

Pingers reduce the activity of Burmeister's porpoise around small-scale gillnet vessels

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ABSTRACT: Incidental mortality (bycatch) in gillnet fisheries is a major threat to many cetacean populations. Acoustic alarms or pingers are a widely adopted management tool used to deter dolphins and porpoises from nets; however, their efficacy is largely species- and fishery-dependent. As such, results from experimental trials may have limited transferability to poorly studied species or fisheries. Here, we investigated the effect of pingers on the behaviour of Burmeister's porpoise *Phocoena spinipinnis* in the vicinity of the Peruvian small-scale driftnet fleet. Over a 4 yr period (2009–2012), 116 control (without pingers) and 94 experimental (with pingers) fishing sets were observed, and porpoise acoustic activity around nets was recorded using passive acoustic loggers (C-PODs). We modelled variation in detection rates as a function of pinger use and habitat covariates, and found that in regions of preferred habitat associated with cooler (17–18°C), shallow waters (within the 100 m isobath), the use of pingers lead to an 86 % reduction in porpoise activity around nets. Our results suggest that pingers are likely to be particularly effective at deterring Burmeister's porpoises from fishing nets, and given the vast capacity of this and other fleets in the region, may substantially reduce mortality. This study also emphasizes the potential of passive acoustic monitoring to determine the effectiveness of bycatch mitigation measures, both for species for which visual observations are scarce, and also in regions where gathering statistically meaningful bycatch rates is logistically challenging.

KEY WORDS: By-catch mitigation · Artisanal fisheries · Behavioural avoidance · Acoustic alarm · Passive acoustic monitoring · Marine mammal · *Phocoena spinipinnis* · C-POD · Peru

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1. INTRODUCTION

Incidental capture (bycatch) of marine mammals in gillnet fisheries is recognized as their most serious global threat, with hundreds of thousands of individuals estimated to be killed each year (Read et al. 2006, Reeves et al. 2013). Several management strategies have been proposed to reduce interactions, including time–area fishery closures (e.g. Murray et al. 2000), modifications to fishing gear (e.g. Trippel et al. 2003) or the use of sound-emitting devices called acoustic alarms or pingers (e.g. Kraus et al. 1997).

While it is widely acknowledged that effective fisheries management is best achieved through multiple interventions (Read 2013, van Beest et al. 2017), the use of pingers is the most widely adopted measure, likely due to its perceived lower cost, and because it does not require drastic changes to fishing behaviour or gear (Dawson et al. 2013). Indeed, since the early 2000s, pingers have been mandated in numerous fisheries, including in the California–Oregon driftnet fishery (Barlow & Cameron 2003) and the Gulf of Maine bottom-set gillnet fishery (Read 2013), both in the USA, as well as in many gillnet fisheries within

the European Union (Kastelein et al. 2007, Sørensen & Kindt-Larsen 2016).

Pingers emit intermittent sounds, mostly in the frequency range 10–130 kHz, with the aim to alert animals to the presence and location of nets. They have been shown to substantially reduce bycatch rates of many cetacean species, including harbour porpoises *Phocoena phocoena* (Kraus et al. 1997, Trippel et al. 1999, Palka et al. 2008, Larsen & Eigaard 2014) and several species of dolphins and beaked whales (Bordino et al. 2002, Barlow & Cameron 2003, Carretta et al. 2008). Concurrently, studies of behavioural responses have proved useful in determining the mechanisms by which pingers reduce entanglement (Cox et al. 2001, Leeney et al. 2007, Hardy et al. 2012, Kyhn et al. 2015, Kindt-Larsen et al. 2019); these are particularly informative for regions, fisheries, or species where it is logistically challenging to generate sample sizes large enough to determine statistically significant changes to bycatch rates, for example where the bycatch rate of a particular species is low (Dawson et al. 1998, 2013).

Several decades of study have indicated that the efficacy of pingers is largely case- or species-specific, often linked to the experimental protocol or operational characteristics of the fishery, as well as the behaviour of species studied (reviewed in Dawson et al. 2013). For example, while pingers elicit aversive behaviours in harbour porpoises which are largely consistent across studies (Cox et al. 2001, Culik et al. 2001, Carlström et al. 2009, but see ICES 2018), results have been mixed for other species such as Hector's *Cephalorhynchus hectori* and bottlenose dolphins *Tursiops truncatus* (Stone et al. 1997, 2000, Cox et al. 2004, Leeney et al. 2007, Waples et al. 2013, Snape et al. 2018). In addition, while experimental studies allow researchers to control for potentially confounding operational or environmental factors (Northridge et al. 2017), results may not always be scaled up to real fishery situations, in part due to logistical, political or economic factors, such as a lack of compliance or inappropriate use of gear (Cox et al. 2007, Carretta & Barlow 2011, Dawson et al. 2013, Read 2013) or high levels of ambient noise (Hardy et al. 2012). As experiments may have limited transferability to poorly studied regions or species, studying animal behaviour in appropriate fishery settings is crucial for understanding the effectiveness of particular interventions (Barlow & Cameron 2003, Dawson et al. 2013, Martin & Crawford 2015).

The small-scale driftnet fishery in Peru has among the highest bycatch rates of small cetaceans of any fishery, with an estimated annual (incidental and

directed) take of 10 000–20 000 dolphins and porpoises (Read et al. 1988, Van Waerebeek & Reyes 1990, 1994, Mangel et al. 2010); yet, little is known about its impact on local small cetacean populations. Indeed, there is widespread concern about the population status of Burmeister's porpoise *Phocoena spinipinnis* (Jefferson & Curry 1994, Reeves et al. 2005), a little-known porpoise endemic to South America. It overlaps with fisheries throughout most of its range (Jefferson & Curry 1994, Clay et al. 2018), and the Peruvian population has been intensely harvested since at least the 1960s by small-scale fishers (Clarke 1962, reviewed in Read et al. 1988). In the 1970s, it was estimated that over 100 tonnes of porpoises were sold in fish markets each year (Read et al. 1988 and references therein). In the late 1980s and early 1990s, annual catches were estimated to be at least a few thousand individuals based on direct accounts of landings (Van Waerebeek & Reyes 1994). More recently, port inspections and on-board fisheries observers have revealed a decrease in the composition of catch relative to other cetaceans, suggesting long-term population declines (Van Waerebeek & Reyes 1994, Mangel et al. 2010, Tzika et al. 2010). While no formal population assessments have been made, Burmeister's porpoise has recently been uplisted from 'Data Deficient' to 'Near Threatened' by the International Union for the Conservation of Nature, predominantly as a result of ongoing threats from fisheries in Peruvian waters (Félix et al. 2018).

Here, we expanded upon a recent study which used passive acoustic monitoring from a small-scale fisheries platform to document the distribution and habitat use of Burmeister's porpoise in Peruvian waters in the absence of pingers (Clay et al. 2018), to test for an effect of pinger use on porpoise detections. The study took place as part of a larger experimental trial comparing bycatch rates of control (without pingers) and experimental (with pingers) fishing sets (Mangel et al. 2013). Pingers significantly reduced bycatch rates of small cetaceans when species were grouped together, however differences were not significant when each species was analyzed separately (Mangel et al. 2013). We tested for differences in acoustic detections between control and experimental sets while controlling for variation according to habitat characteristics. Due to their close relatedness to harbour porpoises and similarly shy nature (based on anecdotal evidence; Van Waerebeek et al. 2002), we predicted that pingers would elicit a comparable behavioural response in Burmeister's porpoises (Carlström et al. 2009, Hardy et al. 2012, Kindt-Larsen et al. 2018).

2. MATERIALS AND METHODS

2.1. Study design and data collection

The study was conducted from 2 small-scale surface driftnet fishing vessels, with trips monitored out of the port of Salaverry (8° 14' S, 78° 59' W) in northern Peru, between April 2009 and December 2012. The fishery targets elasmobranchs, predominantly smooth hammerhead *Sphyrna zygaena*, blue *Prionace glauca*, short-fin mako *Isurus oxyrinchus* and common thresher *Alopias vulpinus* sharks and eagle rays *Myliobatis* spp., yet many other species are incidentally caught, including cetaceans, sea turtles, seabirds and billfish (Mangel et al. 2010, Alfaro-Shigueto et al. 2010). Multifilament nets, which are approximately 1.5–2 km long, 14 m in height and have a stretched mesh of 19.1–25.4 cm, are set at the sea surface during late afternoon and recovered the next morning. Fishing trips last 8.2 d on average, with a mean 7.4 sets trip⁻¹ and mean net soak time of 13 h (Mangel et al. 2010, 2013). Small cetacean meat is regularly used as bait as it is perceived by fishers to improve shark catch, and is obtained both by har-

pooning animals at the start of the trip, or from bycatch during the trip (Mangel et al. 2010). Detailed descriptions of the fishery are provided by Alfaro-Shigueto et al. (2010) and Mangel et al. (2010), and the pinger trial in Mangel et al. (2013).

A visual depiction of the experimental setup is provided in Fig. 1. Monitored vessels did not deviate from normal procedures or fishing locations. Throughout a fishing trip, nets were set either continuously with pingers in experimental sets (n = 6 trips), without pingers in control sets (n = 11), or alternated between the 2 treatments over the course of a fishing trip (n = 19). The 2 vessels were always at least 5 km apart (mean: 44 km) when fishing, and fishing sets within trips were separated temporally (mean: 11 h) and spatially (mean: 30 km), so for trips which alternated between the 2 treatments, it was unlikely that pinger use directly influenced subsequent control sets. Dukane Netmark™ 1000 pingers, which have been used in numerous trials (e.g. Kraus et al. 1997, Trippel et al. 1999, Barlow & Cameron 2003), were attached to the lead-line of the net at a depth of approximately 14 m and with a spacing of 200 m (Mangel et al. 2013). The pingers emit a tone of

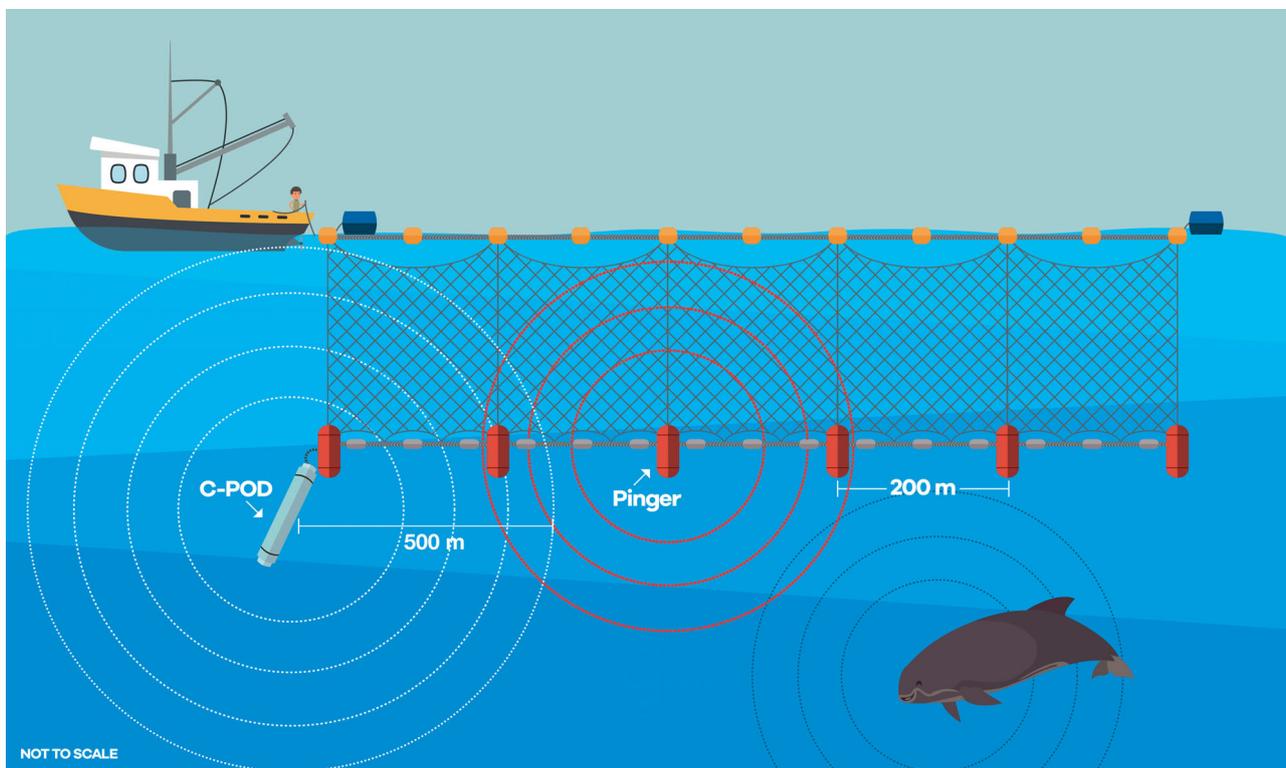


Fig. 1. Experimental design, showing a fishing net with pingers spaced every 200 m along the lead-line of the net, along with a passive acoustic logger (C-POD) deployed at the vessel end of the set. Both the maximum area ensounded by pingers (red circle) and the maximum detection range of Burmeister's porpoises *Phocoena spinipinnis* by the C-POD (white circles), are hypothesized to be similar (ca. 400–600 m), based on studies of harbour porpoises. The setup for control sets was the same, except that pingers were not present. Note that there are portions of the net that are not detected by the C-POD

300 ms duration every 4 s and have a fundamental frequency of 10–12 kHz, with a source level range of 120–146 dB. Battery levels were checked before each trip and after every set to make sure the pinger was functioning. For 3 experimental sets, pingers were deemed not to be working, and so these were removed from analyses.

A passive acoustic logger (C-POD) was deployed at each fishing set by attachment to the lead-line after the net was set and recorded acoustic activity from a depth of approximately 12–14 m for the set duration. Each device was recovered at the start of the following haul (*sensu* Clay et al. 2018). In total, 6 C-PODs were used throughout the study, and all devices were used both in the presence and absence of pingers, but no more than one was used at the same time by the same vessel. Fisheries observers were trained in C-POD deployment and maintenance, and at the start of each set, recorded the GPS position of the vessel, the sea surface temperature (SST) with a handheld Enviro-Safe[®] thermometer and sea state using the Beaufort scale (Clay et al. 2018). While no studies have documented the detection range of C-PODs for Burmeister's porpoise, for harbour porpoise the maximum detection range is around 400–650 m (Tougaard et al. 2006, Culik et al. 2015). This is broadly similar to the maximum range at which pingers are audible to harbour porpoise, which is thought to be around 450–600 m (Trippel et al. 1999, Carlström et al. 2002, Culik et al. 2015, Kindt-Larsen et al. 2019). Thus, for sets with pingers it was assumed C-PODs were logging echolocation behaviour of porpoises largely within the area ensonified by pingers (see Fig. 1). However, we note that the audible ranges of C-PODs and pingers are likely to be highly variable and dependent on device specifications, porpoise orientation and environmental factors such as ambient noise levels, sea state, water depth, temperature and bottom topography (Carlström et al. 2002, 2009, Tregenza 2014, Culik et al. 2015). Although several species of dolphins (predominantly, common *Delphinus capensis*, dusky *Lagenorhynchus obscurus* and bottlenose dolphins *Tursiops truncatus*) are regularly observed around and caught by Peruvian drift-net vessels (Mangel et al. 2010, Clay et al. 2018), we did not consider the effect of pingers on dolphin activity in this study because the detection range of dolphins by C-PODs is much larger (ca. 1000 m; Philpott et al. 2007) than the audible ranges of pingers to animals, and it is also currently challenging to distinguish between different delphinid species using C-PODs.

2.2. Data processing

C-POD files were downloaded and processed using the accompanying C-POD.exe v.2.032 software (Tregenza 2014). The in-built click train detection algorithm identifies cetacean click trains as well as other noise sources (such as boat sonar), and differentiates the former into narrow-band high frequency (NBHF) echolocation of porpoises and the broadband clicks of many dolphin species. We used both the standard KERNO and the GENENC encounter classifier, the latter of which was developed specifically to differentiate between NBHF and broadband echolocation in regions where dolphins and porpoises coexist (Tregenza 2014, see Clay et al. 2018 for further details). Only click trains classified as medium or high quality ('Cet Mod' and 'Cet Hi') were selected, and clicks were inspected visually; this process was conducted blind to treatment type, in order to remove false positives (Tregenza 2014, Clay et al. 2018). Data were exported for each fishing set as detection positive minutes (DPM), which is a standard measure of time spent around C-PODs by echolocating animals, and which also represents relative density (Tregenza 2014, Williamson et al. 2016). Additionally, as there is evidence harbour porpoises avoid bottlenose dolphins in parts of their range (e.g. Jacobson et al. 2015, Nuutila et al. 2017), we hypothesized that the presence of dolphins may also influence Burmeister's porpoise distribution. As a result, for each set we noted the presence or absence of broadband (i.e. dolphin) echolocation to include as a covariate in models.

2.3. Statistical analysis

We modelled the effect of pinger treatment on porpoise DPM using generalized linear mixed models (GLMMs). Burmeister's porpoise distribution and habitat use is influenced both by static and dynamic features, in particular bathymetric depth (hereafter depth) and SST (Clay et al. 2018); as such, we included these variables in models to account for spatio-temporal variation in activity not linked to pinger use. For each fishing set location we extracted depth, obtained from the General Bathymetric Chart of the Oceans (GEBCO, www.gebco.net), in ArcGIS v.10.1 (ESRI). Two sets were removed prior to analysis, as GPS coordinates were not recorded. Also, 2 control sets with porpoise bycatch had notably high acoustic activity (see Table 1; Clay et al. 2018). As we could not be sure whether high activity indicated increased time spent around nets or was the result of

animals vocalizing while drowning in the net, these 2 sets were also removed.

Covariates initially considered were depth, SST, sea state, and the factors treatment (with or without pingers), the presence/absence of dolphin activity, season (which was split into quarters: 1 = January–March; 2 = April–June; 3 = July–September; 4 = October–December) and bait use (yes or no) (Mangel et al. 2010, 2013, Clay et al. 2018). In order to reduce the number of parameters included in minimum adequate models and because some variables contained missing values, we assessed the importance of the covariates sea state, bait use and dolphin presence, as standalone predictors of DPM in models and compared these with null models using Akaike's information criterion (AIC) scores. Their inclusion resulted in models with higher AIC scores, so the 3 variables were not considered for further analysis. The resulting minimum adequate model included the covariates quarter, treatment, depth, SST as a linear and quadratic variable (to model non-linear relationships) and the log-transformed duration of time recorded for each set as an offset. We also included the 2-way interactions between treatment and habitat covariates (depth and SST) to test the prediction that pingers would elicit a greater response in regions where they are more likely to be detected, i.e. in regions of favourable habitat. Generalized variance inflation factors (GVIFs) were used to assess collinearity between variables using a cut-off of 3 (Zuur et al. 2009). Depth was square-root transformed to confirm to the assumption of normality, and depth and SST were standardised before inclusion by subtracting the mean and dividing by the standard deviation. We initially considered several combinations of variables as random effects: trip identity, year, C-POD identity, as well as trip identity nested within year and trip identity nested within C-POD identity. C-POD units were substituted in and out of the trail at various stages while other devices were undergoing maintenance. As a result, C-POD identity and year were correlated so the two were never included in the same model. We compared models with different random effect structures using AIC, and the best supported model (i.e. with the lowest AIC score) was that with just trip identity as the random effect. As other variables explained negligible variance as random effects, they were removed from subsequent models.

We initially modelled the response variable (i.e. DPM) using a Poisson error distribution; however, visualization of model fit revealed that the data were overdispersed, i.e. the variance was larger than the

mean; as such, we chose a negative binomial distribution with a log link (Zuur & Ieno 2016), in the R package 'glmmTMB' (Magnusson et al. 2017). As there were a few very large data points, likely reflecting the clustered spatio-temporal distributions of animals and the inherently large variation in acoustic detections (Williamson et al. 2016), we considered 2 parameterizations of the negative binomial according to the relationship between the mean (μ) and variance (σ^2): (1) where the variance increases linearly with the mean, as $\sigma^2 = \mu(1 + \alpha)$, with $\alpha > 0$; and (2) where the variance increases in a quadratic manner with the mean, as $\sigma^2 = \mu(1 + \mu / \theta)$, where $\theta > 0$ (Hardin & Hilbe 2007). For the majority of fishing sets, no porpoise activity was detected (over 80% of observations were zeros), and so we also included a zero-inflation parameter, which describes the probability of observing extra zeros that are not generated by the negative binomial (conditional) model (Zuur et al. 2009). We compared model fit for both parameterizations of the negative binomial model by examining overdispersion and plotting residuals against fitted values and covariates (Zuur & Ieno 2016), and we assessed model complexity by comparing AIC values (Harrison et al. 2018). The zero-inflated negative binomial with variance which increased linearly with the mean was chosen as the model that fit the data best (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m626p197_supp.pdf) (Zuur et al. 2009, Zuur & Ieno 2016). Model selection was conducted for all possible combinations of predictors, whereby models were ranked by AIC values according to their degree of parsimony. Where multiple models were ≤ 2 AIC units of the best supported model, the most parsimonious model (i.e. that with the fewest parameters) was chosen (Burnham & Anderson 2004). We repeated our analysis (above) on a much reduced sample size of sets occurring within the 100 m isobath to determine if the results were consistent if we only considered areas where porpoises were most likely to be detected. Unless otherwise specified, all analyses were conducted in the statistical program R v.3.3.1 (R Core Team 2014) and means are presented \pm SE.

3. RESULTS

Over the study duration (April 2009–December 2012), 210 sets were observed in 25 calendar months; 116 control sets over 30 trips and 94 experimental sets over 25 trips (Table 1). Effort was not spread evenly across seasons (Fig. 2a) and logistical con-

Table 1. Characteristics of control (no pingers) and experimental (with pingers) fishing sets observed during the study, and Burmeister's porpoise *Phocoena spinipinnis* activity recorded by passive acoustic loggers (C-PODs) deployed on fishing nets. Values are numbers or means \pm SE (range)

	Treatment	
	Control (no pingers)	Experimental (pingers)
No. of trips	30	25
No. of sets	116	94
Depth (m)	451 \pm 66 (1–4173)	506 \pm 68 (22–3584)
Sea surface temperature ($^{\circ}$ C)	20.0 \pm 0.2 (15–25)	20.6 \pm 0.2 (16–25)
No. of sets with porpoise bycatch	2	0
C-POD recording duration (h)	11.0 \pm 0.3 (1.8–18.9)	10.2 \pm 0.3 (1.5–14.9)
No. of porpoise positive sets	25	11
Detection positive minutes (DPM) h ⁻¹	0.0119 \pm 0.0037 (0–0.2999)	0.0005 \pm 0.0002 (0–0.0129)

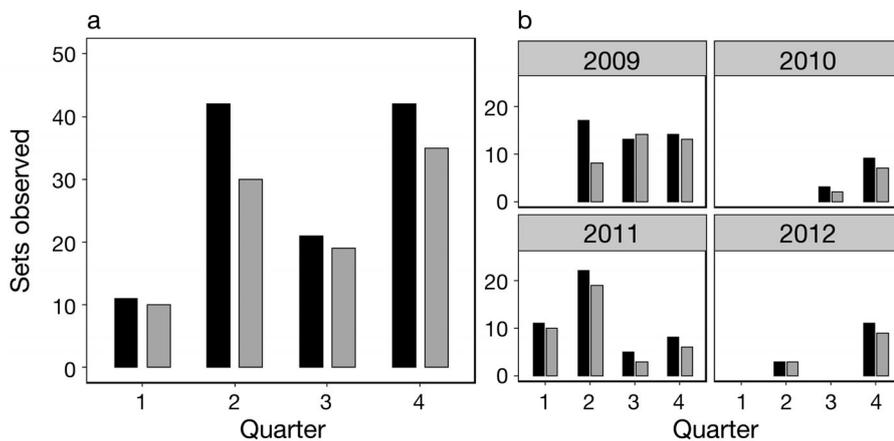


Fig. 2. Distribution of control (no pingers, black) and experimental (pingers, grey) fishing sets observed by quarter for all years (a) together and (b) separately, from the port of Salaverry in northern Peru, over the study duration. Quarter 1: Jan–Mar; 2: Apr–Jun; 3: Jul–Sep; 4: Oct–Dec

straints prevented monitoring in the first half of 2010 and parts of 2012 (Fig. 2b). As a result, a greater number of sets were observed in April–June and October–December (2nd and 4th quarters, respectively) (Fig. 2a), yet the ratio of control to experimental sets was fairly similar across years and seasons (Fig. 2b). C-PODs attached to fishing nets logged a total of 2236 h (93.2 d): 1279 and 957 h for control and experimental sets, respectively, with a mean of 11.0 ± 0.3 and 10.2 ± 0.3 h set⁻¹, respectively. A greater proportion of control (22%, n = 25) than experimental (12%, n = 11) sets recorded porpoise occurrence (i.e. at least 1 click train detected; Table 1). Two porpoise bycatch events were recorded in control sets, while no porpoises were caught in experimental sets. While there appeared to be a greater number of control than experimental sets in near-shore waters (Fig. 3), there was no significant difference in the depth of control and experimental sets (Wilcoxon rank-sum test,

$W = 4811.0$, $p = 0.206$; Table 1). In contrast, control sets were located in slightly cooler waters than experimental sets (by 0.6° C; Wilcoxon rank-sum test, $W = 4305.5$, $p = 0.013$; Table 1).

The interaction between treatment and at least one habitat covariate was included in the 6 best supported models explaining variation in echolocation activity, indicating a habitat-related effect of pingers on porpoise behaviour (Table 2). The most parsimonious model included the interaction between depth and treatment, the linear relationship with SST and quarter. Echolocation activity decreased with increasing depth for both

treatments, such that little activity was detected in waters deeper than 100 m (Figs. 3 & 4). However, the slope of the relationship between depth and activity in the absence of pingers was much steeper than with pingers (Table 2, Fig. 4). Regardless of treatment type, porpoise DPM was higher in cooler waters (17 – 18° C), and marginally higher in October–March than other months (Table 2).

Within core porpoise habitats (identified as depth ≤ 100 m and SST $\leq 18^{\circ}$ C), C-PODs attached to nets with pingers recorded significantly less acoustic activity than without pingers (Table 2). Indeed, pinger use resulted in a mean modelled 85.7% (53.2–94.9% depending on the depth) reduction in activity around fishing nets within the 100 m isobath, with 2.78 DPM h⁻¹ (95% CI: 0.19–5.36) for control sets and 0.40 DPM h⁻¹ (95% CI: 0.00–0.88) for experimental sets (Fig. 4c). Wide confidence intervals (CIs) around estimates, particularly for control sets, highlight

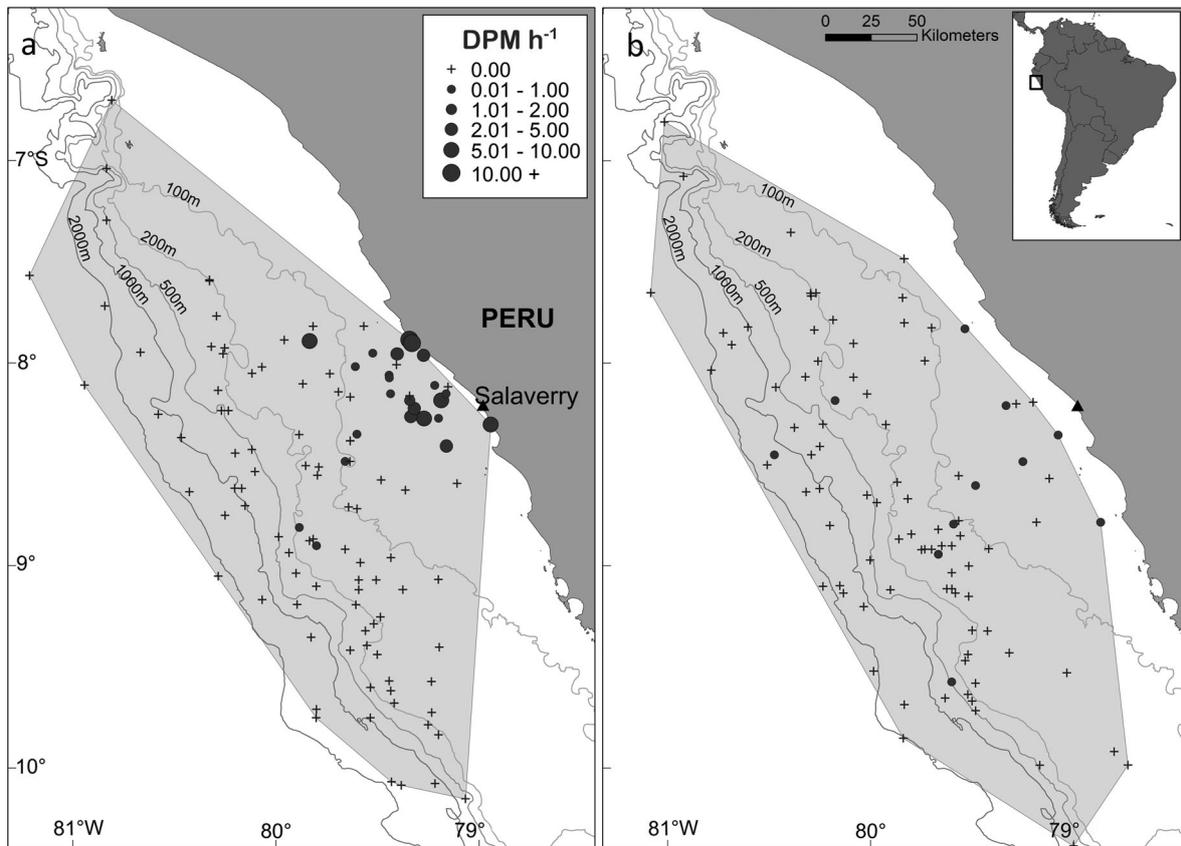


Fig. 3. Locations and activity (detection positive minutes [DPM] h⁻¹) of Burmeister's porpoise *Phocoena spinipinnis* around (a) control (without pingers) and (b) experimental (with pingers) fishing sets observed between April 2009 and December 2012 from the port of Salaverry in northern Peru (triangle). Locations of sets where small cetaceans were recorded as present and absent are shown by circles and crosses, respectively; circle size represents porpoise activity. Grey lines: 100, 200, 500, 1000 and 2000 m isobaths

large natural variability in detection rates (Fig. 4); indeed, regardless of model structure, residual plots showed that there was still some variance which was not sufficiently explained by our covariates (Fig. S1). We repeated our analysis just considering sets within the 100 m isobath, and the best supported model retained the covariates depth, treatment and quarter (Table S1, Fig. S2), emphasizing that differences between the 2 treatment types were robust to sampling effects.

4. DISCUSSION

Our experimental study in an operational fishery revealed that pingers substantially reduce the acoustic activity of Burmeister's porpoises in the vicinity of gillnets. We found that porpoises were less likely to be detected around experimental than control fishing sets. In addition, DPM, a proxy for time

spent by echolocating animals around C-PODs, was markedly reduced (by 86 %) in regions of preferred habitat, despite large variation in detection rates between fishing sets. Burmeister's porpoise is predominantly coastal and prefers cooler waters in the north of its range (Van Waerebeek et al. 2002, Mangel et al. 2010, Clay et al. 2018), and as expected, for both control and experimental sets, the number of DPM reduced with increasing depth and SST. Indeed, acoustic activity of porpoises was restricted to a fairly narrow coastal region where the majority of foraging appears to occur (<100 m depth and <50 km from the shore; Clay et al. 2018). Our modelling approach enabled us to control for unequal sampling in time and space as well as variation in detections along an oceanographic gradient. Yet, regardless of whether we included all sets or just those situated in preferred porpoise habitat (within the 100 m isobath), we found that acoustic detections were consistently lower in the presence of pingers.

Table 2. Generalized linear models testing for the effect of treatment (sets with or without pingers) and habitat variables on Burmeister's porpoise *Phocoena spinipinnis* activity (detection positive minutes [DPM] h⁻¹). (a) Selection of the top 10 best supported models; the most parsimonious model is in **bold**. (b) Parameter estimates (\pm SE) on a log-link scale of the most parsimonious model. AIC: Akaike's information criteria; logLik: log likelihood; Δ AIC: change in AIC from the best supported model. Depth and sea surface temperature (SST) were standardized by subtracting the mean and dividing by the standard deviation. SST was modelled as both a linear (SST) and a quadratic (SST²) variable

(a)				
Covariates	AIC	logLik	df	Δ AIC
Treatment \times (depth + SST + SST ²) + quarter	351.91	-161.96	14	0.00
Treatment \times depth + SST + SST ² + quarter	352.53	-164.16	12	0.42
Treatment \times depth + SST + quarter	352.89	-165.44	11	0.98
Treatment \times (depth + SST) + quarter	352.95	-164.48	12	1.04
Treatment \times depth + SST + SST ²	354.79	-168.39	9	2.88
Treatment \times (depth + SST + SST ²)	355.63	-166.82	11	3.72
Depth + SST + SST ²	356.41	-171.20	7	4.50
Depth + SST + SST ² + quarter	356.93	-168.46	10	5.01
Treatment + depth + SST + SST ² + quarter	357.95	-167.98	11	6.04
Depth + SST + quarter	358.12	-170.06	9	6.21
(b)				
Parameter	Estimate			
Intercept (control, 1 st quarter)	-8.17 \pm 0.93			
Treatment (experimental)	1.06 \pm 0.71			
Depth	-3.60 \pm 0.71			
SST	-0.82 \pm 0.27			
Treatment (experimental):depth	2.69 \pm 0.82			
2nd quarter	-0.33 \pm 0.82			
3rd quarter	-0.70 \pm 0.86			
4th quarter	0.85 \pm 0.79			

Our study was conducted as part of a larger trial which found that pingers reduce the bycatch rate of small cetaceans (dolphins and porpoises combined) by 37% (Mangel et al. 2013). Yet this reduction was not significant when examined at the species level (Mangel et al. 2013) with 5 and 3 individuals bycaught in 195 and 156 control experimental sets, respectively. In our study, 2 and 0 porpoises were bycaught in 116 and 94 control and experimental sets, respectively, which represents a slightly lower bycatch rate. Nonetheless, through passive acoustic monitoring of fishing activity, we were able to generate large enough sample sizes to determine statistically significant differences between the 2 treatment types with lower monitoring effort (213 sets monitored here compared to 351 in Mangel et al. 2013). We emphasize that studying behaviour using passive acoustic techniques may be particularly useful in regions or fisheries where it is logistically challenging to generate large enough sample sizes to test for differences in bycatch rates (Dawson et al. 1998, 2013), or for species for which visual observations are scarce, such as

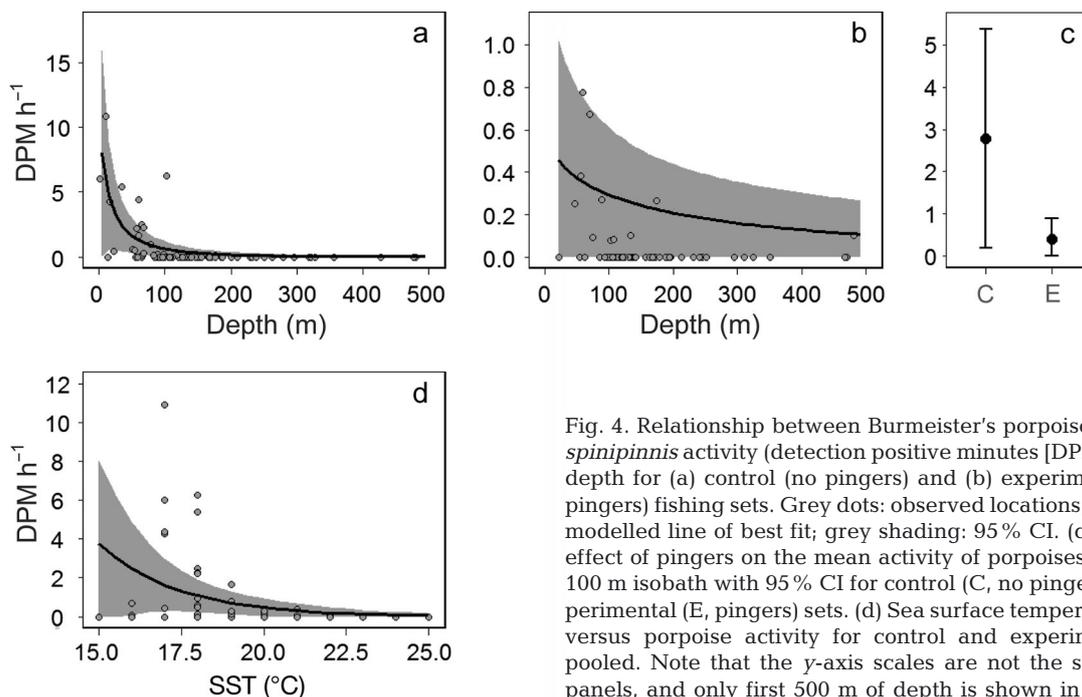


Fig. 4. Relationship between Burmeister's porpoise *Phocoena spinipinnis* activity (detection positive minutes [DPM] h⁻¹) and depth for (a) control (no pingers) and (b) experimental (with pingers) fishing sets. Grey dots: observed locations; black line: modelled line of best fit; grey shading: 95% CI. (c) Modelled effect of pingers on the mean activity of porpoises within the 100 m isobath with 95% CI for control (C, no pingers) and experimental (E, pingers) sets. (d) Sea surface temperature (SST) versus porpoise activity for control and experimental sets pooled. Note that the y-axis scales are not the same for all panels, and only first 500 m of depth is shown in (a) and (b)

the congeneric vaquita *Phocoena sinus* (Jaramillo-Legorreta et al. 2017) or finless porpoise *Neophocaena* spp. (Amano et al. 2017).

The majority of studies testing behavioural responses to pingers have focussed on harbour porpoises (reviewed in Dawson et al. 2013), while other porpoise species have mostly been neglected (Amano et al. 2017) despite evidence of long-standing interactions with gillnets (Jefferson & Curry 1994). Observational studies have consistently found that pingers displace harbour porpoises by at least one to several hundred metres from nets (e.g. Laake et al. 1998, Cox et al. 2001, Carlström et al. 2009), while passive acoustic monitoring studies have noted fewer detections (by 50–100%) in the presence of pingers (Cox et al. 2001, Carlström et al. 2009, Hardy et al. 2012, Kyhn et al. 2015). Given their similarly shy behaviour (Van Waerebeek et al. 2002, Read 2009), we predicted that pingers would elicit comparable responses in the Burmeister's porpoise to the harbour porpoise. The reduced number of detections of Burmeister's porpoise in the presence of pingers supports our initial prediction. Indeed, our results indicate that porpoises may still encounter fishing nets, but are much less likely to remain in their vicinity for long periods of time in the presence of pingers, reducing the risk of entanglement (Clay et al. 2018).

Several hypotheses have been proposed to explain the mechanisms by which pingers reduce small cetacean entanglements. One original hypothesis suggested that they encourage animals to echolocate, making them aware of the presence of the net (Kraus et al. 1997), but there has been little evidence to support this (except see Culik et al. 2015). In particular, several studies noted a drop rather than an increase in detection rates (Cox et al. 2001, Carlström et al. 2009). The most widely accepted hypothesis states that the sounds are aversive and displace animals from the vicinity of the pinger (Kraus et al. 1997, Kastelein et al. 2000, Dawson et al. 2013). This is supported by increased evidence that harbour porpoises are sensitive and show aversive responses to anthropogenic noise sources (Pirotta et al. 2014, van Beest et al. 2018). While passive acoustic techniques allowed us to monitor cetacean activity for the duration of each set, we acknowledge that our results are limited in that we were not able to observe the movements of animals in relation to nets or pingers (e.g. Cox et al. 2001). Also, gillnets were longer than the likely detection range of porpoises by C-PODs, and so presumably there were sections of the net that were not detected (Clay et al. 2018). As such, we cannot conclude that reduced DPM around experimental

nets represents displacement rather than reduced vocal activity. Nevertheless, porpoises are highly vocal, and rarely stop echolocating (for navigation, foraging and social interactions; Wisniewska et al. 2016, Sørensen et al. 2018), and so it seems unlikely that they would be present within the vicinity of pingers for such long periods of time and remain completely silent. Additionally, given porpoises produce clicks of high directionality, there is also a chance that porpoise detections could have been missed if animals were not oriented towards the C-PODs (Cox et al. 2001, Tregenza 2014); although as porpoises move in the direction of their sound beam this would imply a lower density nearer to the logger.

Recently, the conservation status of Burmeister's porpoise was uplisted from 'Data Deficient' to 'Near Threatened', principally due to ongoing fisheries interactions in Peru (Félix et al. 2018) as well as the genetic isolation of Peruvian animals from those in Argentina and Chile (Rosa et al. 2005). As such, conservation efforts focussed on the regulation of porpoise–fishery interactions are urgently required. While the number of individuals caught per trip is relatively low compared to some other species, such as common dolphins, an estimated 200 porpoises are caught each year by gillnet vessels from the port of Salaverry alone (Mangel et al. 2010). As this fleet represents only ca. 2% of gillnet vessels operating in Peru (Mangel et al. 2010, Estrella Arellano & Swartzman 2010 and references therein), it is likely that even low bycatch rates are unsustainable.

There are several outstanding issues that may need to be addressed before a fleet-wide implementation of pingers can be fully recommended (Mangel et al. 2013). Firstly, we did not consider dolphin species which are also frequently recorded as bycatch (Mangel et al. 2010) due to the challenges of species identification, and because the range at which C-PODs can detect dolphins is generally much larger than that for porpoises, meaning that C-PODs could potentially be detecting dolphins outside the range at which they hear pingers (Tougaard et al. 2006, Philpott et al. 2007). As dolphins are regularly recorded around and captured by fishing vessels (Mangel et al. 2010, Clay et al. 2018), a better understanding of how they respond to pingers is important for their conservation, particularly given that pinger-related reductions in bycatch rates were not as pronounced in this fishery as recorded elsewhere (Dawson et al. 2013, Mangel et al. 2013). Also, it is possible that pingers might temporarily exclude animals from foraging habitats (Dawson et al. 2013, van Beest et al. 2017). However, if pingers displace porpoises by sev-

eral hundred metres (Laake et al. 1998, Culik et al. 2001), based on the number of vessels that operate out of the port of Salaverry each year (Mangel et al. 2010), we estimate that the exclusion zone is likely to be less than one-quarter of 1% of the available habitat (defined as the fishing area within the 100 m isobath) at any given time. While this is a crude approximation, the real value would have to represent a much higher percentage before a significant effect of habitat exclusion on porpoise behaviour is likely. As such, it appears that in this region, the benefits of reduced mortality through the widespread use of pingers are likely to greatly outweigh their limitations. Further studies investigating the effective detection range of C-PODs and pingers using an array design (e.g. see Kindt-Larsen et al. 2019), would help establish the ideal number and spacing of pingers on nets, which may reduce both the cost to fishers and sublethal effects of noise pollution on porpoises.

As porpoises use a fairly narrow coastal region, it is possible that mitigation measures such as pingers could be focussed within this region (i.e. within the 100 m isobath). However, long-term trials of pingers in fisheries elsewhere indicate that they are unlikely to be adopted or used appropriately unless mandated (Dawson et al. 2013). Notwithstanding, there are complex socio-economic issues in the region such as poverty, a lack of governance of small-scale fisheries and direct take of small cetaceans both for bait and for domestic consumption (Mangel et al. 2010, 2013, Alfaro-Shigueto et al. 2010). For example, while dolphins are generally used as bait, porpoises are preferred for human consumption (70% consumed on the boat or at home; Mangel et al. 2010). Nonetheless, over 40% of small cetacean bycatch is discarded unused which suggests bycatch is often unwelcome (Mangel et al. 2010), and that there is scope to reduce entanglement rates substantially. This is supported by anecdotal evidence that fishers are generally receptive to the use of pingers (Pro Delphinus pers. comm.). Successful management of fishing practices is likely to be best achieved through cultural changes or economic incentives, such as providing fishers with alternatives to using cetacean bait. While the cost of equipping a net with pingers (over USD 1000) is substantial, an incentive-based approach, either through domestic eco-certification programs or external pressure through legislative frameworks such as the US Marine Mammal Protection Act (MMPA), might contribute towards uptake of mitigation if fishers are able sell their products at higher profit margins (Williams et al. 2016, Lent & Squires 2017).

5. CONCLUSIONS

Our finding that pingers substantially reduce porpoise detections suggests that they may be effective at reducing porpoise entanglements in the Peruvian small-scale driftnet fishery, and potentially other gillnet fisheries throughout South American waters. Given the multi-species nature of bycatch in Peruvian small-scale (artisanal) fisheries, further investigations into the effect of pingers on the behaviour of sympatric dolphin species would be highly advantageous. Nonetheless, the scale of bycatch in small-scale fisheries in the south-east Pacific (Mangel et al. 2010, Alfaro-Shigueto et al. 2018) indicates that the immediate and direct benefits of reduced mortality through use of pingers are likely to be substantial.

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