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RESEARCH ARTICLE

Passive acoustic tracking of the three-dimensional movements and acoustic behaviour of toothed whales in close proximity to static nets

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Abstract

1. Entanglement in net fisheries (static and drift) is the largest known cause of direct anthropogenic mortality to many small cetacean species, including harbour porpoise (*Phocoena phocoena*), in UK waters. Despite this, little is known about the behaviour of small cetaceans in proximity to nets.
2. We have developed a passive acoustic monitoring (PAM) system for tracking the fine-scale three-dimensional (3D) movements of echolocating cetaceans around actively fishing nets by localising their acoustic clicks. The system consists of two compact four-channel acoustic recorders with sample-synchronised sensor packages that use 3D motion tracking technology to accurately log orientation, depth, water temperature and ambient light level. Two recorders were used in tandem, with each one attached to and floating above the net floatline. The system can be deployed during normal fishing operations by a trained researcher or experienced fisheries observer. Recordings were analysed in PAMGuard software and the 3D positions of echolocating animals in the vicinity of the system were calculated using an acoustic particle filter-based localisation method.
3. We present findings from four deployments in UK waters (each 1–2 days in duration) in which 12 distinct harbour porpoise encounters yielded a sufficient number of detected clicks to track their movements around the net. The tracks show a variety of behaviours, including multiple instances of animals actively foraging in close proximity to the fishing net.
4. We show that a relatively inexpensive PAM system, which is practical to deploy from active fishing vessels, is capable of providing highly detailed data on harbour porpoise behaviour around nets. As harbour porpoises are the one of the most difficult species to localise, this methodology is likely to be suitable for elucidating the behaviour of many other toothed whale species in a variety of situations.

KEYWORDS
acoustic localisation, bycatch, gill net, harbour porpoise, passive acoustic monitoring

1 | INTRODUCTION

Fisheries bycatch (unintended mortality) of non-target species in fishing gear is the largest known cause of direct anthropogenic-related mortality in toothed whales. Over 300,000 toothed whales are estimated killed in fishing gear every year globally (Read et al., 2006) which has resulted in significant declines in the conservation status of many toothed whale populations (Brownell Jr et al., 2019). Among the various different types of fishing gear, synthetic static or drift nets (moored or drifting panels designed to entangle or gill target fish species) account for the majority of bycatch of smaller toothed whales (Read, 2008). Bycatch in static nets is considered to be the primary factor in the near certain imminent extinction of the vaquita (Thomas et al., 2017), probably contributed to the extinction of the baiji dolphin (Turvey et al., 2007), and could be at least partially responsible for an 87% decline in delphinid populations in the Indian Ocean (Anderson et al., 2020).

Static nets are generally considered to be of low environmental impact, as the net mesh size enables relative selectivity for target species and size, and they do not cause significant widescale habitat damage that can be associated with bottom trawling and dredging (e.g. Hiddink et al., 2006; Jennings et al., 2001). However, the chronic and widescale nature of cetacean bycatch associated with net fisheries is a significant conservation concern and has prompted research into various mitigation approaches. These have included the use of acoustic deterrents (e.g. pingers) to warn non-target animals of net presence (Dawson et al., 2013), changing the net materials to make them more acoustically reflective (e.g. Trippel et al., 2008) deploying nets in different configurations or altering fishing profiles (Palka, 2000), and/or the spatio-temporal closure of fisheries (e.g. Dawson & Slooten, 1993; Murray et al., 2000). However, with decades of focus on developing mitigation strategies for bycatch, there still remains very little information on the mechanism by which toothed whales, which have highly sophisticated acoustic sensory abilities, become caught in nets.

This sparsity of information is partially explained by the difficulty in collecting fine-scale data on toothed whale behaviour around fishing nets. Methodologies with very limited monitoring ranges, such as underwater video cameras, have a low probability of recording encounters between non-target animals and the net. Other visual methods can be effective if the net is in very shallow water and animal behaviour can be viewed from a high vantage point (Nielsen et al., 2012) but this is limited to a small number of fishing grounds and, given the low frequency of entanglements for a given net, is impracticable. Another option would be to use biologging tags which can provide exceptionally high-resolution data on behaviour, including 3D underwater tracks and acoustic behaviour (e.g. Tyack et al., 2006; Wisniewska et al., 2016). However, tagging wild animals is difficult and they may never approach a net, leading to no relevant data being collected.

All toothed whale species studied thus far produce transient pulsed sounds (clicks) to hunt and sense their surroundings via echolocation (Au, 1993). By deploying acoustic listening devices that can record these clicks, we can detect animal presence, classify species and call type (e.g. Roch et al., 2021), a methodology which is broadly termed passive acoustic monitoring (PAM). PAM provides a powerful, non-invasive approach to study soniferous species and is advantageous in that it allows for the monitoring of a specific area of interest (such as in the immediate vicinity of fishing gear Bayless et al., 2017), enables long periods of recording, is relatively unaffected by weather and light conditions, and can be used to detect behavioural cues, such as foraging and social interaction. Acoustic data can also be used to determine the positions of animals underwater, thereby providing a potential method to obtain fine-scale acoustic and 3D movement data. Tracking beaked whales in deep water (Gassmann et al., 2015), localising multiple sperm whales (Hirotsu et al., 2010) and quantifying the behaviour of porpoises around tidal turbines (Gillespie et al., 2021) are just some of the many potential applications for acoustic localisation; however, despite the potential of this technology, it has only rarely been used to study fisheries interactions with toothed whales (Higashisaka et al., 2018; Maeda et al., 2021; Tiemann et al., 2006).

Harbour porpoises are the most abundant cetacean in UK waters (Hammond et al., 2013) and they also have the highest bycatch rates, with around 1,000 killed annually in UK fisheries (Kingston et al., 2021). They are highly soniferous animals, producing clicks nearly continuously (Linnenschmidt et al., 2013). Porpoises utilise a distinct narrow-band high frequency (NBHF) click for echolocation with a peak frequency centred at around 130 kHz and −3 dB bandwidth of ~16 kHz (Mohl & Andersen, 1973; Teilmann et al., 2002). Unlike many toothed whale species, harbour porpoises do not produce lower frequency tonal vocalisations for social interaction; instead their entire vocal repertoire uses only NBHF clicks with behavioural cues encoded in the rate and amplitude of click trains, for example foraging buzzes and communication calls are identifiable by amplitude and different ranges of inter-click intervals (Clausen et al., 2011; Sørensen et al., 2018). Acoustic data can thus be used to determine whether harbour porpoises are present, infer aspects of their behavioural state and, if the correct configuration of equipment is used, calculate their precise underwater location. Despite this potential, there are only a limited number of studies in which PAM has been applied to study porpoise (or indeed other toothed whales species) bycatch and, of these, the majority have focussed on testing mitigation measures (e.g. Cox & Read, 2004) and/or broad-scale behaviours such as the number of detected foraging buzzes (e.g. Mackay, 2011). Only a few studies have used localising PAM devices to provide insights into porpoise movements around set nets (Higashisaka et al., 2018) and foraging behaviours around gill nets (Maeda et al., 2021). However, as these studies collected bearing data from stereo loggers, it was only possible to obtain relatively coarse localisation information.

There is evidence that both captive (Kastelein et al., 2000) and wild porpoises (Nielsen et al., 2012) can visually and/or acoustically detect nets at sufficient range to avoid them. Thus, harbour porpoise bycatch is likely not simply a case of animals being unable to detect nets but involves hitherto unknown underlying behaviours that potentially lead to dangerous encounters with nets. To describe these likely complex behavioural and ecological interactions, and thus understand the risk factors for porpoise (and other toothed whale) bycatch, there is a requirement for much finer scale behavioural data (accurate 3D underwater tracks) around nets than has been previously collected. Here we describe a compact and easily deployable PAM system, that can be attached at the time of active fisheries gear deployment, to track the 3D movements and acoustic behaviour of harbour porpoises and other echolocating small cetaceans, revealing insights into fine-scale behaviours around actively fishing static nets.

2 | MATERIALS AND METHODS

Determining the position of an animal from received vocalisations (acoustic localisation) can be achieved via a variety of methodological approaches. One of the most common is to calculate the time difference of arrival (TDOA) between a vocalisation received on a number of distributed hydrophones (a hydrophone array) of known location. An ideal hydrophone array for 3D localisation must contain at least four (but ideally many more) hydrophones which are spatially distributed (in latitude, longitude and depth) as far apart as possible while also ensuring that vocalisations will consistently ensonify a sufficient number of hydrophones to allow the source location to be resolved. However, deploying a large number of widely spaced, time-synchronised hydrophones at precisely known positions on an operational gill net is not logistically practical. An alternative approach was therefore adopted which utilised two free floating micro-aperture tetrahedral hydrophone clusters combined with orientation and depth sensors (Figure 1). Each hydrophone cluster enabled the calculation of relative 3D vectors (a horizontal and vertical bearing) to a received echolocation click. The data from the orientation and depth sensors allowed each vector to be geo-referenced and the absolute 3D locations of received vocalisations could then be resolved by calculating the crossing point of two vectors from two adequately separated clusters (Figure 1). The hydrophone clusters and orientation/depth sensors were packaged with autonomous acoustic recorders to create a compact recording device which could be practically deployed on the headline of a gill net. If a porpoise was within localisation range of the devices (see Section 2.4), its position could be continuously recalculated for each received echolocation click and thus its 3D movement tracked over time, enabling fine-scale behavioural data to be obtained.

2.1 | Hardware

Each recording device was subject to constant water movement and so its orientation and depth were continuously changing. To allow for geo-referenced vectors to be accurately calculated, each device had to therefore record time-synchronised depth and orientation data along with four channels of acoustic data.

SoundTrap 4300 devices were used as the basis of the recording system (Ocean Instruments, www.oceaninstruments.co.nz). These four-channel recorders have a maximum sampling rate of 384 kHz, 16-bit resolution, a 2V pp ADC range, an anti-aliasing filter at 160 kHz and 256 GB of storage. An onboard lossless X3 compression algorithm (Johnson et al., 2013) reduced the size of wav files by a factor of ~4, and thus each SoundTrap (as configured here) was typically capable of 4–5 days of continuous recording. An array of four custom-built hydrophones attached to a 3D-printed graphite SLS frame in a tetrahedral configuration with an average aperture of 4 cm was mounted on each SoundTrap. Each hydrophone consisted of a potted 10mm diameter spherical piezo electric element with a sensitivity of approximately −201 dB re 1V/μPa. ETEC 040527D preamplifiers (ETEC, Denmark) provided 20 dB of gain (for an overall clipping level of ~181 dB re 1 μPa pp).

An external sensor package was custom designed and built to allow the SoundTrap to record depth and 3D orientation (heading, pitch and roll) data to allow for the geo-referencing of localisation data. The internal electronics comprised a custom circuit board based around a Sparkfun Pro Micro microcontroller (Sparkfun Ltd, USA) that recorded the sensor data, which were then transmitted to the SoundTrap using RS-485 protocol. The SoundTrap's firmware was modified to read and store the sensor package data at a sample rate of 25 Hz, alongside the current sample time so that orientation data were sample synchronised with acoustic recordings. The orientation sensor was an XSens MTi-3 (first and second generation) (XSens) which recorded data from triple-axis magnetometer, accelerometer and gyroscope sensors, and ran an onboard sensor fusion algorithm to calculate heading, pitch and roll. The onboard sensor fusion algorithm compensated for in situ magnetic field fluctuations and gyroscope drift, providing accurate and reliable geo-referenced orientation data (heading accuracy 1° and pitch accuracy 0.1°). The pressure sensor (MS5837-30BA; Blue Robotics) allowed the depth of the device to be calculated with a resolution of 2 mm and maximum depth-rated to 300 m.

2.2 | Deployment and recovery on a gill net

The recording devices were successfully deployed four times from a fishing boat (<10 m) in an area off the south coast of Cornwall, UK, during normal fishing operations. Both devices were attached to the floatline of the net separated by a distance of 20–60 m (note: the straight-line distance between the devices underwater depended on how the gill net settled on the seabed after deployment). The hydrophones were housed in 6-mm thick HDPE pipe for protection

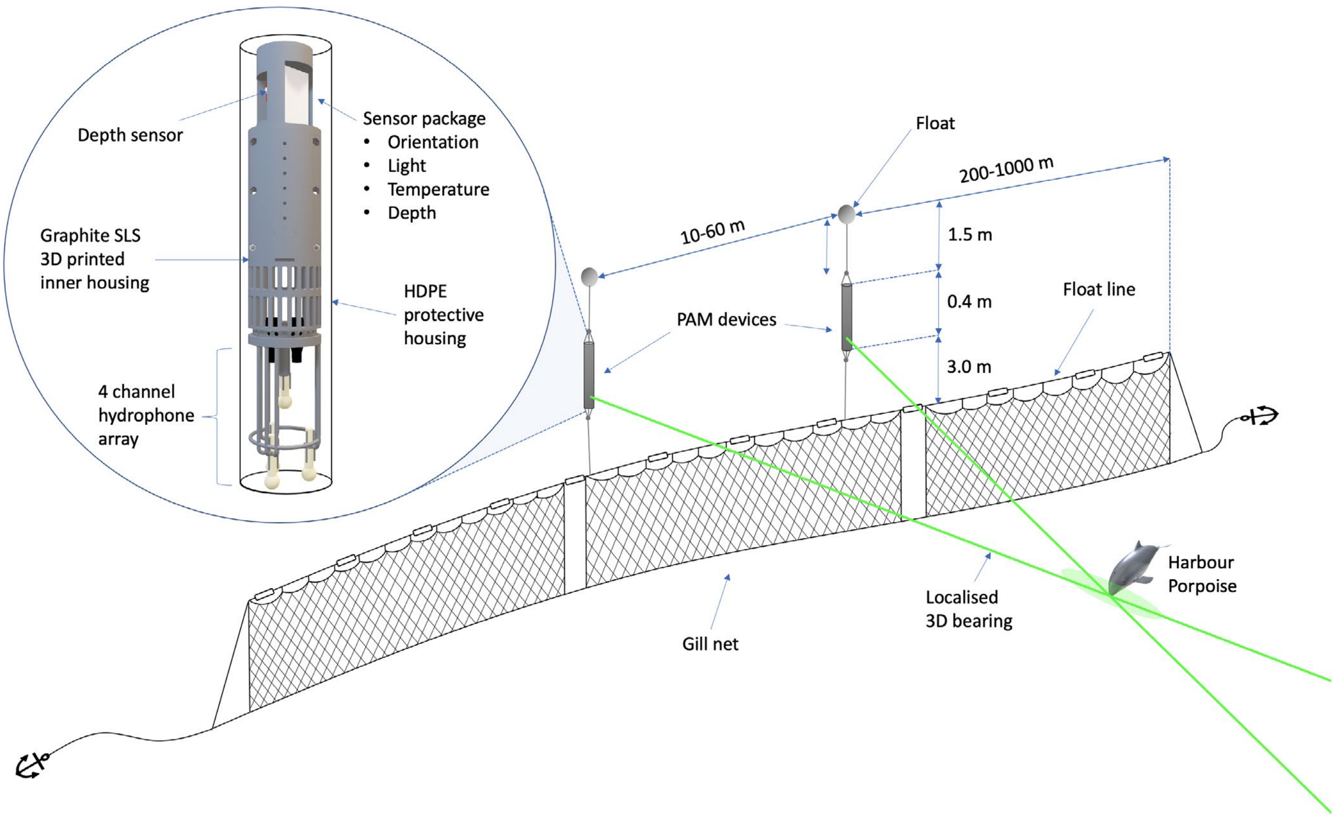


FIGURE 1 Diagram of the localising array (not to scale). Two recording devices were attached to the floatline of a gill net via a 3 m strop line. The recording devices were kept slightly positively buoyant using a small float, allowing them to maintain position in the water column above the floatline without deforming the net. Each device contained a tetrahedral four-element hydrophone cluster which enabled the calculation of 3D localisation vector to the source of a received sound. As a given deployment involved two devices, there was effectively an 8-channel hydrophone array mounted on the net. If both devices detected the same click, the point at which the two vectors intersected indicated the instantaneous 3D location of the animal. Animal movement patterns could then be inferred by interpolating these 3D locations

and clipped to the gill net floatline on a 3 m length of 8-mm braided rope (Figure 1). An incompressible float 125 mm long (Nokalon 5″ trawl headline float [Reg 34758] 630 g buoyancy) was positioned about 1.5 m above both recording devices to help them maintain position above the net in any tidal flow; the slight overall positive buoyancy of each buoy/recorder also minimised any deformation of the nets' fishing profile. Immediately prior to each deployment, the outer housings of each device were tapped against one another to allow for the initial synchronisation of their internal clocks, and then deployed over the stern of the vessel as the nets were being shot; this minimised any risk of instrument entanglement as the net and devices settled on the seabed. The recording devices were recovered when the vessel returned to haul its nets.

2.3 | PAM analysis

2.3.1 | Software workflow

Acoustic data were analysed in PAMGuard 2.00.16e (www.pamguard.org) to automatically detect transients, calculate TDOA measurements within each hydrophone cluster and classify possible porpoise clicks. The resulting transient detections along with their TDOA measurements were imported into MATLAB v2021a (The Mathworks; www.mathworks.com) using the PAMGuard library for MATLAB (https://github.com/PAMGuard/PAMGuardMatlab) and porpoise positive 10 s (ppts) calculated for each device to provide a broad overview of each dataset (see S1.3).

A manual analyst then used PAMGuard's visualisation and annotation tools to mark out and verify porpoise click trains, foraging buzzes/communication calls (inter-click interval [ICI] < 16 ms—from here on referred to collectively as buzzes) and cavitation transients from the deployment vessel. Porpoise encounters in which there were at least 100 detected clicks over a 2-min period were considered candidate encounters for localisation. Porpoise click trains were imported into MATLAB and time aligned by comparing similar ICI patterns in click train sequences simultaneously detected on both devices allowing coherent clicks to be matched (see S1.2). The data from each sensor package were imported into MATLAB and the geo-referenced orientation and depth of the hydrophone clusters were then calculated at the time of each detection.

Orientation data from the sensor packages of each recording device and GPS data from the deployment vessel were used to calculate the latitude and longitude of each recording device on the seabed as detailed in Section 2.3.2.

The time-aligned click trains, geo-referenced hydrophone arrays and latitude and longitude of the recording devices formed the input for a particle filter-based localisation algorithm (see Section 2.3.3) (implemented in MATLAB [Marín, 2022]) which calculated the geo-referenced 3D porpoise tracks around the gill net. A graphical representation of the analysis workflow is shown in Figure 2 and more detailed software settings are available in S1.

2.3.2 | Geo-referencing device position

Although the data from the sensor package compensates for changes in orientation and depth for each recording device, the location of each device on the seabed (once the net has settled and the devices are no longer moving ~10 mins after deployment) is still required for localisation to be possible. An approach similar to that used by Gassmann et al. (2015) was used to calculate the latitude and longitude of each device. This involved the fishing vessel undertaking some additional manoeuvres near the recording devices after their initial deployment and usually required ~15 min to complete. The vessel's track during these manoeuvres was recorded by a handheld Garmin eTrex Legend HCx GPS (Garmin, USA). The known location of the moving boat, together with the calculable localisations of the transients detected from the boats' propellor cavitation, allowed the location of each device on the seabed to be determined (see S2 for details). These locations were assumed to be fixed for the duration of the deployment.

2.3.3 | Localisation and tracking

A porpoise must ensonify at least two of the recording devices for an instantaneous 3D location to be calculated. One analysis approach mirrors the conceptualisation of crossed bearings shown in Figure 1, that is when both devices are ensonified, 3D locations are determined and multiple consecutive locations constitute an animal track. However, this method negates the use of partial location information when just one device is ensonified. To address this, a localisation framework was developed which, rather than localising only simultaneously detected clicks, instead calculated the most likely animal track based on the evolving state of click trains detected on both devices.

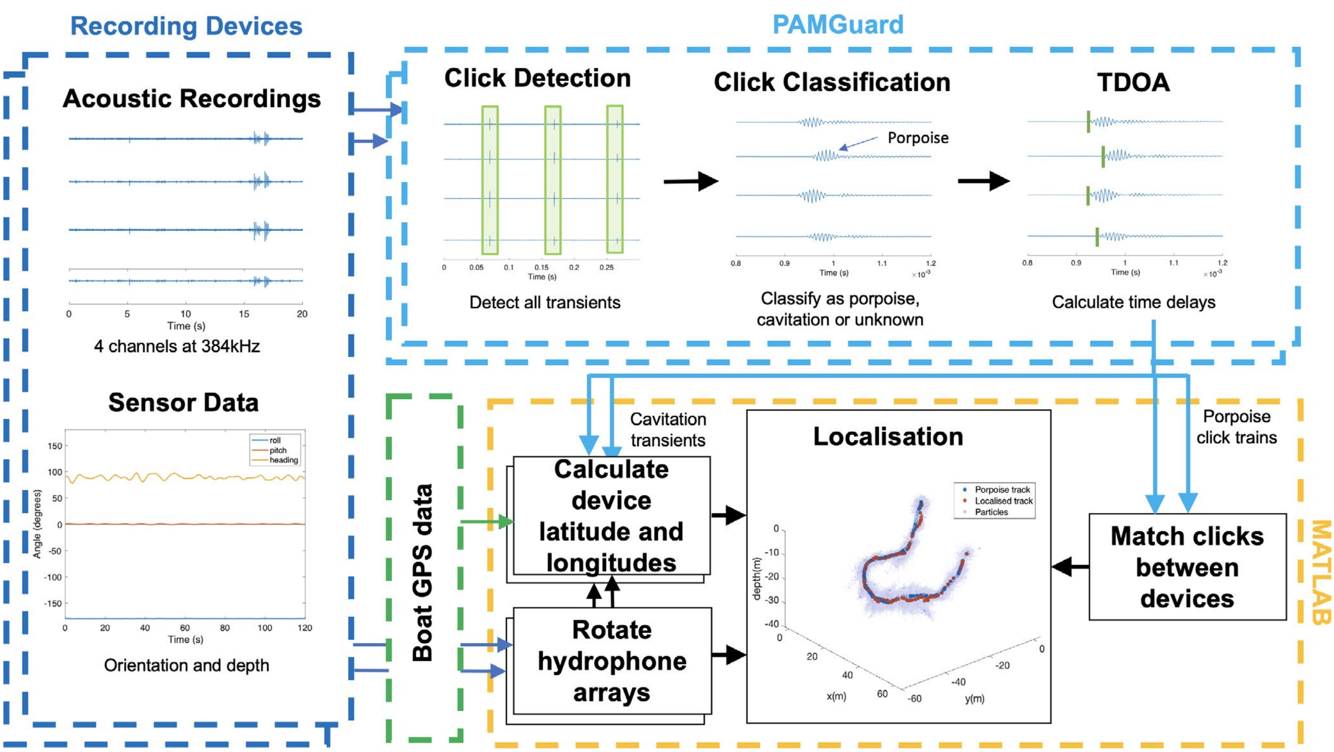


FIGURE 2 The software workflow used to calculate dive tracks from acoustic data. Each recording device recorded acoustics, and device orientation and depth. Porpoise click trains and cavitation transients were extracted from the acoustic data using PAMGuard. The latitude and longitude of each device were calculated using the detected cavitation transients, vessel GPS data and orientation data. Using depth and orientation data from the sensor packages, this then allowed the precise geo-referenced (*x*, *y*, *z*) position of each hydrophone element to be calculated for every detected click. The time delay of arrival (TDOA) of detected porpoise clicks and hydrophone locations formed the input for a particle filter localisation algorithm which calculated the position of detected harbour porpoises. Layered boxes indicate processing that takes place separately for each PAM device

The tracking algorithm was based on a particle filter, and works by randomly producing a set of N particles $\{\alpha_0^{(i)}, i = 1{:}N\}$ which are distributed in (x, y, z) around an initial location. The particle filter starts from the first click detected on both devices with initial location determined using a discrete localisation method. All clicks detected 2 s after the first click are passed to a simplex-based localisation algorithm, where the minimisation function is a slightly modified version of that used in Macaulay et al. (2017) which incorporates multiple clicks (see S3).

Particles are initialised from this localised start location with a uniform set of weights $\{w_0^{(i)} = \frac{1}{N}, i = 1{:}N\}$.

Upon detection of a new click, particles from the previous iteration are resampled by their weight to form a resampled set of particles $\{\overline{\alpha}_{k-1}^{(i)}, i = 1{:}N\}$. A new set of particles $\alpha_t^{(i)}$ is then predicted from the resampled particles based on, in this case, a simple movement model of a harbour porpoise.

$$\begin{bmatrix} x_k^{(i)} \\ y_k^{(i)} \\ z_k^{(i)} \\ \dot{x}_k^{(i)} \\ \dot{y}_k^{(i)} \\ \dot{z}_k^{(i)} \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 & t & 0 & 0 \\ 0 & 1 & 0 & 0 & t & 0 \\ 0 & 0 & 1 & 0 & 0 & t \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} x_{k-1}^{(i)} \\ y_{k-1}^{(i)} \\ z_{k-1}^{(i)} \\ \dot{x}_{k-1}^{(i)} \\ \dot{y}_{k-1}^{(i)} \\ \dot{z}_{k-1}^{(i)} \end{bmatrix} + \begin{bmatrix} t^2/2 \\ t^2/2 \\ t^2/2 \\ t \\ t \\ t \end{bmatrix} a, \quad (1)$$

where x, y, z are the independent Cartesian co-ordinates of the porpoise and $\dot{x}$, $\dot{y}$, $\dot{z}$ are the velocity, or the derivative of x, y, z with respect to time (t), a is a normally distributed acceleration of a typical harbour porpoise with a mean of 0 and a standard deviation of σ_a and k represents concurrent time steps. A second stage ensures that none of the parameters are spatially or biologically impossible via Equation 2.

$$\begin{bmatrix} x_k^{(i)} \\ y_k^{(i)} \\ z_k^{(i)} \\ \dot{x}_k^{(i)} \\ \dot{y}_k^{(i)} \\ \dot{z}_k^{(i)} \end{bmatrix} = \begin{bmatrix} x_k^{(i)} \\ y_k^{(i)} \\ \max\left(\min\left(z_k^{(i)}, 0\right), z\left(x_k^{(i)}, y_k^{(i)}\right)_{seabed}\right) \\ \min\left(\dot{x}_k^{(i)}, v_{max}\right) \\ \min\left(\dot{y}_k^{(i)}, v_{max}\right) \\ \min\left(\dot{z}_k^{(i)}, v_{max}\right) \end{bmatrix}, \quad (2)$$

where $v_{\max}$ is the maximum speed of a harbour porpoise (4 m/s) (Otani et al., 2000) and $z\left(y_k^{(i)}, y_k^{(i)}\right)_{seabed}$ is the depth of the seabed at location $\left(x_k^{(i)}, y_k^{(i)}\right)$. This restricted particles to be between the sea surface and seabed, and prevents unlikely porpoise swim speeds.

For each new particle, the travel time $T_{jk}^{(i)}$ required for a sound wave to travel from the particle location to every hydrophone j is calculated assuming simple linear propagation, that is $\{T_{jk}^{(i)} = \frac{d^{(i)}}{c}\}$ where $d_j^{(i)}$ is the distance from particle i to hydrophone j and c is sound speed (assumed to be 1,500 m/s see S4.5). The recorded orientation, depth and latitude/longitude location of each device allow the geo-referenced position of all hydrophone elements to be determined and thus accurate calculation of $d_j^{(i)}$ for each click detection.

The weights of each particle represent how likely the location is given the received data and are calculated by comparing the time delays calculated for the particle location to the observed time delays of both the recording devices at time k using Equation 3,

$$w_k^{(i)} = \sum_{n=1}^{Nd} \sum_{s \in S} \frac{\left(\tau_{n,k}^{(i)}(s) - t_{n,k}(s)\right)^2}{\varepsilon\left(snr_{n,k}\right)^2}, \quad (3)$$

where $\tau_{n,k}^{(i)}(s)$ is the time delay measurement between hydrophones defined by s which iterates over S, a set that contains all possible combinations of hydrophone pairs. In this case, each device has four hydrophones so $S = \{(1,2), (1,3), (1,4), (2,3), (2,4), (3,4)\}$. $\tau_k^{(i)}(s)$ is then the time delay between sounds arriving at hydrophones defined by each element in S. For example, when $s = (1, 2)$, $\tau_k^{(i)}(s) = T_{1k}^{(i)} - T_{2k}^{(i)}$. ε is the standard error in time delay measurements which is a function of the sound speed error (10 m/s) and the signal-to-noise ratio ($snr_{n,k}$) of the detection click on device n of Nd (i.e. the number of recording devices on the net) at time k (see Section 2.4.1). The weight is then calculated and summed for each recording device. The new weights of all particles are normalised so that $\sum_i^N w_k^{(i)} = 1$.

Thus, the particle filter creates a cloud of particles which evolves over time representing the track of the animal; the weighted mean location of particles at each click detection was considered to be the location of the animal and the 95% confidence interval of particles in each dimension the corresponding 3D uncertainty in the track (Arulampalam et al., 2002; Ward et al., 2003). The particle filter algorithm was run 10 times for each set of time delays using 500 particles per run and results then averaged to produce a track and uncertainty estimates.

2.3.4 | Click-by-click localisation

The performance of the particle filter was compared against a click-by-click localisation algorithm. Unlike the particle filter approach, the click-by-click approach only considered individual clicks coherently detected on both devices. 3D locations were resolved using a simplex minimisation approach based on the received time delays on both devices (see Macaulay et al. 2017 for details).

2.3.5 | Localising buzzes

Buzzes are difficult to localise because they are produced at lower source levels, which usually results in a low received signal-to-noise ratio (SNR). The location of buzzes was therefore calculated as the point on the dive tracks that was closest in time to the buzz. If there was no dive track point within 3 s of the buzz, then its location was considered as unknown in subsequent analysis.

2.4 | Localisation accuracy

The range at which a localising array can accurately track an animal is usually significantly less than the maximum detection range. In the case of porpoises, which produce highly direction clicks, there is a trade-off between detecting clicks coherently on a sufficient number of hydrophones to allow for a location to be calculated and spacing the hydrophones widely enough apart to increase localisation accuracy. Macaulay et al. (2017) suggested that a maximum 30–40 m hydrophone separation resulted in a large number of coherently detected clicks and maximum localisation range of ~200 m (the detection range of porpoises can be up to 1 km; Villadsgaard et al., 2007); however, this was for a wide baseline vertical array. It was therefore necessary to quantify the potential localisation error for the two micro-aperture hydrophone arrays by integrating time delay uncertainty into the localisation calculations using broadcast trials and performing simulations to test the particle filter algorithm.

2.4.1 | Quantifying time delay uncertainty

The particle filter model requires an estimate of time delay uncertainty ($\varepsilon\,(snr)$in Equation 3). The standard error in time delay measurements was estimated at the start of the first deployment by broadcasting simulated porpoise clicks from a fishing vessel using a custom transducer deployed using a rope and terminal weight at 5 m depth. The output set-up is described in detail in Macaulay et al. (2017). To minimise engine noise during these trials, the fishing vessel motored against the tide and then broadcasted the clicks while drifting past the estimated location of the devices. The track of the drifting vessel was recorded using a handheld GPS.

The predicted time delays for each broadcast click were determined using the location of the transducer (from GPS and dive computer) and geo-referenced hydrophone positions. These were compared to the recorded (observed) time delays and the mean difference between the observed and predicted time delays used as a measurment of time delay error with respect to recieved SNR. A constant sound speed uncertainty of ±10 m/s was added to each time delay error measurment and a function $\varepsilon\left(snr_{nk}\right)$ generated; this was used as the uncertainty in time delay measurements for subsequent localisation calculations in Equation 3 (see S4.4). Note that it was critical to up-sample clicks (here, by a factor of 4) to allow for accurate time delay and bearing estimation of the NBHF clicks (Gillespie & Macaulay, 2019).

2.4.2 | Simulation of particle filter accuracy

The particle filter-based localisation approach detailed in Section 2.3.3 considered acoustic data over an entire porpoise encounter in conjunction with an animal movement model. Testing the true 3D localisation accuracy of the PAM array would therefore require a broadcast system which was capable of both broadcasting directional clicks and imitating the diving behaviour of a porpoise. This was impractical and thus a simulation-based approach was employed to test the performance of the particle filter algorithm.

Dive tracks of harbour porpoise were simulated assuming a start location, vertical dive angle, bottom depth and duration drawn from pre-defined distributions (see S4.6 for details). Simulated clicks were generated at regular intervals along the track and corresponding received TDOAs calculated for each recording device. The animal's instantaneous orientation on the track, source level and beam profile (Macaulay et al., 2020) were also used to calculate a received level on the recording devices, allowing the calculation of SNR and thus an estimate of TDOA error for each emitted click. The simulated TDOA values and error estimates were then passed to the particle filter algorithm alongside array positions with an added random offset in the heading orientation of ±1° (the manufacturers quoted heading uncertainty for the orientation sensor) to simulate potential uncertainty in the orientation sensor measurements. In addition, 20% of clicks were randomly removed from each device to simulate non-synchronised detections. The TDOA values were also passed to an individual click-by-click localisation algorithm, which used a Simplex minimisation algorithm to determine a location (see Section 2.3.4). The resulting localised tracks from the particle filter and simplex localisation were compared to the simulated dive tracks to estimate localisation accuracy.

Additional assessments of localisation accuracy can be found in S4.

3 | RESULTS

3.1 | Device locations

Over four deployments a total of 7.3 days (4 TB) of continuous recordings were collected (Table 1). Figure 3 shows the location of the recording devices and gill nets. Porpoises were detected on every deployment; however, only a subset of total number of porpoise positive 10 s (ppts) were suitable for localisation.

In total, over the entire dataset, 13 porpoise encounters were suitable for localisation, resulting in 2.3 hr of recordings containing echolocation click trains and porpoise tracks. A low-profile tangle net (10.5″ [267 mm] monofilament mesh, 10.5 meshes high with a braided floatline with integral flotation) was used in all deployments.

3.1.1 | Localisation accuracy

Figure 4 shows a click spectrogram and bearing–time plot from a single recording device during a porpoise encounter. The bearing–time

TABLE 1 Summary of deployments. The distance between devices is the straight-line distance. The total number of porpoise positive 10 s (ppts) during the entire recording period for each device is shown alongside the total number of ppts which were suitable for localisation

Trip no.	Start date time	Deployment duration (hours)	Separation between devices (m)	Water depth within 200 m range (min/max metres [ref. mean sea level])	Total no. ppts (device 1/2)	No. ppts suitable for localisation (device 1/2)
1	02 October 2018 09:35	50.7	13.4	25.6/31.0	239/282	172/215
2	11 June 2019 10:30	55.3	53.5	19.4/29.3	38/45	11/17
3	11 November 2019 09:47	23.3	58.1	12.4/22.2	31/34	9/17
4	14 November 2019 09:48	48.3	50.8	17.3/27.2	631/514	99/113

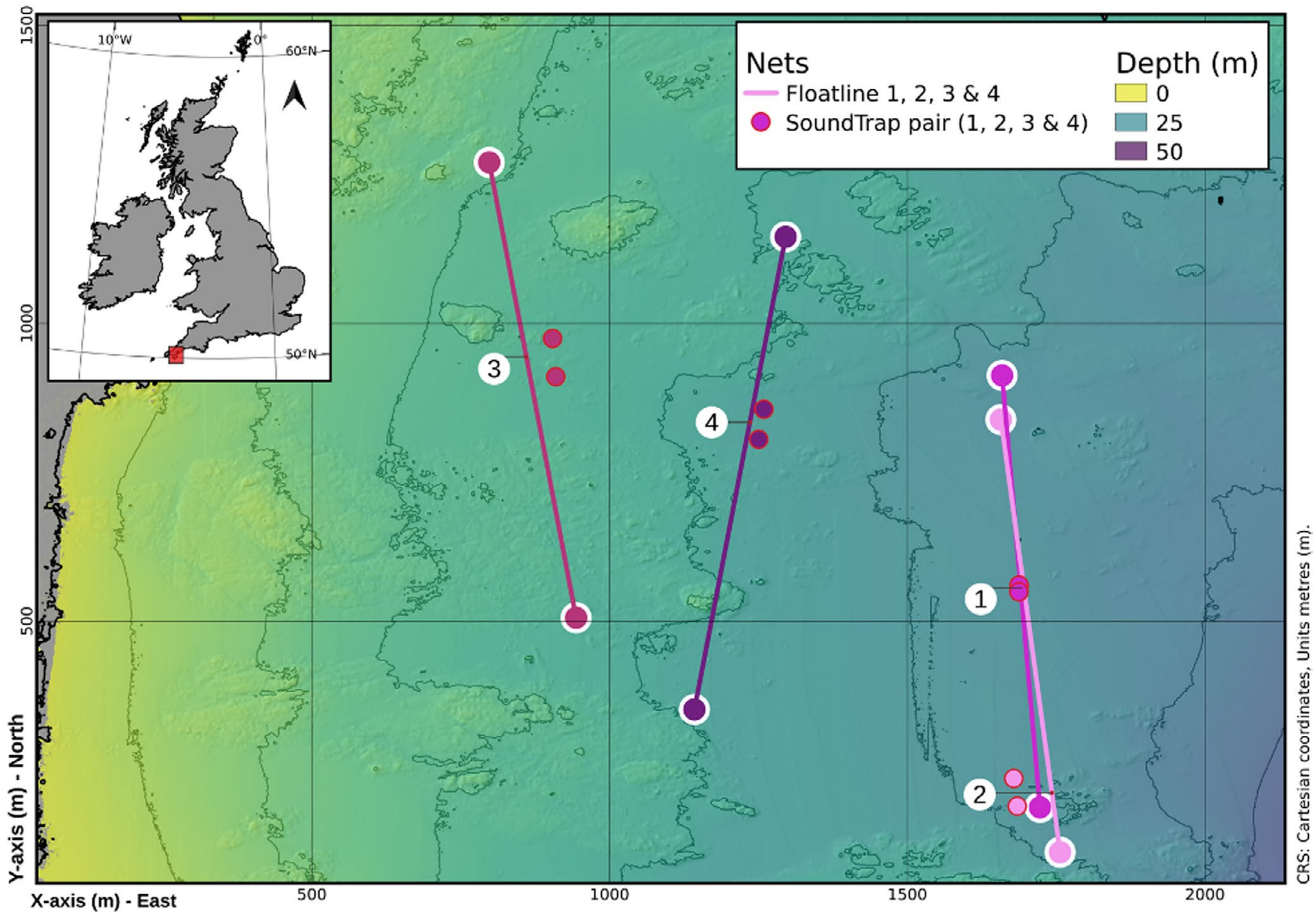


FIGURE 3 Net deployments and device locations. Round dots indicate the ends of the gill net, and the smaller circles indicate the estimated position of the recording devices on the nets when settled on the seabed. Different deployments are colour coded. The net floatline is shown as a straight line between the start and end points of the shooting operation; however, in reality the final net position (and associated devices) will be affected by prevailing tidal and weather conditions and may drift significantly as it sinks and settles on the seabed. Note that in deployment 1 the devices settled close to each other because the net was deployed at a slower speed than usual. The map was generated in QGIS v3.10 QGIS.org, 2021. QGIS Geographic Information System. QGIS Association. http://www.qgis.org. Bathymetric data were provided by the UK Hydrographic Office, Admiralty Maritime Data Solutions Seabed Mapping Service (https://seabed.admiralty.co.uk/)

plot shows both device and geo-referenced bearings alongside the heading measurements from the orientation sensor. The change in heading is reflected in the device referenced data but the geo-referenced bearing track shows a smooth change in bearing, which is what would be expected from an animal passing the device. This indicates that the orientation sensor was accurately compensating for device movement.

Error surfaces for both the particle filter and click-by-click localisation approaches are plotted in Figure 5. Each error surface shows the median error in range/depth between the true

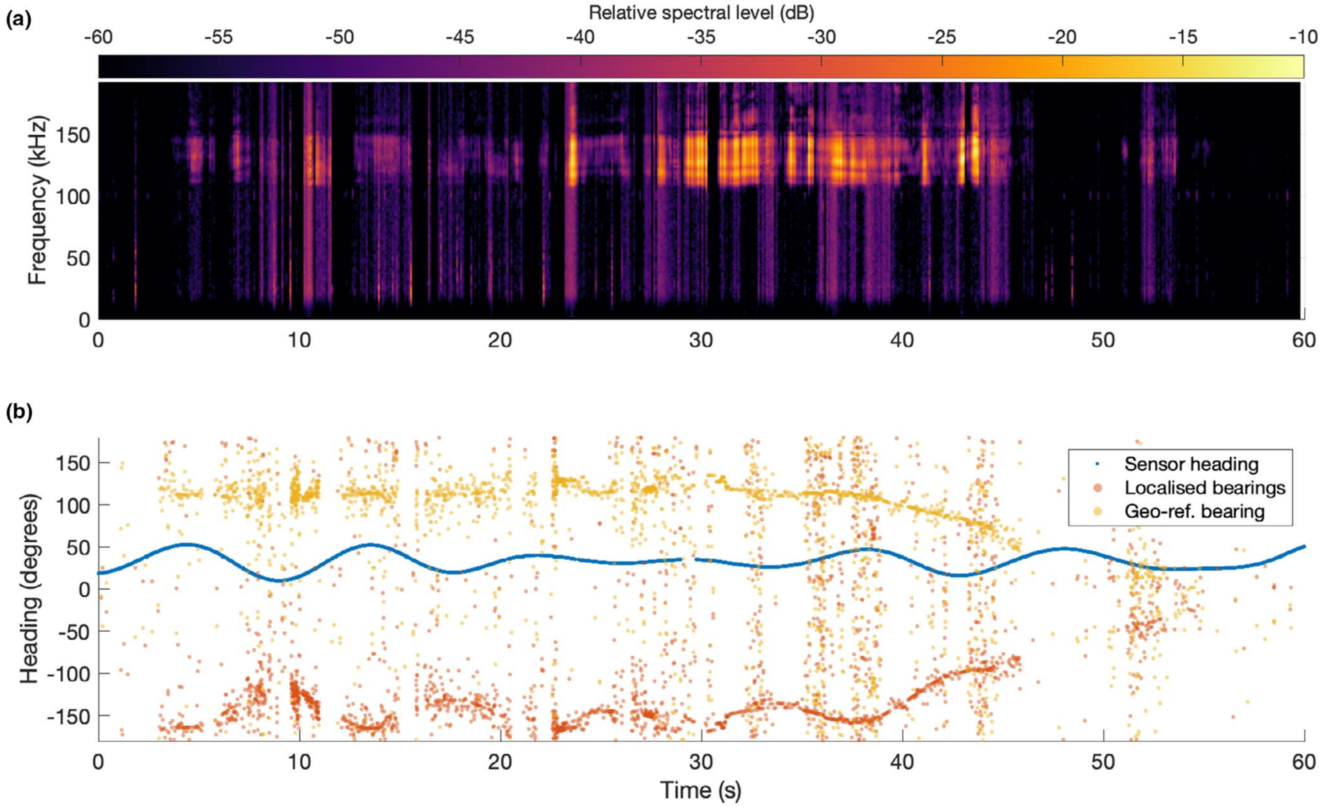
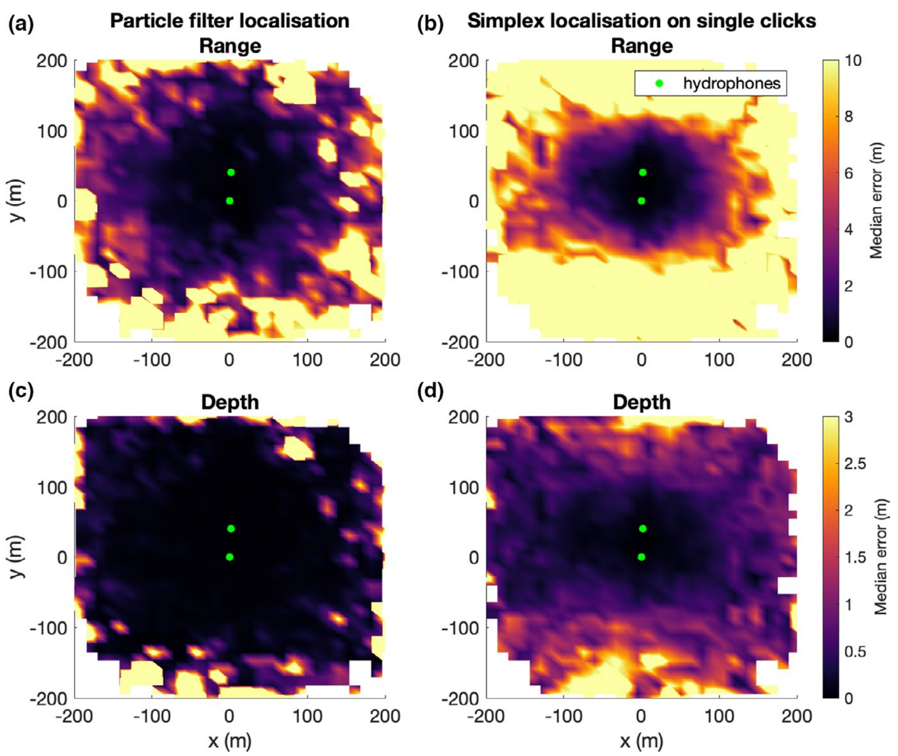


FIGURE 4 Data received on one of the recording devices during a porpoise encounter. Plot (a) shows a spectrogram of all detected transients clearly indicating significant energy in the 100–150 kHz band typical of porpoise clicks. Plot (b) shows the calculated bearings of clicks and heading sensor data. Both the device referenced bearings (red) and geo-referenced bearings (yellow) are shown alongside heading sensor data (blue)

FIGURE 5 The median range and depth error for simulated dive tracks using a particle filter (a, c) and click-by-click localisation (b, d). In total, 1,500 animal tracks were simulated around two recording devices separated by 40 m—the error surface is for all localisations below the PAM devices, that is those at a depth close to the net. Green circles represent the position of the two PAM devices. The particle filter clearly outperforms the click-by-click approach with accurate localisations possible in a ~100 m radius around the net



and localised locations of simulated porpoise tracks below 15 m depth (the net depth in the simulation). The particle filter algorithm performs significantly better in range and depth estimation on simulated data compared to a click-by-click approach, allowing animals to be accurately localised in a roughly uniform 100 m radius around a hydrophone cluster.

TABLE 2 All porpoise encounters over the four deployments. The number of detected clicks and buzzes are the number of manually verified clicks and buzzes within each encounter. The track time is the total time over which the particle filter was able to determine the 3D location of a porpoise. The number of localised buzzes and track points within 10 m of the net floatline assumed that the floatline was 1 m above the seabed. Minimum and maximum estimates for the number of localised buzzes and track time within 10 m are based on the estimated localisation errors. Note that a letter in the encounter serial number indicates an encounter with more than one animal present

Start time	Encounter duration (s)	Track duration (s)	No. detected clicks (device 1/device 2)	No. detected buzzes (device 1/device 2)	No. buzzes within 10 m of floatline (min./max.)	Track time within 10 m of floatline (s) (min./max.)	Encounter serial no.
03 October 2018 04:14:18	606	194	2,087 (800/1,287)	45 (18/27)	9 (2/17)	48.2 (6.2/151.4)	001
03 October 2018 19:43:05	482	186	3,557 (1,887/1,670)	32 (29/3)	0 (0/0)	0.0 (0.0/0.2)	002
04 October 2018 06:29:39	2,329	539	11,464 (4,583/6,881)	152 (69/83)	1 (0/3)	37.8 (2.6/76.4)	003
01 December 2018 17:47:11	380	98	1,652 (757/895)	0 (0/0)	0 (0/5)	10.4 (5.0/17.2)	004
11 November 2019 14:58:07	232	59	1,303 (902/401)	11 (11/0)	4 (0/5)	13.6 (0.0/26.2)	005
14 November 2019 12:48:59	624	250	3,545 (2,176/1,369)	812 (381/431)	5 (0/11)	37.4 (0.0/70.2)	006A
14 November 2019 12:48:59	624	149	3,545 (2,176/1,369)	126 (106/20)	10 (5/16)	28.4 (18.6/41.4)	006B
14 November 2019 21:14:03	726	78	1,181 (778/403)	13 (3/10)	0 (0/0)	0.0 (0.0/0.0)	007
15 November 2019 11:07:21	293	105	1,597 (1,383/214)	1 (0/1)	1 (1/1)	19.2 (14.4/19.2)	008
16 November 2019 00:14:07	132	17	956 (740/216)	5 (2/3)	0 (0/0)	0.2 (0.0/0.4)	009
16 November 2019 00:34:51	366	136	2,597 (1,249/1,348)	43 (14/29)	0 (0/2)	0.0 (0.0/1.0)	010
16 November 2019 00:52:30	446	107	976 (389/587)	14 (6/8)	5 (0/6)	47.8 (2.8/100.8)	011
16 November 2019 01:14:29	822	58	1,236 (725/511)	14 (3/11)	0 (0/0)	0.0 (0.0/0.0)	012

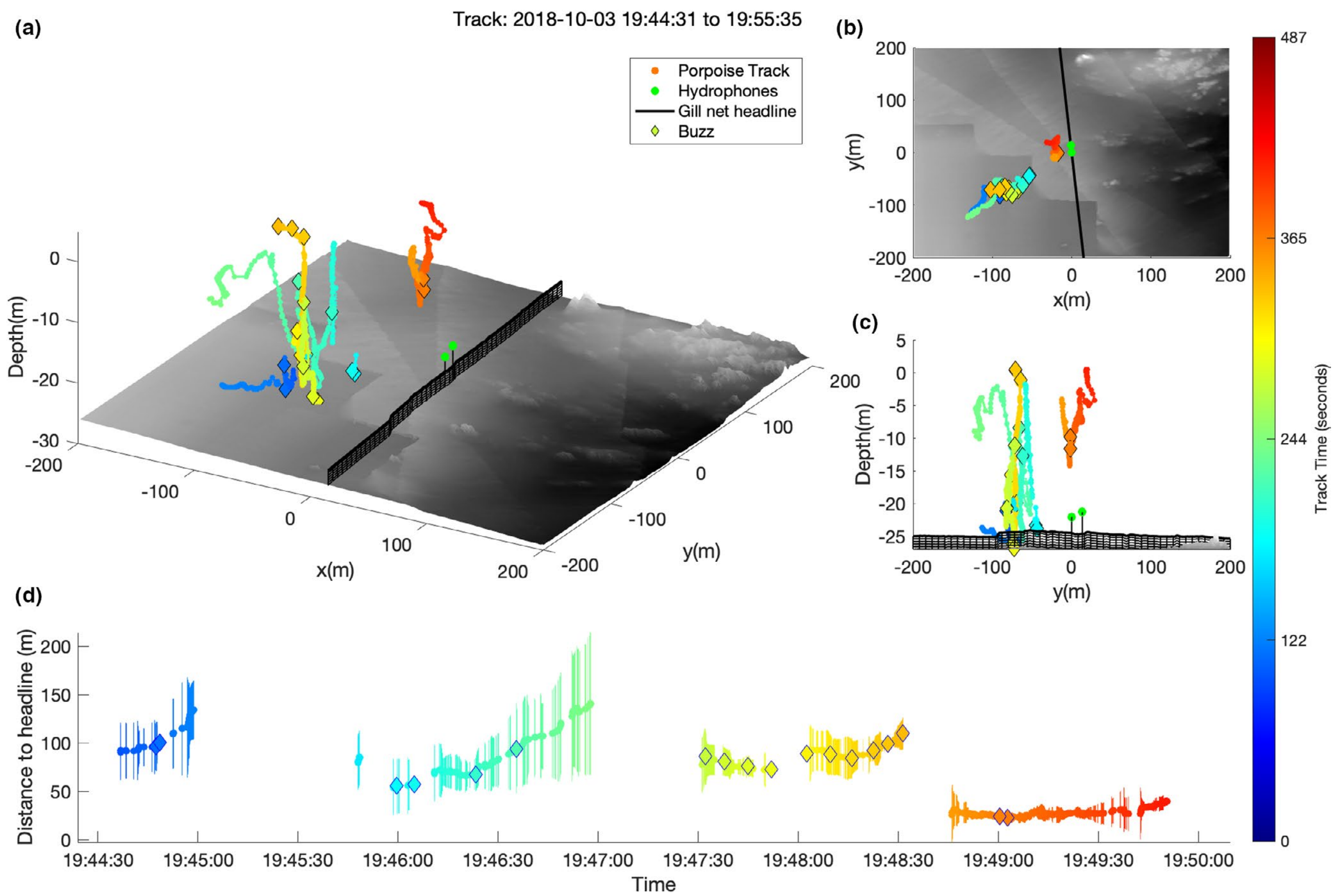


FIGURE 6 Example of a 3D dive track of a single harbour porpoise where the porpoise approaches but does not come within 5 m of the gill net. Plot (a) shows 3D view of the track, including bathymetry and the position of the gill net (black). Note that the gill net was assumed to be in line with the recording devices and 2 m above the seabed. Plot (b) is a top-down view, and plot (c) is the depth profile along the gill net. Plot (d) shows the range of the animal to the closest point on the headline of the gill net with estimated range errors (95% confidence interval). In this example, the animal initially swims away from the net but then turns around, approaches the net and likely moves away again

3.1.2 | Localisation data

All porpoise encounters during the four deployments are summarised in Table 2, including the number of detected echolocation clicks and buzzes. The duration of localised tracks and number of buzzes or calls within 10 m of the gillnet floatline are also shown—note that not all buzzes were localised and a porpoise could be present but not tracked if it was detected on only one device for an extended period (over 5 s). Thus, the number of buzzes and tracks within 10 m of the net floatline is likely a minimum estimate.

An example of the localised tracks during a porpoise encounter is shown in Figure 6. In this encounter, a porpoise is initially diving ~100 m from the net and then after the middle of the encounter (>244 s) appears to approach the net. Towards the end of the encounter (at ~300 s), the porpoise dove towards the gillnet and came within 5 m of the floatline, but then surfaced again. After this point, the animal is not detected suggesting that (because of its narrow beam profile) it is facing away from the net (i.e. moving away). Another dive track is shown in Figure 7, and in this example, a porpoise consistently dives close to the net producing buzzes nearby and at a variety of depths. Both examples demonstrate the detailed and varied behavioural information that can be obtained using this PAM methodology.

4 | DISCUSSION

We have demonstrated that a relatively low-cost PAM system can be practically deployed on actively fishing static nets during normal fishing operations to provide high-resolution information of porpoise movements and acoustic behaviour.

There are numerous benefits to using a PAM-based approach to record behaviour, including relatively low cost, comparative ease of use and the ability to autonomously collect behavioural data from any toothed whale within a specific area of interest. The system here was also highly practical; it could be deployed by a researcher during normal fishing operations and required only 15 min of additional boat time to allow the PAM devices to be located on the seabed.

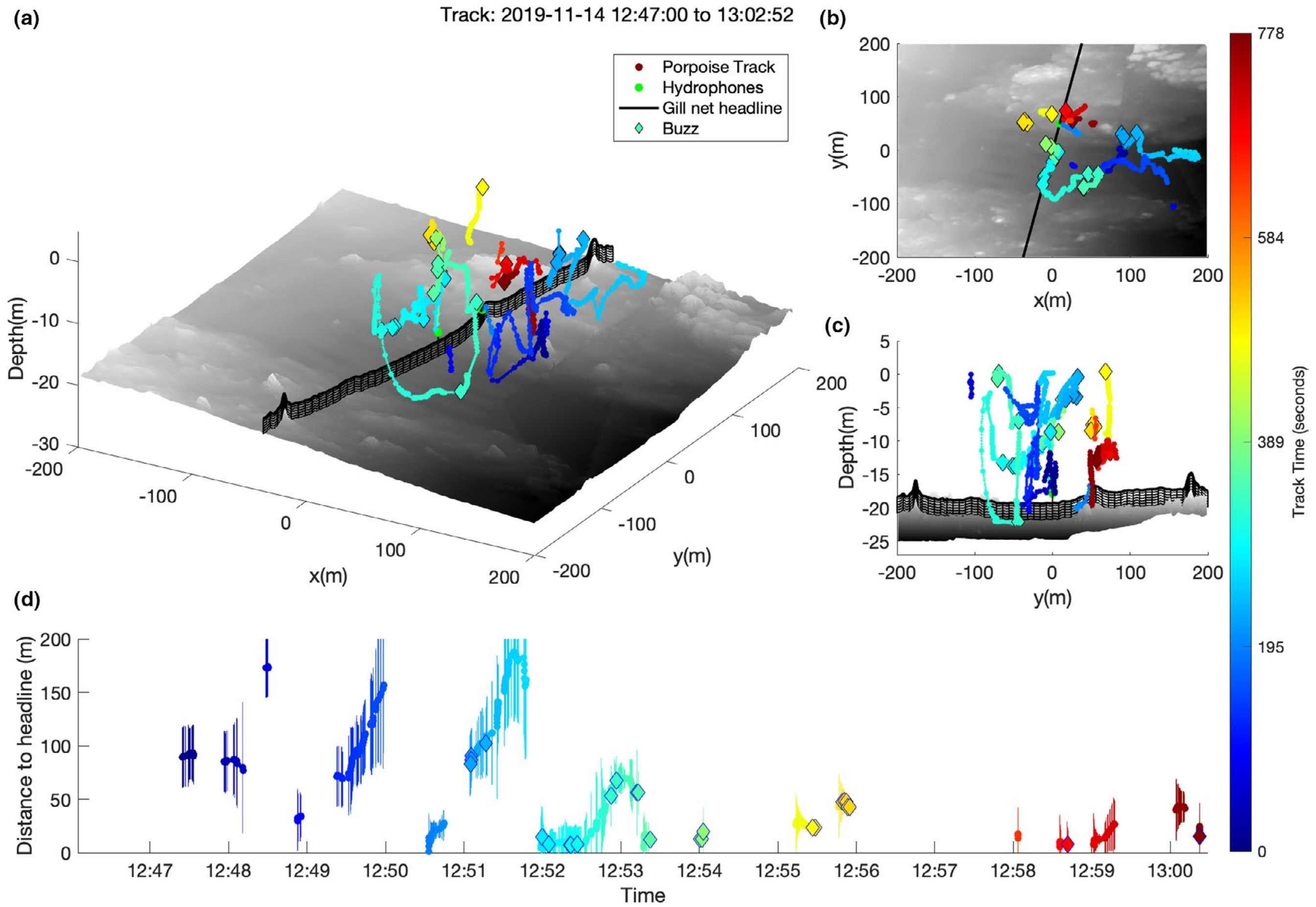


FIGURE 7 Example of a 3D dive track of a single harbour porpoise where the porpoise appears to be actively interacting with the gill net. In this example, the porpoise dives close to the net several times producing foraging buzzes (or possibly communication calls) throughout the water column and in the middle and towards the end of the encounter comes very close (<5 m) to the net

However, there are also limitations in using PAM which must be considered when deploying this localisation system in the future studies. For any PAM study, the probability of detecting and then localising an animal is dependent on the range to the animal (Marques et al., 2013) and so, for example, the close proximity of localised tracks around the nets recorded in Figures 6 and 7 and S5 may give a biased impression of how frequently porpoises were interacting with the net. Thus, control experiments with devices on their own mooring without a net should complement any future larger scale studies. Another important consideration is that the tracks collected by any PAM localisation study are often fragmented because the narrow beam profiles of toothed whales means that, at some orientations relative to the recording devices, they are essentially undetectable unless at very close range (Macaulay et al., 2020). Thus, while our system cannot provide the accuracy or the constant tracking data that might be achieved with tags, it allows behavioural data to be collected continuously at a specific targeted location. This provides the capability to collect a large dataset of track fragments near gill nets (or other at other locations) from multiple animals which, over time, allows for an accurate statistical picture of animal behaviour to be constructed.

Here we set out to demonstrate a proof of concept for tracking porpoise behaviour around gill nets, and in doing so collected the highest quality behavioural data ever recorded in a toothed whale bycatch study. The fine-scale movements that can be obtained by this system will allow researchers to explore a number of different aspects of toothed whales bycatch. For example, the continued deployment of this PAM system over large spatial ranges and temporal scales would provide a large dataset on toothed whale behaviour around nets that could form the basis of an exploratory model into bycatch risk. Fine-scale tracks and calibrated received levels could also provide unique insights into a toothed whale's acoustic sensory perception of nets during the typical encounter (see Malinka et al., 2021) helping us further understand why they might become entangled. In addition to investigating the natural behaviour of animals around nets, acoustic localisation could be used to help test mitigation strategies by resolving the behavioural basis which makes a mitigation measure effective. This would help us understand why mitigation measures work, or do not work, and thus could broadly predict how effective they are likely to be.

Finally, although this particular use-case has focused on gill nets, the methods described here have other applications for investigating bycatch in other fisheries (e.g. deployment in trawl nets) and/or any study which requires an easy to deploy acoustic localisation system. Harbour porpoises are a particularly challenging species for acoustic localisation because the low received SNR (due to relatively low source levels and high attenuation) and the multi-cycle narrow band nature of their clicks make accurate time delay calculation difficult (Gillespie & Macaulay, 2019). Thus, because this system was capable of tracking porpoises, it can be assumed that it is just as (or likely more) effective for other toothed whale species. This approach to acoustic localisation is therefore highly adaptable and can be utilised in any study which requires an understanding of the fine-scale behaviour of toothed whale species (or other consistently vocalising species) in a particular area.

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CONFLICT OF INTEREST

There is no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.M. and S.N. conceived the ideas and designed the methodology; J.M., R.S. and M.O. designed and constructed the hardware; A.K., J.M. and A.C. collected the data; J.M. analysed the data; J.M. and D.G. developed PAMGuard and MATLAB code; J.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/2041-210X.13828.

DATA AVAILABILITY STATEMENT

PAMGuard software and SoundTrap recorders are open source. Coding libraries, 3D print and PCB files are available on Zenodo 10.5281/zenodo.6045759 (Jamie Mac., 2022). Acoustic detections (processed PAMGuard data), GPS and sensor package data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.v9s4mw6xv. Note that the GPS locations have been altered to comply with data protection regulations but still allow for the methods to be replicated. The raw acoustic data (>4 TB) can be requested from the authors.

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SUPPORTING INFORMATION

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