MODELS FOR PREDICTING NITROGEN TENSIONS AND DECOMPRESSION SICKNESS RISK IN DIVING BEAKED WHALES

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1 ABSTRACT

The work presented in this paper constitutes the second stage of a long-term project that aims to develop a model to predict the risk of decompression sickness (DCS) occurring during any given dive by beaked whales, particularly *Ziphius cavirostris* or *Mesoplodon densirostris*. The motivation for this work comes from the need to quantify the relative hazards associated with dive behaviours exhibited by these species following their exposure to mid-frequency active sonar.

During the first stage of this project, static diffusion was identified as the most likely mechanism of bubble growth that may give rise to the DCS-like, gas embolic disease observed in mass-stranded whales following sonar exposure. This finding highlighted the need for a model of how the nitrogen tensions in the tissues of diving odontocetes evolve during diving. In this paper, the results of a parameter sensitivity study conducted on such a model are presented. This model is to be modified to make its output specific to the two beaked whale species. As such, the aim of these tests was to identify the relative magnitude with which the parameters affect the output of the model, so as to prioritise the order in which they should be quantified empirically in these species. The results showed that of the parameters tested, the assumed depth of lung collapse was the strongest determinant of the model output. This was followed by the relative Ostwald solubility coefficients for nitrogen chosen for the various tissue types, and then the perfusion of both individual tissue 'types' and the tissues as a whole.

It is intended that the tissue nitrogen tensions predicted by the current model will be modified to be specific to the beaked whales of interest in line with the results of the parameter sensitivity study presented here. The resulting model will then be combined with the theory of bubble growth via static diffusion to produce the final version of the model, which will be capable of predicting the risk of DCS occurring during any dive by either *Ziphius cavirostris* or *Mesoplodon densirostris*. This model will then be used to identify the behaviours theoretically conferring the highest risk of DCS, so that they may then be compared with those actually observed during controlled exposure experiments such as those currently underway in the Bahamas.

2 BACKGROUND

While there is little historical information about beaked whale strandings from much of the world, no mass strandings involving three or more individuals were reported prior to the early 1960s. This approximately co-incides with the first usage of mid-frequency sonar [1;2]. The link between beaked whale strandings and the use of military sonar has received increased attention in recent years after Simmonds and Lopez-Juardo noted the spatial and temporal coincidence of mass stranding events with naval manoeuvres in 1991 [3]. Many confirmed incidences have been noted

since then, including strandings in Greece in 1996 [4], Madeira in 2000 [5], the Bahamas in 2000 [6] and the Canaries in 2002 [7;8].

Necropsies conducted on whales stranded during the Canary Islands incident revealed that the whales suffered from symptoms consistent with DCS [7;8], including lesions associated with gas bubbles. The discovery of such DCS-like symptoms in beaked whales was both controversial and unexpected, since it had always been assumed that whales would have evolved anatomical, behavioural and physiological adaptations to buffer them from the effects of such diseases [9]. It is speculated that these DCS-like symptoms are directly caused by gas embolism[1], with the gas bubbles forming in the blood and tissues *in vivo* from stabilised gas bubble nuclei already present in the tissues. Explaining how these nuclei might grow to sizes that can cause such injuries is therefore pivotal to understanding the cause of this DCS-like disease in beaked whales, and provides the motivation for this paper.

Knowledge of the mechanism underlying bubble growth in beaked whales is required to conduct accurate modelling of how bubble nuclei may be expected to grow to sizes that could result in tissue damage and DCS-like injuries in the whales. Previous work by Potter [10] and the current authors [11] showed that rectified diffusion occurring as a result of exposure to sound pressure waves is unlikely to be the primary mechanism of such growth. The model of bubble growth via rectified diffusion produced during the first stage of the current study [11] showed that, for the assumed conditions (see below), the sound only had an effect on the maximum bubble radius reached at intensities above 200 dB (re. 1 μPa), see Figure 1 below. These are unlikely to be attained at the position of the whale. It should be noted that this modelling work was conducted for specific assumed conditions wherein, prior to sound exposure, the tissues were supersaturated with nitrogen to 300% of their initial nitrogen content at sea level (as consistent with Houser et al. [12]) and contained pre-existing bubble nuclei which all initially had radii of 10 μm. Such assumptions are chosen as those most favourable to bubble growth within the regime of realistic parameters.

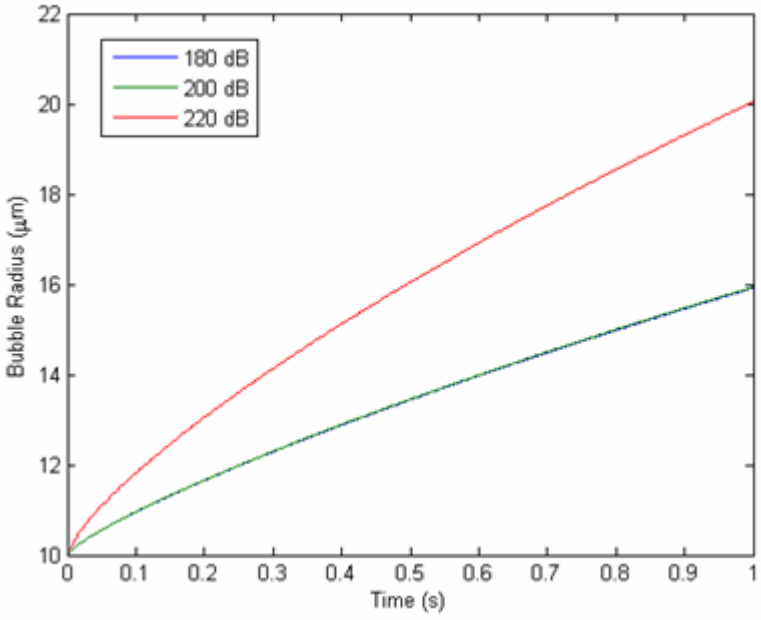

Figure 1. Predicted growth of a bubble of initial radius 10 μm by rectified diffusion in acoustic fields of different amplitudes. (Note that the 180 dB and 200 dB curves overlay each other indicating that at these source levels, static[2] diffusion is the dominant cause of bubble growth).

[1] An embolism is a blockage or occlusion of a blood vessel.
[2] Static diffusion occurs when the partial pressure in a liquid is greater than that in a bubble. Gas leaves the liquid and enters the bubble causing it to grow. Static diffusion may occur in the absence of an acoustic field.

The conclusion from this evidence, that rectified diffusion was unlikely to be the primary mechanism of bubble growth in the whale's tissues, is consistent with other authors' findings [10;13]. Static diffusion, as the favoured alternative mechanism of bubble growth in the tissues, has also been shown experimentally *ex vivo* to be capable of causing the growth of bubble nuclei to sizes that, if it occurred *in vivo*, could cause DCS following their initial acoustic destabilisation [14]. This observation adds weight to the evidence that static diffusion is the most likely cause of bubble growth in whales.

Having identified static diffusion as the most likely cause of bubble growth in the tissues, at least one key item of knowledge is required in order to provide the possibility of predicting the likelihood of resulting bubble growth and DCS risk in the future. That item is, specifically, knowledge of how the gas tensions[3] evolve in the tissues of the diving whales. The evolution of nitrogen tensions are of particular interest, because nitrogen is both biologically inactive and abundant in the body. The model tested in this paper performs that task. Later work will refine this model to include two more components. This first component consists of experimentally derived values specific to the beaked whales of interest for the parameters identified in this paper as being important determinants of the model output. The second component is the ability to predict bubble growth and so estimate the commensurate risk of DCS being incurred during diving. As previously stated, completion of this refined model will enable the identification of those behavioural responses (exhibited in response to sonar exposure) that theoretically confer the highest risk of DCS. These putative high-risk behaviours can then be compared with those dive profiles which are actually observed during the controlled exposure experiments currently underway in the Bahamas [15].

3 THE MODEL

The work presented here is a reconstruction of part of an existing model by Fahlman *et al*. [16]. This model was originally designed to model nitrogen tension evolution in the tissues of diving dolphins, but has the potential to be equally applicable to beaked whales through changing the values of the input parameters. In this model the nitrogen tensions in the tissues are calculated from the difference between the nitrogen tensions in the blood and the tissues themselves at each time instant. The blood is considered as circulating in discrete 'packages', with one package exchanging gas at the lungs and one exchanging gas at the tissues at any one time, as shown in figure 2 on the next page. The tissues of the body are also divided into 'compartments', each containing tissues with similar physical properties. These compartments are: the 'central circulation', containing the heart, liver, kidneys and alimentary tract; 'fat', containing fat, skin, bone and connective tissue; 'muscle' and 'brain'. The perfusion[4] of each compartment is modelled as being proportional to the level of metabolic activity in each tissue. These features combine to make the model a fairly good representation of the physiology it simulates.

This model enables the nitrogen tensions in the tissues to be predicted from any given input dive profile. Another model, which treats the body as being constituted of the same tissue compartments and uses a similar set of differential equations is that of Zimmer and Tyack [17]. However, Zimmer and Tyack's model considers the blood in a different way, treating the arterial and venous blood as two homogeneous pools within which the nitrogen tension has a single value. It was decided that for the purposes of the model we eventually aim to produce, it would be more appropriate to calculate the nitrogen tensions arising in the tissues in the same way as was used by Fahlman *et al*., as this seems to provide a more accurate representation of the physiology we wish to model here.

[3] Nitrogen tension is the partial pressure of nitrogen dissolved in a solid, in this case tissue.
[4] Perfusion is defined as the rate of blood flow to an area of the body.

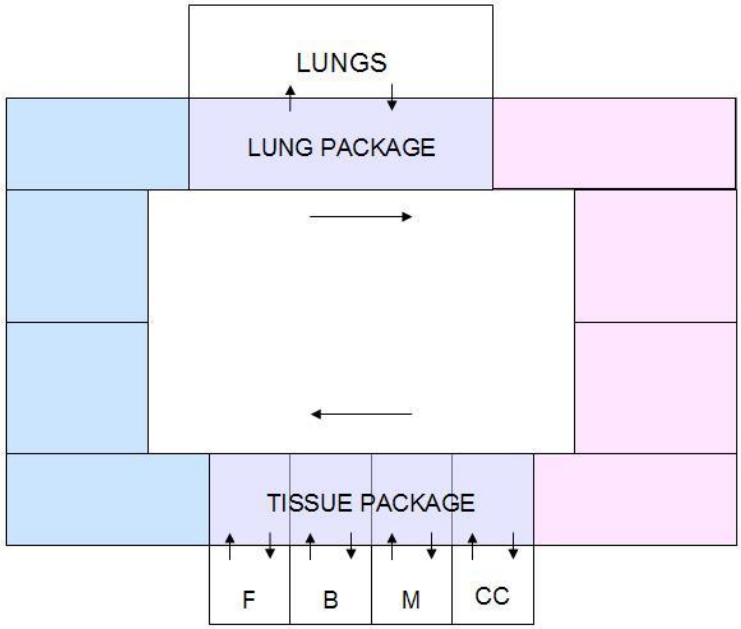

Figure 2. A diagrammatic representation of the model of Fahlman *et al*. [16] showing how the blood is considered as discrete packages which circulate from the lungs to the tissues. The tissue compartments are fat (F), brain (B), muscle (M) and central circulation (CC).

Our own implementation of the model by Fahlman *et al*. was validated against the original via the reconstruction of 'figure 2' in that paper, which showed the nitrogen tensions predicted to arise in each tissue compartment as a result of a hypothetical dive by a dolphin to 25 m, which was assumed to continue until all of the tissues were saturated. The results of this reconstruction are shown in figure 3 below.

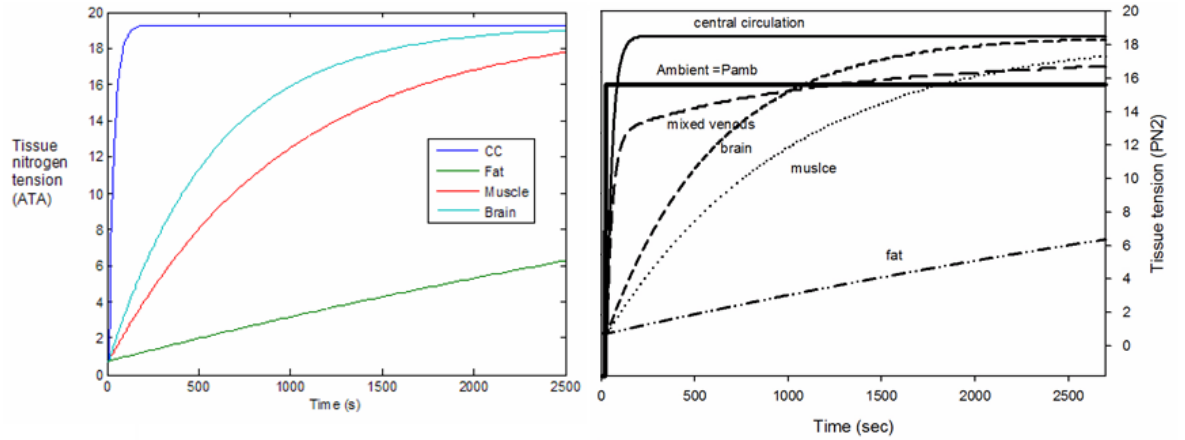

Figure 3. Figure 2 modified from Fahlman *et al*. (2006) [16] shown to the right of the same figure produced by our implementation of the model on the left. Both plots depict the evolutions of nitrogen tissue tension (PN2) expressed in atmospheres (ATA).

Having confirmed our accurate reproduction of the original model, our implementation was then used to model how the nitrogen tensions experienced by the tissues of the dolphins that took part in Ridgway and Howard's experiments involving a series of dives to 100 m [18] would have changed during diving. This enabled the model output to be validated against the results of these field

experiments. This dive series was then used as the model input for each of the subsequent model sensitivity tests.

4 MODEL SENSITIVITY TESTS

A series of parameter sensitivity tests were conducted on the model to identify which of the parameters not currently quantified in the beaked whale species of interest were the strongest determinants of the model output. The parameters included in these tests were the assumed depth of lung collapse, the Ostwald solubility coefficients[5] of nitrogen in each of the tissues compartments, (defined as the volume of nitrogen dissolved per volume of solute per atmosphere of partial pressure of nitrogen at a given temperature), the perfusion of the tissues as a whole, and the perfusion of individual tissue compartments. The aim of this work was to establish the order of priority that should be given to these parameters in terms of conducting experiments to quantify their values in beaked whales.

This model, as reported by Fahlman *et al*. [16], has only been validated against measured physiological and anatomical data for one cetacean species, specifically the bottlenose dolphin (*Tursiops truncatus*). This validation was based measurements made by Ridgway and Howard [18] in an experiment involving animals undergoing a sequence of dives. Fahlman *et al* were able to exploit direct physiological measurements and the, relatively, well understood anatomy of this species. In seeking to apply a similar model to beaked whales the underlying lack of physiological and anatomical data presents a challenge. Zimmer and Tyack [17] chose to overcome this problem using a variety of techniques, including allometric scaling (scaling between species based on body mass) of parameters. We chose to centre our sensitivity analysis about the parameters used to characterise bottlenose dolphins, since these are currently the only parameters that have been validated against experimental data. One should note that our objective is to rank the parameters in terms of their influence on the model output, and not to measure the parameter sensitivity *per se*.

The results of these model sensitivity tests are shown in figure 4 below. Figure 4a clearly shows that an increase in the assumed depth of lung collapse in the whales has a large effect on increasing the maximum percentage saturation with nitrogen reached in the tissues during diving. Of all the parameters tested here, this has been shown to be the strongest determinant of the model output. Figure 4b shows that increasing the solubility of nitrogen in the tissues of one compartment, in this case the central circulation, relative to that in the others also has a strong influence on the model output. The effect of increasing the total perfusion of the tissues, as shown in figure 4c, is less influential, although these results still show a clear effect on the model output. It can also be seen in figure 4d that the values chosen for the relative perfusion of each of the tissue compartments has a strong effect both on the perfusion to the other compartments and on the model output. Taking these results together, it is clear that each of the parameters tested here will need to be quantified specifically in the beaked whale species of interest, in order to produce a model capable of accurately simulating how the nitrogen tensions in each of the tissue compartments changes during a dive by a beaked whale. It should be noted that the order of priority given to the quantification of each of these parameters should not solely be dependent upon the magnitude of the effect of each parameter on the model output as identified above. Care should also be taken to account for the accuracy with which measurements for each parameter could be made.

[5] The Ostwald solubility coefficient is the constant of proportionality in Henry's law, i.e. it relates the equilibrium concentration of a dissolved gas in a liquid to the partial pressure in an adjacent gas.

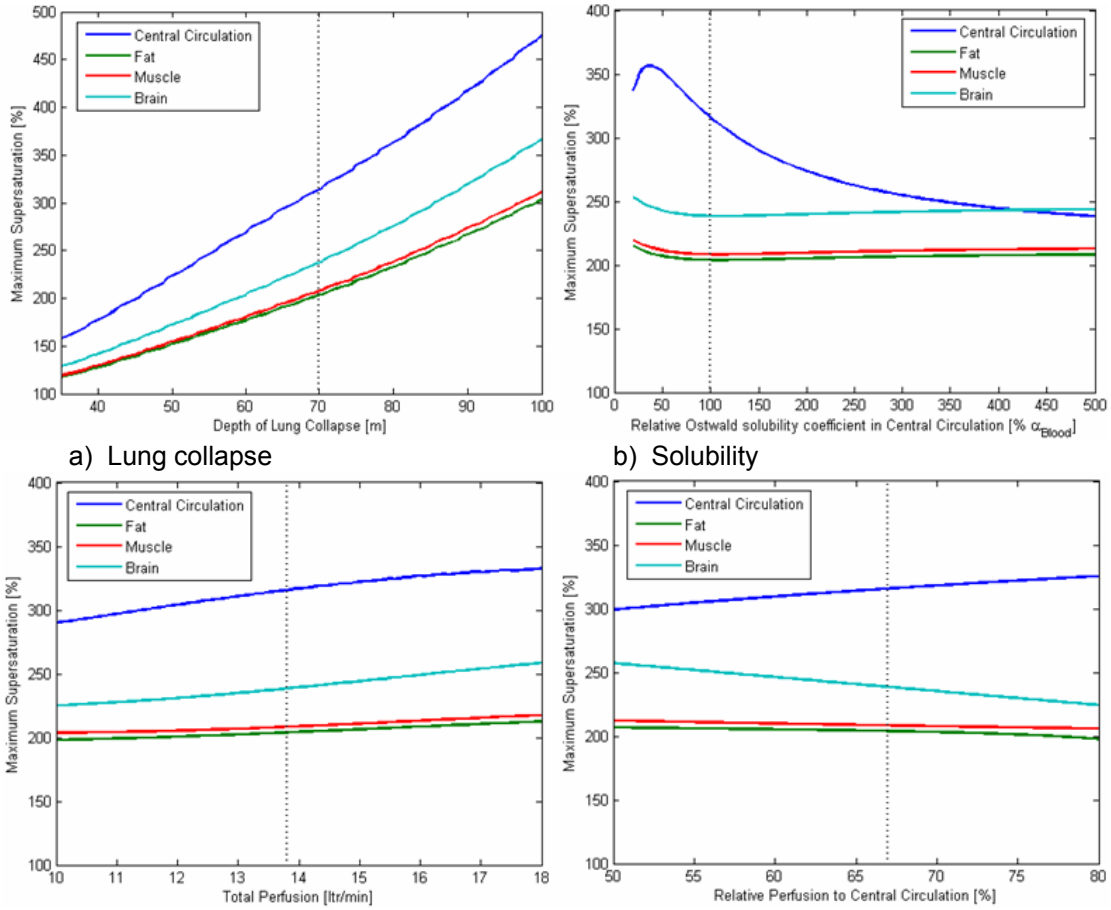

Figure 4. Graphs showing maximum supersaturation level reached in each tissue compartment relative to that at sea level as a function of perturbations of various model parameters. a) The assumed depth of lung collapse, b) the Ostwald solubility coefficient for nitrogen in the central circulation compartment relative to that in the blood, c) the total perfusion of the tissues, and d) the perfusion of the central circulation compartment relative to the perfusion to all the other tissue compartments (the overall perfusion is kept fixed for each configuration). The dotted line on each graph represents the value used in the original model by Fahlman *et al*. [16].

5 DISCUSSION

The comparison of the output of our implementation of the model of Fahlman *et al*. [16] with the original in figure 3 clearly shows that we have been able to reproduce that part of their model accurately. The parameter sensitivity tests conducted on the model reveal that it will be necessary to determine values for each of the parameters tested empirically, although the measurement of the depth of lung collapse in beaked whales should be given the highest priority, as it has been predicted here to be the parameter with the strongest influence on the model output.

The increase in the maximum percentage saturation of the tissues with nitrogen reached during diving with increases in three of the parameters - the assumed depth of lung collapse, the total perfusion to the tissues, and the relative perfusion of individual tissue compartments - can all be explained by the increase in the volume of nitrogen supplied to the tissues with the increasing hydrostatic pressure during dive decent prior to the 'collapse' of the lungs. However, the results

that show the effect of changing the Ostwald solubility coefficients for nitrogen chosen for each of the tissue compartments upon the maximum nitrogen saturation levels reached in the tissues shows a more complex relationship. Here it is suggested that there are two effects combining to produce the results observed. Increasing the solubility of nitrogen in a tissue compartment increases the absolute volume of nitrogen required to saturate the tissues to a given level, so that the maximum percentage saturation reached during a dive will decrease with increasing nitrogen solubility. Contrary to this, at low nitrogen solubility values, a smaller volume of the circulating nitrogen gas can pass into the tissues during the time period for gas exchange than can pass for higher solubility values, so that the total volume of nitrogen that enters the tissues during a dive is much lower, and therefore the maximum percentage saturation level reached is also lower. It is therefore suggested that the interplay between these two factors explains the results shown in figure 4b.

From the work presented here, it is clear that the next stage of this research should be to design and undertake experiments to quantify each of the parameters tested in the sensitivity tests, in order to produce a model that is more specific to *Ziphius cavirostris* and *Mesoplodon densirostris*. In addition to this, it will be necessary to find a method of estimating the probability and extent of bubble growth within each of the tissue compartments, along with the resulting DCS risk, in order to produce the model capable of estimating the DCS risk from any beaked whale dive profile, as described at the start of the paper. The model of Zimmer and Tyack discussed earlier links tissue nitrogen tensions with bubble growth [17]. This model uses a dive profile of *Ziphuis cavirostris* recorded in the Ligurian Sea [19] as the basis of estimating whether bubble nuclei of various sizes would be expected to grow within the tissue compartments used by Fahlman *et al*. [16] as a result of the nitrogen tensions reached in these tissues during this dive. The maximum size of bubble nucleus that could exist within the tissues without growing was identified in this way, and the maximum nitrogen tension reached within each tissue compartment upon surfacing from the dive, which would not result in the growth of such bubble nuclei, was then calculated. It is intended that a similar model will be developed using the current model presented here, with the species specific values for the parameters found to be strong determinants of the current model output identified here substituted into it, to calculate the nitrogen tensions resulting from dive profiles recorded for both *Ziphius cavorstris* and *Mesoplodon densirostris*. Critical stable bubble nucleus sizes will then be calculated in much the same way as was done by Zimmer and Tyack, along with the critical tissue nitrogen tensions upon surfacing. The results determined using this model will therefore be specific to the two beaked whale species of interest here.

Once the model just described has been produced, it will be possible to predict the risk of DCS resulting from any given behavioural response by beaked whales to sonar exposure, and therefore to identify the behaviours that incur the highest risk to the whales. These will then be compared with those observed during controlled exposure experiments. This will establish which behaviours, if any, are causing these species to suffer DCS-like injuries and mass strand in the way that has been observed. It will also facilitate the comparison of alternative mitigation procedures, since one can use the model to infer risk of inducing DCS by examining the modified diving behaviour in reacting to the mitigation protocol.

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