Science Advances

Supplementary Materials for

Cheap gulp foraging of a giga-predator enables efficient exploitation of sparse prey

Simone K. A. Videsen et al.

Corresponding author: Peter T. Madsen, peter.madsen@bio.au.dk

Sci. Adv. **9**, eade3889 (2023) DOI: 10.1126/sciadv.ade3889

The PDF file includes:

Supplementary Text Figs. S1 to S14 Table S1 Legends for audio S1 to S3 Legends for movies S1 to S6 Legend for data S1 References

Other Supplementary Material for this manuscript includes the following:

Audio S1 to S3 Movies S1 to S6 Data S1

Scaling of lunge costs

Humpback whales are among the smaller rorqual whales and are hypothesized to have both smaller mass specific and absolute costs associated with feeding lunges compared to the larger fin (Balaenoptera physalus) and blue whales (Balaenoptera musculus) (6, 27, 83-86). This is due both to their smaller size and the allometric increase in mass-engulfment capacity in larger rorquals, which increases their mechanical costs of lunging (6, 87, 88). To investigate whether the humpback whales from this study were performing cheaper lunges mass specifically than the larger fin and blue whales we compared our data to that of one tagged fin whale tagged off Tasiilaq, East Greenland during September 2017, with 28.7 hours of tag data (Fig. S13) and two blue whales from a previous published study (bw180827-46 and bw180905-53) (Fig. S14) (29, 89). The same methodology for breath and lunge detection was implemented as previously described. Even though the data consists of only three whales, these show a very similar trend in relative lunge cost compared to that of humpback whales (Fig. S10, Fig. 2). Using the same modelling approach as we used with humpback whales (glmmPQL, poisson family, log link and corrected for autocorrelation but with no random effect of ID since N=1 or 2), the results were: for the fin whale, $log(breaths) = 4.1162+0.007753 \cdot lunges)$, slope = 0.53 (estimated from minimum and maximum values) and for the blue whales $\log(breaths) = 3.4591+0.01528 \cdot lunges)$, slope = 0.56 (estimated from minimum and maximum values). When estimating the absolute cost of a lunge for the fin and blue whales we used the same procedure as for humpback whales but used a body mass of 45t for fin whales (55, 90) and 100t for blue whales (55) to calculate TLC (eq. 2). This resulted in estimates for the maximum energy invested in performing a lunge of 1.35MJ for fin whales and 2.98MJ for blue whales, thus the absolute break-even costs increased as expected for these larger whales, but the mass specific costs are very similar. However, as fin and blue whales have a larger engulfment capacity than humpback whales with a mean of $41m^3$ and $86m^3$ respectively (11, 27), the density of prey can be as low as 0.01kg m⁻³ and still meet the maximum break-even cost of lunging (~396g of krill for fin whales and ~872g of krill for blue whales), assuming an energetic value for krill of 3800kj kg⁻¹ (9, 74). Thus, the estimated break-even prey density for the tagged fin and blue whales is slightly smaller than the value estimated for the larger set of humpback whales in our study. When computing the mechanical work done, it appears that the tagged fin and blue whales with an estimated weight of 45t and 100t perform maximum mechanical work of around 7.5 J/kg, which is slightly smaller, but comparable to the maximum value we estimate for the tagged humpback whales of 8.3J/kg.



Fig S1. Lunge detection from multi-sensor tag data.

A) dive profile of a humpback whale (mn08_146a) with detected lunges (red circles), B) spectrogram of the sound recording for the same time segment (FFT length: 4096 samples at 96 kHz sampling rate, overlap: 80%, Hann window), C) jerk signal of lunges calculated from accelerometer data, and D) roll and pitch angles during lunge events calculated from accelerometer data.



Fig. S2 Breaths sounds of tagged whale. Section of dive profile for mn10_146a showing breath sounds with associated jerk peaks (blue triangles). This figure has an accompanying sound clip (Audio S1). A) dive depth in meters showing a surfacing interval followed by a dive descent, B) the jerk values over the same interval, and C) the corresponding spectrogram for the recorded sound (FFT length: 2048 samples at 96 kHz sampling rate, overlap: 50%, Hann window).



Fig. S3 Breath sounds of tagged whale and conspecifics. Section of audio data for mn10_132a showing breath sounds recorded from both the tagged whale and other nearby animals. Only the breaths of the tagged whale are apparent in the jerk (marked by blue triangles). This figure has an accompanying sound clip (Audio S2). A) shows the dive depth of the tagged whale confirming that it is at the surface, B) jerk values for the same time interval C) spectrogram for the recorded sound (FFT length: 2048 samples at 64 kHz sampling rate, overlap: 50%, Hann window).



Fig. S4 Breaths of a tagged swimming whale. Section of dive profile of mn10_155a showing an interval of near-surface travel with breaths at each surfacing (Audio S3). A) dive depth, B) corresponding jerk (breaths marked with blue triangles) and C) spectrogram of the recorded sound (FFT length: 2048 samples at 96 kHz sampling rate, overlap: 50%, Hann window).



Fig. S5. Autocorrelation function of model residuals showing the temporal correlation. (A) Before and (B) after the inclusion of an auto-regressive structure of lag 1 (AR1) in the GLMM.



Fig. S6. Histogram of model residuals from the GLMM. Residuals for hourly segments with no lunges are shown in red and segments with lunges are shown in white.



Fig. S7. PaCO₂ distribution in relation to body weight. Data and plot from (67) (red dots), with a histogram of our modelled EO₂ (the fractional oxygen uptake), using eq. 6, superimposed. Weddell seal (*Leptonychotes weddellii*) (91), bottlenose dolphins (*Tursiops truncatus*) (42, 53, 92), California sea lion (*Zalophus californianus*) (93), Patagonia sea lion (*Otaria flavescens*) (94), Grey seal (*Halichoerus grypus*) (95) and harbor porpoise (*Phocoena phocoena*) (54) (blue dots).



Fig. S8 Yearly life cycle of a humpback whale. The circle represents a year of a humpback whale's life. Each plot depicts estimated probable distributions of breathing rate (96). The grey dots in feeding and breeding ground plots represent measured breathing rates in this study and in a previous study (15). Respiration data have not been measured during migration.



Fig. S9 Calculated FMR on feeding grounds versus lunge rate extrapolated to 24hr. Each point represents the calculated field metabolic rate (FMR) for each tagged whale in Table S1, and the number of lunges detected in the accelerometer and depth data.



Fig. S10 The relationship between hourly lunge and breath rates for tagged humpback, fin and blue whales. Data come from 23 humpback whales (grey), a single fin whale (tagged for 28.7 hours off Tasiilaq, Greenland, green), and two blue whales (*89*) (blue).



Fig. S11. Estimated FMR of free-swimming humpback whales compared to scaling equations proposed for marine mammals. Violin plot of daily average field metabolic rate of 30t humpback whales is based on our estimated annual energy expenditure (Fig. 3). Blue dot shows estimated daily FMR of humpback whales targeting krill in the eastern North Pacific and the red dot shows estimated daily FMR of humpback whales off the West Antarctic Peninsula targeting krill (*11*). These two data points arise from yearly prey ingestion and are corrected for somatic growth and reproduction costs and scaled to a 30t whale. Each line represents proposed scaling equations for the FMR of marine mammals (*25, 97, 98*).

Fig. S12. Dive profiles of all tagged humpback whales included in our analysis. The title of each sub-plot corresponds to whale ID in Table S1. The top panel in each figure displays lunge and breath counts in 1 hour time blocks. The lower panel shows the dive profile with detected lunges (red circles).









































Fig. S13. Dive profile of a tagged fin whale. Title of plot corresponds to whale ID. First panel displays lunge and breath counts in 1 hour time blocks. Second panel shows the dive profile with lunges (red circles).



Fig. S14. Dive profile of tagged blue whales (89). Title of plot corresponds to whale ID. First panel displays lunge and breath counts in 1 hour time blocks. Second panel shows the dive profile with lunges (red circles).

Table S1.

Whale ID	Tagging	Tag	Analyzed	Breathing	Lunge rate
	location	deployment	data interval	rate (min ⁻¹)	(h^{-1})
		duration (h)	(start-end, s)		
Mn07_192a	Nuuk fjord,	4.9	3600-17550	1.21	20.9
	Greenland				
Mn07_203a	Nuuk fjord,	24.3	3600-87399	0.77	13.5
	Greenland				
Mn08_146a	Nuuk fjord,	5.8	3600-20984	1.27	29.4
	Greenland				
Mn08_152a	Nuuk fjord,	4.9	3600-17525	1.90	55.8
	Greenland				
Mn08_153a	Nuuk fjord,	5.9	3600-21071	1.68	46.8
	Greenland				
Mn08_155a	Nuuk fjord,	4.8	3600-17126	1.53	38.1
	Greenland				
Mn08_156a	Nuuk fjord,	5.8	3600-21038	1.27	28.5
	Greenland				
Mn08_158a	Nuuk fjord,	3.6	3600-12857	1.68	44.3
	Greenland				
Mn08_160a	Nuuk fjord,	5.3	3600-18923	1.71	37.6
	Greenland				
Mn10_133a	Wilhelmina	22.7	13900-81859	1.01	19.1
	Bay, Antarctica				
Mn10_139a	Wilhelmina	20.7	3600-74564	1.24	38.7
	Bay, Antarctica				
Mn10_144a	Wilhelmina	17.9	3600-64560	1.57	60.7
	Bay, Antarctica				
Mn10_146a	Wilhelmina	20	31132-71912	0.94	15.4
	Bay, Antarctica				
Mn10_151a	Wilhelmina	20.3	19000-73190	1.19	26.2
	Bay, Antarctica				
Mn10_155a	Wilhelmina	24.1	3600-86827	0.89	14.5
	Bay, Antarctica				
Mn10_155b	Wilhelmina	21.9	3600-78730	1.12	3.3
	Bay, Antarctica				
Mn12_179a	Disko bay,	6.4	3600-22952	1.49	2.4
	Greenland				
Mn12_180a	Disko bay,	6.4	3600-23213	0.77	2.2
	Greenland				
Mn12_184a	Disko bay,	7.2	3600-26032	1.27	6.9
	Greenland				
Mn12_185a	Disko bay,	11.1	3600-40056	1.01	43.9
	Greenland				

Tag deployment details and data overview

Mn17_251a	Tasiilaq,	34.9	3600-116457	1.04	9.8
44	Greenland				
Mn17_255a	Tasiilaq,	32.3	3600-97060	1.05	13
42	Greenland				
Mn17_255b	Tasiilaq,	26.9	3600-125889	1.18	14.7
43	Greenland				

Movie S1.

Onboard video of a bottom lunge. All video samples were recorded with a CATS tag on humpback whales.

Movie S2.

Onboard video of a bubble-net lunge.

Movie S3.

Onboard video of a lunge feeding on fish.

Movie S4.

Onboard video of a lunge with dense prey.

Movie S5.

Onboard video of a whale swimming and breathing.

Movie S6.

Onboard video of a logging whale breathing.

Audio S1.

Breath sounds recorded by a Dtag attached to a logging humpback whale.

Audio S2.

Breath sounds from the tagged whale and nearby conspecifics recorded by a Dtag.

Audio S3.

Breath sounds recorded by a Dtag attached to a travelling humpback whale.

Data S1

Hourly counts of lunges and breaths for each individual whale

REFERENCES AND NOTES

- J. A. Goldbogen, P. T. Madsen, The evolution of foraging capacity and gigantism in cetaceans. *J. Exp. Biol.* 221, jeb166033 (2018).
- G. J. Slater, J. A. Goldbogen, N. D. Pyenson, Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proc. R. Soc. B Biol. Sci.* 284, 20170546 (2017).
- R. E. Shadwick, J. Potvin, J. A. Goldbogen, Lunge feeding in Rorqual Whales. *Physiology* 34, 409–418 (2019).
- M. Simon, M. Johnson, P. T. Madsen, Keeping momentum with a mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *J. Exp. Biol.* 215, 3786–3798 (2012).
- D. E. Cade, A. S. Friedlaender, J. Calambokidis, J. A. Goldbogen, Kinematic Diversity in Rorqual Whale Feeding Mechanisms. *Curr. Biol.* 26, 2617–2624 (2016).
- J. A. Goldbogen, J. Calambokidis, D. A. Croll, M. F. McKenna, E. Oleson, J. Potvin, N. D. Pyenson, G. Schorr, R. E. Shadwick, B. R. Tershy, Scaling of lunge-feeding performance in rorqual whales: Mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Funct. Ecol.* 26, 216–226 (2012).
- A. Acevedo-Gutiérrez, D. A. Croll, B. R. Tershy, High feeding costs limit dive time in the largest whales. J. Exp. Biol. 205, 1747–1753 (2002).
- J. A. Goldbogen, J. Calambokidis, D. A. Croll, J. T. Harvey, K. M. Newton, E. M. Oleson, G. Schorr, R. E. Shadwick, Foraging behavior of humpback whales: Kinematic and respiratory patterns suggest a high cost for a lunge. *J. Exp. Biol.* 211, 3712–3719 (2008).
- J. A. Goldbogen, D. E. Cade, D. M. Wisniewska, J. Potvin, P. S. Segre, M. S. Savoca, E. L. Hazen, M. F. Czapanskiy, S. R. Kahane-Rapport, S. L. DeRuiter, S. Gero, P. Tønnesen, W. T. Gough, M. B. Hanson, M. M. Holt, F. H. Jensen, M. Simon, A. K. Stimpert, P. Arranz, D. W. Johnston, D. P. Nowacek, S. E. Parks, F. Visser, A. S. Friedlaender, P. L. Tyack, P. T. Madsen, N. D. Pyenson, Why

whales are big but not bigger: Physiological drivers and ecological limits in the age of ocean giants. *Science* **366**, 1367–1372 (2019).

- M. F. Czapanskiy, M. S. Savoca, W. T. Gough, P. S. Segre, D. M. Wisniewska, D. E. Cade, J. A. Goldbogen, Modelling short-term energetic costs of sonar disturbance to cetaceans using high-resolution foraging data. *J. Appl. Ecol.* 58, 1643–1657 (2021).
- M. S. Savoca, M. F. Czapanskiy, S. R. Kahane-Rapport, W. T. Gough, J. A. Fahlbusch, K. C. Bierlich, P. S. Segre, J. Di Clemente, G. S. Penry, D. N. Wiley, J. Calambokidis, D. P. Nowacek, D. W. Johnston, N. D. Pyenson, A. S. Friedlaender, E. L. Hazen, J. A. Goldbogen, Baleen whale prey consumption based on high-resolution foraging measurements. *Nature* **599**, 85–90 (2021).
- C. Lockyer, Growth and energy budgets of large baleen whales from the Southern Hemisphere, in Mammals in the Seas (FAO Fish. Ser. no. 5, 1981) vol. 3, pp. 379–487.
- 13. L. Ratnarajah, A. R. Bowie, D. Lannuzel, K. M. Meiners, S. Nicol, The biogeochemical role of baleen whales and krill in Southern Ocean nutrient cycling. *PLOS ONE* **9**, e114067 (2014).
- 14. J. Roman, J. J. McCarthy, The Whale Pump: Marine Mammals Enhance Primary Productivity in a Coastal Basin. *PLOS ONE* **5**, e13255 (2010).
- 15. L. Bejder, S. Videsen, L. Hermannsen, M. Simon, D. Hanf, P. T. Madsen, Low energy expenditure and resting behaviour of humpback whale mother-calf pairs highlights conservation importance of sheltered breeding areas. *Sci. Rep.* **9**, 771 (2019).
- 16. A. Fahlman, J. van der Hoop, M. J. Moore, G. Levine, J. Rocho-Levine, M. Brodsky, Estimating energetics in cetaceans from respiratory frequency: Why we need to understand physiology. *Biol. Open* 5, 436–442 (2016).
- N. C. Heglund, M. A. Fedak, C. R. Taylor, G. A. Cavagna, Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57–66 (1982).

- P. S. Segre, J. Potvin, D. E. Cade, J. Calambokidis, J. Di Clemente, F. E. Fish, A. S. Friedlaender, W. T. Gough, S. R. Kahane-Rapport, C. Oliveira, S. E. Parks, G. S. Penry, M. Simon, A. K. Stimpert, D. N. Wiley, K. C. Bierlich, P. T. Madsen, J. A. Goldbogen, Energetic and physical limitations on the breaching performance of large whales. *eLife* 9, e51760 (2020).
- P.-E. Mårtensson, E. S. Nordøy, A. S. Blix, Digestibility of krill (Euphausia superba and Thysanoessa sp.) in minke whales (Balaenoptera acutorostrata) and crabeater seals (Lobodon carcinophagus). *Br. J. Nutr.* **72**, 713–716 (1994).
- W. T. Gough, D. E. Cade, M. F. Czapanskiy, J. Potvin, F. E. Fish, S. R. Kahane-Rapport, M. S. Savoca, K. C. Bierlich, D. W. Johnston, A. S. Friedlaender, A. Szabo, L. Bejder, J. A. Goldbogen, Fast and Furious: Energetic Tradeoffs and Scaling of High-Speed Foraging in Rorqual Whales. *Integr. Org. Biol.* 4, obac038 (2022).
- E. M. Chenoweth, K. M. Boswell, A. S. Friedlaender, M. V. McPhee, J. A. Burrows, R. A. Heintz, J. M. Straley, Confronting assumptions about prey selection by lunge-feeding whales using a process-based model. *Funct. Ecol.* 35, 1722–1734 (2021).
- 22. D. E. Cade, N. Carey, P. Domenici, J. Potvin, J. A. Goldbogen, Predator-informed looming stimulus experiments reveal how large filter feeding whales capture highly maneuverable forage fish. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 472–478 (2020).
- 23. F. Christiansen, A. M. Dujon, K. R. Sprogis, J. P. Y. Arnould, L. Bejder, Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere* 7, e01468 (2016).
- 24. W. H. Dawbin, The seasonal migratory cycle of humpback whales. *Univ. Calif. Press*, 145–170 (1966).
- 25. T. M. Williams, M. Peter-Heide Jørgensen, A. M. Pagano, C. M. Bryce, Hunters versus hunted: New perspectives on the energetic costs of survival at the top of the food chain. *Funct. Ecol.* **34**, 2015–2029 (2020).

- 26. M. Diaz Gomez, D. A. S. Rosen, A. W. Trites, Net energy gained by northern fur seals (Callorhinus ursinus) is impacted more by diet quality than by diet diversity. *Can. J. Zool.* **94**, 123–135 (2016).
- 27. S. R. Kahane-Rapport, J. A. Goldbogen, Allometric scaling of morphology and engulfment capacity in rorqual whales. *J. Morphol.* **279**, 1256–1268 (2018).
- 28. D. P. Nowacek, A. S. Friedlaender, P. N. Halpin, E. L. Hazen, D. W. Johnston, A. J. Read, B. Espinasse, M. Zhou, Y. Zhu, Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLOS ONE* 6, e19173 (2011).
- D. E. Cade, S. M. Seakamela, K. P. Findlay, J. Fukunaga, S. R. Kahane-Rapport, J. D. Warren, J. Calambokidis, J. A. Fahlbusch, A. S. Friedlaender, E. L. Hazen, D. Kotze, S. McCue, M. Meÿer, W. K. Oestreich, M. G. Oudejans, C. Wilke, J. A. Goldbogen, Predator-scale spatial analysis of intrapatch prey distribution reveals the energetic drivers of rorqual whale super-group formation. *Funct. Ecol.* 35, 894–908 (2021).
- 30. M. Bejder, D. W. Johnston, J. Smith, A. S. Friedlaender, L. Bejder, Embracing conservation success of recovering humpback whale populations: Evaluating the case for downlisting their conservation status in Australia. *Mar. Policy* 66, 137–141 (2016).
- 31. P. Stevick, J. Allen, P. Clapham, N. Friday, S. Katona, F. Larsen, J. Lien, D. Mattila, P. Palsbøll, J. Sigurjónsson, T. Smith, N. Øien, P. Hammond, North Atlantic humpback whale abundance and rate of increase four decades after protection from whaling. *Mar. Ecol. Prog. Ser.* 258, 263–273 (2003).
- 32. A. S. Friedlaender, R. B. Tyson, A. K. Stimpert, A. J. Read, D. P. Nowacek, Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Mar. Ecol. Prog. Ser.* **494**, 281–289 (2013).
- 33. S. K. A. Videsen, M. Simon, M. Johnson, P. T. Madsen, F. Christiansen, Cryptic vocal behavior of foraging humpback whales on feeding grounds in West Greenland. J. Acoust. Soc. Am. 150, 2879– 2887 (2021).

- L. M. M. López, P. J. O. Miller, N. Aguilar de Soto, M. Johnson, Gait switches in deep-diving beaked whales: Biomechanical strategies for long-duration dives. *J. Exp. Biol.* 218, 1325–1338 (2015).
- 35. D. E. Cade, S. R. Kahane-Rapport, B. Wallis, J. A. Goldbogen, A. S. Friedlaender, Evidence for size-selective predation by Antarctic humpback whales. *Front. Mar. Sci.* **9**, 747788 (2022).
- 36. P. J. O. Miller, A. D. Shapiro, V. B. Deecke, The diving behaviour of mammal-eating killer whales (Orcinus orca): Variations with ecological not physiological factors. *Can. J. Zool.* 88, 1103–1112 (2010).
- 37. S. Isojunno, D. Sadykova, S. DeRuiter, C. Curé, F. Visser, L. Thomas, P. J. O. Miller, C. M. Harris, Individual, ecological, and anthropogenic influences on activity budgets of long-finned pilot whales. *Ecosphere* 8, e02044 (2017).
- 38. W. F. Dolphin, Ventilation and dive patterns of humpback whales, Megaptera novaeangliae, on their Alaskan feeding grounds. *Can. J. Zool.* **65**, 83–90 (1987).
- 39. A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, G. M. Smith, *Mixed Effects models and Extensions in Ecology with R* (Statistics for Biology and Health, Springer New York, 2009).
- 40. W. N. Venables, B. D. Ripley, *Modern Applied Statistics with S* (Statistics and Computing, Springer New York, 2002).
- 41. T. M. Williams, T. L. Kendall, B. P. Richter, C. R. Ribeiro-French, J. S. John, K. L. Odell, B. A. Losch, D. A. Feuerbach, M. A. Stamper, Swimming and diving energetics in dolphins: A stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. *J. Exp. Biol.* 220, 1135–1145 (2017).
- 42. A. Fahlman, S. H. Loring, G. Levine, J. Rocho-Levine, T. Austin, M. Brodsky, Lung mechanics and pulmonary function testing in cetaceans. *J. Exp. Biol.* **218**, 2030–2038 (2015).
- 43. A. Fahlman, M. J. Moore, D. Garcia-Parraga, Respiratory function and mechanics in pinnipeds and cetaceans. *J. Exp. Biol.* **220**, 1761–1773 (2017).

- 44. E. A. Wahrenbrock, G. F. Maruschak, R. Elsner, D. W. Kenney, Respiration and metabolism in two baleen whale calves. *Mar. Fish. Rev.* **36**, 3–8 (1974).
- 45. J. L. Sumich, Direct and indirect measures of oxygen extraction, tidal lung volumes and respiratory rates in a rehabilitating gray whale calf. *Aquat. Mamm.* **27**, 279–283 (2001).
- 46. A. Krogh, Physiology of the Blue Whale. Nature 133, 635–637 (1934).
- 47. A. J. Armstrong, W. R. Siegfried, Consumption of antarctic krill by minke whales. *Antarct. Sci.* **3**, 13–18 (1991).
- A. S. Blix, L. P. Folkow, Daily energy expenditure in free living minke whales. *Acta Physiol. Scand.* 153, 61–66 (1995).
- F. Christiansen, M. H. Rasmussen, D. Lusseau, Inferring energy expenditure from respiration rates in minke whales to measure the effects of whale watching boat interactions. *J. Exp. Mar. Biol. Ecol.* 459, 96–104 (2014).
- 50. W. F. Dolphin, Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. *Can. J. Zool.* **65**, 354–362 (1987).
- 51. P. F. Scholander, Experimental investigations on the respiratory function in diving mammals and birds. *I kommisjon hos Jacob Dybwad.* **22** (1940).
- L. Rojano-Doñate, B. I. McDonald, D. M. Wisniewska, M. Johnson, J. Teilmann, M. Wahlberg, J. Højer-Kristensen, P. T. Madsen, High field metabolic rates of wild harbour porpoises. *J. Exp. Biol.* 221, jeb185827 (2018).
- 53. S. H. Ridgway, B. L. Scronce, J. Kanwisher, Respiration and deep diving in the bottlenose porpoise. *Science* **166**, 1651–1654 (1969).
- 54. J. Z. Reed, C. Chambers, C. J. Hunter, C. Lockyer, R. Kastelein, M. A. Fedak, R. G. Boutilier, Gas exchange and heart rate in the harbour porpoise, Phocoena phocoena. *J. Comp. Physiol. B.* 170, 1–10 (2000).

- 55. C. Lockyer, Body weights of some species of large whales. ICES J. Mar. Sci. 36, 259–273 (1976).
- G. L. Kooyman, E. E. Sinnett, Mechanical properties of the harbor porpoise lung, Phocoena phocoena. *Respir. Physiol.* 36, 287–300 (1979).
- 57. G. L. Kooyman, Respiratory adaptations in marine mammals. Am. Zool. 13, 457–468 (1973).
- G. L. Kooyman, M. A. Castellini, R. W. Davis, Physiology of diving in marine mammals. *Annu. Rev. Physiol.* 43, 343–356 (1981).
- C. R. Olsen, F. C. Hale, R. Elsner, Mechanics of ventilation in the pilot whale. *Respir. Physiol.* 7, 137–149 (1969).
- 60. M. C. I. Martins, C. Miller, P. Hamilton, J. Robbins, D. P. Zitterbart, M. Moore, Respiration cycle duration and seawater flux through open blowholes of humpback (Megaptera novaeangliae) and North Atlantic right (Eubalaena glacialis) whales. *Mar. Mamm. Sci.* 36, 1160–1179 (2020).
- 61. D. M. Bramble, D. R. Carrier, Running and breathing in mammals. Science 219, 251–256 (1983).
- 62. W. R. Stahl, Scaling of respiratory variables in mammals. J. Appl. Physiol. 22, 453-460 (1967).
- 63. P. J. Ponganis, G. L. Kooyman, M. A. Castellini, Determinants of the aerobic dive limit of Weddell seals: Analysis of diving metabolic rates, postdive end tidal Po₂'s, and blood and muscle oxygen stores. *Physiol. Zool.* 66, 732–749 (1993).
- A. Fahlman, M. Brodsky, S. Miedler, S. Dennison, M. Ivančić, G. Levine, J. Rocho-Levine, M. Manley, J. Rocabert, A. Borque Espinosa, Ventilation and gas exchange before and after voluntary static surface breath-holds in clinically healthy bottlenose dolphins, Tursiops truncatus. *J. Exp. Biol.* 222, jeb192211 (2019).
- 65. N. K. Iversen, H. Malte, E. Baatrup, T. Wang, The normal acid–base status of mice. *Respir. Physiol. Neurobiol.* **180**, 252–257 (2012).
- 66. W. O. Fenn, H. Rahn, A. B. Otis, A theoretical study of the composition of the alveolar air at altitude. *Am. J. Physiol.* **146**, 637–653 (1946).

- J. P. Mortola, J. Seguin, End-tidal CO2 in some aquatic mammals of large size. *Zoology (Jena)* 112, 77–85 (2009).
- 68. J. L. Sumich, Oxygen extraction in free-swimming gray whale calves. *Mar. Mamm. Sci.* **10**, 226–230 (1994).
- 69. J. L. Sumich, Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, Eschrichtius robustus. *Can. J. Zool.* **61**, 647–652 (1983).
- L. P. Folkow, A. S. Blix, Metabolic rates of minke whales (Balaenoptera acutorostrata) in cold water. *Acta Physiol. Scand.* 146, 141–150 (1992).
- 71. A. S. Kennedy, A. N. Zerbini, O. V. Vásquez, N. Gandilhon, P. J. Clapham, O. Adam, Local and migratory movements of humpback whales Atlantic Ocean. *NRC Res. Press.* 18, 9–18 (2014).
- 72. R. G. Chittleborough, Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Mar. Freshw. Res.* 16, 33–128 (1965).
- 73. A. A. Cabrera, E. Schall, M. Bérubé, P. Anderwald, L. Bachmann, S. Berrow, P. B. Best, P. J. Clapham, H. A. Cunha, L. Dalla Rosa, C. Dias, K. P. Findlay, T. Haug, M. P. Heide-Jørgensen, A. R. Hoelzel, K. M. Kovacs, S. Landry, F. Larsen, X. M. Lopes, C. Lydersen, D. K. Mattila, T. Oosting, R. M. Pace, C. Papetti, A. Paspati, L. A. Pastene, R. Prieto, C. Ramp, J. Robbins, R. Sears, E. R. Secchi, M. A. Silva, M. Simon, G. Víkingsson, Ø. Wiig, N. Øien, P. J. Palsbøll, Strong and lasting impacts of past global warming on baleen whales and their prey. *Glob. Chang. Biol.*, 28, 2657–2677 (2022).
- 74. A. Clarke, The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. J. *Exp. Mar. Biol. Ecol.* 43, 221–236 (1980).
- 75. F. R. Merkel, J. F. Linnebjerg, O. G. N. Andersen, N. P. Huffeldt, T. Jansen, R. Hedeholm, M. Frederiksen, Changing winter diet of thick-billed murres (Uria lomvia) in southwest greenland, 1990s versus 2010s. *Can. J. Zool.* **99**, 1080–1088 (2021).

- 76. C. Lockyer, in *Approaches to Marine Mammal Energetics*, A. C. Huntley, D. P. Costa, G. A. J. Worthy, M. A. C. Huntley, Eds. (Society for Marine Mammalogy, 1987), pp. 183–203.
- 77. R. Hedeholm, P. Grønkjær, S. Rysgaard, Energy content and fecundity of capelin (Mallotus villosus) along a 1,500-km latitudinal gradient. *Mar. Biol.* **158**, 1319–1330 (2011).
- W. A. Montevecchi, J. Piatt, Composition and energy contents of mature inshore spawning capelin (*mallotus villosus*): Implications for seabird predators. *Comp. Biochem. Physiol. Part A Physiol.* 78, 15–20 (1984).
- D. Pauly, A. W. Trites, E. Capuli, V. Christensen, Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* 55, 467–481 (1998).
- 80. C. S. Baker, L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley, J. H. Straley, Population characteristics and migration of summer and late-season humpback whales (*Megaptera Novaeangliae*) in southeastern Alaska. *Mar. Mamm. Sci.* 1, 304–323 (1985).
- 81. S. Villegas-Amtmann, L. K. Schwarz, J. L. Sumich, D. P. Costa, D. P. C. Peters, A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* 6, 1–19 (2015).
- C. Lockyer, Review of baleen whale reproduction and implications for management. *Rep. Int. Whal. Comm.* 6, 27–50 (1984).
- J. A. Goldbogen, N. D. Pyenson, R. E. Shadwick, Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* 349, 289–301 (2007).
- 84. J. Potvin, D. E. Cade, A. J. Werth, R. E. Shadwick, J. A. Goldbogen, Rorqual Lunge-Feeding Energetics Near and Away from the Kinematic Threshold of Optimal Efficiency. *Integr. Org. Biol.* 3, obab005 (2021).
- 85. S. R. Kahane-Rapport, M. S. Savoca, D. E. Cade, P. S. Segre, K. C. Bierlich, J. Calambokidis, J. Dale, J. A. Fahlbusch, A. S. Friedlaender, D. W. Johnston, A. J. Werth, J. A. Goldbogen, Lunge filter

feeding biomechanics constrain rorqual foraging ecology across scale. *J. Exp. Biol.* **223**, jeb224196 (2020).

- 86. J. A. Goldbogen, J. Potvin, R. E. Shadwick, Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proc. R. Soc. B Biol. Sci.* 277, 861–868 (2010).
- 87. W. T. Gough, P. S. Segre, K. C. Bierlich, D. E. Cade, J. Potvin, F. E. Fish, J. Dale, J. Di Clemente, A. S. Friedlaender, D. W. Johnston, S. R. Kahane-Rapport, J. Kennedy, J. H. Long, M. Oudejans, G. Penry, M. S. Savoca, M. Simon, S. K. A. Videsen, F. Visser, D. N. Wiley, J. A. Goldbogen, Scaling of swimming performance in baleen whales. *J. Exp. Biol.* **222**, jeb204172 (2019).
- 88. J. Potvin, J. A. Goldbogen, R. E. Shadwick, Metabolic expenditures of lunge feeding rorquals Across scale: Implications for the evolution of filter feeding and the limits to maximum body size. *PLOS ONE* 7, e44854 (2012).
- D. E. Cade et al., Super-group data archive. Stanford Digital Repository (2021); https://purl.stanford.edu/rq794kc6747.
- 90. C. Lockyer, T. Waters, Weights and anatomical measurements of northeastern atlantic fin (*Balaenoptera Physalus*, Linnaeus) and Sei (*B. Borealis*, Lesson) whales. *Mar. Mamm. Sci.* 2, 169– 185 (1986).
- 91. G. L. Kooyman, D. H. Kerem, W. B. Campbell, J. J. Wright, Pulmonary gas exchange in freely diving weddell seals Leptonychotes weddelli. *Respir. Physiol.* **17**, 283–290 (1973).
- 92. A. Fahlman, M. Brodsky, R. Wells, K. McHugh, J. Allen, A. Barleycorn, J. C. Sweeney, D. Fauquier, M. Moore, Field energetics and lung function in wild bottlenose dolphins, *Tursiops truncatus*, in Sarasota bay Florida. *R. Soc. Open Sci.* 5, 171280 (2018).
- 93. A. Fahlman, J. Meegan, A. Borque-Espinosa, E. D. Jensen, Pulmonary function and resting metabolic rates in California sea lions (Zalophus californianus) on land and in water. *Aquat. Mamm.* 46, 67–79 (2020).

- 94. A. Fahlman, J. Madigan, Respiratory function in voluntary participating patagonia sea lions (*Otaria flavescens*) in sternal recumbency. *Front. Physiol.* **7**, 528 (2016).
- 95. J. Z. Reed, C. Chambers, M. A. Fedak, P. J. Butler, Gas exchange of captive freely diving grey seals (Halichoerus grypus). *J. Exp. Biol.* **191**, 1–18 (1994).
- 96. M. Allen, D. Poggiali, K. Whitaker, T. R. Marshall, R. A. Kievit, Raincloud plots: A multi-platform tool for robust data visualization. *Wellcome Open Res.* **4**, 63 (2019).
- 97. M. Kleiber, Metabolic turnover rate: A physiological meaning of the metabolic rate per unit body weight. *J. Theor. Biol.* **53**, 199–204 (1975).
- 98. K. A. Nagy, Field metabolic rate and body size. J. Exp. Biol. 208, 1621–1625 (2005).