not explicitly a reduction in foraging) to piling ranging from 2.2 – 33 km (summarised in Brandt et al. 2018, Southall et al. 2019, Brown et al. 2023).

To represent this variety of effect ranges, we used radii of 6 km, 12 km and 36 km (calculated as the maximum observed effect plus a 3 km buffer) as the maximum distances from the noise source at which foraging disruption would occur. We then calculated the time it would take for a harbour porpoise to swim from its starting location to ‘safety’ (the distance at which no response is detected, and foraging can resume; Table 6 and Figure 16A). A range of swim speeds was also selected to represent variation in harbour porpoise swim speed estimates in the literature, including both travelling and fleeing speeds. These speeds were 1.2, 2.0 and 3.0 ms^{-1} (Verfuß et al. 2009, Kastelein et al. 2018).

Lastly, while one study has suggested behavioural responses up to 72 hrs following the cessation of piling, this claim is poorly supported (Brandt et al. 2011). Other sources suggest that harbour porpoise activity within 25 km of the source will return to baseline levels within 16.8 hours following disturbance for unmitigated pile-driving (Dähne et al. 2013), or 5-6 hrs for pile-driving combined with acoustic deterrent devices or bubble curtains (Dähne et al. 2017). In addition, various studies cite deterrent effects of 6-10 hrs up to ~15 km distance from piling (Geelhoed et al. 2018, Nabe-Nielsen et al. 2018, Rose et al. 2019), with the probability and magnitude of response increasing closer to the piling location (Graham et al. 2019, Brown et al. 2023). On this basis, we selected 12, 15 and 18 hrs as maximum response durations in order to get an overview of model results when extreme disturbance effects are included. Individual disturbance effects for a maximum response of 12 hrs were arbitrarily set at 12, 8, 6, 4, 2 and 1 hrs, with increasing distance from the noise source. This sequence was then scaled for maximum durations of 15 and 18 hrs (Figure 16B).

Table 6. Effect of disturbance (number of foraging hours lost) as distance/speed, where distance is the maximum disturbance distance - the animal's location in relation to the piling vessel at the start of piling. Maximum disturbance distances are based on the spatial extent of responses present in Brandt et al. (2018), Southall et al. (2019) and Brown et al. (2023). Swim speeds are taken from Verfuß et al. (2009) and Kastelein et al. (2018).

Maximum disturbance distance (km)	Distance from source (km)	Swim speed 1.2 (ms^{-1})	Swim speed 2.0 (ms^{-1})	Swim speed 3.0 (ms^{-1})
6	0.5	1.27	0.76	0.51
	1	1.16	0.69	0.46
	2	0.93	0.56	0.37
	3	0.69	0.42	0.28
	4	0.46	0.28	0.19
	5	0.23	0.14	0.09
12	1	2.55	1.53	1.02
	2	2.31	1.39	0.93
	4	1.85	1.11	0.74
	6	1.39	0.83	0.56
	8	0.93	0.56	0.37
	10	0.46	0.28	0.19
36	3	7.64	4.58	3.06
	6	6.94	4.17	2.78
	12	5.56	3.33	2.22
	18	4.17	2.50	1.67
	24	2.78	1.67	1.11
	30	1.39	0.83	0.56

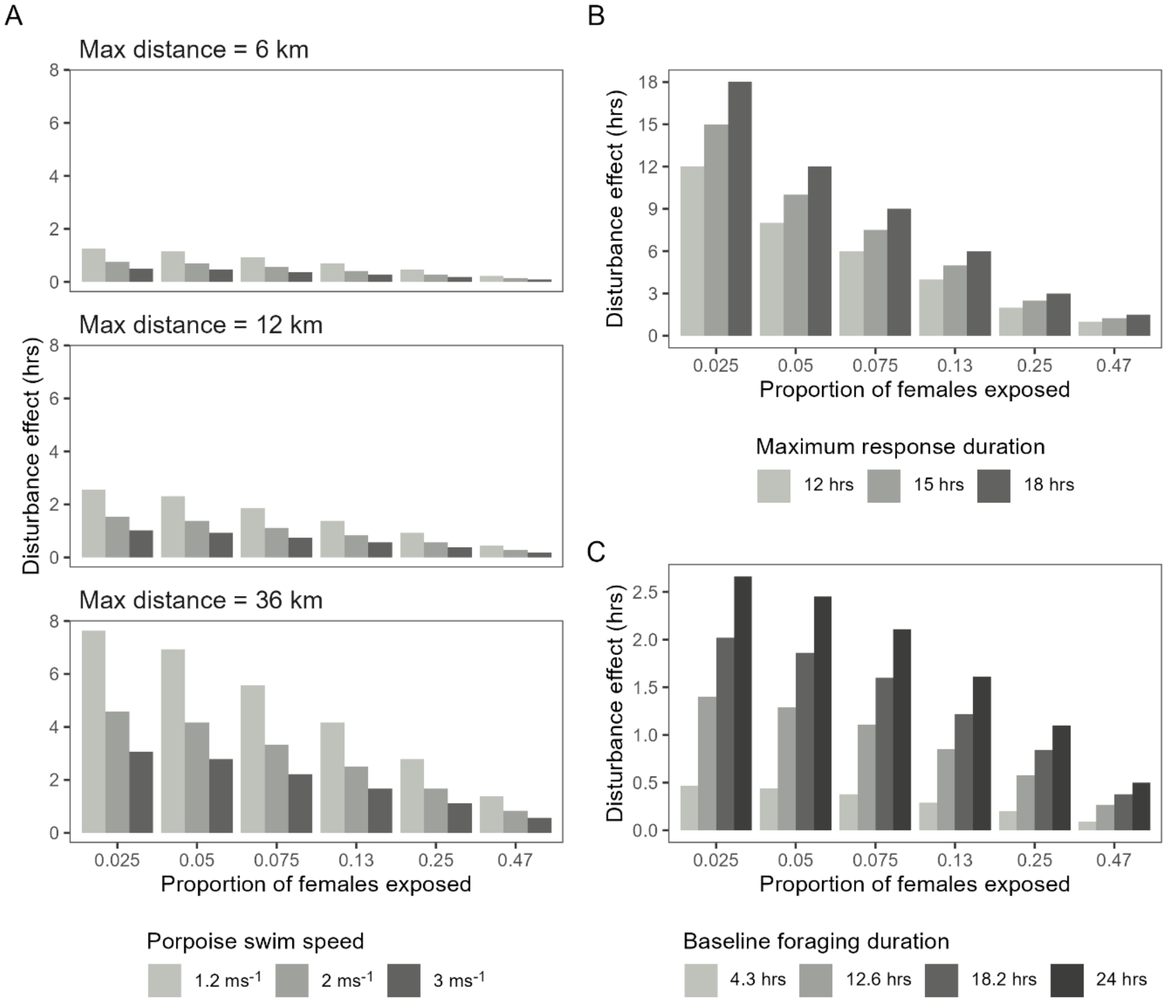

Figure 16. Effect of disturbance (lost foraging hours) for differing proportions of females in the population, where higher proportions of females are those located further from piling activities and lower proportions experience higher effects of disturbance and are located closer to piling. Effects of disturbance are determined by A) the time taken to swim from the animal's location at the start of piling to the maximum disturbance distance: 6 km, 12 km, and 36 km, B) arbitrary scale based on three maximum response durations (12, 15 and 18 hrs), and C) baseline foraging durations when harbour porpoises are not disturbed multiplied by estimated reduction in foraging with distance from piling.

9.2 Additional review of studies and their utility in informing disruption in harbour porpoise foraging

Many studies refer to disturbance of harbour porpoise from piling noise. However, as the intensity of the sound individuals experience decreases with increasing distance from the sound source, all responses of harbour porpoise exposed to piling noise are not necessarily equal. Southall et al. (2019) outlined a scale capturing a range of severities of responses of free-ranging marine mammals to exposure events in the context of individual vital rates, considering impacts on overall survival along with effects on feeding and reproduction. Under this framework, response scores 0-5 encompass stages up to and including the onset of avoidance behaviour, when individuals actively move away from the source and experience reduced foraging success during the exposure period. Response scores 6-9 are associated with the most severe behavioural changes, including reductions in foraging success extending beyond the exposure period, increases in energy expenditure exceeding the normal daily baseline, and prolonged displacement from foraging habitat resulting in impacts to individual heath or mortality (see Table 3 in Southall et al 2019). Therefore, these higher severity responses are the ones of concern within the context of energetic disruption, such that they may impact vital rates. It is therefore important to consider the types of behavioural responses taken by harbour porpoise to various levels of piling noise, rather than simply whether they are disturbed or not, as these can help determine the extent to which sound exposure has a tangible impact on vital rates. Building on sections above, and the review by Brown et al. (2023) we summarise many of the available studies to provide a summary of the observed responses (if information on porpoise foraging is available, this was included). We highlight important caveats that caution against verbatim use of ranges used in studies without careful considerations of methodologies employed and data limitations.

Reference: Brandt et al. (2011). Studied offshore windfarm: Horns Rev II.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• This study analysed data collected from a TPOD gradient system to investigate the impacts of piling on harbour porpoise, using minutes per hour during which at least 1 click was detected (or porpoise positive minutes per hour, PPM/h) as a proxy for porpoise activity at various distances from the construction site. • Overall detection rates were very low across the study sites – especially close to the piling locations. • Porpoise activity decreased by 100% in the first hour after pile driving, remaining below normal for 24-72 hrs 2.6 km from the piling site, with a negative effect out to a mean distance of 17.8 km.	• The duration of the impact of piling on harbour porpoise activity in this study was quantified by time between porpoise positive minutes (PPM) and hours (PPH) reaching average pre-exposure levels and the first local maximum, without considering variation in mean PPM/PPH for each TPOD position. • Both baseline and during piling PPM/PPH were very low in several POD locations. Baselines were also collected at different times of year. • Other factors potentially impacting harbour porpoise activity such as water depth and the presence of pre-existing windfarm structures were also not considered, and the model revealed a significant effect of month on PPM/PPH but this was not corrected for in the final results. The baseline was only a 6-week period in April-May ahead of a piling programme occurring intermittently over a 5 month periods. Therefore, baseline period may not be reflective of patterns over a longer time frame or a different time of year.

Reference: Carstensen et al. (2006). Studied offshore windfarm: Nysted.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Used TPODS to monitor echolocation activity of porpoise. • During construction wait times between HP encounters increased from 6 hrs in the baseline period to 3 days in the windfarm area, an increase 6 times larger than the reference area. • Steel sheet pile installation saw an increase in wait time of 4 to 41 hrs in the construction and reference areas. • Indicates occurrence and therefore habitat use of HP changes during construction as HP appeared to leave the windfarm.	• Study did not appear to test if wait times differed for the baseline in the construction site and the reference area prior to the study (i.e. only considered 'impact' with no consideration of natural behaviour). Wait time could be inherently higher in one than the other before construction even started, which risks the results showing the effect of piling on HP presence was lower/higher than was actually the case. • Wait time also varied with 'month' but construction was only in the summer. • Doubts regarding the effect on porpoises further than 15.7 km where first waiting time was still significantly higher than the baseline, but this was the furthest distance from the piling that the authors had data for.

Reference: Dähne et al. (2013). Studied offshore windfarm: Alpha Ventus.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Visual monitoring of HP prior to and during construction and operation with line transect surveys from 2008 to 2010. SAM click loggers from 2008 to 2011 1-50km from the centre of the wind farm. • Lowest HP density during construction in 2009. Reduced density observed during piling up to 20km from source. • Acoustic data also showed negative impact of piling on porpoise detection rates <10.8km from source with increased detection rates further from source (25-50km) suggesting some form of displacement occurred.	• Although the authors provide evidence that displacement had occurred there is little information about how long it took for porpoise occurrence to return to baseline conditions, so the extent of the disturbance caused by piling is difficult to infer. • Despite visual and acoustic data, the authors did not note down any behaviours observed which would have been useful to see if porpoises were foraging in the areas they were displaced from and therefore the potential impacts of disturbance from the area. The authors claim that this is a key foraging area for porpoise, hence such information would be useful. • Construction work was "unintentionally carried out during a period of low detection rates" in 2009, difficult to separate effects of seasonal variation in porpoise occurrence and effects of human activities at that time, affecting baseline density.

Reference: Dähne et al. (2017). Studied offshore windfarm: Dan Tysk.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Porpoise presence decreased up to only 12 km from the source with a bubble curtain as opposed to the 18-25 km reported without.	• No assessment of behaviour made. Only considered displacement. • Very little baseline data as C-POD time series before pile driving was only 3 hours much shorter period than that over which data was collected after pile driving, therefore results are susceptible to stochastic day to day variation in porpoise activity and presence at the study site (c.f. results of Graham et al 2019).

Reference: Geelhoed et al. (2018). Studied offshore windfarm: Gemini.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Aerial surveys indicate avoidance 15-25 km from piling. • PAM indicates avoidance distance of 10-20 km during piling.	• Although there were baseline aerial surveys, no PAM baseline before piling commenced. • PAM detected porpoises during piling whilst the aerial surveys did not. • No statistical relationship between distance from piling and porpoise activity. • No mention of different behaviours observed from porpoise after piling, though the authors discuss that individual variability and the importance of the area for feeding could contribute to determining the extent of the response of porpoise to piling noise, the authors do not try to address this with data.

Reference: Nehls et al. (2015). Studied offshore windfarm: Borkum West II.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• the authors compared disturbance of harbour porpoise from pile driving with and without a 'big bubble curtain' (BBC). • Harbour porpoises were disturbed up to 15 km from the construction site when there was no BBC as evidenced by decreased detection rates (porpoise positive minutes per hour). • Use of a BBC appeared to reduce harbour porpoise disturbance as the radius of disturbance was only about 5 km.	• Looked at the effect of using a BBC on harbour porpoise disturbance more than the nature of the disturbance itself, with no reference to different porpoise behaviours and no indication of whether normal foraging was occurring between 5 and 15 km with the BBC. • Reference periods were always 9 hrs before piling events given than no pile strikes had occurred within the last 24 hrs.

Reference: Tougaard et al. (2009). Studied offshore windfarm: Horns Rev.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Looking at changes in inter encounter intervals from clicks detected with TPODS, harbour porpoise appeared to react to piling, with increases in inter encounter interval during and after pile driving compared to before. • “Zone of responsiveness” at least 20 km from piling site.	• the authors compared inter encounter intervals during pile driving to other times throughout the construction period, not necessarily a true baseline for the area. • No record of behaviours detected during study such as foraging or feeding, these were only briefly mentioned in the discussion. • Similarly to Carstensen et al 2006, no grading of response with distance from piling site, concerning as the extent of response to disturbance could have been greater than 20 km.

Reference: Teilmann and Carstensen (2012). Studied offshore windfarm: Nysted.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Authors suggest that harbour porpoise activity has not yet recovered at Nysted Offshore wind farm since its installation in 2001-2002 (this was a 2012 study). • However, compared to a reference area there was relatively high echolocation activity in the later operation period compared to during the construction period and earlier operational periods. Indicates that strong negative effects of construction on harbour porpoise has decreased as time has passed, the authors suggest maybe because porpoise are becoming habituated to the wind farm or because of positive effects of the wind farm structures serving as artificial reefs.	• Lots of p-values, for example need to be cautious when interpreting their BACI contrasts in the discussion as the authors tested differences in various measures (click PPM, PPM, encounter duration and waiting time) between the study and reference areas 60 times. • the authors talk about echolocation but not in the context of feeding behaviours. Hard to tell the extent to which the wind farm has impacted harbour porpoise foraging. • The baseline period was much shorter than all the other periods combined.

Reference: Thompson et al. (2010). Studied offshore windfarm: Beatrice Demonstrator Project.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Significantly fewer harbour porpoise detections in June 2006 during piling, compared to June 2007 when piling had ceased. Number of detections stayed about the same at nearby reference site (Lossiemouth).	• Porpoise detections were low at the reference site before and after construction, not sure how helpful it is as a comparison. • Looked at hours per day porpoises were detected, quite a coarse measurement to get an idea of porpoise activity. • No discussion of feeding or foraging behaviour, or idea about the maximum distance from the piling where porpoises were disturbed.

Reference: Rumes et al. (2017). Studied offshore windfarm: Nobelwind.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Results suggest that porpoise up to 20 km from piling are displaced, with reductions in detections up to this distance and increased detections beyond this distance during piling. • Extrapolating noise measurements led to an estimated noise level of 159 dB re 1µPa (Lz-p) at 20 km, this is close to the major disturbance threshold proposed by previous work (Bailey et al 2010).	• Results suggest that porpoise up to 20 km from piling are displaced, with reductions in detections up to this distance and increased detections beyond this distance during piling. • Extrapolating noise measurements led to an estimated noise level of 159 dB re 1µPa (Lz-p) at 20 km, this is close to the major disturbance threshold proposed by previous work (Bailey et al 2010).

Reference: Graham et al. (2019). Studied offshore windfarm: Beatrice.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Decreasing probability of response/distance at which disturbance was detected to pile driving over time as more locations were piled, less conservative view of the impact of piling on harbour porpoise than in other studies, suggesting that they may become habituated to piling over time. • Suggest that the use of ADDs may elicit a larger response to piling than piling alone. • Assuming not an effect of acoustic masking, increased vessel activity could also impact harbour porpoise disturbance.	• Decreasing probability of response/distance at which disturbance was detected to pile driving over time as more locations were piled, less conservative view of the impact of piling on harbour porpoise than in other studies, suggesting that they may become habituated to piling over time. • Suggest that the use of ADDs may elicit a larger response to piling than piling alone. • Assuming not an effect of acoustic masking, increased vessel activity could also impact harbour porpoise disturbance.

Reference: Benhemma-Le Gall et al. (2021). Studied offshore windfarm: Beatrice and Moray East.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Looked at foraging activity, inferred foraging from the presence of buzzes in acoustic data. • Porpoise displacement up to 12 km from the construction site, the probability of detecting buzzes increased with distance from the construction site and decreased with higher levels of vessel intensity and background noise. • Looks as if foraging activity as well as occurrence shifts when porpoises are displaced by piling, the effect was similar at both sites analysed.	• Construction was in 2017, 2018 and 2019 but baseline data was collected in 2010 and 2011, this is quite a large difference and the importance of the area to harbour porpoise foraging could have changed in that time. • Looked at buzzes and distance from piling but not clear how long it took for buzzing rates to return to normal once piling had ceased.

Reference: Thompson et al. (2020). Studied offshore windfarm: Beatrice.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• With use of ADDs, harbour porpoise returned to within 1 km of playback more than two hours afterwards, with times to next detection much longer with ADD than without.	• Assuming that a lack of acoustic detections means no animals but could also mean a change in acoustic behaviour. • The authors didn't actually really look at the effect of piling itself on porpoise, mostly the effect of ADDs on dispersing harbour porpoises. Not that helpful unless other studies also used ADDs to minimise risk of injury to animals nearby to construction site on onset of piling, which is quite commonly done. • No mention of behaviours impacted by ADDs/piling, just that some disturbance was detected according to acoustic data.

Reference: Brandt et al. (2009). Studied offshore windfarm: Horns Rev II.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Harbour porpoise left areas close to the construction site for a median of 16.6 hrs and a maximum of 74.2 hrs after piling. • Recovery time exceeded breaks between piling events meaning harbour porpoise displacement could have lasted for the whole of the construction period.	• This study and many others used seal scarers/ADDs, although this seems standard variable use of them makes it more difficult to compare the results of harbour porpoise displacement from different studies.

Reference: van Beest et al. (2018). Studied offshore task: Harbour porpoise responses to airgun.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Tagged harbour porpoise and then exposed them to an airgun ("noise level estimates of 135–147 dB re 1 µPa2s (sound exposure level)"). • Of the 5 porpoises tagged, one rapidly moved away, two exhibited shorter and shallower dives, and the remaining two did not exhibit any changes in behaviour. • Natural behaviours weren't resumed in those which responded until 24 hrs after exposure.	• Only 5 individuals tagged and those tagged showed variability in responses, difficult to scale up these results to make inferences about the rest of the population. • Airgun noise was used instead of pile driving.

Reference: Macaulay et al. (2023). Studied offshore task: Probability of detecting porpoise clicks.

Contributes to knowledge of disruption of foraging or any disruption	Caveats/limitations about the utility of this study
• Used data from acoustic tags deployed on 22 harbour porpoises showed that changes in behaviour state (between pelagic foraging, benthic foraging, and non-foraging) have a significant effect on the probability of detecting porpoise clicks in a given area. • Probability of detecting an animal within a snapshot of time (1s) was highest for pelagic feeding but varied between behavioural states and between the day and night. However, the probability of detecting a single click during different behavioural states did not differ much between day and night. • During the day harbour porpoise are expected to spend around 25% of their time pelagic feeding, 25% of their time benthic feeding and 50% of their time not foraging. • During the night harbour porpoise are predicted to spend 60% of their time pelagic feeding, 15% of their time benthic feeding and 25% of their time not foraging- there was lots of individual variability, but general pattern emerged of porpoise spending the majority of their time in the night pelagic feeding.	• Doesn’t contribute directly to knowledge of how foraging is disrupted by piling but could be informative as suggests, based on these animals that ~50-70% of the time that porpoises were tagged they were using buzz sounds associated with foraging (Figure 4, Macaulay, et al 2023).

10 Appendix 2 – Density dependence analysis – parameters

Table 7. Default parameters of the harbour porpoise IBM used for establishing the relationship between population size and prey density.

Parameter	Description	Value	Unit
R_{max}	Max. prey density	10	MJ m^{-3}
δ	Prey turn-over rate	0.05	d^{-1}
V	Whale to prey volume scalar	1e6	m^3
Rbeta_mu	Desired mean of beta distribution used to generate stochasticity in R_{max} Rescaled to a mean of 1.0 before multiplication	0.25	-
Rbeta_sd	Desired standard deviation of beta distribution used to generate stochasticity in R_{max}	0.055	-
maxage	Maximum age	40	yrs.
ageminrepro	Minimum age for reproduction	3	yrs.
l_b	Length at birth	70	cm
l_∞	Female asymptotic length	160	cm
$l_{\infty,m}$	Male asymptotic length	160	cm
k	Von Bertalanffy growth rate female	0.0015	d^{-1}
k_m	Von Bertalanffy growth rate male	0.0015	d^{-1}
ω_1	Mass-length scaling constant	5.9e-05	kg $cm^{-\omega_2}$
ω_2	Mass-length scaling exponent	2.67	-
ϕ_R	Prey encounter rate scalar	1.0	m^3 d^{-1} $kg^{-2/3}$
ϕ_L	Lactation scalar	3.55	MJ d^{-1} $kg^{-2/3}$
T_P	Length of gestation	305	d
T_L	Age at weaning (duration of lactation)	250	d
T_N	Calf age at which female begins to reduce milk supply	120	d
T_R	Age at which prey feeding efficiency is 50%	130	d
T_D	Mean waiting period before onset of pregnancy	0.0	d
F_{neo}	Reserve mass constant in pregnancy threshold	5.77	kg
F_{ini}	Initial reserve mass of female	5.893	kg
ξ_c	Shape parameter for decrease in milk supply with calf age	0.5	-
ξ_m	Shape parameter for starvation-induced reduction in milk supply	-3.0	-
θ_F	Relative cost of maintaining reserves	0.2	-
ρ	Target body condition in summer	0.24	-
ρ_s	Starvation body condition in summer	0.13	-
ρ_w	Target body condition in winter	0.35	-
$\rho_{s,w}$	Starvation body condition in winter	0.24	-
η	Steepness of assimilation response	20	-
γ	Shape parameter for effect of age on resource foraging efficiency	4.0	-
σ_M	Field metabolic maintenance scalar	5.5	MJ $kg^{-3/4}$ d^{-1}

Parameter	Description	Value	Unit
σ_G	Energetic cost per unit structural mass	30	MJ kg^{-1}
σ_L	Efficiency of conversion of mother's reserves to calf tissue	0.860	-
μ_s	Starvation mortality scalar	0.2	d^{-1}
h_g	Fetal survival rate over entire gestation period	0.803	-
$\epsilon_{+,\uparrow}$	Anabolic efficiency of reserve conversion when rho is increasing or constant	55	MJ kg^{-1}
$\epsilon_{-,\uparrow}$	Catabolic efficiency of reserve conversion when rho is increasing or constant	20	MJ kg^{-1}
$\epsilon_{+,\downarrow}$	Anabolic efficiency of reserve conversion when rho is decreasing	28	MJ kg^{-1}
$\epsilon_{-,\downarrow}$	Catabolic efficiency of reserve conversion when rho is decreasing	35	MJ kg^{-1}
start_summer	Start of summer season	182	d
start_winter	Start of winter season	335	d
end_summer	End of summer season	258	d
end_winter	End of winter season	60	d
start_recep	First day in the year when implantation can occur	202	d
end_recep	Last day in the year when implantation can occur	222	d

Table 8. Summary statistics of the sensitivity analysis of parameter δ and census time

version	variable	# replicates	mean	SD	5% quantile	95% quantile
base	K	120	11417.424	73.143	11307.900	11539.950
base	N_{start}	120	0.018	0.001	0.016	0.020
base	PGR	120	1.090	0.003	1.086	1.097
base	Prey intercept	120	2.338	0.090	2.202	2.493
base	Prey slope	120	-1.338	0.090	-1.493	-1.202
Delta = 0.01	K	20	2442.950	19.086	2414.275	2479.425
Delta = 0.01	N_{start}	20	0.086	0.008	0.073	0.100
Delta = 0.01	PGR	20	1.090	0.006	1.084	1.100
Delta = 0.01	Prey intercept	20	2.976	0.078	2.892	3.097
Delta = 0.01	Prey slope	20	-1.976	0.078	-2.097	-1.892
Delta = 0.1	K	20	22306.825	143.996	22109.150	22516.500
Delta = 0.1	N_{start}	20	0.009	0.001	0.008	0.011
Delta = 0.1	PGR	20	1.090	0.003	1.085	1.096
Delta = 0.1	Prey intercept	20	2.246	0.085	2.129	2.348
Delta = 0.1	Prey slope	20	-1.246	0.085	-1.348	-1.129
t0 = 163	K	20	13587.550	66.624	13503.775	13680.025
t0 = 163	N_{start}	20	0.019	0.001	0.018	0.021
t0 = 163	PGR	20	1.088	0.003	1.084	1.091
t0 = 163	Prey intercept	20	2.424	0.089	2.297	2.552
t0 = 163	Prey slope	20	-1.424	0.089	-1.552	-1.297

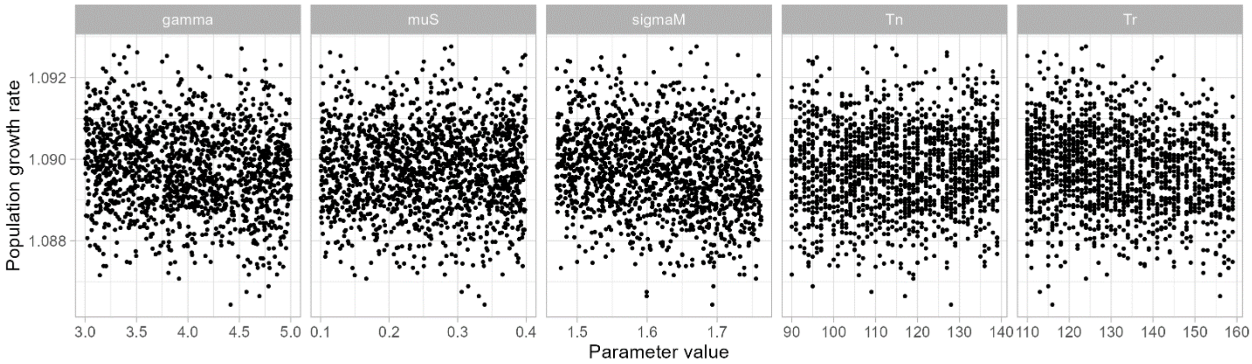

Figure 17. Partial effect of ABC parameters (panels) on the estimated population growth rate. Each point corresponds to a single simulation.

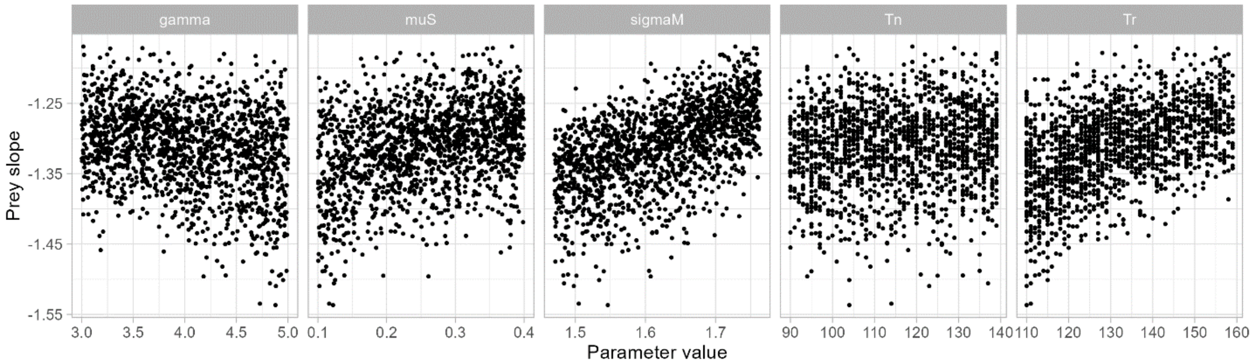

Figure 18. Partial effect of ABC parameters (panels) on the estimated prey-abundance slope. Each point corresponds to a single simulation.

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