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Could beaked whales get the bends?
Effect of diving behaviour and physiology on modelled gas exchange for three species: *Ziphius cavirostris*, *Mesoplodon densirostris* and *Hyperoodon ampullatus*

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A mathematical model, based on current knowledge of gas exchange and physiology of marine mammals, was used to predict blood and tissue tension N_2 (P_{N_2}) using field data from three beaked whale species: northern bottlenose whales, Cuvier's beaked whales, and Blainville's beaked whales. The objective was to determine if physiology (body mass, diving lung volume, dive response) or dive behaviour (dive depth and duration, changes in ascent rate, diel behaviour) would lead to differences in P_{N_2} levels and thereby decompression sickness (DCS) risk between species. Diving lung volume and extent of the dive response had a large effect on end-dive P_{N_2}. The dive profile had a larger influence on end-dive P_{N_2} than body mass differences between species. Despite diel changes in dive behaviour, P_{N_2} levels showed no consistent trend. Model output suggested that all three species live with tissue P_{N_2} levels that would cause a significant proportion of DCS cases in terrestrial mammals. Cuvier's beaked whale diving behaviour appears to put them at higher risk than the other species, which may explain their prevalence in strandings after the use of mid-frequency sonar.

1. Introduction

Multiple mass strandings of beaked whales have been documented over the last decade following acoustic exposure to anthropogenic sounds (reviewed in Cox et al., 2006). In terms of species composition, Cuvier's beaked whale (*Ziphius cavirostris*) have predominated, with Blainville's beaked whale (*Mesoplodon densirostris*) also occurring in several events, and occasional occurrence of other beaked whale species (northern bottlenose whale *Hyperoodon ampullatus*, and Gervais' beaked whale *M. europaeus*, Simmonds and Lopez-Jurado, 1991; Cox et al., 2006). Gas-bubble disease, induced through a precondition of tissue N_2 supersaturation coupled with a behavioural response to acoustic exposure, has been suggested as a possible pathologic mechanism for these beaked whale deaths (Jepson et al., 2003; Cox et al., 2006).

Beaked whales dive deeply more frequently than most other cetacean species (Hooker and Baird, 1999; Baird et al., 2006, 2008; Tyack et al., 2006; Minamikawa et al., 2007) and this behaviour has been suggested to result in tissue N_2 supersaturation. It is possible that these mammals live continuously with elevated levels of N_2 (Cox et al., 2006) which could render them prone to decompression sickness (DCS) if they altered their diving behaviour. Suggestions include disturbance caused by an acoustic signal that could (1) affect the normal diving behaviour, e.g. increased or decreased surface interval, ascent rate, or dive duration, leading to increased supersaturation, thereby increasing DCS risk, (2) the acoustic signal could activate existing stabilized bubble nuclei allowing them to grow by passive diffusion, and/or, (3) drive activated bubbles to expand through rectified diffusion (Cox et al., 2006). Each of these hypotheses assumes that these breath-hold diving marine mammals live with significantly elevated blood and tissue tension N_2 (P_{N_2}) levels.

Increasing concentrations of N_2 have been observed in bottlenose dolphin (*Tursiops truncatus*) tissues following trained repetitive dives (Ridgway and Howard, 1979), in freely diving Weddell seals (*Leptonychotes weddellii*, Falke et al., 1985) and forced diving Weddell, harbour (*Phoca vitulina*) and elephant seals (*Mirounga angustirostris*, Kooyman et al., 1972). Houser et al. (2001) used the results published by Ridgway and Howard (1979) in a theoretical model based on gas diffusion to show that beaked whale diving patterns (based on simulated dive data) could lead to chronic tissue accumulation of N_2 gas. Their simulations illustrated the potential increase in N_2 caused by relatively shallow (100 m, 9 min)

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dives with short (1 min) surface intervals. However, their simulated time at the surface (5 min at surface in 60 min of diving) was much shorter than recorded from logged field-data (30–38% time spent at the surface, Hooker and Baird, 1999), suggesting that re-evaluation of DCS risk based on logged-data would be valuable. Zimmer and Tyack (2007) have previously estimated blood and tissue P_{N_2} values for a Cuvier's beaked whale, and also emphasized the danger of repetitive shallow dives rather than deep dives per se. However, both of these previous models incorporated the assumption that alveolar collapse is immediate and occurs at a pre-determined depth (~70 m, Zimmer and Tyack, 2007). Here we use a revised model (described in Fahlman et al., 2009) which incorporates the recent lung collapse model developed by Bostrom et al. (2008) and the circulatory adjustments of the diving response (Fahlman et al., 2006).

Since sonar-related strandings have occurred for several species of beaked whale, we compare and contrast results for previously published time depth recorder data (Hooker and Baird, 1999; Baird et al., 2006, 2008) from Cuvier's beaked whale (referred to as *Ziphius*), Blainville's beaked whale (referred to as *Mesoplodon*) and northern bottlenose whale (referred to as *Hyperoodon*). We investigate how differences in behaviour and physiology would affect end-dive tissue and blood P_{N_2} and thus the susceptibility to DCS-like symptoms.

Whole body N_2 saturation is a reliable index of DCS risk in terrestrial animals of varying body size (Berghage et al., 1979). To predict DCS risk in beaked whales it is therefore important to use a gas exchange model that has been calibrated against empirical data and to compare these estimated levels against those in terrestrial mammals. A previously published model that has been calibrated against known tissue and blood N_2, O_2 and CO_2 levels in several different species of marine mammals (Fahlman et al., 2009) was used and we (1) examined the predicted blood and tissue N_2 levels resulting from differences in normal diving behaviour (dive depth and duration). Several of the recorded beaked whale strandings appear to have contained a disproportionate number of subadult whales (Freitas, 2000; Anon., 2001; Martin et al., 2004), possibly suggesting an effect of body mass (M_b). Together with our lack of knowledge of the dive response or diving lung volume in these species, we therefore investigate (2) the effect of changes in body mass (M_b), diving lung volume (and changes in pulmonary shunt), and cardiac output ($\dot{Q}_{tot}$) on blood and tissue P_{N_2} levels. In terms of behaviour, in addition to looking at dive depth and duration, we (3) assessed whether changes in ascent rate (Jepson et al., 2003; Zimmer and Tyack, 2007) and diel changes in diving behaviour (Baird et al., 2008) would influence the likelihood of DCS in these whales, the latter of which could help direct mitigation efforts for sonar-related threats to these whales. While we do not know the underlying physiology for these species, this comparison enables us to determine whether differences in dive behaviour or in the aspects of physiology we investigate using this model could explain possible differences in estimated P_{N_2} and thereby DCS risk.

2. Material and methods

2.1. Model

The first model, Model A, was adapted from the breath-hold model developed by Fahlman et al. (2006) with addition of pulmonary shunt and exchange of O_2 and CO_2 as detailed in Fahlman et al. (2009) and summarized below. The body was partitioned into four different tissue compartments (brain, fat, muscle, and central circulation) and one blood compartment (arterial and mixed venous). The central circulatory compartment included heart, kidney, liver and alimentary tract while the muscle compartment included muscle, skin, bone, connective tissue and all other tissues (Fahlman et al., 2009).

Gas exchange occurred between lung and blood and between blood and each compartment. The same assumptions were used for the blood N_2 stores as those detailed in Fahlman et al. (2006). The $\dot{Q}_{tot}$ and fraction of blood to each tissue were not fixed and could be varied to mimic diving bradycardia and changes in regional blood flow due to peripheral vasoconstriction. Hence, cardiovascular changes seen in freely diving animals could be simulated (Zapol et al., 1979; Andrews et al., 1997; Froget et al., 2004).

Unless specified, in the instances in which we had no direct anatomical or physiological data for the species in this study, we used the data reported for the Weddell seal (Davis and Kanatous, 1999). We used a model that predicted alveolar volume (V_A) with depth (Bostrom et al., 2008) and estimated pulmonary shunt from the ratio between V_A and the total alveolar capacity (TAC) as previously detailed (Fahlman et al., 2009). The relative size of each compartment was estimated from data reported by Mead (1989) for the genus *Mesoplodon* and from Scholander (1940) for the genus *Hyperoodon*, as 57.0% for muscle, 3.0% for central circulation, 0.2% for brain, 20.7% for fat and 19.1% for blood. It was assumed that the relative proportion of each compartment remained constant between species and for animals of different size.

A second variation (Model B) was derived from Model A, and this was used to determine the extent to which the diving bradycardia affected inert gas uptake. The mass specific $\dot{Q}_{tot}$ ($s\dot{Q}_{tot}$) was estimated as detailed in the appendix. The resulting $s\dot{Q}_{tot}$ at the surface was 206 ml min^{-1} kg^{-1} for *Mesoplodon* (M_b = 1000 kg), 172 ml min^{-1} kg^{-1} for *Ziphius* (M_b = 2050 kg) and 138 ml min^{-1} kg^{-1} for *Hyperoodon* (M_b = 5000 kg). For model A, it was assumed that $\dot{Q}_{tot}$ during diving was 50% of that at the surface, while for model B it was 12.5%.

Blood flow distribution to each tissue at the surface was assumed similar to that measured in forced dived Weddell seals resting at the surface (Zapol et al., 1979; Fahlman et al., 2009). During diving, we assumed that blood flow was directed to each tissue according to the metabolic rate ($\dot{V}_{O_2}$) of that tissue and the available O_2 in the tissue (see Fahlman et al., 2009 for details on how tissue $\dot{V}_{O_2}$ and O_2 stores were estimated). Consequently, during diving both Model A and B assumed that 80% of $\dot{Q}_{tot}$ was directed to the central circulation, 1% to the muscle, 12% to the brain and 7% to the fat.

Table 1

Estimated body mass (kg), metabolic rate ($\dot{V}_{O_2}$, l O_2 min^{-1}) and O_2 store (l) for the central circulation (CC), muscle (M), brain (B), fat (F), lung (L), and blood (Bl) compartments for Blainville's beaked whale (*Mesoplodon densirostris*), Cuvier's beaked whale (*Ziphius cavirostris*) and northern bottlenose whale (*Hyperoodon ampullatus*).

Genus	Body mass (kg)	Metabolic rate (l O_2 min^{-1})					O_2 store (l)						
		CC	M	B	F	Total	CC	M	B	F	L	Bl	Total
Mesoplodon	1000	0.6	0.7	0.04	0.08	1.4	0.05	41	0.02	1.7	3.1	61	106
Ziphius	2050	1.0	1.2	0.06	0.14	2.4	0.1	84	0.04	3.6	6.4	124	218
Hyperoodon	5000	2.0	2.4	0.12	0.27	4.8	0.2	204	0.10	8.7	16	303	532

2.2. *Tissue metabolic rate and O_2 stores*

The metabolic rates for each tissue compartment were estimated from the data presented in Davis and Kanatous (1999, Table 1). The O_2 available during a dive came from lung, blood and tissue stores (mainly muscle, see below). The Ostwald solubility coefficient was used to calculate the dissolved O_2 content in blood and we used a value of 0.0261 l O_2 l^{-1} blood (Weathersby and Homer, 1980). The same solubility coefficient was used to estimate O_2 content of muscle and central circulation. For the fat and brain compartment we used a value of 0.133 l O_2 l^{-1} tissue.

In addition to dissolved O_2, the muscle compartment was assumed to contain a significant amount of endogenous O_2 bound to myoglobin and available for muscle metabolism. When calculating the total O_2 stored in the muscle compartment, we assumed that 49% of the total M_b was skeletal muscle, i.e. the muscle compartment was composed of a variety of tissues not all having myoglobin, with a specific gravity of 1.06 kg l^{-1} (Kayar et al., 1997). We used the reported myoglobin concentration (63 g kg^{-1} muscle, Butler and Jones, 1982) reported for *Hyperoodon* and an O_2-binding capacity of 1.34 ml O_2 (STPD) g^{-1} muscle tissue (Stephenson, 2005). The muscle was assumed to be completely saturated at the beginning of a trial run, i.e. the initial conditions.

The blood was assumed to have a hemoglobin (Hb) concentration of 0.26 kg l^{-1} blood and the same O_2-binding capacity as myoglobin (Stephenson, 2005). Initially, it was assumed that arterial blood was 97% saturated and venous blood 87% saturated. The resulting O_2 stores for each species is reported in Table 1. Body mass for each species was estimated based on data recorded from stranded animals (Heyning, 1989; Mead, 1989) or from length-weight equations and length estimates (Bloch et al., 1996; Whitehead et al., 1997).

2.3. *Lung compression and pulmonary shunt*

The model published by Bostrom et al. (2008) was used to estimate alveolar volume at depth (DV_A). Initial parameters used to estimate DV_A were: total lung capacity (TLC, total respiratory volume), the volume of the upper respiratory system, including trachea and bronchi (V_T), and maximal alveolar volume (V_A), i.e. $TLC = V_T + V_A$. It was assumed that gas exchange occurred only in the alveoli and when $DV_A = 0$, no gas exchange occurred. For all species, TLC was assumed equal to that reported for the bottlenose whale (25 ml kg^{-1}, Scholander, 1940). Dead space volume was assumed to be 9% of TLC (Bostrom et al., 2008). For our investigation of an animal diving with a lung volume lower than TLC, the reduction in gas volume was taken from the alveolar gas space. That is, $DV_A = DV_L - V_T$. Thus, for a 1000 kg beaked whale diving on a DV_L that was 50% of TLC: TLC = 25 l, V_T = 2.25 l, DV_L = 12.5 l, DV_A = 10.25 l.

Estimated DV_A was used to compute pulmonary shunt, sometimes also termed venous admixture (see Eq. (4) in Fahlman et al., 2009). The power function ($1\text{-shunt} = a\cdot(DV_A\cdot V_A)^{-b}$, Bostrom et al., 2008; Fahlman et al., 2009) established from harbour seal data was used to establish the relationship between pulmonary shunt and estimated $DV_A\cdot V_A{}^{-1}$.

2.4. *Dive data and estimated P_{N_2} levels*

The dive data used to estimate blood and tissue P_{N_2} levels were previously published for *Ziphius* and *Mesoplodon* by Baird et al. (2006, 2008) and for *Hyperoodon* by Hooker and Baird (1999). Two dive traces were used for each species, and summary statistics for each dive series are presented in Table 2. Each dive trace is indicated by the species abbreviation and the duration of the trace (e.g. Md_{78} is a 78-h trace for *M. densirostris*).

Table 2

Animal code, logger attachment duration (Duration), number of dives (*n*), mean (± 1 SD) dive duration (DD), surface interval duration (SI), maximum (Max) and mean depth (Mean) for dive data used for estimation of tissue and blood N_2 tensions for two Blainville's beaked whales (*Mesoplodon densirostris*, Baird et al., 2006, 2008), two Cuvier's beaked whales (*Ziphius cavirostris*, Baird et al., 2006, 2008) and two northern bottlenose whales (*Hyperoodon ampullatus*, Hooker and Baird, 1999). A dive was defined as a submergence to a depth >5 m for >10 s. Shallow dives were >5 m and ≤50 m, intermediate dives were >50 m and ≤200 m, and deep dives were >200 m. Number of dives in parentheses follows removal of the initial P_{N_2} equilibrium period (see text for details).

Animal code	Duration (h)	Shallow dives					Intermediate dives					Deep dives				
		n	DD (min)	SI (min)	Max (m)	Mean (m)	*n*	DD (min)	SI (min)	Max (m)	Mean (m)	*n*	DD (min)	SI (min)	Max (m)	Mean (m)
Md_{22}	22	108 (105)	4.5 ± 3.6	0.3 ± 0.6	16 ± 9	10 ± 6	18 (12)	10.1 ± 2.6	0.2 ± 0.3	119 ± 48	72 ± 30	11 (7)	38.9 ± 17.4	1.3 ± 1.0	886 ± 424	537 ± 263
Md_{78}	78	186 (186)	6.9 ± 5.5	1.6 ± 1.3	25 ± 15	18 ± 12	62 (58)	12.4 ± 2.6	2.1 ± 1.7	101 ± 51	63 ± 32	46 (39)	40.1 ± 16.8	1.9 ± 1.6	818 ± 407	509 ± 243
Zc_9	9	5 (0)	0.7 ± 0.2	0.2 ± 0.3	12 ± 7	7 ± 4	1 (0)	13.8	–	69	22	11 (0)	41.3 ± 20.1	3.2 ± 1.1	786 ± 505	513 ± 314
Zc_{34}	34	70 (64)	5.0 ± 7.1	0.5 ± 0.8	19 ± 11	12 ± 8	6 (5)	12.2 ± 6.3	0.7 ± 0.9	64 ± 15	48 ± 12	32 (24)	45.2 ± 24.2	1.4 ± 1.0	716 ± 459	468 ± 278
Ha_2	2	9 (0)	1.8 ± 1.4	1.2 ± 1.1	11 ± 2	7 ± 1	5 (0)	9.0 ± 2.6	1.2 ± 1.4	106 ± 21	60 ± 20	3 (0)	18.9 ± 7.5	0.04 ± 0.03	475 ± 322	259 ± 181
Ha_{28}	28	120 (73)	1.7 ± 1.7	1.6 ± 1.6	14 ± 10	6 ± 6	18 (8)	9.2 ± 2.9	1.6 ± 0.9	113 ± 43	73 ± 32	24 (11)	34.9 ± 10.9	1.3 ± 0.6	992 ± 347	585 ± 179

A dive was defined as a submergence for >10 s to a depth >5 m. Dives were separated into shallow, intermediate and deep dives depending on the maximum depth recorded. For all species, shallow dives were defined as >5 m and $\leq$50 m, intermediate dives were >50 m and $\leq$200 m, and deep dives were >200 m. These categories were based on the assumption that shallow dives <50 m may serve to reduce bubble formation and be potentially helpful as decompression dives (Fahlman et al., 2007), intermediate dives 50–200 m are likely to include gas exchange for a high proportion of the dive, whereas deep dives >200 m will almost certainly have no gas exchange beyond this depth and so the lungs are likely to be collapsed for a portion of the dive (Bostrom et al., 2008). Within these categories we present mean maximum dive depth (the maximum depth reached during the dive), mean dive depth (the average depth of the dive), and surface interval (the time spent at the surface between dives). For each dive series, tissue and blood P_{N_2}s were estimated throughout the entire duration of the series. Following this, we extracted the end-dive P_{N_2} values for each dive and these end-dive levels are presented for different categories of dives for each series.

To look at diel changes in dive behaviour and how these affect estimated blood and tissue P_{N_2}, the dive data were divided into day (D) or night (N) based on location and times for each dive. We used sunrise and sunset to separate D and N (http://aa.usno.navy.mil/data/docs/RS_OneDay.php, Table 4), for the longer traces (*Md*$_{22}$, *Md*$_{78}$, *Zc*$_{34}$ and *Ha*$_{28}$).

3. Results

The average hourly dive rate was significantly different ($P < 0.01$) between *Ziphius* (2.5 dives h^{-1}) and *Hyperoodon* (7.1 dives h^{-1}), but neither was different from the hourly dive rate of 5.0 dives h^{-1} for *Mesoplodon* ($P > 0.3$, Mixed model ANOVA). There was no difference in the proportion of shallow ($P > 0.4$), intermediate ($P > 0.1$) or deep dives ($P > 0.5$) between species.

Except for the short 2-h dive trace from *Hyperoodon*, the mean dive duration, maximum and mean dive depths for deep dives were similar between individuals and species. For intermediate dives, both the mean and maximum dive depth was shallower for *Ziphius* compared with *Mesoplodon* and *Hyperoodon* (Table 2). For all species, there was a significant correlation between the maximum depth and the mean depth for each dive ($P < 0.05$).

3.1. Predicting tissue and blood P_{N_2} model variations

Rather than assigning an arbitrary initial P_{N_2} at the start of the dive trace, we simply assumed this matched with surface N_2 at the model outset. For tissues with a fast time constant (central circulation and brain), a diving P_{N_2} equilibrium was established during the first few dives while for tissues with a slow time constant, equilibrium took several hours (Fig. 1). To avoid bias we therefore removed the initial 4 h for *Mesoplodon*, 8 h for *Ziphius* and 13 h for *Hyperoodon*. We also excluded the 9 h data set for *Ziphius* (*Zc*$_9$) and the 2 h data set for *Hyperoodon* (*Ha*$_2$). Therefore, the number of dives reported in Table 2 includes all dives and the number within parentheses is the number of dives after excluding the initial period until equilibrium. Equilibrium values converged when the model was started with different initial conditions and the time to equilibrium was the same.

Model A (50% bradycardia) generally showed highest P_{N_2} levels for *Ziphius*, although high fast tissue P_{N_2} levels were also seen for intermediate dives of *Hyperoodon* (Table 3 Model A). Predicted end-dive P_{N_2} increased linearly with mean dive depth (Fig. 2A) or dive duration (Fig. 2B) until a maximum at which time estimated mixed venous P_{N_2} (Pv_{N_2}) levelled off. Comparing between dive classes and body compartments, end-dive P_{N_2} for central circulation increased

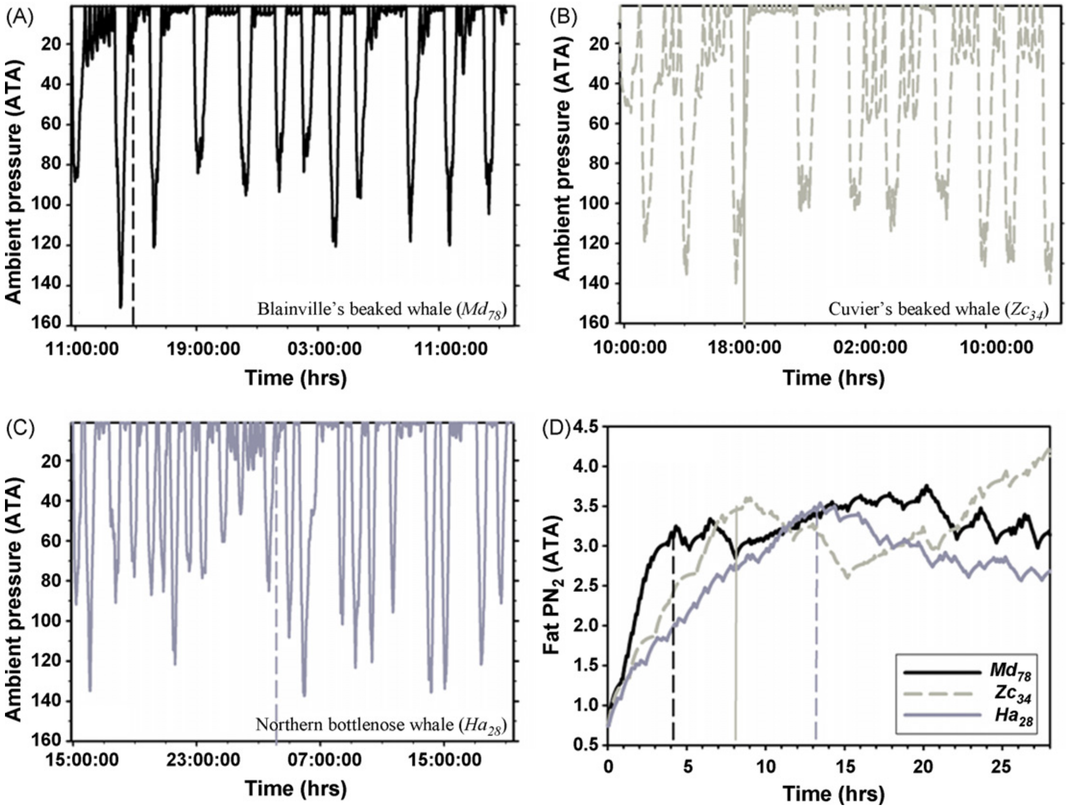

Fig. 1. Dive trace for: (A) Blainville's beaked whale (*Md*$_{78}$); (B) Cuvier's beaked whale (*Zc*$_{34}$); (C) northern bottlenose whale (*Ha*$_{28}$); and (D) estimated fat P_{N_2} against time of dive trace showing the time to equilibrium (broken vertical lines) for each of these.

Table 3

Sensitivity analysis of standard model (A: 50% bradycardia) and that with more extensive dive response (B: 12.5% bradycardia) on N_2 levels in each of the four tissue compartments and mixed venous blood (V). Tissue compartments are central circulation (CC), muscle (M), brain (B), fat (F). See text for details on the variation of physiological variables for each model. Dive data sets used were a 78 h (*Md*$_{78}$) and a 22 h (*Md*$_{22}$) trace for Blainville's beaked whales, a 34 h (*Zc*$_{34}$) trace from a Cuvier's beaked whale and a 28 h (*Ha*$_{28}$) trace from a northern bottlenose whale.

ID	Model	Body mass (kg)	Mean end-dive P_{N_2} (ATA)														
			Dives <50 m					Dives >50 m and Dives <200 m					Dives > 200 m				
			CC	M	B	F	V	CC	M	B	F	V	CC	M	B	F	V
Md$_{22}$	A	1000	1.5	1.0	1.6	2.4	1.2	3.8	1.1	4.2	2.7	2.0	3.8	1.1	4.0	2.6	2.0
Md$_{78}$	A	1000	1.9	1.0	2.1	3.1	1.3	3.2	1.1	3.6	3.3	1.8	4.3	1.1	4.4	3.3	2.2
Zc$_{34}$	A	2050	1.8	1.3	1.8	3.3	1.5	4.1	1.5	4.2	3.6	2.4	4.9	1.5	5.0	3.7	2.6
Ha$_{28}$	A	5000	1.2	1.0	1.6	3.0	1.1	4.6	1.0	4.7	3.0	2.2	4.8	1.0	4.7	3.1	2.2
		Mean	**1.6**	**1.1**	**1.8**	**2.9**	**1.3**	**3.9**	**1.2**	**4.2**	**3.2**	**2.1**	**4.4**	**1.2**	**4.6**	**3.2**	**2.2**
Md$_{22}$	B	1000	1.6	1.1	1.6	1.9	1.3	4.4	1.2	4.1	1.9	2.2	5.5	1.1	4.6	2.0	2.6
Md$_{78}$	B	1000	2.1	1.1	2.3	2.6	1.5	4.2	1.2	4.0	2.6	2.2	5.5	1.1	5.1	2.6	2.5
Zc$_{34}$	B	2050	1.6	1.5	2.1	2.4	1.6	3.7	1.7	3.7	2.4	2.4	6.2	1.7	5.5	2.8	3.1
Ha$_{28}$	B	5000	1.0	1.0	1.6	1.9	1.0	3.8	1.0	3.0	1.9	1.9	4.8	0.9	3.9	1.9	2.1
		Mean	**1.6**	**1.2**	**1.9**	**2.2**	**1.3**	**4.0**	**1.3**	**3.7**	**2.2**	**2.2**	**5.5**	**1.2**	**4.8**	**2.3**	**2.6**

by 107% for *Mesoplodon* (146% and 67%), 131% for *Ziphius* and 275% for *Hyperoodon* for the intermediate compared with the shallow dives ([intermediate-shallow]/shallow × 100, Table 3). For the deep dives, end-dive P_{N_2} for central circulation only increased by an additional 1–34% (Table 3). Similar changes were seen for the brain, with end-dive P_{N_2} increasing substantially as depth increased (shallow to intermediate, Table 3). For muscle and fat, end-dive P_{N_2} did not change much and even decreased in some cases for deeper dives (Table 3).

3.2. *The effect of cardiac output, $\dot{Q}_{tot}$, on estimated tissue and blood P_{N_2}*

With enhanced diving bradycardia ($\dot{Q}_{tot}$, 12.5% of the surface value during diving), central circulation P_{N_2} and Pv_{N_2} generally increased while fat P_{N_2} decreased in all animals and at all depths (Table 3, Model A vs. B). A greater dive response (i.e. reduction in $\dot{Q}_{tot}$) only resulted in lower end-dive P_{N_2}s for all body compartments for intermediate and deep dives of *Hyperoodon* (Table 3, Model A vs. B). For *Mesoplodon and Ziphius* results were more variable depending on body compartment.

3.3. *The effect of diving lung volume (DV_L) on estimated tissue and blood P_{N_2}*

To investigate the effect of partial inhalation on N_2 levels, we varied DV_L for each dataset and examined the effect on model output (Model A) for blood (Fig. 3) and tissue P_{N_2}. As diving lung volume was reduced, end-dive P_{N_2} decreased for all tissues and for Pv_{N_2}. For the shallow dives, a 75% reduction in DV_L reduced mixed venous P_{N_2} by between 12% and 19% for all individuals and species except *Md*$_{22}$, for which the reduction was only 4% (Fig. 3A). The reduction in end-dive P_{N_2} for central circulation and muscle were similar to Pv_{N_2} and ranged between 5% and 21%, while it was substantially higher for brain (range: 9–31%) and fat (range: 28–51%).

A 75% reduction in DV_L reduced Pv_{N_2} between 16% and 43% for the intermediate depth dives. For the deep dives, the same reduction in DV_L resulted in a reduction in Pv_{N_2} between 32% and 45% (Fig. 3B and C). Interestingly, it appeared that end-dive Pv_{N_2} decreased exponentially toward a minimum value for the shallow and intermediate dives but this became more or less linear for the deep dives (Fig. 3). The reduction in end-dive P_{N_2} for the tissue compartments varied between animals without any obvious trends except that as depth increased the relative reduction in end-dive P_{N_2} increased. The most notable exception was the fat compartment for which the reduction against DV_L appeared to be relatively unaffected by the dive depth and when DV_L was reduced by 75% the end-dive P_{N_2} reduction ranged between 33% and 49% for all depths, presumably due to the slow response time of this tissue.

3.4. *The effect of body mass, M_b, on estimated tissue Pv_{N_2}*

While Model A did not indicate any obvious trends in end-dive P_{N_2} against M_b when the species were compared (Table 3), we were concerned that this might be due to species-specific differences in dive trace profiles. We therefore ran the model for each

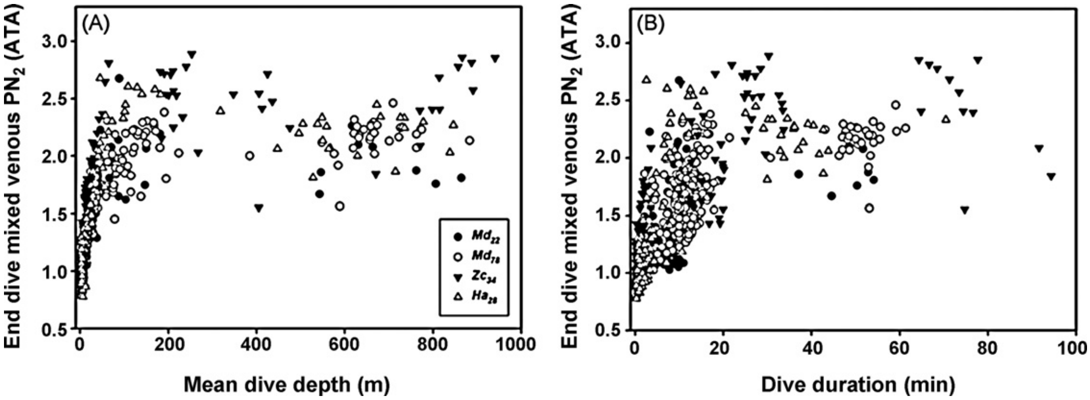

Fig. 2. Estimated end-dive mixed venous P_{N_2} against (A) mean dive depth or (B) dive duration for each of the dive traces.

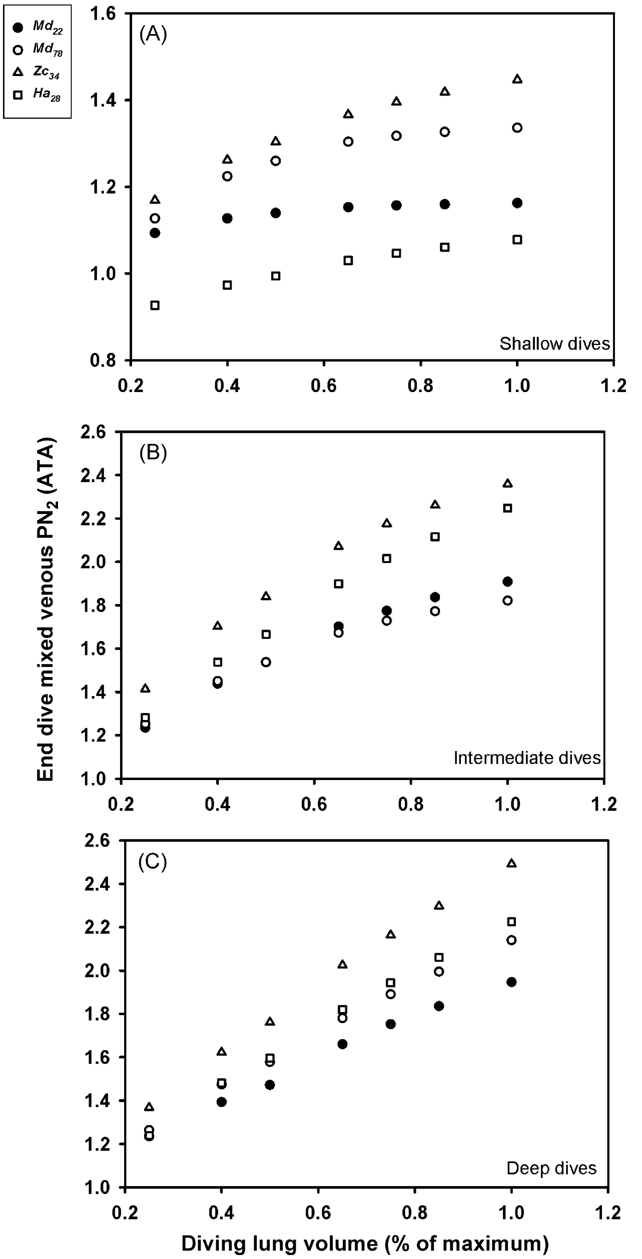

Fig. 3. Average predicted end-dive mixed venous P_{N_2} (ATA) against proportion of diving lung volume (% of maximum) for the entire dive trace for (A) shallow, (B) intermediate and (C) deep dives for two Blainville's beaked whales (*Md₂₂* and *Md₇₈*), one Cuvier's beaked whale (*Zc₃₄*) and one northern bottlenose whale (*Ha₂₈*).

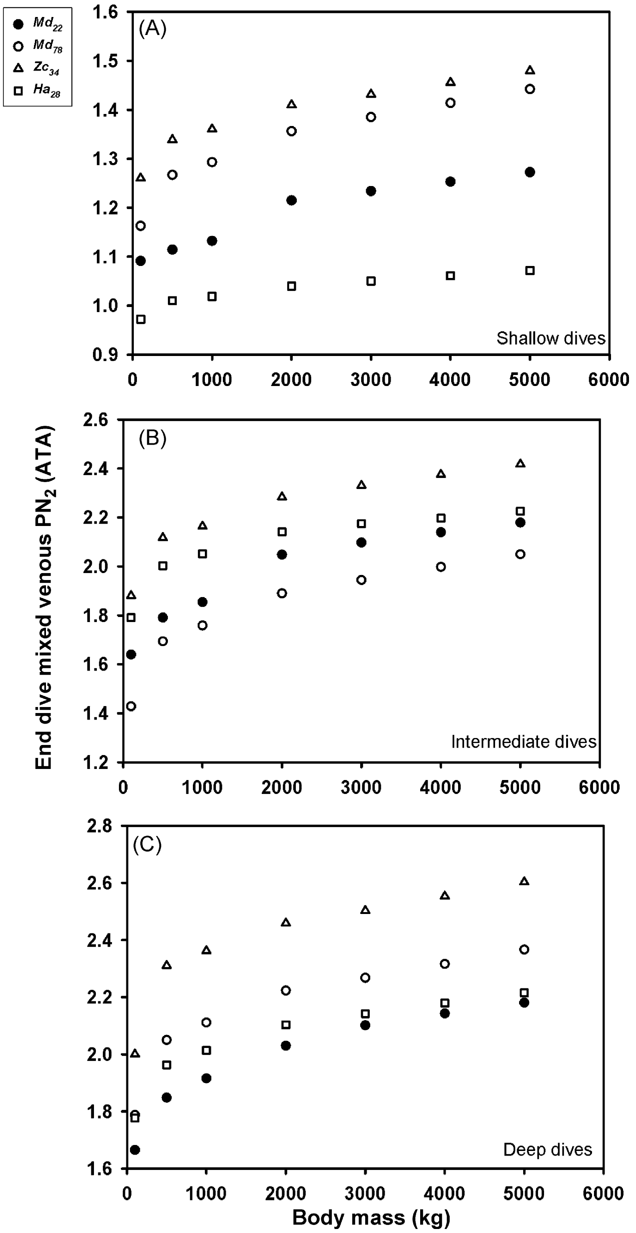

Fig. 4. Average predicted end-dive mixed venous P_{N_2} (ATA) against varying body mass (kg) for the entire dive trace for (A) shallow (B) intermediate and (C) deep dives for two Blainville's beaked whales (*Md₂₂* and *Md₇₈*), Cuvier's beaked whale (*Zc₃₄*) and northern bottlenose whale (*Ha₂₈*).

dive trace and varied M_b within each (Fig. 4). As M_b decreased from 5000 kg to 100 kg, end-dive mixed venous P_{N_2} decreased exponentially for all depths (Fig. 4). From 5000 kg to 500 kg the reduction was linear by between 2% and 14% for the shallow dives (Fig. 4A), 7% to 21% for the intermediate dives (Fig. 4B) and 3% to 18% for the deep dives (Fig. 4C). Muscle and brain P_{N_2} also decreased with a reduction in M_b, central circulation P_{N_2} decreased or increased between 17% and 27%, while fat P_{N_2} increased between 4% and 40%.

3.5. The effect of ascent rate on estimated tissue and blood P_{N_2}

Some beaked whale dives appear to show a deceleration in the ascent rate prior to surfacing. This was first noted for northern bottlenose whales (Hooker and Baird, 1999) but is also apparent in the near surface waters for several of the dives analyzed here. To determine how such changes in ascent rate would affect end-dive P_{N_2}, we modified one of the dives from the *Mesoplodon* 78-h trace (Fig. 5). Model A was used to determine end-dive P_{N_2} for this dive trace before and after the ascent rate had been modified as the whale approached the surface. When $Pv_{N_2} >$ ambient N₂ pressure (P_{amb}) bubbles may form, and the extent of the supersaturation is a measure of the risk of DCS (Fahlman et al., 2001). As the ascent rate increased for the modified dive trace, the P_{N_2} gradient between mixed venous blood and the ambient pressure increased rapidly and then decreased rapidly as the animal surfaced. A similar increase was seen in the partial pressure gradient for the original dive profile but here the gradient remained elevated as the animal slowly approached the surface.

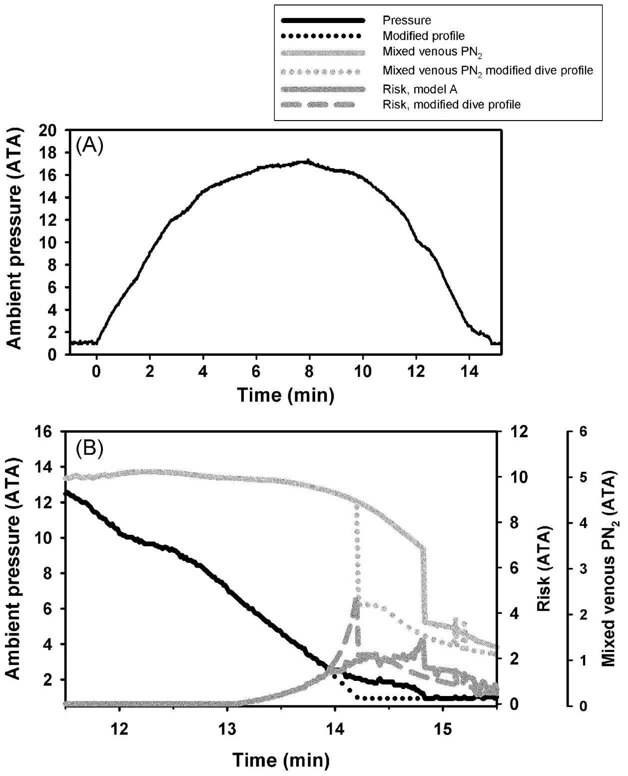

Fig. 5. One 15 min dive to 160 m from a 78 h dive record from Blainville's beaked whale showing (A) pressure against time and (B) pressure during the ascent (solid black line). The black dotted line is for a hypothetical dive in which the ascent rate is maintained rather than decreased as the whale approaches the surface. The solid and dotted lines are predicted mixed venous P_{N_2} for the actual and hypothetical dive trace, respectively, while the blue solid and dotted line is the instantaneous risk. The instantaneous risk was described based on the pressure history of the dive and the estimated mixed venous N_2 tension (Pv_{N_2}) and defined as; $r=(Pv_{N_2}-P_{amb})\cdot P_{amb}{}^{-1}$, where r is the instantaneous risk. By this definition, r is 0 at any time when $Pv_{N_2} < P_{amb}$ (Fahlman et al., 2001).

3.6. Diel variation in dive behaviour and estimated tissue and blood P_{N_2}

The three species varied in the extent of differences between dive profiles in the day and night (see examples in Fig. 1), with Cuvier's beaked whales showing the most pronounced differences in decreased frequency of dives >200 m, and increased frequency of dives <50 m at night (see also Baird et al., 2008).

There was no clear cut consistent elevation of end-dive P_{N_2} for day vs. night across all species. The two *Mesoplodon* traces differed in their day/night differences in both behaviour and resulting end-dive P_{N_2} (Table 4). This was most striking for shallow dives with the 22-h trace showing higher values in the day while the 78-h trace showed higher values at night. For the latter, it appears that the increase in maximum and mean dive depth, and dive duration at night increased end-dive P_{N_2} for all tissues and mixed venous blood despite the 75% increase in the surface interval (Md_{78} N vs. D, Table 4). For the 22-h trace, only the fast tissues and the mixed venous blood changed as dive depth changed without concomitant changes in dive duration or surface interval (shallow dives, Table 4). For *Hyperoodon* and *Ziphius*, a reduction in dive depth and duration during shallow dives at night reduced end-dive P_{N_2} for the slow tissues (fat and muscle).

The intermediate dives showed some of the highest end-dive P_{N_2} levels, particularly for the fast tissues of both *Hyperoodon* at night and for *Ziphius* in the day, associated with deeper and longer dives (Table 4). For the 22-h *Mesoplodon* trace deep dives, end-dive P_{N_2} increased in the day for fast tissues (central circulation and brain) despite lower depths and shorter duration dives. In contrast, the only significant increase for the 78-h *Mesoplodon* trace deep dives was for slow tissue (fat) at night (Table 4). The number of deep dives per hour for *Hyperoodon* increased at night although the depth and duration were reduced, which resulted in an increase in muscle, brain and fat end-dive P_{N_2}.

For the shallow dives, there was a significant correlation between dive duration and the duration of the surface interval that followed a dive both during the night and day for Md_{78}, Md_{22} and Zc_{34} ($P<0.001$), but there was no correlation for intermediate or deep dives ($P>0.7$). For Ha_{28} there was no relationship between dive duration and subsequent surface interval for any depth.

4. Discussion

This work uses gas exchange models of diving to analyze the effect of physiology (extent of diving bradycardia, diving lung volume and body mass) and diving behaviour (dive depth and duration, variation in ascent rate, and diel variation) on tissue and blood P_{N_2} levels and thereby the risk of decompression sickness in three species of beaked whales. The near impossibility of conducting physiological experiments on beaked whales necessitates such a modelling approach.

Overall, our work concurs with previous modelling efforts showing that blood flow (Fahlman et al., 2006, 2007) and the level of pulmonary shunt (Bostrom et al., 2008; Fahlman et al., 2009) during diving will greatly affect blood and tissue P_{N_2} levels. The dive behaviour of *Ziphius*, with longer dives and shorter surface intervals compared with the other species (Tables 2 and 4) resulted in estimated tissue and blood P_{N_2}s that were generally higher for all depth ranges (*Zc34*, Model A, Table 3). Zimmer and Tyack (2007) previously published estimated blood and tissue P_{N_2} values for a Cuvier's beaked whale. They used the assumption that alveolar collapse is immediate and occurs at a pre-determined depth (~70 m, Zimmer and Tyack, 2007). While they did not report end-dive Pv_{N_2} values, end-dive P_{N_2} for the central circulation reached 1.6 ATA, for the brain reached 1.3 ATA, and for muscle and fat reached values as high as 2.0 ATA (see Fig. 2 in Zimmer and Tyack, 2007). Equivalent values in the current study are generally higher (Table 3) emphasizing the importance of properly understanding how gas exchange changes with depth.

4.1. The importance of long dive profile series for estimation of Pv_{N_2} and DCS risk

Although the deep and long dives of beaked whales are remarkable in themselves, alone these would be unlikely to trigger DCS. Rather it is the accumulation of dives that would result in sequential increase of N_2 in tissues causing a higher risk of DCS. As Scholander noted, "by repeated dives, conditions as regards diving disease would certainly tend to be worse on account of an accumulation of invaded N_2. There is every reason to believe that this risk exists unless there is sufficient ventilation between dives" (p. 112, Scholander, 1940).

Our analysis demonstrated that models which incorporate gas exchange within multiple body compartments will necessitate longer datasets particularly for larger animals. Short datasets are not a problem for tissues with short time constants, e.g. the central circulation and brain, as these tissues rapidly reach a equilibrium state in which end-dive P_{N_2} remains more or less constant (see Fahlman et al., 2006). However, tissues with a long time constant, such as fat, are highly dependent on the length of the data set (Fig. 1). End-dive P_{N_2} for these tissues slowly increases with each repeated dive and only reaches equilibrium after hours (Fig. 1) or even days (Fahlman et al., 2007).

Table 4

Animal identification (ID), number of dives (n) during day (D) or night (N), mean maximum dive depth (Max, m), mean depth (Mean, m), mean dive duration (DD, min), mean surface interval duration (SI, min), estimated tissue and mixed venous (V) P_{N_2} (ATA) for central circulation (CC), muscle (M), brain (B), fat (F) using Model A (50% bradycardia) for a 78 h (Md_{78}) and a 22 h (Md_{22}) Blainville's beaked whale dive trace, a 34 h (Zc_{34}) Cuvier's beaked whale dive trace and a 28 h (Ha_{28}) northern bottlenose whale dive trace. Number of dives is that after removing dives before equilibrium.

ID	*n*	Day/night	Max	Mean	DD	SI	CC	M	B	F	V
			Dives <50 m								
Md_{22}	37	D	19 ± 10	13 ± 7	4.4 ± 3.2	0.3 ± 0.5	1.7 ± 0.6	1.0 ± 0.1	1.8 ± 0.7	2.4 ± 0.3	1.3 ± 0.2
Md_{22}	68	N	14 ± 9[†]	9 ± 5[†]	4.5 ± 3.8	0.4 ± 0.6	1.4 ± 0.4[†]	1.0 ± 0.1	1.5 ± 0.5[†]	2.3 ± 0.3	1.1 ± 0.2[†]
Md_{78}	117	D	19 ± 12	13 ± 8	5.2 ± 5.0	1.2 ± 1.0	1.6 ± 0.7	1.0 ± 0.1	1.7 ± 0.7	3.0 ± 0.2	1.2 ± 0.2
Md_{78}	69	N	35 ± 14[†]	26 ± 12[†]	9.8 ± 5.0[†]	2.1 ± 1.5[†]	2.5 ± 0.8[†]	1.1 ± 0.1[†]	2.7 ± 0.8[†]	3.1 ± 0.3[†]	1.5 ± 0.3[†]
Zc_{34}	13	D	22 ± 9	14 ± 6	1.5 ± 0.9	0.2 ± 0.2	1.7 ± 0.7	1.4 ± 0.2	1.7 ± 0.5	3.7 ± 0.5	1.5 ± 0.3
Zc_{34}	51	N	18 ± 11	12 ± 9	5.9 ± 7.8	0.6 ± 0.9	1.7 ± 0.8	1.3 ± 0.1[†]	1.8 ± 0.8	3.2 ± 0.3[†]	1.4 ± 0.3
Ha_{28}	44	D	14 ± 9	7 ± 6	1.8 ± 1.8	1.4 ± 1.2	1.2 ± 0.5	1.0 ± 0.1	1.6 ± 0.6	2.9 ± 0.6	1.1 ± 0.2
Ha_{28}	29	N	13 ± 10	6 ± 7	1.4 ± 1.4[‡]	2.0 ± 2.0	1.1 ± 0.6	1.0 ± 0.2[‡]	1.7 ± 0.7	2.6 ± 0.5[†]	1.1 ± 0.2
			Dives >50 m and <200 m								
Md_{22}	7	D	138 ± 38	80 ± 26	10.4 ± 2.3	0.1 ± 0.1	3.4 ± 0.7	1.1 ± 0.1	3.9 ± 0.7	2.4 ± 0.4	1.8 ± 0.3
Md_{22}	5	N	88 ± 47[†]	59 ± 34	9.8 ± 3.3	0.3 ± 0.4	3.8 ± 0.9	1.2 ± 0.1	4.1 ± 0.9	2.7 ± 0.4	2.0 ± 0.4
Md_{78}	30	D	126 ± 50	76 ± 35	12.2 ± 2.5	1.8 ± 1.1	3.3 ± 0.7	1.1 ± 0.1	3.8 ± 0.7	3.2 ± 0.3	1.8 ± 0.2
Md_{78}	28	N	72 ± 33[†]	47 ± 18[†]	12.8 ± 2.6	2.5 ± 2.0[‡]	3.2 ± 0.5	1.1 ± 0.1	3.5 ± 0.6[†]	3.3 ± 0.2	1.8 ± 0.2
Zc_{34}	2	D	74 ± 18	58 ± 10	18.7 ± 4.6	1.8 ± 0.1	4.7 ± 0.6	1.6 ± 0.2	4.9 ± 0.5	4.0 ± 0.8	2.6 ± 0.2
Zc_{34}	3	N	60 ± 14	43 ± 10	8.9 ± 4.2	0.2 ± 0.2	3.9 ± 0.6	1.5 ± 0.2	3.9 ± 0.8	3.4 ± 0.2	2.2 ± 0.3
Ha_{28}	4	D	81 ± 14	51 ± 8	8.8 ± 2.1	1.6 ± 0.5	4.4 ± 0.4	1.0 ± 0.1	4.5 ± 0.4	3.0 ± 0.6	2.1 ± 0.1
Ha_{28}	4	N	146 ± 36[†]	94 ± 32[†]	9.6 ± 3.6	1.2 ± 0.3[‡]	5.1 ± 0.7[†]	1.1 ± 0.1[†]	5.1 ± 0.5[†]	3.3 ± 0.4[†]	2.4 ± 0.3[†]
			Dives > 200 m								
Md_{22}	5	D	730 ± 447	419 ± 246	33.4 ± 19.3	1.2 ± 1.0	4.0 ± 0.4	1.0 ± 0.1	4.2 ± 0.4	2.2 ± 0.7	2.0 ± 0.2
Md_{22}	2	N	1159 ± 205[‡]	745 ± 139[†]	48.6 ± 7.8[‡]	1.6 ± 1.0	3.4 ± 0.2[†]	1.1 ± 0.1	3.7 ± 0.1[†]	2.4 ± 0.4	1.8 ± 0.1
Md_{78}	22	D	730 ± 491	437 ± 281	34.4 ± 19.0	1.5 ± 1.4	4.2 ± 0.4	1.1 ± 0.1	4.4 ± 0.4	3.0 ± 0.6	2.1 ± 0.2
Md_{78}	17	N	944 ± 193[†]	612 ± 120[†]	48.2 ± 1.7[†]	2.6 ± 1.7[†]	4.3 ± 0.2	1.2 ± 0.1[‡]	4.4 ± 0.2	3.4 ± 0.2[†]	2.2 ± 0.1
Zc_{34}	17	D	666 ± 509	419 ± 293	43.5 ± 25.5	1.5 ± 1.0	4.6 ± 0.7	1.5 ± 0.3	4.7 ± 0.7	3.5 ± 0.9	2.5 ± 0.4
Zc_{34}	7	N	844 ± 275	594 ± 196[‡]	49.7 ± 21.2	1.1 ± 1.0	4.8 ± 0.4	1.3 ± 0.1	5.0 ± 0.3	3.2 ± 0.3	2.5 ± 0.1
Ha_{28}	4	D	1230 ± 190	704 ± 97	39.4 ± 11.2	1.3 ± 0.6	4.7 ± 0.6	1.0 ± 0.1	4.5 ± 0.4	2.7 ± 0.8	2.2 ± 0.2
Ha_{28}	7	N	753 ± 301[†]	467 ± 165[†]	30.4 ± 8.9[†]	1.2 ± 0.6	4.8 ± 0.4	1.1 ± 0.1[†]	4.8 ± 0.3[‡]	2.8 ± 0.4	2.3 ± 0.2

P-values represent differences between day and night.

[†] $P < 0.05$.

[‡] $P < 0.1$.

It has previously been suggested that tissues with slow time constants could help buffer P_{N_2} at the beginning of a dive bout, but they would be a liability after a long bout and possibly lead to dive bout terminations (Fahlman et al., 2007). Consequently, these models require sufficient data for the N_2 levels to reach equilibrium so that appropriate conclusions can be made. With this dataset, it took *Mesoplodon* 4 h (Md_{78}), *Ziphius* 8 h (Zc_{34}) and *Hyperoodon* 13 h (Ha_{28}) to reach steady state values for the slow tissues (Fig. 1). The lower mass specific $\dot{Q}_{tot}$ in larger whales appears to increase the time to equilibrium and emphasizes the need for longer dive traces from larger species. To avoid such a bias others have increased the tissue P_{N_2} at the start of the dive trace (Zimmer and Tyack, 2007). However, it is unclear without the analysis presented in Fig. 1, what starting value should be chosen and we therefore do not advocate this approach.

4.2. The effect of cardiac output, $\dot{Q}_{tot}$, on estimated tissue Pv_{N_2}

The dive response is primarily thought to extend the aerobic dive duration by conserving available O_2 to the core (heart and brain), but it has been suggested that this redistribution of blood flow is also a useful mechanism for altering inert gas uptake (Scholander, 1940; Ponganis et al., 1999; Fahlman et al., 2007). This makes intuitive sense and one study showed that mixed venous P_{N_2} could be reduced by as much as 45% when an animal exhibited diving bradycardia during the descent and bottom phase with a reduced ascent rate and a pre-surface tachycardia (Fahlman et al., 2006). However, that study only analyzed a 1-h dive bout consisting of 23 dives. A more recent theoretical study, estimating tissue and blood P_{N_2} levels in deep diving king penguins during a foraging trip, showed that an increase in blood flow during diving led to an increased P_{N_2} at the end of an extended dive bout in some tissues (muscle and fat P_{N_2}), but a substantial reduction in P_{N_2} in brain and central circulation (Fahlman et al., 2007). These surprising results suggest that the diving related reduction in blood flow does not always reduce N_2 levels during repeated diving. The results in the current study suggest a similarly complex relationship between end-dive P_{N_2} and blood flow during diving. A reduction in $\dot{Q}_{tot}$ generally increased end-dive P_{N_2} in fast tissues while it caused a reduction in P_{N_2} in fat (Table 3). Consequently, modelling predicts that blood flow adjustment is an efficient strategy for reducing end-dive N_2 levels in diving animals. However, as the circulatory system is also responsible for removing CO_2 and supplying O_2, blood flow changes to each tissue are a trade-off between the need to exchange metabolic gases and the need to reduce DCS risk. The question is to what extent blood flow changes are used as a means to reduce extreme P_{N_2} without ischemic injury and this will be an interesting area of research.

4.3. The effect of diving lung volume, DV_L, on estimated tissue Pv_{N_2}

Adjustment of DV_L can help adjust the depth at which the alveoli collapse (Bostrom et al., 2008) and increase the level of the pulmonary shunt (Eq. (6A) and (6B), in Fahlman et al., 2009), thereby reducing the N_2 taken up during the dive (Kooyman and Sinnett, 1982). As most species of marine mammals (e.g. cetaceans, otariid seals) dive on either full or partial inhalation, we tested how efficient this adjustment would be for beaked whales to modify gas exchange during a dive. Fahlman et al. (2009) concluded that end-dive Pv_{N_2} decreases with a decreasing $DV_{Ao} \cdot V_D{}^{-1}$ ratio and that gas exchange and the level of pulmonary shunt cannot be investigated separately because they are correlated. Thus, gas tensions reported from gas exchange models that do not account for the pulmonary shunt should be viewed with caution and conclusions from such studies may have to be re-assessed (Fahlman et al., 2006, 2007; Zimmer and Tyack, 2007).

While previous work showed that pre-dive exhalation or partial inhalation is an efficient way to reduce the collapse depth, and thereby limit gas exchange at depth, this investigation was only done for a single dive (Fahlman et al., 2009). Visual observations suggest that beaked whales dive on inhalation (Baird and Hooker, unpublished observations), but the actual DV_L is not known and may vary between dives. We were therefore interested in determining the extent to which DV_A affects tissue and blood P_{N_2} in whales that dive repeatedly. In the current study, Model A suggested that a 75% reduction in DV_L decreased end-dive Pv_{N_2} by as much as 43% and 45% for the intermediate and deep dives, respectively (Fig. 3B and C), while the reduction for shallow dives was only between 6% and 19% (Fig. 3A). Consequently, pre-dive exhalation appears to be most efficient for reducing end-dive P_{N_2} during intermediate or deep dives and one would therefore expect larger variation in DV_L during shallow dives.

4.4. The effect of body mass, M_b, on estimated tissue Pv_{N_2}

There is an allometric relationship between M_b and resting metabolic rate (RMR), or $\dot{Q}_{tot}$, between species (e.g. Kleiber, 1975). As inert gas uptake and removal is affected by $\dot{Q}_{tot}$, one would expect that DCS risk correlates with M_b. In fact, past studies have shown a correlation between DCS risk and M_b, both within and between animal species (Berghage et al., 1979; Lillo et al., 2002) and the allometric mass exponent between M_b and DCS risk was shown to be 0.79 for seven species of terrestrial mammals (Fahlman et al., 2006), ranging from 22 g to 78 kg (Berghage et al., 1979). Therefore, even with similar end-dive Pv_{N_2} levels, one would expect larger animals to be more susceptible to DCS. Assuming the physiology of DCS is the same between species, and that metabolic rate and $\dot{Q}_{tot}$ scales to the same mass exponent, it would be expected that *Hyperoodon* would be most susceptible for the same end-dive P_{N_2} level, followed by *Ziphius* and *Mesoplodon* (Table 1). In addition to physiological adjustment, i.e. dive related changes in DV_L, $\dot{Q}_{tot}$ and blood flow distribution, dive behaviour is another way for species of different size to reduce blood and tissue P_{N_2} and therefore reduce the risk of DCS.

Running Model A for a range of M_bs for each dataset allowed us to investigate if differences in dive behaviour affected estimated end-dive Pv_{N_2}. Irrespective of changes in M_b, *Ziphius'* dive profile had the highest end-dive P_{N_2}s for each depth range (Fig. 4), suggesting that the dive behaviour of Cuvier's beaked whales makes them most susceptible to suffer DCS. Interestingly, this is the species that appears to be particularly sensitive to anthropogenic sound and their diving behaviour may be an underlying factor for this observstion (Cox et al., 2006).

In general, reduction in body size showed decreasing end-dive P_{N_2}s for most body compartments, which would suggest that larger animals would be at increased risk of DCS for the same dive profile (Figs. 4 and 6). However, results for central circulation were variable, and fat P_{N_2} increased with decreasing M_b. It is possible that higher fat P_{N_2} in smaller animals could be linked to the prevalence of immature and sub-adult animals in strandings (Freitas, 2000; Anon., 2001; Martin et al., 2004). Current experimental work detailing the behavioural response to anthropogenic sound may help shed some light on this.

4.5. Calculating DCS risk

There is a good correlation between M_b and the saturation pressure resulting in 50% DCS in terrestrial mammals after a rapid decompression (Berghage et al., 1979). If we assume that Pv_{N_2} is a reliable measure of the overall saturation of an animal, estimated end-dive Pv_{N_2} levels from the beaked whales allow a comparison with terrestrial species (Fig. 6). It appears that all three species of beaked whales live with end-dive Pv_{N_2} levels that would result in a high incidence of severe DCS in terrestrial mammals. Although our estimated N_2 levels probably have an uncertainty of at least 20%, it is clear that these whales live with high blood and tissue N_2 levels during most of their lives.

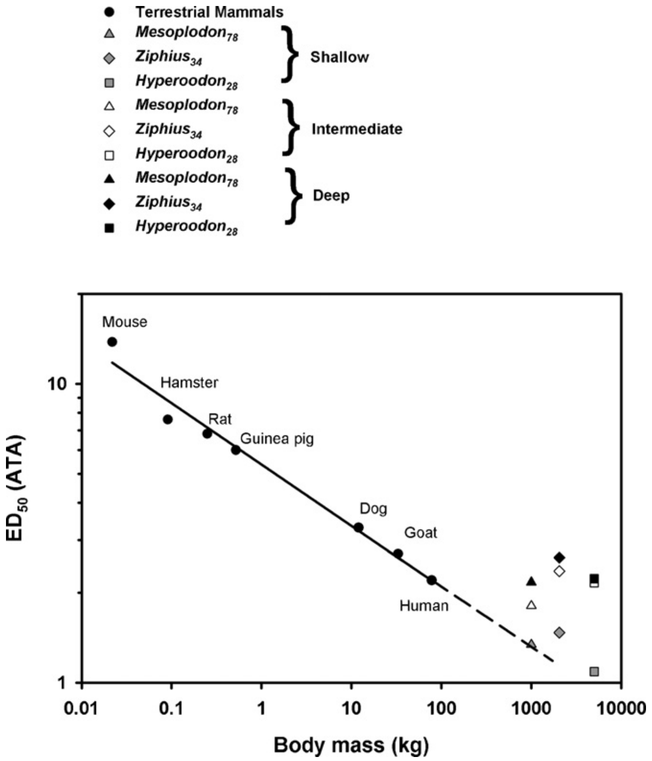

Fig. 6. Estimated N_2 saturation pressure (ATA) that would result in 50% decompression sickness (DCS) in a range of terrestrial animals after a rapid decompression (Flynn et al., 1971; Berghage et al., 1979). Black circles are tissue saturation P_{N_2} for terrestrial animals. The solid line indicates the best fit regression $\log ED_{50} = 0.730 - 0.205 \cdot \log M_b$. Open and grey symbols are average mixed venous inert gas tension (Pv_{N_2}) for Blainville's beaked whale (*Md₇₈*), Cuvier's beaked whale (*Zc₃₄*) and northern bottlenose whale (*Ha₂₈*) using Model A.

How do they avoid DCS during routine diving? One possibility is that there is a minimum pressure difference, or threshold, that is necessary to form bubbles from pre-existing nuclei (Tikuisis and Gerth, 2003). For example, in a 70 kg human the P_{N_2} saturation pressure to cause 50% DCS was 2.2 ATA while in a 1000 kg, 2000 kg and 5000 kg animal the predicted values were, respectively 1.3 ATA, 1.1 ATA and 0.9 ATA, values not very different from P_{amb} at the surface (0.74 ATA). If we assume that the relationship holds for end-dive Pv_{N_2} for large whales ($M_b > 1000$ kg), this would have resulted in a 50% DCS incidence for the intermediate and deep dives for all species. It has been shown that repeated decompression stress in terrestrial mammals reduces DCS risk (Montcalm-Smith et al., 2005). Consequently, the DCS incidence in Fig. 6 is probably much less in acclimated animals such as deep diving whales.

Although beaked whales appear to dive on inhalation (Hooker and Baird, unpublished observations), this may not be a full inhalation. If DV_L were 50% of TLC, this would reduce end-dive Pv_{N_2} for *Ziphius* during deep dives by 25% (Fig. 3C) resulting in an end-dive P_{N_2} of 1.96 ATA. This is still a high saturation partial pressure, but because of the sigmoidal shape of the DCS risk curve against saturation pressure (Dromsky et al., 2000), small changes in inert gas load (5%) result in large changes in DCS risk (50%, Fahlman et al., 2001; Fahlman and Kayar, 2003).

4.6. Ascent rate

Decompression sickness research on terrestrial mammals shows a distinct relationship between ascent rate and DCS risk (Flynn and Lambertsen, 1971; Fahlman and Kayar, 2003). In the mouse, the decompression rate from 13.8 ATA to 1 ATA resulting in a 50% DCS was ~0.58 ATA s^{-1}, or 5.8 m s^{-1} (see Fig. 9 in Flynn and Lambertsen, 1971). As the decompression rate was reduced to 0.13 ATA s^{-1} (1.3 m s^{-1}), an ascent rate similar to those reported in these three species of beaked whales (Hooker and Baird, 1999; Baird et al., 2006, 2008), the incidence decreased to ~28% (Flynn and Lambertsen, 1971).

Modelling efforts on diving mammals, on the other hand, have reported divergent results when investigating the effect that changes in ascent rate has on tissue and blood P_{N_2} (Houser et al., 2001; Fahlman et al., 2006, 2007; Zimmer and Tyack, 2007). Fahlman et al. (2006) suggested that a reduction in the ascent coupled with an increase in $\dot{Q}_{tot}$ close to the surface could reduce Pv_{N_2} by as much as 45%. Zimmer and Tyack (2007), on the other hand, reported that an increase in the ascent rate after a deep dive from 1 m s^{-1} to 20 m s^{-1} actually decreased end-dive tissue P_{N_2}.

For the data in Fig. 5 the ascent was increased at a depth of 15 m (2.5 ATA) and the animal rapidly (within a few seconds) decompressed to the surface (1 ATA). The spike in supersaturation that results from a more rapid ascent rate may overcome the threshold necessary to initiate bubble formation and growth while a more gradual ascent keeps tissue P_{N_2} at a moderate level above P_{amb}, reducing the risk of bubble formation (Fig. 5). Thus, the effect of changes in ascent rate will differ depending on the blood and tissue P_{N_2} and the ambient pressure (depth). When tissue $P_{N_2} < P_{amb}$, the ascent rate should be high to prevent further uptake of N_2. When tissue $P_{N_2} > P_{amb}$ the risk increases for bubbles to form and grow (Tikuisis and Gerth, 2003). At this time, a reduction in the ascent rate helps to safely remove N_2 from the tissues. Consequently, the effect of changes in ascent or descent rate is complicated and depends on several variables. An increase in ascent rate could either increase or decrease end-dive Pv_{N_2} depending on the previous dive history. While some diving species reduce their ascent rate as they approach the surface, possibly to reduce end-dive Pv_{N_2} levels (e.g. penguins and elephant seals, Fahlman et al., 2006), beaked whales have the lowest ascent rates in midwater between 300 and 600 m (Tyack et al., 2006). This suggests that beaked whales either do not experience tissue and blood P_{N_2} levels that put them at risk of DCS or that they have other strategies to deal with an excessive N_2 load. In Cuvier's and Blainville's beaked whales, Tyack et al. (2006) noticed that deep foraging dives were commonly followed by a series of shallower dives. This dive behaviour has been suggested as an alternate strategy to deal with elevated N_2 levels and help reduce DCS risk (Fahlman et al., 2007). Thus, diving mammals and birds may use different strategies to deal with excessive levels of N_2 and the choice may depend on the need to also exchange O_2 and CO_2 (Fahlman et al., 2009).

The natural dive profiles of marine mammals are less severe than those used in DCS research using terrestrial animals as models. Nevertheless, our results suggest that beaked whales probably live with N_2 levels that would elicit DCS in non-diving mammals. That diving marine mammals at least experience N_2 levels that would result in bubble formation during an immediate ascent has been empirically shown in bycaught animals where bubbles were observed while stranded animals showed little evidence of bubbles (Moore et al., 2009). If the natural diving behaviour of these whales is significantly altered this could well result in DCS symptoms.

4.7. Diel variation in dive behaviour and estimated tissue and blood P_{N_2}

Changes in diving behaviour between day and night are relatively common and often associated with diel changes in prey distribution. Although not thought to be related to changes in prey distribution, Baird et al. (2008) reported that Blainville's and Cuvier's beaked whales spend proportionally more time at in shallow depths (<100 m) at night. If such behavioural changes affect P_{N_2} levels and DCS risk, this could present a simple mitigation avenue if disturbing whales is less likely to have dangerous consequences at night vs. in the day, for example.

In this study, the data showed a clear diel divergence in dive depth and duration for all species, and these were also apparent in the estimated tissue and blood P_{N_2} (Table 4). Notable was the change in dive mode for *Ziphius*, in which deep dives (>200 m) were more common during the day while shallow dives (<50 m) were more common at night (Table 4). Unlike *Mesoplodon* and *Hyperoodon*, *Ziphius* showed few diel changes in maximum and mean dive depth and duration within each dive category, yet their behaviour resulted in higher blood and tissue P_{N_2} levels during the day (Table 4).

The much higher estimated blood and tissue P_{N_2} in *Ziphius* compared with either *Mesoplodon* or *Hyperoodon* (Figs. 3, 4 and 6), indicate that mean dive depth and duration is a poor index for estimating DCS risk and that more subtle behavioural differences exist that differentiate diving physiology in these species. In other words, looking at the dive characteristics alone (depth and dive duration) is less useful than to investigate the dive trace as a whole. Although longer dives or shorter surface intervals will result in elevated levels of N_2, it appears that fat P_{N_2} in beaked whales reaches a more or less steady value during natural dives (Fig. 1). Thus, each dive and surface interval will only have an effect against a background "reservoir" P_{N_2} level. Therefore, for modelling efforts to be useful at unravelling the physiological constraints, real dive profiles encompassing diel changes as well as seasonal alterations in dive behaviour need to be considered.

It has been proposed that short and shallow dives following a series of deep dives may serve to reduce tissue and blood supersaturation ($P_{amb} - P_{N_2}$) and thereby DCS risk (Fahlman et al., 2006, 2007, 2009). To reduce DCS risk, the shallow decompression dives need to be deep enough to reduce supersaturation but shallow enough to allow removal of N_2 (Fahlman et al., 2007). Such dive behaviour was observed in both *Mesoplodon* (Fig. 1A e.g. short shallow dives following the deep and long dive ending at 19:43) and *Ziphius* (Fig. 1B), but less so in *Hyperoodon* (Fig. 1C). This agrees with the dive data reported by Tyack et al. (2006) where it was reported that both *Mesoplodon* and *Ziphius* perform very shallow dives (<20 m) in the period between deep dives. This dive behaviour could be an important feature to reduce supersaturation and bubble formation in *Mesoplodon* and *Ziphius*. If sonar activity interrupts this behaviour this could result in a higher risk of DCS.

4.8. Additional adaptations to reduce DCS risk?

The interplay between diving lung volume, gas exchange within different body compartments, the extent of bradycardia, and alterations in dive depth, dive duration and dive history suggest that, despite some leeway, beaked whales generally live with elevated blood and tissue N_2 levels, and therefore a high risk of DCS. Yet it is only under unusual circumstances that DCS symptoms are observed, suggesting the possibility that they may have additional specialized adaptations to reduce DCS risk during their normal diving routine. Research has shown a potential link between bubbles and nitric oxide levels in terrestrial mammals (Wisloff et al., 2004; Mollerlokken et al., 2006). It has been suggested that nitric oxide alters the endothelial interface and reduces bubble nuclei, thereby preventing formation of bubbles. It is possible that diving marine mammals and birds have a vascular anatomy that prevents bubble nuclei forming or that they have elevated levels of nitric oxide during diving that reduces the likelihood of bubble formation. A better understanding of the physiology of these animals will be important to determine the reasons for the apparent relationship between anthropogenic noise and mass strandings (Cox et al., 2006). Such knowledge may also result in important information to prevent DCS in human divers.

4.9. Summary

While management of O_2 has been the central tenet in understanding what limits the duration of a dive, our current modelling effort suggests that deep diving whales permanently live with blood and tissue P_{N_2} levels that elicit a high incidence rate of DCS in terrestrial animals. Thus, it is possible that diving mammals may have to end foraging at times when the N_2 levels become too high. The dive behaviour of *Ziphius* was different from both *Mesoplodon* and *Hyperoodon*, and resulted in higher predicted tissue and blood N_2 levels. While the prevalence of Cuvier's beaked whales stranding after naval sonar exercises could be explained by a higher abundance of this species in the affected areas, our results suggest that species differences in behaviour and/or physiology may also play a role.

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Appendix A.

A typographical error was discovered in Eq. 5 in Fahlman et al. (2009). The equation used in this and the previous study (Fahlman et al., 1990) to estimate $s\dot{Q}_{\mathrm{tot}}$ was

$$s\dot{Q}_{\mathrm{tot}} = s\dot{Q}_{\mathrm{tot}HS} \cdot \left(\frac{\mathrm{M}_b^{-0.25}}{34^{-0.25}} \right)$$

where $s\dot{Q}_{\mathrm{tot}HS}$ is $s\dot{Q}_{\mathrm{tot}}$ from the harbour seal ($8.0\,\mathrm{ml\,kg^{-1}\,s^{-1}}$, Ponganis et al., 1990), 34 the assumed M_b of the harbour seal and M_b the mass of the species of beaked whale.

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