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Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration

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Abstract

Cetaceans exhibit an exceptionally wide range of body mass that influence both the capacities for oxygen storage and utilization; the balance of these factors is important for defining dive limits. Furthermore, myoglobin content is a key oxygen store in the muscle as it is many times higher in marine mammals than terrestrial mammals. Yet little consideration has been given to the effects of myoglobin content or body mass on cetacean dive capacity. To determine the importance of myoglobin content and body mass on cetacean diving performance, we measured myoglobin content of the *longissimus dorsi* for ten odontocete (toothed whales) and one mysticete (baleen whales) species ranging in body mass from 70 to 80 000 kg. The results showed that myoglobin content in cetaceans ranged from 1.81 to 5.78 g (100 g wet muscle)⁻¹. Myoglobin content and body mass were both positively and significantly correlated to maximum dive duration in odontocetes; this differed from the relationship for mysticetes. Overall, the combined effects of body mass and myoglobin content accounts for 50% of the variation in cetacean diving performance. While independent analysis of the odontocetes showed that body mass and myoglobin content accounts for 83% of the variation in odontocete dive capacity. © 2000 Elsevier Science Inc. All rights reserved.

Keywords: Cetaceans; Myoglobin; Body size; Diving capacity; Odontocetes; Mysticetes

1. Introduction

Cetaceans exhibit a 2200-fold increase in body mass from the smallest species, the 55 kg vaquita (*Phocoena sinus*; Evans, 1987), to the largest species, the 122 000 kg blue whale (*Balaenoptera musculus*; Laurie, 1933). Such a wide range of body masses results in an exceptionally large range of metabolic rates and capacities for oxygen storage in comparison to other marine mammal groups. Although both factors will impact diving

capability (Kooyman et al., 1981), there is little information concerning the advantages or disadvantages associated with extreme body size and the capacity to adapt the mammalian body for prolonged periods of submergence. One important adaptation for diving exhibited by a wide range of diving mammals is the storage of oxygen in the skeletal muscles (Castellini and Somero, 1981). Myoglobin acts as the primary oxygen carrier in the skeletal muscles of these mammals. When perfusion to a muscle region is decreased, oxygen depletion of that area is retarded by the release of myoglobin-bound oxygen into the tissue (Salathe and Chen, 1993). Elevated myoglobin content in the skeletal muscle enables aerobic

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metabolism to be maintained during apnea and appears to be an important adaptation for diving in birds and mammals. Consequently, myoglobin concentration is 10–30 times greater in the locomotor muscles of aquatic birds and mammals than in the muscles of their aerial or terrestrial counterparts (Kooyman, 1989).

For the species studied to date, cetaceans demonstrate a higher reliance on muscle oxygen stores than other marine mammal groups including pinnipeds. For example, ≈ 33 , 38, and 51% of the total body oxygen store is found in the skeletal muscle of beluga whales (Shaffer et al., 1997), bottlenose dolphins (Williams et al., 1993) and narwhals (Williams unpublished observation), respectively. In comparison, otariids and phocids sequester a higher proportion of the total oxygen store in the blood; less than 33% of the oxygen reserve of pinnipeds is found in the skeletal muscle (Kooyman, 1989). A non-diving mammal, the human, stores only 15% of its oxygen reserve in the skeletal muscle.

In contrast to numerous investigations on pinniped muscles (Scholander, 1940; Lenfant et al.,

1970; George et al., 1971; Castellini and Somero, 1981; Lydersen et al., 1992; Ponganis et al., 1993; Thorson 1993), comparatively few studies have examined the skeletal muscles of cetaceans or the adaptations of their muscles for diving. One previous study suggested that cetaceans with higher muscle myoglobin contents show longer dive durations (Snyder, 1983). A complicating factor, however, is the effect of body mass on dive performance in this diverse marine mammal group. In view of this, we examined the myoglobin content of the primary locomotor muscles of 11 species of cetaceans, ranging in size from the 70 kg common dolphin to the 80 000 kg bowhead whale. These data were then correlated with reported values for maximum dive duration for each species. We found that both muscle myoglobin content and body mass explained nearly 50% of the variation in dive performance across cetacean species. Differences in foraging behavior between the two cetacean suborders, odontocetes (toothed whales) and mysticetes (baleen whales), suggest that foraging behaviors may further influence these relationships.

Table 1

Myoglobin contents for the *longissimus dorsi* of the cetacean species examined in this study^a

Cetacean species	<i>n</i>	[Mb] (g [100 g wet muscle] ⁻¹)
<i>Odontocetes</i>		
Common dolphin (<i>Delphinus capensis</i>)	3	3.58 ± 0.32
Common dolphin (<i>Delphinus delphis</i>)	7	3.55 ± 0.27
Harbor porpoise (<i>Phocoena phocoena</i>)	2	4.03 ± 0.32
Striped dolphin (<i>Stenella coeruleoabla</i>)	1	5.78
Northern right whale dolphin (<i>Lissodelphis borealis</i>)	1	1.81
Pacific white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	2	3.45 ± 0.25
Bottlenose dolphin (<i>Tursiops truncatus</i>)	6	2.66 ± 0.16
Pygmy sperm whale (<i>Kogia breviceps</i>)	1	4.33
Beluga whale (<i>Delphinapterus leucas</i>)	5	3.44 ± 0.39
Cuvier's beaked whale (<i>Ziphius cavirostris</i>)	2	4.32 ± 0.15
<i>Mysticetes</i>		
Bowhead whale (<i>Balaena mysticetus</i>)	5	3.54 ± 0.33

^a All values are for site 1 illustrated in Fig. 1. *n*, represents the number of specimens for each species. Values are given as the mean ± 1 S.E.M.

2. Materials and methods

2.1. Animals

Muscle samples were obtained from ten odontocete species and one mysticete (Table 1). The cetaceans examined in this study were acquired from strandings, incidental fishery catches, or subsistence hunts. Muscle samples were taken only from mature animals that were considered in excellent condition based on their external appearance (i.e. no bloating or large external cuts). Depending on the availability of specimens, one to seven individuals of each species were analyzed.

2.2. Muscle sample collection

For the bowhead and beluga whales, muscle samples were collected on site soon after death. For all other species, whole carcasses were frozen at 0°C shortly after death and muscle samples were taken within 6 months postmortem. All muscle samples were stored at -80°C until analysis. Muscle samples were taken from the midbelly of the *longissimus dorsi* (Fig. 1). The *longissimus dorsi* is the primary locomotor muscle of

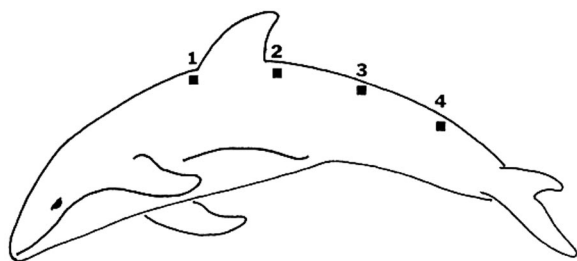


Fig. 1. Sample sites for skeletal muscle in cetaceans. Numbered black squares indicate the four areas along the *longissimus dorsi* where the muscle samples were taken. All muscles were sampled from the midbelly region at each site. Samples (≈ 6 g) were obtained from site 1 for all of the specimens in this study.

cetaceans and is one of two muscles that power the dolphin upstroke (Pabst, 1993). Recent research suggests that there is a gradient in myoglobin content between the midbelly and the peripheral regions of the *longissimus dorsi* of cetaceans (Harrison and Davis, 1998). The midbelly appears to contain the highest concentration of myoglobin. In addition, a small gradient in myoglobin content is found along the length of the muscle, with the area below the dorsal fin showing the highest content (Harrison and Davis, 1998). Sample site 1 in the present study (Fig. 1) was chosen to reflect the highest myoglobin content for the *longissimus dorsi* of each species. When available, samples were also taken from three other sites along the muscle (sites 2, 3, and 4; Fig. 1) for comparative purposes.

2.3. Myoglobin content

Myoglobin content ([Mb]), measured in g Mb (100 g wet muscle) $^{-1}$ was determined using the procedure of Reynafarje (1963). Slightly thawed muscle samples (≈ 0.5 grams) were minced in a low ionic strength buffer (40 mM phosphate, pH = 6.6), and sonicated (Sonifier Cell Disrupter Model W185D, Heat systems-Ultrasonics, Inc.) for 2–3 min on ice. The buffer to tissue ratio was 19.25 ml buffer per g wet tissue. The samples were centrifuged at -4°C and 28 000 g for 50 min (Sorvall RC-5B refrigerated superspeed centrifuge, DuPont Instruments). The clear supernatant was drawn, and bubbled at room temperature with pure CO for approximately 8 min. We added 0.02 g of sodium dithionite to ensure a complete reduction. The absorbance of

each sample was read at room temperature at 538 and 568 nm on a spectrophotometer (Shimadzu UV-visible spectrophotometer Bio spec-1601). All samples were run in triplicate.

2.4. Standards for the assays

Myoglobin contents were determined for the main locomotory skeletal muscles of a New Zealand white rabbit and a 7 day old Northern elephant seal pup, and compared to previously published values. The [Mb] of the seal pup in the present study, 2.4 ± 0.2 g (100 g wet muscle) $^{-1}$, was similar to a previously published value for a 1–14 day old northern elephant seal pup (Thorson, 1993). The [Mb] for rabbit muscle, 0.08 ± 0.06 g (100 g wet muscle) $^{-1}$, was similar to previous reports for a New Zealand white rabbit (Castellini and Somero, 1981).

2.5. Dive duration

Maximum dive times for each species were obtained from previous studies that used time-depth recorders (TDRs) or trained animals. Timed observations of dive durations for wild, uninstrumented animals were included only if no other data source was available. *Kogia breviceps* was not used in the diving analyses because the only dive data available for this species was acquired from a rehabilitated animal that had been housed in a shallow pool for several months before release (Hohn et al., 1995). We used maximum dive durations rather than average dive times in these analyses for several reasons. First, few diving records for cetaceans report average dive durations; of the 15 species used in our analyses, only six have average dive times reported in the literature. Second, average values are a poor indicator of an animal's diving capabilities. This is illustrated by comparing average and maximum dive durations of the six cetacean species for which both values are available. Average dive duration is 1.1 min for the harbor porpoise (Westgate et al., 1995), 0.4 min for the Pacific white-sided dolphin (Black, 1994), 0.4 min for the bottlenose dolphin (Mate et al., 1995), 12.9 min for the beluga whale (Martin et al., 1993), 38 min for the sperm whale (Watkins et al., 1993), and 6.3 min for the bowhead whale (Wursig et al., 1984). These values represent less than 20% of the maximal dive durations reported for these species. The

beluga and sperm whales are exceptions; their average dive durations are 70 and 52% of their maximum dive durations, respectively. Similar to studies examining aerobic function in terrestrial mammals (Weibel et al., 1987), we have chosen to use extreme performance in this study to understand the physiological capacities of diving in cetaceans.

2.6. Statistics

Variability between the myoglobin contents of skeletal muscle sites, and between species was determined by Kruskal–Wallis one way analysis of variance on ranks. In addition, Dunn's method for all pairwise comparison procedures was used for interspecies comparisons. Species specific muscle myoglobin contents determined in the present study were combined with previously published values for other cetacean species for further analyses. The inclusion of previously reported values ensured that the myoglobin-dive duration relationships determined in this study were inclusive of as many cetacean species possible. The same species were subsequently used in body mass-dive duration relationships. Least squares methods were used for the linear regressions of myoglobin content versus maximum dive duration, and for body mass in relation to maximum dive duration. The regressions for body mass were plotted on logarithmic scales due to the large range in body mass (70–80 000 kg). The reported linear equation for this plot was log transformed. Significance of the regressions was determined using an *F*-test. A Pearson correlation test was used to determine the correlation between body mass and muscle myoglobin. The simultaneous effects of body mass and muscle myoglobin content on maximum dive performance were assessed using a forward stepwise regression. Results were considered significant when $P \leq 0.05$. All statistical tests were calculated using standard software programs (Sigma Stat, Jandel Scientific, 1995).

3. Results

3.1. Myoglobin content

Myoglobin contents for each of the four sampling sites and the average value for the four sites were not significantly different in 10 specimens of

Lagenorhynchus obliquidens, *Delphinus delphis* and *Delphinus capensis* ($H = 1.11$, $df = 4$, $P = 0.89$). Therefore, values for site 1 (Fig. 1) are used as a representative of the entire muscle; these are reported as mean values ± 1 S.E.M.

Myoglobin contents for the *longissimus dorsi* of cetaceans measured in this study are presented in Table 1. There was a 3-fold increase in myoglobin content from the lowest value in the Northern right whale dolphin, 1.81 g (100 g wet muscle)⁻¹, to the highest value in the striped dolphin, 5.78 g (100 g wet muscle)⁻¹. The one mysticete examined in this study, the bowhead whale, had a myoglobin content of 3.54 g (100 g wet muscle)⁻¹; that was within the mid-range of values for the odontocetes. The interspecific differences in myoglobin contents were significant ($H = 18.37$, $df = 10$, $P = 0.049$, $n = 11$) although an all pairwise test was unable to identify the particular species that were different.

For review, previously published myoglobin contents for the skeletal muscles of cetaceans are presented in Table 2. The combined myoglobin data for all cetacean species, including previously reported values and data from the present study, show that the range of myoglobin values for the mysticetes (0.91–3.54 g [100 g wet muscle⁻¹]) are at the lower range of myoglobin values for the odontocetes (1.81 to 7.87 g [100 g wet muscle⁻¹]) (Tables 1 and 2).

3.2. Myoglobin content and body mass relationships with dive capacity

The results of the literature search for the accumulation of the body mass and dive capacity data for the cetacean species used in the analyses for this study are presented in Table 3.

Myoglobin content of the skeletal muscle correlated poorly with maximum dive duration for all cetaceans ($r^2 = 0.28$, $F = 5.03$, $P = 0.04$, $n = 15$). When the two cetacean suborders were analyzed independently, we found that the correlation increases for odontocetes while the relationship for mysticetes was not significant (Fig. 2). For odontocetes, maximum dive duration increased with myoglobin content according to the relationship:

Odontocete maximum dive duration

$$= 8.31 \text{ Mb} - 13.10 \quad (r^2 = 0.36, F = 5.69, P = 0.04, n = 12)$$

Table 2
Previously reported myoglobin contents for cetacean skeletal muscle

Cetacean species	[Mb] (g [100 g wet muscle] ⁻¹)	References
<i>Odontocetes</i>		
Indus river dolphin (<i>Platanista indi</i>)	2.6	(Blessing, 1972)
Spotted dolphin (<i>Stenella attenuata</i>)	2.54	(Castellini and Somero, 1981)
Spinner dolphin (<i>Stenella longirostris</i>)	5.5	(Dolar et al., 1999)
Fraser's dolphin (<i>Lagenodelphis hosei</i>)	7.1	(Dolar et al., 1999)
Humpback dolphin (<i>Sousa chinensis</i>)	2.5	(Harrison and Davis, 1998)
Narwhal (<i>Monodon monoceros</i>)	7.87	(Williams unpubl. observ.)
False killer whale (<i>Pseudorca crassidens</i>)	6.3	(Harrison and Davis, 1998)
Northern bottlenose whale (<i>Hyperoodon ampullatus</i>)	6.34	(Scholander, 1940)
Sperm whale (<i>Physeter macrocephalus</i>)	5.03	Avg. of Scholander (1940) and Tawara (1950)
<i>Mysticetes</i>		
Sei whale (<i>Balaenoptera borealis</i>)	0.91	(Tawara, 1950)
Fin whale (<i>Balaenoptera physalus</i>)	2.42	Avg. of Scholander (1940) and Hochachka and Foreman (1993)

Table 3
Body mass and maximum dive durations for cetaceans^a

Cetacean species	Mass ^d (kg)	Max. dive (min)	Method ^b	References ^c
<i>Odontocetes</i>				
Common dolphin (<i>Delphinus capensis</i>)	70 ^e	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Common dolphin (<i>Delphinus delphis</i>)	70 ^e	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Harbor porpoise (<i>Phocoena phocoena</i>)	70 ^h	5.35	TDR	(Westgate et al., 1995)
Spotted dolphin (<i>Stenella attenuata</i>)	75 ^e	4.7	TDR	(Perrin et al., 1987; Scott et al., 1993)
Northern right whale dolphin (<i>Lissodelphis borealis</i>)	115 ^e	6.25	O	(Jefferson et al., 1993; Leatherwood and Walker, 1979)
Pacific white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	120	6.2	E	(Whole body specimen mass from present study; Black, 1994)
Bottlenose dolphin (<i>Tursiops truncatus</i>)	200 ^e	8	E	(Evans, 1987; Ridgway and Harrison, 1986)
Pygmy sperm whale (<i>Kogia breviceps</i>)	363 ^e	12	TDR	(Evans, 1987; Hohn et al., 1995)
Beluga whale (<i>Delphinapterus leucas</i>)	1400 ^f	18.3	TDR	(Bryden, 1972; Martin et al., 1993)
Narwhal (<i>Monodon monoceros</i>)	1500 ^h	25	TDR	(Heide-Jørgensen and Dietz, 1995)
Cuvier's beaked whale (<i>Ziphius cavirostris</i>)	2953 ^f	30	O	(Bryden, 1972; Houston, 1991)
Northern bottlenose whale (<i>Hyperoodon ampullatus</i>)	6700 ^e	60	O	(Evans, 1987; Reeves et al., 1993)
Sperm whale (<i>Physeter macrocephalus</i>)	36,700 ^g	73	TDR	(Omura, 1950; Watkins et al., 1993)
<i>Mysticetes</i>				
Sei whale (<i>Balaenoptera borealis</i>)	23,000 ^g	20	O	(Lockyer and Waters, 1986; Martin, 1990)
Fin whale (<i>Balaenoptera physalus</i>)	33,000 ^g	14	TDR	(Lockyer and Waters, 1986; Watkins et al., 1981)
Bowhead whale (<i>Balaena mysticetus</i>)	80,000 ^e	31	TDR	(Evans, 1987; Wursig et al., 1984)

^a Species: listed are limited to those with known myoglobin contents and dive behaviors.

^b Dive data acquired by: TDR, time depth recorder; E, experimental dive; or O, observation.

^c References: body mass reference first, followed by dive duration reference.

^d Mass given, unless otherwise noted in table, is represented as.

^e Average mass for the species.

^f Calculated mass from body length-mass equations.

^g Mass corrected by 6% for loss associated with piecemeal weighing.

^h Estimated mass of animal from which dive data was acquired.

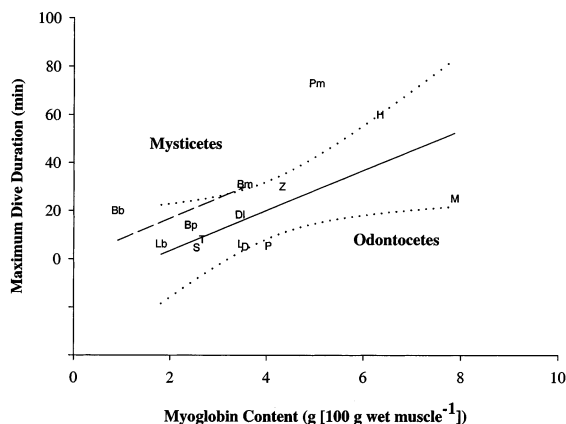


Fig. 2. Maximum dive duration in relation to skeletal muscle myoglobin content for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 1, Table 2, and Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).

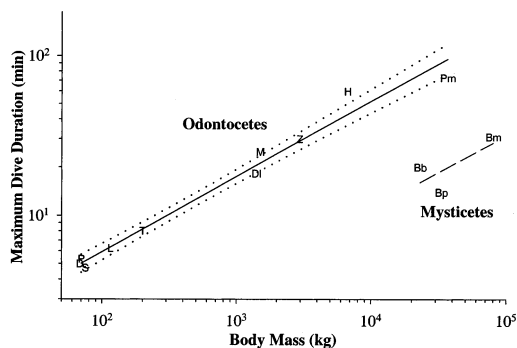


Fig. 3. Maximum dive duration in relation to body mass for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens* and *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).

where duration is in min and muscle myoglobin is in g Mb (100 g wet muscle)⁻¹. For mysticetes, the relationship between myoglobin content and maximum dive duration was not significant ($r^2 = 0.33$, $F = 0.48$, $P = 0.61$, $n = 3$).

Similar results were found for the body mass and dive capacity analyses. A significant correlation was found between maximum dive duration and body mass for all cetaceans in this study ($r^2 = 0.72$, $F = 33.49$, $P < 0.001$, $n = 15$). Again the relationships differed between the two cetacean suborders. Odontocetes exhibit a significant correlation between maximum dive duration and body mass (Fig. 3) according to the relationship:

Odontocete max. dive duration

$$= 0.68 (\text{body mass})^{0.47}$$

$$(r^2 = 0.98, F = 463.92, P < 0.001, n = 12)$$

where duration is in min and body mass is in kg. The same relationship was not significant for mysticetes ($r^2 = 0.54$, $F = 1.15$, $P = 0.48$, $n = 3$) (Fig. 3).

Pearson correlation tests showed that cetacean muscle myoglobin content and body mass, and odontocete muscle myoglobin content and body mass are not correlated ($r = -0.08$, $P = 0.77$, $n = 15$ and $r = 0.49$, $P = 0.16$, $n = 10$, respectively). Because these two variables are independent, we ran forward stepwise regression analyses to determine the combined influence of these two characteristics (muscle myoglobin content and body mass) on maximum dive duration. For all cetaceans combined, muscle myoglobin content and body mass together explained 50% of the variation in maximum dive duration across species (myoglobin $r^2 = 0.28$, $P = 0.017$; body mass $r^2 = 0.22$, $P = 0.042$). For odontocete species only, body mass and muscle myoglobin together explained 83% of the variation in maximum dive duration across odontocete species (body mass $r^2 = 0.69$, $P < 0.001$; myoglobin $r^2 = 0.14$, $P = 0.023$). A similar test for the mysticete species was not possible due to the small sample size available for analyses.

4. Discussion

Limits to aerobic diving are determined by the size of the oxygen store as well as the rate in which this store is utilized. Because skeletal mus-

cles provide the power for swimming, an important factor in determining maximum dive duration of marine mammals is size of the on-board oxygen stores to support metabolic processes at the level of the working skeletal muscle (Hochachka, 1986). Previous studies have demonstrated that aerobic metabolic processes within the muscle may be maintained during prolonged periods of submergence by utilization of oxygen stored in myoglobin (Kooyman, 1989). From the present study it appears that the combined effect

of muscle myoglobin content as well as body mass dictates the limits to diving performance in cetaceans. As discussed below, feeding behaviors unique to odontocetes and to mysticetes may have refined these relationships over evolutionary time.

By itself, myoglobin content of the skeletal muscle is a poor predictor of maximum dive duration when cetaceans are considered as a single group (Fig. 4). However, when the two cetacean suborders are analyzed independently, we find a close correlation between myoglobin content and maximum dive duration, particularly for the odontocetes (Fig. 2). Thus, the four odontocete species exhibiting the longest maximum dive durations (25–73 min) have high myoglobin contents ranging from 4.32 to 7.87 g (100 g wet muscle)⁻¹. In comparison, short duration divers among the odontocetes with maximum dive durations of 5 to 18.3 min maintain comparatively lower myoglobin contents (1.81 to 4.03 g [100 g wet muscle]⁻¹). These results suggest that high myoglobin content within the skeletal muscles serves as an important adaptation for prolonging dive duration in odontocetes. Indeed, some of the longest dives for cetaceans occur among the odontocetes, including the narwhal, Cuvier's beaked whale, Northern bottlenose whale, and sperm whale (Table 3).

In contrast to the results for odontocetes, the relationship between myoglobin content and maximum dive duration for mysticetes was not significantly correlated (Fig. 2). This may be due in part to the low sample size available for analysis for the mysticetes (Tables 1 and 2). These results differ from Snyder (1983) who suggested that large cetaceans have elevated myoglobin contents that correspond to increased dive duration. The results also differ from the pattern reported for pinnipeds, a mammalian group that demonstrates a distinct positive correlation between myoglobin content and maximum dive time (Fig. 4). Furthermore, pinnipeds may be subdivided into two groups, shorter diving otariids that maintain low myoglobin contents and longer diving phocids with higher myoglobin contents. The current study did not find a similar distinction between the two groups of cetaceans, the mysticetes and odontocetes (Fig. 4).

The wide range of body masses among cetacean species has a demonstrable effect on the range of maximum dive durations reported for these mammals (Table 3). Although body mass was posi-

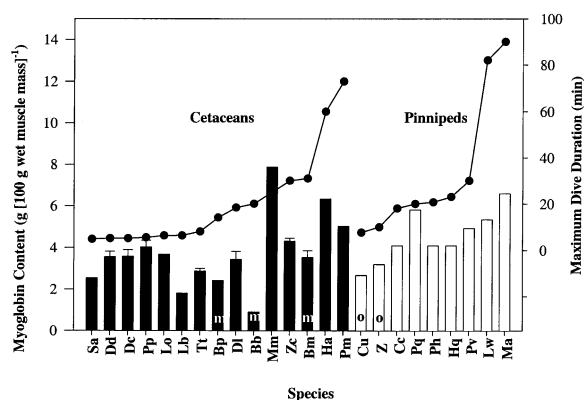


Fig. 4. Muscle myoglobin content (bars) and maximum dive duration (—●—) for cetaceans (black bars) and pinnipeds (white bars). Individual species are presented in order of increasing dive duration. 'm' denotes mysticetes and 'o' denotes otariids. Initials denote genus and species. Note that our calculations show that in pinnipeds, myoglobin concentration correlates with maximum dive duration according to the relationship, $\text{dive duration} = 18.7 [\text{Mb}] - 51.4$ ($r^2 = 0.58$, $F = 9.82$, $P = 0.017$, $n = 9$). The relationship between maximum dive duration and myoglobin content is more variable in cetaceans as described in the text. See Table 1, Table 2, and Table 3 for cetacean references. (Sa, *Stenella attenuata*; Dd, *Delphinus delphis*; Dc, *Delphinus capensis*; Pp, *Phocoena phocoena*; Lb, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*; Tt, *Tursiops truncatus*; Bp, *Balaenoptera physalus*; Dl, *Delphinapterus leucas*; Bb, *Balaenoptera borealis*; Mm, *Monodon monoceros*; Zc, *Ziphius cavirostris*; Bm, *Balaena mysticetus*; Ha, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*). Pinniped references Otariids: Cu, *Callorhinus ursinus*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Gentry et al., 1986); Z, *Zalophus californianus*: [Mb] (Castellini and Somero, 1981), Dive (Feldkamp et al., 1989). Phocids: Cc, *Cystophora cristata*: [Mb] and Dive (Scholander, 1940); Pg, *Phoca groenlandica*: [Mb] and Dive (George et al., 1971); Ph, *Phoca hispida*: [Mb] (Lydersen et al., 1992), Dive (Parsons, 1977); Hg, *Halichoerus grypus*: [Mb] (Scholander, 1940), Dive (Lavigne and Kovacs, 1988); Pv, *Phoca vitulina*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Kooyman et al., 1972); Lw, *Leptonychotes weddelli*: [Mb] (Ponganis et al., 1993), Dive (Castellini et al., 1993); Ma, *Mirounga angustirostris*: [Mb] (Thorson, 1993), Dive (Le Boeuf et al., 1993).

tively correlated with maximum dive duration for cetaceans, the effect of body mass differs between the two cetacean suborders. A strong correlation between body mass and maximum dive duration was found for odontocetes; the same relationship was not significant for mysticetes (Fig. 3). Again, this may have been related to the small sample size of mysticetes examined. To maintain equivalent sample sizes for the myoglobin-dive duration and body mass-dive duration analyses, we limited our analyses to those species in which myoglobin content was measured or known. Although it was difficult to draw conclusions in the present study, previous investigations have reported a positive correlation between body mass and dive duration for mysticetes (Schreer and Kovacs, 1997).

For Weddell seals (Kooyman et al., 1983), other pinnipeds (Costa, 1991), and the pekin duck (Hudson and Jones, 1986) large body size provides an advantage for diving in terms of the absolute size of oxygen stores and relative decrease in mass specific metabolic rate. Similarly, both muscle myoglobin content and body mass influence dive capacity in cetaceans. These two characteristics explain nearly 50% of the variation in dive performance across a wide range of cetacean species including odontocetes and mysticetes. When odontocetes are considered separately, muscle myoglobin content and body mass accounts for 83% of the variation in dive performance.

Increased body size preadapts large cetaceans for prolonged dive durations due to two factors; (1) an increase in the absolute muscle mass and consequently an increase in absolute muscle oxygen stores; and (2) a decrease in mass specific metabolic rate. Metabolic rate only increases by a mass exponent 0.75 for resting mammals (assuming cetaceans follow the same allometric trend presented for other animals by Kleiber 1975) and by 0.71 for swimming transport costs in marine mammals (Williams, 1999). The lower mass specific energetic demands of large cetaceans in comparison to smaller cetaceans slow the relative depletion of oxygen during breath-hold. Thus, the larger cetacean is able to prolong its dive time beyond that of smaller cetaceans despite similar mass specific muscle oxygen stores. A comparison of the 80 000 kg bowhead whale and the 70 kg common dolphin demonstrates these relationships. These species represent two size extremes among cetaceans that have similar myoglobin

contents in the locomotor muscles (Table 1). Based on the Kleiber (1975) regression, the mass specific metabolic rate of the common dolphin is 10 times greater than that of the bowhead whale. The theoretical consequence is a lower oxygen utilization rate for the larger cetacean, and sparing of limited oxygen stores in the skeletal muscle. With similar myoglobin contents per gram of muscle, the difference in oxygen utilization rate permits longer dive durations in the larger cetacean. TDR records support this, and we find a 6-fold greater maximum dive duration for the bowhead whale in comparison to the common dolphin (Table 3). Admittedly, further research is required to provide empirical evidence regarding the scaling of oxygen demand in this taxonomic group. However, these simple calculations demonstrate the importance of body size on metabolic rate and its potential effect on diving performance.

Despite the small sample sizes for mysticetes in this study, it appears that the relationships between myoglobin content and maximum dive duration (Fig. 2) and body mass and maximum dive duration (Fig. 3) are different for the two cetacean sub groups. One possible explanation for this is differences in preferred feeding behaviors and consequently different selective pressures for prolonged diving in odontocetes and mysticetes. The largest species in this study, the bowhead whale, dives between 0.1–31 min with an average dive duration of 12.08 ± 9.15 min (Wursig et al., 1984). These whales are described as skimmer feeders and forage primarily at the water surface, exhibiting a stereotypic basic pattern of short dive durations (Wursig et al., 1984; Dorsey et al., 1989). Other mysticete species show similar surface foraging behaviors. For example, in the Gulf of California and coastal California the majority of dives by fin whales rarely exceed 12 min and 200 m in depth (Croll personal communication). This depth represents only 12 times the animals' body length and suggests that large mysticetes may rarely approach their physiological limits for diving. In view of this, many species of mysticetes may be under little selective pressure for developing physiological adaptations, such as high myoglobin contents, that prolong dive duration. Conversely, the sperm whale, the largest odontocete, forages at depths of up to 2250 m (Ridgway and Harrison, 1986) for durations of 73 min (Watkins et al., 1993). When feeding behavior is

taken into account, it is not surprising that large odontocetes show exceptionally high myoglobin contents in the skeletal muscles while large mysticetes do not (Figs. 2 and 4, Tables 1 and 2).

In summary, the results of the present study demonstrate how myoglobin concentration in the skeletal muscles and body mass mutually influence dive duration in cetaceans. These two characteristics combined account for nearly 50% of the variation in dive capacity across cetacean species that vary in body mass from 70 to 80 000 kg. As found for other marine mammals, enhanced oxygen storage capacity due to high myoglobin concentrations is an important adaptation for diving in cetaceans. Balancing this store and oxygen utilization rate will dictate the duration of aerobically supported dives for these animals (Kooyman, 1989). Due to the wide range of body masses among cetaceans, differences in oxygen utilization rate as modulated by mass specific metabolic rate, is an especially important factor in defining aerobic dive capacity. Differences observed between the two cetacean suborders suggest that odontocetes and mysticetes have been under different selective pressures for developing physiological adaptations for prolonged dive duration. Among cetaceans, mysticetes show average myoglobin contents and rely on the relatively low oxygen consumption rates associated with large body size to support relatively short dives. The trend for smaller odontocetes is elevated muscle myoglobin contents prolonging dive durations. Large odontocete species, such as the bottlenose whale and sperm whale, combine both large body mass and high myoglobin contents in the skeletal muscles. As a result, these cetaceans are capable of prolonged dives at remarkable depths making them the champion divers among cetaceans.

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