

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

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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

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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 digital tags (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](#)

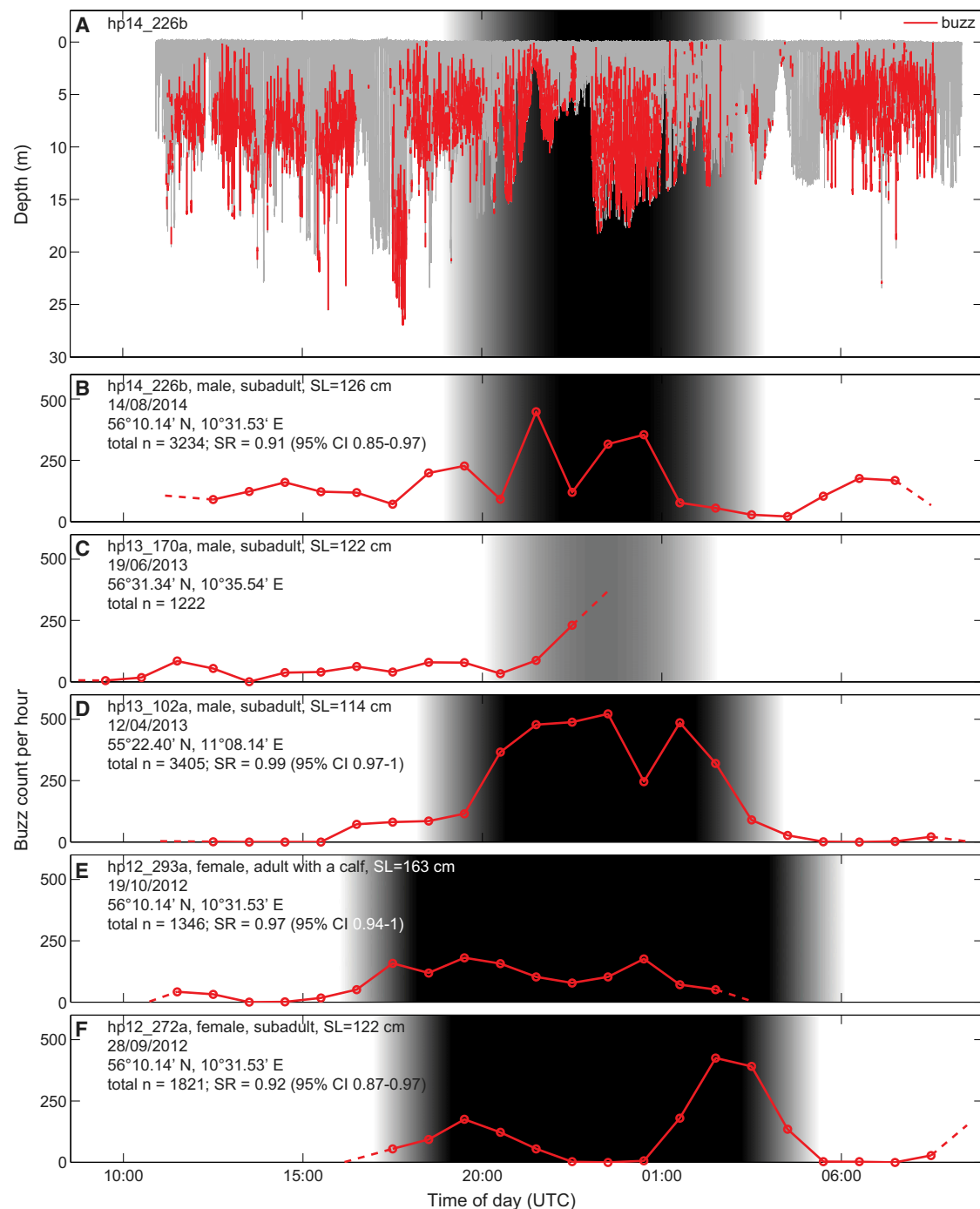


Figure 1. Buzz Rates Indicative of Prey Encounter Rates of Echolocating Harbor Porpoises

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

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

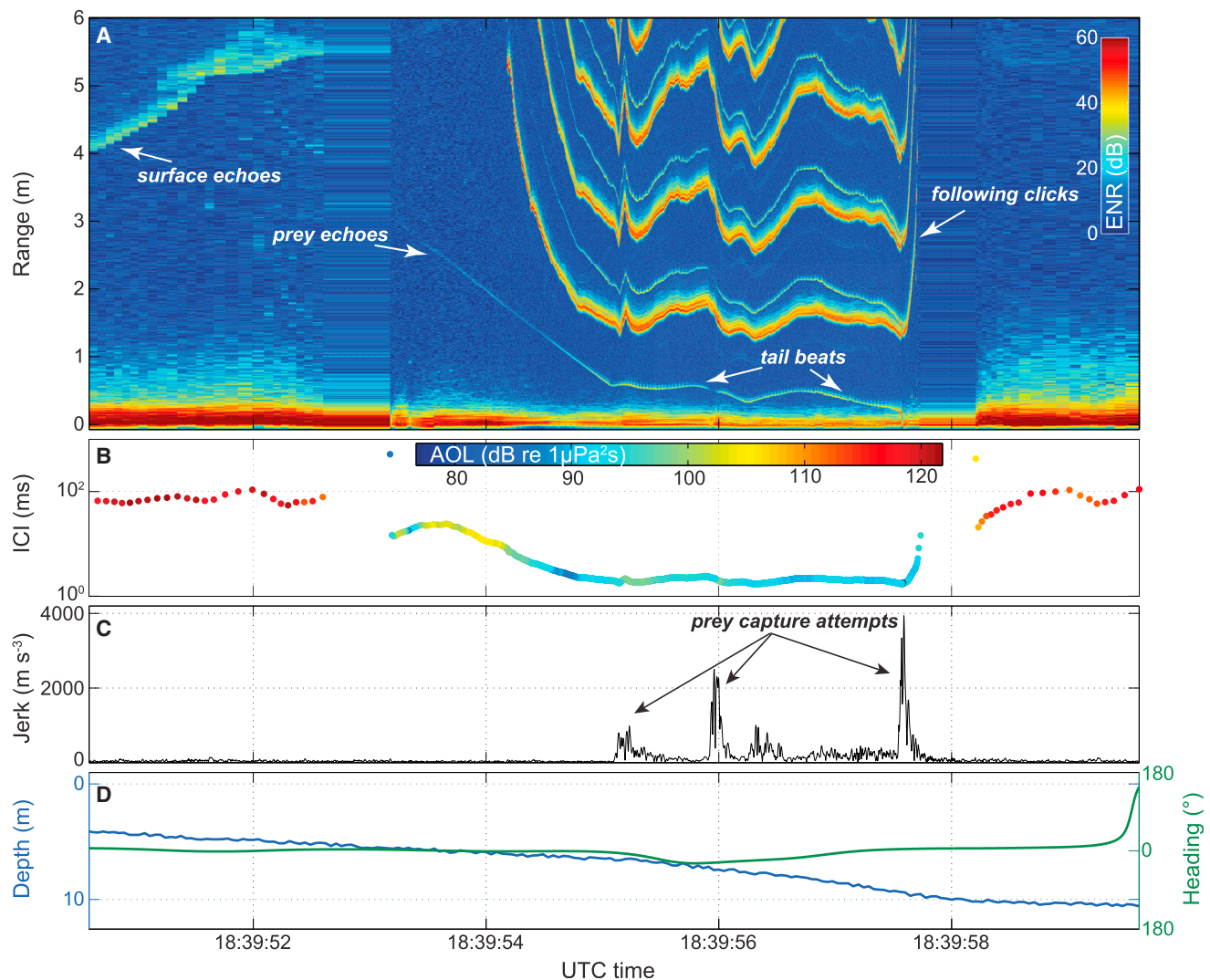


Figure 2. Approach and Probable Capture of a Prey by a Harbor Porpoise

(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 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. (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.

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

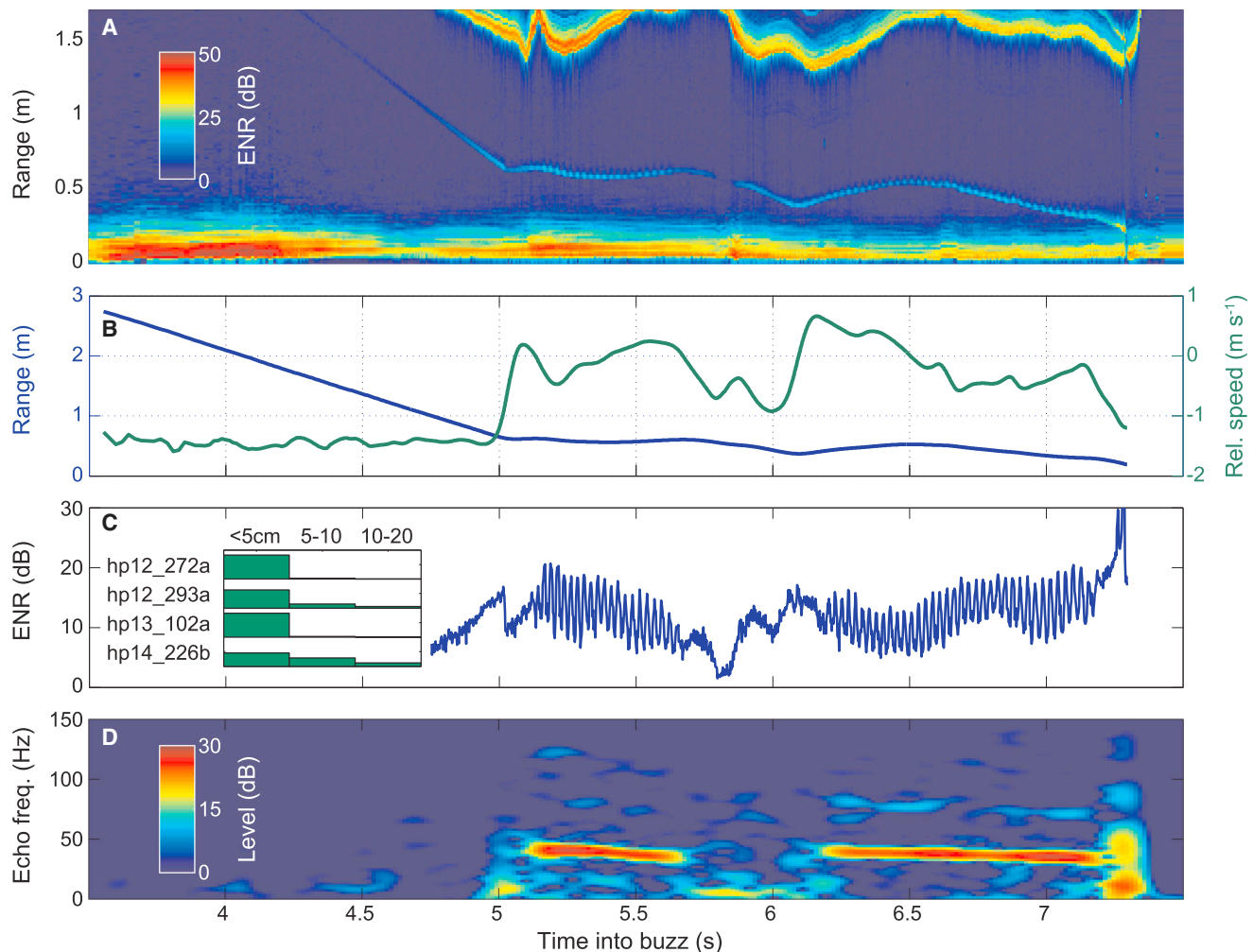


Figure 3. Determination of Prey Behavior and Size

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

(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 (BL) 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.

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 also 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.

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.

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Supplemental Information

Ultra-High Foraging Rates of Harbor Porpoises

Make Them Vulnerable to Anthropogenic Disturbance

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Supplemental Table

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 echograms for each animal were evaluated for capture success. Echograms without clear prey echoes or judged inconclusive were treated as missing data. A sensitivity analysis explored three scenarios for the behaviour of the missing data: 1) all uncategorised buzzes were failures; 2) all uncategorized buzzes were successes; 3) the uncategorised 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. See also Supplemental Experimental Procedures.

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

Supplemental Experimental Procedures

Data collection

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

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

Data analysis

Buzz count

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

Prey capture success rate

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

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

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

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

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

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

Prey size estimation

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

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

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