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NOTE

Using audio and UAS-based video for estimating tidal lung volumes of resting and active adult gray whales (*Eschrichtius robustus*)

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Understanding how a species' metabolic rate varies in different behavioral contexts is useful in filling a variety of knowledge gaps, from quantifying prey requirements and foraging efficiencies of individuals to estimating total resource requirements of populations and to detecting impacts of anthropogenic disturbances. Survey responses reported by McHuron et al. (2022) have ranked field metabolic rates (FMR) as a key critical question to be addressed in future marine mammal energetic studies. FMR represent daily means of short-term estimates of O_2 consumption rates, \dot{V}_{O_2} . This in turn can be calculated as the products of three ventilatory variables: tidal lung volume (V_T , the volume of air exchanged with each breath), f_v ventilation frequency) and ΔO_2 (% O_2 extraction of inhaled air). Tidal lung volume represents some variable fraction of an animal's total lung capacity and is the subject of this study.

Here we describe a novel approach to estimate V_T of actively foraging adult gray whales and compare those to V_T estimates of gray whales studied in Laguna San Ignacio, Baja California Sur, Mexico, a winter breeding/calving lagoon, 1978–1985. Foraging whales were monitored in shallow coastal waters along the central Oregon coast with unoccupied aircraft systems (UAS) during summer, 2016–2020. These foraging whales are members of a

subset of the Eastern North Pacific gray whale population known as the Pacific Coast Feeding Group (PCFG). Adult status of foraging whales was assumed if body lengths (L_b) were greater than 10.5 m (Rice & Wolman, 1971). All monitored winter lagoon whales were observed in close association with calves of the year and were considered to be adult females, fasting and lactating (Rice & Wolman, 1971). These females were monitored from small boats as they "logged" at the surface or swam slowly against tidal currents, and were assumed to be in a resting state, as the metabolic costs associated with milk production, exclusive of the energy value of its lipid content, are assumed to be negligible (Costa & Gentry, 1986; McHuron et al., 2023).

Ventilatory behaviors of gray whales typically include very rapid exhalation/inhalation events as they surface, followed by submerged breath holds of varying duration and depth. During inhalation, intercostal and diaphragm muscles stretch elastic lung and diaphragm tissues that rapidly recoil during exhalation ((Piscitelli et al., 2013) to produce and maintain high ventilatory air flow rates through most of inhalation and exhalation durations. In previous studies, direct spirometry was used to measure exhalation and inhalation durations, ventilatory flow rates and tidal lung volumes (V_T) of four temporarily restrained young gray whales (Figure 1), including two calves

temporarily stranded in a winter lagoon (Kooyman et al., 1975) and two calves held in human care at SeaWorld, San Diego for more than a year each (Gigi II in 1971-1972 and JJ in 1997-1998; Sumich, 2001; Wahrenbrock et al., 1974). All four whales were partially submerged during sampling and were breathing voluntarily. The effects, if any, of partial stranding on the subject whales' ventilatory mechanics are unknown, but are assumed to be less for the young subject animals than for adults.

Sumich and May (2009) have previously shown that, for all four whales' measured V_T values, when pooled, were found to vary directly with the square of body length (L_b) and with the exhalation durations of (t_{EX} ; Equation 1). In Figure 2, the eight individual sampling regressions that were pooled by Sumich and May (2009) are plotted as separate linear regressions indicating no apparent allometric change with increasing body size.

$$V_T = -7.24 \cdot 2.14 \cdot t_{EX} \cdot L_b^2; \quad r^2 = 0.92 \quad (1)$$

Extrapolating allometric relationships from young animals to adults can be problematic. However, the high r^2 value of Equation 1, the similarity of the regressions plotted in Figure 2 over a five-fold range of body masses (1,175-6,026 kg) and the similar $t_{EX}:L_b$ ratios of approximately 0.1 for active calves ($L_b = 5-7$ m; Sumich, 2021) and adults (see Table 1 and Figure 4 below)

all support our extrapolation of Equation 1 to estimate V_T of adult-sized gray whales.

In a PCFG summer foraging area along the central Oregon coast, video recordings and photogrammetric body lengths (L_b) of PCFG whales were obtained using UAS conducted for other unrelated studies (unpublished data; see Torres et al., 2022 for methods). Only video clips that included 10 or more sequential surfacing events of foraging whales were analyzed.

For a total of 299 surfacing events, we measured the duration of each surfacing from the beginning of the exhale to the end of the immediately following inhale. As the nares in the middle of most surfacing events were obscured by the whale's blow and transitions from exhale to inhale could not be seen (Figure 3), we assumed that, over several successive ventilatory events, t_{EX} equaled each surfacing duration divided by 2.

To test that assumption, we examined all 20 of the 299 individual surfacing events from 19 foraging whales that clearly showed the middle portions of the surfacing events not obscured by the blow to determine if there was an observable change in the shape of the nares that might indicate the transition from an exhale to an inhale, as described by Nazario et al. (2022) for minke (*Balaenoptera bonaerensis*) and humpback (*Megaptera novaeangliae*) whales. We observed that the nares are elongated

during the exhale and visibly flared and widened at the presumed transition point from exhale to inhale. We noted the time stamp of each observed transition point and compared it to the time stamp of the actual midpoint of the same exhalation/inhalation surfacing event. We found no significant difference between the time of observed changes in the appearance of the nares and the actual mid-point times (mean difference = 0.005 s, $t = 0.1059$, $p = .918$, 95% CI[-0.09, 0.10]; Kolmogorov-Smirnov normality test of differences: $p = .679$). These results support our approach of dividing by 2 each surfacing duration to estimate t_{EX} . Results are summarized in Table 1 and plotted in Figure 4.

For comparative purposes, body masses (M_b) are estimated with Equation 2 (Sumich et al., 2013) from body length (L_b) and body girth (G_b) values using a mean $G_b:L_b$ ratio of 0.50 that represents the "lean" condition of the seasonal variation in body condition related to alternating feasting:fasting cycles of adults (Perryman & Lynn, 2002; Rice & Wolman, 1971; Sumich et al., 2013). This approach excludes the seasonally acquired, but metabolically quiescent, stored lipid load from biasing mass estimates. Mean V_T values for each whale were calculated using Equation 1 and are plotted against their calculated M_b in Figure 5. Mean $V_T \cdot M_b^{-1} = 0.021$ (2.1%).

$$M_b = 28.5 \cdot G_b^{1.17} \cdot L_b^{.73} \quad (2)$$

To obtain a comparison with foraging whales, exhalation sounds of fasting adult females exhibiting low activity levels in winter lagoons were recorded with a directional microphone from small boats. Their t_{EX} values were determined from audio spectrograms of the recordings (Figure 6, adapted from Sumich, 2001). Acoustic signal strengths of inhalation sounds were much weaker than those of exhalations and were not analyzed. Lacking individual L_b values, the photogrammetrically determined L_b values of north-migrating lactating females (Perryman & Lynn (2002; $M \pm SD = 12.3 \text{ m} \pm 0.54$) are used here to represent L_b for the demographically similar cohort of fasting winter lagoon whales prior to their northward migration. Results are summarized in Table 2.

Individual L_b values of fasting females were not available, so the mean and standard deviations of their t_{EX} and L_b values (from Table 2) were entered into Stella Professional Modeling and Simulation software (2015; Version 1.5.2; iSee systems, Lebanon, NH; and see Sumich, 2021). The Stella model computationally links variables as definable drag-and-drop objects to iteratively generate populations of V_T and $V_T \cdot M_B^{-1}$ values by randomly combining the normal distributions of t_{EX} and L_b listed in Table 2. Each simulation was run 1,000 times and the mean and standard deviation values for V_T and $V_T \cdot M_B^{-1}$ were

calculated (Table 3).

Mass-relative ratios of V_T ($V_T \cdot M_B^{-1}$) are useful for comparisons across subject groups of different sizes, behavior states and taxonomic groups. Our $V_T \cdot M_B^{-1}$ estimates for foraging whales (2.1%) are somewhat higher than those found earlier for gray whale calves (1.8%-1.9%; Sumich, 2021). Our results also indicate that foraging whales express $V_T \cdot M_B^{-1}$ values 35%-40% higher than resting lagoon females (Table 3, Figure 6). This difference likely reflects different behavior states, activity intensities and consequent O_2 demands of the two groups. We have two caveats regarding these lagoon V_T values as representative estimators of resting gray whale V_T . First, lactating females offload several metric tons of stored lipids over the course of a fasting winter lagoon season, altering their body compositions, densities, and presumably their buoyancies (Sumich, 1986 and see Beck et al., 2000, for a pinniped example). Second, the lagoon individuals included in this study were stationary at the sea surface or were swimming slowly, achieving little hydrodynamic lift from forward momentum. For either of these situations, these whales may intentionally retain more of their total lung capacity for buoyancy compensation by reducing their V_T , thus complicating our interpretation of our estimated V_T values.

No $V_T \cdot M_B^{-1}$ measurements of other mysticete species at any age

are available for comparison. The $V_T \cdot M_B^{-1}$ ratios of both fasting lagoon whales and foraging whales are intermediate between the resting V_T predicted by Stahl's (1967) allometric regression for terrestrial mammals at rest (1%; Figure 7) and that of Fahlman et al. (2020) for small to medium-sized odontocetes (~3%-5%; Figure 7).

Over the past 8 years, gray whales have experienced a 46% reduction in population size (Eguchi et al., 2023), prompting concerns about changing climate-driven oceanographic conditions negatively impacting gray whale prey availability. The method described here for estimating V_T of gray whales, especially with the use of UASs to simultaneously establish body lengths and monitor breathing rates and of individual whales, provides a new tool for developing more robust estimates of gray whale \dot{V}_{O_2} and FMR to better understand the resource requirements of this cetacean species.

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rehabilitation, facilitated by a letter of authorization issued by the NOAA-NMFS Southwest Regional Office (Sumich, 2021).

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TABLE 1 Summary of expiration data derived from UAS video for foraging gray whales.

Foraging whales	
<i>n</i> whales	19
<i>n</i> surfacing events examined	299
$M \pm SD$ L_b	12.2 m \pm 0.61
$M \pm SD$ of individual t_{EX}	1.22 s \pm 0.13

TABLE 2 Summary t_{EX} data for fasting adult female gray whales measured acoustically for whales that included 10 or more sequential surfacing events.

Fasting females	
n whales	11
n surfacing events examined	153
$M \pm SD$ L_b	12.3 m \pm 0.55 ^a
$M \pm SD$ of individual t_{EX}	0.94 s \pm 0.19

^a From Perryman and Lynn (2002).

TABLE 3 Simulation model results for fasting whales' V_T and $V_T \cdot M_B^{-1}$

$M \pm SD V_T$	278 L \pm 60
$M \pm SD M_{b-lean}$ (Equation 4)	18,353 kg \pm 2,389
$M \pm SD V_T \cdot M_B^{-1}$	1.6% \pm 0.34

FIGURE 1 Left: Spirometer in place over JJ's blowholes. Right: Example of a typical spirometer trace showing high flow rates throughout most of an exhalation/inhalation event (adapted from Sumich & May, 2009). Flow rates are integrated over time to obtain V_T .

FIGURE 2 Scatterplots and least squares regressions of V_T as functions of $t_{EX} \cdot L_b^2$ (adapted from Sumich & May, 2009) for each of eight sampling series of four different whales (JJ, GG, GK1 *Balaenoptera bonaerensis*, and GK2) between 1 and 14 months of age and spanning a five-fold range of body masses.

FIGURE 3 Time sequence of video frames illustrating a typical exhalation/inhalation surfacing event. Video clips of individual surfacing events were played at 25% normal frame rate to measure total duration of surfacing events to the nearest 0.01 s and divided by 2 to estimate t_{EX} .

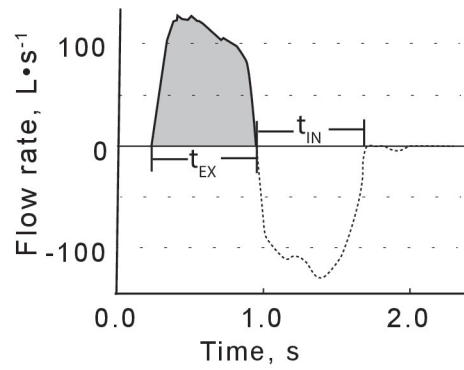
FIGURE 4 Scatterplot of mean expiration duration (t_{EX}) values against body length (L_b). Error bars = $\pm 1 SE$. Least squares regression forced through the origin: $t_{EX} = 0.1000 \cdot L_b$, $r^2 = 0.298$.

FIGURE 5 Scatterplot, least squares linear regression of foraging whales' mean calculated tidal lung volumes (liters) on calculated body masses (meters). Overall mean V_T is 382 L. Gray = 95% CL.

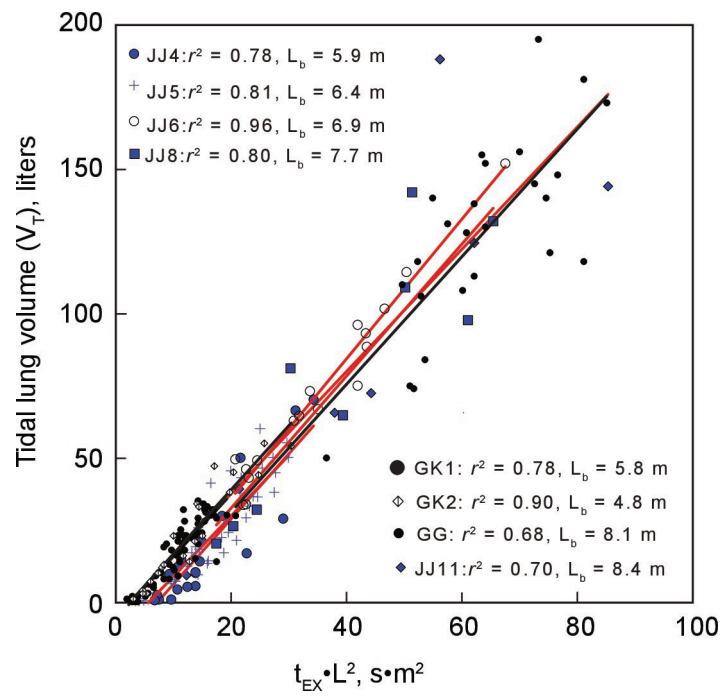
FIGURE 6 Relative power spectrum (top) and frequency spectrogram

(bottom) of a single exhalation/inhalation event (adapted from Sumich, 2001).

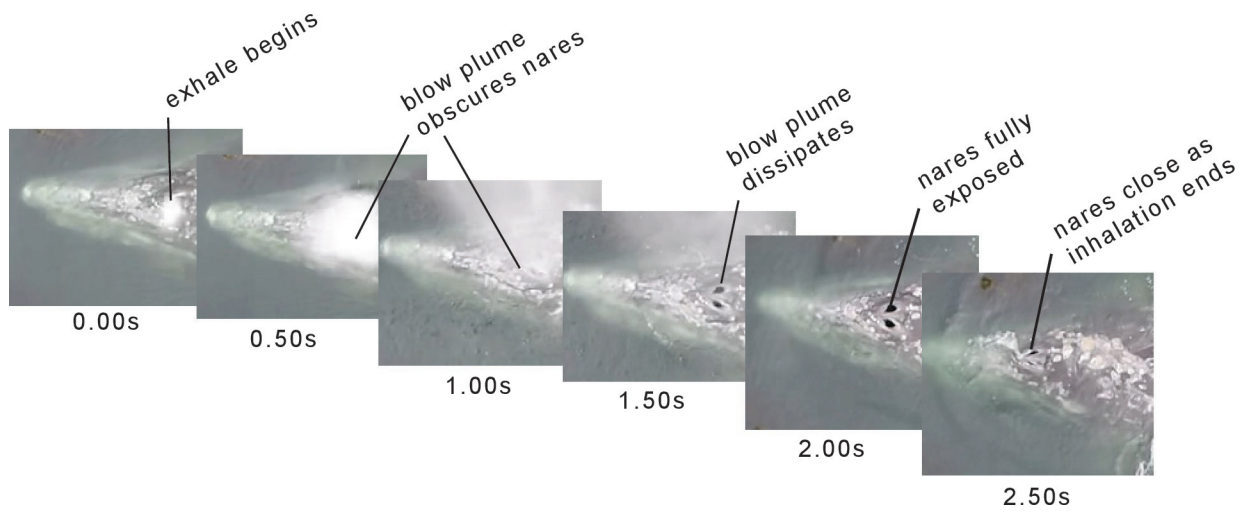
FIGURE 7 Comparison of estimated mean mass-relative tidal lung volumes ($V_T \cdot M_b^{-1}$) of adult foraging (heavy solid line) and fasting ●) gray whales with five species of odontocetes at rest (Fahlman et al., 2020). Regressions for tidal lung volume on body mass at 1%, 3%, and 5% are indicated.



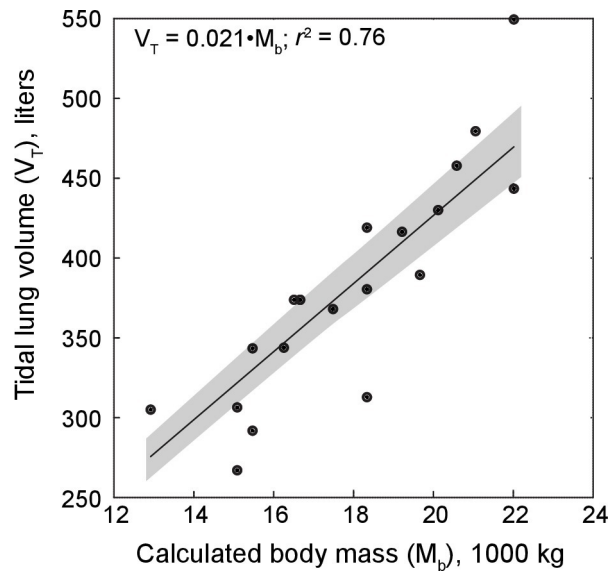
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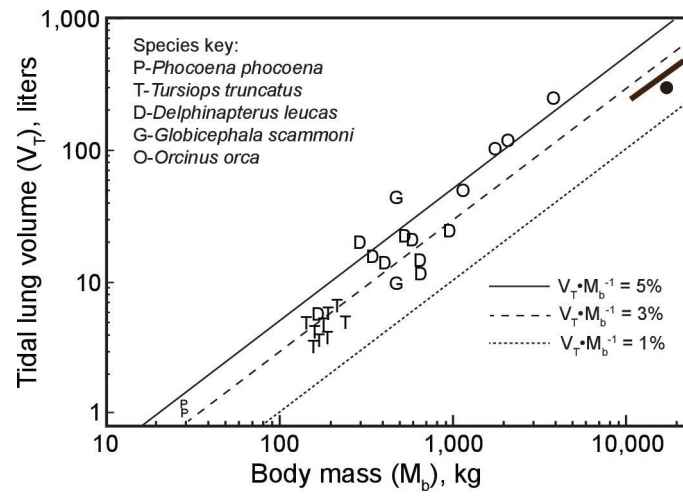
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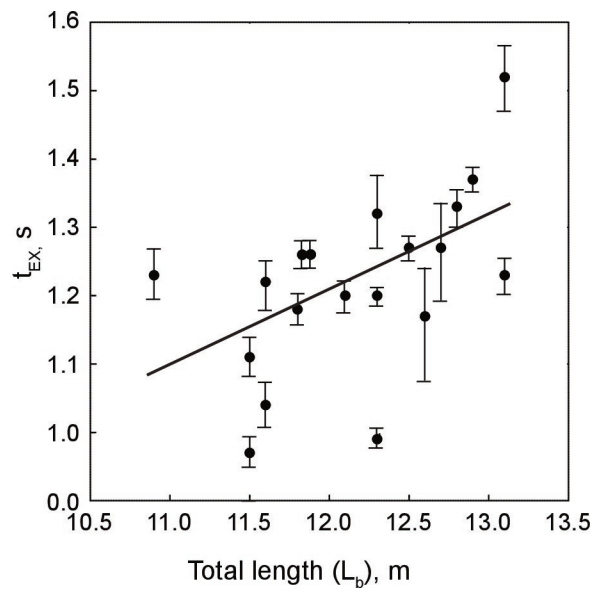


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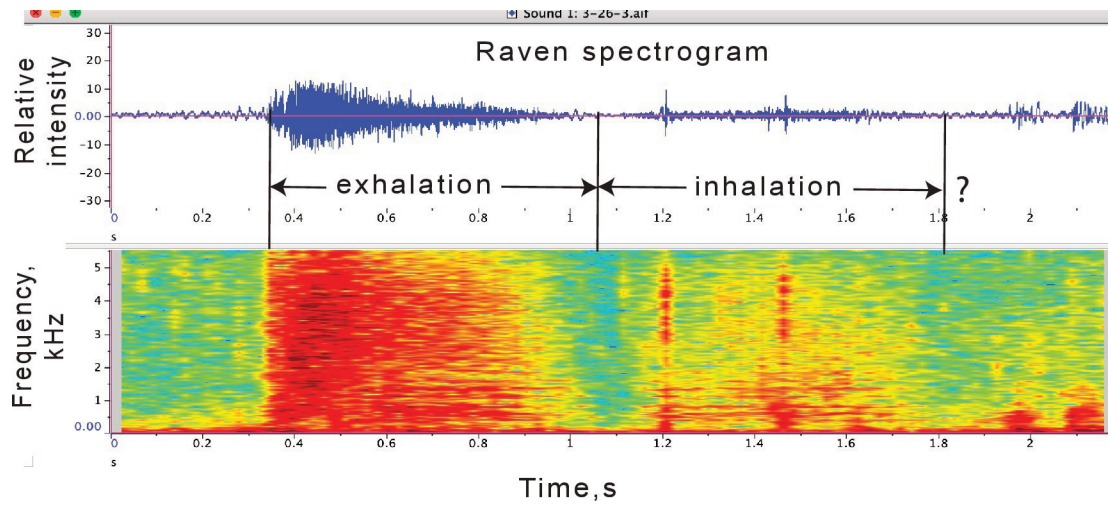


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5552_fig 4.ai



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