



Concurrent bycatch and population assessments of Burmeister's porpoises in northern Peru reveal unsustainable levels of mortality

Clara Ortiz-Alvarez^{1,2,*}, Ruth Ortés-Villauriz³, Jeffrey C. Mangel^{2,4}, Joanna Alfaro-Shigueto^{2,5}, Sonja Heinrich¹

¹Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, East Sands, St Andrews KY16 8LB, United Kingdom

²ProDelphinus, Lima 15074, Perú

³Marine Biological Research Centre, University of Southern Denmark, Kerteminde 5300, Denmark

⁴Centre for Ecology and Conservation, University of Exeter, Cornwall TR10 9FE, United Kingdom

⁵Grupo de Investigación 'Soluciones para la Biodiversidad', Carrera de Biología Marina, Universidad Científica del Sur, Lima 15067, Perú

*Corresponding author. Sea Mammal Research Unit, Scottish Ocean Institute, University of St. Andrews, East Sands, St Andrews KY16 8LB, UK.

E-mail: caoa1@st-andrews.ac.uk

Abstract

Fisheries-related mortality has been a threat to Burmeister's porpoises in Peru for decades. However, the magnitude of its impacts on porpoise populations has not been assessed. This study reports the first concurrent abundance and bycatch estimates to evaluate the status of Burmeister's porpoises in northern Peru. We conducted systematic line transect surveys with 770 km of effort and concurrent towed passive acoustic monitoring as well as semi-structured interviews with gillnet fishers from Salaverry. We recorded 87 porpoise sightings during 9 survey days in February 2023 using a repurposed gillnet fishing vessel and trained observers. Using density surface modelling of the line transect sighting data Burmeister's porpoise abundance was estimated at 1 696 individuals (CV = 0.23) in the 3 500 km² study area. Porpoise distribution showed a spatial gradient with highest densities close to shore (<25 km) and in shallow waters (≤50 m). Visual and acoustic detections and fishers' descriptions of bycatch areas matched closely in space. The majority (66%) of fishers interviewed (*n* = 32) reported porpoise bycatch in the previous year. For the area matching the abundance survey, the estimated mean bycatch rate per vessel was 6 porpoises/year which equates to an annual bycatch of 420 (95% CI: 210–700) porpoises when scaled to the entire artisanal gillnet fishing fleet of Salaverry. We then considered the potential biological removal reference limit to put into context abundance and bycatch estimates in the study area which shows that current bycatch rates by far exceed sustainable limits and highlights the urgent need for bycatch mitigation measures.

Keywords: Burmeister's porpoise; abundance; bycatch; Peru; interviews; density surface modelling

Introduction

Off the coast of Peru, the upwelling ecosystem of the Humboldt Current System (HCS) is a highly productive but oceanographically variable region exposed to El Niño Southern Oscillations (Swartzman et al. 2008, Gutiérrez et al. 2016). The HCS supports important megafauna and large artisanal fisheries of around 18 000 vessels that employ over 50 000 people and represent the main source of marine products for domestic consumption (Castillo Mendoza et al. 2018, Salazar et al. 2020). These artisanal fleets overlap substantially with marine megafauna which has led to high levels of human-induced mortality of small cetaceans, sea turtles, seabirds, and non-target elasmobranchs from accidental catch (bycatch) and intentional take for bait and wild meat (Awkerman et al. 2006, Mangel et al. 2010, Alfaro-Shigueto et al. 2011, Pajuelo et al. 2018).

Small cetaceans have been subject to exploitation for at least the last five decades in Peru with some of the highest levels globally of documented fisheries-related mortalities (Read et al. 1988, Van Waerebeek and Reyes 1994b, Mangel et al. 2010). Reports from the early 1990's suggested that

around 15 000–20 000 cetaceans were killed per year, with the highest bycatch rates in ports located in northern and central Peru (Van Waerebeek and Reyes 1994b). Gillnets have been the main fishing gear involved in small cetacean bycatch in Peru (Van Waerebeek et al. 2002, Mangel et al. 2010, Campbell et al. 2020) and are used by around 7 900 vessels (~40%) of the artisanal fishing fleet, targeting over 200 coastal and pelagic fish species (Castillo Mendoza et al. 2018). Even though gillnets are set along the Peruvian coastline, they are most frequently used by fishers from northern and central ports (6°24'S–13°20'S) (Castillo Mendoza et al. 2018). The gillnet fishing fleet from one northern port, Salaverry (8°13'S, 78°58'W), was estimated to catch around 2 400 small cetaceans (CI: 1 092–4 303) per year from 2002 to 2007 (Mangel et al. 2010). Salaverry port harbours about 140 gillnet fishing vessels (Castillo Mendoza et al. 2018). This port has a long history of high bycatch of small cetaceans (Van Waerebeek et al. 1997, Campbell et al. 2020) and has been a focal area for studies of small cetaceans and their interactions with fisheries (Mangel et al. 2010, Mangel et al. 2013, Clay et al. 2018).

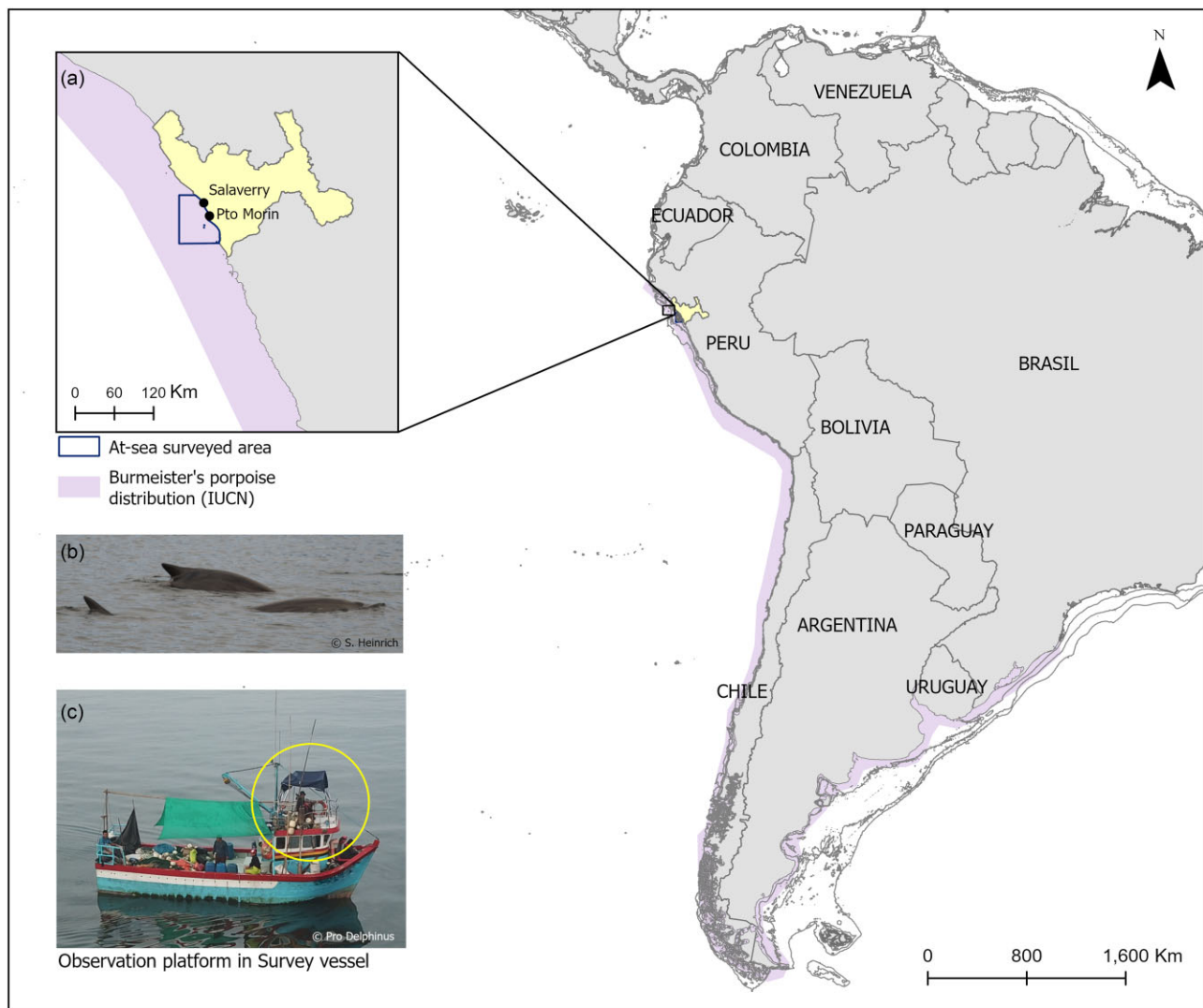


Figure 1. Distribution range of Burmeister's porpoise in South America (shade area) taken from the IUCN website (Félix et al. 2018). (a) Inset map shows the study area off Puerto Morin and Salaverry port (polygon), (b) photo of three Burmeister's porpoises to illustrate species characteristics; note the photo was taken in southern Chile (by S. Heinrich), and (c) observation platform (circle) on the repurposed fishing vessel used during at-sea surveys.

The Burmeister's porpoise (*Phocoena spinipinnis*) is one of the main small cetacean species affected by bycatch in the gillnet fisheries in Peru, with reports of 200–600 porpoises caught per year from each of the five ports that were assessed (Van Waerebeek and Reyes 1994a, Van Waerebeek et al. 1997, Mangel et al. 2010). Burmeister's porpoises occur in neritic and continental shelf waters from Peru to southern Brazil (Fig. 1). There are no abundance estimates for Burmeister's porpoises anywhere, but bycatch has been reported throughout their range (Reyes and Brownell, Jr 2025). The species has been classified as Near Threatened on the IUCN Red List of Species, but the Peruvian porpoise population would likely qualify for a more severe threat listing if more information was available (Félix et al. 2018).

Burmeister's porpoises are cryptic and challenging to observe at sea given their unobtrusive surfacing behaviour and backward sloping small dorsal fins. It is thus no surprise that they are one of the least observed small cetacean species in South America. Based on mostly incidental sightings and records of bycaught specimens, Burmeister's porpoises seem to occur in coastal waters up to 55 km from shore and in wa-

ter depths of <200 m (Goodall et al. 1995, Molina-Schiller et al. 2005, Clay et al. 2018). The lack of information on porpoise ecology limits our understanding of how environmental processes and anthropogenic threats affect Burmeister's porpoises. It also hampers an evaluation of the impacts of bycatch on porpoise populations and makes it difficult to devise and implement effective management strategies for conservation (Sucunza et al. 2020, Hammond et al. 2021b).

This study presents the first estimate of abundance for Burmeister's porpoises derived from vessel-based line transect surveys off northern Peru and density surface modelling (DSM). For cryptic species, such as porpoises, visual detections can be complemented by passive acoustic detections with towed hydrophones (Akamatsu et al. 2001, Gerrodette et al. 2011, Booth et al. 2013, Fleming et al. 2018). Burmeister's porpoises produce narrow-band high frequency (NBHF) clicks, with no spectral energy below 100 kHz, similar to those of other porpoise species (Reyes Reyes et al. 2018). Although Burmeister's porpoises co-occur with several delphinid species in Peru, their NBHF clicks are sufficiently distinct to enable robust acoustic species identification (ProDelphinus unpub-

lished data). Thus, our study trialled the use of passive acoustic methods alongside visual surveys to establish the feasibility of this approach and corroborate the sighting data and the observed distribution pattern.

When abundance is known, human-induced mortality such as bycatch can be put into perspective. Information on bycatch rates is usually gathered via on-board observer programmes or fisher interviews (Moore et al. 2010). Independent onboard observer programmes are considered ideal to obtain high quality information about bycatch but are usually not feasible in the large and unregulated fleets of small-scale fisheries (Lewison et al. 2004, Northridge and Fortuna 2008, Moore et al. 2010, Panagopoulou et al. 2017, Dewhurst-Richman et al. 2020). Interviews with fishers represent an alternative and attainable low-cost method to determine the characteristics and rates of fisheries bycatch (Moore et al. 2010, Pilcher et al. 2017, Alfaro-Shigueto et al. 2018, Ortiz-Alvarez et al. 2020, Costanza et al. 2021). We interviewed gillnet fishers from Salaverry to investigate the scale of current porpoise bycatch and compare the reported level of fisheries-related mortality with the estimated porpoise abundance to better understand the conservation concerns about Burmeister's porpoises in northern Peru.

Methods

At-sea surveys

At-sea surveys focussed on the coastal waters off the nationally important fishing port Salaverry (8°13'S, 78°58'W) in northern Peru where substantial porpoise bycatch had been recorded previously (Mangel et al. 2010). Surveys were conducted over 9 days from 11 to 19 February 2023 using a 9 m long repurposed artisanal gillnet fishing vessel (Fig. 1) with an inboard engine. The fishing vessel was not engaged in fishing activities during our surveys, but all crew had experience fishing in these waters.

All surveys were conducted as day trips during daylight hours from the small port Puerto Morin (8°24'S, 78°53'W) to the south of Salaverry (Fig. 1). Puerto Morin provided access to different coastal habitat types (including islands and protected areas) and offered safe overnight anchorage for the vessel. Given the logistic constraints of starting and ending in the same port each day, triangular blocks of connected transect lines were preferred over zig-zag or parallel line placement. The resulting star-shape design provided efficient and representative coverage of the study area of 3 500 km² encompassing coastal waters up to 40 km (25 nm) offshore. Surveys started at first light around 6 a.m. and lasted 8–10 h. During the surveys, the vessel maintained passing mode (i.e. the vessel did not deviate from the transect line) and a constant speed of 5–6 knots (maximum vessel speed), which facilitated towing a hydrophone array (see below) and enhanced opportunity for observers to sight porpoises.

The survey team consisted of trained observers (from the NGO ProDelphinus) and data recorders who rotated positions every 30 min. The data recorders logged the sighting and effort data, liaised with the vessel crew, and monitored the safe towing of the hydrophones. The data recorders (and crew) were instructed not to cue observers onto a sighting but could support them during species ID and group size estimates once the sighting had been called. The two designated observers were positioned on either side of the vessel and on top of the

wheelhouse (Fig. 1, inset), which served as a secure (fenced) observation platform with an average observer eye height of 4.9 m above sea level. Prior to the surveys all observers received training in distance estimation including the use of a 'porpoise model' floated at different distances from the vessel. During surveys the observers searched for Burmeister's porpoises with naked eyes but had 10 × 42 reticle binoculars available for closer inspection, species identification, and assistance with distance estimation. When a sighting occurred, the observer provided an estimate of the radial distance and the angle to the sighting using an angle board affixed to the centre line of the vessel. Radial distance estimates were later multiplied by the sine of the respective angles to calculate the perpendicular distances to all sightings. The observers also provided species identification and a relative measure of their confidence in species ID (low, medium, and high), cue of detection, an estimate of group size, and the number of calves present. The predominant behavioural state at first sighting and the animals' movement direction in relation to the vessel (towards, away, and neutral) were recorded as an indication of potential responsive movement of porpoises to the vessel.

All sighting and effort data were recorded using a rugged tablet with a customised CyberTracker app (www.cybertracker.org/) that logged GPS positions every 10 s. These data were used to plot survey track lines and sightings. Sighting conditions were recorded when observers rotated or whenever conditions changed and included sea state (Beaufort scale), swell height (m), presence of sun glare, and a relative index for sightability of porpoises, reflecting the observers' perceptions of sighting conditions in four categories (3 = poor, 2 = moderate, 1 = good, and 0 = excellent).

Porpoise density and abundance estimation

We used DSM to estimate porpoise abundance which involved modelling porpoise density as a function of spatial and environmental co-variables along the track lines and using this model to estimate density for the entire study area (Miller et al. 2013). Only medium to high confidence sightings of porpoises made in Beaufort sea state of <3 and with good to excellent sightability were used in the analyses.

The detection function was fitted to the perpendicular distances to estimate the effective strip half-width (esw). We tested Half normal and Hazard rate functions and inclusion of categorical covariates Beaufort sea state, sightability, and observer with untruncated and truncated distances. The truncation distance was set at 200 m following standard distance sampling methods to exclude the most distant detections (Buckland et al. 2001). The best fitting model was selected using Akaike's information criterion (AIC) and was used to obtain the average detection probability (P). Given the single platform set up, we could not estimate a correction factor for imperfect detection on the transect line [i.e. $g(0)$ potentially not being 1]. Models for the detection function were created using the package Rdistance (McDonald et al. 2025) in the statistical software R (version 4.4.3, R Development Core Team 2025).

For the DSM, track lines were split into segments of 1 km length with a buffer of 100 m either side (total width of 200 m) based on the calculated esw. Criteria to define segment length were based on the resolution of the available environmental

co-variate data ensuring minimal variation within each segment and the calculated esw (Miller et al. 2013). We considered water depth, sea surface temperature (SST), chlorophyll *a* concentration (Chl *a*), shortest distance to coast, as well as spatial variables (X and Y coordinates, in Universal Transverse Mercator, UTM). Given the coastline layout, the X-coordinates reflect distance patterns from the coast whereas Y-coordinates captured potential longitudinal patterns along the coast (north–south). Water depth data (m) were available on a 15 arc-second grid (GEBCO Compilation Group 2023). Monthly composites of satellite-derived SST and Chl *a* were available at 1 km (MUR SST Analysis fv04.1) and 4 km (Aqua MODIS, NPP, L3SMI) resolutions, respectively (NOAA ERD-DAP version 2.23) (NOAA 2023). Upon closer inspection, SST and Chl *a* did not vary sufficiently spatially during our short-term study to provide biological insights and were therefore not considered further. Thus, five variables were available for each segment: spatial coordinates X and Y derived at the midpoint of each segment, shortest distance to coast calculated from the segment's geographical midpoint, median water depth (m), and standard deviation (SD) of water depth as a proxy of rugosity to capture changes in the sea floor elevation (Forney et al. 2023). Depth and derived values were calculated for the segment area using zonal statistics (following Franchini et al. (2020)). Only segments surveyed in Beaufort sea state of <3 and with good to excellent sightability were used in the analyses.

Generalized additive models (GAMs) were built using the estimated abundance of porpoises per segment (via the Horvitz–Thompson estimator) as the response variable and different combinations of median depth, SD of depth, and X and Y coordinates as covariates. X-coordinates, median depth, and shortest distance to the coast were not used in the same model to avoid issues of collinearity. Tweedie and negative binomial distributions were considered with the different covariate combinations. The best model was selected using AIC and considering deviance explained and model fit. Model diagnostics were checked for satisfactory fit using the `gam.check` function. The variance of the predicted density estimates including uncertainty from the detection function was calculated following Miller et al. (2022a) with asymptotic confidence intervals obtained using the delta method. All modelling was undertaken in the statistical software R (version 4.4.3 R Development Core Team 2025) with the libraries Distance (Miller et al. 2016) and DSM (Miller et al. 2022b).

The best model was used to predict porpoise density on a grid with 2 km x 2 km cell sizes and density estimates were summed for total abundance across the 3 500 km² study area. We explored potential effects of segment and grid cell sizes by repeating the analyses for different combinations of survey segments (1 or 2 km lengths) and prediction grid cell sizes (1 and 4 km²), but these did not affect the results or conclusions (different models not shown). We therefore present model outputs for segments of 1 km length and a prediction grid of 2 km x 2 km. For each grid cell, median depth and SD of depth were calculated. X/Y-coordinates and shortest distance to coast were determined at the grid cells' centre points. The coefficient of variation (CV) of the estimates were plotted across the prediction grid to give an overview of spatial variation in uncertainty. All mapping and data preparation were conducted with the software QGIS v. 3.36.1 (QGIS Development Team 2024).

Complementary acoustic detections of porpoises

A hydrophone array consisting of two SoundTraps 4300 HF (Ocean Instruments, New Zealand equipped with two HTI-96-Min hydrophones, High Tech, Inc.) contained in a flooded towbody (Barlow 2021) was towed around 180 m behind the vessel whenever conditions allowed. The main requirement was for water depth to be >12 m depth to ensure sufficient clearance for safe towing of the hydrophone array. Each hydrophone had a sampling rate of 288 kHz, which captured most of the porpoise click energy but cut off some of the upper frequency content. We note that this should not have affected click detection given porpoise click characteristics (ProDelphinus unpublished data). After each survey, the recordings were downloaded and Burmeister's porpoise clicks were identified using bespoke classifiers developed during this study (Ortíz-Villauriz et al. unpublished data) using the software PAMGuard (Version 2.02.07, 2023) (Gillespie et al. 2009). The trigger threshold was set to 10 dB above the background noise. A four-pole Butterworth high pass pre-filter was set at 70 kHz, and an eight-pole Butterworth high pass trigger filter was set at 100 kHz to identify potential porpoise clicks in the recordings. Clicks were further classified as noise, potential Burmeister's porpoise clicks or remained unclassified. A control frequency band at 50–90 kHz (considered noise) was compared against a test band at 110–144 kHz (porpoise click frequencies). Whenever the control band exceeded the test band by 2 dB, the detection was classified as noise. Clicks identified as potential porpoise clicks were checked manually using the spectrogram view of PAMGuard. Only NBHF clicks that occurred in click trains were considered as indication of porpoise presence. As no other NBHF click-producing species occur in our study area, there was no risk of misidentification with other odontocete species. Only manually confirmed porpoise click trains were paired with the vessel's GPS tracks using the time stamps of detection to derive location information and were mapped alongside visual detections to inspect overlap (Fig. 2). Click train detections were also associated with 1 km segments to calculate the number of segments and percentage of segments with acoustic detections and segments with concurrent visual and acoustic detections.

Fisher interviews for porpoise bycatch estimation

We conducted in-person interviews with the captains of artisanal gillnet fishing vessels from Salaverry to characterize Burmeister's porpoise bycatch. These interviews were part of a larger effort to study fisheries–cetacean interactions along the Peruvian coastline (ProDelphinus, unpublished data). We attempted to interview at least 20% of the captains with vessels registered in Salaverry ($n = 140$) based on the last fisher census conducted by the Peruvian fisheries authorities (Castillo Mendoza et al. 2018). Interviewers liaised with local contacts to determine the best time and place to encounter fishers and used a snowball method to identify further interviewees. All interviews were conducted by trained and experienced personnel from the NGO ProDelphinus using semi-structured questionnaires based on the protocol developed by Pilcher et al. (2017) and Alfaro-Shigueto et al. (2018). The questionnaires consisted of 49 open and closed questions covering a wide range of bycatch-related aspects. For the purpose of this study, we only considered information from 18 questions related to fishers' background and Burmeister's porpoise bycatch. Fishers' background information included age, main occupation, and

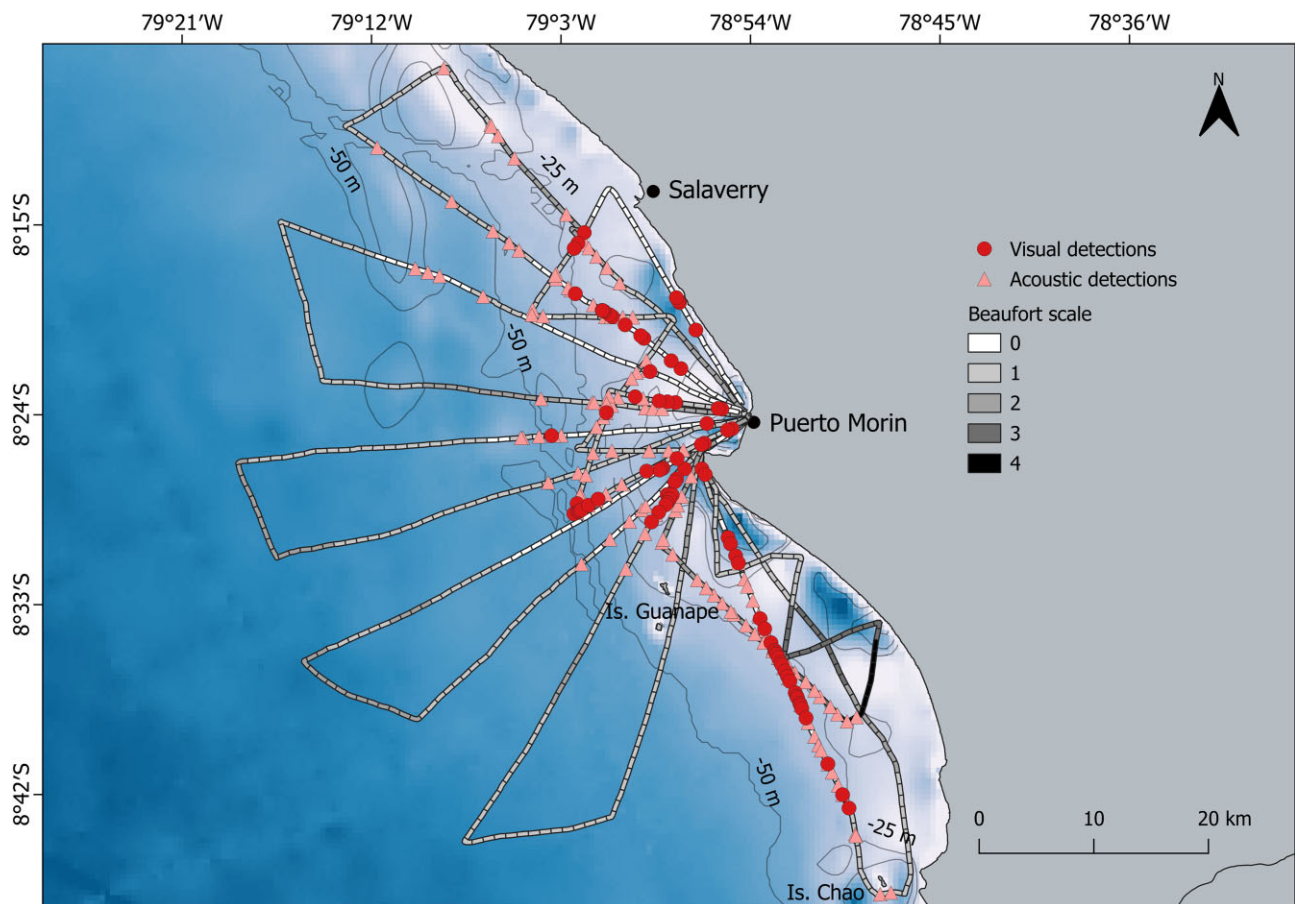


Figure 2. Visual (circles) and acoustic (triangles) detections of Burmeister's porpoises off Puerto Morin overlaid on survey track lines indicating the sea state (Bft) in 1 km segments.

fishing experience (age they started fishing). Bycatch-related questions aimed to characterize the nature of cetacean bycatch, including the species caught, months when bycatch occurred, distance from the coast at which bycatch events usually occurred, and the estimated number of porpoises caught in the previous year (2022). We focused on fishing activities and animals caught in the previous year to reduce recall bias (Costanza et al. 2021, Tubbs and Berggren 2024). Information about fishing grounds, target catch species, and characteristics of the fishing gear (mesh size, measure between opposite knots, in inches) involved in bycatch was also collated. To better understand spatial patterns of porpoise bycatch, fishers were asked to draw on printed maps the extent of their fishing grounds and mark areas where porpoise bycatch occurred. Clean paper copies of the maps were used for each fisher. To reduce knowledge bias (Tubbs and Berggren 2024), all questions included 'no response' and 'do not know' options which were considered in the analysis (Pilcher et al. 2017). Interviewers used printed species guides to assist fishers in small cetacean identification (Moore et al. 2010, Turvey et al. 2013) and performed screening questions which involved asking fishers to describe species to ensure correct identification (Tubbs and Berggren 2024). Interviewers also provided an independent post-hoc assessment of the reliability of a participant's responses. This included a self-assessment of an interviewer's perception of the integrity of information provided by the interviewee based on confidence, knowledge, and honesty ratings (Pilcher et al. 2017, Alfaro-Shigueto et al. 2018, Tubbs

and Berggren 2024). Only interviews considered reliable and with high confidence ratings were included in the following analyses.

Prior to being asked questions, each participant had to consent to be interviewed and was informed of the study's aims, that participation was voluntary and anonymous and who would have access to the information provided and data storage.

Descriptive analysis

Only interviews considered reliable were used to calculate the percentage of fishers reporting bycatch and the number of animals bycaught in the previous year. Temporal patterns of porpoise bycatch were investigated using the proportion of fishers reporting bycatch per month, using the total number of fishers engaged in fishing activities per month as the basis. Spatial patterns of fishing effort and bycatch were derived from the hand-drawn areas on the maps which were photographed, imported into Geographic Information System (GIS), georeferenced, and then overlaid to generate composite maps.

Bycatch estimation for the vessel-based survey area

For comparison with the abundance estimate, we calculated a porpoise bycatch rate in the area covered during our vessel-based surveys. For fishers who identified areas inside and outside of the vessel-based survey area, we calculated the number of porpoises likely captured inside the vessel-surveyed area

from the total number reported by each fisher scaled by the overlap of their bycatch area with our survey area. For fishers who reported not to have had porpoise bycatch, a value of zero was included in the resampling. We used ordinary non-parametric bootstrap with 10 000 replications to generate the mean and confidence intervals of porpoise bycatch per vessel. All analyses were performed using the boot package in the statistical software R (version 4.4.3, R Development Core Team 2025). Overall porpoise bycatch in 2022 was then estimated for our study area by scaling the estimated mean number of porpoises caught per vessel by the number of gillnet vessels from Salaverry expected to have bycatch inside the vessel-based survey area.

Contextualizing porpoise bycatch rates and abundance

We used the potential biological removal (PBR) control rule to contextualize the bycatch and abundance estimates and to provide a perspective on the reported fisheries-related mortality of Burmeister's porpoises off Salaverry. The PBR formula is comprised of three parameters: the minimum abundance estimate (N_{MIN}) multiplied by one-half of the maximum intrinsic rate of population growth ($0.5R_{\text{MAX}}$) and a recovery factor (F_R) (Wade 1998). N_{MIN} was derived as the 20th percentile of the log-normal distribution (Bettridge 2023) of the model-based abundance estimate and corresponding CV obtained from the best fitting dsm-model. We chose the default value for R_{MAX} of 0.04 for cetaceans and F_R of 0.5 as recommended for species with unknown population trends (Wade 1998, Punt et al. 2020, Wade et al. 2021). We also used a reverse approach and considered the estimated annual bycatch level in our study area as a putative PBR reference limit. Using the same equation and solving for N_{MIN} gave an indication of the number of porpoises required under the estimated level of bycatch to meet the PBR control rule to reach or maintain an optimal sustainable porpoise population (Wade 1998).

Results

At-sea surveys

A total of 770 km of line transect survey effort were completed during 9 consecutive days, with daily surveys averaging 87 km in length (min: 40 km, max: 98 km). During surveys 90 sightings of Burmeister's porpoises were recorded, of which three sightings had low confidence in species identification and were not included in the subsequent analyses. Using the remaining 87 porpoise sightings, the encounter rate was estimated at 0.12 (SD $\pm$ 0.13) porpoise sightings/km. Mean group size was of 1.6 (SD $\pm$ 0.7) individuals with a maximum group size of 4. Only 5 sightings contained a calf. No porpoises were seen beyond the 50 m depth contour or further than 25 km from the coast with 94% of sightings recorded in waters shallower than 25 m and within 20 km (11 nm) from the coast (Fig. 2). Almost all observed groups (94%) showed a neutral orientation towards the vessel. Only one mother-calf pair was observed heading away from the vessel. Most surveys were conducted in sea states of 0–2 Bft (Beaufort) including the offshore areas and deeper waters (where no sightings were made). Twenty three percent of the survey effort (175 km) was conducted in 0 Bft, 57% (437 km) in 1 Bft and 15% (119 km) in 2 Bft. Only some nearshore sections in the southern part were surveyed in 3–4 Bft, which represented 5% (39 km) of the survey

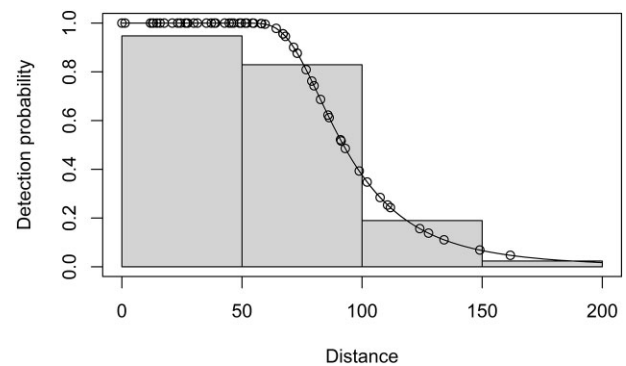


Figure 3. Frequency distribution of perpendicular distances of porpoise sightings ($n = 84$) with the detection curve fitted using Hazard rate model and truncation distance of 200 m.

effort. Visual detections of porpoises were registered only in conditions of <3 Bft and in good to excellent sighting conditions (Fig. 2). Thus, only segments surveyed in conditions when porpoise sightings occurred were included in the DSM analyses.

Over 95% of acoustic detections also occurred within 20 km from the coast and in waters shallower than 50 m matching the distribution of porpoise sightings (Fig. 2). Of the 731 1 km-long segments of the transect lines, there were 56 segments (8%) with visual detections and 134 (18%) with acoustic detections with a 34% overlap between these (Fig. 2). Passive acoustic monitoring allowed for detection of porpoises in all sea states including in 3–4 Bft when no sightings occurred. The overall spatial pattern of porpoise occurrence was consistent between visual and acoustic detections (Fig. 2). For example, both visual and acoustic methods yielded many porpoise detections inshore and to the south of Guañape island, but detections varied between survey days with different sea states. The independently collected PAM data corroborates the visual sighting data to be representative of porpoise distribution during the survey period.

Porpoise density and abundance estimation

Of the 87 porpoise sightings, only three had perpendicular distance values >200 m, so truncation distance was set to 200 m. The best model for the detection function used Hazard rate with truncated distances and no covariates. Detection probability was highest close to the track line and declined substantially after 100 m (Fig. 3). Average detection probability (P) was estimated at $P = 0.49$ (CV = 0.08) and effective strip half-width (esw) at 100 m.

The best-fitting DSM model used a Tweedie distribution with a log link and retained shortest distance to the coast and Y coordinates (Table 1, Fig. 4). It explained 29.6% of the deviance and model diagnostics showed a good fit to the data. Predicted density per grid cell ranged from 0 to 34 porpoise/4 km² and summed to a total abundance of 1 696 porpoises (95% CI: 1 087–2 648; CV = 0.23) in the 3 500 km² study area. The model that retained median depth and Y coordinates had a higher AIC and lower deviance explained (21.7%, Table 1) but gave a nearly identical estimate of abundance of 1 748 porpoises (95% CI: 1 144–2 674; CV = 0.22). We present predicted density surface maps for both models (Fig. 5) as the spatial pattern in the predicted densities from the depth model (Fig. 5, panel right side) better reflect the observed spatial

Table 1. Summary of candidate models incorporating different combination of variables.

Model components	Significance of covariates		Exp. Dev	AIC
Y-coordinate	0.22		6.1%	629.9
Depth (median)	<0.001	–	13.6%	607.3
Depth (median) + Y-coordinate	<0.001	0.07	21.7%	599.4
Shortest distance to coast	<0.05	–	19.4%	592.9
Shortest distance to coast + Y-coordinate	<0.05	<0.05	29.6%	578.5

Shown are the significance of model covariates, % of deviance explained (Exp. Dev.) and AIC. In bold selected models.

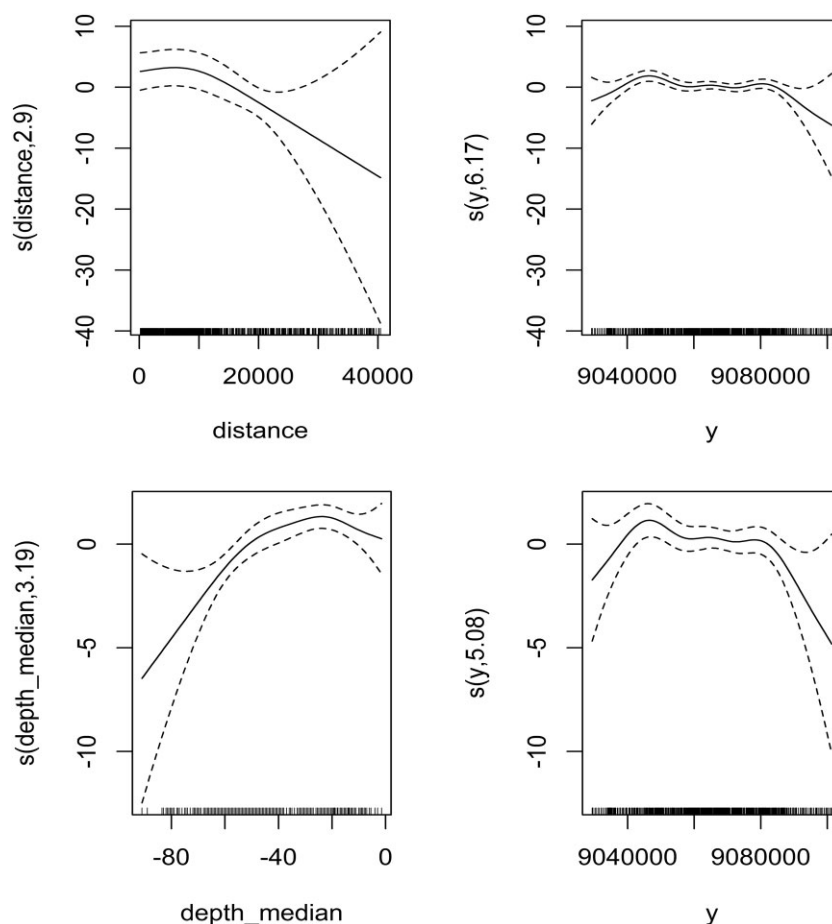


Figure 4. (Upper panels) Smooth terms of shortest distance to the coast (m) and spatial coordinate (y) for porpoise density. (Lower panels) Smooth terms of median depth (m) and spatial coordinate (y) for porpoise density. Dashed lines represent 95% confidence intervals. Rug plots indicate co-variate values covered by survey effort (segments).

distribution of Burmeister's porpoises when compared with the visual and acoustic detections.

Predicted porpoise densities (from both models) were highest in the inshore and southern parts of the study area between Gunaep and Chao islands (Fig. 5). Predictions from the depth model also captured some higher density areas of porpoises between Puerto Morin and Salaverry (Fig. 5, panel right side) which also matched information reported by fishers (see below).

Fisher interviews for porpoise bycatch estimation

Descriptive analysis

A total of 36 interviews with vessel captains were conducted at Salaverry port. However, four interviews were excluded because the interviewers considered the responses to contain

contradictions in answers or errors in the reliable identification of Burmeister's porpoises. The 32 remaining interviews represent 23% of the total number of gillnet vessels registered in Salaverry. The mean age of fishers interviewed was 50-year-old ($SD \pm 10$ yrs) with an average fishing experience of 33 ($SD \pm 13$) years, (min: 6 yrs, max: 60 yrs). Thirty-one (97%) fishers reported fishing as their main occupation and 23 (72%) fished all-year around. Some fishing grounds extend from 4°S to 18°S, and beyond 100 nm from the coast (Fig. 6), but the majority of fishing effort was concentrated between San Jose (7°21'S, 79°27'W) and Pucusana (12°25'S, 76°47'W) and within the first 100 nm (Fig. 6).

Twenty-one fishers (66%) reported to have had porpoise bycatch during the previous year (2022) with 11 (52.4%) fishers reporting bycatch of 2–10 porpoises, 7 (33.3%) fishers said they caught 15–40 porpoises, and 3 (14.3%) fishers reported

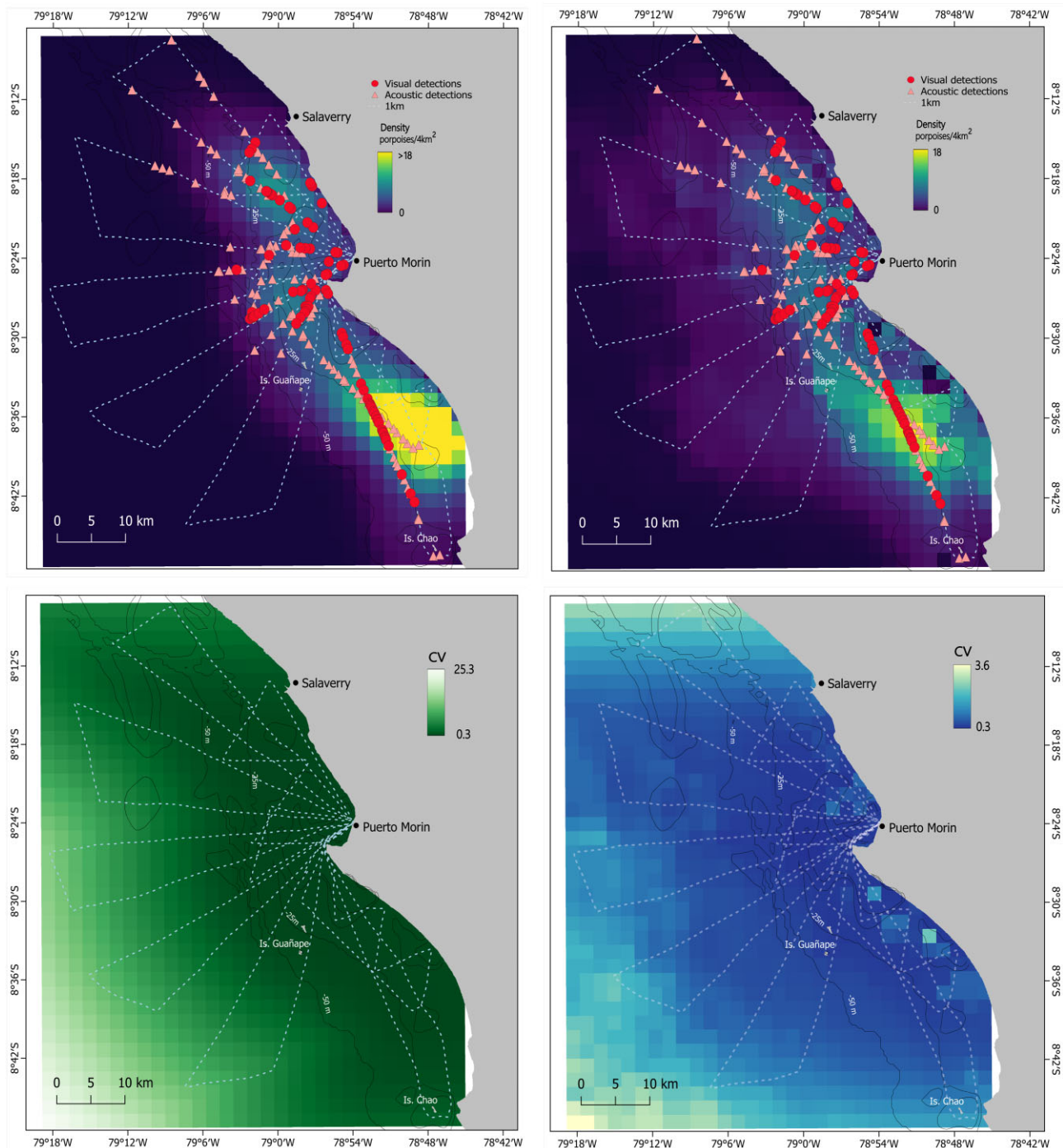


Figure 5. (Upper panels) Estimated density of Burmeister's porpoises overlaid with visual (circles) and acoustic (triangles) detections, and (lower panels) associated uncertainty (CV) of the estimates. (Left panels) Results from the model incorporating shortest distance to shore (m) and Y-coordinates, and (right panels) results from model incorporating median depth (m) and Y-coordinates.

bycatch of up to 100 porpoises. Fishers' self-reported numbers sum to a total of 541 Burmeister's porpoises captured in 2022. Porpoise bycatch was reported to occur in most months but 71% of fishers identified February as the month with more bycatch events.

Twenty of the 21 fishers reporting bycatch were able to pinpoint areas on maps where bycatch events had occurred (Fig. 6). Bycatch was reported from San Jose (7°21'S, 79°27'W) to Supe (10°48'S, 77°44'W), but most fishers identified bycatch areas close to Salaverry (Fig. 6) and within

the first 10 nm (19 km) from the coastline. Only 4 (17%) fishers reported to have bycatch beyond 10 nm from the coast. Sixteen fishers reported porpoise bycatch inside our vessel-based survey area (Fig. 6) and of those, six fishers highlighted bycatch near islands such as Macabi, Guañape, and Chao. There was close congruence of fisher-identified bycatch areas in our study area and our observed porpoise distribution (Fig. 4, Fig. 6 inset).

Sixty-five percent of fishers reported rays (*Myliobatis* sp) as their target catch when Burmeister's porpoise were bycaught

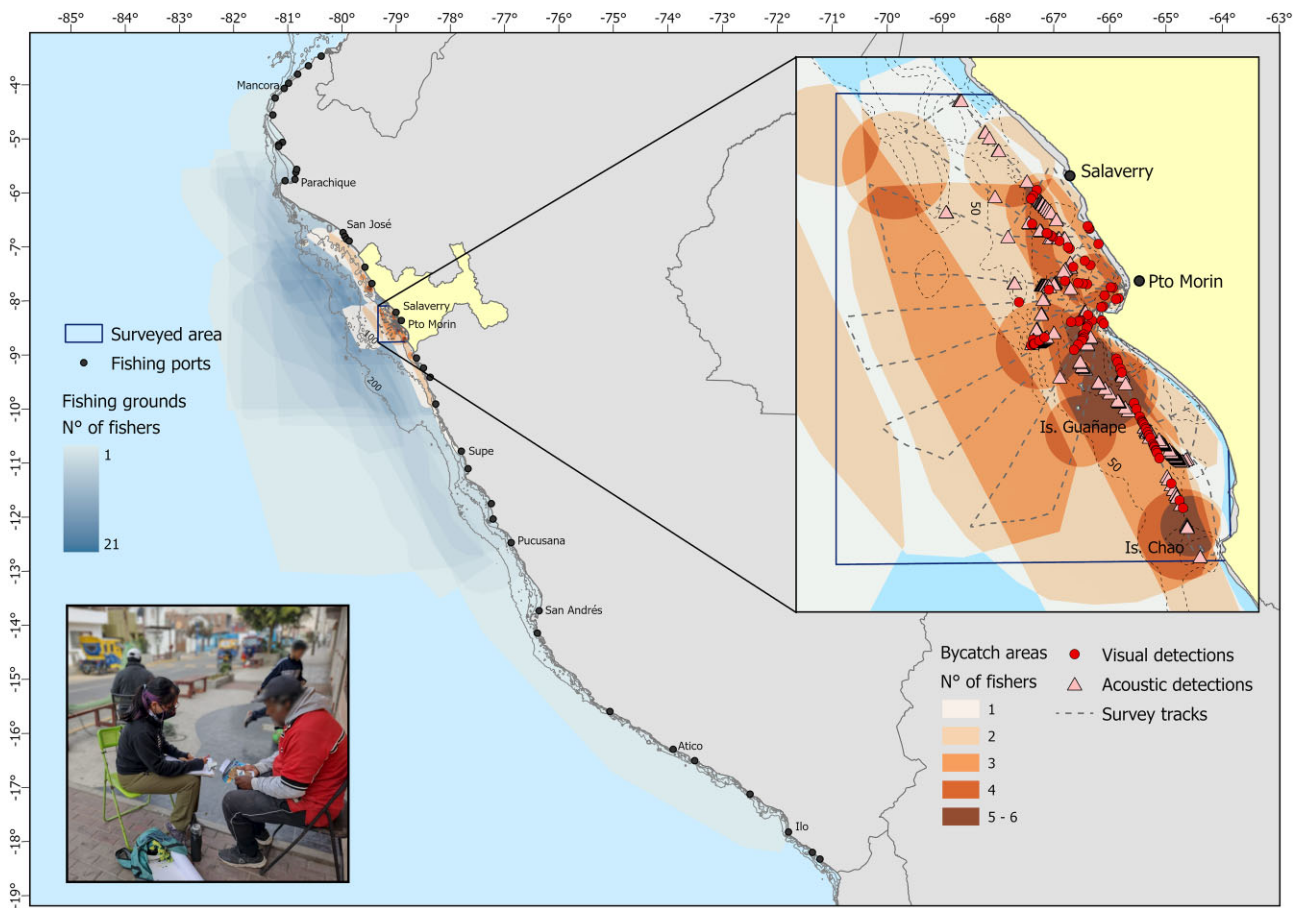


Figure 6. Fishing grounds (large map left, shades of blue) and areas of Burmeister's porpoise bycatch (overlay and inset right, shades of orange) reported by fishers from Salaverry during interviews. Inset map shows a close-up of our vessel-based survey area (polygon) along with visual (circles) and acoustic (triangles) detections of Burmeister's porpoises.

followed by those fishing for striped mullet (*Mugil cephalus*) (17%) or other bony fishes (18%). Rays were targeted mostly with surface driftnets of 14 inches mesh size, but mid-water driftnets and bottom nets of different mesh sizes (7–15 inches) were also used. Bony fishes were targeted with surface and midwater driftnets of smaller mesh sizes (2.5–8 inches).

Bycatch estimation for the vessel-based survey area

From the total number of fishers interviewed, 16 (50%) reported to have bycatch inside the survey area. Estimated mean porpoise bycatch inside our study area was 6 porpoises per vessel per year (95% CI: 3–10 porpoises). By extrapolating the bycatch estimate per vessel to the Salaverry gillnet fleet of 140 vessels, we estimated that 420 (95% CI: 210–700) porpoises were captured inside the study area in 2022.

Contextualising porpoise bycatch rates and abundance

We applied the PBR control rule to provide a perspective on porpoise abundance and bycatch estimates off Salaverry. Using the abundance estimate of 1 696 porpoises ($CV = 0.23$) from the best DSM-model provided an N_{MIN} of 1 425 porpoises and a PBR reference limit of 14 porpoises. In contrast, using the estimated bycatch of 420 porpoises in the study area as the PBR reference limit would require at least 42 000 porpoises to reach or maintain an optimal sustainable population.

Discussion

In Peru, Burmeister's porpoises have been known almost exclusively from dead individuals bycaught in fisheries (Reyes and Brownell 2025). Here, we present the first estimates of abundance and fine-scale distribution of Burmeister's porpoises off the coast of Peru obtained using dedicated at-sea surveys. We show that it is both feasible and effective to apply line transect methodology using a repurposed fishing vessel to detect porpoises at sea. Although the single platform survey set up did not allow us to estimate the number of animals missed on the track line [i.e. apply $g(0)$ correction], the estimated detection probability and effective strip half-width are well within the range expected for cryptic species and the type of survey platform used (Barlow et al. 1997, Dawson et al. 2004, Gerrodette et al. 2011, Kuit et al. 2021, Li et al. 2023). Abundance estimates for porpoises are generally considered to be biased low without $g(0)$ correction. For example, for harbour porpoises uncorrected estimates of detection probability were two to four times larger than the $g(0)$ corrected estimates (Hammond et al. 2013, Hammond et al. 2021a, Zerbini et al. 2022) which, if not addressed, would have led to abundance to be underestimated by the same magnitude. Assuming that our uncorrected detection probability could be biased high by similar quantity would mean that there could be more than twice as many porpoises in our study area than estimated. Any bias in this order of magnitude would not affect any of the

conclusions drawn (see below), and there is no indication that our estimates were afflicted by worse biases. We were fortunate to have excellent survey conditions with calm seas (≤ 2 Bft) and no swell present across the study area which greatly facilitated detecting porpoises visually. A small portion of the transect lines (5% of survey effort) to the south was covered in higher seas states (3–4 Bft) and was excluded from further analysis to reduce visibility bias. We also surveyed this southern area again on a different day in good conditions with many porpoise sightings (Fig. 2) which were included in the analyses reducing potential spatial bias in survey coverage.

We used acoustic detections of porpoises to confirm that the spatial pattern of visual detections provided a good representation of porpoise distribution. In most areas where we had sightings, we also had acoustic detections with the hydrophone array towed 180 m behind the vessel. Given porpoise echolocation characteristics, the animals must have remained well within 100 m of the transect line and the towed hydrophones to have been detected (Clausen et al. 2021). Although acoustic detections can, in some circumstances, be used to correct for animals missed on the transect line (Ollier et al. 2023), there is no established process of using this to correct the overall abundance estimation. Our acoustic analysis did not allow identification of distinct detection events that could be associated reliably with individual sightings, but a more detailed analysis could be explored in the future. Behavioural changes to avoid an approaching vessel have been described for other porpoise species (Akkaya Bas et al. 2017, Oakley et al. 2017), but we did not observe any obvious short-range avoidance behaviours of Burmeister's porpoises. We cannot rule out porpoises having responded to the vessel over larger distances. There is no indication of responsive movements in the shape of the detection function.

Model-based abundance of Burmeister's porpoises was estimated at 1 696 individuals (CV = 0.23) in the 3 500 km² study area off Salaverry. The second best DMS-model with depth instead of distance to coast as co-variate produced a near identical estimate (1 748 porpoises, CV = 0.22) but seemed to better reflect porpoise distribution when compared to the visual and acoustic detections (Fig. 5). Both observed and predicted porpoise distributions showed a clear spatial gradient from inshore to offshore areas with highest densities of Burmeister's porpoises in shallow waters (<50 m depth) and within the first 25 km from the coast. Porpoises were conspicuously absent from offshore transects (including no acoustic detections) despite excellent survey conditions. More extensive surveys across broader environmental conditions and longer time frames are needed to understand if this distribution is consistent across seasons and climatic events (e.g. El Niño events).

In this study, we relied on fishers' knowledge through interviews to characterize and estimate porpoise bycatch. This approach has been applied widely to gain insights into species ecology and conservation issues including bycatch (Liu et al. 2017, Alfaro-Shigueto et al. 2018, Ayala et al. 2019, Ortiz-Alvarez et al. 2020, Costanza et al. 2021), due to its cost-effectiveness and ease of implementation compared to on-board observer programmes (Moore et al. 2021). While it is not possible to fully verify the accuracy of self-reported data, we addressed common sources of bias—such as recall bias, misidentification, and response bias—by following the established best-practice approach (Pilcher et al. 2017, Costanza et al. 2021). This included limiting questions to a specific time frame (e.g. past year) and incorporating verifi-

cation questions to confirm species identification. All interviews were conducted one-to-one to reduce peer influence and encourage honest processes (Ayala et al. 2019, Tubbs and Berggren 2024). Although there are some limitations to non-probabilistic methods such as snowball sampling, this approach has shown to enhance respondents' trust—since referral come from previous participants (Tubbs and Berggren 2024)—and is suitable for engaging dispersed, hard to reach communities while still capturing a representative sample of fishers' knowledge (Ayala et al. 2019, Tubbs and Berggren 2024). In our case, interviewed fishers had an average of 33 years of experience, providing valuable information grounded in extensive experience.

Fishers mainly identified shallow areas within the first 10 nm (19 km) from the coast and near islands as bycatch hotspots off Salaverry. These locations are consistent with porpoise bycatch areas reported two decades ago by on-board observers in the same fisheries (Mangel et al. 2010). Bycatch hotspots also aligned with the observed and predicted higher density areas for Burmeister's porpoises identified during the vessel-based surveys (Figs 4 and 6). Fishers reported that Burmeister's porpoise were bycaught most frequently in nets targeting rays which matches observations from the early 2000s (Mangel et al. 2010). Two species of eagle rays, *Myliobatis peruvianus* and *M. chilensis*, are the main target species for net fisheries in Salaverry (Mangel et al. 2010, Mangel et al. 2013, Marín Soto et al. 2017). Nets used for rays have mesh sizes up to 19 inches (Marín Soto et al. 2017, Salazar et al. 2020) which fit with the nets of 14-inch mesh size used frequently by fishers in this study. Burmeister's porpoises and eagle rays are known to prey on Peruvian anchovies (*Engraulis ringens*) when these forage fish congregate inshore (Reyes and Van Waerebeek 1995, García-Godos et al. 2007, Coasaca-Céspedes et al. 2018, Gonzalez-Pestana et al. 2021, Peña-Cutimbo et al. 2025). This spatial overlap between anchovy predators might explain why Burmeister's porpoise are bycaught frequently in surface and mid-water driftnets targeting rays. Some porpoise bycatch also occurred in bottom set nets for bony fishes that are well known to cause porpoise entanglements (Read et al. 1988, Read 2008, Van Waerebeek and Reyes 1994a). The diet of Burmeister's porpoises is not well studied but Peruvian anchovies and demersal fish species have been listed as common prey species (Reyes and Brownell 2025). A better understanding of porpoise habitat use and diet is needed before targeting particular fisheries or gear types for bycatch mitigation measures.

The majority of Salaverry fishers reported bycatch of Burmeister's porpoises with individual reports summing to over 540 porpoises caught in 2022 between San Jose and Supe. Bycatch levels are likely to vary between years, but it is unlikely that the level reported for 2022 was exceptionally high. Our interview-based estimate is consistent with historic estimates for Salaverry gillnet fishers of 105–699 porpoises caught annually obtained via on-board observer programmes (Mangel et al. 2010). The fishers interviewed in this study represent only around 23% of all vessels registered in Salaverry. In addition, there are more than a dozen smaller fishing coves with artisanal gillnet fishers (Fig. 1) that also fish in the same area with unknown levels of bycatch. Thus, the reported bycatch is a minimum estimate based on only a fraction of the active fishing fleet.

In order to compare bycatch levels and porpoise abundance, we rescaled the reported bycatch to the survey area and

extrapolated to all fishers registered in Salaverry likely fishing in the study area. The resulting estimate of 420 Burmeister's porpoises bycaught annually off Salaverry by Salaverry fishers constitutes around 1/4th of the estimated abundance of 1 700 porpoises in the same area. The PBR reference limit for a porpoise population of around 1 700 individuals is only 14 porpoises per year. Conversely, a population of over 42 000 porpoises would be required to maintain or recover its optimum sustainable size under the reported bycatch level of hundreds of porpoises per year. This order of magnitude mismatch remains even if our abundance estimate might be biased low (see above). For example, doubling our abundance estimate still falls several tens of thousands of porpoises short for the reported bycatch level to be considered sustainable. Conversely, the bycatch level would need to be 30 times smaller to be sustainable under the estimated abundance of porpoises in the study area. Given this persistent mismatch, the current (and historic) levels of fisheries-related porpoise mortality cannot be considered sustainable, and it is likely that the number of porpoises estimated for Salaverry now represent a fraction of their past abundance.

There are some important caveats to the comparisons above but these should not distract from the conclusion that Peruvian Burmeister's porpoises have long been subject to unsustainable levels of bycatch and the current population size might be severely reduced (see also Félix et al. (2018)). Our survey area captured only a small portion of Burmeister's porpoise habitat in Peru (Fig. 1). For the observed level of bycatch (let alone the bycatch from all fishing fleets) to be sustainable however, there would need to be many tens of thousands of porpoises in other parts of Peru that range along the coast as one mixing population (and considered one stock). Seasonal changes in porpoise distribution either along the coast or inshore–offshore are possible but currently unknown. Burmeister's porpoise habitat seems to be limited to neritic waters out to 200 m depth (Goodall et al. 1995, Molina-Schiller et al. 2005, Clay et al. 2018). The continental shelf is much narrower in southern than northern Peru which limits availability of suitable habitat for porpoises. A better understanding of distribution and habitat use is needed to identify important porpoise habitat and its overlap with human activities. Extending spatial survey coverage to obtain abundance and bycatch estimates for the entire Peruvian coastline should be considered a high research priority.

We used the PBR approach only to contextualize bycatch and abundance estimates. We do not propose to apply the PBR reference limit to manage bycatch of Salaverry fishers. The PBR reference limit is a conservative estimate of animals that can be removed from a defined stock without impacting an optimal sustainable population (Wade 1998). Although stock structure has not been defined for Burmeister's porpoises, Peruvian Burmeister's porpoises are considered genetically distinct from Chilean and Argentinian populations (Rosa et al. 2005). Weak but significant genetic differences were also found between Peruvian porpoises sampled <200 km apart which might indicate sub-population structuring (Rosa et al. 2005). Further research is needed to clarify existence of population structure in Peruvian Burmeister's porpoises as sub-populations would be more vulnerable to human-caused mortality and have a higher risk of extinction (Frankham et al. 2002, Read 2008). Porpoises also face many other pressures including reduced prey availability from overfishing and intensifying climatic events (e.g. El Niño), pollution, coastal

developments (García-Cegarra et al. (2024)), and infectious diseases, e.g. highly pathogenic avian influenza that caused mass mortalities among marine mammals in Peru (Leguia et al. 2023).

Potential bycatch mitigation measures

The integration of genetics, demographics, and environmental factors have been recommended to define conservation objectives and management actions (Paudel and Koprowski 2020). However, such types of research may require some time to be planned and implemented. Immediate actions should focus on bycatch mitigation measures. Studies conducted in Peru have shown that pingers and light emitting diodes reduced small cetacean bycatch in fishing nets (Mangel et al. 2013, Clay et al. 2019, Bielli et al. 2020). Those devices are, however, relatively costly and require careful maintenance which limit their uptake and effective use by small-scale fishers (Dawson et al. 2013, Secchi et al. 2022). Low-cost acoustic alarms such as rattling or reflective plastic bottles have shown some success in reducing bycatch of some small cetaceans (Sucunza et al. 2024) but did not yield promising results when trialled with small cetaceans in Peru (ProDelphinus, unpublished data).

Other approaches should be explored urgently such as operational changes in fishing practices (Secchi et al. 2022), avoiding areas of high likelihood of bycatch or high density areas of Burmeister's porpoises. Potential areas for spatial mitigation measures are Guañape, Chao, and Macabi islands which are already part of the protected area system in Peru (DS-N°024–2009-MINAN). Having protected areas already in place represents an opportunity to facilitate the development of monitoring plans and bycatch mitigation measures in coordination with government representation and local communities within an existing institutional framework. In fisheries that use overnight net soaking times (Mangel et al. 2010), adapting practice to monitor nets or modify soak times might help to increase the likelihood of finding and releasing porpoises alive. Bespoke training guides and workshops for fishers to learn to handle and release entangled marine mammals and sea turtles alive have already been implemented in Peru (Córdova-Zavaleta et al. 2020, ProDelphinus 2025). Such live release efforts should be promoted among fishers and monitored for effectiveness.

Given the importance of fishing for local communities, bycatch mitigation actions should be co-developed and implemented in consultation with fishers to consider their expertise in fishing practises and concerns about the effect of these actions on their livelihoods (Senko et al. 2014, Alava et al. 2019). Involving fishers can lead to more successful adoption and compliance with changes in fishing practice through community buy-in and social pressures (Danilewicz et al. 2010, Senko et al. 2014, Secchi et al. 2022). The engagement of government authorities is also key in the development of effective bycatch mitigation strategies. Fisheries management authorities should aid in the implementation of monitoring programmes to evaluate the species population status and the effectiveness of the adopted interventions considering biological/ecological factors and socioeconomic implications for the local communities (Danilewicz 2007). Bycatch mitigation plans require clear, achievable, measurable, and time-bound goals (Gilman et al. 2022) that are monitored to allow for responsive and effective interventions when required. Monitoring programmes should be collaborative between authorities and local

communities to avoid trust issues (Alava *et al.* 2019). Having a monitoring plan is key for assessment and improvements to achieve the bycatch mitigation goals. Gaining support of influential members of the fishing community and setting positive examples can promote wider participation and better engagement across fishers (Danilewicz 2007). Putting in place strategies requires political will and appropriate assignation of resources. Notwithstanding the difficulties and regardless of the preferred strategies, we emphasize the immediate and critical need to implement bycatch mitigation measures to ensure that viable population(s) of Burmeister's porpoises remain along the Peruvian coast.

Conclusions

This study presents the first estimate of abundance for Burmeister's porpoises in the northern part of Peru (and anywhere in their range). Porpoise density in neritic waters during summer was highest close to shore and in shallow water and overlapped with important gillnet fishing areas which was reflected in reported bycatch of 100s of porpoises per year. The high and unsustainable levels of bycatch described in this study alongside the long history of bycatch (Van Waerebeek and Reyes 1994a, Van Waerebeek and Reyes 1994b, Van Waerebeek *et al.* 2002) raise serious concerns for the long-term survival of Burmeister's porpoises in Peru. Bycatch mitigation measures should be implemented as a matter of urgency and require the active participation of fishers and governmental authorities. Further research is also needed to better understand porpoise population structure and assess abundance of Burmeister's porpoises and their interactions with fisheries along the entire Peruvian coast.

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Author contribution

Conceptualization: Clara Ortiz-Alvarez, Sonja Heinrich, Jeffrey C. Mangel, Joanna Alfaro-Shigueto. Data curation: Clara Ortiz-Alvarez, Ruth Ortés-Villauriz. Formal analysis: Clara Ortiz-Alvarez, Ruth Ortés-Villauriz. Funding Acquisition: Clara Ortiz-Alvarez, Sonja Heinrich, Joanna Alfaro-Shigueto,

Jeffrey C. Mangel. Investigation: Clara Ortiz-Alvarez, Sonja Heinrich, Methodology: Clara Ortiz-Alvarez, Ruth Ortés-Villauriz, Sonja Heinrich. Project Administration: Clara Ortiz-Alvarez, Joanna Alfaro-Shigueto. Resources: Clara Ortiz-Alvarez, Ruth Ortés-Villauriz, Sonja Heinrich. Software: Clara Ortiz-Alvarez, Ruth Ortés-Villauriz. Supervision: Sonja Heinrich. Validation: Sonja Heinrich. Visualization: Clara Ortiz-Alvarez. Writing—original draft: Clara Ortiz-Alvarez. Writing—review & editing: Sonja Heinrich, Joanna Alfaro-Shigueto, Jeffrey C. Mangel, Ruth Ortés-Villauriz

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Data availability

At-sea survey data will be available at <https://doi.org/10.17630/bd08e679-8c7f-41d5-97ad-b99038a4fadd> after an embargo period. Fishers interview data underlying this article cannot be shared publicly as the terms of participants' consent do not allow the data to be made publicly available. These data will be shared on reasonable request to the corresponding author.

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