

Auditory impairment from acoustic seal deterrents predicted for harbour porpoises in a marine protected area

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Abstract

1. Management interventions to reduce human–wildlife conflict can have unintended consequences for non-target species. Acoustic deterrent devices (ADDs) are used globally by the aquaculture sector. However, the potential for these sound emissions to impact non-target species, such as cetaceans, has not yet been quantified at population relevant spatial scales.
2. To better understand the extent of potential impacts on cetaceans, such as harbour porpoises, we used acoustic modelling to investigate levels of ADD noise throughout the west coast of Scotland and across a Special Area of Conservation (SAC) for this species.
3. Using an energy-flux acoustic propagation model and data on aquaculture sites known to be using ADDs, we predicted the spatial extent of ADD noise on the Scottish west coast from 1 February 2017 to 31 January 2018. Noise maps were produced to determine the risk of auditory impairment for harbour porpoises under a range of scenarios which assumed single or multiple ADDs and simultaneous use across all sites.
4. The acoustic propagation model performed well when tested against field measurements up to 5 km, with 98% of sound exposure level (SEL) predictions within $\pm 10\%$ of the measurements. Predictions of SELs over a 24-hr period suggested extensive temporary hearing loss zones (median radius: ~28 km) for harbour porpoises around aquaculture sites. Assuming a single device at each site, 23% of the harbour porpoise SAC was predicted to be exposed to ADD noise sufficient to induce a temporary threshold shift, and under the worst-case scenario (multiple, continuously running devices per site with an aggregate duty cycle of 100%), levels exceeding permanent threshold shift could reach 0.9% of the SAC.
5. *Policy implications.* This study highlights the potential for ‘collateral damage’ from interventions such as acoustic deterrent devices (ADDs) which are intended to reduce human–wildlife conflicts with pinnipeds but may affect the long-term health and habitat use of non-target species. This is especially true for harbour porpoises which are protected under the EU and UK Habitats Regulations. The aquaculture

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industry, policymakers and regulators in countries where ADDs are used should consider these findings when attempting to mitigate pinniped depredation.

KEYWORDS

acoustic deterrent devices (ADDs), anthropogenic noise, aquaculture, harbour porpoise, human-wildlife conflict, marine protected areas, noise pollution

1 | INTRODUCTION

Human-wildlife conflicts are widespread and can be damaging to wild animals and people (Redpath et al., 2013). Conflicts arise from predation of animals reared for human use, perceived competition for resources, contamination or damage to resources and property, and disruption to construction activities (Nunny, 2020). To reduce conflicts, interventions are sought to lessen interactions. One example is the increasingly widespread use of man-made sound ('acoustic deterrents') to deter wildlife from activities including water storage, aviation and farming on land (Bomford & O'Brien, 1990), and fishing, offshore construction and aquaculture in marine environments (Götz & Janik, 2013; Mikkelsen et al., 2017). Acoustic signals are used to discourage predation, displace species away from harmful stimuli, or reduce damage to resources and property (Bomford & O'Brien, 1990; Schakner & Blumstein, 2013).

In the marine context, acoustic deterrent devices [ADDs; or acoustic harassment devices (AHDs)], produce loud sounds (source levels ≥ 185 dB re 1 μ Pa RMS), within the mid- to high-frequency range (2–40 kHz; Lepper et al., 2014) and are audible to marine mammals (pinnipeds: 50 Hz–86 kHz; small cetaceans: 150 Hz–160 kHz; NMFS, 2018). ADDs are used globally in coastal areas where aquaculture production can extend over large spatial scales to reduce pinniped depredation (Coram et al., 2014).

Exposure to ADD noise has the potential to exceed levels estimated to cause temporary threshold shifts (TTS) in cetaceans (Schaffeld et al., 2019), and may induce behavioural changes, increasing the energetic demands on individuals (Mikkelsen et al., 2017). Additionally, ADDs can exclude animals from key habitats over long periods (Morton & Symonds, 2002).

The Scottish aquaculture sector is the third largest finfish producer globally, and production (primarily Atlantic Salmon *Salmo salar*) is widespread across western Scotland (Kenyon & Davies, 2018). Individual sites are widely distributed along the coast to reduce cumulative impacts of eutrophication, chemical pollution and disease outbreaks. Depredation events by harbour *Phoca vitulina* and grey seals *Halichoerus grypus* on this coast are frequently reported by the sector (Coram et al., 2014). ADDs were first introduced in the mid-1980s (Coram et al., 2014) to counteract this issue and reduce the practice of shooting seals for which, until recently, licences were granted (Marine (Scotland) Act 2010; Scottish Government, 2020).

Harbour porpoises *Phocoena phocoena* are protected under the EU and UK Habitats Regulations and occur in high densities around the Scottish west coast (Booth et al., 2013). In 2016, much of this area was designated a Special Area of Conservation (SAC) for this

species. This SAC is the second largest for harbour porpoises in the UK and Europe (13,813.9 km²), and aims to provide protection and maintain favourable conservation status of this population (NatureScot, 2020). The SAC overlaps considerably with aquaculture production (Figure 1), which has led to concerns that impacts from this industry may compromise its Conservation Objectives (NatureScot, 2020).

ADDs are not currently licensed in Scotland and their use at individual aquaculture sites thus remains poorly documented (Coram et al., 2014). Data gaps include the number of devices per site, duty cycles, and their acoustic source levels. The geographic spread of ADD noise along much of the Scottish west coast is increasing (Findlay et al., 2018), highlighting the need for a more quantitative understanding of the spatial extent of this noise to identify areas where harbour porpoises may be affected (Coram et al., 2014).

This study uses an acoustic propagation model to predict the spatial extent of ADD noise from the aquaculture industry across the west coast of Scotland and within the designated harbour porpoise SAC. These noise maps are then used to examine areas which may be impacted and predict zones of potential auditory impairment for harbour porpoises.

2 | MATERIALS AND METHODS

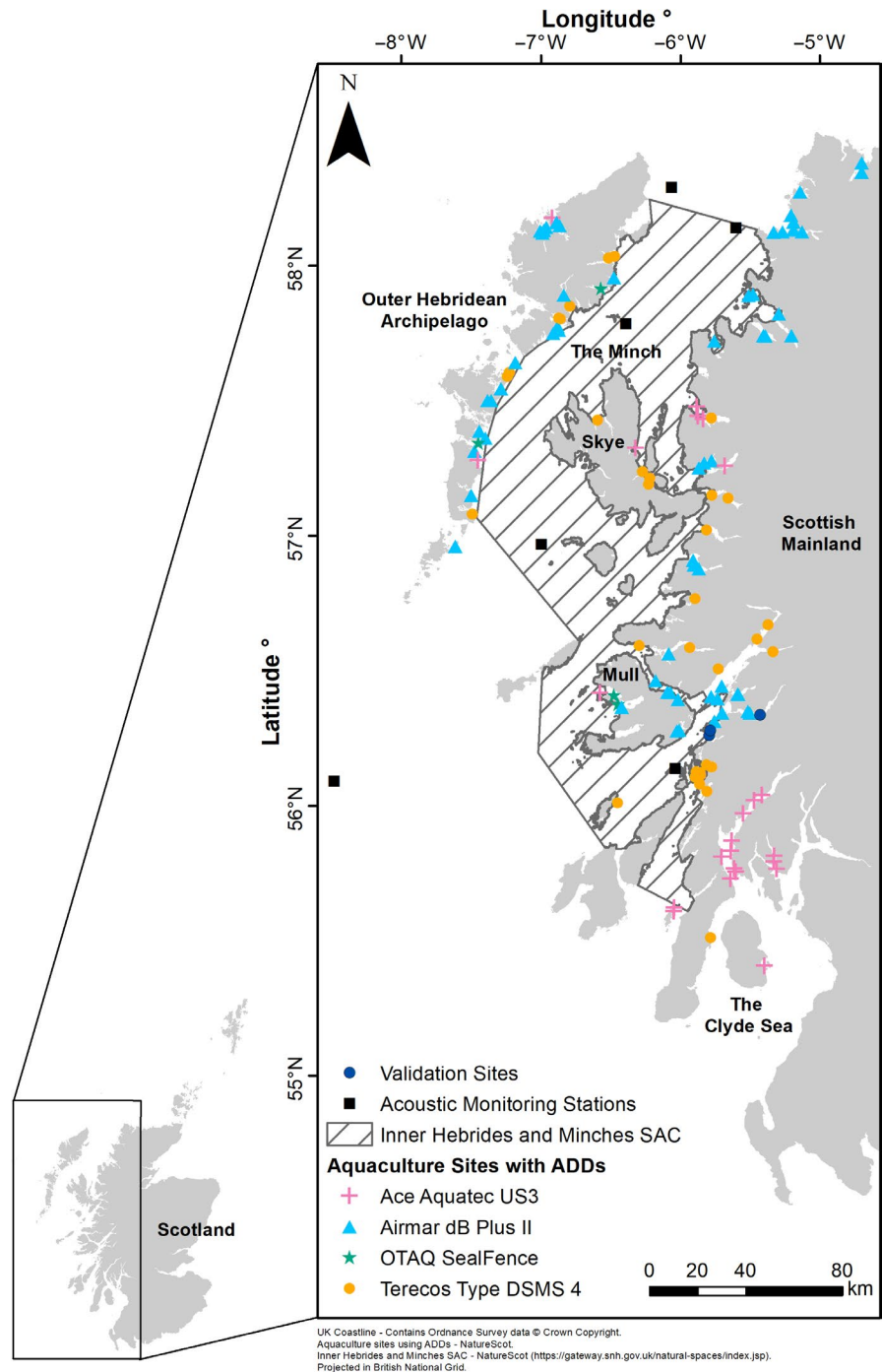
The study area extends from the Scottish mainland to beyond the Outer Hebridean Archipelago (Figure 1; 55°N–59°N and 4°W–9°W). This temperate, shallow (<300 m), coastal shelf environment, is topographically complex with numerous islands, sounds and sea lochs (Mcintyre & Howe, 2010).

Locations of aquaculture sites using ADDs during a 1-year period (1 February 2017 to 31 January 2018) were obtained from information submitted to the Marine Scotland – Licensing Operations Team in fulfilment of seal shooting license applications (NatureScot, 2018), and consequently may not include all sites using ADDs in 2017. Four ADD types (Ace Aquatec US3, Airmar, OTAQ SealFence and Terecos Type DSMS-4) were reported at 120 sites (Figure 1).

2.1 | Acoustic propagation model

An energy-flux acoustic propagation model (Weston, 1971) was implemented in MATLAB (MathWorks® 2018b). Energy-flux models are two-dimensional, range-dependent models which account for

FIGURE 1 Map of the west coast of Scotland showing the locations of aquaculture sites using acoustic deterrent devices (ADDs) between the 1 February 2017 and 31 January 2018 (NatureScot, 2018), the *Inner Hebrides and Minches* Special Area of Conservation (SAC) for harbour porpoises, the three validation sites and the six acoustic monitoring stations



bathymetry, sound speed, seabed reflectivity and are widely used for higher frequency (>1 kHz) sources located in shallow waters (Sertlek & Ainslie, 2014). Propagation loss from each aquaculture site was calculated for all 1/3 octave frequency bands (TOBs) centred between 2 and 40 kHz (Lepper et al., 2014).

Energy source levels (ESLs; dB re $1 \mu\text{Pa}^2\text{s-m}^2$ RMS over 1 s; ISO, 2017) expressed in TOBs between 2–40 kHz for ADDs were taken from the literature (Lepper et al., 2014; see Figures S1–S2 in Supporting Information for further details).

Bathymetric data were obtained from the European Marine Observation and Data Network (EMODnet) Bathymetry Consortium (<http://www.emodnet-bathymetry.eu/>; 115×115 m), and

OceanWise maps via the EDINA Marine Digimap (<https://digimap.edina.ac.uk/marine>; 30×30 m). These data were combined into a bathymetric grid with 112-m resolution using the RASTER package in R (Hijmans, 2018) and corrected for mean tidal depth. Combination of these datasets was necessary to improve accuracy along the coastline and in sea lochs where aquaculture sites are located. Bathymetric values were extracted at 100-m intervals along 360 radials extending 100 km from each source. Four sites were excluded due to poor bathymetric data at the source. To improve computation efficiency, the bathymetry-dependent component of propagation loss (integral and minimum depth; Weston, 1971) were pre-computed and interpolated from values extracted along

radials into computational grids (112-m resolution) for each aquaculture site, and applied in calculations of propagation loss.

Seabed acoustic properties (sound speed, density and attenuation) of the four main sediment types: coarse, mixed, mud and sand (EMODnet Geology Project; <http://www.emodnet-geology.eu/>; Jensen et al., 2011) were averaged and incorporated as a single model parameter, the seabed bottom loss (see Figure S3; Table S1; Weston, 1971). Water column properties were extracted from the West Scotland Coastal Ocean Modelling System (WeStCOMS-FVCOM; Aleynik et al., 2016). Seasonally variable values (temperature: 7–14°C; salinity: 3–34.5 ppt) were used to calculate an average annual sound speed profile for use in calculations of propagation loss (Weston, 1971). The sensitivity of model predictions to changes in seabed sediment type and sound speed is illustrated in the Supporting Information (Figures S3–S5; Tables S1–S2).

2.2 | Validation of the acoustic propagation model

The energy-flux model was validated by comparing predictions with measurements of ADD signals at three sites: (a) Firth of Lorne (56°21.837'N, 5°32.633'W); (b) Sound of Kerrera (56°23.008'N, 5°32.081'W); and (c) Loch Etive (56°26.954'N, 5°12.409'W; Figure 1). These sites exhibit a range of environmental conditions typical of Scottish aquaculture sites, but without contaminating noise from ADDs.

An Airmar ADD (<https://www.gaelforcegroup.com>) was deployed at 10-m depth, a typical deployment depth in Scottish aquaculture. The signal was recorded for ~1 min at intervals of ~100 m up to 1 km, and then at 2 and 5 km, in four directions around the device. The true range between the ADD and each recording was recorded via GPS (Garmin eTrex). Recordings were made using a SoundTrap 300 HF (sensitivity –188.4 dB re 1 V/μPa; Ocean Instruments Ltd.) sampling at 144 kHz, suspended at 10-m depth.

PAMGuide (Merchant et al., 2015) was used to calculate the average TOB Sound Exposure Level (SEL; dB re 1 μPa²s over 1 s). For each measurement location, SELs were modelled by applying the same methodology and model parameters as described above. Agreement (±10% error) between measured and modelled SELs was then assessed for all TOBs.

2.3 | Potential for auditory impairment in harbour porpoises

The potential for predicted levels to exceed published thresholds for TTS and permanent threshold shift (PTS) in harbour porpoises was estimated using non-impulsive acoustic thresholds for very high-frequency (VHF) cetaceans (SELs: TTS = 153 dB re 1 μPa²s and PTS = 173 dB re 1 μPa²s; Southall et al., 2019). Non-impulsive thresholds were used following recommendations made by Southall et al. (2007) which state that although these devices can produce pulsed signals, they are emitted in such a rapid fashion that some mammalian auditory systems are likely to perceive them as

continuous. Although there are no internationally harmonised noise impact criteria (Lucke et al., 2020), these threshold values are often used by regulators to assess zones of potential auditory impairment (NMFS, 2018; Southall et al., 2019).

VHF cetacean auditory weighting was applied to TOB (*f*; Equations 1 and 2) SELs for the three ADD types (ESL_w; Equation 1). ESL_w were calculated over a 24-hr period, consistent with the TTS/PTS accumulation period (ESL_{w,24h}; Equation 1; NMFS, 2018). Each aquaculture site was assumed to deploy: (i) a single device (Airmar: 52.4% duty cycle, Terecos: 6.7% duty cycle (Lepper et al., 2014); and Ace Aquatec: 5% duty cycle (pers. comms. Pyne-Carter)); or (ii) multiple devices. There is a lack of information on aggregate duty cycles of sites with multiple devices. The operation of up to 20 devices per site is common practice in Scotland (Northridge et al., 2010). As a proxy for aggregate duty cycles of multiple overlapping devices, we used either 75% or 100%. Duty cycles were calculated as the percentage of time a device was 'on' in seconds over a 24-hr period (*T*; Equation 1).

$$ESL_{w,24h}(f) = ESL_w(f) + 10 \log_{10}(T), \quad (1)$$

The weighted SEL accumulated within a range cell over a 24-hr period (SEL_{w,24h}; dB re 1 μPa²s; Equation 2; ISO, 2017) at each TOB centre frequency was computed as follows:

$$SEL_{w,24h}(f) = ESL_{w,24h}(f) - PL(f), \quad (2)$$

where *PL*(*f*) is the associated propagation loss. Broadband (2–40 kHz) weighted SEL_{w,24h} was then computed via an energy summation across all frequencies.

Modelled ADD noise maps were used to calculate the median radial distance around aquaculture sites, and the percentage area of the harbour porpoise SAC in which an animal could exceed the TTS/PTS exposure thresholds for energy accumulated over a 24-hr period.

2.4 | Ambient sound analysis

Ambient sound (ISO, 2017) data were collected over 1 year at six acoustic monitoring stations within the study area (Figure 1; COMPASS EU INTERREG VA Programme; www.compass-ocean-science.eu). SoundTrap 300 HF acoustic recorders were deployed for up to 4 months, moored ~3 m above the sea floor in depths ranging from 45 to 110 m, and programmed to record on a 20/40-min on/off duty cycle at a sampling rate of 96 kHz.

PAMGuide was used to calculate median TOB sound pressure levels (SPL; dB re 1 μPa) for each site. Median TOB SPLs were weighted for VHF cetaceans (Southall et al., 2019; see Figure S6) and accumulated over a 24-hr period (SEL_{w,24h}). The median broadband (2–40 kHz) SEL_{w,24h} for each site was then computed via an energy summation across all frequencies, and the median SEL_{w,24h} for all sites combined was calculated (see Table S3) and used in ADD noise maps to represent ambient sound levels. A signal-to-noise ratio (SNR) of 0 dB was used for mapping the extent of ADD signal propagation.

2.5 | Exposure to ADD noise by stationary and fleeing harbour porpoises

To understand how different behaviours could affect the potential for animals to be exposed to levels of ADD noise exceeding auditory impairment thresholds, hypothetical noise exposure scenarios assuming stationary and straight-line fleeing animals were investigated. These were based on minimum, average and maximum swim speeds reported in the literature (see Table S4).

Modelled scenarios started with the animal at distances of 1, 100, 500, 1,000 and 5,000 m from a single Airmar ADD. Animals were assumed to remain stationary or swim in a straight line away from the source. Range-dependent SEL_w was accumulated at 1-s intervals up to a duration of 24-hr along each straight line, with no auditory recovery assumed to occur within this period (NMFS, 2018).

3 | RESULTS

3.1 | Validation of the acoustic propagation model

The Airmar playback signal was strongest between 8 and 12.5 kHz. The SNR outside these frequencies was too low for accurate validation. Overall, good agreement was found between measured and modelled SELs at distances up to at least 5 km with 98% of predictions falling within $\pm 10\%$ of measurements (Figure 2), and under- or

over-prediction varying with validation site and source–receiver distance (see Appendix S2, Table S5; Figure S7).

3.2 | Predicted spatial extent of ADD noise

Maps of ADD noise indicated that, when assuming continuous ADD use over a 24-hr period and regardless of duty cycle, over 11.8% (15,966 km²) of the Scottish west coast study area was ensouffied by ADD noise exceeding the broadband (2–40 kHz) median ambient sound level accumulated over a 24-hr period (132.5 ± 1.4 dB re $1 \mu\text{Pa}^2\text{s}$) by more than 10 dB (Figure 3; see Figures S6–S8; Table S3). When assuming a single device at each aquaculture site (Figure 3a), the maximum weighted $SEL_{w,24h}$ was 218 dB re $1 \mu\text{Pa}^2\text{s}$ and occurred within ~ 100 m of sites. As expected, $SEL_{w,24h}$ decreased with increasing distance from the source but could remain 10 dB above ambient sound levels (>142.5 dB re $1 \mu\text{Pa}^2\text{s}$) at considerable distances (>60 km; Figure 3). $SEL_{w,24h}$ was highest in areas where aquaculture sites were located close together, or in narrow sounds and sea lochs. For example, the Sound of Mull, a narrow strait (~ 168 km²) with four aquaculture sites, was ensouffied by $SEL_{w,24h}$ in excess of 145 dB re $1 \mu\text{Pa}^2\text{s}$ (Figure 3a).

Changes in sound speed and sediment type had a limited influence on predicted $SEL_{w,24h}$. For example, assuming an average sediment type, the comparison of extreme sound speed values (1,485.9 and 1,501.2 m/s) yielded median differences of 0.3 ± 0.02 dB, while

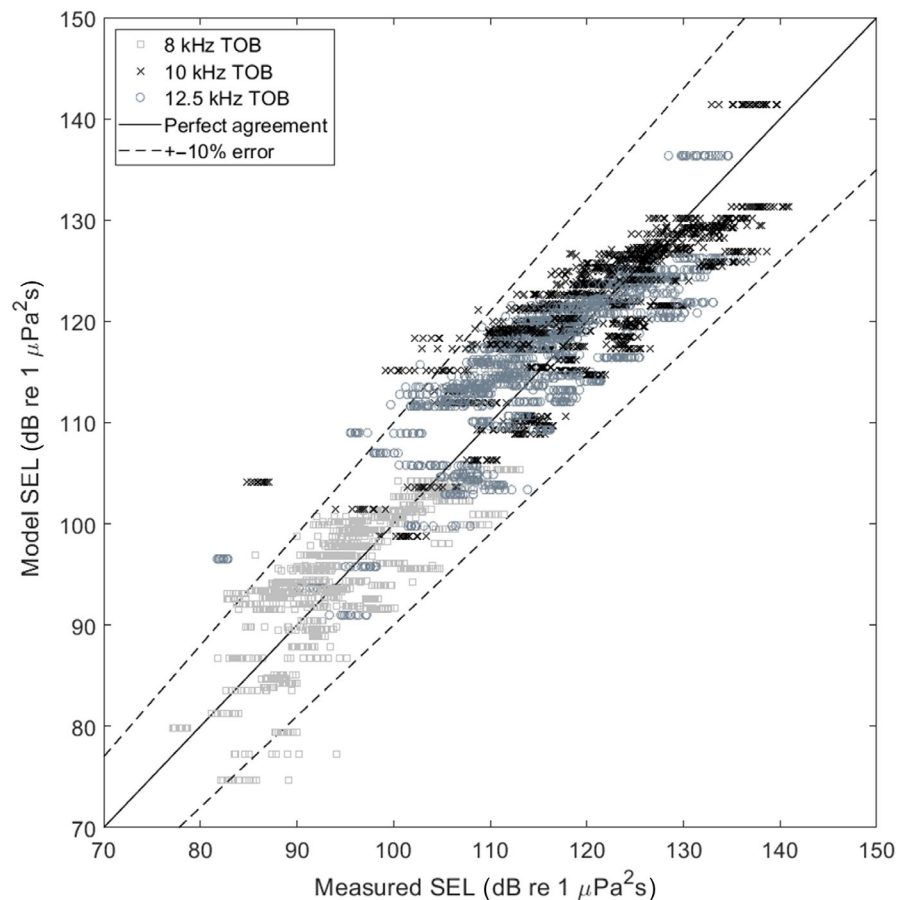


FIGURE 2 Measured versus modelled sound exposure levels (SELs; dB re $1 \mu\text{Pa}^2\text{s}$) for TOBs with centre frequencies from 8 to 12.5 kHz. Solid line indicates perfect agreement and dashed line indicates $\pm 10\%$ error

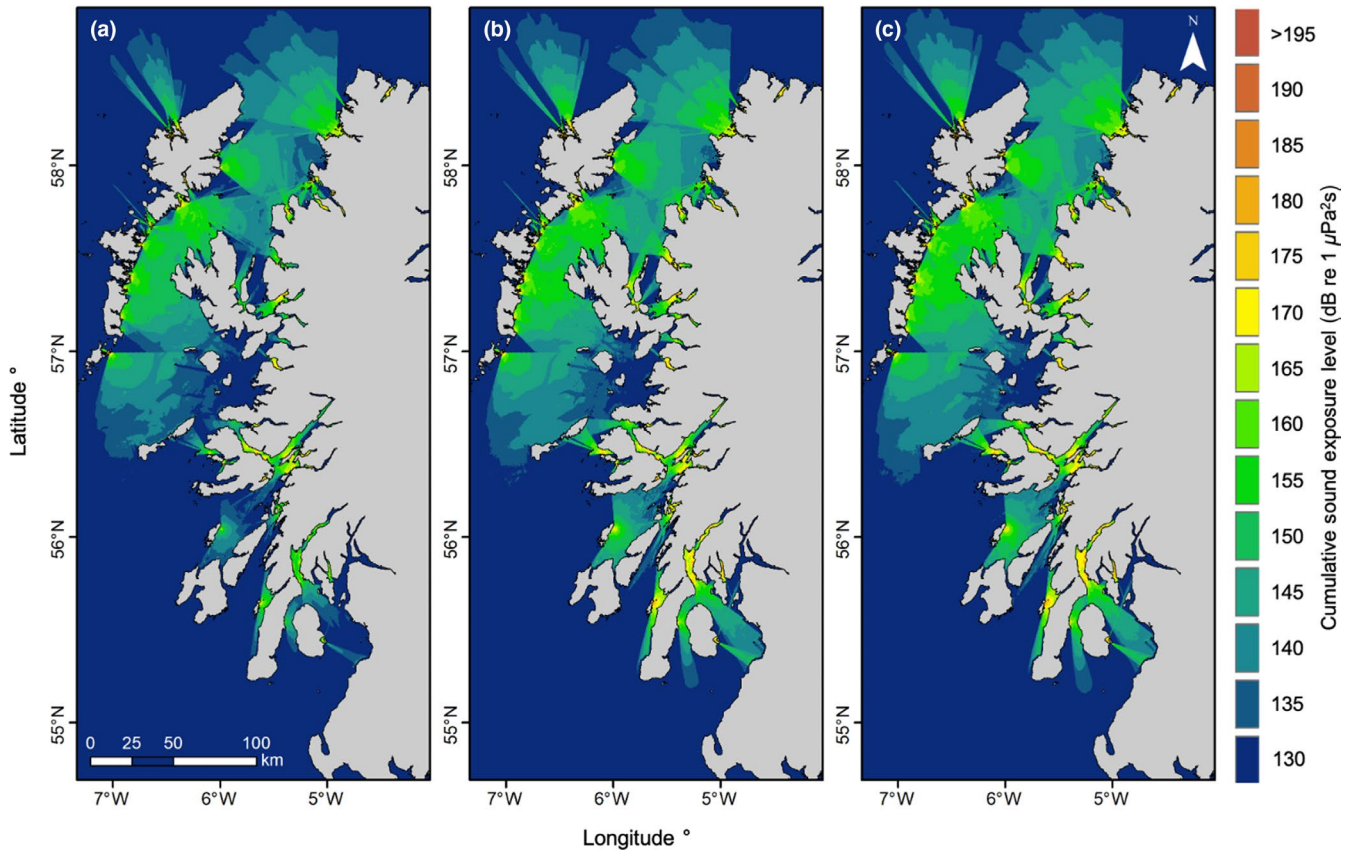


FIGURE 3 Very high-frequency cetacean weighted 24-hr cumulative sound exposure levels (dB re $1 \mu\text{Pa}^2\text{s}$). Maps include the outputs of aquaculture sites using Ace Aquatec US3, Airmar, and Terecos Type DSMS-4 acoustic deterrent devices (ADDs) with (a) a single device (5, 6.7, 52.4%), (b) 75% and (c) 100% duty cycles, between 1 February 2017 and 31 January 2018 (NatureScot, 2018)

varying sediment type and keeping sound speed constant made between -1.5 ± 0.1 dB (mud) and $+1.33 \pm 0.03$ dB (coarse) difference to $\text{SEL}_{w,24h}$ when compared to the average sediment type as assumed in the model (see Figure S5; Table S2).

When increasing the aggregate ADD duty cycle to 75% and 100% (Figure 3b,c), the maximum $\text{SEL}_{w,24h}$ increased to 220 and 221 dB re $1 \mu\text{Pa}^2\text{s}$, respectively at ~ 100 m from source. Accordingly, in these scenarios, areas exceeding 142.5 dB re $1 \mu\text{Pa}^2\text{s}$ (75% = 21,406.5 km^2 ; 100% = 23,517.3 km^2) were larger than for the single-device scenario (15,966 km^2).

3.3 | Potential for auditory impairment in harbour porpoises

Predicted $\text{SEL}_{w,24h}$ exceeded the TTS threshold in large areas around aquaculture sites, and across the entire west coast of Scotland (Figures 3 and 4). For a single device at each site, the predicted TTS radius ranged from 11 to 53 km (median: 28 km; Figure 4a). Predicted PTS radii were 0.2–0.9 km (median: 0.5 km; Figure 4b). Increasing the aggregate duty cycle at a site increased median distances for TTS and PTS. The radius of predicted TTS zones were increased to 20–70 km (median: 44 km) for 75%, and 23–72 km (median: 46 km)

for 100% respectively (Figure 4a). Predicted PTS distances increased to 0.3–1.3 km for 75% (median: 0.7 km) and 0.4–2 km for 100% (median: 1 km; Figure 4b).

Large areas of the harbour porpoise SAC were predicted to be ensonified by ADD noise levels exceeding auditory impairment thresholds for the species. For the single-device scenario, 23% (3,177.2 km^2) of the SAC had predicted $\text{SEL}_{w,24h}$ that exceeded TTS exposure thresholds (Figure 5). In this scenario, 0.2% of the SAC (27.6 km^2) was at high enough levels to exceed PTS thresholds. In scenarios with higher aggregate duty cycles, these percentages were increased (TTS: 75% duty cycle = 33% (4,558.6 km^2); 100% duty cycle = 37% (5,111.1 km^2); and PTS: 75% duty cycle = 0.6% (82.8 km^2); 100% duty cycle = 0.9% (124.3 km^2); Figure 5).

3.4 | Exposure to ADD noise by stationary and fleeing harbour porpoises

Both stationary and straight-line fleeing animal scenarios indicated the potential for auditory impairment thresholds to be exceeded in harbour porpoises. The greatest exposure was incurred by animals closest to the ADD at onset (1 m; Table 1). In this scenario, both stationary and fleeing harbour porpoises (travelling ≤ 1.5 m/s; see Table S4) would

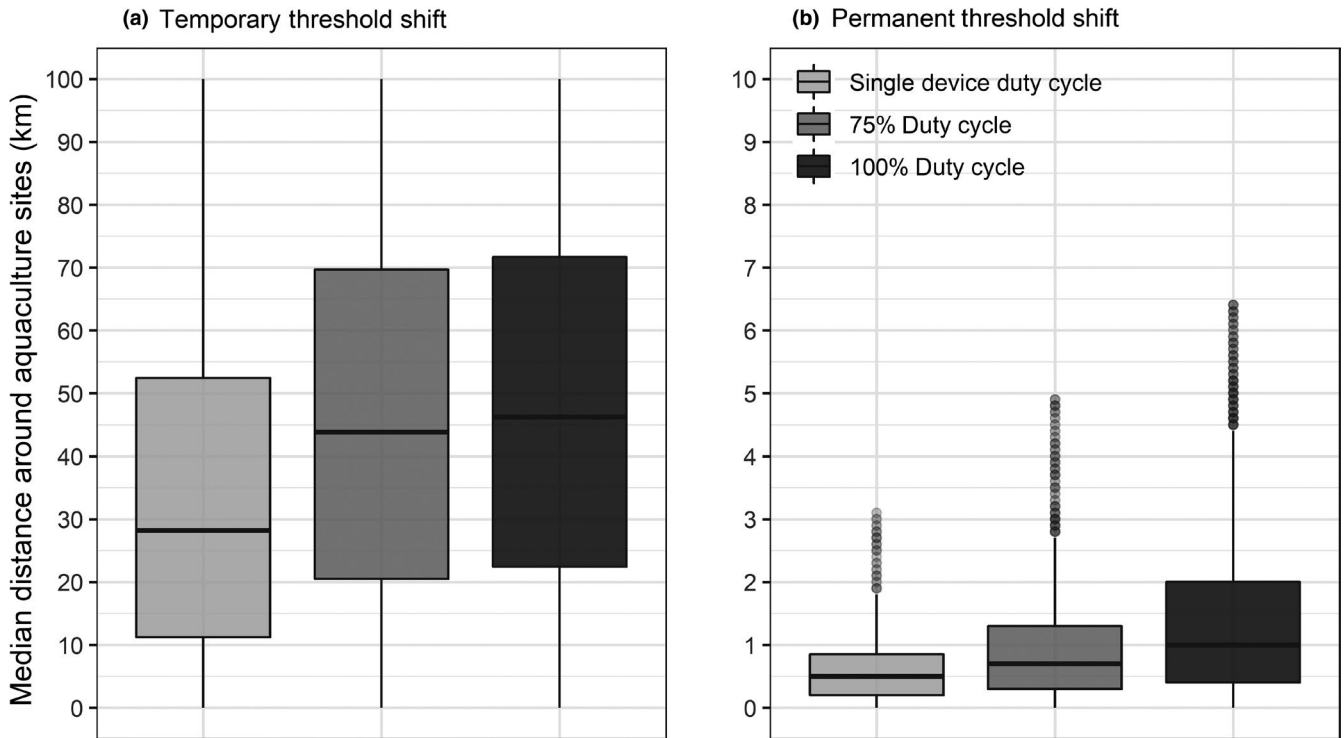


FIGURE 4 Median distance around all aquaculture sites where acoustic deterrent device (ADD) noise levels were predicted to exceed (a) temporary threshold shift (TTS) or (b) permanent threshold shift (PTS) levels over a 24-hr period for different duty cycles of devices [single device (5%, 6.7% or 52.4%), 75% and 100%]. Figure shows the median value (solid line), the 25th and 75th percentiles (boxes), the range without outliers (whiskers) and outliers (circles)

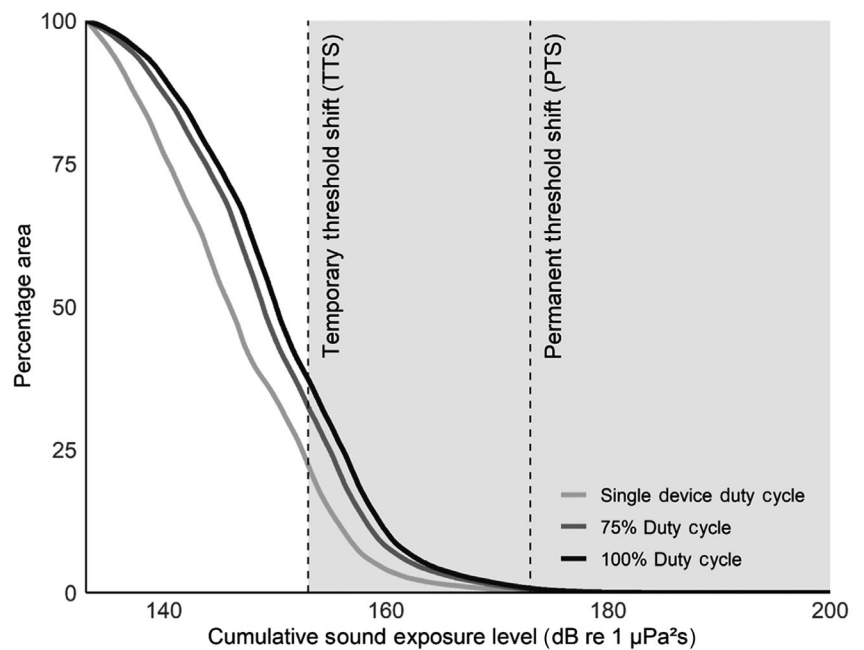


FIGURE 5 Percentage area of the Inner Hebrides and Minches Special Area of Conservation (SAC) for harbour porpoises exceeding 24-hr very high-frequency cetacean weighted cumulative sound exposure levels (dB re 1 µPa²s) which could exceed thresholds for temporary threshold shift (TTS) or permanent threshold shift (PTS). Results illustrate variable duty cycles [single device (5%, 6.7% or 52.4%), 75% or 100%]

Cumulative sound exposure level (dB re 1 µPa²s)	Percentage area		
	Single device duty cycle	75% Duty cycle	100% Duty cycle
TTS	23	33	37
PTS	0.2	0.6	0.9

Distance at onset of ADD (m)	Swim speed (m/s)	Temporary threshold shift (TTS = 153 dB re 1 $\mu\text{Pa}^2\text{s}$)		Permanent threshold shift (PTS = 173 dB re 1 $\mu\text{Pa}^2\text{s}$)	
		Time (s)	Distance (m)	Time (s)	Distance (m)
1	0	1	1	1	1
	0.15	1	1	1	1
	1.5	1	1	1	1
	2.8	1	1	NA	NA
	4.3	1	1	NA	NA
100	0	35	100	3,458	100
	0.15	36	104.4	NA	NA
	1.5	46	168	NA	NA
	2.8	61	269.8	NA	NA
	4.3	85	464.5	NA	NA
500	0	190	500	18,923	500
	0.15	196	528.4	NA	NA
	1.5	317	974.5	NA	NA
	2.8	1,512	4,732.6	NA	NA
	4.3	NA	NA	NA	NA
1,000	0	589	1,000	NA	NA
	0.15	658	1,097.7	NA	NA
	1.5	NA	NA	NA	NA
	2.8	NA	NA	NA	NA
	4.3	NA	NA	NA	NA
5,000	0	30,434	5,000	NA	NA
	0.15	NA	NA	NA	NA
	1.5	NA	NA	NA	NA
	2.8	NA	NA	NA	NA
	4.3	NA	NA	NA	NA

TABLE 1 Time (s) and distance (m) over a 24-hr period at which stationary or straight-line fleeing harbour porpoise would exceed TTS/PTS levels at variable distances from an Airmar ADD at its onset. NA values indicate no predicted auditory impairment

exceed PTS thresholds within 1 s (Table 1). With increased distance at ADD onset, the overall exposure decreased (Table 1). At an onset distance of 100 m, all porpoises would exceed TTS thresholds within 85 s and up to 464.5 m from the device regardless of swimming speed (Table 1; Figure 6). At 500 m, porpoise fleeing at ≤ 2.8 m/s would exceed TTS thresholds within 25 min (Table 1). At 1,000 m, animals would exceed TTS thresholds if fleeing at 0.15 m/s within 11 min and at a distance of 1,097.7 m (Table 1). At 5,000 m, TTS thresholds were predicted only in stationary animals (Table 1). Only stationary animals at 100 and 500 m were predicted to exceed PTS thresholds when assuming a single ADD (Table 1; Figure 6).

4 | DISCUSSION

Our results make evident that noise from ADDs used by the aquaculture industry can propagate far beyond the immediate vicinity of aquaculture sites. Target and non-target species could therefore be affected over large distances. Given model assumptions, estimates

of ADD noise for 2017 predicted that 15,966 km² (11.8%) of the Scottish west coast study area was ensounded by SEL_{w,24h} in excess of 142.5 dB re 1 $\mu\text{Pa}^2\text{s}$, with large areas around aquaculture sites (median radius: ~ 28 km) potentially exceeding TTS levels for harbour porpoises. When assuming a single device at each site, 23% of the harbour porpoise SAC was predicted to fall within a TTS zone and when assuming the worst-case scenario (multiple devices per site running continuously and producing an aggregate duty cycle of 100%) the PTS zone could reach 0.9% of the SAC. Thus, the attempt to manage the conflict between aquaculture and pinnipeds through the use of ADDs could be creating an unintended impact on another protected species at habitat-wide scales ($> 3,177.2$ km² of the SAC).

4.1 | Methodological limitations

Our results are based on an acoustic propagation model with a number of assumptions. Principally heterogeneities such as temperature, salinity and different sediment types were not included. Alternative

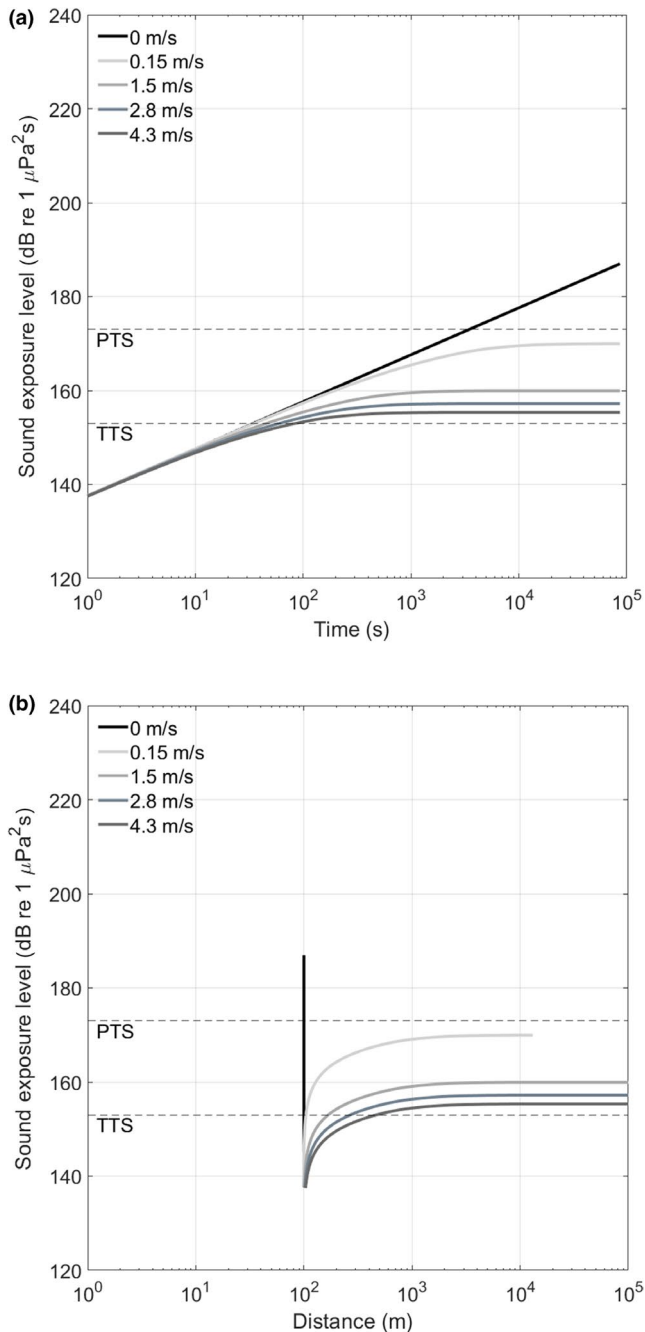


FIGURE 6 Very high-frequency cetacean weighted sound exposure levels (SEL_w ; dB re $1 \mu Pa^2 s$) for stationary and fleeing harbour porpoise accumulated at 1-s intervals up to 24 hr. Figure indicates SEL_w over (a) time (s) and (b) distance (m) assuming the animal is at 100 m from an Airmar acoustic deterrent device (ADD) at its onset. Dashed lines indicate temporary threshold shift (TTS) or permanent threshold shift (PTS)

models (e.g. Ray Tracing; Porter & Liu, 1994) can incorporate this detail, but are computationally expensive given the large number of sources in this study (Lepper et al., 2014). The potential influence of changes in sound speed and sediment type on $SEL_{w,24h}$ predictions were assessed, and results indicated that both parameters had a limited effect on model predictions ($< \pm 1.5$ dB; see Figure S5; Table S2).

Effective quiet, defined as the maximum SPL that will fail to produce a significant threshold shift regardless of exposure duration and accumulation (NMFS, 2018), has been estimated in harbour porpoises as ≤ 124 dB re $1 \mu Pa$. However, this can only be applied with confidence up to 4 kHz (Kastelein et al., 2012). Given that the main frequencies of ADDs in this study lie between 2 and 40 kHz (Lepper et al., 2014), the use of this estimate was deemed inappropriate in the context of this study. Future assessments of thresholds for effective quiet at frequencies exceeding 4 kHz would be useful to improve confidence in auditory impairment predictions from mid- to high-frequency sources, such as ADDs.

To examine model accuracy, we compared our predictions against field measurements. High levels of agreement were found for peak ADD frequencies (8–12.5 kHz) up to the furthest measurement at a distance of about 5 km (98% within $\pm 10\%$ error; Figure 2). Variation in SELs was dependent on validation site and source–receiver distance. At sites 1 and 2, measurements within 200 m were lower than model estimates and higher at greater distances. At site 3 (Loch Eive) measurements were lower than estimates for all distances (see Table S5; Figure S7), which is likely due to the strong water-column stratification (Mcintyre & Howe, 2010), creating complex propagation conditions. Validation results confirm that for peak ADD frequencies the energy-flux modelling approach provided reliable estimates up to at least 5 km. Assessments of lower- and higher-frequency ADD signal components, and at distances exceeding 5 km would have improved confidence in model accuracy but were outside the scope of this study.

Predicting the precise acoustic outputs of sites with ADDs is challenging because there is currently no requirement to report how these devices are being used (Coram et al., 2014). The total number of sites using ADDs, the number of active devices, aggregate duty cycles and their acoustic source levels are therefore poorly documented. We used data submitted in fulfilment of seal shooting license applications in 2017 to model the simultaneous acoustic outputs of ADDs from 120 sites, assuming these sites used either a single device or multiple devices continuously over a 24-hr period. More recent data, which were not available when this study was conceived and carried out, suggest that in 2017, 128 aquaculture sites on this coastline used ADDs, and that sites often deployed multiple ADDs, which were switched on continuously for 89% of stocked days per year (Scottish Government, 2021). Consequently, estimating noise levels for higher aggregate duty cycles as done in this study may be a realistic approximation for the multiple ADD use scenario which appeared to be common on the Scottish west coast in 2017. Addressing uncertainties in industry use of ADDs at Scottish aquaculture sites could further refine our overall results.

4.2 | Conservation implications

Harbour porpoises occur in relatively high densities in the inshore waters off western Scotland (Booth et al., 2013), leading to large parts of the area being designated an SAC for the species in 2016.

Our study estimates that much of this area was potentially ensounded by ADD noise which could remain high ($SEL_{w,24h} > 142.5$ dB re $1 \mu Pa^2s$) at considerable distances (>60 km) from aquaculture sites, particularly when higher aggregate duty cycles were assumed. Higher $SEL_{w,24h}$ were especially apparent where multiple aquaculture sites were closely grouped, and in narrow sounds and sea lochs. For example, in the Sound of Mull where four aquaculture sites used Airmar and Terecos ADDs (Figure 1), noise levels increased by 10 dB at higher duty cycles (Figure 3).

Furthermore, our results indicate several large areas of Scottish inshore waters would be exposed to noise levels potentially high enough to exceed TTS and PTS exposure thresholds (Figures 3 and 4). Radial distances of zones of TTS threshold exceedance ranged between 11 and 72 km depending on duty cycle (Figure 3), and in many areas PTS thresholds were exceeded at ranges of 0.2–2 km from the source (Figure 4). These estimates of zones for potential auditory impairment are based on the NMFS (2018) criteria, which are mostly derived from acute noise exposure experiments. Despite a lack of studies on hearing impacts from chronic noise exposure in marine mammals, it is worth noting that evidence from human studies suggests that the mammalian ear can incur permanent impairment from chronic exposure at lower noise levels compared to acute noise exposure (Themann & Masterson, 2019). This is of particular importance given the predictions of high noise levels from ADDs for much of the Scottish west coast. This study therefore highlights a potential ecological risk to the species within a SAC designated for their protection.

Theoretical behavioural simulations of harbour porpoise exposure to the onset of a single Airmar ADD predicted exceedance of PTS thresholds in only stationary animals up to 500 m, and the potential for TTS threshold exceedance at >1 km from the source when considering worst-case scenarios of animals slowly (<0.15 m/s) fleeing in a straight line. While such simulations can help assess exposure risk in individuals, due to a lack of fine-scale behavioural data around aquaculture sites, this risk assessment is sensitive to several assumptions. For example, simulations assumed animals experience no auditory recovery during exposure, but ADDs used by the Scottish aquaculture sector produce intermittent signals and therefore some auditory recovery is likely to occur between signal pulse trains or sweeps (see Figure S1). However, during the deployment of multiple devices (Northridge et al., 2010) where continuous noise is expected (75% and 100% duty cycles), periods where auditory recovery could occur are likely to be significantly reduced. Hearing loss is dependent on several interacting factors including exposure level and duration, repetition rate, directionality of hearing, and changes in vertical dive behaviour (van Beest et al., 2018; Kastelein et al., 2005; Mikkelsen et al., 2017; NMFS, 2018; Northridge et al., 2010). Hence, the results presented here may over- or under-estimate exposure in porpoises responding to ADD noise.

Our results predict that large areas within the SAC are chronically exposed to high noise levels from ADDs (Figure 3; Figure S8), making potential re-distribution to quieter areas challenging. It has been suggested that cetaceans may remain within high noise environments

even when there is risk of auditory impairment depending on a) the context of previous exposures (Ellison et al., 2012), and b) their motivation to remain within an area when the habitat is of high value for foraging, resting or reproducing (Forney et al., 2017). Evidence indicates that harbour porpoises will utilise areas around aquaculture sites using ADDs (Northridge et al., 2010). Individuals may therefore be willing to remain within high noise environments, such as those predicted (Figure 3), increasing their exposure to noise.

While harbour porpoise echolocation is concentrated in the very high-frequency range (120–140 kHz), porpoise best hearing sensitivity occurs between ~ 10 and 140 kHz (Kastelein et al., 2017). This range encompasses the peak frequencies of the ADDs considered in this study. It is unknown how a reduction in hearing sensitivity at these frequencies (2–40 kHz) might affect the ecology of harbour porpoises. But, auditory impairment could reduce dynamic range, frequency discrimination and passive listening space, with implications for navigation or predator/prey detection (Götz & Janik, 2013; Kastelein et al., 2019; Pine et al., 2019; Tougaard et al., 2015). Chronic noise disturbance also has the potential to disrupt feeding behaviour, making individuals vulnerable to starvation if experienced over extended periods due to their high metabolic demands (Booth, 2020). Chronic degradation of their acoustic habitat and the potential for auditory impairment could therefore have serious long-term consequences for harbour porpoise populations in Scottish inshore waters.

Globally ADDs have been recommended as a non-lethal method of mitigating pinniped depredation at aquaculture sites. This study highlights the potential for auditory impairment from ADD noise to non-target species such as harbour porpoises, at distances exceeding 28 km from aquaculture sites, amounting to over 23% of a designated porpoise SAC. Alternative mitigation options to reduce depredation have been trialled at aquaculture sites globally, such as improved net tensioning, use of different net materials, multiple nets and improved animal husbandry (Coram et al., 2014). The use of ADDs as mitigation to reduce interactions by pinnipeds has implications for sympatric, protected species such as harbour porpoises. These unintended consequences might extend over large portions of the coastal habitats of target and non-target species which are also used in aquaculture production. The aquaculture industry, policymakers and regulators in countries where these devices are used should therefore consider these findings when weighing the efficacy of ADDs against other mitigation measures.

5 | CONCLUSIONS

Human activities in marine and terrestrial environments are leading to widespread conflicts with wildlife. The increasing and long-term use of ADDs to deter pinnipeds from aquaculture sites globally has the potential to have unintended impacts on non-target species. This study used an acoustic propagation model to investigate the predicted spatial extent and potential for non-target cetaceans, such as harbour porpoises, to be exposed to ADD noise at levels which

may exceed auditory impairment thresholds. Due to a lack of information, a number of assumptions were made with regards to how ADDs are deployed by the aquaculture sector. However, our findings underscore the need to consider the potential for 'collateral damage' from management interventions such as ADDs for non-target species at aquaculture sites worldwide.

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AUTHORS' CONTRIBUTIONS

C.R.F., N.D.M., D.R. and B.W. conceived the study; A.F., N.D.M. and D.A. aided with analysis; C.R.F. performed the analysis and wrote the manuscript. All authors contributed to writing and reviewing draft manuscripts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.j6q573ndq> (Findlay et al., 2021).

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REFERENCES

- Aleynik, D., Dale, A. C., Porter, M., & Davidson, K. (2016). A high resolution hydrodynamic model system suitable for novel harmful algal bloom modelling in areas of complex coastline and topography. *Harmful Algae*, 53, 102–117. <https://doi.org/10.1016/j.hal.2015.11.012>
- Bomford, M., & O'Brien, P. H. (1990). Sonic deterrents in animal damage control: A review of device tests and effectiveness. *Wildlife Society Bulletin*, 18, 411–422. <https://www.jstor.org/stable/3782740>
- Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, 36, 195–208. <https://doi.org/10.1111/mms.12632>
- Booth, C. G., Embling, C., Gordon, J., Calderan, S. V., & Hammond, P. S. (2013). Habitat preferences and distribution of the harbour porpoise *Phocoena phocoena* west of Scotland. *Marine Ecology Progress Series*, 478, 273–285. <https://doi.org/10.3354/meps10239>
- Coram, A., Gordon, J., Thompson, D., & Northridge, S. (2014). *Evaluating and assessing the relative effectiveness of acoustic deterrent devices and other non-lethal measures on marine mammals* (pp. 1–145). Scottish Government.
- Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2012). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology*, 26, 21–28.
- Findlay, C. R., Aleynik, D., Farcas, A., Merchant, N. D., Risch, D., & Wilson, B. (2021). Data from: Auditory impairment from acoustic seal deterrents predicted for harbour porpoises in a marine protected area. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.j6q573ndq>
- Findlay, C. R., Ripple, H. D., Coomber, F., Froud, K., Harries, O., van Geel, N., Calderan, S. V., Benjamins, S., Risch, D., & Wilson, B. (2018). Mapping widespread and increasing underwater noise pollution from acoustic deterrent devices. *Marine Pollution Bulletin*, 135, 1042–1050. <https://doi.org/10.1016/j.marpolbul.2018.08.042>
- Forney, K. A., Southall, B. L., Slooten, E., Dawson, S., Read, A. J., Baird, R. W., & Brownell, R. L. (2017). Nowhere to go: Noise impact assessments for marine mammal populations with high site fidelity. *Endangered Species Research*, 32, 391–413. <https://doi.org/10.3354/esr00820>
- Götz, T., & Janik, V. M. (2013). Acoustic deterrent devices to prevent pinned depredation: Efficiency, conservation concerns and possible solutions. *Marine Ecology Progress Series*, 492, 285–302. <https://doi.org/10.3354/meps10482>
- Hijmans, R. J. (2018). *raster: Geographic data analysis and modeling*. Retrieved from <https://cran.r-project.org/package=raster>
- ISO. (2017). *ISO 18405:2017 'Underwater acoustics - Terminology'*. International Organization for Standardization. Retrieved from <https://www.iso.org/standard/62406.html>
- Jensen, F. B., Kuperman, W. A., Porter, M. B., & Schmidt, H. (2011). *Computational ocean acoustics* (2nd ed., W. M. Harmann, A. Ando, W. L. Au, A. B. Baggeroer, N. H. Fletcher, C. R. Fuller, W. A. Kuperman, J. L. Miller, M. R. Schroeder, & A. I. Tolstoy, Eds.). Springer. <https://doi.org/10.1007/978-1-4419-8678-8>
- Kastelein, R. A., Gransier, R., Hoek, L., & Olthius, J. (2012). Temporary threshold shifts and recovery in a harbor porpoise (*Phocoena phocoena*) after octave-band noise at 4 kHz. *Journal of the Acoustical Society of America*, 132, 3525–3537. <https://doi.org/10.1121/1.4757641>
- Kastelein, R. A., Helder-Hoek, L., & Van de Voorde, S. (2017). Hearing thresholds of a male and a female harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America*, 142, 1006–1010. <https://doi.org/10.1121/1.4997907>
- Kastelein, R. A., Helder-Hoek, L., van Kester, R., Huisman, R., & Gransier, R. (2019). Temporary hearing threshold shift in Harbor Porpoises (*Phocoena phocoena*) due to one-sixth Octave Noise Band at 16 kHz. *Aquatic Mammals*, 45, 280–292. <https://doi.org/10.1578/AM.45.3.2019.280>
- Kastelein, R. A., Janssen, M., Verboom, W. C., & de Haan, D. (2005). Receiving beam patterns in the horizontal plane of a harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America*, 118, 1172–1179. <https://doi.org/10.1121/1.1945565>
- Kenyon, W., & Davies, D. (2018). *Salmon farming in Scotland*. Scottish Parliament, 36 pp. Retrieved from <https://digitalpublications.parliament.scot/ResearchBriefings/Report/2018/2/13/Salmon-Farming-in-Scotland>
- Lepper, P. A., Gordon, J., Booth, C., Theobald, P., Robinson, S. P., Northridge, S., & Wang, L. (2014). *Establishing the sensitivity of cetaceans and seals to acoustic deterrent devices in Scotland*. Scottish Natural Heritage Commissioned Report No. 517. Scottish Natural Heritage. Retrieved from <https://www.nature.scot/naturescot-commissioned-report-517-establishing-sensitivity-cetaceans-and-seals-acoustic-deterrent>
- Lucke, K., Martin, B. S., & Racca, R. (2020). Evaluating the predictive strength of underwater noise exposure criteria for marine mammals.

- Journal of the Acoustical Society of America*, 147, 3985–3991. <https://doi.org/10.1121/10.0001412>
- McIntyre, K. L., & Howe, J. A. (2010). Scottish west coast fjords since the last glaciation: A review. *Geological Society, London, Special Publications*, 344, 305–329. <https://doi.org/10.1144/SP344.21>
- Merchant, N. D., Fristrup, K. M., Johnson, M. P., Tyack, P. L., Witt, M. J., Blondel, P., & Parks, S. E. (2015). Measuring acoustic habitats. *Methods in Ecology and Evolution*, 6, 257–265. <https://doi.org/10.1111/2041-210X.12330>
- Mikkelsen, L., Hermannsen, L., Beedholm, K., Madsen, P. T., & Tougaard, J. (2017). Simulated seal scarer sounds scare porpoises, but not seals: Species-specific responses to 12 kHz deterrence sounds. *Royal Society Open Science*, 4, 170286. <https://doi.org/10.1098/rsos.170286>
- Morton, A. B., & Symonds, H. K. (2002). Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES Journal of Marine Science*, 59, 71–80. <https://doi.org/10.1006/jmsc.2001.1136>
- NatureScot. (2018). *Data extract from Marine Scotland Seal Licensing Return, released under the Environmental Information (Scotland) Regulations 2004 by NatureScot, 2018*. Retrieved from <https://donst.aniford.typepad.com/files/snh-foi-25-april-2017-document-7-adds-used-only.xlsx>
- NatureScot. (2020). *Conservation and Management Advice: Inner Hebrides and the Minches SAC*. NatureScot. Retrieved from <https://apps.snh.gov.uk/sitelink-api/v1/sites/10508/documents/59>
- NMFS. (2018). *Technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing: Underwater acoustic thresholds for onset of permanent and temporary threshold shifts* (pp. 1–178). National Oceanic and Atmospheric Administration. Retrieved from <https://www.fisheries.noaa.gov/resource/document/technical-guidance-assessing-effects-anthropogenic-sound-marine-mammal-hearing>
- Northridge, S. P., Gordon, J., Booth, C., Calderan, S., Cargill, A., Coram, A., Gillespie, D., Lonergan, M., & Webb, A. (2010). *Assessment of the impacts and utility of acoustic deterrent devices*. Final Report to the Scottish Aquaculture Research Forum, Project Code SARF044 (pp. 1–39). Scottish Aquaculture Research Forum.
- Nunny, L. (2020). Animal welfare in predator control: Lessons from land and sea. How the management of terrestrial and marine mammals impacts wild animal welfare in human–wildlife conflict scenarios in Europe. *Animals*, 10, 1–24. <https://doi.org/10.3390/ani10020218>
- 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>
- Porter, M. B., & Liu, Y. C. (1994). Finite-element ray tracing. *Theoretical and Computational Acoustics*, 2, 947–956.
- Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., Amar, A., Lambert, R. A., Linnell, J. D. C., Watt, A., & Gutiérrez, R. J. (2013). Understanding and managing conservation conflicts. *Trends in Ecology & Evolution*, 28, 100–109. <https://doi.org/10.1016/j.tree.2012.08.021>
- Schaffeld, T., Ruser, A., Woelfing, B., Baltzer, J., Kristensen, J. H., Larsson, J., Schnitzler, J. G., & Siebert, U. (2019). The use of seal scarers as a protective mitigation measure can induce hearing impairment in harbour porpoises. *Journal of the Acoustical Society of America*, 146, 4288–4298. <https://doi.org/10.1121/1.5135303>
- Schakner, Z. A., & Blumstein, D. T. (2013). Behavioral biology of marine mammal deterrents: A review and prospectus. *Biological Conservation*, 167, 380–389. <https://doi.org/10.1016/j.biocon.2013.08.024>
- Scottish Government. (2020). *Animals and Wildlife (Penalties, Protections and Powers) (Scotland) Bill*. Scottish Government.
- Scottish Government. (2021). *Acoustic deterrent device (ADD) use in the aquaculture sector*. Parliamentary Report. Scottish Government.
- Sertlek, Ö. H., & Ainslie, M. A. (2014). A depth-dependent formula for shallow water propagation. *Journal of the Acoustical Society of America*, 136, 573–582. <https://doi.org/10.1121/1.4884762>
- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., & Tyack, P. L. (2007). Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquatic Mammals*, 33(4), 411–414. <https://doi.org/10.1578/am.33.4.2007.411>
- Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., Nowacek, D. P., & Tyack, P. L. (2019). Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. *Aquatic Mammals*, 45(2), 125–232. <https://doi.org/10.1578/am.45.2.2019.125>
- Themann, C. L., & Masterson, E. A. (2019). Occupational noise exposure: A review of its effects, epidemiology, and impact with recommendations for reducing its burden. *Journal of the Acoustical Society of America*, 146, 3879–3905. <https://doi.org/10.1121/1.5134465>
- Tougaard, J., Wright, A. J., & Madsen, P. T. (2015). Cetacean noise criteria revisited in the light of proposed exposure limits for harbour porpoises. *Marine Pollution Bulletin*, 90, 196–208. <https://doi.org/10.1016/j.marpolbul.2014.10.051>
- van Beest, F. M., Teilmann, J., Hermannsen, L., Galatius, A., Mikkelsen, L., Sveegaard, S., Balle, J. D., Dietz, R., & Nabe-Nielsen, J. (2018). Fine-scale movement responses of free-ranging harbour porpoises to capture, tagging and short-term noise pulses from a single air-gun. *Royal Society Open Science*, 5. <https://doi.org/10.1098/rsos.170110>
- Weston, D. E. (1971). Intensity-range relations in oceanographic acoustics. *Journal of Sound and Vibration*, 18, 271–287. [https://doi.org/10.1016/0022-460X\(71\)90350-6](https://doi.org/10.1016/0022-460X(71)90350-6)

SUPPORTING INFORMATION

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