

Disturbance effects on harbour porpoises

Research projects within the framework of the environmental monitoring program of Gemini offshore wind farm



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Author: Dr. F. Heinis

HWE Consultancy
Graaf Wichmanlaan 9
1405 GV Bussum
The Netherlands

Commissioned by: GEMINI Buitengaats C.V.

Contact: Luuk Folkerts

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1 Introduction

1.1 Background

Gemini offshore wind farm is located in the Dutch part of the North Sea, 85 km north of the coast of Groningen. The Gemini wind farm consists of 150 wind turbines, totalling 600 MW and two offshore high voltage stations. Start of construction was mid-2015. Gemini is fully operational since 2017.

As part of Gemini's environmental monitoring program, the presence of harbour porpoises in and around the wind farm was measured with a network of 15 passive acoustic monitoring devices (CPODs, see Figure 1), both prior to the construction of the wind farm and in the year in which the monopiles were driven (2015). In addition, aerial surveys were performed in a wide area around the wind farm. The results of these research efforts have been reported in two reports from Wageningen Marine Research (Geelhoed et al. 2015; Geelhoed et al. 2018).

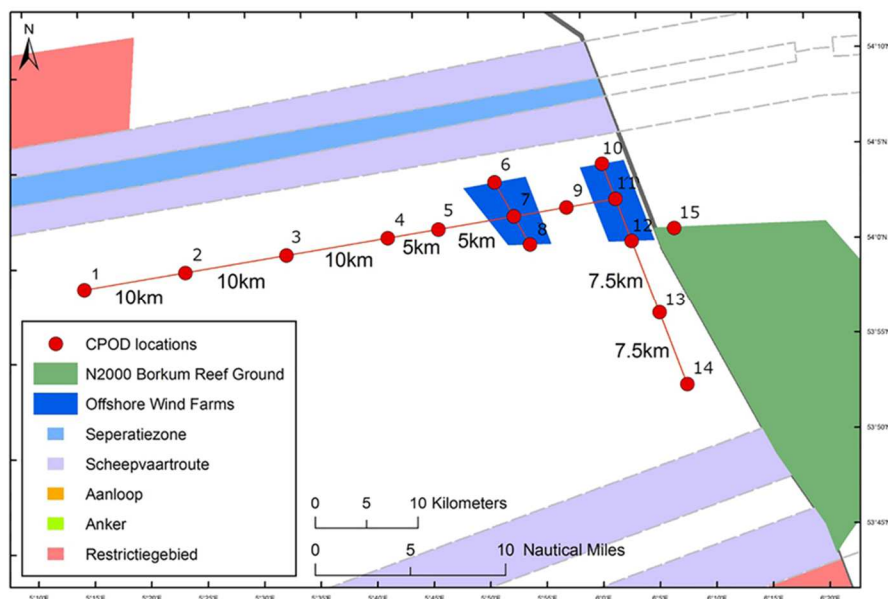


Figure 1: Location of the CPODs

Post construction follow-up research within the framework of the environmental monitoring program of Gemini wind farm has focused on filling in a number of important knowledge gaps about the effects of disturbance caused by impulsive underwater sounds on the fitness of harbour porpoises. This knowledge at the individual level could then, in combination with the results of the field research carried out during the construction, be used to estimate with more certainty through model calculations what the (cumulative) effects of impulsive noise on the harbour porpoise population are.

This report gives an overview of and summarizes the results of the work done with (part) funding from Gemini. The full reports of the research projects are included as appendices to this report.

1.2 Effects of pile-driving sound on harbour porpoises

Underwater sounds caused by human activities at sea can have a negative impact on marine fauna. Loud sounds can impair hearing, resulting in temporary hearing loss (TTS) or even permanent hearing damage (PTS). Ecologically relevant sounds can be masked, or the behaviour of the animals can change in such a way that their foraging efficiency decreases.

Harbour porpoises (*Phocoena phocoena*) are particularly susceptible to disturbance by underwater noise. Harbour porpoises have been shown to respond to pile-driving sounds by swimming away from the

construction sites (Carstensen et al., 2006; Brandt et al., 2011; Dähne et al., 2013) and from locations where seismic surveys take place (Thompson et al., 2013; van Beest et al., 2018). Harbour porpoises live in the cold waters of the northern hemisphere (Kanwisher and Sundnes 1965, Gaskin, 1992) and are relatively small compared to other toothed whales. Due to their relatively large body surface area in relation to the volume, they lose a lot of energy due to heat radiation and conduction to the surrounding water compared to other, larger marine mammal species (Feldman and McMahon, 1983). To maintain a stable body temperature, their food intake must be sufficient. The species has a higher metabolism than land mammals of comparable size (Kanwisher and Sundnes, 1965 and 1966; Kanwisher, 1971; Reed et al., 2000). Consequently, harbour porpoises must eat often to get enough energy. It has been shown that harbour porpoises living in the wild can follow up to 550 small prey (fish) per hour with a high catch success (Wisniewska et al., 2016). The large number of preys with a low energy content per prey means that a high foraging efficiency is needed for survival. Even a small decrease in foraging efficiency due to anthropogenic disturbance could already have an impact on the fitness of this species.

To estimate possible effects on the population dynamics of the harbour porpoise, various models are being developed, such as the Population Consequences of Acoustic Disturbance model (PCAD, National Research Council, 2005), the Interim Population Consequences of Disturbance model (iPCoD; Harwood et al., 2014; King et al., 2015) and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea model (DEPONS; Nabe-Nielsen et al., 2014). Important input parameters for these models are the birth and death rates, which are influenced by the energy consumption of the species and the available prey. Much of this required information is missing for most marine mammals, and therefore estimates are based on results of expert elicitation (Donovan et al., 2016).

1.3 Overview of research performed

In order to better predict the effect of acoustic disturbance on the population dynamics of harbour porpoises, more information is needed about the energetics of this species and about the effect of noise on foraging efficiency. Instead of performing field research during the operational phase of the Gemini wind farm, experimental research was carried out into the effect of anthropogenic sounds on swimming speed, food intake and energy consumption. Subsequently, the information obtained together with results from other recently conducted research was used for an update of the transfer functions in the Interim PCoD model with the results of a new expert elicitation.

In the period 2017 - 2018 this has been implemented in the following way:

1. Three controlled experiments with harbour porpoises have been conducted by SEAMARCO with the aim of collecting new data on the effects of pile-driving noise on swimming speed and the ability to find food, but also to collect more general data on the food intake of harbour porpoises.
2. After these results became available, an international 1-day symposium was organized in June 2018 for (selected) specialists, regulators and licensing authorities in which the most recent results, including the above-mentioned results, were presented and discussed.
3. Following this workshop, a two-day expert elicitation workshop was held, in which the most recent knowledge presented during the symposium could be applied. This workshop focused on the effects of noise disturbance on foraging behavior and thus on the fitness of porpoises and seals. In a previous workshop, held in February 2018 and co-financed by Gemini, the focus was on transfer functions related to the effects of PTS. The aim of both workshops was that by applying recent insights, both in the biological / ecological field and in the field of the expert elicitation process, the Interim PCoD model could calculate more realistic effects on the population.
4. The results of the two expert elicitations were subsequently processed by SMRU / University of St. Andrews in the summer and fall of 2018 and incorporated in a new version of the Interim PCoD model. This version was used to update the Dutch Framework for assessing the cumulative effects of OWF-construction on harbour porpoises (Heinis et al. 2019).
5. In 2016, a publication by Wisniewska et al. raised a debate in the scientific community about the potential negative effects of disturbance on harbour porpoises (Hoekendijk et al. 2018; Wisniewska et al. 2018). Wisniewska et al. (2016) suggested that even a moderate level of

anthropogenic disturbance in the busy shallow waters they share with humans may have severe fitness consequences at individual and population levels. This triggered Cormac Booth to analyze the energetic consequences of lost foraging opportunities for harbour porpoises by using Wisniewska's published DTAG-data and combining them with published data on energy requirements and diet composition.

2 Controlled experiments by Seamarco

2.1 Effect of pile-driving sounds on swimming speed (funded by Gemini & RWS)

If the swimming speed of harbour porpoises is affected by anthropogenic sounds, there may be repercussions for the foraging behaviour. Swimming speed data are also needed to calculate the sound levels that harbour porpoises may experience when they swim away from a piling site, and are thus important for estimating the likelihood that porpoises exposed to anthropogenic sound will experience TTS (temporary hearing threshold shift, i.e. temporarily reduced hearing), and if they do, the magnitude of that TTS.

For this study, video recordings of a captive 7-year-old male harbour porpoise were analysed for swimming speed in quiet conditions and during exposure to play backs of pile-driving sounds (Figure 1).

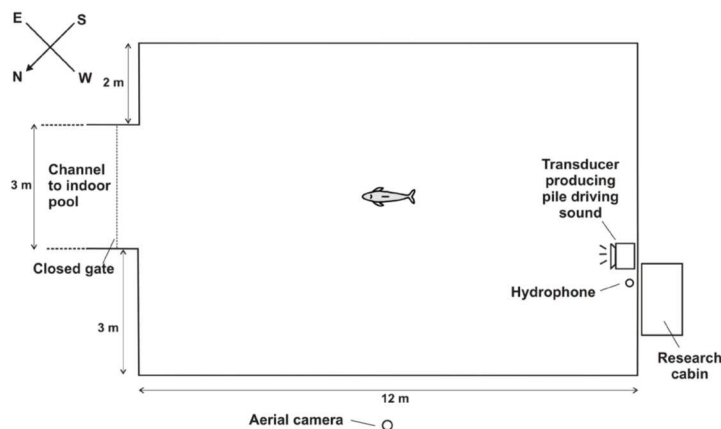


Figure 1 Top scale view of the outdoor pool study facility, showing the study animal, the aerial camera, the underwater transducer producing the pile driving sounds, and the hydrophone used to listen to the pile driving sounds and ambient noise. Also shown is the research cabin which housed the video and audio equipment and the operator.

The results of the analyses showed that during quiet baseline periods, the mean swimming speed of the porpoise was 4.3 km/h corresponding with a mean distance of 2.2 km in 30 min. Even at the lowest SPL tested (130 dB re 1 μ Pa), the mean swimming speed was significantly greater than during baseline periods. At the highest SPL (154 dB re 1 μ Pa), the mean swimming speed was 7.1 km/h, resulting in a mean distance of 3.6 km in 30 min. Swimming speed did not decline significantly during the 30-min test periods (Figure 2).

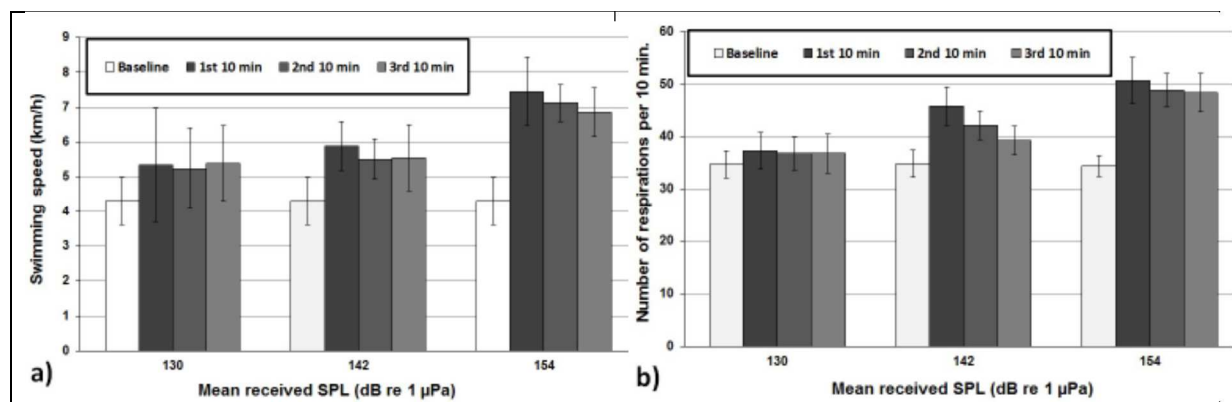


Figure 2 (a) The mean swimming speed (\pm SD; $n = 10$) of a male harbour porpoise (M02) during baseline periods and during the first, second, and third 10-min sections of the 30-min test periods in which he was exposed to pile driving playback sounds at a mean received SPL of 130, 142, and 154 dB re 1 μ Pa. (b) The mean respiration rates during the same periods. For single-strike SELs, subtract 9 dB from the SPL levels shown.

Discussion – implications of the results from this study

Driving one mono-pile into the substrate usually takes about 2 h. Based on the swimming speed observed in the present study at a mean received SPL of 154 dB re 1 μ Pa (\sim 7 km/h; a speed that can probably be maintained sustainably by harbour porpoises), a harbour porpoise that is near a pile driving site when piling begins may swim approximately 14 km away from the site during the piling activity. The increase in swimming speed during fleeing from a piling site may lead to an increase in energy expenditure and could have ecological implications for the porpoise if insufficient prey is available.

The impact of sound on hearing depends on a combination of the received SPL and the exposure duration. In modelling the impact of piling sound on harbour porpoise hearing, the exposure time is often fixed (e.g., the time it takes to drive a particular mono-pile a certain depth into the substrate), but the SPL received by a porpoise during the piling process depends on its location at the onset of piling, the local propagation conditions, and the animal's swimming speed and direction.

Publication

The results from this study were published in *Aquatic Mammals* by Kastelein et al. (2018a). The full paper is attached to this report in Appendix 1.

2.2 How do impulsive sounds affect feeding ability?

2.2.1 Effect of pile-driving sounds on efficiency of catching fish (funded by Gemini)

Sounds produced during the construction of offshore wind turbines may affect the foraging efficiency of harbour porpoises. Sounds produced during pile driving are in the low-frequency range, so they are not expected to interfere with the high-frequency echolocation signals of harbour porpoises by masking. However, pile-driving sounds may distract harbour porpoises from foraging. In order to feed, porpoises first have to find a fish, usually by means of echolocation, since water transparency is low in their natural environment, such as the North Sea. Then they have to catch the fish: when a fish is close to their mouths, they suck it into their mouth cavity by withdrawing their tongue. This requires good timing which may be reduced if the porpoise is distracted by sounds.

To investigate the relationship between pile-driving sounds and fish capture, an experimental set-up was designed to measure the effects of impulsive, interrupted sounds on the ability of harbour porpoises to catch fish (Figure 3). The experiment was carried out with a 4-year-old male (M06) and a 7-year-old female (F05). The two animals performed a fish-catching task while they were exposed to quiet conditions and to impulsive pile-driving playback sounds at three (M06) or four (F05) mean received single-strike sound exposure levels (SEL_{ss}) between 125 and 143 dB re 1 μ Pa²s (see appendix 1 for details).

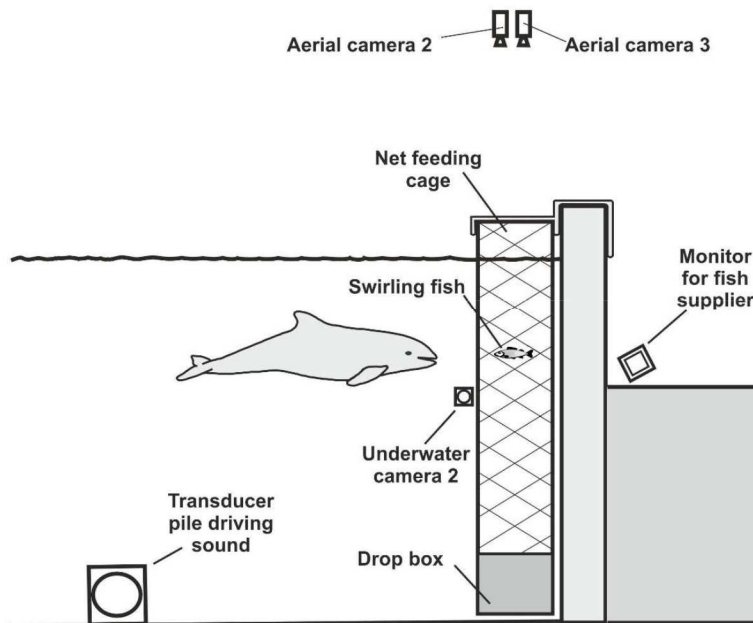


Figure 3 Schematic representation of the experimental set-up (lateral view) used for the fish catching task. Reproduced from Kastelein et al. 2019a.

From the results it appeared that the two study animals differed in their fish-catching success rate at all sound levels: the female tested was generally less adept at catching fish than the male – even in quiet conditions. When impulsive sound was introduced, it was found that as sound exposure increased, the number of capture attempts by the female that were terminated before capturing the prey increased. However, failure rate was consistent across trials. For the younger male, sound exposure appeared to have little effect with the animal achieving high success rates regardless of the tested sound exposure levels (up to 143 dB SEL_{SS}).

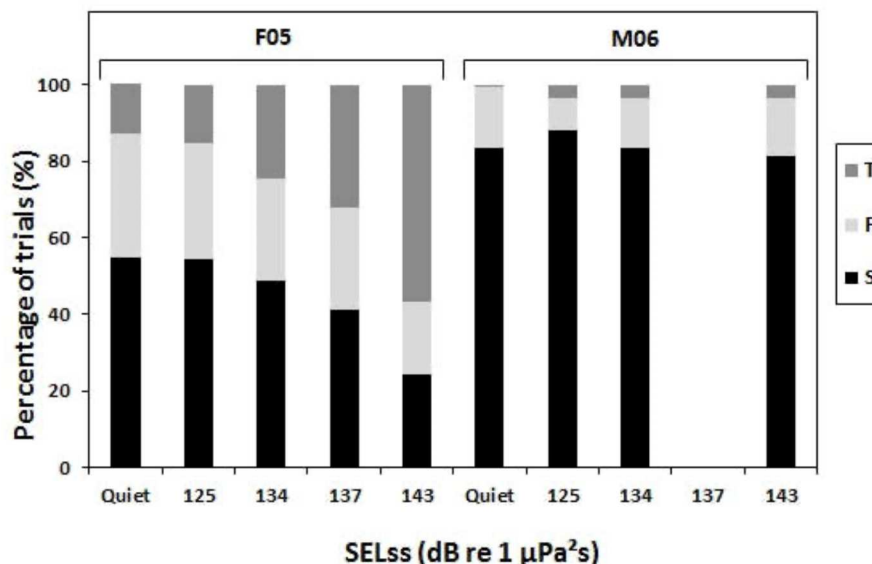


Figure 4 The outcomes of fish-catching trials, shown as percentages of the number of trials for each SEL_{SS}. T = termination, F = failure and S = successful fish capture. F05 = female, M06 = male.

Discussion – implications of the results from this study

The results suggest that loud pile-driving sounds are likely to affect foraging negatively in some harbour porpoises, by decreasing their catch success rate and increasing the termination rate of their fish-catching attempts; the severity of the effects is likely to increase with increasing pile-driving SEL_{SS}. However,

individual differences in responses to sound, termination rates, and fish-catching success (even in quiet conditions) may complicate the quantification of the impacts of pile-driving sounds on harbour porpoises.

Publication

The results from this study were published in *Aquatic Mammals* by Kastelein et al. (2019a). The full paper is attached to this report in Appendix 2.

2.2.2 Effects of fasting on body mass and blubber thickness (funded by Rijkswaterstaat)

To determine what the possible consequences of reduced foraging success resulting from disturbance by pile-driving sounds could be on the animal's health, the same individuals as in the study described in 2.2.1 were the subject of another experiment (Kastelein et al. 2019b). This time animals fasted for 24 hours (in separate experiments in each of the four seasons) and the changes in body mass and condition were monitored. A past study on another male harbour porpoise indicated that in natural conditions there were seasonal fluctuations in blubber mass (Kastelein et al. 2018b). Animals are leaner in the summer to cope with the higher water temperatures and putting on blubber to a greater extent for the winter months (when water temperatures are much lower). In all seasons, the effect of fasting for 24h was that body mass reduced by ~3-6%. This tells us that in cases where animals cannot find suitable prey, the overall condition of the animal is reduced.

2.2.3 Maximum food intake after a period of food deprivation (funded by Gemini)

The next logical question, once understanding that animals may lose condition if they cannot find food for 24 hours, is: how much food can they regularly eat and how fast can they recover from food deprivation? This question is relevant in assessing the impact of pile-driving on harbour porpoises, because it cannot be excluded that animals, once disturbed, are limited in their access to suitable preys. It has been shown that harbour porpoises flee tens of kilometres from areas where offshore percussion pile driving occurs. While travelling, harbour porpoises are probably less efficient in catching prey (see above § 2.2.1), and in the area that they flee to, sufficient suitable preys may not be available. After piling has stopped, or once a porpoise has reached an area where the Sound Exposure Level is below the threshold for disturbance, can the animal make up for lost time by increasing its foraging rate? Recovery after a period of food deprivation depends on how much fish a porpoise can ingest over time. That depends not only on the fish available to the porpoise, but also on the number of fish a porpoise can eat when it encounters prey.

In this study, following fasts lasting between 2 and 24 hours, the food intake of four porpoises was monitored. Whilst a typical feed (for these captive animals) was ~20% of their daily energy requirements, following fasting the animals routinely ate over 35% of their requirements in a single bout of feeding, with some of them consuming between 60-90% of their energy needs in a single feed. Animals were also ready to feed again only two hours later, indicating animals can consume large amounts, digest it quickly and be ready to feed again. This might shed light on how the species can cope with the patchy nature of their prey species, where animals may have to travel between, or search for suitable food patches (losing weight during this time, before feeding readily).

Publication

The results from this study were published in *Aquatic Mammals* by Kastelein et al. (2019c). The full paper is attached to this report in Appendix 3.

3 Harbour porpoise resilience using DTAG data (partly funded by Gemini)

Research has shown that noise disturbance can disrupt the behaviour of harbour porpoises. The significance of such disturbance for their survival and ability to reproduce is, however, unclear. As harbour porpoises are relatively small, these animals may be vulnerable to starvation when disturbed due to their high energy requirements (Wisniewska *et al.* 2016). Important parameters determining harbour porpoise energy balance are the size and energy content of prey, their foraging behaviour and their energetic requirements for homeostasis, growth, and reproduction. In the study, partly funded by Gemini, Booth (2019) used data from novel tags put on wild animals published by Wisniewska *et al.* (2016), which recorded information about how often and how much they were trying to catch fish. By combining these data with reviews of what fish porpoises in the area would eat and how much energy they contained (Andreasen *et al.* 2007), it was possible to explore whether or not animals obtained enough energy. These analyses showed a broad range of plausible levels of energy intake, in line with those from captive studies (Kastelein *et al.* 1997, Lockyer *et al.* 2003, Kastelein *et al.* 2018b, Rojano-Doñate *et al.* 2018). Metabolizable energy intake estimates were most strongly affected by variations in target prey size and to a lesser extent, by the foraging intensity of porpoises. In all but the worst-case scenarios, harbour porpoises appear to be well equipped for their ecological niche due to their generalist diet, consisting of a range of moderate to high energy-density prey combined with ultra-high foraging rates and high capture success. If animals can find suitable prey, porpoises may be capable of recovering from some lost foraging opportunities. Minimizing disturbances is, however, important for their health.

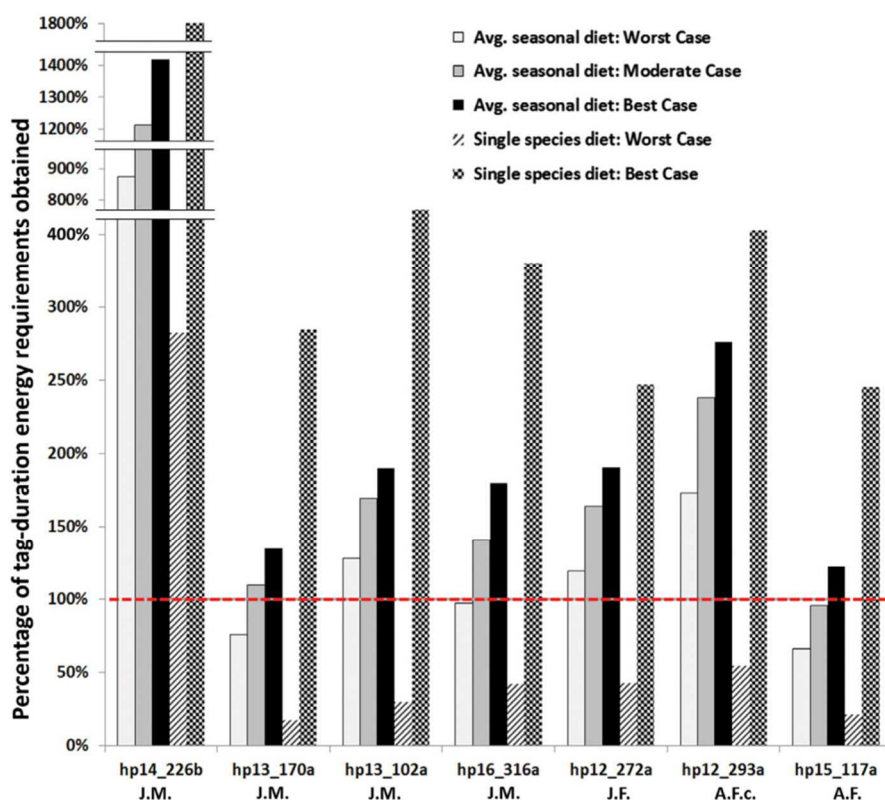


Figure 5. Best- and worst-case scenarios of obtained metabolizable energy from each of the tagged harbour porpoises relative to their estimated energy requirements over the tag duration (from Rojano-Doñate *et al.* 2018). Note the broken y-axis. The red dashed line shows the 100% energy requirement for each individual over the tag duration. J.M. = juvenile male; J.F. = juvenile female; A.F.c. = adult female with calf; A.F. = adult female (no calf)

Publication

The results from this study were published in *Marine Mammal Science* by Booth (2019). The full paper is attached to this report in Appendix 4.

4 Updating of the Interim PCoD model

4.1 INPAS symposium (funded by Gemini)

The effects of Impulsive Noise on Porpoises and Seals (INPAS) meeting was held in 2018 as a one-day symposium presenting the latest research on marine mammals and impulsive sound. The purpose of the symposium was to bring together scientists, regulators, industry, and environmental groups to present and discuss the big picture of impulsive sound on marine mammals.

The symposium captured some of the latest updates in research on marine mammals and impulsive noise (see Appendix 5) – with a focus on species occurring in the North Sea – and provided an excellent opportunity to keep discussions advancing. The meeting was structured such that the presentations were built around three broad thematic questions (with overlap across these themes):

- What is disturbance and when does it occur?
- What is the effect of disturbance on individuals?
- What is the significance of disturbance, *i.e.* what is the effect on populations?

An additional benefit of the INPAS symposium, was that it provided a foundation for a 2-day, closed expert elicitation to update the interim Population Consequences of Disturbance (iPCoD) model for the effect of disturbance (see 4.2.2). The insights gained during the INPAS meeting were hugely beneficial to the subsequent expert elicitation (and significant updates to the iPCoD model).

Abstracts of the presentations are included in Appendix 5.

4.2 New expert elicitations for harbour porpoise and seals

4.2.1 Expert elicitation workshop on effects of PTS (partly funded by Gemini)

The Interim Population Consequences of Disturbance (iPCoD) framework was developed by SMRU Consulting and the University of St Andrews in 2013 to forecast the potential effects on marine mammal populations in UK waters of any disturbance and permanent threshold shifts (PTS). The iPCoD framework was designed to assist decision making in a situation where there is only limited knowledge about the potential effects of these developments on marine mammals. The iPCoD framework was developed with the quantification of the effect of disturbance on vital rates determined via expert elicitation, conducted in 2013. The elicitation was carried out using an online questionnaire and at the time was recognised as an interim solution to the evaluation of these effects.

The objective of the expert elicitation workshop described here was to update the transfer functions on the effects of PTS on the probability of survival and of giving birth to a viable young of harbour porpoise, bottlenose dolphins, harbour seals and grey seals via an expert elicitation (in the form of probability distributions). The workshop was held in St Andrews, UK over three days on Tuesday 6th – Thursday 8th March 2018.

A number of general points came out in discussions as part of the elicitation. These included that PTS did not mean animals were deaf, that the limitations of the ambient noise environment should be considered and that the magnitude and frequency band in which PTS occurs are critical to assessing the effect on vital rates, that a larger TTS could precede a PTS and the mechanisms by which a PTS could affect vital rates. In advance of the elicitation, the exact noise stimuli (low frequency broadband pulsed noise), the frequency range and magnitude of PTS predicted (as a result of exposure) and the species/age classes were discussed and a scope for the elicitation agreed. As part of the formal elicitation, experts agreed on the wording of each question and definitions for each parameter to be elicited. For each of the species of interest (harbour porpoise, harbour seal/grey seal & bottle nose dolphin), rounds of elicitation were carried out for the effect of the agreed PTS on the survival of dependents (calves/pups), juveniles, mature females and on the probability of giving birth to viable offspring.

The result of this updated elicitation differed significantly from the original expert elicitation outputs conducted in 2013. Overall, experts indicated that the effects of a 6 dB PTS in the 2-10 kHz band was unlikely to have a large effect on survival or fertility of the species of interest. Effects were considered to be smallest for porpoises and seals and slightly larger in bottlenose dolphins, though experts noted that the broader range of plausible outcomes for dolphins was due to potential uncertainty in how the defined PTS would impact dolphins (which use lower frequency for communications and for some foraging calls), not necessarily that they were definitely more sensitive. It should be noted, however, that for all species experts indicated that the most likely predicted effect on survival or fertility as a result of 6 dB PTS was likely to be very small (i.e. <5 % reduction in survival or fertility). In general, the experts indicated that the defined PTS was likely to have a slightly larger effect on calves/pups and juveniles than on the survival or fertility of mature females.

The **full report** of the expert elicitation workshop on the effects of PTS on vital rates of harbour porpoises, grey seals, harbour seals and bottlenose dolphins by Booth & Heinis (2018) is included in Appendix 6.

4.2.2 Expert elicitation workshop on effects of disturbance (funded by Gemini)

The objective of this workshop was to update the transfer functions on the effects of disturbance on the probability of survival and of giving birth to a viable young of harbour porpoise, harbour seals and grey seals via an expert elicitation (in the form of probability distributions). To achieve this, a two-day workshop was held in Amsterdam, The Netherlands from 13-14 June 2018. The invitation for this workshop was sent to a leading group of experts on physiology, behaviour, energetics, statistics and the effects of noise on marine mammals and spanning the species of interest. In addition, the attendees' experience spans the fields of veterinary pathology, physics, physiology and behaviour.

To support the elicitation for harbour porpoises, a dynamic energy budget (DEB) model was available and used during the elicitation to aid discussions regarding the potential effects of missed foraging opportunities on survival and reproduction. It is important to note that no DEB model was available for the seal species in the elicitation. For the elicitation the Sheffield Elicitation Framework (SHELF) using SHELF v.3.0 was employed. For each quantity of interest each expert was asked to provide his/her individual judgements regarding a number of parameters: the plausible limits, median, lower and upper quartiles. The experts were then asked to input their personal judgements into SHELF and distributions were fitted to each individual expert judgement with the best statistical fit. During the process, the mechanisms experts had considered in making their individual judgements were discussed among the group before consensus distributions were agreed upon.

As with the 2013 iPCoD elicitation, experts agreed the focus should be on the potential for disturbance to be caused by exposure to low frequency broadband pulsed (LFBP) noise (e.g. pile-driving, airgun pulses). Disturbance was defined as when no feeding (or nursing) was taking place on the day of disturbance as a result of exposure. This means that in a day of disturbance there is a period of zero energy intake for the disturbed individual. Experts agreed that harbour porpoises, grey & harbour seals are likely to be sufficiently different in life history strategy and in their sensitivity to noise that the effects of disturbance on each group is likely to be different and were therefore, where possible, elicited separately. The experts' judgements for harbour porpoises were based on the assumption that, on average, the behaviour of the animals classified as being disturbed will be altered for 6 hours (within a single day – the day of disturbance), and that no feeding will take place during this time. This was agreed by experts following review of grey and published literature. For seals, the experts' judgements were based on the assumption that, on average, the behaviour of the individual seals classified as being 'disturbed' using this approach will be altered for much less than 24 hours by exposure to LFBP noise sources like pile-driving (though it was not possible to define a discrete value for the number of hours that disturbance effects are likely to last due to a lack of evidence of significant behavioural responses for these species). Experts cited a lack of knowledge of exactly if/how disturbance affects seals energy expenditure and intake.

The results of this updated elicitation show significant differences over those of the original expert elicitation conducted in 2013. Overall, experts indicated that the effects of disturbance were likely to be less severe than previously estimated. This was largely driven by new empirical data collected and published since then, and the presentation of the DEB model which helped to guide discussions and test expert theories

presented during the workshop of the critical vital rates to focus on. In addition, the face-to-face element of the workshop was important. This allowed discussion and prior agreement of question wording with experts which is fundamental to a successful elicitation. The biggest effects changes from the 2013 elicitation were for harbour porpoises in which the effects of disturbance were considered to be reduced (even when basing judgements on a disturbance resulting in a 6-hour period of zero energy intake). The estimated effects of disturbance were smaller for harbour and grey seals than for harbour porpoises, and both seal species had reduced effect sizes compared to the 2013 elicitation. This was due to experts' discussions about seal life history, fat reserves and species responsiveness.

The new transfer functions derived in this exercise indicate a smaller 'effect size' than in the 2013 expert elicitation and therefore will be reflected in new iPCoD scenarios. Where a large number of animals are predicted to experience some degree of disturbance following exposure to low frequency broadband pulsed noise, this may make a large difference to the population trajectories predicted by iPCoD.

The **full report** of the expert elicitation workshop on the effects of disturbance on vital rates of harbour porpoises, harbour seals and grey seals is included in Appendix 7.

5 Contribution of GEMINI to filling of knowledge gaps

In 2016, the Dutch Government started an extensive and long-term research programme on the effects of offshore wind energy in the Dutch part of the North Sea on marine life, including birds and bats (Wozep). Before 2016, the research was not centralized as individual wind farm owners who were awarded permits were required to monitor and investigate the effects of their own wind farm. This was also the case for GEMINI. However, part of the original monitoring requirements that were designed more than 5 years before the wind farm was actually built in 2015, were later adapted with the main research questions of the Wozep programme in mind.

In the Wozep programme, the following main knowledge gaps for harbour porpoises were identified:

1. Sound propagation as a consequence of pile-driving;
2. Thresholds for disturbance/behavioural effects and for effects on hearing (TTS and PTS = Temporary and Permanent Threshold Shifts);
3. Number of disturbed animals resulting from construction activities (mainly pile-driving);
4. Impact of disturbance on vital rates, *i.e.* on survival and/or fertility;
5. Assumptions in the Interim PCoD model about population development and demographic parameters.

Ad 1. Sound measurements during the construction of the GEMINI wind farm were used to improve the Aquarius sound modelling considerably (Binnerts et al. 2016; De Jong et al. 2018). This led to the TNO Aquarius 4 model (a Wozep project), on which the sound mapping for the updated calculations of the cumulative effects of offshore wind farm construction on harbour porpoises was based (KEC 3.0, Heinis et al. 2019).

Ad 2. The results of the CPOD measurements during the construction of the GEMINI wind farm reported by Geelhoed et al. (2018) were incorporated by Nabe-Nielsen and colleagues in the DEPONS-model version 2.0 (<https://depons.eu>). The results on the effect of pile-driving sound on swimming speed (see §2.1) can be used to estimate the number of harbour porpoises that experience TTS or PTS (see Heinis et al. (2015) for the principles of calculations).

Ad 3. Although a lot of valuable field measurements on sound propagation and behavioural responses of harbour porpoises were done near the GEMINI wind farm, it has as yet not been possible to use these data to estimate the number of harbour porpoises disturbed by pile-driving sound more precisely.

Ad 4. Most of the work funded by Gemini and summarized here was and will be used to make better predictions about the potential impact of disturbance on the vital rates of harbour porpoises and consequently on the population of these relatively small marine mammal species. The results of the studies performed by Seamarco on the energetics of harbour porpoises (see §2.2.2 and §2.2.3) formed important inputs for the energetic model that was used during the Expert Elicitation workshop on Disturbance and that led to the 2018 update of the Interim PCoD model. The updated Interim PCoD model could, subsequently, be used to estimate the cumulative effects on harbour porpoises of offshore wind farm construction until 2030. The discussions on the energetic consequences of disturbances of harbour porpoises in the field, and the impact of wind farm construction in particular, are not died yet. The results of the studies by Ron Kastelein (see §2.2.1) and Booth (see Chapter 3) have given valuable contributions for the assessment of these effects.

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APPENDICES

APPENDIX 1

Kastelein, R.A., S. van de Voorde & N. Jennings, 2018a. Swimming Speed of a Harbor Porpoise (*Phocoena phocoena*) During Playbacks of Offshore Pile Driving Sounds. *Aquatic Mammals* 44: 92 – 99, DOI 10.1578/AM.44.1.2018.92.

APPENDIX 2

Kastelein, R.A., L.A.E. Huijser, S. Cornelisse, L. Helder-Hoek, N. Jennings, & C.A.F. de Jong, 2019a. Effect of Pile-Driving Playback Sound Level on Fish-Catching Efficiency in Harbor Porpoises (*Phocoena phocoena*). *Aquatic Mammals*, 45: 398 – 410, DOI 10.1578/AM.45.4.2019.398.

APPENDIX 3

Kastelein, R., L. Helder-Hoek, C.G. Booth, N. Jennings & M. Leopold, 2019c. High Levels of Food Intake in Harbor Porpoises (*Phocoena phocoena*): Insight into Recovery from Disturbance. *Aquatic Mammals*, 45: 380 – 388, DOI 10.1578/AM.45.4.2019.380.

APPENDIX 4

Booth, C.G., 2019. Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Mar. Mam. Sci.* 2019: 1 – 14.

APPENDIX 5

Abstracts for INPAS 1: June 2018 (Amsterdam, The Netherlands)

APPENDIX 6

Booth, C., and F. Heinis, 2018. Updating the Interim PCoD Model: Workshop Report - New transfer functions for the effects of permanent threshold shifts on vital rates in marine mammal species. Report Code SMRUC-UOA-2018-006.

APPENDIX 7

Booth, C., F. Heinis & J. Harwood, 2019. Updating the Interim PCoD Model: Workshop Report – New transfer functions for the effects of disturbance on vital rates in marine mammal species. Report Code SMRUC-BEI-2018-011.

APPENDIX 1

Swimming Speed of a Harbor Porpoise (*Phocoena phocoena*) During Playbacks of Offshore Pile Driving Sounds

Ronald A. Kastelein,¹ Shirley Van de Voorde,¹ and Nancy Jennings²

¹Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands
E-mail: researchteam@zonnet.nl

²Dotmoth, 1 Mendip Villas, Crabtree Lane, Dundry, Bristol BS41 8LN, UK

Abstract

The loud sounds produced under water during offshore percussion pile driving for the construction of wind turbines may affect harbor porpoises (*Phocoena phocoena*). Kastelein et al. (2013b) exposed a porpoise in a quiet pool to playbacks of underwater pile driving sound at several mean received sound pressure levels (SPLs; range: 130 to 154 dB re 1 μ Pa) and suggested that harbor porpoises at sea swim away from offshore pile driving locations (moving tens of km), thus reducing their received SPL. The speed at which they swim both determines the acoustic exposure and impacts the energetic costs of a behavioral response. Therefore, information on swimming speed is important for estimating the potential impact of pile driving sounds on the hearing, the energetics, and the population dynamics of harbor porpoises. The video recordings from the Kastelein et al. (2013b) study were analyzed for swimming speed. During quiet baseline periods, the mean swimming speed of the porpoise was 4.3 km/h, and he swam a mean distance of 2.2 km in 30 min. Even at the lowest SPL tested (130 dB re 1 μ Pa), his mean swimming speed was significantly greater than during baseline periods. At the highest SPL (154 dB re 1 μ Pa), his mean swimming speed was 7.1 km/h, and he swam a mean distance of 3.6 km in 30 min. Swimming speed did not decline significantly during the 30-min test periods, and a speed of \sim 7 km/h appears to be sustainable for harbor porpoises.

Key Words: acoustics, behavior, disturbance, habitat, marine mammals, noise, odontocete, offshore wind farms, temporary threshold shift, wind turbines, swimming speed

Introduction

Coastal waters support high densities of marine fauna and are heavily used by humans producing noise through, for example, oil and gas industry operations and, more recently, the construction of wind turbines. Although alternative methods of attaching wind turbines to the sea floor are being investigated, installation still commonly involves percussion pile drivers which produce loud impulsive sounds. Offshore pile driving with hydraulic hammers for wind turbine installation at sea produces impulsive sounds at a rate of \sim 35 to 65 strikes/min, and placing one mono-pile may take a few hours. The duration of the signal and sound pressure level (SPL) of the sounds depend on the distance from the pile at which they are measured. The sound energy released into the environment during percussion pile driving can be reduced by noise mitigation systems such as cofferdams or bubble screens (Bellmann, 2014).

The high-amplitude sounds produced under water during offshore pile driving may affect marine mammals (Bailey et al., 2010). A marine mammal that is potentially affected is the harbor porpoise (*Phocoena phocoena*) because it has a wide distribution in the coastal waters of the northern hemisphere (Bjorge & Tolley, 2008) and because this small odontocete has hearing that is acute and functional over a very wide frequency range (Kastelein et al., 2002, 2009, 2010, 2017). Kastelein et al. (2013a) determined the 50% hearing threshold of a harbor porpoise for playbacks of pile driving sound when background noise levels were low (below levels occurring during Sea State 1). The 50% detection threshold sound exposure levels (SELs) for the first sound of the series (no masking) was \sim 73 dB re 1 μ Pa²s (see Kastelein et al., 2013a, for signal parameters).

Multiple sounds in succession (series) caused a \sim 5 dB decrease in hearing threshold. These hearing thresholds, together with propagation conditions

and background noise levels, can be used to calculate the distance to which piling sound is audible to harbor porpoises. However, ecologically, it is more important to discover at which SPL pile driving sounds become uncomfortable to harbor porpoises or at which SPL their behavior changes in response to the sounds.

Only when a sound has an effect on the physiology and/or behavior of an animal can it directly affect its chance of survival or reproduction. Kastelein et al. (2013b) exposed a porpoise in a quiet pool to playbacks of underwater pile driving sound (46 strikes/min; signal duration: 126 ms) at five SPLs to determine the behavioral response threshold SPL. The results suggested that, at sea, harbor porpoises are likely to move tens of km (~20 km, depending on the propagation conditions and ambient noise) away from offshore pile driving locations; this estimated distance is in the same order of magnitude as that observed in wild harbor porpoises near pile driving sites (Carstensen et al., 2006; Tougaard et al., 2009; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014).

Harbor porpoises swimming away from piling areas at sea reduce their received SPL of the piling sounds. The speed at which they swim away determines both the acoustic energy received by their ears (cumulative SEL) and the energetic cost of locomotion—the faster they swim, the greater the energetic cost. Information on swimming speed and endurance is important for estimating the impact of pile driving sounds on both the hearing and energetics of harbor porpoises. The information can also be used to estimate the effect of pile driving sounds on harbor porpoise population dynamics. The Population Consequences of Acoustic Disturbance (PCAD) framework (National Research Council, 2005) was implemented to generate the Interim Population Consequences of Disturbance (iPCoD) model (King et al., 2015) and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS) model (Nabe-Nielsen et al., 2014), provides an energetics-based approach to estimate population dynamics effects.

Therefore, with the above points in mind, the objective of the present study was to measure and compare the swimming speed of a captive harbor porpoise during quiet baseline periods and during 30-min exposures to playbacks of pile driving sounds at three SPLs (Kastelein et al., 2013b). These outputs can provide useful insights into assessments of the energetic costs of disturbance for individuals and contribute to population-level model assessments.

Methods

Study Animal and Facility

The male study animal, identified as Porpoise 02, was 7 y old at the time of the study; his body weight was around 38 kg, his body length was 146 cm, and his girth at axilla was ± 73 cm. His hearing was assumed to be representative of animals his age of the same species; it was similar to that of two other young harbor porpoises (Kastelein et al., 2002, 2009, 2010, 2017). He received four meals of fish per day.

The study animal was kept at the SEAMARCO Research Institute, the Netherlands, in a pool complex specifically designed and built for acoustic research, consisting of an indoor pool (described in detail by Kastelein et al., 2010) and an outdoor pool (12 × 8 m, 2 m deep) in which this study was conducted (Figure 1). The walls of the outdoor pool were made of plywood covered with polyester and 3-cm thick coconut mats with their fibers embedded in 4-mm thick rubber (reducing reflections mainly above 25 kHz). The bottom was covered with sand. The water circulation system and the aeration system for the biofilter were made as quiet as possible, and they were switched off before sessions and kept off during sessions so that there was no current in the pool. The equipment operator was out of sight of the study animal in a research cabin next to the pool (Figure 1; see also Kastelein et al., 2013b).

Equipment, Playback Sounds, and Experimental Procedure

The study animal's behavior was filmed from above by a waterproof camera (Conrad – 750940) with a wide-angle lens and a polarizing filter to prevent saturation of the video image by glare from the water surface. The camera was placed on a pole 9 m above the water surface on the north-western side of the pool (Figure 1). The entire surface of the pool was captured on the video image. The output of the camera was fed through a video multiplexer (MX-8 – CSX) which added the time and date to the images. Thereafter, the output was digitized by an analog-to-digital converter (König – grabber) and stored on a laptop computer (Medion – MD96780).

A recording of pile driving sound sequences made at sea from an offshore wind farm was played back in the pool as a WAV file. For details of the playback sounds, the sound transmitting and recording equipment, and the background noise, see Kastelein et al. (2013b). The SPL distribution in the pool was measured at 77 locations in the horizontal plane and at three depths. Because Porpoise 02 used the entire pool during the test periods with pile driving sound, the mean received

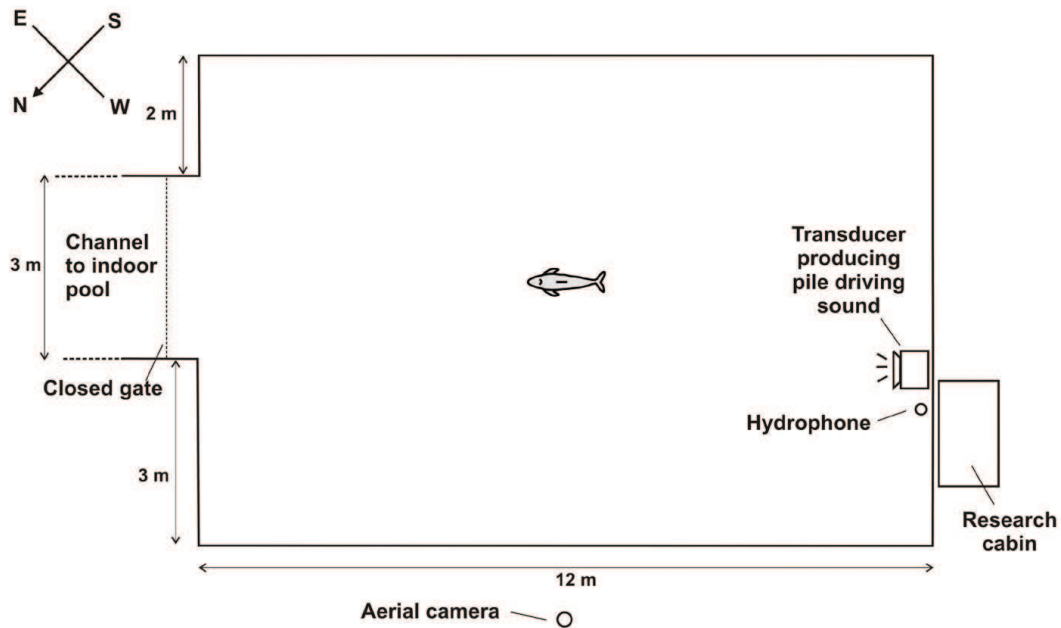


Figure 1. Top scale view of the outdoor pool study facility, showing the study animal, the aerial camera, the underwater transducer producing the pile driving sounds, and the hydrophone used to listen to the pile driving sounds and ambient noise. Also shown is the research cabin which housed the video and audio equipment and the operator.

SPL per source level was calculated from all 231 measurements. Per depth, levels decreased slightly with increasing distance from the transducer (see Kastelein et al., 2013b, for details). The pile driving sound sequences were played back at three source levels within a 24 dB range (12 dB steps), resulting in mean received root-mean-square SPLs of 130, 142, and 154 ± 3 dB re $1 \mu\text{Pa}$; single-strike (t_{90}) SELs of 121, 133, and 145 ± 2.7 dB re $1 \mu\text{Pa}^2\text{s}$; and zero-to-peak SPLs of 145, 157, and 169 ± 3 dB re $1 \mu\text{Pa}$ (Kastelein et al., 2013b). The levels near a pile driving site at sea are much higher than those that could be produced in the pool.

The transducer producing the playback sequences was positioned in the water at the southwestern end of the pool at the start of each day (Figure 1). Sessions consisted of a 30-min baseline period (no sound emission), followed by a pause of random length (no sound emission; no recordings), followed by a 30-min test period (piling sound sequence emission). The pause was included so that the animal could not predict when the test period would start. It takes ~ 2 h to drive a mono-pile into the substrate, but test periods were only 30 min long to minimize negative impact or stress. Generally, one session was conducted per day, 5 d/wk, beginning between 0900 and 1600 h. During the test and baseline periods, only the operator in the research cabin was allowed within 10 m of the pool, and she sat very still.

During each test period, the playback of pile driving sounds was transmitted at one of the three SPLs, and each level was tested in ten periods, resulting in 30 test periods in all. The three levels were tested in random order. To prevent potential masking of the sounds by background noise, tests were not carried out during rainfall or when wind speeds were above Beaufort 4 (during the tests, the background noise level was below that observed at sea during Sea State 1; Knudsen et al., 1948). The data collection period was between June and August 2012.

Analysis

Software (*Kinovea*) was used to measure the distance Porpoise 02 swam in each session from the video recordings by tracking the animal automatically frame-by-frame. In $\sim 10\%$ of the videos, the study animal was difficult to track due to glare, shadows, or waves, so the playback speed was reduced by 25 to 200% to allow easier manual tracking in sections where the porpoise could not be tracked automatically. The 30-min video recordings were analyzed in sections of 10 min to determine whether Porpoise 02's speed changed during the test period. Images of the tracked path in each 10-min section were stored. Calibration was done by means of the 1 m marks on the sides of the pool. To account for the perspective of the images, the calibration was done both from the side of the pool nearest to the

camera and from the side farthest from the camera; the mean was used for the calculations. In addition to the ten 30-min test periods per SPL, data were collected from ten random baseline periods.

Porpoise 02's swimming speed was calculated from the distance he traveled. For statistical analysis, we considered only the swimming speed. An ANOVA on swimming speed was conducted with the crossed factors level (SPL, including the baseline: SPL = 0) and 10-min section. The interaction term between the two factors was initially included but was removed from the final analysis as it was not significant. Data conformed to the assumptions of the tests, and the level of significance was 5% (Zar, 1999).

In addition to the swimming speed and distance traveled, the respiration rates were also counted in the baseline and test periods. These data have already been reported by Kastelein et al. (2013b). Respiration rates for the relevant SPLs are presented in the "Results" section for comparison with the swimming speeds from the present study.

Results

During baseline periods, the mean swimming speed of Porpoise 02 was 4.3 km/h, and he swam a mean distance of 2.2 km in 30 min. The study animal used most of the pool during most of the test periods. A tracked swimming path from a representative test period at the maximum SPL tested (154 dB re 1 μ Pa) showed that he did not avoid the location of the underwater transducer (Figure 2). During the test periods, Porpoise 02 increased his mean swimming speed relative to during baseline periods and, thus, the mean distance he swam in the 30-min periods (Table 1; Figure 3a).

Analysis showed that Porpoise 02's swimming speed was similar in the three 10-min sections of the test periods. However, swimming speed was significantly affected by the SPL factor (Table 2). The interaction term between the two factors had been removed from the final analysis as it was not significant, showing that the combined pattern of effects of the 10-min sections and SPL was similar for all SPLs. *Post-hoc* tests showed that the

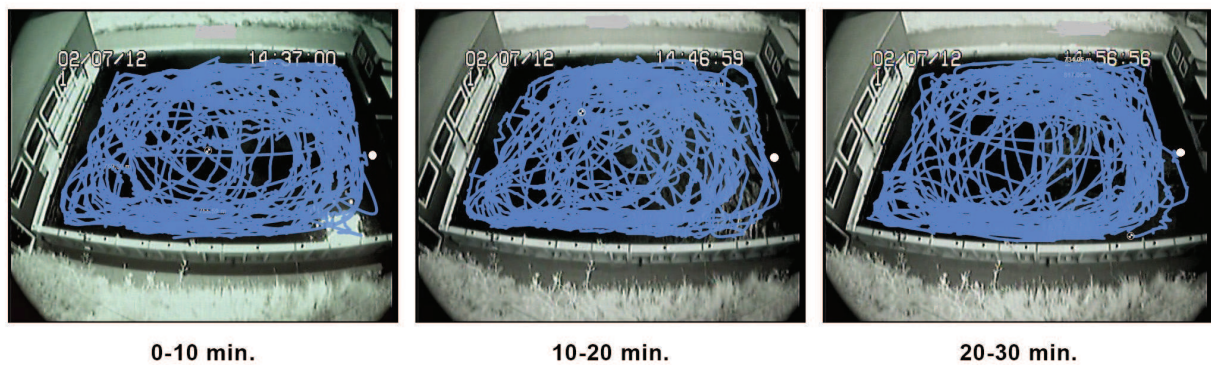


Figure 2. Example of the swimming tracks of the harbor porpoise (*Phocoena phocoena*) during three consecutive 10-min sections of a 30-min test period in which he was exposed to pile driving playback sound at a mean received SPL of 154 ± 3 dB re 1 μ Pa (from left to right: 0 to 10 min, 10 to 20 min, and 20 to 30 min). The study animal used most of the pool and did not avoid the underwater transducer (indicated by the white dot on the right-hand side of the pool). Due to the reverberations in the pool, the SPL distribution was fairly homogenous. Pool dimensions: 12 m \times 8 m; 2 m deep.

Table 1. The mean (\pm SD) swimming speed by the harbor porpoise (*Phocoena phocoena*) during quiet baseline periods and during the 30-min test periods in which he was exposed to pile driving playback sounds at three mean received SPLs ($n = 10$ for each SPL). Also included are the results of the *post-hoc* tests carried out after the ANOVA, which showed that the swimming speed was significantly affected by the SPL (Table 2). In the *post-hoc* tests, the same letters indicate the mean received SPLs between which *post-hoc* tests showed no significant difference in the swimming speed.

Mean received SPL dB re 1 μ Pa	Mean (\pm SD) swimming speed (km/h)	<i>Post-hoc</i> test
Sea State 1 (baseline)	4.3 (\pm 0.7)	A
130	5.3 (\pm 1.1)	B
142	5.6 (\pm 0.7)	B
154	7.1 (\pm 0.6)	C

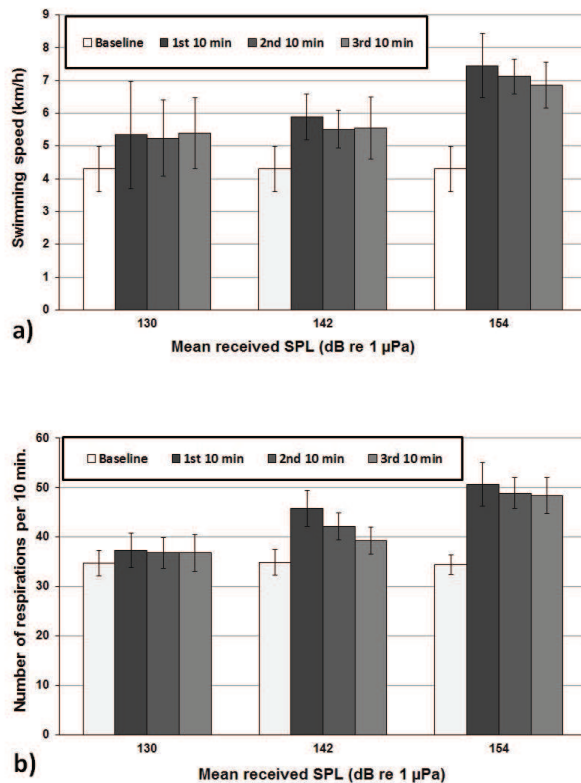


Figure 3. (a) The mean swimming speed (\pm SD; $n = 10$) of Porpoise 02 during baseline periods and during the first, second, and third 10-min sections of the 30-min test periods in which he was exposed to pile driving playback sounds at a mean received SPL of 130, 142, and 154 dB re 1 µPa. (b) The mean respiration rates during the same periods (selected levels from Kastelein et al., 2013b). For single-strike SELs, subtract 9 dB from the SPL levels shown.

swimming speed was significantly lower in the baseline periods and higher in periods with the highest SPL (SPL = 154 dB re 1 µPa). Swimming speed in test periods with SPL = 130 and 142 dB re 1 µPa was similar but significantly different to that in the baseline periods and in the highest exposure level periods (Table 1).

The respiration rate (reported by Kastelein et al., 2013b) showed a similar pattern as the swimming speed (Figure 3b).

Discussion

Evaluation of Experimental Approach

Only a small gradient in pile driving playback sound SPL occurred in the pool (Kastelein et al., 2013b), so Porpoise 02 used the entire pool even when he experienced the highest source level of the pile driving playback exposures (there were no relatively quiet locations to which he could swim).

Behavioral effects during exposure to pile driving sound occurred when the background noise between the impulsive sounds was very low (lower than the sound during Sea State 1, as in this study). Under higher background noise conditions, effects are expected to be less clear, as responses of harbor porpoises to sounds decrease as the signal-to-noise ratio decreases (Kastelein et al., 2011).

Within sessions, the swimming speed seemed to decrease slightly at the highest level (Figure 3a), but this was not statistically significant. When the same harbor porpoise was exposed to the same pile driving playback sounds in another study, his hearing showed a 2.2-dB temporary threshold shift after 30 min (Kastelein et al., 2016). This means that the SPL perceived by the animal was gradually reduced so that after the 30-min test period, the pile driving sound appeared to the study animal to be 2.2 dB less loud than at the start of the period.

The sound field, the sound levels (including background noise level), and the durations of baseline and test periods were appropriate for assessing the effects of the piling sounds on the swimming speed in the harbor porpoise.

Increased Swimming Speed as a Response to Pile Driving Sounds

To evaluate the impacts of pile driving sounds on harbor porpoise swimming speeds, it is important to understand how the swimming speeds observed in the present study compare to maximum known swimming speeds and to general swimming speeds, and whether the observed swimming speeds are sustainable.

It is difficult to relate the swimming speed observed during the highest SPL (7.1 km/h) to the

Table 2. Results of ANOVA to evaluate changes in the harbor porpoise's swimming speed in the 10-min sections of each test period, taking into account the SPL (included as a factor); df = degrees of freedom, Adj. MS = adjusted mean square, F = test statistic, and p = significance. For *post-hoc* test results, see Table 1.

Source of variation	df	Adj. MS	F	p
SPL	3	41.34	45.96	0.000
10-min section	2	0.45	0.51	0.601
Error	108	0.90		

maximum swimming speed of the harbor porpoise. In the 22 y in which captive harbor porpoises have been observed by the first author, including in a large floating pen (34 m \times 20 m; 3.5 m deep at the sides and 5 m deep in the centre) and in the large pool used in the present study (12 m \times 8 m; 2 m deep), they never swam much faster than during pile driving playback at the highest SPL used in the present study. The swimming speeds observed during pile driving playback were similar to those seen during rainfall when porpoises tend to increase their swimming speed. During rainfall in the pool used in the present study, an adult female harbor porpoise similar in size to the study animal swam at a mean speed of 5.8 km/h (SD \pm 0.4 km/h; n = 3; measured over 5 min).

Some information on the general swimming speeds of wild harbor porpoises is available. Gaskin et al. (1975) calculated mean horizontal displacement rates of porpoises in the wild from very high frequency (VHF) transmitter tracking data and obtained swimming speeds ranging from 1.6 to 2.2 km/h (maximum 6.7 km/h). Otani et al. (2000) reported a mean horizontal swimming speed of 3.2 km/h; 90% of the time the speed was below 5.4 km/h, and the highest speed recorded was 15 km/h. Brandt et al. (2013a, 2013b) reported swimming speeds for harbor porpoises fleeing from seal scarers of between 4.7 and 11.5 km/h (mean 5.8 km/h). Linnenschmidt et al. (2013) recorded the minimum swimming speeds of three free-ranging porpoises as 8.0, 2.6, and 4.0 km/h. Although swimming speed data are scarce and difficult to compare due to differences in methodology (VHF transmitters, data loggers, and tracking routes as in the present study), circumstances (feeding, traveling, and fleeing), and ways of reporting (maximum speed, speed range, and the time a speed could be maintained), the swimming speeds observed in the present study are similar to those observed in the wild.

The harbor porpoise in the present study could maintain the maximum observed mean swimming speed (7.1 km/h) for at least 30 min. Two observations suggest that he was not performing at maximum capacity: (1) as the test periods ended, his respiration rate immediately returned to normal; and (2) within 1 min after exposure to pile driving sounds in a similar study, the same animal participated in a behavioral hearing test which required him to use subtle pectoral fin and tail fluke movements to achieve a very precise body position and stay under water for at least 1 min (Kastelein et al., 2016).

Otani et al. (2001) studied the rate of oxygen consumption and the energetic cost of locomotion in captive harbor porpoises and found that oxygen consumption increased with

swimming speed according to a cubed function. The minimum cost of transport during underwater swimming in the harbor porpoise is 2.39 to 2.43 J/kg/m at an average swimming speed of between 4.7 and 5.4 km/h. However, the porpoises usually swam more slowly (thus conserving energy) and dove aerobically. This explains why harbor porpoises can dive repeatedly and continuously without resting for extended periods at the sea surface, and it suggests that a swimming speed of up to 5.4 km/h requires little energy (Otani et al., 2001).

In response to sounds, the respiration rate of the study animal showed a similar pattern as the swimming speed (Figure 3), suggesting that the parameters are correlated: greater exertion costs more energy and, thus, requires more oxygen. The respiration rate did not increase during the 30-min test periods even at the highest SPL, suggesting that the study animal could maintain a speed of 7.1 km/h relatively easily. The results from the present study suggest this speed to be sustainable for harbor porpoises for at least 30 min.

The Response Threshold for Harbor Porpoises at Sea

Harbor porpoises may flee from locations where they are exposed to pile driving sounds at broadband SPLs \geq ~142 dB re 1 μ Pa under low ambient noise conditions (Kastelein et al., 2013b). This “142 dB SPL behavioral threshold” corresponds (due to the sounds’ duration) to a broadband single-strike SEL threshold of ~133 dB re 1 μ Pa²s in the present study. However, the behavioral threshold SEL is probably only valid for the spectrum that the porpoises were exposed to by Kastelein et al. (2013b) and in the present study (same spectrum as in Kastelein et al., 2013b). As the distance to the piling site increases, the spectrum changes; high frequencies are more easily absorbed by sea water than low frequencies. The hearing sensitivity of harbor porpoises is frequency-dependent. Hearing is more sensitive at higher frequencies than at lower frequencies (Kastelein et al., 2017), so it is likely that the study animal of Kastelein et al. (2013b) reacted to the high-frequency components of the broadband pile driving playback sound. Therefore, it is not realistic to compare broadband SPLs at sea (Remmers & Bellmann, 2016) directly with the broadband 133 dB re 1 μ Pa²s SEL threshold. We recommend that SEL measurements should be weighted—for instance, with the weighting function proposed by the National Marine Fisheries Service (NMFS) (2016), although this weighting function is proposed to only set SEL limits to prevent permanent hearing threshold shift. Weighting of SEL may also be important in setting sound level limits to prevent behavioral disturbance.

Conclusion

In the wild, harbor porpoises have been observed swimming away from pile driving sites to distances of tens of km (Dähne et al., 2013; Haelters et al., 2014). As they move away from a sound source, harbor porpoises reduce the SPL they receive. Porpoises probably begin to swim away from a piling site before piling starts as activities such as shipping, hoisting, and positioning the pile create underwater sounds that may deter them.

Driving one mono-pile into the substrate usually takes about 2 h. Based on the swimming speed observed in the present study at a mean received SPL of 154 dB re 1 μ Pa (\sim 7 km/h; a speed that is probably sustainable for harbor porpoises), a harbor porpoise that is near a pile driving site when piling begins may swim approximately 14 km away from the site during the piling activity. The increase in swimming speed during fleeing from a piling site may lead to an increase in energy expenditure and could have ecological implications for the porpoise if insufficient prey is available.

The impact of sound on hearing depends on a combination of the received SPL and the exposure duration. In modelling the impact of piling sound on harbor porpoise hearing, the exposure time is often fixed (e.g., the time it takes to drive a particular mono-pile a certain depth into the substrate), but the SPL received by a porpoise during the piling process depends on its location at the onset of piling, the local propagation conditions, and the animal's swimming speed and direction.

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APPENDIX 2

Effect of Pile-Driving Playback Sound Level on Fish-Catching Efficiency in Harbor Porpoises (*Phocoena phocoena*)

Ronald A. Kastelein,¹ Léonie A. E. Huijser,¹ Suzanne Cornelisse,¹
Lean Helder-Hoek,¹ Nancy Jennings,² and Christ A. F. de Jong³

¹Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands
E-mail: researchteam@zonnet.nl

²Dotmoth, 1 Mendip Villas, Crabtree Lane, Dundry, Bristol BS41 8LN, UK

³TNO Acoustics and Sonar, Oude Waalsdorperweg 63, 2597 AK, The Hague, The Netherlands

Abstract

The foundations of offshore wind turbine parks are often constructed by means of percussion pile driving. Broadband impulsive sounds generated by pile driving may disturb and distract marine mammals such as harbor porpoises (*Phocoena phocoena*); their concentration may be reduced, affecting the skills they need for foraging (e.g., timing and precision) or reducing their ability to catch prey and, thus, their foraging efficiency. The resulting reduction in fitness may eventually lead to population declines. Therefore, it is important to understand the effects of these anthropogenic sounds on the ability of harbor porpoises to catch fish. Two captive harbor porpoises (porpoise F05 and porpoise M06) performed a fish-catching task (i.e., retrieving dead fish from a net feeding cage) while they were exposed to low ambient noise (quiet conditions) and impulsive pile-driving playback sounds at three (porpoise M06) or four (porpoise F05) mean received single-strike sound exposure levels (SELs) between 125 and 143 dB re 1 μPa^2 s. The two study animals differed in their fish-catching success rate at all noise levels, including under quiet conditions: Porpoise F05 was less likely to catch fish than porpoise M06. They also responded differently to increasing SELs: Only porpoise F05 was significantly more likely to terminate trials and less likely to catch fish as SELs increased above 134 dB, but her trial failure rate remained unaffected by increasing SELs. The time taken to catch a fish did not vary with SELs but was slightly longer for porpoise F05 than for porpoise M06. Results suggest that high-amplitude pile driving sounds are likely to negatively affect foraging in some harbor porpoises by decreasing their catch success rate and increasing the termination rate of their fish-catching attempts; the severity of the effects is likely to increase with increasing pile driving SELs. However, individual

differences in responses to sound, termination rates, and fish-catching success (even in ambient conditions) may complicate the quantification of the impacts of pile driving sounds on harbor porpoises.

Key Words: anthropogenic sound, distraction, behavior, foraging, harbor porpoise, odontocete, marine mammal, individual variation, pile driving, wind park

Introduction

In the coming decades, many wind turbine parks will be built in the North Sea and in nearby waters (<https://www.actu-environnement.com/media/pdf/news-29718-scenario-2020-eolien-Europe-WindEurope.pdf>) within the geographic range of the harbor porpoise (*Phocoena phocoena*; Rice, 1998). Impulsive sounds are produced during the construction of offshore wind turbines by means of percussion pile driving (so far, the most commonly used method). It may take several thousand blows (depending on the pile diameter and length, and the composition of the substrate) to drive one pile into the sea floor in a time period of 2 to 3 h. Typically, one pile is placed per day, and the construction of an entire offshore wind park may take months. The broadband high-amplitude sounds produced during offshore percussion pile driving have most of their energy below 1 kHz (Bailey et al., 2010; Gabriel et al., 2011; Norro et al., 2013), so they are not expected to mask the high-frequency echolocation signals used by harbor porpoises (around 125 kHz, narrow band; Møhl & Andersen, 1973). However, at certain received levels, percussion pile driving does affect the behavior of harbor porpoises (Carstensen et al., 2006; Tougaard et al., 2009; Bailey et al., 2010; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014).

Apart from the most commonly used percussion pile driving method, vibratory pile driving is sometimes used, which also produces broadband high-amplitude sounds. The effect of vibratory pile driving sounds on echolocation vigilance has been investigated in another odontocete, the bottlenose dolphin (*Tursiops truncatus*; Branstetter et al., 2018). The vibratory sounds have energy up to 80 kHz, so their spectra overlap with those of the echolocation signals of bottlenose dolphins. While the echolocation performance of two of the five dolphins used in the study was unaffected, the remaining three almost completely stopped echolocating during their first exposure to the highest sound level, suggesting that these dolphins were distracted by the sounds (Branstetter et al., 2018). Wild bottlenose dolphins exposed to vibratory pile driving sounds (with energy in the 0 to 80 kHz range) may temporarily stop echolocating and, thus, stop foraging (Branstetter et al., 2018).

Pile driving sounds are unlikely to mask the echolocation signals of harbor porpoises, but they may distract foraging harbor porpoises since porpoises use echolocation to find, track, and catch prey items (DeRuiter et al., 2009; Miller, 2010; Wahlberg et al., 2015). When closing in on their prey, usually small to medium-sized fish (Sveegaard et al., 2012; Wisniewska et al., 2016), harbor porpoises produce very rapid echolocation click sequences (DeRuiter et al., 2009). They catch a fish by grabbing it with their teeth or by sucking it into their mouth cavity by withdrawing their tongue (Kastelein et al., 1997b). This requires precision and good timing, skills that may be impaired if the porpoise is distracted by underwater anthropogenic sounds. Such effects of sound have been observed in fish; they made more prey-handling errors in the presence of intermittent sound (Purser & Radford, 2011; Shafiei Sabet et al., 2015).

Harbor porpoises are relatively small and inhabit the cold temperate waters of the Northern Hemisphere (Rice, 1998), so their thermoregulation imposes energetic challenges (Lockyer, 2007). Because of their high relative heat loss and rapid life history, harbor porpoises have been referred to as “aquatic shrews” (Kanwisher & Sundnes, 1965). To sustain their high metabolic rates, harbor porpoises must spend a large portion of their time feeding (Wisniewska et al., 2016, 2018; Hoekendijk et al., 2017); and if their foraging is interrupted, they are susceptible to starvation (MacLeod et al., 2007). Although the resilience of harbor porpoises to anthropogenic disturbances is debated (Wisniewska et al., 2016, 2018; Hoekendijk et al., 2017), distraction of foraging harbor porpoises by pile driving sounds may have particularly detrimental impacts because of

the species’ biological traits. If exposure to sounds produced during wind park construction routinely affects harbor porpoise foraging and animals cannot compensate, then in the long term, the population dynamics of the species may be affected.

Policymakers need to assess to what extent acoustic disturbances are likely to affect the population dynamics of marine mammals in order to make informed wildlife management decisions. Several theoretical models are being developed, such as the Population Consequences of Acoustic Disturbance model (PCAD; National Research Council, 2005), and model principles have been implemented in mathematical frameworks such as the Interim Population Consequences of Disturbance model (iPCoD; King et al., 2015) and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea model (DEPONS; Nabe-Nielsen et al., 2014, 2018). These models require input parameters such as the number of animals that will be significantly affected by a noise disturbance, the energetic needs of a species (DEPONS), the relevant food availability (DEPONS), and other parameters affecting the vital rates (birth and death rates). So far, most of the information that is needed is lacking for most marine mammal species, though estimates for input parameters for the iPCoD model have been made via an expert elicitation method (Donovan et al., 2016).

The goal of this study was to contribute towards a more accurate assessment of an input parameter for models of acoustic disturbances for the harbor porpoise. The effect of pile-driving playback sounds on the efficiency (success rate and speed) of attempts by harbor porpoises to catch fish in a controlled environment is quantified.

Methods

Study Animals

The two harbor porpoises that participated in the study, an adult female and a subadult male, had both been found stranded on the North Sea coast and had been rehabilitated. The long duration of their rehabilitation deemed the porpoises unsuitable for release, and they were therefore made available for research. The female (identified as porpoise F05) was ~11 mo old when she stranded; the male (identified as porpoise M06) was ~7 mo old. At the time of the study, both animals were healthy and in good physical condition. Porpoise F05 had reached her maximum body length (154 cm) and was 7 years old. Her weight varied between 43 and 46 kg during the study period. Porpoise M06 was 4 years old and still growing (130 cm). His weight varied between 30 and 34 kg during the study period.

Food Consumption

The harbor porpoises were normally fed four to five times a day on a diet of thawed sprat (*Sprattus sprattus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and squid (*Loligo opalescens*). Vitamin supplements (Akwavit; Arie Blok Animal Nutrition, Woerden, The Netherlands) were added to the thawed fish. Fish were fed to the porpoises at a temperature of $\sim 4^{\circ}\text{C}$. The fish were weighed digitally (5 g accuracy), and the mass of each fish species eaten during each meal was recorded. During experimental fish-catching sessions, only thawed sprats were used (~ 15 cm long). Before a session began, the sprats were dropped into a bucket of sea water, and only those that sank were used (i.e., those which did not contain gas).

Study Area

The study was conducted at the Sea Mammal Research Company (SEAMARCO) Research Institute in the Netherlands. The animals were kept in a pool complex consisting of an outdoor pool (12×8 m; 2 m deep; Figure 1) connected via a channel (4×3 m; 1.4 m deep) to an indoor pool (8×7 m; 2 m deep). The bottom was covered

with a 20-cm-thick layer of sloping sand on which aquatic vegetation grew and invertebrates lived. Skimmers kept the water level constant. Sea water was pumped directly from the Eastern Scheldt, a lagoon of the North Sea, into the water circulation system; partial recirculation through biological and sand filters ensured year-round water clarity and quality.

The pool water temperature was measured once per day and varied between 2 and 15°C during the study period. The minimum and maximum air temperatures over each 24-h period were also recorded. The mean daily air temperature ranges (2.3 to 16.9°C in winter and 5.7 to 26.9°C in summer) and salinity ($\sim 3.4\%$) experienced during the study period by the captive study animals were similar to those experienced by wild conspecifics in the North Sea (occurring ~ 200 m away on the other side of the dyke in the Eastern Scheldt).

Net Feeding Cage

To quantify fish-catching efficiency, fish were offered to the harbor porpoises under water in a custom-built net feeding cage (Figure 2). The cage was made of monofilament transparent twine net with a mesh size of 12 cm. The entire back of

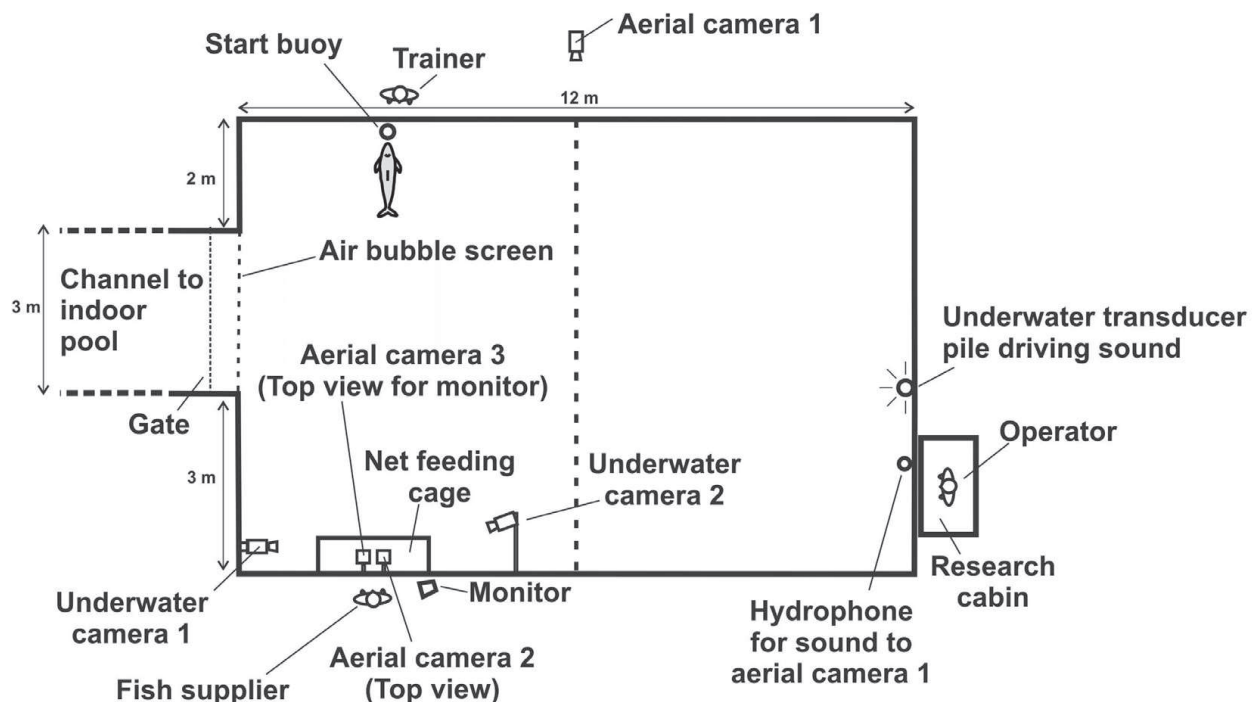


Figure 1. The outdoor pool used for the study, showing the location of the test harbor porpoise (*Phocoena phocoena*) at the start buoy, the net feeding cage, the underwater transducer, and the various aerial and underwater cameras. Also shown is the research cabin which housed the sound-producing, sound-monitoring, and video-recording equipment and the operator. During the sessions, the test porpoise remained to the left of the dashed central imaginary demarcation line. An air-bubble screen reduced the high-frequency components of the impulsive broadband pile driving sound that could reach the indoor pool where the non-test porpoise was housed while the test porpoise participated in the study.

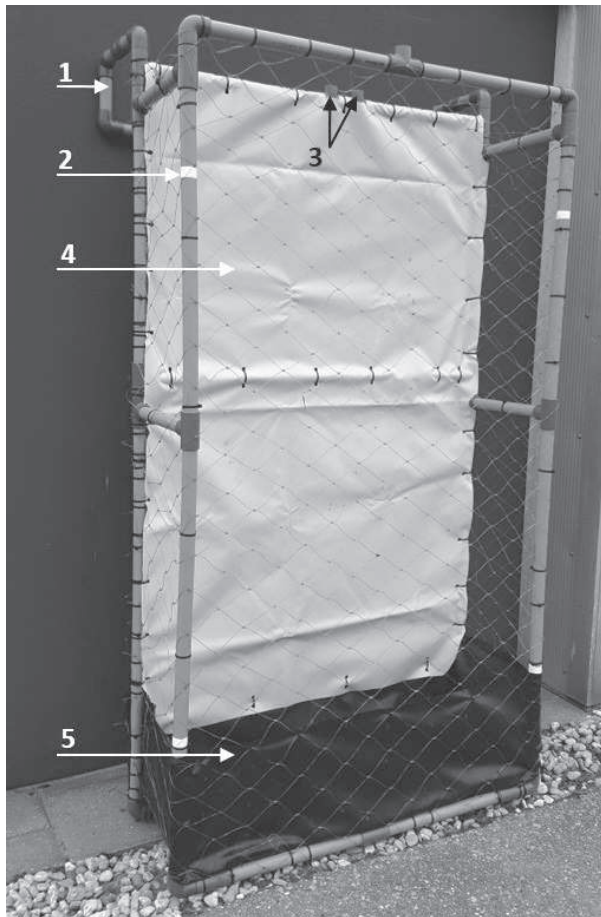


Figure 2. The net feeding cage (104 cm wide, 188 cm high, and 36 cm deep) which was placed in the water and attached to the side of the pool by the suspension system (1) when in use. The white markings (2) indicate the water level during fish-catching trials. Top view camera mounting locations are shown (3; aerial cameras #2 and 3; see Figure 1). The back of the net feeding cage (4) was covered with white pond liner so that fish remained in the cage. Fish that were not caught by the harbor porpoise fell into the drop box (5) made of black pond liner.

the cage was covered with white pond liner so that the fish could not swirl through the meshes at the back and get stuck between the cage and the side of the pool. The lower sides and front of the net cage were covered with black pond liner (36 cm high) so that the porpoises could not access a fish once it had reached the bottom of the net cage within this so-called drop box.

Background Noise and Stimulus Measurements

Unless stated otherwise, acoustic terms and definitions follow *ISO 18405 Underwater Acoustics – Terminology* (ISO, 2017). The background noise and pile driving sounds were measured via three hydrophones (Brüel & Kjaer [B&K] – 8106) with a multichannel high-frequency analyzer (B&K PULSE – 3560 D) and a laptop computer with B&K PULSE

software (*Labshop*, Version 12.1; sample frequency used: 524,288 Hz). Before analysis, the recordings were high-pass filtered (cut-off frequency 100 Hz; 3rd order Butterworth filter; 18 dB/octave) to remove low-frequency sounds made by water surface movements. The system was calibrated with a pistonphone (B&K – 4223). The received sound pressure of the impulsive pile driving sounds was analyzed in terms of unweighted single-strike sound exposure level (SEL_{ss}) in dB re 1 $\mu\text{Pa}^2\text{s}$.

Fish-catching sessions were not performed under unfavorable weather conditions such as rain or hard wind (i.e., Beaufort wind force 6 or more). Raindrops falling on the water surface may distract the harbor porpoises or distort the images made by the top view cameras. Strong wind may move the water surface, thereby changing the random swirling pattern of fish in the net feeding cage. In addition, when the wind came from the south, sessions were not performed if the Beaufort wind force was 4 or more, as under these conditions; the fish always moved towards the back of the net cage where the porpoise could not reach them. Only the people involved in the tests were allowed within 15 m of the pool during sessions, and they were required to stand still. During test conditions without pile driving sounds, the background noise in the pool was below that typical of sea state 0 (see Kastelein et al., 2012).

Pile-Driving Playback Sound

The sound intended to distract the harbor porpoises consisted of playbacks of a series of offshore percussion (impulsive) pile driving sounds recorded at 800 m from a 4.2-m diameter pile being driven into the sea bed as the foundation for a wind turbine for the Dutch offshore wind farm “Egmond aan Zee” in the North Sea. No mitigation, such as bubble screens, was used. The strike rate was 2,760/h. A WAV file was made of a series of consecutive pile-driving strike sounds. The original recordings were sampled at 65 kHz and band-pass filtered between 50 Hz and 32.5 kHz. For the generation of the WAV files used in the study, signals were resampled to 88.2 kHz.

A random section of five strikes from the digitized original recording of a series of pile driving sounds (WAV file) was played back repeatedly by a laptop computer (ASUS PC 1001 PXD) with *Adobe Audition*, Version 3.0, to a digitally controlled attenuator. The output went through a custom-built variable passive low-pass filter (set to 125 kHz), after which it went to a power amplifier (East & West Inc. – LS5002), which drove the transducer (Lubell – LL1424HP) through an isolation transformer (Lubell – AC1424HP). The transducer was placed at the southwestern end of the pool at 2 m depth (~10 m away from the net

feeding cage; Figure 1). The linearity of the transmitter system used for the pile-driving playback sound deviated at most by 1 dB within a 42 dB range.

The sound distribution was measured both in the general area where the harbor porpoises swam during the sessions (6 × 7 m, 1-m grid on the left side of the central dashed line in Figure 1; 42 locations) and up to 1 m from the net feeding cage (four locations). The SELss was measured at three depths per location (0.5, 1.0, and 1.5 m below the surface). Three strikes were recorded per depth and location over a 10-s period. The analysis of a single strike was done for a 500-ms time window. The average received SELss (dB re 1 $\mu\text{Pa}^2\text{s}$) of the played back impulsive sound, as experienced by the harbor porpoises when they were near the net feeding cage, was calculated as the power average of all 12 individual measurement positions (four locations, three depths at each). There were only small differences in SELss per position, showing that the sound field near the net feeding cage was fairly homogeneous (Table 1).

Both study animals were tested during exposure to pile driving sounds at SELss = 125 dB, 134 dB, and 143 dB re 1 $\mu\text{Pa}^2\text{s}$. Porpoise F05 responded differently (she showed a profound reaction by increasing swimming speed) to the highest level than porpoise M06, so exposure to SELss = 137 dB re 1 $\mu\text{Pa}^2\text{s}$ was added to show a response gradient. Porpoise M06 was not exposed to pile driving sound at SELss = 137 dB re 1 $\mu\text{Pa}^2\text{s}$ because his pattern of behavior remained constant at the highest and lower levels. Therefore, based on the study animals' behavior, the pile driving sounds were played back at three levels for porpoise M06 and at four levels for porpoise F05. The highest amplitude was the maximum level that could be produced by the sound emitting system: a mean SELss of 143 dB re 1 $\mu\text{Pa}^2\text{s}$ in the swimming area of the porpoise (the waveform is shown in Figure 3a). The background noise

level in the pool, converted to SELss based on a t_{90} pulse duration of 151 ms, was measured to be in the range between 50 and 65 dB re 1 $\mu\text{Pa}^2\text{s}$ in the one-third octave bands between 100 Hz and 10 kHz. The spectrum and level of the playback sound in the pool (Figure 3b) resembled the spectra of pile driving sounds recorded in shallow water at 7 km from a North Sea pile driving site (Remmers & Bellmann, 2016). Below 600 Hz, the energy at sea could not be replicated in the pool due to the characteristics of the transducer and the dimensions of the pool.

Experimental Procedure

Before each session, the harbor porpoises were not fed for approximately 2 h to ensure that their motivation to feed was strong and consistent. While they were in the indoor pool, the transducer and the net feeding cage were lowered into the outdoor pool, and the video cameras were activated (Figure 1). Then, the test porpoise for that session was asked to swim into the outdoor pool. The non-test porpoise was kept in the indoor pool and was tested once the session with the first animal had been completed. The air-bubble screen (Figure 1) was lowered during each session; this reduced the high-frequency components of the pile driving sound in the indoor pool so that the non-test animal was not disturbed by it.

The fish-catching task required skill, concentration, and prior training (which had taken 2 wks). Once the test porpoise had stationed at the start buoy near the trainer, 8 m from the net feeding cage (Figure 1), the fish supplier held a fish just under the water surface in the middle of the top of the net cage (always in the same position; the fish was held horizontally, parallel to the pool wall, with its ventral side pointing downwards; Figure 4). The trainer counted out loud from one to three, then gave a hand signal and the vocal command "search" to send the porpoise to the net cage. The fish supplier released the fish

Table 1. The four mean (\pm standard deviation [SD]) exposure levels (expressed as SELss and peak level) and t_{90} of the pile-driving playback sound in the area where the harbor porpoises (*Phocoena phocoena*) swam during the fish-catching sessions ("Overall"; $n = 126$ locations) and in the 1 m area around the net feeding cage ("Cage"; $n = 12$ locations).

Porpoise	Mean SELss (dB re 1 $\mu\text{Pa}^2\text{s}$) \pm SD		Mean t_{90} (ms) \pm SD		Mean peak level (dB re 1 μPa^2) \pm SD	
	Overall	Cage	Overall	Cage	Overall	Cage
F05 & M06	125 \pm 2	123 \pm 1	151 \pm 11	158 \pm 11	148 \pm 2	146 \pm 1
F05 & M06	134 \pm 2	132 \pm 1	151 \pm 11	158 \pm 11	157 \pm 2	155 \pm 1
F05	137 \pm 2	135 \pm 1	151 \pm 11	158 \pm 11	160 \pm 2	158 \pm 1
F05 & M06	143 \pm 2	141 \pm 1	151 \pm 11	158 \pm 11	166 \pm 2	164 \pm 1

when the trainer began counting with the word “one.” After releasing the fish, the fish supplier sat down and was not visible to the porpoise. During each session, the porpoise and net feeding cage were filmed simultaneously by five cameras (Figure 1): one underwater camera on each side of the net cage (Rollei Actioncam 300), one aerial top view camera (Rollei Actioncam 300) on a 1.5 m high pole, and one aerial camera on a 6-m-high pole for a top view of the swimming tracks (GoPro Hero 3; Figure 1). Another aerial camera

(Conrad), connected to a monitor (camera 3 in Figure 1), allowed the fish supplier to see whether the fish was caught or not without distracting the porpoise.

As the harbor porpoise swam towards the net feeding cage (usually taking ~ 3 s for the 8 m distance), the fish slowly swirled down through the water column (mean swirling time between surface and drop box, where the fish was no longer accessible to the porpoise: 30 s; SD: 6 s; range: 14 to 40 s; $n = 30$). Once the porpoise reached

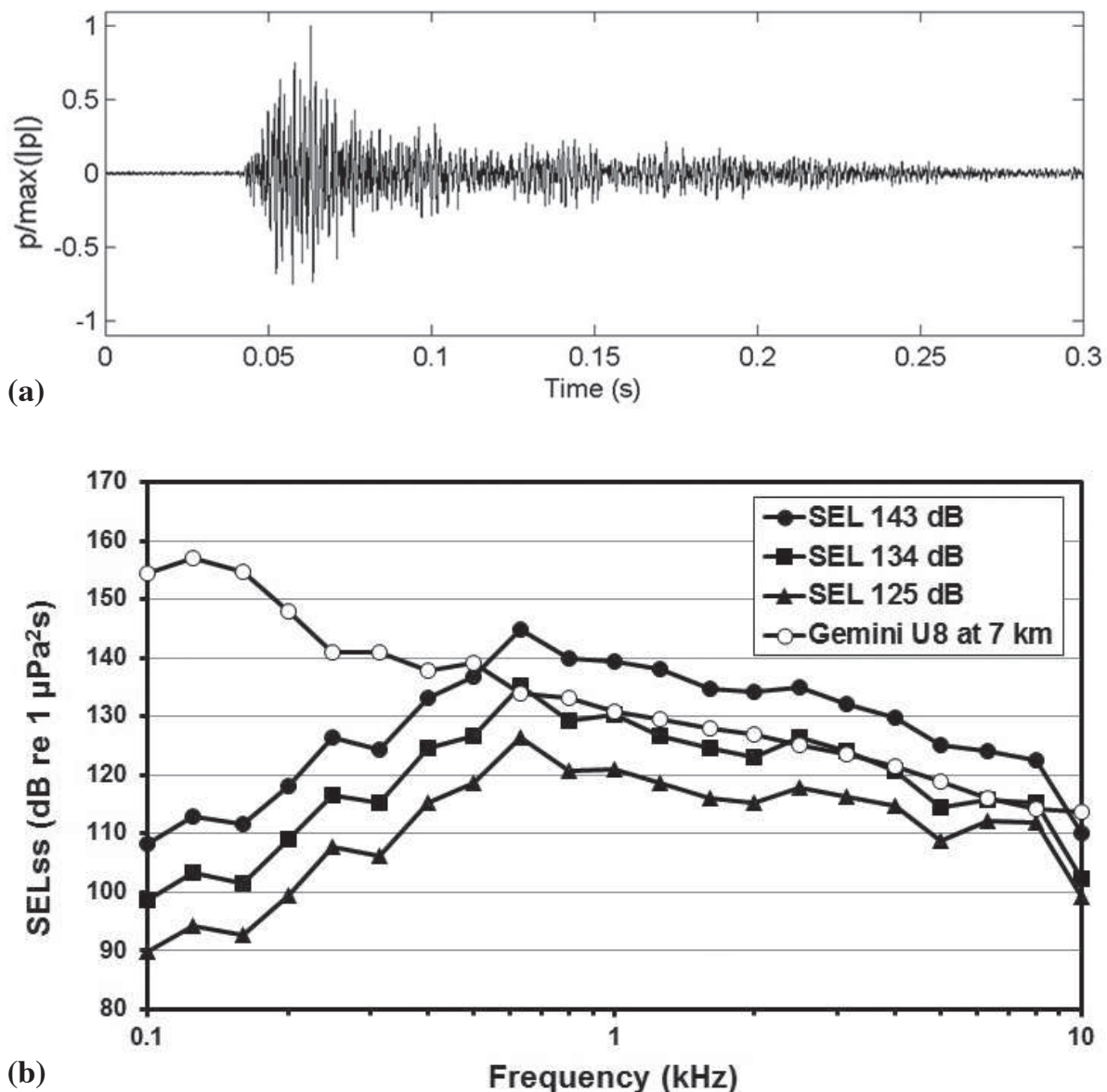


Figure 3. (a) The waveform of a pile-driving playback sound in the pool, measured at a distance of 2 m from the source and at a depth of 1.5 m; and (b) the one-third octave (base-10) band spectra of a pile-driving playback sound in the pool measured at the same location (at source levels corresponding to a mean SELss in the pool part used by the porpoises during the sessions of 125, 134, and 143 dB re $1 \mu\text{Pa}^2\text{s}$), and, for comparison, the one-third octave band spectrum of a pile driving sound recorded at 7 km distance from a North Sea pile driving site (Remmers & Bellmann, 2016).

the net cage, it (1) sucked or grabbed the fish through the net and ingested it (“catch” or “success”), (2) tried to catch the fish but was unable to so the fish ended up in the drop box (“failure”), or (3) abandoned any attempt to catch the fish before the fish reached the drop box (“termination”; in some cases, no attempt to capture the fish was made, but the porpoise always swam towards the net cage).

To catch a fish before it fell into the drop box, the harbor porpoise had to be in the right place (vertically and horizontally), and the fish had to be near a hole in the net. The position of the fish was partially determined by chance as it swirled down through the water, but it could be manipulated by currents created by the mouth of the porpoise (suction) or by movement of its entire body. After each trial, the porpoise returned to the trainer at the start buoy and was then sent back to the net feeding cage for the next trial.

Each session consisted of 20 trials per harbor porpoise, and both porpoises were tested in random order once a day, usually in the afternoon. Sessions were conducted either in the low background noise level of the pool or during playbacks of the pile driving sound at three or four (depending on the animal) source levels. Sessions were conducted in random order; during sessions with pile driving sound, the sound was played back throughout the session (one strike every 1.2 s; 47 strikes/min). Data collection took place between October 2017 and March 2018.

Data Collection and Analysis

The outcome of each trial (success, failure, or termination) was recorded by the fish supplier at the net feeding cage. A separate nominal logistic regression (Hosmer & Lemeshow, 2000) was used for each animal to assess the effects of the factor SELs on the outcome of each trial, with successful fish capture as the reference event and the quiet condition as the reference level of SELs.

Video recordings of successful trials were analysed to quantify the catch time—the time between the moment a fish was released (when the trainer at the buoy said “one”) and when the fish was caught. All catch times were quantified by the same person, mostly using the video recordings made by top view aerial camera #2 mounted on the net cage (Figures 1 & 2). On the rare occasions when a trial outcome was not clearly visible on these video images, the video recordings from underwater cameras #1 and 2, mounted on either side of the net cage, were used. A general linear model (Zar, 1999) was used to evaluate the effect of the factors “porpoise” and “SELs” on the catch time (which was log transformed to bring it close to normal distribution). Assumptions of general

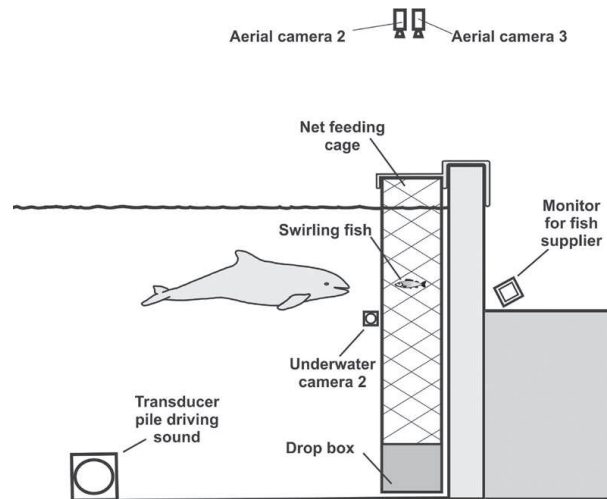


Figure 4. A schematic representation (lateral view) of the experimental set-up used for the fish-catching task.

linear models were checked for and mostly met. Some slight departures from homogeneity of variances and normality occurred in the data, but models are robust to such departures. All statistical analysis was conducted with *Minitab 18*; the significance level was set at 5% (Zar, 1999).

Results

In all, 1,640 trials were conducted in 57 sessions: 1,060 trials with porpoise F05 and 580 with porpoise M06. The sample size for porpoise M06 was lower than for porpoise F05, mainly because only three SELs were tested. Overall, 991 trials resulted in a successful fish catch, 373 trials resulted in failure, and 276 trials were terminated. Responses differed greatly between the two study animals: Compared to porpoise F05, porpoise M06 was much more likely to capture fish successfully, less likely to fail to catch a fish, and less likely to terminate trials (Figure 5). The harbor porpoises also used different fish-catching techniques. Porpoise F05 approached the net feeding cage forcefully, swimming fast, slowing down at the last moment, and sometimes swimming on her back (i.e., with her dorsal fin pointing down), thus causing water displacement; she then used a biting technique to grab the fish. Porpoise M06 used either this biting and grabbing technique or the suction technique (i.e., sucking the fish into his oral cavity by quickly withdrawing his tongue; Kastelein et al., 1997b). Porpoise F05 was observed to increase her swimming speed at SELs above 134 dB re 1 $\mu\text{Pa}^2\text{s}$, whereas porpoise M06 maintained a constant swimming speed.

For porpoise F05, the nominal logistic regression model revealed a statistically significant

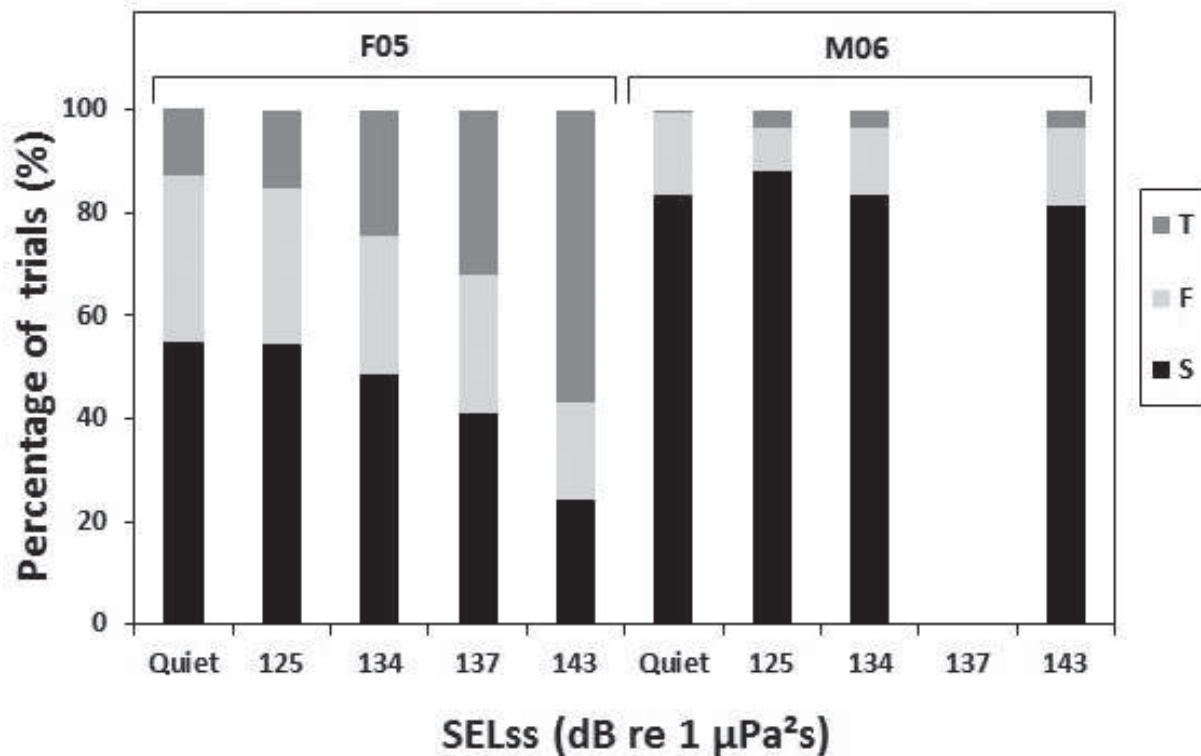


Figure 5. The outcomes of fish-catching trials, shown as percentages of the number of trials for each SELss (in total, there were 1,060 trials with porpoise F05 and 580 with porpoise M06). Outcomes are shown as T = termination, F = failure, and S = successful fish capture. Porpoise M06 had a higher overall success rate than porpoise F05. For porpoise F05 only, success rate declined with increasing SELss (from 134 dB re 1 µPa²s), as failure rate remained approximately constant and termination rate increased. Porpoise M06 was not tested during exposure to pile driving sound at 137 dB re 1 µPa²s because his pattern of behavior remained constant even at the highest level (143 dB re 1 µPa²s). Porpoise F05 did behave differently at the highest level, so the 137 dB re 1 µPa²s SELss was added to show a response gradient.

correlation between the outcome of the trials and the terms in the model ($G = 96.8$; $p = 0.000$). Trials were significantly more likely to be terminated when the SELss was 134 dB re 1 µPa²s or above (Logit 1, comparing termination with success; Table 2); SELss had a significant effect on trial outcome in Logit 1 ($\chi^2 = 79.2$; $p = 0.000$) but not in Logit 2 (comparing failure with success, $\chi^2 = 1.98$; $p = 0.739$). The odds of termination were ~10 times higher when SELss was 143 dB re 1 µPa²s than in quiet conditions (odds ratio = 9.79, $p = 0.000$). Thus, as the SELss increased, there was an increasing likelihood of trial termination, but the trial failure rate was not affected by SELss (Logit 2; Table 2).

For porpoise M06, the nominal logistic regression model revealed that there was no statistically significant correlation between the outcome of the trials and the terms in the model ($G = 7.25$; $p = 0.298$).

The mean catch time in successful trials was 11.7 ± 4.2 s ($n = 985$). Analysis of the log-transformed catch times showed that they were not

affected by SELss but were affected by porpoise (Table 3); porpoise F05 had slightly longer catch times than porpoise M06 (untransformed and uncorrected means \pm SD: F05, 12.0 ± 4.2 s, $n = 495$; M06, 11.5 ± 4.1 s, $n = 490$).

Discussion and Conclusions

Substantial individual variation in the responses of the two captive harbor porpoises to underwater sound was seen in the present study, which was in line with results of research on bottlenose dolphins (Branstetter et al., 2018). The fish-catching ability of porpoise F05 was negatively influenced by pile driving sounds, while porpoise M06's performance remained constant in the presence of the playback sound. Porpoise M06's capture success rate was higher than porpoise F05's in general and was unaffected by the pile-driving sound playbacks, even at the highest SELss. As the noise level increased above SELss = 134 dB re 1 µPa²s, fish-catch success declined for porpoise F05, and she was more likely to terminate trials, especially

Table 2. Results of the nominal logistic regression model to assess the effects of SELss on the outcome of each trial (success, failure, or termination) for porpoise F05. The reference outcome is S (successful catch). Logit 1 relates S to T (termination) and shows that trials were significantly more likely to be terminated when the SELss was 134 dB or above. The odds of termination were ~10 times higher when SELss was 143 dB re 1 $\mu\text{Pa}^2\text{s}$ than in quiet conditions (odds ratio = 9.79). Logit 2 relates S to F (failure) and shows that SELss had no significant effect on the trial failure rate.

Predictor	Coefficient \pm SE	Z	p	Odds ratio	95% CI (Lower-upper)
Logit 1: (T/S)					
Constant	-1.4 \pm 0.2	-7.49	0.000		
SELss = 125 dB	0.2 \pm 0.3	0.62	0.536	1.18	0.70-1.99
SELss = 134 dB	0.7 \pm 0.2	2.99	0.003	2.11	1.29-3.43
SELss = 137 dB	1.2 \pm 0.3	4.66	0.000	3.26	1.98-5.36
SELss = 143 dB	2.3 \pm 0.3	7.80	0.000	9.79	5.52-17.38
Logit 2: (F/S)					
Constant	-0.5 \pm 0.1	-3.81	0.000		
SELss = 125 dB	-0.1 \pm 0.2	-0.37	0.715	0.92	0.63-1.38
SELss = 134 dB	-0.1 \pm 0.2	-0.38	0.706	0.92	0.62-1.39
SELss = 137 dB	0.1 \pm 0.2	0.48	0.630	1.11	0.72-1.72
SELss = 143 dB	0.3 \pm 0.3	0.94	0.346	1.34	0.73-2.47

Table 3. Results of the general linear model on the dependent variable “catch time” (log transformed) in successful trials only to evaluate the effects of the factors “porpoise” and “SELss.” Source = source of variation, *df* = degrees of freedom, Adj SS = adjusted sum of squares, and Adj MS = adjusted mean squares.

Source	<i>df</i>	Adj SS	Adj MS	F value	p value
SELss	4	0.1664	0.04160	2.02	0.090
Porpoise	1	0.0915	0.09147	4.44	0.035
Error	979	20.1856	0.02062		
Total	984	20.4332			

at the highest SELss (Figure 5). This suggests that her ability to catch fish was negatively affected by the increasing sound levels, most of all by decreasing her motivation to complete a trial. In addition, as porpoise F05 was observed to increase her swimming speed at SELss above 134 dB, she might have increased the task’s difficulty (and thus decreased the chance of success) in some trials herself by displacing more water than usual (see below) and pushing the fish temporarily out of reach. During such trials, which only rarely occurred, a decreased motivation might have led porpoise F05 to decide not to wait for the fish to come within reach again before it reached the drop box.

The decline in fish-catch success and the increase in trial termination seen in porpoise F05 when unweighted broadband SELss increased above 134 dB suggest that some harbor porpoises may experience a *distraction threshold* for percussive pile driving sounds, approximately between 125 and 134 dB re 1 $\mu\text{Pa}^2\text{s}$. *Distraction* is defined herein as the involuntary diversion of attention from one stimulus or set of stimuli to another. In this case, the decrease in success rate for porpoise F05 suggested that the (auditory) stimuli of playback pile driving sounds diverted her attention from the fish-catching task. Since actual echolocation activity was not measured in this study, we can only speculate that the decrease in fish-catch

success rate exhibited by porpoise F05 was caused by a decrease in vigilance behavior similar to that in the bottlenose dolphins tested by Branstetter et al. (2018). Besides distraction, *aversive stimuli*, such as loud sounds, may influence motivation-related behaviors, as has been shown for grey seals (*Halichoerus grypus*; Götz & Janik, 2010). For instance, avoidance behavior may be induced, and foraging behavior may be suppressed. The latter seems to be the case for porpoise F05: at the highest SELss, she terminated over half of all trials, even though hunger was the intrinsic motivation for both porpoises to perform the task. This decrease in motivation is also consistent with the findings by Branstetter et al. (2018). Finally, the increase in swimming speed observed in porpoise F05 for the highest SELss is consistent with the behavioral response of captive harbor porpoises to pinger-like sounds observed by Teilmann et al. (2006). In their study, Teilmann et al. also measured a concurrent increase in heart rate, indicating stress. The concept of stress, however, is difficult to define, and more accurate measurements of stress in relation to sound exposure would require a physiological approach (e.g., Romano et al., 2004). Regardless, stress could have been a factor contributing to distraction from and/or a decrease in motivation to perform the fish-catching task.

Surprisingly, the catch times in successful trials remained stable for porpoise F05 with increasing SELss. When the same harbor porpoises involved in the present study were asked to perform a fish-searching task while exposed to various intermittent and continuous sounds at two different levels in another behavioral response study, search times were also found to be stable (Kok et al., 2018).

Individual differences in the harbor porpoises' approach to the fish-catching task also became apparent: porpoise F05 terminated trials more readily than porpoise M06 (Figure 5), and she took slightly longer to catch fish in successful trials. In a study of prey-searching behavior by the same porpoises, Kok et al. (2018) found that porpoise M06 spent less time searching than porpoise F05.

The two harbor porpoises certainly had different fish-catching techniques. Porpoise M06 approached the net feeding cage relatively slowly and used either the biting and grabbing technique or the suction technique. He sometimes pushed himself as far as possible into the net to reach the fish. Porpoise F05 did not use the suction technique and did not push into the net cage. She sometimes rotated horizontally and grabbed the fish through the net while swimming with her dorsal fin pointing down. It is not known whether this twisting maneuver is normal during prey capture by harbor porpoises, as it is for lunge-feeding blue whales (*Balaenoptera musculus*;

Goldbogen et al., 2013) and for squid-hunting sperm whales (*Physeter macrocephalus*; Miller et al., 2004). Using electronic tags, Akamatsu et al. (2010) observed rolling dives in finless porpoises (*Neophocaena phocaenoides*) in which the porpoises often rotated their bodies more than 60° around the body axis in a dive bout. This behavior occupied 31% of the dive duration, and the rolling dives were associated with extensive searching effort. The authors suggest that the finless porpoises searched extensively for targets and rolled their bodies to enlarge the search area by changing the narrow beam axis of their biosonar. Though echolocation was not recorded, occasional checks with a hydrophone and a bat detector showed that the harbor porpoises in the present study did use echolocation in addition to vision when approaching the net cage with the fish.

The suction technique in harbor porpoises was described in detail by Kastelein et al. (1997b). The biting and grabbing technique and the suction technique have also been observed in harbor seals (*Phoca vitulina*; Marshall et al., 2014). In the setting of the present study, porpoise F05 was a less effective forager than porpoise M06. Porpoise F05 approached the net cage at higher speeds than porpoise M06 and, because of her speed and because she was bigger than porpoise M06, she displaced more water and produced more waves, which sometimes pushed the fish towards the back of the net cage, thus making it more difficult to retrieve the fish.

Measurements in shallow parts of the North Sea (34 m deep) show that the spectrum of the playback sound at a broadband SELss = 134 dB re 1 $\mu\text{Pa}^2\text{s}$ in the present study resembles the spectrum of pile driving sounds recorded at 7 km from a pile driving site at frequencies above about 500 Hz (Remmers & Bellmann, 2016). The corresponding unweighted broadband SELss measured in the field was 163 dB re 1 $\mu\text{Pa}^2\text{s}$. However, harbor porpoises can probably sense the distance to a sound source due to reverberations, which may affect their reaction to a sound apart from the received SELss. Porpoises have a low hearing sensitivity for low-frequency sounds, so pile driving sounds with a frequency content below 500 Hz, which could not be reproduced in this playback study, are unlikely to be relevant for their behavioral response (Tougaard et al., 2015). However, individual differences in both fish-catching success (even in ambient conditions) and termination rates may complicate the quantification of the impacts of percussion pile driving sounds on harbor porpoises. Individual differences in responses to sound found in both bottlenose dolphins (Branstetter et al., 2018) and in harbor porpoises (present study) could be due to differences

in a wide range of factors that may, or may not, be quantifiable, such as sex, motivation, age, history, reproductive state, body condition, degree of need for food, or character.

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APPENDIX 3

High Levels of Food Intake in Harbor Porpoises (*Phocoena phocoena*): Insight into Recovery from Disturbance

Ronald A. Kastelein,¹ Lean Helder-Hoek,¹ Cormac Booth,²
Nancy Jennings,³ and Mardik Leopold⁴

¹Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands
E-mail: researchteam@zonnet.nl

²SMRU Consulting, New Technology Centre, North Haugh, St Andrews, KY16 9SR, UK

³Dotmoth, 1 Mendip Villas, Crabtree Lane, Dundry, Bristol BS41 8LN, UK

⁴Wageningen Marine Research, Ankerpad 27, 1781 AG, Den Helder, The Netherlands

Abstract

If harbor porpoises (*Phocoena phocoena*) are impaired in their foraging ability because they need to move away from anthropogenic sound sources, their fitness may be reduced. Understanding how much harbor porpoises can eat after a disturbance, and how quickly they can replenish their energy reserves, is important for assessing the significance of disturbances. After fasting for various time periods (2 to 24 h), four captive harbor porpoises, housed in water and air temperatures similar to those encountered by wild conspecifics, were fed a structured diet of meals larger than usual (each normal meal was 20% of the daily food mass requirement). A few times they were fed *ad libitum*, but this led to severe constipation, so this feeding method was abandoned for welfare and health reasons. The food ingested over a period of one hour following fasting for 2 to 24 hours was quantified (i.e., mass, volume, and as a percentage of normal daily food mass intake in that period). The results show that, in contrast to established belief, harbor porpoises can eat a large percentage (up to ~98%) of their normal daily food mass intake in a single feeding bout without showing physical problems. Adult animals of around 155 cm in body length can eat up to ~3 kg (~2,700 ml) in one feed. If food is abundantly available after a period of fasting due to a disturbance, wild harbor porpoises could eat a large percentage of their daily energetic requirement in one feeding bout to compensate for the period of fasting. However, if food availability is limited in terms of prey numbers, size, or species, or if the fish are widely dispersed (so that more time is required to find and capture them), this may limit or reduce the speed of the recovery of body mass and blubber layer.

Key Words: odontocete, body condition, nutrition, meal size, diet, energetics, recovery from disturbance, iPCoD, DEPONS

Introduction

Harbor porpoises (*Phocoena phocoena*) are one of the smallest of all toothed whales, so they have greater body surface area to volume ratios than other, larger species (Andersen, 1981). This geometry causes them to potentially lose a great deal of energy through radiation and conduction to the surrounding water (Feldman & McMahon, 1983). To offset these losses, harbor porpoises have blubber with a relatively high insulation value (Worthy & Edwards, 1990), which is thicker in relation to their body size than that of larger odontocetes (Koopman et al., 1996; Koopman, 1998; Kastelein et al., 2018a). Due to seasonally changing water temperatures in the geographical range of the harbor porpoise, seasonal changes in blubber thickness and, thus, body mass occur regularly (Kastelein et al., 1997c, 2018a; Lockyer et al., 2003). Despite this increased insulation, harbor porpoises have a higher metabolic rate than terrestrial mammals of similar body mass and larger odontocetes (Yasui & Gaskin, 1986; Kastelein et al., 1997a, 2018a; Reed et al., 2000; Williams & Maresh, 2016; Rojano-Doñate et al., 2018), so they need to consume relatively large amounts of food to maintain a stable body temperature of ~36°C (Kastelein et al., 1990). Their high metabolic rate means that harbor porpoises are particularly sensitive to disturbance that prevents them from feeding. Harbor porpoises may stop feeding when they need to evade larger marine mammals that feed on them, such as killer whales (*Orcinus orca*; Dahlheim & White, 2010) and grey seals (*Halichoerus grypus*; Leopold et al., 2015), or when they flee from loud anthropogenic sound sources (Dähne et al., 2013).

A prominent offshore sound source in the North Sea is pile driving, which is used to place the foundations of offshore wind turbines. Currently, most offshore wind farms are constructed by means of percussion pile driving, which causes impulsive sounds with a high sound pressure level (SPL). Driving a single pile into the sea floor may take up to 3 h, and several piles can be placed per day in one wind park. Harbor porpoises are deterred from percussion piling sites at distances of up to tens of kilometers (Carstensen et al., 2006; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014; Rumes et al., 2017). During percussion pile driving sound exposure, harbor porpoises may swim at a speed of ~7 km/h when leaving the area, which is probably faster than their general swimming speed (Kastelein et al., 2018b). Assuming they swim away from pile driving sites in a straight line and can maintain that speed, it would take them about 1.5 to 3 h to get 10 to 20 km away from a site (see Dähne et al., 2013; Rumes et al., 2017). As porpoises likely do not forage during flight, this scenario means that a porpoise fleeing from a pile driving site would fast for up to 3 h and would subsequently need to compensate for the food missed during those 3 h and the energetic cost of fleeing.

As a small odontocete, the harbor porpoise is predated on by great white sharks (*Carcharodon carcharias*; Arnold 1972), other odontocetes such as killer whales (Ford et al., 1998), bottlenose dolphins (*Tursiops truncatus*; Ross & Wilson, 1996), and pinnipeds such as grey seals (Haelters et al., 2012). This means that porpoises often have to flee when encountering predators. Therefore, the species is probably adapted to disturbance on a certain time scale. Not feeding for 3 h is well within the normal range of behavior observed in wild harbor porpoises (Wisniewska, 2016, 2018); sometimes little foraging effort was observed for 9 to 12 h. However, if the disruption is unexpected and/or prolonged such that it impedes normal foraging behaviour, the consequences can be significant. Kastelein et al. (2019) showed that harbor porpoises lose ~4% of body mass and ~1 mm in blubber layer following a 24-h fasting period. It is not clear how readily individual harbor porpoises can make up for lost foraging opportunities through increased subsequent food intake.

Extremely high feeding rates on small fish have been observed in wild harbor porpoises (Wisniewska et al., 2016, 2018). Although this may not be representative of general porpoise feeding behavior since larger fish are found in the stomachs of many stranded or bycaught porpoises (Hoekendijk et al., 2017), it suggests that porpoises may be able to compensate after periods of fasting. Recovery (i.e., replenishing the blubber layer and regaining lost body mass) after a period of fasting depends on the availability of sufficient suitable prey, on the

energetic content of that prey, on the energy it takes to capture the prey, and on how much prey a porpoise can physically ingest. The amount of fish that harbor porpoises can eat before reaching satiation is thought to be limited by the size of the forestomach (Kastelein & Lavaleije, 1992; Figure 1). The forestomach, having an uninflated volume of around 500 ml in adult porpoises (Kastelein, pers. obs), can expand to contain food. Analysis of otoliths suggests that the forestomach of a harbor porpoise can hold at least 1.9 kg of fish (Sveegaard et al., 2012). Recovery from fasting also depends on foraging efficiency, ingestion, and digestion speed, the latter determining how soon a porpoise can feed again after it has filled its forestomach.

The goal of this study is to quantify the amount of food a harbor porpoise can eat in a short period of time (during a single feed) in order to understand how disturbance resulting in fasting might impact individuals. This information can be used to inform models that have been developed for the harbor porpoise to aid in the assessment of the population consequences of disturbance (e.g., Interim PCoD: King et al., 2015; and DEPONS: Nabe-Nielsen et al., 2018).

Methods

Study Animals

Four stranded and rehabilitated harbor porpoises were available for the study, each for a different period of time (Table 1). Their ages on arrival at the Dolfinarium Harderwijk rehabilitation center were estimated based on their length (after van Utrecht, 1978; Gaskin et al., 1984). During the study, all four animals were in good physical condition. Their age, body length, girth at axilla, and body mass ranges during the study are shown in Table 1. Three of the four were still growing, and all showed expected seasonal variation in body mass and girth.

Study Area

The study was conducted at the SEAMARCO Research Institute, the Netherlands (51° 32' N, 3° 55' E). The animals were kept in a pool complex consisting of an outdoor pool (12 × 8 m; 2 m deep) connected via a channel (4 × 3 m; 1.4 m deep) with an indoor pool (8 × 7 m; 2 m deep). The bottom of each pool was covered with a 20-cm-thick layer of sand on which aquatic vegetation grew and invertebrates lived. Sea water was pumped directly from the Eastern Scheldt, a semi-enclosed tidal estuary of the North Sea, into the water circulation system, with partial recirculation through biological and sand filters. The pool water temperature ranged from -2 to +24°C throughout the year. The minimum and maximum air temperatures over each 24-h period ranged from -8 to 34°C. The air and

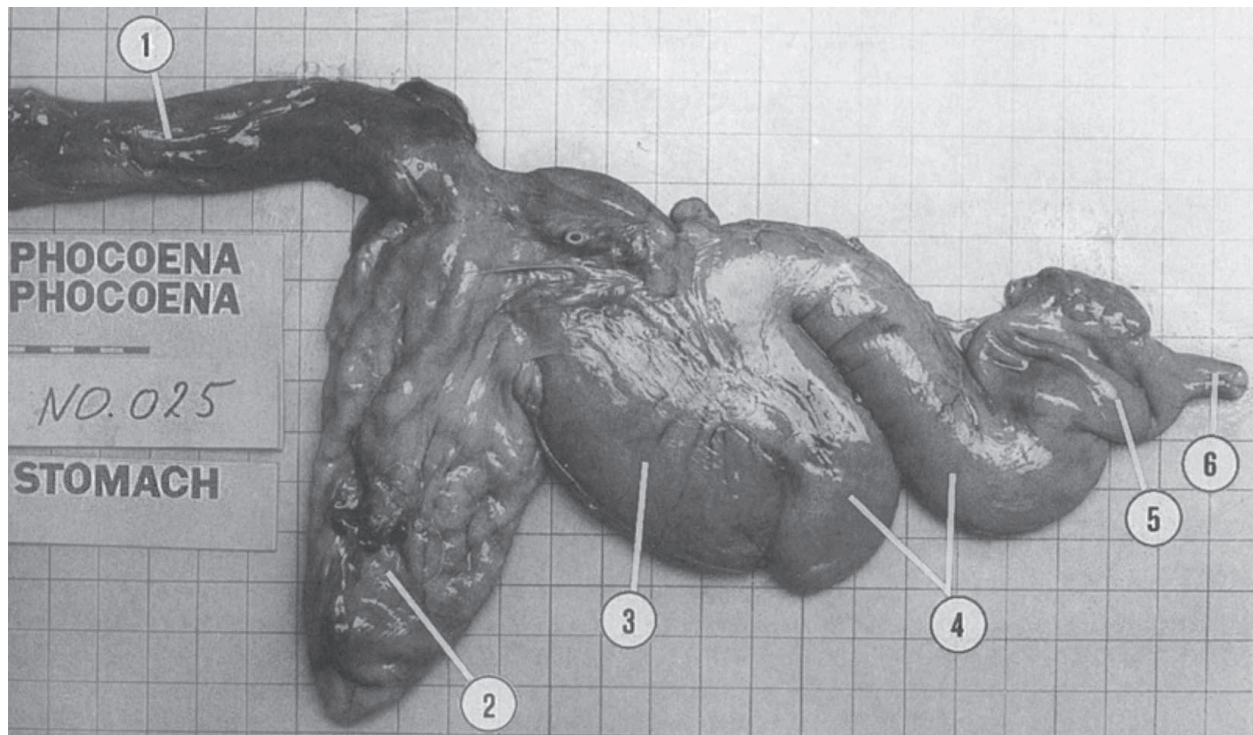


Figure 1. Part of the digestive tract of a harbor porpoise (*Phocoena phocoena*), showing from left to right (1) the esophagus, (2) the empty (expandable) forestomach, (3) the fundic (main) stomach, (4) the pyloric (connecting) stomach, (5) the duodenal ampulla, and (6) the beginning of the duodenum (small intestine) (from Kastelein & Lavaleije, 1992, with permission). The background grid squares are 2×2 cm.

Table 1. Genders, age range (giving an indication of the study period for each animal), total body length, girth at axilla, and body mass of the four study animals. Note the individual difference in body sizes per age.

Porpoise identification (M = male, F = female)	Age range (year)	Total body length range (cm)	Girth at axilla range (cm)	Body mass range (kg)
Subadult to Adult M02	3-6.5	133-147	68.0-78.0	30.6-39.1
Subadult M04	3-3.5	129-132	69.5-77.0	28.2-33.3
Adult F05	6-7	153-155	77.0-84.5	39.7-44.1
Subadult M06	3-4	127-130	73.0-81.0	27.9-32.2

water temperatures and salinity ($\sim 3.4\%$) experienced by the study animals were similar to those experienced by wild conspecifics in the North Sea (wild porpoises occurred 200 m away from the pool on the other side of the dyke in the Eastern Scheldt).

Feeding

The harbor porpoises were routinely fed a diet of thawed sprat (*Sprattus sprattus*; 7.9 kJ/g), herring (*Clupea harengus*; 6.5 kJ/g), and mackerel (*Scomber scombrus*; 7.7 kJ/g). Based on the daily diet composition, the caloric energy density of the diet was approximately 7.1 kJ/g. The porpoises were fed fish at a temperature of $\sim 4^\circ\text{C}$. The fish were weighed digitally (1 g accuracy), and the summed mass of fish of each species eaten during each meal

was recorded. Feeding session length was usually 15 min, but occasionally up to 60 min. The volume of the fish species, as measured by water displacement, was 1,000 g sprat, ~ 950 ml; 1,000 g herring, ~ 600 ml; and 1,000 g mackerel, ~ 750 ml.

The study animals were typically (on $\sim 95\%$ of days) fed five times a day, with the daily amount divided equally over five meals ($\sim 20\%$ in each feed). No food was available to the animals during the evening and night (1600 to 0830 h). The initial food passage time in harbor porpoises is ~ 2.5 h (Kastelein et al., 1997b), and they regain their appetite (based on degree of performance in psychophysical research) starting about 2 h after eating a meal consisting of $\sim 20\%$ of the normal daily food requirement (Kastelein, pers. obs.).

When the present study began, it was the intention to feed the harbor porpoises *ad libitum* after the normal 16-h fasting period during the night: feeding would be stopped only when an animal dropped the fish that it was offered, started to play with it instead of ingesting it immediately, or swam away from the feeding station for several minutes. However, *ad libitum* feeding was done only a few times—with porpoise M02 twice, with F05 three times, and with M06 twice—during 60-min feeding sessions in which they were not asked to perform specific behaviors. Two of the animals became very lethargic after these meals and showed signs of severe constipation during the rest of the day (they experienced cramps, which were indicated by them moving their tail stocks below their bodies). After one feed, gas bubbles came out of the mouth of porpoise M06. The feces, which are normally watery and dark green, became thick and beige during the day of the *ad libitum* feeding, also indicating constipation. After this, due to welfare and health concerns, *ad libitum* feeding sessions were discontinued.

Data were collected on meals that were limited by staff but were larger than normal (> 20% of the porpoises' normal daily food mass intake). In these staff-limited meals, the amount of food offered was determined by the staff before each feeding session began. The harbor porpoises always ate all the food that was offered to them. These large meals occurred when weekly or biweekly body mass measurements were lower than expected, or when a feed had been missed (usually because staff were occupied with other animals) and was compensated for in the next feed. The large meals did not result in the animals showing any kind of discomfort. In all cases, the animals had not eaten for at least 2 h and for up to 24 h before they were fed (a broad time-frame, as these were opportunistic data), which meant that their forestomachs were likely empty when feeding began. The data were collected at various frequencies in each study animal but not more often than once a week. Staff elicited trained behaviors from the harbor porpoises during the feeds. The total amount of food ingested within 1 h (the maximum length of feeding sessions) was recorded. In these dedicated feeding sessions, the food was given quickly (generally during ~15 min), given in small increments during the hour, or given as two smaller meals during the hour (because two animals were usually fed in alternation in a training session). The data were collected between July 2008 and September 2017.

Results

When they were fed *ad libitum*, porpoises F05 and M06 ate up to 100% of their mean daily food intake during the previous week in one meal (Figure 2), but this caused severe constipation.

Porpoise M02 ate 85% of his daily food intake during the previous week in one meal without showing digestive problems.

When their food intake in one meal after at least 2 h of fasting was high, but limited by staff, the harbor porpoises ate between 38 and 98% of the normal daily food mass intake (i.e., mean daily food intake during the previous week; Figure 2). The porpoises did not suffer the digestive problems that were seen after *ad libitum* feeds. However, in staff-limited feeds, porpoise M06 ate similar amounts as during *ad libitum* feeds without showing signs of constipation, perhaps because the food given in staff-limited feeds was more spread out over the hour.

Data from both *ad libitum* and staff-limited feeds are combined and summarized in Table 2. Although we do not assume that the caloric content had an effect on the meal size ingested, the energy content of the food is also given in Table 2 and Figure 2.

Discussion and Conclusion

In this opportunistic study, variability occurred in the amount of food the harbor porpoises ate, both within and between individuals. This was as expected because the following parameters were not kept constant between feeds:

- The amount of fish offered (*ad libitum* or limited by staff)
- The time since the last meal (2 to 24 h)
- The season, which is related to energy requirements (Kastelein et al., 2018a)
- The fish given (species, size)
- The time taken to feed (15 to 60 min)
- The behavior of the animals (stationary in the water near the feeding station or free swimming)
- Whether or not the porpoises were required to perform behaviors to obtain fish
- Placement of the fish (in the porpoise's mouth or in the water)
- Individual differences (forestomach size or appetite)
- The reason for ending the feed (in the *ad libitum* feeds: dropping fish, playing with fish, or swimming away from the feeding station)

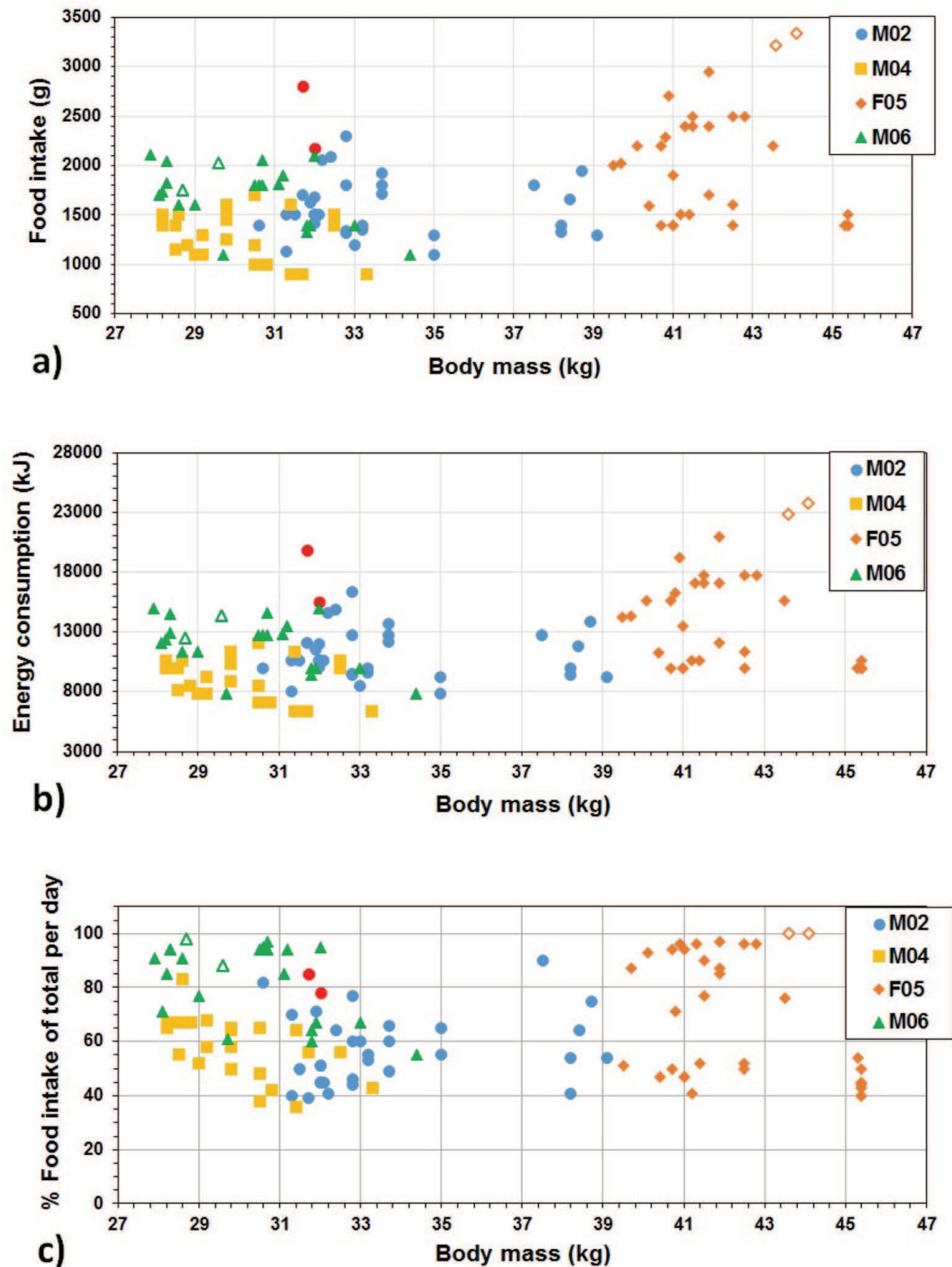


Figure 2. Food intake by four harbor porpoises in 1 h expressed in (a) grams, (b) kJ, and (c) as a percentage of mean daily food mass intake after at least 2 h of fasting. The four open symbols (porpoises F05 and M06) indicate feeds in which the animals were allowed to eat *ad libitum* (maximum food intake in one meal), becoming lethargic and showing signs of constipation (two data points from F05 overlap). The solid red dots were meals during which porpoise M02 was fed *ad libitum* but did not show signs of any discomfort afterwards. The other solid symbols show feeds that were limited in quantity by staff but larger than the usual ~20% of the normal daily food mass intake. In these staff-limited feeds, the porpoises always ate all the food that was offered.

Table 2. The mean, standard deviation (SD), and range of mass, energy content, and volumes of meals eaten in large meals by four harbor porpoises after a minimum of 2 h of fasting. Data from *ad libitum* feeds and staff-limited feeds are combined. For comparison, normal meals were ~20% of the daily food mass intake. *N* = sample size.

Porpoise	Meal mass (g)				Energy content meal (kJ)			Meal volume (ml)		% of daily food mass intake	
	Mean	SD	Range	<i>N</i>	Mean	SD	Range	Mean	Range	Min	Max
Subadult to Adult M02	1,619	365	1,100-2,800	34	11,500	2,590	7,800-19,900	1,295	880-2,240	39	90
Subadult M04	1,284	239	900-1,700	28	9,120	1,700	6,400-12,100	1,028	720-1,360	36	83
Adult F05	2,209	546	1,400-3,337	22	15,680	3,900	9,940-23,700	1,767	1,120-2,670	38	100
Subadult M06	1,635	338	1,000-2,110	22	11,600	2,400	7,100-15,000	1,308	800-1,688	44	97

Most of the data were collected opportunistically, so it is not possible to unravel the individual roles (if any) of each of these parameters. More studies would be needed to evaluate the factors affecting the amount of food harbor porpoises can eat in one meal.

While the intention of this study of captive animals was to provide insight into the maximum amount of food that wild harbor porpoises could ingest to overcome lost foraging opportunities due to disturbance, we recognize that the results may not be directly translatable. When they were fed *ad libitum* without being asked to perform trained behaviors, porpoises F05 and M06 showed signs of severe discomfort after the feed. Wild porpoises would not ingest such a large amount of fish in one meal without expending energy and time to capture the fish which might impact the speed with which the first stomach is filled and, thus, the chance of the feeling of discomfort. The study animals were kept in similar water and air temperatures to wild porpoises, in large pools with sea water, and swam most of the day like their conspecifics, so their energy requirements and food intake may have been similar. However, in common with most other captive harbor porpoises, the study animals were not fed during the night, whereas wild harbor porpoises do feed at night. The context of porpoises in the wild varies depending on geographic location (e.g., water depth, fish species preyed upon, and local temperatures), season, and year. Both wild and captive porpoises show population-related body size differences (for instance, North Sea and Baltic populations; Møhl-Hansen, 1954; Lockyer, 1995; Learmonth et al., 2014), as well as individual differences in body size, metabolism, gender, age, health, reproductive state, etc.

Sveegaard et al. (2012) estimated that the forestomach of a harbor porpoise could contain at least 1.9 kg of fish. The present study shows that

an adult porpoise (the size of the largest animal in the present study, porpoise F05) can eat ~3 kg of fish, and that the forestomach can expand to contain a volume of up to 2,700 ml (about six times the volume of an empty forestomach; Table 2). In the wild, if harbor porpoises encounter a sufficiently large school of fish when they are hungry, they can probably eat at least 85%, and possibly 100%, of their daily food mass intake in a short period of time (< 1 h). Wisniewska et al. (2016, 2018) suggest that wild harbor porpoises made up to 200 to 550 successful prey capture attempts per hour. They can digest food rapidly (initial passage time is ~2.5 h; Kastelein et al., 1997b) and then eat more. Therefore, after periods of fasting that may result from disturbances, as long as food is abundantly available, harbor porpoises can probably recover quickly. A high metabolism works both ways: when insufficient food is available, an animal can lose mass quickly; but if food is readily available and can be ingested quickly, rapid mass gain is possible.

The lowest amount of food consumed following at least 2 h of fasting was 36% of daily food mass intake in 1 h (Table 2). Wild harbor porpoises take approximately 3 h to flee a pile driving site (Dähne et al., 2013; Rumes et al., 2015). If only poor-quality prey are available, or if prey are dispersed, porpoises may need to feed almost all day and night to ingest sufficient energy to recover after fasting for a few hours. Wisniewska et al. (2016) observed that wild harbor porpoises had periods of low foraging activity (lasting 6 to 12 h, often during daylight hours) and periods of increased foraging activity (lasting 3 to 4 h, often in darkness). This suggests that harbor porpoises can increase their activity when they encounter a suitable prey patch or suitable conditions for efficient foraging. It is unclear whether these foraging patterns, observed by Wisniewska et al. (2016), are unusual for harbor porpoises in the wild or

whether they are representative of the species (Hoekendijk et al., 2017).

Given their small size and thermoregulatory constraints, harbor porpoises are believed to be under constant pressure to forage effectively and frequently to survive (Read & Hohn, 1995). Depending on the season, healthy porpoises can lose approximately 1 kg of body mass if they do not eat for 24 h, during which time they would normally eat 2 to 2.5 kg (Kastelein et al., 2019). If suitable prey is abundant, harbor porpoises are likely to be able to recuperate quickly from disturbances. However, little is known about the availability of food in areas that wild harbor porpoises may flee to or about their foraging behavior when they are disturbed. If they reduce their foraging effort or if food availability is limited (e.g., diurnally, seasonally, annually, or geographically), recovery of body mass may be compromised.

As a recommendation for future policymakers and managers, prey availability should be studied just outside a radius of ~20 km of pile driving locations (representing a 3-h swim for harbor porpoises), as part of environmental impact assessments for offshore pile driving. Each pile takes around 3 h to drive into the sea bed, and pile driving often continues for several hours each day. If disturbances occur in quick succession, if suitable prey were not abundant to begin with, or if disturbances influence prey availability, harbor porpoises may lose too much body mass and become hypothermic and susceptible to disease.

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APPENDIX 4

ARTICLE



Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance

Cormac G. Booth 

SMRU Consulting, New Technology Centre,
University of St Andrews, St Andrews, UK

Correspondence

Cormac G. Booth, SMRU Consulting, New
Technology Centre, North Haugh, St
Andrews, Fife KY16 9SR, UK.
Email: cgb@smruconsulting.com

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Abstract

Research has shown that noise disturbance can disrupt the behavior of harbor porpoises. The significance of such disturbance is unclear. However, these animals may be vulnerable to starvation when disturbed due to their high energy requirements. Important parameters determining harbor porpoise energy balance are the size and energy content of prey, their foraging behavior and their energetic requirements for homeostasis, growth, and reproduction. Energy intake can be estimated using published data from tagged animals. Such analysis indicates a broad range of plausible levels of energy intake, in line with those from captive studies. Metabolizable energy intake estimates were most strongly affected by variations in target prey size and to a lesser extent, by the foraging intensity of porpoises. In all but the worst case scenarios, harbor porpoises are well equipped for their ecological niche due to their generalist diet, consisting of a range of moderate to high energy-density prey combined with ultra-high foraging rates and high capture success. If animals can find suitable prey, porpoises may be capable of recovering from some lost foraging opportunities. Minimizing disturbances is, however, important for their health. Further research into prey and the environment are required to fully test the assumption of vulnerability.

KEYWORDS

diet, disturbance, energetics, foraging, harbor porpoise, noise

1 | INTRODUCTION

The energy balance for any species is governed by the effort they expend to acquire food, the energetic value of that resource and how the energy acquired is utilized. This forms a cost–benefit equation, where the costs are represented by the energy expenditure involved in prey capture and that expended to maintain body processes, such as thermoregulation, growth, and reproduction. Marine mammals exhibit a wide range of life strategies, from large, long-lived species with long, interbirth intervals, to smaller species that reach sexual maturity early and produce a large number of offspring. Efficient foraging (maximizing benefits while minimizing costs) is, therefore, an essential element in the survival and reproduction of smaller species. Insights into energy acquisition and expenditure are therefore critical to developing an understanding of a species and its role in a changing ecosystem.

A number of studies have explored how energy budgets influence lifestyle (Kastelein, Hardeman, & Boer, 1997; Lockyer, 2007; McLellan et al., 2002). Harbor porpoises have short, stocky bodies, (females: length 160 cm and weight 60 kg; males: 145 cm and 50 kg) (Bjørge & Tolley, 2018). They are found throughout the cold, temperate waters of the Northern Hemisphere. In order to cope with relatively cold waters (and resulting thermoregulatory pressures) they require close proximity to food supplies and regular feeding due to their lack of major fat stores and their limited energy reserves (Lockyer, 2003). Heat loss is considered to be managed via cyclical shifts in energy intake to build up and then shed a blubber layer throughout the year (Rojano-Doñate et al., 2018). Female harbor porpoises are considered to be “income breeders” (Read, 2001; Read & Hohn, 1995), i.e., they balance the costs of pregnancy and lactation by increased food intake rather than depending on fat stores. These are evolutionary adaptations to a life that includes short-term periods of feast and famine.

A number of studies, using acoustic monitoring, have determined that harbor porpoises change their distribution and/or behavior following exposure to high-intensity, broadband noise sources (such as pile-driving, which is commonly used during the construction of offshore wind farms (Brandt et al., 2018; Dähne et al., 2013; Haelters, Dulière, Vigin, & Degraer, 2015) and lower intensity sources (Dyndo, Wiśniewska, Rojano-Doñate, & Madsen, 2015; Mikkelsen, Hermannsen, Beedholm, Madsen, & Tougaard, 2017). Reduced detection rates are often encountered during and following exposure to noise. It has been demonstrated that animals sometimes stop vocalizing in response to noise and therefore likely cease foraging (Wisniewska et al., 2018b). Near fasting has been shown to cause seasonally dependent variations in reduction of porpoise body mass of between 3.0% and 5.4% following 24 hr of near-fasting (Kastelein, Helder-Hoek, Jennings, van Kester, & Huisman, 2019). Whether porpoises can compensate following gaps in foraging requires further research on prey abundance, availability and the most limiting factors affecting porpoise health (assessed in this study). Kastelein et al. (2019) indicated that, following fasting, harbor porpoises can eat a large percentage (>90%; ~12–20 MJ) of their normal daily energy requirements in a 1 hr feeding bout and will then feed again shortly (without physical issues). What constitutes a significant disturbance (i.e., one that affects an animal's probability of survival or reproducing) remains a critical knowledge gap (King et al., 2015; Nabe-Nielsen et al., 2018).

Studies of porpoise diet in the North and Baltic Seas indicate that they ingest a wide range of prey types, typical of a generalist feeder, focusing on one or two prey species over short temporal scales (Andreasen et al., 2017; Börjesson, Berggren, & Ganning, 2003; Leopold, 2015; Ross, Andreasen, & Andersen, 2016; Santos & Pierce, 2003; Santos et al., 2004; Sveegaard et al., 2012). While there is significant temporal and spatial variation in the dominant prey species, the most commonly observed prey types include Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), sprat (*Sprattus sprattus*), and herring (*Clupea harengus*). Sandeels (Family *Ammodytidae*) and goby species (Family *Gobiidae*) also feature in their diet and may be important regionally (e.g., Andreasen et al., 2017; Santos et al., 2004). Diet varies with age and season with respect to both prey selection and prey size (Andreasen et al., 2017). Importantly, prey type differs in quality, with energy densities varying significantly from 4.2 kJ/g (wet mass) in whiting, to 7.6 kJ/g in sprat, parameters that also vary seasonally and with body length (Pedersen & Hislop, 2001; Wanless, Harris, Redman, & Speakman, 2005). Further, the lipid content, and therefore their seasonally dependent

value as food, of these fish vary. Overall, food intake and energy generation for porpoises is complex as they may forage on different species throughout the year.

Recent studies have deployed acoustic tags (DTAGs) on harbor porpoises and used the data collected to assess their vocalization and foraging behavior (Wisniewska et al., 2016, 2018a, 2018b). Acoustic click signatures, for males and females of different ages, in the audio recordings were used to estimate the number of foraging attempts made by tagged porpoises and to determine their success rates. The size of the targeted prey was also estimated. The majority of tagged animals foraged more during the night than during the day (as measured by daytime buzz-positive minutes [BPM] vs. night-time BPM) (Wisniewska, 2018b). Similarly, estimates of daily energy expenditure for tagged animals range from 7.8 to 31.0 MJ day⁻¹ (corresponding to 0.25–0.59 MJ day⁻¹ kg⁻¹ of body mass). Further, it has been shown that exposure of animals to high levels of shipping noise can result in short-term disruptions in foraging (Wisniewska et al., 2018b). Despite these advances, our understanding of harbor porpoise vulnerability to disturbance is incomplete (summarized in Hoekendijk, Spitz, Read, Leopold, & Fontaine, 2018; Wisniewska et al., 2018a). Critical to understanding harbor porpoise vulnerability to missed foraging opportunities is an assessment of likely net energy gain at any time versus energy demands. The objective of this study was to utilize published studies to assess the effectiveness of harbor porpoises as foragers, what a bout of foraging might mean energetically for animals and how this learning informs how vulnerable harbor porpoises may be to disturbance. To achieve this, the data presented in (Wisniewska et al., 2016, 2018a) have been combined with our understanding of porpoise diet and the energy derived from different prey (e.g., Andreasen et al., 2017; Spitz, Mourocq, Schoen, & Ridoux, 2010; Wanless et al., 2005). These elements are used to estimate a plausible range of energy intake over the tag duration and, using the energy requirements of the same individuals (Rojano-Doñate et al., 2018), generate insights into the energy budget of harbor porpoises.

2 | MATERIALS AND METHODS

2.1 | Model development

Information on the individual tagged porpoises (ID, stage class, sex, standard length, month of tagging) and porpoise foraging parameter estimates (buzz rate, success rate of foraging attempt, size of prey targeted) were taken from recent papers (Wisniewska et al., 2016, 2018a) (Table 1). The animals were tagged between 2012 and 2016 in the Kattegat, at the mouth of the Baltic Sea (see Figure S1 in Wisniewska et al., 2018b). One tagged animal was referenced as “hp15_116a” in Wisniewska et al. (2018a), but as “hp15_117a” in Wisniewska et al. (2018b) and (Rojano-Doñate et al., 2018). These animals have the same tag date, length, tag deployment duration, and buzz count across the two studies and therefore are considered to be the same animal (with modified ID code) and have been treated as such in this study.

The total metabolizable energy intake for each tagged porpoise i (ME_i) was estimated using Equation 1.

$$ME_i = S_i \times C_i \times A \times \sum_{f=1}^F \sum_{p=1}^{P_f} (W_{f,p} \times d_{f,p} \times E_{f,q_i} \times k_{f,q_i,o_i}) \quad (1)$$

where S_i is the individual-specific rate of attempted captures that were successful; C_i is the number of capture attempts by that individual (“buzzes” as a proxy for capture attempts and success rate from Wisniewska et al., 2016, 2018a; summarized in Table 1 and Table S1); and A is assimilation efficiency (from Lockyer, 2007; Yasui & Gaskin, 1986). F is the main fish species recorded in porpoise diet by life stage and time of year (from Andreasen et al., 2017; summarized in Table 2 and Table S1). Each species f occurs in a number of 1 cm size bins/classes (P_f) in the range 3–20 cm. $W_{f,p}$ is the weight (in grams) of each fish species f given size class p and is equal to $a_f L_{f,p}^{b_f}$, where $L_{f,p}$ is the integer length (in centimeters) of fish in that size class, and a_f and b_f are constants that vary across different

TABLE 1 Information on tagged porpoises used in this study, derived from Wisniewska et al. (2016, 2018a).

ID	Sex	Class	SL (cm)	Dur. (hr)	Month	Buzzes	Buzz hr ⁻¹	SR %	Target prey size (cm)		
									<5	5–10	10–20
hp14_226b	M	J	126	20.0	Aug	3,234	153	91% (85–97)	53%	34%	13%
hp13_170a ^a	M	J	122	15.3	Jun	1,222	60	NA	NA	NA	NA
hp13_102a	M	J	114	22.7	Apr	3,405	162	99% (97–100)	95%	4%	1%
hp16_316a	M	J	113	39.1	Nov	5,715	146	NA	NA	NA	NA
hp12_272a	F	J	122	17.8	Sep	1,821	106	92% (87–97)	96%	3%	1%
hp12_293a ^b	F	A	163	16.4	Oct	1,346	86	97% (94–100)	75%	17%	8%
hp15_117a	F	A	170	12.4	Apr	906	73	NA	NA	NA	NA

Note: ID = code provided by Wisniewska et al. (2016, 2018a) in the form: [species][year]_[JulianDay]. Sex = the sex of the tagged animal, M = male, F = female. Class = the stage class of the animal, J = juvenile, A = adult. SL (centimeters) = the length of the tagged porpoise in centimeters. Dur. (hr) = the duration in hours of the tag deployment in which data was collected on the animal (from start of foraging to tag release). Month = the month in which the animal was tagged. Buzzes = the total number of buzzes estimated for the tag duration. Buzz hr⁻¹ = the total number of buzzes estimated divided by the tag duration. SR% = the estimated mean (and 95% confidence intervals) success rate of capture attempts by the tagged porpoises. Target prey size = prey size targeted by the tagged porpoises in Wisniewska et al. (2016, 2018a), derived from Figure 3C in Wisniewska et al. (2016). NA = data not available for that individual.

^aTag data only collected during daylight hours.

^bThis adult female was present with a calf.

TABLE 2 Seasonal prey mass composition derived from fig. 4 of Andreassen et al. (2017) for juveniles and adult porpoises (based on 339 stomach contents).

Stage class	Seasonal prey mass composition (%)							
	Juveniles				Adult			
	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Prey species/group								
Atlantic Cod	6%	18%	55%	29%	32%	18%	41%	55%
Whiting	1%	3%	17%	2%	4%	1%	1%	2%
Herring	38%	27%	9%	5%	9%	30%	17%	29%
Sprat	9%	10%	2%	5%	0%	7%	0%	1%
Sandeel family	0%	2%	1%	0%	0%	14%	6%	0%
Eelpout	10%	10%	0%	5%	0%	6%	24%	0%
Gobies family	30%	28%	10%	38%	1%	10%	4%	8%
Others	5%	2%	6%	15%	4%	14%	7%	5%

Note: Q1 = January–March; Q2 = April–June; Q3 = July–September; Q4 = October–December.

fish species (sources summarized in Table 3 and Table S1). $d_{f,p}$ is the estimated proportion of fish species f belonging to size class p from Wisniewska et al. (2016) (Table 1 and Table S1); E_{f,q_i} is the energy density (in kilojoules/gram wet weight) of each fish species f in the quarter during which each porpoise was tagged, q_i (Table 2); and is the proportion of fish species f in the porpoise diet in quarter q_i (from Anderson et al., 2017; summarized in Table 3 and Table S1), given the ontogenetic stage o_i of the tagged porpoise (juvenile or adult). Where foraging parameter estimates were not available for individual porpoises, the values provided for the most closely related individual were used. For example, no information on the success rate of foraging attempts was available for animal hp13_170a (a juvenile) and, therefore, the estimate for animal hp12_272a, (a similar sized juvenile) was used. The latter had the lowest success rate in the study and is, therefore, a conservative estimate. Similarly, the success rate for hp15_117a

TABLE 3 Weight-length relationships and energy density for prey species considered in this study. Gobies value taken as a proxy from grey gurnard and red mullet.

Prey species	Weight-length parameters			Energy density	
	a	b	Reference	Value (kJ/g)	Reference
Atlantic Cod	0.0143	2.9126	Silva et al. (2013)	4.2	Lawson et al. (1998)
Whiting	0.0166	2.7708	Silva, et al. (2013)	4.2 ^a	Pedersen and Hislop (2001)
Herring	0.00603	3.0904	Coull et al. (1989)	6.0 ^a	Pedersen and Hislop (2001)
Sprat	0.00211	3.4746	Coull et al. (1989)	7.6	Wanless et al. (2005)
Sandeel family	0.00124	3.32	Coull et al. (1989)	5.0 ^a	Pedersen and Hislop (2001)
Eelpout	0.003	4.0957	Coull et al. (1989)	5.1	Spitz et al. (2010)
Gobies family	0.0056	3.3081	Silva et al. (2013)	4.4	Plimmer (1921)
Four-bearded rockling	0.0035	3.1062	Coull et al. (1989)	5.5	Spitz et al. (2010)
Horse mackerel	0.0034	3.2943	Coull et al. (1989)	6.0	Spitz et al. (2010)
Saithe	0.0085	3.0242	Silva et al. (2013)	4.2	Spitz et al. (2010)
Haddock	0.0092	3.1026	Silva et al. (2013)	4.4 ^a	Pedersen & Hislop (2001)
Sole	0.0036	3.3133	Coull et al. (1989)	5.0	Spitz et al. (2010)
Flounder	0.0087	3.0978	Coull et al. (1989)	3.0	Plimmer (1921)

^aDenotes where there was evidence of energetic density varying seasonally and with fish length, this was accounted for in analyses, but only an average value is presented here.

(an adult female) was not presented in Wisniewska et al. (2018a) so the foraging success data for animal hp12_293a (the only other adult female tagged) was used.

Estimates of the prey sizes targeted (derived from tailbeat frequency of fish detected on the DTAG) by the porpoises were presented for four of the individuals tagged (in Wisniewska et al., 2016). For the purposes of this study, the proportions of different prey sizes were digitally extracted using WebPlotDigitizer (version 4.0, <https://automeris.io/WebPlotDigitizer/>) (Table 1). In the published studies (Wisniewska et al., 2016, 2018a), porpoises primarily targeted fish that had body lengths of 3–10 cm and displayed proportions for prey sizes <5 cm, 5–10 cm, and 10–20 cm. Therefore, it was assumed that the smallest prey targeted was 3 cm and the largest was 20 cm corresponding to the minimum and maximum fish length targets specified. The lower value of this range is consistent with the size of the main prey items for Danish (Kattegat) harbor porpoises (Andreasen et al., 2017; Ross et al., 2016). Where data on targeted prey size were not available for individuals, the closest available estimate of target prey for a suitable proxy was used. For example, for animal hp13_170a, no estimates of target prey size were available, therefore the data from hp12_272a (a similar sized juvenile, see above) were used. Similarly for individuals hp16_316a (juvenile male) and hp15_117a (adult female) no target prey size estimates were available and so estimates from hp13_102a (juvenile male) and hp12_293a (adult female), respectively, were used in the calculations. These proxies also represent a minimum estimate, as they targeted predominantly small prey sizes (which have lower energy content than larger fish).

For this analysis the most likely target prey species, based on stomach contents of either stranded or bycaught animals, was considered. Data reported for 339 harbor porpoises (either bycaught or stranded) in the Western Baltic Sea and Kattegat between 1980 and 2011 has been utilized (Andreasen et al., 2017). Geographically, the study areas for diet and porpoise tagging overlap and so, this study focuses on these key prey species. In their analyses the samples comprised; males ($n = 183$), females ($n = 156$), juveniles ($n = 228$) and adults ($n = 111$). They determined that 91% of the stomach contents were comprised of: Atlantic cod (mean length = 23 cm, length range = 2.6–56.9 cm), whiting (mean = 14.9 cm, range = 2.9–46.6 cm), herring (mean = 17.7 cm, range = 2.6–30.6 cm), sprat (mean = 10.3 cm, range = 3.0–15.9 cm), sandeels spp. (mean = 15.1 cm, range = 4.1–21.0 cm), eelpout (or burbot,

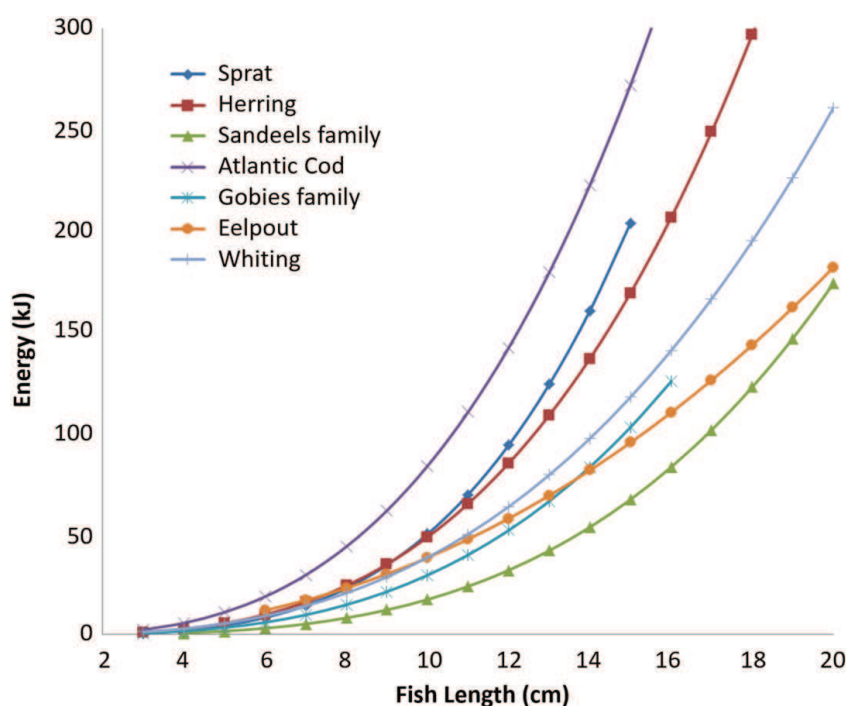


FIGURE 1 The relationship between average fish length (centimeters) and energy (kilojoules) for a range of harbor porpoise prey items (though seasonal and length-specific variations exist; see Equation 1). Fish length for each species is limited by the observed range of prey in stomach contents from Andreasen et al. (2017).

Zoarces viviparus) (mean = 19.6 cm, range = 6.0–28.7 cm), gobies spp. (mean = 4.9–5.8 cm, range = 2.5–12.7 cm), and the remaining diet items (“others”) mostly comprised of sole (*Solea solea*), flounder (*Platichthys flesus*), gadoids (Family *Gadidae*, excluding cod and whiting), Atlantic horse mackerel (*Trachurus trachurus*), and four-bearded rockling (*Enchelyopus cimbrius*) (length range = 5.7–35.3 cm). Since mass is a cubic function of fish length (and the caloric value of a fish is a product of mass), larger prey offer substantially greater energy gains to the animal (Figure 1). Prey sizes used in analyses were based on the quoted size ranges (Andreasen et al., 2017); for example, eelpout <6 cm were not observed in the stomach contents of harbor porpoises, so it was assumed that any eelpout consumed were >6 cm. Metabolizable energy obtained for an animal was estimated from a range of values for assimilation efficiency values from the literature and were between 74% (Yasui & Gaskin, 1986) and 90%–95% (Lockyer, 2007). ME estimates were scaled by tag duration in (Table 1) and allometrically using mass estimates (Table S2).

2.2 | Sensitivity analysis of ME_i

To understand the sensitivities of calculations ME , the relative importance of each of the variables in Equation 1 was assessed. Some of the variables are nonindependent (i.e., a change in one results in a change in the other, for example, d the estimated proportion of fish in a size class) and so a classic sensitivity analysis was not possible. Collinearity between the variables was assessed using the *vif* and *GGally* packages. Energy density and proportions of different fish species in the diet f were found to be strongly correlated. Therefore a series of linear models with standardized ME estimates, variable combinations with interactions fitted across the nonindependent variables were assessed and the best model selected (determined by AIC). Model order was iteratively adjusted to ensure that results were not biased by the order of fitting of variables. To calculate the relative importance of each variable in the best model the contribution of each variable using the absolute value of the t -statistic for each model parameter was undertaken using *varImp* (in the *caret* package) (Kuhn, 2008). All relative importance assessment steps were implemented in R (version 3.4, <https://cran.r-project.org/>).

2.3 | Energy balance

Rojano-Doñate et al. (2018) estimated the field metabolic rates (FMR) for each of the tagged animals reported in previous studies (Wisniewska et al., 2018a, 2018b;). These FMR estimates were corrected in the current study using the reported tag durations to calculate the energy balance for these tag deployments (Table S2, Equation 2).

$$\text{Energy balance} = \frac{ME_i}{ER_i} \quad (2)$$

where ME_i is the metabolizable energy intake for each tagged porpoise i (from this study) and ER_i is the energy requirement estimate for the same tagged porpoise i from Rojano-Doñate et al. (2018) over the tag duration. Five short-term energy balance scenarios were assessed (detailed in Table S3). The first three scenarios dealt with the “average seasonal porpoise diet” (following dietary patterns observed in Andreasen et al., 2017), the “best case” (highest ME obtained and lowest ER estimates over the tag duration), “moderate case” (best estimate of ME obtained and ER), and “worst case” (lowest ME obtained and highest energy requirement estimates) scenarios were assessed. Finally, two scenarios investigated single species diet: the lowest and highest energy single prey species—defined as “single species–worst and best case” (see Table S3 for further details). For these single species analyses only prey that were a significant component of the relevant quarterly diet were considered (from Table 2). This avoided the inclusion of prey that were unlikely to be in the diet of the tagged porpoise. These scenarios provides a range of plausible values of ME ingested by the tagged animals and allow a better understanding of the role of prey caloric value in assessments of energy balance.

3 | RESULTS AND DISCUSSION

3.1 | Estimates of ME obtained by tagged porpoises

Estimates of potential metabolizable energy gained by seven different harbor porpoises were derived from published data (foraging records and diet studies) (Andreasen et al., 2017; Wisniewska et al., 2016, 2018a) under several different prey availability scenarios (Figure 2, Table S3). As expected there was considerable variance between the animals with two juvenile males providing the most extreme values: animal hp14_226b (juvenile male) was an outlier, as it

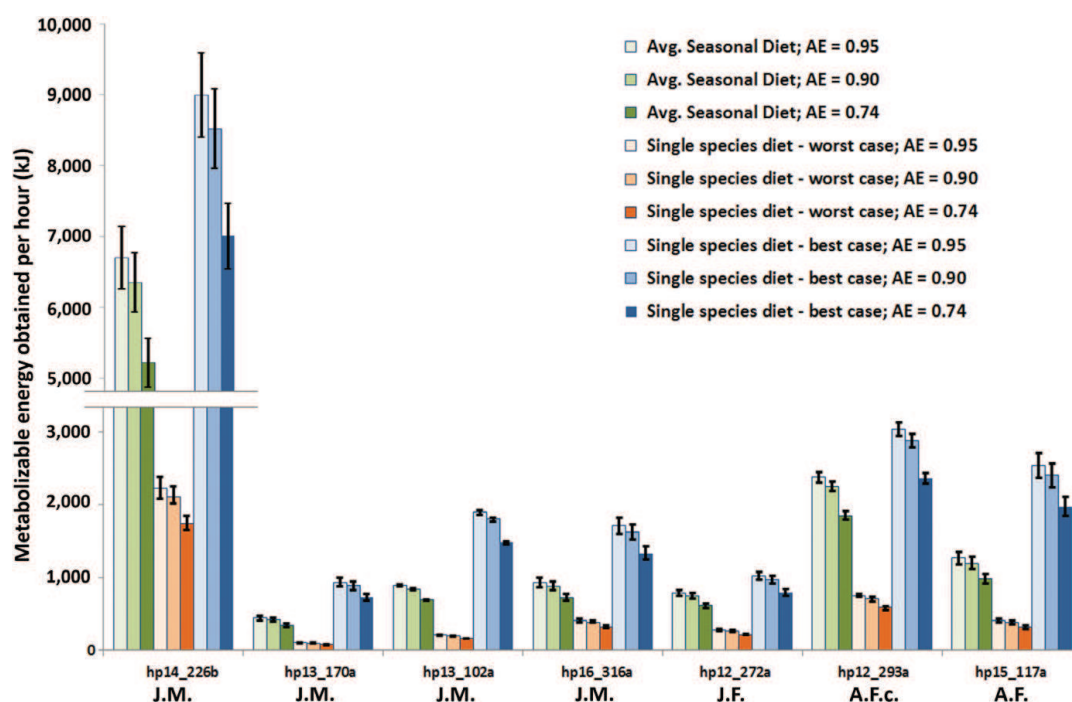


FIGURE 2 Estimates of average metabolizable energy obtained per hour (allometrically scaled) for each tagged porpoise from Wisniewska et al. (2016, 2018a). Note the broken y-axis. Error bars indicate the range of successful capture rates for each individual. The height of the main bars are a product of the total number of capture attempts, the prey species foraged on and the size of the prey. AE = assimilation efficiency. J.M. = juvenile male; J.F. = juvenile female; A.F.c = adult female with calf; A.F. = adult female (no calf).

TABLE 4 Sensitivity analysis of factors affecting *ME* intake estimates for the “average seasonal diet” scenarios. The relative importance of each variable was calculated using the absolute value of the *t*-statistic for each model parameter. Variables in italics denote variables fitted as interaction terms. Variables are ordered by *t*-statistic.

Variable	Symbol	<i>t</i> -statistic
<i>Proportion of fish in each size class^a</i>	<i>d</i>	38.773
Number of successful captures ^a	SC	7.223
Assimilation efficiency ^b	A	3.999
<i>Proportion of fish species in diet^c</i>	<i>k</i>	3.718

^aData sourced from Wisniewska et al. (2016).

^bData sourced from Lockyer (2007) and Yasui and Gaskin (1986).

^cData sourced from Andreasen et al. (2017) (see Table S1 for sources).

appeared to be targeting larger prey items and correspondingly had the highest *ME* values. Estimates for animal hp13_170a were lower, ranging between 2.6 and 3.3 kJ h⁻¹ kg⁻¹ and this fits with the observation that the animal was not tagged during hours of darkness. For the other animals, males and females, plus nursing females, most of the values of *ME* fitted between the two extremes described above. For all the animals, single species diets are predicted to give the highest *ME* values for the best case, whereas worst cases were calculated to fall below the values for average seasonal diet (derived from the stomach contents of bycatch and stranded animals (Figure 2).

To understand the drivers of the variance in *ME* described above, an assessment was made of the most important variables in Equation 1 (Table 4). The single most important factor was the size of prey item targeted, with fish of 5–10 cm and 10–20 cm resulting in the highest *ME* estimates (*t*-statistic: 37.77). The next most important variable was the number of successful captures by each tagged porpoise (a product of the total number of capture attempts—buzzes from the DTAG record and the estimated success rate—from Wisniewska et al. (2016) (*t*-statistic: 7.22). Finally, the assimilation efficiency of the ingested prey of the porpoises (*t*-statistic: 3.99) and the prey species (*t*-statistic: 3.72) were the least important variables.

3.2 | Energy balance assessment

To gain a better understanding of the *ME* estimates above, the energy requirements were incorporated into the assessment of energy balance for the tagged porpoises (using the same five scenarios) (Figure 3). Only in the worst case scenarios (both average seasonal and single species diets) did the energy capture fall below the calculated requirement (Figure 3). In most cases prey capture and energy intake were up to 1.5–two-fold greater than the calculated demand. This applied particularly to individual hp13_170a where tagging only covered the period (daytime) with the lowest foraging effort (Wisniewska et al., 2016). In nearly all examples the lowest energy yield came from the scenario that is least realistic—“single species diet-worst case” (Figure 3).

In the majority (>70%) of scenarios considered, animals obtained >100% of their energy requirements over the tag deployment. Among the juvenile animals hp14_226b, the animal obtained >100% in all scenarios and hp13_170a (only tagged during daylight hours) obtained >100% in all but the worst case scenarios (average and seasonal diets). All remaining juveniles obtained less than 100% of requirements only in a scenario with the “single species-worst case” prey species available. For the adults females tagged, the female without a calf only obtained >100% in 2 out of 5 scenarios, while the female accompanying a calf obtained >100% of required energy in 3 out of 10 scenarios.

3.3 | Model interpretation

This study predicts the energy intake and energy expenditure of tagged harbor porpoises, with the objective of gaining a better understanding of their vulnerability to disturbance. This is the first time that an energy balance has been estimated for harbor porpoises using data from field experiments on wild harbor porpoises and their prey. The analyses in

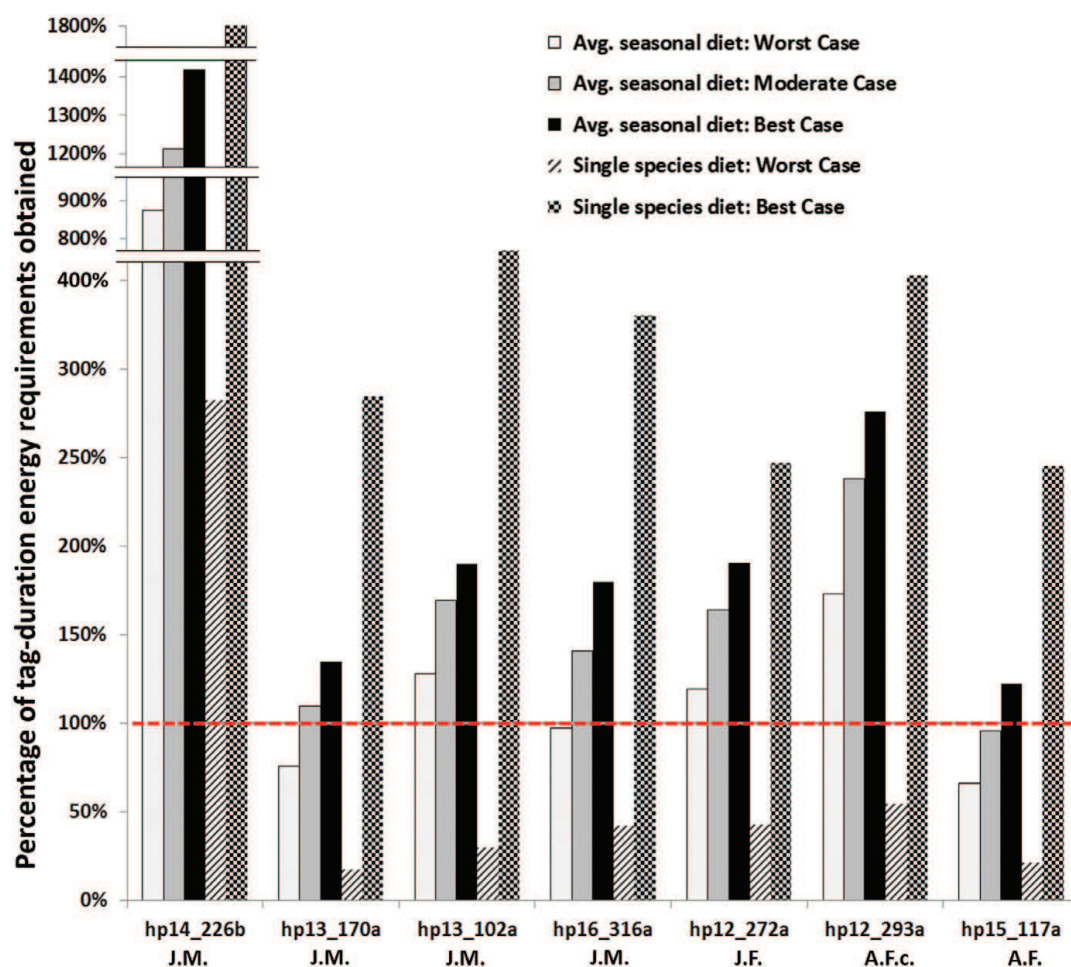


FIGURE 3 Best and worst case scenarios of obtained metabolizable energy for each of the tagged harbor porpoises relative to their estimated energy requirements over the tag duration (from Rojano-Doñate et al., 2018). Note the broken y-axis. The red dashed line shows the 100% energy requirement for each individual over the tag duration. J.M. = juvenile male; J.F. = juvenile female; A.F.c = adult female with calf; A.F. = adult female (no calf).

this study are built primarily on three previous studies; on the foraging behavior and energy requirements of seven tagged harbor porpoises. The animals tagged represent a very small sample size from which to draw conclusions.

Porpoises have been described to exist on an “energetic knife-edge” (e.g., Wisniewska et al., 2016) due to their life strategy. The estimates presented in this study indicate how inclusion of prey quality (specifically prey size distribution and energetic density) can meaningfully advance this research area. Critical, here, is the consideration of prey species, target size, and energy content when assessing how a species exists in its ecological niche. Ultra-high foraging rates can translate into ultra-high energetic intake when the energy density of potential prey species are considered. The range of metabolizable energy intake estimates generated in this study (Figure 2 and Figure 3) indicate a very broad range of plausible outcomes for the foraging observed in the tagged porpoises. However, the majority of case studies generating energy intake estimates >100% of energy requirements. Only under a worst-case scenario, were the tagged harbor porpoises predicted to only capture a small portion of their daily energy requirements. Such animals would indeed be vulnerable to disturbance via missed foraging opportunities. However, the worst case chosen is an extreme in which individuals are poor foragers (with low digestive efficiency) and with access only to atypical single species diet.

Some specific data sets do give further pause for thought. Animal hp14_226b, a juvenile male, was an outlier, with very high ME estimates, driven primarily by the animal targeting larger prey items (~47% of items >5 cm in length) and to a lesser extent, relatively high foraging rates (153 hr^{-1}) (from Wisniewska et al., 2016). Obviously it is possible that target prey size was overestimated. If the animal was feeding on the lowest energy prey available (or on a species not considered in this analysis) the ME values might fall back into the normal range for the other six

animals. Given the cube relationship between size and mass (i.e., size and energetic content) (Figure 1) overestimating the size of the prey would generate such high values of ME. It is also possible that the DTAG recorded buzzes from other porpoises in close proximity to the tagged animals (Stimpert et al., 2014). Animal hp13_170a exhibited low ME values but was only tagged during the day. The low buzz rate (60 hr^{-1}) may not have captured the peak foraging for that individual, as tagged animals in inner Danish waters appeared to increase foraging during the night (Wisniewska et al., 2018b) (discussed further below). Equally capture success rates may be overestimated. No other foraging success data exist for harbor porpoises by which to make more detailed comparisons. The intake estimates in this study are comparable with those for captive studies (both juvenile and adults: not adjusted for assimilation efficiency), which range between 646 and $1,304 \text{ kJ hr}^{-1}$ (Rojano-Doñate et al., 2018); 333 and $1,042 \text{ kJ hr}^{-1}$ (Kastelein et al., 1997); 681 and $1,479 \text{ kJ hr}^{-1}$ (Lockyer, Desportes, Hansen, Labberté, & Siebert, 2003), and 375 and $1,083 \text{ kJ hr}^{-1}$ (Kastelein, Helder-Hoek, & Jennings, 2018) (all estimates scaled to hours from daily estimates). The ME estimates in this stage mostly range from 323 to 996 kJ hr^{-1} in juveniles (hp14_226b was much higher), 921 to $1,350 \text{ kJ hr}^{-1}$ for an adult with no calf (but potentially pregnant), and 1,795 to $2,452 \text{ kJ hr}^{-1}$ for the female with a calf. Therefore the ME estimates in this study are in line with captive studies on harbor porpoises.

In the wild, it is likely that harbor porpoises are equipped to survive short periods (e.g., ~12 or more hours) with little energy intake. As generalists they exploit productive patches and the corollary to this is that they must also encounter less productive regions. Tagged animals were observed to forage more during periods of darkness (Wisniewska et al., 2016, 2018a, 2018b). It is implicit in this observation that harbor porpoises endure periods of 10–12 hr where foraging effort is greatly reduced (e.g., see Figure 2 in Wisniewska et al., 2016). The implication here is that the feeding overnight sustains the periods of nonfeeding behavior. Such behavior may reflect travel between foraging patches, periods of reduced activity to allow digestion of prey or a preference for foraging more during the night, when prey might be easier to catch. Kastelein et al. (2019) indicated that captive porpoises have a large extensible forestomach and, following a fasting period, are capable of ingesting >90% of their energy requirements (i.e., ~12–20 MJ) in a 1-hr period and were able to feed again shortly afterwards. How well this observation translates into free-living porpoises is not clear, but it is likely that food is less readily available in the wild than in captivity. In the specific context of disturbance, it is important to note that the location of tagged animals featured a high density of vessel traffic and offshore wind farm developments. These animals are likely to be regularly exposed to a range of anthropogenic noise sources, for example, see Figure S1 in Wisniewska et al. (2018b) and the data, therefore, reflect the foraging behavior, energy expenditure, and energy intake estimates in this study in an already perturbed environment.

Periodic “over-feeding” or *hyperphagia* has been established to be a key part of the lifestyle of a range of taxa. These include fish (e.g., Jobling & Johansen, 1999), reptiles (e.g., Castoe et al., 2013), birds (e.g., Guillemette, Richman, Portugal, & Butler, 2012) and both terrestrial (e.g., Wu & Storey, 2016) and marine mammals (e.g., Goldbogen & Madsen, 2018). It is also a strategy employed periodically by any predator with variable prey (e.g., migrating birds, hibernating mammals, central place foragers; e.g., Barnard & Brown, 1987). It has long been hypothesized that long-term energy intake over weeks to months is well-matched with energy expenditure (Kennedy, 1953). DTAG deployments provide a brief (hours), but important, snapshot of foraging behavior. Potentially they could capture periods of hyperphagia, but conversely, they may capture periods where expenditure cannot be balanced by intake. Therefore, hyperphagia is either indicative of some compensatory behavior or of some degree of building up reserves to support the animal between prey-dense patches. Harbor porpoises are known to exploit prey-rich patches over the short-term before engaging in larger scale movements over longer periods (Nielsen et al., 2018; Read & Westgate, 1997). Such a phenomenon could explain the extreme excesses in short-term energy intake relative to predicted expenditure in some cases (Figure 3).

Another possibility is that energy expenditure is underestimated. Tidal volume is increased following exercise (Fahlman et al., 2016; Ridgway, Scronce, & Kanwisher, 1969) and wild animals are considered to be exercising more than captive subjects (which were used to calibrate the respiration rates of wild animals in Rojano-Doñate et al., 2018). Consequently, the existing estimates of FMR for the tagged porpoises represent underestimates for foraging (and likely active) porpoises. If that is the case, the estimates of energy requirements obtained in Figure 3 would be reduced, but not sufficiently to change the conclusions of this analysis. Rojano-Doñate et al. (2018) highlighted the

FMR estimates from free-ranging porpoises indicated that porpoises required a minimum of 15 kJ of energy intake per minute. In over two thirds of the scenarios considered in this study, this minimum threshold was exceeded. The analyses presented here are for porpoises in inner Danish waters and therefore energy intake estimates may be different in other areas where other prey (with different energy content) are available.

The harbor porpoise diet suggests the species to be a generalist, with a wide range of prey available to the species (as observed in Andreassen et al., 2017; Santos & Pierce, 2003; Santos et al., 2004). Stomach contents data from Andreassen et al. (2017) suggest porpoises typically feed on larger prey than identified in acoustic targets by Wisniewska et al. (2016, 2018a), which might indicate the estimates of ME presented in this study could be underestimates. The assessment of viable prey types (upon which energetic calculations are based) is from stomach contents analysis of 339 harbor porpoises. Andreassen et al. (2017) corrected for residence time of stomach contents in their analyses and, therefore, they can be considered a robust assessment of the likely prey size targeted by porpoises in the region. However, the stomachs were collected between 1980 and 2011 and represent a generalist species diet over an extended period, but one that falls outside the tagging period, which may not be indicative of recent foraging trends in Kattegat harbor porpoises. One cannot rule out that the tagged animals were feeding on a species not documented or considered here and a number of studies have questioned the value of data derived from bycaught or stranded animals (e.g., Leopold, 2015; Ross et al., 2016).

One of the biggest sensitivities in this study are the estimates of the energy obtained per fish, which is driven primarily by fish length and to a lesser extent, the energetic content of prey. The assessment of the size of prey targets from Wisniewska et al. (2016) was limited to a subset of the animals tagged (0.9%–1.6% of available prey capture attempts in juveniles and 2.2% in adults) and thus potentially a large source of error in derived energy intake in this study. In the generation of prey length estimates, the tailbeat frequency of return echoes (converted to muscle contraction time) was used based on the previous analysis by Wardle (1975). This approach is sensitive to the values chosen for maximum swimming velocity, maximum stride length and the precision with which tailbeat frequency is measured. An example is presented in Wisniewska et al. (2016) for a fish of “body length <5 cm” (fig. 4D). This is derived from the values for maximum stride length of 0.8, maximum swimming velocity of 1.4 m/s, and tailbeat frequency of 36 Hz (measured from the echoes recorded on DTAGs) integrated using the equation from Wardle (1975). Repeating this analysis it can be determined that the fish length estimate in this example is 4.9 cm. Wardle and Videler (1980) provide a review of cases where observations show that fish species frequently exceed the theoretical maximum suggested in the earlier study (Wardle, 1975). Maximum stride length ranges between 0.6 and 0.8 (based on available empirical measures; Wardle, 1975), but using the lower stride length value suggests prey target size of 6.5 cm (an increase of 1.6 cm from the original estimate). Videler and Wardle (1991) indicate that stride lengths are low when fish are accelerating and so a value of 0.6 may be more appropriate for a prey item fleeing a predator over a short time period. The only prey species with a published stride length considered here is the Atlantic cod (0.6–0.62) (Videler & Wardle, 1991) and maximum burst swimming speeds (as would be observed during a predation event) are available for species such as herring (4.6 m/s), whiting (2.2 m/s) and Atlantic cod (1.9 m/s) (read from fig. 4 in He, 1993). Use of these swimming speeds in the prey size estimation (using the default of stride length of 0.8, tailbeat 36 Hz) would result in fish length estimates of 16.1 cm for herring (corresponding to an additional 67 kJ per fish) and 7.7 cm for whiting (an additional 11.8 kJ per fish). Use of the stride length and maximum burst velocity for cod (from the studies above) leads to an estimated fish target length of 8.9 cm (an additional 16.8 kJ per fish). In addition, even a small shift to larger prey can result in a significant increase in energy obtained, for example, from a 4 cm sandeel spp. (0.54 kJ) to a 5 cm sandeel spp. (1.14 kJ) represents a doubling of energy to the animal. When considering that tagged animals were observed making peak foraging attempts of between 200 and 500 hr⁻¹, such differences are critical in assessing the vulnerability of harbor porpoise as a species. We cannot say here if fish length estimates used are systematically underestimated, but if that is the case, then the estimates of metabolizable energy intake for each individual could be considered conservative (and size estimates would also better match estimates derived from stomach contents analyses). The intention here is to specifically highlight some of the sensitivities in this approach and the consequences for estimating energy—that is, the type and size of prey are critical to modeling energetic calculations and assessments of vulnerability. The studies by Rojano-Doñate et al. (2018), Wisniewska et al. (2016), and Wisniewska et al. (2018b) represent novel and exciting approaches to using acoustic tag data for studying

eco-physiology. Understanding the prey environment (and its quality) for harbor porpoises and other marine mammal species remains an important topic for which further field research is required. A greater knowledge of the abundance, distribution of harbor porpoise prey, their movements, and variations in porpoise metabolic costs is required to understand the ecology of this species and their susceptibility to perturbation.

3.4 | Conclusions

A holistic approach has been taken to understanding the energy balance for harbor porpoises. The results indicate a broad range of plausible levels of energy intake for tagged harbor porpoises indicating that these animals, in all but the worst case scenarios, are capable of exploiting the ecological niche into which they have evolved. This reflects their generalist diet and ultra-high foraging rates. These results may also inform the species susceptibility to disturbance and the drivers of capacity to cope with disrupted foraging (either via environmental variability or if caused by noise disturbance). Minimizing disturbances is important as other pathways may affect animal health but this study highlights porpoises may have some elasticity in recovering following short lost foraging opportunities (or the local absence of suitable prey), like any patch forager. Robust assessments of vulnerability to disturbance require consideration of the prey energy content and the size of prey being targeted as these are critical drivers of energy balance. Furthermore, an appreciation of the abundance, distribution and quality of prey is critical to understanding species ecology and the potential effects of disturbance.

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COMPETING INTERESTS

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AUTHOR CONTRIBUTIONS

Booth carried out all reviews, analysis, and writing in this manuscript.

ORCID

Cormac G. Booth  <https://orcid.org/0000-0002-5804-3455>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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APPENDIX 5

Abstracts for INPAS 1: June 2018 (Amsterdam, The Netherlands)

The symposium was chaired by, René Dekeling – Project Leader: Sound in the Marine Environment, Ministry of Infrastructure and Water Management, Netherlands.

Jakob Tougaard from Aarhus University, Denmark provided a general introduction keynote to set the scene for the INPAS symposium. From there, the following presentations were made with lots of time for discussions to explore where this research field needs to go next and how to effectively fill our gaps in knowledge.

Impact areas – Christ de Jong et al. – TNO Acoustics and Sonar, The Hague, The Netherlands

An essential step in assessing impacts is to determine the area around the source in which the impulsive noise may have a significant impact on porpoises and seals. The likeliness for effects on the behaviour (e.g. avoiding the sound source) or on the hearing (particularly PTS) to occur depends on the dose of sound to which the animals are exposed. Acoustic models for sources, such as marine pile driving, airgun arrays for seismic surveys and explosions, and for sound propagation in the marine environment have been developed to quantify the sound distribution around the source. A short update will be given on the current status of the models and the associated uncertainties. Significant effects are assumed to occur when the sound exposure quantity exceeds a defined threshold value. Recent developments suggest that incorporation of animal hearing sensitivity in that quantity provides a more robust impact assessment, though further research is required.

Avoidance of pile driving by harbour seals; results of an animal-borne telemetry study – Gordon Hastie et al. – Sea Mammal Research Unit, St Andrews, UK.

The Wash (southern North Sea) is an area of extensive wind farm development and hosts >3,500 harbour seals. To quantify interactions with wind farms, we deployed GPS-tags on 24 seals prior to wind farm development (2003-2005) and on 25 seals during wind farm construction and operation (2012). Using the GPS data, we compared seal distribution between pre-development and during both construction and operation, and during the construction phase between piling and non-piling periods. Results showed no significant decrease in seal abundance within operational wind farms; in fact, one seal appeared to be attracted to the turbine foundations. Further, there was no large-scale displacement of seals during construction overall. However, during piling periods, seal abundance was significantly reduced up to 25 km from the piling; there was a 19 to 83% (95% CIs) decrease in usage compared to non-piling periods, equating to a mean estimated displacement of 440 seals.

Uncontrolled sound exposure experiments: behavioural reactions of wild grey seals to pile-driving – Geert Aarts et al. – Wageningen Marine Research, Wageningen University & Research

Pile-driving during the construction of offshore windfarms produces high energy, broad spectrum sound that can be detected by marine mammals, causing changes in behaviour that could reduce condition and reproductive potential. Grey seals (*Halichoerus grypus*) are abundant predators in the North Sea, but their responses to anthropogenic sounds are still largely unknown. To examine if movement and behaviour could be influenced by pile-driving, we tracked grey seals during the construction of the Luchterduinen windfarm in 2014 and Gemini windfarm in 2015. Reactions of the grey seals to the pile driving were diverse, and included: altered surfacing or diving behaviour, and changes in swim direction including swimming away from the source, heading into shore or travelling perpendicular to the incoming sound, or coming to a halt. Also, during a large number of exposures, the seals did not appear to change their diving behaviour or movement. The change in behaviour most often observed in response to pile-driving was a decline in the descent speed, which suggests a transition from foraging (diving straight down to the bottom), to more horizontal movement. The analysis showed that these changes in behaviour were on average larger and occurred more frequent at smaller distances (<30km) from the pile driving events.

Porpoise displacement at different noise levels during construction of an offshore windfarm – Isla Graham et al. – Lighthouse Field Station, University of Aberdeen, UK.

A key area of uncertainty in the assessment of the potential impacts of offshore developments remains the extent of marine mammal displacement to different levels of underwater noise. Recent environmental

assessments have used range-dependent acoustic models that predict unweighted single-pulse sound exposure levels, but information on the likely responses of harbour porpoises at different received levels is lacking. In 2017, the foundations of the 84-turbine Beatrice Offshore Windfarm (BOWL) were piled. Harbour porpoise responses were studied using passive acoustic monitoring in two phases during the initial and later stages of pile installation. Changes in porpoise occurrence in response to piling noise, vessel activity and acoustic deterrent devices were estimated using echolocation detectors (CPODs) moored at different distances from the construction vessel. Underwater noise levels were recorded using autonomous noise recorders (SM2Ms and SoundTraps). A porpoise behavioural dose-response curve was estimated from these data and factors affecting variation in responses at different received levels and distances from construction activity were explored. These results will inform impact assessments and measures to mitigate the impact of underwater noise from marine renewable technologies on marine mammals.

Porpoise disturbance during noise mitigated construction of seven offshore wind farms – Miriam J. Brandt et al. – Bioconsult SH GmbH, Germany

Disturbance effects of offshore windfarm (OWF) construction on harbour porpoises were investigated using acoustic porpoise monitoring data and noise measurements at the first seven large-scale OWFs in the German Bight between 2010 and 2013. Six OWFs were constructed mainly under active noise mitigation systems (NMS), one without. Based on GAM analyses, declines in porpoise detections were found at noise levels exceeding 143 dB re 1 $\mu\text{Pa}^2\text{s}$ (SEL05) and up to 17 km from piling (14 km for piling events with NMS). Effect size, however, declined with distance and decreasing noise level and was greater at piling events without NMS: Porpoise detections during piling measured at 10-15 km distance from piling declined by 50 % without NMS but only by 17 % with NMS when compared to 25-48 h before piling. When effect distance during piling was investigated in dependence of the noise levels measured at 750 m distance, there was a clear reduction in disturbance range when noise was reduced down to 165 dB SEL05. Further noise reduction, however, did not further reduce effect ranges on porpoises. Potential reasons for this are discussed.

Porpoise foraging and disturbance based on acoustic tags – Jonas Teilmann et al. – Aarhus University, Denmark

Understanding where and how marine mammals acquire food is essential to management and conservation, in particular for species challenged by high metabolic demands. By using acoustic behavioural tags (DTAG) to study how often echolocating porpoises forage in the Danish Straits. Porpoises forage with on average 80 buzzes per hour for adults and 125 buzzes/hour for juveniles, amounting to a mean of 1920-3000 prey pursuits over a 24-hour period. Based on echoes from the tail beats of the chased fish, we estimated the target fish size to be mostly below 5 cm in length. Assuming the weight of each fish to be around 1 g, and a 90% prey capture success rate, a juvenile porpoise would consume 2.7 kg/24 h, which is roughly 10% of the body weight. Tagged porpoises encountered vessel noise 17–89% of the time and occasional high-noise levels coincided with vigorous fluking, bottom diving, interrupted foraging, leading to significantly fewer prey capture attempts at received levels greater than 96 dB re 1 mPa (16 kHz third-octave).

*Harbour porpoise (*Phocoena phocoena*) energetics and fish catch ability related to offshore pile driving – Ron Kastelein, et al. – SEAMARCO, Netherlands*

Results from studies under controlled conditions give information on the potential impact of pile-driving noise on harbour porpoise energetics. Upon exposure of two porpoises to playbacks of pile driving sound (SELss between 134 and 152 dB re 1 $\mu\text{Pa}^2\text{s}$), their ability to catch fish was negatively affected. In both animals, the number of aborted trials increased, and one was also less successful in catching the prey. The potential impact of decreased foraging was studied measuring the effect of fasting for 24 h on the body condition in 4 seasons. It showed that the average body mass loss (up to 4%) was greatest in autumn and lowest in summer. Some insight into the potential ability to recover from periods of food deprivation could be derived from the study in which four porpoises were fed larger meals than usual. If food is abundantly available after a period of fasting, harbour porpoises can eat a large percentage (~ 95%) of their daily food requirement in one feeding bout. One should take into account that the daily requirement varies with the season, being the highest in winter.

Can short, medium and long-term elements of energetics and physiology help understand the effects of disturbance on harbour and grey seals – David Thompson, SMRU

By necessity modelling exercises such as PCOD or IBMS must make simplifying assumptions about prey acquisition, food processing and short, medium and long term energetics. Predators on the other-hand are making sophisticated fine-tuned decisions about foraging and diving behaviour in the context of:

- short term energetic/oxygen consumption constraints; divers face absolute unavoidable constraints in individual dives due to limited oxygen stores. How they deal with these has important implications for foraging efficiency
- satiation constraints; short term limits (e.g. stomach capacity), medium term limits (e.g. food processing) and long term limits (e.g. lean tissue growth or fat storage capacity) will all influence foraging efficiency.
- long term energetic goals; e.g. reproductive v growth.

All of these factors will influence how successfully seals exploit their environment and how their responses to anthropogenic disturbance will affect their foraging efficiency and long term status. In this talk I will use information from grey and harbour seals to try to address some of the implications of this mismatch in level of detail for energetics models and their predictions of disturbance effects.

Forecasting the population consequences of disturbance: insights from simple bioenergetics models – John Harwood – Centre for Research into Environmental and Ecological Modelling, University of St Andrews, UK.
The PCoD conceptual framework provides a comprehensive structure for developing models to forecast the population consequences of disturbance (defined as a deviation in an animal's physiology or behaviour from patterns occurring without predator or human influences). However, there is limited empirical information on the effects of disturbance on an animal's health (usually measured by its energy reserves), and on the effects of variations in health on individual vital rates (survival, probability of giving birth, and age at first reproduction). Simple bioenergetic models can provide insights into how disturbance that results in either reduced energy intake or increased energy expenditure may affect an individual's health. The importance of these effects depends on when during the individual's life cycle disturbance occurs and on the species' life history strategy. The same models can also provide predictions of the potential effects of changes in health on vital rates. However, these predictions depend on how an individual chooses to use its own energy reserves if these are depleted.

Using individual-based models to assess impacts of disturbances on marine populations – lessons learned from the DEPONS project – Jacob Nabe-Nielsen – Aarhus University, Aarhus, Denmark

Agent-based models are unique in allowing population impacts of anthropogenic disturbances to emerge from their impact on individual animals. In the DEPONS model individual animals get deterred by noise, which reduces their foraging efficiency and potentially also their fitness. It has been parameterized based on movement and distribution data for harbor porpoises to assess population impacts of wind farm construction. These impacts were negligible when simulating the construction of a realistic number of wind farms in the North Sea. They only became visible when increasing simulated noise levels to let animals respond up to 20–50 km from the construction area. In that case the population impacts depended on the piling schedule. This demonstrates how agent-based models can be used for spatial planning to reduce impacts of anthropogenic disturbances based on well understood processes and empirical data.

A harbour seal IBM – an attainable management tool? – Bernie McConnell et al. – SMRU, UK

A quantification and modelling of harbour seal movement is required to predict the consequence of environmental change on both population distribution and movement connectivity. One approach to this challenge is a mechanistic individual based model (IBM) of seal movement. IBMs predict emergent behaviour from physiological capabilities and constraints using a set of biologically realistic behaviour rules within a simulated ecological environment. A simple prototype harbour seal IBM has been constructed with two currencies: energy and information (following Nabe-Nielsen et al., 2013). This model is now being developed and expanded. A major challenge is to find and parameterise the appropriate level of complexity that can be supported by data and yet can also provide realistic, defensible, and useful outputs. The model is scalable such that it will be able to incorporate future information about individual response to anthropogenic disturbance and to the consequence of individual condition on population demographic parameters.

APPENDIX 6



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Updating the Interim PCoD Model: *Workshop Report - New transfer functions for the effects of permanent threshold shifts on vital rates in marine mammal species*

Authors:	Cormac Booth & Floor Heinis
Report Code:	SMRUC-UOA-2018-006
Date:	20 th June 2018

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Executive Summary

The Interim Population Consequences of Disturbance (iPCoD) framework was developed by SMRU Consulting and the University of St Andrews in 2013 to forecast the potential effects on marine mammal populations in UK waters of any disturbance and permanent threshold shifts (PTS). The iPCoD framework was designed to assist decision making in a situation where there is only limited knowledge about the potential effects of these developments on marine mammals. The iPCoD framework was developed with the quantification of the effect of disturbance on vital rates determined via expert elicitation, conducted in 2013. The elicitation was carried out using an online questionnaire and at the time was recognised as an interim solution to the evaluation of these effects. The objective of this study was to update the transfer functions on the effects of PTS on the probability of survival and of giving birth to a viable young of harbour porpoise, bottlenose dolphins, harbour seals and grey seals via an expert elicitation (in the form of probability distributions).

To achieve this, a workshop was held in St Andrews, UK over three days on Tuesday 6th – Thursday 8th March 2018. In preparation for the workshop, we reached out to a leading group of experts on noise-induced (and natural) threshold shifts on marine mammals in general, and spanning the species of interest. In addition, the attendees' experience spans the fields of veterinary pathology, physics, physiology, behaviour and energetics.

A number of general points came out in discussions as part of the elicitation. These included that PTS did not mean animals were deaf, that the limitations of the ambient noise environment should be considered and that the magnitude and frequency band in which PTS occurs are critical to assessing the effect on vital rates, that a larger TTS could precede a PTS and the mechanisms by which a PTS could affect vital rates. In advance of the elicitation, the exact noise stimuli (low frequency broadband pulsed noise), the frequency range and magnitude of PTS predicted (as a result of exposure) and the species/age classes were discussed and a scope for the elicitation agreed. As part of the formal elicitation, experts agreed the wording of each question and definitions for each parameter to be elicited. For each of the species of interest, rounds of elicitation were carried out for the effect of the agreed PTS on the survival of dependents (calves/pups), juveniles, mature females and on the probability of giving birth to viable offspring.

The result of this updated elicitation is a significant difference over original expert elicitation outputs conducted in 2013. Overall experts indicated that the effects of a 6 dB PTS in the 2-10 kHz band was unlikely to have a large effect on survival or fertility of the species of interest. Effects were considered to be smallest for porpoises and seals and slightly larger in bottlenose dolphins, though experts noted that the broader range of plausible outcomes for dolphins was due to potential uncertainty in how the defined PTS would impact dolphins (which use lower frequency for communications and for some foraging calls), not necessarily that they were definitely more sensitive. It should be noted, however, that for all species experts indicated that the most likely predicted effect on survival or fertility as a result of 6 dB PTS was likely to be very small (i.e. <5 % reduction in survival or fertility). In general experts indicated that the defined PTS was likely to have a slightly larger effect on calves/pups and juveniles than on mature females survival or fertility.

The new transfer functions derived in this exercise indicate a much smaller 'effect size' than in the earlier expert elicitation and therefore will be reflected in new iPCoD scenarios. Where a large number of animals are predicted to experience some degree of PTS following exposure to low frequency broadband pulsed noise, this may make a large difference to the population trajectories predicted by iPCoD.

We recommend that research effort is directed to address the knowledge gaps currently estimated using expert elicitation (for both the effects of PTS and disturbance on vital rates). It is assumed that not all knowledge gaps will be filled and as with the new (2018) elicitation updating the 2013 transfer functions, there will likely be value in revisiting the 2018 elicitations, in light of new learning. However we emphasise that the focus on funding research studies to replace the elicited relationships with empirically derived ones and where appropriate validating the existing relationships.

1 Introduction

1.1 An Introduction to the interim PCoD framework

In 2005, a panel convened by the National Research Council of the United States National Academy of Sciences (NRC) published a report on biologically significant effects of noise on marine mammal populations (NRC, 2005). The panel developed what they referred to as a “conceptual model” that outlines the way marine mammals respond to anthropogenic sound, and how the population level consequences of these responses could be inferred on the basis of observed changes in behaviour. They called this model Population Consequences of Acoustic Disturbance or ‘PCAD’ (Figure 1).

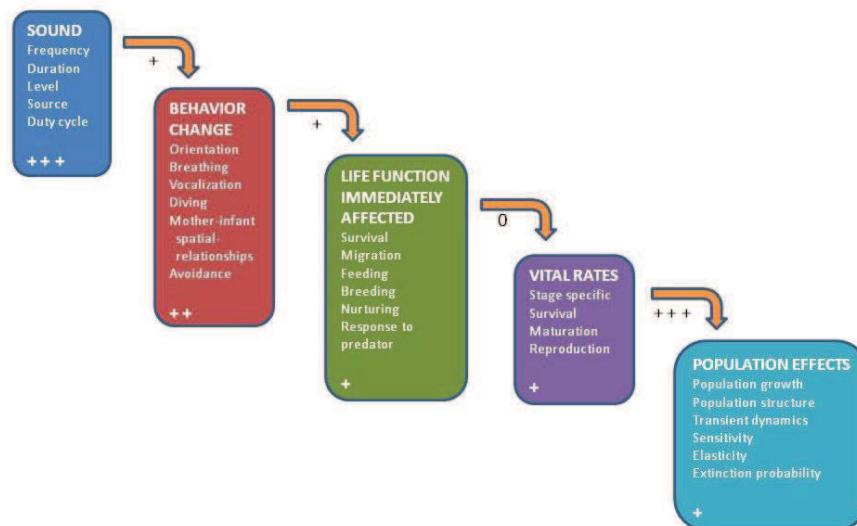


Figure 1 - The Population Consequences of Acoustic Disturbance (PCAD) model developed by the National Research Council’s panel on the biologically significant effects of noise. After Fig. 3.1 in NRC (2005). The number of + signs indicates the panel’s evaluation of the relative level of scientific knowledge about the links between boxes, 0 indicates no knowledge. These links were described by the panel as “transfer functions”.

In 2009, the United States Office of Naval Research (ONR) set up a working group to transform this conceptual model into a formal mathematical structure and to consider how that structure could be parameterised using data from a number of case studies. The ONR working group also extended the PCAD model to consider forms of disturbance other than noise, and to address the impact of disturbance on physiology as well as behaviour. The current version of that model, which is based on case studies of elephant seals, coastal bottlenose dolphins, northern right whales and beaked whales, is now known as PCoD (Population Consequences of Disturbance). It is shown in Figure 2 and described in more detail in New et al. (2014).

The PCoD model provides a framework for assessing how disturbance may affect both the behaviour and physiology states of an individual, and how changes in these states may influence that individual’s vital rates (see Glossary) either directly (an acute effect) or indirectly via its health (a chronic effect). For example, exposure to high levels of sound may result in hearing damage (a physiological effect) through a permanent increase in the threshold for hearing at a particular frequency (Permanent Threshold Shift - PTS). This could have an acute effect on survival, because the affected individual might be less able to detect predators. It could also have a chronic effect on reproduction via the individual’s health, because it might be less able to locate and capture prey. Similarly, behavioural changes in response to disturbance could have an acute effect on survival if they result in a calf being separated from its mother. They could have a chronic effect on reproduction, via body condition, if they result in the disturbed animal spending less time feeding or in activities that conserve energy, such as resting.

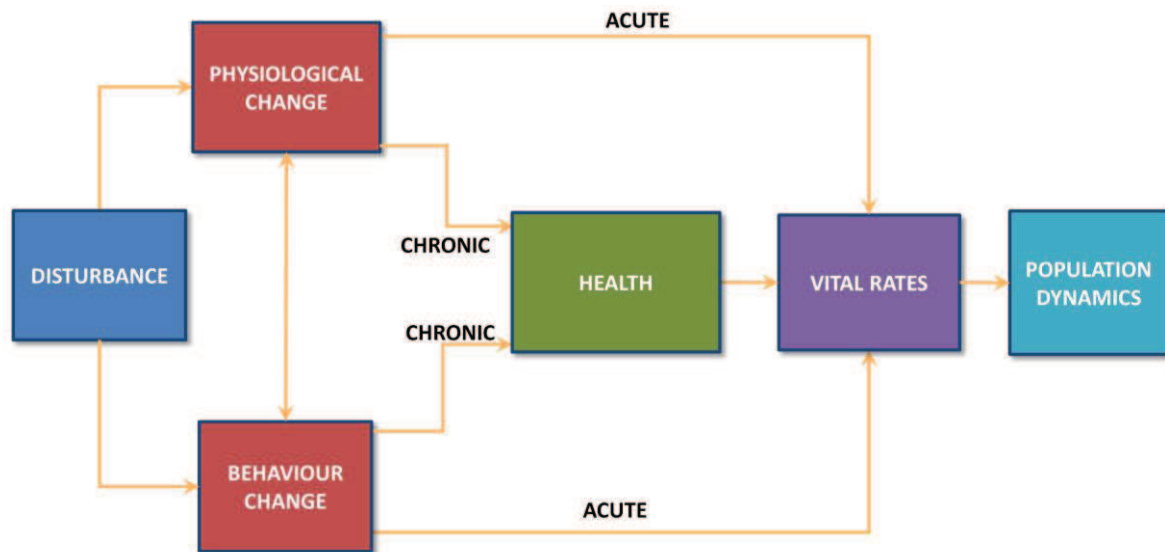


Figure 2 - The PCoD model of the population consequences of disturbance developed by the ONR working group on PCAD (modified from Fig.4 of New et al., in press). See Glossary for a definition of the terms used in the diagram.

Using case studies of elephant seals (Schick et al. 2013, New et al. 2014) and bottlenose dolphins (New et al. 2013), it was possible to show how changes in behaviour in response to disturbance could affect the energy reserves of adult females, and to estimate the implications of these changes for the probability of giving birth and offspring survival. The consequences of these changes for population dynamics could then be inferred from the number of animals that might be affected by disturbance and the size of the population of which they are part. A similar approach to assess the potential impacts of wind farm operation on harbour porpoises in Inner Danish Waters (Nabe-Nielsen et al. 2011) and North Sea (Nabe-Nielsen et al. 2018).

Unfortunately, the empirical information that is required to parameterise the PCoD model developed by the ONR Working Group does not exist for the five species considered in the iPCoD model. We have therefore used a simplified version of this model (Figure 3) which was developed at the workshop on 'Assessing the Risks to Marine Mammal Populations from Renewable Energy Devices' (Lusseau et al. 2012). The information required to quantify the potential effects of behavioural and physiological changes on vital rates, shown by the dotted lines in Figure 3, was obtained using an expert elicitation process (Runge et al. 2011, Martin et al. 2012) which is described in the next section.

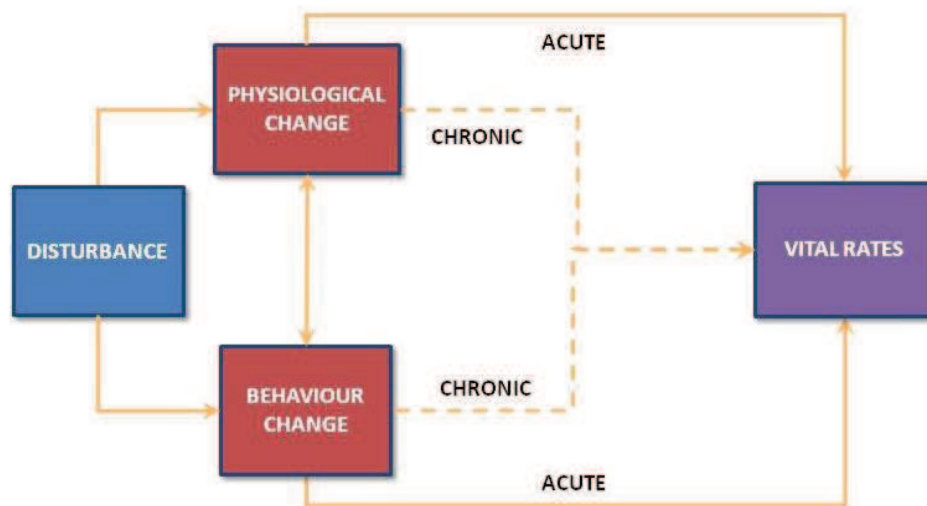


Figure 3 - A simplified version of the PCoD model shown in Figure 2 that is being used in the interim PCoD approach. The transfer functions that determine the chronic effects of physiological change and behavioural change on vital rates are represented with dotted lines to indicate that the form of these functions has been determined using the results of an expert elicitation process rather than using empirical evidence. See Glossary for definitions of the terms used in this diagram.

The Interim Population Consequences of Disturbance (iPCoD) framework was developed by SMRU Consulting and the University of St Andrews in 2013 to forecast the potential effects on marine mammal populations in UK waters of any disturbance, hearing damage (via permanent threshold shifts (PTS)) or collisions that might result from the construction or operation of offshore renewable energy devices. A detailed description of the approach can be found in Harwood et al. (2014) and King et al. (2015).

1.2 Expert elicitation

Expert elicitation is a formal technique, first developed in the 1950s and 60s (Brown 1968, O'Hagan et al. 2006), that is now widely used in a range of scientific fields to combine the opinions of many experts in situations where there is a relative lack of data but an urgent need for conservation or management decisions (Runge et al. 2011, Martin et al. 2012). Specifically, Morgan (2014) indicates: "Expert elicitation should build on and use the best available research and analysis and be undertaken only when the state of knowledge will remain insufficient to support timely informed assessment and decision making". Martin et al. (2012) describe how this technique can be used to access substantive knowledge on particular topics held by experts and such techniques have been discussed and used widely in recent years (e.g. MacMillan and Marshall 2006, Aspinall 2010, Knol et al. 2010, European Food Safety Authority 2014, Sibley et al. 2015). Perhaps the most high profile use in the environmental sector has been in the assessment of risks from climate change (Lenton et al. 2008) and predictions of future sea level rise (Bamber and Aspinall 2013). The technique can also be used to translate and combine information obtained from multiple experts into quantitative statements that can be incorporated into a model, minimize bias in the elicited information, and ensure that uncertainty is accurately captured. The formal process of expert elicitation therefore avoids many of the well documented problems, heuristics and biases that arise when the judgements of only a few experts are canvassed or where expert knowledge is sought in an unstructured manner (Kynn 2008, Kahneman 2011, Morgan 2014). In the field of marine mammals, a number of elicitations have been conducted in recent years involving the project team and seeking to improve the methods for marine mammal issues (e.g. Booth et al. 2014, Tollit et al. 2016).

1.3 Project Objectives

The iPCoD framework was designed to assist decision making in a situation where there is only limited knowledge about the potential effects of these developments on marine mammals. The iPCoD framework was developed with the quantification of the effect of disturbance on vital rates determined via expert elicitation, conducted in 2013. The elicitation that was carried out, was at the time recognised as an interim solution to the evaluation of these effects. There remains an urgent need for additional scientific research to address the knowledge gaps that were identified by Harwood et al. (2014).

Since its initial release (v1.0) in February 2014 on the Marine Scotland Science website¹ the tool was updated with amendments to the code and helpfiles in October 2014 (v1.1). Since then, the iPCoD tool has been used for a number of offshore wind developments in Germany, Netherlands, France and the UK (and possibly others) (e.g. Heinis et al. 2015, Brandt et al. 2016, Booth et al. 2017) and has been used to explore the potential population level effects of collisions of a range of species with marine renewable energy devices in the UK. Also during this time, SMRU Consulting and John Harwood have developed the tool further to improve the model framework. Since the initial interim PCoD framework was developed, it has proved possible to develop PCoD models for a number of marine mammal species (King et al. 2015, van Beest et al. 2015, Booth et al. 2016, Harwood and Booth 2016, Nabe-Nielsen and Harwood 2016, Tollit et al. 2016), some using expert elicitation approaches to fill data gaps. Carrying out these referenced expert elicitations has led to significant advances in our understanding of elicitation processes and the refinement of methods in eliciting expert opinion. The first elicitation, carried out in 2013-14, was carried out via an online elicitation, in which questions were posed and experts were invited to provide answers to them. Although a Delphi approach was conducted (a second round of elicitation where feedback was provided to experts), we have learned from subsequent elicitations, the value of discussion and prior-agreement of question wording with experts (see Section 2) is important to a successful elicitation. As such, with the advances in knowledge in how to conduct expert elicitations with marine mammal experts and increased knowledge of the marine mammalian auditory system and mechanisms affecting vital rates, now we seek to upgrade the interim PCoD model by updating the expert elicitation step of the framework. Specifically, exploring how the Permanent Threshold Shifts (PTS) affect the vital rates of marine mammal populations.

Therefore, the objective of this study was to update the transfer functions on the effects of PTS on the probability of survival and of giving birth to a viable young (see Glossary) of harbour porpoise, bottlenose dolphins, harbour seals and grey seals via an expert elicitation. The effects of disturbance on these vital rates will be assessed as part of a second elicitation workshop later in 2018. Below we describe the expert elicitation process that was undertaken and present the updated transfer functions.

2 Expert Elicitation

2.1 Elicitation workshop

A workshop was held in St Andrews, UK over three days on Tuesday 6th – Thursday 8th March 2018. Here, we provide a brief summary of the scope of the workshop and how the effects of PTS were considered in this elicitation. In section 3 we present the results of the workshop in the form of output distributions.

The workshop attendees are shown below (Table 1). In preparation for the workshop, we reached out to a leading group of experts on noise-induced (and natural) threshold shifts on marine mammals in general and

¹ <http://www.gov.scot/Topics/marine/science/MSInteractive/Themes/pcod>

spanning the species of interest (see Appendix 2). In addition, the attendees' experience spans the fields of veterinary pathology, physics, physiology, behaviour and energetics.

Table 1 - Workshop participants

Name	Affiliation	Role
Darlene Ketten	Woods Hole Oceanographic Institute (USA)	Invited expert
Jakob Tougaard	Aarhus University (Denmark)	Invited expert
Dorian Houser	National Marine Mammal Foundation (USA)	Invited expert
Ron Kastelein	SEAMARCO (Netherlands)	Invited expert
Klaus Lucke	JASCO Applied Sciences (Australia)	Invited expert
Peter Tyack	Sea Mammal Research Unit (UK)	Invited expert
Paul Thompson	University of Aberdeen (UK).	Invited expert
Cormac Booth	SMRU Consulting (UK)	PI and Facilitator
Floor Heinis	HWE Consultancy (Netherlands).	Recorder
Vincent Janik	Sea Mammal Research Unit (UK)	Observer*
Gordon Hastie	Sea Mammal Research Unit (UK)	Observer*
Francesca Marubini	Hartley Anderson Ltd (Consultant to BEIS)	Observer

The workshop began with a series of presentations from the facilitator/PI (Booth) outlining the interim PCoD model, the 2013 elicitation and outlining the scope of the elicitation. Following those discussions, some of the attending experts presented some of their research and reviews on how thresholds manifest, what is known from empirical studies and the different aspects of marine mammalian hearing and the effects of noise on auditory systems.

Following those discussions, the group focused on refining the scope of the elicitation. An important part of expert elicitation is ensuring there is total clarity on the questions being asked (as 'linguistic uncertainty' can impact elicitations (e.g. Knol et al. 2010)). For this elicitation, it was critical to specify the species of interest, the noise stimuli under consideration, the amount of permanent threshold shift expected from exposure to the noise stimuli, the frequency band in which PTS was expected to manifest (i.e. where the shift in hearing threshold would occur) and the vital rates potentially impacted. Therefore, this represents an update from the 2013 elicitation, where experts were asked to consider PTS as a binary response (i.e. animals had PTS or not, but the amount was not defined). In 2013, experts were asked to participate in a survey to focus on the potential population consequences of changes in hearing ability resulting from PTS as a result of exposure to broadband impulsive noise (e.g. pile-driving, airgun bursts). We hypothesized that the vital rates most likely to be affected by PTS are survival (for all age classes) and the probability of giving birth (fertility).

Southall et al. (2007) defined the onset of temporary threshold shifts (TTS) as "*being a temporary elevation of a hearing threshold by 6 dB*" (in which the reference pressure for the dB is 1μPa). Although 6 dB of TTS is a somewhat arbitrary definition of onset, it has been adopted largely because 6 dB is a measurable quantity that is typically outside the variability of repeated thresholds measurements. The onset of PTS was defined as a non-recoverable elevation of the hearing threshold of 6 dB, for similar reasons. Based upon TTS growth rates obtained from the scientific literature, it has been assumed that the onset of PTS occurs after TTS has grown to 40 dB. The growth rate of TTS is dependent on the frequency of exposure, but is nevertheless assumed to occur as a function of an exposure that results in 40 dB of TTS, i.e. 40 dB of TTS is assumed to equate to 6 dB of PTS.

2.2 Elicitation Methods

The objective of an expert elicitation is to construct a probability distribution to accurately represent the knowledge and beliefs of an expert or group of experts regarding a specific Quantity of Interest (QoI). Here our

QoI was the effects of PTS on the probability of survival and probability of a successful birth (fertility) in different stage classes of harbour porpoise, harbour seal and grey seal and bottlenose dolphin. We employed the Sheffield Elicitation Framework (SHELF) approach in the expert elicitation (Oakley and O'Hagan 2016), using the SHELF v.3.0 (www.tonyohagan.co.uk/shelf) in the workshop. For each QoI, which has a true value (which is unknown, and we'll call 'X'), each expert was asked to provide their individual judgements regarding a number of parameters; the plausible limits, median, lower and upper quartiles. The plausible limit was defined such that it may be theoretically possible for the true value of X to lie outside these limits, but that the expert would regard it as extremely unlikely that X was outside this range. We asked for the plausible limits first to try to avoid well-known biases of *overconfidence* (where experts do not consider extreme cases for X) and *anchoring* (where experts start with a value of X in mind). Following that, the experts were asked to specify their median value for X (such that there is equal probability that the true value of X lies above or below the median (but within the plausible limits). Finally, experts were asked to provide lower and upper quartile values for X. The exact structure of each question was agreed with experts in advance of the elicitation and all required definitions were specified and agreed in advance.

The experts were then asked to input their personal judgements into a web-interface form (Figure 4) and to send the data to the facilitator (via the form). The judgements were then input into SHELF and distributions fitted to each individual expert judgement with the best statistical fit (determined in SHELF as the distribution with the lowest sum of squares value). The facilitator then presented the anonymised individual judgements of all experts together to the group (Figure 5). During the process, the mechanisms experts had considered in making their individual judgements were discussed among the group.

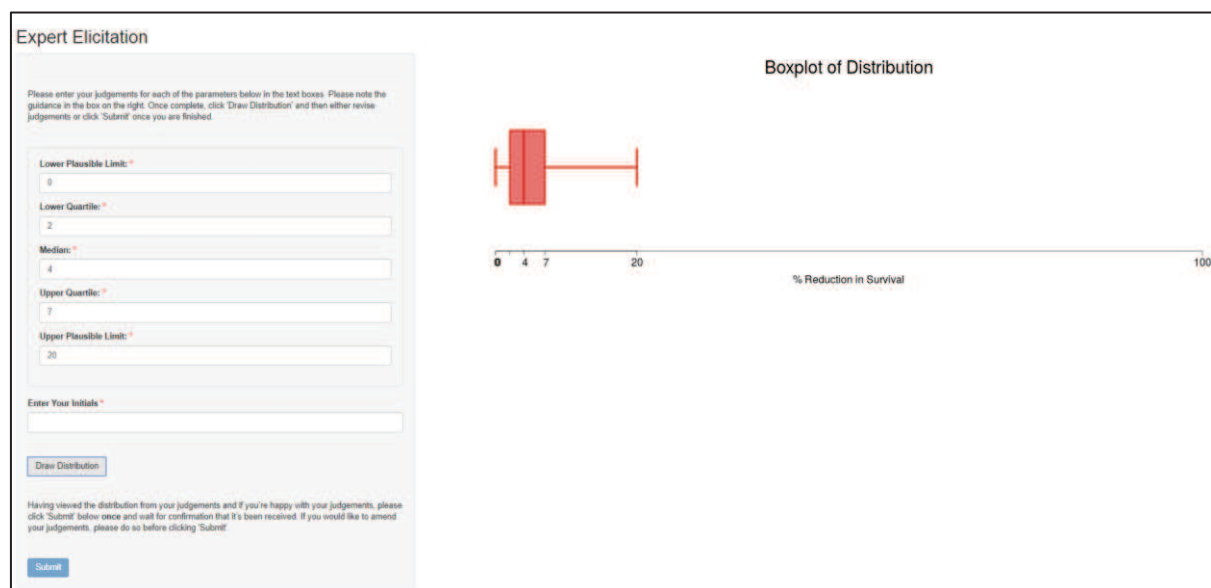


Figure 4 - Example screengrab of online tool used to collate individual expert judgements

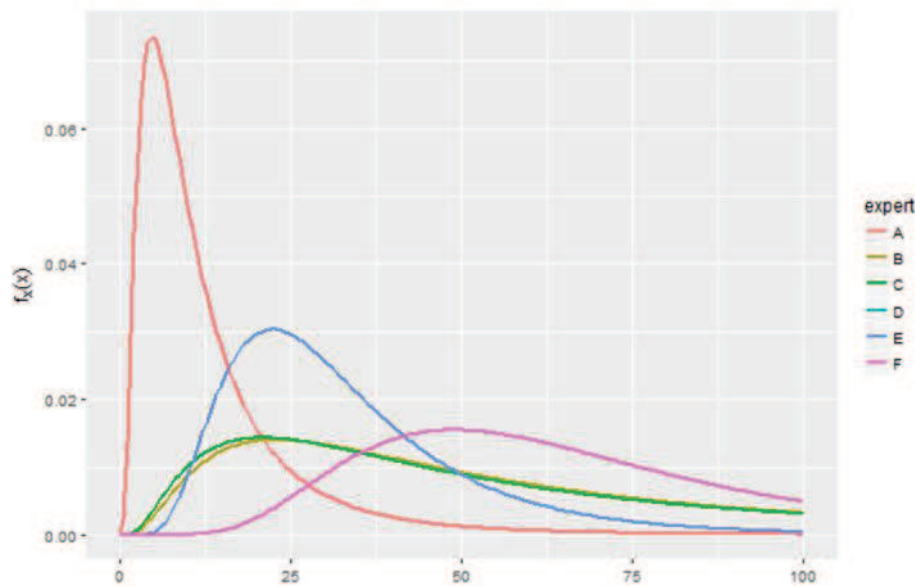


Figure 5 - Example fitting of example individual judgements (not of the effects of PTS on vital rates) fitted in SHELF v3.0

Experts were asked to justify any different judgements to ensure that the range of judgements had been discussed openly. Following this, the group was asked to reach a ‘group consensus’ judgement (in the form of a probability distribution). It is important to note here (and stated clearly to experts), that there was no expectation that the experts would reach complete agreement on a probability distribution for our QoI. That is because it is unlikely that there is one single distribution that would be accepted as perfectly representing the opinion of all experts. Instead, we asked experts to discuss and agree upon a distribution representing the reasoned opinions of a theoretical external observer, called a Rational Impartial Observer (or RIO). The RIO would not have identical views to any one of the experts but would instead find some merit in all the differing arguments or justifications – and give some weight to each. Using the SHELF software, this RIO consensus distribution was determined using either the *elicit* function (in cases where there were large disparities between individual expert judgements) or via a mathematical aggregation in which a weighted linear pool (where there was significant overlap in individual expert judgements).

The statistical analysis used to estimate the parameters of the relationships required by the interim PCoD model from the results of this ‘effects of PTS’ elicitation are described by Donovan et al. (2016).

3 Results

3.1 General Discussions

During the workshop there was extensive discussion among experts in defining the scope of the elicitation into the effects of PTS on vital rates. These included that PTS did not mean animals were deaf, that the limitations of the ambient noise environment should be considered and that the magnitude and frequency band in which PTS occurs are critical to assessing the effect on vital rates, that a larger TTS could precede a PTS and the mechanisms by which a PTS could affect vital rates. We discuss each of these in the paragraphs below.

From the outset, experts were keen to stress that PTS did not mean that animals were deaf – but that PTS meant a reduction in hearing sensitivity in a specific frequency range. In addition, it was highlighted that marine mammals suffer conductive hearing loss as part of a natural aging process (and that older animals have a high incidence of disease and specifically ear infections, further affecting hearing loss). It was also noted there was a large natural variability in hearing sensitivity across animals sampled (e.g. see Castellote et al. 2014); therefore, it was important to realise that reduced hearing ability does not necessarily mean a less fit animal (i.e. an animal of lower fitness).

Experts agreed that in considering the impact of threshold shifts, ambient noise should also be considered because some species' ability to hear in their environment will be limited as a result of ambient noise more so than by their hearing ability. For example, there are regions with high levels of natural ambient noise (e.g. ice, wind activity, tidal activity, ground waves, and snapping shrimp) and other anthropogenic sources contributing to the baseline environment (e.g. chronic exposure to shipping noise). Experts also discussed whether different species were likely to be hearing limited by ambient noise ('noise-limited'), or by their hearing sensitivity (threshold- or sensitivity-limited). More specifically, an animal would be considered 'noise limited' if noise interferes with the detection of the signal. To determine the signal-to-noise ratio required to detect the signal, the critical ratio is often used (e.g. see Yost and Shofner 2009). For Gaussian noise (i.e., noise with a Gaussian (normal) amplitude distribution), the critical ratio is informative for how much above the background noise the signal must be in order to be detectable by an animal. In most real world cases, at least below 20 kHz, signal detection is likely noise limited. (At ultrasonic frequencies, where ocean noise is low, this may not be the case - e.g., at echolocation frequencies for dolphins and porpoises). Conversely, an animal would be considered 'threshold limited' if that noise is sufficiently below the threshold of hearing that it does not interfere with the detection of the signal. As such, it is implied that the noise would be at least a critical ratio below the threshold of hearing (this is the true physiological limit to the system's signal detection ability). They suggested that, because of the frequencies of best hearing sensitivity and the use of sound in species life history, seals were likely to be hearing limited by ambient noise much of the time but that echolocation frequencies for odontocetes are unlikely to be noise limited because the frequencies are much higher than the frequencies of the dominant ambient noise sources.

The magnitude of PTS and the bandwidth affected are important factors in determining impact. The group had a general discussion and review of papers on threshold shifts and the magnitude (i.e. the amount (in dB) of shift) and band over which shifts occur (i.e. over what frequency range is hearing sensitivity reduced). It was agreed that PTS typically occurs following a temporary shift, but at a lower magnitude compared to the TTS (i.e. following a large temporary shift hearing sensitivity improves but never returns to baseline) and that the ultimately remaining PTS has a smaller bandwidth than the original TTS (i.e. this occurs over a smaller frequency range than the original temporary shift)(see Figure 6 for an illustration of these two points).

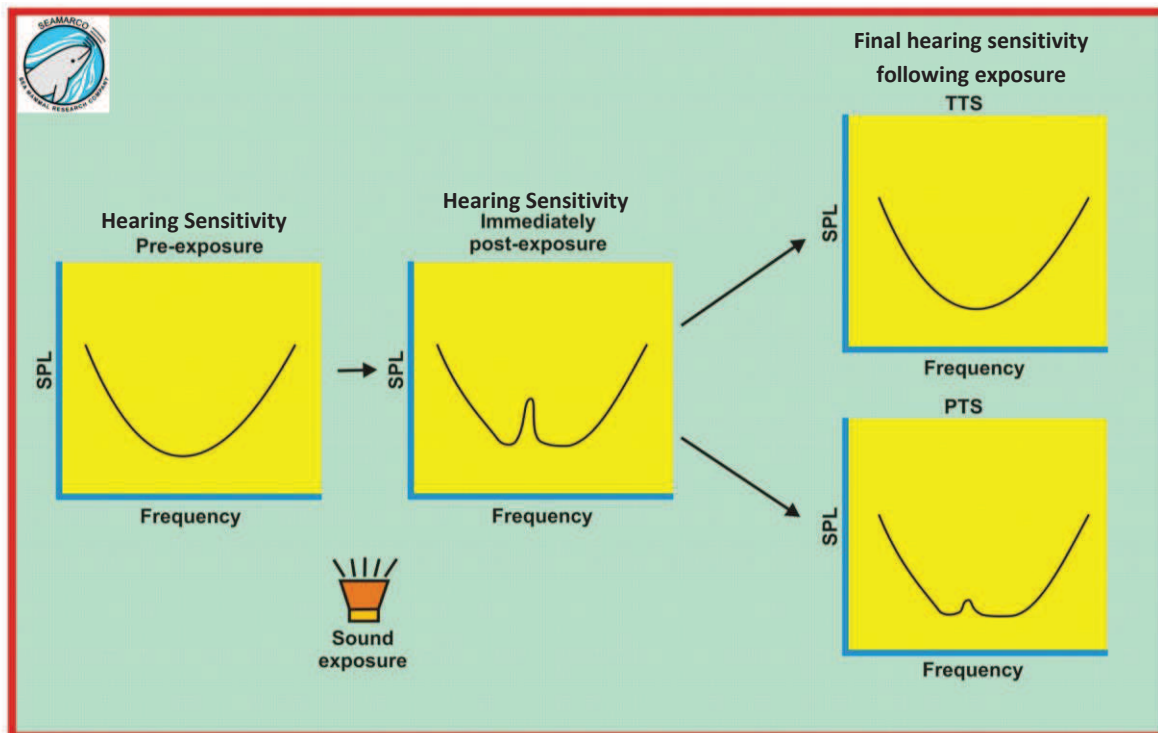


Figure 6 - Conceptual figure showing a hypothetical hearing sensitivity curve (i.e. audiogram) pre-exposure (left), the TTS occurring immediately post-exposure (centre) and the two potential outcomes of temporary threshold shift (TTS) where the pre-exposure sensitivity is achieved (top right) and where a permanent threshold shift (PTS) occurs (no return to pre-exposure sensitivity)(bottom right). Note that the frequency range and magnitude of resulting PTS are smaller than the range and magnitude of the threshold shift immediately post-exposure. Reproduced with permission from Ron Kastelein, SEAMARCO.

Experts agreed that how permanent thresholds manifest is still relatively poorly understood. Experts discussed that recovery from TTS induced by impulsive sounds is usually relatively fast, because the magnitude of TTS is small. However, this is not always the case and although few studies of PTS in marine mammals exist, Kastak et al. (2008) twice exposed a single harbour seal to a 4.1 kHz pure tone with a maximum received sound pressure level (SPL) of 184 dB re 1 μ Pa for a duration of 60 s (SEL = 202 dB re 1 μ Pa²s) and that this led to a temporary threshold shift in excess of 50 dB at 5.8 kHz which resulted in an apparent permanent shift of between 7-10 dB when the animal was tested again two months following exposure. A recent study indicated that despite a high SPL exposure to octave-band white noise centred around 4 kHz, resulting in a 44 dB TTS in a harbour seal, the animal's hearing sensitivity had recovered to pre-exposure levels within four days (Kastelein et al. 2013a). The lead author (Kastelein) for this latter paper was present at the workshop and highlighted that once the animals were experiencing this TTS, the seals did not show any altered behaviour and reacted normally to vocal commands, despite these high threshold shifts. But it is important to consider that in most cases, before an animal experiences a (potentially) small PTS, they will likely have a period of time with a larger, temporary shift as observed in Kastak, et al (2012).

The role and relative importance of hearing as a sense in marine mammals was discussed and whilst many agreed that this would likely be a primary sense, it was not the only sense; animals likely used other means such as taste, touch (via vibrissae in pinnipeds) and vision in navigating and exploiting their environment. However, critically, the reliance of different senses will be species-specific, and this was taken into account by experts in their judgements. Furthermore, experts discussed the role of hearing in foraging, communicating, reproduction and navigation/orientating and how a PTS in a specific frequency band would affect an animal's abilities and therefore the mechanism by which PTS could impact an individual's survival or fertility.

In considering how any PTS could affect vital rates (i.e. probability of survival, probability of fertility), experts discussed the mechanisms by which this could occur. In general, experts noted that where communication has a significant social or reproductive function, that this might be a means by which survival and/or reproduction are affected. Experts noted however that PTS would likely occur over a small frequency range and that much of the energy of communication signals either fell outside the likely range affected by PTS (see section 3.2.2) or that the loss of part of the signal would likely not affect detection of the communication signals. Experts discussed the role of hearing in navigation and orientation and the ability of animals to detect and resolve shipping sources and general orientation (e.g. potential cues like waves crashing). For porpoises loss of sensitivity in low frequencies was not likely to affect foraging (as their echolocation is high frequency). Experts considered that taste, visual and tactile senses may be important to help explain breeding aggregations (in porpoises) and returning to haulouts (seals) each year and acknowledged there may be an auditory cue. In dolphins, experts predicted that animals could potentially have a reduction in sensitivity in the PTS band without an effect on their functioning (because the agreed PTS likely affects a narrow range and information will be available above and below the affected PTS band).

The experts noted that whilst it's a poorly understood field, the age of acquisition of PTS could be important; in young animals, hearing loss was predicted to be more problematic, especially in recently weaned animals (presumably lacking independent foraging experience). In older animals it was expected that the gained experience (e.g. on prey behaviour, characteristics of frequented environment etc.) would perhaps make animals more tolerant to PTS.

3.2 Elicitation scope

3.2.1 What noise stimuli are we considering

As with the 2013 iPCoD elicitation, experts agreed we would focus on the potential for PTS caused by exposure to low frequency broadband pulsed (LFBP) noise (e.g. pile-driving, airgun pulses).

3.2.2 At what frequencies does PTS manifest following exposure to pile-driving noise?

Experts discussed and agreed that the elicitation should focus on a PTS occurring in the 2-10 kHz band (note: this does not equate to a PTS occurring across this entire range, but within this band). This was based on where TTS (and PTS) had been observed in empirical studies. Following exposure to low frequency broadband pulsed noise, TTS was typically observed 1.5 octaves (see Appendix 1 - Glossary) higher than the centre frequency of the exposure sound for seals and porpoise (Kastelein et al. 2012a, Kastelein et al. 2012b, Kastelein et al. 2013a, Finneran 2015). For piling noise and airgun pulses, most energy is between ~30 Hz- 500 Hz, with a peak usually between 100 – 300 Hz and energy extending above 2 kHz (e.g. Kastelein et al. 2015a, Kastelein et al. 2016). Experts noted that exposure to impulsive noise induces TTS in a relatively narrow frequency band in both seals and porpoises (reviewed in Finneran 2015) and for such LFBP noise stimuli, there was a high probability that if threshold shifts occurred, they would manifest somewhere between 2-10 kHz (Kastelein et al. 2017). The lead author (Kastelein) noted that the frequency distribution of airgun shots in those experiments are more similar to a pile-driving spectrum in the field than the pile-driving play-backs and therefore are valid for consideration here. Experts noted there was some evidence, from experiments in cats, for very high frequencies to be affected following high intensity exposures (Liberman and Kiang 1978) though it's important to stress this has not yet been established in marine mammals and therefore was not considered formally in the elicitation.

3.2.3 What magnitude of PTS should be considered?

Experts considered how exposure to LFBP noise would result in PTS and the exposures necessary for this to occur to allow an elicitation of different magnitudes of PTS. Experts noted that in most cases, before an animal

experiences a (for example) 6 dB PTS, they will likely have a period of time with a larger, temporary shift as observed in, for example, Kastak, et al (2012). During the workshop, an *ad hoc* analysis was performed by the experts in attendance to explore the possible magnitude of PTS the species of interest could experience (using TTS growth rate for the species or closely related species). This process is described in Appendix 3.

Experts agreed it was unlikely that seals or bottlenose dolphin would experience more than 6 dB of PTS in the 2-10 kHz frequency band following exposure to LFBP due to low growth rates (under low duty cycle conditions). We elicited on the effects of 6 dB PTS for all species and all classes. For the porpoise part of the elicitation, experts calculated a worst case PTS of 24 dB. In the workshop there was limited time to elicit, but an additional elicitation for the effects of 18 dB PTS was calculated for mature female survival (see section 3.3.2).

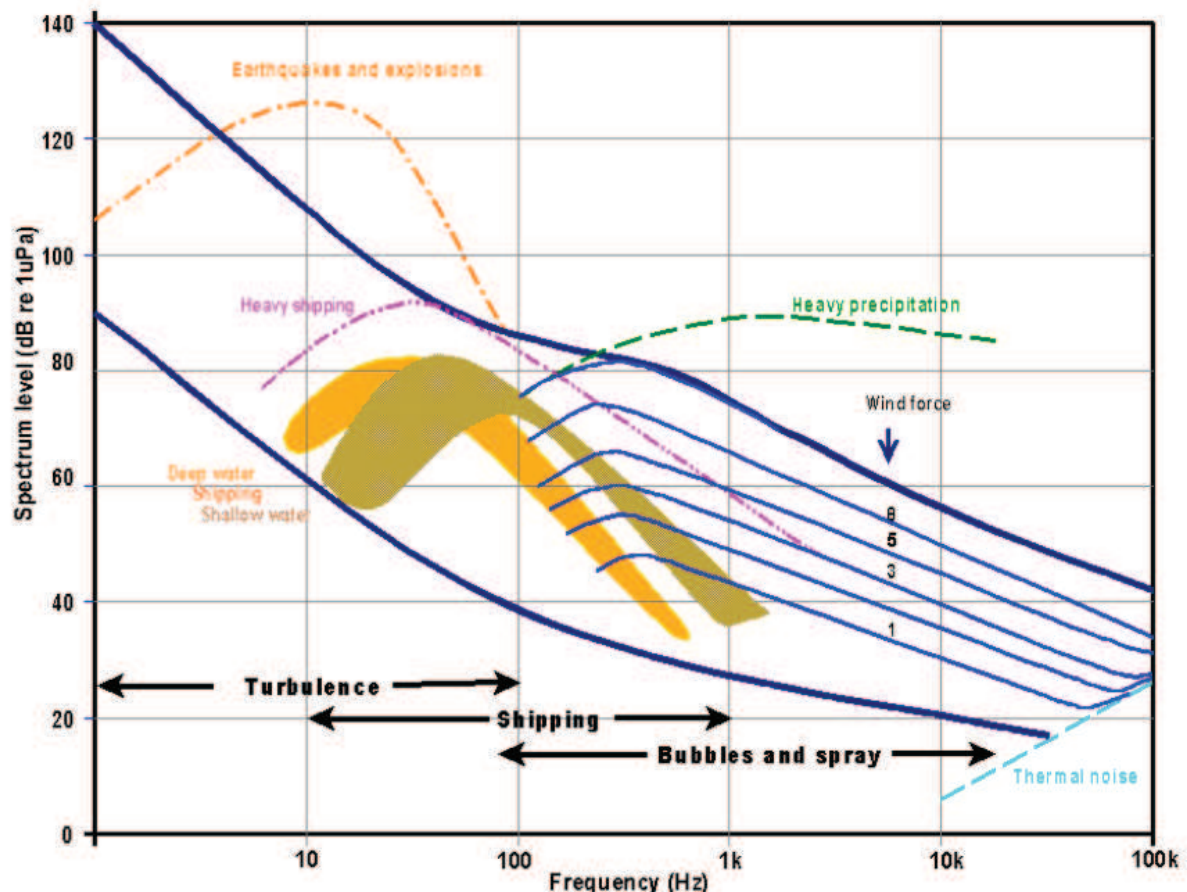


Figure 7 -- Composite of ambient noise spectra. From Harland et al. (2005).

3.2.4 Does PTS affect different species differently?

Experts agreed that grey & harbour seals appear to have comparable hearing, because audiograms, life history and vocalisation ranges are similar and, therefore, no separate EE for grey and harbour seals would be required (i.e. the effects of PTS on the vital rates of harbour seals and grey seals could be elicited together). It was also agreed that harbour porpoises and bottlenose dolphins should be elicited separately due to differences in audiogram, life history and vocalisation behaviour.

3.2.5 Does PTS affect different age classes differently?

Experts were comfortable with the breakdown of age classes used in iPCoD: dependent calves, juveniles (from weaning until sexually maturity) and adults (mature females). For seals and harbour porpoises experts agreed that the effects on survival would be sufficiently similar (though possibly via different mechanisms) for calves/pups and juvenile animals so they could be elicited together, but for bottlenose dolphins these should be elicited separately to account for the experts judgements of different effects on survival for these classes.

3.3 Elicitation outputs

3.3.1 Harbour seal and grey seal

3.3.1.1 Effects on seal fertility

The experts were asked to provide individual judgements (in isolation) on the effect of PTS on seal fertility. Following individual judgements, they were presented to the group and experts explored and achieved a group (RIO) consensus as shown below (Figure 8). An example of the individual judgements and resulting consensus judgement (via RIO) are shown in Appendix 4. See Appendix 5 for the questions in the expert elicitation.

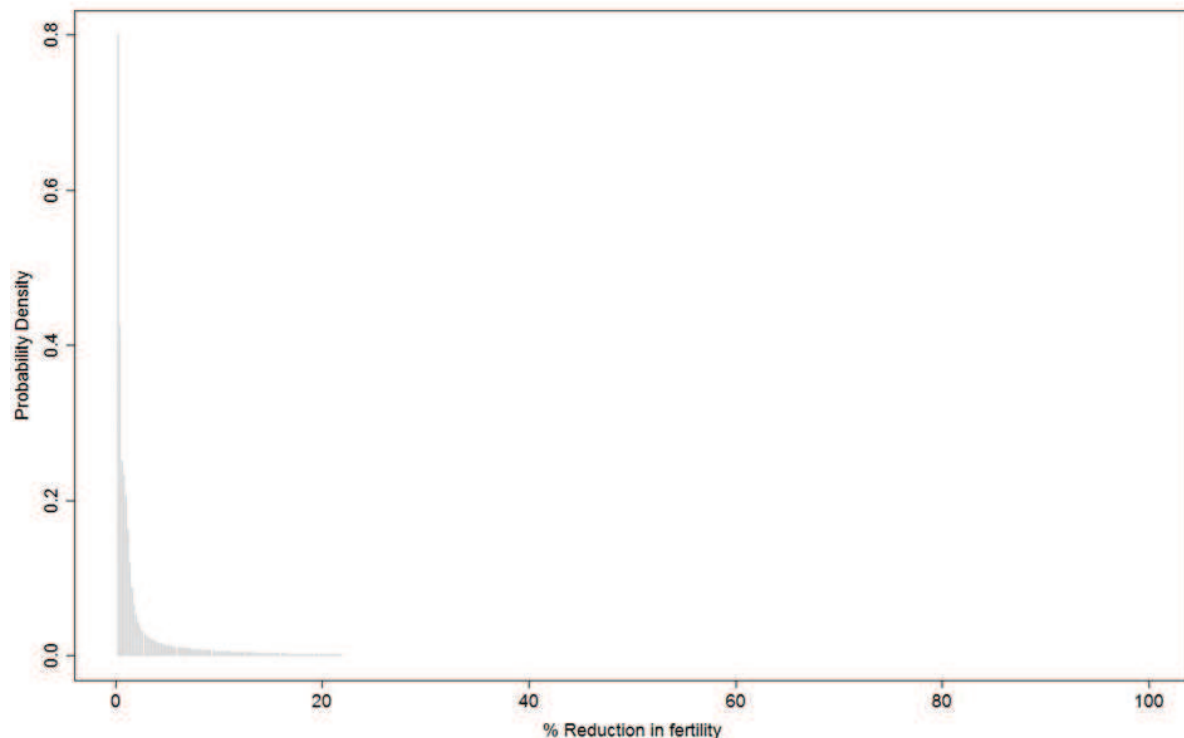


Figure 8 – Probability distribution showing the consensus distribution for the effects on fertility of a mature female (harbour or grey) seal as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

Experts felt that the overall effect of the defined PTS (see section 3.2) on seal fertility was low as there were limited mechanisms by which fertility could be impacted by a narrowband reduction in hearing sensitivity. Experts felt it was unlikely that the defined PTS would affect foraging but that there was some uncertainty around the role of hearing on foraging. This uncertainty meant that the experts acknowledged that if hearing was important in phocid seal foraging that there was a possible mechanism for PTS to affect fertility by a reduction in body condition due to a reduction in foraging efficiency caused by PTS. Experts thought there was a small chance of communication being impacted, affecting breeding opportunities, but acknowledged this was unlikely given most vocalisations are below 2 kHz (Van Parijs et al. 2003, Bjørgesæter et al. 2004, Sabinsky et al. 2017) and

therefore would be unaffected by the PTS specified above. Overall, experts agreed that the final selected range and upper plausible limit reflected the current scientific uncertainty in the true value of how the defined PTS could affect harbour or grey seal fertility, but that the most likely effect on fertility was very low (i.e. below a 5% reduction in fertility) (Figure 8).

3.3.1.2 Effects on seal survival

Mature females

The experts were asked to provide individual judgements (in isolation) on the effect of PTS on seal survival. Following individual judgements, they were presented to the group and experts explored and achieved a group (RIO) consensus as shown below (Figure 9). See Appendix 5 for the questions in the expert elicitation.

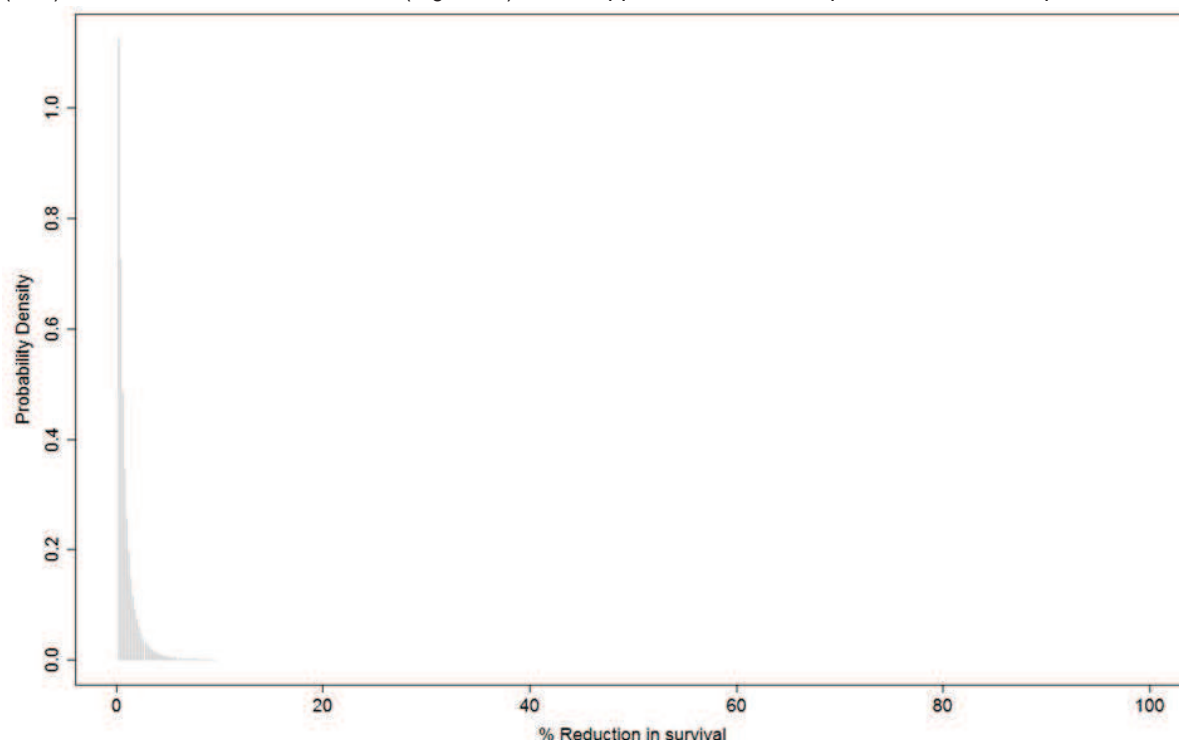


Figure 9 - Probability distribution showing the consensus distribution for the effects on survival of a mature female (harbour or grey) seal as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

Experts felt that the overall effect of the defined PTS (see section 3.1) on mature female seal survival was low as there were limited mechanisms by which survival could be impacted by a narrowband reduction in hearing sensitivity. As with the fertility elicitation, experts felt it was unlikely that the defined PTS would affect foraging but it was acknowledged that it was possible to affect survival (via reduced body condition) given the uncertainty in the role of hearing in foraging. However, experts considered that seals had other well-developed senses for foraging, e.g. tactile senses which might be more important to foraging. Experts thought the most likely mechanisms by which survival could be impacted was via reduced ability to detect predators (e.g. killer whales (if vocal) or dogs (when hauled out) or vessels/shipping (and the potential for collision), but that animals would not be heavily affected by this. Overall, experts agreed that the final selected range and upper plausible limit reflected the current scientific uncertainty in the true value of how the defined PTS could affect harbour or grey seal survival, but that the most likely effect on survival was very low (i.e. below 5% reduction in survival).

Pups/Juveniles

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 10). See Appendix 5 for the questions in the expert elicitation.

Experts noted in their justifications that a number of factors contributed to their judgements. These included that the condition of pups will be dependent on the condition of the mother. In addition that there are uncertainties about how communication might be affected by the defined PTS. However experts thought it was unlikely communication would be heavily impacted as recognition is typically by smell. Experts felt there was an increased risk of predation and/or disturbance from gulls, dogs, humans and marine predators in naïve animals. In addition, experts acknowledged it was possible that pups could potentially be exposed in utero and therefore get PTS (though this is poorly understood), but still the overall risk to survival was low (given the limited impact on foraging etc.). Overall, experts agreed that the final selected range and upper plausible limit reflected the current scientific uncertainty in the true value of how the defined PTS could affect harbour or grey seal pup or juvenile survival, but that the most likely effect on survival was very low.

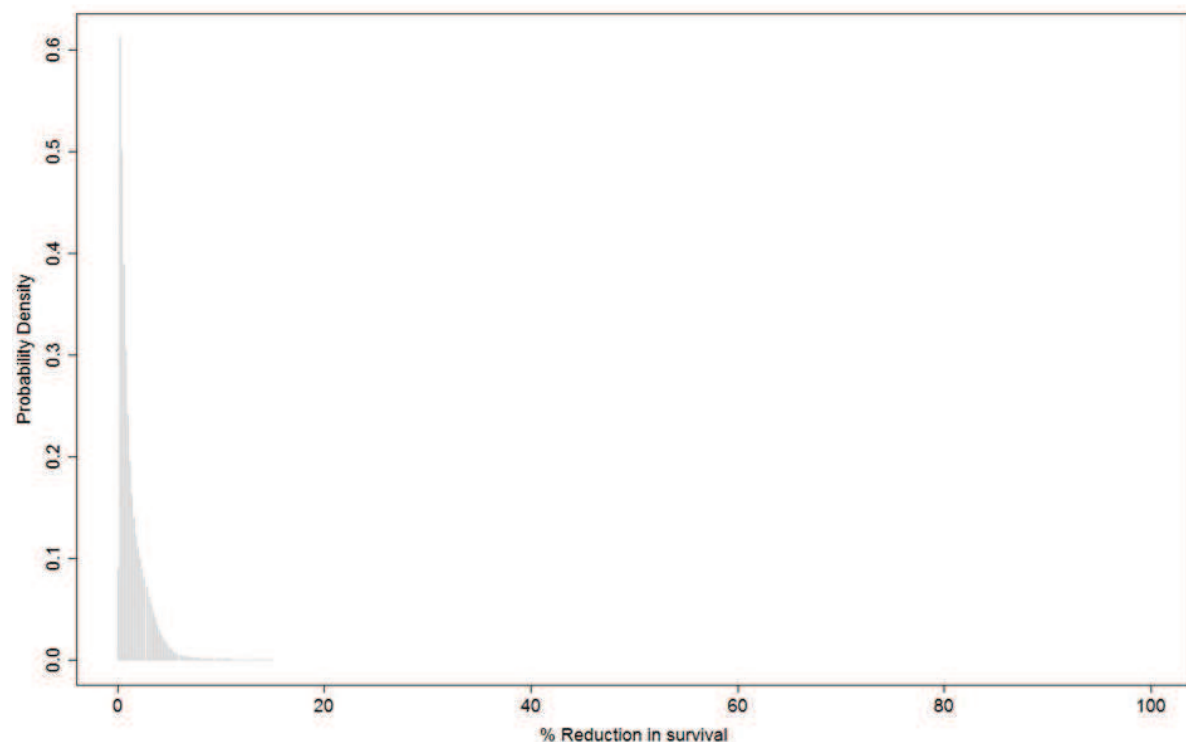


Figure 10 - Probability distribution showing the consensus distribution for the effects on survival of juvenile or dependent pup (harbour or grey) seal as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

3.3.2 Harbour porpoise

3.3.2.1 Effects on harbour porpoise fertility

The experts were asked to provide individual judgements (in isolation) on the effect of PTS on harbour porpoise fertility. Following individual judgements, they were presented to the group and experts explored and achieved a group (RIO) consensus as shown below (Figure 11). See Appendix 5 for the questions in the expert elicitation.

Overall, experts felt that there was an extremely low risk of harbour porpoise fertility being affected by the defined PTS, because foraging is unlikely to be affected as echolocation signals are well outside the PTS band.

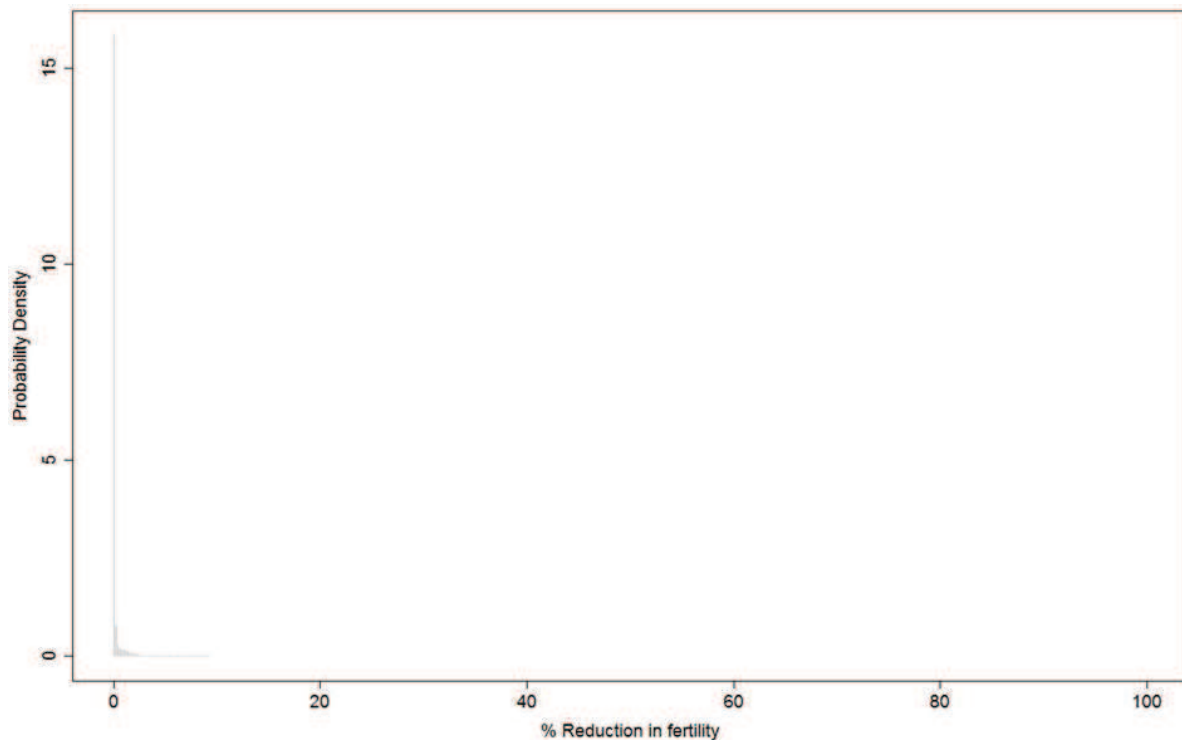


Figure 11 - Probability distribution showing the consensus distribution for the effects on fertility of a mature female harbour porpoise as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

3.3.2.2 *Effects on harbour porpoise survival*

Mature females

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 8). The same process was also followed for the effect of a larger magnitude PTS (18 dB) on mature female survival and the group (RIO) consensus is shown below (Figure 13). See Appendix 5 for the questions in the expert elicitation.

Experts felt that the impacts of both defined PTS magnitudes on mature female porpoise survival were likely to be low, because both fell outside the key frequency range used in foraging. Experts felt there might be a small increase in effect on survival via reduced detection of predators or vessels/shipping, but that because significant energy is present outside the defined PTS band, it was considered that animals would not be heavily impacted by such occurrences (if they occur). Experts noted that even with a larger PTS (18 dB), animals (in this frequency band) would still be ambient noise limited most of the time. Experts thought, given the scientific uncertainty, that there was a slightly higher probability of an effect on survival from a 18 dB PTS (compared to a 6 dB PTS) and captured this in the RIO consensus distribution accordingly (Figure 12 vs Figure 13).

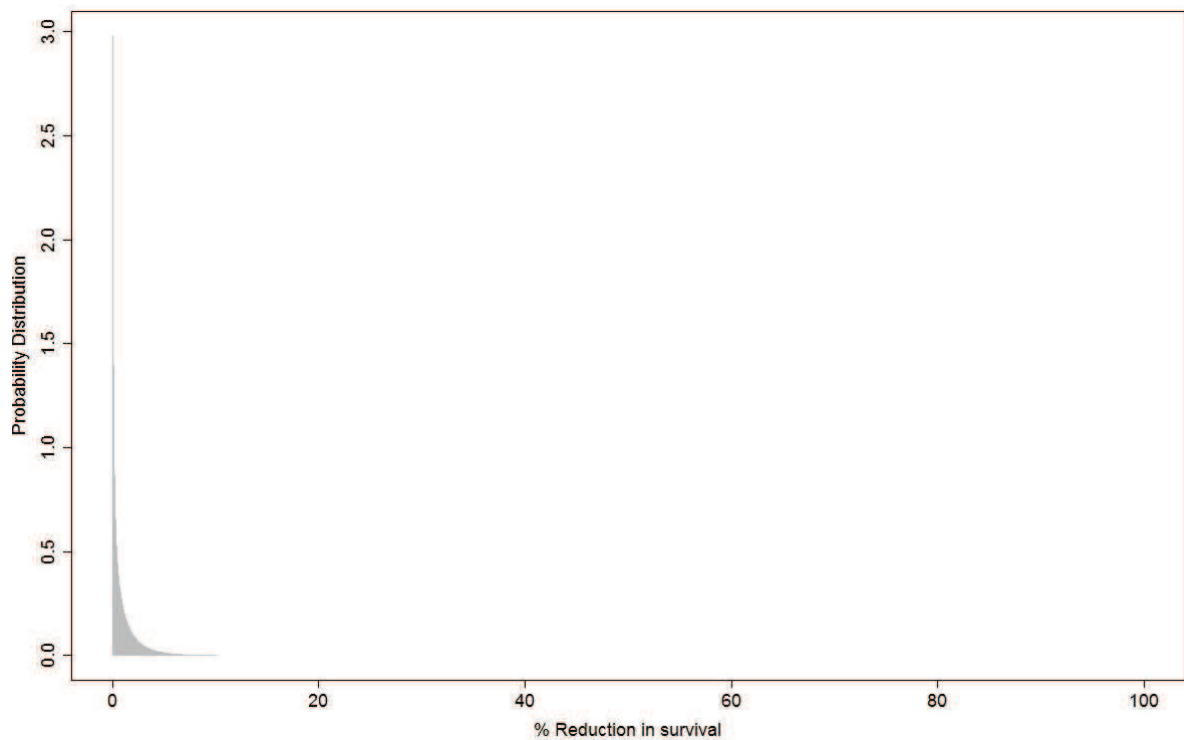


Figure 12 - Probability distribution showing the consensus distribution for the effects on survival of a mature female harbour porpoise as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

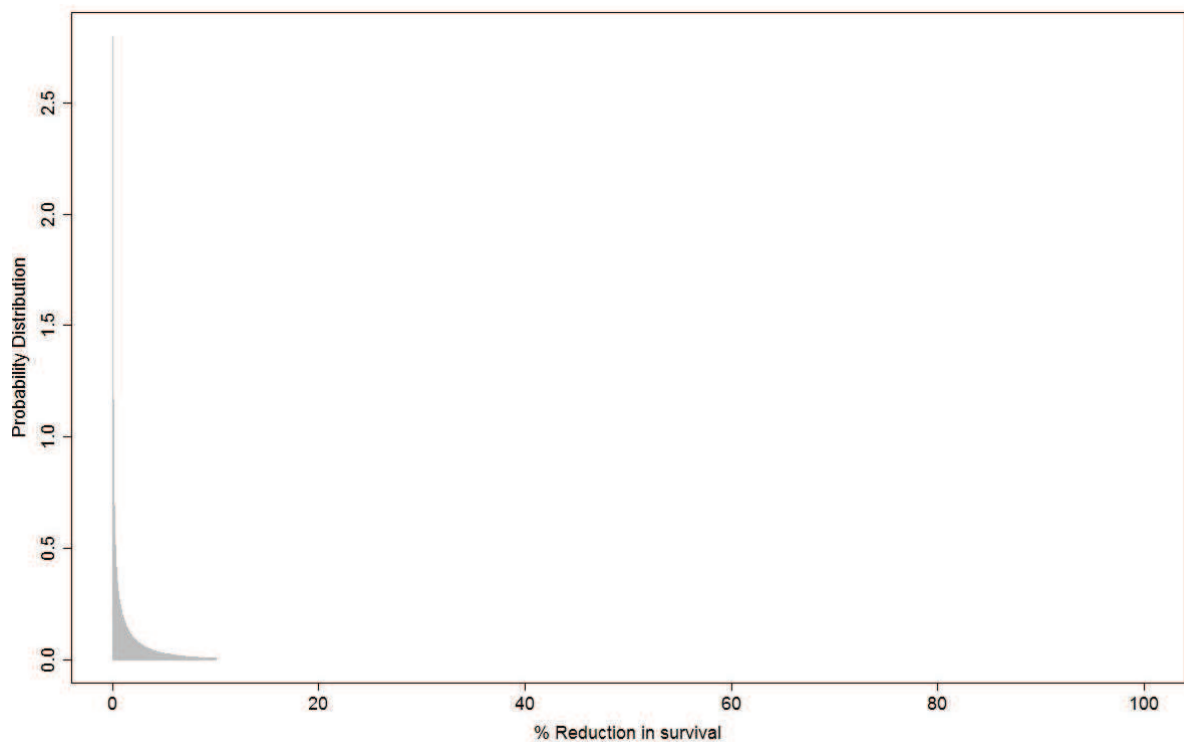


Figure 13 - Probability distribution showing the consensus distribution for the effects on survival of a mature female harbour porpoise as a consequence of a maximum 18 dB of PTS within a 2-10 kHz band.

Calves/Juveniles

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 14). See Appendix 5 for the questions in the expert elicitation.

Experts noted in their justifications that a number of factors contributed to their judgements. These included that the condition of calves will be dependent on the condition of the mother, and that there are uncertainties about how communication might be affected and an increased risk of separation as a result of the defined PTS. Experts also felt there was an increased risk of predation from marine predators (e.g. seals, bottlenose dolphins) in naïve porpoises. Overall, experts agreed that the final selected range and upper plausible limit reflected the current scientific uncertainty in the true value of how the defined PTS could affect harbour porpoise survival, but that the most likely effect on survival was very low.

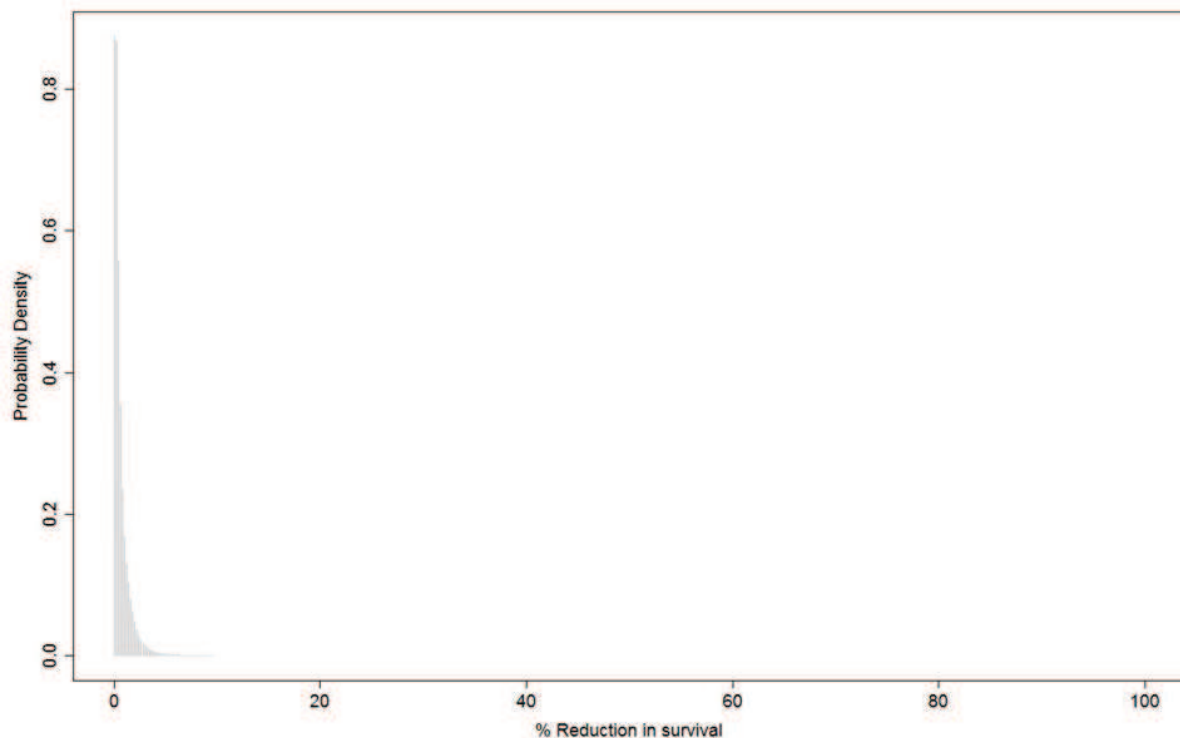


Figure 14 - Probability distribution showing the consensus distribution for the effects on survival of juvenile or dependent calf harbour porpoise as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

3.3.3 Bottlenose dolphins

3.3.3.1 Effects on bottlenose dolphin fertility

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 15). See Appendix 5 for the questions in the expert elicitation.

Experts felt that the effects of the defined PTS on fertility was likely to be small, but noted it was larger than for the other species considered in this elicitation. Experts thought that foraging and foraging related communication might be affected as this may fall in the affected PTS band, leading to reduced foraging success and finally reduced body condition, thereby impacting fertility. Experts noted that a 6 dB PTS would not be considered to have a large impact on communication for foraging and therefore a small effect was the most likely outcome in animals with the defined PTS.

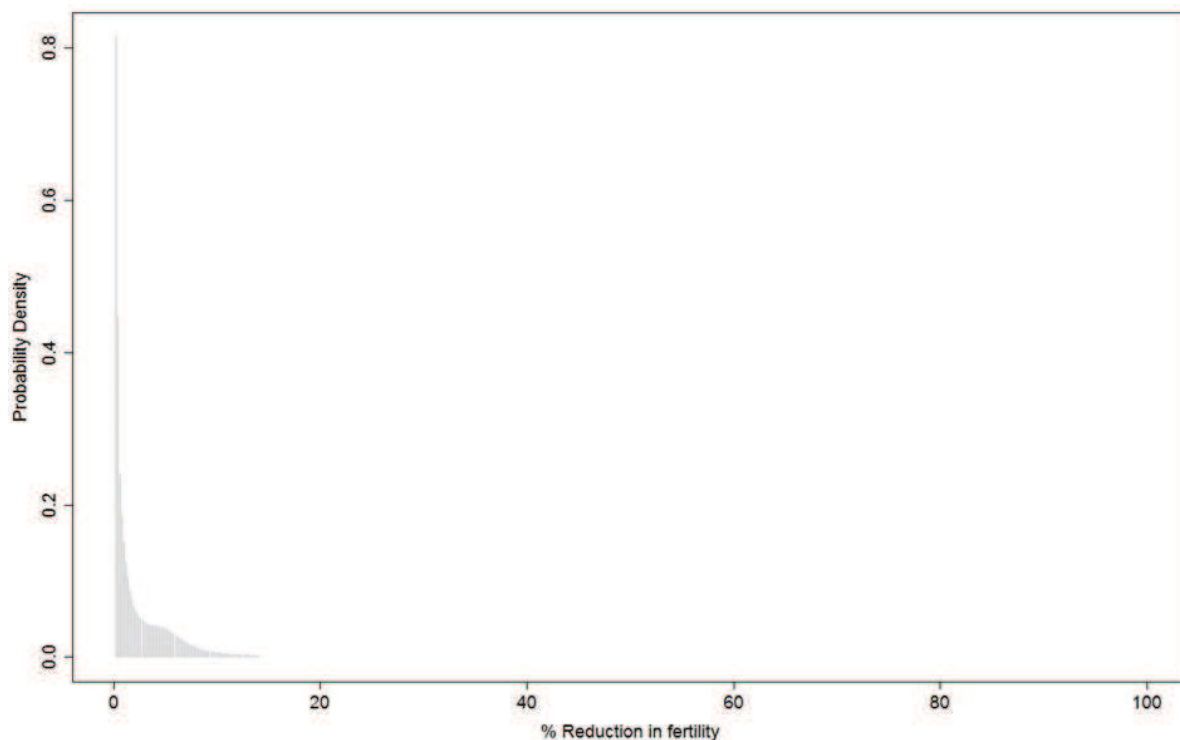


Figure 15 - Probability distribution showing the consensus distribution for the effects on fertility of mature female bottlenose dolphin as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

3.3.3.2 *Effects on bottlenose dolphin survival*

Mature females

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 16). See Appendix 5 for the questions in the expert elicitation.

Experts felt that the most likely mechanisms by which the defined PTS could impact the survival of mature female bottlenose dolphins was via foraging cues, such as brays of conspecifics (Janik 2000) being impacted (i.e. detected less frequently leading to missed feeding opportunities) and because communication appears to have an important survival function in social species like bottlenose dolphins. Experts felt that a reduced ability to detect vessels/shipping (potentially increasing the risk of collision in areas of heavy vessel use) might have some small impact on the probability of survival, but overall the risk of PTS affecting survival was low.

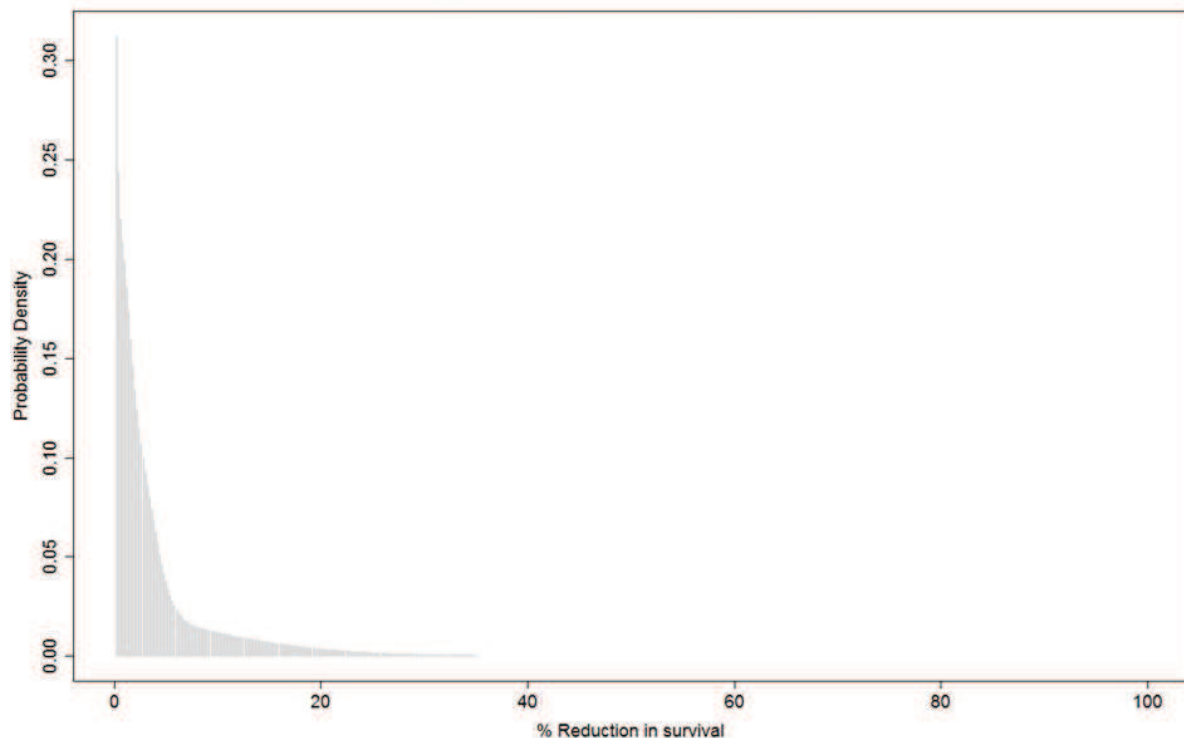


Figure 16 - Probability distribution showing the consensus distribution for the effects on survival of mature female bottlenose dolphin as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

Juveniles/Calves

The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 17). See Appendix 5 for the questions in the expert elicitation.

Experts felt that as with mature females the most likely mechanisms by which the defined PTS could impact the survival of juvenile bottlenose dolphins was via foraging cues being impacted and because communication appears to have an important survival function in social species like this species. Experts felt that a reduced ability to detect vessels/shipping (potentially increasing the risk of collision in areas of heavy vessel use) might have some small impact of the probability of survival, but overall the risk of PTS affecting survival was low, but with a slightly larger range of plausible outcomes than for mature female survival.

For bottlenose dolphin calves, the question was defined as: “What is the reduction in probability of survival (for a bottlenose dolphin calf) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?” where a calf is defined as an animal dependent on their mother. The experts provided individual judgements before moving towards a group (RIO) consensus shown below (Figure 18).

Experts felt that the same justifications as for mature females and juveniles applied, but that calves were also dependent on the foraging success (and thus condition) of their mothers. In addition experts noted the importance of social communication between mother and calf and because calves were naïve/inexperienced (leading to an increased risk of separation), the probability of an effect on survival was slightly increased over juveniles and mature females.

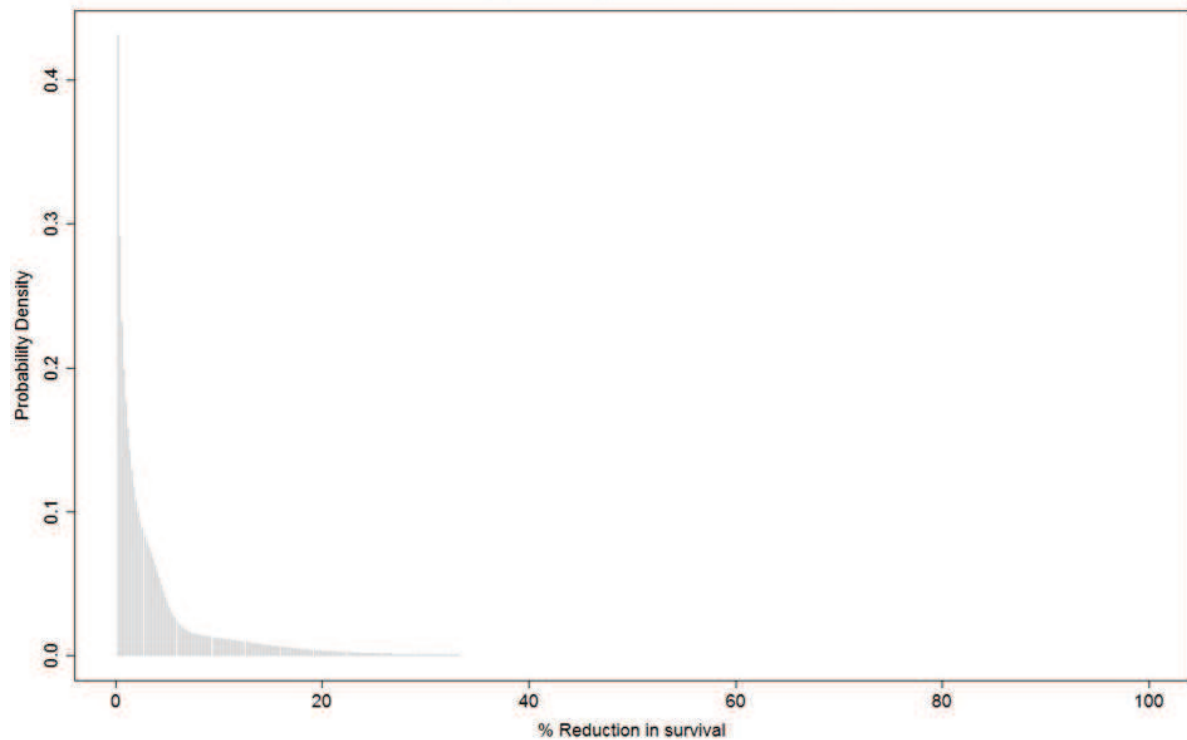


Figure 17 - Probability distribution showing the consensus distribution for the effects on survival of juvenile or dependent calf bottlenose dolphin as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

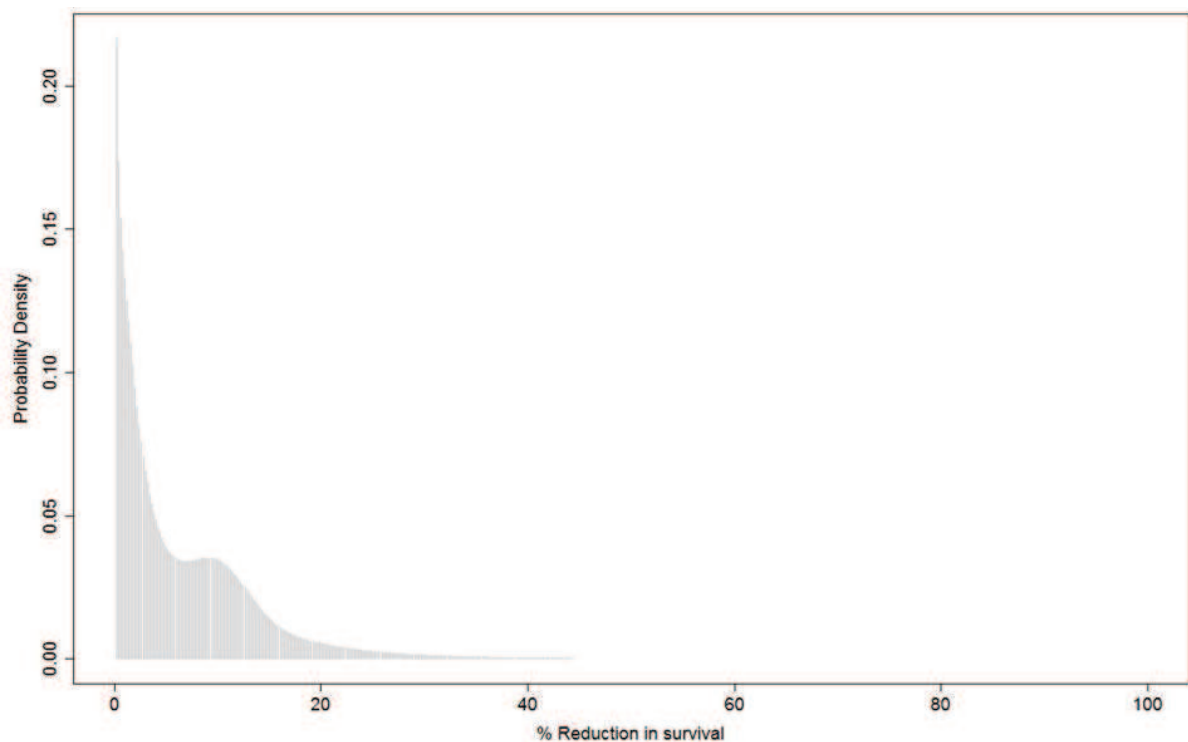


Figure 18 - Probability distribution showing the consensus distribution for the effects on survival of dependent calf bottlenose dolphin as a consequence of a maximum 6 dB of PTS within a 2-10 kHz band.

4 Discussion

The objective of this project was to update the transfer functions of the interim PCoD model relating to the effects of PTS on fertility and the probability of survival in harbour porpoise, harbour seal, grey seal and bottlenose dolphin. This was conducted via a new expert elicitation exercise. The result of this updated elicitation is a significant difference over original expert elicitation outputs conducted in 2013. Overall experts indicated that the effects of a 6 dB PTS in the 2-10 kHz band was unlikely to have a large effect on survival or fertility of the species of interest. Effects were smallest for porpoises and seals and slightly larger in bottlenose dolphins, though experts noted that the broader range of plausible outcomes for dolphins was due to potential uncertainty in how the defined PTS would impact dolphins (which use lower frequency for communications and for some foraging calls), not necessarily that they were definitely more sensitive. It should be noted, however, that for all species experts indicated that the most likely effect on survival or fertility as a result of 6 dB PTS was likely to be very small (i.e. <5 % reduction). In general experts indicated that the defined PTS was likely to have a slightly larger effect on calves/pups and juveniles than on survival or fertility of mature females.

The new transfer functions derived in this exercise indicate a much smaller 'effect size' than in the earlier expert elicitation and therefore will be reflected in new iPCoD scenarios. Where a large number of animals are predicted to experience some degree of PTS following exposure to LFBP, this may make a large difference to the population trajectories predicted by iPCoD.

It is important to note that experts highlighted that, in most cases, TTS will occur before a PTS and this could have an impact. For example, Kastak et al. (2008) observed a TTS in excess of 50 dB in harbour seal which resulted in a PTS of 7 dB. In iPCoD, this might also be captured in the period under which animals would be considered 'disturbed' (i.e. impaired ability for a period of days), but this should be considered. Based on the mechanisms and results above (Section 3), if large TTSs do occur prior to PTS, this is most likely to affect bottlenose dolphins and potentially seals, but is less likely to affect harbour porpoises due to PTS in the 2–10 kHz band being outside the important frequency range for echolocation. In all species, the same mechanisms as discussed in Section 3 above are likely to be those potentially affected.

Harwood et al (2014), with respect to the interim PCoD model and original elicitation, highlighted: *"This expert elicitation process was designed specifically to provide parameter values for the functions that form part of the [iPCoD] model. Those values should not be used to infer how disturbance might affect vital rates outside of the context of this model. In addition, the expert elicitation and the subsequent analysis of the results from the elicitation process were designed to capture the uncertainty expressed by individual experts, and the variability among experts in their opinions. It would therefore be entirely inappropriate to derive simple summary statistics from this analysis."* As such, we recommend that the probability distribution outputs of this expert elicitation should be used in the context of the wider interim PCoD model (i.e. as part of iPCoD simulations). Furthermore, we also concur with the statement made in 2014 stressing *"the interim nature of this approach, which was developed to deal with the current situation, where there are limited data on the way in which changes in behaviour and hearing sensitivity may affect the ability of individual marine mammals to survive and to reproduce. The research that is needed to improve our knowledge and understanding of these processes has been identified by (Harwood and King 2012) and some of this work is currently underway."* We hope that this work will stimulate new rounds of research funding to advance our empirical knowledge base in these fields to support or replace the need of expert elicitation in the transfer functions.

4.1 Next steps

Following the successful update of the PTS –vital rate transfer functions (i.e. the relationship between animals experiencing PTS and their vital rates potentially being affected), it is planned that the new distributions (i.e. Figure 8-18) will be integrated into the iPCoD software and made publically available via download of the tool. This is expected to be completed by autumn 2018.

In June 2018 a second expert elicitation workshop is planned, in which the relationship between disturbance and vital rates will be the focus. Following that workshop it is intended the new distributions will be integrated into the iPCoD software.

We recommend that research effort is directed to address the knowledge gaps currently estimated using expert elicitation (for both the effects of PTS and disturbance on vital rates). It is assumed that not all knowledge gaps will be filled and as with the new (2018) elicitation updating the 2013 transfer functions, there will likely be value in revisiting the 2018 elicitations, in light of new learning. However we once again stress that the focus on funding research studies to replace the elicited relationships with empirically derived ones and where appropriate validating the existing relationships.

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6 Appendix 1 - Glossary

Below is the glossary of acronyms and terms used in the Interim PCOD protocol (from Harwood et al. 2014).

Acronym / Term	Definition
Acute effect	The direct effect of a change in behaviour or physiology on vital rates
Ambient noise	That part of the total noise background observed with a non-directional hydrophone which is not due to the hydrophone and its manner of mounting or to some identifiable localised source of noise (Urick 1984)
Background noise	All acoustic sound detected in the environment at a time, including all sound in the ocean, and excluding the signal of interest, system noise, electrical noise and self-noise.
Body condition	A measure of an individual's energy stores. In marine mammals, usually blubber thickness or total body lipid
Chronic effect	The indirect effect of a change in behaviour or physiology on vital rates via individual health.
dB	Decibel. Unless stated, this is a short-hand for dB re 1µPa – 'e.g. a 6 dB permanent threshold shift'.
Delphi process	An established process whereby experts are asked to reconsider their opinions in the light of what other experts have said in answer to the same set of questions
Expert elicitation	A formal technique for combining the opinions of many experts. Used in situations where there is a relative lack of data but an urgent need for conservation decisions
Fertility	The probability that an individual adult female will give birth to a viable offspring in any particular year
Fitness	A relative term reflecting the potential contribution of the genotype of an individual to future generations. The fittest individuals leave the greatest number of descendants relative to the number of descendants left by other individuals in the population
Gaussian noise	Noise with a Gaussian amplitude distribution – see Normal distribution.
Health	All internal factors that may affect individual fitness and homeostasis, such as condition , and nutritional, metabolic, and immunological status
Normal distribution	A function that represents the distribution of many random variables as a symmetrical bell-shaped graph.
NRC	National Research Council of the United States National Academy of Sciences
Octave	In acoustical measurements, sound pressure level is often measured in octave bands, and the centre frequencies of these bands are defined by ISO - 31.5 Hz, 63 Hz, 125 Hz, 250 Hz, 500 Hz, 1 kHz, 2 kHz, 4 kHz, 8 kHz, 16 kHz to divide the audio spectrum into 10 equal parts. Octave Definition IEC 801-30-09, logarithmic frequency interval between two sounds whose fundamental frequency ratio is two
ONR	US Office of Naval Research

PCAD	Population Consequences of Acoustic Disturbance
PCOD	Population Consequences of Disturbance
PTS	Permanent Threshold Shift: a non-recoverable elevation of the hearing threshold that occurs under conditions that cause a 40dB temporary shift in the threshold (TTS) for hearing at a particular frequency
RIO	Rational Impartial Observer. A term used in Expert Elicitation: The RIO would not have identical views to any one of the experts but would instead find some merit in all the differing arguments or justifications
SEL	Sound Exposure Level
TTS	Temporary Threshold Shift: a recoverable elevation of the hearing threshold at a particular frequency
Uncertainty	Incomplete information about a particular subject. In this report, we are only concerned with those components of uncertainty that can be quantified
Vital Rates	The probability that an individual will survive from one year to the next, the probability that an individual adult female will give birth in one year

7 Appendix 2 – Expert Background

Prior to the experts, in alignment with the SHELF protocol, we asked experts to provide a brief summary of their background and highlight any vested interests in the expert elicitation process on the consequences of PTS.

Dorian Houser is a biologist with over 20 years of experience investigating marine mammal bioacoustics and hearing through both behavioural and neurophysiological methods. He works for the National Marine Mammal Foundation, a U.S.-based non-profit with interests in improving marine mammal conservation, and has particular interest in conservation as it relates to the impact of anthropogenic sound on marine mammals.

Jakob Tougaard is trained in animal bioacoustics, with emphasis on physiology of hearing and has worked with issues relating to underwater noise and marine mammals over the last 20 years. He provides independent advice to a broad range of stakeholders, including government agencies and private and public enterprises, and does not represent any particular stakeholder viewpoint.

Darlene Ketten is a marine scientist and neuroanatomist whose research focuses on the biomechanics of underwater hearing in marine mammals, fishes, invertebrates, and turtles and on mechanisms of hearing loss from noise, trauma, and disease. She stated in advance of the workshop (upon request): “I, Darlene Ketten, am a research scientist with expertise in the area of marine mammal hearing and more broadly in the pathology and mechanisms of hearing loss in humans and other mammalian species. I do not have any vested interests in the topic of this meeting and its outcome other than to represent current knowledge in my area of expertise.”

Klaus Lucke is an expert in: sensory biology in marine animals; assessing impacts of anthropogenic sound on the hearing system of marine vertebrates; and, performing underwater acoustic measurements. He currently works for JASCO Applied Science, providing scientific guidance on hearing and noise-induced effects in marine animals in all aspects of underwater sound. He has previous and ongoing advisory work for various national and international regulatory bodies.

Peter Tyack is a behavioural ecologist who studies acoustic communication and social behavior in marine mammals. He has developed experimental approaches to measure the relationship between acoustic exposure and behavioural response in marine mammals. His primary interest is in integrity of the scientific process advising policy.

Paul Thompson has expertise in: variation in behaviour, reproduction and survival in relation to natural and anthropogenic stressors, developed through integration of individual based studies of seabirds, seals and seal cetaceans. He noted the following relating to vested interests: current or recent membership of advisory groups for NERC, SCOS, Marine Scotland Science & ORJIP; current or recent contracts from renewables industry, BEIS and Marine Scotland for work related to impacts of noise on marine mammals; and, independent advisory work for several different offshore wind developers.

Ron Kastelein has 35 years of experience with (behavioural) hearing studies with marine mammals of which the last 8 years with TTS research. He runs SEAMARCO and stated they have no vested interest in the outcome of the elicitation process.

8 Appendix 3 – Magnitude of PTS calculations

The following process was followed:

1. Experts determined the worst-case, unweighted sound exposure level (SEL) for an animal starting the exposure adjacent to, for example, a pile driving activity, which was 220 dB re 1 $\mu\text{Pa}^2\text{s}$ SEL.
2. Experts used the unweighted threshold for the onset of TTS and then used the difference between the threshold and the max SEL received to determine the SEL excess. (Note - experts used unweighted SEL and thresholds because we did not have access to the weighting functions and noise files during the workshop).
3. This was combined with the growth rate of TTS (i.e. by how much TTS increases (in dB) with each increasing dB of sound exposure) using average growth rate values for the harbour porpoise from 1-2 and 6-7 kHz data for 10% duty cycle exposures, harbour seal data from Kastelein's studies (Kastelein et al. 2013b, Kastelein et al. 2015b), and the 3-10 kHz data from Finneran's research on bottlenose dolphins using fatiguing stimuli in the 3-10 kHz range (Finneran et al. 2005, Finneran et al. 2010, Finneran and Schlundt 2013). These references are presented in National Marine Fisheries Service (2016). The growth rate data was used to determine when PTS onset would occur (i.e., at 40 dB of TTS). In both cases, the growth rate in this frequency range is low (<1.0 dB/dB SEL) (due to low duty cycle appropriate for pile driving/airgun pulses).
4. Once the PTS onset (6 dB) was determined, PTS was accumulated at the same growth rate as for TTS up to the maximum of 220 dB SEL.

For bottlenose dolphin, experts used the onset of TTS for the beluga (Finneran et al. 2002), since it had the lowest threshold for TTS onset for a mid-frequency odontocete exposed to an impulsive sound. For seals and porpoises TTS onset thresholds were based on their respective threshold values (harbour porpoise and phocid in water)(Kastelein et al. 2012b, National Marine Fisheries Service 2016).

Once experts had the amount of PTS, experts compared the elevated threshold to the sum of the average background noise in the North Sea (Figure 7)(for the frequencies of interest) and the critical ratio (see Yost and Shofner 2009) for each of the species. This was used to estimate whether the animal would still be noise limited or not. Experts calculated the new threshold based on the average threshold across frequencies in the band of interest and then added the different levels of PTS (6, 12, 18, 24 dB). That value was compared to the noise spectral density and critical ratio to determine if it could be achieved by exposure to the LFBP noise stimuli of interest.

9 Appendix 4 - Expert Elicitation Judgement - Example

9.1 Example 2018 Individual & Consensus Judgements

Below we show two figures from the 2018 elicitation to show the first (individual judgements) and second phase (consensus judgements) from the elicitation. Only two figures have been shown as this is merely an indicative case to show how individual and consensus judgements may differ.

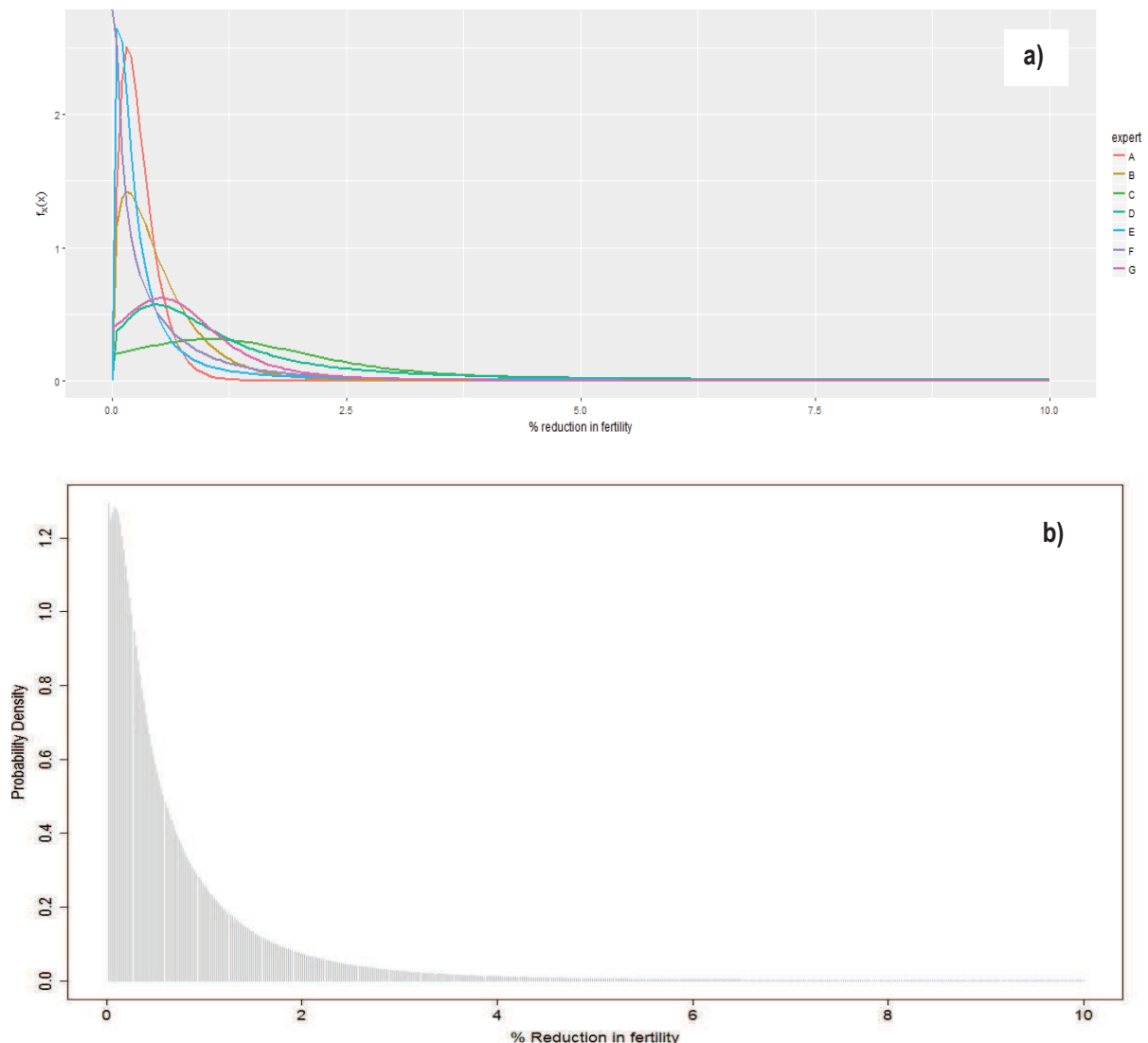


Figure 19 - Example outputs from the 2018 elicitation on the effects of the stated PTS on seal fertility, showing a) the individual judgements and b) the final consensus judgement. Note the x axis has been condensed to allow comparison of individual and consensus judgement.

10 Appendix 5 – Expert Elicitation Questions

In consultation with the experts in attendance, the following questions were answered by experts during the expert elicitation (results in Figure 8-18):

‘What is the reduction in the fertility (for a mature female seal) you judge (as a probability distribution) to occur as a consequence of a maximum 6 dB PTS within a 2-10 kHz band?’ where fertility was defined as the probability of a successful birth by individual adult female in a year’

'What is the reduction in probability of survival (for a mature female seal) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?'

'What is the reduction in probability of survival (for a seal pup or juvenile seal) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where a pup is defined as an animal dependent on their mother and a juvenile is defined as the stage from becoming nutritionally independent through to sexual maturity.

'What is the reduction in the fertility (for a mature female harbour porpoise) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where fertility was defined as the probability of a successful birth by individual adult female in a year'

'What is the reduction in probability of survival (for a mature female harbour porpoise) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?'

'What is the reduction in probability of survival (for a porpoise calf or juvenile porpoise) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where a calf is defined as an animal dependent on their mother and a juvenile is defined as the stage from becoming nutritionally independent through to sexual maturity.

'What is the reduction in the fertility (for a mature female bottlenose dolphin) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where fertility was defined as the probability of a successful birth by individual adult female in a year'.

'What is the reduction in probability of survival (for a mature female bottlenose dolphin) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?'

'What is the reduction in probability of survival (for a juvenile bottlenose dolphin) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where a juvenile is defined as the stage from becoming nutritionally independent through to sexual maturity (likely age 2-9 in this species).

'What is the reduction in probability of survival (for a bottlenose dolphin calf) you judge (as a probability distribution) to occur as a consequence of a maximum 6dB PTS within a 2-10 kHz band?' where a calf is defined as an animal dependent on their mother.

APPENDIX 7



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Updating the Interim PCoD Model: Workshop Report - New transfer functions for the effects of disturbance on vital rates in marine mammal species

Authors:	Cormac Booth, Floor Heinis & John Harwood
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Executive Summary

The Interim Population Consequences of Disturbance (iPCoD) framework was developed by SMRU Consulting and the University of St Andrews in 2013 to forecast the potential effects on marine mammal populations in UK waters of any disturbance and permanent hearing loss (threshold shifts, PTS). The iPCoD framework was designed to assist decision making in a situation where there is only limited knowledge about the potential effects of these developments on marine mammals. The iPCoD framework was developed with the quantification of the effect of disturbance on vital rates determined via expert elicitation, conducted in 2013. The elicitation was carried out using an online questionnaire and at the time was recognised as an interim solution to the evaluation of these effects. The objective of this study was to update the transfer functions on the effects of disturbance on the probability of survival and of giving birth to a viable young of harbour porpoise, harbour seals and grey seals via an expert elicitation (in the form of probability distributions).

To achieve this, a two-day workshop was held in Amsterdam, The Netherlands from 13-14 June 2018. To deliver the workshop, we invited a leading group of experts on physiology, behaviour, energetics, statistics and the effects of noise on marine mammals and spanning the species of interest. In addition, the attendees' experience spans the fields of veterinary pathology, physics, physiology and behaviour.

To support the elicitation for harbour porpoises, a dynamic energy budget (DEB) model was available and used during the elicitation to aid discussions regarding the potential effects of missed foraging opportunities on survival and reproduction. It is important to note that no DEB model was available for the seal species in the elicitation. For the elicitation we employed the Sheffield Elicitation Framework (SHELF) using SHELF v.3.0. For each quantity of interest each expert was asked to provide their individual judgements regarding a number of parameters; the plausible limits, median, lower and upper quartiles. The experts were then asked to input their personal judgements into SHELF and distributions were fitted to each individual expert judgement with the best statistical fit. During the process, the mechanisms experts had considered in making their individual judgements were discussed among the group before a consensus distributions were agreed upon.

As with the 2013 iPCoD elicitation, experts agreed we would focus on the potential for disturbance to be caused by exposure to low frequency broadband pulsed (LFBP) noise (e.g. pile-driving, airgun pulses). Disturbance was defined as when no feeding (or nursing) was taking place on the day of disturbance as a result of exposure. This means that in a day of disturbance there is a period of zero energy intake for the disturbed individual. Experts agreed that harbour porpoises, grey & harbour seals are likely to be sufficiently different in life history strategy and in their sensitivity to noise that the effects of disturbance on each group is likely to be different and were therefore, where possible, elicited separately. The experts' judgements for harbour porpoises were based on the assumption that, on average, the behaviour of the animals classified as being disturbed will be altered for 6 hours (within a single day – the day of disturbance), and that no feeding will take place during this time. This was agreed by experts following review of grey and published literature. For seals, the experts' judgements were based on the assumption that, on average, the behaviour of the individual seals classified as being 'disturbed' using this approach will be altered for much less than 24 hours by exposure to LFBP noise sources like pile-driving (though it was not possible to define a discrete value for the number of hours that disturbance effects are likely to last due to a lack of evidence of significant behavioural responses for these species). Experts cited a lack of knowledge of exactly if/how disturbance affects seals energy expenditure and intake.

The results of this updated elicitation show significant differences over those of the original expert elicitation conducted in 2013. Overall, experts indicated that the effects of disturbance were likely to be less severe than previously estimated. This was largely driven by new empirical data collected and published since then, and the presentation of the DEB model which helped guide discussions and test expert theories presented during the workshop of the critical vital rates to focus on. In addition the face-to-face element of the workshop was

important. This allowed discussion and prior-agreement of question wording with experts which is fundamental to a successful elicitation. The biggest effects changes from the 2013 elicitation were for harbour porpoises in which the effects of disturbance were considered to be reduced (even when basing judgements on a disturbance resulting in a 6 hour period of zero energy intake). The estimated effects of disturbance were smaller for harbour and grey seals than for harbour porpoises, and both seal species had reduced effect sizes compared to the 2013 elicitation. This was due to experts' discussions about seal life history, fat reserves and species responsiveness.

The new transfer functions derived in this exercise indicate a smaller 'effect size' than in the 2013 expert elicitation and therefore will be reflected in new iPCoD scenarios. Where a large number of animals are predicted to experience some degree of disturbance following exposure to low frequency broadband pulsed noise, this may make a large difference to the population trajectories predicted by iPCoD

We recommend that research effort is directed to address the knowledge gaps currently estimated using expert elicitation (for both the effects of PTS and disturbance on vital rates). We stress then need to focus on funding research studies to replace the elicited relationships with empirically derived ones, and, where appropriate, validating the existing relationships. It is assumed that not all knowledge gaps will be filled, and, as with the new (2018) elicitation updating old transfer functions, there will likely be value in revisiting the 2018 elicitations in light of new learning (and the development of DEB models for more species).

1 Introduction

1.1 An Introduction to the interim PCoD framework

In 2005, a panel convened by the National Research Council of the United States National Academy of Sciences (NRC) published a report on biologically significant effects of noise on marine mammal populations (NRC, 2005). The panel developed what they referred to as a “conceptual model” that outlines the way marine mammals respond to anthropogenic sound, and how the population level consequences of these responses could be inferred on the basis of observed changes in behaviour. They called this model Population Consequences of Acoustic Disturbance or ‘PCAD’ (Figure 1).

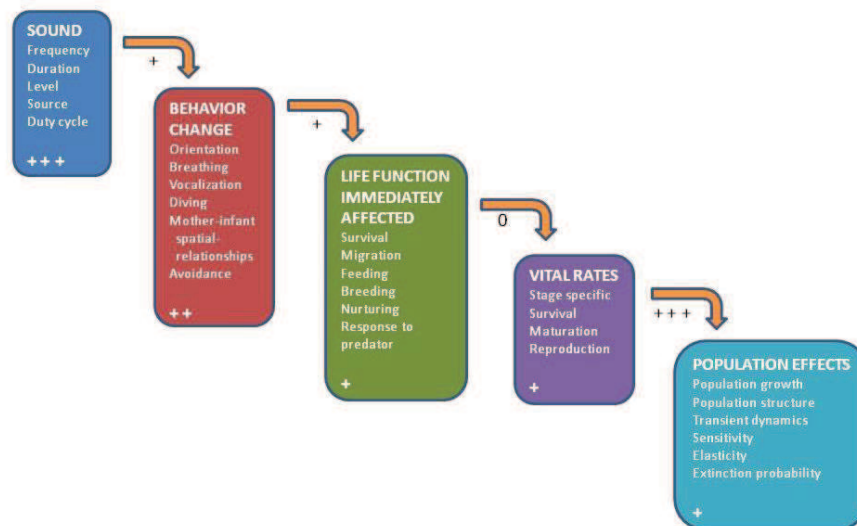


Figure 1 - The Population Consequences of Acoustic Disturbance (PCAD) model developed by the National Research Council's panel on the biologically significant effects of noise. After Fig. 3.1 in NRC (2005). The number of + signs indicates the panel's evaluation of the relative level of scientific knowledge about the links between boxes, 0 indicates no knowledge. These links were described by the panel as “transfer functions”.

In 2009, the United States Office of Naval Research (ONR) set up a working group to transform this conceptual model into a formal mathematical structure and to consider how that structure could be parameterised using data from a number of case studies. The ONR working group also extended the PCAD model to consider forms of disturbance other than noise, and to address the impact of disturbance on physiology as well as behaviour. The current version of that model, which is based on case studies of elephant seals, coastal bottlenose dolphins, northern right whales and beaked whales, is now known as PCoD (Population Consequences of Disturbance). It is shown in Figure 2 and described in more detail in New et al. (2014).

The PCoD model provides a framework for assessing how disturbance may affect both the behavioural and physiological states of an individual, and how changes in these states may influence that individual's vital rates (see Glossary) either directly (an acute effect) or indirectly via its health (a chronic effect). For example, exposure to high levels of sound may result in hearing damage (a physiological effect) through a permanent increase in the threshold for hearing at a particular frequency (Permanent Threshold Shift - PTS). This could have an acute effect on survival, because the affected individual might be less able to detect predators. It could also have a chronic effect on reproduction via the individual's health, because it might be less able to locate and capture prey. Similarly, behavioural changes in response to disturbance could have an acute effect on survival if they result in a calf being separated from its mother. They could have a chronic effect on reproduction, via body condition, if they result in the disturbed animal spending less time feeding or in activities that conserve energy, such as resting.

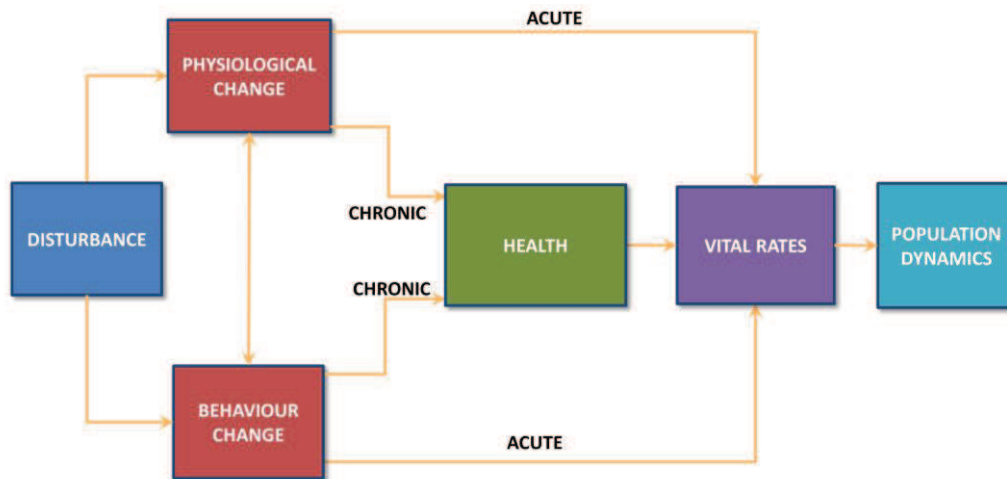


Figure 2 - The PCoD model of the population consequences of disturbance developed by the ONR working group on PCAD (modified from Fig. 4 of New et al., 2014). See Glossary for a definition of the terms used in the diagram.

Using case studies of elephant seals (Schick et al. 2013, New et al. 2014) and bottlenose dolphins (New et al. 2013), it was possible to show how changes in behaviour in response to disturbance could affect the energy reserves of adult females, and to estimate the implications of these changes for the probability of giving birth and offspring survival. The consequences of these changes for population dynamics could then be inferred from the number of animals that might be affected by disturbance and the size of the population of which they are part. A similar approach has been undertaken to assess the potential impacts of wind farm operation on harbour porpoises in Inner Danish Waters (Nabe-Nielsen et al. 2011) and North Sea (Nabe-Nielsen et al. 2018).

The Interim Population Consequences of Disturbance (iPCoD) framework was developed by SMRU Consulting and the University of St Andrews in 2013 to forecast the potential effects on marine mammal populations in UK waters of any disturbance, hearing damage (via permanent threshold shifts (PTS)) or collisions that might result from the construction or operation of offshore renewable energy devices. The term ‘interim’ describes that this model was completed with a step parameterised via expert elicitation. A detailed description of the approach can be found in Harwood et al. (2014) and King et al. (2015). Unfortunately, the empirical information that is required to parameterise the PCoD model developed by the ONR Working Group does not exist for the five species considered in the iPCoD model. We have therefore used a simplified version of this model (Figure 3) which was developed at the workshop on ‘Assessing the Risks to Marine Mammal Populations from Renewable Energy Devices’ (Lusseau et al. 2012). The information required to quantify the potential effects of behavioural and physiological changes on vital rates, shown by the dotted lines in Figure 3, was obtained using an expert elicitation process (Runge et al. 2011, Martin et al. 2012), which is described in the next section.

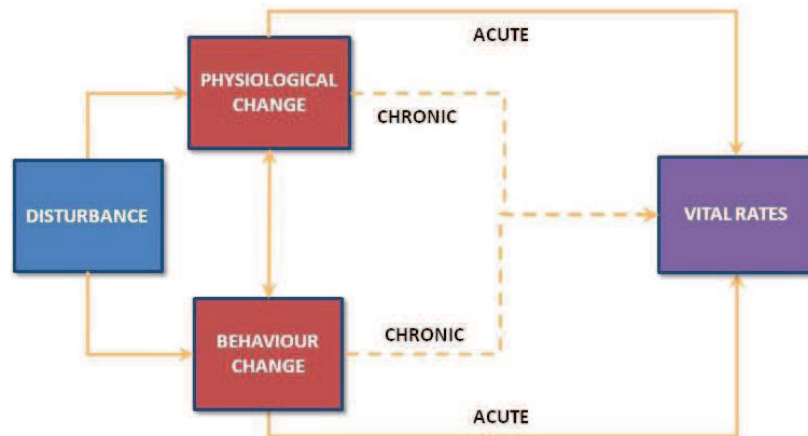


Figure 3 - A simplified version of the PCoD model shown in Figure 2 that is being used in the interim PCoD (iPCoD) approach. The ‘transfer functions’ that determine the chronic effects of physiological change and behavioural change on vital rates are represented with dotted lines to indicate that the form of these functions has been determined using the results of an expert elicitation process rather than using empirical evidence. See Glossary for definitions of the terms used in this diagram.

1.2 Expert elicitation

Expert elicitation is a formal technique, first developed in the 1950s and 60s (Brown 1968, O'Hagan et al. 2006), that is now widely used in a range of scientific fields to combine the opinions of many experts in situations where there is a relative lack of data but an urgent need for conservation or management decisions (Runge et al. 2011, Martin et al. 2012). Specifically, Morgan (2014) indicates: “Expert elicitation should build on and use the best available research and analysis and be undertaken only when the state of knowledge will remain insufficient to support timely informed assessment and decision making”. Martin et al. (2012) describe how this technique can be used to access substantive knowledge on particular topics held by experts and such techniques have been discussed and used widely in recent years (e.g. MacMillan and Marshall 2006, Aspinall 2010, Knol et al. 2010, European Food Safety Authority 2014, Sivle et al. 2015). Perhaps the most high profile use in the environmental sector has been in the assessment of risks from climate change (Lenton et al. 2008) and predictions of future sea level rise (Bamber and Aspinall 2013). The technique can also be used to translate and combine information obtained from multiple experts into quantitative statements that can be incorporated into a model, minimize bias in the elicited information, and ensure that uncertainty is accurately captured. The formal process of expert elicitation therefore avoids many of the well-documented problems, heuristics and biases that arise when the judgements of only a few experts are canvassed or where expert knowledge is sought in an unstructured manner (Kynn 2008, Kahneman 2011, Morgan 2014). In the field of marine mammals, a number of elicitations have been conducted in recent years involving the project team and seeking to improve the methods for marine mammal issues (e.g. Booth et al. 2014, Tollit et al. 2016).

1.3 Project Objectives

The iPCoD framework was developed with the quantification of the effect of disturbance on vital rates determined via expert elicitation, conducted in 2013. This elicitation was, at the time, recognised as an interim solution to the evaluation of these effects. There remains an urgent need for additional scientific research to address the knowledge gaps that were identified by Harwood et al. (2014).

Since its initial release (v1.0) in February 2014 on the Marine Scotland Science website, the tool was updated with amendments to the code and helpfiles in October 2014 (v1.1). Since then, the iPCoD tool has been used for

a number of offshore wind developments in Germany, Netherlands, France and the UK (and possibly others) (e.g. Heinis et al. 2015, Brandt et al. 2016, Booth et al. 2017), and has been used to explore the potential population-level effects of collisions of a range of species with marine renewable energy devices in the UK. During this time, SMRU Consulting and John Harwood have also developed the tool further to improve the model framework. Since the initial iPCoD framework was developed, it has proved possible to develop PCoD models for a number of marine mammal species (King et al. 2015, van Beest et al. 2015, Booth et al. 2016, Harwood and Booth 2016, Tollit et al. 2016) for harbour porpoises, beaked whales, sperm whales and Cook Inlet beluga respectively (with some using expert elicitation approaches to fill data gaps). Carrying out these referenced expert elicitations has led to significant advances in our understanding of elicitation processes and the refinement of methods in eliciting expert opinion. The first elicitation, in 2013-14, was carried out via an online elicitation, in which questions were posed and experts were invited to provide answers to them. Although a Delphi approach was conducted (a second round of elicitation where feedback was provided to experts), we have learned from subsequent elicitations that discussion and prior-agreement of question wording with experts (see Section 2) is important to a successful elicitation. As such, with the advances in knowledge in how to conduct expert elicitations and an increased understanding of marine mammal energetics and the mechanisms of how disturbance could impact affecting vital rates, we now seek to upgrade the iPCoD model by updating the expert elicitation step of the framework. Specifically, exploring how the effects of disturbance affect the vital rates of marine mammal populations.

Therefore, the objective of this study was to update, via expert elicitation, the ‘transfer functions’ that represent the effects of disturbance on the probability of survival and of giving birth to a viable young (see Glossary – Appendix 1) of harbour porpoise, harbour seals and grey seals. The effects of permanent threshold shifts (PTS) on these vital rates in the iPCoD model were assessed as part of an elicitation workshop in March 2018 (Booth and Heinis 2018).

2 Expert Elicitation

2.1 Elicitation workshop

A two-day workshop was held in Amsterdam, The Netherlands from 13-14 June 2018, taking place immediately following the INPAS symposium¹ at the same venue on 12 June. Here, we provide a brief summary of the scope of the workshop and how the effects of disturbance were considered in this elicitation. In section 3 we present the results of the workshop in the form of probability distributions.

The workshop attendees are shown below (Table 1). In preparation for the workshop, we invited a leading group of experts on physiology, behaviour, energetics, statistics and the effects of noise on marine mammals, spanning the species of interest (see Appendix 2). In advance of the workshop, all of the experts completed an online training course for expert elicitation: <https://bit.ly/2LnPm22>.

Table 1 - Workshop participants. * - denotes that person was part of the project team

Name	Affiliation	Role
Christina Lockyer	Age Dynamics (Norway)	Invited expert
Fredrik Christiansen	Murdoch University (Australia)	Invited expert
Ailsa Hall	Sea Mammal Research Unit (UK)	Invited expert

¹ A one-day symposium presenting the latest research on the impacts of impulsive noise on marine mammals: <http://www.inpas.nl/>.

Carol Sparling	SMRU Consulting (UK)	Invited expert
Sophie Smout	Sea Mammal Research Unit (UK)	Invited expert
Garry Stenson	Department of Fisheries and Oceans (Canada)	Invited expert
Jacob Nabe-Nielsen	University of Aarhus (Denmark)	Invited expert
Cormac Booth	SMRU Consulting (UK)	PI and Facilitator*
Floor Heinis	HWE Consultancy (Netherlands).	Recorder*
John Harwood	Sea Mammal Research Unit (UK)	Observer*
Alex Brown	Hartley Anderson Ltd (Consultant to BEIS)	Observer

2.2 Harbour porpoise bioenergetic model

To support the elicitation for harbour porpoises, a dynamic energy budget (DEB) model was available and used during the elicitation to aid discussions regarding the potential effects of missed foraging opportunities on survival and reproduction. The harbour porpoise model was based on a generalised DEB model, originally parameterised for the North Atlantic population of long-finned pilot whales (*Globicephala melas*) by Hin et al. (in prep.). That model describes the way in which the life history processes (growth, reproduction and survival) of a female and her calves depend on the way in which assimilated energy is allocated between different processes (Lockyer 2007, Kooijman and Kooijman 2010, Lika and Kooijman 2011). Energy can temporarily be stored in a reserve compartment, which functions as a buffer between incoming and outgoing energy flows (De Roos et al. 2009). This reserve compartment is mainly stored internally (in and around visceral organs and muscle), but also in blubber (Lockyer 2007), and can be mobilized to serve energetic needs. The size of this reserve controls various life history functions (Lockyer 2007, Miller et al. 2011), and therefore links the effects of disturbance and environmental conditions to survival and reproduction. To control for differences in absolute size during ontogeny, 'reserve level' (reserve mass over total body mass) is used as a measure of individual body condition. A good body condition is required for successful calf recruitment (pregnancy and lactation) and a poor body condition (in the case of harbour porpoise a reserve level less than 0.2, based on data from starving animals in Koopman et al. (2002)) compromises survival and decreases life expectancy.

Changes in length with age are modelled using a von Bertalanffy growth curve parameterised with appropriate values from Table 3 of Lockyer (2003). Core body mass (i.e. total mass less reserve mass) is estimated using the relationship in Lockyer and Kinze (2003).

Environmental productivity is modelled by a variable R (resource density) that represents the maximum potential assimilated energy provided by prey in the local environment (i.e. we do not model prey energy density or digestibility explicitly). Actual energy intake is determined by an individual's body size (large individuals can consume more than small ones), and its body condition (individuals that are close to the maximum permitted body condition consume less than those that are in poor condition). This allows individuals to compensate for the effects of disturbance on foraging by consuming more prey in subsequent foraging bouts if sufficient environmental resources are available. Maximum permitted body condition in winter is set at 0.4, based on data in Lockyer (2007). However, Lockyer (2007) and Kastelein et al. (2018) have documented marked seasonal variations in the body weight of North Sea harbour porpoises, suggesting that body condition is generally much lower during the summer months, so maximum body condition in summer is set at 0.25 (see Figure 4). Because the blubber component of an individual's energy reserves plays an important role in thermoregulation, the model also considers a situation where the threshold level for starvation-related mortality tracks the maximum body condition (shown by the higher of the two dotted red lines in Figure 4).

The model assumes that a sexually mature female only becomes pregnant when the total energy content of her reserves is greater than the sum of the threshold for starvation mortality plus the costs of growing a foetus to

term. Following Lockyer (2003), the gestation period is assumed to be 10 months, and the duration of lactation is set at 8 months. A calf's foraging ability was assumed to increase steadily with age, attaining 50% efficiency at 200 days of age. The calf's demand for milk is determined by its size and body condition. Females are assumed to meet all of this demand when they are in good body condition, but to reduce milk supply if their body condition approaches the threshold for starvation-related mortality. Initially, R is set at a level such that it is just possible for a female that became pregnant at age 3 years to raise a calf successfully.

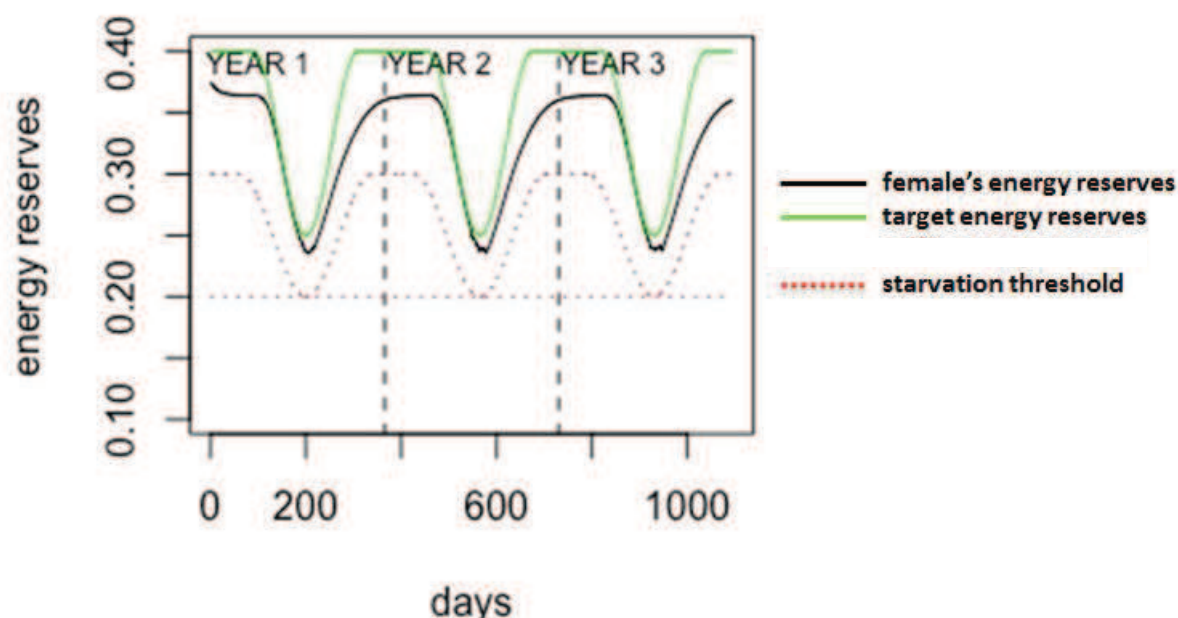


Figure 4 - An example of predicted changes in the energy reserves (expressed as a proportion of total body mass) of a female porpoise over the course of three reproductive cycles. The black line shows changes in the female's energy reserves, the green line is the maximum permitted energy reserve at a particular time of year, the upper dashed red line is a threshold for starvation-related mortality that tracks changes in maximum permitted energy reserves and the lower dashed line represents a constant threshold for starvation-related mortality. Births occur on 1 June each year (e.g. day 152 in year 1).

It is important to note that no DEB model was available for the seal species in the elicitation.

2.3 Elicitation Methods

The objective of an expert elicitation is to construct a probability distribution to accurately represent the knowledge and beliefs of an expert or group of experts regarding a specific Quantity of Interest (QoI). Here our QoI was the effects of disturbance on the probability of survival and probability of a successful birth (fertility) in different stage classes of harbour porpoise, harbour seal and grey seal. We employed the Sheffield Elicitation Framework (SHELF) approach in the expert elicitation (Oakley and O'Hagan 2016), using SHELF v.3.0 (www.tonyohagan.co.uk/shelf) in the workshop. For each QoI, which has a true value (which is unknown, and we'll call 'X'), each expert was asked to provide their individual judgements regarding a number of parameters; the plausible limits, median, lower and upper quartiles. The plausible limit was defined such that it may be theoretically possible for the true value of X to lie outside these limits, but that the expert would regard it as extremely unlikely that X was outside this range. We asked for the plausible limits first to try to avoid well-known biases of *overconfidence* (where experts do not consider extreme cases for X) and *anchoring* (where experts start with a value of X in mind). Following that, the experts were asked to specify their median value for X (such that there is equal probability that the true value of X lies above or below the median (but within the plausible limits). Finally, experts were asked to provide lower and upper quartile values for X. The exact structure of each

question was agreed with experts in advance of the elicitation and all required definitions were specified and agreed in advance.

The experts were then asked to input their personal judgements into a web-interface form (Figure 4) and to send the data to the facilitator (via the form). The judgements were then input into SHELF and distributions fitted to each individual expert judgement with the best statistical fit (determined in SHELF as the distribution with the lowest sum of squares value). The facilitator then presented the anonymised individual judgements of all experts together to the group (Figure 5). During the process, the mechanisms experts had considered in making their individual judgements were discussed among the group.

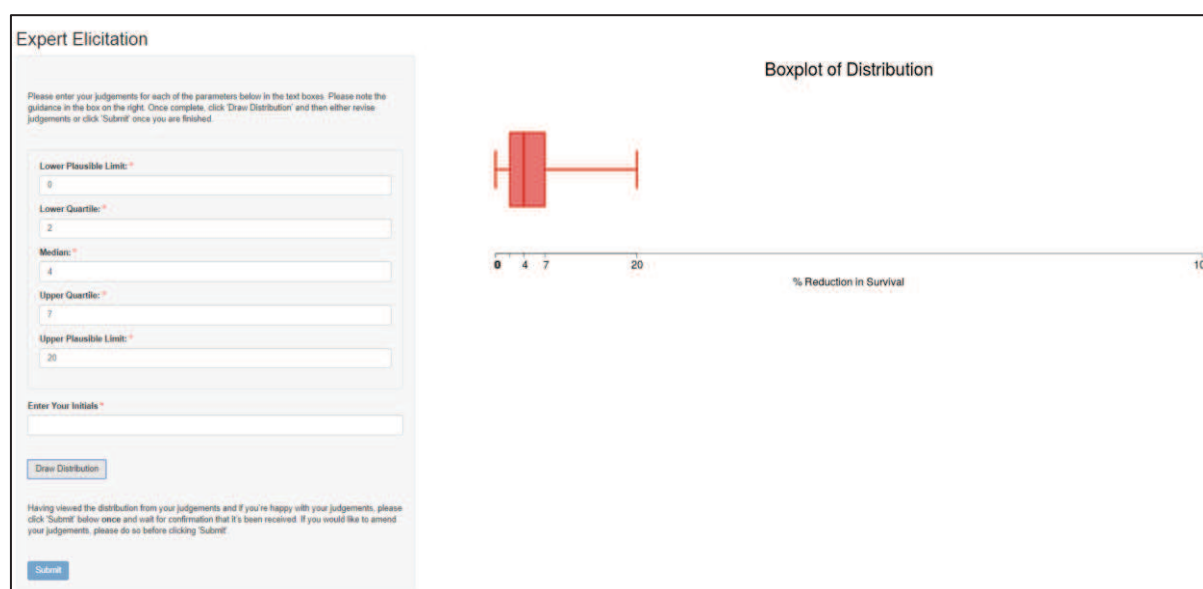


Figure 5 - Example screengrab of online tool used to collate individual expert judgements.

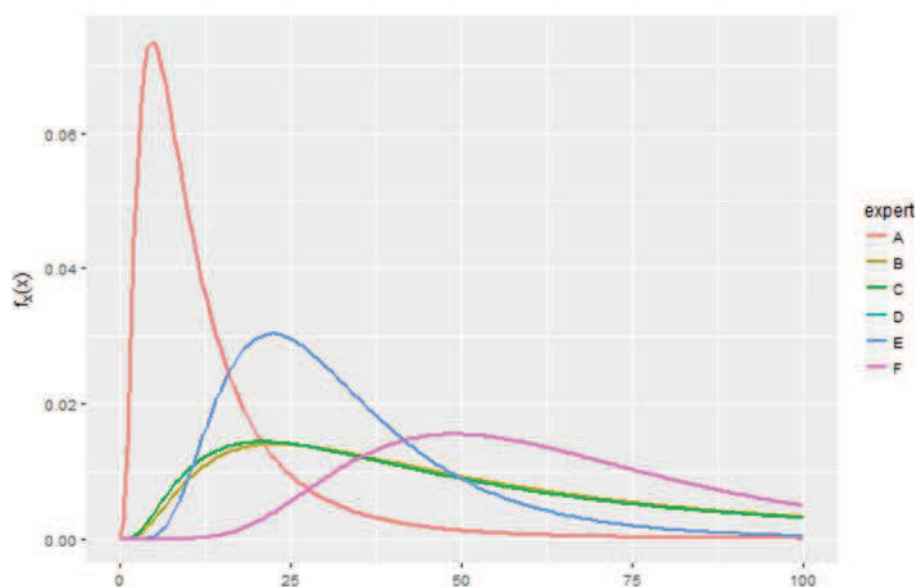


Figure 6 - Example fitting of example individual judgements fitted in SHELF v3.0.

Experts were asked to justify any different judgements to ensure that the range of judgements had been discussed openly. Following this, the group was asked to reach a 'group consensus' judgement (in the form of a probability distribution). It is important to note here (and stated clearly to experts), that there was no expectation

that the experts would reach complete agreement on a probability distribution for our QoI. That is because it is unlikely that there is one single distribution that would be accepted as perfectly representing the opinion of all experts. Instead, we asked experts to discuss and agree upon a distribution representing the reasoned opinions of a theoretical external observer, called a Rational Impartial Observer (or RIO). The RIO would not have identical views to any one of the experts but would instead find some merit in all the differing arguments or justifications – and give some weight to each. Using the SHELF software, this RIO consensus distribution was determined using either the *elicit* function (in cases where there were large disparities between individual expert judgements) or via a mathematical aggregation in which a weighted linear pool (where there was significant overlap in individual expert judgements).

The statistical analysis used to estimate the parameters of the relationships required by the iPCoD model from the results of this ‘effects of disturbance’ elicitation are described by Donovan et al. (2016).

3 Results

3.1 Elicitation scope and definitions

The workshop began with a series of presentations from the facilitator/PI (Booth) outlining the iPCoD model, the 2013 elicitation and outlining the scope of the elicitation. Following those discussions, John Harwood presented on the development and outputs of a generalised DEB model developed as part of the PCoD+ (ONR supported - N000141612858) project and some of the attending experts presented some of their research and reviews on how different species might be affected by noise and the effects of disturbance on critical life functions. As part of these discussions, the scope of the elicitation was defined.

3.1.1 What noise stimuli are we considering

As with the 2013 iPCoD elicitation, experts agreed we would focus on the potential for disturbance to be caused by exposure to low frequency broadband pulsed (LFBP) noise (e.g. pile-driving, airgun pulses).

3.1.2 How do we define disturbance for this elicitation?

We defined disturbance as when “the behaviour of the animals is classified as being disturbed when no feeding (or nursing) is taking place on the day of disturbance”, where possible, for a defined period of time - see section 3.1.3 and 3.1.4. This means that in a day of disturbance there is a period of zero energy intake for the disturbed individual.

3.1.3 Does disturbance affect different species differently?

Experts agreed that harbour porpoises, grey and harbour seals are likely to be sufficiently different in life history strategy and in their sensitivity to noise that the effects of disturbance on each group is likely to be different and were therefore, where possible, elicited separately.

3.1.4 How long do the effects of disturbance last in different species?

In general, the number of animals predicted to be disturbed during 1 day of piling is calculated using an estimate of the density of animals in a specified impact area around the piling activity (the same is typically true regarding calculating exposure to LFBP noise sources). The experts’ judgements for harbour porpoises were based on the assumption that, on average, the behaviour of the animals classified as being disturbed will be altered for 6 hours (within a single day – the day of disturbance), and that no feeding (or nursing) will take place during this time. This was agreed by experts following review of available information (including telemetry, aerial surveys, PAM surveys). This is described further in section 3.3.1. For seals, the experts considered that it was not

possible to define a discrete value for the number of hours in a day that disturbance effects are likely to last, due to a lack of evidence of significant behavioural responses for these species; experts cited a lack of knowledge of exactly if/how disturbance affects seals energy expenditure and intake. Consequently, experts' judgements for seal were based on the assumption that, on average, the behaviour of the individual seals classified as being 'disturbed' using this approach will be altered for much less than 24 hours by exposure to LFBP noise sources like pile-driving.

Experts noted that the 2013 elicitation outputs are very precautionary. This is because assuming a day of disturbance results in 24 hours of no foraging would be considered a very strong reaction. Experts felt that a more realistic length of disturbance would be much less than that (i.e. a day of disturbance results in less than a 24 hours cessation in foraging). Experts also stressed that, in their judgements, they were taking into account the potential interactive effects of multiple exposures to piling close together in time/space, or the possibility of displacement (even temporary) into areas where another anthropogenic stressor main impact them (or a natural stressor like local carrying capacity).

3.1.5 Does disturbance affect different age classes differently?

Through the course of elicitation and discussion it was agreed that the most likely effect of disturbance was on fertility and on the survival of young animals, particularly harbour porpoise calves and 'weaned of the year' (i.e. post-wean fast to first birthday) seals. Each class was elicited separately. Following extensive discussion among experts, having defined the disturbance we are considering in the workshop, no mechanisms were determined by which the survival of mature female or juvenile (> 1 year old) harbour porpoise or seals would be significantly impacted by disturbance (i.e. such that it would impact survival) and therefore it was agreed that these would not be elicited. This was also informed by the DEB model for harbour porpoises, which indicated that many days of disturbance (each day defined as 6 hours without energy intake) would be required to affect an adult porpoise's survival. Experts considered that the seal species were likely more robust to lost energy intake than harbour porpoises and so an even larger number of days of disturbance would be required. Therefore these were not elicited.

As a different approach was taken in 2018 compared to the 2013 elicitation, we have summarised the differences between the stage-classes in the two elicitations (note that bottlenose dolphins and minke whales were not within the scope of this workshop):

Parameter	Elicited in 2013	Elicited in 2018
harbour porpoise fertility	✓	✓
harbour porpoise calf survival	✓	✓ (see note 1)
harbour porpoise juvenile survival	✓	
grey seal fertility	✓	✓
grey seal pup survival	✓	- (see note 2)
harbour seal fertility	✓	✓
harbour seal pup survival	✓	- (see note 2)
grey seal juvenile survival	✓	✓ (see note 3)
harbour seal juvenile survival	✓	

Notes: 1. In 2018, it was agreed that the consideration of 365 days for harbour porpoise calf survival included the key period of sensitivity of weaning and the couple of months which follow (through to first birthday); after that period, animals were likely to be robust to disturbances being considered and, therefore, a separate elicitation for juvenile survival was not required.

2. In 2018, when considering dependent pup survival, experts thought that it was unlikely that pups would be exposed to disturbance unless a development was very close to a pupping site. Consequently,

a separate elicitation for this parameter was not completed. If near to a pupping site, the sensitivity would be similar to that for HP calves.

3. In 2018, the experts concluded that while the differences in resilience of grey and harbour seal fertility warranted two separate elicitations, the same did not apply to juvenile survival and so a single elicitation resulting in a distribution to be applied to either species was appropriate.

3.1.6 Elicitation question structure

In this elicitation we are interested in generating distributions that provide information on two parameters. Firstly, estimates (and associated uncertainty) on the number of days of disturbance that an individual of a species can 'tolerate' before it has any effect of their vital rates. That is, how many days of disturbance would an individual need to experience before a specific vital rate was reduced at all. Secondly we are interested in estimates (and associated uncertainty) of the number of days of disturbance the same individual would need to experience to reduce the vital rate to zero (i.e. for survival this means death, for fertility, this means no chance of producing a viable offspring). In order to achieve this, the experts were asked to provide judgements on two separate questions for each species-vital rate combination to capture estimates for the above parameters. These were named as question A and B respectively and subsequent probability distributions in section 3.3 reflect that.

3.2 Harbour porpoise

3.2.1 General discussion

Experts agreed that harbour porpoises would be more susceptible to the effects of disturbance than either of the seal species, due to the species limited energy stores and income breeder reproductive strategy (the costs of pregnancy and lactation are almost exclusively fuelled by recent energy intake). Most mature females of the species were considered likely to be producing one calf each year and so fuelling pregnancy and lactation simultaneously. The experts agreed that porpoises are generalist feeders and so prey on a wide range of prey species and that their tolerance or resilience to disturbance would be driven by the availability of suitable prey. Experts noted there was a wide variability in observed 'deterrence time' (i.e. the duration of disturbance) ranging from 2-36 hours, but agreed that on average the duration of disturbance by an event, i.e. when animals are not feeding, is likely to be much less than 24 hours (see also 3.3.2). This was based in data published by Brandt et al. (2018) and Van Beest et al. (2018). There was a lot of discussion about the foraging capabilities of the species, noting that the limited available data in this area indicates animals may forage mostly at night and have limited activity during the day, and therefore have some capacity not to feed for up to 12 hours (e.g. as observed in Wisniewska et al. 2016, Wisniewska et al. 2018). Similarly animals in captivity are not fed during the night (Kastelein, pers comm.).

In general, experts felt that juvenile animals would not be as efficient as adults in gathering food initially and this might be a mechanism by which young animals are impacted (though this was expected to be limited to the first year). Experts agreed that the birth period is the most critical as during this early stage calves are entirely dependent on their mother. In addition, the weaning period was identified as an important period as if foraging is impacted at this stage it could affect calf survival. This latter conclusion is supported by outputs from the DEB model (**Error! Reference source not found.**Figure 7), which suggest that the most significant effects of disturbance on maternal and calf energy reserves (and therefore potentially on their survival) occur during the second half of lactation, when calves are increasingly dependent on their own foraging efforts which are not yet as efficient as those of adults.

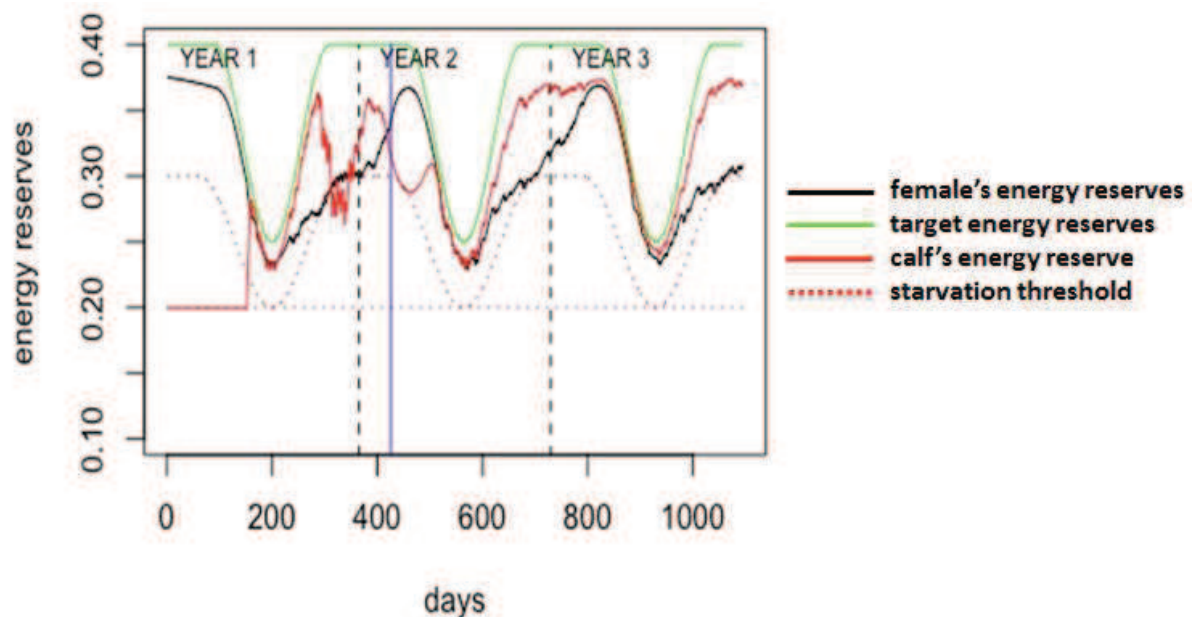


Figure 7 - Predicted changes in the energy reserves (expressed as a proportion of total body mass) of a female porpoise and the first calf she produces, over the course of three reproductive cycles (resource level = 2.37). The female and calf experience disturbance that results in no feeding for 6 hrs on 50 randomly spaced days during the lactation period (which runs from day 152 to day 426 for the first calf).

Therefore, the elicitation focused on the effects of disturbance on calf survival (covering the period post-weaning described above) and fertility. Juvenile (> 1 year old) and mature female survival were agreed to be unlikely to be significantly affected by disturbance (as by this developmental stage they are considered to be relatively robust), and this was supported by the DEB model.

3.2.2 Notes on the use of iPCoD

In general, the number of animals predicted to be disturbed during 1 day of piling is calculated using an estimate of the density of animals in a specified impact area around the piling activity (the same is typically true regarding calculating exposure to LFBP noise sources). As noted above, the experts' judgements were based on the assumption that, on average, the behaviour of harbour porpoises classified as being disturbed will be altered for 6 hours, and that no feeding will take place during this time. We note that, if the actual impact calculations used a threshold resulting in a shorter duration of disturbance, iPCoD is likely to over-estimate the population-level effects of the piling activity, because the individuals will probably be disturbed, on average, for longer than was assumed. Conversely, if a larger impact duration (i.e. disturbance lasting >6 hrs) was used in the impact assessment calculations, the population-level effects projected in iPCoD are likely to be under-estimates. Experts noted that they were not considering the potential interactive effects of multiple exposures to piling close together in time/space or possibility of displacement (even temporary) into areas where another anthropogenic stressor (or a natural stressor like local carrying capacity) may impact them.

3.2.3 Elicitation outputs

3.2.3.1 Effects on harbour porpoise fertility

Questions:

Harbour porpoise – **fertility**

- A. *“On the basis that an individual is disturbed and not feeding for an average of 6 hours, how many days of disturbance do you judge that a pregnant female harbour porpoise can ‘tolerate’, before the disturbance has any effect on its fertility.”*
- B. *“On the basis that an individual is disturbed and not feeding for an average of 6 hours, how many days of disturbance do you judge would be required to reduce the fertility of the same individual to zero.”*

Where ‘fertility’ is the probability of a successful birth.

The experts were asked to provide individual judgements (in isolation) on the effect of disturbance on harbour porpoise fertility. Following individual judgements, they were presented to the group and experts explored and achieved a RIO consensus as shown below (**Error! Reference source not found. A & B**).

Experts explored the different possible mechanisms by which harbour porpoise fertility could be impacted by disturbance (i.e. one that results in animals not feeding for an average of six hours). As the final third of the year is the most critical (the end of the lactation period for mothers and the beginning of new pregnancies), only in scenarios where animals received repeated exposure throughout the year this would result in significant impacts on fertility. Experts also agreed that it was very unlikely an animal would terminate a pregnancy early as typically the energy reserves of the mother tend to be sufficient (i.e. close to the target level) at this time of year.

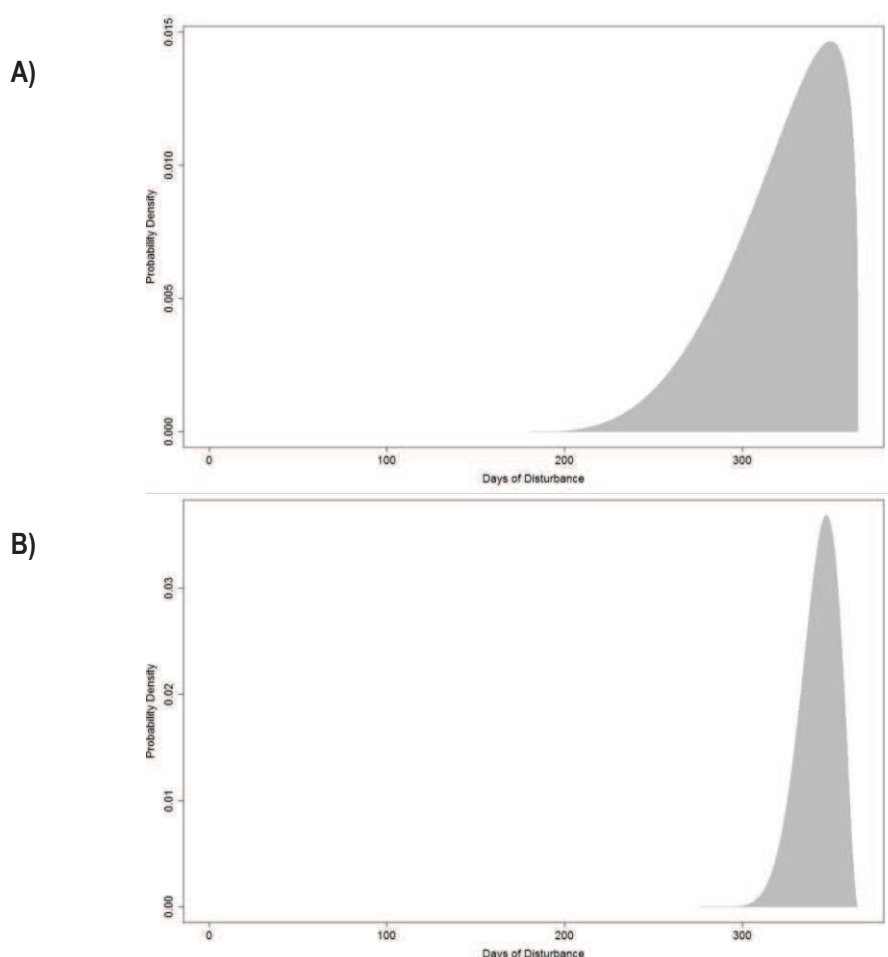


Figure 8 - Probability distributions showing the consensus of the EE for the effect of disturbance on harbour porpoise fertility - A) the number of days of disturbance (i.e. days on which an animal does not feed for 6 hours) a pregnant female could ‘tolerate’ before it has any effect on fertility and B) the number of days required to reduce the fertility of the same individual to zero.

3.2.3.2 Effects on harbour porpoise calf survival

Questions:

Harbour porpoise - **calf survival**

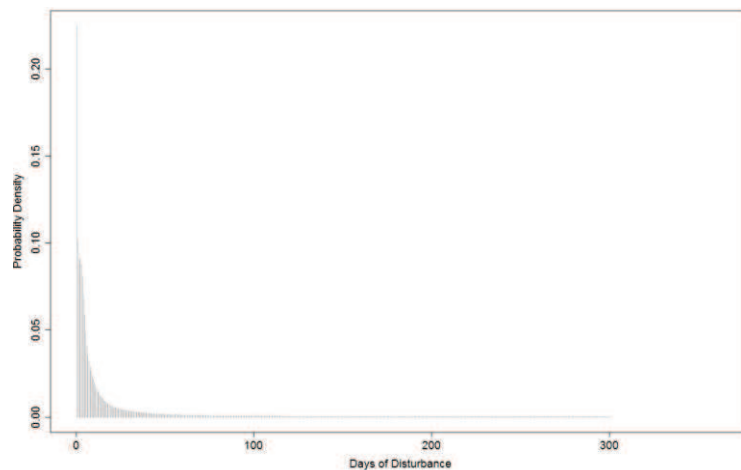
- A. “On the basis that an individual is disturbed and not feeding for an average of 6 hours, how many ‘days of disturbance’ do you judge that an individual **harbour porpoise** mother:calf pair can ‘tolerate’, before the disturbance has any effect on the calf’s probability of survival.”
- B. “On the basis that an individual is disturbed and not feeding for an average of 6 hours, how many ‘days of disturbance’ do you judge would be required to reduce the survival of the same calf to zero.”

Where a ‘calf’ is an individual <1 year-old.

The experts provided individual judgements before moving towards a RIO consensus shown below (**Error! Reference source not found.** A & B). Experts discussed and agreed that the most critical period for the calf is just after birth; during that period, target energy level is declining (because of increasing water temperatures) and energy requirements of the mother are lower. Experts considered it is unlikely that the mother cannot fulfil the milk need of the calf and because milk production by the mother is demand driven, the calf can also compensate as energy reserves drop. The difficult period was considered to be the 7-10 days of the calf’s life where any disturbance could have an effect, because the calf cannot miss a feeding period of 6 hours. The next sensitive period for the calf are the months before winter when it is still (partly) dependent on the mother and has to build up reserves (see Figure 7). At that time, the mother also has to build up her reserves and will reduce the milk supply as her reserves approach the starvation threshold (as under such a scenario her own survival will be prioritised over that of the calf).

With these discussions in mind, the experts considered that there are critical periods in the first year where calf survival could be reduced by a relatively small number of days of disturbance but that a moderate number of days would be required to reduce calf survival to zero (and these would be focused at the critical junctures identified above).

A)



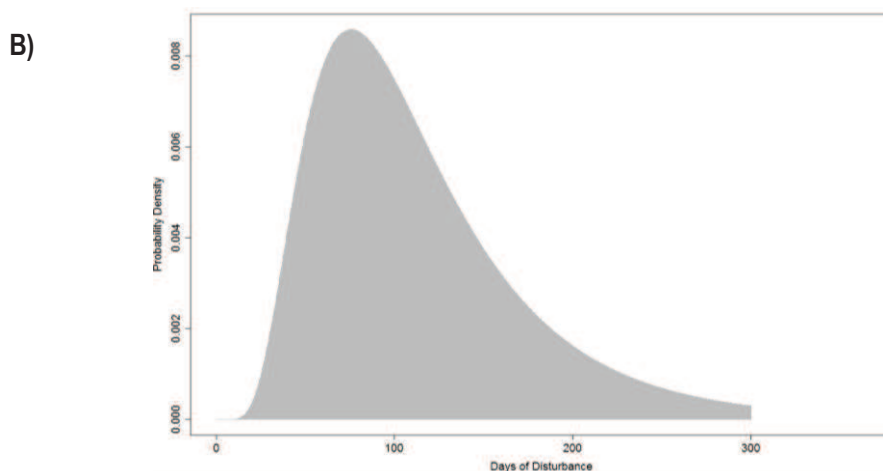


Figure 9 - Probability distributions showing the consensus of the EE for the effect of disturbance on harbour porpoise calf survival - A) the number of days of disturbance (of 6 hours zero energy intake) a mother:calf pair could 'tolerate' before it has any effect on survival and B) the number of days required to reduce the survival of the same individual to zero.

3.3 Harbour and grey seal elicitations

3.3.1 General Discussions

During the workshop experts discussed the knowledge base for considering the effects of disturbance on the two North Sea seal species. Experts agreed that whilst the species were well studied, in the context of assessing the effects of disturbance, there were relatively few studies from which to draw. First experts considered the first iPCoD elicitation, carried out in 2013, and agreed that these results are likely to be overly precautionary because it assumed that a day of disturbance results in a 24 hour period with no foraging (i.e. no energy intake during this period). Experts considered the true effects of disturbance were likely to be much more short-lived (e.g. Russell et al. 2016).

In general, both seal species were considered to have a reasonable ability to compensate for lost foraging opportunities due to their life history and adequate fat stores. Harbour seals were generally thought to be more sensitive than grey seals because of their smaller body size and because of their more 'intermediate' reproductive strategy (between income and capital breeder). They were also considered to be more sensitive to other stressors, potentially with a lower response threshold than grey seals. In both species, the post-weaning period was determined to be a sensitive period where disturbance (i.e. reduced energy intake) may impact survival. In harbour seals, juvenile animals were typically considered to be coastal foragers and so less likely to be exposed to disturbances.

During the workshop, the focus of the elicitation was agreed among experts that it should be on the most vulnerable vital rates to disturbance. These were identified (through discussions of species knowledge, life history strategies and in places supported by the DEB model) as fertility and the survival of 'weaned of the year' animals. Mature female survival and juvenile survival (>1 year) were considered to be unlikely to be significantly affected by disturbance. Whilst pups were also considered to have vulnerable periods, experts agreed it was extremely unlikely animals at this age would be exposed to disturbance, due to their proximity to land.

3.3.2 Notes on the use of iPCoD

In general, the number of animals predicted to be disturbed during 1 day of piling is calculated using an estimate of the density of animals in a specified impact area around the piling activity (see Box 1). The experts' judgements were based on the assumption that, on average, the behaviour of the individual seals classified as

being 'disturbed' using this approach will be altered for much less than 24 hours (though it was not possible to define a discrete value for the number of hours that disturbance effects are likely to last due to a lack of evidence of behavioural responses to noise for these species). Under these scenarios, disturbed animals will not feed (and therefore have no energy intake).

Box 1

We note that, if the actual calculations of the number of animals disturbed are calculated using a noise level threshold for a more intense (i.e. longer lasting) disturbance than we have considered here, iPCoD is likely to underestimate the population-level effects of the piling activity, because the individuals will be disturbed, on average, for longer than was assumed by experts. Conversely, if a threshold for a less intense disturbance was used in the impact assessment calculations, the population-level effects are likely to be overestimated. It was noted by experts that they were not taking into account the potential interactive effects of multiple exposures to piling close together in time/space or the possibility of displacement (even temporary) into areas where another anthropogenic stressor (or a natural stressor like local carrying capacity) may impact them.

3.3.3 Elicitation outputs

3.3.3.1 Fertility questions

Harbour seal and grey seal – **'fertility' (elicited separately)**

- A. "How many days of disturbance do you judge that a pregnant female harbour seal/grey seal can 'tolerate', before the disturbance has any effect on its 'fertility'."
- B. "How many days of disturbance do you judge would be required to reduce the fertility of the same individual to zero."

Where 'fertility' is the probability of giving birth to a pup that survives until the end of the post-weaning fast.

3.3.3.2 Effects on harbour seal fertility

The experts were asked to provide individual judgements (in isolation) on the effect of disturbance on harbour seal fertility. Following individual judgements, they were presented to the group and experts explored and achieved a RIO consensus as shown below (Figure 10 A & B). The main mechanisms the experts considered were that animals would acquire sufficient energy to grow a pup and to feed the pup satisfactorily when it is born. Experts considered that if animals were disturbed on feeding grounds this could have a greater effect than for animals that are transiting through an area (as any deviations and extra energy expenditure as a result was considered minor). Experts thought that a female in bad condition might not be able to feed the pup well and therefore moderate levels of disturbance might be sufficient to reduce fertility. However, experts agreed that females would need to be exposed to a moderate to high level of disturbance in order for fertility to be reduced to zero. The large amount of uncertainty in the range of days of disturbance required to reduce fertility reflected the uncertainty in how animals would be affected by disturbance.

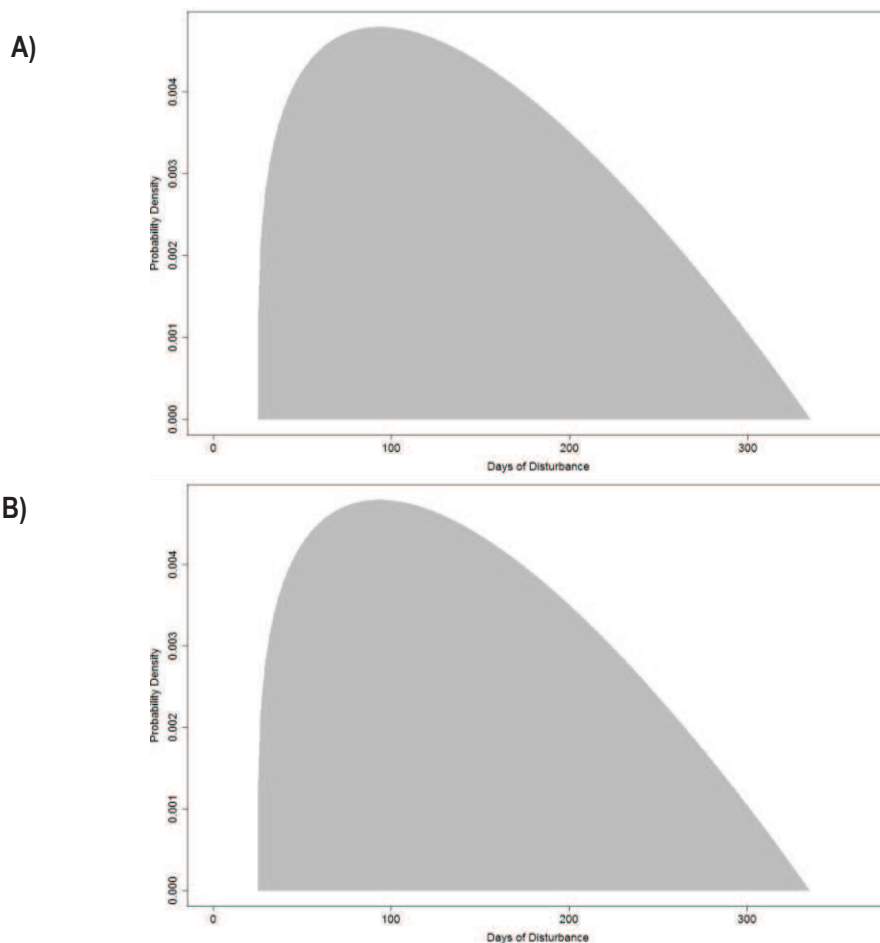


Figure 10 - Probability distributions showing the consensus of the EE for the effect of disturbance on harbour seal fertility- A) the number of days of disturbance a pregnant female could ‘tolerate’ before disturbance has any effect on fertility and B) the number of days required to reduce the fertility of the same individual to zero.

3.3.3.3 *Effects on grey seal fertility*

The experts were asked to provide individual judgements (in isolation) on the effect of disturbance on grey seal fertility. Following individual judgements being made, they were presented anonymously to the group and experts explored and achieved a RIO consensus as shown below (Figure 11 A & B). Experts indicated that in general, grey seals would be much more robust than harbour seals to the effects of disturbance. This was because they have greater energy stores to draw from and were considered to have more adaptable and/or generalist foraging strategies. Experts also noted that harbour seals would typically be considered to be more responsive to noise and that grey seals might be more tolerant (citing inter-species interactions between the two, harbour seals tended to leave when grey seals appear). Experts once again noted that it was unlikely that animals would ever be disturbed such that they would not feed for 24 hours and the species were generally robust to disturbance; as such, they would require a large number of days of disturbance to reduce fertility at all and extreme scenarios of repeated and significant disturbance in order to reduce grey seal fertility to zero. However, there could be a scenario in which feeding is disrupted on multiple sequential days and if this would occur, it might reduce animals’ body condition such that fertility could be impacted. If prolonged disturbance resulted in a move to a different foraging spot, this could be suboptimal for the individuals. We noted in the elicitation, insufficient time was allowed for refining the plausible limits for grey seal fertility, resulting in abrupt ends to the elicited probability distributions. This is unlikely to affect model forecasts in iPCoD, but should be avoided in future elicitations.

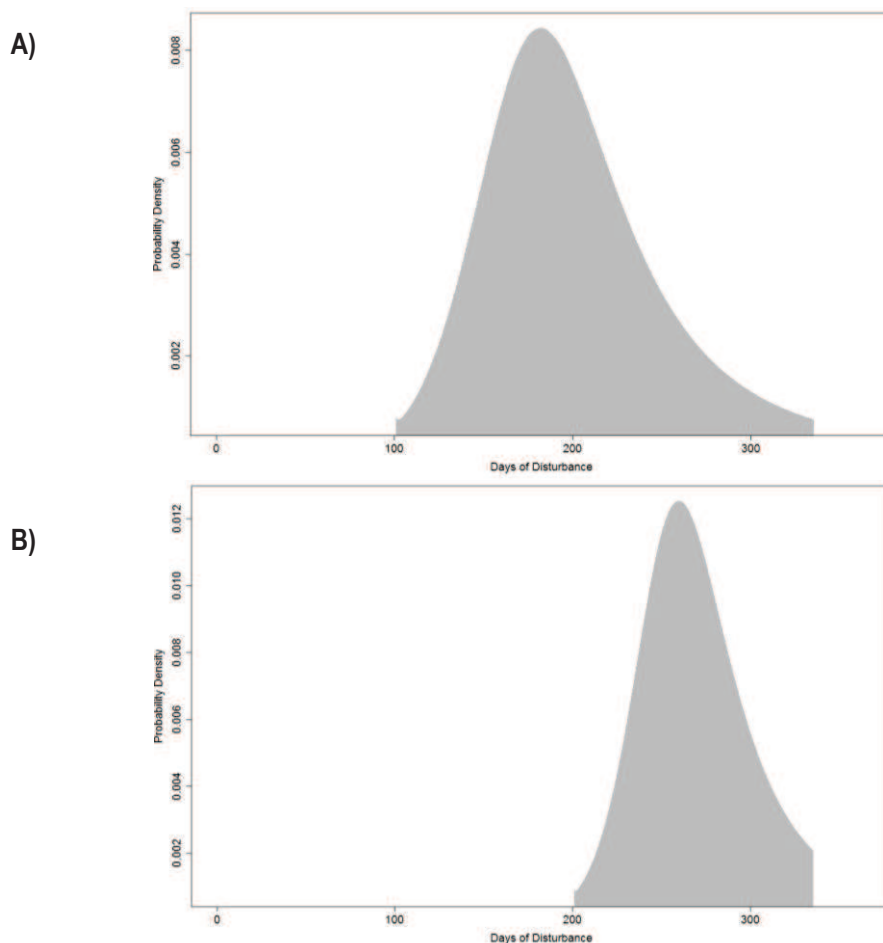


Figure 11 - Probability distributions showing the consensus of the EE for the effect of disturbance on grey seal fertility- A) the number of days of disturbance a pregnant female could 'tolerate' before disturbance has any effect on fertility and B) the number of days required to reduce the fertility of the same individual to zero.

3.3.3.4 Effects on seal 'weaned of the year' survival

Questions:

Harbour seal and grey seal – 'young of the year' survival (elicited together)

- A. "How many days of disturbance do you judge that a weaned young of the year **harbour seal/grey seal** can 'tolerate', before the disturbance has any effect on its probability of survival in the same year."
- B. "How many days of disturbance do you judge would be required to reduce the survival of the same individual to zero."

Where 'weaned young of the year' is an individual from post-weaning fast to 1st birthday.

The experts were asked to provide individual judgements (in isolation) on the effect on 'weaned of the year' survival (for grey and harbour seals combined). Following individual judgements being made, they were presented anonymously to the group and experts explored and achieved a RIO consensus as shown below (Figure 12Error! Reference source not found. A & B). Experts indicated that a pup is given a lot of fat by its mother, that both species undergo a post-weaning fast whilst on land (2-3 weeks in grey seals, 2-2.5 weeks in harbour seals) and that following this fasting there is a 2-3 month window in which animals will be particularly vulnerable to missed foraging opportunities as a result of disturbance; during this time, it might only take a small number of days to reduce the probability of survival. There was a broad range of values representing the uncertainty in this phenomenon and because there is likely to be large variation between years (driven by

environmental variability affecting mother condition). We noted in the elicitation, insufficient time was allowed for refining the plausible limits for grey seal fertility, resulting in abrupt ends to the elicited probability distributions. This is unlikely to affect model forecasts in iPCoD, but should be avoided in future elicitations.

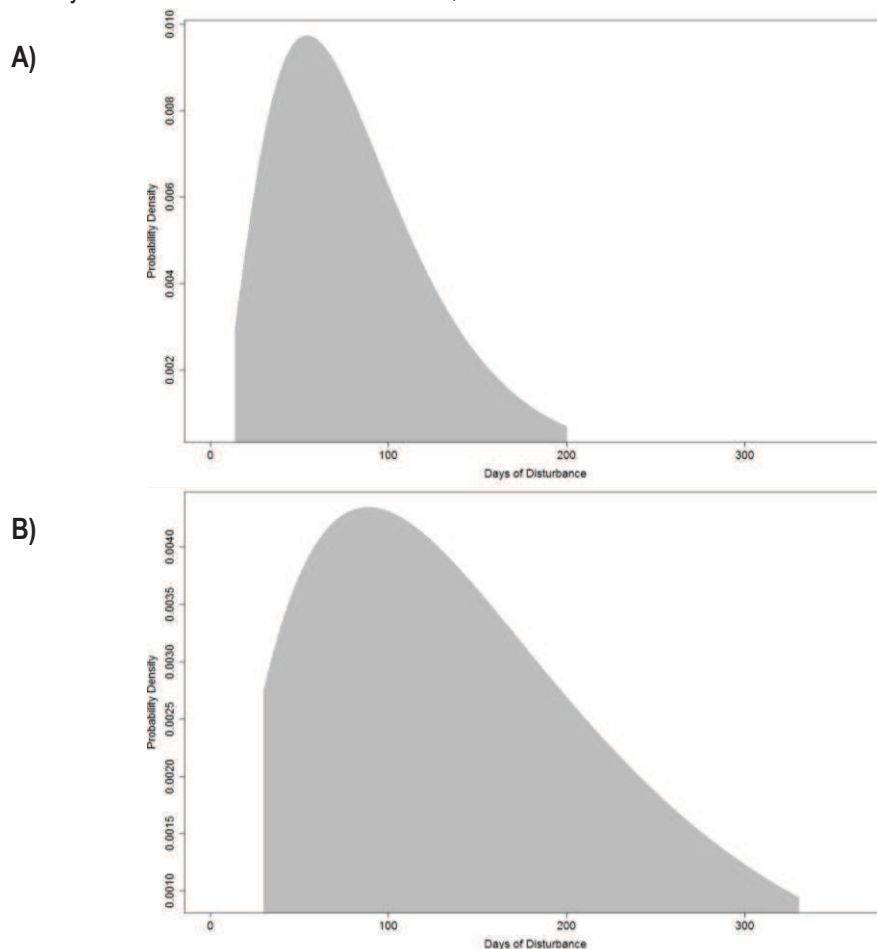


Figure 12 - Probability distributions showing the consensus of the EE for the effect of disturbance on harbour and grey seal 'weaned of the year' survival - A) the number of days of disturbance such a seal could 'tolerate' before it has any effect on survival and B) the number of days required to reduce the survival of the same individual to zero.

4 Discussion

Experts indicated that the effects of disturbance as a result of exposure to LFBP noise had the potential to affect survival and fertility but the distributions elicited were species- and stage class-specific. Grey seals were considered to be the most tolerant of the three marine mammal species for which distributions were elicited and this was broadly due to their foraging behaviour and life history strategy. Harbour seals were generally more susceptible than grey seals but more robust to disturbance than harbour porpoises. Because experts identified that fertility and survival of calves/weaned of the year were the most vulnerable stages, in general it is expected that the new transfer functions derived in this exercise indicate changes compared to the earlier expert elicitation and therefore will be reflected in new iPCoD scenarios (also because some vital rates were not considered likely to be affected, they've been removed from the model – which results in fewer animals likely to be disturbed such that it affects their survival). For most species the effects of disturbance are likely to be slightly reduced compared to the 2013 elicitation, because overall the experts judgements were that animals of each species were more tolerant of the effects of disturbance following the discussions in the 2018 elicitation workshop. Overall, experts identified that both the seal species were more difficult to carry out elicitations for than harbour

porpoise due to a lack of evidence of significant behavioural responses for these species. A DEB model for the seals species is missing, but experts noted that for porpoises the results of the model helped in guiding more informed judgments for harbour porpoise. Construction of the model involved compiling the data available (as parameter inputs) which experts would be considering (and indeed many of the experts in attendance had been involved in the data collection) and provided a means of visualising the variations in condition throughout the year and potential effects of reducing feeding opportunities on individuals in different life stages.

Harwood et al (2014), with respect to the iPCoD model and original elicitation, highlighted: *“This expert elicitation process was designed specifically to provide parameter values for the functions that form part of the [iPCoD] model. Those values should not be used to infer how disturbance might affect vital rates outside of the context of this model. In addition, the expert elicitation and the subsequent analysis of the results from the elicitation process were designed to capture the uncertainty expressed by individual experts, and the variability among experts in their opinions. It would therefore be entirely inappropriate to derive simple summary statistics from this analysis.”* As such, we recommend that the probability distribution outputs of this expert elicitation should be used as part of iPCoD simulations. Furthermore, we also concur with the statement made in 2014 stressing *“the interim nature of this approach, which was developed to deal with the current situation, where there are limited data on the way in which changes in behaviour and hearing sensitivity may affect the ability of individual marine mammals to survive and to reproduce. The research that is needed to improve our knowledge and understanding of these processes has been identified by Harwood and King (2012) and some of this work is currently underway.”*

Following the successful update of the disturbance–vital rate transfer functions (i.e. the relationship between animals experiencing disturbance and their vital rates potentially being affected, Figures 5-10 above), the new distributions have been integrated into the iPCoD software and made publicly available via download of the tool.

4.1 Next steps

The utility of such a model for the other species in the iPCoD model (harbour seal, grey seal, bottlenose dolphin and minke whale) to support (and eventually replace) future expert elicitation was discussed and is described below. Experts agreed that the inclusion of bioenergetics models in the expert elicitation process was an important aid. Such a model was available only for harbour porpoise at the time of the workshop, but the available models could be developed for other species such as bottlenose dolphin, minke whale and also the two North Sea seal species. The development of these kinds of bioenergetics models could also advance PCoD modelling and be used to prioritise research within the PCoD framework. We recommend that research effort is directed to address the knowledge gaps currently estimated using expert elicitation (for both the effects of PTS and disturbance on vital rates). It is assumed that not all knowledge gaps will be filled and as with the new (2018) elicitation updating the 2013 transfer functions, there will likely be value in revisiting the 2018 elicitations, in light of new learning. However, we once again stress that the focus on funding research studies to replace the elicited relationships with empirically derived ones and, where appropriate, validating the existing relationships.

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6 Appendix 1 - Glossary

Below is the glossary of acronyms and terms used in the Interim PCOD protocol (from Harwood et al. 2014).

Acronym / Term	Definition
Acute effect	The direct effect of a change in behaviour or physiology on vital rates
Body condition	A measure of an individual's energy stores. In marine mammals, usually blubber thickness or total body lipid
Chronic effect	The indirect effect of a change in behaviour or physiology on vital rates via individual health.
Delphi process	An established process whereby experts are asked to reconsider their opinions in the light of what other experts have said in answer to the same set of questions
DEB model	Dynamic Energy Budget model. Here describes the way in which the life history processes (growth, reproduction and survival) of a female and her calves depend on the way in which assimilated energy is allocated between different processes.
Expert elicitation	A formal technique for combining the opinions of many experts. Used in situations where there is a relative lack of data but an urgent need for conservation decisions
Fertility	The probability that an individual adult female will give birth to a viable offspring in any particular year
Fitness	A relative term reflecting the potential contribution of the genotype of an individual to future generations. The fittest individuals leave the greatest number of descendants relative to the number of descendants left by other individuals in the population
Health	All internal factors that may affect individual fitness and homeostasis, such as condition , and nutritional, metabolic, and immunological status
NRC	National Research Council of the United States National Academy of Sciences
ONR	US Office of Naval Research
PCAD	Population Consequences of Acoustic Disturbance
PCOD	Population Consequences of Disturbance
PTS	Permanent Threshold Shift: a non-recoverable elevation of the hearing threshold that occurs under conditions that cause a 40dB temporary shift in the threshold (TTS) for hearing at a particular frequency
RIO	Rational Impartial Observer. A term used in Expert Elicitation: The RIO would not have identical views to any one of the experts but would instead find some merit in all the differing arguments or justifications
Uncertainty	Incomplete information about a particular subject. In this report, we are only concerned with those components of uncertainty that can be quantified
Vital Rates	The probability that an individual will survive from one year to the next, the probability that an individual adult female will give birth in one year

7 Appendix 2 – Expert Background

Prior to the expert elicitation, in alignment with the SHELF protocol, we asked experts to provide a brief summary of their background and highlight any vested interests in the expert elicitation process on the consequences of disturbance.

Garry Stenson is a research scientist employed by Fisheries and Oceans, Canada. Success in this project will benefit me by providing a method that can be applied in a Canadian context. He carries out research on the ecology and abundance of marine mammals in the North Atlantic, particular ice breeding seals. A major focus of his research is on factors influencing reproductive rates in harp seals.

Fredrik Christiansen's PhD and most of his postdoctoral research focuses on understanding the population consequences of disturbance on marine mammals, in particular baleen whales. As part of this research he is trying to understand the relationship between body condition and vital rates (survival and reproduction), and identify the lower thresholds in body condition at which survival and reproduction is compromised. Knowledge of this threshold will help determine the level of disturbance required to negatively affect the vital rates of baleen whales. He identified no conflict of interest in relation to the outcome of the elicitation workshop on the effects of disturbance on North Sea harbour porpoises, harbour seals and grey seals.

Carol Sparling's research history focuses on the energetics of grey seals and she has extensive experience in assessing the effects of anthropogenic noise on marine mammal species. She is a colleague of PI Booth, working for SMRU Consulting, a marine mammal consultancy.

Christina Lockyer's field of expertise relates to harbour porpoises life history - age, growth and reproduction - and aspects of feeding and bioenergetics. Possible stakeholder interests might include involvement in any future projects related to this seminar/workshop, should there be funding opportunities for specific tasks related to my field of expertise.

Ailsa Hall's expertise is in factors affecting survival (disease, exposure to contaminants and toxins and physiological constraints etc.). She stated: "I do not have any vested interests as I am not a stakeholder in any wider processes, my role at SMRU is to provide independent expertise scientific advice to a wide range of stakeholders from governments and their agencies to NGOs and other charitable organisations."

Ron Kastelein has experience with hearing, behavioural response, and energetics studies with harbour seals and harbour porpoises. His company, SEAMARCO, has no vested interest in the EE.