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Research



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First detailed insights into harbour porpoise behaviour during a bycatch event

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Bycatch in static nets is the greatest cause of anthropogenic mortality in small cetaceans globally; however, the mechanism underlying how animals with highly sophisticated biosonars become entangled in nets is still poorly understood and represents a key information gap. During the deployment of a multi-hydrophone passive acoustic monitoring system, we tracked the three-dimensional movements and acoustic behaviour of harbour porpoises (*Phocoena phocoena*) during a rarely observed bycatch event. These data provide, to our knowledge, the first comprehensive insights into the behaviour of a harbour porpoise (or any small-toothed whale) prior to and during a bycatch event in static nets. It also included behavioural information related to a second animal that was in close proximity but did not interact with the net. The results indicated that the porpoises were foraging around the net prior to the bycatch event, that the by-caught animal lifted the net by approximately 7 m while entangled and that the two animals were potentially a social unit, with the surviving porpoise exhibiting unusual communication behaviour for several hours after the bycatch occurred. Understanding behaviours prior to and during a bycatch event could significantly improve bycatch mitigation strategies in static net fisheries, and this paper demonstrates a new method for how this can be achieved.

1. Introduction

Gill, entangling and trammel nets (collectively termed static, set, or passive nets) are widely used by commercial (large and small-scale), subsistence, and recreational fisheries throughout the world and are concentrated mainly in continental shelf waters [1]. While static nets are highly size selective with respect to target

species [2,3] and have lower habitat impact than mobile gears [4,5], they are often highlighted as a concern in relation to the accidental capture (bycatch) of endangered, threatened and protected (ETP) species. These include marine mammals [6,7], seabirds [8,9], turtles [10,11] and elasmobranchs [12,13].

Globally, more than 300 000 odontocetes (toothed whales) are estimated to be bycaught annually, and the majority of bycatch (84%) is attributed to static net fisheries [14]. Bycatch in static nets poses a conservation threat to many affected odontocete populations [15] and is considered the primary factor in the significant depletion of some populations [16,17]. In the United Kingdom (UK), small cetacean (dolphin and porpoise) bycatch in static nets is estimated to be approximately 1000 individuals per year [18].

Static nets are typically constructed of three main components: a weighted lead line to keep the gear on or near the seabed, mesh panels (typically monofilaments) that act as the catching element of the gear, and a buoyant float line to suspend the mesh panels in the water column [19]. The specific configurations (i.e. buoyancy regime, mesh size, mesh material, mesh panel length and height, mesh twine thickness, hanging ratio and weighting regime) and operational patterns (e.g. location, season, water depth, soaking time) of different static nets vary widely, and these varying attributes can affect the risk of bycatch within and across taxa [20]. Technical mitigation approaches have been developed and tested to try and reduce cetacean bycatch, including gear modifications such as the use of different net materials and mesh sizes (e.g. [21,22]) and gear attachments such as passive reflectors (e.g. [23]), acoustic diverters (ADDs; e.g. [24]) and light-emitting diodes (e.g. [25]). Some technical approaches may have limited applicability because of practicality, cost, species-specific efficacy and/or associated unintended consequences. For example, extensively used ADDs, which produce aversive sounds to deter animals from nets, may also introduce significant noise pollution [26,27] and/or attract non-target species, such as seals [28,29]. Increasing the output frequency of ADDs can make them audible to fewer species and reduce noise pollution because higher frequency sounds are absorbed more quickly in seawater. However, this approach means that more devices are required along a net to maintain effectiveness, which increases operational complexity and thereby reduces the practicality for routine use. Such trade-offs exist across existing technical mitigation approaches, which must achieve bycatch reduction levels sufficient to meet management and conservation objectives while simultaneously maintaining productive, profitable and safe fisheries.

Much of the existing scientific literature on ETP bycatch has focused on estimating mortality levels and undertaking bycatch mitigation studies (e.g. [7,30–31]). Less emphasis has been placed on investigating environmental, behavioural and operational factors associated with or causing bycatch occurrence [20,29]. Despite growing research and management attention on the topic, the specific details of what happens prior to, during and after bycatch events (which occur below the sea surface) remain largely unknown. Studies on the echolocation abilities of captive animals suggest that small cetaceans, which have highly sophisticated acoustic sensory abilities, can detect the presence of nets at ranges between 25 and 55 m for dolphins and less than 10 m for porpoises [33]. Some studies theorize that porpoises may not be able to detect nets at sufficient distances to avoid them; i.e. they have insufficient time to change direction, which may be further exacerbated by distraction during foraging or masking of weak echoes from the net by fish or other targets [33,34]. However, captive animals, on which many of these studies are based, generally click at lower source levels than wild animals [35,36], and studies of wild porpoises have recorded larger net detection ranges of greater than 80 m [37,38]. More recent studies on the ability of porpoises to acoustically discriminate between closely spaced targets suggest that porpoises should be capable of resolving both a fishing net and nearby prey [39], so acoustic masking of nets is unlikely.

Understanding the behavioural and ecological contexts, as well as the physical mechanisms that lead to bycatch, is a fundamental yet understudied research area. Knowledge of how and why animals become bycaught would provide an evidential basis for developing or modifying mitigation approaches. New approaches based on animal behaviour may rely specifically on understanding behavioural responses to deterrent devices and/or modifying the characteristics of nets that are most implicated in elevated bycatch risk. Once a new mitigation approach has been developed, then comparing behavioural data from modified nets to known baseline behaviours would allow for rapid assessment of likely effectiveness before committing to costly and time-consuming control trials [40]. Knowledge of the fine-scale behaviour of small cetaceans around static nets and the mechanisms behind bycatch are therefore key information gaps in bycatch research that could facilitate more effective mitigation approaches.

While aspects of ‘acoustic’ behaviour have been previously used in bycatch research (e.g. [31,41,42]), only a few studies have investigated the fine-scale movement of small cetaceans around nets using

visual methods such as theodolites and drones [40,43]. Passive acoustic monitoring (PAM) has several advantages over these methods: it can work in deep water, in all sea states and during nocturnal periods and has been used to estimate the position of animals underwater (e.g. [44,45]). Harbour porpoises are highly vocal [46,47] and therefore are considered good candidate species for PAM. They use narrow-band high-frequency (NBHF) clicks for echolocation, with rapid sequences of clicks indicating a foraging attempt [48,49] or a communication call [50,51]. They produce no other types of easily detectable sounds, which makes them arguably the most difficult small cetaceans to acoustically localize because recording instruments require very high sample rates and NBHF clicks are fundamentally difficult to localize [52]. However, harbour porpoises are also the most abundant cetacean in UK waters [54] and suffer the highest bycatch rates, with approximately 1000 killed annually in UK fisheries. Therefore, even though acoustic localization is difficult to achieve for porpoises, its ability to provide much-needed data on porpoise movement and behaviour is invaluable. Several attempts have been made to determine porpoise movements around nets using acoustic localization [42,54]. These previous attempts have calculated relatively coarse positional information, such as bearings to detected echolocation clicks rather than full three-dimensional tracks. To address this capability gap, a multi-hydrophone acoustic monitoring system that can be deployed on actively fishing nets to track the full three-dimensional movements and acoustic behaviour of harbour porpoises and other echolocating small cetaceans was developed [55].

The hydrophone system was deployed on multiple occasions on actively fishing static nets off Cornwall in the southwest UK between 2017 and 2019, and enabled the estimation of three-dimensional tracks of several animals around nets. This study was a proof of concept and did not aim to record a bycatch event occurring because, despite the comparatively high levels of porpoise bycatch around the UK, the probability of detecting an actual bycatch event in any particular section of a net is extremely low [18]. However, in 2019, during one deployment, a porpoise was bycaught approximately 20 m from the monitoring array, providing the first detailed insights into how porpoise bycatch occurs in a static net.

In this paper, we describe this bycatch event and present the three-dimensional movement and acoustic behaviour of the bycaught porpoise and a second animal that was in close proximity before, during and after the bycatch occurred. We also used depth sensor data recorded from the event and from a subsequent net force experiment that aimed to replicate the bycatch event to estimate how far the bycaught animal was able to lift the net in the water column. We discuss how this information, along with the characteristics of potential acoustic distress calls, might be useful for informing future bycatch mitigation research directions.

2. Material and methods

2.1. Acoustic tracking array

Acoustic localization methods detailed in Macaulay *et al.* [55] were used to track the three-dimensional movements of porpoises around actively fishing gill nets. Two PAM devices were deployed on the float line of a gill net separated by approximately 50 m (figure 1). Each device contained a compact tetrahedral hydrophone array along with depth and orientation sensors, which enabled the calculation of geo-referenced three-dimensional vectors (a horizontal and vertical bearing) to received echolocation clicks. If a harbour porpoise click was received on both devices, then the point at which the two resulting three-dimensional vectors crossed was the estimated position of the animal. As a porpoise swam around the net, regularly producing echolocation clicks, its position was continuously re-calculated, and thus, its three-dimensional movement was tracked over time.

2.2. Acoustic analysis

Acoustic data were processed using PAMGuard software [56] to automatically detect and classify high-frequency transient sounds (clicks) and calculate the difference in arrival time between the hydrophones on each device. An expert analyst then marked out the porpoise click trains using the visualization and annotation tools in PAMGuard. If two animals are present, then these appear as two different sequences of clicks separated by bearing in the PAMGuard-bearing time display, allowing analysts to identify and annotate clicks produced by multiple animals. Potential foraging behaviour (i.e. an approach phase and/or buzz) or calls were identified by marking rapid-click sequences with an inter-click interval below 40 ms for at least 20 consecutive clicks (see the supplementary material, S4.1). The analyst graded the

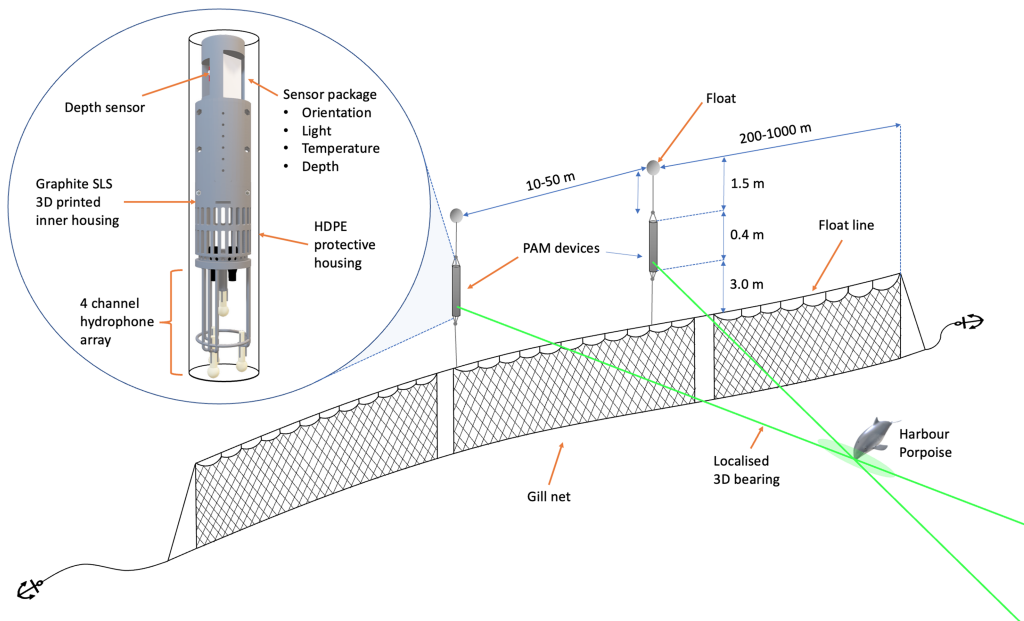


Figure 1. Diagram of the localizing array (not to scale). Two PAM devices were attached to the float line of a gill net via a 3 m drop line. The devices were kept slightly positively buoyant using a small float, allowing them to maintain position in the water column above the float line without deforming the net. Each device contained a tetrahedral four-element hydrophone array, which enabled the three-dimensional localization vector to the source of a received sound. This allowed a direction to a harbour porpoise to be determined upon the detection of an echolocation click. If both devices detected the same click, the point at which the two vectors crossed was the three-dimensional location of the animal.

quality of rapid-click sequences between one and three based on the amplitude and waveform of individual clicks within the sequence. Grade 3 was applied if multiple clicks appeared distorted, suggesting a low signal-to-noise ratio because the foraging approach/buzz or call was produced further from the device or off-axis. Grade 1 was applied to rapid click sequences with clear near-on-axis clicks. Grade 2 was applied if the analyst was uncertain if it should be graded as 1 or 3. Note that the interclick interval (ICI) was not considered in the grading procedure.

2.2.1. Acoustic localization

Manually annotated clicks were imported into MATLAB using the PAMGuard library for MATLAB (<https://github.com/PAMGuard/PAMGuardMatlab>), and click trains, excluding potential foraging approaches/buzzes or calls, were localized using the methods in [55].

2.2.2. Buzzes and communication calls

All annotated rapid-click sequences were imported into Matlab and mapped to tracks based on time and direction, indicating which animal they probably originated from.

To investigate calling behaviour, rapid-click sequences, which contain potential foraging behaviour and communication calls, were converted to ICI versus time contours. Because the annotated rapid-click sequences were based on automatically detected clicks, there were occasions where a single click may have been missed or two individual clicks were recorded as one by PAMGuard. This caused occasional artificial spikes in the ICI/time contours. To remove these, a 'spike-removal' algorithm was implemented, which removed spikes but crucially preserved the shapes of the contours based on Kalkan [57].

The data suggested that most detected click sequences were calls (see the supplementary material, S4); in order to visualize the relationship between different types of calls, a t-distributed stochastic neighbour embedding (t-SNE; [58]) algorithm was used to cluster similar ICI contours; a 100×100 pixel image, showing a line plot of each contour with the y -axis representing the ICI from 0 to 16 ms and the x -axis time from 0 to 500 ms, was input into Matlab's tsne function (perplexity = 30); note that these ICI and time limits removed many of the presumed foraging click sequences from the data (see the supplementary

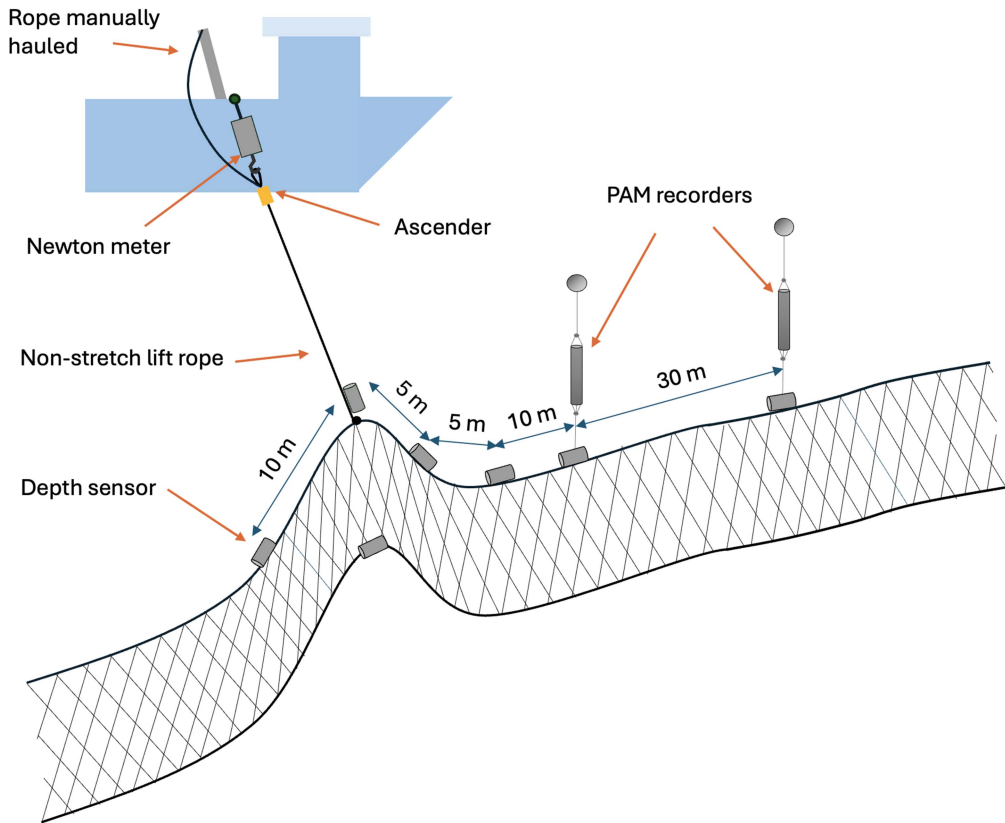


Figure 2. Diagram of the lifting force experiment. The net was hauled upwards with several depth sensors placed along the headline. The force required to lift the net was measured by a Newton meter attached to the vessel. The depth sensors recorded the movement of the net and could then be used to calibrate the force exerted by the porpoise after it became bycaught.

material, S4.1 and S4.2). A small image of each contour was then plotted on an image with respect to the output two-dimensional embeddings from the t-SNE algorithm. Contours were coloured by time to explore the relationships between the call types and the sequencing of the bycatch event.

2.2.3. Depth sensor data

Depth sensor data were extracted from the acoustic recorders and imported into MATLAB. The devices were suspended on 3 m stops from the float line; thus, although the sensor data do not provide the absolute depth of the net, they can be used as a useful proxy for net movements, in this case indicating how the bycaught porpoise altered the position of the net.

2.2.4. Estimating porpoise movements on the net

The porpoise became entangled approximately 20 m from the nearest hydrophone and depth sensor. As it presumably attempted to escape from the net, it lifted it upwards, causing the nearest depth sensor to rise in the water column. However, given the distance between the device and the bycatch position, the sensor will not have lifted as far as the net where the bycatch occurred. To estimate how far the porpoise may have lifted the net, we conducted an additional experiment. A gill net of the same type and length was deployed with the PAM system in the same configuration as during the bycatch event. Small depth sensors (Cefas Technology – Model DST G5_LL) were added to the net, as shown in figure 2. A non-stretch surface line was attached to the floatline 20 m from one of the acoustic recorders to replicate the relative positions of the bycaught porpoise and the nearest acoustic recorder. After the net was deployed and had settled on the seabed, the surface line was used to pull the net to the surface through a climbing ascender. The force on the net was measured approximately every metre using a Newton meter. The depth sensors deployed along the net were used to compare depths at various distances from the lifting point.

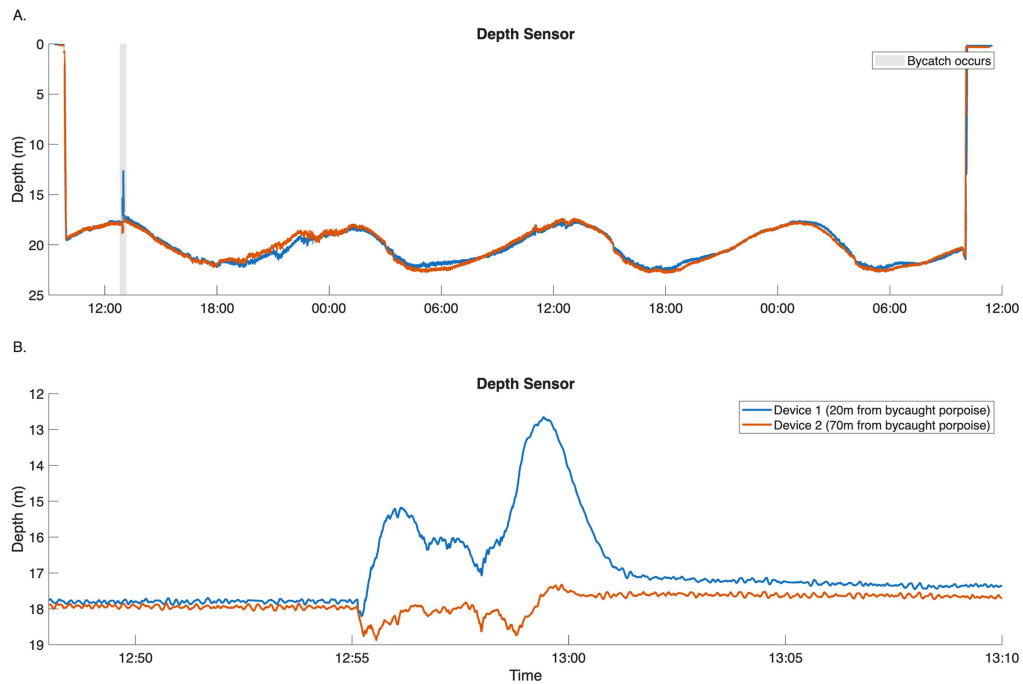


Figure 3. Depth of the recording devices on the gill net over the entire deployment period (A) and during the bycatch event (B). The devices are attached via a 3 m strop to the headline of the gill net and thus can be used as a proxy for the float line height of the net. The bycatch event is highlighted in the time depth record by a grey shaded area in (A). (B) shows a detailed view of the highlighted event, as indicated by an abrupt change in depth over a 5 min period.

3. Results

3.1. Deployment

A monofilament gill net (267 mm stretched mesh, 10.5 meshes high, 10 mm braided float line with a foam core, twine diameter of 0.65 mm and a length of six nets at 120 m per net) was deployed in November 2019 at a depth of approximately 25 m off the coast of Cornwall during normal fishing operations. A single male bycaught porpoise was recovered upon hauling the net. Its length, from the rostrum to the notch of the tail fluke, was measured to be 115 cm. The total soaking time of the net was 48.25 hours. The exact location and time are withheld for anonymity.

3.2. Timeline of the bycatch event

The bycaught porpoise was recovered from the net near the recording devices, and depth sensor data could therefore be used to pinpoint the exact time of the bycatch event. In general, the hydrophone array changes depth slowly and predictably according to the tidal cycle. At 12:55:06 (approx. 18 min after low water), there was an abrupt change in the depth of both devices, indicating the time the bycaught porpoise became entangled and presumably attempted to swim to the surface, as shown in figure 3. At the location of the closest recorder, approximately 20 m from the bycatch, the net is pulled upwards in two main bursts during a 4 min period. The closest device rose approximately 3 m over a period of approximately 53 s before settling slightly and then lifted again approximately 5 m over a period of approximately 84 s. The more distant recorder, approximately 70 m from the bycaught porpoise, sank slightly—presumably because the gear was being stretched and becoming more taut. At 12:59:25, the closest device begins to sink slowly back towards the seabed, indicating the point at which the animal is assumed to have asphyxiated.

3.3. Swim tracks and summary of the bycatch event

Acoustic data immediately before, during and after the bycatch event were processed and indicated that there were two porpoises near the gill net in the vicinity of the hydrophone array before the

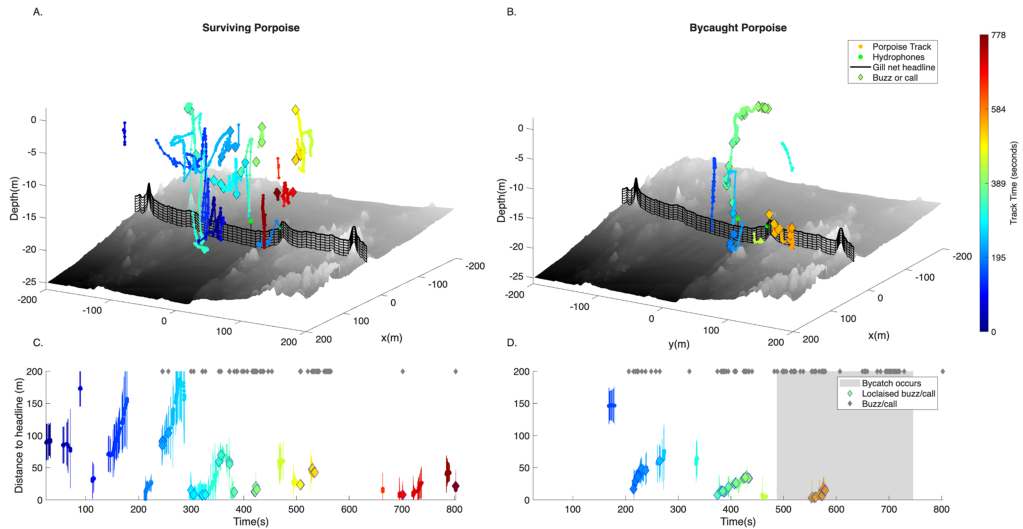


Figure 4. Three-dimensional tracks of two harbour porpoises leading up to a bycatch event, showing the three-dimensional tracks of (A) the surviving porpoise and (B) the bycaught porpoise. Tracks are coloured by time, and foraging/calls are indicated by coloured diamonds. (C) and (D) show the estimated horizontal range to the net headline, with coloured diamonds indicating the range of detected foraging/calls. The error bars represent the 95% confidence interval range error estimated by the localization algorithm. Note that it is not possible to localize all detected clicks, and so detected (but not localized) foraging/calls are indicated by grey diamonds at the top of (C) and (D). The grayscale shaded area beneath each scene is a representation of the seabed (bottom topography) at the location. The plots demonstrate that both animals made multiple dives close <5 m to the net before the bycatch occurred. After the bycatch, the bycaught porpoise makes a series of calls, many of which could not be resolved to three-dimensional locations.

bycatch event. Localization estimates were used to differentiate between the tracks of the two animals, as shown in figure 4. Both animals were diving throughout the water column and came close to the net for approximately 8 min prior to the bycatch occurring. During this period, rapid sequences of clicks (probably foraging approaches/buzzes; see §2.2) were detected, indicating that the animals were actively foraging, including close to the net.

At approximately 375 seconds (figure 4D), one of the porpoises was localised approximately 7 meters from the headline of the gill net with several likely foraging approaches/buzzes detected as it then surfaced. 15 seconds after last being detected near the sea surface, it was localised 2–7 m from the net and, from the depth sensor data (figure 3) became entangled <20 seconds after that. At this point localisation is less accurate because the net was deformed by the bycaught animal (one bycaught porpoise track during the bycatch event was removed as it was clearly incorrect). Between the point of entanglement and the presumed time of asphyxiation (§3.4), a total of 51 calls were detected from the bycaught porpoise and 15 calls from the second animal. An animation of the dive tracks is available in the supplementary material, S3.

3.4. Acoustic behaviour

The recorded acoustic behaviour of the porpoises changed markedly after the bycatch event occurred. Figure 5 shows the acoustic behaviour alongside the depth profile of the recording device closest to the bycatch. Before the bycatch occurred, both animals were echolocating and producing rapid sequences of clicks with variable ICIs that were indicative of foraging behaviour. Immediately after the bycaught porpoise became entangled, both animals switched to producing rapid-click sequences with an ICI centred at approximately 4–7 ms, which corresponds with the predominant ICI used by porpoises for communication calls [51]. The bycaught animal produced calls from the time it was bycaught until the presumed time of death, with a median ICI of 4 ms (see the supplementary material, S4.2). The surviving porpoise produced calls for approximately the first minute after the bycatch began and then appeared to produce only echolocation clicks.

At 13.02:45, approximately 4 min after the bycaught porpoise is assumed to have died, the surviving porpoise produced fewer echolocation clicks (clicks that are not part of a call or buzz) and switched to regularly producing probable communication calls with a median ICI of approximately 6 ms (see the supplementary material, S4.2). At 13.54, 59 min after the bycatch occurred, the calls became less

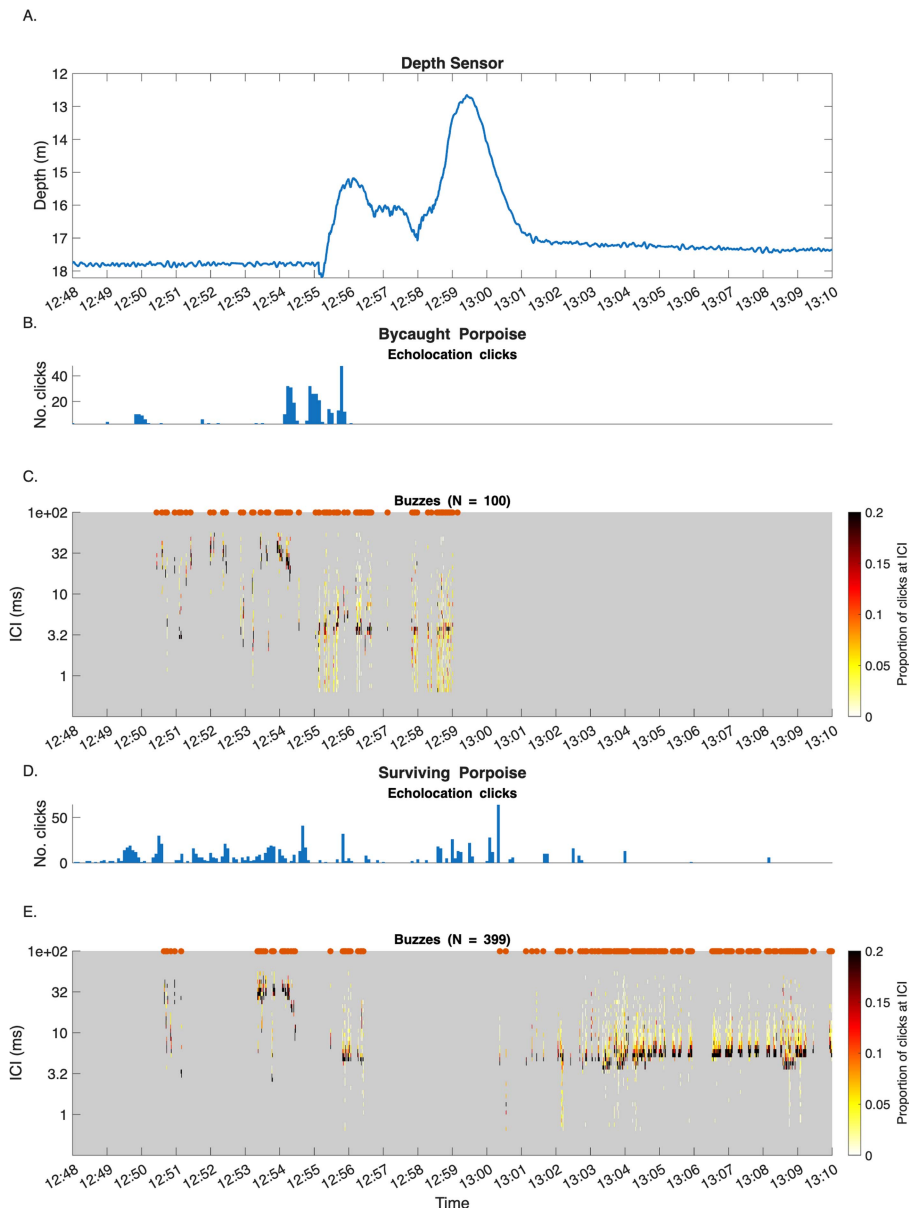


Figure 5. Timeline of the echolocation and communication behaviour of the two porpoises before and after the bycatch event. (A) is the depth of the recording device closest to the bycaught porpoise. (B) and (D) show the number of clicks (excluding foraging buzzes and calls) per 5 s for the bycaught and surviving porpoise, respectively. (C) and (E) are ICIgrams of the bycaught and surviving porpoise, respectively. ICIgrams show the density of ICIs for a given time interval (10 s). Before the bycatch event, the ICI is relatively evenly distributed, indicating that the porpoises are probably foraging, but during and after the event, the ICI is far more constrained—with most clicks having an ICI of approximately 5 ms, suggesting that the porpoises move from foraging to communication.

frequent, and at 14.47, echolocation clicks were detected in higher numbers again, although it is uncertain whether these belonged to the surviving porpoise or another animal. Similar periods of calls without much or any associated echolocation activity were then recorded in two shorter periods over the next 3 h, as shown in figure 6. In total, 607, 78 and 41 calls were detected during these three periods of unusual calling activity, respectively.

3.4.1. Communication call types

Rapid sequences of clicks (i.e. calls or foraging approaches/buzzes) marked as high or medium quality were clustered using a t-SNE algorithm, and the output was plotted on a two-dimensional scatter plot (figure 7), with each point representing a small image of the ICI contour. Similar-shaped contours are closer together, and more dissimilar contours are farther apart; however, the distance between points

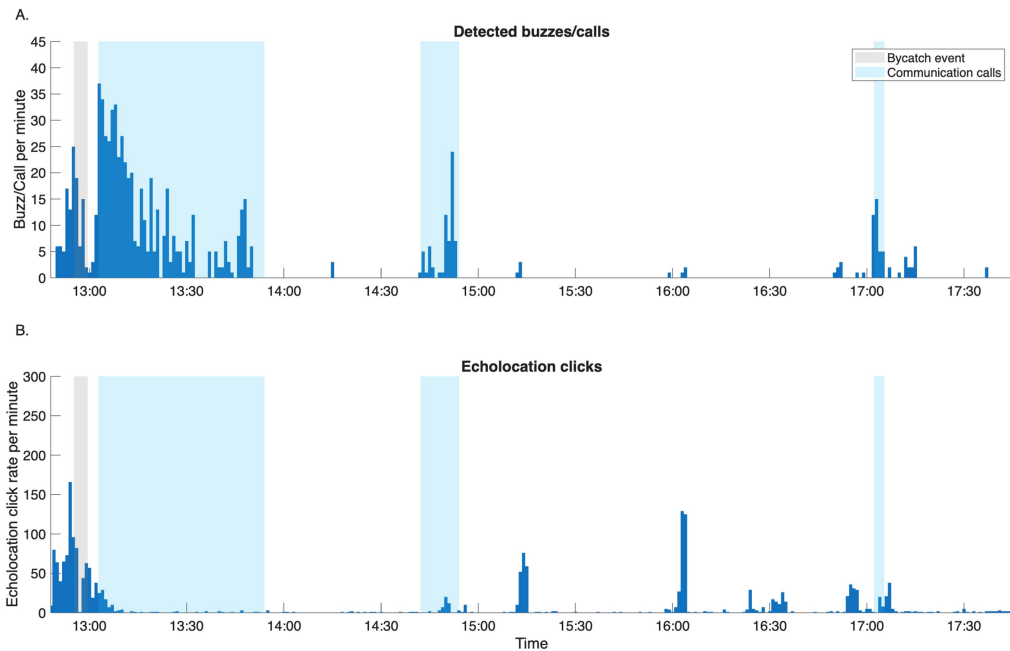


Figure 6. The number of calls or foraging approaches/buzzes per minute (A) and echolocation clicks (B) detected before and after the bycatch event—marked in grey. At approximately 13.03 after the porpoise has presumably asphyxiated, there are an unusual number of presumed calls (607) with very little echolocation activity until 13.54. This was followed by two shorter periods of continuous calling without much, or any, associated echolocation activity (blue highlighted areas). Note that this plot includes all clicks, calls and buzzes detected on the recorders and therefore includes vocalizations from both porpoises prior to the bycatch event. An audio file and animation of the acoustic behaviour are available in the supplementary material, S2.

is not quantitatively meaningful. The contours were coloured by time period as follows: before the bycatch occurred (blue), during the entanglement to the presumed point of asphyxiation (red), 30 min after asphyxiation (grey) and more than 30 min after asphyxiation (black). There appears to be a clustering of red contours in the bottom right quadrant during the bycatch event and less well-defined clustering before and after the bycatch event, indicating that the characteristics of some of the calls during the bycatch event were distinct compared with the other periods.

3.5. Net force

To evaluate the likely force exerted by the bycaught animal, a test net with the same mesh size and length and similar anchors as the net used during the bycatch event was deployed on three successive occasions in a subsequent experiment carried out in October 2025. During each deployment, the net was manually lifted in the water column to simulate the behaviour of the net during the bycatch event. It was apparent that the force needed to lift the net was extremely variable because of sea conditions and difficulty keeping the boat in position. In addition, as soon as hauling stopped, the net would settle in position, and within a few seconds, the force decreased significantly. Therefore, it was not possible to measure the force required to pull the net to different depths accurately. However, the net depth sensors allowed the shape of the net to be modelled as it was hauled to the surface; this was calculated by interpolating between the depth sensors, assuming that the total distance along the net between each depth sensor was fixed (figure 8). A second-order polynomial fit between the recorded depth data and depth sensor data at the haul point indicated that the bycaught porpoise probably lifted the net headline to a depth of 13.6 m ($r = 0.947$, 95% confidence interval (CI) [10.52, 16.67]), indicating that during the bycatch event, it pulled the net approximately 7.22 m (CI [4.15, 10.3]) towards the sea surface.

4. Discussion

We have recorded and described, in a previously unseen level of detail, a small cetacean bycatch event that occurred unexpectedly within the range of a hydrophone array that was deployed to track the three-dimensional movements and acoustic behaviour of cetaceans around fishing gear. While a single event

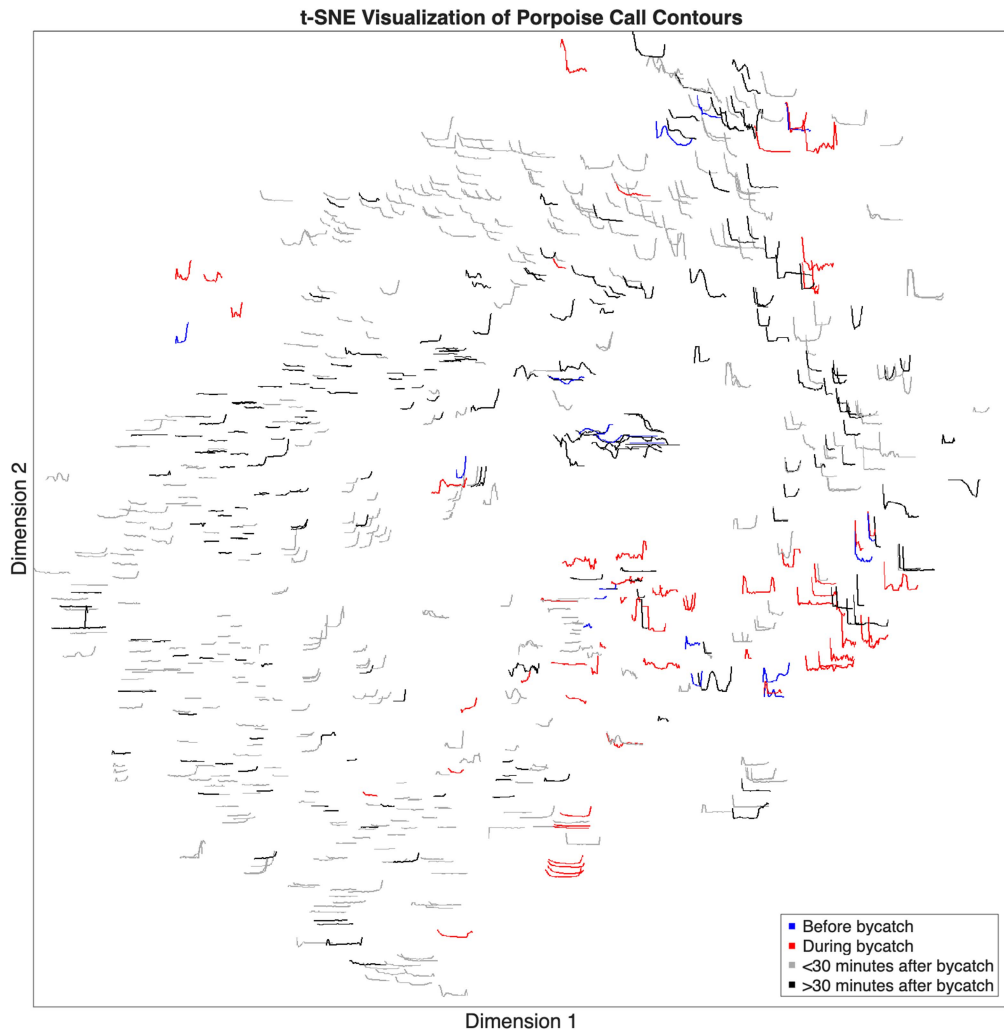


Figure 7. Call contours clustered using a t-SNE algorithm and coloured by time period during the bycatch event—before the bycatch occurred (blue), during the entanglement to the presumed point of asphyxiation (red), 30 min after asphyxiation (grey) and greater than 30 min after asphyxiation (black). Each point is a small image of the ICI contour. ICI contours that are closer together are more similar and farther apart less similar; however, the absolute distance between contours has little quantitative meaning.

may not represent the full extent of small cetacean behaviour when bycatch occurs, it nonetheless provides unique insights into the possible acoustic and physical responses of animals when interacting with a fishing net. This provides information that both improves the fundamental understanding of entanglement in nets and presents new avenues for future applied research to help mitigate bycatch.

Initially, two porpoises are detected near the net for approximately eight minutes before the bycatch event occurs (figure 4). Both animals are actively foraging throughout the water column. While the precise position of the net is uncertain, the estimated positions of the animals appear to show them coming within a few meters of the net and foraging, suggesting that they can detect and evade the net, at least at close ranges. Data collected during other deployments of the hydrophone array have recorded many occasions where porpoises are present close to the net without becoming entangled [55]. This suggests that bycatch is not simply a case of animals being unable to detect a net and blindly swimming into it, but may instead represent a temporary lapse in sensory perception, perhaps as animals are distracted during prey-capture attempts. If it is the case that porpoises can acoustically resolve a net and potential prey, and most evidence to date suggests that at short ranges, they can [33,35,39], then mitigation approaches that try to make a net more acoustically visible (e.g. pearl beads [59]) may work by reducing the likelihood of these occasional lapses in sensory perception.

While the physical position of the animals provides important information, the acoustic behaviour of both porpoises also provides key insights into the bycatch event. Before the bycatch occurs, most detected rapid click sequences appear to be foraging approaches/buzzes with a variable ICI. After bycatch

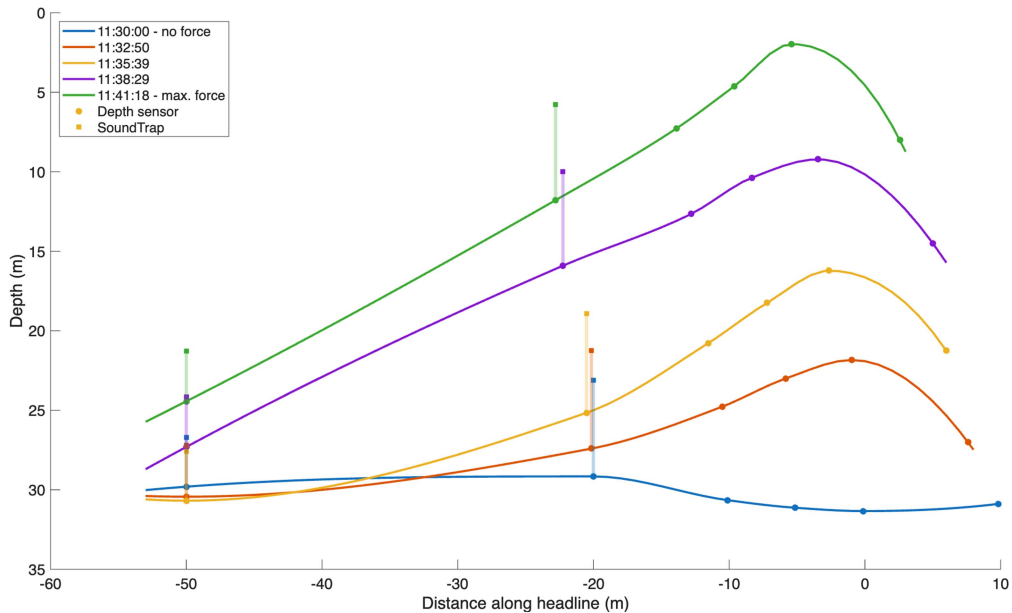


Figure 8. The shape of the net as it is hauled to the surface. The depth data plotted in figure 3 indicate that the porpoise managed to lift the net so that the depth sensor on the recorder reached 13 m depth. Modelling the net deformation indicates that this corresponds to the porpoise lifting the headline to 13.16 m ($r = 0.947$, 95% CI [10.52, 16.67]) depth.

occurs, both animals immediately switch to acoustic activity, which is more typical of communication calls (figure 5). After the bycaught porpoise died, for a period of time, the second animal produced only communication calls without any associated echolocation clicks (figure 6). These findings indicate that the two animals may have been part of a social unit and that the unusual calling behaviour during and after the bycatch event could indicate a stress-mediated social response. The length of the bycaught porpoise (1.15 m) indicates that it was probably a subadult, suggesting the possibility of a mother–calf pair.

Information on porpoise communication is rare, and only a few studies have described porpoise communication calls in the wild [51,60]. Sørensen *et al.* [51] demonstrated that porpoise communication calls from wild tagged animals in Denmark have an ICI distribution centred at approximately 6 ms (-2.3 for $\log_{10}(\text{ICI})$). In the present study, there were consistent call types (figure 7; supplementary material, S4.2 and S4.3), with most calls comprising a flat section at 5–7 ms with down and up sweeps greater than 6 ms, which is generally in line with the ICI distributions calculated by Sørensen *et al.* [51]. The calls during the bycatch event had a lower median ICI of approximately 4 ms, suggesting that these calls had a different purpose and may have been associated with distress (see the supplementary material, S4.2). Most of the call contours do not appear to closely match those recorded from captive porpoises in Clausen *et al.* [50]. This is significant because it has been suggested that porpoise calls can be used to deter animals from nets [61,62], and the warning calls used in those studies were initially derived from Clausen *et al.* [50]. Our data suggest that either the call types recorded here were out of the behavioural context explored in Clausen *et al.* [50] (e.g. calls associated with distress) or that different geographical locations have an impact on call characteristics. The possible ‘distress calls’ recorded during the bycatch event provide a potential route to improve acoustic deterrent mitigation approaches based on biomimicry, but more research is needed to properly describe porpoise call types, especially with respect to geographical variability and behavioural context.

The movement of the net in the water column during the bycatch event also provides interesting and potentially important information and indicates that porpoises can exert considerable force during bycatch events. The results show that the bycaught animal lifted the closest hydrophone (20 m from the bycatch) by approximately 5 m (figure 3). Subsequent experiments indicate that, at the position of the bycatch, the net lifted by 7.22 m (CI [4.15, 10.3]; figure 8). We were unable to accurately estimate the force required to do this because of practical complications with the net lifting experiment. Future attempts to quantify the force exerted will need to be carried out under very calm conditions so that the movement of the boat does not interfere with the results. However, this study has demonstrated that large marine animals, such as porpoises, can probably exert significant force when they become entangled. This highlights potential avenues for evidence-based gear modifications that combine animal

force and gear strength considerations into net designs that could allow larger animals to escape while maintaining target catch rates. This type of approach has the significant benefit of not requiring any additional gear attachments which can be associated with practical, cost and, potentially, safety issues, and if designed appropriately would potentially be close to operationally invisible; making it easier for vessels to incorporate into their normal working routines.

Finally, this study demonstrated the potential of localizing PAM systems and depth sensors to monitor fishing nets. The PAM system described here can track any regularly vocalizing animal around a static net, meaning that it is effective for most species of toothed whales [63,64]. The recording hardware can be deployed with minimal training and is relatively inexpensive compared with other monitoring devices, meaning that it can potentially be scaled widely to other fisheries where cetacean bycatch occurs. This would provide detailed data on the behaviours that lead to entanglement and thus more effectively inform mitigation strategies across a wide range of toothed whale species. We have also demonstrated that there is potential in simply monitoring net movements using depth sensors (figure 3; supplementary material, S1). Routine attachment of depth sensors on nets could provide a method to estimate animal/net interaction rates independently of fishers and/or observers. The DST sensors used in the net haul experiment are low cost, extremely compact and capable of long-term recording and are practical for use in static net fisheries. However, without additional equipment, such as an associated PAM system, they would not allow identification of bycaught taxa or species.

4.1. Data caveats

The localizing array used in this study provided, to our knowledge, the most detailed information on porpoise behaviour around nets to date. However, there are several important caveats to note in relation to the data analysis. Localization in such dynamic environments is technically difficult, and large errors can occur because of uncertainty in received time delays, the position of devices and magnetic distortions altering headings. Porpoises have narrow beam profiles, which means that only a portion of clicks are detected on recording devices. Dive tracks are therefore fragmented, and it can be challenging to associate tracks with specific animals if more than one is present. An expert analyst used visualization tools to associate the track fragments; however, some subjectivity was involved in this process, which can introduce errors into the localization results. Additionally, while static nets would not generally be expected to move significantly over the timespan of a few minutes, horizontal movement of the net during the bycatch event is unknown, meaning that the precise location of the bycaught porpoise after entanglement is not certain.

5. Conclusion

We have demonstrated that data from passive acoustic tracking can provide unique behavioural insights into how porpoises interact with nets and the mechanism of bycatch. The two porpoises recorded in this study were foraging around the net before the bycatch occurred, and the bycaught animal then lifted the net headline, attempting to escape before it died. Both porpoises markedly altered their acoustic behaviour during the bycatch event, and after the bycaught animal had asphyxiated, the surviving porpoise continued making calls for several hours. While the accidental bycatch of marine mammals or other protected taxa is unfortunate, this study provides key information that can inform new bycatch mitigation strategies moving forward. Our results indicate that animals were present and foraging around the nets before entanglement, suggesting that bycatch is not simply a case of porpoises randomly swimming into nets but probably a lapse in sensory perception, possibly when focusing on foraging. Mitigation strategies that enhance the reflectivity of nets, such as pearl beads, may therefore prove effective. Acoustic deterrents that warn animals of danger may also work to prevent lapses in sensory perception or deter animals from foraging near nets; the distress calls recorded during the bycatch event could potentially support the development of effective biomimicry deterrence. Finally, the porpoise was able to lift the net 7 m while entangled—further research on the force the porpoise exerted on the net could help fine-tune the design of nets that would enable larger animals to break free from them.

Ethics. A full ethics statement for this work was submitted to the University of St Andrews Biology Department and accepted (BL16688).

Data accessibility. Acoustic data processed in PAMGuard are available from the Dryad Digital Repository [55]. Note that this contains all the required acoustic information to replicate the study, e.g. all the detected transient sounds,

bearings to each sound, and waveform snippets along with soundscape information. The raw acoustic data are close to 1 TB and too large to be hosted online. It can be shared via a hard drive on a reasonable request. Note that these data are strictly protected under the GDPR, and so GPS co-ordinates, exact times, and any other identifying information have been anonymized. The relevant code and examples of usage for this research work are stored in GitHub: <https://github.com/macster110/soundnet> and have been archived within a Zenodo repository [65].

Supplementary material is available online [66].

Declaration of AI use. There was minimal use of AI. Some AI was used to assist in aspects of coding - for example asking Copilot questions on how to make graphs certain colours etc. AI code was manually checked. AI was used to check spelling and grammar.

Authors' contributions. J.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing—original draft, writing—review and editing; A.K.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing; A.C.: conceptualization, investigation, methodology, validation, writing—review and editing; J.H.: methodology, resources, writing—review and editing; M.O.: resources, software, writing—review and editing; R.J.S.: methodology, software, writing—review and editing; S.N.: conceptualization, project administration, supervision.

All the authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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