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Synthetic communication signals influence wild harbour porpoise (*Phocoena phocoena*) behaviour

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We used our novel and programmable Porpoise Alarm (PAL, patd.) to synthesize life-like, electronic harbour porpoise communication signals based on those described for captive animals. In the Little Belt, Denmark, we employed PAL (source level 158 ± 1 dB p–p re 1 μPa@1 m; centroid frequency 133 ± 8.5 kHz) to synthesize three aggressive click train types termed “A”, “F3” and “M1” to naive, free-living harbour porpoises. Via theodolite tracking (372 h of total visual effort spread over 10 expeditions) we found that, depending on signal type, porpoises either avoid or become attracted to PAL: Signal types “A” and “F3” are slight deterrents, porpoises increasing minimum range (+23 to 32 m, respectively), whereas “M1” attracts porpoises, reducing range (by −29 m). As determined via archival acoustic detectors (AADs), both signals “F3” and “M1” led the animals to significantly intensify their click rate (by +10% and 68%, respectively) while signal “A” led to a significant reduction (−59%). We propose that equipping fishing gear with PAL emitting signal “F3” could potentially reduce porpoise by-catch by increasing (1) awareness through enhanced echolocation and (2) distance to the nets. Detection probability and radius of PAL/AAD tandems could be improved by emitting signal “M1” to focus porpoise echolocation signals on the AAD. The signal may also be useful in luring animals away from hazards, which may be helpful for conservation measures prior to the onset of harmful acoustic activities such as pile-driving, seismic exploration or ammunition clearance.

Keywords: harbour porpoise; *Phocoena phocoena*; click communication; field experiments; by-catch mitigation; acoustic surveys; instrumentation

Introduction

Fishery by-catch

In a recent study, Reeves et al. (2013) show that 75% of odontocete species, 64% of mysticetes, 66% of pinnipeds and all species of sirenians and marine mustelids have been recorded as gillnet by-catch over the past 20 years. By-catch remains a critical issue demanding urgent attention if further losses of marine mammal diversity and abundance are to be prevented. Between 2000 and 2009, the number of harbour porpoise carcasses found annually along the German Baltic Sea coast increased from 25 to 152 year^{-1}. In 47–86% of those carcasses that were relatively well preserved, by-catch was identified as the mortality cause (Herr et al. 2009; Koschinski and Pfander 2009). Latest figures

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(2012, Eva Wehrmeister, pers. comm. to C. Dorrien) show a decrease in strandings to 72 animals. The reason for this is unclear.

Warning the animals of widely spread hazards such as gill nets (Vinther and Larsen 2004; Orphanides and Palka 2013; Scheidat et al. 2013) by increasing their minimum distance to the threat (Kraus et al. 1997) and raising their awareness by increasing their echolocation intensity (Koschinski et al. 2006) could reduce the risk of collision and entanglement. To reduce by-catch in fisheries, currently employed acoustic deterrent devices (ADDs), also called pingers, produce aversive noise.

Several hypotheses were brought forward on the mechanism of pinger deterrence in marine mammals in general (e.g. Götz and Janik 2013). Dawson et al. (2013) suggested that acoustic devices are most effective in reducing by-catch of neophobic species such as porpoises. Culik et al. (2001) showed that porpoises maintain a safety distance of several 100 m to ADD-equipped nets. However, they simultaneously reduce echolocation intensity (Cox et al. 2001; Culik et al. 2001; Berggren et al. 2002; Carlström et al. 2009; Hardy et al. 2012) and therefore may become entangled between too widely spaced (Berggren et al. 2002) or defective pingers (Palka et al. 2008; Carretta and Barlow 2011). Furthermore, maintaining large safety distances may lead to exclusion from parts of the habitat. We also assume that porpoises fail to establish a connection between the aversive noise and the threatening nets: monofilament gillnets become only discernible for the biosonar of porpoises at very close range (estimates range from 8 to 25 m, Koschinski et al. 2006), and if the animals are actively echolocating, which is not always the case even in the absence of pingers (Akamatsu et al. 1994; Koschinski et al. 2006; Linnenschmidt 2007). One of the major aims of our study was therefore to develop a new acoustic method to overcome these drawbacks.

In general, acoustic signals are likely to induce avoidance if they are similar to signals for which the subject has made a negative association (Coram et al. 2014). This will most likely be the case with predator signals. Avoidance will become stronger if repeatedly reinforced by non-lethal predator encounters, and weaken in the absence of reinforcement. However, Bomford and O'Brien (1990) reviewed the use of aversive sound to exclude terrestrial pests and concluded more generally that biologically significant signals would have an effect: in terrestrial species alarm signals are often used. Whereas such calls are not known to be commonly used by marine mammals (Coram et al. 2014), Clausen et al. (2011) identified a variety of aggressive harbour porpoise signals in animals in captivity. This offered a promising alternative to the acoustic deterrents used to date.

Detection and population estimates

A recent estimate of the remaining vaquita population, which only occurs in a small range in the north-east of the Gulf of California, yielded only 150 animals (Jaramillo-Legorreta et al. 2007). The closely related harbour porpoises were once numerous in the Baltic Sea south and east of the Belt region but today the population is estimated in the low thousands: Scheidat et al. (2008) give combined estimates for the German Exclusive Economic Zone in Kiel Bight, Mecklenburg Bight and the German waters of the Baltic proper ranging between 457 (March 2003; $CV = 0.97$) and 4610 (May 2005; $CV = 0.35$). Further east, in the Baltic Proper, porpoise detection densities are very low, with only three detections in Polish coastal waters (Gillespie et al. 2005) and an estimate of <600 porpoises in a 43,000 km^2 study area in international waters of the Baltic Sea block (Hiby and Lovell 1996).

Reliable detection of endangered marine mammal species or populations in their remaining habitat (e.g. Jaramilllo-Legorreta et al. 2013; Benke et al. 2014; cf. Culik 2011, for review) or within close range of hazardous activities such as ammunition clearance, seismic exploration or pile-driving is a pre-requisite for specific protective measures (Koschinski 2011; Brandt et al. 2013). However, harbour porpoise detection by observers on airplanes or ships, or via archival acoustic detector (AAD) is fraught with low detection ranges and probabilities: trackline detection probability $g(0)$ from aircraft (Laake et al. 1997) is only 0.079–0.292. Ship-based detection probability during good weather (sea state < 1.5) decreases from 0.8 to less than 0.2 within 0–300 m from the ship (Reay 2005).

In passive acoustic monitoring, $g(0)$ reaches only 0.1–0.3, with an effective detection range of only 22–104 m (Kyhn et al. 2012). The reason for low acoustic detection probabilities is believed to be discontinuous echolocation by the animals as well as by their echolocation signals being rarely focused on the receiver: porpoise signals are narrow beam with a 3-dB aperture of only 13° in the horizontal plane (Koblitz et al. 2012). As a consequence, confidence intervals for population estimates of rare porpoise species or populations are very large (Barlow and Gerrodette 1997; Benke et al. 2014). We propose here that acoustic measures capable of attracting the attention of the target species would be helpful in increasing detection range and probability, to the benefit of protective measures.

Porpoise communication signals

For echolocation as well as for communication, members of the Phocoenidae seemingly only produce narrowband high-frequency (NBHF) clicks arranged in specific click trains (Clausen et al. 2011). NBHF clicks have durations of approximately 100 μs, high directionality, centre frequencies around 130 kHz, and source levels (SLs) of up to 205 dB pp re 1 μPa, 1 m (Villadsgaard et al. 2007). During behavioural studies in the Fjord & Belt Centre, Kerteminde, Clausen et al. (2011) observed five types of behaviour between male, female and juvenile animals, each associated with particular communication click trains characterized by either constant click rates, upsweep chirps or a combination of both. For the reasons stated by Bomford and O'Brien (1990), four of these signal types, observed during grooming, contact, approach or swimming in echelon did not qualify for our objectives. Only those characterized during aggressive interactions (Clausen et al. 2011, see details later) served as a template to programme and generate *de novo* (as opposed to playback of recordings) life-like communication sounds with our new patented, self-contained synthetic porpoise click train generator Porpoise Alarm (PAL; DPM Pat. Nr.: 10 2011 109 955). We tested this in the field on naive harbour porpoises and recorded their reaction visually via theodolite tracking and acoustically with AADs.

Our investigations were aimed at identifying specific porpoise communication signals for different tasks: (1) to increase the distance of porpoises to the PAL, while simultaneously increasing their echolocation rate, two prerequisites for the development of a new method to reduce the risk of collision and entanglement in fishing gear, and (2) to enhance detection by using PAL signals to attract and focus harbour porpoises to a PAL/AAD tandem within acoustic range and leading them to significantly increase their echolocation rate.

Methods

Click train generator PAL

The autonomous, synthetic click and click train generator PAL (Figure 1; patd. by Boris Culik and Matthias Conrad) is an omni-directional transmitter, except for a cone of

Figure 1. Self-contained synthetic porpoise signal generator “PAL” (dimensions: 30 cm long, 9 cm diameter). Top: the housing is made of 10 mm polyoxymethylene. Bottom: programmable electronics board with protruding omni-directional signal transducer (> 1 month autonomy).

approximately 90° aperture in the long axis behind the spherical sound transducer, owing to the air-filled housing. Each PAL (centroid frequency 133 kHz, SL calibrated in the test tank of L-3 Communications ELAC Nautik GmbH, 158 + 1 dB p–p re 1 μPa @ 1 m) can be programmed via personal computer and purpose-built software to generate individual porpoise-like clicks as well as various click train patterns consisting of constant click rates, up- or downsweep chirps and any combination of these, with freely programmable repetition rates and pauses.

We attempted to match aggressive harbour porpoise communication signals (*sensu* Clausen et al. 2011) as closely as possible. Specifically, we tested three signal types termed “A”, “M1” and “F3” differing in duration, number of upsweep chirps, click rate per second and repetition rate per minute (Table 1; Figure 2). Signal “F3” imitates the 3d aggressive signal recorded by Clausen et al. (2011) from a female towards a male. “F3” is composed of two upsweep-chirps and has a total duration of 1.22 s, beginning with a click rate of 173 clicks s^{-1} and ending with 959 clicks s^{-1}. This signal was repeated at approximately 20 s intervals. “M1” corresponds to the first signal recorded from a male towards a female (one upsweep chirp, 0.47 s duration, 130–911 clicks s^{-1}, repeated three times per minute). Finally, signal “A” matches their general description of aggressive porpoise signals (see “Discussion” section) but does not replicate any of their recordings in particular (1.14 s duration, two upsweep chirps, 437–774 clicks s^{-1}, seven repetitions per minute). As shown in field recordings (Figure 2) using an AAD (CPOD, Chelonia, Mousehole, UK, details provided later), all three click train types were emitted at 133 kHz, without

Table 1. Characteristics of the three PAL-generated synthetic porpoise communication signals.

Signal	Click train duration (s)	Upsweep 1 (clicks s^{-1})	Upsweep 2 (clicks s^{-1})	Repetition rate (N $\min^{-1}$)
A	1.14	437–565	658–774	7
F3	1.22	173–507	519–959	3
M1	0.47	130–911		3

Notes: As shown in Figure 1, signals are composed of up to two consecutive upsweep chirps.

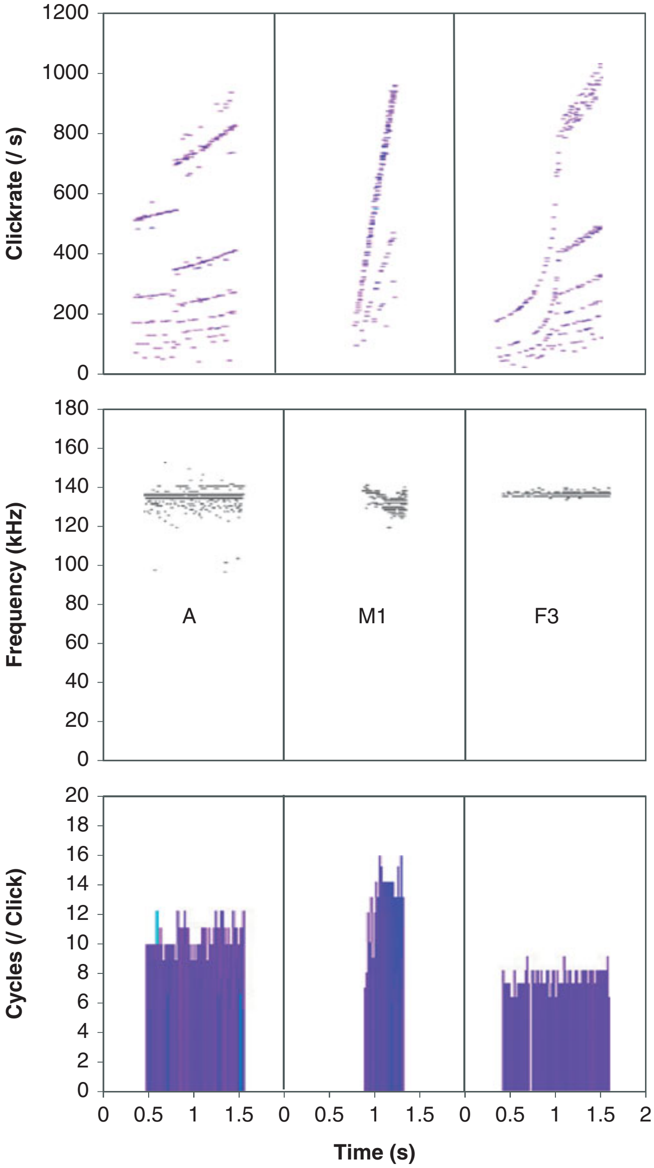

Figure 2. Field recordings via CPOD of the three synthetic communication signals tested in this study. Top: click rate (s^{-1}; NB: click rates emitted by PAL correspond to the higher values shown, lower data points stem from clicks lost in indirect propagation paths); middle: frequency distribution (kHz); bottom: number of cycles per click. The three signals differ with respect to the number of upsweep chirps (two in signals “A” and “F3”, one in signal “M1”), duration and total number of clicks produced (Table 1).

harmonics at lower frequencies. Individual clicks consisted of 8–14 cycles, a variability which is probably an artefact of field measurements.

All PALs were tested prior to and after deployment (acoustically by checking sound transmission and visually by checking the light emitting diode on electronics board) as well as during experiments via archival CPOD recordings. Independently of each other, and independent of porpoise presence, PALs would operate for 15 min (treatment) followed by 15-min silence (controls) and so on. Because observers could neither see nor hear which PAL was active at any one time, this effectively resulted in a blind approach.

Acoustic buoys

During experiments, we equipped up to four mooring buoys (80 cm diameter), each with one calibrated PAL and CPOD AAD (Chelonia). CPOD is a self-contained, calibrated archival acoustic data analyser, with an omni-directional hydrophone with centre frequency of 130 kHz (sensitivity -208 dB re 1 V μPa^{-1}) and a range of 20–160 kHz (for further details, see http://www.chelonia.co.uk/c-pod_standardisation.htm). CPOD and PAL were strapped to each other in tandem and end-to-end and secured at their midpoint at 4 m depth, to ensure vertical orientation in currents. Buoys were moored outside the shipping lane, along the 8 ± 0.5 m depth contour, at least 320 m apart from the next acoustic buoy using an anchor and an anchor stone. This distance was required to avoid recording signals from adjacent PAL/CPOD tandems. Normally buoys were deployed on the Strib side of the Little Belt only, except during the expedition involving RV Clupea, when two buoys were deployed on either side of the Little Belt (Figure 3, Table 2 for deployment details). Until July 2013, CPOD/PAL buoys were deployed only during daytime. Thereafter, buoys were left at sea night and day, for the full period of a field trip.

CPOD uses digital waveform characterization to select cetacean clicks and log the time, centre frequency, sound pressure level, duration and bandwidth of each click (for more details, see http://www.chelonia.co.uk). All acoustic data were filtered and analysed using the software CPOD.exe (ver. 2.042) to produce cp3 output files. We used the following software-specific parameters: train filters: all Q; kerno classifier: NBHF, Other Cet, Sonar, unclassed; click filter: 120–150 kHz. Because the CPOD software repeatedly failed to exclude PAL signals during processing and generation of the output files, all data-sets were also inspected visually and every synthetic PAL signal (clearly recognizable by its repetitive pattern, constant frequency and duration) in the cp3 file was excluded manually in the process. Data output was the number of net porpoise clicks per minute.

Study area and set-up

All experiments took place during the summers of 2012 and 2013 in Danish waters between the towns of Fredericia and Strib at sea state <2. Here, the Little Belt is only 1.35 km wide and water depths reach 46 m in the middle of the channel (Figure 3). During daylight hours, from a land-based research platform in Strib, approximately 13.5 m above sea water (55° 32,609 N; 9° 46,162 E) and facing north, we determined surfacing positions of individual porpoise groups using a programmable electronic theodolite (Geodimeter total station 620). This recorded horizontal and vertical angles to the nearest 10^{-4} degree and time to the nearest 10^{-1} s with a data storage capacity of several thousand data-sets. Instrument height above sea level was determined at intervals for tide correction by determining the vertical angle to a calibrated gauge attached to a submerged structure near shore. Distance to the gauge, which also served as our reference point, was measured using the built-in laser range finder. On station we had two to three observers scanning the area during most of the daylight hours. During one field trip (Table 2), we also deployed the German RV "Clupea" on the Fredericia side of the Little Belt with three to four additional observers simultaneously scanning the area to spot harbour porpoise groups and report these via radio to the theodolite station.

Figure 3. Study area in the Little Belt, DK, between the towns of Fredericia and Strib (maps courtesy of Google Earth). The theodolite was positioned in Strib facing north. Marine navigation buoys marked "Nav", research buoy positions marked red. Up to four research buoys each carrying a PAL and CPOD tandem were deployed simultaneously: up to four on the Strib side and up to two on the Fredericia side. RV Clupea was only available in September 2012. For details, see Table 2.

Table 2. Details on field experiments conducted in the Little Belt, DK to the north of Strib.

Observation platforms	Signal	Start date	End date	Visual effort (h)	CPOD/PAL buoys (*n*)
Theodolite	A	27 Aug. 2012	30 Aug. 2012	38	2
Theodolite	A	10 Sep. 2012	12 Sep. 2012	26	2
Theodolite/RV Clupea	A	21 Sep. 2012	4 Oct. 2012	82	4
Theodolite	M1	20 April 2013	22 April 2013	25.9	2
Theodolite	M1	02 May 2013	6 May 2013	47.5	3
Theodolite	M1	27 May 2013	28 May 2013	21.4	3
Theodolite	F3	10 June 2013	12 June 2013	28.8	3
Theodolite	F3	24 July 2013	27 July 2013	41.7	3
Theodolite	F3	27 Aug. 2013	29 Aug. 2013	27.6	4
Theodolite	F3	25 Sep. 2013	28 Sep. 2013	32.9	4

We conducted a total of 10 field trips of 2–13 days duration between August 2012 and September 2013, with 9–200 days pause in between. Our aim was to reduce possible porpoise response attenuation with time as well as pseudo-replication by reducing the probability of testing the same animals: As shown by Teilmann et al. (2008), 23% of porpoises in the Little Belt can be expected to be visiting, spending 2 days or less in the area, whereas 77% are foraging, staying more than 2 days. In total, we visually surveyed the area for 371.8 h: three field trips in summer/autumn of 2012 to test the effect of signal "A" on harbour porpoise behaviour (146 h of visual effort); three field experiments between April and May 2013 to test the effect of signal "M1" (94.8 h) and four field expeditions between June and September 2013 to test signal "F3" (131 h).

Data analysis was conducted in EXCEL using standard trigonometric functions to determine interpolated height above sea level, buoy and porpoise surfacing position (cf. Würsig et al. 1991; Müller 2013 for details). From theodolite data and for each signal type, we determined the distance between the nearest CPOD/PAL acoustic buoy and surfacing harbour porpoise groups (mean group size 1.9–2.2). In order to avoid pseudo-replication, we only used the minimum surfacing distance (MSD) for each porpoise group *sensu* Dawson et al. (2013):

(a) when the PAL was off (controls; repeated surfacings of the same group in the vicinity of a PAL *after* the device had switched off were discarded) and
(b) when the PAL was on (experiment).

Only a few groups remained within detection range (details provided later) 15 min and more, beginning with PAL off. For these, we recorded two values, as mentioned.

Site-specific sound propagation

Site-specific sound propagation parameters were determined in order to derive acoustic harbour porpoise, PAL and CPOD ranges (Figure 4). We used the calibrated PAL as a porpoise signal generator and deployed it by boat at 6 m depth in 12 m deep water (determined by hand-held echosounder, Hondex PS 7), at various ranges (Garmin GPS 12) from the calibrated CPOD moored just North of the theodolite position (Figure 3).

SL of the PAL is related to received levels (RLs) of the CPOD and transmission loss (TL; all in dB p–p re 1 μPa @ 1 m) by

$$\mathrm{SL} = \mathrm{RL} + \mathrm{TL}$$

RL was converted from recorded CPOD data (P, in Pa) via

$$\mathrm{RL} = 20 \log \left(\frac{P}{P_0} \right)$$

where P is pressure in Pa and $P_0 = 10^{-6}$ Pa.

We assumed TL to be best described by the shallow water sound propagation model appropriate for depths <200 m (Richardson et al. 1995), as

$$\mathrm{TL} = 10 \log R_1 + 10 \log R_2 + \alpha R_1$$

with R_1 = PAL–CPOD distance (m), $R_2 = 0.5 \times$ water depth (m) and sound absorption $\alpha = 0.04\,\mathrm{dBm}^{-1}$ (at 135 kHz; salinity 35 ppt; Richardson et al. 1995).

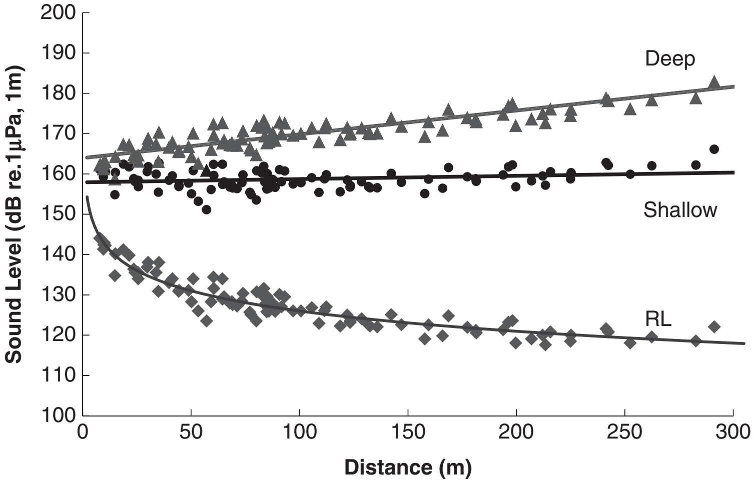

Figure 4. Site-specific sound propagation. RL: original received levels (diamonds, $n = 95$) measured via CPOD (in dB p–p re 1 μPa @ 1 m) at various distances from the PAL in the Little Belt near Strib [logarithmic fit, RL (dB) = $-7.24 \ln D$ (m) + 159; $R^2 = 0.896$]. Shallow: re-calculation of SLs (round dots) using the shallow water propagation model yields a constant value, irrespective of distance [linear fit, SL (dB) = 0.008 D (m) + 158; $R^2 = 0.048$]. Deep: as opposed to this, re-calculating the SL using the deep water propagation model (triangles) overestimates SL as well as TL with distance and is inappropriate for this area [linear fit, SL (dB) = 0.056 D (m) + 164; $R^2 = 0.759$]. For details, see text.

As shown in Figure 4, this shallow water propagation model (dots) yields an almost constant back-calculated SL of the PAL irrespective of distance to the CPOD: the slope is not significantly different from zero (slope = 0.0076 dB m^{-1}, $R^2 = 0.0476$). The calculated *y*-intercept is 158 dB and corresponds well to the SL generated by the calibrated PAL.

As opposed to this, applying the deep water, spherical propagation model of Richardson et al. (1995), where TL = 20 Log R_1 (Figure 4, triangles) overestimates propagation loss and consequently SL. This yields a significant overestimate of back-calculated PAL SL with distance (0.056 dB m^{-1}) and re-calculated SL for a source at 250 m is 20 dB higher than the actually produced SL.

Detection range

For analysis of visually obtained porpoise behaviour data, we needed to consider the acoustic range of harbour porpoises, PAL and CPOD. We calculated detection ranges for a variety of combinations: (1) two types of weather with different ambient noise levels (NLs); (2) three types of porpoise orientation, either towards (0°), sideways (90°) or away (180°) and (3) porpoises either as sound detectors or as sound source (Table 3).

We used the following assumptions for weather conditions: fair (wind force 0 Bft, no rain; NL = 67 dB p–p re 1 μPa @ 1 m) and foul (wind 7 Bft, strong rain; NL = 87 dB p–p re 1 μPa @ 1 m; Urick 1983; Richardson et al. 1995). We conservatively assumed porpoise SL = 178 dB (data from the Little Belt, Villadsgaard et al. 2007) when the acoustic beam hits the detector head on (±6.5°, Koblitz et al. 2012), but only 141 dB sideways (animal at 90°) and 134 dB when the animal faces with its tail to the detector (180° ± 45°; Hansen et al. 2008). Harbour porpoise hearing is very sensitive, with a critical ratio

Table 3. Calculated acoustic detection ranges.

Detection	Range (m)	Sea state (Bft) 0	Sea state (Bft) 7
HP → CPOD	Head on	670	280
	Side	50	1
	Tail on	13	0
PAL → HP	Head on	460	120
	Side	340	50
	Tail on	240	20

Notes: HP, harbour porpoise; CPOD, archival acoustic detector; PAL, programmable synthetic communication signal generator. Head on: porpoises facing towards ± 6.5°; side: porpoises parallel (90°); tail on: porpoises facing backwards (180° ± 45°).

(CR) = 38 dB (135 kHz) and directional, with a directivity index (DI) of 11.7 dB (e.g. when the animals are at 180° to the detector; Kastelein et al. 2005). We assumed that a sideway orientation would result in +6 dB.

The PAL is an omni-directional sound source with an SL of 158 dB p−p re 1 μPa @ 1 m. The CPOD is an omni-directional receiver with a CR = 47.5 dB (at 135 kHz; Dähne et al. 2013). Detection range was defined as the distance from the sound source where signal excess (SE) > 0, with SE = SL − (TL + NL + CR + DI).

Results

Detection range

From the calculations based on published data (see earlier), we derived that in fair weather a CPOD can detect a harbour porpoise clicking "head on" from a distance of 670 m, but if the animal is facing sideways or away, detection range falls to 50 and 13 m, respectively (Table 3). However, a PAL transmitting at the site of the detector would be heard at distances of at least 460 m (head on), 340 m (sideways) and 240 m (tail on). Since it is impossible to determine the orientation of the porpoises under water, we conservatively assumed animals to be able to detect PAL signals during our acoustic experiments conducted in fair weather at a distance of 300 m from each PAL/CPOD acoustic buoy and truncated all visual data-sets accordingly, to avoid conclusions based on false positives or false negatives.

MSD to acoustic buoys

From theodolite data, we determined the MSD of porpoises to acoustic buoys (Table 4). Data obtained during controls (PAL off) were compared by analysis of variance (ANOVA) to ascertain that all values were comparable between one experiment and the next. This was confirmed ($F = 1.22$, critical $F = 3.05$, $p = 0.29$, df = 181), and all control data were pooled (mean 144 m, 95% CI = 11.3 m, $n = 182$).

Subsequently, we used ANOVA to determine whether MSD differed between pooled control and the three treatments (signal types "A", "F3" and "M1") and found this to be highly significant ($F = 5.31$, critical $F = 2.62$, $p = 0.0013$, df = 379). *Post hoc* analysis (Tukey test) showed that surfacing distance during emission of any of the three signal types was significantly different from controls (pairwise comparison of controls with

Table 4. Surfacing distance of harbour porpoise groups to acoustic buoys (via theodolite tracking).

	Signal			
	A	F3	M1	PAL off pooled
PAL off				
Mean min. dist. (m)	151	131	148	**144**
95% CI	19.6	20.1	18.7	**11.3**
Median	144	115	141	**131**
Obs (*n*)	66	58	58	**182**$^{a,\ b}$
Mean group size (*n*)	2.3	1.9	2.2	
PAL on				
Mean min. dist. (m)	**174**^{a}	**163**$^{b,\ c}$	**119**$^{a,\ c}$	
95% CI	**18.8**	**18.4**	**27.1**	
Median	**189**	**167**	**101**	
Obs (*n*)	**68**	**77**	**53**	
Diff. PAL off/on (m)	**+ 30**	**+ 19**	**− 25**	

Notes: Values during controls (PAL off) were pooled and compared to synthesized signals “A”, “F3” and “M1”. Mean min. dist., mean minimum distance (m); CI, 95% confidence interval; diff PAL off/on, difference between pooled PAL off values as opposed to emitting the specific signal type. Pairwise comparisons significant at $\alpha = 0.01$ level (a), $\alpha = 0.05$ level (b, c). For details, see text.

signals “A” and “M1” was significant at $\alpha = 0.01$ level, comparison of controls with signal “F3” at $\alpha = 0.05$ level). Pairwise comparisons between signals “A” and “M1” and between “F3” and “M1” were also highly significant (at $\alpha = 0.01$ level), but comparison between signals “A” and “F3” was not (at $\alpha = 0.05$ level).

Comparison of treatments with pooled controls (Table 4) shows that signal “A” leads the animals to increase their mean distance to the PAL (from 144 m during PAL off to 174 m during PAL on) by 30 m. Porpoise response to signal “F3” is similar with a 19 m increase. The right-shift in distance distribution during PAL on is clearly visible in both cases (Figure 5). The response of harbour porpoises to signal “M1” is the complete opposite (mean distance to PAL only 119 m), and animals come significantly closer (− 25 m). With “M1” porpoises repeatedly swum directly to the acoustic buoy to investigate it more closely (26.4% of sightings within the 20 m range; Figure 5).

Acoustic reaction to synthetic signals

For all CPOD data-sets, we determined the number of clicks received per minute during 15-min PAL off as compared to the 15 min during PAL on and 15 min when PAL was off again (Table 5; Figure 6). Data-sets with only 1 min of click activity within the 45-min period were discarded. Because the numbers of received clicks per minute varied between daytime and night-time, as well as from one approach to the next, we standardized each interval with respect to itself by calculating the percentage of clicks for each minute with respect to the total number of clicks observed in that 45-min interval. This enabled us to compare across all the data-sets and gives every interval in the data-set the same weight.

Within each treatment category (signals “A”, “F3” and “M1”), statistical comparison between the proportion of clicks emitted during each of the three 15-min phases shows significant differences [ANOVA with arcsine transformed percentage values *sensu* McDonald (2009), at $\alpha = 0.0001$]. With signal “A” (Table 5; Figure 6), mean click rate dropped from 2.78% (control) to 1.15% (PAL on) and then increased again to 2.73% (control). Click activity during signal “A” was only 41% of previous control. With signal

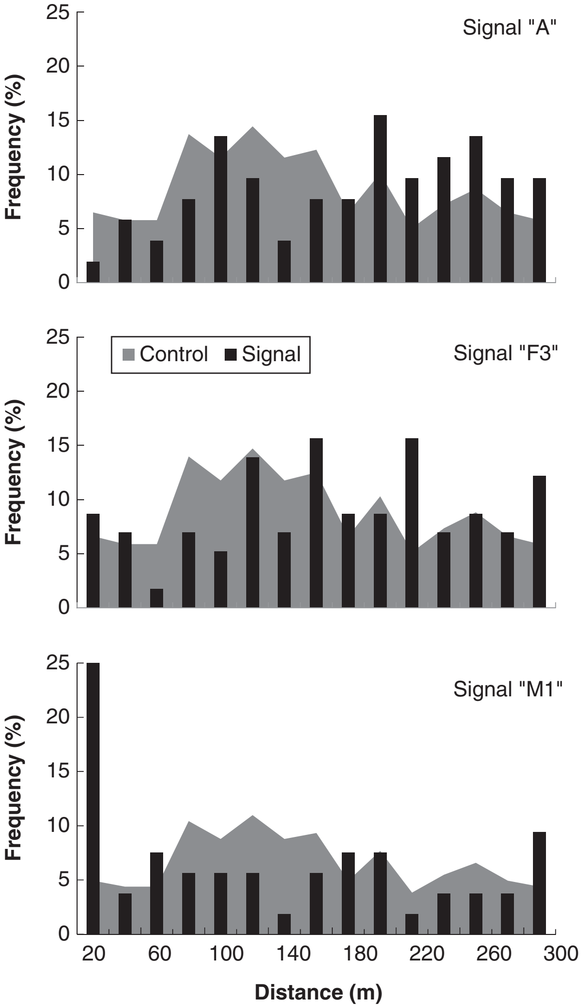

Figure 5. Frequency distribution of minimum porpoise surfacing distance (*D*) to the PAL/CPOD acoustic buoys as determined via theodolite. Control (PAL off): grey-shaded area in background. Signal (PAL on): dark bars. (A) Signal “A”: right shift in distance: dark bars extend beyond shaded area at far range. (B) Signal “F3”: less pronounced right shift. (C) Signal “M1”: surfacing distance is shifted to the left and there is a concentration of surfacings in the 0–20 m range (for details, see text and Table 4).

“F3”, mean click rate rose from 2.26% (control) to 2.49% (PAL on) and then dropped to 1.92% (control). Click activity with signal “F3” was 110% of previous control. The highest click rates were induced by signal “M1” and click rate increased to 168% of controls (3.07% during PAL on as opposed to 1.83% during control).

More profound analysis relating porpoise surfacing distance to acoustic behaviour recorded via CPOD was only possible in the very few cases where the animals remained within 300 m of one of the buoys prior to (control) and during PAL operation. This was observed four times with signal “M1” (Figure 7). Click activity (bars) of porpoise groups swimming at approximately 150–250 m from the detector (tracked via theodolite, black line) is at first low (0–25 min^{-1}). This changes significantly as the PAL is active

Table 5. CPOD data obtained during PAL experiments with three synthetic signal types.

	PAL off	PAL on	Pal off	Difference on/off (%)
Signal A				
Observations (*n*)	727	727	727	
Mean click (%)	2.78	1.15	2.73	41
Raw (click min^{-1})	4.74	1.99	4.79	
Signal F3				
Observations (*n*)	634	634	634	
Mean click (%)	2.26	2.49	1.92	110
Raw (click min^{-1})	17.89	17.2	17.21	
Signal M1				
Observations (*n*)	119	119	119	
Mean click (%)	1.83	3.07	1.76	168
Raw (click min^{-1})	5.07	9.48	5.46	

Notes: Number of observations = number of 15-min intervals for each signal type. Mean click % = proportion of clicks emitted in any 1 min within the 45-min interval. Raw = mean number of clicks min^{-1} within 15-min interval. For details, see text and Figure 5.

(shaded area): the porpoises approach the detector to within 10 m and click at higher rates (> 100 min^{-1}). After a few minutes, the animals leave.

Discussion

PAL to determine local acoustic range

The spherical TL model used by Villadsgaard et al. (2007) for the Little Belt works reasonably well within the first tens of metres, but over larger distances they found it to overestimate SL by approximately 1 dB per 10 m. Our results largely agree with theirs: we determined acoustic range within 300 m of the AAD and found the spherical TL model to overestimate back-calculated SL by 0.7 dB per 10 m. We therefore used the shallow water propagation model of Richardson et al. (1995) instead (Figure 4) to find that back-calculated values for SL were independent of PAL distance to the CPOD. The use of our calibrated, programmable, self-contained, easy-to-operate sound source PAL (Figure 1) to produce signal types and frequencies corresponding to those of the target species proved to be very helpful for this task. As opposed to this, the effort required by Villadsgaard et al. (2007) for their range estimations was very substantial. We propose that PAL may help to simplify *in situ* calibration of acoustic detectors and characterization of site-specific properties (cf. also Gauger et al. 2012). It is currently employed by researchers in Scotland and Denmark for this purpose.

Averse reaction to aggressive signals "A" and "F3"

PAL was programmed to emit aggressive signals based on those recorded on captive harbour porpoises by Clausen et al. (2011). Their recordings of the upsweeping, high repetition rate click trains emitted by a male and a female porpoise and involving a calf during aggressive interactions in the enclosure had a duration between 0.3 and 3 s. Minimum click rates ranged from 150 to 500 s^{-1} (male towards calf) and 100–630 s^{-1} (mother towards male), while maximum click rates were 900–1100 and 750–1050 s^{-1}, respectively. According to Clausen et al. (2011),

> "The aggressive sequences were sometimes made up of one click train and other times consisted of up to three click trains."

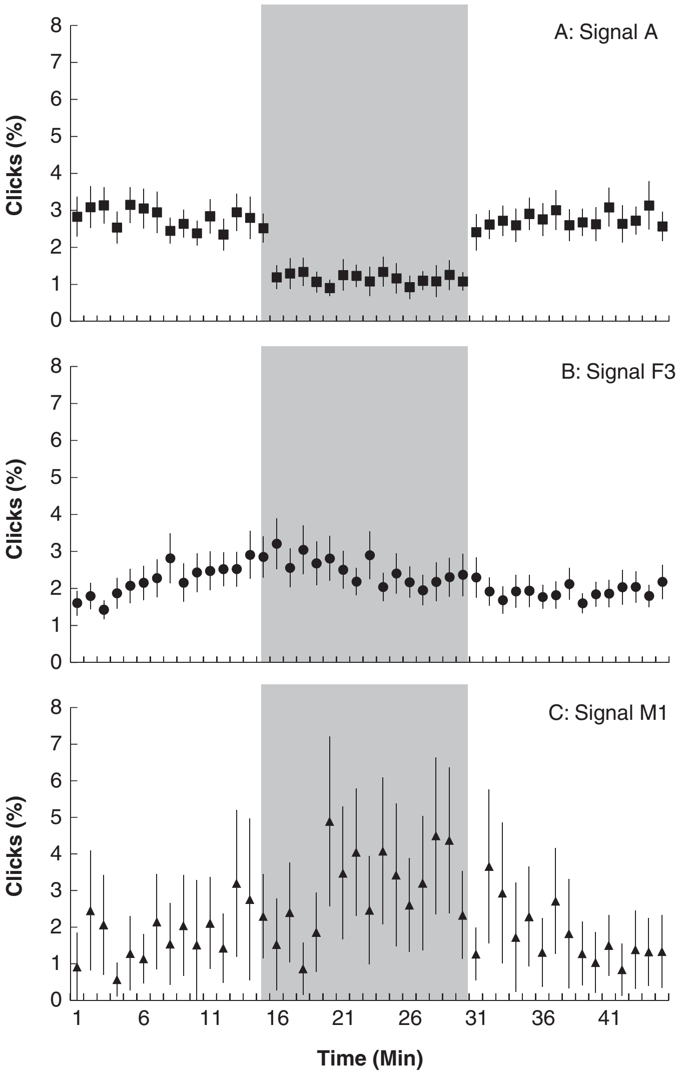

Figure 6. Harbour porpoise click intensity (mean percentage per minute of total clicks recorded during 45-min observation) during the 15 min before, during (shaded) and after PAL operation. (A) Signal "A": mean click activity per minute drops to 41% during PAL on. (B) Signal "F3": mean click activity increases to 110% during PAL on. (C) Signal "M1": mean click activity increases to 168% during PAL on (all as opposed to controls in the 15-min period before PAL on; for details, cf. Table 5).

All three signal types investigated in our study match these criteria (Table 1; Figure 2). According to Clausen et al. (2011):

> The "aggressive" porpoise would suddenly turn towards the subject of aggression (either the calf or the male) and emit a high repetition rate click pulse often while performing a rapid scanning movement of its head. The receiving porpoise always fled after receiving this directed high repetition rate.

Due to the narrow acoustic beam, this head movement would result in a highly variable RL, which could not be reproduced here. But although SL (and due to the omni-directional PAL, RL) in our experiments was constant, our synthetic signals "A" and "F3" entice a similar

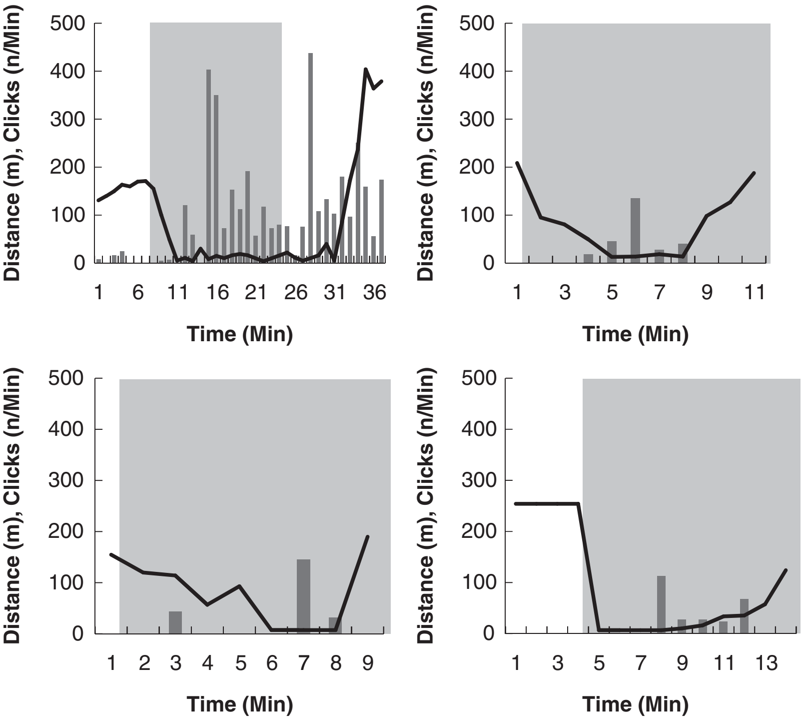

Figure 7. Four examples for the reaction of porpoise groups to PAL signal "M1", recorded on different days between 21 April and 27 May 2013. PAL transmitted during shaded periods. The figures show porpoise range (black line, m) to the signal source (theodolite data) and simultaneous animal click intensity (bars, $n\,\mathrm{Min}^{-1}$, CPOD data). In all four cases, the animals approached the PAL, increased their click rate and left within minutes.

reaction: porpoises within hearing distance move away and increase their surfacing distance to the active PAL. This confirms the assumption of Clausen et al (2011) that the information seems to be encoded in the click repetition rates, rather than, for example, in the SL.

Observed avoidance to "F3" and "A" is moderate: porpoises only increase their mean distance to the acoustic buoys by 19–30 m, respectively, as opposed to PAL off (Table 4). This is far less intensive than the effect of deterring signals of standard ADDs. Culik et al. (2001) found that with a Pice pinger, mean porpoise approach distance increased from 150 m (controls) to 530 m, a difference of 380 m or more than 10 times that observed here. Similarly, the mean distance increased from 431 m (controls) to 752 m when a Dukane NetMark 1000 pinger was active (Berggren et al. 2002), a difference of 321 m. Viewed by itself, porpoise avoidance reaction to the PAL signals "F3" and "A" would not be expected to reduce by-catch.

Echolocation response

Whereas ADDs were found to reduce echolocation activity in porpoises, reaction to PAL is dependent on the type of the signal emitted. After exposing porpoises to pinger-like sounds (100–140 kHz; 153 dB; 200 ms; every 4 s) Teilmann et al. (2006) observed a reduction in echolocation intensity. This was confirmed by Carlström et al. (2009), who monitored echolocation rates around simulated bottom-set nets equipped with Dukane NetMark 1000 pingers, observing a reduction between 50% and 100%. Recently, Hardy et al. (2012) reported a similar reaction to the "banana" pinger (Fishtec Marine, Dartington, UK). Reduced echolocation activity would prevent the animals from obtaining the sensory information required to avoid net collision and entanglement and entails that ADDs cannot be considered an end point in the development of acoustic by-catch mitigating devices.

Unfortunately, Clausen et al. (2011) do not report on the acoustic reaction of animals towards their vocal aggressors. We find here that depending on signal type, porpoise reaction ranges from a strong decrease in echolocation activity with signal "A" to a moderate increase with signal "F3". It appears that signal "A" (increased distance and reduced echolocation) elicits a similar but weaker response as compared with pingers. This effect is not helpful to reduce by-catch: signal "A" and more so pingers may lead animals to collide with nearby, but unmarked nets or with unmarked net sections: Carretta and Barlow (2011) found that cetacean by-catch was 10 times higher with ≥1 malfunctioning pinger compared to nets without pinger failure. They hypothesize that cetaceans might misinterpret the gaps in acoustic coverage as safe passages they can cross acoustically "blindfolded".

Signal type, including click rate, duration and form seem to be crucial for the provoked reaction. Koschinski et al. (2003) showed that harbour porpoises could be stimulated to increase echolocation activity by exposing free-living animals to synthesized low-frequency offshore windmill noise (peak SL: 128 dB re 1 $\mu Pa^2 Hz^{-1}$ at 1 m; maximum sound energy between 30 and 800 Hz). In a later study, Pleskunas and Tregenza (2005) found an increase in porpoise click activity after the emission of a very brief synthetic click train (130 kHz, repeated every 4 s, duration 0.4 s, SL: 130 dB re 1 μPa). However, Kindt-Larsen (2008) tested a type of "porpoise alerting sound (PAS)" pingers generating porpoise-like click trains, although with very high click rates (pulses between 50 and 2500 clicks s^{-1}; 110 kHz; SL: 126–138 dB p–p re 1 μPa @ 1 m) with ambiguous results. She concluded that signal composition and propagation required more attention.

As opposed to this, our results with signal "F3" confirm earlier findings in the Kerteminde aquarium and at sea. There, we recorded an increase in porpoise echolocation activity directed at an earlier version of the PAL emitting signal "F3" (repetition rate 8.9 min^{-1}; Culik and Winkler 2011). With the same reasoning as earlier, we assume that increased distance to the stimulus and at the same time, increased bioacoustic awareness could possibly reduce the risk of becoming entangled in PAL-equipped nets and perhaps also in nearby unequipped nets.

Many previous studies (see review by Coram et al. 2014) report a reduction in responsiveness to acoustic deterrents over time, often referred to as "habituation". However, Dawson et al. (2013) found that there was no diminution of the response of cetaceans (as measured by by-catch rates) to long-term exposure to pingers. Because PAL produces biologically significant signals, with reinforcement occurring during inter-specific interactions, we do not expect habituation over time. We have only opened a door to synthetic communication, and currently conducted tests with PAL in monitored commercial gillnet fisheries will have to prove this.

Positive reaction to signal "M1" and detection range

The active space estimated by Clausen et al. (2011) for harbour porpoises using aggressive signals in the wild is up to 250 m, assuming an SL of 155 dB. This is somewhat lower than our estimates: the PAL generates a SL of 158 dB and for fair weather (no rain or wind) we estimated a maximum range to receiving porpoises (Table 3) of 460 m. Conservatively assuming harbour porpoise signals in the wild to have a minimum SL of 178 dB

(Villadsgaard et al. 2007), we estimate a CPOD detection range of up to 670 m in fair weather (head on). However, when the animals are not oriented towards the CPOD, range estimations drop to as low as 13 m when the animals face with their tail to the AAD, which compares well with the literature (Clausen et al. 2011). In poor weather, this is further reduced and CPOD may only record harbour porpoises if these face the AAD head on at close range (Table 3).

Stenback (2006) tested interactive pingers and observed a variety of behavioural reactions. Normally, porpoises would show a clear avoidance reaction towards the displacement sound generated by these pingers. However, some mother–calf pairs were observed approaching and repeatedly triggering the device through increased click activity without showing any avoidance towards the provoked displacement noise. A similar reaction was observed with our signal "M1", albeit in the absence of calves: the observations shown in Figure 7 are from April to May, that is before the start of the calving season (pers. obs. Boris Culik, Siebert et al. 2006).

Porpoises in the Fjord & Belt Centre stem from the Danish Belt Sea and their semi-natural enclosure communicates acoustically with Kerteminde harbour (Verfuß et al. 2005). We therefore assumed that the aggressive communication signals observed in captivity and synthesized in the PAL study would match those used by the same population in the nearby wild, including the Little Belt. Therefore, reaction to the "aggressive" signal "M1" was unexpected. Clausen et al. (2011) had recorded this signal on the male towards the female as well as in several of their recordings of the female towards the calf. Our signal "M1" matched this very well and completely lacked, for example, low repetition click train components recorded in communication calls associated with other behaviour such as approach, contact, echelon or grooming. Nevertheless, signal "M1" did not cause an avoidance or flight response but significantly attracted wild porpoises and led them to intensify their echolocation (Figures 5–7).

While the reason for attraction by "M1" remains unclear, this effect could be used to improve acoustic detection probability of the animals. As shown in the introduction, $g(0)$ in acoustic monitoring reaches only 0.1–0.3, because of the intermittent echolocation and the narrow echolocation beam of porpoises, requiring, in a figurative sense, that porpoises "hit" the AAD to ensure detection. As shown in Table 3 actively "calling" harbour porpoises with signal "M1" at the site of the AAD would potentially increase detection radius in fair weather to at least 240 m, if signal M1 made them turn around and focus their signals on the AAD. This is the range within which porpoises should be able to hear the PAL even when swimming away from it. In bad weather, most porpoises would go undetected by a CPOD, lest their signals hit the detector head on. Our simple model shows that even under these conditions, PAL could substantially improve detection radius and presumably probability. We assume the impact on the animals to be small: our calculations show that in fair weather, PAL would only be heard within a radius of 460 m (head on) to 240 m (tail on). The signal also seems to lose its attraction within 10–20 min (Figure 7), a rather short-lived effect.

Conclusions

Electronic communication signals synthesized *de novo* by PAL can be used to influence harbour porpoise behaviour. Signal "F3" leads harbour porpoises to increase their surfacing range to the sound source, while at the same time raising their echolocation rate. This combination is very different from what is observed during the deployment of acoustic deterrents and could enable porpoises to avoid acoustically marked nets or other obstacles, while simultaneously decreasing their chance of collision with other, unmarked hazards in their path. To test whether signal "F3" might be useful to avoid harbour porpoise by-catch in set gill nets, we have developed a fisheries version of PAL which is being tested at present in North and Baltic Sea commercial gillnet fisheries.

Signal "M1" is an effective stimulator and entices animals within hearing range to approach and significantly intensify their echolocation, thereby increasing their chance of detection by a passive acoustic detector moored at the same site. With the "right tone", PAL may positively contribute in acoustically detecting low-density populations such as the endangered vaquita in the Gulf of California (Jaramilllo-Legorreta et al. 2013) or harbour porpoises in the eastern Baltic Sea (Benke et al. 2014). Signal "M1" would also increase the chance of detecting dispersed harbour porpoises prior to hazardous marine activities such as seismic exploration, pile-driving or ammunition clearance. Another usage could be to lure animals out of hazardous areas such as tide-affected rivers. Preliminary trials showed promising results.

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Notes

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