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Harbour porpoises respond to small boats by speeding up and moving away

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Abstract

Recreational boats are common in many coastal waters, yet their effects on cetaceans and other sensitive marine species remain poorly understood. To address this knowledge gap, we used drone videos to quantify how harbour porpoises (Phocoena phocoena) responded to a small motorboat approaching at different speeds (10 or 20 knots). The experiment was carried out in shallow waters near Funen, Denmark (55.51° N, 10.79° E) between July and September 2022. Porpoises moved further away from the boat path during approaches at both boat speeds. In addition, porpoises swam faster when approached at 20 knots but not when approached at 10 knots, and they had a higher likelihood of moving away from the boat path when approached at 10 knots but not at 20 knots. Importantly, the received sound level did not depend on how fast the boat approached, suggesting that differences in porpoise responses were related to the speed of the boat's approach rather than to sound itself. The porpoises' behaviour during the minute where the boat was closest did not differ from their behaviour before boat exposure, indicating that the direct impact of small vessels on porpoise behaviour was most likely small. Nevertheless, repeated exposure to noise from small vessels could influence porpoises' foraging efforts and cause them to relocate from disturbed areas. The approach used in this study increases our understanding of recreational boats' impact on harbour porpoises and can be used to inform efficient mitigation measures to help conservation efforts.

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Page heading title: Harbour porpoises' reactions to small boats

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Abstract

Recreational boats are common in many coastal waters, yet their effects on cetaceans and other sensitive marine species remain poorly understood. To address this knowledge gap, we used drone videos to quantify how harbour porpoises (*Phocoena phocoena*) responded to a small motorboat approaching at different speeds (10 or 20 knots). The experiment was carried out in shallow waters near Funen, Denmark (55.51° N, 10.79° E) between July and September 2022. Porpoises moved further away from the boat path during approaches at both boat speeds. In addition, porpoises swam faster when approached at 20 knots but not when approached at 10 knots, and they had a higher likelihood of moving away from the boat path when approached at 10 knots but not at 20 knots. Importantly, the received sound level did not depend on how fast the boat approached, suggesting that differences in porpoise responses were related to the speed of the boat's approach rather than to sound itself. The porpoises' behaviour during the minute where the boat was closest did not differ from their behaviour before boat exposure, indicating that the direct impact of small vessels on porpoise behaviour was most likely small. Nevertheless, repeated exposure to noise from small vessels could influence porpoises' foraging efforts and cause them to relocate from disturbed areas. The approach used in this study increases our understanding of recreational boats' impact on harbour porpoises and can be used to inform efficient mitigation measures to help conservation efforts.

KEYWORDS: behavioural response; boat disturbance; drone footage; motorboat; *Phocoena phocoena* ; recreational vessels; underwater noise

Introduction

As small boats become more prevalent in coastal waters worldwide they increasingly interfere with wildlife (Davenport & Davenport, 2006; Hermannsen et al., 2019; Carreño & Lloret, 2021). In particular, species that use sound for foraging, navigating, and communicating, such as the harbour porpoise (*Phocoena phocoena*), are continuously at risk of being disturbed. Vessel traffic is known to affect porpoise behaviour (Dyndo et al., 2015; Wisniewska et al., 2018; Frankish et al., 2023), and can potentially influence the animals' foraging success, fitness and population dynamics (Oakley, Williams, & Thomas, 2017; Wisniewska et al., 2018; Lusseau, Kindt-Larsen, & van Beest, 2023). However, as opposed to large vessels, studies investigating how animals react to small boat disturbances or how long their responses last are particularly lacking. Considering the overlap of small boat traffic with harbour porpoise habitats and the overlap between the frequency range of boat noise and porpoise hearing (Hermannsen et al., 2019; Hao & Nabe-Nielsen, 2023), such knowledge is important for improving the conservation of porpoises and other cetaceans.

Cetaceans have been reported to exhibit different types of behavioural responses to approaching vessels, including changes in speed, altered diving behaviour and spatial avoidance (Janik & Thompson, 1996). Orcas (*Orcinus orca*) move in less predictable patterns when disturbed by vessels (Williams, Trites, & Bain, 2002) and bottlenose dolphins (*Tursiops truncatus*) sometimes increase their inter-breath interval, speed and alter their surfacing behaviour in response to approaching boats (Lemon et al., 2006; Nowacek et al., 2001). Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) exhibit short-term erratic movements when approached by boats (Bejder et al., 2006) while harbour porpoises have been observed to porpoise more often, move away, dive to the bottom, and to display interrupted foraging when exposed to vessel noise (Dyndo et al., 2015; Wisniewska et al., 2018; Frankish et al., 2023). However, to assess the potential health impact of such behavioural changes it is important to quantify how the animals' behaviour changes when exposed to boat disturbance. This is challenging as it is difficult to assess the exact distance between animals and boats as well as observe changes in animal behaviour from a distance.

Over the past few years, the development of increasingly advanced drones (unmanned aerial systems) has made it easier to observe cetacean behaviours remotely and non-invasively (Álvarez-González et al., 2023; Nowacek et al., 2016; Rees et al., 2018; Sprogis et al., 2020). Compared to traditional observations from boats or from land, drones have the advantage that they can hover over an animal while continuously collecting high-quality data (Koh & Wich, 2012; Rees et al., 2018; Morimura & Mori, 2019). They also make it possible to quantify detailed behavioural changes and how these are related to features in the environment, including the distance to a boat (Koh & Wich, 2012; Chabot & Bird, 2015). With these advantages, drones hold great potential for enhancing our understanding of how anthropogenic disturbances affect marine animals like harbour porpoises.

In this study we used a drone to quantify behavioural changes in harbour porpoises as they were approached by a small boat at a constant speed (either 10 or 20 knots). Given the reactions described above, we hypothesized that porpoises would respond to this disturbance by speeding up, by moving away from the boat's path (distance moved away and probability of doing so), turning more abruptly, diving deep and breathing less often. We also investigated whether they responded more strongly to boats that moved fast than to slow boats, considering animals might get more scared towards rapid changes in approaching distance or noise levels. Furthermore, we compared porpoise behaviour when the boat was nearby with their natural behaviour (i.e., prior to boat approach) and explored how rapidly porpoises resumed their natural behaviour to assess if small boats are likely to have long-term effects on porpoises. We measured the sound level at different distances to the boat to determine if porpoise responses were mostly related to the sound level or to the speed at which the boat approached. As porpoises are strictly protected in European waters (Council Directive 92/43/EEC, 1992), studies of how animals react to small boats, like the present study, are important for informing management.

Materials and methods

Study site and experiment design

To investigate how harbour porpoises responded to approaching boats, we conducted an experiment using a research boat while monitoring porpoise movements with a DJI Phantom 4 Pro v2.0^{TM} drone with a mounted camera recording in 4K resolution (4096 × 2160 pixels) and up to 60 frames per second. The camera was equipped with polarizing filters to avoid sun glare in the video footage. The experiment was carried out in Romsø Sound, located by the eastern coast of Funen, Denmark (55.51° N, 10.79° E; Fig. 1), which is recognized as an important habitat for harbour porpoises (Sveegaard et al., 2011). The experiment took place between 11th July – 10th September 2022, with a total of 20 days spent in the field collecting data (see Fig. 1 for dates when videos were recorded). We conducted the experiments on days with favourable weather conditions, i.e., sea state [?]2 (Douglas scale), wind speed <10 m/s, and without rain. It was done at water depths between 1–7 m to ensure a clear view of the porpoises in the drone footage. The research boat used in the experiment was a 5.5 m Pioner Multi III, powered by an 80 hp outboard engine. Boat tracks were collected using a portable GPS (Garmin GPSMAP 78s). Previous studies have suggested that drones flying at low altitudes (10–23 m) have minimal impact on cetacean behaviours (Ramos et al., 2018; Fettermann et al., 2019; Aubin et al., 2023), and when flown above 5 m, they have negligible effects on underwater noise levels (Christiansen et al., 2016). In our experiment, we maintained the drone's flight height between 10–30 m to minimize its impact on porpoises while keeping track of the animals when they were diving deep. We did not observe obvious reactions from porpoises to the drone. Our selection of 10 and 20 knots as experimental speeds was based on the observed travelling speed for motorboats equipped with outboard engines (without sails) in Danish waters; 10 knots corresponds to mean travel speed while 20 knots corresponds to fast moving vessels (Hao & Nabe-Nielsen, 2023).

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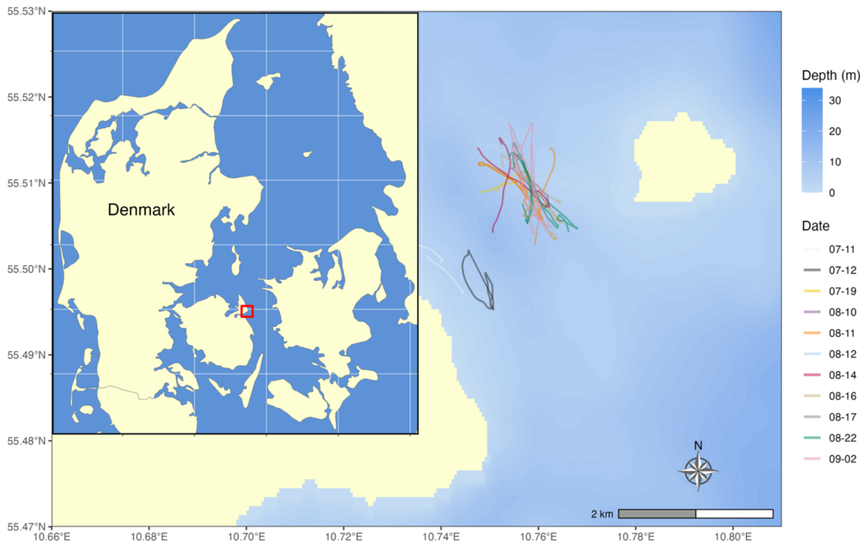

Fig. 1 Area where porpoises were exposed to boat disturbance. The red rectangle in the top left map indicates the location of the study area; coloured lines show the boat tracks on different dates during fieldwork. The country map was extracted using the "rnaturalearth" package for R (Massicotte & South, 2023). Bathymetry data were obtained from https://emodnet.ec.europa.eu/en/bathymetry.

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Fig. 2 Experimental setup.

Each experiment consisted of three phases (see Fig. 2 for experimental setup): 1) Before exposure (phase 1), the research boat had the engine turned off >300 m from any porpoise. The distance was >400 m in the 20 knots experiments to ensure porpoises had as much time to react to the boat as in the 10 knot experiments. Upon sighting porpoises, we launched the drone to obtain video footage of their behaviour for 1.5 min. We only analysed data from the last minute of this phase for comparison with data collected during the exposure phase. 2) During exposure (phase 2) the boat started to gradually increase speed over 30 s while moving towards the drone, passing the porpoise without changing direction. Due to variations in currents and waves, the maximum speed (10 or 20 knots) varied by up to 2 knots among trials. We aimed to pass the target porpoise at a distance of 25 m (henceforth called the closest point of approach, CPA) and continued until the boat was >300 m away from the porpoise. If the porpoise was diving, we estimated its location based on the position of the drone. When comparing porpoise behaviour "before" and "during" exposure, we used data from the one minute centred around CPA and from the last minute of phase 1. 3) After exposure (phase 3), we turned off the engine and observed the porpoise for another 1.5 minutes with the drone. To limit the influence of external variables on porpoise behaviour, we only conducted experiments when there were no moving vessels <1 km from the porpoise. Each group of porpoises was only approached once, and we focused on one animal in each trial. After each trial we moved more than one kilometre away and waited for minimum of 30 min before approaching another porpoise to minimize the risk of exposing the same animal twice. Throughout the experiment period, the echo sounder of the boat was switched off.

On the last day of the fieldwork, we measured underwater noise levels at varying distances from the boat. A stationary recorder (Sound trap, OceanInstruments, New Zealand; 576 kHz sampling rate, 16 bits, clipping level 176 dB re 1 µPa p, as determined by relative calibration) was suspended 2.7 m below the surface and

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attached to a buoy. This was done in the same area where exposure experiments were conducted. Following this preliminary setup, we drove the boat from a distance of >300 m to pass the recorder at speeds of either 10 or 20 knots. The boat was stopped when it was >300 m away from the recorder. This process was repeated twice for each boat speed. The boat's geographical coordinates were recorded using a portable GPS (Garmin GPSMAP 78s).

Data handling

We used the Drone Video Measure tool (Version 1.1.1; Egemose, 2021) to extract location, swimming state and body length of the target porpoise (one location per second). Body length was measured from the tip of its nostrum to the fluke notch. This length was used as an indicator of the age of the porpoise (following Stepien et al. 2023). Each porpoise was measured up to three times from different locations (see porpoises' body length in Table A1 in Appendix A). The swimming state was categorized as either shallow-dive (porpoise body shape clearly visible; including breathing animals) or deep-dive (porpoise under the water, body shape not clearly visible; Fig. 3). To calculate the porpoise's speed and horizontal turning angles between successive moves, we applied the "adehabitatLT" package (Calenge, 2006) to porpoise locations (one per second). To quantify whether an animal tried to avoid the boat and its tendency to move away from the boat track, we calculated the distance between the boat track and the porpoise at two successive boat locations (i.e., one second apart; Fig. A1 in Appendix A). To ensure that porpoise tracks were temporally aligned with the boat tracks we compared the clocks in the boat GPS and in the drone at the point where the boat became visible in the drone video footage. When needed, we calibrated the drone clock based on the time difference between the GPS's. The location measurement accuracy was 2.4±1.5 m when the drone was 30 m above the porpoise (Brennecke et al., 2022).

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Fig. 3 Examples of porpoise swimming states a. Shallow dive, non-breathing; b. Deep dive; c. Shallow dive, breathing. Images were obtained from zoomed-in drone videos.

Data where the porpoise was lost in the video footage for more than five seconds during boat approaches (i.e. phase 2 before CPA) were excluded from all analyses. Thus, out of 27 recorded videos, only 17 (8 for boats moving at 10 knots; 9 for 20 knots) were selected for analysing variations in porpoise behaviour in relation to the distance to the boat, but 16 (7 data of 10 knots, as the porpoise was lost in one of the experiments after boat approach; 9 data of 20 knots) videos were used to determine if the animals' behaviour during exposure (1 min around CPA) differed from their pre-exposure behaviour, and to explore how long it took porpoises to return to their natural behaviour after the disturbance.

Data analysis

To analyse how porpoises responded to the approaching boat (i.e., phase 2 before CPA, using Dataset 1; Fig. A2 in Appendix A), we built six models for each boat speed, with either movement speed, change in distance from boat path (i.e., avoidance distance, Fig. A2), probability of moving away from the boat path, absolute turning angle, probability of diving deep or breathing as a response variable. In all models we used $\log_{10}$(distance) as the independent variable, as sound levels are generally proportional to the logarithm of the distance to the sound source. Individual ID was included as a random effect, and an AR1 model was used to account for temporal autocorrelation. To determine whether porpoises altered their speeds or absolute turning angles when the boat approached, we used generalised linear mixed effects models (GLMMs) with each behaviour as a Gamma distributed response variable (we used a Gamma distribution instead of Gaussian because variance of residuals was not homogenous after transformation, and neither of the response variables can be negative). Porpoise speeds and absolute turning angles were cube root transformed in all statistical analyses to improve spread of data (i.e. make it more normally distributed). To identify whether porpoises

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tended to move further away from the boat path as the boat approached, we used a linear mixed effects model (LME) with avoidance distance to the boat path (Fig. A2) as the response variable. To examine how the probability that porpoises were avoiding the boat path, deep-diving, or breathing depended on distance to the boat, we built three GLMMs with each behaviour as a binary response variable. We used the Newey-West variance estimator (by adding "sandwich" argument) to re-estimate standard errors and associated significance levels (Newey & West, 1986), which accounts for autocorrelation between observations by inflating estimated standard errors (Lennon, 1999). To estimate the uncertainty of model predictions, we calculated 95% confidence intervals (CI) for each model. We used the Wilson score interval (Wilson, 1927) for probabilities associated with avoiding the boat, diving deep and breathing, because it had better coverage probability for binomial proportion (Brown, Cai, & DasGupta, 2001).

To explore whether porpoises responded differently to the boat depending on whether it approached at 10 knots and 20 knots, we used the same methods and model types as described above for each behaviour, except that we included boat speed (categorical) and the interaction between boat speed and $\log_{10}$(distance) in the models.

To evaluate whether porpoises changed their behaviours during boat exposure compared with before exposure (using Dataset 2; Fig. A2), we constructed GLMMs with experiment phase (before/during exposure; categorical) as an independent variable and individual ID as a random effect. We accounted for temporal autocorrelation using the same method as above. To assess whether porpoises moved faster or turned more abruptly, we used GLMMs with either porpoise speed or absolute turning angle (both in their cube root forms with Gamma distribution) as response variables. To test whether the probability of diving deep or breathing was higher, we fitted binomial models. We fitted separate models for the 10 and 20 knot experiments. We used the "nlme" package (Pinheiro et al., 2007) to fit all LME models, and the "glmmTMB" and "glmmAdaptive" packages (Brooks et al., 2017; Rizopoulos, 2022) to fit all GLMMs.

To assess how long it took porpoises to resume their pre-disturbance behaviour, we used generalized additive models (GAMs; using Dataset 3; Fig. A2) with either porpoise speed, absolute turning angle, or probability of diving deep as response variables and time relative to the CPA as predictor (H_0: the independent variables have no effect on the response). Individual ID was included as random effect (bs = "re"). Models were fitted using a Gamma distribution for speed or turning angle. For the probability of diving deep we used a binomial distribution. A k-value of 5 for the smooth term was chosen to limit the risk of model overfitting. We fitted GAMs using the "mgcv" package for R (Wood, 2012).

We used one-tail tests to compute the statistical significance (i.e., $p < 0.025$ is of significance) for models evaluating how porpoises responded to the approaching boat. Statistical significance was attributed to a p-value of less than 0.05 across all other models. We estimated the proportion of variance in the response variables attributed to the independent variables by computing both marginal R-Squared ($R^2{}_m$: variance explained by only fixed factors) and conditional R-Squared ($R^2{}_c$: variance explained by both fixed and random factors). The boat passed the porpoises at an average distance of 26 m (range: 9-40 m) during the 10 knots experiment and at an average distance of 22 m (range: 4-55 m) during the 20 knots experiment.

To investigate how received noise levels were related to distance to the research boat, we used MATLAB (version 2022b) to analyse the recorded data. Noise levels (in dB re 1 µPa rms, 1 s average) were calculated at full bandwidth (0.1-150 kHz) and at the 1/3 octave (TOL) 16 kHz frequency band. To investigate how noise levels changed over time for the two boat speeds, we calculated noise increments per 10 seconds for both frequency bands.

Ethical note

The research protocol was approved by the Danish Environmental Protection Agency and by the University of Southern Denmark's Animal Ethics Committee for non-license requiring experiments, under the authority of the Danish Animal Ethics Inspectorate (DVO approval number: 2022/07). The potential harm to porpoise individuals was very limited, as animals only had a risk of being disturbed when the boat was moving, i.e.,

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typically for 4–7 min. During before- and after-exposure observations, the boat was stationary with the engine turned off. We did not use the echo sounder at any time. To minimise the risk of exposing the same animal twice we waited >0.5 hours and then moved to a new different area >1 km away after each experiment. Porpoises resumed their natural behaviours shortly after exposure.

Results

Porpoises' behavioural response to an approaching boat

A small motorboat approaching at 20 knots caused animals to swim faster (z =-3.05, p =0.002, $R^2{}_m$ =0.20), although the swimming speed varied considerably among individuals ($R^2{}_c$ =0.93; Fig. 4a). No significant change was observed at 10 knots (z =-0.57, p =0.568; Fig. 4a). Porpoises tended to move further away from the boat track when approached by boats at 10 or 20 knots, and there was only little variation among individuals (10 knots: t =-4.57, p <0.001, $R^2{}_m$ =0.12, $R^2{}_c$ =0.19; 20 knots: t =-2.28, p =0.023, $R^2{}_m$ =0.05, $R^2{}_c$ =0.05; Fig. 4b). However, the probability of moving away from the boat track depended on the boat speed (p =0.02, interaction term between $\log_{10}$(distance) and boat speed). Specifically, porpoises were more inclined to move away when approached at a speed of 10 knots (z =-2.37, p =0.002, $R^2{}_m$ =0.13, $R^2{}_c$ =0.28; Fig. 4c). Although most animals started moving away from the boat track when the boat was 100–200 m away, some animals did not move away till the boat was very close (Fig. A3 in Appendix A). Turning angles did not increase as the boat approached (z =-1.06, p =0.289 for 10 knots; z =0.11, p =0.908 for 20 knots), and neither did the probability of using deep dives (z =-2.20, p =0.027 for 10 knots; z =-1.21, p =0.226 for 20 knots). Additionally, porpoises did not breathe less often (z =1.88, p =0.060 for 10 knots; z =1.28, p =0.200 for 20 knots). Model residuals for porpoises' speed, distance that moving away from the boat track and absolute turning angle indicated our modelling approaches were appropriate (Fig. A4 in Appendix A).

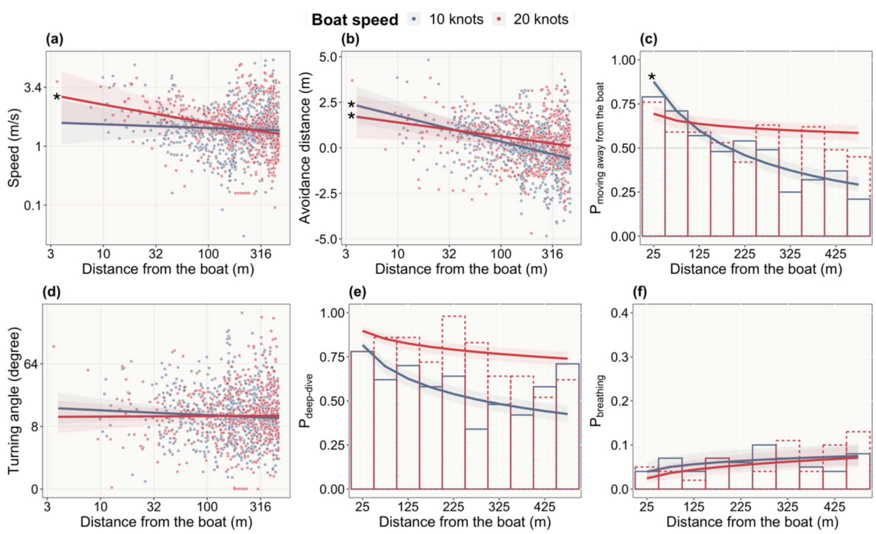

Fig. 4 Observations (dots) and model estimates (lines) of porpoise behavioural responses to an approaching boat (averaged across animals; data from phase 2 before the closest point of approach, i.e. CPA). X-axis values were back-transformed from their logarithms. In a and d, values on the y-axis were back-transformed from their cube root; in b, c and d, bars show observed frequencies of a specific behaviour at each distance range. Shaded areas show 95% confidence intervals. * denotes significant models (p <0.025).

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Porpoise behaviour before and during exposure

The porpoises' behaviour during the minute where the boat was closest did not differ significantly from their behaviour before the experiment started (their speed, absolute turning angles, and the probability of diving or of breathing, were the same; $p > 0.05$ for all variables and both boat speeds; Fig. 5).

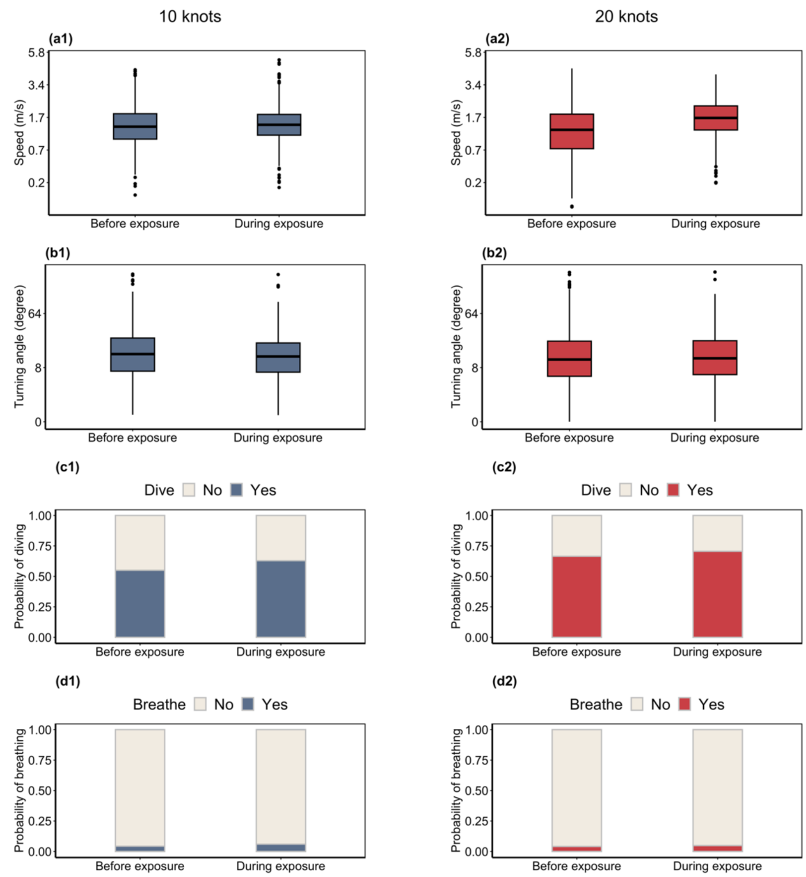

Fig. 5 Porpoise behaviour before (phase 1) and during (phase 2) boat exposure, measured over a period of one minute. The values on the y-axis of a1, a2, b1, and b2 were transformed back from their cube root form.

Time before resuming pre-disturbance behaviour

Porpoise speeds varied in the course of the experiments (10 knots: $p < 0.001$, $R^2 = 0.083$; 20 knots: $p < 0.001$, $R^2 = 0.17$). This was particularly evident in the 20 knots experiments, where animals tended to move faster when the boat approached, then slowing down <50 seconds after the boat had passed. When the boat approached at 10 knots, this response trend seemed not as clear (Fig. 6). However, many animals moved as fast when the boat was not in motion as they did when the boat was nearby. Additionally, porpoises were more likely to dive deep as the boat approached at 10 knots, decreasing rapidly after it passed ($p < 0.001$, $R^2 = 0.11$). But no similar trend was observed at 20 knots ($p = 0.09$). Although the results presented above did not suggest that porpoises turned more steeply or that they were more likely to dive deep when approached by boats, the GAM analyses indicated that the porpoises' horizontal movements (10 knots: $p = 0.003$, $R^2 = 0.029$; 20 knots: $p < 0.001$, $R^2 = 0.028$) changed significantly in the course of the experiments. It is, however, worth noting that time relative to CPA explained a very small proportion of the variation in this behaviour.

The probability of breathing remained unchanged throughout the experiments for both speeds ($p > 0.05$ for both boat speeds).

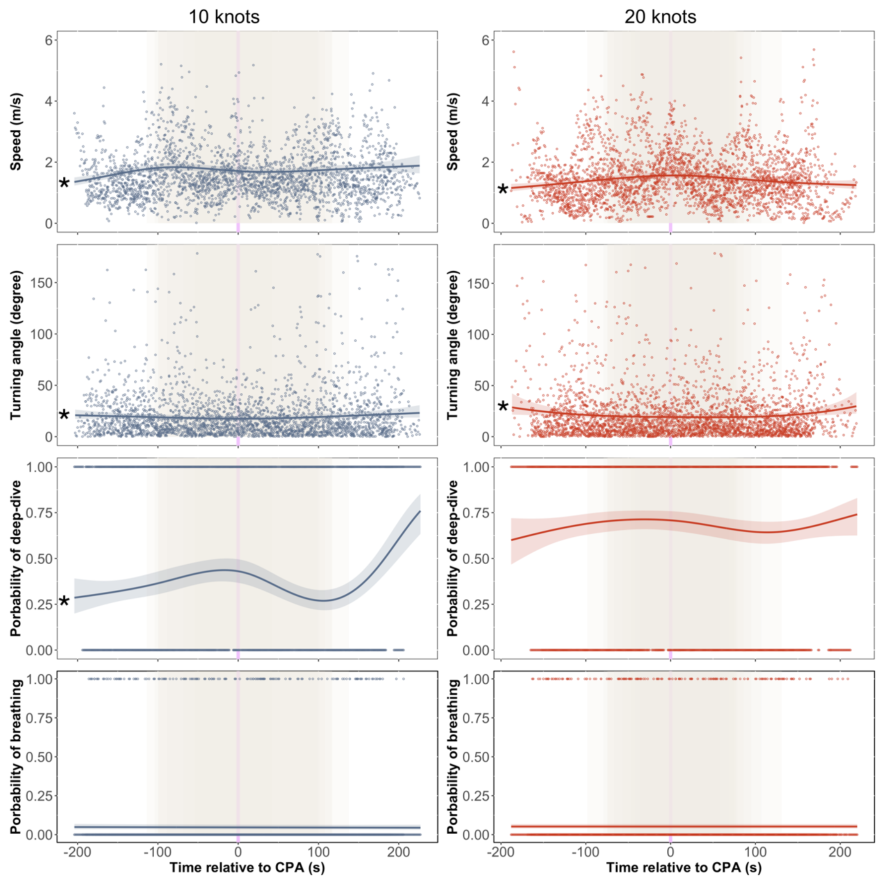

Fig. 6 Observations (dots) and model estimates (smooth curves) of variations in porpoise behaviour during the exposure experiments (phase 1, 2 and 3). Shaded areas along smooth curves show 95% confidence intervals. The vertical purple lines represent the closest point of approach (CPA). The shaded light brown areas indicate the periods where the boat was in motion (i.e. phase 2). * denotes statistically significant models ($p < 0.05$).

Sound received from an approaching boat

As the boat moved towards the CPA at 10 knots, the TOL 16 kHz sound level increased from approximately 90 to 115 dB while the broadband sound level (0.1 to 150 kHz) increased from 110 to 135 dB. The increase in sound level was similar at 10 knots (TOL 16k: 27.2–31.6 dB; Broadband: 26.6–29.4 dB) and 20 knots (TOL 16k: 26.1–29.4 dB; Broadband: 26.3–30.3 dB) for both sound frequency bands (Fig. 7). The broadband sound level was 17 dB higher than the TOL 16 kHz band level at CPA. At a speed of 10 knots, the mean absolute change in noise level per 10 seconds was 3 dB for broadband levels and 5.1 dB for 16 kHz TOL. Conversely, at 20 knots, the corresponding changes were 5.1 dB for broadband levels and 5.3 dB for the 16 kHz TOL. In the 10-knot scenario, the most rapid change in sound levels occurred during the 10 seconds around CPA, where changes in sounds reached 14.3 dB and 17.9 dB for broadband and 16 kHz TOL, respectively. In the 20-knot recordings, these changes were even more pronounced; 22.0 dB per 10 s for broadband and 27.4 dB per 10 s for 16 kHz TOL.

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Importantly, porpoises exhibited obvious reactions, including speeding up and moving away from the boat, when the approaching boat was within the range of 100–200 m. This coincided with a rapid rise in sound levels that started occurring from around 200 m with noise levels at 100–105 dB at 16 kHz TOL (Fig. 4 and 7). After the boat had passed, the sound levels rapidly decreased (Fig. 7).

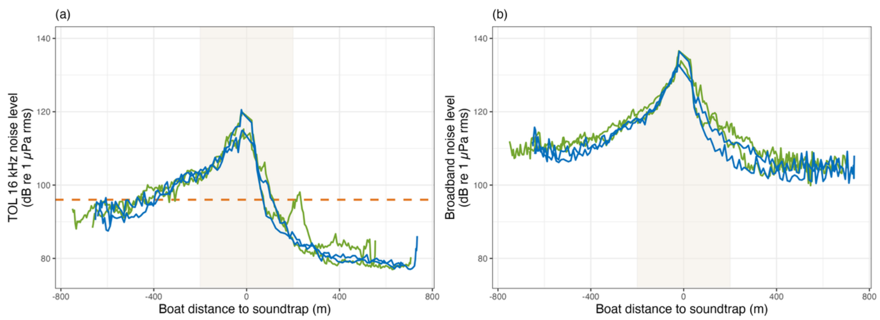

Fig. 7 Received sound levels (1-ws averages) measured within (a) 1/3 Octave (TOL) centred at 16 kHz and (b) broadband (0.1–150 kHz) from various distances of a boat approaching at 10 or 20 knots; negative distance values mean the boat was approaching the acoustic data logger. The dashed horizontal orange line indicates the threshold of porpoises' behavioural reactions to noise reported by Wisniewska et al. (2018). Shaded areas indicate distance ranges where most porpoise reactions appeared to take place, as based on raw data.

Discussion

Porpoises started moving faster when approached by small boats at 20 knots, and they had a higher likelihood moving away from the path of the boat when approached at 10 knots. Additionally, porpoises tended to move further away from the boat path (i.e. avoidance distance is longer) when approached at either 10 or 20 knots (Fig. 4). After the boat had passed, the animals quickly slowed down again, and their movements during the minute where the boat was closest did not differ from their behaviour before the experiment started (Figs. 5 and 6). Earlier research has suggested that either the absolute received noise level or rate of increase in received noise level may trigger porpoise responses to vessels (Wisniewska et al., 2018). In our study, noise levels recorded by the acoustic data logger independently of the drone experiments, were the same when the boat moved at 10 and 20 knots when measured at a specific distance. This was the case both for TOL 16 kHz and broadband sound (Fig. 7), suggesting that the differences in porpoise reactions to boats approaching at different speeds is due to the rate of change in noise level, rather than the noise level itself. It also suggests that the porpoises' reaction to small boats depend on their capacity to predict boat movements, and thereby assess the level of potential danger.

Although there was considerable variation among individuals in observed behaviours, animals generally speeded up (in 20 knots) and moved away from the boat path when the boat was <100–200 m away (Fig. 4a and b). At this distance sound had reached the levels at 100–105 dB at 16 kHz TOL, corresponding to a rapid increase in sound intensity (Fig. 7). Porpoises have been reported to change behaviour at noise levels exceeding 95–96 dB re 1 μPa at the TOL 16 kHz frequency band (Tougaard, Wright, & Madsen, 2015; Wisniewska et al., 2018), which aligns with our observations. However, the observed noise level is below the threshold of 123 dB re 1 μ Pa at 0.25-63 kHz octave bands reported by Dyndo et al. (2015). The reason may be that in the study by Dyndo et al. (2015), porpoises were kept in a net pen, and regularly exposed to specific boat passages over 10 years. Thus, they could not necessarily be assumed to behave naturally prior to disturbance.

We had expected porpoises to turn more abruptly when approached by a boat, which would have resulted in less predictable movements. However, we did not observe changes in turning angles as the boat approached. This contrasts with the observations of Black Sea harbour porpoises in Istanbul Strait, Turkey, which tended to turn more when vessels were nearby but were less likely to turn when the vessel was further away (>400 m; Baş et al. 2017b). We also expected porpoises to dive more when disturbed by a vessel, as has previously been reported for animals in the inner Danish waters (Wisniewska et al., 2018; Frankish et al., 2023), but this was not the case. One possible explanation is that the water was less than 7 m deep, which may not be enough to allow porpoises to avoid boats by diving to the bottom. Additionally, we had expected animals to breathe less often when the boat approached, thus allowing them to dive longer, but we did not observe any change in this behavioural metric. Nevertheless, we observed two instances of porpoises exhibiting porpoising behaviour before the CPA, and we failed to follow seven porpoises during boat approaches as they dove too deep and did not resurface in the same area (10 knots: 4 instances; 20 knots: 3 instances). These observations collectively suggest that boats may represent a significant disturbance to porpoises at close ranges although the strength and type of response is likely context dependent. The reactions of porpoises appear to be contingent on whether they are able to predict the movements of vessels, and as small pleasure boats sometimes move in a very unpredictable manner, they may in reality disturb porpoises more than we report in this study.

Our findings did not entirely support our initial hypothesis that higher boat speeds lead to stronger behavioural reactions, but porpoises reacted differently to boats approaching at 10 knots and 20 knots. For instance, at 10 knots, they were more likely to move away from the boat, but they did not start moving faster. Animals reacted to a boat approaching at 20 knots by swimming faster, but then they did not have higher likelihood to move away from the boat path. Porpoises sometimes accelerated rapidly when the boat was approximately 100 m away, suggesting that these animals possess the ability to assess the level of danger and adapt their avoidance strategies accordingly. The lack of an increase in the probability of moving away from the boat at 20 knots may be that porpoises have too little time to determine the appropriate avoidance direction when the boat was close, leaving them with only the option to speed up to avoid the boat.

Although porpoises responded to approaching boats by speeding up and moving away from the boat path, their behaviour during the minute where the boat was closest did not differ from their pre-disturbance behaviour (Fig. 5). Additionally, after the boat passed at a speed of 20 knots, animals soon started to reduce their speeds, while their speeds never increased much when they were approached at 10 knots. Variations in diving probability and turning angle further did not seem to reflect proximity to the boat (Fig. 6). These results indicate that the direct impact of the boat was brief, and that the behaviour observed for many of the animals during exposure was similar to their – often highly variable – behaviour before the experiment started.

The short-term impacts observed in this study might be due to the use of a single boat in this study, and due to the predictability of its path during our experiments. In reality, porpoises are likely to encounter vessels traveling at different speeds and that make abrupt turns, which would make it more risky for them to decide not to respond to approaching boats. Studies in different locations, such as South Carolina, U.S., and Cardigan Bay, U.K., found that erratic approaches and the presence of multiple vessels had more pronounced negative effects on cetacean behaviour and movement patterns (Mattson, Thomas, & St. Aubin, 2005; Veneruso et al., 2011). Another factor that may influence the porpoises' behaviour is that our study area is close to a marina with 700 boats; during the summer around 300 boats approach the marina per day (source: https://www.kertemindehavn.dk/kerteminde-marina/). The porpoises are therefore used to boat traffic, which may cause them to respond less to approaching vessels than animals in quieter areas, as has previously been observed in some cetaceans (Stevens, Allen, & Bruck, 2023).

One important take-home message of our study is that animals differ considerably in their response to approaching vessels, as well as in their natural movement patterns (Fig 6, Fig. A3 and Table A1 in Appendix A). While some animals appeared to react to the vessel, others moved faster and turned more prior to exposure. The observed differences in reactions illustrate why it is important to study a random sample

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of the population, rather than merely report an apparent change in behaviour for a few animals far from a vessel or other disturbances. The observed variability in movement behaviours likely arises from the fact that different animals are involved in behaviours that are more important to them than the approach of a boat. For example, harbour porpoises usually mate between July and August in Danish waters (Sørensen & Kinze, 1994), and two of the animals in our study were chasing each other or attempting to mate, which potentially diverted their attention from the approaching boat.

Animals with calves are likely to attempt to stay together with their calf, and hence to react less to the boat than average animals. In our study there were six mother-calf pairs (Fig. A3; Table A1 in Appendix A), but a visual inspection of their movement patterns (Fig. A3) did not suggest that mothers or calves reacted differently to the approaching boat than other animals. However, as mothers and calves did not always stay closely together during the observation period, it is challenging to conclusively determine whether the boat had a negative impact on the pairs. In addition to mating and nursing behaviour the porpoises may also be engaged in different kinds of foraging behaviours and differ in age and health status, all of which influence their movements and contributes to masking any impact of an approaching boat.

Other species of cetaceans have been reported to respond to vessels in ways that resemble those observed in this study. For example, bottlenose dolphins (S. M. Nowacek, Wells, & Solow, 2001; Marley et al., 2017), and killer whales (Williams, Trites, & Bain, 2002; Williams et al., 2009) exhibit altered movement patterns in response to vessel disturbances. However, killer whales, in contrast to porpoises in our study, exhibited larger turning angles between successive dives in the vicinity of boats, which is something we did not observe for porpoises. This may partly be due to the shorter time interval between consecutive moves in our study, which automatically reduces the occurrence of sharp turns. Humpback whales have been observed to dive more frequently in the presence of whale-watching vessels and to move away when the vessel was within 100 m (Stamation et al., 2010). While previous research regarding bottlenose dolphins (Papale, Azzolin, & Giacoma, 2012; Baş, Amaha Öztürk, & Öztürk, 2015; Baş, Christiansen, Öztürk, Öztürk, Erdoğan, et al., 2017) found that animals reacted more negatively to faster vessels, our observations indicate that porpoises responded distinctively to the approaching boat at different speeds. However, it is uncertain whether faster vessels have led to increased energy expenditure in the animals here.

Our findings that the impact of boats is brief for harbour porpoises corresponds to what has previously been reported in other species of cetaceans. For instance, in Yaldad Bay, Chile, Chilean dolphins (*Cephalorhynchus eutropia*) rapidly resumed their natural behaviour after encountering boats, possibly as an energy conservation measure (Ribeiro, Viddi, & Freitas, 2005). However, notably, individuals engaged in foraging took longer to return to their natural behaviours than those that did not forage. A similar trend was observed in Indo-Pacific bottlenose dolphins in areas with high vessel traffic, where short-term responses to boats were even less pronounced (Bejder et al., 2006). This diversity in responses highlights that cetaceans differ in their sensitivity to vessel disturbances, and that they adopt different strategies to avoid them. This emphasizes the need for context-specific impact assessments.

The widespread presence of recreational boats exposes cetaceans to high levels of disturbance. In Danish waters, where our study was conducted, recreational boats are often found in areas that are important harbour porpoise habitats (Hao & Nabe-Nielsen, 2023). In such habitats even seemingly minor avoidance responses to individual boats may influence the porpoises' foraging behaviour and energy budgets due to repeated exposure. In areas with limited food resources, missed foraging opportunities could lead to energy deficits and reduced reproductive rates (Lusseau, 2004). In addition to vessel disturbances, porpoises are affected by bycatch, chemical pollutants, and climate change (MacLeod et al., 2007; Pierce et al., 2008; Nabe-Nielsen et al., 2014), and amplifying cumulative impacts could ultimately alter population dynamics (Nabe-Nielsen et al., 2018; Gallagher et al., 2021). This emphasizes the need for holistic assessments of the combined impacts of different stressors, and to do this, it is important to study the impacts of each stressor in isolation. This requires an experimental setup, like the one we have used here, where we provide the first direct results on how harbour porpoises react to approaching vessels in Danish waters.

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Data availability

The raw data used for the analysis in this study, including porpoise locations, swimming states, boat locations and recorded boat noise levels, is accessible on Dryad (https://doi.org/10.5061/dryad.q83bk3jq8). The corresponding R scripts used for conducting the analysis and calculating porpoise's avoidance behaviour from the boat track are also available at the same location.

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Author contributions

All authors contributed to writing the manuscript. Xiuqing Hao, Héloïse Hamel, Magnus Wahlberg, Jacob Nabe-Nielsen and Caitlin Kim Frankish contributed to the study conception and design. Material preparation, data collection and analysis were performed by Xiuqing Hao, Héloïse Hamel, Céline Hagerup Grandjean, Ivan Fedutin, and Magnus Wahlberg. All authors read and approved the final manuscript.

Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

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Appendix A:

Hosted file

`image8.emf` available at https://authorea.com/users/753863/articles/723942-harbour-porpoises-respond-to-small-boats-by-speeding-up-and-moving-away

Fig. A1 Calculation of porpoise's reaction to an approaching boat at time t1. If avoidance distance >0, the porpoise is avoiding the boat. If assuming porpoises remain neutral to boat disturbance, the avoidance distance from the boat track would be around 0, and the probability of moving away from the boat track is close to 0.5.

Hosted file

`image9.emf` available at https://authorea.com/users/753863/articles/723942-harbour-porpoises-respond-to-small-boats-by-speeding-up-and-moving-away

Fig. A2 Summary of the datasets used in the analysis for different models (T_0 indicates the time when the boat starts moving; T_{CPA} represents the time at closest point of approach; T_1 indicates the time when the boat stops moving)

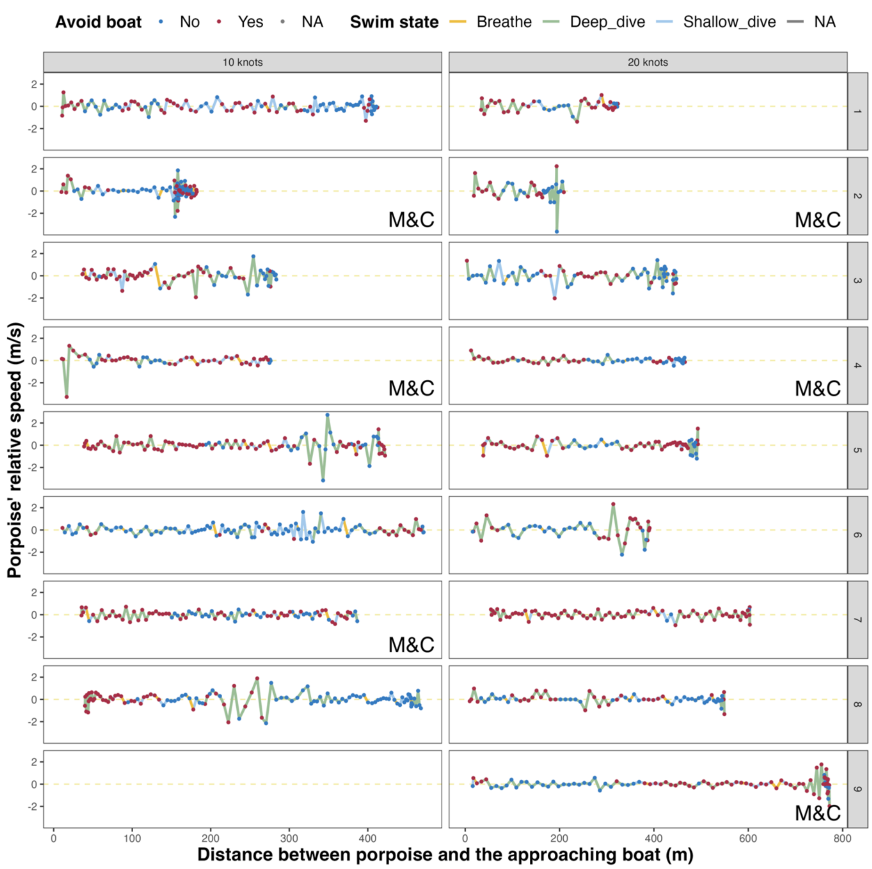

Fig. A3 Individual porpoise's behaviour when a boat approached from when it started moving (at per second interval) to before the closest point of approach (CPA) at 10/20 knots. Porpoise's relative speed is the difference between speed at T $_{t+1}$ and T_t. M&C indicates mother-calf pair was involved in the corresponding experiment.

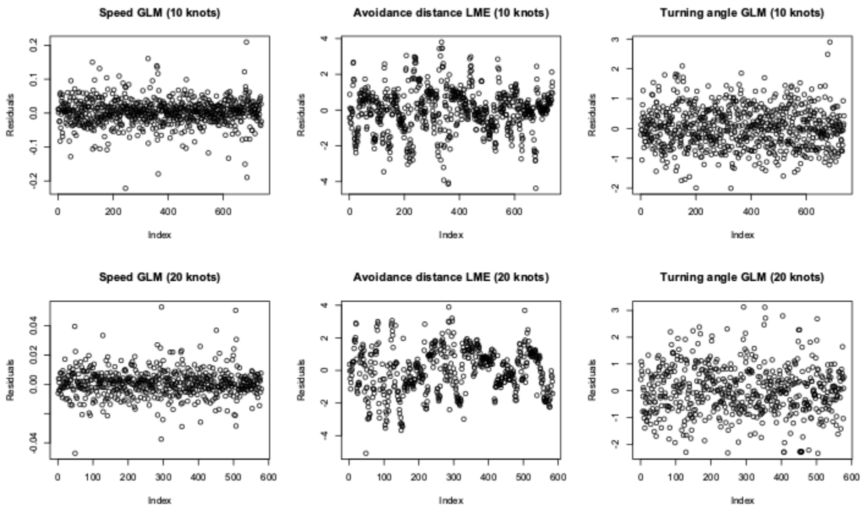

Fig. A4 Model residuals for porpoises' behaviours in relation to their distance to the boat. Speed and absolute turning angles were transformed to their cube root form with a Gamma distribution; Avoidance distance was modelled with a Gaussian distribution.

Boat speed (knots)	ID	Length (m, mean)	SD	Group size	Identity
10	10_1	1.36	0.02	1	
	10_2	1.82	0.07	2	mother
	10_3	1.48	0.03	1	
	10_4	1.83	0.03	2	mother
	10_5	1.46	0.03	1	
	10_7	2.21	0.06	3	mother
	10_8	1.33	0.02	1	
20	20_1	1.55	0.03	1	
	20_2	1.61	0.04	1	mother
	20_4	1.06	0.00	2	calf
	20_5	1.53	0.02	1	
	20_6	1.56	0.03	1	
	20_7	1.78	0.08	1	
	20_8	0.80	0.01	1	
	20_9	1.57	0.05	2	mother

Table A1 Summary of porpoise metadata. Porpoise age can be inferred from Stepien et al. (2023) according to body length. Group size was determined as the number of porpoises at the beginning of each experiment.

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