

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29

**Ultra-high foraging rates of harbour porpoises make them vulnerable to anthropogenic disturbance**

Danuta Maria Wisniewska<sup>1,2</sup>, Mark Johnson<sup>3</sup>, Jonas Teilmann<sup>2</sup>, Laia Rojano Doñate<sup>1</sup>, Jeanne Shearer<sup>3</sup>,  
Signe Sveegaard<sup>2</sup>, Lee A. Miller<sup>4</sup>, Ursula Siebert<sup>5</sup> and Peter Teglberg Madsen<sup>1,6</sup>

<sup>1</sup>Zoophysiology, Department of Bioscience, Aarhus University, Building 1131, C. F. Moellers Alle 3, DK-8000 Aarhus C, Denmark.

<sup>2</sup>Marine Mammal Research, Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark.

<sup>3</sup>Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews KY16 8LB, Scotland.

<sup>4</sup>Sound and Behaviour Group, Institute of Biology, University of Southern Denmark, Campusvej 55, DK-5230 Odense M, Denmark.

<sup>5</sup>Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Werftstrasse 6, 25761, Buesum, Germany

<sup>6</sup>Murdoch University Cetacean Research Unit, School of Veterinary and Life Sciences, Murdoch University, Perth, WA, 6150, Australia

\*Corresponding author: [danuta.wisniewska@bios.au.dk](mailto:danuta.wisniewska@bios.au.dk), +45 26644639

30 **Summary**

31 The question of how individuals acquire and allocate resources to maximize fitness is central in  
32 evolutionary ecology. Basic information on prey selection, search effort and capture rates are critical  
33 for understanding a predator's role in its ecosystem and for predicting its response to natural and  
34 anthropogenic disturbance. Yet for most marine species, foraging interactions cannot be observed  
35 directly. The high costs of thermoregulation in water requires that small marine mammals have  
36 elevated energy intakes compared to similar-sized terrestrial mammals [1]. The combination of high  
37 food requirements and their position at the apex of most marine food webs may make small marine  
38 mammals particularly vulnerable to changes within the ecosystem [2–4], but the lack of detailed  
39 information about their foraging behaviour often precludes an informed conservation effort. Here, we  
40 use high resolution movement and prey echo recording tags on five wild harbour porpoises to  
41 examine foraging interactions in one of the most metabolically challenged cetacean species. We report  
42 that porpoises forage nearly continuously day and night, attempting to capture up to 550 small (3-10  
43 cm) fish prey per hour with a remarkable prey capture success rate of >90%. Porpoises therefore  
44 target fish that are smaller than those of commercial interest, but must forage almost continually to  
45 meet their metabolic demands with such small prey, leaving little margin for compensation. Thus, for  
46 these “aquatic shrews”, even a moderate level of anthropogenic disturbance in the busy shallow  
47 waters they share with humans may have severe fitness consequences at individual and population  
48 levels.

49

50

51

52

53

54

55

56

57

58

59 **Results**

60 The harbour porpoise (*Phocoena phocoena*), the smallest cetacean inhabiting cold temperate  
61 waters of the Northern Hemisphere, has been described as “living life in the fast lane” [5]. Compared to  
62 other toothed whales, it matures at an earlier age, reproduces more frequently and has a shorter life  
63 span [5]. Its small size in cold water gives rise to a high relative heat loss, and limits the amount of  
64 energy it can store with respect to its metabolic rate, making it sensitive to starvation [6,7]. Harbour  
65 porpoises are therefore hypothesized to feed at high rates year-round, capturing up to 10% of their  
66 body weight in fish per day [6,7] to support their metabolic requirements.

67 Porpoises, like other toothed whales, use echolocation to find, track and intercept individual  
68 prey, producing distinctive low-level, rapid click sequences, termed buzzes, when closing on prey  
69 [8,9]. The first deployments of sound detecting tags on harbour porpoises assumed a stereotyped  
70 acoustic behaviour during prey pursuits [9], and recorded low rates of possible feeding events,  
71 between 5 and 62 per day [10]. Although, the settings of the deployed tags likely led to an  
72 underestimation of the number of possible feeding events, the results suggest that these predators  
73 must target relatively large, energy-rich prey with high success rates to meet their predicted metabolic  
74 demands. This is inconsistent with the stomach contents of bycaught and stranded individuals [11]  
75 which suggest a main food source comprising large numbers of relatively small fish prey, primarily  
76 <25 cm and frequently <5cm in length. If porpoises do target large fish, the extent of their dietary  
77 overlap with commercial fisheries may be greater than hitherto assumed. Conversely, given that  
78 porpoises inhabit some of the most industrialized waters of the world’s oceans, targeting very small  
79 prey at high rates would mean that even moderate behavioural disruptions induced by common  
80 anthropogenic stressors in their shallow water habitats (e.g. [12]) could have immediate and serious  
81 consequences for their fitness.

82 To resolve these conflicting reports on porpoise feeding behaviour, we investigated the  
83 foraging performance of five harbour porpoises using new high resolution sound and movement  
84 recording DTAGs [13]. These suction cup attached loggers acquire continuous 16-bit stereo sound at  
85 500 kHz/channel while also sampling seven channels of movement sensors at up to 625 Hz. Analysis  
86 of the 15-23 hour deployments (Supplemental Experimental Procedures) revealed between 1222 and  
87 3405 buzzes giving prey encounter rates of 0-200/hour during the day and 50-550/hour after dusk  
88 (figure 1). Dive profiles and sea-floor echoes (see for example video S1) indicated that porpoises  
89 switched between near-surface, pelagic and benthic foraging during the day, but performed primarily  
90 pelagic dives at night. Click sound levels during buzzes were often very low (figure 2B), and the

91 acoustic behaviour leading up to buzzes was variable, likely explaining the low detection rate of  
92 feeding attempts in earlier acoustic tagging studies [10].

93 To evaluate prey capture success, we formed echograms of sound envelopes synchronized to  
94 outgoing clicks during buzzes (figure 2), thereby visualizing the self-generated auditory scenes  
95 experienced by porpoises during prey pursuit [8,13]. Given the complexity of these scenes, we used  
96 trained assessors to judge if prey were captured. Four evaluators were presented with figures  
97 containing the echogram, inter-click intervals, depth profile and differential acceleration (i.e., jerk  
98 [8,14] (figure 2, video S1). Evaluators looked for decreasing prey echo return times during buzzes  
99 accompanied by fast changes in acceleration indicative of a strike when the target was close [8,14] and  
100 lack of prey echoes after the strike, interpreting these as successful captures (Supplemental  
101 Experimental Procedures). Based on 100 buzzes rated as success or fail per animal the success rate of  
102 four porpoises was estimated at 0.91 - 0.97 (figure 1), with Cohen's kappa coefficient of inter-rater  
103 agreement of 0.49 - 0.91 (mean±SD: 0.73±0.11) (see Supplemental Experimental Procedures for  
104 details). Sliding of the suction-cup attached tag on a fifth animal (figure 1C) precluded reliable  
105 echogram evaluation. Prey echo traces frequently contained cyclic variations in echo level caused by  
106 the tail movements of escaping fish (figures 2 and 3). Frequency analysis of these modulations  
107 (figure3, Supplemental Experimental Procedures) on 30 randomly selected echograms per individual  
108 showed that the porpoises were primarily targeting fish with maximum body lengths of 3-10 cm.

109

## 110 **Discussion**

111 Despite the fundamental importance of foraging interactions for survival and fitness, fine-scale  
112 information on predation is scarce for many species in the wild and most particularly for aquatic  
113 animals. Advanced biologging tags have enabled studies of hunting in terrestrial (e.g. cheetahs [15])  
114 and marine (e.g. pilot whales [16]) predators, but it is rarely possible to obtain concurrent information  
115 about prey behaviour. Here we overcome this by using the echolocation signals produced by porpoises  
116 themselves to track prey, effectively tapping into the predators own sensory system. The low ambient  
117 noise in the frequency range used by harbour porpoises coupled with click repetition rates of more  
118 than 500 per second during buzzes enable detailed visualizations of individual prey encounters  
119 (figures 2 and 3).

120 Tagged porpoises foraged nearly continuously, targeting small prey with remarkably high  
121 capture success rates. Stomachs of adult harbour porpoises can accommodate up to 1.9 kg of food [17],  
122 but the passage time of food through the digestive tract is short at about 140 minutes [2] supporting

123 the ultra-high intake rates measured here. Prey sizes of 3-10 cm estimated in this study from tailbeat  
124 echo modulations are in general smaller than prey found in stomach contents of bycaught individuals  
125 [17]. This discrepancy [11] could indicate a bias towards detecting remains of larger prey in stomach  
126 contents, diet shift of porpoises towards smaller prey in recent years or differences in the study area.  
127 In either case, the consistently small fish targeted by the four porpoises with measurable echograms  
128 suggest that their diet has little overlap with commercial fisheries.

129           Very little is known about the foraging rates of small cetaceans, but compared to larger toothed  
130 whales, instrumented with similar tags, the high buzz rates documented here for porpoises are truly  
131 exceptional: on a daily basis they are about an order of magnitude higher than those reported for  
132 sperm whales [18], beaked whales [19] and pilot whales [16]. These deep-diving species must allocate  
133 more time for transport between mesopelagic prey and the surface, but, even at the base of foraging  
134 dives, their capture attempts are far less frequent than those of porpoises. The disparity in feeding  
135 rates likely reflects bigger, and hence more energetic, prey items, being selected by the deep-diving  
136 species. However, porpoises must require a higher energy intake per kilogram of body weight to meet  
137 their high mass-specific metabolic rate resulting from a low surface-to-volume ratio and consequential  
138 elevated heat loss per unit mass compared to toothed whales that are 10-700 times heavier [20]. Thus  
139 porpoises seem to be compelled by their small body size, cold water habitat and chosen prey size to  
140 hunt and capture 1000's of fish per day.

141           Whether marine mammals in general have elevated metabolic rates compared to their  
142 terrestrial counterparts has been a topic of debate [21]. However, recent reviews convincingly support  
143 earlier predictions [1] that small marine mammals do have field metabolic rates 2-3 times higher than  
144 similar-sized terrestrial mammals [20]. With their high estimated daily energy expenditures,  
145 porpoises have been described as “aquatic shrews” [1]. Our results show that, like shrews, porpoises  
146 must feed nearly continuously to support their high metabolic demands, leaving very little margin to  
147 compensate for changes in their environment. Failure to acquire sufficient energy when operating on  
148 an energetic knife-edge may have rapid and severe fitness consequences, giving them low resilience to  
149 disturbance: individual porpoises have been reported to starve to death in less than a week [22]. The  
150 effects of frequent anthropogenic disturbance [12] and changes in the marine ecosystem [2] on the  
151 foraging efficiency of porpoises and other small marine mammals in cold water should therefore be of  
152 prime importance in future research.

153

154

155 **Experimental Procedures**

156 Details of experimental procedures can be found within Results, and in the legends for figures 2 and 3.  
157 A full description can be found in Supplemental Experimental Procedures.

158 **References**

- 159 [1] Kanwisher J, Sundnes G. Physiology of a small cetacean. *Hvalrad Skr* 1965;48:45–53.
- 160 [2] MacLeod CD, Santos MB, Reid RJ, Scott BE, Pierce GJ. Linking sandeel consumption and the  
161 likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change  
162 mean more starving porpoises? *Biol Lett* 2007;3:185–8. doi:10.1098/rsbl.2006.0588.
- 163 [3] Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, et al. Trophic downgrading of  
164 Planet Earth. *Science* 2011;333:301–6. doi:10.1126/science.1205106.
- 165 [4] Block B, Jonsen I, Jorgensen S. Tracking apex marine predator movements in a dynamic ocean.  
166 *Nature* 2011;475:86–90. doi:10.1038/nature10082.
- 167 [5] Read AJ, Hohn A. Life in the fast lane : the life history of harbor porpoises from the Gulf of Maine.  
168 *Mar Mammal Sci* 1995;11:423–40. doi:10.1111/j.1748-7692.1995.tb00667.x.
- 169 [6] Kastelein RA, Hardeman J, Boer H. Food consumption and body mass of harbour porpoises  
170 (*Phocoena phocoena*). In: Read AJ, Wiepkema PR, Nachtigall PE, editors. *Biol. Harb. Porpoise,*  
171 *Woerden, The Netherlands: De Spil Publishers; 1997, p. 217–33.*
- 172 [7] Lockyer CH, Desportes G, Hansen K, Labberté S, Siebert U. Monitoring growth and energy  
173 utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. *NAMMCO Sci Publ*  
174 2003;5:107–20. doi:10.7557/3.2743.
- 175 [8] Wisniewska DM, Johnson M, Nachtigall PE, Madsen PT. Buzzing during biosonar-based  
176 interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. *J Exp Biol*  
177 2014;217:4279–82. doi:10.1242/jeb.113415.
- 178 [9] DeRuiter SL, Bahr A, Blanchet M-A, Hansen SF, Kristensen JH, Madsen PT, et al. Acoustic  
179 behaviour of echolocating porpoises during prey capture. *J Exp Biol* 2009;212:3100–7.  
180 doi:10.1242/jeb.030825.
- 181 [10] Linnenschmidt M, Teilmann J, Akamatsu T, Dietz R, Miller LA. Biosonar, dive, and foraging  
182 activity of satellite tracked harbor porpoises ( *Phocoena phocoena* ). *Mar Mammal Sci*  
183 2013;29:E77–97. doi:10.1111/j.1748-7692.2012.00592.x.
- 184 [11] Borjesson P, Berggren P, Ganning B. Diet of harbor porpoises in the Kattegat and Skagerrak  
185 Seas: accounting for individual variation and sample size. *Mar Mammal Sci* 2003;19:38–058.  
186 doi:10.1111/j.1748-7692.2003.tb01091.x.
- 187 [12] Dyndo M, Wisniewska DM, Rojano-Doñate L, Madsen PT. Harbour porpoises react to low levels  
188 of high frequency vessel noise. *Sci Rep* 2015;5:11083. doi:10.1038/srep11083.
- 189 [13] Johnson M, Aguilar Soto N, Madsen PT. Studying the behaviour and sensory ecology of marine  
190 mammals using acoustic recording tags: a review. *Mar Ecol Prog Ser* 2009;395:55–73.  
191 doi:10.3354/meps08255.
- 192 [14] Ydesen KS, Wisniewska DM, Hansen JD, Beedholm K, Johnson M, Madsen PT. What a jerk: prey

- 193 engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca*  
194 *vitulina*). *J Exp Biol* 2014;2239–43. doi:10.1242/jeb.100016.
- 195 [15] Wilson A, Lowe J, Roskilly K. Locomotion dynamics of hunting in wild cheetahs. *Nature*  
196 2013;498:185–9. doi:10.1038/nature12295.
- 197 [16] Aguilar Soto N, Johnson M, Madsen PT, Díaz F, Domínguez I, Brito A, et al. Cheetahs of the deep  
198 sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J Anim Ecol*  
199 2008;77:936–47. doi:10.1111/j.1365-2656.2008.01393.x.
- 200 [17] Sveegaard S, Andreassen H. Correlation between the seasonal distribution of harbour porpoises  
201 and their prey in the Sound, Baltic Sea. *Mar Biol* 2012;159:1029–37. doi:10.1007/s00227-012-  
202 1883-z.
- 203 [18] Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL. Deep-diving foraging behaviour of  
204 sperm whales (*Physeter macrocephalus*). *J Anim Ecol* 2006;75:814–25. doi:10.1111/j.1365-  
205 2656.2006.01101.x.
- 206 [19] Madsen P, Aguilar Soto N, Arranz P, Johnson M. Echolocation in Blainville’s beaked whales  
207 (*Mesoplodon densirostris*). *J Comp Physiol A* 2013;199:451–69. doi:10.1007/s00359-013-0824-  
208 8.
- 209 [20] Williams TM, Maresh JL. Exercise energetics. In: Mellish C&, editor. *Mar. Mammal Physiol.*  
210 *Requisites Ocean Living*, Madison, WI.: SPi Global; 2015, p. 47–68.
- 211 [21] Innes S, Lavigne DM. Do cetaceans really have elevated metabolic rates? *Physiol Zool*  
212 1991;64:1130–4.
- 213 [22] Kastelein R, Sijs S Van der. Blubber thickness in harbour porpoises (*Phocoena phocoena*). In:  
214 Read AJ, Wiepkema PR, Nachtigall PE, editors. *Biol. Harb. porpoise*, Woerden, The Netherlands:  
215 De Spil Publishers; 1997, p. 179–99.

216

## 217 **Acknowledgements**

218 This work was funded by the German Bundesamt für Naturschutz (BfN). DMW and PTM were also  
219 supported by the Danish National Research Foundation (FNU) and the Carlsberg Foundation, and MJ  
220 was also supported by the Marine Alliance for Science and Technology Scotland (MASTS) and by a  
221 Marie Curie-Sklodowska award. We thank A. Galatius, L. Mikkelsen, M.V. Jensen, L. Hermannsen, M. de  
222 Freitas, M. Dyndo, B. McDonald, M. Ladegaard, R. Dietz, A. Hansen and B. Hansen as well as all the  
223 helpful fishermen and the skilled pilot (U. Gosewinkel) involved in tag deployments and recoveries. P.  
224 Meyer, M. Dyndo, S. Videsen and A. E. M. Schrøder are thanked for help with data processing. We thank  
225 T. Hurst at Woods Hole Oceanographic Institution for constructing some of the tags used in this study,  
226 and R. Holst for help with the supplemental video. We thank the referees for their constructive  
227 comments that helped improve the manuscript.

228

229 **Author contribution**

230 DMW, MJ, PTM, JT, SS, LAM, US designed the study. DMW, JT, SS, PTM and LRD collected the data. MJ  
231 developed the tags and echographic analysis methods. DMW, MJ, LRD, JS and PTM were responsible  
232 for programming, data analysis and interpretation. DMW, MJ and PTM wrote the manuscript. All  
233 authors provided comments to improve the manuscript.

234

235 **Figure legends**

236 **Figure 1. Buzz rates indicative of prey encounter rates of echolocating harbour porpoises. A.**

237 Example dive profile from one porpoise. Individual buzzes are marked in red. The shaded area  
238 represents twilight (grey) and night (black). **B-F.** Hourly buzz counts for the five porpoises as recorded  
239 by attached tags. Numbers for the first and last incomplete hours are depicted with dashed lines. The  
240 animal's sex, age class, standard length (SL), tagging date and location, as well as the total number of  
241 buzzes (N) and the animal's estimated success rate (SR, mean and 95% confidence intervals) are  
242 provided in each panel. The digits in the names of the individuals indicate the year and Julian day of  
243 tag deployment. See also Supplemental Experimental Procedures, Table S1 and Video S1.

244 **Figure 2. Approach and probable capture of a prey by a harbour porpoise. A.** Echogram (see also

245 Video S1), displaying sonar clicks and echoes recorded by a DTAG-3 tag attached to the porpoise about  
246 5 cm behind its blowhole (i.e. about 20 cm from the tip of the animal's rostrum). The image is a stack  
247 plot of sound envelopes synchronized to the outgoing clicks, as in an echosounder display. The y-axis  
248 indicates time elapsed from emitted clicks to returning echoes, expressed as target range from the  
249 sound source below the blowhole using a sound speed of  $1500 \text{ ms}^{-1}$ . Clicks emitted at rates of more  
250 than 125 Hz, corresponding to inter-click intervals shorter than the 8 ms time-window chosen here,  
251 are displayed repeatedly making subsequent buzz clicks form a pattern akin to harmonics in the stack  
252 plot. The colour scale indicates echo-to-noise ratio (ENR) on a dB scale. Amplitude variations in the  
253 prey echo track individual tail strokes of the fish when it tries to escape (see figure 3A for details of the  
254 fish echo trace). **B.** Inter-click intervals (ICI) colour-coded for apparent output level (AOL) of  
255 echolocation clicks showing a 30 dB reduction in output energy during buzzes. **C.** Norm of jerk, i.e. the  
256 vector magnitude of the rate of change of acceleration as recorded by the tag. The high magnitude  
257 peaks most likely reflect rapid movements in the gular region during generation of suction. **D.** Depth  
258 (blue) and heading (green) of the tagged porpoise over the same interval. To evaluate prey capture  
259 success, similar figures were formed for a subset of buzzes for four of the tagged porpoises, and were  
260 presented to four evaluators.

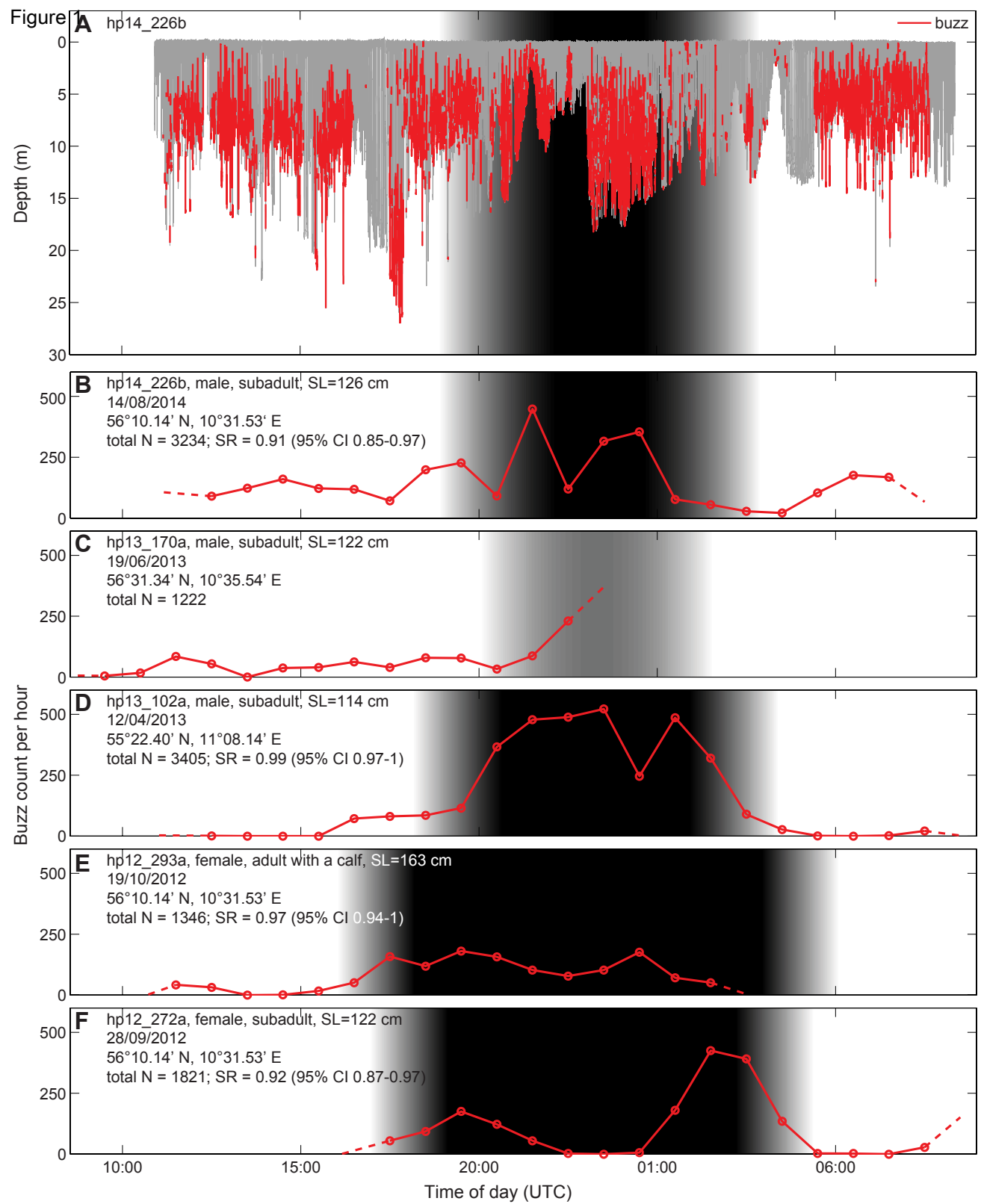


261 **Figure 3. Determination of prey behaviour and size.** **A.** Expanded view of the echogram in figure 2  
262 showing the echo level variation due to prey tailbeats (ENR – echo-to-noise ratio). **B.** Range (blue) and  
263 closing speed (green) to the prey extracted from the echogram using a two-state Kalman-Rauch filter  
264 to track the prey echo. Negative values of relative speed indicate when the porpoise is closing on the  
265 prey while positive values occur when the prey and predator draw apart. **C.** Received level at the tag of  
266 each prey echo tracked by the Kalman filter, expressed as root-mean-squared (RMS) echo-to-noise  
267 ratio. The prey appears to respond to the approaching porpoise at a distance of 65 cm from the sound  
268 source (50 cm from the anterior rostrum) and oscillations in the echo level thereafter indicate tail  
269 strokes of the escaping fish. **D.** Spectrogram of the echo level (interpolated to a regular time grid)  
270 showing the frequency (rate) of tail strokes. Each tail stroke requires two muscle contractions so the  
271 36 Hz stroke rate here implies a contraction time of 14 ms. As minimum contraction time (and  
272 therefore highest stroke rate) is a function of body length and water temperature, the maximum prey  
273 size can be deduced from the stroke rate in echograms, in this case  $BL < 5\text{cm}$ . This is corroborated by  
274 the escape speed of the prey: Assuming that the porpoise maintains its initial closing speed of 1.4 m/s  
275 throughout the chase, the prey must attain a similar speed at seconds 5.5 and 7.5 when the net speed  
276 is 0. This speed is consistent with a 5 cm fish stroking at 36 Hz with a stride of 0.8 BL. Inset in panel C  
277 shows the proportion of fish sizes targeted by the tagged porpoises as inferred from tailbeat rates in  
278 30 randomly-selected echograms per animal.

279

### 280 **Supplemental Information**

281 Supplemental Information includes Supplemental Experimental Procedures, one video and one table.



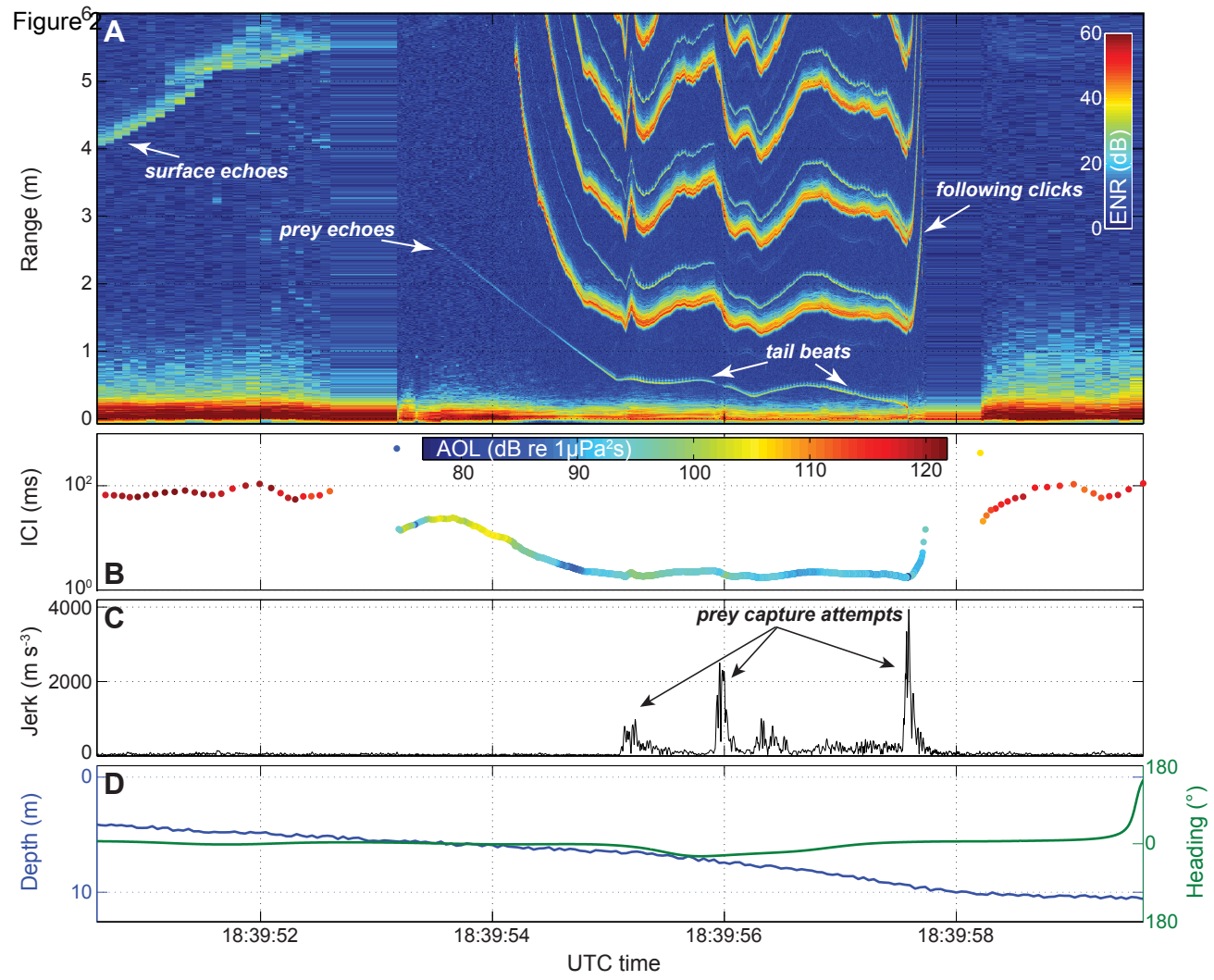
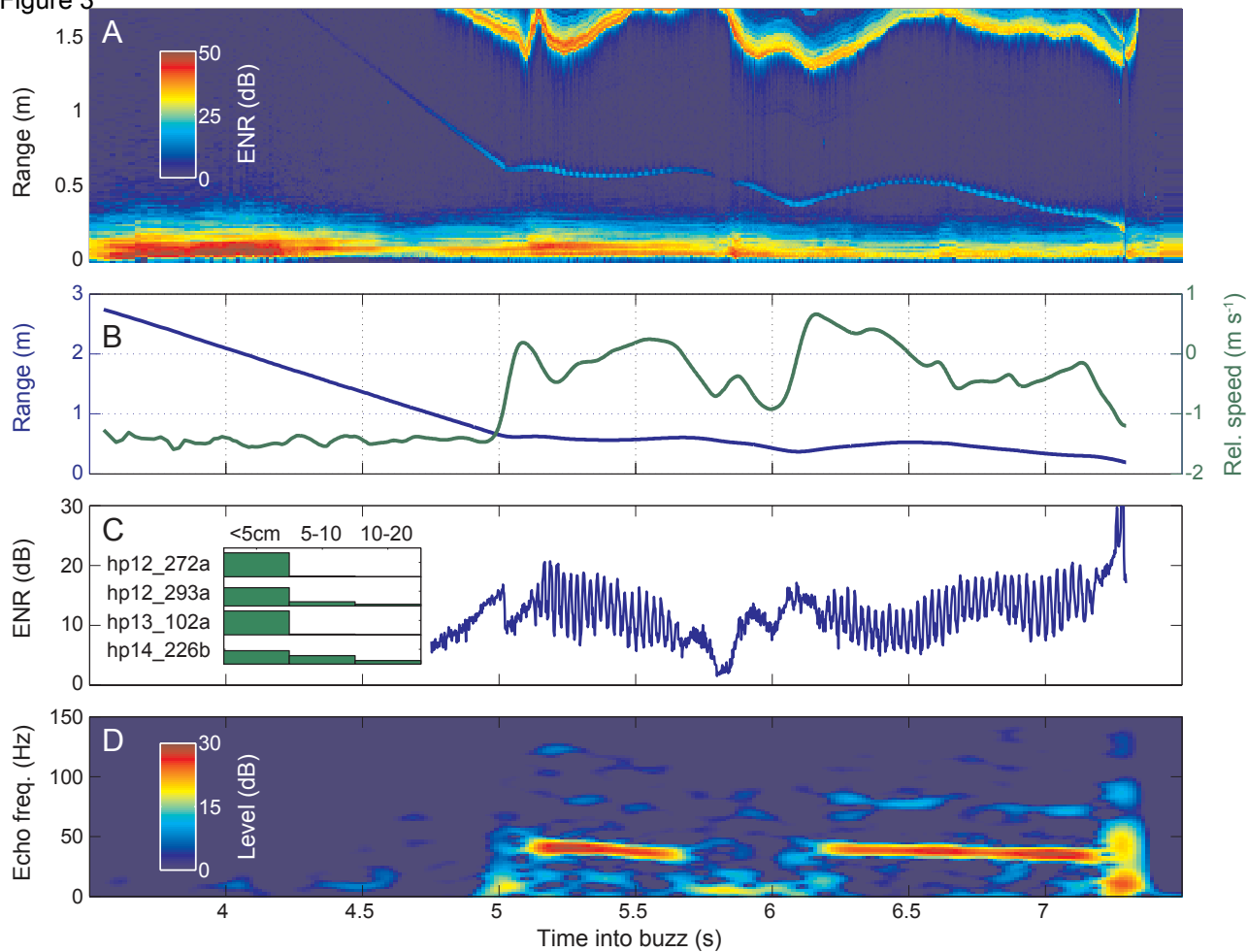


Figure 3



**1 Supplemental Information**

2 Supplemental Information includes Supplemental Experimental Procedures, one video and one table.

1 *Supplemental Tables*

2 **Table S1. Related to Figure 1. Estimates of the success rate of prey capture, based on an echogram scoring procedure by four evaluators.** In the procedure, a subset of  
 3 echograms for each animal were evaluated for capture success. Echograms without clear prey echoes or judged inconclusive were treated as missing data. A sensitivity  
 4 analysis explored three scenarios for the behaviour of the missing data: 1) all uncategorized buzzes were failures; 2) all uncategorized buzzes were successes; 3) the  
 5 uncategorized buzzes were considered to come from the same distribution as the judged data (random). The latter scenario (shaded cell) was assumed for the final estimates.  
 6 See also Supplemental Experimental Procedures

Individual	Total buzz count	Sensitivity Analysis				
			<i>Inconclusive echograms</i>			
hp14_226b	3234	<i>Echograms with no echoes</i>		<b>Missing are failures</b>	<b>Missing are random</b>	<b>Missing are successes</b>
			<b>Missing are failures</b>	73%	86%	88%
			<b>Missing are random</b>	77%	91%	92%
			<b>Missing are successes</b>	78%	91%	93%
hp13_102a	3405	<i>Echograms with no echoes</i>		<b>Missing are failures</b>	<b>Missing are random</b>	<b>Missing are successes</b>
			<b>Missing are failures</b>	80%	91%	92%
			<b>Missing are random</b>	87%	99%	99%
			<b>Missing are successes</b>	88%	99%	99%
hp12_272a	1821	<i>Echograms with no echoes</i>		<b>Missing are failures</b>	<b>Missing are random</b>	<b>Missing are successes</b>
			<b>Missing are failures</b>	80%	88%	89%
			<b>Missing are random</b>	84%	92%	93%
			<b>Missing are successes</b>	84%	92%	93%
hp12_293a	1346	<i>Echograms with no echoes</i>		<b>Missing are failures</b>	<b>Missing are random</b>	<b>Missing are successes</b>
			<b>Missing are failures</b>	58%	74%	80%
			<b>Missing are random</b>	72%	97%	98%
			<b>Missing are successes</b>	77%	98%	98%

## 1 ***Supplemental Experimental Procedures***

### 2 *Data collection*

3           Between September 2012 and August 2014, five porpoises, incidentally trapped in pound nets along the  
4 Danish coast of Kattegat and the Belt Seas, were equipped with DTAG-3 digital multisensor tags [S1,S2]. Upon  
5 discovering a porpoise in the net, the fishermen closed the mouth of the net to prevent the animal from escaping.  
6 Tagging personnel arrived within 24 hours. For tagging, the porpoise was carefully lifted on to a fishing boat  
7 and placed on a soft pad on the deck. Its sex was determined, body condition evaluated and standard length  
8 measurement taken. Only animals considered to be in good health were equipped with a tag. Porpoises were  
9 handled on the boat for 3-15 minutes before being released a few hundred meters from the net.

10           The suction-cup attached tag was placed dorsally about 5 cm behind the blowhole (i.e. about 20 cm  
11 from the tip of the rostrum) to ensure good quality recordings of the outgoing clicks and to maximize the chance  
12 of recording faint prey echoes. Animal movements were coupled to the tag through a square array of 4 x 50mm  
13 diameter soft silicone suction cups giving a semi-rigid attachment. The DTAG-3 tag used here sampled 16-bit  
14 stereo audio at 500 kHz (clip level of 179 dB re 1 $\mu$ Pa, -3dB frequency of 164 kHz), as well as three-dimensional  
15 acceleration, magnetic field and pressure sensors at between 250 Hz and 625 Hz, giving 18 – 44 hours of  
16 continuous recording depending on configuration. The tag detached passively after about 24 hours and was  
17 recovered with the aid of aerial VHF tracking. Prior studies on porpoises have used a sound event recording tag  
18 called the A-tag [S3–S5]. Whereas the DTAG records sound continuously, the A-tag detects transients with  
19 energy up to above 200 kHz and registers the time of occurrence, the amplitude and bearing of these signals  
20 within a predefined bandwidth [S6]. Its detection threshold of 142 dB re 1 $\mu$ Pa [S5] does not allow for recording  
21 of low amplitude buzz clicks or faint prey echoes which are recorded by the DTAG (see figures 2 and 3, and  
22 video S1).

### 23 *Data analysis*

#### 24 Buzz count

25           Data processing and subsequent analysis were performed using Matlab R2013b (MathWorks Inc.). The  
26 tag acoustic recordings were manually audited aurally and by visual inspection of spectrograms (Hamming  
27 window, FFT size 512, 75% overlap) computed over 5-second segments of the data, and high-repetition-rate  
28 click sequences were marked. Fast click sequences associated with continuous echolocation were defined as  
29 foraging buzzes accompanying prey capture attempts [S7], while isolated click sequences with generally higher  
30 received levels were classified as pulsed communication sounds [S8], and were excluded from further analysis.  
31 Signals from the tagged animal were discriminated from conspecific clicks based on their more broadband  
32 characteristics (likely due to the proximity and placement of the tag; see [S9]), typically higher received levels,  
33 and association with a low-frequency component that should only be discernible at short ranges from the source  
34 [S10]. All audits were verified by a second auditor before being submitted to further analysis. Although a small  
35 number of errors may arise in ascribing clicks to the tagged animal or in classifying buzzes, given the number of  
36 foraging sequences examined here, such occasional misclassifications will not influence the overall conclusions.  
37 Following Wisniewska et al. [S11], we used a marked dip in the distributions of inter-click-intervals at 15 ms to  
38 define the onset and cessation of buzzes. As animals switched between benthic, pelagic and surface foraging,  
39 they adapted their acoustic behaviour and it was difficult in some cases to determine whether a buzz sequence  
40 constituted a series of buzzes on multiple prey items, or a long pursuit of a single prey that escaped multiple  
41 times. The latter was assumed to be conservative leading to a potential underestimate in the total buzz count.

#### 42 Prey capture success rate

43           Synchronized sound and accelerometry data were examined to evaluate prey capture success during  
44 buzzes for four of the tagged porpoises (early sliding of the tag on the fifth porpoise precluded recording good  
45 quality prey echoes). Given the large and diverse number of buzzes for the four individuals (ranging from 1821  
46 to 3405), only a subset of buzzes was investigated in detail with buzzes being picked at random for each animal  
47 (without replacement using randperm in Matlab) Stack plots, or echograms [S2,S12,SS13], of sound envelopes  
48 synchronized to the outgoing click, as in echosounder images, were formed for these buzzes to visualize the  
49 self-generated acoustic scenes experienced by the porpoises during prey pursuits (figures 2A and 3A). Sound  
50 data were high-pass filtered at 105 kHz using a 50-sample symmetric FIR filter and the envelope was then  
51 computed as the magnitude of the Hilbert transform. To guide interpretation of echograms, the rate of change of  
52 acceleration, or jerk, was plotted synchronously with each buzz. Rapid muscle movements in the gular region  
53 are produced by many aquatic predators including toothed whales when attempting to capture active prey

1 [S14,S15] and these generate high-magnitude jerk peaks [S12,S13]. To simplify the plot, the jerk magnitude,  
2 computed as the norm of the triaxial jerk (i.e. the square root of the sum of the squared value in each axis [S16])  
3 at each time instant, was plotted.

4 For each analysed buzz, the echogram and jerk were combined with plots of the inter-click interval and  
5 depth profile in a four panel figure (akin to figure 2 and video S1). As echograms are often complex to interpret,  
6 four trained assessors were asked to estimate capture success for these buzzes. Assessors considered prey  
7 capture attempts successful when the prey echo trace converged close to the animal near the end of the buzz, did  
8 not re-emerge after the buzz, and was accompanied by a high jerk peak. Initial processing of the data showed  
9 that prey echoes were not always clearly visible in the echograms, or the echo traces could not always be  
10 followed to the conclusion of the buzz sequence. Therefore, we developed a two-stage questionnaire, in which  
11 the evaluators were asked 1) whether prey echoes were present in each echogram; and if so, 2) whether they  
12 considered the capture attempt to be a success, a failure, or uncertain.

13 The number of buzzes required to estimate success rate from echograms produced for each porpoise  
14 was calculated using standard survey sampling [S17]. For a margin of error of 10%, some 91-94 conclusive  
15 echograms are required depending on the number of buzzes produced per animal. To homogenize the  
16 methodology a sample size of 100 buzzes was used per animal. Buzzes for which the echogram had no  
17 detectable echo or for which capture was deemed inconclusive by an evaluator were replaced with a new  
18 randomly-selected buzz from the same animal until 100 conclusive results were obtained. The randomness of  
19 the subsampling procedure ensures that buzzes from all foraging modes are selected in the proportion that they  
20 occur. However, the proportion of conclusive buzzes may be less balanced if prey in one foraging mode tend to  
21 produce weak echoes or are more readily masked by echoes from the surface or sea-floor.

22 The final assessment was obtained by merging the answers of the four evaluators, with the accepted  
23 result being the one with most votes. Agreement between assessors was quantified using a weighted Cohen's  
24 Kappa [S18], where a score of 1 was given for agreeing answers, 0 for definite answers that did not agree (i.e.  
25 failure vs. success), and 0.5 for buzzes that were rated as success or failure by some assessors and inconclusive  
26 by others.

27 Echograms without clear prey echoes or judged inconclusive were treated as missing data. We  
28 performed a sensitivity analysis to examine how these uncategorised buzzes might influence the overall success  
29 rate. We considered extreme scenarios in which all uncategorised buzzes were considered to be either success or  
30 failures. The overall success rate was then recalculated including these buzzes in the sample (table S1). The final  
31 success rate estimates (shaded cells in table S1) assumed that the missing data were drawn from the same  
32 distribution as the data with conclusive prey echoes. 95% confidence intervals around these estimates were  
33 computed assuming a normal distribution.

#### 34 Prey size estimation

35 Prey size estimation was performed on the same echograms as for the prey capture analysis.  
36 Echograms were evaluated visually and the first 60 per individual with clear prey echoes and modulations  
37 indicative of tailbeats (see figure 3) were selected for analysis. The selected echograms were plotted with high  
38 resolution and a supervised Kalman filter was used to track prey echoes. The Kalman filter had range and  
39 closing speed as states and the state variances were adjusted to achieve a close visual match between the echo  
40 track and the actual prey echoes. Kalman tracks were terminated whenever the prey echo became too faint for  
41 reliable tracking, and multiple tracks were generated for each echogram if the prey echo appeared in disjoint  
42 segments. The tracks define the echo range at the time of each outgoing click. To analyse echo modulation, the  
43 RMS echo intensity was calculated in a 90% energy window constrained to fall within  $\pm 80 \mu\text{s}$  (equivalent to  $\pm 6$   
44 cm in range) of the Kalman track point for each click. The result of this step is a sequence of echo intensity  
45 values at irregular times corresponding to outgoing clicks. After applying a length-3 median filter to reduce  
46 outliers, the intensity time series was plotted and sub-sequences with at least 4 consecutive intensity  
47 modulations and RMS modulation depth  $> 1$  dB were identified for spectral analysis. After mean removal, a  
48 Lomb-Scargle periodogram was used to estimate the spectral peak of each sub-sequence. As tailbeats could  
49 produce asymmetric intensity modulations depending on the aspect of the prey with respect to the acoustic  
50 beam, a two harmonic model was used to assess goodness of fit. In this model, echo intensity was modelled as  
51 having a sine and cosine component at the spectral peak frequency and at twice this frequency. The four  
52 coefficient model was evaluated by performing a least-squares fit to the intensity sub-sequence and recording  
53 the  $r^2$  of the fit. Sub-sequences with  $r^2 > 0.5$  were retained and the spectral peak frequency in the 30 echograms  
54 with highest  $r^2$  per individual were taken as a sample of prey tailbeat frequencies. The  $r^2$  in this sample was, in  
55 most cases, greater than 0.75. The tailbeat frequencies (figure 3) were then converted to maximum muscle



1 contraction times (i.e., max contraction time = 0.5/frequency) from which the maximum prey size could be  
2 estimated for the average water temperature at the time of tagging using the relationship in [S19]. For this we  
3 assume that escaping fish will swim at close to their maximum capabilities. Although this seems likely, our  
4 method will over-estimate the size of fish that swim below their capacity.  
5

## 6 **Supplemental References**

- 7 [S1] Johnson MP, Tyack PL. A digital acoustic recording tag for measuring the response of wild marine  
8 mammals to sound. *IEEE J Ocean Eng* 2003;28:3–12. doi:10.1109/JOE.2002.808212.
- 9 [S2] Johnson M, Aguilar de Soto N, Madsen P. Studying the behaviour and sensory ecology of marine  
10 mammals using acoustic recording tags: a review. *Mar Ecol Prog Ser* 2009;395:55–73.  
11 doi:10.3354/meps08255.
- 12 [S3] Akamatsu T, Wang D, Wang K, Naito Y. Biosonar behaviour of free-ranging porpoises. *Proc Biol Sci*  
13 2005;272:797–801. doi:10.1098/rspb.2004.3024.
- 14 [S4] Akamatsu T, Teilmann J, Miller L a., Tougaard J, Dietz R, Wang D, et al. Comparison of echolocation  
15 behaviour between coastal and riverine porpoises. *Int Symp Underw Technol UT 2007 - Int Work Sci*  
16 *Use Submar Cables Relat Technol 2007* 2007;54:520–6. doi:10.1109/UT.2007.370755.
- 17 [S5] Linnenschmidt M, Teilmann J, Akamatsu T, Dietz R, Miller LA. Biosonar, dive, and foraging activity of  
18 satellite tracked harbor porpoises (*Phocoena phocoena*). *Mar Mammal Sci* 2013;29:E77–97.  
19 doi:10.1111/j.1748-7692.2012.00592.x.
- 20 [S6] Akamatsu T, Matsuda A, Suzuki S, Wang D, Wang K, Suzuki M, et al. New stereo acoustic data logger  
21 for free-ranging dolphins and porpoises. *Mar Technol Soc J* 2005;39:3–9.  
22 doi:10.4031/002533205787443980.
- 23 [S7] DeRuiter SL, Bahr A, Blanchet M-A, Hansen SF, Kristensen JH, Madsen PT, et al. Acoustic behaviour  
24 of echolocating porpoises during prey capture. *J Exp Biol* 2009;212:3100–7. doi:10.1242/jeb.030825.
- 25 [S8] Clausen KT, Wahlberg M, Beedholm K, Deruiter S, Madsen PT. Click communication in harbour  
26 porpoises *Phocoena phocoena*. *Int J Anim Sound Its Rec* 2010;20:1–28.
- 27 [S9] Madsen PT, Wisniewska D, Beedholm K. Single source sound production and dynamic beam formation  
28 in echolocating harbour porpoises (*Phocoena phocoena*). *J Exp Biol* 2010;213:3105–10.  
29 doi:10.1242/jeb.044420.
- 30 [S10] Hansen M, Wahlberg M, Madsen PT. Low-frequency components in harbor porpoise (*Phocoena*  
31 *phocoena*) clicks: communication signal, by-products, or artifacts? *J Acoust Soc Am* 2008;124:4059.  
32 doi:10.1121/1.2945154.
- 33 [S11] Wisniewska DM, Johnson M, Beedholm K, Wahlberg M, Madsen PT. Acoustic gaze adjustments during  
34 active target selection in echolocating porpoises. *J Exp Biol* 2012;215:4358–73.  
35 doi:10.1242/jeb.074013.
- 36 [S12] Johnson M, Madsen PT, Zimmer WMX, de Soto NA, Tyack PL. Beaked whales echolocate on prey.  
37 *Proc R Soc B Biol Sci* 2004;271:S383–6. doi:10.1098/rsbl.2004.0208.
- 38 [S13] Wisniewska DM, Johnson M, Nachtigall PE, Madsen PT. Buzzing during biosonar-based interception of  
39 prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. *J Exp Biol* 2014;217:4279–82.  
40 doi:10.1242/jeb.113415.
- 41 [S14] Werth A. A kinematic study of suction feeding and associated behavior in the long-finned pilot whale,  
42 *Globicephala melas* (Traill). *Mar Mammal Sci* 2000;16:299–3. doi:10.1111/j.1748-  
43 7692.2000.tb00926.x.
- 44 [S15] Higham TE, Day SW, Wainwright PC. The pressures of suction feeding: the relation between buccal  
45 pressure and induced fluid speed in centrarchid fishes. *J Exp Biol* 2006;209:3281–7.  
46 doi:10.1242/jeb.02383.

- 1 [S16] Ydesen KS, Wisniewska DM, Hansen JD, Beedholm K, Johnson M, Madsen PT. What a jerk: prey  
2 engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). J Exp  
3 Biol 2014;2239–43. doi:10.1242/jeb.100016.
- 4 [S17] Kish L. Survey sampling. New York, NY: J 1965.
- 5 [S18] Cohen J. Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit.  
6 Psychol Bull 1968.
- 7 [S19] Wardle CS. Limit of fish swimming speed. Nature 1975;255:725–7.

**Video S1. Related to Figures 1 and 2. Echolocation of prey by a harbour porpoise during a night-time pelagic dive.**

**LEFT:** Approximate three-dimensional path of a foraging harbour porpoise (individual hp14\_226b, see figure 1) estimated by dead reckoning using pressure, accelerometer and magnetometer data recorded by the DTAG-3 tag. The track is colour-coded by root-mean-squared (RMS) jerk in 0.5-s windows. Durations of buzzes are shown by wide segments in the horizontal projection of the track. The stationary pins (black on the projection, purple on the track) indicate the end of each buzz. The moving pins (red-filled on the projection, grey-filled on the track) illustrate the movement of the porpoise. The plot covers the entire 75-s dive during which the porpoise performed 24 buzz sequences.

**RIGHT: Top panel.** Echogram displaying sonar clicks and echoes in the same dive as LEFT recorded by the tag attached to the porpoise about 5 cm behind its blowhole (i.e. about 20 cm from the tip of the animal's rostrum). The y-axis indicates the time elapsed from emitted clicks to returning echoes expressed as target range from the sound source by the blowhole using a sound speed of  $1500 \text{ ms}^{-1}$ . Clicks emitted at inter-click intervals (ICIs) shorter than the 13.3 ms time window presented here are displayed repeatedly in the vertical axis, causing the subsequent buzz clicks to form a pattern resembling harmonics in a spectrogram. The colour scale indicates signal energy from blue (faint) to red (intense). Echoes from the water surface and the seafloor indicate that the porpoise was hunting about 2-3 m above the seafloor. Since prey echo traces in all 24 buzzes converged close to the animal near the end of the buzzes, did not re-emerge following the buzzes and were accompanied by rapid changes in acceleration (in **C**), all 24 prey pursuits probably ended with captures. **2<sup>nd</sup> panel.** Inter-click intervals colour-coded for relative energy of the signals from blue (faint) to red (intense). **3<sup>rd</sup> panel.** Norm jerk, i.e. the vector magnitude of the rate of change of acceleration as recorded by the tag. The high magnitude peaks likely reflect rapid movements in the gular region during generation of suction. **Bottom panel.** Depth (blue) and roll (green) of the porpoise. The step changes in roll are due to the limits of the y-axis and occur when the animal rolls by more than 180 degree around its body axis.



Click here to access/download

**Supplemental Movies & Spreadsheets**  
Wisniewska\_et\_al\_VideoS1\_small.mov

