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

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The giant orca whales are believed to have a massive food turnover driven by a high-intake lunge feeding style aptly described as the world’s largest biomechanical action. This high-drag feeding behavior is thought to limit dive times and constrain orcas to target only the densest prey patches, making them vulnerable to disturbance and habitat change. Using biologging tags to estimate energy expenditure as a function of feeding rates on 23 humpback whales, we show that lunge feeding is energetically cheap. Such inexpensive foraging means that orcas are flexible in the quality of prey patches they exploit and therefore more resilient to environmental fluctuations and disturbance. As a consequence, the food turnover and hence the ecological role of these marine giants have likely been overestimated.

INTRODUCTION

Orca gigantism evolved some 5 Ma ago in response to increased concentrations of small prey driven by the onset of seasonally intensified upwelling regimes in the ocean (1, 2). Central to this radiation of giga-predators was the evolution of a bulk feeding strategy (1) where tens of tons of water are engulfed in a single mouthful and then filtered in baleen to harvest small fish and zooplankton (Fig. 1). Before opening their parachute-like mouths, lunge feeding orcas must accelerate to 3 to 5 m/s to maximize the engulfed water volume and reduce prey escapes (4, 5). The resulting high kinetic energy is lost as the whale decelerates because of the momentum transferred to the engulfed water as well as the increased drag from the distended body profile (3, 5). The high drag of lunge feeding suggests high foraging costs, and this inference has been used to explain the unusually short dive times of orcas (6–8). Humpback whales (Megaptera novaeangliae), for example, perform foraging dives that are an order of magnitude shorter than the similar-sized sperm whale (Physeter macrocephalus) (9). The predicted high cost of lunge feeding also implies that orcas must selectively target dense, high-quality prey patches. This requires in turn that they are capable of assessing prey patch quality (6), although the sensory modalities to support such assessment remain unknown.

Their extreme body size and apparent reliance on dense prey suggest that orcas may be highly susceptible to feeding disruptions due to climate change, anthropogenic noise, and competition with fisheries (10, 11). Extrapolating the presumed large food turnover of orcas to prewhaling population levels also leads to the conclusion that they exert substantial top-down control on high-latitude marine food chains (11, 12), thereby contributing to global carbon turnover (13). Such cosmopolitan giga-predators may even act as ecosystem engineers, effectively farming prey by nutrient cycling (11, 14). However, these profound ecological top-down effects involve the presumption that lunge feeding in giant orcas is energetically costly, a hypothesis that has not been field-tested. Here, we address that hypothesis by measuring the absolute energetic costs of lunge feeding in humpback whales. As capital breeders, humpback whales must meet their annual energetic requirement during a short foraging period in nutrient-rich, high-latitude foraging grounds (12, 15). We used high-resolution biologging tags to record lunge feeding and breathing rates as a proxy for energy expenditure of humpback whales in two polar feeding areas.

RESULTS AND DISCUSSION

We analyzed 338 hours of high-resolution biologging data from 23 whales containing 6633 lunges and 23,416 breaths (table S1). The energetic cost of lunge feeding was quantified from the relationship between feeding and breathing rates in 1-hour intervals (fig. S12). Compared to whales on the breeding grounds (15), we found that whales on the feeding grounds had elevated breathing rates even when not lunging (generalized linear mixed effects model (GLMM) intercept on feeding ground: 61.2 ± 3.3 breaths hour<sup>−1</sup> versus breeding ground: 42 ± 12 breaths hour<sup>−1</sup> (15), Fig. 2 and fig. S8). However, when feeding, there was only a small increase in breathing rate (mean = 0.58 breath/lunge, Fig. 2) as lunge rate increased for humpback whales in both feeding areas (Fig. 2).

Using a Monte Carlo modeling approach based on estimated distributions of lung tidal volumes and oxygen uptakes (Fig. 3 and fig. S7), we converted breath counts into estimates of energy turnover. We find that the median estimated costs of an average lunge is just 0.77 MJ for a 30-t humpback whale. Even when using the 95% percentile of estimated energy turnover per breath to account for potentially heavier breathing after exercise (16), we find that an average lunge has a maximum metabolic cost of 1 MJ (Fig. 3). If all of this energy is invested in muscle action during the active part of the lunge, a 30-t humpback whale performs maximum
mechanical work of no more than 8.3 J/kg of body mass per lunge (Eq. 8), assuming a muscle efficiency of 25% (17). This is comparable to the mass-specific mechanical work done by a terrestrial animal climbing 87 cm vertically, for example, a human walking up three steps of stairs. As the active part of a lunge lasts 5 to 10 s (4, 5), the mean power output is around 1 Watt/kg (equivalent to a jogging human) when a lunging whale is fluking to gain speed before mouth opening (18). Despite the high speeds and massive water engulfment of lunges, this moderate power output combined with the short active duration of lunges results in low mass-specific energy costs. Consequently, the very short dives of rorquals cannot be explained by the energetic expense of lunge feeding (7) but instead may be a result of proximate epipelagic food that places little selection pressure on high-oxygen stores and prolonged dive times (9).

Converting the median metabolic cost of a lunge of 0.77 MJ into absolute prey mass gives a break-even cost of 225 g of prey using an average value of 3800 kJ kg\(^{-1}\) wet weight (ww) (9, 11) and a digestive efficiency of 90% (19). Thus a 30-t humpback whale expends net zero energy in a lunge that yields merely 225 g of prey in the approximately 21 m\(^3\) of engulfed water (11), equivalent to one capelin m\(^{-3}\) or about 10 krill m\(^{-3}\). Despite the persistent narrative that lunges are highly energetic (4, 6–8, 20), our median lunge cost estimate of 0.77 MJ is within the range of estimates from biomechanical models that report costs between 0.5 and 2.6 MJ per lunge (6, 18, 20–22). Thus, both our field respirometry estimates and biomechanical modeling of acceleration and speed data from biologging show that foraging costs are low in humpback whales despite a high-drag feeding mechanism. Low foraging costs and high engulfment capacity in rorquals mean that these giant predators can feed efficiently on relatively sparse prey. This frees humpback whales from their assumed strict reliance on dense, high-quality prey patches and helps explain the diversity of foraging styles and prey types exploited by this species (5). Given the low break-even ingestion, humpback whales can perhaps even use lunging as a patch assessment tool, obviating the need for sophisticated sensory means to assess prey patch quality.

However, low-cost foraging does not free humpback whales from a time crunch caused by their migratory lifestyle. Humpback whales perform annual long-distance migrations between productive high-latitude feeding grounds and warmer sheltered waters where successful mating and breeding depend on good body condition (23). Because humpback whales scarcely feed on the breeding grounds, the energy spent there is fueled by energy reserves.
that an adult humpback whale performs some 60,000 ± 15,000
that have high mass-specific metabolic rates. Thus, humpback whales exert some top-down control over high-latitude marine food webs, particularly in prewhaling ecosystems, but perhaps no more so than other marine endotherms such as the smaller, but much more abundant sea birds and pinnipeds (11). Our estimated average intake of 3.8 kg/lunge allows for a reevaluation of the prey patch densities required to support feeding humpback whales (11). The engulfment capacity of humpback whales is 15 to 27 m³ with a mean of 21 m³ per lunge (11, 27). Assuming a 50% catch rate of prey (22), an average prey density of 0.37 kg m⁻³ is needed to obtain an average of 3.8 kg of prey per lunge, which is within the observed krill and fish densities in feeding areas (11, 21, 28, 29). Remarkable footage of feeding humpback whales show that they sometimes engulf particularly dense prey patches [movie S4; (22, 29)] to achieve extraordinarily high foraging efficiencies. In these extreme cases, peak densities from echo sounder.
surveys (11, 21, 22, 29) suggest that humpback whales may ingest tens of kilograms of prey per lunge, but our estimated average intake show that such very successful lunges are rare (movies S1 to S3). Instead, food returns per lunge are likely to be log-normally distributed (29) over a season with fewer rich patches interspersed with many more poor ones. Thus, low-cost foraging in humpback whales, and likely other orca species such as fin and blue whales (fig. S10), enables much greater flexibility in foraging behavior than recent studies suggest (10). Rather than lunge feeding representing an evolutionary cul de sac restricting orca foraging strategies to exploit a wide density range of tiny prey species on their high-latitude feeding grounds during short foraging seasons. Such flexibility may make humpback whales less vulnerable to variability in prey patch density due to environmental change or human disturbance (10), perhaps explaining the rapid recovery of many subpopulations from whaling (30, 31).

MATERIALS AND METHODS

Tag data

Between 2007 and 2017 16 adult (>10 m) humpback whales were tagged with digital animal-borne loggers in three locations in Greenland: Nuuk fjord, Disko Bay, and fjords around Tasilaq (table S1). The research in Greenland was carried out under permits issued by The Ministry of Fishing, Hunting and Agriculture, Greenland Self Government to the Greenland Institute of Natural Resources, according to §35 of the executive order no. 12 of 22 December 2014. In addition, seven adult humpback whales were tagged in 2010 in Wilhelmina Bay, on the Western Antarctic Peninsula (table S1). The research in Antarctica was conducted under National Marine Fisheries Service Permit 808-1735, Antarctic Conservation Act Permit 2009-014, and Duke University Institutional Animal Care and Use Committee A049-112-02. The whales were all equipped with noninvasive suction cup tags, either Dtag version 2 or 3 or CATS tags (Customized Animal Tracking Solutions; www.cats.is/cats-cam/). Both tag types recorded continuous high-resolution sensor data from the whale including pressure and accelerometer data (sampling rate Dtag: 50 Hz, 200 Hz; sampling rate CATS tag: 400 Hz). The Dtag also recorded continuous stereo sound (sampling rates: 48, 64, 96, or 120 kHz, 16 bit) from two hydrophones and the CATS tag recorded video from a forward-pointing video camera (1280 × 720p high-definition resolution) during periods with sufficient light. All whales were tagged from a small motorized vessel that approached slowly from behind (4, 32). To minimize effects of behavioral reactions to tagging in the data analysis, the first hour of tag data was excluded from all analyses sensu (10). Tag attachment durations varied between 3.5 and 34.9 hours (table S1). All Dtags were deployed with a preset galvanic
release, but the suction cup–attached tags sometimes came off prematurely because of rubbing, breaching, or high-intensity swimming.

**Detection of lunges**

The short burst of fluking during lunge feeding can be detected by sudden changes in the acceleration recorded by animal–attached tags (4, 8) (fig. S1). An automated detector was used to identify jerk peaks [i.e., transients in the differential of acceleration; see methodology in (33)] in the tag recordings. As other high-intensity activities such as excessive fluking (34), breaching (15, 18), and rubbing also give rise to an increase in jerk signal, every detected jerk peak was inspected for stereotyped changes in pitch and roll sensu (4, 5). Furthermore, foraging lunges were verified if a jerk peak was associated with an increase and rapid decrease in flow noise as the whale accelerates forward and then decelerates (fig. S1) (4). This was checked in all Dtag data by listening to, and inspecting spectrograms of, the corresponding sound recording.

Deployments with CATS tags did not record any sound; therefore, when available, video recordings were used to verify jerk-detected lunges. Video cues for lunges included a visible mouth opening with a simultaneous jerk peak (movies S1 to S4). When video was not available, lunge events were inferred from jerk peaks and changes in pitch and roll (4, 5, 35). For each whale, the tag data were divided into 60-min bins, and for each time bin, the number of lunge events were identified.

**Detection of breaths**

Field and video observations of humpback whales show that they generally breathe every time they surface. Breaths were therefore identified by first detecting every time the whale surfaced (36, 37). The rapid air flow and muscle movements when whales breathe create a jerk transient (i.e., pulse in the differential of acceleration; for example, see movies S5 and S6) that can be detected in the accelerometer data collected by the tags, and this was used to validate breath detections derived from surfacing times. To verify each breath and identify breaths during periods of logging and surface behavior, a 60-s interval of the dive profile with superimposed accelerometer data and jerk together with a spectrogram of the sound was visually and aurally inspected for all Dtag data (15, 36). In case of multiple animals breathing simultaneously, only breath sounds with an associated jerk peak were marked as breaths of the tagged whale (for examples, see figs. S2 to S4, audio S1 to S3, and movies S5 and S6) (8, 15). If breath sounds were masked by high-intensity splashes when surfacing, the whale was presumed to respire if roll and pitch values corresponded to an upright whale (37). Breathing sounds were especially difficult to detect during periods of logging and surface traveling in rough seas because of splash sounds on the tag, which also influenced the jerk signal. These periods of uncertainty were therefore excluded from the analysis, amounting to less than 7% of the data. Only complete continuous 1-hour segments for each animal were analyzed (table S1). Breaths from the three whales tagged with CATS tags were marked in the same way as for the Dtag data. Because no audio was available, marked breaths were validated using video, where either a blow or opening of nostrils were visible (movies S5 and S6). Breathing rates for all whales in the study had an overall median of 1.2 ± 0.31 breaths min⁻¹, which matches well with previously reported breathing rates of 1.15 ± 0.97 breaths min⁻¹ for humpback whales on feeding grounds based on 603.3 hours of visual observations (38).

**Model selection and validation**

Because both the numbers of breaths and lunges per hour are count data, a GLMM with a Poisson error distribution and log link function was developed to investigate the relationship between number of lunges (explanatory variable) and number of breaths (response variable) in hourly time segments. The GLMM was developed in R v.4.0.3 using the glmmpQL function (39) in the Mass package (40). To account for repeated measurements from the same individuals, whale ID was included as a random effect on both the intercept and slope parameters. Model validation tests were performed to ensure that all model assumptions were met. To investigate homogeneity of variance, scatter plots of residuals versus fitted values and residuals versus explanatory variables were visually examined. Normality of residuals was investigated in histograms of residuals. Overdispersion was tested by dividing the residual deviance with the residual degrees of freedom, with a ratio value (dispersion parameter, φ) above 1 indicating overdispersion (the mean of the variance is larger than the mean). There was no sign of overdispersion in our model (φ = 0.82). The data were visually inspected for temporal autocorrelation (nonindependence between data points), using autocorrelation function (ACF) plots, and we found that model residuals were correlated with a lag of 1. To account for this, an AR1 temporal autocorrelation structure with lag 1 was included in the model (fig. S5). The data were also checked for zero inflation by comparing residuals of data subsets with no lunges against data subsets with one or more lunges (fig. S6). Both the conditional (variance explained by the fixed and random effects) and marginal (variance explained by fixed effects only) $R^2$ were calculated for the model. The marginal $R^2$ for the model explained 29% of the variance in the data, whereas the conditional $R^2$ for the model explained 80% of the variance in the data.

**Estimation of energetic turnover per breath**

The oxygen uptake per breath (VO₂breath) is given by the volume of air exchanged in one breath (the so-called tidal volume, $V_T$) and the fraction of the oxygen in the inhaled air the whale takes up (the extraction coefficient, EO₂)

\[
VO_2^{\text{breath}} = V_T \cdot EO_2 \cdot F_{I,O_2}
\]

(1)

where $F_{I,O_2}$ is the fraction of oxygen in atmospheric air of 0.2095. These parameters, or their combination, are readily measured in standard respirometry setups with smaller trained marine mammals using, for example, flow-through respirometry (41) or a pneumotachometer and a fast gas analyzer (42, 43). However, while these methods have been used on young gray whale calves (Eschrichtius robustus) in captivity (44, 45), they are logistically impossible to use on large whales at sea. Accordingly, researchers have pursued means to use Eq. 1 to estimate VO₂breath in large, wild cetaceans by making assumptions about the values of $V_T$ and EO₂ for known or estimated body masses. First used by Krogh (46) and later by others (47–50), this modeling approach often involves the assumption that $V_T$ is a high, fixed value of the total lung capacity (TLC). This notion is based on early observations from restrained and hence perhaps stressed marine mammals (51) that reported $V_T$ values very close to the vital capacity (VC), the maximum possible
Most modeling approaches also assume a high fixed EO tidal volume). While a recent study show that this approach of assuming fixed VT and EO can be unexpectedly accurate in estimating the FMR of harbor porpoises (Phocoena phocoena) (52), it has attracted criticsim for being overly simplistic (16) on the basis of observations from free-moving, trained marine mammals showing that both VT and EO are lower and more dynamic than often assumed (53, 54). Thus, because VT and EO are related to the level of exercise (42) and where the breath is made in the dive cycle (16, 53), it is inherently difficult to reliably estimate the oxygen turnover for any particular breath made by a wild cetacean (16). Nevertheless, because any animal on average must be in physiological steady state, the method of estimating VO2 from the parameters of Eq. 1 lends themselves to quantification of the probability density function of energy turnover per breath for a period of several dive cycles if the appropriate mean and variance of VT and EO can be modeled. Here, we pursue that logic to estimate the energy turnover per breath in wild humpback whales using a Monte Carlo modeling approach, where random samples from the probability density functions of VT and EO are multiplied to form a probability density function of VO2 breath.

Using a standard body mass of 30 t for an adult humpback whale (18, 55), we estimate the TLC from the equation (56)

\[
TLC = 0.135 \cdot M_b^{0.92}
\]

We then estimate the VC (the highest possible VT) to be a high proportion (85%) of TLC sensu (42, 57–59).

\[
VC = 0.85 \cdot TLC
\]

Drone footage of open nares during breaths in wild humpback whales (60) suggests that VT, like for any other breathing mammal (61), is variable. To embrace that variability in our modeling, we created a probability density distribution of VT with a mean of 0.6 of VC sensu (44) and an SD of 150 liters, corresponding to 0.1 of VC, resulting in a 5 to 95% confidence interval for VT from 0.4 to 0.8 of VC (Fig. 3A). Using a mean of 0.6 VC which is about four times the value for resting terrestrial mammals (62) and two times higher than for smaller, free-moving marine mammals (16) may lead to consistent overestimation of VT and hence VO2 per breath in wild humpback whales. However, because we test the hypothesis that lunge feeding is expensive, we deliberately wish to bias toward overestimating lunge costs. Thus, by using a VT distribution from 0.4 to 0.8 of VC, we ensure that the extreme consequences of even the highest consistent VT are propagated in the modeling allowing us to put a maximum cap on VO2 breath.

The extraction coefficient of the lung (EO2) can be up to 80% after prolonged breath holds in diving marine mammals (53, 63) but drops to a quarter of that after a number of breaths during a surfacing interval (64). This complicates the estimation of EO2 for an individual breath in a wild animal, but because the blood pH for any mammal (65) must be stable around 7.4, we can use the lung gas equation to estimate the distribution of average realized EO2 over longer time periods.

The lung gas equation describes the relationship between alveolar CO2 and O2 at a given inspired PO2 and a respiratory gas exchange ratio (R). This was first given by (66)

\[
P_{A}O_2 = P_{I}O_2 - \frac{P_{A}CO_2}{R} + \frac{F_{I}O_2 \cdot P_{A}CO_2 \cdot (1 - R)}{1 - (1 - R)F_{I}O_2}
\]

where P_{A}O2 and P_{A}CO2 are the alveolar oxygen and carbon dioxide partial pressures, P_{I}O2 and F_{I}O2 the inspired oxygen partial pressure and fractional concentration, and R is the respiratory exchange ratio. Assuming that CO2 is in equilibrium across the lung membrane, we can replace P_{A}CO2 with P_{A}O2, and rewriting the original Eq. 4, we get

\[
P_{A}O_2 = P_{I}O_2 - \frac{P_{A}CO_2}{R} \left[ 1 - (1 - R)F_{I}O_2 \right]
\]

The extraction coefficient EO2 is defined in terms of the expired oxygen partial pressure, but because of the high tidal volume, the dead space fraction becomes so low we can write

\[
EO_2 = \frac{P_{I}O_2 - P_{A}O_2}{P_{I}O_2} \approx \frac{P_{I}O_2 - P_{A}O_2}{P_{A}O_2}
\]

Thus, EO2 can be estimated if P_{A}CO2 can be either measured or estimated with reasonable certainty. Direct measurements of P_{A}CO2 in large free-roaming cetaceans is impossible, but here, we exploit the fact that P_{A}CO2 on average is unexpectedly stable across both terrestrial mammals and all measured marine mammals [fig. S7; (67)] between 30 and 56 mmHg. Using Eqs. 5 and 6, these P_{A}CO2 values translate into EO2 values between 0.24 and 0.45. EO2 can for any given breath be both higher and lower, but in the steady-state situation where the blood pH is 7.4 and the body temperature is 37°C, the mean EO2 per breath cannot be higher than 0.35. To estimate VO2 breath, we therefore assume a mean EO2 in our probability density function of 0.35 with 5 and 95% confidence interval of 0.3 and 0.4, consistent with previously measured P_{A}CO2 values (42, 45, 67, 68) (fig. S7). This use of Eqs. 3, 5, and 6 also shows that previous assumptions (47–50, 69, 70) of average EO2 of 0.5 are physiologically untenable.

**Yearly energy expenditure and prey intake in a lunge**

To estimate the yearly prey consumption of free-living humpback whales, we used our measured breathing rates on feeding grounds (median = 1.2 breaths min\(^{-1}\)) and previously published breathing rates on breeding grounds (median = 0.7 breaths min\(^{-1}\)) (fig. S8) (15). Because, to our knowledge, data on breathing rates of migrating humpback whales are unavailable, we assumed that the value for migrating, but largely fasting individuals would be half way between that on feeding grounds and on breeding grounds (median = 0.95 breaths min\(^{-1}\)). This assumption is based on previous observations showing a positive correlation between breathing rate and swim speed in gray whales (E. robustus) (69) and minke whales (Balaenoptera acutorostrata) (49) in conjunction with calculated faster swim speeds for migrating humpback whales compared to when they are on their breeding grounds (71). We then modeled a distribution of each breathing rate with an SD of 0.2 of the mean (fig. S8).

The time spent on feeding, migrating, and breeding during a year has been shown to vary between humpback whale populations, as well as with sex, maturity, and migration routes (24, 71, 72). Thus, the duration of effective feeding (120 days, SD 15 days), migration (145 days, SD 15 days) and breeding (100 days, SD 15 days) periods during a year was modeled to incorporate this variability. Using the
distributions of breathing rates and total times spent in each activity in a year, we estimated the probability distribution of total number \(N_{\text{breath, year}}\) of breaths in a year (Fig. 3F). We then used this to estimate the total yearly FMR distribution by multiplying random samples from the \(N_{\text{breath, year}}\) distribution with random samples from the probability distribution of energetic turnover per breath (Eq. 7).

\[
\text{FMR}_{\text{year}} = N_{\text{breath, year}} \cdot \text{VO}_{2, \text{breath}} \cdot \varepsilon_{\text{O}}
\]  

(7)

Here, \(\varepsilon_{\text{O}}\) is the energetic value of oxygen, which is 20.08 kJ-liter\(^{-1}\). Daily FMR on the feeding ground was calculated in the same fashion using the total number of breaths in a day, \(N_{\text{breath, day}}\) (Fig. 3E).

To convert yearly energy requirements to prey mass, we used the mean energetic value of capelin and krill, two common humpback whale prey types in their feeding areas (35, 73). The prey energetic density of krill varies with species, sex, and time of year (74). For a common Antarctic krill type, \textit{Euphausia superba}, the energetic value has been measured at 3.8 to 5.4 MJ kg\(^{-1}\) ww (9, 74). Similar values were found for krill species in Greenland and Iceland (\textit{Thysanoessa raschii} and \textit{Meganyctiphanes norvegica}) 3.9 to 6.4 MJ kg\(^{-1}\) ww (75, 76) and for two other species of krill (\textit{Thysanoessa spinifera} and \textit{Euphausia pacifica}) 2.94 to 3.8 MJ kg\(^{-1}\) ww (21). For capelin (\textit{Mallotus villosus}, Osmeridae) in Greenland, the energy density is, on average, 4.2 MJ kg\(^{-1}\) ww (77) but can also vary between sex and season (78). Therefore, to account for a mixed diet, we took the average of these two prey energetic values (11, 79). The ingested prey energy further depends on the digestive assimilation coefficient, which in baleen whales, like for other marine mammals, has been estimated to be \(\sim 90\%\) (19). Accounting for the digestive assimilation coefficient, the available energy density per kilo of prey consumed is 3.6 MJ kg\(^{-1}\) (i.e., 4 MJ*0.9). It is important to note that some prey types of humpback whales have a much higher energetic density per kilo [up to 6 to 10 MJ kg\(^{-1}\) (75)] and by targeting these energetic prey a humpback whale would need to ingest less prey mass per lunge and per feeding season (tons) for the same yearly energetic requirement (MJ). If such prey are targeted consistently, we overestimate the prey weights per lunge and yearly-required prey tonnage.

To estimate how much prey a humpback whale needs to ingest on average during a lunge to meet its overall energy costs, we first modeled effective feeding days, i.e., the number of days in which the whale actively feeds while on feeding grounds, with an average of 120 days and an SD of 15 days based on previous observations (11, 80). By dividing random samples from the annual prey requirement distribution in tons by random samples from the modeled distribution of the effective number of feeding days, we can then estimate the distribution of needed daily prey consumption for a pregnant humpback whale on the feeding grounds (6549 ± 1623 MJ, 1.8 ± 0.5 t). To get the required average prey intake per lunge, we divided random samples from the daily prey consumption distribution with random samples from the distribution of number of daily lungen to find that the mean estimated intake per lunge should be around 3.8 kg of mixed prey (13.8 ± 7.4 MJ, 3.8 ± 2 kg) (Fig. 3I). Pregnant female humpback whales will have an increased energy need to fuel the growth of their calf during pregnancy and after birth while lactating. Earlier studies on baleen whales have estimated the cost of gestation and lactation at \(\sim 20\%\) of total energy cost over a 2-year period (81, 82), thus, a pregnant female need to ingest 20% more energy during two subsequent feeding seasons. If we allocate that to extra food consumption during each feeding season then a reproducing female humpback whale needs to ingest 18.8 ± 4.5 t (67,800 ± 16,300 MJ) more prey than a nonreproducing female each feeding season to produce a viable calf every 2 years.

**The cost of a lunge**

The hourly breathing rates of humpback whales increased with increased lunge rates (Fig. 2). The cost (expressed in number of breaths) of performing a lunge can be estimated on the log-scale from the fitted model parameters \[\log (\text{Breaths}) = 4.1134 + 0.0069 \cdot \text{Lunges}\]. When back transforming the predicted values of the GLMM to the arithmetic scale however, the regression line between the relationship between number of breaths and number of lungen becomes curvilinear because of the log-link being used in the model (Fig. 2). To obtain a mean estimate of the cost per lunge, we therefore calculated the overall increase in number of breaths from 0 to 88 lungen (the full range of lunge values observed) and divided it by the maximum number of lungen (i.e., 88), which is equivalent to the slope of a linear regression line fitted between the number of breaths and number of lungen on the arithmetic scale. The estimated slope was 0.58, which corresponds to a marginal lunge cost of 60% the energetic turnover of an average breath. We found the same slopes if we binned the breath and lunge data over 0.5- or 2-hour epochs.

A lung ventilation corresponds to a median energy turnover of 1.33 ± 0.3 MJ (Fig. 3D). To account for heavier breathing during exercise (16), i.e. a high \text{VO}_{2, \text{breath}}, we used the 95% percentile of the distribution of energetic turnover per breath (1.76 MJ) when calculating the maximum cost associated with lunging. The maximum energetic cost of a lunge was thereby calculated to be 1.02 MJ (Cost of lunge = 0.58*energetic turnover per breath of 1.76 MJ) and the median cost calculated to be 0.77 MJ (Cost of lunge = 0.58*energetic turnover per breath of 1.33 MJ). If the whales are digesting while foraging, part of these elevated breathing rates with increasing lunge rates will be due to specific dynamic action costs, but we conservatively assume these to be zero thereby, if anything, overestimating lunge costs.

Assuming an assimilation efficiency of 90% (19), and an average calorific value of prey, the median cost of a lunge corresponds to 225 g of prey or a maximum of 298 g using the 95% [using the average value of 3800 kJ kg\(^{-1}\) krill ww (9, 11, 74)]. If we translate the maximum energetic cost of performing a lunge into muscle action, a 30-t humpback whale would perform mechanical work of about 8.3 J kg\(^{-1}\) of body mass per lunge (Eq. 8), assuming a muscle efficiency of 25%. In comparison, the same mass-specific mechanical work would be done by a terrestrial animal climbing ~87 cm vertically (Eq. 9).

**Mechanical work**

\[
\text{Mechanical work} = \frac{I}{\text{kg}} = \frac{1 \times 10^6 \text{ J}}{30,000 \text{ kg}} \cdot 0.25
\]  

(8)

**Potential energy**

\[
\text{Potential energy} (J) = \text{mass (kg)} \cdot 9.82 \left(\frac{\text{m}}{\text{s}^2}\right) \cdot \text{height (m)}
\]  

(9)

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

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The PDF file includes:

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Legend for data S1
References

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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 whale (*Balaenoptera physalus*) and blue whale (*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·lunges, slope = 0.53 (estimated from minimum and maximum values) and for the blue whales log(breaths) = 3.4591+0.01528·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 41m³ and 86 m³, 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.
Tag deployment details and data overview

<table>
<thead>
<tr>
<th>Whale ID</th>
<th>Tagging location</th>
<th>Tag deployment duration (h)</th>
<th>Analyzed data interval (start-end, s)</th>
<th>Breathing rate (min⁻¹)</th>
<th>Lunge rate (h⁻¹)</th>
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<tbody>
<tr>
<td>Mn07_192a</td>
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</table>
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


51. P. F. Scholander, Experimental investigations on the respiratory function in diving mammals and birds. *I kommisjon hos Jacob Dybwad.* **22** (1940).


