

Current Biology

Ultra-High Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance

Highlights

- Harbor porpoises forage nearly continuously day and night to meet energy needs
- Porpoises hunt up to 550 small fish prey per hour with a >90% capture success rate
- Targeted sizes of fish overlap little with commercial fisheries
- Even moderate disturbance may have severe fitness consequences for porpoises

Authors

Danuta Maria Wisniewska, Mark Johnson, Jonas Teilmann, ..., Lee A. Miller, Ursula Siebert, Peter Teglberg Madsen

Correspondence

danuta.wisniewska@bios.au.dk

In Brief

Wisniewska et al. use echoes from prey targeted by wild harbor porpoises to study their foraging. They show that this small cold water predator lives on an energetic knife-edge, hunting small fish nearly continuously day and night with extreme capture rates. Such intense foraging may make this species especially vulnerable to human disturbance.

Ultra-High Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance

Danuta Maria Wisniewska,^{1,2,*} Mark Johnson,³ Jonas Teilmann,² Laia Rojano-Doñate,¹ Jeanne Shearer,³ Signe Sveegaard,² Lee A. Miller,⁴ Ursula Siebert,⁵ and Peter Teglberg Madsen^{1,6}

¹Zoophysiology, Department of Bioscience, Aarhus University, Building 1131, C.F. Moellers Alle 3, 8000 Aarhus C, Denmark

²Marine Mammal Research, Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

³Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews KY16 8LB, Scotland

⁴Sound and Behaviour Group, Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark

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

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

*Correspondence: danuta.wisniewska@bios.au.dk

<http://dx.doi.org/10.1016/j.cub.2016.03.069>

SUMMARY

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

RESULTS

The harbor porpoise (*Phocoena phocoena*), the smallest cetacean inhabiting cold temperate waters of the Northern Hemi-

sphere, has been described as “living life in the fast lane” [5]. Compared to other toothed whales, it matures at an earlier age, reproduces more frequently, and has a shorter lifespan [5]. Its small size in cold water gives rise to a high relative heat loss and limits the amount of energy it can store with respect to its metabolic rate, making it sensitive to starvation [6, 7]. Harbor porpoises are therefore hypothesized to feed at high rates year-round, capturing up to 10% of their body weight in fish per day [6, 7] to support their metabolic requirements.

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

To resolve these conflicting reports on porpoise feeding behavior, we investigated the foraging performance of five harbor porpoises using new high-resolution sound and movement recording DTAGs [13]. These suction cup attached loggers acquire continuous 16-bit stereo sound at 500 kHz/channel while also sampling seven channels of movement sensors at up to 625 Hz. The tagging was carried out under permission from the Danish Forest and Nature Agency (NST-3446-00016) and the Animal Welfare Division (Ministry of Justice, 2010-561-1801). Analysis of the 15–23 hr deployments (Supplemental

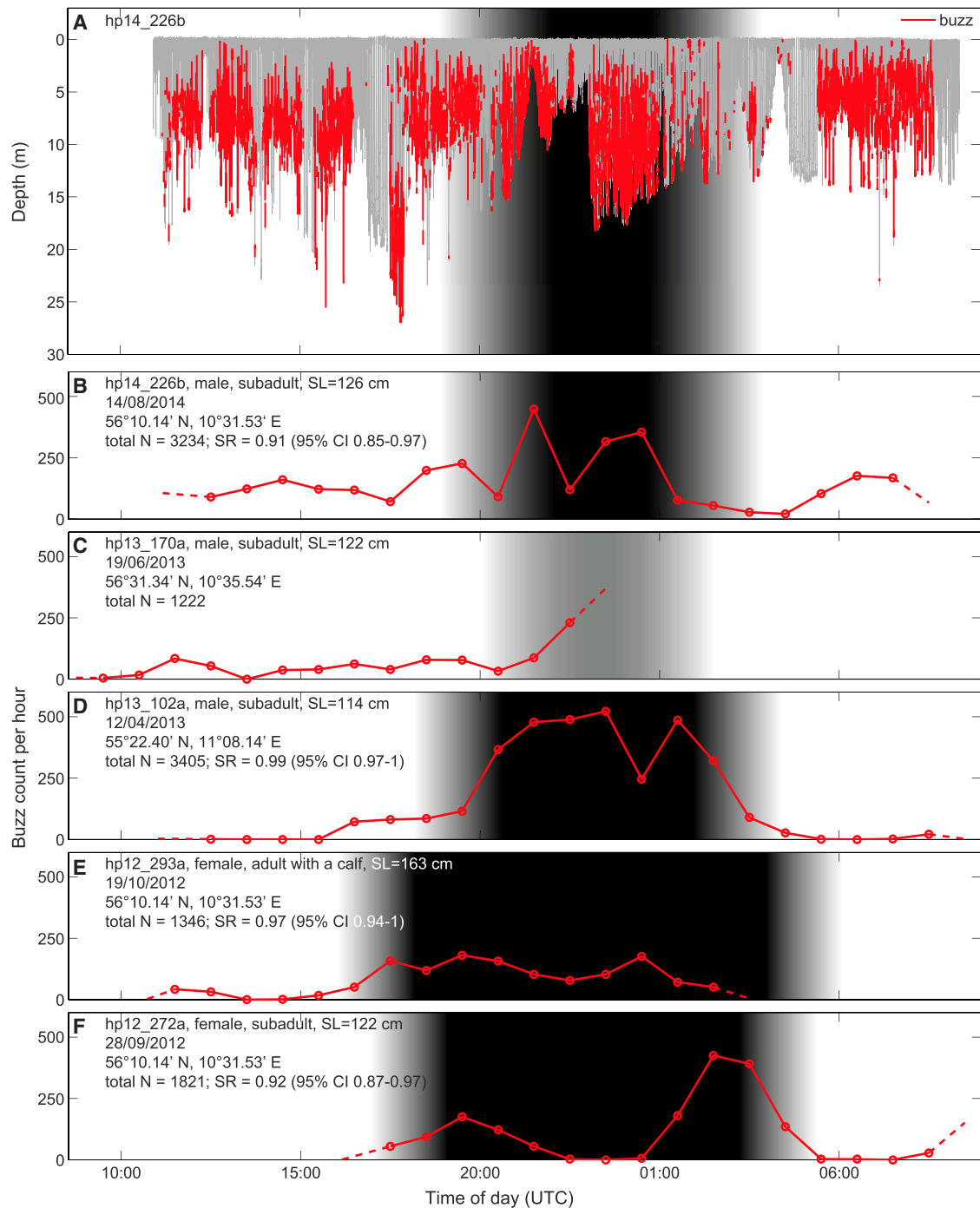


Figure 1. Buzz Rates Indicative of Prey Encounter Rates of Echolocating Harbor Porpoises

(A) Example dive profile from one porpoise. Individual buzzes are marked in red. The shaded area represents twilight (gray) and night (black).

Q4 (B–F) Hourly buzz counts for the five porpoises as recorded by attached tags. Numbers for the first and last incomplete hours are depicted with dashed lines. The animal's sex, age class, standard length (SL), tagging date, and location as well as the total number of buzzes (n) and the animal's estimated success rate (SR; mean and 95% confidence intervals) are provided in each panel. The digits in the names of the individuals indicate the year and Julian day of tag deployment. See also [Supplemental Experimental Procedures, Table S1](#), and [Movie S1](#).

[Experimental Procedures](#)) revealed between 1,222 and 3,405 buzzes, giving prey encounter rates of 0–200/hour during the day and 50–550/hour after dusk ([Figure 1](#)). Dive profiles and

sea-floor echoes (see for example [Movie S1](#)) indicated that porpoises switched between near-surface, pelagic, and benthic foraging during the day but performed primarily pelagic dives **Q2**

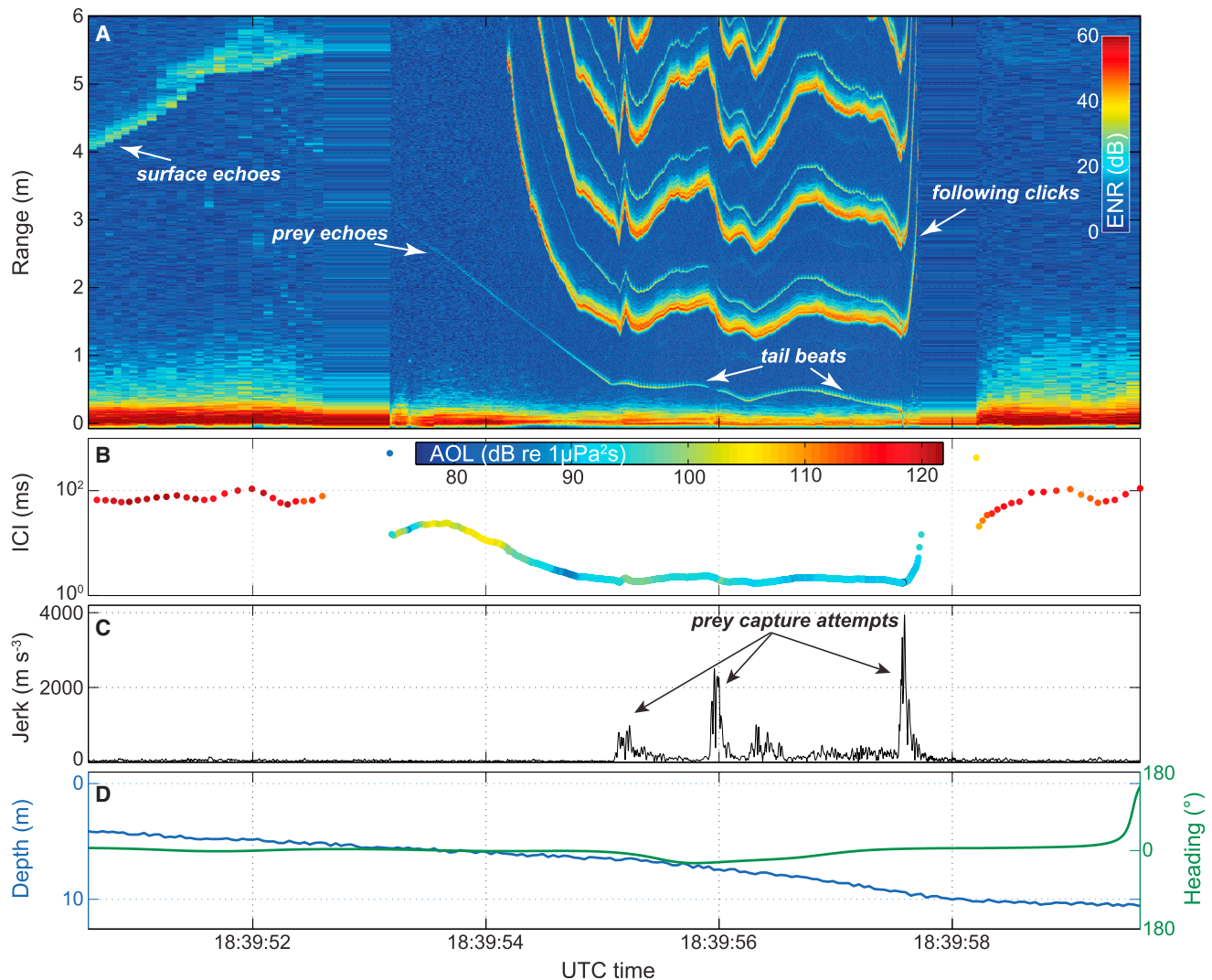


Figure 2. Approach and Probable Capture of a Prey by a Harbor Porpoise

(A) Echogram (see also [Movie S1](#)) displaying sonar clicks and echoes recorded by a DTAG-3 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 image is a stack plot of sound envelopes synchronized to the outgoing clicks, as in an echosounder display. The y axis indicates time elapsed from emitted clicks to returning echoes, expressed as target range from the sound source below the blowhole using a sound speed of $1,500 \text{ ms}^{-1}$. Clicks emitted at rates of more than 125 Hz, corresponding to inter-click intervals (ICIs) shorter than the 8-ms time window chosen here, are displayed repeatedly, making subsequent buzz clicks form a pattern akin to harmonics in the stack plot. The color scale indicates echo-to-noise ratio (ENR) on a dB scale. Amplitude variations in the prey echo track individual tail strokes of the fish when it tries to escape (see [Figure 3A](#) for details of the fish echo trace). (B) ICI color-coded for apparent output level (AOL) of echolocation clicks showing a 30-dB reduction in output energy during buzzes. (C) Norm of jerk, i.e., the vector magnitude of the rate of change of acceleration as recorded by the tag. The high magnitude peaks most likely reflect rapid movements in the gular region during generation of suction.

Q5

(D) Depth (blue) and heading (green) of the tagged porpoise over the same interval. To evaluate prey capture success, we formed similar figures for a subset of buzzes for four of the tagged porpoises and presented them to four evaluators.

at night. Click sound levels during buzzes were often very low ([Figure 2B](#)), and the acoustic behavior leading up to buzzes was variable, likely explaining the low detection rate of feeding attempts in earlier acoustic tagging studies [10].

To evaluate prey capture success, we formed echograms of sound envelopes synchronized to outgoing clicks during buzzes ([Figure 2](#)), thereby visualizing the self-generated auditory scenes experienced by porpoises during prey pursuit [8, 13]. Given the complexity of these scenes, we used trained assessors to judge

whether prey were captured. Four evaluators were presented with figures containing the echogram, inter-click intervals, depth profile, and differential acceleration (i.e., jerk; [8, 14]) ([Figure 2](#); [Movie S1](#)). Evaluators looked for decreasing prey echo return times during buzzes accompanied by fast changes in acceleration indicative of a strike when the target was close [8, 14] and lack of prey echoes after the strike, interpreting these as successful captures ([Supplemental Experimental Procedures](#)). Based on 100 buzzes rated as success or fail per animal, the

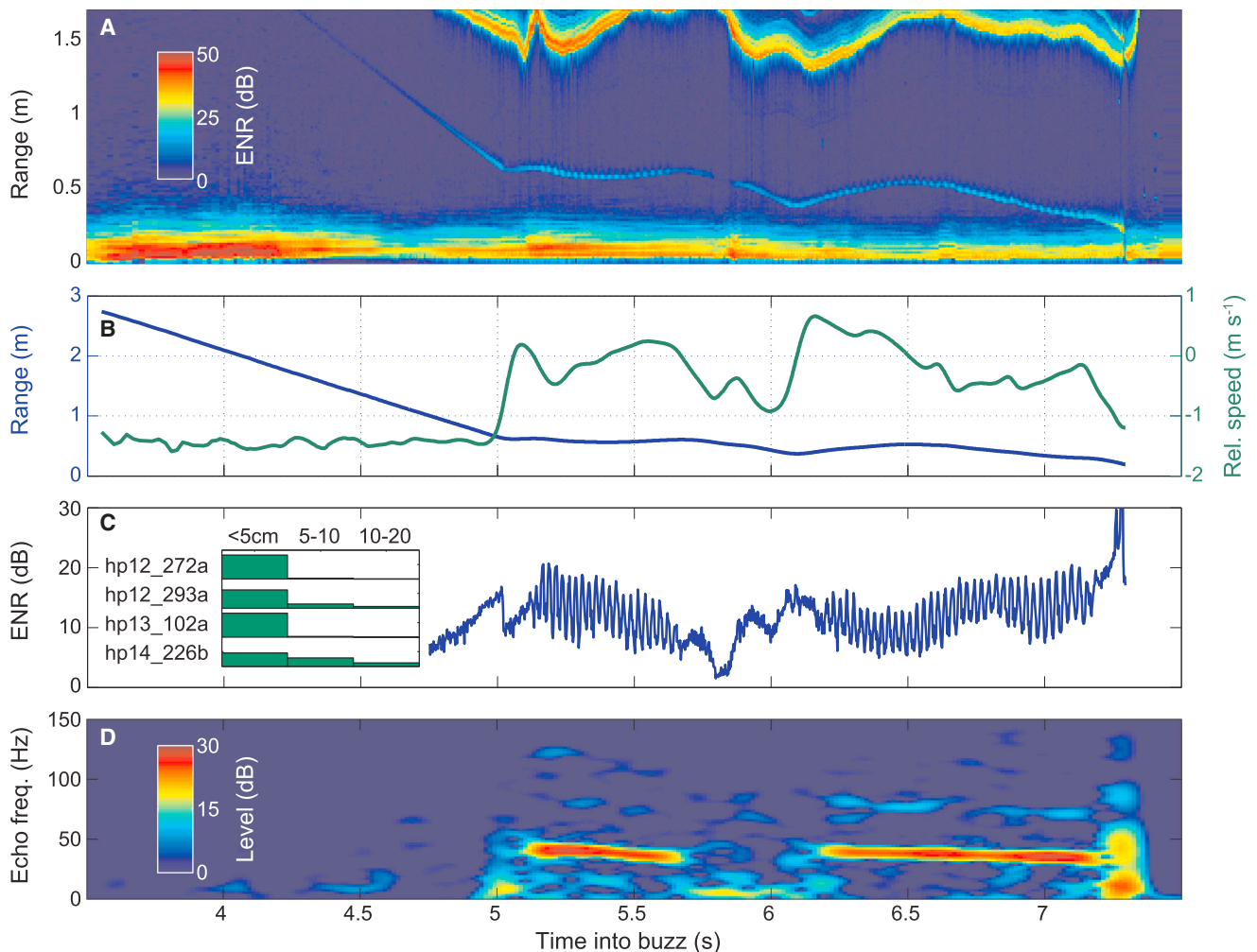


Figure 3. Determination of Prey Behavior and Size

(A) Expanded view of the echogram in Figure 2 showing the echo level variation due to prey tailbeats (ENR).

(B) Range (blue) and closing speed (green) to the prey extracted from the echogram using a two-state Kalman-Rauch filter to track the prey echo. Negative values of relative speed indicate when the porpoise is closing on the prey, while positive values occur when the prey and predator draw apart.

(C) Received level at the tag of each prey echo tracked by the Kalman filter, expressed as root-mean-squared (RMS) ENR. The prey appears to respond to the approaching porpoise at a distance of 65 cm from the sound source (50 cm from the anterior rostrum), and oscillations in the echo level thereafter indicate tail strokes of the escaping fish.

(D) Spectrogram of the echo level (interpolated to a regular time grid) showing the frequency (rate) of tail strokes. Each tail stroke requires two muscle contractions, so the 36-Hz stroke rate here implies a contraction time of 14 ms. As minimum contraction time (and therefore highest stroke rate) is a function of body length and water temperature, the maximum prey size can be deduced from the stroke rate in echograms, in this case BL < 5 cm. This is corroborated by the escape speed of the prey: assuming that the porpoise maintains its initial closing speed of 1.4 m/s throughout the chase, the prey must attain a similar speed at seconds 5.5 and 7.5 when the net speed is 0. This speed is consistent with a 5-cm fish stroking at 36 Hz with a stride of 0.8 BL. Inset in (C) shows the proportion of fish sizes targeted by the tagged porpoises as inferred from tailbeat rates in 30 randomly selected echograms per animal.

Q6

success rate of four porpoises was estimated at 0.91–0.97 (Figure 1), with Cohen's kappa coefficient of inter-rater agreement of 0.49–0.91 (mean \pm SD: 0.73 \pm 0.11) (see Supplemental Experimental Procedures for details). Sliding of the suction cup attached tag on a fifth animal (Figure 1C) precluded reliable echogram evaluation. Prey echo traces frequently contained cyclic variations in echo level caused by the tail movements of escaping fish (Figures 2 and 3). Frequency analysis of these modulations (Figure 3; Supplemental Experimental Procedures) on 30 randomly selected echograms per individual showed

that the porpoises were primarily targeting fish with maximum body lengths of 3–10 cm.

DISCUSSION

Despite the fundamental importance of foraging interactions for survival and fitness, fine-scale information on predation is scarce for many species in the wild and most particularly for aquatic animals. Advanced biologging tags have enabled studies of hunting in terrestrial (e.g., cheetahs [15]) and marine (e.g., pilot

whales [16]) predators, but it is rarely possible to obtain concurrent information about prey behavior. Here, we overcome this by using the echolocation signals produced by porpoises themselves to track prey, effectively tapping into the predators' own sensory system. The low ambient noise in the frequency range used by harbor porpoises coupled with click repetition rates of more than 500 per second during buzzes enable detailed visualizations of individual prey encounters (Figures 2 and 3).

Tagged porpoises foraged nearly continuously, targeting small prey with remarkably high capture success rates. Stomachs of adult harbor porpoises can accommodate up to 1.9 kg of food [17], but the passage time of food through the digestive tract is short at about 140 min [2], supporting the ultra-high intake rates measured here. Prey sizes of 3–10 cm estimated in this study from tailbeat echo modulations are in general smaller than prey found in stomach contents of bycaught individuals [17]. This discrepancy [11] could indicate a bias toward detecting remains of larger prey in stomach contents, diet shift of porpoises toward smaller prey in recent years, or differences in the study area. In either case, the consistently small fish targeted by the four porpoises with measurable echograms suggest that their diet has little overlap with commercial fisheries.

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

Q3

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

EXPERIMENTAL PROCEDURES

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

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, one table, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.03.069>.

AUTHOR CONTRIBUTIONS

D.M.W., M.J., P.T.M., J.T., S.S., L.A.M., and U.S. designed the study. D.M.W., J.T., S.S., P.T.M., and L.R.-D. collected the data. M.J. developed the tags and echographic analysis methods. D.M.W., M.J., L.R.-D., J.S., and P.T.M. were responsible for programming, data analysis, and interpretation. D.M.W., M.J., and P.T.M. wrote the manuscript. All authors provided comments to improve the manuscript.

ACKNOWLEDGMENTS

This study was partly funded by the Federal Agency for Nature Conservation under the contract Z1.2-5330/2010/14 and the BfN-Cluster 7 “Effects of underwater noise on marine vertebrates.” D.M.W. and P.T.M. were also supported by the Danish National Research Foundation (FNU) and the Carlsberg Foundation, and M.J. was also supported by the Marine Alliance for Science and Technology Scotland (MASTS) and by a Marie Curie-Sklodowska award. We thank A. Galatius, L. Mikkelsen, M.V. Jensen, L. Hermannsen, M. de Freitas, M. Dyndo, B. McDonald, M. Ladegaard, R. Dietz, A. Hansen, and B. Hansen as well as all the helpful fishermen and the skilled pilot (U. Gosewinkel) involved in tag deployments and recoveries. P. Meyer, M. Dyndo, S. Videsen, and A.E.M. Schröder are thanked for help with data processing. We thank T. Hurst at Woods Hole Oceanographic Institution for constructing some of the tags used in this study and R. Holst for help with the supplemental movie. We thank the referees for their constructive comments that helped improve the manuscript.

Received: February 22, 2016

Revised: March 25, 2016

Accepted: March 30, 2016

Published: May 26, 2016

REFERENCES

1. Kanwisher, J., and Sundnes, G. (1965). Physiology of a small cetacean. *Hvalråd. Skr.* 48, 45–53.
2. MacLeod, C.D., Santos, M.B., Reid, R.J., Scott, B.E., and Pierce, G.J. (2007). Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biol. Lett.* 3, 185–188.
3. Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., et al. (2011). Trophic downgrading of planet Earth. *Science* 333, 301–306.
4. Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., et al. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90.
5. Read, A.J., and Hohn, A.A. (1995). Life in the fast lane: the life history of harbour porpoises from the Gulf of Maine. *Mar. Mamm. Sci.* 11, 423–440.
6. Kastelein, R.A., Hardeman, J., and Boer, H. (1997). Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In *The Biology of the Harbour Porpoise*, A.J. Read, P.R. Wiepkema, and P.E. Nachtigall, eds. (De Spil Publishers), pp. 217–233.

7. Lockyer, C.H., Desportes, G., Hansen, K., Labberté, S., and Siebert, U. (2003). Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. NAMMCO Scientific Publications 5, 107–120.
8. Wisniewska, D.M., Johnson, M., Nachtigall, P.E., and Madsen, P.T. (2014). Buzzing during biosonar-based interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. *J. Exp. Biol.* 217, 4279–4282.
9. Deruiter, S.L., Bahr, A., Blanchet, M.-A., Hansen, S.F., Kristensen, J.H., Madsen, P.T., Tyack, P.L., and Wahlberg, M. (2009). Acoustic behaviour of echolocating porpoises during prey capture. *J. Exp. Biol.* 212, 3100–3107.
10. Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R., and Miller, L.A. (2013). Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). *Mar. Mamm. Sci.* 29, E77–E97.
11. Börjesson, P., Berggren, P., and Ganning, B. (2003). Diet of harbor porpoises in the Kattegat and Skagerrak Seas: accounting for individual variation and sample size. *Mar. Mamm. Sci.* 19, 38–58.
12. Dyndo, M., Wiśniewska, D.M., Rojano-Doñate, L., and Madsen, P.T. (2015). Harbour porpoises react to low levels of high frequency vessel noise. *Sci. Rep.* 5, 11083.
13. Johnson, M., Aguilar de Soto, N., and Madsen, P.T. (2009). Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Mar. Ecol. Prog. Ser.* 395, 55–73.
14. Ydesen, K.S., Wisniewska, D.M., Hansen, J.D., Beedholm, K., Johnson, M., and Madsen, P.T. (2014). What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *J. Exp. Biol.* 217, 2239–2243.
15. Wilson, A.M., Lowe, J.C., Roskilly, K., Hudson, P.E., Golabek, K.A., and McNutt, J.W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* 498, 185–189.
16. Aguilar Soto, N., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., and Tyack, P. (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* 77, 936–947.
17. Sveegaard, S., Andreasen, H., Mouritsen, K.N., Jeppesen, J.P., Teilmann, J., and Kinze, C.C. (2012). Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. *Mar. Biol.* 159, 1029–1037.
18. Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T., and Tyack, P.L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* 75, 814–825.
19. Madsen, P.T., de Soto, N.A., Arranz, P., and Johnson, M. (2013). Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*). *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 199, 451–469.
20. Williams, T.M., and Maresh, J.L. (2016). Exercise energetics. In *Marine Mammal Physiology. Requisites for Ocean Living*, M.A. Castellini, and J.-A. Mellish, eds. (CRC Press), pp. 47–68.
21. Innes, S., and Lavigne, D.M. (1991). Do cetaceans really have elevated metabolic rates? *Physiol. Zool.* 64, 1130–1134.
22. Kastelein, R.A., van der Sijs, S.J., Staal, C., and Nieuwstraten, S.H. (1997). Blubber thickness in harbour porpoises (*Phocoena phocoena*). In *The Biology of the Harbour Porpoise*, A.J. Read, P.R. Wiepkema, and P.E. Nachtigall, eds. (De Spil Publishers), pp. 179–199.