DTU Aqua
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Lotte Kindt-Larsen, Magnus Wahlberg, David Lusseau, Floris van Beest, Mollie E. Brooks, Thomas Noack, and Gildas Glemarec

DTU Aqua Report no. 480-2025

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Cover photo: Harbour porpoise photographed in Romsø study area. Photo: Hèloïse Hamel

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Preface

The work presented here was funded by the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency via the project 'Reduction of harbour porpoise bycatch in protected area/Reduktion af marsvine-bifangst i områder, hvor marsvin er beskyttede' (grant agreement number 33113-B-17-097). The project leader was Lotte Kindt-Larsen, and the project was carried out in cooperation with University of Southern Denmark and Aarhus University. The project period was from 2018 to 2022.

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1 Summaries

1.1 Danish summary

Projektets overordnede formål var at undersøge hvorledes marsvins adfærd påvirkes i forhold til akustiske alarmer, såkaldte pingere. I projektet er der lagt vægt på undersøgelser af pingers effektive rækkevidde, hvordan marsvin reagerer på pinger signalerne, modeller for hvordan marsvin påvirkes af pingere og fysiske drone observationer af pingernes effekt. Yderligere har der været fokus på at monitere bifangster af marsvin i Nordsøen.
Projektet har været opdelt i 5 arbejdspakker:
Arbejdspakke 1: Observation af marsvin i forhold til forskellige nye pingertyper.
Arbejdspakke 2. Afstandsforsøg med nye pingertyper i fiskeriet.
Arbejdspakke 3: Bifangst af marsvin og langtidseffekt af pingere i Nordsøen
Arbejdspakke 4. Modellering af pingernes effekt.
Arbejdspakke 5: Formidling af viden

Arbejdspakke 1 havde som hovedformål at observere hvordan marsvin påvirkes af forskellige pingere. Arbejdspakken har først lavet kontrollerede målinger af pingerne for at have retvisende data for hvilke lyd-landskaber marsvinene udsættes for, når de svømmer ind i områder, hvor der anvendes pingere. I alt er der undersøgt fire pingere, som viser store variationer i både lydstyrker og frekvenser. Arbejdspakke 1 har også lavet direkte observationer af marsvin ved brug af droner. Arbejdet har bestået i at nedsænke pingere i nærheden af vilde marsvin. Herefter er marsvinens adfærd blevet studeret når pingeren er blevet aktiveret. Resultatet har vist, at pingere kan forårsage meget stærke af undgåelsesreaktioner, hvilket forklarer pingernes effektivitet i at reducere bifangst, når de anvendes i fiskeriet. Forsøget viste dog også, at 25% af dyrene ikke reagerede på pingerne hvilket antyder, at der er stor diversitet i marsvins affærdsreaktioner i forhold til pingere. Resultaterne peger dog på vigtigheden af at forstå pingernes effekt før de fx implementeres i områder, som er vigtige for marsvin.

For at undersøge pingernes langtidsvirken blev der sat lyttebøjer på forskellige afstande fra en specielt designet pinger, som var henholdsvis tændt og slukket. Hvert forsøg varede 2-6 måneder og blev foretaget på to forskellige lokaliteter. Derved kunne det undersøges hvor effektive pingers er til at holde marsvin på afstand. Der blev afprøvet to typer af ‘banana pingers’ med lydsignaler ved 40-70 kHz. Resultaterne fra dette er indbygget og brugt under arbejdspakke 4.

Arbejdspakke 2 har haft som hovedformål at udføre forsøg med forskellige afstande mellem pingere i fiskeriet. Årsagen er, at en øget afstand mellem pingere vil bidrage til at nedsætte fiskeriets udgifter til indkøb af pingere og reducere udledningen af støj. I alt er der blevet udført 3 forsøg. Det første blev udført i 2020 men pga. Covid19 blev samarbejdet udfordret, da DTU ikke havde mulighed for at instruere fiskeriet ordenligt i, hvordan forsøget skulle udføres. Resultaterne fra dette forsøg var derfor ikke valide. I 2021 blev det andet forsøg udført. Her blev forsøg udført hvor pingerene var sat med afstande på henholdsvis 200 og 500 meter. Resultatet viste, at når pingerene var sat med en afstand på 200m blev bifangsten reduceret med 90%, hvor når pingerne blev sat med en afstand på 500m, reducerede de bifangsten med 51%. Da usikkerheden på de 90% reduktion ved 200 meters afstand var stor og effekten ved 500 m afstand er lille, blev der udført endnu et forsøg i 2022. Her blev pingere igen sat med 200 og 500 meters afstand. Yderligere blev der fremstillet en ny type pinger, med et højere lydniveau, i håb om at øge effektiviteten, når pingerne blev sat med 500meters afstand. Resultaterne viste et fald i effektiviteten både når pingerne blev sat med 200 og 500meters afstand til henholdsvis 51 og 36%. De nye pingerne med et højere lyd niveau viste dog en reduktion på 77%. Årsagen til den lavere effekt i 2022 er ukendt. Men fiskeren observerede et særligt stort antal marsvin og juvenile makreller i perioden. Dette kan have forsaget, at marsvinene haft deres sonar fokuseret på føde og derved ikke har haft opmærksomheden rettet mod lydene, og kun når lydniveauet har været højt nok, har de undgået garnet.

Arbejdspakke 3 har fokuseret på monitering af bifangst i Nordsøen, da kun observationer af ældre dato findes for bifangster i området. Denne arbejdspakke har derfor fokuseret på at indhente nye data omkring bifangsten af marsvin i Nordsøen. I 2019 indgik DTU Aqua et samarbejde med et kommercielt fartøj der udelukkende fisker med garn I Nordsøen om at monitere bifangster af beskyttede arter, herunder marsvin. Fartøjet fik derfor installeret et kamera overvågningssystem og fartøjet er blevet moniteret fra 2019-2022. I alt er der moniteret 584, 756 og 628 dage i henholdsvis 2019, 2020 og 2021. De reelle tal er ikke angivet i rapporten, selvom DTU Aqua er i besiddelse af disse, da dataet er af særligt sensitiv karakter. Men alle data er indrapporteret til ICES og er anvendt i modelleringer for den totale bifangst af marsvin for Nordsøen.

Arbejdspakke 4 har undersøgt hvorledes marsvine populationen påvirkes når/hvis pingere implementeres i fiskeriet. Her er dels data fra arbejdspakke 2 blevet anvendt, men særligt har arbejdet fokuseret på, at udvikle modeller og udføre forskellige simuleringer til at besvare dette. Modelleringsarbejdet viste, at selvom pingerne kan være en effektiv forvaltningsmetode, er det vigtigt, at overveje implementeringsplanen, da effektiviteten af planen afhænger af denne. Hvis der fx er en lav anvendelse af pingerne og de derfor ikke virker optimalt, kan dette modvirke gevinsterne ved reduceret bifangst. Denne sidstnævnte effekt er sandsynligvis medieret af en indflydelse på reproduktionshastigheden. For at opdage denne effekt vil det derfor være nødvendigt at sikre, at overvågningsprogrammer omfatter observationer, der gør det muligt at estimere denne parameter ud over estimering af bifangstraten. Et sådan tiltag vil sikre, at fiskeriet ikke er den eneste faktor, der kan hjælpe med at nå bevaringsmålene for marsvin.

Arbejdspakke 5 har sørget for at resultaterne fra projektet er blevet videreformidlet. Dette har medført følgende: Videnskabelige artikler (5), hvoraf 2 allerede er publicerede, konference bidrag (4), møde præsentationer (4) og præsentationer i arbejdsgrupper (3).

1.2 English summary

The overall purpose of the project was to investigate how the behavior of harbor porpoises is affected in relation to acoustic alarms, so called pingers. In the project, the main focus was on studies of the effective range of pingers, their long-term effects, how porpoises reacts to the pinger signals and models of pingers effect on porpoises. Furthermore, monitoring of porpoise bycatch of porpoises have been conducted in the North Sea.

The project has been divided into 5 work packages:
Work package 1: Observations of porpoises in relation to different pinger-types.
Work package 2. Distance trials with new types of pingers in the field
Work package 3: Bycatch of porpoises and long-term effects of pinger use in the North Sea

Work package 4. Modeling the pinger effect.
Work package 5: Outreach of the project.

The main task of Work package 1 was to observe how porpoises were affected by different pingers. The first part conducted acoustic measurements of the pingers in order to have accurate data for which soundscapes the porpoises are exposed to when they swim into areas where pingers are used. In total, four pingers have been examined. These show large variations in both in source level and frequencies. Work package 1 furthermore conducted direct observations of porpoises using drones. Here pingers were deployed in the vicinity of wild porpoises and the behavior of the porpoises was then followed when the pinger was activated. The results showed that pingers can cause very strong avoidance responses, which explains the effectiveness of the pingers in reducing bycatch when used in fisheries. However, the experiment also showed that 25% of the animals did not respond to the pingers, which suggests that there is great diversity in porpoises' behavioral reactions to pingers. However, the results point to the importance of understanding the effect of the pingers, for example if they are implemented in areas that are particularly important for porpoises.

To investigate the long-term effectiveness of pingers, acoustic recorders were deployed at different distances from a specially designed pinger. The pinger emitted sounds in on and off cycles. Each trial lasted 2-6 months and was repeated at two locations. In this way, it was possible to investigate, how effective pingers are in keeping porpoises at a distance. Two types of 'Banana pingers' with sound signals at 40-70 kHz were tested. The results were used under WP 4.

The main purpose of Work package 2 was to test the effectivity of the pingers when the spacing between the pingers was increased. The reason is that an increased distance between pingers can reduce fishing expenses for the purchase of pingers and reduce the emission of noise pollution in the sea. A total of 3 experiments were conducted. The first trial was carried out in 2020, but due to Covid19 it was not possible to make a proper setup. The results from this trial were therefore invalid. In 2021, the second attempt was carried out. Here, pingers were set with 200 and 500 meter spacings. The result showed, that when the pingers were set with 200m distance, they reduced the bycatch of porpoises by 90%, while when the pingers were set with 500m spacing, they reduced the bycatch by 51%. The 90% reduction, however, showed large uncertainties. Thus, a third trial was conducted in 2022. Again, the pingers were set with 200 and 500 meter spacings. In, however, collaboration with the manufacturer, a new type of pinger with a higher sound level was made. The idea was to increase the efficiency when the pingers were set with 500m distance. Unexpectedly, the results from the last trial showed that the pingers were less effective both when the pingers were set with 200 and 500 meter spacings (51 and 36% reduction respectively). However, the new louder pinger with the higher source level showed a reduction of 77%. The reason for the low effect in 2022 is unknown. However, the fishers observed large numbers of porpoises and juvenile mackerel during the period. This could suggest that the porpoises had their sonar locked on prey items and thereby only played attention when the source level was loud enough.

Work package 3 focused on monitoring bycatch in the North Sea. In 2019, DTU Aqua and a commercial gillnet fishing vessel began a collaboration to monitor bycatch of protected species including porpoises. The vessel had a camera surveillance system installed and the vessel has been collected video footage during the full trial of the project. A total of 584, 756 and 628 days have been monitored in 2019, 2020 and 2021 respectively. The data processing from 2022 is still ongoing as the fisher has decided to continue the data collection despites the project has ended. All data has been reported to ICES and are used in modeling of the total bycatch of porpoise for the North Sea.

Work package 4 has investigated how the porpoise population is affected when/if pingers are implemented in the fishery. Here, data from work package 2 has been used, but the work has also focused on developing models and carrying out various simulations to answer this.
In the modeling work, it was found that the pingers can be an effective management intervention to reduce bycatch. However, it was also shown that when designing such a management intervention, it is important to consider the implementation plan, as the effectiveness of the plan depends on it. If, for example, there is a low use of pingers on the net and they therefore do not work optimally, this can counteract the gains from reduced bycatch. This latter effect is probably mediated by an influence on the reproduction rate. In order to detect this effect, it will therefore be necessary to ensure that monitoring programs include observations that make it possible to estimate this demographic parameter in addition to estimating the bycatch rate. Such a measure will ensure that fisheries are not the only carrier of management interventions to help achieve conservation objectives for these species.

Work package 5 has applied for the results from the project to be further disseminated. This has resulted in the following: Scientific articles (5), of which 2 have already been published, conference contributions (4), Meeting presentations (4), Presentations in working groups (3).

2 Introduction

Within the EU, favorable conservation status of the harbour porpoise is enacted by several EU legislations. The reason is mainly the risk of bycatch within the gillnet fisheries, which may have effects on the status of several populations. Even though gillnet fisheries are considered as low impact fisheries due to little seabed impact, high selectivity and low fuel consumption (Suuronen et al. 2012), some gillnet fisheries have high bycatch rates of harbour porpoises and other marine mammals and sea birds (Lewison et al. 2014). In European waters the harbour porpoise is protected with the Habitat Directive both as an Annex II and Annex IV species implying that the populations have to be maintained at favourable conservation status and deliberate actions of killing, disturbance and habitat deterioration shall be prohibited (EC 1992). All Annex II species will further be protected by a spatial network called Natura2000. The driving forces behind Natura2000 is, besides the Habitat Directive, the Bird Directive (EC 1979), which purpose is to protect biodiversity. According to the Natura2000 framework, EU member states are obliged to nominate candidate protected areas in their waters to the EU Commission and within 6 years establish legislation to implement the areas as special areas of conservation and prepare management plans (EC 2007).

Furthermore, the regulation on the conservation of fisheries resources and the protection of marine ecosystems through technical measures (EU 2019) require EU Member States to develop and implement measures to reduce the bycatch hereunder the use of acoustic alarms, so called pingers. The idea behind the pinger is to have an aversive effect and displace the porpoises from the vicinity of the pinger (Dawson et al. 2013). One of the first studies demonstrating a positive effect of pingers was conducted as a field experiment in the Gulf of Maine gillnet fishery. The study was designed as a blind controlled experiment, testing if bycatch of harbour porpoise could be reduced by using Dukane NetMark1000 pingers (source level 132dB re 1 µPa@1m, frequency 10kHz). There was a significant reduction (85%) in bycatch of harbour porpoises when pingers were used (Kraus et al. 1997). Since then, many more studies have tested the effect of different types of pingers. Dawson et al. (2013) reviewed 14 experiments on effect of pingers on porpoise bycatch. Only three studies did not have statistical power to conclude any bycatch reducing effect of the pingers. The reasons for the missing effect were lack of bycatch on both pinger and control nets (Carlström et al. 2002), pingers having several faults (Northridge et al. 1999) and small sample size (Morizur et al. 2009). Due to the many positive results in reducing the bycatch of porpoises in gillnets fisheries, IWC (2000) and Dawson et al. (2013) thus concluded that pingers do reduce bycatch of porpoises and further experimentation on pinger effects in reducing bycatch of porpoises is unnecessary.

Even though pingers are very useful in reducing bycatch of harbour porpoise, there are some important issues that need to be considered, hereunder effective range, habituation, habitat exclusion, appropriate pinger spacing, effects on the population, functionality and enforcement. The purpose of this project was to investigate how the behavior of porpoises are affected in relation to pingers. In the project, the focus was mainly on investigations of the effective range of the pingers, habituation effects and how the porpoises are affected by the pingers on a population level.

The project was built into five sections. WP 1: “Observation of porpoises in relation to pinger-types" serves to investigate how porpoises react to pingers on a very fine scale. WP 2: “Distance trials with new types of pingers in the field”, will test how increased pinger spacing affects the bycatch level. WP 3: “Bycatch of porpoises and long-term effects in the North Sea” investigates bycath in the North Sea where WP 4: “Modelling of the pinger effects” will use models to investigate the effect of pinger use. Last WP 5: “Outreach of the project” will descibe where the knowledge obtained in the project has been presented.

3 Observations of porpoises in relation to different pinger-types (WP1)

3.1 Introduction and objectives

In terms of reducing bycatch of harbour porpoises pingers have shown to be a very effective tool (Dawson et al. 2013). Overall, three main types of pingers have been developed, 1) the “constant” deterring pinger; 2) the “randomized” deterring pinger and 3) the “alerting” pinger. The “constant” has a constant frequency at 10kHz with multiple harmonics and pulses played every 4 second (Kraus et al. 1997). The “randomized” use a range of frequencies e.g. 50—120 kHz and radomized signals (Larsen et al. 2013) whereas the “alerting” pinger plays signals around 133 ± 8.5 kHz and emits series of one to three signals at random followed by a randomised pause of 4–30 s (Chladek et al. 2020).

Most assessment of pinger efficiency to reduce bycatch and alter the behaviour of porpoises have focussed on the effect on bycatch in commercial fishing trials.

Fine-scale porpoises behavioural response to pingers has only been studied to a small extent. Such data may be important for better understanding how to avoid porpoises being bycaught. One reason for the few behavioural studies is that porpoises are difficult to observe in the wild as they spend most of their lives below the surface. Recent developments in passive acoustics, tags and drones indicate that such techniques may be very useful when studying cetacean behaviour.
Despites pinger are implemented by EU the regulation they have only been used to as less extent in Danish waters (EU 2019). A large part of the Danish fishing fleet are not covered by the regulation as many vessels are below 12 meters. In addition, the enforcement of boats covered by the regulation has not been effective. If, however, pingers were to be used more frequently, for example within Natura200 sites there would be an increasing risk of both habitat exclusion or habituation to pinger sounds. Therefore, more knowledge on how pingers affect fine-scale behaviour of porpoises is needed.

The objective of WP1 is to gather knowledge on how porpoises behave in relation to different pinger types, by using both drones and passive acoustics to observe the animals.

3.1.1 Pinger measurements

Methods

Four different commercially available pingers were measured during 5 min at a depth of 1 m, with a hydrophone (TC4014, Reson Aps.) placed at 1 m distance horizontally along the normal to the pinger axis (the pinger was held vertically in the water). The hydrophone was connected via a custom-made amplifier and filter (30 dB, 0.1-200 kHz 4-pole filter) to a NI USB-9162 and further by USB to a laptop running a custom-made Labview program (ver. 2021; National Instruments; programmed by Alain Moriat). Analysis was made in a custom-made Matlab program (ver. 2022; Mathworks, Inc.). The hydrophone had previously been calibrated by reciprocity calibration in the frequency range from 30 to 150 kHz. For each signal, the duration was extracted using a 95% energy window, from which also the RMS source level was estimated. Spectral analysis was made by using an FFT covering the entire signal (frewquency resolution varying, but around or below 1 Hz). Spectrograms were plotted using 512 points, Hanning window and 50% overlap.

Results/discussion

The pinger parameters are given in Table 1. The source level did not vary significantly between the Aquamark100, Banana and Future Oceans pingers, whereas it was much reduced in the PAL pinger. The PAL pinger also had a much higher frequency content than the other pingers. This is all explained by the fact that the PAL pinger is supposedly working as an alerting, rather a scaring, device. The duration of the signals are all longer than measured hearing integration times of porpoises, indicating that they the detectability of the signals are optimized.

Table 1. Results of calibrations of pingers. Values are mean, followed by min and max in parenthesis. Minimum and maximum frequency is estimated as the lowest –10 dB and highest –10 dB points re frequency peak in the signal power spectrum.

	Aquamark 100	**Banana**	**Future Oceans**	**PAL (Baltic)**
Number of signals	25	41	81	29
Number of signal types	8	8	4	1
Signal interval (s)	12 (3.8-23)	7.5 (3.0-12)	4.2 (4.2-4.2)	11 (1.2 -29)
Source level (dB re 1 µPa rms @ 1m)	127 (125-128)	129 (128-130)	135 (131-137)	112 (109-113)
Source level (dB re 1 µPa pp @ 1m)	143 (138-146)	148 (146-150)	146 (145-148)	135 (133-137)
Signal duration (ms)	301 (211-361)	274 (211-318)	274 (266-282)	802 (795-806)
Frequency peak (kHz)	51 (46-61)	70 (69-71)	66 (64-68)	131 (130-134)
Minimum frequency (kHz)	45 (37–61)	59 (53-65)	66 (64-68)	59 (58-62)
Maximum frequency (kHz)	67 (49-80)	93 (71-132)	67 (64-68)	141 (139-143)

3.1.2 Short- and long-term responses to pingers by wild porpoises

Introduction/objective

Our purpose was to observe the detailed reactions of the porpoises to pinger sounds. There are concerns that current pingers may be too efficient in scaring porpioses, thereby excluding them from habitats. Another concern is that there may be individual differences in the reactions to sounds. We addressed these concerns by playback experiments on wild porpoises, where the detailed response in several individuals could be described.

Methods

To study short-term reactions, we observed porpoises with a drone (DJI Phantom 4Pro) while submerging a Fishtech banana pinger (emitting sounds with a frequency emphasis of 40-80 kHz) at 200-500 m distance from the animals (Figure 3-1). A Soundtrap (Ocean Instruments, model HF300) with GPS unit was deployed by the boat to monitor the pinger emissions, and the background noise conditions. Drone and Soundtrap recordings were synchronized by tapping the Soundtrap while filming it with the drone at the end of the experiment. Analysis was made with software developed by Prof. Henrik Midtiby, University of Southern Denmark. For details, see Brennecke et al. (2022).

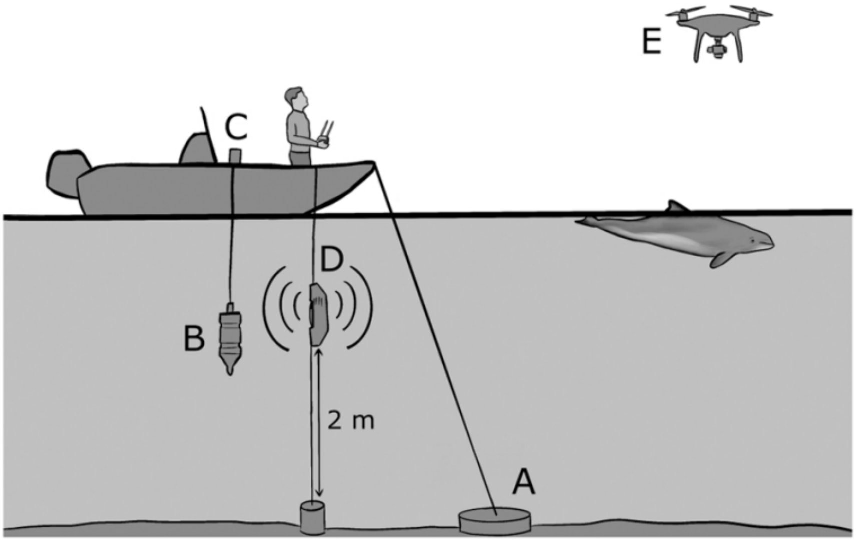

Figure 3-1. Experimental Experimental setup for observing animals during pinger trials From: Brennecke et al. (2022), where details about the setup can be found.

Results/discussion

The methodology and results are described in detail in Brennecke et al. (2022). The results of 16 pinger trials and 10 control trials (deploying a non-functional pinger) are seen in Figure 3-2. Many animals disappeared from the visual field after playback started, indicating that they either dove to the bottom or rapidly swam away. Out of 8 porpoises that could be followed for one minute after playback, 4 showed strong responses, whereas four did not show any responses. This calls for precautions in interpreting the effect of pingers on porpoises, as there may be large individual differences in their reactions, both depending on their 'personality' (some animals being more skittish than others) and on their current behavioural activities (e.g., animals engaged in feeding or mating may be less prone to respond than animals travelling).

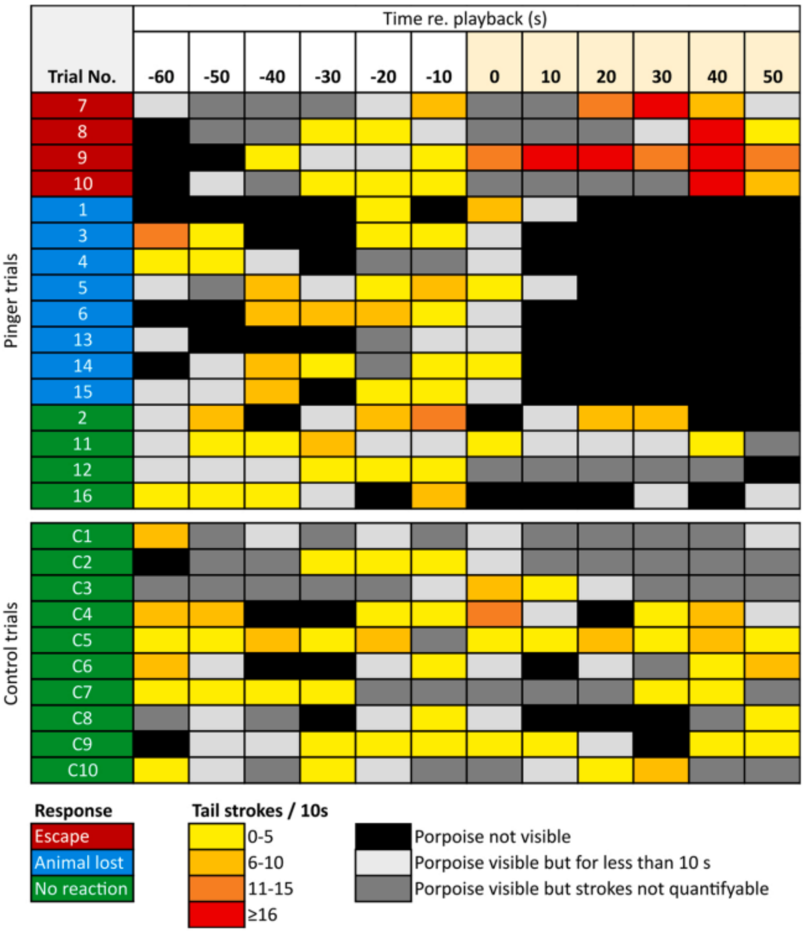

Figure 3-2. Summary of pinger playback with drone observations of the animals' reactions.

3.1.3 Reactions to pingers when using c-pod arrays

Introduction/objective

In this task porpoise reactions to pingers have been studied. The idea was to test changes in in porpoise echolocation patterns in the presence and absence of two different pinger types over time by use of c-pods. Two questions were addressed. Firstly, to which level do pingers affect porpoise echolocation activity at different distances and secondly, do porpoises habituate to the pinger signals.

Methods

The 2 experiments were conducted in the coastal waters of Denmark. The first trial was conducted in Jammerland Bay, great Belt, Denmark (Experiment 1), where the second was conducted in the waters close to Romsø, Great Belt, Denmark (Experiment 2).

Experiment 1

The first experiment was deployed on the 26th of June 2019 and retrieved on the 24th of April 2020. A triangle array of 13 c-pods was deployed at approximately 7-10 m depts. The array had a single modified Banana pinger attached to the center c-pod of the array. The C-pods were placed in distances of 0, 100, 200, 300, 400, 500, 600 and 700 meters from the banana pinger.

The modified banana pinger emitted randomized pings with harmonics with a frequency between (50-120kHz). The mean source level was 145 dB re 1 uPa@1m (RMS) +/- 3dB. The modified Banana pinger was turned on and off an internal clock. The cycle was 24 hours on and 26 hours off. The cycle was chosen to simulate a fishery where nets a set for 24 hours however to limit the effect of diurnal variation, the time was chosen to be longer.

The functionally of the modified banana pinger was verified by the C-pod closest to the pinger. The pinger source level was mesured before and after deployment in a 3m diameter 3 m deep cylindrical tank with a Reson 4014 hydrophone that had been calibrated by the method of reciprocity. All C-pods were calibrated before and after deployment using the methodology described in Dähne et al. (2013).

Experiment 2

The second experiment was conducted between the 10th of August and the 1st of February 2020. A triangle array of 13 C-pods was deployed at 4-6 m depts. The array had a single modified Banana pinger attached to the center C-pod of the array. The C-pods were placed in distances of 0, 100, 200, 400, 500, 600 700 meters to the banana pinger in the same constellation as in Experiment 1. The modified banana pinger emitted different signals with frequencies between (40-80kHz). The modified Banana pinger was turned on and off an internal clock. The cycle was 24 hours on and 26 hours off. The cycle was chosen to simulate a fishery where nets a set for 24 hours. The time was however chosen to be longer in order to limit the effect of diurnal variation.

The functionality of the modified babana pinger was verified by the Cpod closest to the pinger. The pinger source level was mesured before and after deployment in a 3m diameter 3 m deep cylindrical tank with a Reson 4014 hydrophone that had been calibrated by the method of reciprocity. All C-pods were calibrated before and after deployment using the methodology described in Dähne et al. (2013).

Data analysis of both experiments

The data was analysed as done by Kindt-Larsen et al. (2019). The echolocation clicks recorded on the C-PODs were analysed in the C-POD software (C-POD V2.035, Chelonia Ltd.). As indicators of porpoise presence only clicks in trains (>5 clicks) classified as high and moderate-probability cetacean trains with a frequency spectrum 125–145 kHz was used. Both types of pinger signals could easily be identified in the C-POD data, thus making it possible to identify the pinger cycles. Hours when the pinger was changing between on and off were eliminated from the trials to remove recordings of any porpoises that had been exposed both to pinger sounds and silent periods

The model was fitted individually for each combination of experiment and distance to the pinger. The full model included the following terms:

$$Y=\beta 0+\beta 1 pinger+\beta 2\ time+\beta 3 clock+\beta 4 click+\beta 5 pinger:\ halftime,$$

where the response variable *Y* is the number of porpoise clicks (in trains/hour). *Pinger* indicate if the pinger cycle was on or off, *time* was the time from the start to the end of the experiment, and *clock* was a categorical effect from 1 to 12 representing 2 h time intervals of the day. *Click* was defined as the natural logarithm of the number of clicks (in trains/hour) plus 1 in the previous hour and was included to model auto-correlation in the observed time-series of clicks.

The log-transformation was required due to AIC value for this model was better compared to when the variable was untransformed. *Pinger:halftime* was included to analyze habituation effects, and is defined as the interaction between the *pinger* variable and an indicator variable *halftime* that has a value of one whenever the data point stems from the second half of the experiment. This implies that two distinct pinger effects are estimated in the model if *pinger:halftime* is significant, one for each halftime of the experiment. All model selection was based on AIC.

Approximate confidence bounds were constructed by parametric bootstrapping and *P*-values were calculated using the likelihood ratio test for model reduction. All analyses were made in the R 3.4.1 statistical package (R Core Team) using the package pscl (Zeileis *et al*. **2008**).For further information see Kindt-Larsen et al. 2019.

All results are reported and used under WP 4.

4 Distance trials with new types of pingers in the field (WP2)

4.1 Introduction and objectives

In Europe, mandatory use of pingers is regulated through the European Union's Council Regulation *2019/1241* (EU 2019). Pingers have proven to be very effective at reducing bycatch of small cetaceans in gillnets but they also have some disadvantages, which are limiting their acceptance by fishers and environmentalists. The disadvantages include high costs, noise pollution, habituation/ reduced effectiveness, exclusion from important habitats and alerting seals to the nets to depredate on the catch.

The regulation includes technical specifications and deployment rules for the use of pingers. With respect to pinger spacing, the maximum spacing between 2 pingers follows the advice of the pinger manufacturers, giving 200 for the Banana (Fishtek Marine). Earlier studies have however shown that pingers could be deployed with larger spacing than suggested by the managers (Larsen et al. 2013) and still remain effective, while a number of the disadvantages mentioned above would be reduced.

Because of the results demonstrated by Larsen et al. (2013), today Danish fishers can fish with the double spacing (455m instead of 200m) if they use the "AQUAmark100" pinger. This pinger, is, however, very heavy and fishers have complained that it drags down the nets thus changing the buoyancy of the net. Furthermore, the pinger has no options for changing battery or to check the battery level of the pinger. These negative effects have made the fishers reluctant to use the pingers despite the Regulation *2019/1241.*

The objective of WP2 was to investigate whether it is possible to increase the distance between "banana pingers" to more than what is specified by the manufacturer. As this will reduce noise pollution, costs of pinger implementation, and the risk of habitat exclusion.
Thus, it was decided to test a newer type of pinger, the so called "Banana". The banana pinger emits randomised pings with harmonics in frequencies between 50kHz- 120kHz and with a source level of 145dB+/- 3dB@1m. It has no effect on the net buoyancy and fishers could have the opportunity to check the battery level of the pingers.

4.1.1 Banana Pinger trials

Objective

The objective of this study was to quantify the effect of Banana pingers when they were spaced with either 200 or 500m.

Methods

The study was conducted in the Danish Turbot fishery in the North Sea in collaboration with a commercial fisher using a large gillnet vessel (18m). The study was separated into three trials, all investigating the effect of the Banana pinger (Fishtek Marine). The Banana pinger plays randomised pings with harmonics in frequencies between 50kHz- 120kHz and with a source level of 145dB+/- 3dB@1m. The pinger is 185mm x 52mm x 120mm in size and weigh 229 grams including battery Figure 4-1.

Figure 4-1. Picture of Banana Pinger (Fishtek Marine)

The project was planned to have 1/3 of the net-fleets pingers spaced with 400m, 1/3 of the net-fleets with 200m spacing and 1/3 of the net-fleets as control (no pingers). The pingers were placed in the headline between the nets.

The trials were instructed by DTU staff, however the monitoring of the trials was done by CCTV. The vessel was equipped with the REM system developed by Anchorlab Ltd, Denmark. The system comprised a control box, a position sensor (global positioning system; GPS) and 2 waterproof closed-circuit television (CCTV) cameras. The control box included a computer that monitored sensor status and activated image recording. All components were connected to the control box placed in the wheelhouse. One camera was positioned to view the net when it was breaking the water surface prior to the entry of the hauler as many porpoises tends to feel out as this point due to their heavier weight in air. The system was programmed to switch on while leaving port and off when entering port, determined by the GPS positions of the outer range of the harbours. All data was uploaded to DTU Aqua through a 4G wireless connection while in port.

All video footage was examined by the trained DTU Aqua viewers. The videos were played back at a rate 4-5 times faster than real time, depending on the image quality. For all data, position, haul soak time, net-fleet length, number of bycaught porpoises and pinger usage was noted. Furthermore, the fisher had an additional logbook. He also noted position, haul soak time, net-fleet length, number of bycaught porpoises and pinger usage.

Data analysis

The data was analysed using generalized linear mixed models (GLMMs) with negative binomial distributions (log-link) to allow for overdispersion in the count data. Each model included an offset of log of soak time (hours) plus log of haul length (meters) so that estimated model coefficients would be in terms of a bycacth rate per hour and meter. Each model also included a random effect of either date or trip to account for temporal variation in bycatch due to factors other than pingers and soaking time and haul length. We used AICc, i.e. small-sample size corrected Akaike Infomramtion Criteria, to check if date or trip was a better random effect. Analyses were done in R. Models were fit using glmmTMB and effect plots were done using sjPlot. For statistical inference, we used Wald-z statistics of the estimated parameters from the GLMMs.

Results

As the study was separated into 3 trials the results from each trial are presented separately below.

Trial 1

The first trial was conducted between 12th of June – 2nd of July 2020. A total of 13 hauls were conducted, however all were invalid as the pingers were not attached correctly.

Table 4-1. Tables the different type of hauls and the number of hauls conducted in trial 1.

Type of haul	**Number of hauls**
Invalid	13 (spacing's were mixed, between control pingered nets)
Control	0
200 m spacing	0
500 m spacing	0
Total	**13**

Trial 2

The second trial was conducted between 30th of June 2021- 27th of July 2021. During the period 77 net fleets was hauled. In total 43 hauls were collected with 500m spacing and 3 hauls with 200m. Thirty hauls was collected as control hauls and none haul had to be excluded from the analysis as the pingeres was mixed with 200 and 500 meter spacings. The net fleets had a mean length of 6,9km and a mean soak time of 152 hours.

Table 4-2. Tables the different type of hauls and the number of hauls conducted in trial 2.

Type of haul	**Number of hauls**
Invalid	1 (200m and 500m spacing's were mixed)
Control	30
200 m spacing	3
500 m spacing	43
Total	**77**

Figure 4-2 shows the number of porpoises caught per km net-fleet per 100 hours of soak time from the raw data from trial 2. Where Figure 4-3 shows the model output. The model output demonstrates that when the pingers were spaced with 200m the bycatch was reduced by 90% compared to no pingers while when spacing them with 500m the rate was reduced by 51%.

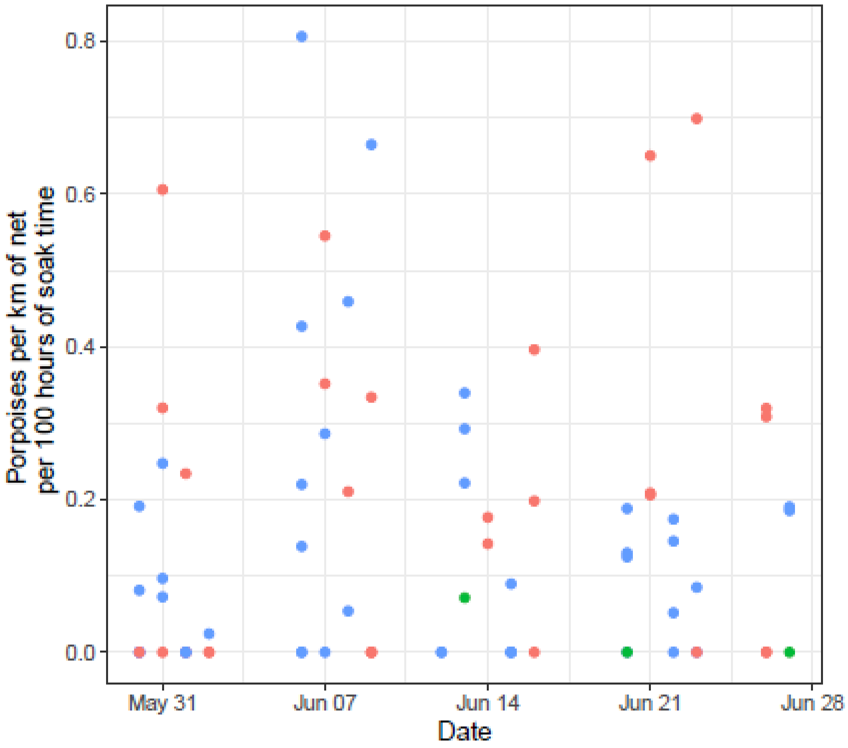

Figure 4-2. Figures number of bycaught porpoises per km of net-fleet per 100hours of soaktime. Blue, red and green dots are when pingers are spaced with 500m, control and 200m respectively.

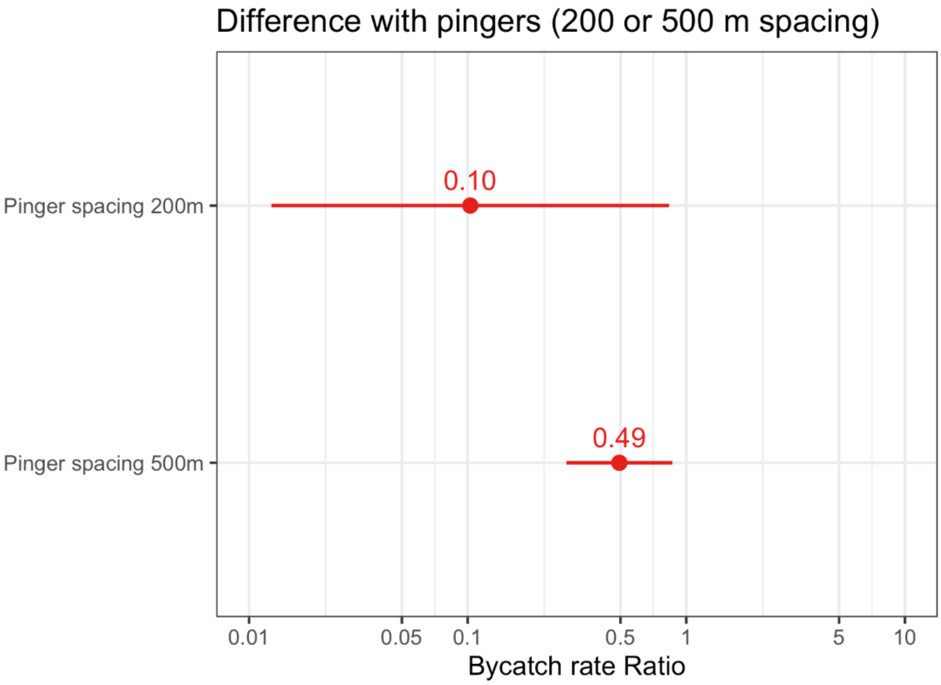

Figure 4-3. Model output showing the effect of the pingers when spaced with 200 and 500m respectively.

Trial 3

The third trial was conducted between 11th of May 2022- 5th of July 2022. During the period 130 net fleets was hauled. In total 59 hauls were collected with 500m spacing and 18 hauls with 200m. Fifty-nine hauls was collected as control. As the results in Trial 2 showed a reduction of only 51% when spacing the pingers with 500m a new lauder pinger was built. The idea was to test if it was possible to have a higher reduction (<80%) if the same signal was used however with a higher SPL but keeping the 500m spacing. Thus, a new type of pinger was built. The pinger was built as a prototype “Red banana” (Figure 4-4) The frequency, signals and weight were the same as the one. The SPL was however increased to 155dB and the pingers were made in red enabling the fishers to separate the two pinger types.

In trial 3 the net fleets had a mean length of 8.4 km and a mean soak time of 140 hours.

Figure 4-4. Pictures the “red banana” pinger.

Tabel 4-3. Tables the different type of hauls and the number of hauls conducted in trial 3.

Type of haul	Number of hauls
Invalid	None
Control	59
200 m spacing	18
500 m spacing	59
Red-Banana, 500m spacing	4
Total	**140**

Figure 4-5 shows the number of porpoises caught per km net-fleet per 100 hours of soak time from the raw data from trial 2. Here it can be seen that after the 8th of June the number of porpoises bycaught per km net-fleet increased. Figure 4-6 shows the model output. From the model output in can be seen that that when the pingers were spaced with 200m the bycatch was reduced by 51% while when spacing them with 500m the effect was reduced by 36%. Red pingers with 500m spacing had wide confidence intervals in the model results due to few hauls, but the best estimate was that they give 77% reduction in bycatch.

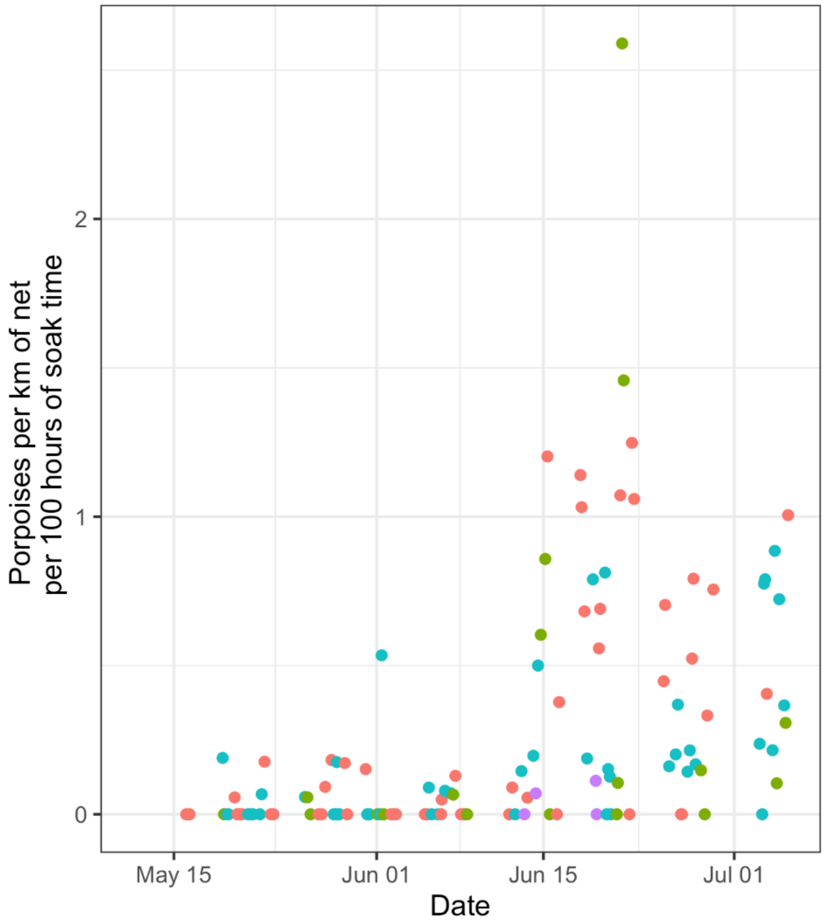

Figure 4-5. Figures the number of bycaught porpoises per km of net-fleet per 100hours of soak-time. Blue, red, purple and green dots are when pingers are spaced with 500m, control, 500m (red-banana) and 200m respectively.

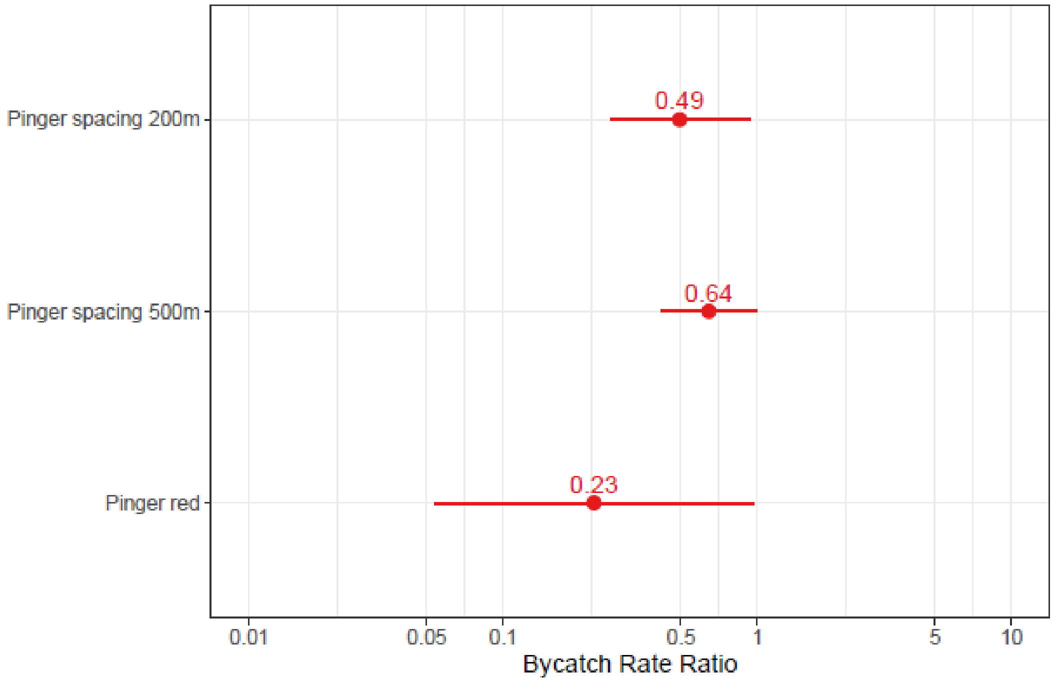

Figure 4-6. Model output showing the effect of the pingers when spaced with 200, 500m, 500m (red-banana) respectively.

Discussion and conclusions

The results from both *Trial 2* and *3* show that banana pingers do reduce bycatch of porpoises significantly. The level of reduction, however, strongly depends on the spacing of the pingers and differences were seen between years.

The results from *Trial 2* indicate that bycatch was reduce by 90% and 51% when spacing the pingers with 200m and 500m respectively. Despite the uncertainties measured with the 200m spacing, the results fit well with the spacing recommended by the manufacturer.

In contrast, earlier results of pinger spacing trials support the argument that pingers are effective at longer ranges than the manufacturers' recommended spacings. This is, however, difficult to compare as different pingers emit different sounds. Larsen et al. (2013) investigated the effect of AQUAmark100. The AQUAmark100 had a source level between 136 to 145 dB re. 1 µPa @ 1 m. which is very similar to the source level of the Banana pinger (145 +/- 3dB). The recommended space of the AQUAmark100 was like the Banana 200 m. However, Larsen et al. (2013) revealed that when spacing Aquamark100 with 455 m, bycatch of harbour porpoise was reduced by 100%, and even when the pingers were spaced 585 m, bycatch was reduced by 82%. The results from Trial 3 however reviled another result. Here the bycatch was only reduced by 51% and 36% when spacing the pingers with 200m and 500m respectively. The Red Banana however showed an effect of 77% reduction. The effect of the 200m and the 500m spacing is much lower compared to Trial 2; the potential reasons for this are numerous, but first is the battery. Battery life is essential for pingers to function properly. The crew were asked to inspect the battery life of all pingers, during the full duration of the trial. The fishers claim that this was done, however they did mention that the pingers slowed in their flash responds and suggested that the signal might not have been fully functional. The batteries were thus exchanged to make sure of the full functionality, during the trial. However, one could suggest that all batteries should have been exchanged in all pingers from the beginning to make sure that no such doubts can raise. Secondly, a very rare phenomenon of high bycatch rates was seen in the data set. Until the 8th of June, the bycatch rate the for control, 200m, and 500m was below 0,3 bycaught porpoises per km of net per 100 hours of soak-time. However, after that date the level increased drastically and many values was recorded between 0.3 and 1.5 bycaught porpoises per km of net per 100 hours of soak-time see Figure 4-5. The reason for this cannot be conclusively explained, but the fisher and crew stated that massive amounts of porpoises were seen in the area. They stated that they saw hundreds of porpoises in the area which is not a normal sight for them. They believed that the reason for the high amount of porpoises was due to an inflow of high densities of juvenile mackerel. Large amounts of mackerel can attract predators like the porpoise. It, however, has not possible to verify this explanation as no fish or porpoise surveys were done within the time frame of the trial. Another way to document the large amount of mackerel was if these could have been seen on the video footage of the catches. However, as mesh size is above 200 m juvenile mackerel cannot be gilled in the turbot fishery. The only way the mackerel was documented was on the echo sounder of the vessel, but these recordings were not saved as the echo sounder is only used for real time purposes. Thus, unfortunately, no known documentation exists from these events.

However, if this is the explanation and the reason why there are many porpoises in the area is due to large food sources, the pingers should still have prevented the porpoises from getting bycaught. However, as this was not the case, understanding why becomes crucial when understanding the way pingers work. From Trial 2 of this study and in many other trails, the results show that pingers do work (Dawson et al. 2013) however it might be that when the porpoises are too “busy” feeding they don’t show the same reaction as when they are milling. Kastelein et al. 1995 studied porpoise net entanglement in a pool. Here it was documented that when introducing live fish or other porpoises, the test porpoise became distracted, which induced a higher entangle rate. Their observations therefore indicate a possibility of porpoises having their sonar locked on other targets. Another explanation could be the sound level. When a lot of activity is ongoing the sound level increases in the water thus masking the sound emitted from the pingers. This explanation can be supported by the results from the red pinger trials which had a higher sound level thus making the pingers more audible to the porpoises.

Another issue that has been raised when using pingers is that malfunctioning pingers or when pingers are missing can lead to increases in the bycatch rate. One can say that our study also investigated this issue, as the net-fleets with 500m spacings is similar to a net-fleet with 200m spacing where every second pinger is malfunctioning. Murray *et al*. (**2000**) found that in situations where one or more 10 kHz pingers on a net had malfunctioned, thereby increasing the distance between functioning pingers, the bycatch rate of porpoises increased. This result is however not supported in our findings as the 500m still had reduction effect when compared to the control nets.

5 Bycatch of porpoises and long-term effects of pinger use in the North Sea (WP3)

5.1 Introduction

Monitoring of marine mammal bycatch has been conducted worldwide. In 1992, the Council of the European Community adopted the Habitats Directive on conservation of natural habitats and of wild fauna and flora, which obliges member states to protect and conserve the populations of marine mammals (EC 1992).

Furthermore, EU member states are obliged to fulfil Council Regulation *2019/1241*, which lays down measures concerning the incidental catches of cetaceans in fisheries (EU 2019). In short, the regulation promulgated, that Member states should minimise the impact of fishing activities on marine ecosystems, monitor the incidental captures and killings of protected cetaceans and ensure that the captures do not have a significant impact on the species concerned. It also requires that Member states collect scientific information and techniques on developments to reduce the incidental captures of cetaceans, implement acoustic deterring devices in areas and fisheries with known or foreseeable high levels of cetacean bycatch and establish the technical specifications for the efficiency of such devices. In Denmark, Council Regulation *2019/1241* proclaims that acoustic devices (pingers) should be prescribed in ICES-area IV and section IIIa. The pingers are obligatory for vessels larger than 12m in all gillnet fisheries with net fleets of ≤400m and on gillnets with mesh sizes of ≥220mm (EU 2019). Different from directives, regulations are legally binding throughout every Member State and enter into force on a set date in all Member States.

Bycatch monitoring can be conducted using a number of different methods, including onboard observers, self-reporting or electronic monitoring (EM). The EM systems provide video footage, time and position of all net hauls and bycatches of marine mammals. In 2012 DTU Aqua compared results between EM and fishers' logbooks and found that the EM system gave more reliable results, as fishers, in many cases, did not observe the bycatch while working on the deck because the bycatch had already dropped out of the net before coming on board. Furthermore, very high coverage percentages at low cost, compared to on-board observers, could be obtained with EM (Kindt-Larsen et al. 2012).

5.1.1 Bycatch and long-term pingers usage

Objective

The objective of this trial was (1) to collect data needed for the pinger spacing trials under WP.2, (2) to monitor the long-term effects of pinger usage and (3) to record bycatch of porpoises in the North Sea commercial gillnet fishery. The goal was to monitor all fishing events from 2 vessels for a period of one year.

Methods

In cooperation with Ministry of Food, Agriculture and Fisheries DTU Aqua announced the need for of vessels to monitor bycatch of porpoises in North Sea gillnet fishery. The announcement was made through the local fishing chairmen and meetings was arranged with local fishers. After the meetings interested fishers could sign up for the project.

All trials were conducted on voluntarily basis and the participating fisher could however, get additional quotas of cod (from the Danish National research quota), when the contract with terms and conditions was accepted from both sides. The conditions followed a standard procedure which are used for all Danish gillnets vessels monitored by EM systems.

When joining the project the vessel was equipped with an Electronic Monitoring system developed by Anchorlab Ldt. The system comprised a control box, a position sensor (global positioning system; GPS) and 2 waterproof closed-circuit television (CCTV) cameras. The control box included a computer that monitored the sensor status and activated image recording. One camera was positioned to view the net when it was breaking the water surface prior to the entry of the hauler, as many porpoises falls out of the net at this position, due to their heavier weight in air compared to water. The second camera recorded the sorting table. All data was uploaded by the 4G network when the vessel was within range of the net.

Once all data was uploaded the data was analysed by trained DTU staff within the Anchorlab software. The viewer recorded the time and position each net haul, including net-lenght, soak-time, pinger usage and bycatch of porpoises.

Results

Fishing effort

Unfortunately, only one vessel signed up for the task. However, instead of one year, the fisher agreed to collect data for the full duration of the project. This, of cause, increased the amount of data collected under the project tremendously. The vessel joined in 2019 where 584 net-hauls were collected. In total more than 2468 net-hauls has been monitored see Table 5-1.

Table 5-1. Total number of gillnet hauls monitored within the project.

	Total number of net-hauls covered
2019	584
2020	756
2021	628
2022	350+ (still ongoing)

Figure 5-1 shows the number of days at sea per ICES squares which have been covered during the trial. The data from 2022 is, however, not included on the figure as the vessels has continued to collect data after the end of the project. The full data set will thus be avaible in the beginning of 2023.

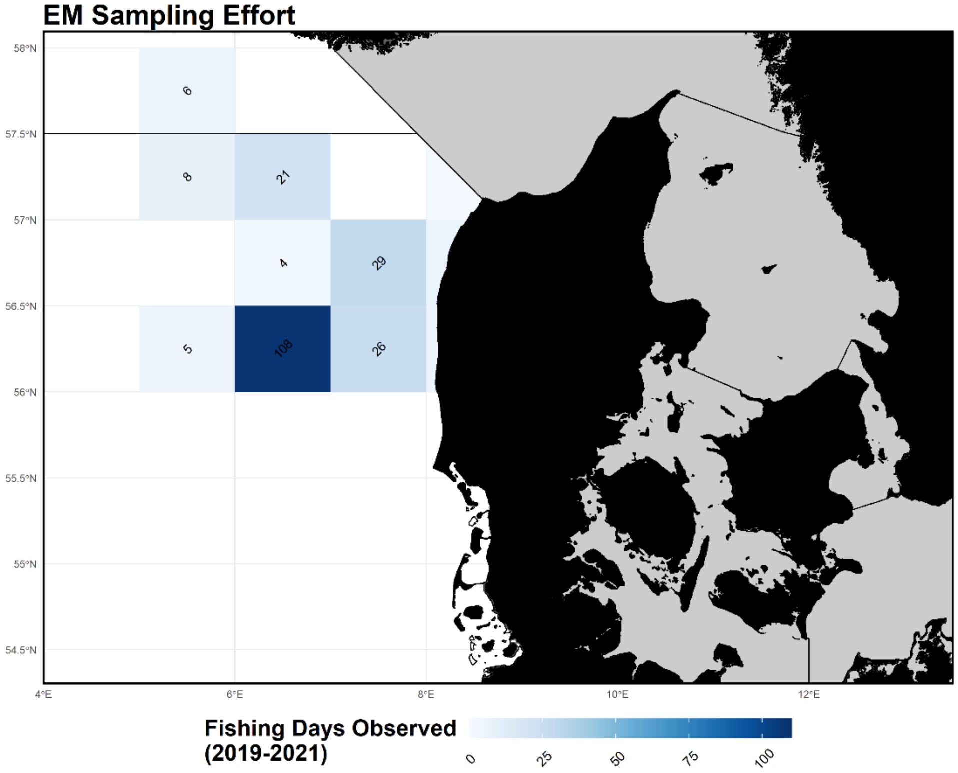

Figure 5-1.Total number of fishing days covered by EM monitoring from 2019-2021.

Pinger usage

In terms of pinger usage the first goal of WP.4 was to monitor bycatch of porpoises when different pinger spacings where tested in WP.2 when pingers are used in the commercial fisheries. The results of these pinger trials are thus reported under WP.2. (See WP. 2 page 17)

The second goal was to monitor bycatch in relation to the long term pinger usage. As mentioned in the introduction the there are rules in place for pinger usage in the North Sea (EU 2019). However, the vessel which signed in for the project was only obliged to use pingers within a small part of this fishery (turbot fishery, meshes >220mm). The vessel only conducted this fishery within a short time of the year, most often only in June. It was thus not possible to monitor the effects of the long-term usage, as e.g., habituation effect most likely happens over longer time periods than 1 month.

Bycatch monitoring

The third goal of this WP was to monitor bycatch of porpoises in the North Sea. This was done with great success and the amount of observed effort is reported in fishing effort section "*fishing effort*" above. However, bycatch of protected species is highly sensitive data, and as only one vessel has been monitored it is not possible to report on the specific numbers. However, DTU holds these data, and the data can be used when GDPR rules are taken into account. Data have been used within ICES WGBYC (Working Group on BYCatch of protected species). WGBYC have thus used the data to gather information of bycatch of porpoises for the full North Sea population.

Data are used in the following ICES reports:

ICES. 2020. 'Report of the Working Group on Bycatch of Protected Species (WGBYC). ICES.

ICES. 2021. ‘Report of the Working Group on Bycatch of Protected Species (WGBYC). ICES.
ICES. 2022. ‘Report of the Working Group on Bycatch of Protected Species (WGBYC). ICES.
Furthermore, the data are used in a model-based prediction of the total porpoise bycatch in Swedish and Danish gillnets fisheries. Here the porpoise bycatch data from this trial was linked with data from the long-term monitoring programme using electronic monitoring (EM) systems in Denmark. Since 2010 Danish gillnet vessels (outside the North Sea) have collected data on porpoise bycatch and gillnet fishing effort on a fine spatial and temporal scale. These observations were used to develop a model aiming to predict bycatch rates, given the operational and ecological characteristics of each haul observed with EM in Danish waters. A GLMM was used to predict the number of bycatches of each haul and the mean quarterly distribution of bycatches in the different areas, hereunder the coastal North Sea, the Skagerrak, the Sound, and the Belt Seas. The data revealed yearly and seasonal variations in bycatches both within and between fishing areas. Between 2010 and 2020, the total mean bycatch was estimated averaged to 2113 animals (95% CI: 1012-4387) per year for all areas. Further the results showed a spatio-temporal variation. The results further concluded that that fishing characteristics are key determinants of porpoise bycatch and that classical approaches which do not account for these features produces biased bycatch rates.

More detailed information the methods and bycatch estimates can be found in the paper listed below.
Kindt-Larsen, L., Glemarec, G., Berg, C. W., Königson, S., Kroner, A. M., Søgaard, M., & Lusseau, D. (2023). Knowing the fishery to know the bycatch: bias-corrected estimates of harbour porpoise bycatch in gillnet fisheries. Proceedings of the Royal Society B, 290(2002), 20222570.

Discussion/conclusion
This is the first trial to collected data on porpoise bycatch in the North Sea since the observer trials made in 2000 (Vinther and Larsen 2004). The study was planned to cover two vessels for 1 year and monitor both the bycatch and the effectiveness of pingers when they are used with different distances (WP2) and monitor the long-term effect of pingers. Unfortunately, only one vessel signed up for the trial however the fisher agreed to monitor the vessel during the full duration of the project. Despites the loss of having only one participating vessel the coverage of all fishing event for a long-time scale (almost 4 years) gave new insights in porpoise bycatch both in terms of areas, seasonal and temporal variation and which gear factors that significantly affects the bycatches.

6 Modelling of the pinger-effect (WP4)

6.1 Calibrations 2 pinger types

Calibration of the individual based model: porpoise responses to pinger noise.
In this section, we aimed to improve and calibrate the pinger noise avoidance framework within the Indiviual-Based Model of van Beest et al. (2017) with new empirical data to ensure that porpoise agents responded to different types of pinger noise with deterrence movements that lead to temporary declines in harbour porpoise densities in the vicinity of active pingers as observed in nature.

To do so, we first conducted three experimental field studies (at Reersø in 2019, at Romsø in 2020 and at Jammerland Bay in 2017) where we collected porpoise click data using passive acoustic monitoring during periods with and without pingers emitting noise. For an overview of the setup of each experiment see section 3.1.3. In Jammerland Bay, we tested the effect of the AQUAmark100 pinger, producing randomized broadband high frequency (20-160 kHz) signals (Aquatec Group Ltd. `www.netpinger.net`). In in Reersø we tested the effect of the Banana pinger (plays randomised pings with harmonics in frequencies between 50kHz- 120kHz and with a source level of 145dB+/- 3dB@1m.) on porpoise deterrence behaviour and in Romsø we tested the effect of the 10kHz pinger (300 ms at 4 s intervals 132 dB re 1 µPa@1m (RMS).

The field data testing the AQUAmark100 pinger showed a significant reduction in the number of porpoise clicks at distances ≤400 m when the pinger was on compared to when the AQUAmark100 pinger was off, but this reduction was not significant at distances further away (Figure 6-1A). The mean decline in number of porpoise clicks recorded was 85.5% (range: 80.4−91.6%) and 52.1% (47.5−57.6%) at 0 and 400 m distances and 30% (24.8−39.4%) and 11% (9.2−14.4%) at 800 and 1600 m distances, respectively (Figure 6-1B).

The field data testing the Banana pinger did not show a significant reduction in the number of porpoise clicks at distances ≤800 m when the pinger was on compared to when the Banana pinger was off (Figure 6-2A). However, the mean decline in number of porpoise clicks recorded was 34.8% (range: 28.8−43.7%) and 16.8% (14.9−19.1%) and 13.7% (12.3−15.6%) at 0, 400 and 800 m distances, respectively (Figure 6-2B).

The field data testing the 10Khz pinger showed a significant reduction in the number of porpoise clicks only at 0 m but not at 400 m distances when the pinger was on compared to when the pinger was off (Figure 6-3A). Here, the mean decline in number of porpoise clicks recorded was 56.9% (range: 53.7−60.4%) and 14.3% (13.1−15.8%) at 0 and 400 m distances, respectively (Figure 6-3B).

Overall, the field experiments revealed that porpoises responded most strongly to the the AQUAmark100, followed by the 10Khz pinger and least to the Banana pinger. The next step was to use the results of the empirical studies to tune the noise deterrence behaviour of porpoise agents in the model by van Beest et al.(Van Beest et al. 2017) using pattern-oriented modelling (POM) (Grimm et al. 2005).

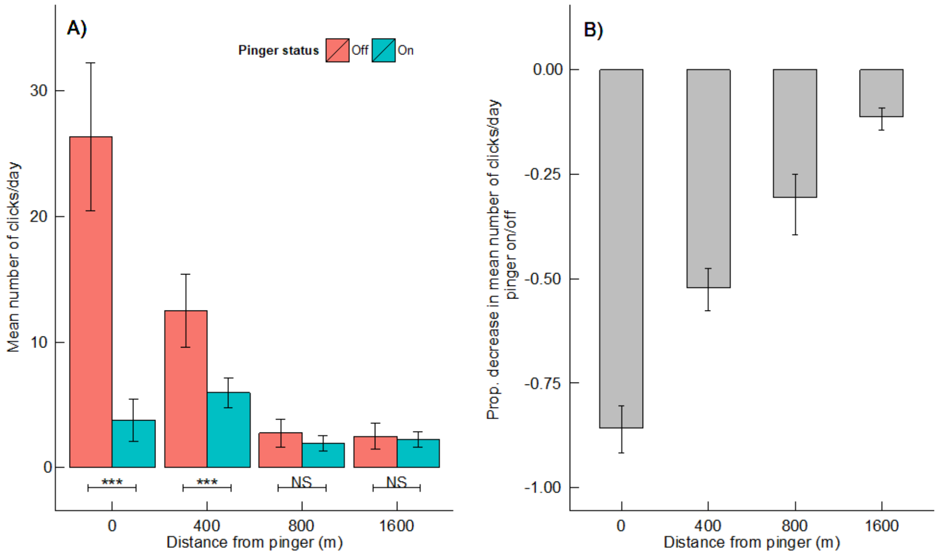

Figure 6-1. Results of a field experiment in Jammerland Bay, Denmark, testing the effect of the AQUAmark100 pinger on harbor porpoise echolocation activity. Panels show the absolute (A) and proportional (B) change in mean daily number of porpoise clicks recorded during pinger on/off cycles as a function of distance from the pinger. Results are re-used with permission from van Beest et al. (2017).

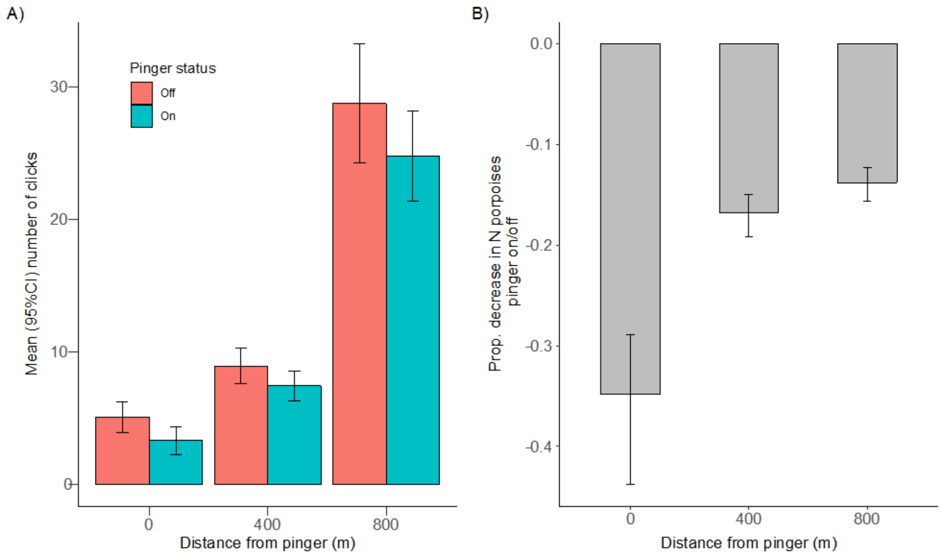

Figure 6-2. Results of a field experiment in Reersø, Denmark, testing the effect of the Banana pinger on harbor porpoise echolocation activity. Panels show the absolute (A) and proportional (B) change in mean daily number of porpoise clicks recorded during pinger on/off cycles as a function of distance from the pinger.

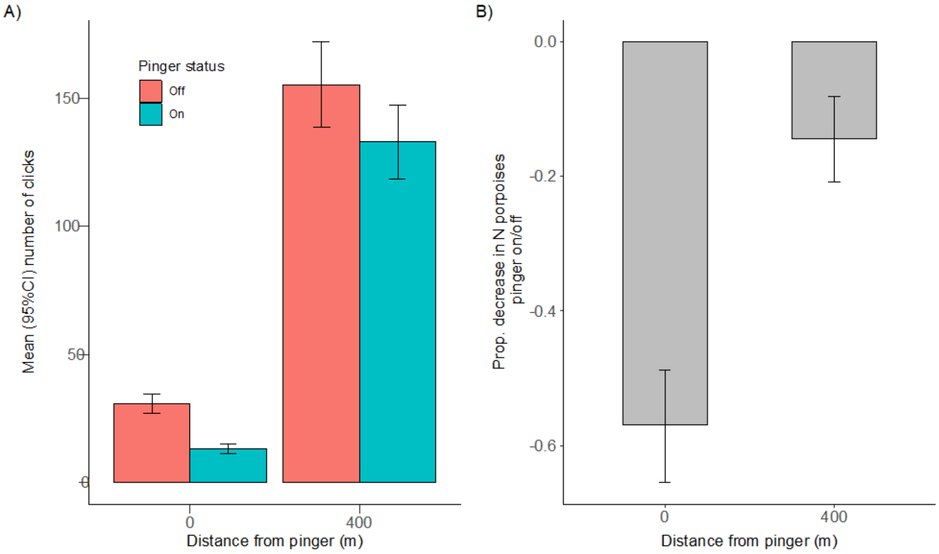

Figure 6-3. Results of a field experiment in Romsø, Denmark, testing the effect of the 10KhZ pinger on harbor porpoise echolocation activity. Panels show the absolute (A) and proportional (B) change in mean daily number of porpoise clicks recorded during pinger on/off cycles as a function of distance from the pinger.

To model underwater noise avoidance behavior of harbor porpoises, the framework of van Beest et al (2017) uses four parameters: the impact factor (unitless measure of sound strength at the noise source), deterrence distance (parameter controlling the distance (m) at which agents respond to noise), deterrence coefficient (unitless parameter controlling the strength of deterrence at the source), and deterrence time (number of 30-min time steps the deterrence effect lasts after the noise has disappeared). We updated this framework by assuming spherical spreading of the sound level received by porpoise agents (Urick 1983), which differs from the linear decrease used in van Beest et al. (2017). Habituation to pinger noise is currently not included in the IBM. We focused the POM analyses on the parameters deterrence coefficient (c) and the impact factor for calibration, as these were the pinger noise parameters that had the largest influence on model results in van Beest et al. (2017). The POM was performed for each pinger type separately and by building a seascape (40×40 km) within the IBM that reflected bathymetry and presence of land as in each area (Jammerland Bay, Reersø and Romsø). We used the same locations for the pinger and C-PODS as in the field studies and the same pinger on/off time cycles. All simulations in the POM procedure covered two simulation years and were replicated 100 times. The data collected in the first simulation year were discarded to allow for a stable population size to emerge (burn-in period). We recorded and used the number of porpoise agents present in the different distance classes from the pinger for each simulation as a proxy for porpoise clicks given that porpoise click frequency is strongly correlated with porpoise density (Kyhn et al. 2012). We ran a series of simulations with a range of values for the impact factor and the deterrence coefficient with the aim to find the values that correctly reproduced the results of the field studies.

The results of the POM procedure revealed that for the AQUAMARK100 an impact factor of 218 and a deterrence coefficient of 0.06 (Figure 6-4) resulted in the same relative reduction in porpoise density at different distances from active pingers as observed in the field (Figure 6-1). For the Banana pinger an impact factor of 215 and a deterrence coefficient of 0.06 (Figure 6-5) resulted in the same relative reduction in porpoise density at different distances from active pingers as observed in the field (Figure 6-2). Finally, for the 10kHz pinger an impact factor of 215 and a deterrence coefficient of 0.3 (Figure 6-6) resulted in the same relative reduction in porpoise density at different distances from active pingers as observed in the field (Figure 6-3).

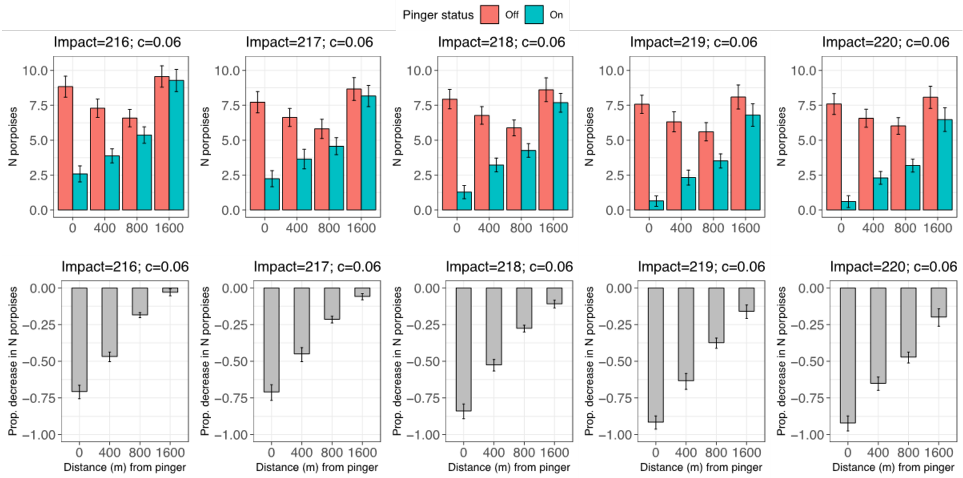

Figure 6-4. Overview of the POM results showing model-based changes in absolute (top panels) and proportional (lower panels) porpoise numbers during pinger on/off cycles as a function of distance from the pinger and impact factor. Simulations with a pinger noise impact level of 218 best replicated the patterns observed in a field experiment using the AQUAmark100 pinger (see Figure 6-1).

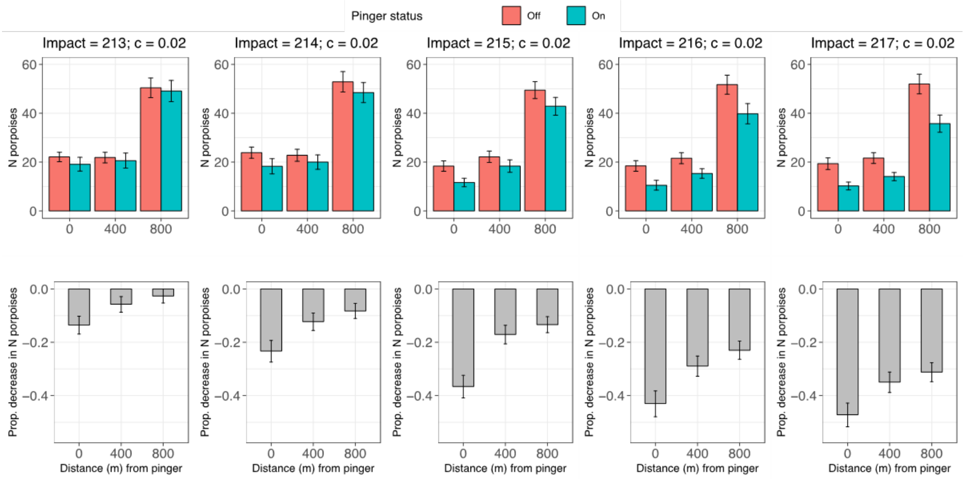

Figure 6-5. Overview of the POM results showing model-based changes in absolute (top panels) and proportional (lower panels) porpoise numbers during pinger on/off cycles as a function of distance from the pinger and impact factor. Simulations with a pinger noise impact level of 218 best replicated the patterns observed in a field experiment using the Banana pinger (see Figure 6-2).

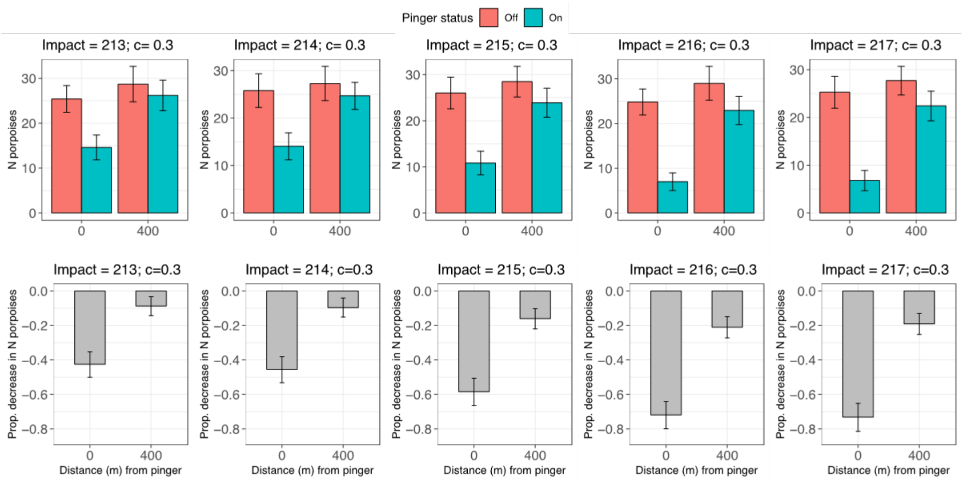

Figure 6-6. Overview of the POM results showing model-based changes in absolute (top panels) and proportional (lower panels) porpoise numbers during pinger on/off cycles as a function of distance from the pinger and impact factor. Simulations with a pinger noise impact level of 218 best replicated the patterns observed in a field experiment using the 10KhZ pinger (see Figure 6-3).

6.2 Understanding the consequences of implementing pinger mitigation for porpoises: estimating the cumulative impacts of noise and bycatch to determine adequate pinger deployment regimes.

6.2.1 Introduction

Ensonification of the oceans is a key biodiversity challenge which can affect a range of species through habitat modification and disturbance. As we aim to deploy sound emitting devices to alert porpoises of net presence, we need to better understand the consequences this ensonification could have on the very same biodiversity target we aim to achieve.

The impact of anthropogenic noise on marine populations is difficult to estimate because this threat typically does not directly kill individuals. Anthropogenic noise can, however, deteriorate cetacean habitat by impairing their ability to carry out essential activities. Biologically-relevant impacts emerge primarily from foraging disruptions, and depending on life history traits and ecological context these disturbances can have population-level consequences (Williams et al. 2006, Lusseau 2014, Nattrass and Lusseau 2016, Pirotta et al. 2018, Keen et al. 2021). Population consequences of disturbances (PCoD), including acoustic disturbances, emerge from a deterioration of the condition of individuals that are repeatedly exposed to foraging disruption in the affected population. In PCoD, condition is taken as an integrative concept of ecological health of individuals (Derous et al. 2020). This decrease in condition then compromises their ability to contribute demographically, via survival and reproduction, to population growth. There are now multiple models of condition-mediated population dynamics available to estimate when PCoD might occur and its severity (New et al. 2013, King et al. 2015, Pirotta et al. 2015, 2018, van Beest et al. 2017, Nabe-Nielsen et al. 2018, Booth et al. 2020, Mortensen et al. 2021). These models can be used to simulate the population consequences of varied noise exposure scenarios and therefore inform management interventions best suited to address conservation objectives (Christiansen and Lusseau 2015, Pirotta et al. 2015, Nabe-Nielsen et al. 2018).

Behavioural responses to underwater noise by individuals are often variable and expected to be influenced by the context in which noise exposure occurs (Ellison et al. 2012). This suggests that there is not one “optimal” dose-response relationship to study the impact of noise exposure on activity disruption. More generally, the elicitation of behavioural responses to risk and fear is context-dependent (Lima and Dill 1990, Frid and Dill 2002, Beale and Monaghan 2004, Lusseau 2014, Gallagher et al. 2017) because the perception of risk and fear is integrated with other motivations to yield behaviour (McFarland 1969, Sibly and McFarland 1976, Lorenz and Kickert 1981, Pirotta et al. 2014). One of the key motivational axes affecting behavioural dynamics and state resulting from fear and risk perception is condition (Sutton and Krashes 2020). Condition can be defined in many ways, particularly depending on fields of enquiries, but here we focus on ecologically-relevant condition, that is the state of individuals affecting their demographic contributions; via either survival or reproduction (Derous et al. 2020). Therefore, PCoD estimation is difficult using simple deterministic models.

Previous studies have used agent-based simulation models to assess changes in harbour porpoise abundance when exposed to bycatch risk (Nabe-Nielsen et al. 2014) and the noise emerging from pingers used for bycatch mitigation (van Beest et al. 2017). The harbour porpoise (*Phocoena phocoena*) bycatch management we face exemplifies the challenge of wicked problem emergence in the management of multiple conservation threats. Harbour porpoises have a unique physiological ecology for a cetacean in that their body condition reacts rapidly to lost opportunities of energy intake (Kastelein et al. 2019b) and at the same time their foraging ecology is plastic, with an ability to have very large energy intakes in one bout (Kastelein et al. 2019a). Therefore, body condition of individuals can fluctuate rapidly with pronounced inter-annual variation in starvation mortalities for the species (Fenton et al. 2017, Murphy et al. 2020). Overall, the population biology of the species is related to this fast physiological pace with higher reproductive rate, younger age at first reproduction and shorter lifespan (Lockyer 1995, 1995, 2007, Lockyer and Kinze 2003, Murphy et al. 2020). These adaptations have the scope to increase the sensitivity of harbour porpoises to the physiological impacts of PCoD, but it is unclear whether those may be compensated by a more resilient population biology (Lusseau 2014, Nattrass and Lusseau 2016, Pirotta et al. 2018). While agent-based models can provide some estimate of system state, their full potential to appraise the shape of the basin of attraction around those equilibria has been understudied (Nardini et al. 2021). Here we extend numerical analyses of agent-based model outcomes to estimate the basin of attraction of equilibria (Nattrass and Lusseau 2016) under different anthropogenic conditions to assess not only whether we can find trade-offs in management interventions that can meet conservation objectives, but also appraise whether those trade-off solutions leave the population in a resilient state. Population dynamical resilience, measured as engineering resilience (Caswell 2000, Nattrass and Lusseau 2016), is crucial to accommodate for stochastic events likely to impact the populations, such as disease outbreaks, which we know will increase in frequency as climate changes (Sanderson and Alexander 2020).

van Beest et al (2017) used multi-agent simulations to show that pinger implementation could be associated with increased mortalities leading to potentially a non-trivial relationship between bycatch rate decrease (gains) and PCoD-related mortalities (losses) as fishing gear are instrumented with pingers. In other words, while high pinger prevalence decreased bycatch, it increased noise induced impacts on demographic contributions. We therefore need now to determine whether pinger implementation could be designed in a way that maximises bycatch rate reduction, minimise PCoD emergence and maintains a resilient population. Here we assess whether changes in pinger prevalence in nets could be used to balance trade-offs in excess mortalities that could still achieve the conservation objectives for the species. Moreover, because the previous model of van Beest et al (2017) did not account for condition mediation in the avoidance response to pinger noise, we integrate here condition mediation to assess whether changes in risk-taking by individuals as their condition deteriorates can ultimately affect population trajectory. As the modelling approach is limited in its ability to extrapolate from the conditions for which the model was tuned, here we focus on changes in key vital rates to understand the consequences of introducing pingers in fishing nets and increasing their prevalence in nets from 0% to 100%.

6.2.2 Methods

Multi-agent model to determine the population consequences of fishing gear modification for harbour porpoises in an existing fishery

Here we use the multi-agent model DEPONS (Disturbance Effects on the Harbour Porpoise population in the North Sea) tuned to the gillnet fisheries exploiting the region between Denmark and Sweden (Figure 1). This model is described in detail in (van Beest et al. 2017) as well as in the TRACE document of DEPONS available at https://github.com/jacobnabe/DEPONS (Nabe-Nielsen et al., 2018).

The model takes a data-driven, bottom-up mechanistic approach where population dynamics emerge from the individuals' competition for a dynamically changing food resource and from altered movements and reduced foraging when porpoises are disturbed by underwater noise. Each porpoise in the model (also called agents) is a 'super individual' and represent approximately 100 individual porpoises, estimated using population counts in the inner Danish waters (Hammond et al., 2017). Movement of porpoise agents switches between fine-scale foraging movements and large-scale dispersal movements. Both movement modes are parameterized and calibrated based on empirical tracking data to ensure that agents have home range sizes, displacement distances and residence times that match those of real porpoises (Sveegaard et al., 2011; van Beest et al., 2018). Switching between the two movement modes is directly determined by the energetic status of the agent. When a porpoise agent manages to locate food resources in a given area, its energy level is maintained or increases, which allows it to reproduce successfully. When foraging success and thus the energy level of a porpoise agent declines for a predetermined amount of time, the porpoise agent switches to large-scale movement behaviour and starts moving towards another potential feeding area. Porpoise agents have a spatial memory of where in the landscape food resources were found previously, which guides their inter-patch movements. If food is not found in previously visited feeding areas (e.g. due to depletion as a result of competition with other porpoise agents), the porpoise's energy level steadily declines, which increases the risk that it abandons its lactating calf or dies. As such, foraging success directly influences individual fitness and population dynamics.

Energy expenditure in the model is determined by the animals' field metabolic rate and movement, which is dependent on season (e.g. water temperature) and by reproductive status, with higher energy use for lactating females. Underwater noise also has a negative effect on the energy level of porpoise agents as any foraging activity is interrupted and deterrence movements away from the sound source lead to increased energy expenditure. Porpoise agents remain deterred to noise for a maximum of 2.5 h, but the extent to which they are deterred is halved at every time step. If a deterred porpoise agent moves far enough away from a sound source so that the sound level is below a predetermined threshold, it stops being deterred and, depending on its energy level, either resumes fine-scale foraging movements or starts dispersal movements. The impact of underwater noise is thus the combination of lost foraging opportunities and increased energy expenditure due to deterrence movements, which influences the energy level of an agent and its probability of reproducing and surviving successfully.

To estimate the population-level consequences of bycatch and pinger deployment, the DEPONS model used in this study has the option to activate gillnet agents (with or without a pinger present). The number, length, location, and soak time of gillnet agents in the IBM seascape are based on empirical data of Swedish and Danish gillnet fisheries. Each gillnet agent is assigned a bycatch probability value, which was calibrated by van Beest et al. (2017) to get a realistic annual bycatch rate for the inner Danish waters landscape. As such, gillnet agents have a direct negative effect on porpoise agents' survival probability. In scenarios where pingers are activated on gillnet agents, the probability of bycatch by gillnet agents is drastically reduced, but porpoise agents are impacted by pinger noise through loss of foraging opportunities and deterrence movements away from pinger noise.

In this study, we built on the pinger noise avoidance framework of van Beest et al. (2017) to ensure that porpoise agents responded to pinger noise with deterrence movements that lead to temporary declines in harbour porpoise densities in the vicinity of active pingers as observed in nature. Briefly, this response, described fully in van Beest et al. (2017), was informed by a previous empirical study estimating the change in porpoise acoustic activity, used as a proxy for presence, at different range of a pinger depending on whether it was enabled or not. The pinger, an Aquamark100 (Kindt-Larsen et al. 2019), was placed in the center of an array of porpoise click detectors (C-PODs, www. chelonia.co.uk) that were placed at 0, 400, 800, and 1600 m from the pinger. An internal clock activated the pinger in cycles of 23 h on (with noise) and 23 h off (without noise). Results of the empirical studies were subsequently used in van Beest et al. 2017 to tune the noise deterrence behaviour of porpoise agents in the model using pattern-oriented modelling (POM) (Grimm et al. 2005). Because in this version of the model the sound level received by porpoise agents, R, was modelled assuming spherical spreading (Urick 1967), which differs from the linear decrease used in van Beest et al. (2017), we redid the POM, by varying the level of sound emitted by the pingers (impact, to reflect those used in the fisheries) and the deterrence coefficient (*c*) of porpoise agents until we identified the combination of values that produced the same decrease in porpoise densities with distance to the pingers in the model as observed during the empirical studies.

Scenarios

Once the deterrence behaviour of porpoise agents was tuned, we explored two gillnet exposure scenarios: one (*pingers only*) in which all areas are available for fishing and net deployment mimics actual gillnet deployment locations and effort in the study region (van Beest et al. 2017), and a second (*pingers and area closure*) where time area closures are implemented but keeping fishing effort constant across the landscape by redistributing fishing effort outside the area closed (see van Beest et al. 2017 for full details). Area closures were implemented in locations and seasons with higher bycatch risk and the fishing effort redistribution was implemented to

mimic the expected compensatory fishing behaviour that would be implemented by fishers in such circumstances (O'Keefe et al. 2014). The stochastic nature of the effort redeployment led to an overall slight drop in fishing effort (by 10%), which would be expected in reality, as fishers would not always be able to fully replace all fishing effort displaced (Smith et al. 2020).
For each scenario, we run 30 replicate simulations of 40 years for each level (n=11) of pinger prevalence treatment in gillnets (from 0% to 100% in 10% increment). For each level, established gillnets were randomly selected to be equipped with pingers with a probability equal to the prevalence set for the treatment level.

Integrating condition-mediation of behavioural responses in existing agent-based model
One shortcoming of current DEPONS implementations is a lack of condition-mediated behavioural responses to noise exposure. Thus, all porpoise agents respond to noise with the same deterrence strength and independent on current condition. However, this is an important feature of PCoD which influences system state and dynamics (Nattrass and Lusseau 2016), and, given the life history traits of harbour porpoises, we assume that it could lead to overestimation of condition-mediated mortalities (Dall and Johnstone 2002). Particularly in our case, harbour porpoises are known to change their behavioural responses to noise exposure over time (Graham et al. 2019, Kindt-Larsen et al. 2019), a functional response that could emerge from changes in body condition (Bejder et al. 2009). It is therefore important to introduce condition-mediation mechanisms in agent's response to noise exposure. Here we introduce three possible functional responses of the movement to noise depending on condition: linear; non-linear; and asymmetrically non-linear, assuming that behavioural response is resilient to condition changes (Figure 6.2.1). This was done by altering the file *Porpoise.java* (function 'deter', lines 1237-1238, https://github.com/jacobnabe/DEPONS).

To do so the length of the deterrence vector (V_D) was associated to the condition of the individuals. The deterrence vector determines the response of porpoises to noise exposure (the direction and magnitude of the movement change). Full details of the variables and functions is available in the TRACE document of DEPONS (Nabe-Nielsen et al. 2018):
Without condition-mediation (unaltered DEPONS):

$$|V_D| = c(R - T) \qquad \text{Eq. 1}$$

Linear condition-mediation:

$$|V_D| = \frac{cE_p}{E_{pmax}}(R - T) \qquad \text{Eq. 2}$$

Non-linear, symmetric condition-mediation:

$$|V_D| = \frac{c}{1 + e^{-E_p + \frac{E_{pmax}}{2}}}(R - T) \qquad \text{Eq. 3}$$

Non-linear, asymmetric condition-mediation:

$$|V_D| = \frac{c}{1 + e^{-1.24E_p + \frac{E_{pmax}}{2}}}(R - T) \qquad \text{Eq. 4}$$

Where c is a tuned deterrence coefficient, which we kept with the same value for Eqs 1-4, R is the sound received level by the porpoise and T the threshold at which sound elicits a deterrence response (if $R<T$, then $V_D=0$). E_p is the energy level of the individual porpoise, a measure of its condition, and E_{pmax} is the maximum value E_p can take (in DEPONS E_p varies from 0 to 20).

The 330 model runs (40-years each) of '*pingers only*' described in the previous section were simulated for each of these four types of condition mediation. When contrasting the outcome of the different functional responses it became apparent that there was no qualitative difference in outcomes and the responses only varied the effect sizes. For simplicity we contrast the inclusion of the non-linear symmetric condition mediation (Eq. 3, yielding the largest effect of the condition functional responses) and the current DEPONS model lacking condition-mediation (Eq. 1) for the main analyses (660 runs across both scenarios).

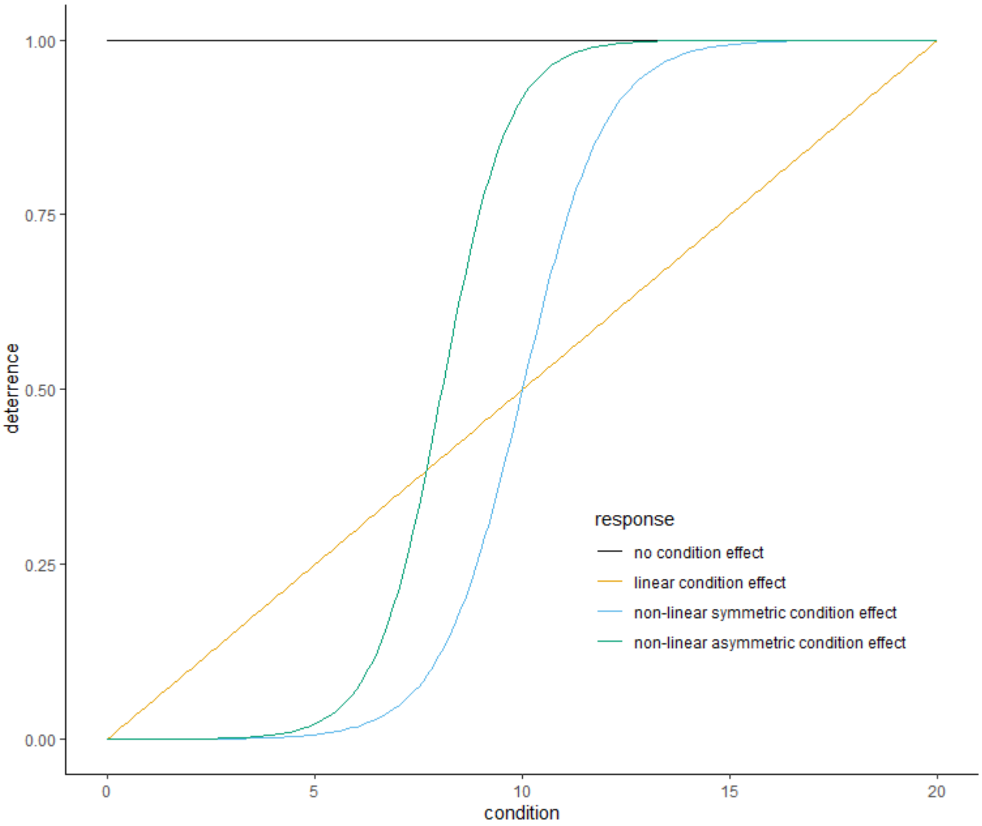

Figure 6.2.1. Functional responses of deterrence depending on condition for the four shapes considered (Eqs. 1 to 4 in the main text). This function then alters the tuned deterrence coefficient, c, (van Beest et al. 2017).

We did not fully reparameterise the DEPONS model to integrate condition mediation i) so as to facilitate comparison with previous work (van Beest et al. 2017) and ii) because we currently do not have data to inform the absolute changes in behavioural response with changes in condition. Instead, we applied the functions described above (eqs. 1-4) to the tuned model described in van Beest et al. (2017). This means that we cannot interpret the absolute change in abundance trajectory between simulations with and without condition mediation. However, we can appraise whether the behaviour of the modelled system changes with the integration of condition mediation (a non-trivial question given the physiological dynamics and population dynamics of the species). Implementation of these changes and simulation outcomes are available at the DEPONS fork: https://github.com/dlusseau/DEPONS.

Estimating changes in population dynamics with changes in pinger prevalence

Here we estimated whether abundance was associated with pinger prevalence, whether the implementation of condition mediation in the model interacted with this association and whether these effects changed depending on the scenarios. We fitted generalised linear mixed effects models (GLMMs) to the abundance time series assuming a Poisson distribution of residuals and accounting for a random effect of run replicates and an autoregressive autocorrelation structure with a lag of 1-year (following preliminary inspection of the autocorrelation of residuals) within run replicates. We fitted models with a categorical fixed effect of prevalence, scenario, and condition mediation function type as well as a potential interaction between those effects. We fitted these models to both the whole 40-year time series and to the last 20 years of the time series. The first set of models account for both long-term behaviour of abundance as well as behaviour as the system moves away from initial conditions (which captures some understanding of reactivity). The latter set accounts for the behaviour of abundance away from initial conditions.
We replicate this modelling process with mortalities, assessing whether the mortality rate changed with prevalence and condition mediation; assuming a Poisson distribution of the residuals of the number of deaths per year and an offset effect of the log of the abundance. We then assessed whether bycatch rate changed with these fixed effects (prevalence, condition mediation and scenario) by fitting similar generalised linear mixed effects models to the proportion of porpoises dying of bycatch out of recorded yearly abundance, assuming a binomial distribution of the residuals.

Finally, as PCoD are most likely to emerge from changes in reproductive rate, we estimated whether the lifetime reproductive success (LRS) of females was associated with the fixed effects. LRS was estimated as the number of weaned calves produced by a female over her lifespan. This count was not offset by the age at death of the female as LRS capture trade-offs between survival and reproductive investment. We complemented this analysis by determining whether the number of calves produced by females by a given age (offset by the age of females when they die) varied across simulation sets and implementing the same models to the proportion of weaned-to-produced calves.

System transient dynamics – basin of attraction of attractors, the resilience of porpoise populations exposed to different scenarios

We can explore the temporal dynamics of the way the population moves away from initial conditions (year 0) towards the levels at which it settles under the different scenarios to understand its resilience in the state in which it settles. This state can be defined by two dimensions which are in the model the primary drivers of population dynamics: abundance and the condition (energy) of porpoises in the population. The latter is a primary driver of population dynamics because it is modelled to directly influence the survival probability and reproductive success of individuals. To do so, we approximated the flow trajectory of the system’s phase portrait in the {abundance, porpoise energy} plane using a general additive model (GAM) relating the change in a bivariate response variable $(\frac{dabundance}{dt}, \frac{denergy}{dt})$

to a spline relationship of the interaction between abundance and average energy level of individual porpoises at time *t*. Fitted values of this GAM provide insights about the system's behaviour by approximating the partial derivatives of the indirectly coupled abundance and energy time series (Nattrass and Lusseau 2016). Hence, this approximates the Poincaré map of the system, providing a similar information to what a Jacobian matrix would for a deterministic model composed of coupled differential equations (Nardini et al. 2021). We then estimated whether the type of basin of attraction changed with prevalence and condition mediation and whether the attractor changed with prevalence and condition mediation by predicting abundance and average porpoise energy from the GAM for $\left(\frac{dabundance}{dt}, \frac{denergy}{dt}\right) = 0$.

We finally estimated the engineering resilience of the system state (Nattrass and Lusseau 2016) by estimating the speed of travel of the system (s) in the (abundance, porpoise energy) plane depending on its distance from the estimate equilibrium:

$$s_t = \sqrt{(\frac{d\widetilde{abundance}}{dt})^2 + (\frac{d\widetilde{energy}}{dt})^2}$$

Eq. 5

Where $\tilde{x}$ is the variable centered and scaled by its standard deviation so that rate of movement on both axes (that have different magnitudes) are comparable. We then estimated changes in speed with distance from the equilibria depending on pinger prevalence, condition mediation and scenario using a GLMM, with a random effect of run replicates and assuming a quadratic effect of 'distance from equilibria' on speed and a gaussian distribution of residuals. All GLMM were implemented in R using glmmTMB (Brooks et al. 2017) and GAM using mgcv (Wood 2017).

6.2.3 Results

The effects of condition-mediation

Condition-mediation functions significantly altered population trajectory with pinger prevalence with the symmetric non-linear function (Eq. 3) being most distinguishable from simulations without condition mediation (Figure 6.2.2). Whether we considered the whole simulated times series or the latter halves, abundance varied with prevalence and, moreover, the effect of prevalence depended on whether condition mediation was implemented or not. As expected, implementing condition mediation increased the realised abundance, particularly for higher pinger prevalence. These effects were more pronounced in the last 20 years of simulations (Figure 2).

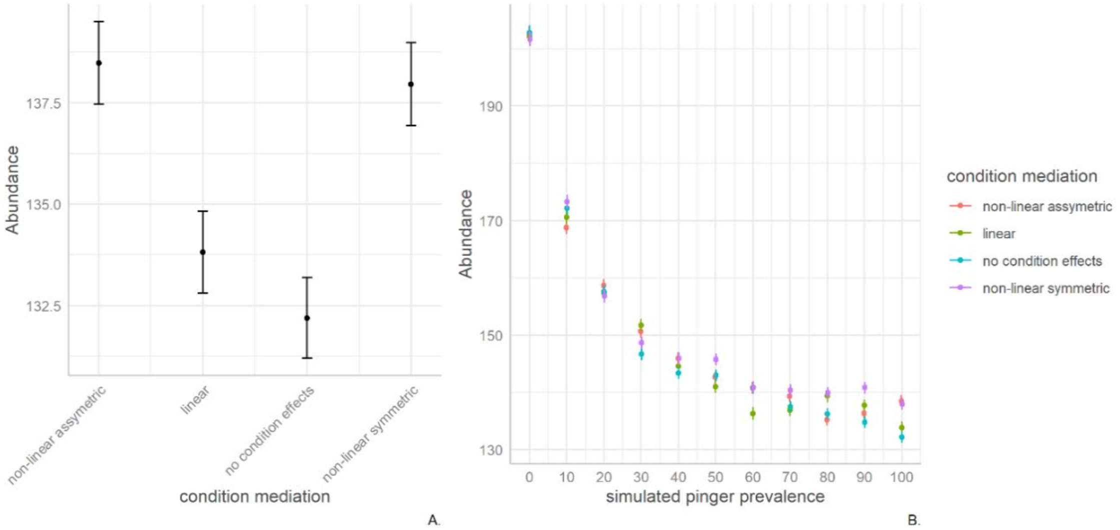

Figure 6.2.2. Predicted partial effects of condition mediation (4 functions, see Methods Eqs 1-4) at pinger prevalence 100% (A) and the interaction between pinger prevalence and condition mediation function (B) when considering the last halves (20 years) of time series. Error bars are 95% confidence intervals around the mean. Prediction from best model when considering pinger-only scenario (condition: χ^2_3=130.5, p<0.00001; prevalence: χ^2_{10}=64263.5, p<0.00001; prevalence x condition: χ^2_{30}=429.3, p<0.00001; 26400 observations; variance associated with replicate runs (n=30): σ = 1.1e-5; variance associated with autocorrelation of year in run: σ = 0.0096, ρ = 0.95).

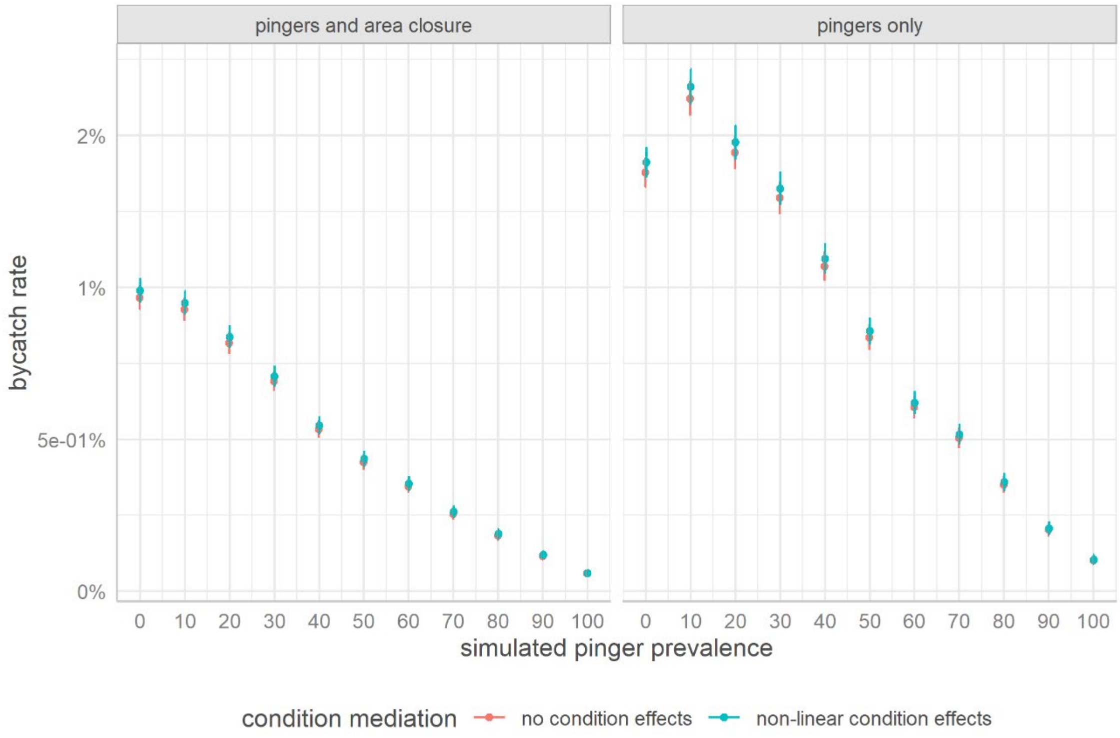

Figure 6.2.3. Predicted annual bycatch rate, estimated as the proportion of individuals dying from bycatch annually out of the annual abundance, depending on condition mediation, pinger prevalence and scenario. Error bars are 95% confidence intervals around the mean.

Bycatch rate changed non-linearly with pinger prevalence in both scenarios (Figure 6.2.3, Tables 6.2.1 & 6.2.2). This non-linearity in bycatch rate is more pronounced in the "*pingers only*" scenario, in other words when bycatch risk is homogeneous across the landscape. The effect of including condition mediation changes through the levels of pinger prevalence being more pronounced at lower levels.

Table 6.2.1. Selection of models based on Akaike Information Criterion (AIC) to determine factors associated with simulated porpoise annual bycatch rates over the last halves (20 years) of times series when simulated populations have moved away from initial conditions. Annual bycatch rate is estimated as the proportion of animal dying from bycatch out of the total abundance that year. Models are generalized linear mixed effect models assuming a binomial distribution of residuals, including a random effect of run (30 replicate runs for each simulation set). There was no support (in model validation) to include an autocorrelation structure. Factors are condition (no condition effects, non-linear condition effects), prevalence of pingers in nets (ranging from 0 to 100% treated as a factorial variable) and TA (implementation of time-area closure). Model retained is in bold.

		Last 20 years	
model	fixed terms	AIC	ΔAIC
1	Condition	85691.8	16482.0
2	Prevalence	71882.8	2673.0
3	Condition+prevalence	71880.0	2670.2
4	Condition*prevalence	71889.8	2680.0
5	TA	82595.2	13385.4
6	TA+condition	82594.2	13384.4
7	TA+prevalence	69288.8	79.0
8	TA+condition+prevalence	69286.2	76.4
9	TA+condition*prevalence	69296.1	86.3
10	TA*condition	82595.9	13386.1
11	TA*prevalence	69212.3	2.6
12	TA*condition+prevalence	69287.4	77.6
13	TA*condition*prevalence	69235.3	25.6
14	TA*prevalence+condition	**69209.8**	**0.0**

Table 6.2.2. Analysis of Deviance table for the best model describing the variance in annual bycatch rate over the last 20 years of simulatiohns (model 14, Table 6,2,1). Variance associated with run ($\sigma = 0.021$).

Terms	χ^2	df	p-value
TA	2546.8	1	<0.000001
Condition	4.6	1	0.03
Prevalence	9234.5	10	<0.000001
TA x prevalence	97.1	10	<0.000001

Females produced calves at a constant rate throughout all simulation sets with predicted average of 3.13 calves (95% CI: 3.126; 3.135, Table 6.2.3) born to a female by the time she reaches 8 years. Females' lifetime reproductive success was also constant with a predicted 2.06 weaned calves produced on average by female porpoises in their lifetime (95%CI: 2.058; 2.072, Table 6.2.4). The rate at which these calves were successfully weaned depended on pinger prevalence and scenario (Figure 6.2.4). Overall, this rate is higher in the pinger only scenario. The weaning rate is also significantly lower when ≥90% of nets have pingers and significantly higher when 10-30% of nets have pingers.

Table 6.2.3. Selection of models based on Akaike Information Criterion (AIC) to determine factors associated with simulated total number of calves born to each female porpoise over their lifespan over the last halves (20 years) of time series when simulated populations have moved away from initial conditions. Models are generalized linear mixed effect models assuming a Poisson distribution of residuals, including an offset of the log of the female's age when she died and a random effect of run (30 replicate runs for each simulation set). Factors are condition (no condition effects, non-linear condition effects), prevalence of pingers in nets (ranging from 0 to 100% treated as a factorial variable) and TA (implementation of time-area closure). Model retained is in bold.

		Last 20 years	
model	fixed terms	AIC	ΔAIC
0	Constant (σ_{run} = 1.3e-5)	**1870448**	**0**
1	Condition	1870450	2
2	Prevalence	1870462	14
3	Condition+prevalence	1870464	16
4	Condition*prevalence	1870477	29
5	TA	1870450	2
6	TA+condition	1870452	4
7	TA+prevalence	1870464	16
8	TA+condition+prevalence	1870466	18
9	TA+condition*prevalence	1870479	31
10	TA*condition	1870454	6
11	TA*prevalence	1870477	29
12	TA*condition+prevalence	1870468	20
13	TA*condition*prevalence	1870511	63
14	TA*prevalence+condition	1870479	31

Table 6.2.4. Selection of models based on Akaike Information Criterion (AIC) to determine factors associated with simulated female lifetime reproductive success (LRS) over the last halves (20 years) of time series when simulated populations have moved away from initial conditions. LRS is estimated as the number of weaned calves a female produced over her lifespan. Models are generalized linear mixed effect models assuming a negative binomial distribution of residuals, including a random effect of run (30 replicate runs for each simulation set). Factors are condition (no condition effects, non-linear condition effects), prevalence of pingers in nets (ranging from 0 to 100% treated as a factorial variable) and TA (implementation of time-area closure). Model retained is in bold.

		Last 20 years	
model	fixed terms	AIC	ΔAIC
0	Constant (σ_{run} = 3.2e-5)	**2319438**	**0**
1	Condition	2319440	2
2	Prevalence	2319455	17
3	Condition+prevalence	2319457	19
4	Condition*prevalence	2319472	34
5	TA	2319440	2
6	TA+condition	2319442	4
7	TA+prevalence	2319457	19
8	TA+condition+prevalence	2319459	21
9	TA+condition*prevalence	2319473	35
10	TA*condition	2319444	6
11	TA*prevalence	2319470	32
12	TA*condition+prevalence	2319461	23
13	TA*condition*prevalence	2319504	66
14	TA*prevalence+condition	2319472	34

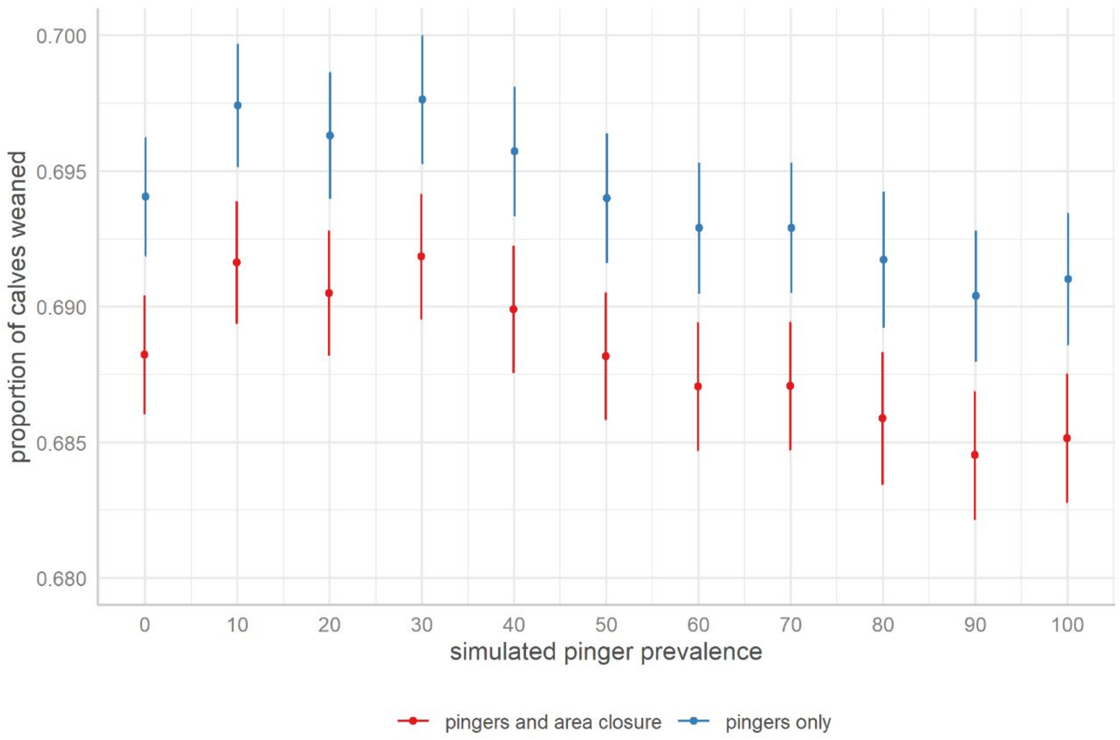

Figure 6.2.4. Predicted proportion of calves born that are successfully weaned in the last 20 years of simulations depending on pinger prevalence and the scenario considered. Error bars are 95% confidence intervals around the mean.

System transient dynamics – potential for extirpation and population resilience

With an observed effect on abundance, it is important to know whether any of the simulation sets may lead to extirpation of the simulated populations. Here we find, given the simulated 40 years, that all simulation sets stabilise around non-zero attractive focus equilibria in the (abundance, porpoise energy) plane along the same isocline (Figure 6.2.5).

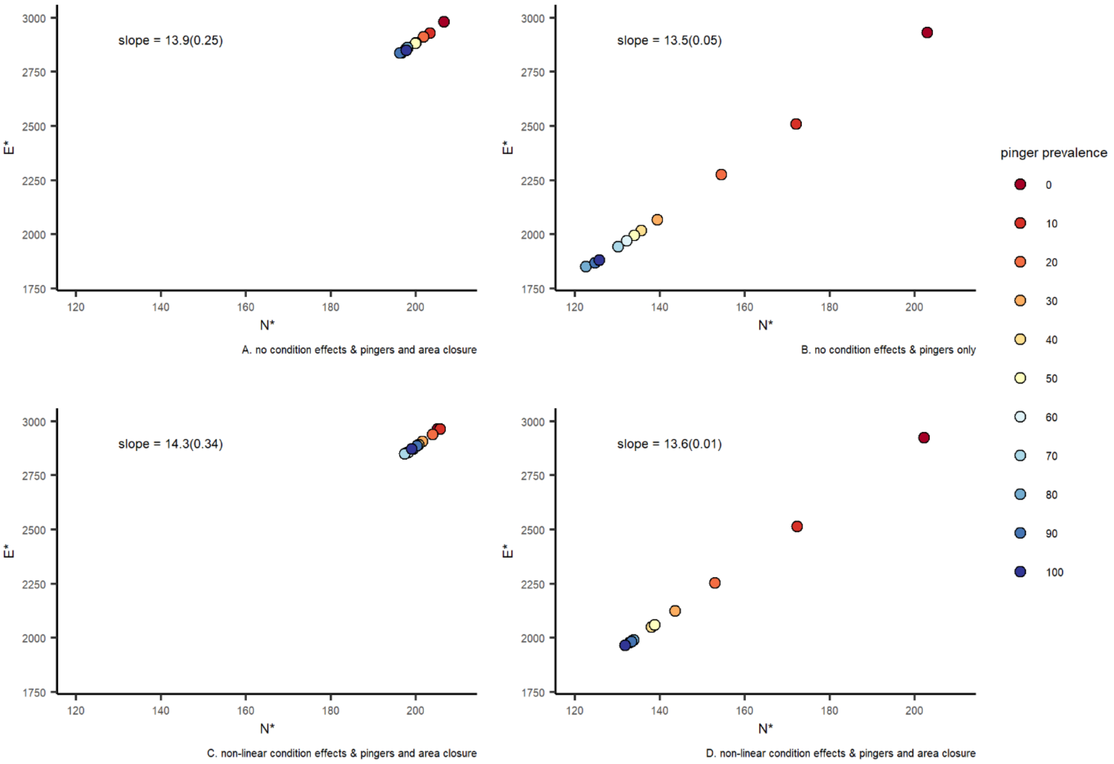

Figure 6.2.5. Estimated equilibria based on the 30 run replicates for each level of condition mediation, scenario and pinger prevalence. Each graph is annotated with the slope of the isocline and its associated standard error.

However, the engineering resilience of the system states varies with pinger prevalence, condition mediation implementation, and scenario (Figure 6.2.6). The estimated basin of attraction is more resilient at zero pinger prevalence because the estimations show that the porpoise population would rapidly travel back to its equilibrium after a disturbance. However, we need to be careful that the absolute magnitude of engineering resilience may be caused by the tuning process rather than being an emergent property of the ecological system as the parameters relating energy to abundance are tuned. When overall bycatch risk is not spatially segregated ("*pingers and area closure*" scenario) the system resilience does not change with pinger prevalence. In the other scenario, we may be observing critical slowdown (van Nes and Scheffer 2007) at high pinger prevalence (the speed of the system becomes slower and more varied as we move away from the equilibria, 0 on the x-axis, with decreasing abundance). This indicates that in this tuned system, with the assumption of a given function relationship between condition and response to noise (Eq. 3), a pinger prevalence of 100% may place the system in danger of a state shift, with alternative equilibria moving away from the current isocline. However, we can see the difference in behaviour at 100% prevalence between scenarios that did not have a condition effect and those that include one. When condition-mediation was considered, the resilience increases again at 100%.

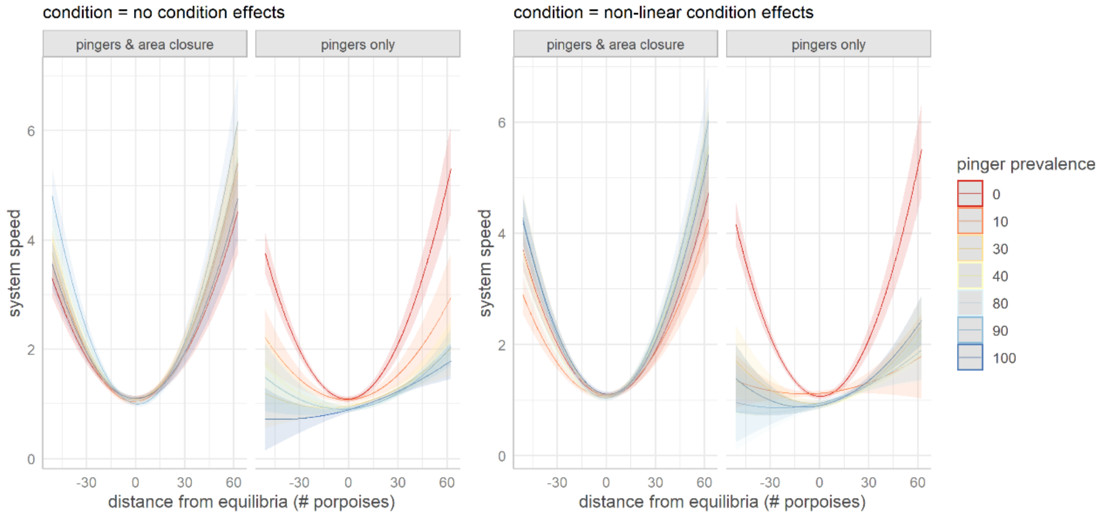

Figure 6.2.6. Predicted speed of travel of the system, a proxy for engineering resilience and the shape of the equilibria's basins of attraction along the abundance axis, given pinger prevalence, condition-mediation, and scenario. The 'flatter' the curve, the less resilient the system is. Error bars are 95% confidence intervals around the mean.

6.2.4 Conclusions

The simulation outcomes depended on the inclusion of condition-mediation, hence it would be important to retain this feature in future PCoD simulation platforms. To fully understand this mechanism, more experimental studies are needed to estimate dose response relationships for behavioural responses to noise exposure depending on an ecologically-relevant measure of body condition (Derous et al. 2020). Here we introduced condition mediation in a pre-tuned model limiting our capacity to assess the absolute magnitude of change in abundance and mortalities associated with condition mediation implementation. Our results are related to the system state, and its associated resilience, to which the model was tuned. As expected from theoretical and empirical studies, PCoD were more likely to emerge from condition-mediated effects on offspring production (Pirotta et al. 2018, Allen et al. 2022). Here we showed that bycatch rate increased at low pinger prevalence in contrast to the simulation of fisheries operating without pingers. This non-linear effect remained in the "*pingers and area closure*" scenario. It is anticipated that pingers at lower prevalence simply increase the movement, via displacement, of harbour porpoises leading them to increase their encounter probability with gillnet unequipped with pingers, and therefore increasing the overall bycatch risk. We can therefore expect this non-linear effect of pinger on bycatch rate to emerge in real life. In the currently tuned model, it takes a prevalence of 30% and above for the bycatch rate to start falling below conditions where there were no management interventions (20% with time area closure implementation). We can therefore conclude that if pingers are implemented in a region they need to be consistently implemented over a significant proportion of the fleet in order to not be counter-productive. We anticipate this outcome to be consistent across a range of tuneable parameters, with varying effect size. It also means that the decision to implement pinger interventions needs to be warranted and implemented with a robust monitoring programme as poor compliance may result in increased bycatch. Current European legislation does not account for this indirect effect and in some cases limits pinger intervention only on part of the fleet (EU 2019). This could have the unintended consequence to increase bycatch depending on the fishing effort covered by pinger deployment. The probability that pinger implementation in fisheries will yield reduced survival probability and reproductive outputs in the population depends on the functional relationship between individual harbour porpoise condition and their demographic contributions. This function is currently approximated, not informed by physiological studies, in a manner that may be useful when applying the precautionary principle to a single impact assessment (Nabe-Nielsen et al. 2018, Pirotta et al. 2018) but which needs to be known more precisely if it is to impact management decisions on trade-offs between multiple or cumulative impacts (Pirotta et al. 2022).

In our simulations the gillnet density, that is the fishing effort, leads to a decreased porpoise abundance as the pinger prevalence in gillnets increases, but a decrease that does not lead to extirpation of the population. Instead, simulated populations reach non-zero equilibria along the same (abundance, porpoise energy) isocline. This effect is lessened when we allow individuals to have a condition-mediated response to pingers. Decreasing gillnet density in high porpoise density area, by introducing time-area closures, simply moves the intercept upwards on this relationship. Hence, while area closure can be a useful tool to decrease pinger density if PCoD elicited by pingers are likely to occur, they do not provide additional functional interventions on the porpoise-fishery system. That is, they do not affect the bycatch probability when a net is encountered but affect bycatch rate by decreasing net encounters. In our model, we assume that this decreased encounter does occur by designing the shift of fishing effort so that displaced effort is placed in low harbour porpoise density locations. Here, we assumed fisher behaviour's response to the area closure to have the maximum effect on net encounter probability in the model. Before area closure are implemented it is crucial to better understand fisher behaviour and the socioecological propensity to spatially and temporally shift fishing effort given that the main contribution of area closures to conservation objectives is through the displacement of fishing effort towards areas that are less used by porpoises. We therefore need to better understand the drivers of fisher behaviour in response to area closure. Fisheries microeconomics factors will influence whether fishers are likely to displace all their effort to nearby low bycatch risk areas. It is possible that costs would prevent them to do so or might jeopardise the sustainability of their activities (O'Keefe et al. 2014, 2021). These socioeconomic functions can be complex, with environmentally-associated inter-annual variation (Smith et al. 2020).

Noise-mediated pinger effects (van Beest et al. 2017) are impacting population abundance by decreasing the reproductive potential of individuals. While pinger prevalence influences mortality as the simulated populations move away from initial conditions, once the populations are closer to equilibria, mortality is only influenced by whether locations with high bycatch risk are not fished once we account for the cost of responding to pingers. However, when close to equilibria the proportion of weaned calves depends on pinger prevalence. In our tuned simulations, the proportion of weaned calves is higher at lower prevalence and significantly lower when pinger prevalence exceeds 80%. As LRS and calf production is estimated to be constant, it is likely that the variation in the proportion of weaned calves can be explained by a selection towards females in better condition. That is, the increased mortality observed is biased towards females in poorer condition, and hence the population average weaning rate is increased by the removal of these females. Such indirect effects could act as selection pressure on the population, changing its phenotypic characteristics. It could also change its vital rates (e.g., age-at-first-reproduction); compensatory measures that are not functionally implemented in our models. Also, this may be the factor affecting the resilience of the simulated population, and hence its ability to cope with added stressors (Nattrass and Lusseau 2016).

In conclusion, we show here that pinger implementation can be an effective management intervention to reduce bycatch rate. However, we also show that when designing such a management intervention it is important to consider that this effectiveness depends on the deployment schedule. If compliance issues are anticipated, and difficult to address and redress, then a low pinger prevalence in nets has the potential to increase bycatch rate. At the same time, at high fishing effort, a high pinger prevalence could lead to PCoD elicitation if the affected population is in a physiological and an ecological context in which we can expect PCoD to emerge (Lusseau 2014, Nattrass and Lusseau 2016), counteracting against the gains made from reduced bycatch rate. This latter effect is likely to be mediated by an influence on reproductive rate. Therefore, to detect this effect, it will be necessary to ensure that monitoring programmes include observations allowing to estimate this demographic parameter in addition to bycatch rate estimation. Moreover, as others have also concluded on multiple occasions (Booth et al. 2020), such a monitoring programme would aid in estimating PCoD more widely and help attribute the impact of multiple human marine activities on harbour porpoise conservation objectives. Such a framework would ensure that fisheries are not the sole bearer on management interventions to help achieve conservation objectives for these species.

7 Outreach of the project (WP5)

7.1 Meetings with partners outside the project team

The results from the project have been presented at the following meetings. All listed meetings are outside the regular project management meetings between the project partners.

1. 2nd June 2022: Fisher meeting, presenting the results to the fishing community of Thorsminde, DK.

2. 27th April 2022: Cooperation meetings, SLU (Sveriges Landbrugs universitet), Thünen (Johann Heinrich von Thünen Institute) and DTU Aqua.

3. 27th September 2022: Presentation to ASCOBANS. Porpoise bycatch assessment and porpoise mortality estimates in Danish and Swedish gillnets.

4. 22th November 2022: Cooperation meetings, SLU (Sveriges Landbrugs universitet), Thünen (Johann Heinrich von Thünen Institute) and DTU Aqua.

7.2 Scientific papers

The project has at this stage resulted in 4 scientific papers.

1. Brennecke, D., Siebert, U., Kindt-Larsen, L., Midtiby, H., Egemose, H., Ortiz, S., Knickmeier, K,. & Wahlberg, M. (2022). Fine-scale behavior of harbor porpoises towards pingers. *Fisheries research: an international journal on fishing technology, fisheries science and fisheries management* 255.

2. Lusseau, D., Kindt-Larsen, L., & van Beest, F. M. (2023). Emergent interactions in the management of multiple threats to the conservation of harbour porpoises. *Science of the Total Environment*, *855*, 158936.

3. Kindt-Larsen, L., Glemarec, G., Berg, C. W., Königson, S., Kroner, A. M., Søgaard, M., & Lusseau, D. (2023). Knowing the fishery to know the bycatch: bias-corrected estimates of harbour porpoise bycatch in gillnet fisheries. *Proceedings of the Royal Society B*, *290*(2002), 20222570.

4. Kindt-Larsen, L., Brooks, M. E., & Glemarec, G. Mind the Gap-Pinger Spacing and Sound Levels Influence Bycatch Rates of Harbour Porpoises. *Available at SSRN 5115164*.

7.3 Conferences

The work has been presented at four international conferences.

1. Brennecke, D., Siebert, U., Kindt-Larsen, L., Midtiby, H.S., Egemose, H.D., Ortiz, S.T., Knickmeier, K., Wahlberg, M. (2019) The fine-scale behavior of harbor porpoises towards pingers. ECS, Barcelona, Spain.
2. Brennecke, D., Siebert, U., Kindt-Larsen, L., Midtiby, H.S., Egemose, H.D., Ortiz, S.T., Knickmeier, K., Wahlberg, M. (2022) The fine-scale behavior of harbor porpoises towards pingers. SMM, Florida, USA.
3. Wahlberg, M. (2022). Introduction to playback experiments. Oral presentation, African Bioacoustic Conference, Skukuza 5th of October 2022.

7.4 Working groups

The work has been presented at the following working groups

1. Wahlberg, M. (2021). Porpoise detection of gill nets. Oral presentation, ICES WGFTFB, 20th of April 2021 (online).
2. Porpoise bycatch assessment and porpoise mortality estimates (2022). WGBYC, ICES Working Group on Bycatch of protected species. La Rochelle, France.
3. Wahlberg, M. (2022). Individualizing small cetaceans. Oral presentation, SMM workshop, Florida, USA, 30th of July, 2022.

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