Harbor porpoise (*Phocoena phocoena*) reactions to pingers

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ABSTRACT

The use of acoustic alarms (pingers) has been mandated in several gill net fisheries around the world. Even though pingers have shown to reduce the incidental catch there are still questions to be answered in relation to effective range, habituation and displacement. In the present studies, the vocalization behavior of porpoises was recorded in response to two different pingers, AQUAmark100 (20–160 kHz) and AQUAmark300 (10 kHz). The Scottish experiment included an AQUA-mark100 pinger running in on/off cycles. The pinger was placed in an array of acoustic click detectors (C-PODs) spaced at different distances from the pinger. In Denmark, three experiments were conducted. One had the same AQUAmark100 pinger placed in a C-POD array. The second and third experiment used an AQUAmark300 pinger running in on/off cycles. Both trial results of the AQUAmark100 revealed significant pinger reduction effects at 0, 200, and 400 m distance; however, the vocalization behavior reveal no signs of habituation. The studies of the AQUAmark300 revealed a significant pinger effect at 0 m distance and either none or 17% reduction at 300 m distance. At one station, however, habituation effects were found indicated by an increase in clicks over time. These results are important in relation to pinger use and thus fisheries management.

Key words: harbor porpoise, *Phocoena phocoena*, pinger, Natura2000, habituation, pinger effect, habitat exclusion, porpoise management.

Incidental bycatch in gill net fisheries is considered one of the biggest threats to harbor porpoises (*Phocoena phocoena*) (Gaskin 1984, Jefferson and Curry 1994, Reeves *et al.* 2013). Bycatch monitoring schemes have documented relatively large takes of harbor porpoises within several gill net fisheries (Tregenza *et al.* 1997, Vinther and Larsen

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2004, Read *et al*. 2006). The use of acoustic alarms (pingers) on gill nets to reduce this incidental bycatch has been mandated in certain designated areas and fisheries in the EU with the adoption of Council Regulation 812/2004 (EC 2004), and in the northeastern United States under the Harbor Porpoise Take Reduction Plans (New England and mid-Atlantic waters) (U.S. Federal Register 1998). A similar approach has been adopted in California by the Pacific Offshore Cetaceans Take Reduction Plan to minimize bycatch of short-beaked common dolphins (*Delphinus delphis*) and other marine mammal species (U.S. Federal Register 1997). In European Union waters, porpoises are further protected in a network of protected areas identified under the Habitats and Bird Directives, known as Natura2000 (EC 1979, 1992). Plans for fisheries regulations in Natura2000 areas are under development in several European Union member states.

Pingers have been shown to be an effective tool to reduce bycatch of harbor porpoises in gill nets (Kraus *et al*. 1997, Gönener and Bilgin 2009, Dawson *et al*. 2013, Larsen and Eigaard 2014). Two main pinger types have been developed. One has a constant frequency (10 kHz) with multiple harmonics and pulses repeated every 4 s (Dukane Netmark100, AQUAmark300, Future Oceans F10), whereas the other uses higher frequencies and randomized signals (Banana pinger, AQUAmark100, STM DDD, Save Wave dolphin saver) and may emit signals at random intervals (AQUAmark100). Even though pingers reduce the bycatch of porpoises, concerns have been raised about high costs, handling problems, noise pollution, habitat exclusion, and habituation (Dawson *et al*. 1998, Gearin *et al*. 2000, IWC 2000, Cox *et al*. 2001). Habituation, defined as "a decrease in response to a stimulus after repeated presentations" (Bouton 2007), is one of the most serious concerns because it might lead to animals ignoring the signals over time as the range over which porpoises are displaced decreases. Experimentally, porpoises have been found to approach pingers more closely over time (Cox *et al*. 2001, Carlström *et al*. 2009), suggesting that habituation to the pingers took place in these two experiments. Despite these concerns, studies in commercial fisheries where pingers are in use have not found evidence of an increase in bycatch rates over time (Palka *et al*. 2008, Carretta and Barlow 2011).

Pingers have only been used to a limited extent in gill net fisheries within the European Union (ICES 2012) and long-term effects have not, therefore, been recorded in European Union waters. If, however, pingers are introduced as part of management plans within Natura2000 sites, it is likely that they will be used more frequently, increasing the risk of either habituation or habitat exclusion. Knowledge on how pingers affect the fine-scale behavior of porpoises is therefore needed.

Porpoises are difficult to observe since they spend most of their time below the sea surface. Passive acoustic monitoring (PAM) takes advantage of the fact that porpoises echolocate (Møhl and Andersen 1973, Akamatsu *et al*. 2007), and PAM has therefore been used to determine porpoise occurrence (Carlström *et al*. 2009, Kyhn *et al*. 2012, Dähne *et al*. 2013).

Our study used PAM to investigate changes in porpoise echolocation patterns in the presence and absence of two different pinger types over time periods of several weeks. Two questions were addressed. Firstly, to which level do pingers affect porpoise echolocation activity at different distances and what does this tell us about the effective range of the pinger? Secondly, do porpoises habituate to the pinger signals?

Materials and Methods

Four experiments were conducted in coastal waters at three different locations: (1) Jammerland Bay, Great Belt, Denmark; (2) St. Andrews Bay, North Sea, Scotland; (3) Gilleleje Flak, Kattegat, Denmark, and (4) again Jammerland Bay, Great Belt, Denmark; (Fig. 1, Table 1). The Scottish experiment was conducted in water depths of 10–15 m, and the area had a tide around 5 m, whereas the Danish experiments were conducted in 7–10 m depths and had a tide around 0.2 m at both sites.

Porpoise echolocation activity was recorded using porpoise click detectors (C-PODs, version 2; Chelonia Ltd., Mousehole, U.K.). C-PODs are self-contained ultrasound monitors that detect tonal clicks such as echolocation signals. The C-POD contains an omnidirectional hydrophone that records short duration sound clicks within a frequency range of 20–160 kHz. For each click, start time, duration, dominant frequency, and sound pressure level are logged and used to recognize click trains of porpoise origin. C-PODs were calibrated for the main frequency of a harbor porpoise click (130 kHz) and standardized to the same acoustic threshold (±3 dB) (see http://www.chelonia.co.uk for further information).

Jammerland Bay, Denmark—AQUAmark100 (Jammerland1)

The initial experiment was conducted between 24 March and 13 June 2010 (Table 1). An array of five C-PODs was set parallel to the coastline (Fig. 1, map A) at approximately 8.5 m depth and 1.5 m above the sea bed. A single modified AQUAmark100 pinger (Aquatec Group Ltd., Basingstoke, U.K.) was attached above the first C-POD in the array. The next four C-PODs were deployed at distances of 200, 400, 800, and 1,600 m from the pinger. The AQUAmark100 pinger emitted eight different signals in random order, two at a constant frequency and six with frequency sweeps (20–160 kHz). The mean source level and duration was 145 dB re 1 µPa@1m (RMS) and 200–300 ms, respectively. The pinger was activated by an internal clock in cycles of 23 h on and off. The 23 h cycle was chosen to simulate a gill net fishery because many gill nets are set for approximately 24 h. The time, however, was reduced to make the pinger start at different times of the day and thus limit effect of the diurnal variation in porpoise echolocation activity (Linnenschmidt *et al.* 2013). The functionality of the internal clock cycles could be verified by the C-POD to which the pinger was attached. As the C-POD also logs pinger sounds these could easily be confirmed with the C-POD software. The experiment was initiated with a baseline period (36 d) recording the porpoises' presence before introduction of the AQUAmark100 pinger (47 d), (Table 1).
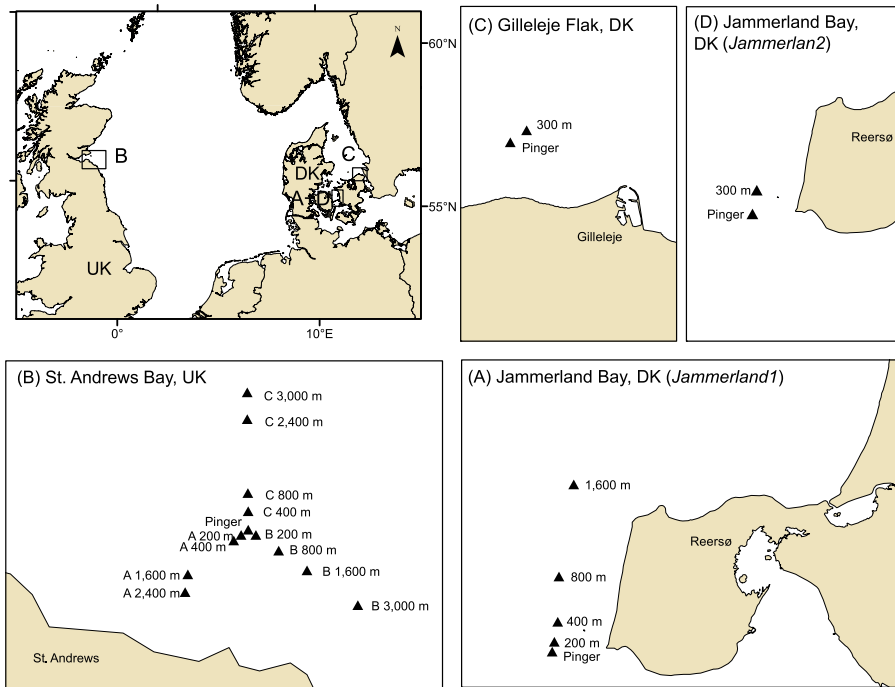
Figure 1. Map of experimental setup in (A) Jammerland Bay, Denmark (*Jammerland1*), (B) St. Andrews Bay, Scotland, (C) Gilleleje Flak, Denmark, and (D) Jammerland Bay, Denmark (*Jammerland2*). At "Pinger" both a pinger and a C-POD were deployed. The triangles indicate the positions of the C-PODs and their corresponding distance to the pinger.

St. Andrews Bay, Scotland—AQUAmark100

The Scottish experiment was conducted between 20 September and 7 December 2010. In Scotland a different array setup was used (Fig. 1, map B) building on experiences and preliminary results obtained during the processing of the data from *Jammerland1.* The preliminary results from *Jammerland1* indicated a pinger effect outwards of 1,600 m (which later turned out to be incorrect, see Results). To ensure, therefore, that the Scottish array included a C-POD station so far from the pinger that the pinger had no effect, this array was extended to include stations at longer distances (2,400 m and 3,000 m). Another concern about the *Jammerland1* experiment was that the array only recorded porpoises in one direction from the pinger (northern direction, Fig. 1, map A). If, for example, the porpoises had only approached the array from either a southern or western direction, the northern stations would be biased, since the animals would not encounter the 0 m station until they had already been exposed to the pinger.

The Scottish experiment thus employed a triangular array to detect porpoises approaching from three directions. A total of 14 C-PODs were

Table 1. Overview of the four experiments.

	Dates	Pinger	Pinger cycles	Comment
Jammerland1				5 C-POD array
Baseline	24 March–28 April 2010	No pinger		No data on 0 m distance
Experiment	28 April–13 July 2010	AQUAmark100	40 on and 41 off	
St. Andrews Bay (Branch A, B, C)				14 C-POD array
Baseline	20 September–5 October 2010	No pinger		
Experiment	5 October–30 October 2010	AQUAmark100	12 on and 13 off	
Recovery	30 October–7 December 2010	No pinger		6 pods collected 5 November 2010
Gilleleje Flak			19 on and 19 off	2 C-POD array
Experiment	3 October 2013–10 November 2013	AQUAmark300		
Jammerland2			16 on and 17 off	2 C-POD array
Experiment	13 March–28 April 2015	AQUAmark100		

deployed in the array (Fig. 1, map B) at 10–15 m depth and placed 1.5 m above the sea bed. Again, a single modified AQUAmark100 pinger running in cycles of 23 h on and off, equal to the one used in *Jammerland1*, was deployed in the center of the array together with two C-PODs. The other 12 C-PODs were deployed at distances of 200, 400, 800, 1,600, 2,400, and 3,000 m. For each distance porpoise clicks were detected by two C-PODs, but on different branches of the array (Fig. 1, map B). The St. Andrews Bay experiment was initiated with a baseline period (16 d) recording the porpoises' presence before the introduction of the AQUAmark100 pinger (26 d) and ended with a recovery period (6–9 d) after the retrieval of the AQUAmark100 (Table 1).

Gilleleje Flak, Denmark—AQUAmark300

The Gilleleje Flak experiment was conducted from 3 October 2013 to 10 November 2013. The results of the Aquamark100 experiments in both St. Andrews Bay and at Jammerland did not reveal any signs of habituation (see Results), which had been identified in earlier experiments with 10 kHz pingers. Cox *et al.* (2001) found habituation effects after 4 d, whereas Carlström *et al.* (2009) found habituation effects after 51 d. To be able to compare our results with those of Cox *et al.* (2001) and

Carlström *et al.* (2009), a simple setup was therefore employed at Gille-leje Flak using the same type of pinger (10 kHz) as in those experiments. Two C-PODs were deployed at 8 m depth, placed 1.5 m above the sea bed with 300 m spacing (Fig. 1, map C). At station 1 a single modified AQUAmark300 pinger was attached to the C-POD. The modified AQUA-mark300 emitted 10 kHz signals lasting 300 ms at 4 s intervals. The source level was 132 dB re 1 µPa@1m (RMS). The pinger was run in cycles of 23 h on and off during the whole experiment.

Jammerland Bay, Denmark—AQUAmark300 (Jammerland2)

The fourth experiment was conducted between 13 March and 28 April 2015. This study was conducted to replicate the experiment from Gille-leje Flak in another area. As in the setup at Gilleleje Flak, two C-PODs were deployed, here at 8 m depth, placed 1.5 m above the sea bed with 300 m spacing (Fig. 1, map D). Again, a single modified AQUAmark300 pinger running in 23 h cycles on/off with the same specifications as mentioned above was attached to the C-POD placed at the first station.

Porpoise Click Classification

The echolocation clicks recorded on the C-PODs were classified as being of porpoise origin by the C-POD software (C-POD V2.035, Che-lonia Ltd.) that automatically filters the data for porpoise clicks by use of a proprietary detection algorithm. Clicks in trains were classified into quality classes of high and moderate-probability cetacean trains. Only clicks in trains from these two classes containing more than five clicks and within the frequency spectrum 125–145 kHz were used as indicators of porpoise presence. Both types of pinger signals could easily be identified in the C-POD data, thus making it possible to iden-tify the pinger cycles. Hours when the pinger was changing between on and off were eliminated from the trials to remove recordings of any porpoises that had been exposed both to pinger sounds and silent periods.

Statistical Analysis

The C-POD output data (clicks in trains) contained many zeros in 23 h periods when the pinger was on (see Appendix S1). Ignoring zero-inflation can cause errors in parameter estimates and bias standard errors (Zuur *et al.* 2009). Thus, when analyzing the data, we evaluated a zero-inflated negative binomial model (Martin *et al.* 2005) as well as an ordinary negative binomial model. Preliminary analyses suggested that the zero-inflated model was more appropriate when the models were compared using the Akaike information criterion (AIC) (Akaike 1974). The regressors of the binomial and negative binomial part of the model were chosen to be identical, and the logit link and log link were used as link functions for the binomial and negative binomial parts of the model, respectively.

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

$$Y = \text{zeroinfl}\left(\beta_0 + \beta_1\, pinger + \beta_2\, time + \beta_3\, clock + \beta_4\, click + \beta_5\, pinger : halftime\right),$$

where the response variable Y is defined as the number of clicks in trains per hour. The covariate *pinger* indicated whether the pinger was on or off, *time* was a continuous variable from the beginning to the end of the experiment, and *clock* was a categorical effect from 1 to 12 representing 2 h time intervals of the day. The covariate *click* was defined as the natural logarithm of the number of clicks in trains/hour plus 1 in the previous hour, and was included to model auto-correlation in the observed time-series of clicks. The log-transformation was chosen since the AIC value for this model was better compared to when the variable was untransformed. The covariate *pinger:halftime* was included to analyze habituation effects, and is defined as the interaction between the *pinger* variable and an indicator variable *halftime* that has a value of one whenever the data point stems from the second half of the experiment. This implies that two distinct pinger effects are estimated in the model if *pinger:halftime* is significant, one for each halftime of the experiment. Model selection was performed using AIC.

The zero-inflated negative binomial model does not directly provide covariate adjusted inference for the exposure effect (the pinger) or other covariate effects. This is because the model consists of a logistic regression for the extra zeroes and a loglinear regression for the negative binomial part, and distinct regression parameters are estimated for both parts. This formulation implies that the overall exposure effect is not multiplicative on the natural scale, but rather it depends on all the other covariates. The "average predicted value" approach (Albert *et al.* 2014) was used to obtain estimates of the overall effects of the pinger and any possible habituation.

The exposure effect size is defined as the average predicted ratio of response means for the unexposed time periods *vs.* the exposed, *i.e.*, an effect size of X can be interpreted as X times more clicks in trains on average when the pinger is off. The habituation effect is defined similarly, *i.e.*, as the ratio of the size of the effect in the first half to the size of the effect in the second half of each experiment.

Approximate confidence bounds were constructed by parametric bootstrapping and *P*-values were calculated using the likelihood ratio test for model reduction. All analyses were made in the R 3.4.1 statistical package (R Core Team 2017) using the package pscl (Zeileis *et al.* 2008).

<center>RESULTS</center>

The first experiment in Jammerland Bay (*Jammerland1*), testing the AQUAmark100, was initiated after a baseline period of 36 d. Unfortunately, the C-POD at 0 m stopped recording after 3 d and consequently no data were collected from this station in the baseline period. During the pinger on/off period, 77 d of recordings were collected resulting in 40 on and 41 pinger-off cycles, except at 0 m distance where the C-POD stopped after a total of 43 on/off cycles. The experiment conducted in St. Andrews Bay had three data collection periods: "Baseline," "Pinger

cycle," and "Recovery," which consisted of 16, 25, and 5–49 d, respectively, resulting in 12 on and 14 off pinger cycles. The reason for the variation in C-POD recording time in the recovery period was adverse weather conditions, postponing the retrieval of some of the C-PODs. The experiment from Gilleleje resulted in a total of 38 d of recording, corresponding to 19 on and 19 off cycles of the AQUAmark300. The experiment from Jammerland (*Jammerland2*) testing the AQUAmark300 resulted in 16 on and 17 off cycles (Table 1). To give an overview of all data recorded, the mean number of porpoise clicks in trains per hour detected at the different distances and grouped according to pinger on/off status is plotted in Figure 2 (baseline and recovery periods omitted). Furthermore, selected time-series of the data are illustrated in Figure 3 (the complete time-series can be found in Appendix S1). Here data have been aggregated by on/off cycles (clicksum), added one and log-transformed (natural log).

Pinger Effect

In *Jammerland1*, the results showed that the number of clicks in trains per hour was significantly lower in "pinger on" compared to "pinger off" periods at 0 ($P < 0.001$), 200 ($P < 0.001$) and 400 m ($P < 0.001$) distance from the AQUAmark100 pinger by factors of 5, 3,
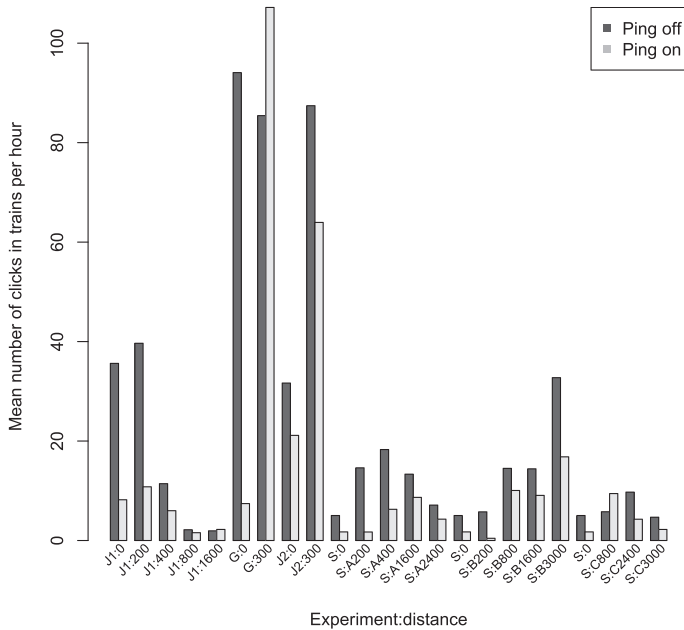

Figure 2. The mean number of porpoise clicks in trains per hour detected at the different distances grouped according to pinger on/off status where baseline and recovery periods are omitted. The Experiment: distance indicates the experiment (J1 = *Jammerland1*, G = Gilleleje Flak, S = St. Andrews Bay, J2 = *Jammerland2*) and its linked distance and branch (only for St. Andrews data).

and 2, respectively. No significant differences were identified in the number of clicks in trains per hour between on and off periods at 800 and 1,600 m distance to the pinger (Fig. 4).

In St. Andrews Bay, the model also revealed a significant difference in the number of clicks in trains per hour between on and off periods at 0 m (4-fold reduction, $P < 0.001$), 200 m (6-fold reduction, $P < 0.001$, branch A; 30-fold reduction, $P < 0.001$, branch B), and 400 m (3-fold reduction, $P = 0.025$, branch A) from the AQUAmark100 pinger (Fig. 5). No effect of the pinger was identified at 800 m or further away except from branch C, where an effect was found at 2,400 m and 3,000 m.

The results from Gilleleje Flak showed a significant pinger effect at 0 m (15-fold reduction, $P < 0.001$), whereas no effect of the AQUA-mark300 pinger could be detected at 300 m (Fig. 6). In *Jammerland2* a
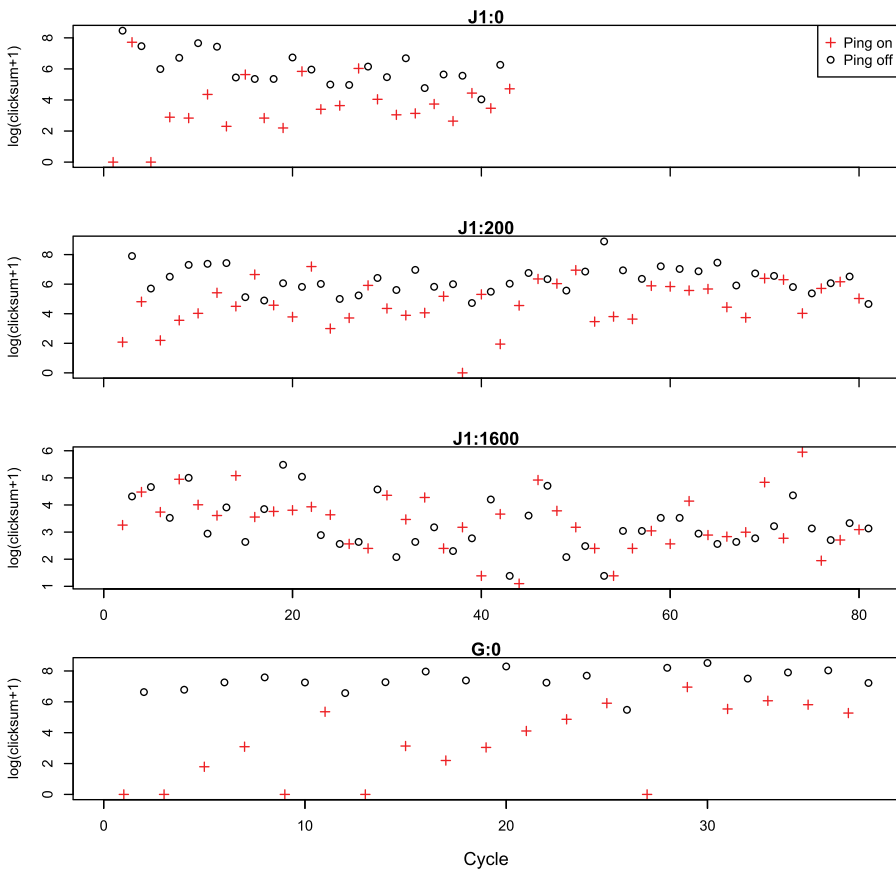

Figure 3. Selected time-series of the data. Data have been aggregated by on/off cycles (clicksum), added one and log-transformed. The latter was chosen to obtain less spread in the values. The heading of each figure corresponds to the experiment (J1 = *Jammerland1*, G = Gilleleje Flak) and its linked distance. The complete time-series of all experiments can be found in Appendix S1).
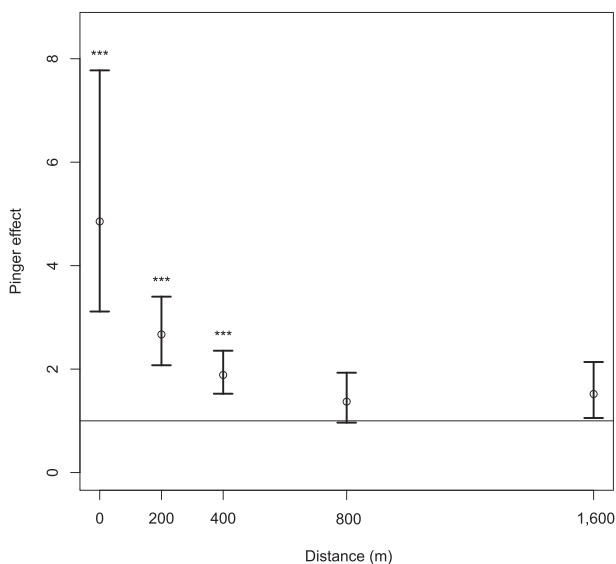
Figure 4. Calculated pinger effect at each monitored distance in Jammerland Bay, Denmark (*Jammerland1*). The predictions were calculated using the final model and the lines indicate 95% confidence intervals (***: $P < 0.001$).

significant but lower reduction was found at 0 m (1.4-fold reduction, $P < 0.001$) and at 300 m (1.2-fold reduction, $P = 0.001$) from the AQUA-mark300 pinger (Fig. 7).

Habituation

All four experiments were analyzed for signs of habituation, defined as a significant difference in the estimated pinger effect in the first half time period compared with the second. In *Jammerland1* (half time period = 40 on/off cycles) and St. Andrews Bay (half time period = 12 on/off cycles), where the AQUAmark100 pinger was used, the analysis showed no signs of habituation. Also, no signs of habituation can be seen in the raw data plots in Figure 3 (J1:0, J1:200) and Appendix S1. The results from Gilleleje Flak testing the AQUAmark300 (half time period = 19 on/off cycles), showed a significant increase in the number of clicks in trains over time at 0 m. Here the habituation effect was estimated at 2.86 (95% CI: 0.88–8.88) indicating the pinger had 2.86 times less effect in the second half of the experiment (15-fold reduction in first half and approximately 5-fold in the second half). This habituation pattern can also be recognized in the simple plot of the raw data (Fig. 3, G:0) by an increase in the number of clicks in on-periods relative to off-periods over time. The same habituation pattern could not be found at *Jammerland2* (half time period = 16 on/off cycles).
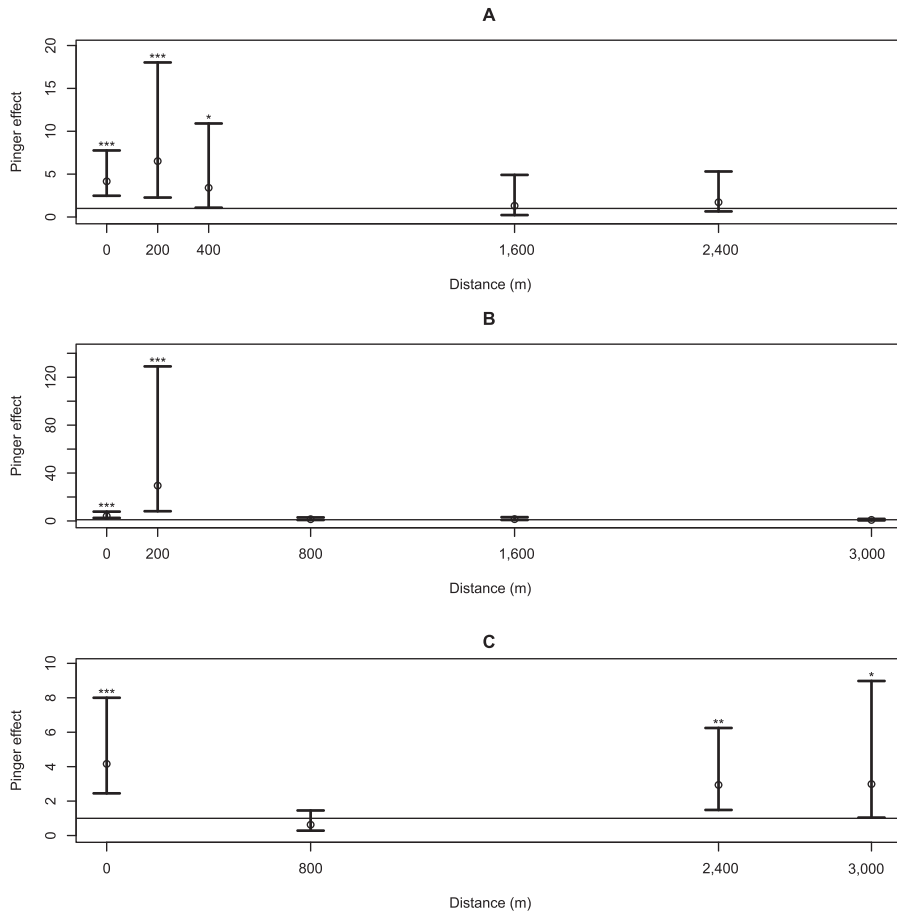
Figure 5. Calculated pinger effect at each monitored distance in St. Andrews Bay, U.K. The letters A, B, and C corresponds to the different branches of the setup. The predictions were calculated using the final model and the lines indicate 95% confidence intervals (*: $P = 0.01–0.05$; **: $P = 0.001–0.01$; ***: $P < 0.001$).

DISCUSSION

The four experiments presented here demonstrated that the presence of a single pinger significantly reduced the number of porpoise clicks in trains per hour. The effect, however, depended on the signal type and area, and habituation could be avoided by varying signals.

In our results the AQUAmark100 pinger had a significant effect out to 400 m in *Jammerland1* and St. Andrews Bay. In *Jammerland1* the pinger effect gradually decreased from a 5-fold (0 m) to a 3-fold (200 m) to a 2-fold (400 m) reduction corresponding to 80%, 67%, and 50% reduction, respectively. This confirms that the pinger effect is decreasing with increasing distance. Larsen *et al.* (2013) found 100% (22 bycatches
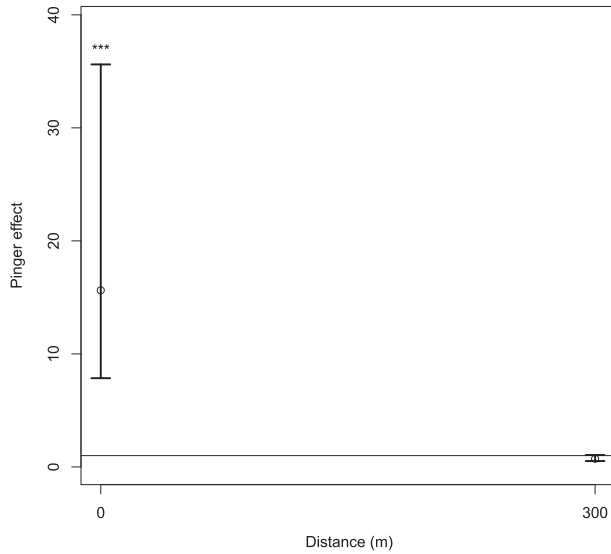
Figure 6. Calculated pinger effect at each monitored distance at Gilleleje Flak, Denmark. The predictions were calculated using the final model and the lines indicate 95% confidence intervals (***: $P < 0.001$).
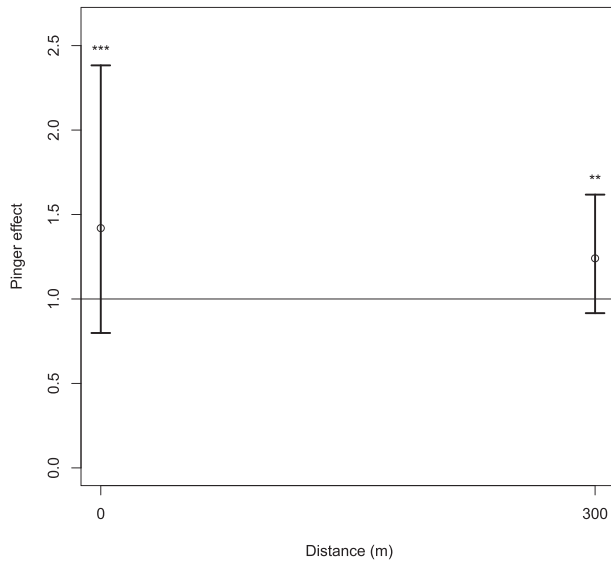

Figure 7. Calculated pinger effect at each monitored distance in Jammerland Bay, Denmark (*Jammerland2*). The predictions were calculated using the final model and the lines indicate 95% confidence intervals (**: $P = 0.001–0.01$; ***: $P < 0.001$).

in 42 control sets *vs*. 0 bycatch in 24 pingered sets) reduction in bycatch rates when the pingers were spaced at 455 m but the efficacy decreased to 78% (22 bycatches in 42 control sets *vs*. 5 bycatches in 43 pingered sets) when the pingers were spaced at 585 m. This suggests that at distances of more than 227 m (the distance covered by a single pinger when the spacing is 455 m) the efficacy begins to decline. In St. Andrews Bay, the same type of pinger showed a greater reduction in porpoise clicks at 200 m (40-fold, 98%), compared to the same distance in *Jammerland1* (3-fold, 67%). However, the confidence bounds at the two areas are wide, indicating that the estimates are not significantly different. Note that fewer data were collected during the St. Andrews Bay experiment, and the shorter time periods increase the CV, thus giving more power to the *Jammerland1* trial.

The triangular setup in St. Andrews Bay gave seemingly contradictory results with respect to the effective range of the pinger as branch C had significant reductions at 2,400 and 3,000 m unlike branches A and B. Such results, however, are possible if the porpoises for some reason always approached the pinger from the A and B sides but never from the C side as illustrated in Figure 8. The figure shows that no porpoises will be recorded at the C branch when the pinger is ON as the pinger prevents them from entering the area around branch C, thus leading to a noncircular effect of the pinger at longer distances. This illustrates the advantages of the triangular setup and demonstrates that pinger displacement will not always be circular but will depend on where the porpoises are in the area.

To our knowledge only one other study has investigated the AQUA-mark100 running in on/off cycles. Hardy *et al*. (2012) found a 50%
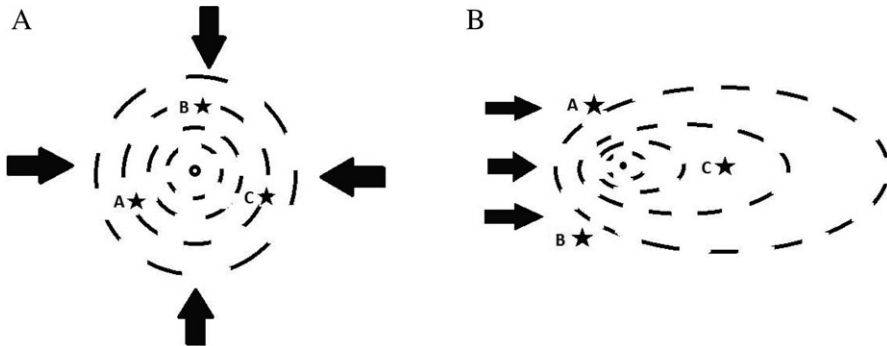

Figure 8. (A) Illustrates that if porpoises approach the pinger evenly from all sides, it does not matter if the C-POD is placed at A, B, or C. For both figures the arrows indicate the porpoise swimming direction, the stars are the C-POD positions and the lines represent the shape of the pinger effect. (B) Illustrates what could happen if the porpoises always approach the pinger from the A and B side but never from the C. The figure shows that few porpoises will be recorded at the C branch when the pinger is ON as the pinger prevents them from entering the area around branch C, thus leading to a spurious effect of the pinger at longer distances.

reduction at 0 m (AQUAmark100, 7 h on/off cycles), which is 30 percentage points less effective than our findings. A possible explanation for the difference is a reduced response to pingers when background noise levels are higher. In areas with high background noise levels, the signal to noise ratio will be reduced (Urick 1983), making it more difficult for the porpoises to detect the pinger signals. The discrepancy could also be caused by differences in sea bed morphology and water depths as shallow waters can lead to multipath sound propagation (Shapiro *et al.* 2009). Hardy *et al.* (2012) found a stronger effect of the pinger in quiet areas compared to noisy areas when testing porpoise responses to the AQUAmark100. All the above factors may influence the results and the effective pinger range is thus expected to vary between different locations. In our study the background noise was not measured but the noise level should be taken into account when testing or implementing pingers in different areas and merits further investigation.

For the AQUAmark300, both the *Jammerland2* and Gilleleje Flak experiments showed a significant reduction in porpoise clicks at 0 m. The effect size differed between sites, as Gilleleje Flak revealed a 15-fold (93%) reduction compared to a 1.4-fold (29%) reduction in *Jammerland2*. Again, a possible explanation for the difference between the areas is a reduced response to pingers where background noise levels are higher. At 300 m no effect was found at Gilleleje Flak and only a 1.2-fold (17%) reduction was found in *Jammerland2.*

Carlström *et al.* (2009) showed that an array of Dukane NetMark 1000 (10 kHz pingers), similar to the AQUAmark300 pinger, reduced porpoise click rates by 50% at a distance of 500 m. The different effect sizes could be due to the differences between pinger brands or by the fact that Carlström *et al.* (2009) used several pingers, as the sound field from several pingers might produce a different reaction by porpoises. In experiments using 10 kHz pingers, high bycatch reduction effects have been found, *e.g.*, 98% reduction (200 m spacing, 92 bycatches in 20 control trips *vs.* 2 bycatches in 20 pingered trips, Gönener and Bilgin 2009), 92% (92 m spacing, 25 bycatches in 423 control sets *vs.* 2 bycatches in 421 pingered sets, Kraus *et al.* 1997), and 77% (100 m spacing, 14 bycatches in 267 control sets *vs.* 3 bycatches in 249 pingered sets, Trippel *et al.* 1999), indicating that the pinger is effective at short distances. Studies examining the pinger effect at longer distances have to our knowledge not been conducted with 10 kHz pingers. However, Murray *et al.* (2000) found that in situations where one or more 10 kHz pingers on a net had malfunctioned, thereby increasing the distance between functioning pingers, the bycatch rate of porpoises increased. These results support our findings of the short effective range for this type of pinger, but differences in the level of effect must be expected due to differences in the factors described above, *e.g.*, depth, bottom type, and background noise levels.

The effect of pingers has traditionally been measured as a bycatch reduction percentage when comparing pingered nets to nonpingered nets in fishing experiments. Bycatch studies on harbor porpoises have reported pinger reduction effects between 77% (Netmark 1000,

Trippel *et al.* 1999) and 100% (*e.g.*, AQUAmark100, Larsen *et al.* 2013), and failures to document effects have been explained by either no bycatch (Carlström *et al.* 2002) or pinger faults (Northridge *et al.* 1999).

To be able to compare our studies to the traditional fisheries bycatch reduction experiments, we assume that the bycatch rate is proportional to the click rate and thus abundance. This assumption is supported by the results of Kindt-Larsen *et al.* (2016) who has shown that bycatch rate is proportional to the porpoise abundance.

An important assumption is that porpoise echolocation is correlated with porpoise density. This correlation has been shown by Kyhn *et al.* (2012) and the relationship has been used to estimate, for example, the abundance and distribution of the Baltic Sea harbor porpoise (Koblitz *et al.* 2014).

An important consideration is whether porpoise echolocation is affected by the pinger signals. Porpoises in captivity have been observed to echolocate less in the presence of pinger sounds (Teilmann *et al.* 2006). This indicates that a porpoise could be present, but silent, in the on-pinger periods and therefore would not be recorded on the C-PODs. Kastelein *et al.* (2000), however, showed that porpoises swam to the farthest end of the pool when exposed to pingers and Culik *et al.* (2001) determined that porpoises tracked with a theodolite were absent from areas in the vicinity of a pinger. We therefore believe that even if porpoises reduce their echolocation in the presence of pinger sounds, they will not remain in close proximity to a pinger.

Another important consideration is that the C-POD does not record only those porpoise clicks originating in close proximity of the C-POD. Culik *et al.* (2015) calculated that C-PODs can detect harbor porpoise clicking "head on" from a distance of 670 m. Because of the narrow beam width of the porpoise sonar (13°, Koblitz *et al.* 2012) the probability of "head on" is only 4% if the porpoise is randomly placed. If the animal is facing sideways or away, detection range falls to 50 and 13 m, respectively (Culik *et al.* 2015). However, as the minimum spacing between two C-PODs in our setup was 200 m and significant differences were still found between two such locations, the effective detection distance of the C-POD must be shorter.

Another point for discussion is the choice of response variable. C-POD data can be extracted in many forms such as porpoise positive minutes, encounters, number of clicks per minute, and number of clicks in trains per hour. In our case we have selected the "number of clicks in trains per hour" as the others could potentially limit variation caused by the pinger. With "number of clicks in trains per hour" there can also be large variation that is not due to the pinger status, but to other factors such as feeding behavior. As we only compare on and off periods from the same location, a location with increased feeding activities will not affect the results. One example, however, could be that pinger sounds may cease all foraging and social behavior, while the animals may remain in the area and only use echolocation for orientation. This could potentially make it more difficult to determine the pinger effect with this type of response variable.

Habituation

Deploying pingers to reduce bycatch represents a case of repeated presentations of a stimulus where no reinforcement is imposed on the porpoises to avoid entanglement. The porpoises may be rewarded for swimming away from the pinger by a reduction in the received level of the pinger sounds, but that is difficult to confirm. A failure to respond, *e.g.*, ignoring the increasing sound level when approaching the pinger is, however, not connected with a learning experience since porpoises most likely will be entangled and drown. Porpoises that have been repeatedly exposed to the same pinger sounds might be expected to show a decrease in avoidance response, *i.e.*, habituate to the pingers. However, habituation will only be a problem in this case if the distance between the porpoise and the pinger becomes too small to avoid entanglement in the net. Thus, as long as bycatch levels do not increase over time, we interpret habituation as a positive response since it will reduce the level of habitat exclusion.

Ideally, habituation should be investigated by using repeated observations of known individuals (Richardson *et al.* 1995), but this is not possible using C-PODs. Potential habituation effects are therefore difficult to assess because it is not known how many times the recorded porpoises have been exposed to the pinger sounds. Nonetheless, evidence of habituation was found. A comparison between the results of the AQUAmark100 and AQUAmark300 experiments showed a difference in habituation to the two pinger types. The 10 kHz AQUAmark300 experiments resulted in an apparent habituation effect over time at Gilleleje Flak (Fig. 3, G:0), whereas no such effect was found in *Jammerland2* or in the studies of the AQUAmark100. Note that data from *Jammerland2* were collected over a shorter time period and a smaller pinger effect was found. Other studies have reported habituation effects in relation to other 10 kHz pingers. Carlström *et al.* (2009) investigated porpoises' acoustic, spatial, and temporal responses to Dukane NetMark 1000 (10 kHz) pingers. They interpreted an increased echolocation rate over time as evidence of habituation. Cox *et al.* (2001) also found a habituation effect in porpoises exposed to a Dukane NetMark 1000. The results of these studies and our own results suggest that porpoises habituate to the simple 10 kHz pingers, whereas our results did not suggest that porpoises habituate to the AQUAmark100. As described earlier, the Dukane NetMark 1000 and the AQUAmark300 pinger emitted the same 10 kHz signal every 4 s. In contrast, the AQUAmark100 emitted eight different signals between 20 kHz and 160 kHz in a random order. The signals and play order of the AQUAmark100 were designed to avoid habituation, and this seems to have been achieved. Our results indicate that porpoises may habituate more easily to a constant signal compared to a mixture of different signals such as those of the AQUAmark100. It could also be that the time span of the experiments were too short for the porpoises to habituate to the AQUAmark100 and the habituation response would first appear at a later stage. Similarly, only short term bycatch reduction experiments (Larsen *et al.* 2013, Larsen and Eigaard 2014) have been conducted with the AQUAmark100. Thus, it has not been

possible to verify if habituation will appear over longer time spans. The duty cycle of the pinger could also have dampened the habituation effect. In this study we had a duty cycle of 23 h on and 23 h off to simulate the usual soak time of 24 h. Both Carlström *et al.* (2009) and Cox *et al.* (2001) had no duty cycles. As porpoises in the vicinity of pingers with a duty cycle will be less exposed to pinger sounds, the habituation response could be delayed. Longer time spans should thus be explored.

Habitat Exclusion

It is clear that pingers can affect porpoise distribution patterns and thus lead to habitat exclusion (Culik *et al.* 2001, Carlström *et al.* 2009), and some level of habitat exclusion is inevitable when using pingers since their function is to keep the porpoises away from the net. However, assessing the exact exclusion zone is difficult as it depends on factors such as pinger type, background noise level, and level of habituation over time. A different way of approaching the issue is through modeling of the effects of habitat exclusion at the population level. The results of the AQUAmark100 from the *Jammerland1* have been incorporated in a spatially explicit individual-based simulation model (IBM). Here it was found that when AQUAmark100 pingers were used in areas of high porpoise usage, the habitat exclusion had a higher impact on the population than the bycatch in the fisheries (van Beest *et al.* 2017). These kinds of model predictions will, however, depend on the pinger type and specific effects of the pinger used. The question of habitat exclusion remains a concern if pingers are used in areas of preferred porpoise habitat (Dawson *et al.* 2013).

Pinger Use in Protected Areas

Porpoise conservation has primarily focused on the use of protected areas, time area closures, and pinger implementation (EC 1979, 1992; Murray *et al.* 2000). Within the European Union, member states are, according to Natura2000, obliged to nominate candidate protected areas in their waters to the European Commission, and within 6 yr establish legislation to implement such areas as special areas of conservation and prepare appropriate management measures (EC 2007). In Denmark, a number of Natura2000 areas have been established based on porpoise satellite tagging data indicating high area usage (Sveegaard *et al.* 2011). At this stage, no management plans exist for the Danish Natura2000 areas. One option would be a requirement for fishermen to use pingers on gill nets to minimize bycatch as done in the United States (Murray *et al.* 2000). The effect of pinger use in such areas, however, is not straightforward and has been the subject of some discussion (ICES 2012). The net benefit of pinger use will depend on the size of the area, its importance for porpoises and the level and distribution of fishing effort in the area. It is likely that the net benefit will need to be assessed on a case-by-case basis. It is possible that larger areas could encompass both porpoises and pingered gill net fisheries at the same time provided the fishery only occupied parts of it. Pinger use in small areas could, however, reduce the number of porpoises in the area that had initially

been established for their conservation. Clearly, some balance is required, though high levels of bycatch should generally be considered a less desirable outcome than some degree of displacement.

The results obtained from the experiments reported here are important in relation to pinger use in porpoise protected areas and for general use of pingers. The experiment revealed that habituation can be avoided by varying signals and the signal type and area affects the pinger effect. All these aspects need to be considered before management plans are drawn up to include pingers as a conservation measure in protected areas.

Concluding Remarks

From a porpoise conservation point of view, the ideal pinger is one that has a very high efficiency in reducing bycatch, habituation only to a point where porpoises are still kept at a safe distance from the nets, and a very small exclusion zone. At the moment, such considerations are not included in the legislation on pinger use in the European Union or in the United States. According to EU Council Regulation 812/2004 (EC 2004), pingers are permitted if they live up to some very basic technical specifications and it is not required that they have been proven to be efficient in reducing bycatch. A manager or a fisherman trying to decide which pinger to use will probably opt for the least expensive, which is not necessarily the most effective.

Conducting traditional bycatch reduction experiments with pingers can be very costly, so comparing the effectiveness of different types and brands of pingers is not something that is easily undertaken. Thus, finding a less costly way of comparing pingers would be very helpful. We believe that the method used in the experiments reported here, *i.e.,* using arrays of click detectors, represents such a method. However, in the clear light of hindsight, we recommend that such experiments should include as a minimum the following elements:

- An array designed to avoid any spurious results stemming from interactions between porpoise travel directions and array design.
- Click detectors that ideally are able to determine the relative position of the porpoises recorded.
- Measurements of background noise levels at each click detector position.
- Measurements of received sound level of the pinger at each click detector position.
- Sufficient time span of the experiment to identify significant habituation effects.

The results from such well-planned and well executed experiments with both existing and new pinger types and brands would be invaluable for both managers and fishermen in reducing bycatch with the smallest possible adverse side-effects.

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Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12552/suppinfo.
Appendix S1. Raw click and time-series of the data.