Lung Mechanics in Marine Mammals

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LONG-TERM GOALS

The long term goal of this study is to develop methods to study lung physiology in live marine mammals and to use these techniques to investigate the mechanical properties of the respiratory system in different marine mammals. This effort is vital to understand how diving mammals manage inert and metabolic gases during diving and will help determine what behavioral and physiological responses increase DCS risk.

OBJECTIVES

Recent theoretical studies have suggested that marine mammals commonly live with elevated blood and tissue N_2 levels, and that they use both physiological and behavioral means to avoid DCS [1, 2]. But what physiological variables are the most important to reduce N_2 levels below those that cause DCS, and how important is a link between behavior and physiology? For example, if the duration of each individual dive was extended, the repeated dives during a bout (a series of repeated dives with a short intervening surface interval) may result in accumulation of N_2 to levels that may cause DCS. A variety of situations, such as sonar exposure, reduction in prey abundance, predator avoidance or environmental change, may result in behavioral changes in dive pattern. Such changes could cause elevated tissue and blood N_2 levels that either result in DCS or force the animal to end a foraging bout prematurely to prevent the formation of inert gas bubbles. Prematurely ending a diving bout reduces

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foraging efficiency and could have detrimental implications for survival. While the results from theoretical studies have to be viewed with caution, sensitivity analyses have indicated that the degree of gas exchange and cardiac output during diving are the most important variables determining N_2 levels in blood and tissue, and thereby the DCS risk. However, current knowledge of how gas exchange is altered by compression of the respiratory system, possibly to the limit of collapse, is rudimentary at best.

The proposed lung collapse depth in the Weddell seal is around 30 m [3] and 70 m for the bottlenose dolphin [4]. In another study, no apparent differences in pulmonary shunt were observed between species with widely different respiratory structure [California sea lion vs. harbor seal, 5]. The results also suggested that complete cessation of gas exchange may not occur until a depth > 150 m [5], even when the animal exhaled before diving. In a previous ONR funded effort, a mathematical model was developed to explain these divergent results (ONR award number N00014-07-1-1098). The results from this work implied that beaked whales commonly experience end-dive N_2 levels that would cause a significant proportion of DCS cases in terrestrial mammals [1]. It was proposed that as the N_2 levels increased they could eventually limit the extent of a dive bout [1, 2, 6, 7]. It was also suggested that the normal dive behavior and physiological adjustments could be important to reduce end-dive P_{N2} [1, 6, 7].

The model results predict that the alveolar-collapse-depth, and thereby the degree of gas exchange, is greatly affected by the compliance values of the different parts of the respiratory system [8].While results from mathematical models should be tested with empirical data, few studies have examined respiratory mechanics of live marine mammals [9, 10]. The model therefore used compliance values from an excised marine mammal lung for the lower respiratory tract, and of an excised trachea from a terrestrial animal for the upper airways [8]. To enhance our ability to predict how anthropogenic sound may interact with gas management during diving, an improved understanding of the physical properties that affect compression of the respiratory system and gas exchange is warranted.

APPROACH

This project is separated into three aims:

Aim 1: We will measure the inspiration ($\dot{V}_{insp}$) and expiration flow rates ($\dot{V}_{\exp}$) during quiet breathing in addition to airway (P_{air}) and esophageal (P_{eso}) pressures. These data will be used to calculate airway resistance, pulmonary and thoracic compliance (pressure-volume relationship). The static compliance values will be compared to the data previously determined in post-mortem marine mammals (Fahlman and Moore, unpublished observation). We hypothesize that deep divers have a more compliant respiratory system that will enhance compression and collapse of the thoracic cavity.

Aim 2: We will monitor end-tidal O_2 and CO_2 in anesthetized, spontaneously breathing marine mammals. We hypothesize that species that dive deeper and for longer duration have significantly lower end-tidal O_2 and higher CO_2 levels.

Aim 3: The experimental results will be compared with data obtained from our previous and on-going hyperbaric CT studies. The combined results will be used to revise a model that predicts the extent of gas exchange for a range of species.

WORK COMPLETED

Aim 1:
In the second year, additional experiments were conducted to estimate the structural properties of the respiratory system of anesthetized pinnipeds (Table 1, Fig. 1). In some animals where euthanasia was planned, we managed to measure both lung mechanics in vivo during spontaneous breathing (dynamic) and mechanical ventilation (static), and the static compliance after euthanasia.

Table 1. Number of samples in each category

	Static compliance		End-tidal		Re-breathing
Species	Live animal	Dead Intact	O_2	CO_2	
California Sea Lion	4	2	5	5	1
Northern fur seal	1	1	1	1	1
Harbor seal	1	-	2	2	1
Elephant seal	1	-	2	2	-

Modifications of the equipment allowed us to accurately measure flow-rates, airway and esophageal pressures during voluntary breathing and mechanical ventilation (Fig. 1).

Aim 2: In the second year we also used a fast response visible spectrum absorption O_2 (Oxigraf X2004) and infrared CO_2 (Servomex Model 15050) analyzer, which allowed measurement of end-tidal respiratory gas composition (ML206, AD Instruments, Fig. 1). In addition, we used an O_2 dilution/re-breathing experiment to estimate residual volume in 3 animals that underwent a terminal anesthesia procedure (Table 1). Our experimental protocol involved sampling of animals that underwent a planned clinical procedure, therefore specific measurements were only available in some animals and the distribution of various measurements is therefore uneven.

Aim 3: Analysis of the data collected from the first year is almost complete and the analysis of the data from the second year is underway. As we have collected respiratory compliance data in both live animals and then in the excised lungs after the animal was euthanized, we plan to compare how well these data compare. We will then compare these data to our previous data from excised lungs collected at Woods Hole Oceanographic Institution. In addition, we also collected data to estimate residual volume in live animals. The procedure was possible in animals that were anesthetized and ventilated on O_2, using the O_2-dilution method. The estimated RV will be compared to those from excised lungs using the water displacement method {Fahlman, 2011 #92}.

RESULTS

Aim 1: We succesfully collected lung compliance data from 7 animals, 4 California sea lions, 1 elephant seal, one harbor seal and 1 Northern fur seal. These data will be combined with the data set of 12 animals, 1 elephant seal and 11 California sea lions, collected in the previous year. In some animals, we were able to collect data from the live animal and then from the excised lung after the animal had been euthanized. Figure 1 shows a representative sample of raw data collected from a sea lion during mechanical ventilation. Figure 2-4 shows analyzed data for the relationship between airway and esophageal pressures and volume during mechanical breathing in an anesthetized Northern fur seal (Fig. 2), Pacific harbor seal (Fig. 3), and California sea lion (Fig. 4). These data indcate that the chest is much more compliant than the lung and agrees with the suggestion that the marine mammal chest provides little resistance to collapse during deep dives.

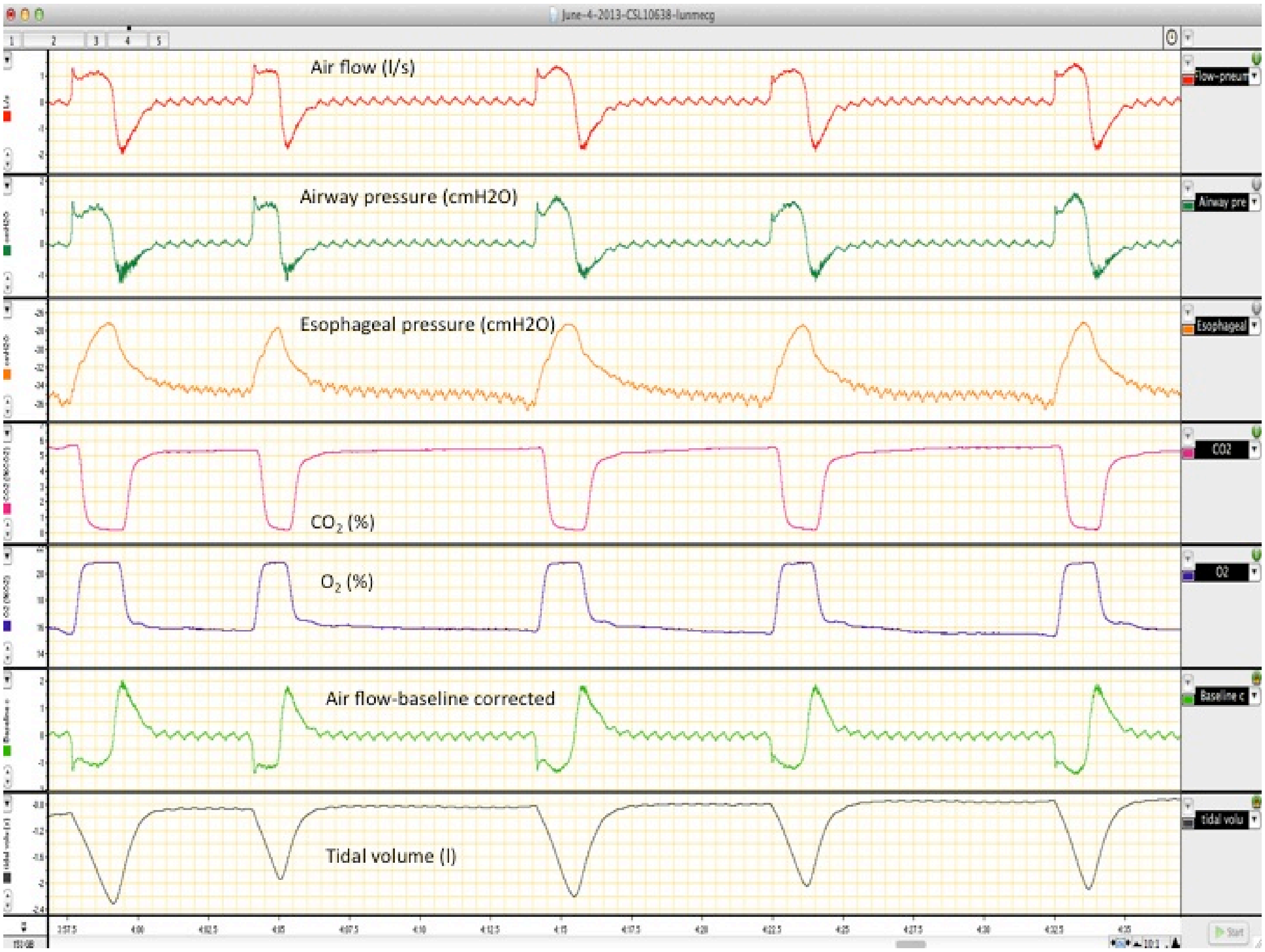

Figure 1. Raw data during mechanical ventilation in an anesthetized California sea lion (CSL10638)

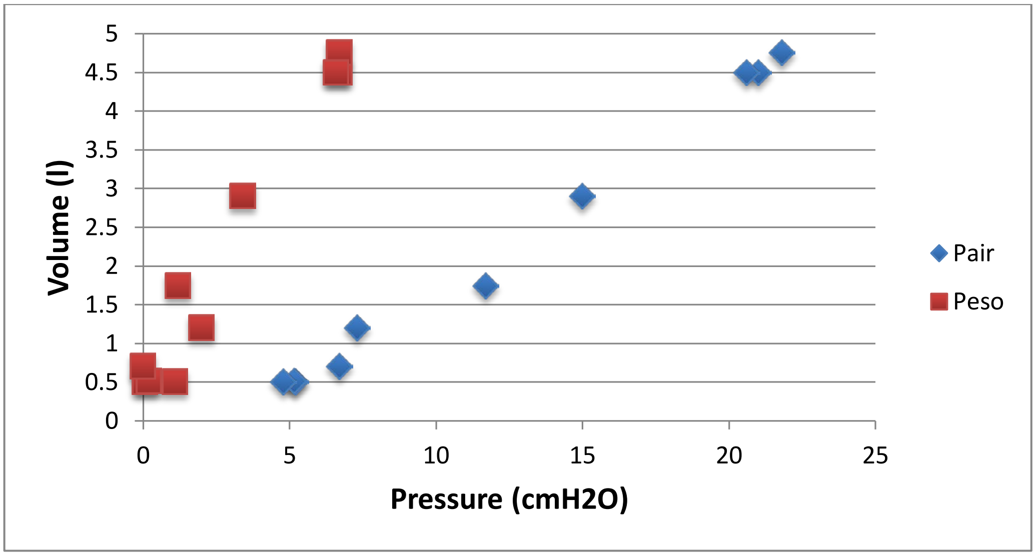

Figure 2. Raw data from mechanical ventilation of a Northern fur seal (NFS266).

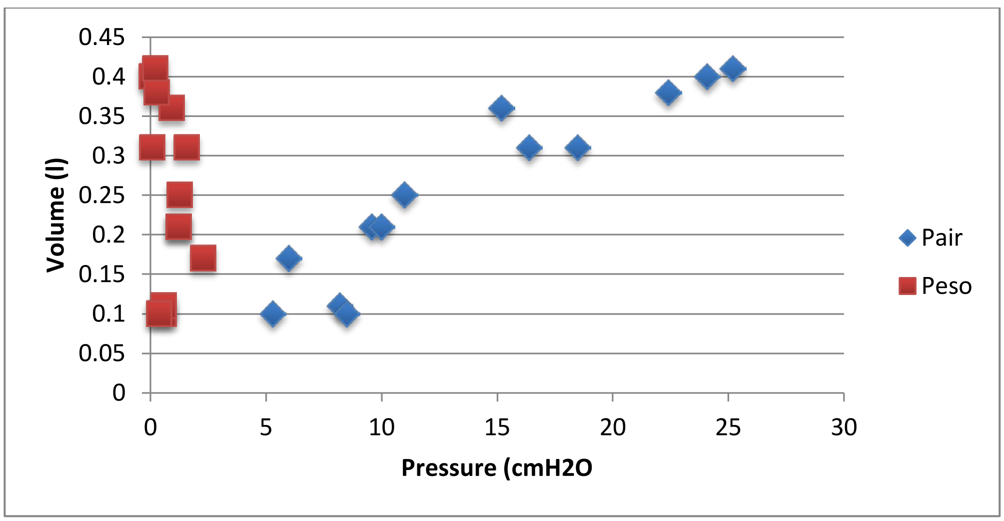

Figure 3. Raw data from mechanical ventilation of a Pacific Harbor seal (HS2328).

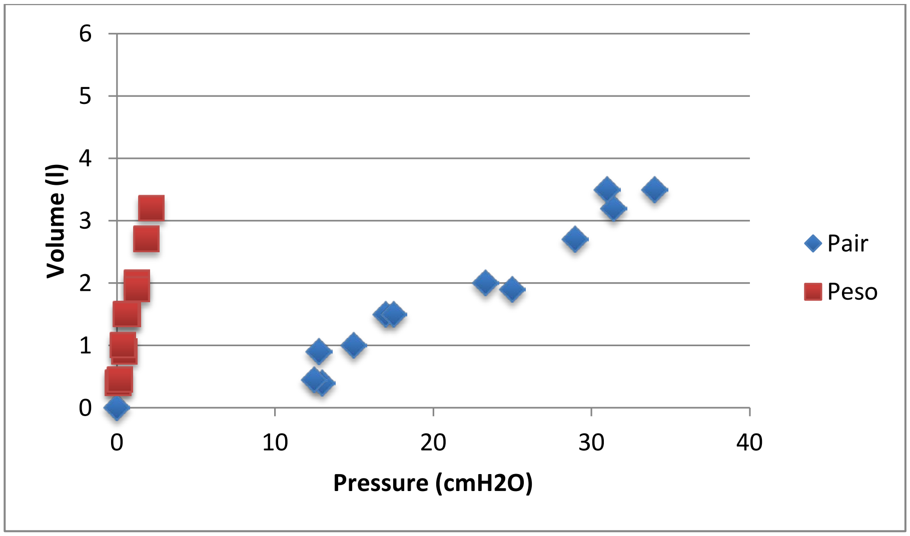

Figure 4. Raw data from mechanical ventilation of a California sea lion (CSL10638).

Aim 2: We collected continuous end-tidal O_2 and CO_2 data in all animals both during voluntary and mechanical ventilation (Fig. 1). These data suggest that sea lions may experience relatively (as compared to terrestrial mammals) high end-tidal PCO_2 levels without apparent problems. In addition, O_2-dilution data were collected with the aim to estimate residual volume.

Aim 3: The data analysis is underway (see Figure 2-4). The analyzed data from live and deceased pinnipeds will be compared with our previous data set in excised lungs from odontocetes and phocids. These data will be used to update our model that predicts the air volumes in the upper (conducting airways) and lower (alveolear space) airways.

IMPACT/APPLICATIONS

This work is intended to enhance our understanding of how the respiratory system responds during diving in marine mammals. The results will provide information that will allow us to provide species specific pressure-volume parameters for the airways. These data will enable more realistic predictions of how the lungs compress to the limit of collapse and improve our understanding how marine mammals manage gases during diving.

The results can be used to determine how changes in dive behavior, including those from man-made interference, affect blood and tissue P_{N_2} levels. Thus, our results will enhance the fundamental understanding and interpretation of avoidance of the effect of anthropogenic sound, and enable knowledgeable decisions about sonar deployment, related training exercises and responses to NGO concerns. This should be of value to the US Navy Marine Mammal Program.

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