

1 First analysis of behavioural responses of humpback whales (*Megaptera*
2 *novaeangliae*) to two acoustic alarms in a northern feeding ground off Iceland

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21 **Abstract**

22 Mitigating cetacean entanglement in fishing industries is of global interest. Strategies include
23 the use of acoustic alarms to warn whales of fishing gear. For baleen whales, responses to
24 acoustic alarms are poorly understood. This behavioural response study compared the
25 behaviour of humpback whales (*Megaptera novaeangliae*) in their feeding grounds off
26 Iceland prior to, during, and after exposure to a low-frequency whale pinger (Future Oceans)
27 and a high-frequency seal scarer (Lofitech Ltd.). Linear mixed effects models and binary
28 generalized linear mixed effects models were used to analyze the effect of the alarms on
29 surface feeding, swimming speed, breathing rate, directness and dive time. We observed a
30 significant decrease in surface feeding and a significant increase in swimming speed during
31 exposure to the whale pinger. Changes in dive time between the phases of a trial differed
32 significantly between individuals indicating that responses may depend on individual or
33 behavioural state. We did not find any significant reactions in response to the seal scarer. In
34 addition to the experimental exposures, a trial of whale pingers on a capelin purse seine net
35 was conducted. Results from this trial showed that whales entered the net from the bottom
36 while the pingers were attached at the top, but the encircled whales were able to locate an
37 opening free of pingers and escape without damaging the net. Our results suggest that whale
38 pingers may be a useful entanglement mitigation tool in humpback whale feeding grounds
39 given that a reduction in feeding around nets likely reduces the risk of whales swimming
40 through them. Pingers may also minimize net damage if whales are encircled by aiding the
41 whales in finding their way out. However, given the uncertain long-term consequences of the
42 behavioural changes reported here, whale pingers are most advisable for short-term use in
43 conjunction with other entanglement mitigation measures.

44 **Introduction**

45 There is global concern over marine mammal bycatch and entanglement in fishing gear (ie.
46 animals becoming incidentally caught in gear and drowning, or escaping, sometimes with
47 gear attached to their body and/or with injuries). Documented impacts of entanglement on
48 cetaceans include injury [1, 2, 3] , exhaustion of energy budgets [4], emaciation and
49 drowning [5, 2]. These impacts at the individual level can lead to increased mortality rates at
50 the population level [6, 7] . Entanglement is known to occur involving many different types
51 of fishing gear [8] and is likely to affect most cetacean species [9] . Apart from impacts on
52 cetacean individuals and populations, entanglement also leads to financial losses to the
53 fishing industry due to loss-of-catch, gear damage or loss and downtime for repairs [10,11].
54 This can be a particularly serious issue in fisheries experiencing large whale, such as
55 humpback whale (*Megaptera novaeangliae*), entanglements.

56 Technologies have been developed with the intent to mitigate marine mammal entanglement.
57 One such technology is acoustic alarms known as “pingers”. These devices can be to attached
58 to fishing gear and emit a tone underwater within the hearing range of target marine
59 mammals [12] . The devices serve to “illuminate” the gear with sound and warn the animals
60 of its presence to encourage them to avoid it. Alternatively, the pingers may simply serve as
61 an annoying, unnatural sound that the animals want to avoid [13]. Since large whales in
62 particular can often escape from or carry away entangling gear, it has been suggested that
63 whales can learn to associate nets and pingers with danger [14] . For cetaceans, specific
64 pinger acoustic alarms have been developed for porpoises, dolphins and beaked whales
65 (odontocetes) as well as baleen whales (mysticetes) with varying degrees of success. The
66 high-frequency porpoise, dolphin and beaked whale pingers have been shown to reduce
67 bycatch of several species [eg. 15, 16, 17, 18], though on the other hand, some studies have

68 found there to be no change or even increased bycatch of some odontocete species with the
69 use of pingers [eg. 19, 20] . Whale pinger and low-frequency acoustic alarm sound
70 experiments have been conducted on baleen whales, including North-Atlantic right whales
71 (*Eubalaena glacialis*) [21], minke whales (*Balaenoptera acutorostrata*) [22], grey whales
72 (*Eschrichtius robustus*) [23], and humpback whales [24, 25, 26, 27, 22]. Results from these
73 experiments were also highly variable. North-Atlantic right whales showed a strong response
74 to alerting sounds [28], and both minke whales and humpback whales also responded during
75 testing of whale alarm prototypes [22]. Humpback whales were also less likely to collide with
76 cod-traps fitted with alarms in Canada [27] and were found to respond to “tone stimuli”
77 within their hearing range in Australia [29]. By contrast, grey whales did not appear to
78 respond to acoustic deterrent sounds though results were inconclusive [23] and the majority
79 of recent research conducted on humpback whales in Australia has concluded there is no
80 clear response to the modern whale pinger alarms, some of which are now sold commercially
81 [24, 25, 26]. Despite this, anecdotal reports do claim that some industries have had lower
82 incidence of humpback whale entanglement with the use of the commercial whale pingers
83 [30, 31].

84 In addition to the pinger acoustic alarms, acoustic deterrent devices (ADDs) have also been
85 developed. Primarily used in the aquaculture industry to ward off seals, these devices produce
86 a loud, high-frequency sound designed to scare away the animals [32]. Though not designed
87 originally for use to deter cetaceans, it has been observed that at least some cetacean species
88 react to the loud sound produced by such a device [33, 34]. Testing of ADDs on cetaceans
89 has found that odontocetes including harbour porpoises [34] , orcas [35] and Pacific white-
90 sided dolphins [36] are deterred by the devices. The only testing of such a device on baleen
91 whales was conducted on minke whales in Iceland, and results showed that they too were
92 deterred from the area with an active ADD [33].

93 Humpback whales are one of the most common cetaceans that frequent the waters off Iceland
94 in the North Atlantic primarily during their feeding season from spring through autumn [37],
95 though some sightings are also recorded in the winter months [38]. The summer-time
96 Icelandic humpback whale population is estimated to be approximately 12,000 individuals
97 [37] with the highest concentration found off the north/northeast coast (Pike et al. 2019
98 submitted). It is thought that the humpback whales' diet in Iceland consists of 60% fish
99 species [39]. The hearing capabilities of humpback whales has been modelled to show that
100 they have hearing sensitivity between 700 Hz and 10 kHz, with maximum sensitivity between
101 2-6 kHz [40]. It has been suggested that hearing is likely the most important sense for baleen
102 whales to orient themselves in their environment [41] and large baleen whales, like the
103 humpback, may have trouble acoustically detecting fishing gear in the water.

104 Commercial fishing is one of the largest industries in Iceland, with 1588 commercial vessels
105 registered in 2018 [42]. The fishing methods used in Icelandic waters are long-line/hand-line,
106 gillnet, trawl, and purse seine [43]. In addition, there are also mussel, oyster, and fish farming
107 operations in coastal Icelandic waters [44, Kristján Phillips pers. comm. 2019, 45]. At least
108 one-quarter of the coastal Icelandic humpback whale population is estimated to have been
109 entangled in fishing gear at least once [46], and virtually all of the fishing methods in the
110 country have reported issues with humpback whales swimming through, and sometimes
111 becoming entangled in, the gear in the water [47, 44]. This has caused gear damage or loss, as
112 well as injury or death to the whales in some cases [46, 47, 48, 49].

113 Currently there are no mitigation methods or regulations in place for minimizing whale
114 entanglement in fishing gear in Iceland, despite growing concern in the local fishing
115 industries. This study conducted the first analysis of behavioural response of free-ranging
116 humpback whales in their northern feeding grounds off the coast of northeast Iceland to the
117 whale pinger acoustic alarm (Future Oceans) and the seal scarer acoustic deterrent device

118 (Lofitech AS ltd.). In addition to the experimental exposure of whales to the acoustic alarms,
119 this study conducted the first trial of the whale pingers in the capelin purse seine fishery in
120 Iceland. Results from this study help to decide if acoustic alarms are likely to effectively
121 mitigate humpback whale entanglement in their feeding grounds and shed light on possible
122 adverse effects of the alarms on natural humpback whale behaviour.

123 **Materials and Methods**

124 **Study area**

125 Trials of the whale pinger acoustic alarm took place in two locations in Northeast Iceland:
126 Skjálfandi Bay and Eyjafjörður (Fig 1). Skjálfandi ($66^{\circ}05'N17^{\circ}33'W$) is an approximately
127 11,000 km² bay well known for predictable humpback whale sightings from spring through
128 autumn during the feeding season. The bay harbours the fishing-turned-whale watching town
129 of Húsavík on the southeast shore [50, 51, 52, A. Gíslason unpubl. data]. Eyjafjörður
130 ($65^{\circ}50'N18^{\circ}07'W$) is an approximately 440km² narrow fjord (S. Jónsson unpubl. data)
131 located approximately 80km west of Skjálfandi Bay. Like Skjálfandi, Eyjafjörður is also well
132 known for humpback whale sightings and harbours fishing and whale watching in the city of
133 Akureyri as well as the towns of Dalvík, Hauganes and Hjalteyri. Trials of the seal scarer
134 acoustic alarm took place only in Skjálfandi Bay.

135 The practical trial of the whale pinger took place in collaboration with a capelin purse seine
136 vessel based in Neskaupstaður in East Iceland. The boat fished for capelin off South Iceland
137 (Fig 1).

138 **Fig 1. Map showing the locations of humpback whale behavioural response trials (1.**
139 **and 2.) using the whale pinger and/or seal scarer, and location where capelin fishing**

140 **with a purse seine net equipped with the whale pingers took place during onboard**
141 **observation (3.).**

142 **Acoustic alarms**

143 Two acoustic alarms were used in the present study. First was the 2016 version of the Future
144 Oceans whale pinger. This device operates on a single 3.6V lithium battery and activates
145 automatically when in contact with saltwater. When active, the alarm produces a 145 decibel
146 re 1 μ Pa tone at 3kHz for 300 ms at 5 sec intervals (Future Oceans) (Fig 2). The second alarm
147 was the Lofitech AS ltd. seal scarer ADD composed of a control box with a 25m long cable
148 with a transducer unit at the end which produces the sound. This control box is powered by a
149 12V marine battery onboard the boat. When active, the alarm produces a 191 decibel re 1 μ Pa
150 sound between 10-20 kHz for 500ms at random intervals of 5-60 sec (Fig 3). A calibration of
151 both acoustic alarm devices was conducted in a harbour to confirm the manufacturers
152 specifications. Each device was lowered 5m into the water and recorded by a Reson 4032
153 hydrophone connected to an Etec amplifier with the sound signal recording to a Microtrack
154 recorder. The whale pinger was recorded at distances of 1, 5, 10 and 20m from the
155 hydrophone, while the seal scarer was recorded at 20, 30 and 40m. The recorded signal from
156 the alarms was compared with a 153 dB rms calibration signal recorded using a calibrator
157 with an adapter for the 4032 Reson hydrophone.

158 **Fig 2. Photograph showing the whale pinger alarm.**

159 **Fig 3. Photograph showing the seal scarer alarm.**

160 The emitted sound from the whale pinger had an actual source level of 137 dB re 1 μ Pa (rms)
161 recorded at a distance of 1 m. The levels at 5, 10 and 20 m were 137 dB, 140 dB and 144 dB
162 re 1 μ Pa (rms) respectively using spherical spreading as transmission loss. Based on previous
163 modelling of the pinger sound, humpback whales are expected to detect the sound at a

164 distance of at least 500m from the source [24, 26]. The seal scarer had an actual source level
165 of 189-198 dB re 1 μ Pa (rms) measured at a distance of 20, 30 and 40 m using spherical
166 spreading (of 20 Log R) as transmission loss.

167 **Experimental exposure to acoustic alarms**

168 Experimental exposures of humpback whales to acoustic alarms were conducted in Skjálfandi
169 Bay in June, July and October 2017, and in June and October 2018. In Eyjafjörður, trials
170 were conducted in May and July 2018. A private boat was used for each trial with a captain
171 and 3-4 researchers and students onboard. Data collected during the trials were recorded with
172 the Logger 2010 computer program (IFAW) and a video recording of each trial was taken
173 using a hand-held video camera (Sony HDR-CX160E handycam). Logger 2010 recorded
174 time, GPS position of the boat, heading of the boat, and any comments that were entered by
175 the student recorder. Trials were attempted when the sea state was considered 3 or less on the
176 Beaufort scale. During a behavioural trial, an individual focal humpback whale was chosen
177 based on the criteria that it was swimming alone and that there were no whale watching boats
178 observing the animal. Photo-identification images of the individual were taken of the unique
179 pattern on the underneath side of the fluke and of the dorsal fin. This was to ensure each
180 individual whale was not exposed to the same device more than once within the same year, to
181 avoid possible habituation to the alarm sound. When photo-identification was complete, the
182 pre-exposure phase (*PrE*) began with the boat following the focal whale from a distance of
183 approximately 100m for 30 mins to obtain a baseline of behaviour of the individual. The
184 100m distance complies with whale watching criteria set forth in many countries around the
185 world to minimize disturbance to the animal [53] while still being within range to collect all
186 necessary data. Each breath the whale took was recorded as “up” and each terminal dive was
187 recorded as “dive” in Logger 2010. Other information was also noted, including if the whale
188 dove with or without raising the fluke, if the whale appeared to be feeding, and if there were

189 other whales in the area. Furthermore, one researcher used an angle-board and rangefinder to
190 obtain the angle to the whale in relation to the boat and the distance to the whale, and this
191 data was also recorded into Logger 2010. If the distance could not be obtained from the
192 rangefinder, one researcher estimated the distance to the whale when it took a terminal dive.
193 The angle-board, rangefinder, and distance estimation were always done by the same
194 researcher (C.J.B) for consistency. Once the *PrE* phase was complete, the boat was
195 positioned beside where the focal whale was seen taking its last terminal dive and the engine
196 was turned off. To begin the 15 min exposure phase (*E*), the whale pinger or the seal scarer
197 was placed off the side of the boat into the water at 5m depth, attached to a rope and buoy
198 similar to Harcourt et al [26] . The breaths, dives, angles, and distances of the focal whale
199 were then recorded in Logger 2010 in the same manner as in *PrE* phase. After the 15 min *E*
200 phase ended, the alarm device was removed from the water and the boat was positioned
201 approximately 100m from the focal whale to follow it and record the same data for an
202 additional 30 mins for the post-exposure phase (*PoE*).

203 **Behavioural variables**

204 **Feeding**

205 The number of surface feeding events was determined by watching the video footage of each
206 phase of each behavioural trial. For each surfacing of the focal whale, surface feeding
207 behaviour was categorized as yes (Y), no (N), or not able to determine (NA). Feeding
208 behaviour was recognized by observing surface lunging behaviour or expanded throat pleats
209 indicating the whale had a full mouth (Fig 4). A surfacing was also categorized as Y if
210 researchers audibly indicated the whale was feeding in the video even though the surfacing
211 was not visible in the footage.

212 **Fig 4. Photographs showing lunge-feeding behaviour and expanded throat pleats used**
213 **to determine if the focal whale was surface feeding in the analysis of the videos.**

214 **Swimming speed**

215 The swimming speed of the focal whale was calculated for each phase of each behavioural
216 trial, when enough data was available. Speed was calculated from each terminal dive to the
217 next terminal dive (and therefore included distance information from when the focal whale
218 was diving and was at the surface).

219 **Breathing rate and dive time**

220 For each phase of each behavioural trial, the breathing rate of the focal whale was calculated
221 as breaths per minute for each surface interval (the time between diving). The time of each
222 dive in seconds in each phase of each trial was also calculated from the time stamps of “dive”
223 and the following “up” recorded in Logger 2010.

224 **Directness index**

225 A directness index (DI) from 0-100, indicating the directness of the swimming pattern of the
226 focal whale, was calculated for each phase of each behavioural trial, when enough data was
227 available. Firstly, the coordinate position of the whale at each terminal dive was calculated.
228 Then, the DI was calculated as the distance between the two end points of the track divided
229 by the sum of the distances between all the points in the track, and the result multiplied by
230 100. A DI of 0 indicates swimming in a complete circle, while a DI of 100 indicates
231 swimming in a straight line.

232 **Analysis of behavioural response variables**

233 We tested the effect of exposure to both acoustic alarms (whale pinger and seal scarer) on
234 four response variables: speed, breathing rate, directness and dive time using linear mixed

235 effects models. Separate models were set up for each acoustic alarm and each response
236 variable. The phase of the trial (*PrE*, *E*, *PoE*) was the only fixed effect predictor variable. To
237 account for the repeated measures within individual whales, trial-ID was included as a
238 random intercept term in all models. Plots of residual versus fitted values revealed that speed
239 and breathing rate needed to be log-transformed to satisfy the modeling assumption of
240 homogeneity of variances. Plots of the autocorrelation function of the residuals revealed
241 significant temporal autocorrelation in the models for $\ln(\text{speed})$, $\ln(\text{breathing rate})$ and dive
242 time. Auto-regressive correlation structures of order 1 were specified in the models for these
243 response variables. Inspection of the plots of the autocorrelation functions verified that this
244 successfully accounted for the observed autocorrelation.

245 Since previous findings suggested individual response to sound can depend on behavioural
246 state [54], individual-specific response variation was incorporated into our models by
247 introducing random slopes for the predictor phase for all response variables. We tested if
248 random intercept and slope models fitted the data better than pure random intercept models.
249 As recommended by Zuur et al. [55] selection of the random effects structure was done prior
250 to selection of the fixed effects structure and was based on a likelihood ratio test comparing
251 the pure random intercept model with the random intercept and slope model. Subsequently,
252 likelihood ratio tests were used to select the optimal fixed effects structure, i.e. to compare
253 models with phase as fixed effect to pure intercept models. For models in which phase had a
254 significant effect, a posthoc pairwise comparison with Bonferroni correction was used to
255 infer between which phases significant changes of the response variable occurred. These
256 statistical analyses were performed using the libraries nlme [56] and multcomp [57] in the
257 statistical software R (R Foundation for Statistical Computing).

258 Surface feeding behaviour was recorded as a binary variable and thus could not be modelled
259 by linear mixed effects models. We fitted a binary generalized linear mixed effects model

260 using the function `glmer` in the `lme4`-package [58]. Model specification and selection was
261 analogous to the protocol described for the linear mixed effects models except for the
262 specification of the autocorrelation structure. Since the `glmer`-function does not allow for the
263 specification of temporal correlation structures, the feeding behaviour at the previous
264 surfacing event (`lag1_feeding`) was included as a fixed effect to account for temporal
265 autocorrelation. Surface feeding behaviour could only be analyzed for whale pinger (WP)
266 trials, because very little surface feeding was observed in all phases of the seal scarer (SS)
267 trials.

268 **Purse-seine trial of the whale pingers**

269 In addition to the individual exposure trials, the whale pingers were also used in a practical
270 application trial on board a capelin purse seine vessel (Börkur NK122) for the 2018 season
271 (January-March) operating out of Neskaupstaður in east Iceland. For the season prior to the
272 trial (January – March 2017), the captain of the vessel kept a log of humpback whale
273 sightings and any encirclements in the net. For the 2018 capelin fishing season, ten pingers
274 were attached to the float line of the purse-seine at a distance of 30-40m from each other,
275 complying with the manufacturer's recommendations. The captain of the vessel kept record
276 of any issues there were with the use of the pingers, and any incidences of whales inside the
277 net. In addition, one researcher (C.J.B.) joined as an onboard observer for one trip (February
278 24-28, 2018). During onboard observations, the track of the vessel and whale sightings were
279 recorded in the SpotterPro app (Conserve.IO) during all transit and active fishing days. The
280 number of net casts and tonnes of fish caught with each cast was also noted. Any
281 encirclements of whales with the net were video recorded for documentation using a hand-
282 held video camera (Sony HDR-CX160E handycam).

283 Results

284 Experimental exposure to acoustic alarms

285 A total of 23 research trips were undertaken in 2017-2018 totalling approximately 83 hours of
 286 effort (Table 1). Of these, enough data for analysis was collected on 14 trips resulting in 9
 287 WP trials and 7 SS trials.

288 **Table 1. Data collection trips undertaken in 2017-2018 with the Date (DD.MM.YY), Location**
 289 **(SB = Skjálfandi Bay, EF = Eyjafjörður), number of hours (Hours), what trial was completed**
 290 **(Trial Complete: na = not available; no usable trial, SS = seal scarer, WP = whale pinger), and**
 291 **the reason the trip did not result in a usable trial (Reason if na).**

Date	Location	Hours	Trial Complete	Reason if na
29.04.17	SB	3.5	na	Whale disappeared during WP exposure phase
03.05.17	SB	4.5	SS	
04.05.17	SB	3	na	No usable whale
04.05.17	SB	3	na	Boat broke down
16.06.17	SB	3.5	WP	
20.06.17	SB	4.5	WP	
27.06.17	SB	4.5	SS	
			SS	
28.06.17	SB	3	WP	
11.07.17	SB	4	na	No usable whale
14.07.17	SB	6.5	WP	
			SS	
21.08.17	SB	2.5	na	Rough seas
01.10.17	SB	3.5	WP	
28.04.18	EF	1.5	na	Rough seas
30.04.18	EF	2	na	Rough seas

02.05.18	EF	4	WP	
08.05.18	EF	5	na	Whale disappeared during WP exposure phase
07.06.18	SB	3.5	WP	
12.06.18	SB	3.5	WP	
11.07.18	EF	3	na	Rough seas
09.10.18	SB	3.5	WP	
15.10.18	SB	3.5	SS	
14.11.18	SB	3.5	SS	
21.11.18	SB	4	SS	

292

293 Fifteen individual whales were used for the successful behavioural trials which produced
 294 usable data (Fig 5). Only one individual whale was used twice, in two separate SS trials, but
 295 these trials were conducted 18 months apart. Fourteen of the individuals could be identified
 296 in the Húsavík Research Center humpback whale catalogues. One individual in Eyjafjörður
 297 was not identifiable beyond confirming that it was only used once in the study.

298 **Fig 5. Table showing the individuals used for each successful behavioural trial (expressed by**
 299 **identification code and nickname), location (SB = Skjálfandi Bay, EF = Eyjafjörður), the device**
 300 **used in the trial and the trial ID number (WP = whale pinger, SS = seal scarer), and the data**
 301 **that was collected in each trial (B = breathing rate, DI = directness index, D = dive time, S =**
 302 **swimming speed, F = feeding). Data codes denoted with an * indicate trials for which data is**
 303 **only available for the pre-exposure and exposure phases.**

304 There were eleven attempts made to complete a WP trial, resulting in nine usable trials. Out
 305 of these eleven attempts, the individual whale was considered lost (disappeared for more than
 306 20 minutes) in three cases (WP1, WP7, WP8). Two out of these three cases did not result in
 307 enough data to be included in the analysis (WP1, WP8). No individuals were lost during SS
 308 trials.

309 Averages of the behavioural response variables for the *PrE*, *E* and *PoE* phases of each WP
 310 trial are shown in Fig 6. Full models for each behavioural response variable included the
 311 experimental phase (*PrE*, *E*, *PoE*) as fixed effect and a random intercept and slope (for
 312 experimental phase) in addition to an autoregressive correlation structure of order 1 as
 313 random effects. Random slope models did not fit the data significantly better than random
 314 intercept models for the behavioural response variables speed, surface feeding, breathing rate
 315 and directness (Table 2). Thus, there was no statistical support for individual variation in
 316 these responses.

317 **Fig 6. Averages of the behavioural response variables breathing rate, dive time, directness and**
 318 **speed for the pre-exposure (PrE), exposure (E) and post-exposure (PoE) phases of each whale**
 319 **pinger (WP) trial. Stars highlight individual whale pinger trials in which the response variable**
 320 **differed significantly between the phases (* uncorrected $p < 0.05$; ** Bonferroni-corrected $p <$**
 321 **0.05). Letters indicate between which phases significant differences occurred. Models for**
 322 **individual whale pinger trials were only calculated for response variables for which overall**
 323 **models found a significant effect of phase or random slope (see Table 3).**

324 **Table 2. Assessment of the random and fixed effects structures of five models explaining the**
 325 **change in a behavioural response variable after exposure to a whale pinger. To test if the effect**
 326 **sizes of the contrasts to the pre-exposure phase differed significantly between individuals, a**
 327 **random intercept and slope model was compared to a pure random intercept model by means of**
 328 **comparison of Akaike Information Criterion (AIC) values and a likelihood ratio test. The fixed**
 329 **effects structure was tested by comparing models with and without the predictor phase.**
 330 **Assessment of random effects was based on models estimated by restricted maximum likelihood,**
 331 **whereas assessment of fixed effects was based on maximum likelihood estimation. Significant p-**
 332 **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	2557.2	2518.2	43	2	<0.001
	Fixed effect phase	2541.6	2545.1	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

333

334 The predictor phase had a significant effect on both speed ($p = 0.006$; Table 2) and surface
 335 feeding ($p = 0.019$; Table 2). Humpback whale speed during the *E* phase was 1.7 times higher
 336 than during the *PoE* phase ($p = 0.0024$; Table 3) and 1.4 times higher than during the *PrE*
 337 phase ($p = 0.11$; Table 3). No significant differences in humpback whale speed were observed
 338 between the *PrE* and *PoE* phases ($p = 0.62$; Table 3). The probability of surface feeding was
 339 significantly lower during the *E* phase than during the *PoE* phase ($p = 0.026$; Table 4). The
 340 reduction in surface feeding from the *PrE* to the *E* phase was marginally significant ($p =$
 341 0.099 ; Table 4). Rates of surface feeding amounted to 11% and 13% in the *PrE* and *PoE*
 342 phases and dropped to 4% in the *E* phase (Fig 7).

343 **Table 3. Posthoc comparison for the predictor phase (*PrE* = pre-exposure, *E* = exposure, *PoE* =**
 344 **post-exposure) in the swimming speed model based on the whale pinger data (See Table 2).**
 345 **Since the response variable speed is ln-transformed, effect is the difference in ln(speed) and**
 346 **e^{\wedge} Effect is the ratio between speeds in the two compared phases. Adjusted p-values are**
 347 **Bonferroni-corrected p-values. Significant p-values are bolded.**

Posthoc Comparison	Effect on ln(speed)	e^{\wedge} Effect	Std. Error	Adjusted p-value
<i>E - PrE</i>	0.35	1.42	0.17	0.11
<i>PoE - PrE</i>	-0.18	0.83	0.14	0.62
<i>PoE - E</i>	-0.53	0.59	0.16	0.0024

348

349 **Table 4. Posthoc comparison for the predictor phase (*PrE* = pre-exposure, *E* = exposure,**
350 ***PoE* = post-exposure) in the surface feeding model based on the whale pinger data (See**
351 **Table 2). Effect and std. error are the effect size on the linear predictor scale and its**
352 **standard error. Adjusted p-values are Bonferroni-corrected p-values. Significant p-**
353 **values are bolded.**

Posthoc Comparison	Effect on surface feeding	Std. Error	Adjusted p-value
<i>E - PrE</i>	-1.02	0.48	0.099
<i>PoE - PrE</i>	0.21	0.26	1
<i>PoE - E</i>	1.22	0.47	0.026

354

355 **Fig 7. Graph showing the probability of surface feeding during whale pinger trials for**
356 **each phase (*PrE* = pre-exposure phase, *E* = exposure phase, *PoE* = post-exposure phase).**
357 **P-values are Bonferroni-corrected p-values obtained in the posthoc comparison (See**
358 **Table 4).**

359 No significant changes in breathing rate ($p = 0.42$; Table 2) and directness ($p = 0.40$; Table 2)
360 were detected in response to exposure to whale pinger sound. The model for dive time was
361 the only case in which a random slope model fitted the data significantly better than a random
362 intercept model ($p < 0.001$; Table 2). Phase of the trial, however, had no significant effect on
363 dive time ($p = 0.79$; Table 2).

364

365 The averages of the behavioural response variables for the *PrE*, *E* and *PoE* phase of each SS
366 trial are displayed in Fig 8. Models of the behavioural response variables were set up in the
367 exact same manner as for the WP trial analysis. Random slope models did not fit the data
368 significantly better than random intercept models for any of the response variables (Table 5).
369 Experimental phase did not have a significant effect on any of the response variables (Table

370 5). Thus, we found no evidence for an individual-specific or shared response of humpback
 371 whales to seal scarer alarm.

372 **Fig 8. Averages of the behavioural response variables breathing rate, dive time,**
 373 **directness and speed for the pre-exposure (PrE), exposure (E) and post-exposure (PoE)**
 374 **phases of each seal scarer (SS) trial.**

375 **Table 5. Assessment of the random and fixed effects structures of five models explaining**
 376 **the change in a behavioural response variable after exposure to a seal scarer. To test if**
 377 **the effect sizes of the contrasts to the pre-exposure phase differed significantly between**
 378 **individuals, a random intercept and slope model was compared to a pure random**
 379 **intercept model by means of comparison of Akaike Information Criterion (AIC) values**
 380 **and a likelihood ratio test. The fixed effects structure was tested by comparing models**
 381 **with and without the predictor phase. Assessment of random effects was based on**
 382 **models estimated by restricted maximum likelihood, whereas assessment of fixed effects**
 383 **was based on maximum likelihood estimation.**

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	1427.3	1418.7	12.6	2	0.002
	Fixed effect Phase	1447.1	1446.5	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

384

385 **Purse-seine trial of the whale pingers**

386 The captain of the participating capelin purse seine vessel did not report any issues with
 387 humpback whales inside the net in the 2017 season and reported that there were generally

388 lower sightings and incidences than in the previous (2016) season. During the 2018 capelin
389 fishing season, the onboard observer recorded 34 individual humpback whale sightings at 7
390 locations during 16 hours of observation (Table 6) with 70.6% (n = 24) occurring while the
391 boat was in the capelin fishing grounds off the south/southwest coast of Iceland. The net was
392 cast 3 times during onboard observation and a total of 1510 tonnes of capelin were caught.
393 Whales at the surface near the vessel when fishing operations were beginning were noted to
394 swim away from the area, with one whale specifically observed turning 180 degrees to go
395 opposite of where the seine net was being set into the water. There were two incidences
396 where humpback whales were encircled in the net fitted with the whale pingers during 2018,
397 once when the onboard observer was present and once when they were not. In both
398 incidences two humpback whales appeared at the surface inside the net once the bottom of
399 the net was being closed, indicating the whales entered from the bottom. During the onboard
400 observation incident, it was noted the whales were “trumpeting” and showed signs of being
401 distressed by the encirclement in the net. In an attempt to release the whales in both cases, the
402 extra line attaching the end of the net to the vessel, without floats or pingers attached, was not
403 brought in towards the boat while the net was closed at the bottom creating an approximately
404 100m wide opening in the side of the net towards the stern. During the onboard observation
405 encirclement, the two whales spent approximately 5 minutes inside the net before locating the
406 opening and escaping without causing any damage. According to the captain the second
407 incident occurred in the exact same manner. The captain and crew reported that whales
408 rarely, if ever, find this opening and escape without further action or damage to the net in
409 previous seasons when the pingers were not in use. Only 270 tonnes of capelin were caught
410 in the cast where the whales were encircled in the net during onboard observation (compared
411 to 690 and 550 tonnes in the other two casts).

412 **Table 6. Effort during onboard observation on the capelin purse seine vessel using the**
 413 **whale pingers including date (DD,MM,YY), time, whale sightings (Mn = humpback**
 414 **whale (*Megaptera novaeangliae*), Bp = fin whale (*Balaenoptera physalus*), location**
 415 **(latitude, longitude), status of the boat, and comments. A * denotes in which sighting**
 416 **two whales were encircled in the net.**

Date	Time	Sightings	Boat Location	Status	Comments
24.02.18	20:00			leaving port	
25.02.18	9:00-12:00	1Mn	63.514593N - 17.864615W	transit	
25.02.18	13:40-15:40	NA		transit	
25.02.18	16:10-18:10	4Mn	63.430734N, - 19.595009W	transit/docking	Two pairs of whales
			63.437207N, - 19.901842W		
26.02.18				in port	
27.02.18	9:30-11:45	9Mn	63.722643N, - 20.818695W	transversing 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		
27.02.18	13:30-16:00	3Mn	63.766879N, - 20.969197W	transversing grounds/fishing	
			63.729173N, - 20.892273W		
			63.784402N, - 20.985329W		
27.02.18	17:00-18:00	3Mn	63.604162N, - 20.773594W	transversing grounds	Pair of whales
			63.596906N, - 20.714554W		
28.02.18	8:35-10:00	6Mn*	63.499573N, - 20.940331W	fishing	Pair of whales
			63.498824N, - 20.937591W		
			63.498249N, - 20.945592W		
			63.500046N, - 20.946389W		
			63.499475N, - 20.9425W		

20.02.18	16:45-18:00	5Mn	63.372122N, - 18.879468W	transit	
			63.36858N, - 18.812109W		
			63.367307N, - 18.774776W		
			63.378524N, - 18.599105W		
			63.382446N, - 18.559984W		
		1Bp	63.369304N, - 18.693336W		

417

418 Discussion

419 Mitigating large whale entanglement in fishing industries is of global interest. This study
420 represents the first in situ experiments testing commercially available acoustic alarms on
421 humpback whales in their North Atlantic feeding grounds off Iceland, and the first study to
422 consider feeding as a behavioural response variable. Results showed that it was significantly
423 less likely to observe surface feeding behaviour during the *E* phase of the WP trials, when the
424 whale pinger was active in the water, compared to when the whales were observed prior to
425 and after exposure. This suggests that the whales reduce or stop surface feeding in response
426 to the pinger. Previous studies have found that humpback whales cease feeding in response to
427 sonar sounds [59], decrease side roll feeding in response to ship noise [60], and decrease
428 detectable lunge feeding behaviour during approaches of whale watching vessels in one of
429 the study sites for this experiment (Skjálfandi Bay) [61], suggesting reduction in feeding may
430 be a common response when whales are exposed to anthropogenic noise. This is the first time
431 a reduction in feeding behaviour has been documented in response to a pinger alarm and we
432 can only hypothesize why the whales would react this way. One possibility is that they are
433 simply distracted by or curious about the sudden introduction of an unnatural and unfamiliar
434 sound in their environment. Since the received sound level from the whale pinger was likely
435 low, it is unlikely that the whales were startled and stopped feeding, and there was no clear
436 indication that they moved away from the sound based on results from the directness index

437 model. However, three out of the eleven individuals involved in attempted WP trials were
438 declared lost (disappeared for more than 20 minutes) during the *E* phase when the whale
439 pinger was in the water. Two out of the three cases (WP1, WP8) did not have enough data to
440 include them in analysis. The first individual (WP1) took one dive approximately 200m away
441 after the *E* phase started and then never resurfaced in sight. The second individual (WP7),
442 which was included in analysis, started traveling and stopped diving with the fluke in the air
443 shortly after the *E* phase began and was last sighted an estimated 1000m away before it was
444 lost. The third individual (WP8) was last seen before the pinger was put in the water to begin
445 the *E* phase and was not seen again within 20 minutes after the *E* phase began. Since the boat
446 was stationary during the *E* phase of the trials, the probability of losing sight of the whale is
447 higher than during the *PrE* and *PoE* phases when the boat is maneuvered. However, trials
448 were only conducted in good weather with good visibility and therefore the complete
449 disappearance in the 15-minute *E* phase was most likely due to a change in behaviour. It is
450 possible that these individuals were disturbed by the pinger sound and moved away.

451 Lien et al. [27] reported that there was an increase in cod catch in traps that had alarms
452 attached than those that did not, suggesting target fish species are not affected by the alarms.
453 Humpback whales are primarily feeding on smaller fish species in the North Atlantic, such as
454 capelin [62]. Fish are modelled to hear at low frequencies below 0.5-1 kHz and react to high
455 intensity sound [63], therefore it is unlikely that the pinger sound affected the prey that the
456 whales were feeding on during the trials. This suggests that the whales responded to the
457 pinger sound directly rather than to a change in prey distribution or behaviour.

458 Whales reducing or stopping their feeding in response to the pinger, could lead to lower
459 incidence of humpback whale encirclement and entanglement in Icelandic fisheries since the
460 whales are likely feeding when these incidences occur. Humpback whales in coastal polar
461 waters have been recorded making an average of 28 feeding lunges per hour in Antarctica

462 [64], and a tagged whale in the primary field site for this study (Skjálfandi Bay) was similiary
463 recorded making an average of 33 feeding lunges per hour [61], suggesting the majority of
464 their time is spent foraging. Furthermore, entanglement of humpback whales has been
465 observed as coinciding with the spawning of one of their main prey species, capelin, in
466 Newfoundland Canada [65] and encirclement of humpbacks in Iceland that were evidently
467 feeding on capelin at the time of the incident was observed during this study. We therefore
468 hypothesize that if the whales stop feeding in the vicinity of fishing gear with active pingers
469 they may be more likely to take notice of the gear and less likely to become entangled or
470 encircled. Therefore, the pingers may be a useful mitigation tool. The whales that were
471 encircled in the purse seine net using the pingers in this study were not surface feeding and
472 entered the net from deeper than 120m while the pingers were near the surface of the water,
473 which may indicate the pingers were not in the correct position to cause the whales to stop
474 feeding and avoid entering the net. Overall, this suggests that if the whales stop feeding in
475 response to the pinger, it may reduce the risk of them becoming entangled or encircled in the
476 fishing gear, but the pingers need to be positioned strategically on the net at the appropriate
477 depth to elicit the reduced feeding response. Further experimentation with the pingers at
478 different depths and tagging of the whales in order to have information about their
479 underwater feeding activity could provide valuable information for this hypothesis.

480 Disruption of feeding behaviour in these whales is cause for concern for negative impacts on
481 the individual, and possibly the population, if pinger use becomes widespread in the fishing
482 industry. Humpback whales need to consume an estimated 1432 Kcal of food per day during
483 the summer feeding season in order to have a large energy storage for their migration and
484 winter breeding season [39]. Insufficient energy stores may lead to decreased ability to
485 migrate or decreased reproductive success, which can furthermore impact the recruitment rate
486 of the population [66]. However, it is important to note that exposure to the whale pinger

487 during the *E* phase was only for 15 minutes, so it is unknown if the whales would habituate to
488 the sound and continue feeding normally after a longer period of time. We did not observe
489 any lasting effect of the whale pinger on surface feeding, suggesting that when the pinger is
490 removed from the water the whale quickly returns to its post-exposure behaviour. Further
491 investigation into the humpback whale's feeding response to low frequency acoustic alarms is
492 recommended for the future in order to determine if this response is consistent within larger
493 sample sizes and if it is detected in other humpback whale feeding grounds. It is also
494 advisable to investigate what the response of the whales is to longer exposure to the alarms to
495 determine if reduction in feeding is only a short-term consequence or is a longer response.
496 Given the uncertainty of the effects of long-term use, the whale pingers may be particularly
497 advisable for fishing methods in which the gear is not in the water for long periods of time
498 such as attached to purse seine nets or suspended in the water from long-line vessels.

499 The whales also significantly increased their swimming speed during exposure to the whale
500 pinger. An increase in humpback whale swimming speed has been documented in response to
501 whale watching boats [67, 68], but has not been reported in previous studies investigating
502 behavioural responses to pingers. Boye et al. [67] found that whales took significantly shorter
503 dives and increased their mean speed in response to boats, while similarly in our study some
504 individual whales significantly decreased their dive time, while overall the whales
505 significantly increased their speed. The increase in speed supports that humpback whales
506 respond to the whale pinger sound. However, further investigation into the whales' behaviour
507 underwater is needed to infer the effect of this reaction on entanglement mitigation.

508 Though similar previous studies were conducted during whale migration opposed to during
509 the feeding season, results from this study were consistent with recent previous finding that
510 there is no consistent, significant behavioural response of humpback whales to the whale
511 pinger in terms of dive time, breathing rate, or directness [24, 25, 26]. There was also no

512 evidence for individual-specific responses in terms of breathing rate or directness, meaning
513 we have no evidence that individuals reacted to the pinger significantly in terms of these
514 variables. The received sound level may have been too low to elicit a detectable behavioural
515 change in terms of these variables, which are behavioural reactions that can indicate the
516 whale was disturbed or startled [28]. The humpback whales foraging in the study sites for this
517 study are also regularly exposed to a lot of anthropogenic noise. Both locations host a high
518 number of whale-watching vessels which target humpback whales primarily for their
519 sightings, as well as industrial ports with associated development and maintenance noise and
520 fishing vessels, cruise ships and cargo ships entering and exiting often. There are also
521 commercial fishing grounds within the waters of both study sites. This may mean that many
522 humpback whales in this area are generally habituated to anthropogenic noise and may not
523 show behavioural changes that would indicate they are significantly disturbed or stressed.
524 There was evidence for individual-specific responses in terms of dive time, even though there
525 was no significant effect of whale pinger exposure on dive time overall. Some individuals
526 significantly increased dive time during the *E* phase while other individuals significantly
527 decreased. This could indicate that individuals just had variable significant reactions when
528 the sound was introduced, which could depend on their behavioural state in the *PrE* phase, as
529 suggested by Southall et al. [54]. It is also possible that individuals were just naturally
530 changing between behavioural states from a long dive period to a short dive period and vice
531 versa during the trials and for some individuals this happened to coincide with the *E* phase of
532 the trial. Further investigation into humpback whale dive time response to low frequency
533 sound, taking into account initial behavioural state and natural changes in behaviour, are
534 necessary to conclude whether dive time changes are in response to the pinger or not.

535 We found no evidence for a significant effect of the seal scarer alarm on humpback whale
536 speed, dive time, breathing rate or directness. In addition, we found no evidence that there

537 were any individual-specific responses to the seal scarer in terms of any of these variables.
538 The seal scarer was measured as having a source level 52 dB louder than the whale pinger
539 and due to this it was hypothesized the whales would have some reaction to the loud sound
540 even though the frequency of the alarm is at the top or slightly above the estimated hearing
541 range of the humpback whales [40]. Hearing in minke whales has more recently been
542 modelled using CT scanning to show their range is higher than what is necessary for their
543 communication [69], and they showed significant behavioural reactions to the seal scarer in
544 Iceland [33], but we found no evidence that this is similar for the humpback whales. This is
545 consistent with the findings of Henderson [70] who also concluded humpback whales do not
546 react to high frequency pingers, though the pinger used in their study was 17-45 kHz higher
547 in frequency than the device used in our study. It is possible that the frequency of the seal
548 scarer was just too high for the humpback whales to hear the alarm well enough to exhibit a
549 significant response, confirming that acoustic entanglement mitigation devices need to target
550 the best-estimated hearing range of the whales. However, the surface feeding behavioural
551 response remains unknown for the seal scarer since there was not enough surface feeding
552 observed in the trials to analyze this.

553 The use of the whale pingers on the capelin purse seine net for one season provided a first
554 insight into the use of the devices in a practical application in Iceland. A pair of whales
555 entered the net fitted with the pingers from the bottom, before it had been closed, twice. Since
556 the pingers were attached along the float line at the top of the net, this made sense that whales
557 may still enter from the bottom, with the net extending down approximately 120m. Despite
558 this, in both cases the whales were able to find their way out of the net through an
559 approximately 100m wide (at the surface) opening to the side of the net without causing any
560 damage and without further intervention methods from the captain (such as putting the boat
561 into reverse to sink the float line), a very rare occurrence according to the captain and crew

562 onboard. This led to an overall positive view of the whale pingers and an increased interest in
563 further trials for use in the Icelandic capelin purse seine fishery to prevent net damage.
564 Suggestions for repositioning the pingers on the net could be considered in the future
565 including attaching the pingers to the lead line at the bottom of the net or sewing specialized
566 pockets for the pingers into the lower portion of the net (Hjörvar Hjálmarsson pers. comm.
567 2018, Geir F. Zoega pers. comm. 2019). These observations also led to hypothesizing about
568 the currently unknown directional hearing capabilities of humpback whales. Ten pingers were
569 spaced approximately every 30-40m along the net measuring 450x120m in total. When the
570 whales were inside the net there was an approximately 100m opening left at the surface by a
571 single rope attaching the net end to the vessel, and the first pinger was attached to the net
572 approximately 30m from the “bag” netting (the net that remains in the water to prevent fish
573 from escaping as the they are hauled on board). This equals an estimated 150m pinger-less
574 space, of which approximately 100m is the opening for the whales to escape through. If the
575 pingers were truly aiding in the humpback whales finding this opening, as is being suggested
576 based on the captain and crew’s experience with whales becoming encircled in the net for
577 several years, this suggests that the whales were able to acoustically detect this 150m pinger-
578 less space where the sound level was lower, and then find the 100m opening. Further trials
579 and observation of whale pinger use on purse seine nets could provide more insight into this
580 hypothesis.

581 Low frequency whale pingers may be a useful tool in preventing humpback whale
582 entanglement and net damage occurring in their feeding grounds based primarily on the
583 findings from this study that the whales reduced their surface feeding behaviour in response
584 to the pinger and exited a purse seine net equipped with pingers without net damage or
585 intervention. The whale pinger also had a significant effect on the swimming speed of the
586 whales in this study, however the implications of this response in terms of entanglement

587 reduction are unknown. The fact that we observed no consistent behavioural reaction to the
588 whale pinger in terms of dive time, breathing rate or directness suggests that the whale
589 pingers do not elicit a stress response in humpback whales although whales increase
590 swimming speed and reduce feeding. No significant reactions to the louder, high-frequency
591 seal scarer alarm in terms of speed, dive time, breathing rate or directness were observed
592 which suggests these alarms are not effective for humpback whales, though their feeding
593 response to such an alarm requires further investigation. Though the whale pingers may be
594 effective in mitigating entanglement, they should be used with caution until further
595 information is known about the longer-term consequences of the reduction in feeding, and
596 may be best suited only for certain, short-term applications in conjunction with other possible
597 entanglement mitigation methods such as seasonal or area restrictions on fishing, and
598 modified fishing gear.

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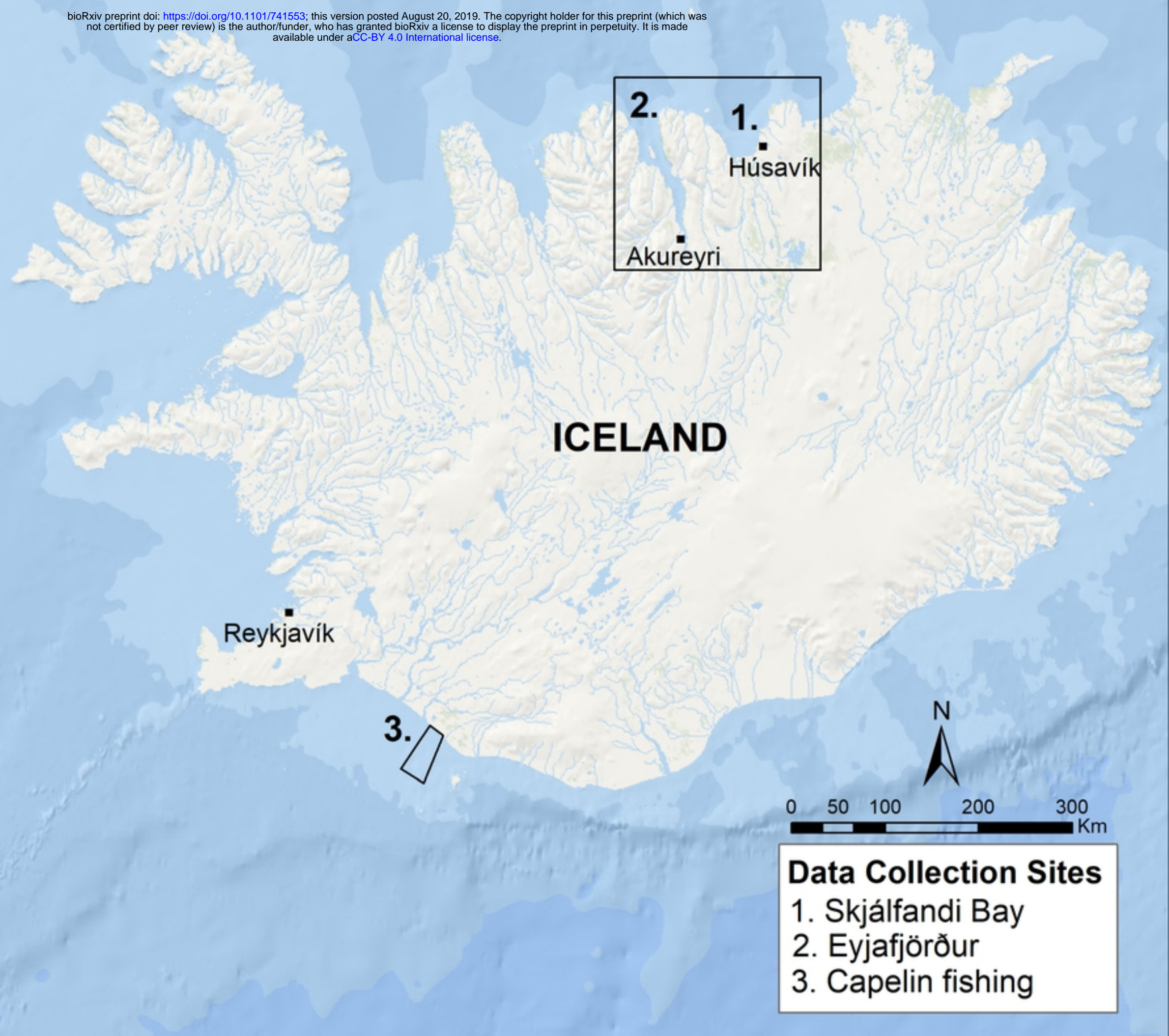
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Figure

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Figure



Figure

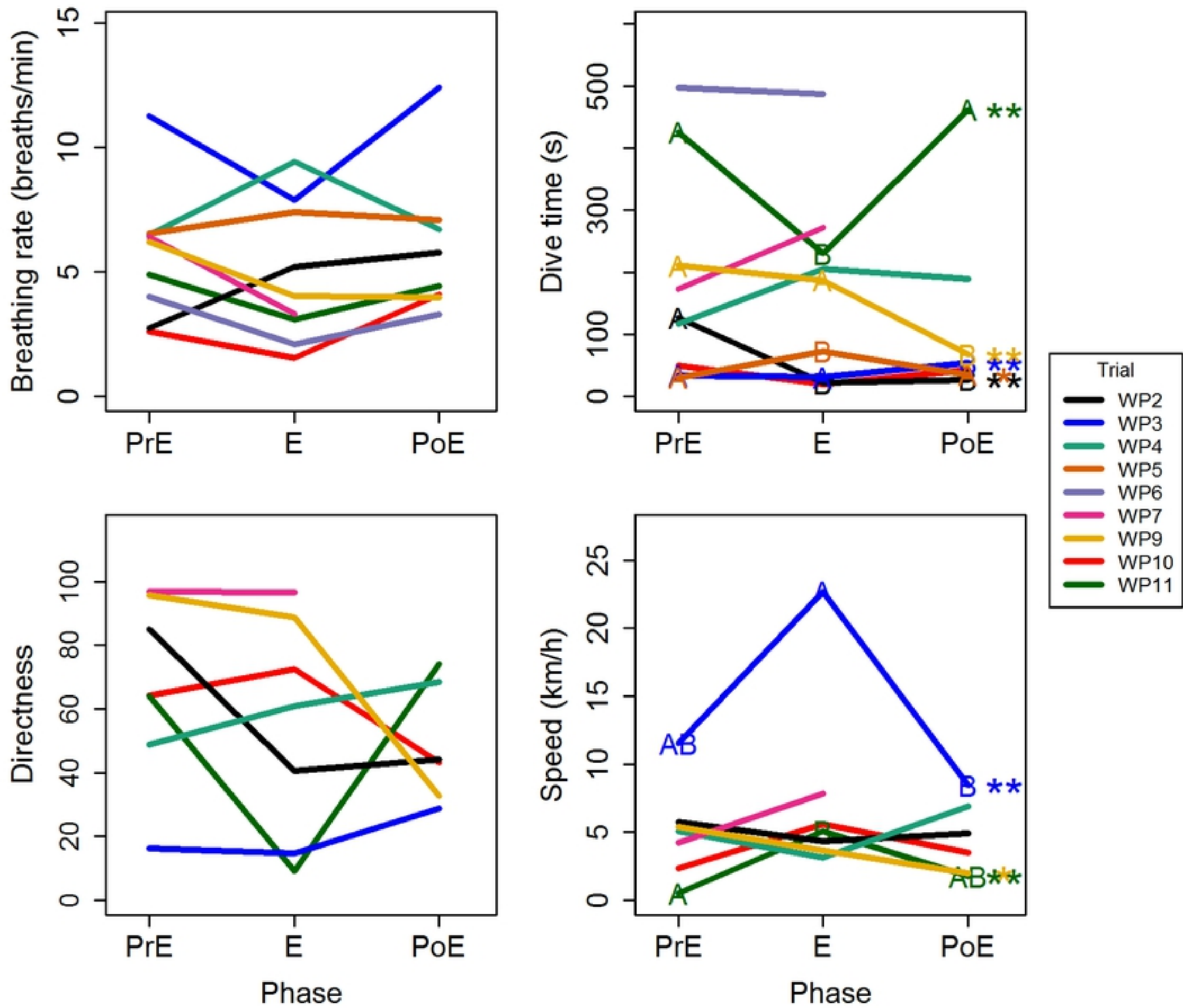


Figure

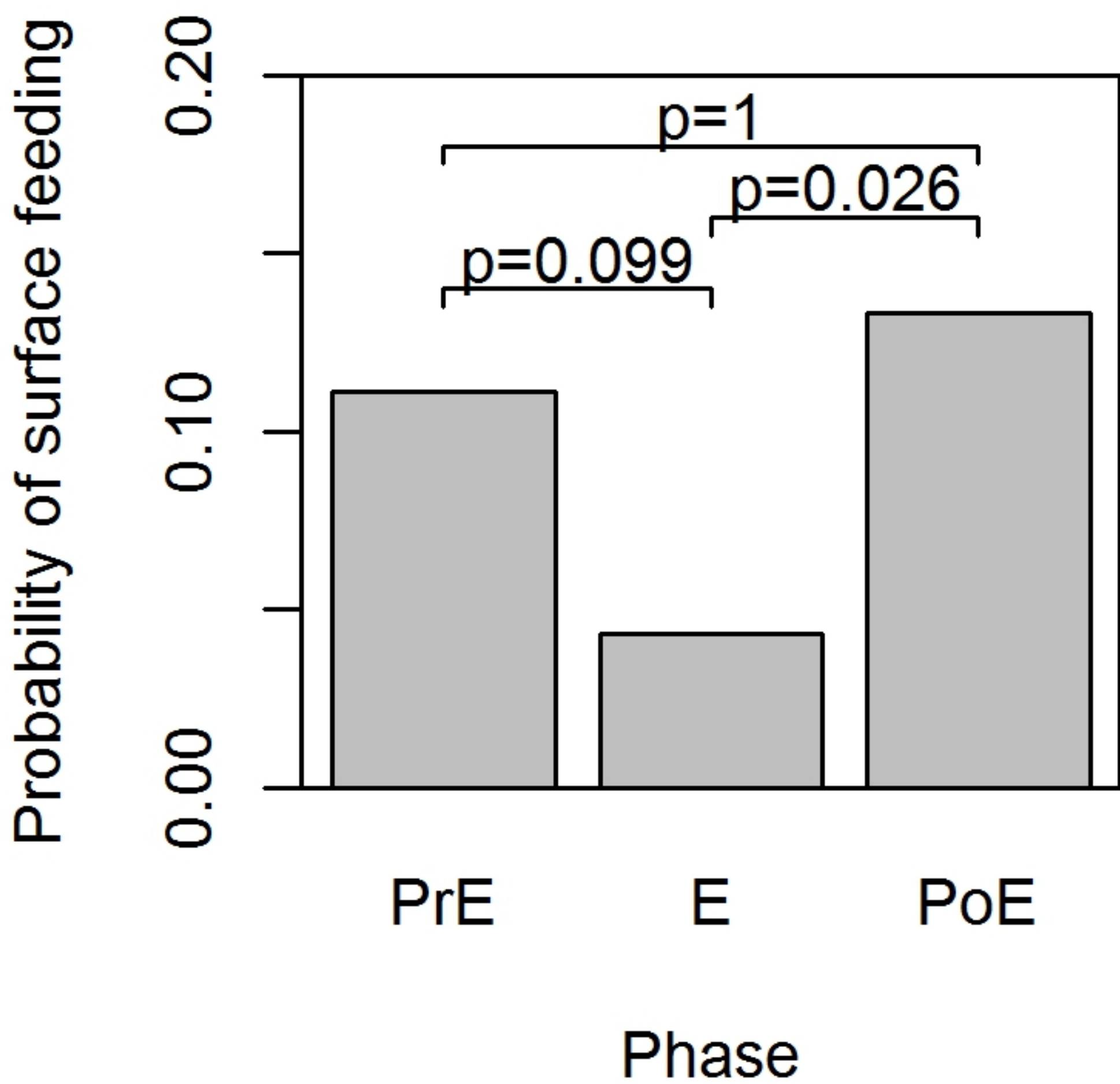
Individual	ID photograph	Location	Device (trial #)	Data
Mn452-Odin		SB	WP2	B, DI, D, S, F
Mn422-Constellation		SB	WP3	B, DI, D, S, F
Mn425-Excalibur		SB	WP4	B, DI, D, S
Mn497-Mystery		SB	WP5	B, D, F
Mn690-Remoladi		SB	WP6	B, D*
Mn598-OneEye		SB	WP7	B, DI, D*, S*
Mn215-Frangia		SB	WP9	B, DI, D, S, F
EF-unknown	Poor quality fluke image	EF	WP10	B, DI, D, S, F
Mn519-Fleur		SB	WP11	B, DI, D, S
Mn597-Cosima		SB	SS1	B, DI, D, S
Mn447-Triplet		SB	SS2	B, DI, D, S
Mn512-CaptainHook		SB	SS3	B, DI, D, S
Mn674-Sully		SB	SS4	B, D, S
Mn750-Chambao		SB	SS5	B, DI, D, S
Mn570-Evero		SB	SS6	B, DI, D, S
Mn597-Cosima	See SS1	SB	SS7	B, DI, D, S

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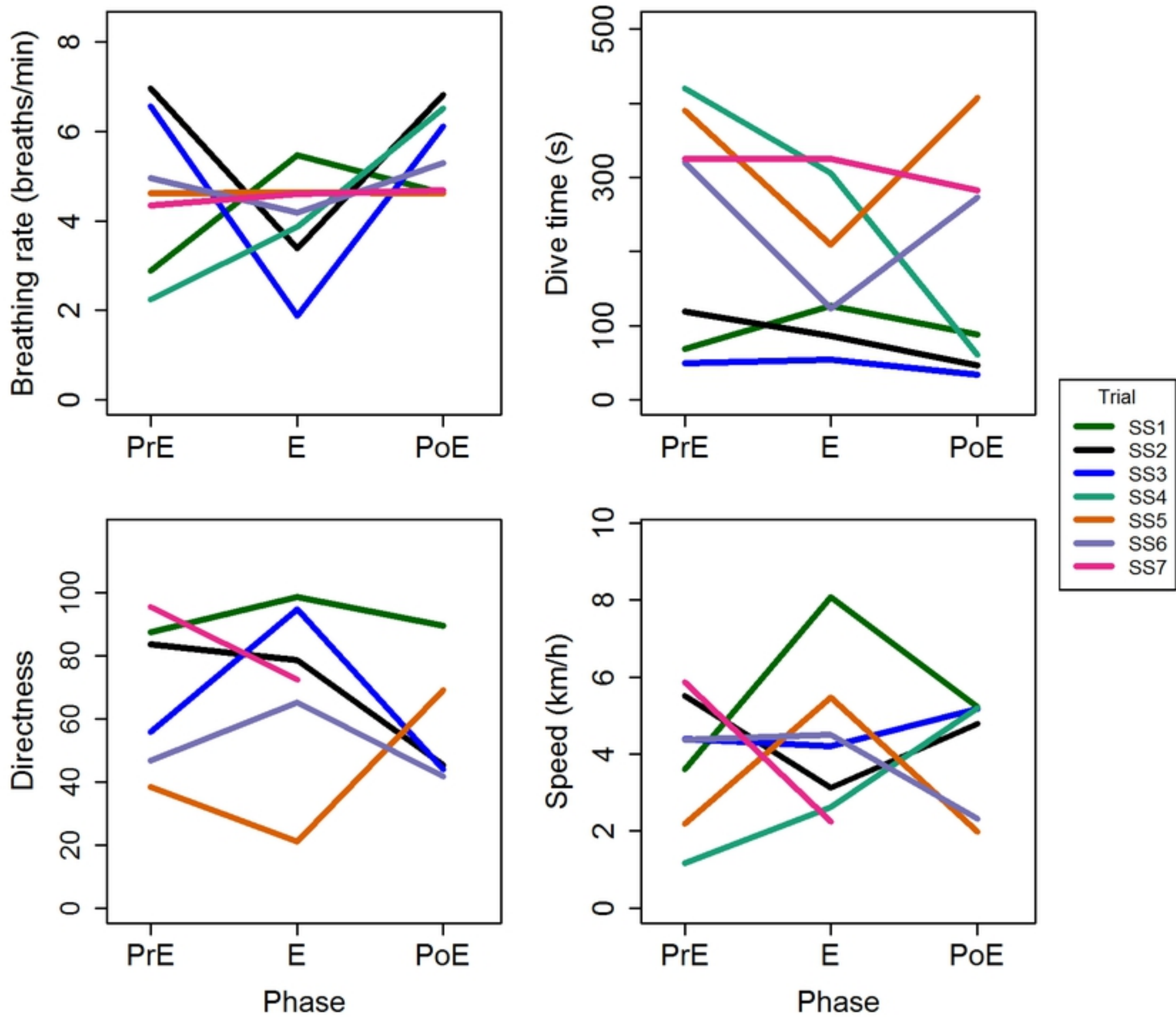
Figure



Figure



Figure



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