



Pingers cause temporary habitat displacement in the harbour porpoise *Phocoena phocoena*

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ABSTRACT: Several studies have shown that pingers mitigate porpoise bycatch and thus pinger use is now mandatory in some fisheries—although the long-term effects of pinger exposure on porpoises have not been well studied. The effects of 2 types of pingers (Airmar: 10 kHz tone; Save-Wave Black Saver: 30–160 kHz sweep) on the presence of wild harbour porpoises, *Phocoena phocoena*, were investigated in 2 areas. Pinger spacing within the areas was similar to that used in commercial fisheries. Two scenarios were tested: (1) pingers were periodically activated and deactivated during 6 periods resembling the deployment and recovery of nets in a gillnet fishery, and (2) pingers were active continuously for 28 d. Acoustic dataloggers (T-PODs) were deployed, 4 within the pinger areas and 3 in control areas, and detected porpoise echolocation activity throughout the entire study. During the periodic-exposure scenario, the porpoise detection rate was reduced by 56% when pingers were active. The reduction was larger for the SaveWave pingers (65%) than for the Airmar pingers (40%). There was a tendency for the encounter rate to increase after the first 2–4 periodic exposures, which could indicate gradual habituation. During the continuous-exposure scenario, the detection rate was reduced by 65% throughout the 28 d with no sign of habituation. In the control areas (2.5, 3 and 5 km distant), neither a decrease nor an increase in detection rate was observed, suggesting that porpoises were displaced either <2.5 km or >5 km away. If pingers are used as deterrent devices, the impact of habitat exclusion must therefore be considered concurrently with mitigation of bycatch, especially when regulating fisheries in Marine Protected Areas.

KEY WORDS: Acoustic deterrent devices · ADD · Small odontocetes · Habituation · Habitat displacement · Bycatch · T-POD · Passive acoustic monitoring · Special Areas of Conservation · Noise pollution

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INTRODUCTION

Throughout its range, the harbour porpoise *Phocoena phocoena* (L., 1758) faces the threat of entanglement in gill nets (e.g. IWC 1994, Read 1994, Vinther 1999, Northridge et al. 2003). So far, the most promising tools to reduce porpoise bycatch are acoustic deterrent devices (ADD), so-called 'pingers', which emit sounds and are mounted on the head rope of gillnets. Since the development of the first prototype

(Lien et al. 1992), many experiments with pingers have been conducted. Behavioral studies with porpoises both in captivity (Kastelein et al. 2001, Teilmann et al. 2006) and in the wild (Cox et al. 2001, Koschinski et al. 2006, Larsen & Krog 2007, Carlstrøm et al. 2009, Hardy et al. 2012) have shown that pingers and pinger-like signals deter porpoises. Moreover, double blind trials conducted in fisheries have shown that pingers reduce porpoise bycatch significantly (Kraus et al. 1997, Trippel et al. 1999, Larsen et

al. 2002) (see Dawson et al. 2013 for a full list of pinger trials and studies). Based on the 92% reduction in the bycatch rate found by Kraus et al. (1997), use of pingers, together with time/area exclusion of fishery and gear modification, was mandated in USA legislation (Harbor Porpoise Take Reduction Plan, www.greateratlantic.fisheries.noaa.gov/protected/porptrp/). However, control hauls undertaken in the fishery found only a 50 to 70% reduction in nets with pingers compared to nets without pingers (Palka et al. 2008). Those authors concluded that the reduced effect was partially caused by the incorrect use of the pingers and by the use of a different mesh-size than that used in Kraus et al. (1997).

In 2004, the Council of the European Union laid down measures concerning incidental catches of cetaceans in European fisheries (EU 2004). The use of pingers was mandated in gill net fisheries over a wide range of the North and Baltic Seas, with full implementation in 2007. However, several essential questions concerning the reactions of porpoises to prolonged pinger exposure remain unanswered. Firstly, the central question is whether a displacement effect caused by pingers may lead to habitat exclusion and, as a consequence, have a larger impact on the survival of porpoise populations than bycatch itself. Secondly, it is important to determine if—and if so, to what extent—porpoises may habituate to or gain useful information from pinger sounds when recurrently exposed to them, i.e. the porpoises may temporarily habituate to the pingers if they, as a consequence of avoiding nets, are not caught. Both Cox et al. (2001) and Carlstrøm et al. (2009) found significant signs of habituation to single pingers in experimental setups without nets, which may not be surprising given the lack of negative reinforcement from the presence of fishing nets. Real fisheries may provide such negative reinforcement and may explain why the results of pinger trials in fisheries do not show increases in bycatch rates over time (Kraus et al. 1997, Trippel et al. 1999, Larsen et al. 2002). As legislation mandates pingers to be placed at intervals of a few hundred meters (depending on pinger type) along the gill net chains (EU 2004), a large number of pingers are used within areas of high gillnet fishery activity. Furthermore, each net deployment may last from a few hours to a few days, which makes the use of pingers in the real fishery very different from previous experimental designs with a single or a few pingers.

The main purpose of this study was to investigate how porpoises would react to long-term exposure to a large number of pingers. Would the porpoises remain in the exposed area, and if not, would they

return to the area after removal of the pingers? Two scenarios were tested: (1) a simulation of the type of exposure experienced in a gillnet fishery in which pingers were deployed and recovered in repeating cycles and (2) a test in which the pingers were continuously active for a longer period (several weeks). Porpoise presence was evaluated using passive acoustic dataloggers (T-PODs).

MATERIALS AND METHODS

Experimental set-up

The experiment was conducted from April to November 2005 in Jammerland Bay in the Great Belt, Denmark (55° 35' N, 11° 5' E). This area was chosen for its high porpoise density (Teilmann 2003), limited depth (10 m maximum) and limited fishing and recreational sailing activity. On April 15, 7 passive acoustic porpoise detectors (T-PODs, Chelonia) were deployed at 4 different locations: 2 T-PODs were positioned 600 m apart in a northern impact area (Impact NE and Impact NW), 2 T-PODs were positioned 600 m apart in a southern impact area (Impact SE and Impact SW) and 3 T-PODs were positioned at control sites (Control N: 5 km north of the northern impact area; Control S: 3 km south of the southern impact area; Control E: between the 2 impact areas, 2.5 km from the nearest pinger) (Fig. 1). The T-PODs were placed between 1.3 and 2.3 km from the shore at ~7 m depth above moraine/muddy sand bottom. They were deployed continuously from April 15 to November 8 and were not interchanged between locations (following the method of Carstensen et al. 2006). Data from the T-PODs were downloaded every 4th week, batteries (6 × 1.5 V lithium D-cell) were replaced and barnacles and mussels were removed from the T-PODs and moorings.

The study was conducted according to the following schedule:

- (1) Baseline (April 15 to May 13): only the T-PODs were in the water, and this period served as the baseline.
- (2) Periodic exposure (May 13 to June 29): the pingers were activated and deactivated cyclically with on and off periods of between 2 and 9 d, dependent on the weather.
- (3) Recovery 1 (June 29 to August 8): no pingers were active (they were physically removed from the buoys).
- (4) Continuous exposure (August 8 to September 5): the pingers were continuously active.

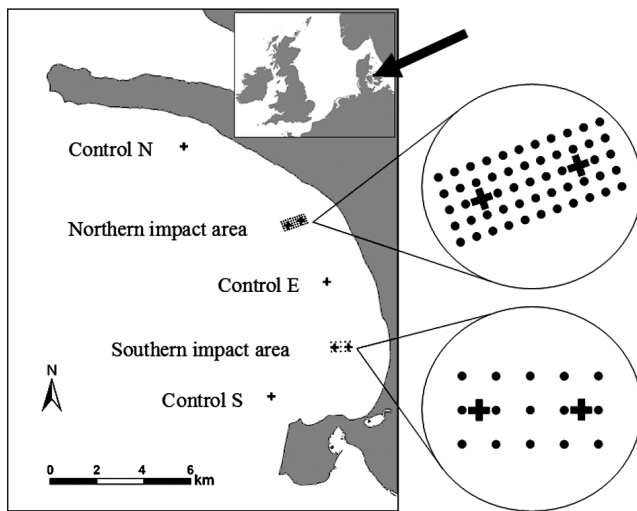


Fig. 1. Experimental setup in Jammerland Bay, the Great Belt, Denmark. Pingers (circles) were spaced 100 m (Northern impact area; Airmar pingers) and 200 m (Southern impact area; SaveWave pingers) apart. The 2 T-PODs (crosses) within each impact area were spaced 600 m apart

(5) Recovery 2+3 (September 5 to November 8): the pingers were removed. This period was split into two subperiods before (Recovery 2) and after (Recovery 3) October 6.

Airmar ($n = 55$; Airmar Technology Corporation) and SaveWave Black Saver ($n = 15$; SaveWave BV) pingers were deployed in the northern and southern impact areas, respectively. All pingers were attached ~ 0.5 m below the surface at the end of 2 m long ordinary fishing buoys (Tonkin cane with styrofoam float and lead weight), which were held in place with 6 mm nylon rope tied to an anchor. The buoys with pingers were spaced 100 m (Airmar) and 200 m (SaveWave) apart for the northern and southern areas, respectively, in agreement with the range and maximum allowed spacing for the 2 pinger types (EU 2004). This setup possibly represents the 'worst case' scenario given that in the fisheries most nets are likely spaced more widely. Thus, an area of ~ 0.6 km² was covered by the pingers in each impact area. All pingers and batteries were new at the time of deployment and were active for about 1400 h during the study. This is well within the battery life given by the pinger manufacturers: 1 yr (8800 h) of continuous operation for the Airmar pingers and 2000 h of continuous operation for the SaveWave pingers. Nevertheless, the batteries of the Airmar pingers were replaced after the Periodic exposure schedule, while the sealed electronics compartment of the SaveWave pingers did not enable battery replacement.

T-PODs

All 7 T-PODs were the new version 3 type (Chelonia; see Kyhn et al. [2008] for a technical description of the T-POD). All T-PODs had identical settings: Target A filter frequency = 130 kHz; Reference B filter frequency = 90 kHz; Selectivity ratio A/B = 5; 'A' filter integration time = Short; 'B' filter integration time = Long; Minimum intensity = 6; Scan limit = 240 clicks; Minimum click duration = 30 μ s. All T-PODs were tested and calibrated in a tank and in the field prior to the study in accordance with Kyhn et al. (2008). Maximum detection range for these T-PODs was about 450 m (Kyhn et al. 2012).

After download, clicks were processed through a classification filter (T-POD.exe ver. 7.41) supplied by the manufacturer. The CET ALL filter setting was used, which retains only the 2 train classes most likely to contain true porpoise clicks (Cet Hi and Cet Low). The detection algorithm remains undocumented but classification is based primarily on variation in inter-click intervals within closely spaced groups of clicks (trains).

Pingers

The Airmar pinger emitted a 300 ms signal at 10 kHz with a nominal source sound pressure level of 132 dB re 1 μ Pa (rms). The signal was emitted once every 4 s. The SaveWave Black Saver pinger emitted frequency modulated sweeps with signal parameters varying randomly within fixed limits. These signals were multiharmonic up-sweeps in the range 30–160 kHz with durations from 200 to 900 ms. Nominal source sound pressure level was 155 dB re 1 μ Pa (rms). Sweeps were emitted every 4 to 16 s. Specifications of the 2 pingers correspond to the Type 1 and Type 2 pinger, respectively, of the European Union pinger directive (EU 2004) and are comparable to the Dukane NetMark 1000 and the PICE pinger, respectively, that have been used in most other pinger studies. Previous studies have found substantial variation in source level both among and within pinger types (Dawson et al. 2013). We measured sound pressure level from both Airmar and SaveWave pingers at distances ranging from 5 m to 1.6 km with a Reson TC4032 hydrophone connected to a Wavebook 512 (500 kHz sampling rate, 12 bit resolution). Recordings were made at seastate 2 Beaufort from one of the corners of each pinger site. One of the Airmar pingers was tested in a tank by Shapiro et al. (2009), who found that at range = 1 m there was up to 4 dB differ-

ence in the source level depending on the recording aspect. At range = 100 m in the field there was up to 10 dB variation in source energy level, but at ranges >100 m the back-calculated source level matched the manufacturer specifications. The difference in received level may be due to the propagation conditions at the study site and/or the reception of signals from multiple pinger units, as the recordings were made from the corner of the pinger site. The Save-Wave pinger was only measured in the field and the recordings were made from the corner of the pinger site and therefore include several pinger units. However, the back-calculated source level from the field recordings confirmed the specifications stated by the manufacturer (see Fig. 5 and Shapiro et al. 2009).

Statistical analysis

T-PODs detect and store the time and duration of likely porpoise echolocation clicks. The T-POD porpoise detections were analysed as so called ‘encounters’ (Carlström 2005, Carstensen et al. 2006) and a porpoise encounter was accordingly defined as a period with echolocation clicks separated by a silent period of at least 10 min. From here on they are termed ‘acoustic encounters’. The daily porpoise acoustic encounter rate was calculated as the observed number of acoustic encounters divided by the period that the T-POD was actively recording. Due to loss of data from some T-POD deployments, the data set was not completely balanced.

Two questions were addressed using the T-POD data. (1) Was there a significant change in daily encounter rate during periods with active pingers compared to periods with inactive pingers and if so, was the change similar for the 2 pinger types? (2) Did the effect of pingers on the daily encounter rate diminish over time, suggesting that porpoises habituated to the signals? These questions were addressed with 2 models described in the next paragraph. First, a model of general pinger effect was used on the entire study period, and second, the effect of individual periods of pinger exposure was tested using the Baseline, Periodic exposure schedule and Recovery 1 periods.

In the first model, changes in porpoise encounters in the impact area relative to the control area were investigated by extending the BACI design (Before-After-Control-Impact; Green 1979) to include 6 periods as opposed to the normal 2. The BACI design can be viewed as a variant of the split-plot design (used when there is a restricted randomisation, here because the pingers were activated and deactivated

at the same time in all areas; see Carstensen et al. 2006), with each day considered as a separate plot since the 6 levels of treatment (periods) were not monitored consistently at all T-PODs. Daily encounter rates (X) were log-transformed after adding 1 to account for zero observations, i.e. $Y = \log(X+1)$, and analysed as normal variants with a mixed model (full model specified):

$$\begin{aligned}
 Y_{ijklm} = & \mu + \underbrace{D_i + p_j + DP_{ij}}_{\text{whole-plot}} + \underbrace{a_k + DA_{ik} + pa_{jk} + DPA_{ijk}}_{\text{split-plot}} \\
 & + \underbrace{s_{l(k)} + DS_{il(k)} + ps_{jl(k)} + DPS_{ijl(k)}}_{\text{split-plot(subarea)}} \\
 & + \underbrace{T_{m(kl)} + DT_{im(kl)} + PT_{jm(kl)} + DPT_{ijm(kl)}}_{\text{split-plot(t-pod)}} + \epsilon_{ijklm}
 \end{aligned} \quad (1)$$

where μ is the overall mean, and effects are given by their first letter: a_k for variation between areas (2 levels: k = control, impact); p_j for variation between periods (6 levels: j = Baseline, Periodic exposure, Recovery 1, Constant exposure, Recovery 2, Recovery 3); $s_{l(k)}$ for variation between subareas nested within the 2 main areas (5 levels: l = Control N, E, and S, and Impact N and S); and $T_{m(kl)}$ for variation between T-PODs nested within subareas (7 levels: m = individual T-PODs). There were 175 d in the design, denoted by D_i (different days indexed by i). In Eq. (1), interactions between these effects are given by their letter combination and subscripts are indices for different levels of the effects in the model, with nesting indicated by parentheses. The model in Eq. (1) has 5 fixed effects (indicated by lowercase letters): p_j (period) describes the different treatments; a_k (area) describes the spatial variation between control areas on one hand and impact areas on the other; pa_{jk} describes the relative change between control and impact areas among periods; $s_{l(k)}$ (subarea(area)) describes the differences between Control N, E, and S, and Impact N and S, respectively; and $ps_{jl(k)}$ (subarea(area) \times period) describes the relative changes between periods within areas. The random effects of the model are indicated by uppercase letters: $T_{m(kl)}$ (t-pod(area \times sub-area)) describes the variation between the T-PODs deployed within Impact N and S (those subareas with multiple T-PODs); D_i (day) describes the temporal variation across the study period; and 8 interactions. The significance of the random effects was tested and non-significant random effects were pooled with the residual variation by backward elimination. The residuals from the resulting model were examined to verify the distributional assumptions.

In the second model, differences between individual Periodic exposures on the encounter rate

were investigated by analysing the first 3 periods with a modification of Eq. (1). As opposed to Eq. (1), where the objective was to investigate differences between periods, the state of the pingers was a main effect with individual Periodic exposures and intermediate periods as a nested effect of this. Thus, the log-transformed encounter rates were analysed as:

$$\begin{aligned}
 Y_{ijklmn} = & \mu + \underbrace{D_i + o_j + DO_{ij} + p_{k(j)} + DP_{k(ij)}}_{\text{whole-plot}} \\
 & + \underbrace{a_l + DA_{il} + oa_{jl} + DOA_{ijl} + pa_{kl(j)} + DPA_{ikl(j)}}_{\text{split-plot}} \\
 & + \underbrace{s_{m(l)} + DS_{im(l)} + os_{jm(l)} + DOS_{ijm(l)} + ps_{km(jl)} + DPS_{ikm(jl)}}_{\text{split-plot(subarea)}} \\
 & + \underbrace{T_{n(ml)} + DT_{in(ml)} + OT_{jn(ml)} + DOT_{ijn(ml)} + PT_{kn(jlm)} + DPT_{ikn(jlm)}}_{\text{split-plot(t-pod)}} + \epsilon_{ijklmn}
 \end{aligned}
 \tag{2}$$

where the modifications to Eq. (1) were that o_j = pinger status (2 levels: j = ON or OFF); and $p_{k(j)}$ = period (6 levels for j = ON [6 Periodic exposures], 7 levels for j = OFF [baseline and 6 periods following the Periodic exposures]). There were 15 random effects in the model in addition to the fixed effects, and non-significant random effects were pooled with the residual variation by backward elimination. The residuals from the resulting model were examined to verify the distributional assumptions.

Marginal means for the different factors of the models were calculated and back-transformed to mean values on the original scale using the moment's transformation of the log-transform (McCullagh & Nelder 1989, p. 285) and subtracting 1 min. The interaction pa_{jk} in Eq. (1) described whether there were significant shifts in the daily encounter rate between the impact and control areas during the 5 periods. In order to investigate the relative changes between 2 periods only, contrasts from the model estimates, similar to the original BACI design (2 periods: before and after), were computed using the 4 marginal means from combinations of the 2 areas and 2 selected periods, e.g. relative change between areas from the Periodic exposures to the Recovery 1. Contrasts were computed similarly for Eq. (2) to investigate different combinations of factor levels.

The statistical analyses were carried out within the framework of mixed linear models (Littell et al. 1996, McCulloch & Searle 2001) by means of PROC MIXED in the SAS system. Statistical testing for fixed effects (F -test) and random effects (Wald Z) were carried out at a significance level of $\alpha = 0.05$. The F -test for fixed effects was partial, i.e. considering the specific contribution of the given effect in addition to all other factors.

RESULTS

At 3 of the 5 sites, the T-PODs recorded data for the entire period (15 April to 8 November). The 2 remaining sites (Control N and Control S) had periods of missing data due to datalogger failures (Fig. 2). The T-POD data contained 8637 porpoise acoustic encounters with most recorded at Control N ($n = 2628$) and Control S ($n = 1682$), and fewer encounters recorded at Control E, Impact NW, NE, SW and SE ($n = 861, 742, 1034, 552$ and 1138 , respectively). Data collected during the 2 h servicing of the instruments were excluded from the analyses, to remove any effects caused by the presence of the service boat. The encounter rates at Control S, Impact NW, NE,

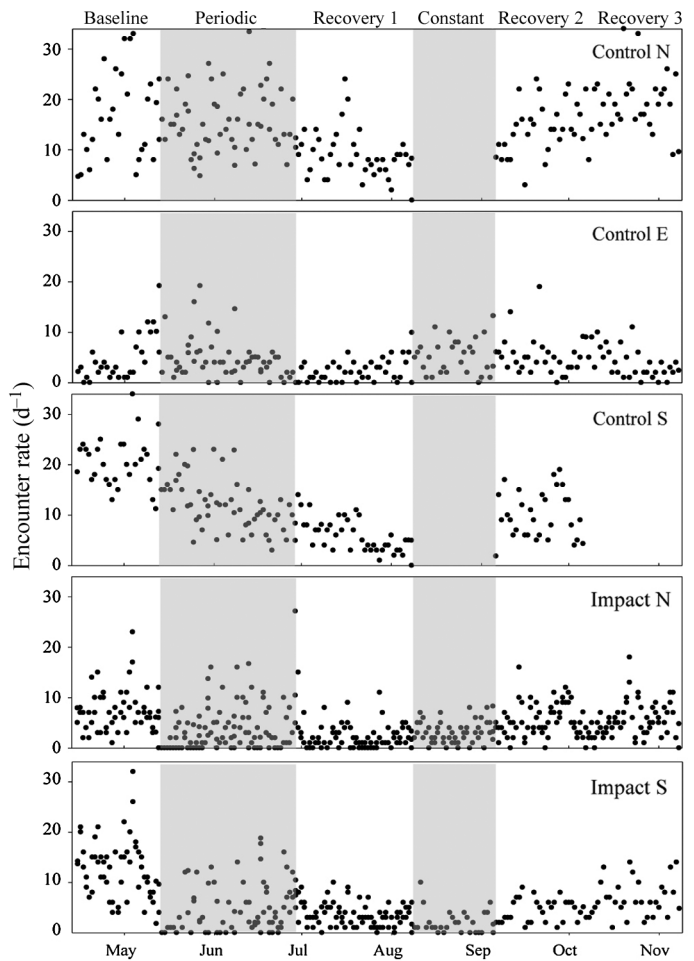


Fig. 2. Daily number of porpoise encounters for each of the 5 areas (Control N, E, S; Impact N, S). Grey columns denote the periods of the Periodic (left) and Constant (right) pinger exposure (all 5 periods of the experiment schedule are indicated at the top of the Control N panel). Each impact plot presents data from the corresponding 2 impact T-PODs. Periods without observations (Control N and S) indicate gaps in data collection

Table 1. Pearson's correlations between stations for the log-transformed number of encounters per day during the Baseline period ($n = 29$ d). Significant correlations ($p < 0.05$) are shown in **bold**

	Impact NE	Impact NW	Control E	Impact SE	Impact SW	Control S
Control N	0.15	0.58	-0.02	0.12	0.11	0.03
Impact NE		0.26	-0.03	0.43	0.41	0.39
Impact NW			0.06	0.47	0.60	0.39
Control E				-0.19	0.02	-0.18
Impact SE					0.56	0.62
Impact SW						0.51

SW and SE were significantly correlated on a daily basis during the Baseline period (Table 1).

General BACI effect of pingers

Many of the random effects in the full model (Eq. 1) were not significant and were consequently pooled with the residual variation. Hereafter, 3 random effects were significant (period \times date: $\sigma^2_{DP} = 0.022$, $p = 0.0270$; area \times date: $\sigma^2_{DA} = 0.029$, $p = 0.0227$; period \times subarea(area) \times date: $\sigma^2_{DPS} = 0.052$, $p = 0.0030$) albeit the variance contribution of these effects was small relative to the residual variation ($\sigma^2 = 0.301$). The fixed factors in the BACI analysis (Eq. 1) were all significant (Table 2). Over the entire study period and taking the loss of data into account, there were ca. 2-fold more encounters in the control area than in the impact area, and within the control subareas Control N had the most encounters (mean [95% confidence interval] 14.6 d^{-1} [13.1; 16.2]) followed by Control S (11.3 d^{-1} [10.0; 12.8]) and Control E (3.4 d^{-1} [3.1; 3.8]). In the impact area the mean encounter rates at Impact N (3.4 d^{-1} [3.1; 3.7]) and Impact S (4.2 d^{-1} [3.8; 4.7]) were different ($p = 0.0526$), albeit not significantly. For the control and impact areas combined the encounter rate decreased from the Baseline (9.7 d^{-1} [8.6; 10.9]) to Periodic exposure (4.9 d^{-1} [4.5; 5.5]) to

Table 2. Before-After-Control-Impact (BACI) analysis of general pinger effect using porpoise daily encounter rates ($n = 1160$ observations). Fixed effects in Eq. (1) were tested by F -test

Effect	df	F	p
Area (a_k)	1,206	241.44	<0.0001
Subarea ($s_{l(k)}$)	3,528	153.50	<0.0001
Period (p_j)	5,206	33.25	<0.0001
Period \times Area (pa_{jk})	5,528	14.07	<0.0001
Period \times Subarea(Area) ($ps_{j(l(k))}$)	12,528	4.92	<0.0001

Recovery 1 (3.4 d^{-1} [3.0; 3.8]) periods, and then increased from the Constant (5.0 d^{-1} [4.1; 5.9]), to Recovery 2 (6.3 d^{-1} [5.6; 7.2]) to Recovery 3 (7.1 d^{-1} [6.2; 8.2]) periods.

The significance of area \times period (pa_{jk} , Table 2) was a combination of significant and non-significant relative changes between the impact and control areas over time (Table 3, Fig. 3). There was a larger decrease in encounter rate in the impact areas from the Baseline to the 2 Exposure periods (Periodic exposure, Constant; $\sim 60\%$)

than from the Baseline to the 3 Recovery periods ($\sim 30\%$). There were no significant differences between the 2 exposure periods or between the 3 recovery periods, but there was a significant partial recovery from the 2 Exposure periods to the 3 Recovery periods (Table 3). These relative changes were also significantly different for subareas within the control and impact areas (Table 2). Impact S had a relatively large decrease in encounter rate from the Baseline to the 1st and 2nd Exposure periods. Changes were smaller and of similar size from the Baseline to the Recovery 1 and Recovery 2 periods (Table 4, Fig. 3). The decrease in encounter rate at Impact S from the Baseline to the Constant exposure period was more than double the decrease from the Baseline to the Periodic exposure at Impact N. In fact, the relative difference between Impact N and S was maintained from the Constant exposure to the Recovery 2 periods.

We also examined if Control E, which was located between the 2 impact areas, deviated from the 2 outer control subareas. Relative to Control N and S, Control E had an increasing encounter rate from the Baseline to the Periodic exposure periods ($F_{2,528} = 5.54$, $p = 0.0042$), from Baseline to Recovery 1 ($F_{2,528} = 7.43$, $p = 0.0007$) and from Baseline to Recovery 2 ($F_{2,528} = 9.12$, $p = 0.0001$), whereas there were no significant changes between Control E and Control N from Baseline to Recovery 3 ($F_{1,528} = 1.96$, $p = 0.1621$). No significant shifts occurred between Control E and the 2 other control sites from the Periodic exposure to Recovery 2 periods, but there was a significant increase in encounters at Control N relative to Control E from the Recovery 2 to the Recovery 3 periods ($F_{1,528} = 6.52$, $p = 0.0110$).

Periodic exposure trial

All the random effects in Eq. (2) were non-significant except for date \times pinger status ($\sigma^2_{DO} = 0.043$, $p = 0.0008$) and date \times subarea(area) ($\sigma^2_{DS} = 0.041$, $p =$

Table 3. Contrasts and their standard error (SE) for relative changes between the control and impact areas for 2 selected periods (First period versus Second period; for definition of periods see 'Materials and methods: Experimental setup') calculated from Eq. (1) estimates (log(X+1)-transformed). The significance of the contrast was estimated by means of a *t*-test, and the relative change and its 95 % confidence interval (in brackets) were calculated as the exponential of the estimate and upper/lower confidence limits minus 1 in accordance with Carstensen et al. (2006). Significant contrasts ($p < 0.05$) are shown in **bold**

1 st period vs. 2 nd period		Estimate	SE	p	Rel. change (%)
Baseline	Periodic	-0.8251	0.1233	<0.0001	-56 [-66; -44]
Baseline	Recovery 1	-0.3361	0.1280	0.0098	-29 [-44; -8]
Baseline	Constant	-1.0379	0.1746	<0.0001	-65 [-75; -50]
Baseline	Recovery 2	-0.3720	0.1400	0.0081	-31 [-48; -9]
Baseline	Recovery 3	-0.3356	0.1464	0.0223	-29 [-46; -5]
Periodic	Recovery 1	0.4889	0.1113	<0.0001	63 [31; 103]
Periodic	Constant	-0.2091	0.1625	0.1985	-19 [-41; 12]
Periodic	Recovery 2	0.4530	0.1251	0.0003	57 [23; 101]
Periodic	Recovery 3	0.4932	0.1317	0.0002	64 [26; 112]
Recovery 1	Constant	-0.7039	0.1660	<0.0001	-51 [-64; -31]
Recovery 1	Recovery 2	-0.0359	0.1294	0.7816	-4 [-25; 24]
Recovery 1	Recovery 3	-0.0015	0.1362	0.9913	0 [-24; 30]
Constant	Recovery 2	0.7172	0.1744	<0.0001	105 [45; 189]
Constant	Recovery 3	0.7024	0.1778	<0.0001	102 [42; 186]
Recovery 2	Recovery 3	-0.0149	0.1464	0.9192	-1 [-26; 31]

0.0122), although the variance contribution from these random effects was ca. 1 order of magnitude smaller than the residual variation ($\sigma^2 = 0.315$). All the fixed effects were significant (Table 5). In the control area there was no significant difference in the encounter rate whether the pingers were active or not (Fig. 4; $p =$

0.8642), whereas there were 54 % fewer encounters in the impact area when the pingers were active ($p < 0.0001$). The decrease in encounter rate was larger at Impact S (65 %, $p < 0.0001$) than at Impact N (40 %, $p < 0.0001$). There was a tendency, but not significant, for the encounter rate to increase during pinger-active periods after the first 2 to 4 Periodic exposures (Fig. 4).

During the first 2 Periodic exposures the impact areas only had ca. 20 % of the Baseline porpoise encounter rate relative to the control areas. During the 3rd–5th Periodic exposures, the encounter rate increased to about 35 % of the Baseline rate and during the 6th Periodic exposure it increased to 57 % of Baseline level (Table 6).

At Impact N there was a significant increase in encounter rate from the 2nd to the 3rd Periodic exposure ($p = 0.0027$), whereas the largest increase at Impact S occurred after the 4th Periodic exposure, although not significant (Fig. 4). There was also a tendency for the intermediate periods between Periodic exposures to have lower encounter rates, but only the periods following the 1st and 2nd Periodic exposures had a significant decline (~35–40 %) from the Baseline levels relative to trends of the control area (Table 6).

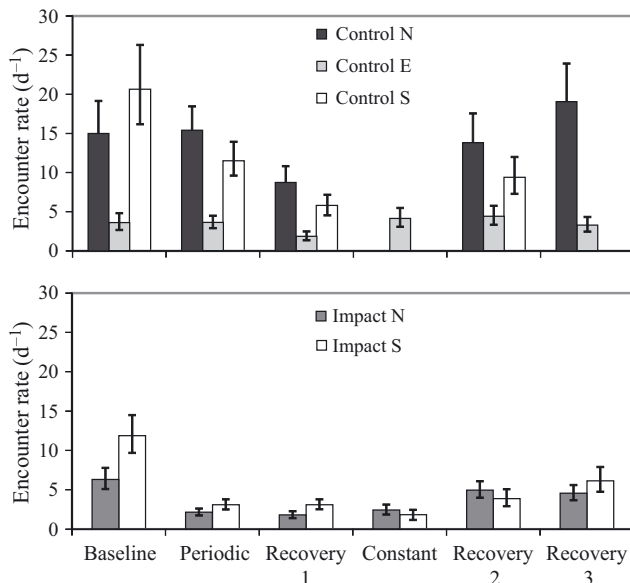


Fig. 3. Estimated marginal mean porpoise encounter rates of the control areas (upper panel) and impact areas (lower panel) for each of the experiment periods, based on back-transformed means. Error bars are 95 % confidence limits

DISCUSSION

Effect of pinger type

Both pinger types had a significant negative effect on the number of acoustic porpoise encounters. The encounter decrease was larger for the SaveWave pingers (65 %) than the Airmar pingers (40 %). The difference in deterrence effect is likely explained by the higher source level, more variable sounds and higher frequencies of the SaveWave pingers. Porpoises have significantly better hearing in the range in which the SaveWave pingers operate, i.e. 50–150 kHz (50 % detection threshold of 46–72 dB re 1 μ Pa (rms); best hearing at 100 kHz with 44 dB threshold). At the 10 kHz frequency at which Airmar pingers operate, porpoise hearing is not as good, even though multiple harmonics may go up into the most sensitive part of the porpoises' hearing range (50 % detection threshold of 62 dB re 1 μ Pa (rms) at

Table 4. Contrasts and their standard error (SE) for relative changes between the Impact N and Impact S areas for 2 selected periods (First period versus Second period; for definition of periods see 'Materials and methods: Experimental setup') calculated from Eq. (1) estimates ($\log(X+1)$ -transformed). The significance of the contrast was estimated by means of a *t*-test and the relative change and its 95% confidence interval (in brackets) were calculated as the exponential of the estimate and upper/lower confidence limits minus 1 in accordance with Carstensen et al. (2006). Significant contrasts ($p < 0.05$) are shown in **bold**

1 st period vs. 2 nd period	Estimate	SE	p	Rel. change (%)
Baseline Periodic	-0.3044	0.1525	0.0463	-26 [-45; 0]
Baseline Recovery 1	-0.1827	0.1551	0.2395	-17 [-39; 13]
Baseline Constant	-0.7866	0.1828	<0.0001	-54 [-68; -35]
Baseline Recovery 2	-0.7661	0.1778	<0.0001	-54 [-67; -34]
Baseline Recovery 3	-0.3118	0.1763	0.0775	-27 [-48; 4]
Periodic Recovery 1	0.1218	0.1379	0.3777	13 [-14; 48]
Periodic Constant	-0.4821	0.1684	0.0044	-38 [-56; -14]
Periodic Recovery 2	-0.4616	0.1630	0.0048	-37 [-54; -13]
Periodic Recovery 3	-0.0073	0.1613	0.9638	-1 [-28; 36]
Recovery 1 Constant	-0.6039	0.1709	0.0004	-45 [-61; -24]
Recovery 1 Recovery 2	-0.5834	0.1655	0.0005	-44 [-60; -23]
Recovery 1 Recovery 3	-0.1291	0.1639	0.4311	-12 [-36; 21]
Constant Recovery 2	0.0205	0.1916	0.9148	2 [-30; 49]
Constant Recovery 3	0.4748	0.1903	0.0129	61 [11; 134]
Recovery 2 Recovery 3	0.4543	0.1855	0.0146	58 [9; 127]

8 kHz) (Kastelein et al. 2002, 2010). Combined with the almost 20 dB lower ambient noise level at higher frequencies (Fig. 5), porpoises likely can hear the SaveWave signals over significantly greater distances than the Airmar signals. The signal to noise ratio (third octave band level) reached 0 dB at about 800 m for the Airmar signal, whereas for the SaveWave signals it was still about 10 dB at 1600 m. This also suggests that porpoises could hear both pingers long before the T-PODs were able to detect porpoise clicks.

In their review of pingers, Dawson et al. (2013) discussed the 4 hypotheses on how pingers work: (1) The sounds of acoustic pingers are generally aver-

Table 5. BACI analysis of periodic pinger exposure using porpoise daily encounter rates ($n = 854$ observations). Fixed effects in Eq. (2) were tested by *F*-test

Effect	df	<i>F</i>	p
Pinger status (α_j)	1,115	21.30	<0.0001
Period ($\beta_{k(j)}$)	11,214	12.92	<0.0001
Area (α_i)	1,460	239.93	<0.0001
Area \times Pinger status ($\alpha\alpha_{ij}$)	1,214	46.00	<0.0001
Area \times Period	11,214	4.55	<0.0001
(Pinger status) ($\beta\alpha_{kl(j)}$)			
Subarea(Area) ($\beta_{m(l)}$)	3,460	53.25	<0.0001
Subarea \times Pinger status(Area) ($\alpha\beta_{jm(l)}$)	3,214	3.47	0.0171
Subarea \times Period status (Area) ($\beta\beta_{km(jl)}$)	33,214	2.18	0.0005

sive and act to displace animals from the vicinity of the pinger; (2) pinger sounds encourage echolocation or otherwise alert the animals to the presence of the net; (3) pinger sounds interfere with the animals' sonar, causing them to leave the area; and (4) pinger sounds act by altering the distribution of prey (Dawson 1994, Kraus 1999, IWC 2000). Dawson et al. (2013) concluded that the most likely explanation, based on all available studies, is that pingers work by deterrence, i.e. scaring porpoises away. However, a few studies also noted that the vocalization rate initially dropped after pingers were introduced, but increased again later (Cox et al. 2001, Carlström et al. 2009); however, the authors could not conclude whether it was because the porpoises reduced their echolocation rate or because they were displaced too far from the T-PODs to be detected. Teilmann et al. (2006) found an initial drop in echolocation rate when 2 captive

porpoises were exposed to pinger-like signals of 1 pulse 4 s^{-1} in 5 min trials. The response, however, waned rapidly and was only present in 3 out of 25 sessions, which was interpreted as habituation to the signals. As also suggested by Cox et al. (2001) and Carlström et al. (2009), the acoustic encounter rate in our study could have dropped as a result of a decreased echolocation rate, rather than due to the porpoises being deterred, or as a combination of both. Nevertheless, some porpoises were acoustically detected in both impact areas during all periods with active pingers. Since we observed a rather gradual increase in acoustic encounters over days and weeks during the Periodic exposures (Fig. 4), the results of this study lend weight to the most parsimonious explanation, the deterrence hypothesis, rather than to the porpoises remaining silent in the area for several days followed by a gradual increase in echolocation rate.

Gradual lessening of response to pinger signals

For the 2 impact areas combined, a strong aversive response was observed during the 1st and 2nd Periodic exposure (the acoustic encounter rate decreased to ~20% of the Baseline level). From there on, the response varied between the 2 impact sites. During the 3rd to the 6th Periodic exposure at the Airmar site (Impact N) the response waned and the acoustic

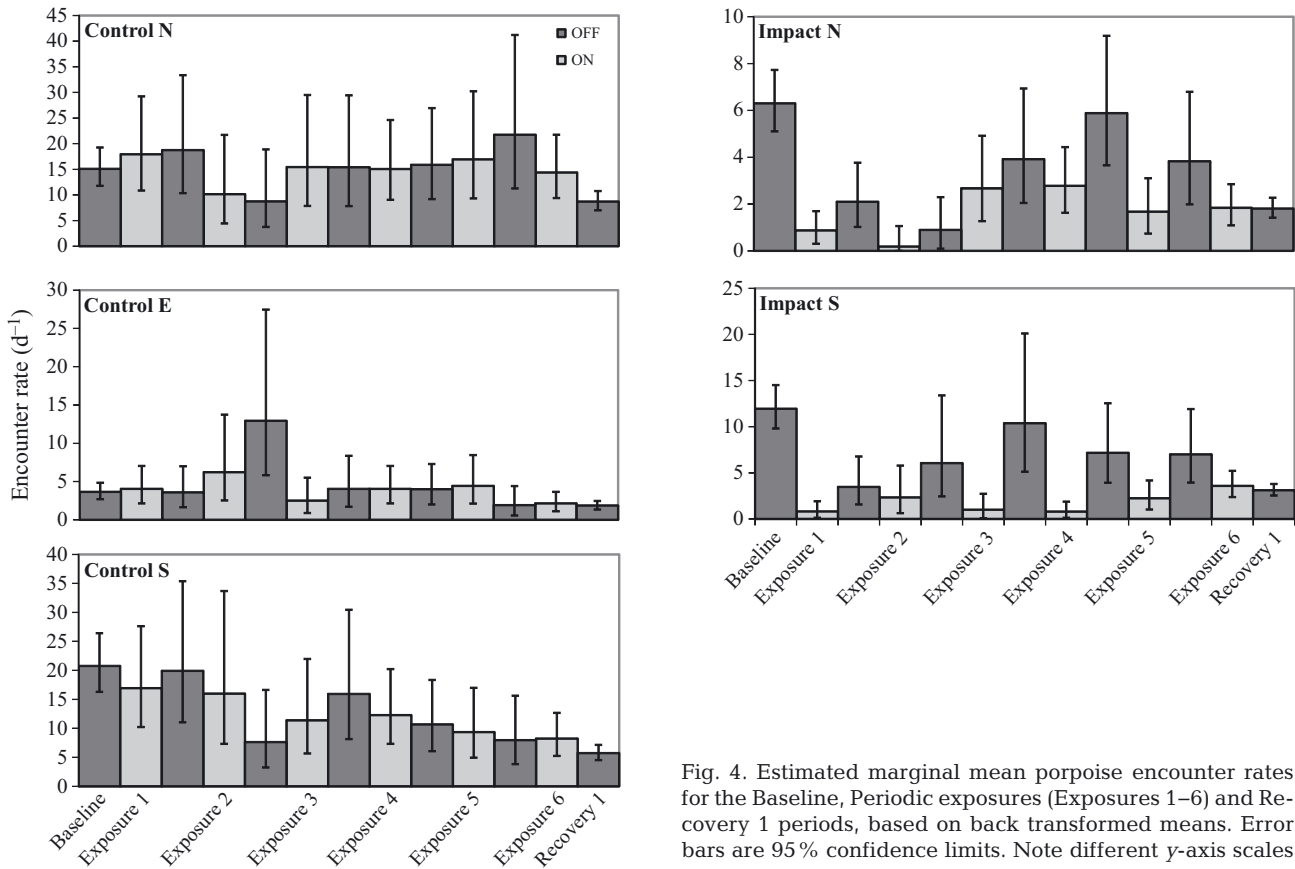


Fig. 4. Estimated marginal mean porpoise encounter rates for the Baseline, Periodic exposures (Exposures 1–6) and Recovery 1 periods, based on back transformed means. Error bars are 95% confidence limits. Note different y-axis scales

encounter rate seemed to stabilise at about 35% of the Baseline level. At the SaveWave site (Impact S) the effect lasted to the 5th and 6th Periodic exposure, where there was an increase in acoustic encounters. At both sites the acoustic encounter rate then in-

creased to 55% of the baseline level during the 6th Periodic exposure (Fig. 4). It is uncertain whether this would indicate a potential further increase in acoustic encounters over time, had the experiment continued. However, during the period of constant exposure that followed, there was no sign of an increase (Fig. 2). In fact, the acoustic encounter rate was about 35% of Baseline level throughout the Constant exposure period. That the relative response was about the same during the 3rd to 5th Periodic exposure and during the Constant exposure could indicate that the effect stabilised.

Table 6. Contrasts and their standard error (SE) for relative changes between the control and impact areas from the Baseline to the 5 intermediate periods between the Periodic exposures ('Second period') calculated from Eq. (2) estimates (log(X+1)-transformed). The significance of the contrast was estimated by means of a *t*-test and the relative change and its [95% confidence interval] were calculated as the exponential of the estimate and upper/lower confidence limits minus 1 in accordance with Carstensen et al. (2006). Significant contrasts (*p* < 0.05) are shown in bold

1 st period vs. 2 nd period	Estimate	SE	p	Rel. change (%)
Baseline 1st exposure	-1.6764	0.2095	<0.0001	-81 [-88; -72]
Baseline After 1st exposure	-1.0105	0.2424	<0.0001	-64 [-77; -41]
Baseline 2nd exposure	-1.5311	0.3043	<0.0001	-78 [-88; -61]
Baseline After 2nd exposure	-0.8692	0.3044	0.0047	-58 [-77; -24]
Baseline 3rd exposure	-1.0000	0.2674	0.0002	-63 [-78; -38]
Baseline After 3rd exposure	-0.2128	0.2673	0.4270	-19 [-52; 37]
Baseline 4th exposure	-1.1767	0.2102	<0.0001	-69 [-80; -53]
Baseline After 4th exposure	-0.0925	0.2242	0.6805	-9 [-41; 42]
Baseline 5th exposure	-1.0373	0.2304	<0.0001	-65 [-77; -44]
Baseline After 5th exposure	-0.1130	0.2480	0.6491	-11 [-45; 46]
Baseline 6th exposure	-0.5617	0.1711	0.0012	-43 [-59; -20]

no sign of an increase (Fig. 2). In fact, the acoustic encounter rate was about 35% of Baseline level throughout the Constant exposure period. That the relative response was about the same during the 3rd to 5th Periodic exposure and during the Constant exposure could indicate that the effect stabilised.

Habituation is measured at an individual level (Thorpe 1966) and the habituation process can be measured as a gradual increase in individual tolerance levels to a stimulus over time (Bejder et al. 2009). We have no information about pinger exposure to the individual porpoises and their responses to the sounds, but we can-

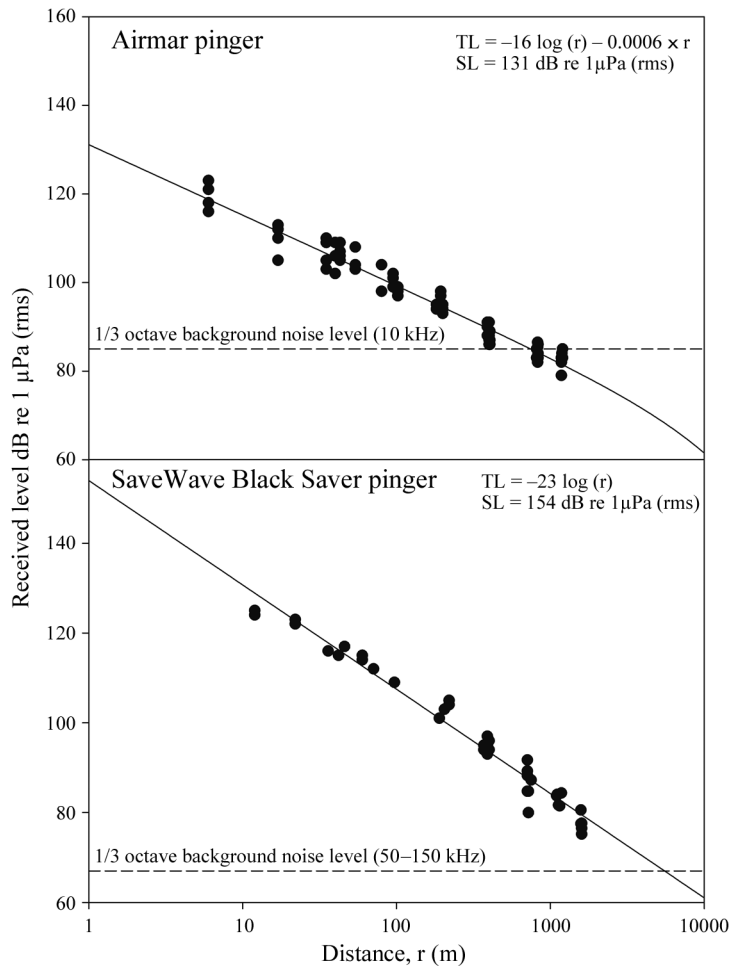


Fig. 5. Received sound levels at various distances (r) from the pingers in the 2 impact areas. Source levels are based on back-calculations. TL = transmission loss. SL = source level. The absorption coefficient is not provided in the SaveWave transmission loss formula as absorption is frequency specific and this pinger operates at varying frequencies

not exclude that some individuals were exposed to the sounds several times and that these sounds were not associated with any negative reinforcement. We measured instantaneous changes in acoustic encounters over time, which are suited to the documentation of differing levels of tolerance towards a sound stimulus within a local population of porpoises over time. Here we may therefore interpret the increasing acoustic encounter rate during the Periodic exposures as a gradual habituation at the population level to the pinger sounds, and this may be a sign that habituation took place within some individuals. We expected to observe more habituation during the Constant exposure than during the Periodic exposure. The fact that results showed the opposite could indicate that animals did not move very far away

from the experiment sites and therefore quickly returned during periods without pinger sounds (Periodic exposure) or that previously unexposed porpoises migrated through the area and chose to stay during these pinger-free periods.

There are several possible explanations as to why we saw an increase in encounter rate over time in this experiment, but not a full recovery to Baseline levels. First of all it may be that some of the porpoises visiting the study area were travelling through the Great Belt rather than utilising the study site permanently, and therefore left the area to continue their travels when the pinger exposure began. The physiological state of an animal may also influence how well it tolerates disturbances. Hungry turnstones (*Arenaria interpres*) tolerated a greater level of disturbances than did well fed individuals (Beale & Monaghan 2004). Phocid seals (*Halichoerus grypus* and *Phoca vitulina*) exposed to different aversive sound stimuli in captivity readily habituated to the sound and associated it with food (Götz & Janik 2010). Thus, the animals were motivated to accept the aversive sound and perhaps both habituated and showed associative learning. On the other hand, Kastelein et al. (2006) in a similar experiment with different types of sound stimuli found that the same 2 seal species did not habituate; however, here the seals were not fed. Harbour seals fled a shorter distance when disturbed by people during the breeding season compared to before and after the breeding season (Andersen et al. 2012). For wild porpoises, for example at our study site, some individuals may tolerate pinger signals better than others due to motivational differences, such as hunger. It may also be that less tolerant porpoises left the area in response to the pingers, resulting in a reduced density of animals, but that a group of porpoises with a more moderate response (Bejder et al. 2009) remained, as acoustic encounters were recorded inside the impact areas even when pingers were active. Nevertheless, the fact that the initial response was a ~80% reduction in acoustic encounters during the first 2 Periodic exposures over 2 to 3 d, points to most porpoises initially leaving the area.

Habitat displacement

In this study there was a displacement effect within each pinger test site, whereas no negative effect of pingers was detected in the control areas 2.5, 3 and 5 km away. It thus seems that the degree of habitat displacement was limited to less than 2.5 km from the

pingers. Kindt-Larsen et al. (2011) found a decrease in porpoise presence (vocalizations detected on T-PODs) up to 1600 m from an active pinger, the maximum distance used in that study. The fact that we did not measure a decrease in acoustic encounters at Control E (between the pinger impact areas) during pinger active trials could indicate that porpoises are not displaced from areas between fishing gears deployed with pingers if the intermediate distance is on the order of a few kilometres. On the other hand, one would expect to see an increase in acoustic porpoise encounters in the 3 control sites during the active pinger trials, if the porpoises were not deterred very far away. That this was not the case means that porpoises either were displaced to areas between the pinger and control areas or that they may have been displaced further away than the immediately surrounding habitats, i.e. >5 km. It may also be that they did not find these immediate habitats to be as suitable as the habitat they were deterred from. Pingers may therefore affect a larger area than the unaffected controls in this study suggest. If fisheries routinely move their nets around within a larger area, it may affect the porpoise density in the entire area if the animals do not move back once the nets have been moved, or it may affect the distribution of porpoises as they may be forced to relocate every few days.

It may be important to discover which sub-group of a population is leaving an area where pingers are used and whether the individual reaction is context specific. Goldbogen et al. (2013) found that blue whale reactions to mid-frequency sonar signals depended on if, and where, the whales were foraging at the time of exposure. If porpoise mother-calf pairs react more cautiously to a potential hazard (i.e. pinger sounds), they may be excluded permanently from an area. Extensive use of pingers could thus have significant consequences for the population if they are used in important harbour porpoise habitats (for example, Special Areas of Conservation), which has been suggested previously (e.g. Culik et al. 2001, Carlstrøm et al. 2002).

In order to limit the pinger exposure to only those porpoises in danger of entanglement, the pinger source level and pinger spacing on nets should thus be adjusted so that pingers are only effective within close range of the nets (a few hundred meters or less), instead of potentially more than a thousand meters. It has been suggested that porpoises may be capable of detecting fishing nets at distances of up to 80 m (Nielsen et al. 2012; but see Dawson & Lusseau 2013, Nielsen et al. 2013). If porpoises are able to detect gillnets up to 80 m away, it may only be relevant to

alert them to a net within this range if they are pre-occupied e.g. by foraging. A reduction in pinger detection range is especially important if gillnet fisheries are to take place inside Special Areas of Conservation where noise from pingers may compromise the favourable conservation status for a strictly protected Annex IV species, like the porpoise (EU Habitats Directive, http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm). Such a pinger could be achieved by using high frequency sweep signals of low source level and sufficiently low duty cycle. Development of such a low source level pinger should be tested directly in a fishery with high bycatch rates, as experimental set-ups without nets do not seem to fairly represent harbour-porpoise decision-making at the time that it counts. Also, experiments with wild porpoises carrying tags recording both sound and 3D movements may show how animals react to different pinger types, if the tagged porpoises are released close to, or by chance found near, active pingers.

Lasting effect

Although to some degree porpoises returned in the 'quiet' periods between the Periodic exposures, the acoustic encounter rate was below expected levels compared to the controls. It cannot be determined whether this was due to a lasting effect of the pinger sound, a confounding effect of the pinger buoys (which were deployed from the 1st Periodic exposure till the end of the 3rd Recovery period), or that the intermediate recovery periods were too short to enable full recovery. Thus, the reduced acoustic encounter rate could reflect a reluctance of the porpoises to re-enter the impact areas when the pinger flags were deployed. However, Carlstrøm et al. (2009) also found that the time to the first acoustic encounter following a pinger trial was significantly longer than when following a control period. This could also explain the fact that even after 2 mo recovery the encounter rate stayed 30% below the Baseline period (in which no buoys were deployed). Porpoises have been shown to use the study area year-round, although predominantly from March to December and peaking from May to December (Sveegaard 2011).

CONCLUSIONS

Both SaveWave and Airmar pingers effectively reduced harbour porpoise presence measured as

acoustic encounters during both the Periodic exposure experiment (mimicking a real fishery) and during the Constant exposure experiment. The number of acoustic encounters increased during the Periodic exposure to Airmar signals, but very little during exposure to SaveWave signals, illustrating a gradual toleration of the Airmar signals over time, which may be caused by habituation of individual porpoises. The reason for the difference in response between the 2 pingers is likely that the Airmar signals were of constant repetition rate, duration and frequency, whereas the SaveWave signals varied in signal type, frequency, duration and repetition rate and were more audible to harbour porpoises. There was, however, no difference in toleration between the pinger types during the Constant exposure experiment. Exposure to the pingers led to a habitat displacement around each pinger site; however, it appeared that displaced porpoises either moved beyond the control sites (i.e. potentially >5 km) or they remained at distances closer than the control sites, i.e. within 2.5 km of the pinger areas. We suggest that future research should focus on developing a low source level pinger that is audible only within close range of a net in order to reduce the accompanying noise pollution and habitat loss.

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