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3 **Single-click beam patterns suggest dynamic changes to the field of**
4 **view of echolocating Atlantic spotted dolphins (*Stenella frontalis*) in**
5 **the wild**

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28 **Short title:** *Biosonar field of view*

30

Abstract

31 Echolocating animals exercise an extensive control over the spectral and temporal properties of
32 their biosonar signals to facilitate perception of their actively generated auditory scene when
33 homing in on prey. The intensity and directionality of the biosonar beam defines the field of
34 view of echolocating animals by affecting the acoustic detection range and angular coverage.
35 However, the spatial relationship between an echolocating predator and its prey changes rapidly,
36 resulting in different biosonar requirements throughout prey pursuit and capture. Here we
37 measured single click beam patterns using a parametric fit procedure to test whether free-ranging
38 Atlantic spotted dolphins (*Stenella frontalis*) modify their biosonar beamwidth. We recorded
39 echolocation clicks using a linear array of receivers and estimated the beamwidth of individual
40 clicks using a parametric spectral fit, cross-validated with well-established composite beam
41 pattern estimates. The dolphins apparently increased the biosonar beamwidth, to a large degree
42 without changing the signal frequency, when they approached the recording array. This is
43 comparable to bats that also expand their field of view during prey capture, but achieve this by
44 decreasing biosonar frequency. This behaviour may serve to decrease the risk that rapid escape
45 movements of prey take them outside the biosonar beam of the predator. It is likely that shared
46 sensory requirements have resulted in bats and toothed whales expanding their acoustic field of
47 view at close range to increase the likelihood of successfully acquiring prey using echolocation,
48 representing a case of convergent evolution of echolocation behaviour between these two taxa.

49

Keywords:

51 Echolocation, directionality, field of view, perception, dolphin, prey capture

52

53 **Introduction**

54 Echolocation has evolved in species as diverse as cave birds, microchiropteran bats, and toothed
55 whales (Griffin, 1958; Schevill and McBride, 1956). In contrast to other sensory modalities such
56 as vision or olfaction, echolocation depends on the production of a signal that travels through the
57 environment and is reflected by objects, resulting in returning echoes that are subsequently
58 detected and processed by the echolocating animal (Griffin, 1958). The acoustic field of view of
59 echolocating predators is defined as the area ahead of the predator that is ensonified sufficiently
60 to produce audible echoes (Jakobsen and Surlykke, 2010) and is given by the angular coverage,
61 termed the beamwidth, and the intensity or range of the sonar. The beamwidth and intensity of
62 emitted signals depend on their spectral and temporal properties and on the acoustic behaviour of
63 the echolocating animal (Moss and Surlykke, 2001). There is increasing evidence that bats and
64 toothed whales exhibit significant control over their biosonar (Jakobsen and Surlykke, 2010;
65 Johnson et al., 2008; Moore et al., 2008; Wisniewska et al., 2012) and it is likely that they
66 actively control the perception of their surroundings through changes in biosonar signals and
67 biosonar field of view (Moss et al., 2011).

68
69 Biosonar signals are characterised by signal parameters that include source level, duration,
70 centroid frequency, bandwidth, and three-dimensional beam pattern. The source level and beam
71 pattern are of prime importance as they define the functional range and spatial coverage of the
72 biosonar system (Madsen et al., 2007; Urick, 1983). The source level (SL, in dB re 1 μ Pa @ 1 m
73 for underwater applications) is the sound pressure level measured on the acoustic axis of the
74 biosonar beam at a reference distance of 1 meter from the source (Urick, 1983). The directivity
75 index (DI, in dB) is the difference between the source level of the source in question and the
76 source level of a hypothetical omnidirectional transducer radiating the same acoustic power
77 (Urick, 1983). As the biosonar intensity drops off with increasing off-axis angle, the half-power
78 beamwidth is defined as the angle at which the source level intensity has decreased to half (-3
79 dB) of the on-axis intensity. Whereas the directivity index is important when discussing sound
80 production efficiency, the beamwidth is a more relevant parameter for understanding how the
81 biosonar system performs in clutter. Focusing the sound energy into a narrow beam restricts the
82 detection of objects to a narrow cone along the axis of the sound beam by increasing their
83 returning echoes and by simultaneously reducing the echoes generated by objects further away

84 from the axis of the biosonar beam. Directional emission of echolocation signals therefore
85 narrows the acoustic field of view of the echolocating animal, facilitating target detection and
86 discrimination within a restricted area and improving long-range biosonar performance through a
87 higher on-axis source level (Madsen and Surlykke, 2013).

88
89 The beamwidth of a biosonar system depends on the dimensions of the sound producing
90 structure and the frequency of the emitted sound so that an increased signal frequency or an
91 enlarged transmitter aperture will result in a narrower biosonar beam (Urlick, 1983). The product
92 of the wave number k and the transducer radius a , given as $ka = (2 \pi / \lambda) * a$ is a useful
93 parameter defining the relationship between the effective transducer aperture and the radiated
94 wavelength λ (Au, 1993) with higher directionality achieved through a higher ka number. This
95 means that animals can increase their biosonar beamwidth by either 1) decreasing the frequency
96 of their outgoing sonar signals, or 2) reducing the effective size of the transmitting aperture (Au,
97 1993).

98
99 The amount of control that echolocating animals have over their biosonar beam is remarkable.
100 Microchiropteran bats producing frequency-modulated echolocation signals reduce call
101 amplitude, frequency content and bandwidth during the foraging buzz (Kalko, 1995). Given the
102 relationship between frequency and directionality, this means that microchiropteran bats modify
103 their biosonar directionality and field of view dynamically during prey pursuit and capture by
104 changing biosonar frequency rather than aperture size (Jakobsen et al., 2012; Jakobsen and
105 Surlykke, 2010). Echolocating delphinids studied so far also demonstrate some control over their
106 biosonar beam. Trained delphinids are capable of changing the source level (Moore and
107 Patterson, 1983), frequency content (Moore and Pawloski, 1990), and directionality (Au et al.,
108 1995) of their biosonar signals, and they control their field of view further by steering the beam
109 direction and by controlling the width of the biosonar beam (Finneran et al., 2014; Moore et al.,
110 2008). Most of these adjustable properties may be linked to changes in biosonar frequency, and it
111 is possible that, like in bats, control over the biosonar field of view is primarily a by-product of
112 frequency control. However, a recent study has suggested that trained harbour porpoises may
113 increase their biosonar beamwidth at close range without concurrent changes in signal frequency
114 (Wisniewska et al., 2012). Whether delphinids modify their beam shape strictly through changes

115 in frequency, as in bats, or may use changes in the size or shape of their sound producing
116 structures to further modify their acoustic field of view remains uncertain, and changes in
117 biosonar beamwidth have yet to be documented from free-ranging animals.

118
119 Here we test whether free-ranging Atlantic spotted dolphins (*Stenella frontalis*) can modify the
120 width of their biosonar beam using a new method capable of estimating the beamwidth of
121 individual clicks from vertical hydrophone array recordings. We demonstrate that echolocating
122 Atlantic spotted dolphins seem to increase their field of view when they approach the recording
123 array, and that a significant part of the beamwidth increase must relate to changes in the
124 functional radiation aperture of the melon. Expanding the biosonar field of view at close range
125 may help prevent rapid prey escape responses from taking the prey out of the acoustic field of
126 view of the approaching predator. Our results suggest that both spectral changes to biosonar
127 clicks and morphological changes to the sound generator may contribute to these biosonar
128 dynamics.

129

130

131

Results

132 We investigated the biosonar field of view using two methods: first, we developed a method for
133 estimating the average (composite) biosonar beam pattern for a series of on-axis echolocation
134 clicks recorded on a one-dimensional array. We then estimated the beamwidth of individual
135 clicks using a parametric fit based on a circular piston model and the amplitude spectra of on-
136 axis clicks recorded across off-axis hydrophones, and we cross-validated these estimates with the
137 composite beamwidth estimate. Finally, we used the parametric spectral fit for estimating the
138 field of view of individual echolocation clicks to show that beamwidth changes as a function of
139 distance from the receiver array, and that these changes are caused in part by changes in
140 frequency, and in part by morphological changes of the sound emitter.

141

1: Composite beam pattern estimation and method validation

142 Test trials with two calibrated transducers emitting directional signals were conducted. During
143 both test trials, the transducer was turned gradually along an axis parallel to the axis of the

144

145 hydrophone array to simulate the click scans of *S. frontalis* and other species of toothed whales
146 that have been recorded with a linear, vertical array (e.g. Madsen et al., 2004).

147
148 To estimate the accuracy of the composite beam pattern, two variants of the same procedure
149 were evaluated. Both variants provided reasonable estimates of the beamwidth (Fig. 1). The
150 traditional error model resulted in negatively biased errors of -19% to -8% beamwidth estimates,
151 whereas the logarithmic error model resulted in smaller errors of -4% to -1% beamwidth
152 estimates (Table 1).

153
154 [INSERT TABLE 1 HERE]

155 [INSERT FIGURE 1 HERE]

156
157 Composite beam pattern estimates were surprisingly robust to low sample sizes. Equivalent
158 piston radius (EPR) confidence intervals were consistently wider during simulations with few
159 on-axis clicks, but the mean EPR was highly stable (Fig. 2). The traditional error model for
160 fitting the piston yielded consistently higher EPR estimates (narrower beamwidth) compared to
161 the logarithmic error model (Table 1, Fig. 2). However, this bias was relatively small, in the
162 order of less than half a degree. A similar evaluation of the impact of sample size on data from
163 Atlantic spotted dolphins revealed that EPR estimates recorded with a 6-element hydrophone
164 array were much more robust to low numbers of on-axis clicks, likely because each click was
165 measured across a larger part of the biosonar beam (Fig. 2).

166
167 [INSERT FIGURE 2 HERE]

168 169 **2: Source parameters of *Stenella frontalis* biosonar clicks**

170 A total of 1035 clicks including 28 on-axis clicks were recorded from wild *S. frontalis*. Of these,
171 19 clicks were recorded within 20 m, with the dolphins milling around the array and often
172 moving in to investigate it. The clicks were typical broadband delphinid echolocation signals
173 (Au, 1993) characterised by short duration and high amplitude (Fig. 3a), with a high centroid
174 frequency and broad bandwidth (Fig. 3b) that corresponds well with the short duration and
175 dominant period in the signal waveform.

176

177 [INSERT FIGURE 3 HERE]

178

179 The source parameters of these oceanic dolphins were characterised by mean back-calculated
180 apparent source level (± 1 s.d.) of 209 ± 4.7 dB re. 1 μ Pa peak-peak, corresponding to 200 ± 4.6 dB
181 re. 1 μ Pa rms over a -10 dB envelope time window. The maximum estimated source level was
182 216 dB re. 1 μ Pa peak-peak, corresponding to 207 dB re. 1 μ Pa rms (Table 2). The spectral
183 parameters reflected the broadband nature of these biosonar clicks. Centroid frequency averaged
184 86 ± 9.0 kHz and centralised RMS bandwidth averaged 33 ± 2.7 kHz, resulting in an average
185 quality factor (Q_{rms}) of 2.6 (Table 2).

186

187 [INSERT FIGURE 3 HERE]

188 [INSERT TABLE 2 HERE]

189

190 Using 19 on-axis *S. frontalis* clicks recorded within 20 m, the logarithmic error model estimated
191 an EPR of 5.0 ± 0.20 cm (mean \pm s.e.m.) with confidence intervals of 4.6 to 5.4 cm (Table 1) for a -
192 3 dB beamwidth of 10.3 degrees in the vertical plane (assuming dolphins were swimming dorsal
193 side up, which seemed to be the predominant swimming orientation for animals near the
194 surface), and a composite DI of 25 dB (BCI: 24.4:25.9 dB) (Table 3). The composite vertical
195 beam pattern and confidence intervals estimated using the logarithmic fitting procedure is shown
196 in Figure 4.

197

198 [INSERT FIGURE 4 HERE]

199 [INSERT TABLE 3 HERE]

200

201 Estimates of beamwidth for individual clicks are necessary to understand whether free-ranging
202 animals shape their biosonar beam to different needs. An estimate of the EPR for each click was
203 derived from the parametric spectral fit (Fig. 5). The EPR was 5.1 ± 0.21 (mean \pm s.e.m.), with
204 95% confidence intervals calculated using the percentile bootstrap method of 4.7 to 5.5 cm
205 (Table 3). These results were cross validated with the results from the composite beam pattern
206 estimates, and the two methods corresponded well with each other (Table 3).

207
208 The parametric fit revealed that the directionality of the biosonar clicks produced by *S. frontalis*
209 changed with range from the recording array: The EPR, and hence the beamwidth of the animal,
210 correlated significantly with the range of the animal to the hydrophone array (Linear regression:
211 $R^2=0.31$, $F_{17}=7.7$, $p=0.013$, $EPR = 0.16 R + 3.15$). There was also a significant negative
212 relationship (best fitting slope of $-0.06 F_c$) between EPR and click centroid frequency in kHz
213 (Linear regression: $R^2=0.35$, $F_{17}=9.0$, $p=0.008$) as would be expected from a relationship
214 between directionality and frequency. We therefore calculated the difference between observed
215 half-power beamwidth and expected half-power beamwidth (given constant EPR and measured
216 centroid frequency of each click), and a negative correlation with range persisted (Linear
217 regression: $R^2=0.26$, $F_{17}=6.04$, $p=0.02$).

218
219 [INSERT FIGURE 5 HERE]

220 [INSERT FIGURE 6 HERE]

221

222 Discussion

223 Echolocating animals exercise a remarkable control over the spectral and temporal properties of
224 their biosonar signals (Kalko and Schnitzler, 1993; Moore et al., 2008; Moore and Pawloski,
225 1990). Dynamic changes to the acoustic field of view (Jakobsen et al., 2013; Wisniewska et al.,
226 2012) may help echolocating animals inspect their surroundings or lock on to specific targets,
227 shaping the perception of their surroundings via changes in the acoustic gaze (Moss, 2010; Moss
228 et al., 2011). Here we show that wild Atlantic spotted dolphins seem to increase their vertical
229 biosonar beamwidth by some 50% over a four-fold decrease in range. Expanding the acoustic
230 field of view during approach, and especially during prey capture, is likely important to ensure
231 that prey remains within the acoustic field of view despite rapid prey avoidance reactions at close
232 range.

233

234 **Vertical arrays provide a robust quantification of the composite biosonar beam pattern** 235 **and the beamwidth of individual clicks**

236 Measuring the biosonar field of view of free-ranging echolocating animals is challenging and
237 requires the use of extensive receiver arrays, acoustic localisation algorithms and conservative

238 on-axis criteria (Madsen and Wahlberg, 2007; Surlykke et al., 2009). Composite beam patterns,
239 defined as the mean beam pattern of a large series of clicks (Au et al., 1986), have been
240 measured for multiple toothed whale species using linear vertical hydrophone arrays (Kyhn et
241 al., 2010; Kyhn et al., 2009; Wahlberg et al., 2011a; Wahlberg et al., 2011b), but the errors
242 inherent in this estimation procedure have never been addressed. We show that the composite
243 beam pattern of toothed whales, quantified as the mean EPR and corresponding biosonar
244 beamwidth, can be reliably estimated using small sample sizes of on-axis biosonar signals
245 derived from echolocation scans in the wild (Fig. 1) where clicks that are on-axis in the
246 horizontal plane are identified using strict selection criteria. Using a modified fitting procedure
247 from previous studies, beam pattern estimates using a vertical array are both accurate, with 1-4%
248 mean errors compared to known source transducers (Fig. 1), and relatively precise, with 95%
249 confidence intervals of the composite DI spanning 1.5-2.0 dB for the sample sizes used here
250 (Table 1). Given the narrow sonar beam of most toothed whales, studies of beam pattern from
251 wild animals often result in a small number of on-axis clicks (Jensen et al., 2013; Madsen et al.,
252 2004; Wahlberg et al., 2011b). The beam pattern estimates were surprisingly robust to small
253 sample sizes of on-axis clicks for artificial transducers (Fig. 2A) and quick convergence for
254 delphinid signals (Fig. 2B), such that a small sample size will yield a realistic estimate of the
255 biosonar beamwidth as long as the array covers a substantial part of the biosonar beam.

256
257 While composite beam pattern estimates may facilitate comparisons of biosonar field of view
258 between species or populations, they are insufficient when addressing causes of variation in the
259 biosonar beam within a dataset. To test whether free-ranging toothed whales such as Atlantic
260 spotted dolphins modify their biosonar beam in the field, we derived an instantaneous estimate of
261 the EPR for individual clicks based on predictable spectral changes (Au, 1993) at increasing off-
262 axis angles (Fig. 5). Cross-validation with the composite beam pattern estimates obtained by
263 fitting a circular piston model with the logarithmic error model indicates that the beam pattern
264 for individual clicks reliably quantifies the biosonar field of view in the plane of the array (Table
265 3). Thus, using the methods developed here, it is possible to obtain estimates of the beam-pattern
266 of individual clicks, assuming axial symmetry, with a one-dimensional array, and to start teasing
267 apart the underlying mechanisms for variations in acoustic field of view. However, given the
268 assumptions of axial symmetry and reliance on criteria to identify on-axis clicks in the horizontal

269 plane, two-dimensional planar arrays should be employed where feasible to quantify close-range
270 fine-scale beam patterns.

271

272 **Free-ranging Atlantic spotted dolphins may increase biosonar field of view at close range**

273 The directionality of biosonar signals allows echolocating animals to detect prey at greater range
274 while reducing the impact of clutter from other nearby but off-axis objects. The broadband
275 biosonar clicks produced by Atlantic spotted dolphins are characterised by a composite DI of 25
276 dB (Fig. 4), which is very similar to that reported for other similar-sized marine toothed whales
277 (Au et al., 1978; Koblitz et al., 2012; Kyhn et al., 2010; Rasmussen et al., 2004; Wahlberg et al.,
278 2011a). Echolocating toothed whales ranging in size across three orders of magnitude have all
279 evolved highly directional biosonar signals with DIs of 23-32 dB (Koblitz et al., 2012; Madsen
280 and Surlykke, 2013). It has been hypothesised that high directionality has been an important
281 evolutionary driver for high echolocation frequencies in toothed whales (Koblitz et al., 2012),
282 driven by the need for a long-range biosonar system in the marine environment (Jensen et al.,
283 2013; Madsen and Surlykke, 2013). However, while a long biosonar detection range can be
284 advantageous when searching for prey in the open ocean, it may pose other challenges when
285 capturing prey at close range.

286

287 Two recent studies have measured changes in the echolocation beam shape and field of view as a
288 function of target range, reaching very different conclusions. Kloepper et al. (2012) reported that
289 a false killer whale, trained to discriminate between objects using echolocation, decreased its
290 biosonar beamwidth by 8% when discriminating between targets at 2.5 m as compared to at 7 m.
291 Even though this change seems counter-intuitive (decreasing SNR at long range where task
292 discrimination is more difficult), the small magnitude of change is unlikely to have an impact on
293 sensory performance. In contrast, harbour porpoises trained to approach and discriminate
294 between two targets showed an increase in beamwidth at close range with more profound
295 sensory implications (Wisniewska et al., 2012).

296

297 Here we show that Atlantic spotted dolphins seem to increase their biosonar beamwidth by
298 almost 50% (-3 dB beamwidth from 8 to 12 degrees) when approaching the recording array with
299 a four-fold decrease in range (Fig. 6). The sample size of our study remains very low and it is

300 likely that a simple linear regression is a poor approximation of how animals modify their
301 acoustic gaze, especially when confronted by live, mobile prey rather than stationary recording
302 arrays. Further lab and field experiments should be performed to verify these results and to tease
303 apart the nature of the relationship between beamwidth and range under different environmental
304 conditions and sensory challenges. However, the increased field of view at short range is
305 comparable to the increasing field of view of trained harbour porpoises (Wisniewska et al., 2012)
306 and bottlenose dolphins (Finneran et al., 2014). This indicates that both phocoenids (family
307 *Phocoenidae*, using narrow-band high-frequency signals) and delphinids (family *Delphinidae*,
308 using broadband biosonar signals) employ a dynamic biosonar beam that allows them to expand
309 their field of view when approaching objects or prey animals, and that these sensory adaptations
310 seem to be important for animals in the wild.

311

312 **Conformational changes in the melon and surrounding air sacs may help modify the**
313 **acoustic field of view independently of changes in biosonar frequency**

314 The functional morphology of the structures associated with sound production in toothed whales
315 is highly diverse (Cranford et al., 1996). Echolocation signals in delphinids seem to be produced
316 at the right pair (Madsen et al., 2013b; Madsen et al., 2010) of sound-producing phonic lips
317 (Norris and Harvey, 1972) and are then guided through the dorsal bursae and the fatty tissue of
318 the melon (Cranford et al., 1996). Early studies suggested that the melon functioned as an
319 acoustic lens to concentrate the sound beam (Wood, 1964). It has been suggested that the melon
320 has an acoustic focal point in front of the melon where the acoustic rays converge (Kloepper et
321 al., 2012) but this hypothesis does not take into account that the sound source itself is placed
322 very close to the melon (Cranford et al., 1996). Finite element models based on computed
323 tomography scans of delphinids (Cranford et al., 2013) instead shows that the melon serves as an
324 acoustic collimator. Indeed, several sound propagation simulations have revealed how the skull
325 and associated air sacs provide the structural basis for the frequency-dependent directionality of
326 toothed whale biosonar beams and simultaneously show that the melon may subsequently
327 modify the shape of the biosonar beam (Aroyan et al., 1992; Cranford et al., 2013). While part of
328 the change in beamwidth reported in our study could be explained by the effect of biosonar
329 frequency, variation in biosonar frequency was limited (Table 2, Figure 6) and changes in
330 beamwidth after taking into account the effect of frequency were significant (Fig. 6C). Such

331 changes could include modifying the geometry of the melon or surrounding air sacs, changing
332 the position of the anterior and posterior bursae, or modifying the actuation of the phonic lips.
333 Both the melon and surrounding air sacs are controlled by complicated epicranial musculature
334 (Cranford et al., 1996; Huggenberger et al., 2009) which likely serves to modify directionality to
335 some degree (Cranford et al., 2013). Similarly, the change in beamwidth that has been observed
336 in the terminal part of prey capture in harbour porpoises also occurred without concurrent
337 spectral changes and has been attributed to conformational changes in the soft structures of the
338 nasal complex (Wisniewska et al., 2012). The extent to which the soft tissue structures in the
339 odontocete forehead may serve to modify directionality defines how much echolocating animals
340 are able to influence their sensory volume. The increase in beamwidth for Atlantic spotted
341 dolphins exceeds 50% (Fig. 6) over a four-fold decrease in range, but the ranges tested do not
342 include the very close target distances that are attained during prey capture attempts, suggesting
343 that greater beamwidth variation is possible. In fact, trained porpoises readily change their
344 beamwidth when investigating an aluminium sphere by 50-100%, and when capturing fish by up
345 to 200% (Wisniewska et al. submitted), demonstrating that the control exercised over their
346 acoustic gaze is quite extensive and may vary significantly depending on the task.

347

348

349 **An adaptable acoustic field of view may allow for long-range prey detection while**
350 **facilitating prey capture at close range**

351 Marine delphinids have likely evolved a highly directional biosonar beam to increase the on-axis
352 source level and thus detection range of possible prey items in the open ocean (Koblitz et al.,
353 2012; Madsen and Surlykke, 2013) and only certain species of freshwater dolphins living in
354 shallow river systems find prey using a short-range, broader biosonar beam (Jensen et al., 2013).
355 Given the high biosonar update rate (typically 1-100 Hz) compared to swim speed (1-5 m/s), it is
356 likely more efficient for an echolocating toothed whale to scan a narrow beam gradually through
357 an environment than it is to swim a greater distance with a shorter but wider biosonar.
358 Blainville's beaked whales depend on significant head-scanning movements of up to ± 10 degrees
359 at rates of some 4 degrees per second when searching for prey patches in the deep ocean
360 (Madsen et al., 2013a; Shaffer et al., 2013), demonstrating how a narrow beam can be
361 sequentially scanned through the environment to search a greater volume of water. However, a

362 narrow beam can be a significant disadvantage when approaching and capturing prey items since
363 rapid escape behaviours at close range might take the prey outside of the acoustic field of view
364 of the approaching predator. Dynamic gaze adjustments, in contrast to a static biosonar beam,
365 allow the approaching predator to increase the width of its field of view during this terminal
366 capture phase, thereby decreasing the likelihood of prey escaping outside the biosonar beam. It is
367 striking that wild delphinids may have comparable gaze adjustment behaviours to trained
368 harbour porpoises (Wisniewska et al., 2012) and echolocating vespertilionid and phyllostomid
369 bats (Brinkløv et al., 2011; Jakobsen and Surlykke, 2010) that all increase their field of view
370 when approaching objects or prey animals. It is likely that shared eco-sensory requirements have
371 led to similar biosonar behaviour in bats and toothed whales to increase the likelihood of
372 successfully acquiring active prey using echolocation, supporting the case of convergent
373 evolution of echolocation behaviour between these highly unrelated lineages.

374

375 **Conclusion**

376 Free-ranging Atlantic spotted dolphins seem to increase their beamwidth independently of
377 centroid frequency when approaching and investigating a recording array. This demonstrates that
378 wild delphinids are capable of adjusting their outgoing sonar beam independently of frequency,
379 likely using conformational changes of the soft tissue structures in the melon. Bats also expand
380 their field of view when closing in on prey, though by changing frequency rather than aperture.
381 An adaptable biosonar beam offers the benefits of long-range target detection with a narrow
382 beam, while enhancing the capacity for tracking and capturing agile prey by increasing field of
383 view at close range.

384

385

385 **Materials and methods**

386

387 **1: Composite beam pattern estimation**

388 **Location:** Ground-truth experiments were conducted at the Fjord & Baelte research facility in a
389 net pen with a water depth of 3 m. An array of 4 Reson TC4034 hydrophones (Reson, Slangerup,
390 Denmark) spaced 0.75 m apart was suspended horizontally from a floating pontoon at a depth of
391 1.5 m. Hydrophones were connected through a custom made 4-channel amplification and
392 filtering box (50 dB gain, 10 kHz high-pass filter, 200 kHz low-pass filter) to two synchronised

393 two-channel National Instruments (National Instruments, Hørsholm, Denmark) USB-6251
394 analogue-to-digital converters (sampling rate 500 kHz, 16 bit) writing data to a laptop using
395 custom-written LabView (National Instruments, Hørsholm, Denmark) sound acquisition
396 software.

397

398 **Calibration signals:** Directional signals were transmitted 7.6 m from the axis of the horizontal
399 array and at a depth of 1.5 m. Test signals were generated with an Agilent Technologies 33220A
400 arbitrary waveform generator (Agilent Technologies, Hørsholm, Denmark) and emitted through
401 two circular piston transducers of different diameter. First, a 10-cycle, 50 kHz test signal was
402 transmitted through an 18 cm diameter Reson TC2116 transducer (Reson, Slangerup, Denmark)
403 at a rate of 10 pulses per second. Afterwards, a 10-cycle, 150 kHz signal was transmitted through
404 a 12 cm diameter Reson TC2130 transducer (Reson, Slangerup, Denmark), also at a rate of 10
405 pulses per second. In both cases, the transducer was positioned approximately in front of
406 hydrophone 2 and turned gradually around the axis parallel to the axis of the hydrophone array
407 so that the beam slowly passed back and forth across the array. Although depth constraints in the
408 Fjord&Baelte facility required a horizontally deployed array, the rotation of the transducer around
409 the axis of the array simulated a delphinid scanning its biosonar beam from side to side across a
410 vertically deployed array in the field.

411

412 **Analysis:** Signals were analysed in Adobe Audition 3.0 (Adobe Systems, Inc.) and MatLab 7.0
413 (MathWorks, Natick, MA, USA) using the same metrics and definitions as for delphinid clicks
414 recorded in the field (Madsen and Wahlberg, 2007). The highest click in each scan was assumed
415 to be pointing towards the axis of the array. The received level on each hydrophone was then
416 calculated as a root-mean-square sound pressure level. The angle of incidence was counted as
417 being within the array aperture if the highest received level was found on one of the inner
418 hydrophones, and the click was discarded from further analysis if this was not the case.
419 Subsequently, the source of the click was localised acoustically using time-of-arrival differences
420 (Spiesberger and Fristrup, 1990) following previous studies (Jensen et al., 2009; Kyhn et al.,
421 2010; Kyhn et al., 2009), after which an initial angle of incidence was calculated to each receiver
422 by assuming that the click was focused on the hydrophone with the highest received level. Then,
423 the theoretical on-axis amplitude and exact angle of incidence relative to the on-axis hydrophone

424 was calculated by fitting a second-degree polynomial through the three points of angle and
425 amplitude, corresponding to the hydrophone with the highest received level and its two
426 neighbouring hydrophones. The peak of the resulting polynomial located between the three
427 hydrophones was defined as the on-axis direction and amplitude of the biosonar beam. Finally
428 the angles and received levels for all hydrophones were calculated relative to the on-axis angle
429 and amplitude.

430

431 **Beam pattern estimation:** The sonar system of bats and toothed whales is often modelled, for
432 mathematical simplicity, as a flat, circular piston oscillating in an infinite baffle (Au et al., 1978;
433 Strother and Mogus, 1970). Building on this model, the transmission beam pattern was estimated
434 numerically using a parametric intensity fit: First, a waveform of an on-axis signal was
435 identified; here we used the signal with the highest back-calculated source level and no apparent
436 reflections. This model on-axis signal was convolved with the angle-specific impulse response of
437 a circular piston with an EPR from 0.5 cm up to 10 cm in 0.05 cm steps. For each step, the
438 expected sound intensity relative to peak on-axis sound intensity was estimated for off-axis
439 values up to the maximum angle of incidence recorded in the dataset, resulting in a modelled
440 beam pattern for each piston size. These modelled values of relative sound intensity were
441 compared to the estimated angle of incidence and measured sound intensity recorded across all
442 hydrophones (see Kyhn et al., 2010). Two variants of the fitting procedure were tested: In the
443 traditional error model, the best fitting EPR was estimated as the piston model minimising the
444 sum of squared errors between the modelled sound intensity and the measured sound intensity
445 values for all recorded clicks. This reflects the method used in previous studies of odontocete
446 beam patterns using linear arrays (Kyhn et al., 2010; Kyhn et al., 2013; Kyhn et al., 2009;
447 Wahlberg et al., 2011a; Wahlberg et al., 2011b). In the logarithmic error model, the modelled
448 and measured sound intensity values were transformed to a decibel scale ($10 \log_{10}[I/I_0]$ where I_0
449 is the on-axis intensity) and the best fitting EPR was estimated as the piston model minimising
450 the sum of squared errors between the log-transformed modelled and measured sound intensity
451 values.

452

453 **Beam pattern confidence intervals:** A non-parametric bootstrap method (Efron, 1979) was
454 constructed to evaluate the variation around the beam pattern estimate. Given that on-axis clicks

455 were derived from different scans, on-axis clicks were assumed to be independent. For a sample
456 size containing N on-axis clicks, individual bootstrap replicates were constructed by randomly
457 sampling N clicks with replacement from the original recorded clicks. In this way, each
458 randomly sampled click included the sound levels recorded across all hydrophones, meaning that
459 this resampling technique is similar to the resampling techniques used for bootstrapping
460 regression. The best-fitting EPR was calculated for each bootstrap as described above. Bootstrap
461 95% confidence intervals (Efron, 1981) were calculated as the 2.5 and 97.5 percentile of the
462 bootstrap distribution of equivalent piston radii and were confirmed to be similar to the
463 confidence intervals based on a normal distribution (Efron, 1981; Efron, 1982). Confidence
464 intervals for final estimates were based on 2000 bootstrap iterations to facilitate percentile
465 confidence intervals (Manly, 1997).

466

467 **Effects of sample size:** We evaluated the effects of sample size on beamwidth estimates of
468 original datasets using a similar bootstrap method by randomly selecting n clicks out of the
469 available N clicks (sampled with replacement), where n was varied between 2 on-axis clicks up
470 to the total sample size (N), in steps of two. For each sample size, 500 bootstrap iterations were
471 made, and the average (as well as confidence intervals) of the estimated EPR was evaluated from
472 the resulting distribution as described above.

473

474 **2: Source parameters of *Stenella frontalis* biosonar clicks**

475 **Recording habitat:** Recordings of Atlantic spotted dolphins (*Stenella frontalis*) were obtained in
476 May 2008 off the west coast of Tenerife, Canary Islands, Spain. Equipment was deployed when
477 encountering groups of spotted dolphins. In several cases, dolphins remained close to the boat for
478 half an hour after stopping the vessel, circling and investigating the vessel and recording array
479 throughout the recording period.

480

481 **Recording equipment:** An array of six Reson TC4034 hydrophones fixed in a hollow PVC tube
482 was suspended vertically between a surface buoy and a 2 kg lead weight. Regular holes in the
483 PVC tube allowed it to fill with water when submerged. The acoustic impedance of the PVC is
484 fairly close to the acoustic impedance of seawater to minimise shadowing and reflections. The
485 top two hydrophones were separated by 1.50 m whereas the remaining hydrophones were

486 separated by 0.75 m. The top and bottom hydrophones were located at approximately 2 m and
487 6.5 m depth. A diagram of this recording setup can be found in Kyhn et al. (2010). Hydrophones
488 were connected through two 4-channel amplifier and filtering boxes (1 kHz high-pass, 200 kHz
489 low-pass filter, 40 dB gain) to 3 synchronised 2-channel National Instrument USB-6251
490 multifunction devices with analogue-to-digital converters running at a sampling rate of 500 kHz,
491 16 bit per channel. Data were written through USB to a Dell laptop with custom made LabView
492 data acquisition software. Hydrophones were calibrated before and after the field experiments
493 using a B&K 4228 piston-phone calibrator (Brüel & Kjær, Nærum, Danmark). The frequency
494 response of the recording chain was flat (± 3 dB) from 1-200 kHz, with a clipping level of 194 dB
495 re. 1 μ Pa (peak). Data acquisition was initiated and terminated manually, and files were stored
496 approximately every minute.

497

498 **On-axis criteria:** Sound files were analysed with custom-written scripts in MatLab 7.0. An
499 automated click extractor isolated echolocation clicks from each recording and displayed the
500 click amplitudes as a function of time. Given the one-dimensional nature of the array, a set of on-
501 axis criteria following Jensen et al. (2009) was employed to minimise the amount of clicks
502 recorded away from the centre of the biosonar beam. A click was analysed only if it fulfilled the
503 following criteria: i) The click had the highest received level in a scan, i.e. a short series of clicks
504 closely spaced in time and resembling a delphinid moving its beam across the array (normally
505 with increasing and then decreasing signal amplitude). ii) The highest received level of the click
506 was recorded on one of the 4 central hydrophones. iii) The direct path of the click was stronger
507 than any surface reflections present.

508

509 **Acoustic localisation:** The source of signals fulfilling these on-axis criteria was then
510 acoustically localised using time-of-arrival differences of the same click to the 6 receivers
511 (Wahlberg et al., 2001). The signal recorded on the third hydrophone (near the centre of the
512 array), excluding any surface reflections, was cross-correlated with the signals recorded on the
513 remaining hydrophones. The time-of-arrival differences were then found by taking the time of
514 the cross-correlation peak relative to the cross-correlation peak of the first hydrophone, so that
515 time-of-arrival localisation (Spiesberger and Fristrup, 1990) was made with respect to the top
516 hydrophone. An average sound speed of 1524 m/s within the first 40 m water depth was

517 measured with a CTD (RBR Data Logger model XR-620 CTD, RBR Global, Ontario, Canada).
518 A two-dimensional acoustic localisation (rotationally symmetric around the axis of the array)
519 was obtained as the least-squared solution to the hyperbola equations formed by each time-of-
520 arrival difference and the corresponding difference in receiver coordinates following equations in
521 Madsen and Wahlberg (2007). Signals that could not be localised were dismissed from further
522 analysis. Clicks that were localised more than 50 m away from the array were removed from the
523 analysis following calibration of localisation accuracy (Kyhn et al., 2010) to ensure a localisation
524 error of less than 3 dB in transmission loss (Jensen et al., 2009).

525

526 **Source parameter estimation:** The range from the sound source to each hydrophone was
527 calculated from source coordinates with the Pythagorean equation. The received levels at the
528 hydrophones were calculated as the peak-peak (pp) and root-mean-square (rms) sound pressure
529 levels within a time window given by the -10 dB end points relative to the peak of the amplitude
530 envelope (Au, 1993; Madsen, 2005), which is reasonable given the high signal-to-noise ratio of
531 the on-axis clicks. The duration of clicks was defined as the time interval between -10 dB end
532 points. An energy flux density measure of click amplitude was calculated as the sum of squared
533 sound pressure values within the -10 dB analysis window (Madsen, 2005). The time between the
534 peak of each click and the previous click was defined as the inter-click interval (ICI: Au, 1993).
535 Subsequently, the click amplitude spectrum was calculated as the 3200-points discrete Fourier
536 transform of a 32-point window centred on the peak envelope of each signal. The amplitude
537 spectrum was squared and divided by its peak value to get the normalized power spectrum. The
538 peak frequency, centroid frequency (defined as the frequency separating the power spectrum into
539 two halves of equal energy) and signal bandwidth (centralised RMS bandwidth, -3 dB power and
540 -10 dB power bandwidth) were calculated from this power spectrum, and the quality factor
541 (Q_{rms}) defined as the centroid frequency divided by the centralised RMS bandwidth (Madsen and
542 Wahlberg, 2007). The apparent source level (ASL_{pp}) was defined as the back-calculated sound
543 pressure level 1m from the source at an unknown angle from the acoustic axis (Madsen and
544 Wahlberg, 2007; Møhl et al., 2000) and calculated according to previous studies (e.g. Madsen et
545 al., 2004) by compensating for the transmission loss between source and receiver. Transmission
546 loss was estimated as the sum of spherical spreading ($20 \log_{10}[R]$) and frequency-dependent
547 absorption (αR) over the range R , using a sound absorption coefficient α of 0.02 dB/m at 85 kHz.

548 To quantify the biosonar beam pattern, we then restricted analysis to signals localised closer than
 549 20 m to ensure high localization accuracy (standard deviation of less than 2% of range) (Kyhn et
 550 al., 2010) and we estimated the composite vertical beam pattern as described above.

551
 552 **Single-click beam pattern:** Biosonar clicks exhibit predictable spectral changes when recorded
 553 off the acoustic axis (Au, 1993; Au et al., 2012; Wahlberg et al., 2011b). Here we use these
 554 changes to estimate the instantaneous EPR from individual clicks using a parametric spectral fit
 555 based on a circular piston model. To do this, we extracted the click waveform recorded on all
 556 receivers in a 32-point window centred on the peak of the envelope. The click with the highest
 557 received level was taken as our best measure of the true on-axis click waveform. We estimated
 558 the corrected angle of incidence in the vertical axis using a second-degree polynomial fit as
 559 described above, and then calculated the angle of incidence for each receiver. Then, the expected
 560 click waveform was modelled for all receivers over a range of simulated circular piston apertures
 561 (EPR of 1-10 cm in steps of 0.005 cm). For each piston aperture, the on-axis waveform was
 562 convolved with the angle-specific impulse response of a circular piston (eq. 1) at the angle of
 563 incidence estimated for each receiver, and the modelled amplitude spectrum obtained through a
 564 fast Fourier transform.

565
 566 The angle-specific, far-field impulse response of a circular piston was defined (Beedholm and
 567 Mohl, 2006) as:

$$568 \quad h(\theta, t) = \frac{4}{\pi T} \sin\left(\cos^{-1}\left[\frac{2t}{T}\right]\right), \text{ with } T = \frac{2a}{c} \sin(\theta) \text{ and defined within } |t| < \frac{T}{2} \quad (1)$$

569 Here, c is the sound speed of the medium, a is the piston radius (EPR), and θ is the off-axis angle
 570 of each receiver.

571
 572 As a measure of the goodness-of-fit of each piston size, we calculated the residual sum of
 573 squared error (SSE) between the observed amplitude spectrum and the modelled amplitude
 574 spectrum for each receiver. Finally, the best-fitting EPR was estimated as the piston size
 575 minimising the total SSE across receivers (Fig. 5). When calculating total SSE, only receivers at
 576 angles between 2 and 25 degrees were used to avoid potential frequency-dependent side-lobes,
 577 but this proved to have a negligible effect on the final fit.

578

579 The half-power beamwidth (HPBW) was then approximated for each click following (Zimmer et
580 al., 2005):

$$581 \quad HPBW = \frac{185^\circ}{ka} = \frac{185^\circ}{EPR \times 2 \times \pi \times f_c / c_0} \quad (2)$$

582 Where k is the wave number, f_c is the centroid frequency of the click, and a is the radius of a
583 circular piston, approximated here as EPR.

584

585 The parametric fit procedure assumes that the piston is flat and circular. Systematic deviations
586 from this assumption might therefore confound results. To account for this, we also estimated the
587 instantaneous aperture size from predictable spectral changes in biosonar signals recorded off the
588 acoustic axis at a known angle (Au, 1993). Clicks recorded off the acoustic axis are expected to
589 have interference dips in the power spectrum as a function of off-axis angle (lower frequency for
590 greater angles) and aperture dimensions (lower frequency for larger aperture) (Beedholm and
591 Mohl, 2006; Wahlberg et al., 2011b). To avoid the circular piston assumption, we assumed only
592 that the sound emitter was finite along the horizontal axis. For a signal transmitted from a line
593 array with length given by $2a$ (in meters) recorded at an angle θ (in degrees) off the acoustic axis
594 of the array, negative interference will occur at a frequency where the difference in travel
595 distance between signals from the edge and centre of the array equals half the wavelength of the
596 signal. For each receiver, we calculated the one-sided amplitude spectrum (16 points) and then
597 extracted the frequency of the first spectral notch (a local minimum of -1 dB or greater)
598 occurring after the peak frequency (Suppl. Fig. 1). The equivalent piston radius (EPR) was then
599 calculated using the frequency f_n of the first spectral notch, recorded at an off-axis angle θ
600 (estimated for each hydrophone relative to the peak of the polynomial) in a medium with sound
601 speed c_0 (1524 m s^{-1}) as:

$$602 \quad EPR_{notch} = 0.5 \times c_0 \times f_n^{-1} \times \sin(\theta)^{-1} \quad (3)$$

603 Only clicks with S/N ratio greater than 10 dB and recorded at angles greater than 2 degrees and
604 less than 25 degrees were used for this analysis. For each individual click, the estimated EPR
605 was taken as the average estimate across hydrophones. This approach yielded very similar results
606 (Suppl. Fig. 2) compared to the parametric fit, and results are therefore included only in
607 supplementary materials.

608

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623

624 **Author contributions**

625 FHJ, MW and PTM designed experiments and calibrations. FHJ, KB and MJ developed
626 analytical methods. FHJ, NAS, MJ and PTM acquired funding and conducted fieldwork. FHJ
627 and MW performed method validation experiments. FHJ, MW, KB, NAS, MJ and PTM drafted
628 manuscript.

629

630 **List of abbreviations**

631 SL Source level
632 DI Directivity index
633 EPR Equivalent piston radius
634 ASL_{pp} Apparent source level, peak-peak
635 ASL_{rms} Apparent source level, root-mean-square
636 ASL_{efd} Apparent source level, energy flux density
637 $Dur_{-10\text{ db}}$ -10 dB envelope duration

638	F_c	Centroid frequency
639	BW_{rms}	Root-mean-square bandwidth
640	BW_{-3db}	-3 dB bandwidth
641	BW_{-10db}	-10 dB bandwidth
642	Q_{rms}	Root-mean-square quality factor
643	HPBW	Half-power beamwidth
644	SSE	Sum of squared error
645	BCI	Bootstrap confidence interval
646	CI	Confidence interval

647

648 Figure captions:

649

650 **Fig. 1: Beam pattern can be accurately estimated using a linear array:** Mean beam pattern
651 estimate of a Reson TC2116 transducer emitting a 50-kHz signal (A) and a Reson TC2130
652 transducer emitting a 150 kHz signal (B) as measured with a 4-hydrophone array. The on-axis
653 sound intensity and angle of incidence from the acoustically localised source to each receiver
654 was estimated through a second-degree polynomial fit (see text). The sound intensity relative to
655 the on-axis intensity is plotted against the angle of incidence for each of 4 receivers recording the
656 same click (squares, colour-coded according to click number). A circular piston model with an
657 aperture minimising the RMS error of received sound intensity on a logarithmic decibel scale
658 (Log method) was fitted to data (dark grey) and 95% confidence intervals for the fit were
659 calculated using a bootstrap method with 2000 replicates (dark grey interrupted lines). The
660 known calibration curve of the transducer is overlaid for comparison (light grey). Note the non-
661 Gaussian error distribution.

662

663 **Fig. 2: Beam pattern estimates are robust to low sample size:** Estimated equivalent piston
664 radius (mean \pm 95% bootstrap confidence intervals) as a function of the number of on-axis clicks
665 (ranging from 2 to the total sample size N in increments of 2) included in the piston fitting
666 procedure. Individual clicks recorded on a 4 channel (A) or 6 channel (B) hydrophone array are
667 sampled with replacement from the total population of on-axis clicks (A: N=23, B: N=19) and a
668 piston fitting procedure implemented as described in the text. Means and confidence intervals

669 were calculated using 500 bootstrap replicates. Note that the baseline grey line for *Stenella*
670 *frontalis* dataset is based on the best-fitting piston model using the full sample size and
671 logarithmic error model, not on the actual (and unknown) EPR.

672

673 **Fig. 3: *Stenella frontalis* echolocation clicks:** A: Waveform of the 4 echolocation clicks of
674 highest amplitude. Waveforms (sample rate 500 kHz) are upsampled (x10 low-pass
675 interpolation), phase-aligned and normalised to the largest pressure excursion for easier
676 comparison. B: Individual log-transformed power spectra (black lines) and mean *Stenella*
677 *frontalis* energy distribution (grey dashed line) derived from all on-axis echolocation clicks.
678 Power spectra are constructed using a 320-point fast Fourier transform based on a 32-point (64
679 μ s) window (resulting in x10 sinc interpolation) centered on the peak envelope of each click.
680 Note that the flatness of the mean energy distribution is partly a result of differences in peak
681 frequency between clicks, whereas individual power spectra exhibit much more spectral
682 variation.

683

684 **Fig. 4: Composite vertical beam pattern of *Stenella frontalis*:** Exact angle of incidence was
685 estimated by fitting a second-degree polynomial to data points consisting of the hydrophone
686 recording the highest source level and the two neighbouring hydrophones. A: Apparent source
687 level difference relative to the estimated on-axis source level is shown as a function of angle of
688 incidence (black squares). A piston model (dark grey line) corresponding to an on-axis *Stenella*
689 *frontalis* click convolved by the angle-specific impulse response of a circular piston with an
690 equivalent piston radius of 5.2 cm was fitted to data. 95% confidence intervals of the estimated
691 beam pattern (Grey interrupted lines) were calculated using a bootstrap method with 2000
692 replicates. B: Polar plot of estimated vertical beam pattern and 95% bootstrap confidence
693 intervals.

694

695 **Fig. 5: Equivalent piston radius estimated for an individual biosonar click using a**
696 **parametric fit:** A: Modelled beam pattern for increasing aperture size (solid lines), relative
697 power as a function of absolute angle measured over 6 receivers (red squares), and modelled
698 beam pattern for a 4.57 cm piston (red dashed line). Receiver 3 (shown in subplot B) highlighted.
699 B: Parametric spectral fit: For each receiver, an observed 16-point amplitude spectrum (red

700 squares) is calculated from the signal waveform. Expected amplitude spectra are calculated by
701 convolving the on-axis signal waveform with the angle-specific impulse response of a circular
702 piston (solid lines, colour-coded according to modelled piston size). C: Individual sum of
703 squared errors for each receiver (coloured lines) and total sum of squared error (black, dashed
704 line) for a signal recorded at a range of 6.4 m and with an estimated EPR of 4.57 cm that
705 minimises the total sum of squared errors across channels.

706

707 **Fig. 6: Dynamic changes in biosonar field of view for Atlantic spotted dolphins:** A:
708 Equivalent piston radius (EPR) (filled circles) estimated for each click through a parametric
709 spectral fit (Fig. 5) and shown as a function of range. Black line represents a significant linear
710 least squares regression ($R^2=0.31$, $F_{17}=7.68$, $p=0.013$) and the grey shaded area represents the
711 95% confidence interval of the linear regression. B: The half-power beamwidth (HPBW) as a
712 function of range. C: Frequency-independent change in beamwidth: Observed HPBW divided by
713 the HPBW that would be expected if beamwidth was determined by a constant EPR (the mean
714 EPR estimated by the parametric fit method) and a changing centroid frequency (measured for
715 each click). Black line represents a significant linear least squares regression ($R^2=0.26$, $F_{17}=6.04$,
716 $p=0.02$), and the grey, shaded area represents the 95% confidence interval of the linear
717 regression. Data points are colour-coded according to centroid frequency of on-axis click.

718

719 **Suppl. Fig 1: Implementation of spectral notch estimation of equivalent piston radius**

720 **(EPR):** Solid lines (colour-coded according to estimated angle of incidence) indicate the
721 interpolated (100x) power spectrum derived at each receiver and offset from the on-axis power
722 spectrum by the difference in estimated peak-to-peak source level. Arrows mark the first spectral
723 notch for each channel (notches were estimated from non-interpolated power spectra), with
724 estimated equivalent piston radius calculated from eq. 1. The total mean equivalent piston radius
725 for this click was 4.05 cm.

726

727 **Suppl. Fig. 2: Dynamic changes in biosonar field of view for Atlantic spotted dolphins**
728 **estimated using spectral notch approach:** A: Equivalent piston radius (EPR) (squares)
729 estimated using the spectral notch method (Suppl. Fig. 1) as a function of range. Black line
730 represents a significant linear least squares regression ($R^2=0.44$, $F_{17}=13.2$, $p=0.002$) and the grey

731 shaded area represents the 95% confidence interval of the linear regression. B: The half-power
732 beamwidth (HPBW) as a function of range. C: Observed HPBW divided by the HPBW that
733 would be expected if beamwidth was determined by a constant EPR (the mean EPR estimated by
734 spectral notch method) and a changing centroid frequency (measured for each click). Black line
735 represents a significant linear least squares regression ($R^2=0.49$, $F_{17}=16.3$, $p=0.0008$), and the
736 grey, shaded area represents the 95% confidence interval of the linear regression.

737

738 **Suppl. Fig. 3: Adjustment of apparent source level and interclick interval with range for**
739 **on-axis Atlantic spotted dolphin biosonar clicks:** A: Apparent source level as a function of
740 range (squares), with a log-linear fit to range overlaid (grey line and confidence intervals). B:
741 Interclick intervals as a function of range (squares). Grey line shows the two-way travel time
742 between the dolphin and the array.

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913 **Tables**914 **Table 1: Validation of composite beamwidth estimation**

915 Values given as means \pm s.e.m. (calculated as the standard deviation of the bootstrap distribution
 916 of means) and with 95% bootstrap percentile confidence intervals in brackets. Third column
 917 represents known values from calibration transducers.

	Traditional error model	Logarithmic error model	Correct
919			
920			
921	TC2116 Transducer (50 kHz)	N=23	N=23
922	EPR (cm)	6.95 \pm 0.14	6.47 \pm 0.11
923		[6.63 : 7.15]	[6.28 : 6.73]
924	-3 dB Beamwidth (degrees)	12.7	13.7
925		[12.4 : 13.4]	[13.2 : 14.1]
926			
927	TC2130 Transducer (150 kHz)	N=12	N=12
928	EPR (cm)	3.11 \pm 0.16	2.60 \pm 0.09
929		[2.75 : 3.29]	[2.50 : 2.79]
930	-3 dB Beamwidth (degrees)	9.86	11.8
931		[9.29 : 11.1]	[11.0 : 12.3]
932			

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936 **Table 2: Source properties of echolocation clicks from Atlantic (*Stenella frontalis*) and**
 937 **Pantropical (*Stenella attenuata*) spotted dolphins**

939		Tenerife, Canary Islands	Bahamas	Oahu, Hawaii
940		(this study)	(Au and Herzing, 2003)	(Schotten et al.,
941		2004)		
942	Species	<i>S. frontalis</i>	<i>S. frontalis</i>	<i>S. attenuata</i>
943	Array type	6-hydrophone vertical	4-hydrophone star	4-hydrophone star
944	ASL _{pp} (dB re. 1 μ Pa)	208.8 \pm 4.7 (max 216)	(max 223)	212 \pm 5
945	ASL _{rms} (dB re. 1 μ Pa)	199.6 \pm 4.6 (max 207)	-	-
946	ASL _{efd} (dB re. 1 μ Pa ² /Hz)	150.6 \pm 4.3 (max 158)	-	150 \pm 4
947	Dur _{.10 dB} (μ s)	12.8 \pm 2.6	-	43 \pm 15
948	F _p (kHz)	78.3 \pm 31.0	-	69.4 \pm 31.3
949	F _c (kHz)	85.6 \pm 9.0	67.2 \pm 25.5	83.4 \pm 16.8
950	BW _{rms} (kHz)	33.1 \pm 2.7	36.4 \pm 11.0	38.7 \pm 6.7
951	BW _{-3 dB} (kHz)	91.1 \pm 18.9	-	79.8 \pm 35.9
952	BW _{-10 dB} (kHz)	128.3 \pm 8.5	-	-
953	Q _{rms}	2.6 \pm 0.2	-	-
954	N	28	1277	314

956 *All values in mean \pm s.d.*

957

958 **Table 3: Directional properties of Atlantic spotted dolphin (*Stenella frontalis*) echolocation**
 959 **clicks**

961 Method	961 Linear Error	961 Logarithmic Error	961 Parametric fit
	962 (Composite)	962 (Composite)	962 (Instantaneous)
963 EPR (cm)	963 5.18 ± 0.23	963 4.99 ± 0.21	963 5.00 ± 0.27
964	964 [4.72 : 5.62]	964 [4.63 : 5.42]	964 [4.51 : 5.56]
965 -3 dB beamwidth (degrees)	965 9.86	965 10.28	
966	966 [9.10 : 10.88]	966 [9.43 : 11.09]	
967 -10 dB beamwidth (degrees)	967 22.05	967 22.95	
968	968 [20.30 : 24.30]	968 [21.07 : 24.78]	
969 DI (dB)	969 25.5	969 25.1	
970	970 [24.6 : 26.2]	970 [24.4 : 25.9]	
971 N	971 19	971 19	971 19

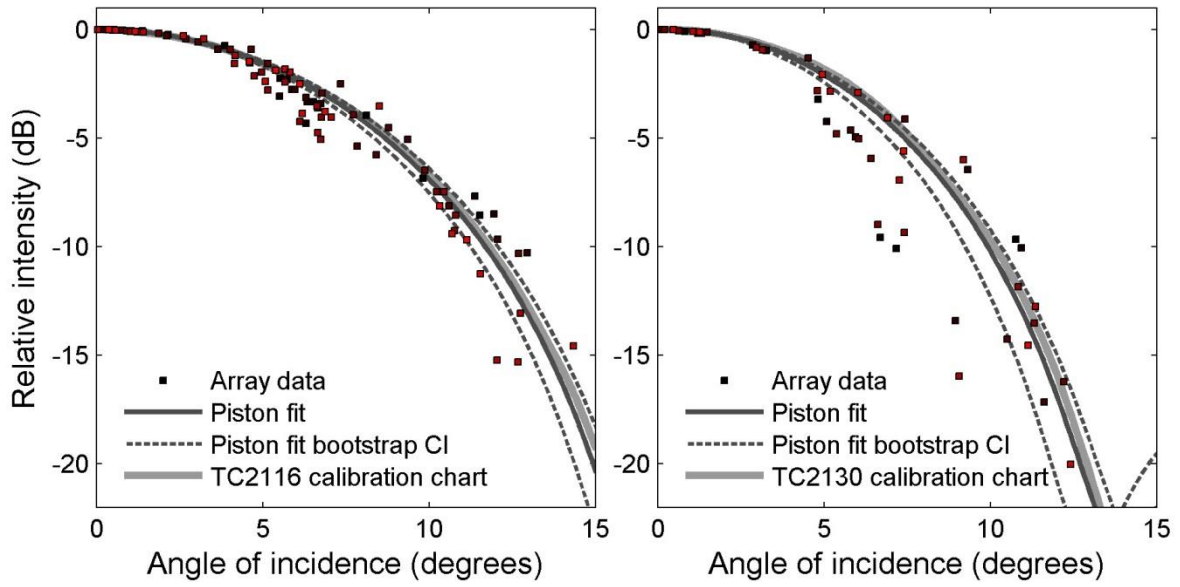
972 *All values given as mean±s.e.m. and with 95% bootstrap confidence intervals in brackets.*

973 *Symmetrical -3 dB and -10 dB beamwidth estimated from the beam pattern of the best fitting*
 974 *circular piston model transmitting an on-axis *Stenella frontalis* biosonar click.*

975 *Composite directionality index (DI) calculated as $20 \text{ Log}_{10}(ka)$ (Madsen and Wahlberg, 2007).*

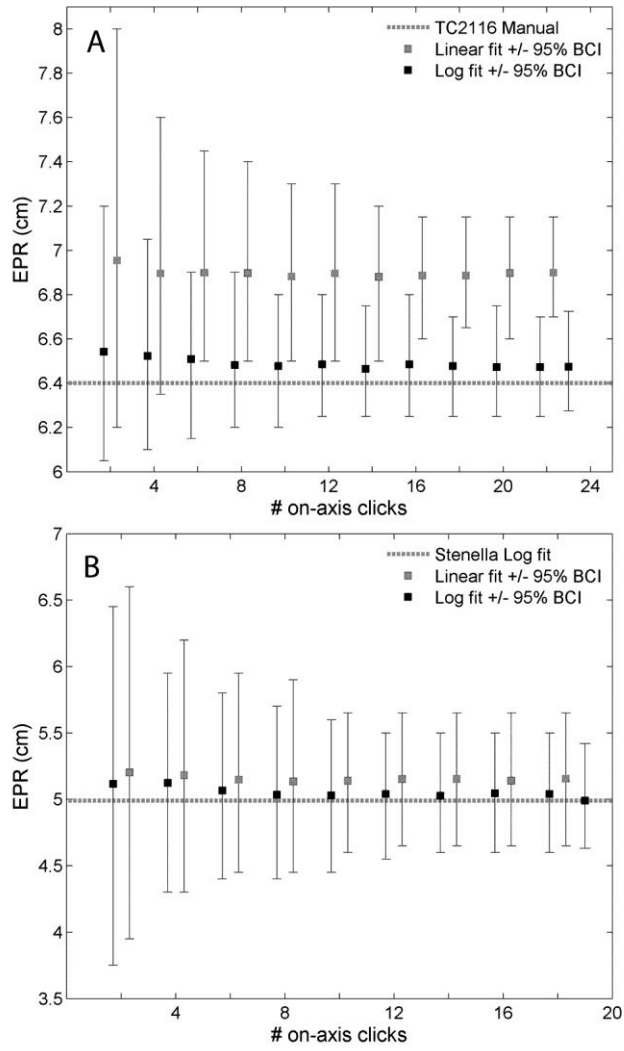
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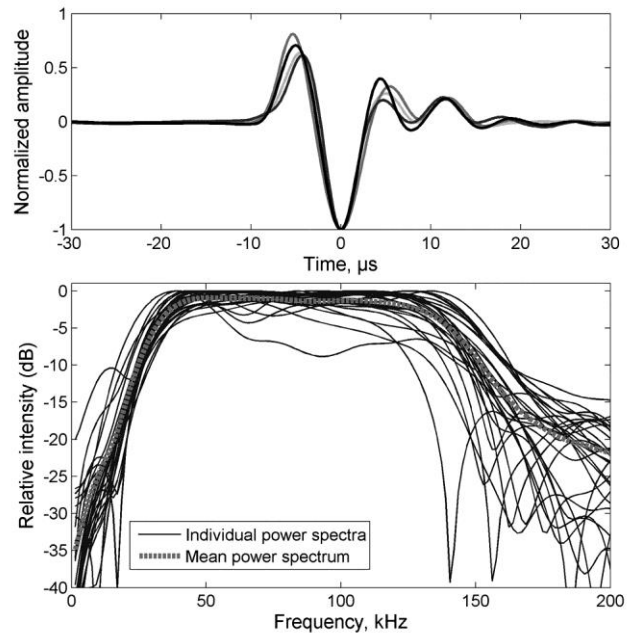
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Figure 1



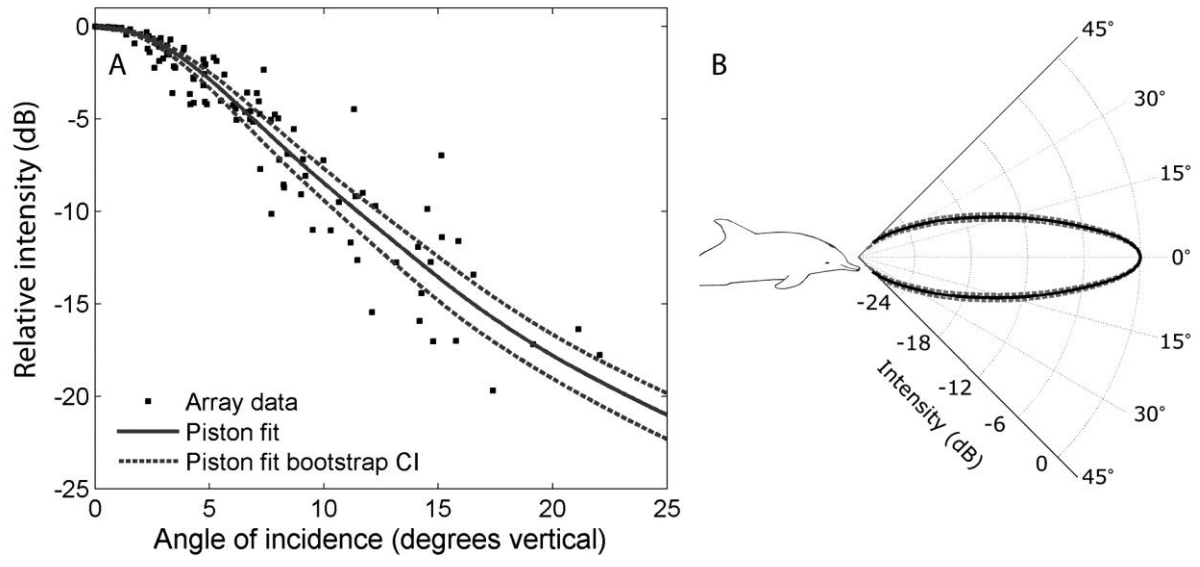
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Figure 2



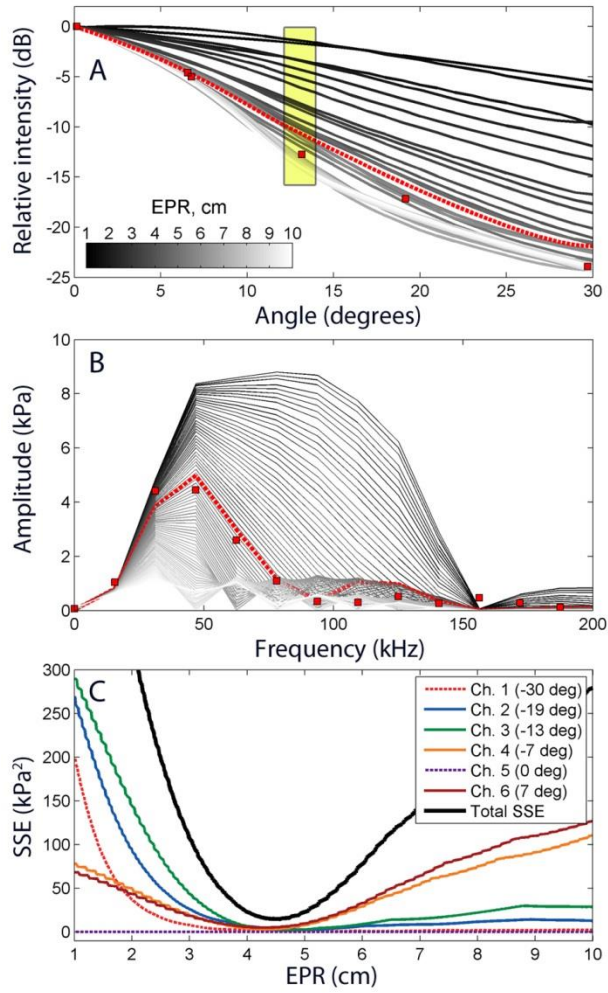
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Figure 3



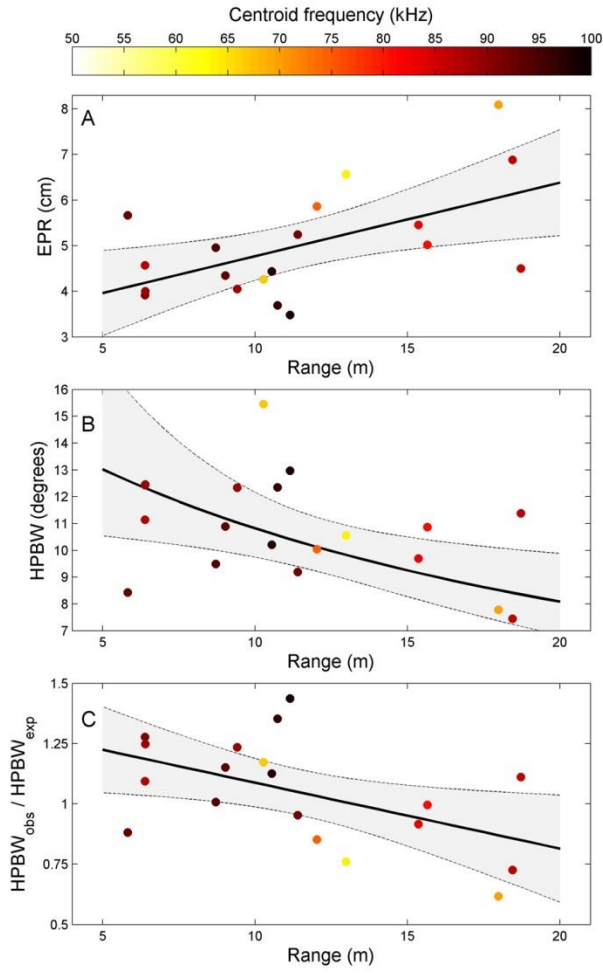
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Figure 4



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Figure 5



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Figure 6