

1 **Heaviside's dolphins (*Cephalorhynchus heavisidii*) relax acoustic**
2 **crystallization to increase communication range**

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13 **Abstract**

14 The costs of predation may exert significant pressure on the mode of communication used by an
15 animal, and many species balance the benefits of communication (e.g. mate attraction) against
16 the potential risk of predation. Four groups of toothed whales have independently evolved
17 narrowband high-frequency (NBHF) echolocation signals. These signals help NBHF species
18 avoid predation through acoustic crypsis by echolocating and communicating at frequencies
19 inaudible to predators such as mammal-eating killer whales. Heaviside's dolphins
20 (*Cephalorhynchus heavisidii*) are thought to exclusively produce NBHF echolocation clicks with
21 a centroid frequency around 125 kHz and little to no energy below 100 kHz. To test this, we
22 recorded wild Heaviside's dolphins in a sheltered bay in Namibia. We demonstrate that
23 Heaviside's dolphins produce a second type of click with lower frequency and broader
24 bandwidth in a frequency range that is audible to killer whales. These clicks are used in burst-
25 pulses and occasional click series but not foraging buzzes. We evaluate three different
26 hypotheses and conclude that the most likely benefit of these clicks is to decrease transmission
27 directivity and increase conspecific communication range. The expected increase in active space
28 depends on background noise but ranges from 2.5 (Wenz Sea State 6) to 5 times (Wenz Sea State
29 1) the active space of NBHF signals. This dual click strategy therefore allows these social
30 dolphins to maintain acoustic crypsis during navigation and foraging, and to selectively relax
31 their crypsis to facilitate communication with conspecifics.

32

33 Keywords: acoustic crypsis, active space, communication, echolocation, Heaviside's dolphin,
34 narrowband high-frequency clicks

35 **Introduction**

36 Social animals inevitably need to balance effective communication with conspecifics against the
37 costs associated with communication, including eavesdropping and potential detection by
38 predators and prey [1]. Trade-offs to decrease predator detection often involve shifting
39 communication to periods or locations with lowered predation risk [2], but such acoustic
40 avoidance can be costly if the social or ecological functions of communication are not fulfilled
41 [3]. Alternatively, animals may use quiet, low-amplitude or high-frequency signals with short
42 detection ranges for social interactions [4] which can be difficult for predators to locate [5].

43

44 In the aquatic environment where light diminishes quickly, cetaceans (whales, dolphins and
45 porpoises) rely on sound as the primary medium for orientation, foraging and communication
46 [6]. In water, sound travels faster and attenuates less than in air [7], increasing the necessity of
47 balancing communication with the associated risk of distant eavesdroppers. Mammal-eating
48 killer whales (*Orcinus orca*) have been shown to fall silent as they hunt so as not to alert their
49 acoustically sensitive prey [8]. Antipredator strategies that decrease the risk of passive detection
50 by predators have potentially large benefits since echolocation used by all toothed whales puts
51 them at heightened risk of detection by eavesdroppers [9]. For example, Blainville's beaked
52 whales (*Mesoplodon densirostris*) only produce sound at depth and remain silent within several
53 hundred metres of the surface, and this has been proposed to represent a strategy to reduce risk of
54 detection by killer whales, which tend not to dive deeper than a few tens of metres [10].

55 Additionally, delphinids [11] and seals [12] seem to suppress vocal activity in the presence of
56 killer whales.

57

58 Toothed whales are grouped into four acoustic categories by the type of biosonar pulses they
59 emit [13, 14]. While most delphinids produce broadband, extremely short biosonar clicks,
60 thirteen species from four separate clades (*Kogiidae*, *Phocoenidae*, *Pontoporiidae*, and 6
61 delphinid species from the genera *Cephalorhynchus* and *Lagenorhynchus*) have evolved a
62 narrowband, high-frequency (NBHF) click type [15, 16] with energy almost exclusively above
63 100 kHz [17]. These four independent cases of convergent evolution have spurred several
64 hypotheses regarding the evolution of NBHF signals [16]. Some authors have argued that NBHF
65 signals exploit a natural low noise window occurring at frequencies above 100 kHz to favour
66 detection in an otherwise noisy environment [18]. Other authors propose that the evolution of
67 NBHF signals and the concurrent loss of producing lower-frequency whistles is evidence for an
68 ‘acoustic crypsis’ strategy [15, 19] where NBHF species have shifted their acoustic signals to
69 frequencies above the hearing limit of killer whales which cuts off around 100 kHz [20]. The
70 ‘acoustic crypsis’ hypothesis has become a commonly accepted explanation for the evolution of
71 NBHF signals [14, 21, 22].

72

73 This cryptic biosonar strategy has had consequences for communication and social behaviour in
74 NBHF species. Many broadband delphinid species produce a wide variety of communication
75 signals [23, 24] including low-frequency calls and whistles that can travel several kilometres
76 underwater [25, 26] and are easily distinguished from foraging sounds. In contrast, NBHF
77 species seem to have lost the ability to whistle [15] and communication is therefore limited to
78 clicks. Both harbour porpoises (*P. phocoena*) [21, 27] and Hector’s dolphins (*C. hectori*) [28] are
79 NBHF species which have been shown to communicate acoustically with short, isolated burst-
80 pulses during social and aggressive encounters. However, there are socio-ecological drawbacks

81 for species constrained to producing NBHF signals for both echolocation and communication.
82 First, the signal repertoire and thus communication complexity [29] is limited, potentially
83 reducing options for resolving and differentiating social interactions with sound. Second,
84 communicating with signals that are also used for echolocation and foraging may increase signal
85 ambiguity for a receiver [30] which then needs to differentiate communication from foraging
86 signals. Finally, as NBHF clicks are highly directional and attenuate rapidly with distance due to
87 high frequency-dependent absorption [22], the detection range for nearby conspecifics is
88 typically short (< 1 km) and dependent on the relative orientation of the source and the receiver
89 [21].

90

91 Heaviside's dolphins (*Cephalorhynchus heavisidii*) are small (< 1.7 m) delphinids endemic to the
92 west coast of southern Africa. They are typically found in shallow coastal waters to
93 approximately 100 m depth [31] in small groups; however, group sizes tend to be slightly larger
94 with more socialising activity than described for other NBHF species [32]. Heaviside's dolphins
95 have only been reported to produce NBHF clicks with little to no energy below 100 kHz, like
96 other NBHF species [33]. Here we present evidence that Heaviside's dolphins produce lower-
97 frequency broadband signals, despite residing in an area with killer whale predation risk. We
98 show that burst-pulses are generally composed of these lower-frequency broadband signals, and
99 thus present evidence of a NBHF species with a dual click type strategy. We discuss three
100 possible theories to explain how the production of these lower-frequency broadband signals may
101 help this species compensate for the socio-ecological trade-offs imposed by communicating with
102 NBHF signals. We use an acoustic model to show that a major advantage of communicating

103 using lower-frequency clicks is that transmission directivity is lower and active space is larger
104 over a wide range of noise levels, thus facilitating social interactions over a greater area.

105

106 **Materials and Methods**

107 Twenty-five hours of acoustic recordings of Heaviside's dolphins were collected in Shearwater
108 Bay, Namibia ($-26^{\circ} 37' S$, $15^{\circ} 05' E$), over 12 days during April and May 2016. Recordings
109 were made by deploying two hydrophones (SoundTrap 300 HF; Ocean Instruments, New
110 Zealand) mounted 1 m apart and suspended 1.5 m below an ocean kayak. Only data from a
111 single hydrophone was analysed for this study. Sound was digitised at a sampling rate of 576
112 kHz with a 16-bit resolution (sensitivity: $-171 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$, flat frequency response: 400 Hz –
113 150 kHz $\pm 3 \text{ dB}$). Behaviour and group size information were collected concurrently with sound
114 recordings (see Supplementary Methods). A land-based observer team stationed at a vantage
115 point (20 m elevation) monitored the presence of cetaceans within the bay.

116

117 *Acoustic data extraction:* Recordings made within a visually estimated 50 m range of dolphins
118 were selected for analysis. Acoustic signals produced by Heaviside's dolphins were identified
119 through visual inspection of a spectrogram display in Adobe Audition CC (Adobe Systems Inc.).
120 Heaviside's dolphin NBHF echolocation clicks have been previously described [33], and only a
121 subset were selected for analysis. We defined three functional groups of signals based on signal
122 context and interclick intervals (ICI, calculated as the time between subsequent clicks [9]). Click
123 trains were defined as series of clicks with ICI exceeding 10 ms. Such click trains are likely
124 echolocation signals produced by the animals. A subset of click trains were composed of lower-
125 frequency, broader bandwidth signals than previously described [33], and we therefore divided

126 click trains into NBHF click trains and broadband click trains by inspecting spectrograms (Fig.
127 1). Foraging buzzes are used during prey capture by echolocating animals [34, 35], including
128 NBHF species [36]. These were defined as click series with ICIs < 10 ms, which were preceded
129 by a slower click train. Since buzzes occurred at the end of a click train, we defined the start of a
130 buzz as the point when the ICI first decreased below 10 ms and the end of the buzz as the point
131 where the click train ended or where the ICI increased to > 10 ms. Finally, we defined burst-
132 pulse signals as discrete, isolated series of high repetition rate clicks that began, persisted and
133 generally ended with interclick intervals < 10 ms following Lammers et al. [37]. Burst-pulses are
134 commonly considered to have an intra-specific communicative function [24, 37, 38], including in
135 NBHF species [21]. Only distinguishable, high-quality pulsed signals measuring > 10 dB above
136 the background noise measured immediately before the signal were selected for further analysis.

137

138 *Acoustic feature extraction:* To quantify temporal differences in repetition rate across signals, we
139 used a click detection algorithm developed in MATLAB 2013B (The MathWorks Inc., USA).
140 We first filtered the input signal with a 6-pole Butterworth bandpass filter (20 kHz - 275 kHz),
141 calculated the signal envelope, and extracted peaks in the envelope that were separated by more
142 than 0.5 ms. Click detections were visually inspected and manually corrected for missed
143 detections. To compare signals with highly variable numbers of clicks, we finally calculated the
144 5th, 50th and 95th percentile ICI across each click series.

145

146 To quantify temporal and spectral differences of component clicks, we extracted the highest
147 amplitude click from each click series following the methods for on-axis click analysis [39, 40].
148 While these signals were recorded from an unknown aspect, the minute difference in the

149 waveform and spectrum of NBHF clicks across varying off-axis angles [41] means that spectral
150 parameters are likely reasonably close to on-axis signals. Individual signals were filtered in
151 MATLAB with a 4-pole Butterworth bandpass filter between 20 kHz and 275 kHz. Individual
152 click power spectra were calculated with a 512-point 50% Tukey window centred on the peak
153 envelope of each click. Spectral and temporal click parameters were calculated according to
154 methods for measuring on-axis click parameters [9, 42].

155

156 *Statistical analysis of signal discrimination:* Signal parameters, including spectral and temporal
157 click parameters as well as interclick intervals, were compared across signal categories using a
158 non-parametric Kruskal-Wallis test and subsequent Dunn’s post-hoc tests for pairwise
159 comparisons in R version 3.4.2 [43, 44]. We then used a Random Forest classifier [45] to
160 measure prediction accuracy as a function of buzz and burst-pulse signal categories using either
161 ICI parameters (5th, 50th and 95th ICI percentiles for each click series), spectral and temporal
162 individual click parameters, or all signal parameters combined to test the potential benefit of
163 spectral differences in decreasing signal ambiguity. The Random Forest classifier was built in
164 MATLAB 2017b using a ‘bagged trees’ ensemble classifier with 30 learners [45]. Prediction
165 accuracy was measured using 5-fold cross-validation to prevent overfitting. To measure
166 consistency in prediction accuracy, a classifier was trained 100 times and prediction accuracy
167 measured for each iteration.

168

169 *Acoustical modelling of detection range:* To test the potential benefit for communication, we
170 modelled the detection range for typical NBHF clicks and for lower-frequency clicks extracted
171 from burst-pulses. We first filtered the input signal with a 6-pole Butterworth bandpass filter (10

172 kHz - 150 kHz), and we used a piston model [46] to estimate changes in transmission beam and
173 empirical measurements of hearing sensitivity of a harbour porpoise [47] to estimate changes in
174 directional hearing. We modelled the detection range (m) for a noise-limited scenario with Wenz
175 Sea State 2 noise levels, and we accounted for changes in transmission loss due to lower
176 frequency-specific absorption. A separate sensitivity analysis was conducted across a 25-dB
177 variation in wind-generated ambient noise (reflecting calm sea conditions to storms) and a 25-dB
178 variation in signal source levels (reflecting the full distribution of on-axis source levels from
179 Heaviside's dolphins [33]) to examine how varying noise conditions and output levels affect the
180 relative change in active space between the two signal types. The full model and sensitivity
181 analysis are described in Supplementary Methods.

182

183 **Results**

184 Acoustic data were collected during recording sessions with Heaviside's dolphins during which
185 foraging, resting, socialising, interacting with the kayak and travelling behaviours were
186 observed. No other cetacean species were sighted visually or detected acoustically during
187 recording sessions. A total of 90 broadband click trains, 706 buzzes and 954 burst-pulses and a
188 subset of 33 NBHF click trains were indexed from recordings made when Heaviside's dolphins
189 were within 50 m of the kayak.

190

191 Broadband click trains and burst-pulse signals were composed of clicks with lower frequency
192 and broader bandwidth (Fig. 1) compared to typical NBHF signals (Table 1). Q-ratios (centroid
193 frequency / RMS bandwidth) are an indicator of click type, and generally burst-pulse signals and

194 broadband click trains had Q-ratios < 5 , whereas NBHF click trains and buzz signals had Q-
195 ratios > 7 (Table 1, Suppl. Fig. 1A).

196

197 Initially, buzz and burst-pulse signals were visually differentiated by the presence or absence of a
198 preceding click train as burst-pulses occur as isolated signals. The measured signal parameters
199 confirmed there were significant differences in both ICI parameters and spectral parameters
200 between these two signal types (Fig. 2; see Supplementary Methods for a full comparison of
201 different signal types). Based on these findings, a Random Forest classification algorithm was
202 implemented to evaluate importance of different parameters and test if discrimination of
203 communication signals (burst-pulses) from feeding signals (buzzes) benefits from spectral
204 differences. The Random Forest classifier demonstrated that ICI parameters were most important
205 for accurate classification of buzz and burst-pulse signal categories (Fig. 2C). Signal categories
206 could be predicted with 97% accuracy using all available parameters (Fig. 2D). Classification
207 accuracy decreased only marginally (95% prediction accuracy) when only interclick interval
208 parameters were included in the model, whereas a larger drop in accuracy was seen when only
209 spectral and temporal click parameters were included in the model (86% prediction accuracy).

210

211 The effect of signal type on beamwidth was two-fold: first, the sidelobes seen in NBHF signals
212 were suppressed because of the broader bandwidth of burst-pulse signals; second, the
213 transmission directivity was lower and consequently sound intensity away from the centre of the
214 sound beam was higher (Fig. 3A). The detection range for NBHF clicks and burst-pulse signals
215 was modelled for a typical 130-kHz NBHF signal and for a burst pulse signal with a centroid

216 frequency of 80 kHz. While detection range depends on the modelled noise levels as well as
217 source and receiver geometry, the estimated detection range was consistently greater for burst-
218 pulse signals at all estimated source and receiver angle combinations (Fig. 3B). The potential
219 gain in active space depended on noise level but was relatively unaffected by large changes in
220 sound source level (Fig. 3C). At wind-generated noise levels corresponding to Wenz Sea State 1
221 (approximately 4-6 knots of wind), the active space of a burst-pulse signal would be around 5
222 times greater than the active space of a NBHF click (Fig. 3C). At an estimated wind-generated
223 noise level corresponding to Wenz Sea State 6 (approximately 28-47 knots of wind), the active
224 space would be approximately 2.5 times greater than for a NBHF click (Fig. 3C).

225

226 **Discussion**

227 Members of the genus *Cephalorhynchus* are thought to have evolved the exclusive use of NBHF
228 biosonar signals to become acoustically cryptic, thereby reducing predation risk by killer whales
229 [15]. This has consequences for the evolution and function of communication signals within the
230 genus, since acoustic communication is thought to be limited to taking place through click series
231 [21, 28]. Here, we show that Heaviside's dolphins produce a second click type that is distinct
232 from normal NBHF clicks by having a lower frequency content and broader bandwidth which
233 circumvents some of the limitations of communicating with NBHF clicks. Heaviside's dolphins
234 produce these lower-frequency broadband signals occasionally in the form of slow click trains
235 but predominately in the form of burst-pulses, presumably used for communication [21, 24, 27,
236 28, 37, 38].

237

238 Communication with burst-pulses is normally achieved using clicks that are nearly
239 indistinguishable from echolocation clicks in delphinids [28, 37] and phocoenids [21, 48], apart
240 from low-frequency pulsed signals such as bottlenose dolphin (*Tursiops sp.*) pops [49] or jaw
241 claps [50]. However, in Heaviside's dolphins, clicks comprising most burst-pulses appear to be a
242 modified and clearly distinguishable version (86% classification success based only on spectral
243 differences: Fig. 2D). Most of the burst-pulses analysed (63%) contained energy beginning at
244 ~50 kHz, which is an octave lower than signals reported for other NBHF species [21, 22, 28, 51].
245 Consequently, most of the recorded broadband signals are well within the hearing limit of killer
246 whales (upper limit at approximately 100 kHz) [20]. This makes these signals risky to produce,
247 especially in Namibia where killer whales are known to occur and predate on cetaceans [52],
248 including Heaviside's dolphins in the study area (Dr J.-P. Roux, personal communication, 2016).

249

250 One explanation for the use of lower-frequency broadband signals could be to reduce signal
251 ambiguity by allowing conspecifics to differentiate communication signals from foraging buzzes.
252 We addressed this theory by using a cross-validated Random Forest classification algorithm with
253 feature vectors containing only ICI parameters, only spectral and temporal click parameters, or
254 containing all parameters combined. Both burst-pulses and foraging buzzes were accurately
255 classified (95% accuracy) by interclick intervals without including spectral and temporal click
256 parameters, so these do not seem to be necessary for accurate discrimination of burst-pulses from
257 foraging buzzes. Rather, it seems likely that ICIs by themselves may allow animals to identify
258 communication signals and it will be interesting to see if that is the case for other NBHF species
259 as well.

260

261 A second, similar explanation for the use of lower-frequency broadband signals is to increase
262 signal complexity in the repertoire, thus allowing for encoding a greater variety of messages.
263 Repertoire complexity could be augmented either by producing non-NBHF communication
264 signals at repetition rates that are also used for foraging signals, or by composing communication
265 signals with different click types. However, we see only little evidence for either of these
266 explanations: burst-pulses were composed predominantly of lower-frequency clicks, with no
267 evidence of burst-pulses composed of different click types, and with repetition rates consistently
268 higher than for other signal types such as click trains or foraging buzzes. However, the lower
269 frequency cut-off did vary between burst-pulses, and it is unclear how much of this is due to off-
270 axis distortion [46, 53] or could be used to encode information.

271

272 Finally, a third possible explanation for the use of these signals is that the lower frequency helps
273 to increase the detection range and thus favours signal detection for nearby conspecifics. High-
274 frequency signals suffer from increased sound absorption as they propagate through water, and
275 thus attenuate faster than lower frequencies [7]. By reducing the predominant frequency, signals
276 will suffer less frequency-dependent absorption and thus travel farther underwater [51]. At the
277 same time, both transmission directivity and receiving directivity will be lower (Fig. 3A), and
278 thus energy will be more equally distributed around the vocalising animal [47, 54]. The modelled
279 detection ranges of NBHF and burst-pulse signals support this hypothesis and show that
280 significant improvements in detection range are possible by switching to lower-frequency burst-
281 pulse signals, especially for receivers that are oriented away from or located outside the centre of
282 the sound beam (Fig. 3B). The relative change in active space is driven mostly by the change in
283 sound radiation and partly by a lower sound absorption and thus is relatively independent of the

284 actual source level and the absolute detection range of the animal (Fig. 3C). Since the noise at
285 NBHF signal frequencies is primarily thermal noise, increasing wind-generated ambient noise
286 decreases the potential gain in active space, but active space remains higher for burst-pulse
287 signals across the entire range of modelled noise levels from Wenz Sea State 1 through Wenz
288 Sea State 6 conditions (Fig. 3C). Furthermore, the change in active space may be greater if
289 animals simultaneously change transmission aperture through manipulations of air sacs or soft
290 tissue structures, such as suggested for echolocating delphinids [46] or harbour porpoises
291 emitting foraging buzzes [55]. Thus, the most likely reason for Heaviside's dolphins to use risky,
292 lower-frequency broadband signals is to circumvent the restrictions in communicating with a
293 short-range, highly directional NBHF signal imposed by shifting their biosonar above the
294 hearing range of killer whales. The estimated increase in active space achieved by the lower-
295 frequency broadband signals is still far less than could be achieved by using whistles [26], thus
296 this secondary click type represents a compromise between remaining acoustically cryptic
297 (especially when foraging) and possessing the ability to communicate over a greater range when
298 necessary.

299

300 It is possible that other NBHF species may take advantage of selectively increasing their active
301 space. Neonatal phocoenids have been reported to produce pulsed signals with a strong low-
302 frequency (~1-3 kHz) content just after birth and begin to exclusively produce NBHF clicks
303 between four [56] and 20 [57] days postnatal. It is not yet understood if this is related to
304 morphological changes or learned call behaviour. Regardless, calves' ability to produce lower-
305 frequency signals with greater active space may be useful for mother-offspring cohesion during
306 the first days of life. Additionally, sporadic broadband clicks and low-frequency (4-16 kHz)

307 whistle sounds have been recorded in the presence of mother and calf pairs of Commerson's
308 dolphins (*C. commersonii*) [58]. Thus, we should not unequivocally dismiss the possibility of
309 finding lower-frequency communication signals in species that are considered acoustically
310 cryptic NBHF species.

311

312 **Ethics**

313 This research was conducted by the "Namibian Dolphin Project" with permission from the
314 Namibian Ministry of Fisheries and Marine Resources and with ethics 252 clearance from the
315 University of Pretoria Animal Use and Care Committee (Reference: ec061-09 AUCC).

316

317 **Data and Materials**

318 The datasets supporting this article have been uploaded to the Dryad as part of the supplementary
319 material and can be referenced as: "Martin M, Gridley T, Elwen S, Jensen F (2018) Data from:
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321 communication range. Dryad Digital Repository. <https://doi.org/10.5061/dryad.64048p0>".

322

323 **Competing Interests**

324 The authors have no competing interests.

325

326 **Authors' Contributions**

327 Conceived and designed the experiments: MJM TG SHE. Performed the experiments and
328 collected data: MJM. Analysed the data: MJM FHJ. Contributed materials and analysis tools:
329 MJM TG SHE FHJ. Acoustic modelling: FHJ. Wrote the paper and approved final submission:
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331

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345

346 **References**

347 1. Bradbury J, Vehrencamp S. Signal design rules. In: *Principles of Animal Communication*.
348 Sunderland, Massachusetts: Sinauer Associates, Inc. 1998. p. 571-618.

- 349 2. Curio E. *The Ethology of Predation*. Berlin, Germany: Springer-Verlag. 1976. p. 1-250.
- 350 3. Ruxton GD. Non-visual crypsis: a review of the empirical evidence for camouflage to senses
351 other than vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 2009. **364**: 549-57.
352 (doi:10.1098/rstb.2008.0228)
- 353 4. Wilson DR, Hare JF. The adaptive utility of Richardson's ground squirrel (*Spermophilus*
354 *richardsonii*) short-range ultrasonic alarm signals. *Can. J. Zool.* 2006. **84**: 1322-30.
355 (doi:10.1139/Z06-120)
- 356 5. Jones KJ, Hill WL. Auditory perception of hawks and owls for passerine alarm calls. *Ethol.*
357 2001. **107**: 717-26. (doi:10.1046/j.1439-0310.2001.00698.x)
- 358 6. Tyack P. Acoustic communication under the sea. In: *Animal Acoustic Communication* (eds.
359 *Hopp SL, Owren MJ, Evans CS*). Germany: Springer. 1998. p. 163-220.
360 (doi:10.1007/978-3-642-76220-8_6)
- 361 7. Clay CS, Medwin H. *Acoustical Oceanography: Principles and Applications*. New York:
362 Wiley-Interscience. 1977.
- 363 8. Deecke VB, Ford JKB, Slater PJB. The vocal behaviour of mammal-eating killer whales:
364 communicating with costly calls. *Anim. Behav.* 2005. **69**: 395-405.
365 (doi:10.1016/j.anbehav.2004.04.014)
- 366 9. Au W. *The Sonar of Dolphins*. New York: Springer-Verlag. 1993. (doi:10.1007/978-1-4612-
367 4356-4)
- 368 10. Aguilar de Soto N, Madsen PT, Tyack P, Arranz P, Marrero J, Fais A, et al. No shallow talk:
369 Cryptic strategy in the vocal communication of Blainville's beaked whales. *Mar. Mamm.*
370 *Sci.* 2012. **28**: 75-92. (doi:10.1111/j.1748-7692.2011.00495.x)

- 371 11. Rankin S, Archer F, Barlow J. Vocal activity of tropical dolphins is inhibited by the presence
372 of killer whales, *Orcinus orca*. *Mar. Mamm. Sci.* 2013. **29**: 679-90. (doi:10.1111/j.1748-
373 7692.2012.00613.x)
- 374 12. Thomas JA, Ferm LM, Kuechle VB. Silence as an antipredation strategy by Weddell seals.
375 Naval Ocean Systems Center San Diego, California. 1989.
- 376 13. Wahlberg M, Beedholm K, Heerfordt A, Møhl B. Characteristics of biosonar signals from
377 the northern bottlenose whale, *Hyperoodon ampullatus*. *J. Acoust. Soc. Am.* 2011. **130**:
378 3077-84. (doi:10.1121/1.3641434)
- 379 14. Fenton BM, Jensen FH, Kalko EK, Tyack PL. Sonar signals of bats and toothed whales. In:
380 *Biosonar* (eds. Surlykke A, Nachtigall P, Fay R, Popper A). New York: Springer. 2014. p.
381 11-59. (doi:10.1007/978-1-4614-9146-0_2)
- 382 15. Morisaka T, Connor RC. Predation by killer whales (*Orcinus orca*) and the evolution of
383 whistle loss and narrow-band high frequency clicks in odontocetes. *J. Evol. Biol.* 2007.
384 **20**: 1439-58. (doi:10.1111/j.1420-9101.2007.01336.x)
- 385 16. Morisaka T. Evolution of communication sounds in odontocetes: A review. *Int. J. Comp.*
386 *Psychol.* 2012. **25**: 1-20.
- 387 17. Au WWL. Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics*. 1997. **8**:
388 137-62. (doi:10.1080/09524622.1997.9753357)
- 389 18. Møhl B, Andersen S. Echolocation: high-frequency component in the click of the harbour
390 porpoise (*Phocoena ph.*). *J. Acoust. Soc. Am.* 1973. **54**: 1368-72.
391 (doi:10.1121/1.1914435)
- 392 19. Andersen S, Amundin M. Possible predator-related adaption of sound production and hearing
393 in the harbour porpoise (*Phocoena phocoena*). *Aquat. Mamm.* 1976. **4**: 56-8.

- 394 20. Szymanski MD, Bain DE, Kiehl K, Pennington S, Wong S, Henry KR. Killer whale (*Orcinus*
395 *orca*) hearing: Auditory brainstem response and behavioral audiograms. *J. Acoust. Soc.*
396 *Am.* 1999. **106**: 1134-41. (doi:10.1121/1.427121)
- 397 21. Clausen KT, Wahlberg M, Beedholm K, DeRuiter SL, Madsen PT. Click communication in
398 harbour porpoises *Phocoena phocoena*. *Bioacoustics*. 2010. **20**: 1-28.
399 (doi:10.1080/09524622.2011.9753630)
- 400 22. Kyhn LA, Tougaard J, Beedholm K, Jensen FH, Ashe E, Williams R, et al. Clicking in a
401 killer whale habitat: narrow-band, high-frequency biosonar clicks of harbour porpoise
402 (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). *PLOS ONE*. 2013. **8**:
403 e63763. (doi:10.1371/journal.pone.0063763)
- 404 23. Tyack P. Population biology, social behavior and communication in whales and dolphins.
405 *Trends Ecol. Evol.* 1986. **1**: 144-50. (doi.org/10.1016/0169-5347(86)90042-X)
- 406 24. Herzing DL. Vocalizations and associated underwater behavior of free-ranging Atlantic
407 spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. *Aquat.*
408 *Mamm.* 1996. **22**: 61-79.
- 409 25. Miller PJ. Diversity in sound pressure levels and estimated active space of resident killer
410 whale vocalizations. *J. Comp. Physiol. A*. 2006. **192**: 449. (doi:10.1007/s00359-005-
411 0085-2)
- 412 26. Jensen F, Beedholm K, Wahlberg M, Bejder L, Madsen PT. Estimated communication range
413 and energetic cost of bottlenose dolphin whistles in a tropical habitat. *J. Acoust. Soc. Am.*
414 2012. **131**: 582-92. (doi:10.1121/1.3662067)
- 415 27. Amundin M. Sound production in odontocetes with emphasis on the harbour porpoise
416 *Phocoena phocoena*. PhD Dissertation. Stockholm, Sweden. 1991.

- 417 28. Dawson SM. Clicks and communication: the behavioral and social contexts of Hector's
418 dolphin vocalizations. *Ethol.* 1991. **88**: 265-76. (doi:10.1111/j.1439-
419 0310.1991.tb00281.x)
- 420 29. Fischer J, Wadewitz P, Hammerschmidt K. Structural variability and communicative
421 complexity in acoustic communication. *Anim. Behav.* 2016. **134**: 229-37.
422 (doi:10.1016/j.anbehav.2016.06.012)
- 423 30. Wiley RH. 2013. Communication as a transfer of information: measurement, mechanism,
424 and meaning. In: *Animal Communication Theory: Information and Influence* (ed. U.
425 Stegmann). Cambridge, UK: Cambridge University Press. 2013. Pp. 113-129.
- 426 31. Elwen S, Meÿer MA, Best PB, Kotze PGH, Thornton M, Swanson S. Range and movements
427 of female Heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-
428 linked telemetry. *J. Mammal.* 2006. **87**: 866-77. (doi:10.1644/05-MAMM-A-307R2.1)
- 429 32. Behrmann CA. Occurrence and group dynamics of Heaviside's dolphins (*Cephalorhynchus*
430 *heavisidii*) in Table Bay, Western Cape, South Africa. MSc Thesis. University of
431 Pretoria, Pretoria, South Africa. 2011.
- 432 33. Morisaka T, Karczmarski L, Akamatsu T, Sakai M, Dawson S, Thornton M. Echolocation
433 signals of Heaviside's dolphins (*Cephalorhynchus heavisidii*). *J. Acoust. Soc. Am.* 2011.
434 **129**: 449-57. (doi:10.1121/1.3519401)
- 435 34. Griffin DR, Webster FA, Michael CR. The echolocation of flying insects by bats. *Anim.*
436 *Behav.* 1960. **8**: 141-54. (doi:10.1016/0003-3472(60)90022-1)
- 437 35. Miller LA, Pristed J, Møshl B, Surlykke A. The click-sounds of narwhals (*Monodon*
438 *monoceros*) in Inglefield Bay, Northwest Greenland. *Mar. Mamm. Sci.* 1995. **11**: 491-
439 502. (doi:10.1111/j.1748-7692.1995.tb00672.x)

- 440 36. Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L, Shearer J, Sveegaard S, et al.
441 Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic
442 disturbance. *Curr. Biol.* 2016. **26**: 1441-6. (doi:10.1016/j.cub.2016.03.069)
- 443 37. Lammers MO, Au WWL, Aubauer R, Nachtigall PE. A comparative analysis of the pulsed
444 emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). In:
445 *Echolocation in Bats and Dolphins* (eds. Thomas JA, Moss CF, Vater M). Chicago,
446 Illinois: The University of Chicago Press. 2004. p. 414-9.
- 447 38. Blomqvist C, Amundin M. High-frequency burst-pulse sounds in agonistic/aggressive
448 interactions in bottlenose dolphins, *Tursiops truncatus*. In: *Echolocation in Bats and*
449 *Dolphins* (eds. Thomas JA, Moss CF, Vater M). Chicago, Illinois: The University of
450 Chicago Press. 2004. p. 425-31.
- 451 39. Madsen PT, Wahlberg M. Recording and quantification of ultrasonic echolocation clicks
452 from free-ranging toothed whales. *Deep Sea Res. Part 1 Oceanogr. Res. Pap.* 2007. **54**:
453 1421-44. (doi:10.1016/j.dsr.2007.04.020)
- 454 40. Jensen FH, Rocco A, Mansur RM, Smith BD, Janik VM, Madsen PT. Clicking in shallow
455 rivers: short-range echolocation of Irrawaddy and Ganges river dolphins in a shallow,
456 acoustically complex habitat. *PLOS ONE*. 2013. **8**: e59284.
457 (doi:10.1371/journal.pone.0059284)
- 458 41. Au WWL, Kastelein RA, Rippe T, Schooneman NM. Transmission beam pattern and
459 echolocation signals of a harbor porpoise (*Phocoena phocoena*). *Journal of the*
460 *Acoustical Society of America*. 1999. **106**: 3699-705. (doi:doi.org/10.1121/1.428221)

- 461 42. Madsen PT, Kerr I, Payne R. Source parameter estimates of echolocation clicks from wild
462 pygmy killer whales (*Feresa attenuata*). *J. Acoust. Soc. Am.* 2004. **116**: 1909-12.
463 (doi:10.1121/1.1788726)
- 464 43. Fox J, Weisberg S. *An R Companion to Applied Regression, 2nd Ed.* Thousand Oaks,
465 California: Sage Publications. 2011.
- 466 44. Ogle D. FSA: Fisheries Stock Analysis. R package version 0.8.16. 2017.
- 467 45. Breiman L. Random Forests. *Machine learning*. 2001. **45**: 5-32.
468 (doi:10.1023/A:1010933404324)
- 469 46. Jensen FH, Wahlberg M, Beedholm K, Johnson M, de Soto NA, Madsen PT. Single-click
470 beam patterns suggest dynamic changes to the field of view of echolocating Atlantic
471 spotted dolphins (*Stenella frontalis*) in the wild. *J. Exp. Biol.* 2015. **218**: 1314-24.
472 (doi:10.1242/jeb.116285)
- 473 47. Kastelein RA, Janssen M, Verboom WC, de Haan D. Receiving beam patterns in the
474 horizontal plane of a harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* 2005.
475 **118**: 1172-9. (doi:10.1121/1.1945565)
- 476 48. Sørensen PM, Wisniewska DM, Jensen FH, Johnson M, Teilmann J, Madsen PT. Click
477 communication in wild harbour porpoises (*Phocoena phocoena*). *Sci. Rep-UK*. 2018. **8**:
478 9702. (doi:10.1038/s41598-018-28022-8)
- 479 49. Connor RC, Smolker RA. 'Pop' goes the dolphin: A vocalization male bottlenose dolphins
480 produce during consortships. *Behaviour*. 1996. **133**: 643-62.
- 481 50. Caldwell MC, Haugen RM, Caldwell DK. High-energy sound associated with fright in the
482 dolphin. *Science*. 1962. **138**: 907-8.

- 483 51. Madsen PT, Carder D, Bedholm K, Ridgway S. Porpoise clicks from a sperm whale nose—
484 Convergent evolution of 130 kHz pulses in toothed whale sonars? *Bioacoustics*. 2005. **15**:
485 195-206. (doi:10.1080/09524622.2005.9753547)
- 486 52. Best PB, Meÿer MA, Lockyer C. Killer whales in South African waters- a review of their
487 biology. *Afr. J. Mar. Sci.* 2010. **32**: 171-86. (doi:10.2989/1814232x.2010.501544)
- 488 53. Wahlberg M, Jensen FH, Soto NA, Beedholm K, Bejder L, Oliveira C, et al. Source
489 parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and
490 *Tursiops truncatus*). *J. Acoust. Soc. Am.* 2011. **130**: 2263-74. (doi:10.1121/1.3624822)
- 491 54. Jakobsen L, Ratcliffe JM, Surlykke A. Convergent acoustic field of view in echolocating
492 bats. *Nature*. 2013. **493**: 93-6. (doi:10.1038/nature11664)
- 493 55. Wisniewska DM, Ratcliffe JM, Beedholm K, Christensen CB, Johnson M, Koblitz JC, et al.
494 Range-dependent flexibility in the acoustic field of view of echolocating porpoises
495 (*Phocoena phocoena*). *Elife*. 2015. **4**: e05651. (doi:10.7554/eLife.05651)
- 496 56. Delgado-Garcia L. Acoustic development and behaviour of odontocete calves. PhD thesis.
497 University of Southern Denmark, Odense, Denmark. 2016.
- 498 57. Li S, Wang K, Wang D, Dong S, Akamatsu T. Simultaneous production of low-and high-
499 frequency sounds by neonatal finless porpoises. *J. Acoust. Soc. Am.* 2008. **124**: 716-8.
- 500 58. Reyes Reyes MV, Tossenberger VP, Iñiguez MA, Hildebrand JA, Melcón ML.
501 Communication sounds of Commerson's dolphins (*Cephalorhynchus commersonii*) and
502 contextual use of vocalizations. *Mar. Mamm. Sci.* 2016. **32**: 1219-33.
503 (doi:10.1111/mms.12321)

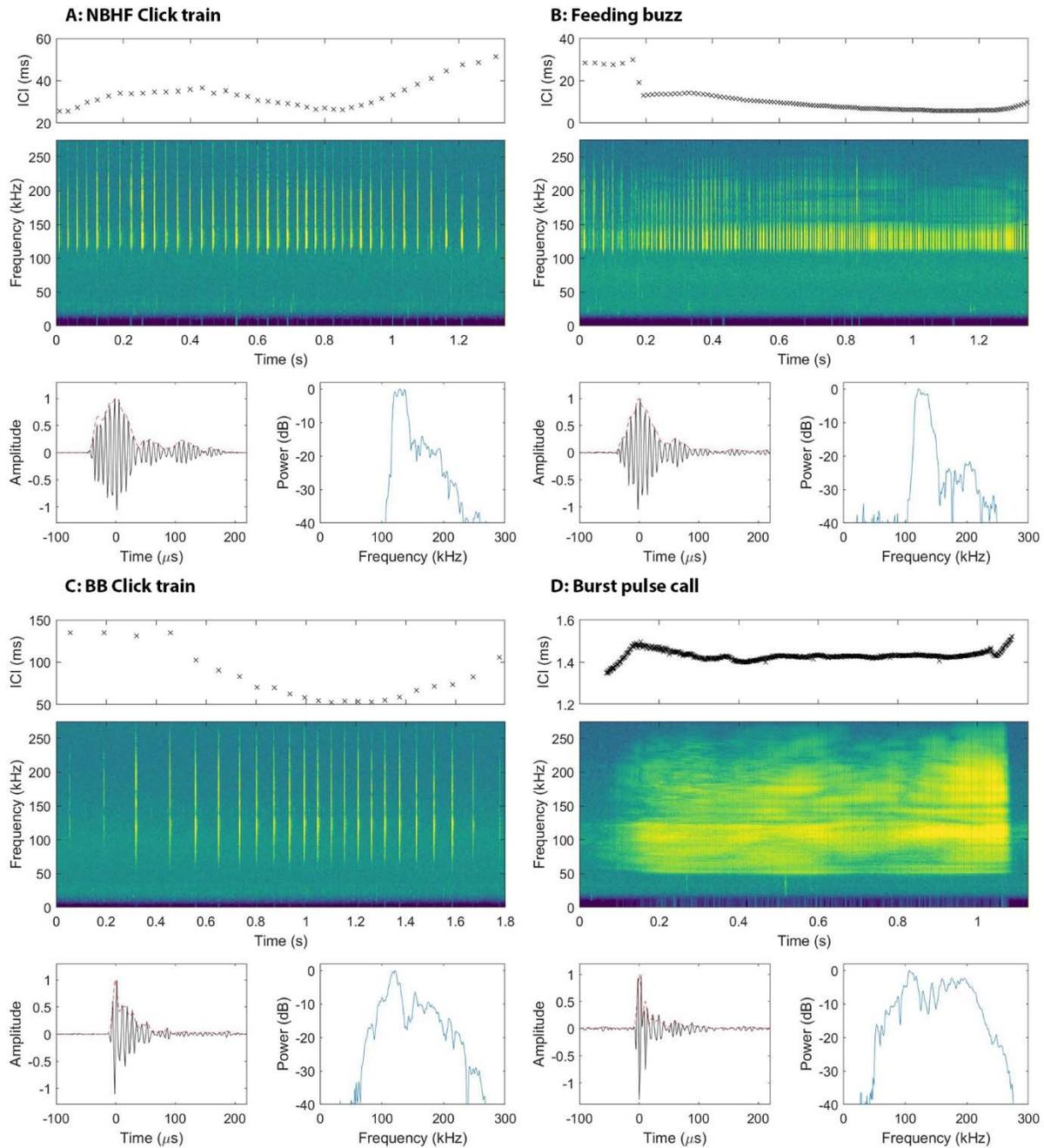
504 Table 1. Biosonar parameters of pulsed signal types produced by Heaviside's dolphins. The median and 5th - 95th percentile values are
 505 reported for each parameter.

Source parameters	NBHF Click Train <i>n</i> = 33		BB Click Train <i>n</i> = 28		Buzz <i>n</i> = 40		Burst-pulse <i>n</i> = 58	
	Median	(5 - 95%)	Median	(5 - 95%)	Median	(5 - 95%)	Median	(5 - 95%)
ICI _{5th} (ms) *	23.5	(14.9 - 41.2)	24.8	(7.8 - 78.9)	6.0	(2.1 - 9.9)	1.5	(1.2 - 1.9)
ICI _{MED} (ms) *	28.9	(22.3 - 55.4)	28.8	(11.7 - 110.1)	7.2	(3.0 - 11.2)	1.6	(1.3 - 2.2)
ICI _{95th} (ms) *	46.1	(29.4 - 104.8)	40.9	(17.4 - 215.8)	10.0	(5.0 - 13.0)	1.7	(1.4 - 3.2)
F _P (kHz) ⁺	127.1	(121.5 - 136.6)	113.6	(78.4 - 141.3)	123.8	(115.8 - 137.3)	112.5	(90.0 - 133.1)
F _C (kHz) ⁺	131.3	(125.3 - 136.9)	110.8	(87.2 - 146.8)	132.4	(124.9 - 143.3)	119.5	(94.4 - 149.0)
BW _{3dB} (kHz) ⁺	15.8	(9.5 - 22.7)	21.4	(4.9 - 79.1)	12.4	(3.3 - 23.7)	16.3	(3.2 - 62.2)
BW _{10dB} (kHz) ⁺	31.5	(22.7 - 69.8)	79.9	(38.1 - 142.5)	37.1	(21.2 - 86.1)	75.4	(31.0 - 137.9)
BW _{RMS} (kHz) ⁺	12.8	(8.2 - 23.2)	27.5	(17.1 - 38.6)	18.3	(10.2 - 31.6)	26.6	(18.1 - 38.7)
Q _{RMS} ⁺	10.2	(5.9 - 15.6)	4.1	(2.8 - 7.1)	7.2	(4.3 - 12.5)	4.4	(3.0 - 6.8)
Dur _{10dB} (μm) ⁺	63.9	(50.6 - 85.1)	37.0	(16.6 - 50.7)	71.1	(42.6 - 129.0)	41.1	(21.1 - 82.3)

* Indicates parameters measured across a click series and ⁺ indicates parameters measured for an individual click
 Abbreviations: ICI_{5th}, ICI_{MED} and ICI_{95th} = 5th, median (50th) and 95th percentile interclick intervals; F_P = peak frequency; F_C =
 centroid frequency; BW_{3dB} = -3 dB bandwidth; BW_{10dB} = -10 dB bandwidth; BW_{RMS} = root mean square bandwidth; Q_{RMS} =
 F_C/BW_{RMS}; Dur_{10dB} = -10 dB click duration

506

507 **Figures**

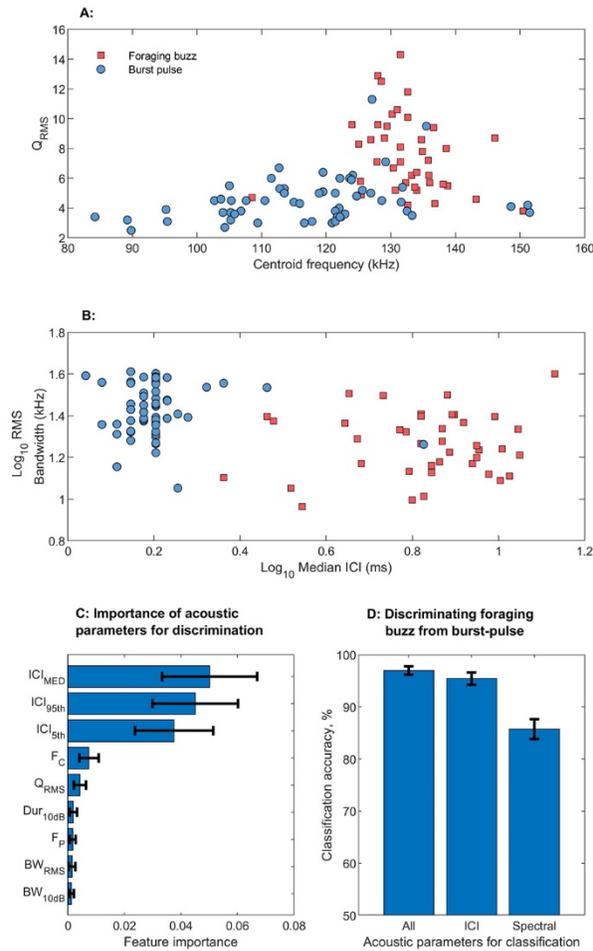


508

509 Figure 1. Examples of Heaviside's dolphin pulsed signal types. A: Narrowband high-frequency
 510 (NBHF) click train, B: Feeding buzz, C: Broadband (BB) click train, and D: Burst-pulse call. For
 511 each signal, the top panel represents the corresponding ICIs of the pulsed signal. Middle panel:

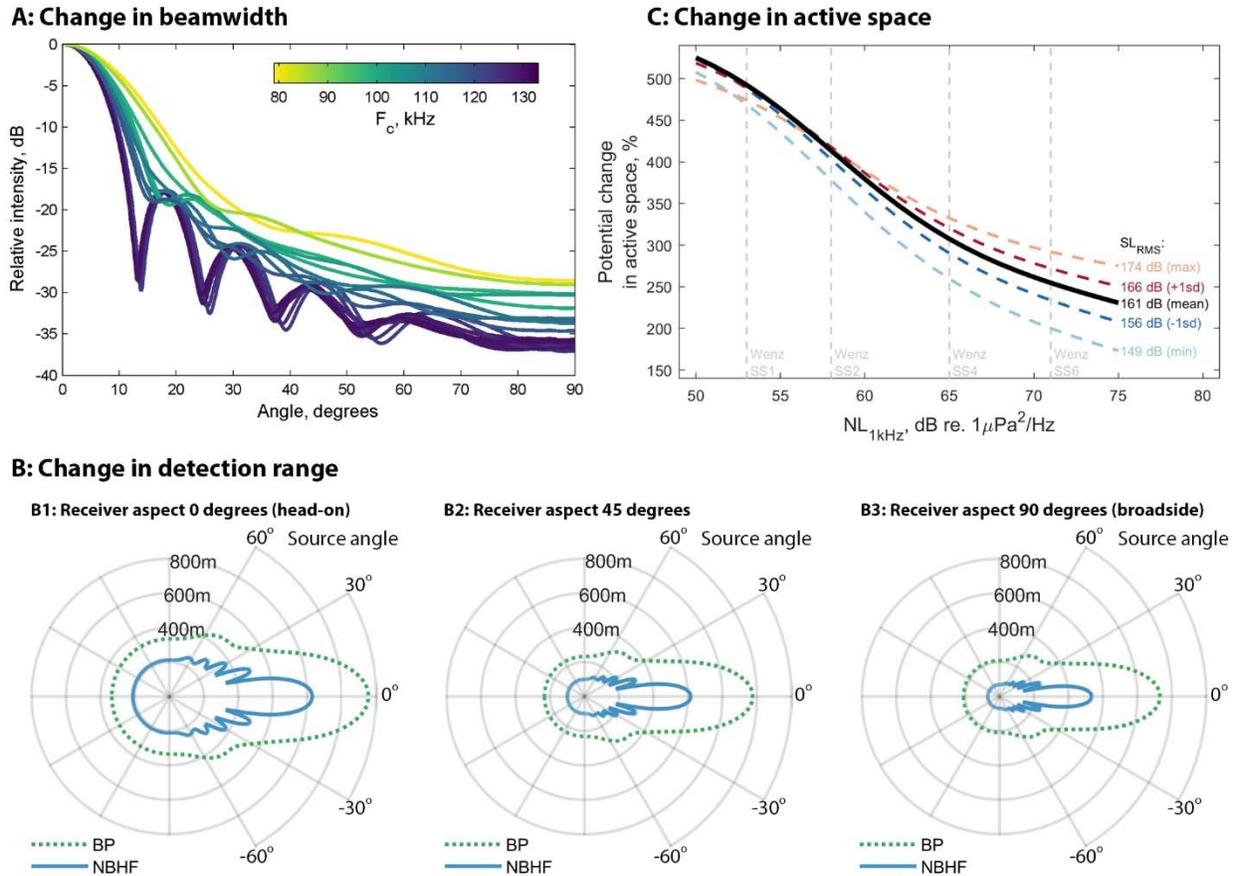
512 spectrogram of the signal (512-pt. FFT, Hamming window, 50% overlap). Bottom left panel:
513 normalised waveform (solid line) and envelope (dashed line) of a single click extracted from the
514 pulsed signal shown in the middle panel (512-pt. rectangular window). Bottom right panel:
515 normalised power spectrum of the extracted click (512-pt. rectangular window, 576 kHz
516 sampling rate).

517



518

519 Figure 2. Signal parameters and discrimination of buzz and burst-pulse signal types. A: Q-ratio
 520 (centroid frequency / RMS bandwidth) as a function of centroid frequency. B: Log-transformed
 521 RMS bandwidth as a function of log-transformed median ICI. C: Relative feature importance of
 522 acoustic signal parameters for classification accuracy. D: Random Forest classification accuracy
 523 following 3 scenarios: discrimination using all signal parameters (All); discrimination using
 524 interclick intervals (ICI); or discrimination using spectral and temporal click parameters
 525 (Spectral). For plots C and D, values are reported as mean (\pm s.d.) for 100 independently trained
 526 Random Forest models. Both feeding buzzes and burst-pulse calls can be accurately classified by
 527 interclick intervals without including frequency, bandwidth, or other individual click parameters.



528

529 Figure 3. Switching to lower-frequency burst-pulse signals increases beamwidth and active
 530 space. A: Transmission beam modelled for 10 standard NBHF clicks and 9 burst-pulse clicks of
 531 varying frequency using a circular piston model. B: Detection range modelled for a typical
 532 NBHF signal (blue solid line) and a lower-frequency (80 kHz) burst-pulse signal (green dashed
 533 line) under Wenz Sea State (SS) 2 noise conditions and with 161 dB RMS source level, with
 534 receivers oriented: toward the source (B1), at a 45° angle to the source (B2), or at a 90° angle to
 535 the source (B3). C: Relative active space for burst-pulse signals compared to the active space of
 536 NBHF signals. Note that while detection range will depend on specific model parameters, the
 537 qualitative relationship between the detection range of NBHF and burst-pulse signals is
 538 consistent under a wide range of noise levels (including Wenz SS1 to Wenz SS6 wind-generated

539 noise, with thermal noise constant) and source levels (covering full range of source levels
540 measured for Heaviside's dolphins in [33]).