Received: 16 February 2021 | Revised: 27 July 2021 | Accepted: 17 September 2021
DOI: 10.1002/aqc.3737

RESEARCH ARTICLE

WILEY

Harbour porpoise (*Phocoena phocoena*) presence is reduced during tidal turbine operation

Laura Palmer[1] | Douglas Gillespie[1] | Jamie D. J. MacAulay[1] | Carol E. Sparling[2] | Debbie J. F. Russell[1] | Gordon D. Hastie[1]

[1]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, Scotland, UK

[2]SMRU Consulting, Scottish Oceans Institute, University of St Andrews, Scotland, UK

Correspondence
Laura Palmer, School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, University of Bristol, Bristol BS8 1TQ, UK.
Email: laura.palmer@bristol.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Number: NE/R015007/1; Scottish Government, Grant/Award Number: MMSS/002/15

Abstract

1. Uptake of tidal turbine technology to generate renewable energy has been partly limited by poor understanding of ecological impacts, including the potential for collisions between cetaceans and rotating turbine blades. To address this concern, it is necessary to identify whether cetaceans behaviourally respond to operating turbines.
2. A turbine in Scotland was instrumented with hydrophones to detect cetacean vocalizations. A generalized additive model was used to investigate temporal variability in harbour porpoise presence close to the turbine. As there were incidentally periods when the turbine was not operating, it was possible to determine the effect of blade rotation, whilst accounting for the potentially confounding effect of tidal flow.
3. Harbour porpoise presence varied intra-annually, diurnally and with tidal state. Peak presence occurred during winter (September–February), at night and at high flow speeds on the flood tide.
4. Porpoises exhibited significant avoidance of the tidal turbine when it was operating; avoidance increased with flow speed, whereby mean porpoise presence was reduced by up to 78% (95% CIs, 51%, 91%) on the flood tide and up to 64% (95% CI, 3%, 91%) on the ebb tide.
5. The temporal variability in encounter rate in the present study highlights that collision risk assessments assuming static densities probably fail to capture the temporal variability of collision risk. Future studies should conduct long-term baseline monitoring to derive encounter rates at larger spatio-temporal scales and as a reference from which to measure change in habitat use. It is also critical that the generality of the avoidance rates presented here is assessed for other sites, turbine types, array sizes and cetacean species. As the tidal industry expands, it will be important to reconcile the benefits of avoidance responses from a collision risk perspective with potential chronic effects of displacement from, or barriers between, important habitats.

KEYWORDS
avoidance rate, collision risk, generalized additive model, marine renewable energy, passive acoustics, porpoise, tidal turbines

1 | INTRODUCTION

In response to climate change, ambitious green energy targets have driven the expansion of the offshore renewable energy sector. Tidal energy production is more predictable than solar, wind or wave energy and is therefore advantageous for serving the electrical grid to meet consumption needs (Sangiuliano, 2017). However, unlike solar and wind, tidal is yet to reach full commercial scale with existing developments still at demonstration phases.

Expansion of the industry is limited, in part, by a lack of data on the potential ecological impacts of tidal energy developments, which has led to cautious uptake of the technology. There is increasing evidence that tidally energetic sites are important habitats for marine mammals, such as harbour porpoises (*Phocoena phocoena*) and delphinids (for review see Benjamins et al., 2015); consequently, there is concern that installing tidal turbines in these habitats could have ecological costs for these species (Wilson et al., 2007). For example, noise emitted by tidal turbines (Schmitt et al., 2018; Pine et al., 2019) could lead to disturbance, resulting in habitat displacement or barrier effects, and there is potential for fatal collisions with turbine blades, as has been observed in the wind farm industry for birds (Zimmerling et al., 2013) and bats (Johnson et al., 2004).

To assess whether these concerns are valid, data on the occurrence and movements of porpoises and dolphins around operational tidal turbines is urgently required. Passive acoustic monitoring (PAM) is a non-invasive method of detecting animals by their vocalizations, and permits continuous monitoring, irrespective of visibility or weather. Passive acoustic monitoring cannot distinguish between individuals that are present but not vocalizing, or individuals that are absent; however, porpoises have extremely high vocalization rates (Wisniewska et al., 2018), for example, a tagged porpoise produced an average of 24,227 clicks/hour (Linnenschmidt et al., 2013), making PAM an effective method to study their occurrence. Passive acoustic monitoring has been used to study cetacean occurrence at a number of tidal sites in the absence (Benjamins et al., 2017; Cox et al., 2017; Nuuttila et al., 2018) and presence of turbines (Malinka et al., 2018; Tollit et al., 2019; Gillespie et al., 2021). The studies around single turbines to date have shown that harbour porpoises are frequently present within tens of metres of tidal turbines when they are operating (Malinka et al., 2018; Gillespie et al., 2021). Additionally, Tollit et al. (2019) found that operation of a turbine led to reduced porpoise activity at monitoring sites 200–230 m away from a tidal turbine, indicating that turbines may elicit behavioural responses. Gillespie et al. (2021) localized porpoises around an operational turbine and showed that individuals evaded the rotor swept area, regardless of turbine operational state. However, a key knowledge gap remains regarding the magnitude and scale of behavioural responses to operational tidal turbines and the consequences for collision risk; for example, it is possible that individuals localized close to the turbine represent only a subset of the population and porpoise presence may be affected at a greater spatial scale than that assessed by Gillespie et al. (2021).

The present study aims to address this knowledge gap by (i) characterizing temporal variation in the probability of porpoise presence around an operational tidal turbine and (ii) assessing whether, and to what extent, there are additional effects related to the operation of the monitored turbine and multiple turbines in the array.

2 | METHODS

2.1 | Tidal turbine and study area

The Inner Sound (58°39'N 3°08'W), is a tidal channel in the Pentland Firth between the Scottish mainland and the island of Stroma (Figure 1). Current speeds in the channel exceed 4 m s^{-1} (Goddign-Murphy, Woolf & Easton, 2013) and water depths are generally less than 40 m (Figure 1). An array of four, horizontal-axis, 1.5 MW turbines (MeyGen, SIMEC Atlantis Energy Ltd) was installed between October 2016 and February 2017. Each turbine is gravity mounted to the sea bed on a three-legged turbine support structure (TSS) with a footprint of 25 × 19 m. The TSS is the yellow structure pictured in Figure 2. One of the turbines (Atlantis Resources Ltd AR1500) was instrumented with a 12-channel hydrophone system (Figure 2). This turbine was chosen as the connection management system was the most accessible for connecting the PAM system. The monitored turbine has 18 m diameter blades with nominal operational speeds of 14 rpm. Usually, the turbine blades began rotating when the flow speed is approximately 0.5 m s^{-1} on either the flood or ebb tide. Depth at the monitored turbine varies between approximately 33 m at peak low tide and 36 m at peak high tide.

Cetacean species sighted in the area include harbour porpoises, white-beaked dolphins (*Lagenorhynchus albirostris*), Risso's dolphins (*Grampus griseus*), killer whales (*Orcinus orca)*, bottlenose dolphins (*Tursiops truncatus*) and short-beaked common dolphins (*Delphinus delphis*) (Reid, Evans & Northridge, 2003; Hammond et al., 2013). Harbour porpoises are the most common cetacean in UK waters (Reid, Evans & Northridge, 2003) and several studies have demonstrated their use of tidally energetic sites (e.g. Benjamins et al., 2017; Cox et al., 2017; Malinka et al., 2018), making them of primary interest from a tidal turbine collision risk perspective.

Harbour porpoise vocalizations are distinctive from other cetaceans in UK waters; they produce narrowband clicks with peak

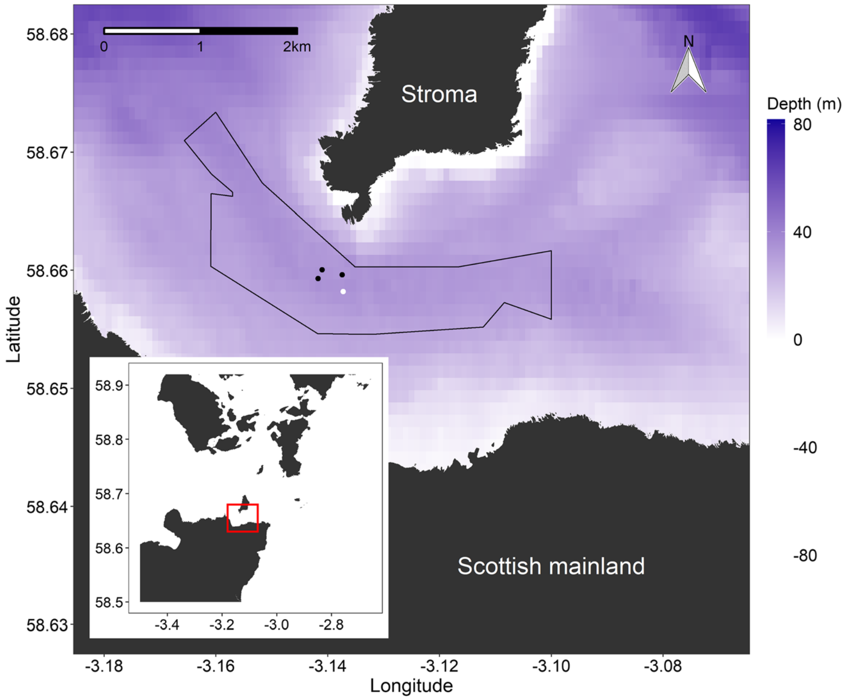

FIGURE 1 (Main) Map of the MeyGen lease area (black polygon) and the four turbines currently installed (points). The monitored turbine is indicated by the white point. (Inset) Map of north-east Scotland where the red rectangle shows the area depicted in the main figure

FIGURE 2 A horizontal-axis tidal turbine similar to the AR1500 turbine in the current study. (Inset; top) one hydrophone cluster. (Inset; bottom) AR1500 during installation. The position of each hydrophone cluster on the turbine support structure is indicated by a red star. Turbine images courtesy of SIMEC Atlantis Energy

frequencies around 130 kHz and mean source levels of 191 dB re 1 μPa peak-to-peak (p–p) @ 1 m (Villadsgaard, Wahlberg & Tougaard, 2007; Kyhn et al., 2013). Most dolphin species produce broadband clicks with source levels up to 228 dB re 1 μPa_{p-p} (Wahlberg et al., 2011), where most energy is contained between 30 and over 100 kHz (Au, 1993).

2.2 | Data collection

The PAM system and its performance are described in Gillespie et al. (2020). The system consists of three tetrahedral hydrophone clusters, one mounted on each leg of the TSS (Figure 2). Data were digitized at 500 kHz and streamed to shore via Ethernet. A computer onshore ran PAMGuard (Gillespie et al., 2008; www.pamguard.org) to process the acoustic data in real time. The PAMGuard click detector was configured to be triggered by transient signals with peak frequencies in the 40–150 kHz detection band that rose >10 dB above a continuous measure of background noise. When triggered, the detector stored short (~1 ms) clips of unfiltered data. The 40 kHz lower frequency bound was selected as there was a strong band of noise present in the data at lower frequencies (Gillespie et al., 2020). While not optimal for the detection of dolphin clicks, which can have peak frequencies at lower frequencies (Soldevilla et al., 2008), the click detector is still triggered by higher-frequency components of the clicks. In addition, noise levels in the 40–150 kHz frequency band were stored once per second. Bearings to clicks from each hydrophone cluster were calculated from time of arrival differences between the four hydrophones within the respective cluster. Clicks were automatically classified as 'harbour porpoise' (see Appendix S1) or 'other' which could include dolphins and/or other sources of noise.

2.3 | Data analysis

An experienced analyst (LP) viewed bearing-time displays of all clicks saved by the PAMGuard click detector *post-hoc* in PAMGuard Viewer. Groups of cetacean clicks with consistent, gradually varying bearings were manually assigned to 'events'. Events were categorized as 'harbour porpoise' or 'dolphin' based on the automatically assigned click type (in the case of harbour porpoise), click frequency characteristics (e.g. peak frequency, bandwidth) and waveforms (click duration). Dolphin events were not classified to species level owing to overlap in click frequencies between sympatric species (Palmer, Brookes & Rendell, 2017). Porpoise or dolphin clicks that occurred within 5 min of another event were assumed to be part of the same event. Conversely, if more than 5 min had passed since the final click of the previous event, the detection was assumed to be independent and was classed as a new event. Only the events with 10 or more clicks were used for further analyses; 10 clicks were enough for the analyst to assess patterns in the click train (e.g. inter-click interval/ bearing change) and a higher threshold was not used to prevent biasing against louder times where fewer clicks may have been detected. It is possible that events could have consisted of multiple individuals; however, this would not impact subsequent statistical analysis as models were based on presence/absence and not counts of individuals. Clicks from this study were localized in Gillespie et al. (2021). The number of events per day was used to estimate mean daily encounter rates which are used directly in collision risk models and hence are useful from a management perspective.

Owing to a low number of dolphin detections, statistical modelling was only conducted for harbour porpoise detections. To examine the temporal variation in porpoise detections, data were divided into 10 min windows. Windows of 10 min were used as larger window sizes could conflate changes in turbine operational state and/or flow speed and small windows may increase temporal autocorrelation.

As described, the PAMGuard click detector was triggered by transient signals in the 40–150 kHz frequency band that increased >10 dB above background noise. Noise in the click detector band increased by up to 20 dB from slack tide to high flows (Gillespie et al., 2020); therefore, the absolute detection threshold was higher (and click detection less likely) during periods of high tidal flow and, if not accounted for, would confound perceived patterns in porpoise presence. Therefore, a single, high noise level and corresponding absolute detection threshold were selected and clicks with received levels below that detection threshold were discarded to provide a uniform probability of detection over time. Several fixed detection thresholds were tested, covering the range of noise levels measured throughout the monitoring period (100–130 dB re 1 μPa in 10 dB increments; see Appendix S2). A value corresponding to a noise level of 110 dB re 1 μPa, or a minimum click amplitude of 138 dB re 1 μPa_{p-p} was selected for subsequent analysis (Appendix S2). Time periods when median noise levels were above 110 dB re 1 μPa were then discarded as detection probability at those times would be negatively biased. Consequently, this precluded analysis of data from periods of highest flow, which also had the highest amplitude noise. When an event had 10 or more clicks with amplitude above the absolute detection threshold, each 10 min window spanning the period between the start and end of the event was marked as porpoise present. Ten-minute windows were marked as absent if they occurred at a time with no event clicks, or if an event that occurred during that period had fewer than 10 clicks with amplitude above the detection threshold.

2.3.1 | Estimating detection range

The range from the turbine at which porpoises could be detected at the threshold noise level was estimated via Monte Carlo simulation and is described in detail in Appendix S3. It is important to highlight that the estimated detection ranges were not used in subsequent statistical analyses and are estimated solely to contextualise the ranges over which behavioural responses were observed.

2.3.2 | Porpoise presence model

A binomial generalized additive model with logit link was fitted to the resultant time series of presence/absence using the function *bam* in the package *mgcv* (Wood, 2017) in R (v. 3.6.0, R Core Team, 2019). Generalized additive models allow complex non-linear relationships between continuous explanatory variables and the response variable, and *bam* is more efficient for large datasets than the standard *gam* function in *mgcv*. Covariates pertaining to time (hour, day of year), tidal state (flow speed and days since new moon) and turbine operation (whether or not turbine was rotating and number of other turbines rotating) were considered (see Table 1 for details). Hour and day of year were fitted as a tensor smooth interaction. Critically, flow speed was fitted as a separate smooth for each operational state of the turbine (rotating/not rotating). The difference between these smooths indicates the effect of turbine operation on porpoise presence at different flow speeds. Turbine rotation (rotating/not rotating) was also included as a separate covariate in the model. *k-values* were determined heuristically. Firstly, $k = 10$ was specified following the methods of Wood (2001). *k-values* were then adjusted by assessing individual plots for evidence of overfitting (wiggliness that did not make biological sense) and using the *gam.check* function to verify that the *k*-value was sufficient (*P*-value > 0.05). This was only necessary for days since new moon and flow speed (Appendix S4; Table S2).

Model validation checks were carried out to assess the reliability of the model coefficients. The *concurvity* function in the *mgcv* library

TABLE 1 Explanatory variables for generalized additive model of harbour porpoise presence. Interactions were fit between (1) hour and day of year and (2) flow speed and turbine rotation (indicated by superscript)

Category	Variable	Description
Temporal	Hour[1]	Discrete variable (0–23) indicating hour of day. Cyclic smooths ensured continuity between the minimum and maximum value of the covariate
	Day of year[1]	Discrete variable (1–365) indicating day of year. Cyclic smooths ensured continuity between the minimum and maximum value of the covariate
Tidal state	Flow speed[2]	Flow speeds at the turbine (m s^{-1}); a continuous variable interpolated to 1 min intervals from modelled data provided by SIMEC Atlantis Energy in 10 min intervals. Positive and negative flow speeds correspond to flood and ebb tides, respectively. The flow speeds were verified using Acoustic Doppler Current Profiler measurements at the turbine (Appendix S4, Figure S1)
	Days since new moon	A discrete variable indicating position in the lunar cycle (0–30). Cyclic smooths ensured continuity between the minimum and maximum value of the covariate
Turbine operations	Turbine rotation[2]	Binary variable indicating whether the monitored turbine was rotating (1) or not rotating (0). Rotation was based on whether the blade speed exceeded 1RPM at any point during the respective 10 min window
	Number of other turbines rotating	Discrete variable describing the number of other turbines in the array that were rotating (0–3)

(Wood, 2017) verified that the levels of multicollinearity between smoothed terms would not lead to unstable coefficient estimates. Residual autocorrelation violates the model assumption that model residuals are independent and if present can result in underestimated uncertainty and lower *P*-values (Redfern et al., 2006). Autocorrelation function plots were examined across the 10 min intervals and revealed that there was autocorrelation in the model residuals. Thus, the model was refitted to account for residual autocorrelation within defined panels of data (using argument *rho* within *bam*; Wood (2017)). This ensured that the parameter estimates and associated *P*-values were robust to the presence of such residual autocorrelation. The model was specified so that residuals within runs of continuous data were permitted to be correlated and where there was a gap in data greater than 6 h, were assumed to be independent; this resulted in 14 independent sections of data. Autocorrelation function plots revealed autocorrelation in the model residuals to approximately 30 lags (or 5 h); 6 h was chosen as it is approximately the length of a tidal window and is therefore more biologically relevant. The value of *rho* was determined by incrementally increasing it from a value of 0.1 and reassessing the autocorrelation function plots; a value of 0.3 was selected for the final model. Autocorrelation function plots of residuals from the original model and the final model with the autocorrelation structure are provided as supporting information (Appendix S4; Figure S2). Significance of variables was determined using Wald's tests implemented via the *anova.gam* function in the *mgcv* library (Wood, 2017). All variables were retained in the final model, irrespective of their statistical significance, to control for natural variation in the probability of porpoise presence before quantifying the effect of turbine operation.

The final model was used to predict the probability of porpoise presence for the range of explanatory covariates. The mean percentage *change* in porpoise presence between turbine operational states (rotating/not rotating) was estimated as a function of flow speed and parametric bootstrapping was used to generate 95% confidence intervals around the change.

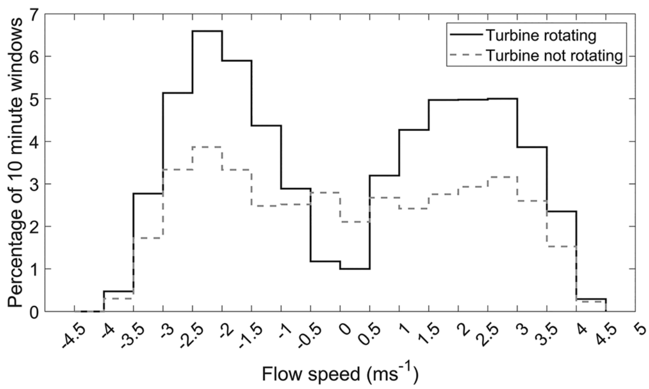

FIGURE 3 Distribution of monitoring effort as a function of flow speed and turbine rotation in the full data prior to noise-adjustment. A bin size of 0.5 m s^{-1} has been used. Negative and positive flow speeds correspond to ebb and flood tides, respectively

3 | RESULTS

The PAM system was operational during 383 days between 19 October 2017 and 31 January 2019, during which 365 days of data were collected. The PAM system was not operational between 23 September 2018 and 19 December 2018 as the turbine was removed for maintenance. Data were collected at all flow speeds and tidal states. Incidentally, there were frequent periods when the monitored turbine did not rotate. These periods were random in relation to tidal phase, and therefore, data were also available for all flow speeds and tidal states when the turbine was not rotating (Figure 3).

Noise varied by up to 20 dB between low and high flows and a 20 kHz tonal sound was present when the turbine was generating power (Gillespie et al., 2020). Whilst rotation of the blades was usually associated with power generation, there were brief periods of rotation without power generation and therefore the 20 kHz tone was not present (574 h; 5.1% of total study period). Individually, these periods generally lasted under 30 min, but in one instance, lasted 350 min.

3.1 | Cetacean detections

There were 814 harbour porpoise events and 32 dolphin events recorded during the 365 days for which data were collected. The mean monthly detection rate was 2.3 (SD = 1.2) harbour porpoise and 0.1 (SD = 0.2) dolphin events per day. However, there was marked intra-annual variation in the mean number of harbour porpoise events per day (Figure 4); the highest detection rate occurred in January 2018 (4.2/day, SD = 0.5) and the lowest detection rate occurred in May 2018 (0.6/day, SD = 0.2). The mean number of dolphin events per day throughout the study period was low, peaking at 0.5/day (SD = 0.2) in September 2018.

A summary of harbour porpoise and dolphin events is presented in Table 2. Thirty-three per cent (271 of 814) of harbour porpoise detections and 28% (9 of 32) of dolphin detections occurred when the monitored turbine was rotating at some point during the detection. Porpoise and dolphin detections occurred when all four turbines in the array were rotating (Table 2).

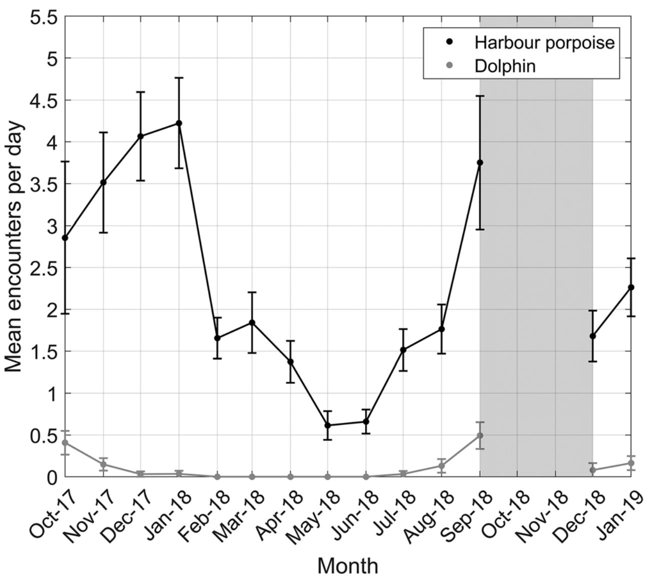

FIGURE 4 Mean number of harbour porpoise (black) and dolphin (grey) detections per monitored day each month. Error bars represent ± one standard error of the mean. No data were collected between 23 September and 19 December 2018 (grey shaded region) as the turbine was removed for maintenance. The monthly number of cetacean detections and days monitored are provided in Appendix S4 Table S1

3.2 | Statistical analysis

Following noise-adjustment, 38,805 (74% of total) 10 min windows were retained for statistical analyses, of which 629 were with porpoise present. The percentage of data at flows above 3 m s^{-1} was markedly reduced (Appendix S4; Figure S3) and therefore subsequent inferences regarding the probability of porpoise presence and behavioural responses to the turbine were limited to a maximum of 3 m s^{-1}.

When noise levels were 110 dB re 1 μPa, the mean probability of detection throughout the water column at 0 m from the turbine was 0.4 (Appendix S3; Figure S1). The probability of detection at 150 m was approximately 0.02; hence, it is unlikely that the detections used in the statistical model were of animals greater than 150 m away. Therefore, it seems reasonable to assume that the scale of behavioural responses estimated by the model is tens of metres to approximately 150 m from the turbine.

Except days since new moon (P = 0.45), all covariates and interactions were significant in the final model (P < 0.001; Appendix S4; Table S2). The model explained 9.0% of the deviance in the response.

The model results showed that there was significant temporal variation in probability of porpoise presence at diurnal and intra-annual scales (P < 0.001; Appendix S4; Table S2). The model predicted peak presence to occur between days 1 and 65 and between days 210 and 365 (Figure 5a). This corresponds approximately to the period between the end of July and the beginning of March. The highest probability of porpoise presence occurred between the hours of 16:00 and 05:00, except from between days 100 and 175 (April to July), when presence was consistently low, irrespective of time of day (Figure 5a). Figure 5b shows how the probability of porpoise presence varied with hour for a range of dates relative to the time of sunrise and sunset. Throughout most of the year porpoise presence was higher during hours of darkness than during daylight hours, although this pattern was less evident in June when the overall probability of presence was low.

Changes in flow speed significantly influenced the probability of porpoise presence around the turbine (P < 0.001; Appendix S4; Table S2). When the monitored turbine was not rotating, presence increased from high flows on the ebb tide to high flows on the flood tide (Figure 5c; left). However, when the turbine was rotating, presence at high flows was reduced relative to when the turbine was not rotating (Figure 5c; right). Further, the model results showed that porpoise presence around the monitored turbine was significantly reduced (P < 0.001; Appendix S4; Table S2) when the three other turbines in the array were rotating.

Turbine rotation led to a significant reduction in the probability of porpoise presence (P < 0.001; Appendix S4; Table S2). The mean percentage *change* in presence when the turbine was rotating compared with not rotating is presented as a function of flow speed in Figure 6. There was no evidence of significant avoidance or attraction at low flows as confidence intervals (CIs) spanned 0%.

TABLE 2 Summary of small cetacean events (≥10 clicks) from October 2017 to January 2019, inclusive

	Harbour porpoise	Dolphin species
Number of events (≥10 clicks)	814	32
Median number of clicks per event	68	851
Mean number of clicks per event (± SD)	154 (250)	1,800 (3,053)
Median event duration (min)	2.0	1.7
Mean event duration (min) (± SD)	3.4 (4.7)	2.5 (2.6)
Maximum event duration (min)	45.9	10.0
Number of events with monitored turbine rotating (>1 rpm)	271	9
Maximum number of turbines rotating during a detection	4	4

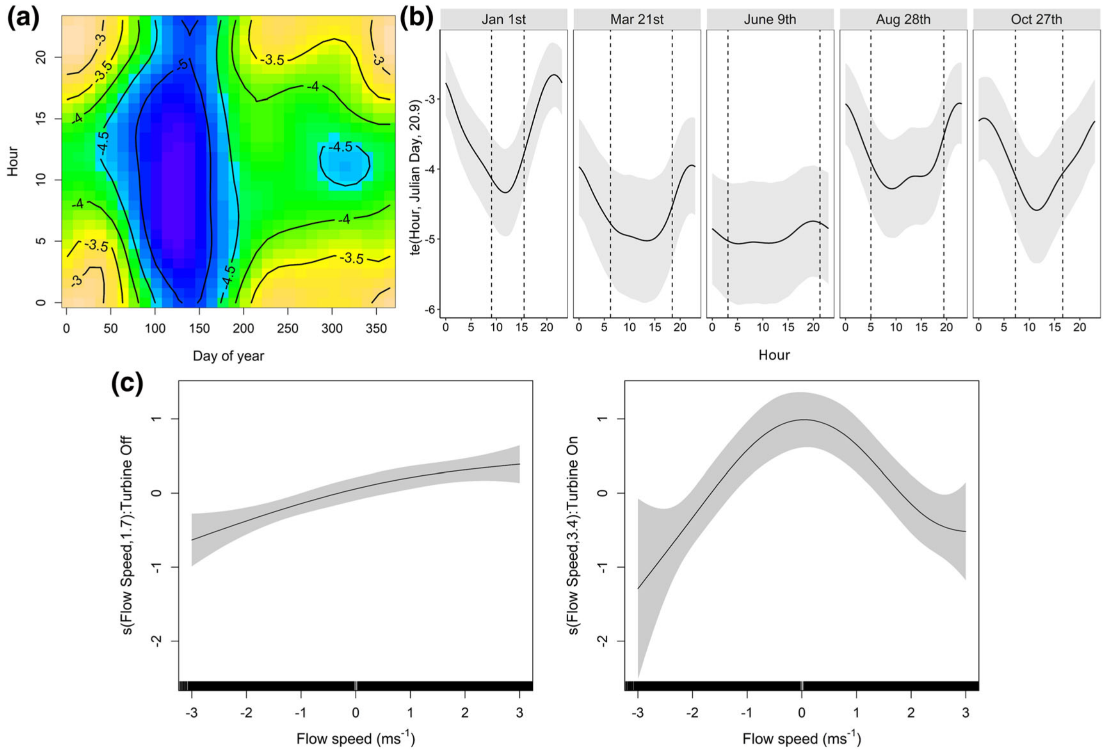

FIGURE 5 Model predicted patterns in the probability of porpoise presence (link scale). Grey shaded regions represent the 95% CIs. (a) Contour plot of the tensor smooth interaction between hour and day of year. Warmer colours (yellow) indicate higher porpoise presence and colder colours (blue) indicate low porpoise presence. (b) Predicted probability of porpoise presence as a smooth function of hour at a range of dates throughout the year. Dashed lines represent the sunrise and sunset times for the given date at the latitude and longitude of the turbine. The number in parentheses indicates the effective degrees of freedom. (c) Predicted probability of porpoise as a smooth function of flow speed when the turbine was not rotating (left) and when the turbine was rotating (right). Negative and positive flow speeds correspond to the ebb and flood tide, respectively. The number in parentheses indicates the effective degrees of freedom. A rug plot is also presented showing that data were available across all flow speeds

However, during operation there was significant avoidance at high flows, which increased with flow speed. On the flood tide, avoidance increased from 33% (95% CI, 6%, 53%) at 1.2 m s^{-1} to 78% (95% CI, 51%, 91%) at 3 m s^{-1}. A similar change in mean avoidance with flow speed was observed on the ebb tide, increasing from 37% (95% CI, 3%, 62%) at 1.8 m s^{-1} to 64% (95% CI, 3%, 91%) at 2.8 m s^{-1}.

4 | DISCUSSION

This study has quantified patterns in harbour porpoise presence in a tidally energetic environment with an operational tidal turbine and, importantly, has demonstrated that porpoises are able to detect and avoid tidal turbines during their operation. Porpoise presence was reduced by up to 78% (95% CI, 51%, 91%) within tens to 150 m of

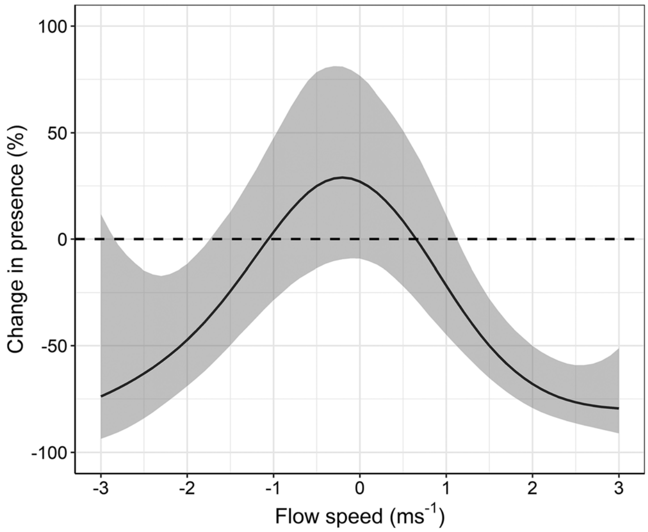

FIGURE 6 Mean percentage change in the probability of porpoise presence between turbine operational states (rotating/not rotating), as a function of flow speed. Shaded regions represent 95% CIs. Changes are calculated based on other model covariates being held at their mean values, or lowest level for factors. All values are also presented in tabular format at 0.1 m s^{-1} intervals in Appendix S4, Table S3

the turbine when it was operating in periods of high flow. These findings have implications for the prediction of collision rates between porpoises and tidal turbines and hence the consenting of future turbine installations.

Whilst the percentage of deviance explained by the model was relatively low (9%), there was sufficient statistical power to identify a significant behavioural response to operation of the turbine. It is not unusual for temporal models of cetacean occurrence to only explain a relatively small amount of the deviance (Holdman et al., 2018) and it is possible that porpoise presence in tidally energetic sites and at the spatial scale monitored is influenced by transient fine-scale hydrographic features that were not considered in this study (Pierpoint, 2008). In general, it is not possible to use passive acoustic data to distinguish between absence, individuals that are present but not vocalizing, or individuals that are not detectable for some other reason, such as their orientation with respect to the receiving hydrophone. Hence, it is possible that behavioural factors could have influenced the temporal patterns in probability of presence and perceived avoidance of the turbine in this study; for example, if porpoises passed over the turbine near the surface, the probability that they would be detected was relatively low (Appendix S3; Figure S1). Further, there is evidence to suggest that porpoises produce higher numbers of vocalizations at night (Wisniewska et al., 2016) and porpoises have been shown to reduce echolocation rates when exposed to noise from other anthropogenic sources such as ships (Wisniewska et al., 2018). Nonetheless, given that porpoises use echolocation to navigate, it seems highly unlikely that they would cease vocalizing when within tens of metres of an audible structure in an environment with strong currents and low visibility.

The results of this study provide important biological insights into how porpoises use tidally energetic environments. Over 365 days, there was a mean of 2.3 porpoise detections per day (SD = 1.2); the temporally varying nature of the encounter rate is also interesting from a collision risk perspective. The highest occurrence of porpoises was during winter months (Figures 4, 5a), which may be driven by prey abundance or availability in the area. Probability of porpoise presence was also higher during the night (Figure 5a, b), although controlled studies suggest that this could be driven by vocalization behaviour, rather than prey activity (Osiecka, Jones & Wahlberg, 2020).

The probability of porpoise presence also varied as a function of tidal state, being greater on the flood tide than the ebb (Figure 5c; left). Porpoise presence has been shown to vary over the tidal cycle at many tidal stream sites, but which phase coincides with peak presence varies markedly between study areas (for review see Benjamins et al., 2015). This variation probably reflects inherent variability in hydrography between sites but ultimately, the apparent preferences are probably driven by enhanced foraging opportunities as hydrodynamic features may mediate prey availability and/or capture efficiency (Zamon, 2001; Zamon, 2003). Further, individual differences may drive apparent preferences such as their experience foraging in tidally energetic areas, their physical condition or the presence of calves (e.g. Pierpoint, 2008).

From an applied perspective, the results show that harbour porpoises exhibit significant avoidance of the turbine during operation (Figure 6). Harbour porpoises have previously been shown to exhibit behavioural changes or spatial avoidance responses to anthropogenic noise sources, including operation of acoustic deterrent devices (Johnston, 2002) and pile driving during installation of offshore wind turbines (Brandt et al., 2011). Independent measurements obtained using drifting hydrophones showed high-amplitude noise associated with operation of the turbine in the 50–1,000 Hz band and at 20 kHz (Risch et al., 2020). Harbour porpoise hearing is relatively poor below 1,000 Hz; however, the 20 kHz component of the turbine noise falls within the most sensitive hearing range for harbour porpoises (Kastelein, Helder-Hoek & Van de Voorde, 2017) and was detectable above ambient noise levels up to 200 m from the turbine (Risch et al., 2020). It is therefore conceivable that this noise may drive the observed avoidance response in this study.

Mean avoidance rates increased with flow speed (Figure 6); however, the mechanism underlying this is unclear. Noise levels between 100 and 200 Hz were increased at higher turbine rotational speeds (Risch et al., 2020) but porpoise hearing sensitivity at these frequencies is relatively poor (Kastelein, Helder-Hoek & Van de Voorde, 2017) and the amplitude of the 20 kHz noise did not increase with turbine rpm (Risch et al., 2020). One plausible explanation may be that porpoises approaching the turbine in higher flows may respond at greater distances to compensate for their increased speed over-ground.

The results also indicate that avoidance behaviour increases with increasing numbers of operational turbines; porpoise presence was significantly reduced when three of the other turbines in the array were operating ($P < 0.001$; Appendix S4; Table S2). Although clearly beneficial from a collision risk perspective, avoidance of tidal turbine arrays could have other ecological consequences for harbour porpoises. How porpoises use the areas where arrays will be placed has a bearing on the potential for these impacts; for example, avoidance of arrays in areas used for transiting between foraging sites may lead to barrier effects. Further, given the scale of the avoidance responses measured here, it is conceivable that porpoises could be displaced from large areas if large numbers of turbines are placed in an important habitat. Tollit et al. (2019) reported decreased click rates at monitoring sites 200–230 m from an operational tidal turbine in Minas Passage, Canada, with simultaneous increases at sites approximately 1.7 km away. Changes in the use of habitats may have chronic energetic effects on individuals which could lead to effects on individuals' vital rates (Kastelein et al., 2001) and ultimately to population-level impacts (King et al., 2015). Whether the avoidance measured in the present study is likely to impact foraging or transitory behaviour is unclear owing to the lack of baseline data on porpoise habitat use and behaviour at the study location. Future studies should aim to collect behavioural data prior to turbine installation to understand how behavioural context and spatial variability may influence avoidance. Further, dedicated array-scale monitoring with networks of hydrophones should be undertaken to allow porpoise movements to be measured through arrays and to determine whether barrier effects or displacement occur as the industry develops.

Unlike many anthropogenic noise sources in the marine environment, tidal turbine noise is likely to be temporally and spatially persistent; it is therefore possible that individuals may habituate to the turbines in the long term. Harbour porpoise responses to other anthropogenic noise sources have been shown to diminish over small temporal scales (Cox et al., 2001; Graham et al., 2019). It was not possible to identify whether habituation may have occurred to the turbines in this study because the identity of individual porpoises cannot be determined. Further, no pre-turbine installation data were collected and the turbine was present and operating periodically for 8 months before monitoring commenced. Therefore, it is unclear whether the avoidance responses detected in this study reflect: (i) the unconditioned responses by naïve individuals moving through the area; (ii) the conditioned responses by individuals resident in the area; or (iii) a combination of these. Importantly, although the present study identified significant avoidance responses, Gillespie et al. (2021) showed that porpoises were still present within 30 m of the turbine when it was operating, which suggests that some individuals may respond at close range, or not at all.

From a management and policy perspective, the results presented here are important for the prediction of collision risk between porpoises and tidal turbines. Collision risk models are used to estimate the number of animals that may collide with turbine blades per unit time (for review see Scottish Natural Heritage, 2016). Typically, these assessments assume a temporally static animal density which probably fails to capture underlying temporal variation and may result in under- or overestimation of collision risk. In future, long-term, site-specific baseline data should be collected to characterize variability in encounter rate over larger spatial and temporal scales prior to collision risk assessment and as a baseline against which to measure change in habitat use. Passive acoustic monitoring is an effective tool to acquire these data for porpoises, but it is essential that the varying probability of detection across the tidal cycle, that would otherwise confound these temporal patterns, is accounted for. Further, the avoidance rates measured in the current study can be considered in future risk assessments. As both porpoise presence and avoidance rate scaled with flow speed, future assessments should also consider a range of flow speeds, using site-specific encounter rates and the respective avoidance rates from this study. However, future research should assess the generality of the avoidance rates presented here for other turbine types and locations. The behavioural responses of other cetacean species must also be addressed in future studies.

The results presented here show that the operation of turbines in these environments can elicit behavioural responses. It will therefore be important to reconcile the clear benefits of avoidance responses from a collision risk perspective with the potential chronic effects of displacement from, or barriers between, important habitats. This will be critical when assessing the longer-term environmental sustainability of tidal energy at the scales envisaged for the industry.

ACKNOWLEDGEMENTS

Funding was provided by the Scottish Government as part of the Marine Mammal Scientific Support Program MMSS/002/15, with additional resources from the Natural Environment Research Council (grant number NE/R015007/1). All procedures and data collection were approved by the University of St Andrews School of Biology Ethics Committee (reference number SEC18014). We thank SIMEC Atlantis Energy for assistance with deploying equipment and providing metadata for this study. We are grateful to members of the project steering group for comments on this manuscript.

CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are archived in the University of St Andrews PURE data repository.

ORCID

Laura Palmer https://orcid.org/0000-0002-3052-8872
Douglas Gillespie https://orcid.org/0000-0001-9628-157X
Jamie D. J. MacAulay https://orcid.org/0000-0003-1309-4889
Carol E. Sparling https://orcid.org/0000-0001-7658-5111
Debbie J. F. Russell https://orcid.org/0000-0002-1969-102X
Gordon D. Hastie https://orcid.org/0000-0002-9773-2755

REFERENCES

Au, W.W.L. (1993). *The sonar of dolphins*. New York: Springer.

Benjamins, S., Dale, A.C., Hastie, G., Lea, A., Scott, B., Wilson, B. et al. (2015). Confusion reigns? A review of marine megafauna interactions with tidal-stream environments. *Oceanography and Marine Biology: An Annual Review*, 53, 1–54. https://doi.org/10.1201/b18733-2

Benjamins, S., van Geel, N., Hastie, G., Elliott, J. & Wilson, B. (2017). Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141, 191–202. https://doi.org/10.1016/j.dsr2.2016.07.002

Brandt, M.J., Diederichs, A., Betke, K. & Nehls, G. (2011). Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series*, 421, 205–216. https://doi.org/10.3354/meps08888

Cox, S.L., Witt, M.J., Embling, C.B., Godley, B.J., Hosegood, P.J., Miller, P.I. et al. (2017). Temporal patterns in habitat use by small cetaceans at an oceanographically dynamic marine renewable energy test site in the Celtic Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141, 178–190. https://doi.org/10.1016/j.dsr2.2016.07.001

Cox, T.M., Read, A.J., Solow, A. & Tregenza, N. (2001). Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? *Journal of Cetacean Research and Management*, 3(1), 81–86.

Gillespie, D., Gordon, J., McHugh, R., McLaren, D., Mellinger, D., Redmond, P. et al. (2008). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Journal of the Acoustical Society of America*, 125(4), 2547. https://doi.org/10.1121/1.4808713

Gillespie, D., Palmer, L., Macaulay, J., Sparling, C. & Hastie, G. (2020). Passive acoustic methods for tracking the 3D movements of small cetaceans around marine structures. *PLoS ONE*, 15(5), 1–16. https://doi.org/10.1371/journal.pone.0229058

Gillespie, D., Palmer, L., MacAulay, J., Sparling, C. & Hastie, G. (2021). Harbour porpoises exhibit localized evasion of a tidal turbine. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(9), 1–10. https://doi.org/10.1002/aqc.3660

Goddign-Murphy, L., Woolf, D.K. & Easton, M.C. (2013). Current patterns in the Inner Sound (Pentland Firth) from Underway ADCP Data. *Journal of Atmospheric and Oceanic Technology*, 30, 96–111. https://doi.org/10.1175/JTECH-D-11-00223.1

Graham, I.M., Merchant, N.D., Farcas, A., Barton, T.R., Cheney, B., Bono, S. et al. (2019). Harbour porpoise responses to pile-driving diminish over time. *Royal Society Open Science*, 6(6). https://doi.org/10.1098/rsos.190335

Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, L., Cañadas, A. et al. (2013). Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation*, 164, 107–122. https://doi.org/10.1016/j.biocon.2013.04.010

Holdman, A.K., Haexl, J.H., Klinck, H. & Torres, L.G. (2018). Acoustic monitoring reveals the times and tides of harbor porpoise (*Phocoena phocoena*) distribution off central Oregon, USA. *Marine Mammal Science*, 35(1), 164–186. https://doi.org/10.1111/mms.12537

Johnson, G.D., Perlik, M.K., Erickson, W.P. & Strickland, M.D. (2004). Bat activity, composition, and collision mortality at a large wind plant in Minnesota. *Wildlife Society Bulletin*, 32(4), 1278–1288. https://doi.org/10.2193/0091-7648(2004)032[1278:BACACM]2.0.CO;2

Johnston, D.W. (2002). The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. *Biological Conservation*, 108(1), 113–118. https://doi.org/10.1016/S0006-3207(02)00099-X

Kastelein, R.A., de Haan, D., Vaughan, N., Staal, C. & Schooneman, N.M. (2001). The influence of three acoustic alarms on the behaviour of harbour porpoises (*Phocoena phocoena*) in a floating pen. *Marine Environmental Research*, 52, 351–371. https://doi.org/10.1016/S0141-1136(01)00090-3

Kastelein, R.A., Helder-Hoek, L. & Van de Voorde, S. (2017). Hearing thresholds of a male and a female harbor porpoise (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, 142(2), 1006–1010. https://doi.org/10.1121/1.4997907

King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L. et al. (2015). An interim framework for assessing the population consequences of disturbance. *Methods in Ecology and Evolution*, 6(10), 1150–1158. https://doi.org/10.1111/2041-210X.12411

Kyhn, L.A., Tougaard, J., Beedholm, K., Jensen, F.H., Ashe, E., Williams, R. et al. (2013). Clicking in a killer whale habitat: Narrow-band, high-frequency biosonar clicks of harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). *PLoS ONE*, 8(5). https://doi.org/10.1371/journal.pone.0063763

Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R. & Miller, L.A. (2013). Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). *Marine Mammal Science*, 29(2), E77–E97. https://doi.org/10.1111/j.1748-7692.2012.00592.x

Malinka, C.E., Gillespie, D.M., Macaulay, J.D.J., Joy, R. & Sparling, C.E. (2018). First *in situ* passive acoustic monitoring for marine mammals during operation of a tidal turbine in Ramsey Sound, Wales. *Marine Ecology Progress Series*, 590, 247–266. https://doi.org/10.3354/meps12467

Nuuttila, H.K., Bertelli, C.M., Mendzil, A. & Dearle, N. (2018). Seasonal and diel patterns in cetacean use and foraging at a potential marine renewable energy site. *Marine Pollution Bulletin*, 129(2), 633–644. https://doi.org/10.1016/j.marpolbul.2017.10.051

Osiecka, A.N., Jones, O. & Wahlberg, M. (2020). The diel pattern in harbour porpoise clicking behaviour is not a response to prey activity. *Nature Scientific Reports*, 10(1), 1–7. https://doi.org/10.1038/s41598-020-71957-0

Palmer, K.J., Brookes, K. & Rendell, L. (2017). Categorizing click trains to increase taxonomic precision in echolocation click loggers. *The Journal of the Acoustical Society of America*, 142(2), 863–877. https://doi.org/10.1121/1.4996000

Pierpoint, C. (2008). Harbour porpoise (*Phocoena phocoena*) foraging strategy at a high energy, near-shore site in south-west Wales, UK. *Journal of the Marine Biological Association of the United Kingdom*, 88(6), 1167–1173. https://doi.org/10.1017/S0025315408000507

Pine, M.K., Schmitt, P., Culloch, R.M., Lieber, L. & Kregting, L.T. (2019). Providing ecological context to anthropogenic subsea noise: Assessing listening space reductions of marine mammals from tidal energy devices. *Renewable and Sustainable Energy Reviews*, 103, 49–57. https://doi.org/10.1016/j.rser.2018.12.024

R Core Development Team. (2019). R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J. et al. (2006). Techniques for cetacean habitat modelling. *Marine Ecology Progress Series*, 310, 271–295. https://doi.org/10.3354/meps310271

Reid, J.B., Evans, P.G.H. & Northridge, S.P. (2003). Atlas of cetacean distribution in north-west European waters. Available at: http://jncc.defra.gov.uk/PDF/CetaceansAtlas_web.pdf

Risch, D., van Geel, N., Gillespie, D. & Wilson, B. (2020). Characterisation of underwater operational sound of a tidal stream turbine. *Journal of the Acoustical Society of America*, 147(4). https://doi.org/10.1121/10.0001124

Sangiuliano, S.J. (2017). Turning of the tides: Assessing the international implementation of tidal current turbines. *Renewable and Sustainable Energy Reviews*, 80, 971–989. https://doi.org/10.1016/j.rser.2017.05.045

Schmitt, P., Pine, M.K., Culloch, R.M., Lieber, L. & Kregting, L.T. (2018). Noise characterization of a subsea tidal kite. *The Journal of the*

Acoustical Society of America, 144(5), EL441–EL446. https://doi.org/10.1121/1.5080268

Scottish Natural Heritage. (2016). Assessing collision risk between underwater turbines and marine wildlife. SNH Guidance Note.

Soldevilla, M.S., Henderson, E.E., Campbell, G.S., Wiggins, S.M., Hildebrand, J.A. & Roch, M.A. (2008). Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. *The Journal of the Acoustical Society of America*, 124(1), 609–624. https://doi.org/10.1121/1.2932059

Tollit, D., Joy, R., Wood, J., Redden, A.M., Booth, C., Boucher, T. et al. (2019). Baseline presence of and effects of tidal turbine installation and operations on harbour porpoise in Minas Passage, Bay of Fundy, Canada. *The Journal of Ocean Technology*, 14, 22–48.

Villadsgaard, A., Wahlberg, M. & Tougaard, J. (2007). Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. *Journal of Experimental Biology*, 210(1), 56–64. https://doi.org/10.1242/jeb.02618

Wahlberg, M., Jensen, F.H., Aguilar Soto, N., Beedholm, K., Bejder, L., Oliveira, C. et al. (2011). Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*). *The Journal of the Acoustical Society of America*, 130(4), 2263–2274. https://doi.org/10.1121/1.3624822

Wilson, B., Batty, R., Daunt, F. & Carter, C. (2007). Collision risks between marine renewable energy devices and mammals, fish and diving birds. Report to the Scottish Executive, Oban, Scotland.

Wisniewska, D.M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S. et al. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, 26(11), 1441–1446. https://doi.org/10.1016/j.cub.2016.03.069

Wisniewska, D.M., Johnson, M., Teilmann, J., Siebert, U., Galatius, A., Dietz, R. et al. (2018). High rates of vessel noise disrupt foraging in wild harbour porpoises (*Phocoena phocoena*). *Proceedings of the Royal Society B: Biological Sciences*, 285(1872), 20172314. https://doi.org/10.1098/rspb.2017.2314

Wood, S. (2001). mgcv: GAMs and generalized ridge regression for R. *R News*, 1(2), 20–25.

Wood, S. (2017). *Generalized additive models: An introduction with R*, 2nd edition. Chapman & Hall/CRC.

Zamon, J.E. (2001). Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography*, 10(4), 353–366. https://doi.org/10.1046/j.1365-2419.2001.00180.x

Zamon, J.E. (2003). Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series*, 261(1), 243–255. https://doi.org/10.3354/meps261243

Zimmerling, R.R., Pomeroy, A.C., D'Entremont, M.V. & Francis, C.M. (2013). Canadian estimate of bird mortality due to collisions and direct habitat loss associated with wind turbine developments. *Avian Conservation and Ecology*, 8(2), 10. https://doi.org/10.5751/ACE-00609-080210

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Palmer, L., Gillespie, D., MacAulay, J. D.J., Sparling, C.E., Russell, D.J.F. & Hastie, G.D. (2021). Harbour porpoise (*Phocoena phocoena*) presence is reduced during tidal turbine operation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–11. https://doi.org/10.1002/aqc.3737