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Behavioural Responses of Humpback Whales (*Megaptera novaeangliae*) to Two Acoustic Deterrent Devices in a Northern Feeding Ground off Iceland

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Abstract

Mitigating cetacean entanglement in fishing gear is of global interest, and strategies include the use of acoustic deterrent devices to warn whales of fishing gear. For baleen whales, responses to these devices are poorly understood. This behavioural response study compared the behaviour of humpback whales (*Megaptera novaeangliae*) in their feeding grounds off Iceland prior to, during, and after exposure to a whale pinger (Future Oceans: 3 kHz, *n* = 9 exposures) and a seal scarer (Lofitech AS Ltd.: 10 to 20 kHz, *n* = 7 exposures) using boat-based focal follows. Linear mixed effects models and binary generalized linear mixed effects models were used to analyze the effect of the devices on breathing rate, dive time, swimming speed, swimming directness, and surface feeding. There was a significant increase in swimming speed and a significant decrease in observed surface feeding during whale pinger exposures. There were no significant behavioural changes that were consistent across individuals during seal scarer exposures. In addition to experimental exposure trials, a field trial of whale pingers on a capelin purse seine was conducted. During this trial, humpback whales were observed entering the net from the bottom while the whale pingers were attached at the top, but the encircled whales were able to locate an opening free of pingers and escape without damaging the net. All in all, the results suggest pingers can be a useful entanglement mitigation tool in humpback whale feeding grounds given that a reduction in feeding around nets likely reduces the risk of whales swimming through them. Furthermore, the use of pingers may also reduce net damage by guiding encircled whales to a pinger-free opening. However, given the observed behavioural changes that may lead to fitness consequences if exposure to pingers is frequent, whale pingers are most advisable for short-term use in conjunction with other entanglement mitigation measures.

Key Words: entanglement, acoustic deterrent device, behavioural response, Iceland, humpback whale, *Megaptera novaeangliae*

Introduction

There is global concern over marine mammal bycatch and entanglement in fishing gear—for example, animals becoming incidentally caught in gear and drowning or incidentally coming into contact with gear and escaping, sometimes with gear attached to their bodies and/or with injuries. Documented impacts of entanglement on cetaceans include injury (Knowlton & Kraus, 2001; Cassoff et al., 2011; Moore et al., 2013), exhaustion of energy reserves (van der Hoop et al., 2017), emaciation (Moore et al., 2013), and drowning (Cassoff et al., 2011; Moore & van der Hoop, 2012). These impacts at the individual level can lead to increased mortality rates at the population level (Volgenau et al., 1995; Robbins et al., 2015). Many different types of fishing gear can cause entanglement (Johnson et al., 2005), and this is likely to affect most cetacean species (Gall & Thompson, 2015). Apart from impacts on cetacean individuals and populations, entanglement also leads to financial losses to the fishing industry because of loss of catch, gear damage or loss, and downtime for repairs (Lien, 1979; Lien & Aldrich, 1982). This can be a particularly serious issue in fisheries incurring large whale entanglements such as those involving humpback whales (*Megaptera novaeangliae*).

Technologies have been developed with the intent to mitigate marine mammal entanglement.

One such technology is low-powered acoustic deterrent devices (ADDs; defined as having source levels ranging from 110 to 179 dB re µPa^2 m^2) known as *pingers* (Ainslie, 2010). These devices can be attached to fishing gear and emit a sound underwater within the hearing range of target marine mammals (Erbe & McPherson, 2012). The devices warn the animals of the presence of gear or simply serve as an annoying, unnatural sound that the animals want to avoid (Kraus, 1999). Alternatively, since large whales in particular can often escape from or carry away entangling gear, researchers also hypothesize that whales can learn to associate nets and pingers with danger (Jefferson & Curry, 1996).

For cetaceans, specific pingers have been developed for porpoises, dolphins, and beaked whales (odontocetes), as well as baleen whales (mysticetes), with varying degrees of success. High-frequency odontocete pingers have resulted in reductions in bycatch (e.g., Kraus et al., 1997; Barlow & Cameron, 2003; Carretta et al., 2008; Mangel et al., 2013), but in other studies, no change or even increased bycatch has occurred (e.g., Soto et al., 2013; Erbe et al., 2016). Whale pinger and low-frequency sound experiments have been conducted on baleen whales, including North Atlantic right whales (*Eubalaena glacialis*; Nowacek et al., 2004), minke whales (*Balaenoptera acutorostrata*; McGarry et al., 2017), grey whales (*Eschrichtius robustus*; Lagerquist et al., 2012), and humpback whales (Harcourt et al., 2014; How et al., 2015; Pirotta et al., 2016) with similar varying results. North Atlantic right whales showed a strong response of swimming to the surface when exposed to 1 kHz alerting sounds (Nowacek et al., 2004), and both minke and humpback whales responded during testing of 4-kHz whale alarm prototypes by making significantly more close approaches and abrupt turns when exposed to active devices (Todd et al., 1992). Humpback whales were also less likely to collide with cod traps fitted with these 4-kHz alarm prototypes in Canada (Lien et al., 1992), and they responded to 2 to 2.1 kHz "tone stimuli" in Australia by swimming away from the sound source (Dunlop et al., 2013). Conversely, grey whales did not appear to respond to 1 to 3 kHz sounds, though results were inconclusive (Lagerquist et al., 2012), and the majority of recent research conducted on humpback whales in Australia concluded that there is no clear response from the whales to the modern 3-kHz whale pingers now sold commercially (Harcourt et al., 2014; How et al., 2015; Pirotta et al., 2016). Despite this, anecdotal reports do claim that some industries have had lower incidence of humpback whale entanglement in their feeding grounds with the use of commercial whale pingers (Fumunda, 2012; Welch, 2016).

High-powered ADDs (defined as having source levels of 189 dB re µPa^2 m^2 and above) are often referred to as *seal scarers* (Ainslie, 2010). They produce a high-intensity, high-frequency sound designed to scare seals away from aquaculture operations (Taylor et al., 1997). Some cetacean species, including harbour porpoises (*Phocoena phocoena*; Brandt et al., 2013), orcas (*Orcinus orca*; Morton & Symonds, 2002), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Morton, 2000), also react to these devices. The only testing of a seal scarer on baleen whales was conducted on minke whales in Iceland, and it was observed that they too were deterred from the area with an active 10 to 20 kHz device (McGarry et al., 2017).

Humpback whales are one of the most common cetaceans that frequent the waters off Iceland in the North Atlantic, primarily during their feeding season from spring through autumn (Pike et al., 2009), though some sightings are also recorded in the winter months (Magnúsdóttir et al., 2014). The summer-time central North Atlantic humpback whale population is estimated to be approximately 10,000 individuals with the highest concentration found off north/northeast Iceland (Pike et al., 2019). Fish species are estimated to constitute 60% of the humpback whales' diet in this area (Sigurjónsson & Víkingsson, 1997). Based on modelling of the hearing capabilities of humpback whales, a lower hearing sensitivity threshold of 700 Hz (Houser et al., 2001), or possibly as low as 200 Hz (Tubelli et al., 2018), and an upper threshold of 9 to 10 kHz (Houser et al., 2001; Tubelli et al., 2018) have been estimated. Their maximum hearing sensitivity is estimated to be between 2 to 6 kHz (Houser et al., 2001). Humpback whale vocalizations, however, have frequency harmonics that range from approximately 20 Hz up to 24 kHz (Thompson et al., 1986; Au et al., 2006), indicating hearing may extend to higher frequencies than have been modeled. Hearing is the most important sense for marine mammals to orient themselves in their environment (Tyack, 2008), and large baleen whales, like the humpback, may have trouble detecting the sounds produced by fishing gear in the water depending on factors such as the acoustic signal produced by different gear types and acoustic masking of these signals (Lien et al., 1990).

Commercial fishing is one of the largest industries in Iceland, with 1,582 commercial vessels registered in 2019 (Statistics Iceland, n.d.). The fishing methods used in Icelandic waters are long-lines/handlines, gillnets, trawls, and seines (International Council for the Exploration of the Sea [ICES], 2019). In addition, there are also mussel, oyster, and fish farming operations, as well as whelk pot-trap fishing, in coastal Icelandic waters (Government of Iceland, n.d.; Young, 2015; Marine and Freshwater Research Institute, 2019; Kristján Phillips, pers. comm., 2019). Estimates indicate that at least one-quarter of the coastal Icelandic humpback whale population has been entangled in fishing gear at least once (Basran et al., 2019), and most Icelandic fisheries have reported issues with humpback whales swimming through, and sometimes becoming entangled in, their gear (Basran, 2014; Young, 2015). These incidences have caused gear damage or loss, as well as injury or death to the whales in some cases (Víkingsson et al., 2004, 2005; Víkingsson, 2011; Basran, 2014; Basran et al., 2019).

Currently, there are no mitigation methods or regulations in place for minimizing whale entanglement in fishing gear in Iceland, despite growing concern over this issue in the local fishing industries. This study conducted the first analysis of behavioural responses of free-ranging humpback whales in their northern feeding grounds off the coast of northeast Iceland to exposure to whale pingers (Future Oceans) and seal scarers (Lofitech AS Ltd.). In addition to the experimental exposures of whales to these ADDs, this study conducted the first field trial of whale pingers in the capelin purse seine fishery in Iceland. This research aims to provide a scientific basis for deciding if these ADDs are likely to effectively mitigate humpback whale entanglement and reduce resulting gear damage in their feeding grounds, and to investigate any potentially adverse effects of the devices on natural humpback whale behaviour.

Methods

Study Area

Experimental exposures of humpback whales to a whale pinger took place in two locations in northeast Iceland: Skjálfandi Bay and Eyjafjörður (Figure 1). Skjálfandi (66° 05' N, 17° 33' W) is a bay with an area of approximately 1,100 km^2 that is known for predictable humpback whale sightings from spring through autumn during their feeding season. The bay harbours the fishing and whale watching town of Húsavík on the southeast shore (Stefánsson & Guðmundsson, 1978; Stefánsson et al., 1987; Einarsson, 2009; A. Gíslason, unpub. data, 2004). Eyjafjörður (65° 50' N, 18° 07' W) is a narrow fjord, approximately 440 km^2 in area, located approximately 80 km west of Skjálfandi Bay (S. Jónsson, unpub. data, 1996). Eyjafjörður is also well known for humpback whale sightings, and it harbours fishing and whale watching in the city of Akureyri as well as the towns of Dalvík, Hauganes, and Hjalteyri. Experimental exposures to a seal scarer took place only in Skjálfandi Bay. The field trial of whale pingers took place in collaboration with a capelin purse seine vessel based in Neskaupstaður in East Iceland. The boat fished for capelin (*Mallotus villosus*) off South Iceland (Figure 1).

Acoustic Deterrent Devices

Two ADDs were used in the present study. The first was the 2016 version of the Future Oceans whale pinger (WP). This WP operates on a single 3.6 V lithium battery and activates automatically when in contact with saltwater. When active, the WP produces a 145 dB re 1 µPa at 1 m tone at 3 kHz for 300 ms at 5 s intervals. The second device was the Lofitech AS Ltd. seal scarer (SS) composed of a control box with a 25-m-long cable with a transducer at the end that produces the sound. This control box is powered by a 12 V marine battery onboard the boat. When active, the device produces a 189 dB re 1 µPa at 1 m sound with a fundamental frequency of 14.5 kHz and a frequency range between 10 to 20 kHz for 500 ms at random intervals of 5 to 60 s.

A calibration of both ADDs was conducted in the harbour in Húsavík (Skjálfandi Bay) to confirm the manufacturer's specifications. Each device was lowered 5 m into the water and recorded by a Reson 4032 hydrophone (also at 5 m depth) connected to an Etec amplifier with the sound signal recording to a Microtrack recorder. The WP was recorded at distances of 1, 5, 10, and 20 m from the hydrophone, while the SS was recorded at 20, 30, and 40 m to avoid the signals being clipped due to the much higher source level of this device. The recorded signals from the devices were compared with a 153 dB re 1 µPa (rms) calibration signal recorded using a calibrator with an adapter for the Reson 4032 hydrophone. The emitted sound from the WP had an actual source level of 137 dB re 1 µPa (rms) calculated from the received level recorded at 1 m. The received levels measured at 5, 10, and 20 m were 123, 117, and 116 dB re 1 µPa (rms), respectively. Based on previous modelling of the WP sound, humpback whales are expected to detect the sound at a distance of at least 500 m from the source (Harcourt et al., 2014; Pirotta et al., 2016). The emitted sound from the SS had an actual source level of 188 dB re 1 µPa (rms) calculated from the received level recorded at 20 m assuming spherical spreading. The received levels measured at 20, 30, and 40 m were 162, 161, and 160 dB re 1 µPa (rms), respectively.

Experimental Exposure Trials

Experimental exposures of humpback whales to the ADDs (experimental exposure trials [EETs]) were conducted in Skjálfandi Bay in June, July, and October 2017, and in June and October 2018. In Eyjafjörður, EETs were conducted in May and July 2018. A different, private boat was used in each location. Both boats were 9-m-long research vessels

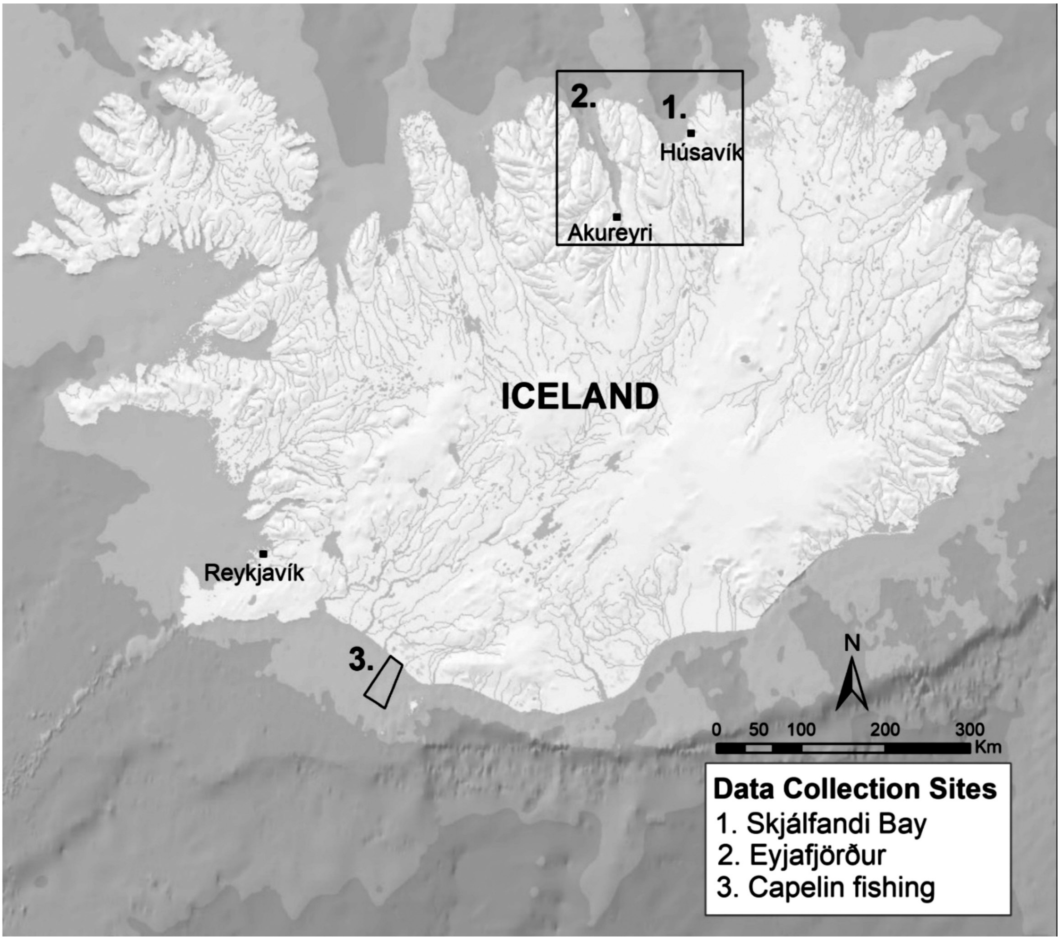

Figure 1. Map showing the locations of humpback whale (*Megaptera novaeangliae*) experimental exposure trials (1. and 2.) using the whale pinger and/or seal scarer, and location where capelin fishing with a purse seine equipped with the whale pingers took place during onboard observation (3.)

from which distance and angle measurements to the whale were conducted from the bow, with the researcher sitting approximately 1 m above the sea surface. Data collected during EETs were recorded with the *Logger 2010* computer program (IFAW); and a hand-held video camera (Sony HDR-CX160E handycam) was used to record the surface behaviours of the whale during each EET. *Logger 2010* recorded time, boat GPS position, boat heading, and any comments that were entered by the data recorder. EETs were attempted when the sea state was considered 3 or less on the Beaufort scale.

During an EET, an individual focal humpback whale was chosen based on the criteria that it was swimming alone and that there were no whale-watching boats observing the animal. Photo-identification images of the individual were taken of the unique pigment pattern on the ventral fluke and of the dorsal fin shape. This was to ensure each individual whale was not exposed to the same device more than once within the same year to avoid possible habituation to the sound. When photo-identification was complete, the pre-exposure phase (PrE) began with the boat slowly following the focal whale from a distance of approximately 100 m for 30 min to obtain the baseline behaviour of the individual; this was considered to be the control phase for each EET. The 100 m distance complies with whale-watching criteria set forth in many countries globally to minimize disturbance (Carlson, 2009) when observing natural behaviour while still being within range to collect all necessary data. This time also allowed for the focal whale to habituate to the presence of the boat, although whales in both study areas encounter boats often so the boat was not a novel stimulus.

Each breath the humpback whale took was recorded as "up," and each terminal dive (when the whale arches the back or lifts the fluke to go down for a deep dive) was recorded as "dive" in *Logger 2010*. Other information was also noted, including if the whale dove with or without raising the fluke, if the whale was surface feeding, and if there were other whales in the area. Furthermore, one researcher used an angle-board and rangefinder to obtain the angle to the whale in relation to the boat and the distance to the whale, and these data were also recorded into *Logger 2010*. If the distance could not be obtained from the rangefinder, this researcher estimated the distance to the whale when it took a terminal dive. This was done conservatively, based on the last recorded distance from the rangefinder, and usually only when the whale was at a distance of 400 m or greater. The angle-board, rangefinder, and distance estimation were always done by the same researcher (CJB) for consistency.

Once the PrE phase was complete, the boat was positioned beside where the focal humpback whale was seen taking its last terminal dive and the engine was turned off. To begin the 15-min exposure phase (E), a single WP or SS was placed off the side of the boat into the water at 5 m depth, attached to a weighted rope and buoy. The breaths, dives, angles, and distances of the focal whale were then recorded in *Logger 2010* in the same manner as in the PrE phase, with the boat remaining stationary. After the 15-min E phase ended, the ADD was removed from the water, the boat was positioned approximately 100 m from the focal whale, and the same data were collected for an additional 30 min for the post-exposure phase (PoE). If the focal whale disappeared from sight for more than 20 min during an EET, it was considered lost, and the EET was ended.

Behavioural Response Variables

Surface Feeding—The number of surface feeding events was determined by watching the video footage of each phase of each EET. For each surfacing of the focal humpback whale, surface feeding behaviour was categorized as yes (Y), no (N), or not able to determine (NA). Feeding behaviour was recognized by observing surface lunging behaviour or expanded throat pleats indicating the whale had a full mouth (Figure 2). A surfacing was also categorized as Y if researchers can be heard in the video commenting that the whale was feeding, even though the surfacing was not visible in the footage.

Breathing Rate and Dive Time—For each phase of each EET, the focal humpback whale's breathing rate was calculated as breaths per min for each surface interval (the time between diving). The time of each dive in seconds in each phase of each EET was also calculated from the time stamps of "dive" and the following "up" recorded in *Logger 2010*.

Directness Index—A directness index (DI) from 0 to 100, indicating the directness of the focal humpback whale's swimming pattern, was calculated for each phase of each EET when enough data were available. First, the coordinate position of the whale at each terminal dive was calculated. Then, the DI was calculated as the distance between the two end points of the track divided by the sum of the distances between all the points in the track, with the result multiplied by 100. A DI of 0 corresponds to swimming in a complete circle, while a DI of 100 corresponds to swimming in a straight line (Williams et al., 2002).

Swimming Speed—The focal humpback whale's swimming speed was calculated for each phase of each EET when enough data were available. Speed was calculated from each terminal dive to the next terminal dive and, therefore, included distance information from when the focal whale was diving and at the sea surface.

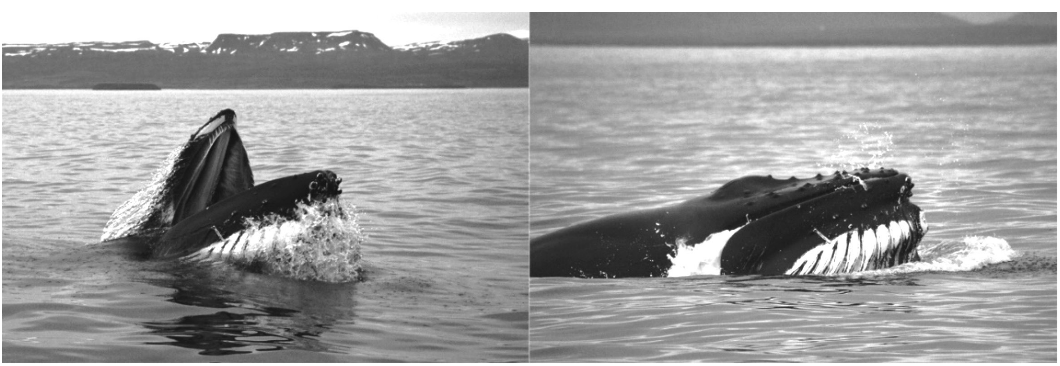

Figure 2. Photographs of lunge-feeding behaviour and expanded throat pleats used to determine if the focal humpback whale was surface feeding in video analysis

Analysis of Behavioural Response Variables

Linear mixed effect models were used to examine the effect of ADD exposure on breathing rate, dive time, swimming speed, and swimming directness. Separate models were set up for each ADD and each of the four response variables. The phase of the EET (PrE, E, and PoE) was the only fixed effect predictor variable. To account for the repeated measures within individual humpback whales, exposure trial-ID was included as a random intercept term in all models. Plots of residual vs fitted values revealed that breathing rate and swimming speed needed to be log-transformed to satisfy the modeling assumption of homogeneity of variances (using natural logarithm [ln]). Plots of the autocorrelation function of the residuals revealed significant temporal autocorrelation in the models for ln(breathing rate), dive time, and ln(speed). Auto-regressive correlation structures of order 1 were specified in the models for these response variables. Inspection of the autocorrelation function plots verified that this approach successfully accounted for the observed autocorrelation.

Since an individual whale's response to sound can depend on behavioural state (Southall et al., 2019) or vary between individuals (Lien et al., 1990), individual-specific response variation was incorporated into the models by introducing random slopes for the predictor variable phase. Likelihood ratio tests were used to determine if random intercept and slope models fitted the data significantly better than pure random intercept models. Selection of the random effects structure was done prior to selection of the fixed effects structure (as recommended by Zuur et al., 2009). Selection of the optimal fixed effects structure (i.e., comparison of models with phase as fixed effect to pure intercept models) was also based on likelihood ratio tests. For response variables in which phase had a significant effect, a post hoc pairwise comparison with Bonferroni correction was used to infer between which phases significant changes of the response variable occurred. Additionally, for response variables in which phase had a significant effect and for response variables for which random slope models were retained in the selected model, separate models and post hoc analyses were calculated for each individual exposure to identify the differences that underlie the significant effect in the overall analysis. The statistical analyses were performed using the 'nlme' (Pinheiro et al., 2014) and 'multcomp' (Hothorn et al., 2008) packages in the statistical software *R* (R Foundation for Statistical Computing).

Surface feeding behaviour was recorded as a binary variable and, thus, could not be modelled by linear mixed effects models. A binary generalized linear mixed effects model was fitted using the function 'glmer' in the 'lme4' package (Bates et al., 2015). Model specification and selection was analogous to the protocol described for the linear mixed effects models except for the specification of the autocorrelation structure. Since the 'glmer' function does not allow for the specification of temporal correlation structures, the feeding behaviour at the previous surfacing event (lag1_feeding) was included as a fixed effect to account for temporal autocorrelation. Surface feeding behaviour could only be analyzed for WP EETs because very little surface feeding was observed in all phases of the SS EETs.

Field Trial of Whale Pingers on a Commercial Purse Seine

In addition to the individual EETs, the effect of WPs was also studied in a field trial. Pingers were fitted on a capelin purse seine used by the vessel *Börkur NK122* operating out of Neskaupstaður in east Iceland for the 2018 season (January to March). For the season prior to this trial (January to March 2017), the vessel captain kept a log of humpback whale sightings and any encirclements by the purse seine. For the 2018 capelin fishing season, 10 WPs were attached to the float line of the purse seine 30 to 40 m apart from each other, complying with the manufacturer's recommendations. The captain kept record of any issues associated with WP use and any incidences of whales inside the purse seine. In addition, one researcher (CJB) joined as an onboard observer for one trip (24-28 February 2018). During onboard observations, the vessel track and whale sightings were recorded in the *SpotterPro* app (Conserve.IO) during all transit and active fishing days. The number of net casts and tonnes of fish caught with each cast were also noted. Any encirclements of whales by the purse seine were video recorded for documentation using a hand-held video camera (Sony HDR-CX160E handycam).

Results

Experimental Exposure Trials

A total of 23 research trips were undertaken in 2017-2018, totalling approximately 83 h of effort (Table 1). Of these, enough data for analysis were collected on 14 trips, resulting in nine WP and seven SS EETs.

Fifteen different individual humpback whales were tested for the 16 EETs that produced enough data to be included in the analysis. Only one individual humpback whale was tested twice, in two separate SS EETs, but these were conducted 18 mo apart. Fourteen of the individuals could be identified in the Húsavík Research Centre humpback whale catalogues. One individual in Eyjafjörður was not identifiable beyond confirming that it was only tested once in the study.

While all seven attempts to complete a SS EET were successful, in three of the 11 attempts to complete a WP EET, the humpback whale disappeared for more than 20 min and was considered lost. Two of these cases did not produce enough data to be included in the analysis.

Whale Pinger—For the WP EETs, there was little evidence for individual- or behavioural state-specific variation in responses. For breathing rate, swimming speed, swimming directness, and surface feeding, models that included a random slope for the predictor phase did not fit the data significantly better than models that only accounted for baseline variation between trials by a random intercept term (Table 2). The model for dive time was the only case in which a random slope model fitted the data significantly better than a random intercept model ($p < 0.001$; Table 2) providing evidence for individual- or behavioural state-specific, divergent responses in terms of dive time. There were four individuals for which a significant effect of phase on dive time was observed, three of which showed significant changes in the E phase (Figure 3). For two of these three individuals (WP2 and WP11), dive time was significantly lower in the E phase than the PrE and/or PoE phases; while for one individual (WP5), dive time was significantly higher in the E phase than in the PrE and PoE phases.

Table 1. Data collection trips undertaken in 2017-2018 with the date (d/mo/y), location (SB = Skjálfandi Bay and EF = Eyjafjörður), number of hours, what experimental exposure trial was completed (Trial complete: NA = not available or no usable trial; SS = seal scarer ID; and WP = whale pinger ID), the data that were collected in each experimental exposure trial (B = breathing rate, DI = directness index, D = dive time, S = swimming speed, and F = feeding), and the reason the trip did not result in a usable trial (Reason if trial NA).

Date	Location	Hours	Trial complete	Data	Reason if trial NA
29/4/17	SB	3.5	NA		Whale disappeared during WP exposure phase
3/5/17	SB	4.5	SS1	B, DI, D, S	
4/5/17	SB	3.0	NA		No usable whale
4/5/17	SB	3.0	NA		Boat broke down
16/6/17	SB	3.5	WP2	B, DI, D, S, F	
20/6/17	SB	4.5	WP5	B, D, F	
27/6/17	SB	4.5	SS2	B, DI, D, S	
			SS3	B, DI, D, S	
28/6/17	SB	3.0	WP3	B, DI, D, S, F	
11/7/17	SB	4.0	NA		No usable whale
14/7/17	SB	6.5	WP4	B, DI, D, S	
			SS4	B, D, S	
21/8/17	SB	2.5	NA		Rough seas
1/10/17	SB	3.5	WP6	B, D*	
28/4/18	EF	1.5	NA		Rough seas
30/4/18	EF	2.0	NA		Rough seas
2/5/18	EF	4.0	WP7	B, DI, D*, S*	
8/5/18	EF	5.0	NA		Whale disappeared during WP exposure phase
7/6/18	SB	3.5	WP9	B, DI, D, S, F	
12/6/18	SB	3.5	WP10	B, DI, D, S, F	
11/7/18	EF	3.0	NA		Rough seas
9/10/18	SB	3.5	WP11	B, DI, D, S	
15/10/18	SB	3.5	SS5	B, DI, D, S	
14/11/18	SB	3.5	SS6	B, DI, D, S	
21/11/18	SB	4.0	SS7	B, DI, D, S	

*Denotes experimental exposures for which data are only available for the pre-exposure and exposure phases

Table 2. Assessment of the random and fixed effects structures of five models explaining the change in a behavioural response variable after exposure to a whale pinger. To test if the effect sizes of the contrasts to the pre-exposure phase differed significantly between individuals, a random intercept and slope model was compared to a pure random intercept model by means of comparison of Akaike Information Criterion (AIC) values and a likelihood ratio test. The fixed effects structure was tested by comparing models with and without the predictor phase. Assessment of random effects was based on models estimated by restricted maximum likelihood, whereas assessment of fixed effects was based on maximum likelihood estimation. Significant *p* values are bolded.

Response variable	Test	AIC (Intercept model)	AIC (Complex model)	Chi-squared	DF	*p* value
Ln(breathing rate)	Random effect slope	471.0	475.0	0	2	1
	Fixed effect phase	461.1	463.4	1.755	2	0.42
Dive time	Random effect slope	2,557.2	2,518.2	43	2	**< 0.001**
	Fixed effect phase	2,541.6	2,545.1	0.479	2	0.79
Directness	Random effect slope	176.7	180.1	0.59	2	0.75
	Fixed effect phase	194.0	196.2	1.833	2	0.40
Ln(speed)	Random effect slope	411.4	414.7	0.73	2	0.69
	Fixed effect phase	412.4	406.1	10.28	2	**0.006**
Surface feeding	Random effect slope	483.3	487.3	0.059	2	0.97
	Fixed effect phase	487.3	483.3	7.97	2	**0.019**

Humpback whale swimming speed differed significantly between the phases of the trial ($p = 0.006$; Table 2; Figure 3). During the E phase, swimming speed was 1.7 times higher than during the PoE phase ($p = 0.0024$; Table 3) and 1.4 times higher than during the PrE phase, though the latter difference was not significant at the 0.05 significance level ($p = 0.11$; Table 3). No significant difference in humpback whale swimming speed was observed between the PrE and PoE phases ($p = 0.62$; Table 3).

Apart from swimming speed, surface feeding differed significantly between phases of the trial ($p = 0.019$; Table 2; Figure 3). The probability of surface feeding was significantly lower during the E phase than during the PoE phase ($p = 0.026$; Table 4). There was also a reduction in surface feeding from the PrE to the E phase; albeit, this was not significant at the 0.05 significance level ($p = 0.099$; Table 4). Rates of surface feeding amounted to 11% in the PrE phase, dropped to 4% in the E phase, and then rose to 13% in the PoE phase (Figure 4). No significant difference in surface feeding was observed between the PrE and PoE phases ($p = 1.00$; Table 4).

No significant effect of phase of the trial on breathing rate ($p = 0.42$; Table 2), dive time ($p = 0.79$; Table 2), or swimming directness ($p = 0.40$; Table 2) was observed (Figure 3), thus providing no evidence for a change in these behavioural response variables that was consistent across individuals in WP EETs.

Seal Scarer—For the SS EETs, there was also little evidence for individual- or behavioural state-specific variation in responses. For breathing rate, swimming speed, and swimming directness, models that included a random slope for the predictor phase did not fit the data significantly better than models that only accounted for baseline variation between trials by a random intercept term (Table 5). The model for dive time was the only case in which a random slope model fitted the data significantly better than a random intercept model ($p = 0.002$; Table 5) indicating that individual- or behavioural state-specific responses in terms of dive time may exist. There were three individuals for which a significant effect of phase on dive time was observed; however, post hoc analysis could only resolve between which phases the significant difference existed for one individual (SS4; Figure 5). For this individual, dive time was significantly lower in the PoE phase when compared to the PrE and E phases.

No consistent response to the SS across individuals was observed for any of the response variables. Phase of the trial did not have a significant effect on breathing rate ($p = 0.55$; Table 5), dive time ($p = 0.10$; Table 5), swimming directness ($p = 0.55$; Table 5), or swimming speed ($p = 0.93$; Table 5).

Field Trial of Whale Pingers on a Commercial Purse Seine

The captain of the participating capelin purse seine vessel did not report any issues with humpback whales inside the purse seine in the 2017 season and reported that there were generally lower sightings and incidences than in the 2016 season. During the 2018 capelin fishing season, the onboard observer

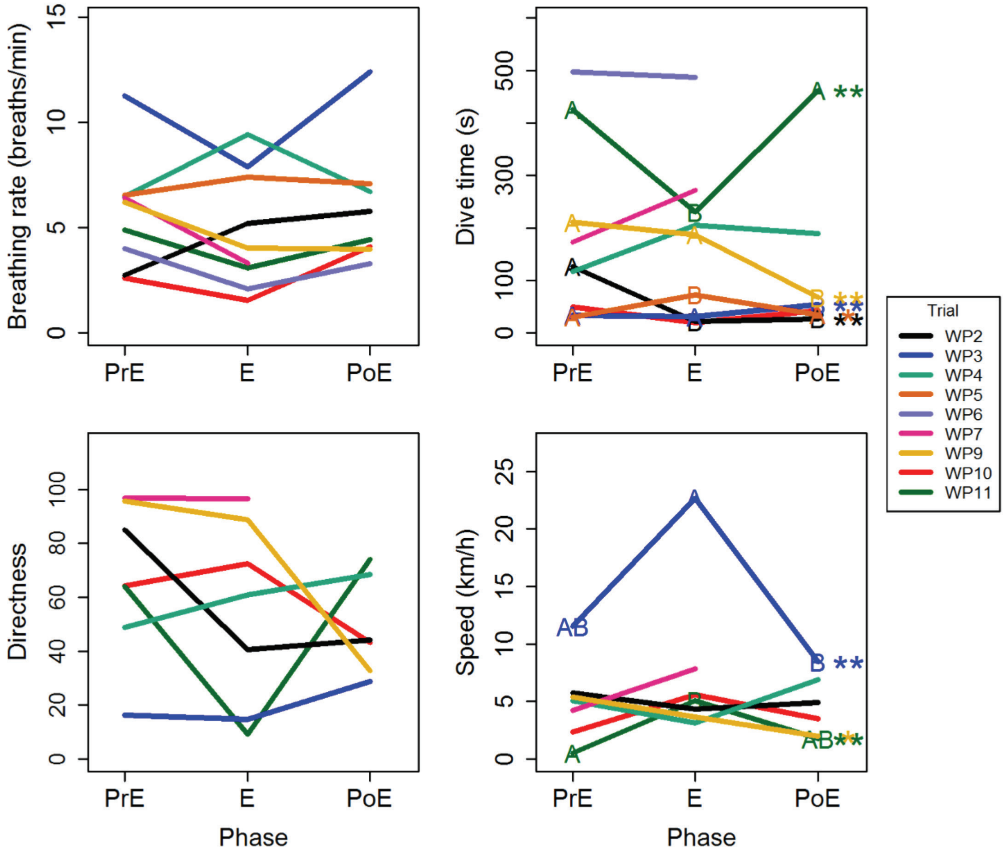

Figure 3. Averages of the behavioural response variables breathing rate, dive time, swimming directness, and swimming speed for the pre-exposure (PrE), exposure (E), and post-exposure (PoE) phases of each whale pinger (WP) experimental exposure trial. Asterisks highlight individual WP exposure trials in which the response variable differed significantly between the phases (*uncorrected: $p < 0.05$; **Bonferroni-corrected: $p < 0.05$). Letters indicate between which phases significant differences occurred. Models for individual WP exposure trials were only calculated for response variables for which overall models found a significant effect of phase or random slope (see Table 3).

Table 3. Post hoc comparison for the predictor phase (PrE = pre-exposure, E = exposure, and PoE = post-exposure) in the swimming speed model based on the whale pinger data (see Table 2). Since the response variable speed is ln-transformed, effect is the difference in ln(speed), and e^Effect is the ratio between speeds in the two compared phases. Adjusted *p* values are Bonferroni-corrected *p* values; significant *p* value is bolded.

Post hoc comparison	Effect on ln(speed)	e^Effect	Std error	Adjusted *p* value
E - PrE	0.35	1.42	0.17	0.11
PoE - PrE	-0.18	0.83	0.14	0.62
PoE - E	-0.53	0.59	0.16	**0.0024**

recorded 34 individual humpback whale sightings at seven locations during 16 h of observation (Table 6). A total of 70.6% ($n = 24$) occurred while the boat was on the capelin fishing grounds off the south/southwest coast of Iceland. The purse seine was cast three times during onboard observations, and a total of 1,510 tonnes of capelin were caught. Whales at the sea surface near the vessel when fishing operations began were noted to swim away from the area, with one whale specifically observed turning 180° to the opposite direction from where the purse seine was being set into the water.

Table 4. Post hoc comparison for the predictor phase (PrE = pre-exposure, E = exposure, and PoE = post-exposure) in the surface feeding model based on the whale pinger data (see Table 2). Effect and std error are the effect size on the linear predictor scale and its std error. Adjusted *p* values are Bonferroni-corrected *p* values; significant *p* value is bolded.

Post hoc comparison	Effect on surface feeding	Std error	Adjusted *p* value
E - PrE	-1.02	0.48	0.099
PoE - PrE	0.21	0.26	1
PoE - E	1.22	0.47	**0.026**

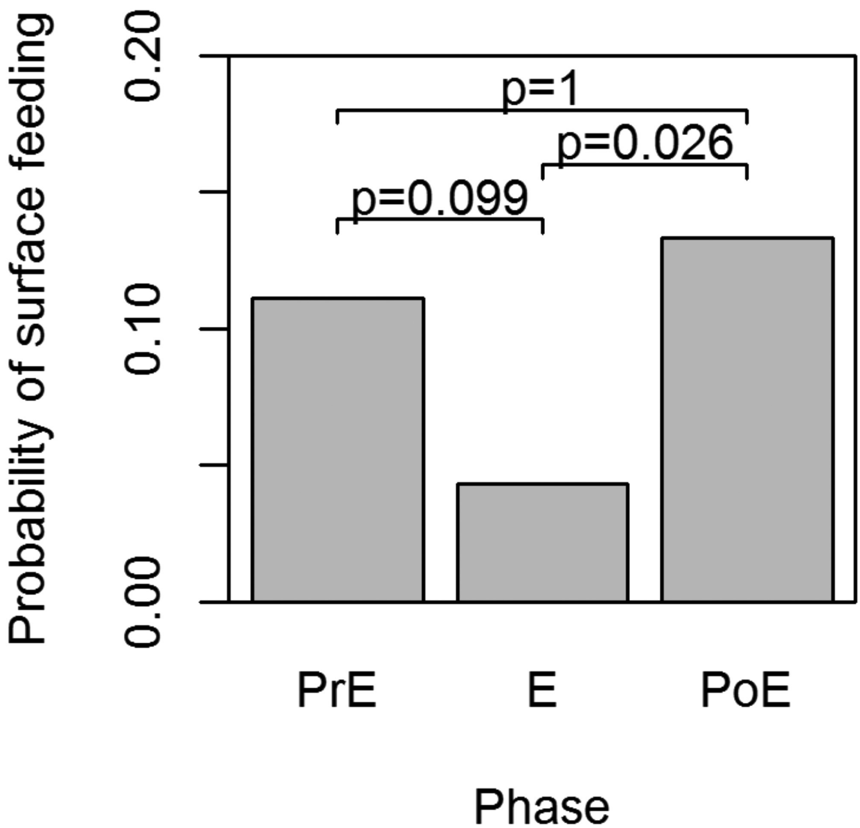

Figure 4. Graph showing the probability of surface feeding during WP experimental exposure trials for each phase (PrE = pre-exposure phase, E = exposure phase, and PoE = post-exposure phase); *p* values are Bonferroni-corrected *p* values obtained in the post hoc comparison (see Table 4).

There were two incidences where humpback whales were encircled by the purse seine fitted with the WPs during the 2018 fishing season: once when the onboard observer was present and once when the observer was not. In both incidences, two humpback whales appeared at the sea surface inside the purse seine once the bottom of the net was being closed, indicating the whales entered from the bottom. When the onboard observer documented the first incident, it was noted the whales were "trumpeting" and showed signs of distress (Weinrich, 1999). In an attempt to release the whales (in both cases), the extra line attaching the end of the purse seine to the vessel was not brought in towards the boat, while the purse seine was closed at the bottom,

Table 5. Assessment of the random and fixed effects structures of four models explaining the change in a behavioural response variable after exposure to a seal scarer. To test if the effect sizes of the contrasts to the pre-exposure phase differed significantly between individuals, a random intercept and slope model was compared to a pure random intercept model by means of comparison of AIC values and a likelihood ratio test. The fixed effects structure was tested by comparing models with and without the predictor phase. Assessment of random effects was based on models estimated by restricted maximum likelihood, whereas assessment of fixed effects was based on maximum likelihood estimation. Significant p value is bolded.

Response variable	Test	AIC (Intercept model)	AIC (Complex model)	Chi-squared	DF	p value
Ln(breathing rate)	Random effect slope	271.8	275.8	0	2	1
	Fixed effect phase	262.2	265.0	1.18	2	0.55
Dive time	Random effect slope	1,427.3	1,418.7	12.6	2	**0.002**
	Fixed effect phase	1,447.1	1,446.5	4.594	2	0.1
Directness	Random effect slope	143.4	147.0	0.4431	2	0.81
	Fixed effect phase	159.6	162.4	1.2	2	0.55
Ln(speed)	Random effect slope	237.4	238.9	2.473	2	0.29
	Fixed effect phase	226.5	230.4	0.138	2	0.93

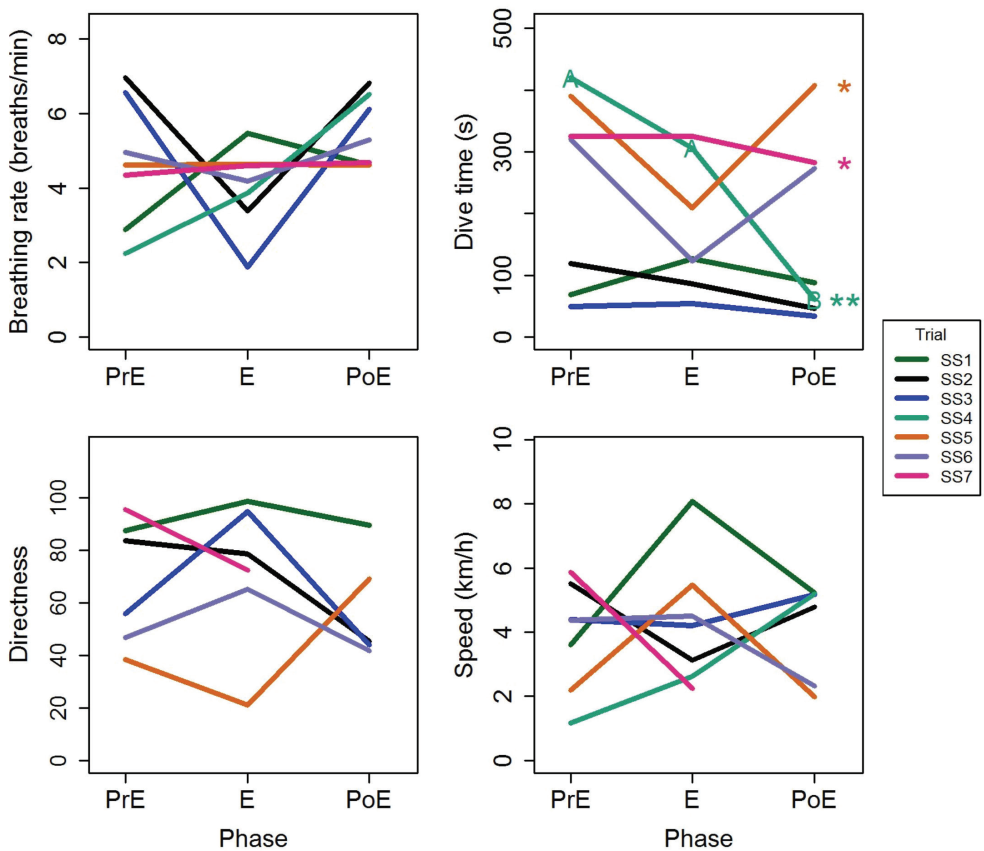

Figure 5. Averages of the behavioural response variables breathing rate, dive time, swimming directness, and swimming speed for the pre-exposure (PrE), exposure (E), and post-exposure (PoE) phases of each seal scarer (SS) experimental exposure trial. Asterisks highlight individual SS exposure trials in which the response variable differed significantly between the phases (*uncorrected: $p < 0.05$; **Bonferroni-corrected: $p < 0.05$). Letters indicate between which phases significant differences occurred. Models for individual SS exposure trials were only calculated for response variables for which overall models found a significant effect of phase or random slope (see Table 5).

Table 6. Effort during onboard observation on the capelin purse seine vessel using the whale pingers, including date (d/mo/y), time, whale sightings (Mn = humpback whale [*Megaptera novaeangliae*] and Bp = fin whale [*Balaenoptera physalus*]), location (latitude, longitude), status of the boat, and comments; NA = not available.

Date	Time	Sightings	Boat location	Status	Comments
24/2/18	2000 h			Leaving port	
25/2/18	0900-1200 h	1 Mn	63.514593N -17.864615W	Transit	
25/2/18	1340-1540 h	NA		Transit	
25/2/18	1610-1810 h	4 Mn	63.430734N, -19.595009W	Transit/docking	Two pairs of whales
			63.437207N, -19.901842W		
26/2/18				In port	
27/2/18	0930-1145 h	9 Mn	63.722643N, -20.818695W	Traversing grounds	
			63.727772N, -20.836443W		
			63.736444N, -20.884974W		
			63.737366N, -20.887947W		Pair of whales
			63.75826N, -20.912274W		
			63.764711N, -20.92963W		Pair of whales
			63.785706N, -20.989416W		
27/2/18	1330-1600 h	3 Mn	63.766879N, -20.969197W	Traversing grounds/ fishing	
			63.729173N, -20.892273W		
			63.784402N, -20.985329W		
27/2/18	1700-1800 h	3 Mn	63.604162N, -20.773594W	Traversing grounds	Pair of whales
			63.596906N, -20.714554W		
28/2/18	0835-1000 h	6 Mn*	63.499573N, -20.940331W	Fishing	Pair of whales
			63.498824N, -20.937591W		
			63.498249N, -20.945592W		
			63.500046N, -20.946389W		
			63.499475N, -20.9425W		
20/2/18	1645-1800 h	5 Mn	63.372122N, -18.879468W	Transit	
			63.36858N, -18.812109W		
			63.367307N, -18.774776W		
			63.378524N, -18.599105W		
			63.382446N, -18.559984W		
		1 Bp	63.369304N, -18.693336W		

*Denotes in which sighting two humpback whales were encircled in the net

creating an approximately 100-m-wide opening in the side of the net towards the stern where there were no WPs, as well as no floats, on the line. During the observer-documented encirclement, the two whales spent approximately 5 min inside the purse seine before locating this opening and escaping without causing any damage. According to the captain, the second incident occurred in the exact same manner. The captain and crew reported that in previous seasons, when the WPs were not fitted on the rest of the purse seine apart from the line creating the opening left for whales to escape, whales rarely, if ever, found this opening and escaped without further action or damage to the purse seine. Only 270 tonnes of capelin were caught in the cast where the whales were encircled by the purse seine during the observer-documented incident (compared to 690 and 550 tonnes, respectively, in the other two casts on the observer trip where no whales were encircled).

Discussion

Mitigating large whale entanglement in fishing industries is of global interest. This study represents the first *in situ* experiments exposing humpback whales to commercially available ADDs in their North Atlantic feeding grounds off Iceland and is the first study to examine changes in surface feeding as a behavioural response to a pinger.

The WP had a significant effect on surface feeding behaviour during WP EETs. Surface feeding was only 4% during the E phase, when the WP was active in the water, compared to 11% prior to and 13% after exposure. This indicates that the whales reduced or stopped surface feeding in response to the WP. Previous studies have found that humpback whales ceased feeding in response to sonar sounds (Sivle et al., 2015), decreased side roll feeding in response to ship noise (Blair et al., 2016), and decreased detectable lunge-feeding behaviour during approaches of whale-watching vessels in one of the study sites for this experiment (Skjálfandi Bay; Ovide, 2017). Therefore, a reduction or cessation of feeding may be a common response of humpback whales to anthropogenic noise.

Humpback whales reducing or stopping feeding when exposed to the WP sound could lead to lower incidence of humpback whale encirclement and entanglement in Icelandic fisheries since the whales are likely feeding when these incidents occur. During the feeding season, humpback whales spend the majority of their time foraging (Friedlaender et al., 2013; Ovide, 2017), and entanglement of the whales has been observed to coincide with spawning of one of their main prey species, capelin, in Newfoundland, Canada (Perkins & Beamish, 1979). Similarly, humpback whales that were evidently feeding on capelin were observed being encircled by a purse seine during the present study. Based on this observation, it can be hypothesized that if the whales stop feeding in the vicinity of fishing gear with active pingers, they may be more likely to take notice of the gear and less likely to become entangled or encircled. This indicates pingers may be a useful mitigation tool. Similarly, Lien et al. (1992) also hypothesized that whales may not notice nets while they are foraging and found that when cod traps set in humpback whale feeding grounds in Canada were fitted with 4-kHz alarm prototypes, the number of whale collisions was significantly reduced.

This study documented a reduction in feeding behaviour in response to a pinger for the first time. We can only hypothesize why the humpback whales reacted as they did. One possibility is that they were simply distracted by or curious about the sudden introduction of an unnatural, unfamiliar sound in their environment as suggested by Lien et al. (1990). Since the received sound level from the WP was likely low (approximately 100 dB at 100 m based on calibration measurements), it is unlikely that the whales were startled and stopped feeding. There was also no clear indication that they moved away from the sound based on results from the directness index model. However, three of the 11 individuals involved in attempted WP EETs were considered lost (disappeared for more than 20 min) during the E phase. Two out of the three individuals (WP1 and WP8) were excluded from the analysis due to lack of data. One individual (WP1) dove and disappeared 35 s after the E phase began; the second individual (WP7) started traveling and stopped taking terminal dives lifting the fluke 23 s after the E phase began and was last sighted an estimated 1,000 m away before it was considered lost; and the third individual (WP8) was recorded taking a terminal dive before the WP was set in the water and was not seen again within 20 min after the E phase began. Since the boat was stationary during the E phase of the trials, the probability of losing sight of the focal whale was higher than during the PrE and PoE phases (when the boat is maneuvered); however, trials were only conducted in good weather with good visibility and, therefore, complete disappearance within 20 min of the E phase beginning was most likely due to a change in behaviour. It is possible that these individuals were disturbed by the WP sound and moved away. Lien et al. (1990) found similar results when testing whale alarm prototypes, reporting that some whales in those experiments moved significantly further away, while some moved significantly closer. However, we cannot rule out the possibility that these whales changed behaviour during the E phase of these trials for some reason unrelated to the pingers, particularly in the case of WP8 in which the whale was not sighted at all during this phase.

Previous research indicates that the responses of the humpback whales observed in the present study are unlikely due to the WP sound impacting the distribution of the prey they were feeding on at the time. Generally, fish species have the highest sensitivity to sounds below 0.5 to 1 kHz (Whalberg & Westerberg, 2005), and humpback whale prey species, such as capelin and krill (*Euphausia* spp.), are hypothesized to have low sensitivity to sound and little behavioural reactions to sound exposure (Brierley et al., 2003; Jørgensen et al., 2004). Therefore, it is unlikely that the WP sound (3 kHz; 137 dB re 1 μPa at 1 m) affected the prey that the whales were feeding on during the EETs and more likely that the whales were responding directly to the WP itself.

The disruption of humpback whale feeding behaviour observed in this study is cause for some concern for potential negative impacts on the individual, and possibly the population, if pinger use becomes widespread in fishing industries. Humpback whales need to consume an estimated 1,432 Kcal of food per day during the summer feeding season to have a large energy storage for their migration and winter breeding season (Sigurjónsson & Víkingsson, 1997).

Insufficient energy stores may lead to decreased ability to migrate or decreased reproductive success, which can impact the recruitment rate of the population (Butterworth et al., 2012). However, it is important to note that exposure to the WP in the present study during the E phase was only for 15 min, so it is unknown if the whales habituate to the sound and continue feeding normally after a longer exposure. No lasting effect of the WP on surface feeding was observed given that there was no significant difference between the PrE and PoE phases, suggesting that when the WP is removed from the water, the whales quickly returned to their pre-exposure behaviour. Based on these findings, the applications in which pingers are used should be chosen carefully to minimize the risk of entanglement and gear damage while also considering the fitness consequences that a reduction in feeding behaviour can have on humpback whales.

The humpback whales in this study that were encircled by the purse seine fitted with the WPs were not surface feeding and entered the net from deeper than 120 m while the WPs were near the sea surface. This may indicate the WPs were not in the correct position to cause the whales to stop feeding and avoid entering the net, suggesting the importance of positioning pingers strategically on gear to obtain the desired result. Further experimentation with pingers at different depths and tagging of whales to gather information about their underwater feeding activity could provide valuable information to further explain how a change in feeding behaviour or increased awareness of the nets could lead to lower incidence of entanglement or encirclement.

Humpback whales significantly increased their swimming speed during exposure to the WP. An increase in swimming speed for these whales has not been reported in previous studies investigating behavioural responses to pingers; however, Todd et al. (1992) reported that humpback whales exposed to 4-kHz alarm prototypes made significantly more abrupt turns towards an active alarm, and abrupt turns have been associated with higher swimming speeds (Edel & Winn, 1978). The increase in speed observed in the present study supports that humpback whales responded to the WP sound, though further investigation into the whales' swimming behaviour is required to infer how this response may relate to entanglement mitigation.

There was no significant behavioural response of humpback whales to the WP in terms of breathing rate, dive time, or swimming directness which is consistent with experiments conducted during whale migration in Australia (Harcourt et al., 2014; How et al., 2015; Pirotta et al., 2016). There was also no evidence for individual- or behavioural state-specific responses in terms of breathing rate or swimming directness, thus there is no evidence that individuals reacted to the WP significantly in terms of these variables. The received sound level may have been too low to elicit a detectable behavioural change in terms of these variables, which are variables that can indicate whether the whale was disturbed or startled (Nowacek et al., 2007) rather than attentive or curious. The humpback whales foraging in the study sites are regularly exposed to considerable anthropogenic noise. Both locations host a high number of whale-watching vessels that primarily target humpback whales for their sightings, as well as industrial ports with associated development and maintenance noise and fishing vessels, cruise ships, and cargo ships entering and exiting often. There are also commercial fishing grounds within the area of both study sites. Therefore, humpback whales in these areas may be habituated to anthropogenic noise and may not show behavioural changes that would indicate they are significantly disturbed or stressed but will still show some behavioural changes when a new, novel sound, such as the WP sound, is introduced.

Response to sound may differ between individuals and may depend on behavioural state (Southall et al., 2019). The results from the dive time models for both the WP and the SS showed no consistent change in dive time across individuals or exposure trials, and the random slope models that account for individual-specific responses fit the data best. While dive time during the E phase significantly increased for some individuals, it significantly decreased for others, which suggests support for individual-specific, divergent responses. An alternative explanation is that individuals may have been naturally switching between a behavioural state of long dive times and a state of short dive times, and this change coincided with the phases of some of the EETs. Given that there was evidence for individual-specific response in dive time for both ADDs, despite there being no consistent response in dive time to either device, and, furthermore, no other significant responses to the SS for any variable, a natural change in behavioural state is considered the most likely explanation of these findings.

There was no evidence for a consistent significant effect of the SS on humpback whale breathing rate, dive time, swimming speed, or swimming directness. The SS had a source level 51 dB re 1 μPa louder than the WP (188 dB re 1 μPa [rms] compared to 137 dB re 1 μPa [rms] based on calibration measurements) and, therefore, it was hypothesized that humpback whales would have some reaction to the high-powered sound even though the frequency of the device is at the top or slightly above their modelled hearing range (Houser et al., 2001). Results from the present study are consistent with findings of Henderson et al. (2016) in which it was also concluded humpback and blue whales (*Balaenoptera musculus*) did not react to high-frequency pingers (though the pinger used in their study was 17 to 35 kHz higher in frequency than the SS used in this study) and with Lien et al. (1990) in which it was determined that high-frequency alarms (7 to 30 kHz higher in frequency than the SS used in this study) did not significantly lower the incidences of humpback whales colliding with gear. It is possible that the frequency of the SS was just too high for humpback whales to hear the device well enough to exhibit a significant response, confirming that ADDs need to target the best-estimated hearing range of the whales.

The use of the WPs on the capelin purse seine for one season provided the first insight into the use of the devices in a practical application in Iceland. On two occasions, a pair of humpback whales entered the purse seine fitted with the WPs from the bottom before it had been closed. Despite the WPs not deterring the whales from entering the purse seine from the bottom, in both cases the whales were able to find their way out through an approximately 100 m wide (at the surface) opening where there were no WPs. The whales escaped without causing any damage to the purse seine and without further intervention methods from the captain (such as putting the boat into reverse to sink the float line). The captain and crew reported that whales escaping the net on their own was a very rare occurrence. This led to an overall positive view of the WPs and an increased interest in further trials for use in the Icelandic capelin purse seine fishery to prevent net damage.

Suggestions for repositioning the WPs on the purse seine could be considered in the future, including attaching them to the lead line at the bottom or sewing specialized pockets for them into the lower portion of the purse seine itself (Hjörvar Hjálmarsson, pers. comm., 2018; Geir F. Zoega, pers. comm., 2019). The observations of humpback whales finding an opening in the net free of pingers in the present study provides insight into the currently unknown directional hearing capabilities of these whales. Ten WPs were spaced approximately every 30 to 40 m along the float line of the purse seine (which measured 450 × 120 m in total). When the whales were inside the purse seine, there was an approximately 100 m opening left at the surface by a single rope attaching the purse seine end to the vessel, and the first WP was attached approximately 30 m from the "bag" netting (the net that remains in the water to prevent fish from escaping as they are hauled on board). This equals an estimated 150 m space without WPs of which approximately 100 m is the opening for the whales to escape through. If the WPs were truly guiding the humpback whales to the opening, as was suggested based on the captain and crew's several years of experience with whales becoming encircled by the purse seine, then possibly the whales were able to acoustically detect this 150 m space. That is, maybe this space with no WPs was devoid of detectable sound and discernible by the whales. If further trials can confirm that humpback whales can be guided to a net opening by pingers, this would indicate that these whales have good directional hearing capabilities.

In conclusion, humpback whales significantly reduced surface feeding in response to WP exposure in their feeding grounds off north Iceland. In addition, when encircled in a purse seine fitted with the WPs, the whales managed to exit the purse seine through a pinger-free opening without causing damage. Since a reduction in feeding around nets likely reduces the risk of whale entanglement or encirclement, these findings suggest that WPs may be effective in mitigating humpback whale entanglement and minimizing fishing gear damage. This is consistent with Lien et al.'s (1992) conclusions that low-powered, low-frequency pingers appeared to be a useful mitigation tool that significantly reduced the incidences of humpback whales colliding with fishing gear. The WP also had a significant effect on whale swimming speed in the present study; however, the implications of this response in terms of entanglement reduction are unknown. No significant reactions to the high-powered, high-frequency SS in terms of dive time, breathing rate, swimming speed, or swimming directness were observed that were consistent across individuals, which indicates these devices are not effective for humpback whales; however, their feeding response to such a device requires further investigation. Results from the present study suggest that pingers may be effective in mitigating humpback whale entanglement and minimizing fishing gear damage in their feeding grounds; however, the devices should be used with caution until further information is gathered on the longer-term consequences of the reduction in feeding. Therefore, pingers may be best suited only for a confined set of short-term applications (e.g., where gear is not left in the water for long periods of time) and used in conjunction with other possible entanglement mitigation methods such as seasonal or area restrictions on fishing and modified fishing gear.

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