

Direct and indirect measures of oxygen extraction, tidal lung volumes and respiratory rates in a rehabilitating gray whale calf

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Abstract

A gray whale neonate, JJ, stranded on January 10, 1997 and held for rehabilitation at SeaWorld, San Diego, was studied to: (1) characterize respiratory patterns for the purpose of remotely monitoring changes in ventilation and oxygen extraction rates over short time-frames and (2) estimate the metabolic rate compared to unrestrained calves in a winter nursery lagoons. Between February and November, fractions of assimilated O₂ values ($[I_{O_2}] - [E_{O_2}]$) ranged from 4.8% to 18.3%, increasing as a function of total duration of the ventilatory cycle immediately prior to each sampled expiration (T_T). Although mean T_T increased two-fold, no change in the relationship between $[I_{O_2}] - [E_{O_2}]$ and T_T with age was apparent. The relationship between $[I_{O_2}] - [E_{O_2}]$ and T_T reported here is similar to, but extended by almost 4 times, that determined by Sumich (1994) for approximately 2-month old, free-swimming gray whale calf. Beginning at approximately three months of age, expiratory flow rates and tidal lung volumes (V_T) were measured periodically with a differential pressure laminar flow element pneumotachograph while the whale was partially stranded. Monitored expiratory flow rates were integrated over the duration of the expiration (T_E) to obtain expiratory V_T , which varied from 2.9 to 3.4% of body mass. A derived relationship between V_T and T_E estimated V_T by acoustically monitoring JJ's expiration sounds and determining T_E and T_T during unrestrained swimming.

Key words: gray whale, respiration, tidal lung volume, oxygen extraction.

Introduction

Breathing rates have sometimes been used to estimate metabolic rates of free-ranging cetaceans. For example, Hampton & Whittow (1976) found that breathing rate correlated with oxygen uptake in a captive Hawaiian spinner dolphin (*Stenella longirostris*). Sumich (1983) thought that breathing

rate and swimming velocity in migrating gray whales (*Eschrichtius robustus*) were consistent with predicted power vs. swim-speed of streamlined homeotherms. These limited observations suggested that breathing rate alone might provide a reasonable index of gray whale respiratory dynamics, and perhaps their metabolic rate. Here, I describe the results of studies on a rehabilitating gray whale calf ('JJ') to explore the relationships among breathing rates, tidal lung volume, and the dynamics of oxygen extraction under relatively controlled conditions.

Materials and Methods

Collection of exhaled lung gas

I collected samples of mixed-tidal expired lung air opportunistically during 1 to 2-hr periods as JJ swam freely about her pool. These samples (ca. 1 to 2 L) of exhaled lung gases were collected with an evacuated latex (2 L) weather balloon, sealed, and then analyzed within 1 hr with a VacuMed[®] oxygen (O₂) and carbon dioxide (CO₂) physiological gas analyzer system calibrated to atmospheric and 6.0% CO₂ and O₂. The concentrations of exhaled CO₂ [E_{CO_2}] and [E_{O₂}] were measured to within 0.1%. I then subtracted the concentration of exhaled oxygen [E_{O₂}] from the concentration of inhaled oxygen ([I_{O₂}]; i.e., 21%) to yield the difference $[I_{O_2}] - [E_{O_2}]$. I did not make any corrections for CO₂ in the exhaled air.

Tidal volume

I made five series of measurements of tidal lung volume (V_T) from early April through November 1997. A differential pressure laminar flow element pneumotachograph (*cf.* Kooyman & Cornell, 1981) was fitted snugly over the blowhole to measure respiratory flow rates during each exhalation/inhalation cycle. During these measurements, the floor of the holding pool was raised to restrict JJ's mobility and allow routine physical examinations



Figure 1. Pneumotachograph in position for obtaining V_T measurements from a rehabilitating gray whale calf (JJ).

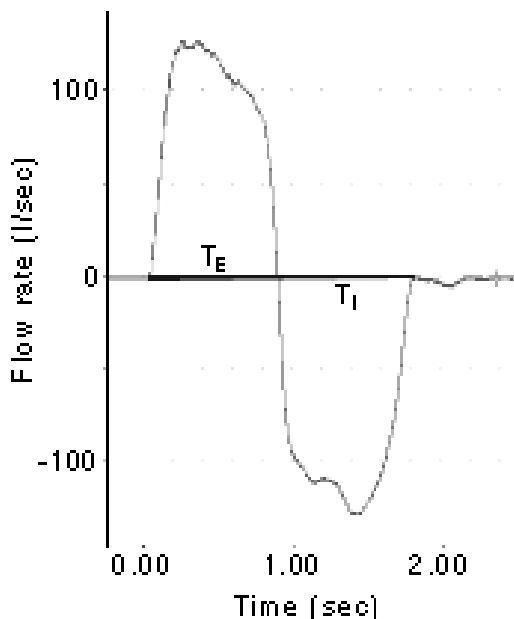


Figure 2. Example of MacLab[®] signal trace of a single exhalation/inhalation event illustrating acoustically determined T_E and $T_I \cdot s^{-1}$. Integrated areas bounded by flow curve above baseline=exhaled V_T ; below baseline=inhaled V_T .

(Fig. 1). I sampled signals from the pneumotachograph at 200 Hz with a MacLab[®] physiological signal processor, recorded those on a laptop computer, and integrated them over the durations of each respiratory cycle to yield exhalation and inhalation tidal lung volume. I also measured the duration of each exhalation (T_E), inhalation (T_I), and maximum rates of gas flow during each of those respiratory events (Fig. 2). I did not measure sequential exhalations and inhalations because the pneumotachograph was placed over the blowholes during one event and then removed during the next

event. Consequently, only exhalation components of each respiration were analyzed.

Respiratory cycle

I measured the duration of the respiratory cycle (T_T) that just preceded the collection of each exhaled sample to the nearest second. I estimated the durations of respiratory cycles ($T_T \pm 1$ s) from continuous recordings of JJ's behavior on Hi-8 mm videotape for 45 to 60 min once every 2–4 weeks starting on 30 January 1997. I then calculated the average cycle durations and derived frequency distributions for each sampling period to characterize JJ's breathing patterns. I also recorded the sounds of exhalations on videotape with a directional microphone to compare with those measured with the pneumotachograph. I only measured exhalations followed by clearly audible inhalations and included only those cycles with acceptable recordings over a minimum of 15 s. I did not consider the sounds of inhalations because they were less audible and more difficult to reliably document and measure. I digitized the acceptable exhalation sounds and measured (± 0.01 s) with the Canary[®] sound analysis program (Fig. 3). Previously, I analyzed recordings of respiratory sounds of gray whale calves in the breeding lagoons using the same methods (Sumich, unpub. data).

Results

Oxygen extraction

I determined the amount of oxygen extracted from inhaled air $[I_{O_2}] - [E_{O_2}]$ during each respiratory cycle for 213 exhalations and the concentration of exhaled carbon dioxide $[E_{CO_2}]$ in 210 exhalations during sampling sessions from February through November 1997. I pooled samples to yield monthly averages.

The concentration of carbon dioxide in exhaled air was unrelated ($P > 0.05$) to the duration of the respiratory cycle (T_T), so I did not consider that variable further. Extraction efficiency for oxygen varied from 4.8% to 18.2%. It increased rapidly with duration of the respiratory cycle, between February and June, for respiratory cycles lasting 30 to 60 s, and more slowly for longer cycles (Fig. 4). The pattern of oxygen extraction efficiency did not change between February and November (Fig. 5).

Tidal volume

Maximum flow rate, average and maximum V_T , and average T_E increased as JJ grew (i.e., versus length=L) through November (Fig. 6). In late November, JJ's respiratory exhalations ($> 300 \text{ L} \cdot \text{s}^{-1}$) exceeded the measurement capabilities of the largest pneumotachographs available.

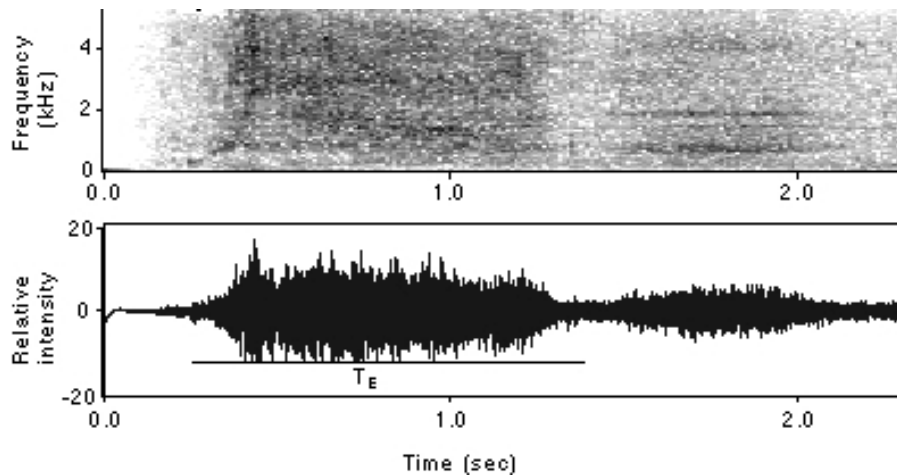


Figure 3. Spectrogram (top) and relative power spectrum (bottom) of a single exhalation/inhalation event. T_E is measured from the beginning of the exhalation to the mid-point between the end of the exhalation and the beginning of the inhalation.

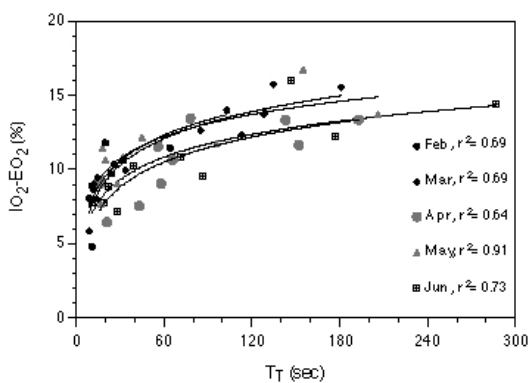


Figure 4. Scatterplots, least squares regression lines, and associated r^2 values of $[O_2]-[E_{O_2}]$ as functions of T_T for five sampling sessions approximately one month apart.

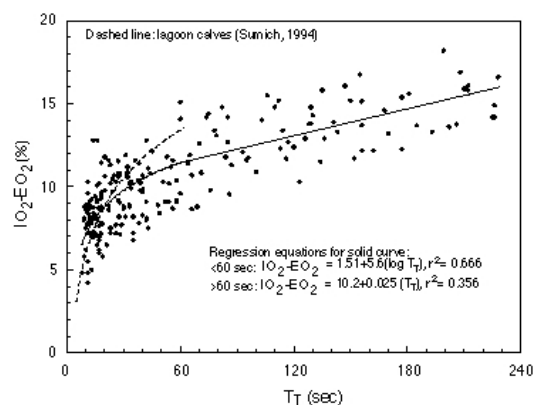


Figure 5. Scatterplot and least squares regressions of pooled sampling sessions of $[O_2]-[E_{O_2}]$ as a function of T_T .

Tidal volume (V_T) increased significantly with both T_E and body length ($P < 0.0001$ for both T_E and L) between April and November; T_E and body length (L) explained most of the variability observed in V_T (multiple $R^2 = 0.875$).

Acoustically derived measures of T_E averaged about 0.5 s in January, increased sharply in February and March to 0.9 s, and then levelled-off at about 1 s (Fig. 7). When the two methods of measuring T_E were compared, the median value of T_E measured acoustically was similar to the maximum value of T_E measured with the pneumotachograph at similar ages (Fig. 8).

Respiratory cycle

The durations of respiratory cycles ranged from 4 to 233 s. The average duration of the respiratory

cycle (T_T) increased from about 30 s in late January to almost 1 min by mid-March, and then remained constant at 50 to 60 s through September (Fig. 9). Respiratory cycles longer than 60 s increased steadily from 10% in January to about 32% by late March. The longest respiratory cycles doubled in length from 2–4 min during that same period.

Discussion

Extraction efficiency

Assimilated oxygen values ($[I_{O_2}]-[E_{O_2}]$) from pooled expired air samples from a captive 2–3 mo-old gray whale, Gigi, II ranged from 8.5 to 12.5% (Wahrenbrock, *et al.*, 1974). Sumich (1986, 1994) found that $[I_{O_2}]-[E_{O_2}]$ values of gray whale

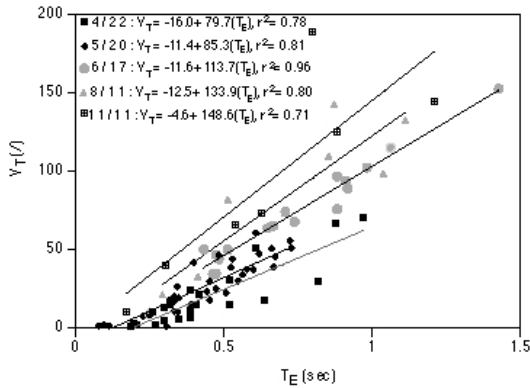


Figure 6. Scatterplots, least squares regressions, and associated r^2 values of V_T as functions of T_E for five sampling sessions between April and November 1997.

calves of similar ages in the breeding lagoons ranged from 5 to 16%, with a large and significant portion of the total variability explained as a function of T_T , presumably the time lung air is maintained in contact with alveolar surfaces. However, only lagoon calves estimated to be 6–10 weeks old could be sampled, and no T_T value in those studies exceeded 64 s. Consequently, the utility of my (1994) regression equation for predicting $[I_{O_2}] - [E_{O_2}]$ values was limited to T_T values of ≤ 1 min.

Tidal volume

The tidal volumes (V_T) for JJ derived from exhalation duration (T_E) ranged from 2.9 to 3.4% of body mass (W), somewhat greater than reported for restrained and temporarily stranded calves (*cf.* Wahrenbrock *et al.*, 1974; Kooyman *et al.*, 1975). The few additional measures of V_T in cetaceans (see Sumich, 1986) range from average values of 2.1% of body volume in a captive yearling gray whale (Wahrenbrock *et al.*, 1974) to 9.4% in pilot whales, *Globocephala melaena*, (Olsen *et al.*, 1969). No studies of captive or restrained whales were designed to measure the typical variability anticipated from unrestrained animals functioning in a normal environment. I assumed that the observed characteristics of JJ's ventilation reflect those of free-ranging calves at similar ages and body size.

Respiratory cycle

A typical ventilatory cycle of gray whale calves consists of a very abrupt exhalation (< 1 s) immediately followed by an equally brief inhalation, then a period of apnea that varies in length, usually associated with submergence (Sumich, 1986). The exhalation/inhalation phase of the cycle is so short that the duration of apnea is essentially equal to the

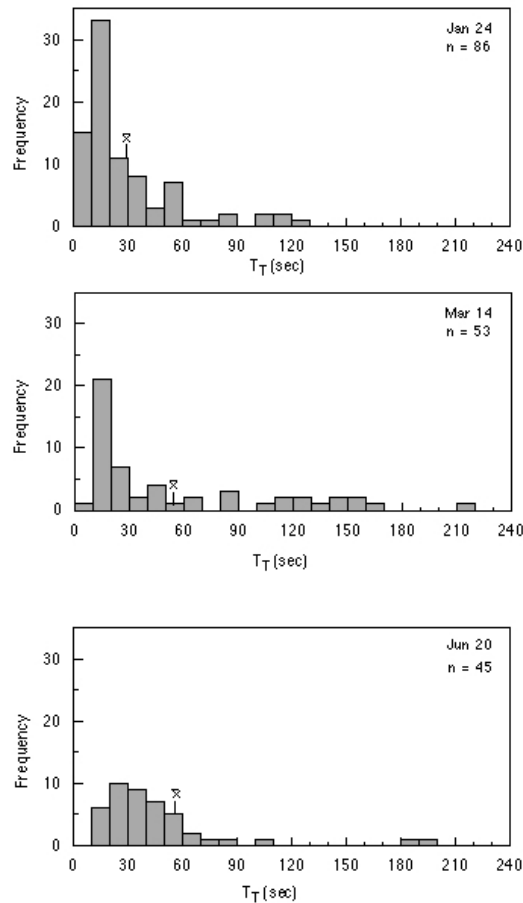


Figure 7. Relationship between T_E and age (calendar day) for JJ and for calves in the breeding lagoons. Vertical line = ± 1 s.d.; sample (n) values are shown for JJ.

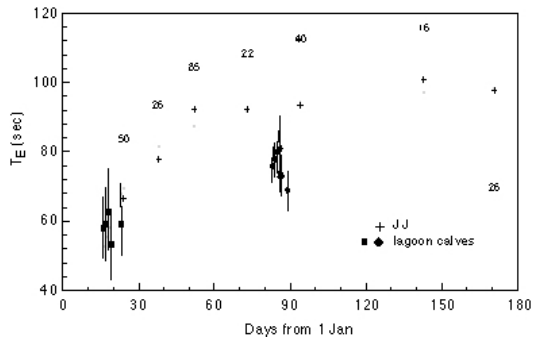


Figure 8. Scatterplot and regression of V_T as a function of T_E in April 1997 (top) and frequency distribution of T_E derived from audio recordings at the same age.

total ventilatory cycle duration (T_T). Average T_T of lagoon calves doubled from 24 s after birth to about 50 s at 2–3 months later when they departed the

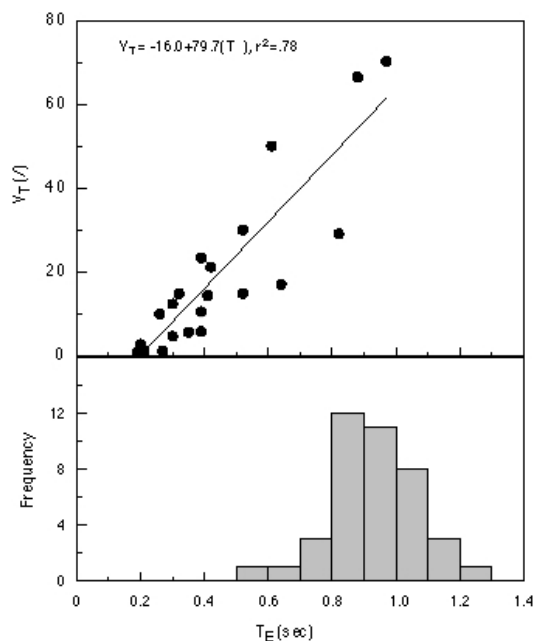


Figure 9. Frequency distributions, in 10-s increments, and average T_T in January (top) and March (bottom) 1997.

lagoons. During the same time maximum T_T increased from 2 to 4 min (Sumich, 1986).

Patterns of respiration in gray whale calves reflect physiological needs and behavioral activity. Presumably, efficient extraction of oxygen from inhaled air occurs by initial rapid transfer of inhaled oxygen to the blood vessels in the alveoli during the first 20 to 30 s of each respiratory cycle, with less exchange afterwards. Uptake of oxygen versus duration of the respiratory cycle was evidently lower for JJ than for calves in the breeding lagoons (*cf.* Sumich, 1994). Nonetheless, there was a clear mode in respiratory frequency at around 20 to 30 s for JJ's respirations, and for all calves while in the breeding lagoons (*cf.* Sumich, 1986). These are also similar to patterns reported for migrating adults and calves (*cf.* Sumich, 1983; Sumich, 1986). The increase in average duration of the respiratory cycle with age corresponds with an increase in the proportion of respiratory cycles longer than 60 s and an increase in the duration of the longest respiratory cycles.

Duration of JJ's exhalations (T_E) increased faster with age and was more variable than those of calves in the breeding lagoons. These differences could be the consequence of the physical constraints imposed

by her holding pool and by the absence of the normal accompaniment and influence of a mother which, prior to weaning, appeared to control the pace of swimming of calves observed in winter lagoons.

JJ's reluctance to exhale completely when the pneumotachograph was placed over her blowholes could account for her shorter measured T_E values with the pneumotachograph in place compared to T_E values obtained from audio recordings. Sumich (1986) reported a similar response by bottlenose dolphins. Because V_T correlates directly with duration of exhalation, data collected with the pneumotachograph evidently underestimated both. I think that monitoring these events with audio-recorders provided a more accurate measure of T_E and, consequently, of estimates of V_T .

Monitoring elements of respiratory cycles of free-ranging gray whales could provide a good index of the whale's metabolic rate. I recommend empirical testing of this hypothesis during future studies of baleen whales, including taking advantage of all possible opportunities to make measurements on stranded and rehabilitating cetaceans.

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