

Allometry of diving capacity in air-breathing vertebrates

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Abstract: Maximum diving depths and durations were examined in relation to body mass for birds, marine mammals, and marine turtles. There were strong allometric relationships between these parameters (\log_{10} transformed) among air-breathing vertebrates ($r = 0.71$, $n = 111$ for depth; $r = 0.84$, $n = 121$ for duration), although there was considerable scatter around the regression lines. Many of the smaller taxonomic groups also had a strong allometric relationship between diving capacity (maximum depth and duration) and body mass. Notable exceptions were mysticete cetaceans and diving/flying birds, which displayed no relationship between maximum diving depth and body mass, and otariid seals, which showed no relationship between maximum diving depth or duration and body mass. Within the diving/flying bird group, only alcidids showed a significant relationship ($r = 0.81$, $n = 9$ for depth). The diving capacities of penguins had the highest correlations with body mass ($r = 0.81$, $n = 11$ for depth; $r = 0.93$, $n = 9$ for duration), followed by those of odontocete cetaceans ($r = 0.75$, $n = 21$ for depth; $r = 0.84$, $n = 22$ for duration) and phocid seals ($r = 0.70$, $n = 15$ for depth; $r = 0.59$, $n = 16$ for duration). Mysticete cetaceans showed a strong relationship between maximum duration and body mass ($r = 0.84$, $n = 9$). Comparisons across the various groups indicated that alcidids, penguins, and phocids are all exceptional divers relative to their masses and that mysticete cetaceans dive to shallower depths and for shorter periods than would be predicted from their size. Differences among groups, as well as the lack of relationships within some groups, could often be explained by factors such as the various ecological feeding niches these groups exploit, or by variations in the methods used to record their behavior.

Résumé : La profondeur et la durée maximales des plongées ont été étudiées en relation avec la masse du corps chez des oiseaux, des mammifères marins et des tortues marines. Il existe de fortes relations allométriques entre ces variables (converties en \log_{10}) chez les vertébrés à respiration aérienne ($r = 0,71$, $n = 111$ dans le cas de la profondeur; $r = 0,84$, $n = 121$ dans le cas de la durée), bien que les points soient fort dispersés de part et d'autre des droites de régression. Il existe également des relations allométriques évidentes entre la capacité de plongée (profondeur et durée maximales) et la masse du corps chez plusieurs des taxons plus petits. Cependant, les cétacés mysticètes et les oiseaux plongeurs/voiliers font exception à cette généralité, puisqu'aucune relation n'a été trouvée chez ces animaux entre la profondeur de plongée maximale et la masse du corps; de même, les otaries constituent également des exceptions, puisqu'il n'y a pas de relation entre la profondeur ou la durée maximales de leurs plongées et leur masse corporelle. Parmi les oiseaux plongeurs/voiliers, il n'y a que chez les alcidés que la relation est significative ($r = 0,81$, $n = 9$ dans le cas de la profondeur). C'est chez les manchots que prévalent les corrélations les plus fortes avec la masse du corps ($r = 0,81$, $n = 11$ dans le cas de la profondeur; $r = 0,93$, $n = 9$ dans le cas de la durée), puis chez les cétacés odontocètes ($r = 0,75$, $n = 21$, dans le cas de la profondeur; $r = 0,84$, $n = 22$ dans le cas de la durée), puis chez les phocidés ($r = 0,70$, $n = 15$ dans le cas de la profondeur; $r = 0,59$, $n = 16$ dans le cas de la durée). Chez les cétacés mysticètes, la corrélation entre la durée maximale et la masse du corps est forte ($r = 0,84$, $n = 9$). Les comparaisons entre les groupes indiquent que les alcidés, les manchots et les phocidés sont des plongeurs exceptionnels compte tenu de leur masse, et que les cétacés mysticètes plongent à des profondeurs moins grandes et pour des périodes moins longues que ne le permettrait de croire leur masse. Les différences entre les groupes ou l'absence de relations chez certains groupes entre la masse et les caractéristiques des plongées résultent souvent de facteurs tels que les variations entre les différentes niches écologiques qu'exploitent ces organismes ou les différences de méthodes utilisées pour enregistrer leurs comportements.

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Introduction

Body size is one of the most important factors influencing how animals interact with their environment, and it has been shown to be an excellent predictive tool in ecology (Peters 1983; Schmidt-Nielsen 1984). Many life-history traits, as well as morphological and physiological traits, of animals

have been compared with body size, including metabolic rate (Kleiber 1961), brain size (Stahl 1965; Jerison 1970), and the cost of locomotion (Brett 1965; Tucker 1973; Greenewalt 1975). Diving behavior in air-breathing vertebrates is highly variable and is dependent on many physiological constraints such as metabolic rate (Scholander 1940; Butler and Jones 1982), oxygen stores (Scholander 1940; Butler and Jones 1982; Snyder 1983), and the ability to metabolize anaerobically (Hochachka and Somero 1984). Since many of these factors have been associated with body size, diving behavior should also be related to body size. This has been shown to be the case in interspecific analyses of diving among alcids and penguins (Piatt and Nettleship 1985; Prince and Harris 1988; Burger 1991) and cormorants (Cooper 1986), and hypothesized or shown in single species by the results of numerous studies (e.g., Irving 1939; Gentry et al. 1986a; Costa 1993; Le Boeuf 1994). Diving air-breathing vertebrates represent an interesting set of organisms for allometric analyses because of their enormous variation in mass, ranging from as small as the 0.09-kg South Georgia petrel (*Pelecanoides georgicus*) (Prince and Jones 1992) to the 145 000-kg blue whale (*Balaenoptera musculus*) (Jefferson et al. 1993), which encompasses more than a millionfold difference.

The study of diving behavior has evolved dramatically over the last 30 years. Originally, the study of diving simply involved observing the behavior. In the 1930s several experimental studies were conducted that provided many insights into how air-breathing animals dive (e.g., Irving 1939; Scholander 1940). More recently, with the availability of remote sensing and recording methods such as sonar (Thompson et al. 1991; Watkins and Tyack 1991; Watkins et al. 1993; Kelly and Wartzok 1996), capillary tubes (Burger and Wilson 1988), and micro-processor-controlled time–depth recorders (TDRs) and satellite-linked TDRs (Kooyman 1981; Kooyman et al. 1983a; Stewart et al. 1989; Wildlife Computers, Woodenville, Wash., U.S.A.), the study of diving has rapidly expanded and diversified. These newer methods have enabled more accurate and rigorous estimates of diving behavior to be made on a broad array of diving animals. The abundance of recent diving research indicated a need for a current review that could address issues such as the comparative diving behavior of various animals and the limitations of different methods used to collect the data.

This paper is a review of available data on observed diving capacity (maximum diving depth and duration) of diving/flying birds (alcids, cormorants, ducks, grebes, loons, and petrels), penguins, cetaceans (odontocetes and mysticetes), pinnipeds (phocids, otariids, and odobenids), sirenians (manatees and dugongs), sea otters, and marine turtles, and a comparison of these values with body mass. Allometric equations were derived for maximum depth and duration versus body mass within and across the major groups mentioned above. The intent of this work was to examine the degree to which diving capacity and body size are related and to explain observed discrepancies from a general pattern. It was expected that the various ecological niches exploited by diving air-breathing vertebrates and the methods used to collect the data would introduce real and artificial variances, respectively. This paper is also intended to be a summary of the available literature and will hopefully serve as a catalyst

to direct research toward species where there is little, outdated, or no diving information.

Methods

Data were collected from the literature on body mass (kg), maximum diving depth (m), maximum diving duration (min), and methods used for data collection. Original sources of information were used whenever possible. For mass, mean values were used when they were available, but sometimes midpoints of ranges or maximum values were utilized if these were the only measurements presented. For sexually dimorphic species, the mass of the gender for which diving behavior was recorded was used if this was available. If diving data were reported for both sexes within a species and their masses were considerably different, the two genders were treated as separate observations. Maximum diving depth and duration were utilized because means were often not presented and these measurements were more highly dependent on the methods used to collect the data and the location and timing of the study.

Allometric relationships were fitted using linear least squares regression of \log_{10} -transformed data for both maximum diving depth and duration against \log_{10} -mass (SYSTAT 1992). Equations were first fitted to the entire data set. The data were subsequently split into two major groups, marine mammals and birds, and new equations were derived for these groups. Subsets of the marine mammal data were then analyzed for mysticetes, odontocetes, phocids, and otariids. Birds were first subdivided into penguins and flying birds. Differences within the bird group were then further tested by dividing the flying birds into those groups for which sufficient data were available to allow comparisons (i.e., alcids, cormorants, and ducks). However, these specific bird groups (except penguins) were not used in the main comparison of all diving vertebrates because of the high variability of the data and small sample sizes. Allometric relationships could not be derived for marine turtles as an independent group because there were too few data on too few species, although this would be warranted taxonomically.

The various equations were compared by testing for homogeneity of slopes and subsequently by analysis of covariance (ANCOVA; SYSTAT 1992) to test for differences in the adjusted means (specifically, differences in the means for a fixed \log_{10} mass; Sokal and Rohlf 1995). Significance was assumed at $\alpha = 0.05$. It must be stressed that the significance test for a regression line does not determine whether a line can be drawn through the data points, but whether the slope of that line is significantly different from 0. Therefore, even nonsignificant regression lines can be compared (Sokal and Rohlf 1995).

Lastly, the hypothetical aerobic dive limit (ADL), defined as the maximum duration of a breath-hold without any increase in plasma lactate levels above resting during or following a dive (Kooyman 1989), and maximum diving depth were calculated as a function of body mass for phocids, birds, otariids, and cetaceans. The predicted standard metabolic rate (SMR) for birds was calculated using $SMR = 13.0M_b^{0.729}$ (Aschoff and Pohl 1970; Kooyman 1989) and that for marine mammals (whose metabolic rates were once thought to be higher than those of terrestrial mammals, but were recently found not to be significantly different; Lavigne et al. 1986) using $SMR = 10.1M_b^{0.75}$ (Kleiber 1961), where M_b is body mass (kg) and SMR is given in millilitres of oxygen per minute. SMR was then divided by body mass to scale it to body size. Diving metabolic rates were only available for phocids (e.g., Kooyman et al. 1973; Castellini et al. 1992b), so for the other groups, metabolic rates while swimming or at sea were used. Diving metabolic rates were assumed to be approximately $2 \times SMR$ for all groups (Eliassen 1960; Kooyman et al. 1973; Baudinette and Gill 1985; Gentry et al. 1986a; Feldkamp et al. 1989; Kooyman 1989; Kooyman and Ponganis 1990; Burger 1991; Castellini et al. 1992b; Costa 1993; Williams et al. 1993), although a second model for otariids was also

derived with a higher diving metabolic rate ($5 \times \text{SMR}$), as suggested by Kooyman (1988b) and Costa (1993). The results of several of the above studies suggested that the metabolic rate during swimming was $2.5 \times \text{SMR}$; however, in agreement with Feldkamp et al. (1989), it was thought that upon submergence, changes occur (e.g., lowering of the heart rate and a decrease in peripheral blood flow; Castellini 1991) which lower this value. Oxygen consumption of swimming cetaceans (specifically bottlenose dolphins (*Tursiops truncatus*)) was found to be near resting levels; however, the resting levels were found to be $2.5 \times$ predicted SMR (Williams et al. 1993).

ADL (min) was calculated as mass-specific oxygen stores ($\text{mL O}_2 \cdot \text{kg}^{-1}$) divided by the mass-specific diving metabolic rate ($\text{mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$). Calculated available oxygen stores ($\text{mL O}_2 \cdot \text{kg}^{-1}$) for the various groups were 58 for birds (specifically measured for king penguins (*Aptenodytes patagonicus*)), 60 for phocids (Weddell seals (*Leptonychotes weddellii*)), 40 for otariids (northern fur seals (*Callorhinus ursinus*)), and 35 for cetaceans (bottlenose dolphins), taken from Kooyman (1989). The resulting equations were $\text{ADL}_{\text{phocids}} = 2.97M_b^{0.25}$, $\text{ADL}_{\text{otariids}} = 1.98M_b^{0.25}$, $\text{ADL}_{\text{cetaceans}} = 1.73M_b^{0.25}$, $\text{ADL}_{\text{birds}} = 2.23M_b^{0.271}$, and $\text{ADL}_{\text{otariids}(5 \times \text{SMR})} = 0.79M_b^{0.25}$.

Maximum diving depths (m) were calculated as $0.5 \times (\text{ADL} \times \text{cruising swim speed})$, where cruising swim speed was assumed to be $1.5 \text{ m} \cdot \text{s}^{-1}$ for all groups (Kooyman 1989). The predicted relationships for ADL and maximum diving depth were compared with observed diving capacities.

Results

The data base compiled for diving air-breathing vertebrates is given in Table 1. All available diving data were used to calculate regression equations regardless of the method of collection. The original intent was to use only data collected by TDRs and maximum depth gauges (MDGs), but this would have eliminated more than half of the data, preventing most intergroup comparisons. Also, eliminating the non-TDR/MDG data did not markedly change the correlations or slopes for depth or duration versus mass (Table 2), although there was a considerable increase in the Y intercepts. Maximum depth and duration were significantly correlated with mass for the entire data set of air-breathing vertebrates (Fig. 1, Table 2). Maximum depth and duration were also significantly correlated with mass for many of the smaller taxonomic groups, except for depth in mysticetes, otariids, and flying birds and duration in otariids. Within the bird group, penguins and alcids had a significant correlation between maximum depth and mass, and only penguins had a significant correlation between maximum duration and mass (Fig. 2, Table 3).

Figure 3 shows the regression lines from observed data, depicted in Fig. 1, along with the predicted relationships calculated for maximum duration (approximated using ADL) and maximum depth. Phocids had the highest predicted diving capacities relative to mass, followed by birds, otariids ($2 \times \text{SMR}$), and cetaceans. If $5 \times \text{SMR}$ had been used for otariids, however, this group would have had the lowest diving capacities. The various predicted lines generally overlapped the overall vertebrate lines; however, the rates at which predicted diving capacities increased with mass were generally lower than for those calculated using the observed data. The small graph at the bottom right of Fig. 3 shows predicted ADLs on a linear scale, showing how predicted diving capacity increases at a slower rate with increasing

mass. It also shows that the influence of mass on ADL is smaller for animals with higher metabolic rates and less oxygen stores.

Comparisons among the various groups were compromised by small and unequal sample sizes and the large variability of the observations within groups; however, several significant differences were found. The regression lines for mysticetes, odontocetes, phocids, and otariids were significantly different across many of these groups. Phocids dove significantly deeper and longer than mysticetes ($p = 0.001$, $n = 21$ for mass-adjusted depth; $p = 0.001$, $n = 25$ for mass-adjusted duration) and odontocetes ($p = 0.003$, $n = 36$ for mass-adjusted depth; $p < 0.001$, $n = 38$ for mass-adjusted duration), and significantly longer than otariids ($p = 0.002$, $n = 29$ for mass-adjusted duration). Odontocetes dove significantly deeper and longer than mysticetes ($p < 0.001$, $n = 27$ for mass-adjusted depth; $p < 0.001$, $n = 31$ for mass-adjusted duration) and significantly shorter than otariids ($p = 0.007$, $n = 35$ for mass-adjusted duration). Mysticetes had a significantly steeper slope for duration versus mass than otariids ($p = 0.041$, $n = 22$). Penguins dove significantly deeper (mass-adjusted depth) than mysticetes ($p = 0.028$, $n = 17$), odontocetes ($p = 0.006$, $n = 32$), otariids ($p = 0.018$, $n = 24$), and flying birds ($p = 0.018$, $n = 51$), and nearly significantly deeper than phocids ($p = 0.063$, $n = 26$). Penguins also dove significantly longer (mass-adjusted duration) than mysticetes ($p < 0.001$, $n = 18$) and odontocetes ($p = 0.001$, $n = 31$), and had a significantly steeper slope for duration versus mass than otariids ($p = 0.002$, $n = 22$) and flying birds ($p = 0.006$, $n = 54$). The flying birds made significantly shorter dives (mass-adjusted duration) than phocids ($p = 0.001$, $n = 61$) and otariids ($p = 0.004$, $n = 58$), and had a significantly less steep slope for duration versus mass than odontocetes ($p = 0.020$, $n = 67$).

Differences within the bird group were seldom significant, which may be due in part to the small sample sizes. Alcids dove significantly deeper and longer than cormorants ($p = 0.005$, $n = 16$ for mass-adjusted depth; $p = 0.027$, $n = 21$ for mass-adjusted duration) and ducks ($p < 0.001$, $n = 24$ for mass-adjusted depth; $p = 0.014$, $n = 23$ for mass-adjusted duration), and significantly deeper than penguins ($p = 0.005$, $n = 20$ for mass-adjusted depth). Neither penguins nor cormorants dove significantly deeper than ducks ($p = 0.050$, $n = 26$ and $p = 0.071$, $n = 22$ for mass-adjusted depth, respectively), although the differences were nearly significant.

Comparisons of birds and mammals showed that the slopes of the depth and duration versus mass lines for birds were significantly steeper than those for marine mammals ($p = 0.002$, $n = 108$ for depth; $p = 0.018$, $n = 118$ for duration). However, when mysticete cetaceans were removed from the data, no significant differences were observed.

Discussion

Diving capacity increased with body mass in broad interspecific comparisons, as was expected. However, this relationship was not significant for some of the smaller taxonomic groups analyzed. The most obvious limitation to an air-breathing animal's diving capacity is its ability to store

Table 1. Adult body mass, maximum diving depth, maximum diving duration, number of observations, and methods used for data collection for air-breathing vertebrates.

Common name ^a	Scientific name	Mass (kg)	Depth (m)	Duration (min)	<i>n</i> ^b	Methods ^c	Sources ^d
Whales, dolphins, and porpoises	Order Cetacea						
Baleen whales	Suborder Mysticeti						
Blue whale	<i>Balaenoptera musculus</i>	145 000	100	50	—	Feeding, line	Jefferson et al. 1993; Harrison and Kooyman 1971; Irving 1939
Right whale	<i>Eubalaena</i> sp.	81 600	184	50	—	Sonar, —	Jefferson et al. 1993; Goodyear 1995; Tinker 1988
Bowhead whale	<i>Balaena mysticetus</i>	79 400	300	80	—	RT, —	Jefferson et al. 1993; Krutzikowsky and Mate 1995; Irving 1939
Fin whale	<i>Balaenoptera physalus</i>	68 000	500	30	—	Line, —	Jefferson et al. 1993; Harrison and Kooyman 1971; Scholander 1940
Gray whale	<i>Eschrichtius robustus</i>	31 800	170	26	—, 11 000	TDR, RT	Jefferson et al. 1993; Evans 1974; Harvey and Mate 1984
Humpback whale	<i>Megaptera novaeangliae</i>	31 700	148	21	300, 5000	Sonar, obs.	Jefferson et al. 1993; Dolphin 1988
Sci whale	<i>Balaenoptera borealis</i>	27 200		15	—	Obs.	Jefferson et al. 1993; Gambell 1985
Bryde's whale	<i>Balaenoptera edeni</i>	20 400		20	—	Obs.	Jefferson et al. 1993; Cummings 1985
Minke whale	<i>Balaenoptera acutorostrata</i>	12 700		17	—	Net	Jefferson et al. 1993; Katona et al. 1993
Toothed whales	Suborder Odontoceti						
Sperm whale (M)	<i>Physeter catodon</i>	51 700	3000 ^e	138	—	Feeding, sonar	Jefferson et al. 1993; Clarke 1976; Watkins et al. 1985
Killer whale (M)	<i>Orcinus orca</i>	10 000	260	15	100, —	Trained, —	Jefferson et al. 1993; Bower and Henderson 1972
Arnoux's beaked whale	<i>Berardius arnuxii</i>	7 500 ^f		70	70	Obs.	Jefferson et al. 1993; Hobson and Martin 1996
Bottlenose whale	<i>Hyperoodon</i> sp.	4 500 ^f	1000	120	—	Line, —	Jefferson et al. 1993; Benjaminsen and Christensen 1979; Irving 1939
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	3 000		30	—	Obs.	Jefferson et al. 1993; Heyning 1989
Pilot whale (M)	<i>Globicephala</i> sp.	2 000	610	20	300, —	Trained, —	Jefferson et al. 1993; Bower and Henderson 1972
False killer whale	<i>Pseudorca crassidens</i>	2 000	300		—	—	Jefferson et al. 1993; Tinker 1988
Narwhal	<i>Monodon monoceros</i>	1 600	1000	20	>600	TDR	Jefferson et al. 1993; Heide-Jørgensen and Dietz 1995
Beluga whale	<i>Delphinapterus leucas</i>	1 600	1000	25	—	TDR	Jefferson et al. 1993; A.R. Martin, personal communication
Bottlenose dolphin	<i>Tursiops truncatus</i>	650	535	12	—	Trained, obs.	Jefferson et al. 1993; Ridgway 1986; Harrison and Kooyman 1971
Pygmy sperm whale	<i>Kogia breviceps</i>	400		12	—	RT	Jefferson et al. 1993; Hohn et al. 1995
Fraser's dolphin	<i>Lagenodelphis hosei</i>	210	500		—	Feeding	Jefferson et al. 1993; Robinson and Craddock 1983
Dwarf sperm whale	<i>Kogia simus</i>	210	300		—	Feeding	Jefferson et al. 1993; Fitch and Brownell 1968
Dall's porpoise	<i>Phocoenoides dalli</i>	200	180		—	Feeding	Jefferson et al. 1993; Morejohn 1979
Irrawaddy dolphin	<i>Orcaella brevirostris</i>	190		12	—	Obs.	Marsh et al. 1989; Marsh et al. 1989
Baiji	<i>Lipotes vexillifer</i>	180		2	—	Obs.	Jefferson et al. 1993; Peixun 1989
Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	180	214	6	100, —	Trained	Jefferson et al. 1993; Hall 1970; Ridgway 1986
Rough-toothed dolphin	<i>Steno bredanensis</i>	150	70	15	—	Line-hp, obs.	Jefferson et al. 1993; Watkins et al. 1987; Miyazaki and Perrin 1994
Atlantic spotted dolphin	<i>Stenella frontalis</i>	143	60	5	—	TDR	Jefferson et al. 1993; Worthy and Davis 1995
Common dolphin	<i>Delphinus delphis</i>	135	258	5	—	TDR	Jefferson et al. 1993; Evans 1971; Ridgway 1986
Pantropical spotted dolphin	<i>Stenella attenuata</i>	120	100	5	—	TDR	Jefferson et al. 1993; Scott et al. 1993

Table 1 (continued).

Common name ^a	Scientific name	Mass (kg)	Depth (m)	Duration (min)	<i>n</i> ^b	Methods ^c	Sources ^d
Southern right whale dolphin	<i>Lissodelphis peronii</i>	116	300	7	—	Feeding, obs.	Jefferson et al. 1993; Baker 1981; Cruickshank and Brown 1981
Northern right whale dolphin	<i>Lissodelphis borealis</i>	115	250	6	—	Feeding, obs.	Jefferson et al. 1993; Fitch and Brownell 1968; Leatherwood and Walker 1979
Ganges River dolphin	<i>Platanista gangetica</i>	108		3	—	Obs.	Jefferson et al. 1993; Reeves and Brownell 1989
Spinner dolphin	<i>Stenella longirostris</i>	77	250	3	—, 500	Feeding, obs.	Jefferson et al. 1993; Fitch and Brownell 1968; Würsig et al. 1994
Harbor porpoise	<i>Phocoena phocoena</i>	60	226	12	8000, —	TDR, exp.	Jefferson et al. 1993; Westgate et al. 1995; Harrison and Kooyman 1971
Vaquita	<i>Phocoena sinus</i>	35 ^f	30		—	Feeding	Jefferson et al. 1993; Fitch and Brownell 1968
Seals, fur seals, sea lions, and walruses	Suborder Pinnipedia						
True seals	Family Phocidae						
Southern elephant seal (M)	<i>Mirounga leonina</i>	4 000	1130	89	25 000	TDR	Jefferson et al. 1993; Hindell et al. 1991
Northern elephant seal (M)	<i>Mirounga angustirostris</i>	2 000	1529	77	35 000	TDR	Jefferson et al. 1993; DeLong and Stewart 1991
Northern elephant seal (F)	<i>Mirounga angustirostris</i>	600	1250	62	20 000	TDR	Jefferson et al. 1993; Le Boeuf et al. 1989
Southern elephant seal (F)	<i>Mirounga leonina</i>	600	1256	120	25 000	TDR	Jefferson et al. 1993; Hindell et al. 1991
Weddell seal (F)	<i>Leptonychotes weddellii</i>	425	741	82	> 20 000	TDR	Jefferson et al. 1993; Testa 1994; Castellini et al. 1992a
Bearded seal (F)	<i>Erignathus barbatus</i>	360	250	25	100 000	TDR	Jefferson et al. 1993; I. Gjertz, personal communication
Hooded seal (M)	<i>Cystophora cristata</i>	350	1000 ^g	52	60 000	TDR	Jefferson et al. 1993; Folkow and Blix 1995
Bearded seal (M)	<i>Erignathus barbatus</i>	260	250	20	100 000	TDR	Jefferson et al. 1993; I. Gjertz, personal communication
Crabeater seal	<i>Lobodon carcinophagus</i>	250	528	11	80 000, 8000	TDR	Jefferson et al. 1993; Nordøy et al. 1995; Bengtson and Stewart 1992
Grey seal (M)	<i>Halichoerus grypus</i>	240	268	23	55 000, —	TDR, —	Jefferson et al. 1993; Hammill et al. 1993; Lavigne and Kovacs 1988
Hooded seal (F)	<i>Cystophora cristata</i>	220	1000 ^g	52	60 000	TDR	Jefferson et al. 1993; Folkow and Blix 1995
Harp seal (F)	<i>Phoca groenlandica</i>	120	370	16	30 000, —	TDR, —	Jefferson et al. 1993; E.S. Nordøy, personal communication; Lavigne and Kovacs 1988
Larga seal	<i>Phoca largha</i>	100	100	10	> 20 000	TDR	Jefferson et al. 1993; Frost et al. 1993
Harbor seal	<i>Phoca vitulina</i>	100	508 ^g	28	500 000, —	TDR, exp.	Jefferson et al. 1993; U. Swain, personal communication; Scholander 1940
Baikal seal	<i>Phoca sibirica</i>	85		68	—	Exp.	Jefferson et al. 1993; Pastukhov 1969
Ringed seal	<i>Phoca hispida</i>	80	222 ^h	26	10 000	Sonic trans.	Jefferson et al. 1993; Kelly and Wartzok 1996
Eared seals	Family Otariidae						
Steller sea lion (F)	<i>Eumetopias jubatus</i>	270	424	16	100 000	TDR	Jefferson et al. 1993; U. Swain, personal communication
Hooker's sea lion (F)	<i>Phocarcos hookeri</i>	160	474 ^k	12	20 000, —	TDR	Jefferson et al. 1993; Gales and Mattlin 1995; Gentry et al. 1987

Table 1 (continued).

Common name ^a	Scientific name	Mass (kg)	Depth (m)	Duration (min)	<i>n</i> ^b	Methods ^c	Sources ^d
South American sea lion (F)	<i>Otaria byronia</i>	140	112 ^h	6	7000	TDR	Jefferson et al. 1993; Werner and Campagna 1993
California sea lion (F)	<i>Zalophus californianus californianus</i>	110	482	15	>1500, >1000	TDR, RT	Jefferson et al. 1993; Melin et al. 1993; Orr and Auriolos-Gamboa 1995
Australian sea lion (F)	<i>Neophoca cinerea</i>	105	92	6	—	TDR	Jefferson et al. 1993; Costa et al. 1989
Galapagos sea lion (F)	<i>Zalophus californianus wollebaeki</i>	80	186	6	3000	TDR	Jefferson et al. 1993; Kooyman and Trillmich 1986b
South African fur seal (F)	<i>Arctocephalus pusillus</i>	80	204	8	1000	TDR	Jefferson et al. 1993; Kooyman and Gentry 1986
Northern fur seal (F)	<i>Callorhinus ursinus</i>	50	207	8	2000	TDR	Jefferson et al. 1993; Gentry et al. 1986b
Guadalupe fur seal (F)	<i>Arctocephalus townsendi</i>	50	82	18	>1000	TDR	Jefferson et al. 1993; Gallo-Reynoso et al. 1995
South American fur seal (F)	<i>Arctocephalus australis</i>	45	170	7	1000	TDR	Jefferson et al. 1993; Trillmich et al. 1986
New Zealand fur seal (F)	<i>Arctocephalus forsteri</i>	40	238	11	700	TDR	Jefferson et al. 1993; Mattlin 1993
Antarctic fur seal (F)	<i>Arctocephalus gazella</i>	35	181	10	60 000	TDR	Jefferson et al. 1993; Boyd and Croxall 1992
Galapagos fur seal (F)	<i>Arctocephalus galapagoensis</i>	30	115	8	3000	TDR	Jefferson et al. 1993; Kooyman and Trillmich 1986a
Walruses	Family Odobenidae						
Walrus (M)	<i>Odobenus rosmarus</i>	1 900	100 ^e	13	—, 1500	Feeding, TDR	Jefferson et al. 1993; Fay and Burns 1988; Wiig et al. 1993
Sirenians	Order Sirenia						
West Indian Manatee	<i>Trichechus manatus</i>	1 600		16	—	—	Jefferson et al. 1993; Irving 1939
Dugong	<i>Dugong dugon</i>	400		8	—	Obs.	Jefferson et al. 1993; Nishiwaki and Marsh 1985
Sea otters	Family Mustelidae						
Sea otter	<i>Enhydra lutris</i>	40	97	4	—	Net, obs.	Jefferson et al. 1993; Newby 1975; Kenyon 1981
Marine turtles	Families Cheloniidae and Dermochelyidae (leatherbacks)						
Leatherback	<i>Dermochelys coriacea</i>	360	1300	37	5000	TDR	Pritchard 1979; Eckert et al. 1989
Loggerhead	<i>Caretta caretta</i>	125	90	99	—	RT	Pritchard 1979; Soma 1985
Kemp's ridley	<i>Lepidochelys kempii</i>	41		167	500	RT	Pritchard 1979; Medonca and Pritchard 1986
Olive ridley ⁱ	<i>Lepidochelys olivacea</i>	38	290		1	Sub.	Kooyman 1989; Landis 1965
Birds	Class Aves						
Penguins	Family Spheniscidae						
Emperor	<i>Aptenodytes forsteri</i>	22.0	534	16.0	16 000	TDR	Burger 1991; Kooyman and Kooyman 1995
King	<i>Aptenodytes patagonicus</i>	13.0	304	8.0	> 10 000	TDR	Burger 1991; Kooyman et al. 1992
Yellow-eyed	<i>Megadyptes antipodes</i>	5.5	56		40	MDG	Seddon and van Heezik 1990; Seddon and van Heezik 1990
Gentoo	<i>Pygoscelis papua</i>	5.5	156	4.5	16 000	TDR	Burger 1991; Williams et al. 1992
Adélie	<i>Pygoscelis adeliae</i>	5.0	175	4.0	30, 600	MDG, TDR	Burger 1991; Whitehead 1989; Naito et al. 1990
Macaroni	<i>Eudyptes chrysolophus</i>	4.6	115	6.3	5000	TDR	Burger 1991; Croxall et al. 1993
Humboldt	<i>Spheniscus humboldti</i>	4.2	80	2.7 ^j	—, 18	MDG, obs.	Burger 1991; Wilson and Wilson 1990; Duffy 1983
Magellanic	<i>Spheniscus magellanicus</i>	3.5	90		60	MDG	Burger 1991; Scolaro and Suburo 1991
Chinstrap	<i>Pygoscelis antarctica</i>	3.5	121	3.0	12 000	TDR	Burger 1991; Bengston et al. 1993
Jackass	<i>Spheniscus demersus</i>	3.2	130	4.0	15, 50	MDG, obs.	Burger 1991; Wilson 1985

Table 1 (continued).

Common name ^a	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n ^b	Methods ^c	Sources ^d
Galapagos Little	<i>Spheniscus mendiculus</i> <i>Eudyptula minor</i>	2.0 ^f 1.2		1.3 69	— 30	Obs. MDG	Del Hoyo et al. 1992; Boersma 1976 Burger 1991; Montague 1985
Loons	Family Gaviidae						
White-billed	<i>Gavia adamsii</i>	5.2	27	1.5	—	Net, obs.	Del Hoyo et al. 1992; Dewar 1924; Sage 1971
Common	<i>Gavia immer</i>	3.6	61	2.0	—	Net, obs.	Del Hoyo et al. 1992; Schorger 1947; Dewar 1924
Black-throated	<i>Gavia arctica</i>	2.4	6 ^e	2.0	35, —	Obs.	Del Hoyo et al. 1992; Dewar 1924; Cramp and Simmons 1977
Red-throated	<i>Gavia stellata</i>	1.7	9 ^e	1.5	200, —	Obs.	Del Hoyo et al. 1992; Dewar 1924
Cormorants	Family Phalacrocoracidae						
White-breasted Japanese	<i>Phalacrocorax carbo lucidus</i> <i>Phalacrocorax capillatus</i>	2.9 2.8		0.9 45	50 10 000	Obs. TDR	Cooper 1986; Cooper 1986 Watanuki et al. 1996; Watanuki et al. 1996
Great Blue-eyed	<i>Phalacrocorax carbo</i> <i>Phalacrocorax atriceps</i>	2.3 2.2	37 125	1.2 5.2	—, 460 —, 700	Net, obs. MDG, TDR	Del Hoyo et al. 1992; Dewar 1924 Burger 1991; Burger 1991; Croxall et al. 1991
Pelagic Shag	<i>Phalacrocorax pelagicus</i> <i>Phalacrocorax aristotelis</i>	2.0 2.0		1.0 80	40 —, 150	Obs. Net, obs.	Del Hoyo et al. 1992; Dow 1964 Del Hoyo et al. 1992; Guyot 1988; Lumsden and Haddow 1946
Bank	<i>Phalacrocorax neglectus</i>	1.8	70	1.1	2,160	MDG, obs.	Del Hoyo et al. 1992; Burger 1991; Cooper 1985
Guanay Red-legged Cape Crowned	<i>Phalacrocorax bougainvillii</i> <i>Phalacrocorax gaimardi</i> <i>Phalacrocorax capensis</i> <i>Phalacrocorax coronatus</i>	1.7 ^f 1.3 1.2 0.8		1.3 ^j 1.0 ^j 92 11	16 70 7 2, 140	Obs. Obs. MDG MDG, obs.	Del Hoyo et al. 1992; Duffy 1983 Cooper 1986; Duffy 1983 Del Hoyo et al. 1992; Burger 1991 Del Hoyo et al. 1992; Burger 1991; Williams and Cooper 1983
Pygmy	<i>Phalacrocorax pygmaeus</i>	0.7		0.7	8	Obs.	Del Hoyo et al. 1992; Cramp and Simmons 1977
Reed	<i>Phalacrocorax africanus</i>	0.6		0.7	30	Obs.	Cooper 1986; Cooper 1986
Ducks	Family Anatidae						
Common eider King eider	<i>Somateria mollissima</i> <i>Somateria spectabilis</i>	2.1 1.8	55 45 ^e	0.8 1.4	—, 300 —, 8	Net, obs. Feeding, obs.	Del Hoyo et al. 1992; Dewar 1924 Del Hoyo et al. 1992; Dewar 1924; Cramp and Simmons 1977
Goosander Velvet scoter Tufted	<i>Mergus merganser</i> <i>Melanitta fusca</i> <i>Aythya fuligula</i>	1.5 1.5 1.2	4 30 ^e 11	2.0 3.0 1.0	100, — — —	Obs. Obs. Net, obs.	Del Hoyo et al. 1992; Dewar 1924 Del Hoyo et al. 1992; Dewar 1924 Del Hoyo et al. 1992; Nilsson 1972; Dewar 1924
Canvasback Scaup Red-breasted merganser	<i>Aythya valisineria</i> <i>Aythya marila</i> <i>Mergus serrator</i>	1.2 1.1 1.1	10 6 ^e 9 ^e	— 1.0 2.0	— 150, — 8, —	Obs. Obs. Obs.	Del Hoyo et al. 1992; Dewar 1924 Del Hoyo et al. 1992; Dewar 1924 Del Hoyo et al. 1992; Dow 1964; Dewar 1924
Common scoter	<i>Melanitta nigra</i>	1.0	30 ^e	0.8	—	Obs.	Del Hoyo et al. 1992; Cramp and Simmons 1977; Dewar 1924
Pochard	<i>Aythya ferina</i>	1.0	6 ^h	1.0	100, —	Obs.	Del Hoyo et al. 1992; Carbone et al. 1996; Dewar 1924
Surf scoter	<i>Melanitta perspicillata</i>	1.0	12 ^e	1.1	—, 20	Obs.	Del Hoyo et al. 1992; Dewar 1924; Dow 1964
Common goldeneye	<i>Bucephala clangula</i>	0.9	9	1.0	—	Obs.	Del Hoyo et al. 1992; Nilsson 1972; Dewar 1924
White-headed	<i>Oxyura leucocephala</i>	0.7	2 ^e	0.7	50	Obs.	Del Hoyo et al. 1992; Cramp and Simmons 1977
Smew	<i>Mergus albellus</i>	0.7	4 ^e	0.8	60, —	Obs.	Del Hoyo et al. 1992; Cramp and Simmons 1977
Long-tailed	<i>Clangula hyemalis</i>	0.7	61	1.2	—	Net, obs.	Del Hoyo et al. 1992; Schorger 1947; Dewar 1924
Grebes	Family Podicipedidae						
Red-necked Great crested	<i>Podiceps grisegena holboellii</i> <i>Podiceps cristatus</i>	1.0 1.0		1.0 30	— 160, —	Obs. Net, obs.	Cramp and Simmons 1977 Del Hoyo et al. 1992; Cramp and Simmons 1977
Western	<i>Aechmophorus occidentalis</i>	0.9		1.2	70	Obs.	Del Hoyo et al. 1992; Forbes and Sealy 1988

Table 1 (concluded).

Common name ^a	Scientific name	Mass (kg)	Depth (m)	Duration (min)	<i>n</i> ^b	Methods ^c	Sources ^d
Horned	<i>Podiceps auritus</i>	0.4	4 ^e	1.2	150, —	Obs.	Del Hoyo et al. 1992; Dewar 1924; Cramp and Simmons 1977
Black-necked	<i>Podiceps nigricollis</i>	0.3	6 ^e	0.8	—	Obs.	Del Hoyo et al. 1992; Cramp and Simmons 1977
Little	<i>Tachybaptus ruficollis</i>	0.2	2 ^e	0.4	100	Obs.	Del Hoyo et al. 1992; Dewar 1924
Alcids	Family Alcidae						
Common murre	<i>Uria aalge</i>	0.9	180	3.4	12 000, 250	Net, RT	Burger 1991; Piatt and Nettleship 1985; Wanless et al. 1988
Thick-billed murre	<i>Uria lomvia</i>	0.9	210	3.7	1000	MDG, TDR	Burger 1991; Croll et al. 1992
Razorbill	<i>Alca torda</i>	0.7	140	0.9	1, 450	Sub., obs.	Burger 1991; Jury 1986; Dewar 1924
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	0.5	65	1.1	15, 3	MDG, exp.	Burger 1991; Burger 1991; Cody 1973
Atlantic puffin	<i>Fratercula arctica</i>	0.5	68	1.9	10, 450	MDG, RT	Burger 1991; Burger and Simpson 1986; Wanless et al. 1988
Pigeon guillemot	<i>Cephus columba</i>	0.5	30	1.1	2, 4	MDG, exp.	Burger 1991; Burger 1991; Cody 1973
Black guillemot	<i>Cephus grylle</i>	0.4	50	1.3	40, —	Net, obs.	Burger 1991; Piatt and Nettleship 1985; Dewar 1924
Cassin's auklet	<i>Ptychoramphus aleuticus</i>	0.2	43	2.0	20, 10	MDG, obs.	Johnsgard 1987; Burger and Powell 1990; Dewar 1924
Dovekie	<i>Alle alle</i>	0.2	35	1.1	—	—, obs.	Burger 1991; Prince and Harris 1988; Dewar 1924
Diving-petrels	Family Pelecanoididae						
South Georgia	<i>Pelecanoides georgicus</i>	0.1	49	6		MDG	Del Hoyo et al. 1992; Prince and Jones 1992

^aGender is indicated in parentheses where appropriate.

^bApproximate number of observations, usually dives (depth and duration, respectively). A dash indicates that the number of observations was not reported or was estimated from feeding. For maximum depth gauges, each observation represents many dives. A single value is listed if numbers were equal for both depth and duration, or if only one parameter was reported.

^cMethods for measuring depth and duration are listed, respectively. If the methods for measuring depth and duration are the same, only one method is listed. Exp., forced dives, usually restrained in various types of tank used for diving or simulating diving; feeding, estimated from known prey depths; line, estimated from the amount of rope let out, allowing for angle of descent; line-hp, line with hydrophone attached; MDG, maximum depth gauge (e.g., capillary tubes); net, caught or tangled in net or trap or on hook; obs., direct observations (e.g., timed with a watch); RT, radio tag; sonar, echo sounding; sonic trans., sonic transmitter; sub., observed from a submarine; TDR, time–depth recorder or satellite-linked time–depth recorder; trained, trained free-swimming dives; —, not reported.

^dSources for mass followed by diving capacity are listed. If sources for depth and duration differ, sources for mass, then depth, and then duration are listed.

^eWater depth where diving occurred; animal is assumed to have been diving to the bottom.

^fMass estimated from the length.

^gDepth limited by the depth range of the pressure sensor.

^hDepth limited by water depth.

ⁱIncorrectly identified and reported as a green turtle in Landis (1965) according to Eckert et al. (1986).

^jEstimated from mean $\pm 2 \times$ SD.

oxygen and to effectively utilize this limited oxygen supply (Scholander 1940; Butler and Jones 1982; Kooyman 1989; Schmidt-Nielsen 1990). The maximum duration for which an animal can stay submerged is directly related to its oxygen storage capacity, rate of oxygen utilization (i.e., metabolic rate and cost of transport), and anaerobic capacity. The maximum depth to which an animal can dive is only indirectly related to oxygen, because it takes time to dive and consequently the deeper an animal dives the longer it has to stay submerged. Speed of locomotion while diving will, of course, influence this relationship to some degree, although diving depth and duration have been shown to be strongly inter-correlated (e.g., Gentry et al. 1986a; Castellini et al. 1992a; Croll et al. 1992; Bengtson et al. 1993). Larger animals generally have more blood, since blood volume (V_b) increases

linearly with body mass (M_b), i.e., $V_b = M_b^{1.0}$ (Peters 1983; Schmidt-Nielsen 1984). Consequently, they will be able to store more oxygen, although many diving species have been shown to have elevated total oxygen stores (Butler and Jones 1982; Kooyman 1989). Also, larger animals have a metabolic advantage in that metabolic rate (MR) increases only 0.75 times as fast as body mass, i.e., $MR = M_b^{0.75}$ (Kleiber 1961), therefore larger animals have lower mass-specific metabolic rates than their smaller counterparts. A lower metabolic rate requires less energy expenditure and therefore a slower utilization of oxygen stores. Since diving capacity is related to the need for oxygen and larger animals need less oxygen per unit mass, it would be expected that larger animals should be able to dive longer and consequently deeper than smaller animals. This is substantiated in that

Table 2. Allometric relationships between \log_{10} diving capacity (maximum depth (m) and duration (min)) and \log_{10} body mass (M_b (kg)) for various groups of air-breathing vertebrates.

Group	n^a	Regression equation ^b	r^c	r^2	p
All	111	Max. depth = $36.31 M_b^{0.33}$	0.71	0.50	<0.001
	121	Max. duration = $1.62 M_b^{0.37}$	0.84	0.71	<0.001
All (TDR or MDG)	57	Max. depth = $68.23 M_b^{0.30}$	0.74	0.55	<0.001
	39	Max. duration = $2.34 M_b^{0.37}$	0.75	0.56	<0.001
Marine mammals	57	Max. depth = $131.83 M_b^{0.13}$	0.32	0.10	0.016
	64	Max. duration = $3.63 M_b^{0.24}$	0.56	0.31	<0.001
Marine mammals without mysticetes	51	Max. depth = $34.67 M_b^{0.39}$	0.65	0.42	<0.001
	55	Max. duration = $1.78 M_b^{0.39}$	0.61	0.37	<0.001
Birds	51	Max. depth = $28.84 M_b^{0.60}$	0.48	0.23	<0.001
	54	Max. duration = $1.35 M_b^{0.50}$	0.69	0.48	<0.001
Pinnipeds	29	Max. depth = $33.88 M_b^{0.43}$	0.60	0.36	0.001
	30	Max. duration = $1.70 M_b^{0.48}$	0.63	0.40	<0.001
Cetaceans	27	Max. depth = $120.23 M_b^{0.11}$	0.31	0.10	0.114
	31	Max. duration = $1.38 M_b^{0.32}$	0.78	0.61	<0.001
Odontocetes	21	Max. depth = $22.91 M_b^{0.42}$	0.75	0.56	<0.001
	22	Max. duration = $0.51 M_b^{0.51}$	0.84	0.71	<0.001
Mysticetes	6	Max. depth = $89.13 M_b^{0.07}$	0.07	0.01	0.895
	9	Max. duration = $0.04 M_b^{0.61}$	0.84	0.71	0.004
Phocids	15	Max. depth = $25.70 M_b^{0.52}$	0.70	0.49	0.004
	16	Max. duration = $3.39 M_b^{0.42}$	0.59	0.35	0.015
Otariids	13	Max. depth = $27.33 M_b^{0.46}$	0.51	0.26	0.073
	13	Max. duration = $6.22 M_b^{0.10}$	0.17	0.03	0.590
Penguins	11	Max. depth = $42.66 M_b^{0.71}$	0.81	0.66	0.003
	9	Max. duration = $0.98 M_b^{0.90}$	0.93	0.86	<0.001
Flying birds	40	Max. depth = $23.99 M_b^{0.21}$	0.14	0.02	0.394
	45	Max. duration = $1.26 M_b^{0.22}$	0.34	0.12	0.023

^aNumber of maximum depth or duration observations.

^bY intercepts for diving capacity were calculated for a mass of 1, since \log_{10} of 1 = 0.

^cPearson's correlation coefficient.

ADL increases with mass (Hochachka and Somero 1984; Gentry et al. 1986a; Kooyman 1989; Costa 1993; Fig. 3 in this study).

Another factor that influences an animal's diving performance is its ability to function beyond its ADL (i.e., anaerobically). The difficulty here is to deal with the end-products of anaerobic metabolism (e.g., lactic acid). Some animals have a high tolerance for these end-products, while others are able to recycle or clear the waste products (Hochachka and Somero 1984). It has been shown that an increase in size also increases an animal's ability to function anaerobically and, hence, increases potential maximum diving time (Hochachka and Somero 1984; Hudson and Jones 1986). Anaerobic metabolism may be fairly unimportant when "normal" or mean diving behavior is considered, since it is considerably less efficient than aerobic metabolism (Kooyman et al. 1983b; Kooyman 1989). The lactic acid produced as a result of anaerobic metabolism is cleared very slowly, therefore anaerobic dives require longer surface time than completely aerobic dives. However, this less efficient metabolism becomes quite important when potential or maximum capacity is considered.

Finally, a direct limitation to the depth to which an animal can dive is hydrostatic pressure. Complications due to pres-

sure include decompression sickness (the bends), high-pressure nervous syndrome (HPNS), mechanical effects of pressure on gas-filled spaces, and problems associated with gases at high pressure (e.g., nitrogen narcosis and oxygen toxicity). Several reviews on this subject have been presented, so it will only be mentioned briefly here (e.g., Ridgway 1986; Kooyman 1988a, 1989; Castellini 1991). Some animals have an unlimited capacity to tolerate the mechanical distortions caused by compression (Kooyman 1988a). In seals, lung and chest compliance are unlimited (Kooyman 1988a). This eliminates the need for intrathoracic pooling of blood to compensate for changes in volume, as would be the case for humans. Problems with gases (e.g., the bends and nitrogen narcosis) are avoided by means of a great reduction in gas exchange between the lungs and blood (Kooyman 1988a, 1989). How other problems, such as HPNS, are dealt with remains a mystery (Kooyman 1989; Castellini 1991). Research has revealed that pressure limitations are not a major factor controlling the diving depths attained by some deep-diving seals (Castellini 1991), which is indicated by the incredible depths attained by many of these animals. Much of this work has been performed on marine mammals and considerably less is known for birds and reptiles.

Fig. 1. Relationships between \log_{10} diving capacity (maximum depth and duration) and \log_{10} body mass for mysticete cetaceans, odontocete cetaceans, flying birds, penguins, otariid seals, and phocid seals (solid lines denote significant results and broken lines nonsignificant results). The thickest lines represent the relationships for the entire data set. These lines include values for sea otters, walruses, sirenians, and marine turtles in addition to the taxonomic groups listed above. e, otariid; f, flying bird; m, mysticete; mu, sea otter; o, odontocete; p, penguin; s, phocid; si, sirenian; t, turtle; w, walrus.

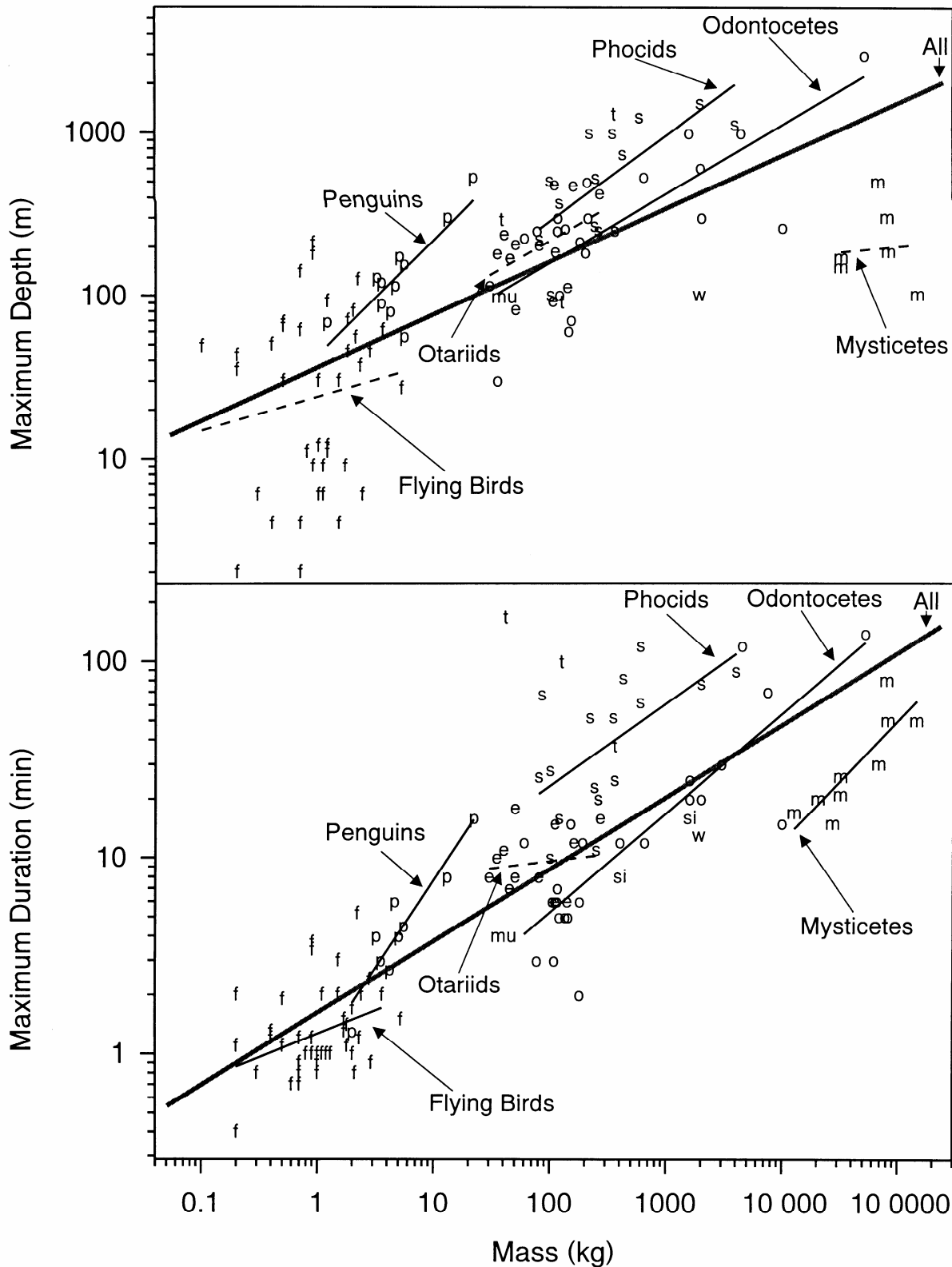


Fig. 2. Relationships between \log_{10} diving capacity (maximum depth and duration) and \log_{10} body mass for alcids, cormorants, ducks, and penguins (solid lines denote significant results and broken lines nonsignificant results). The thickest lines represent the relationships for the entire bird data set. These lines include values for grebes, loons, and petrels in addition to the taxonomic groups listed above. a, alcid; c, cormorant; d, duck; g, grebe; L, loon; p, penguin; pet, petrel.

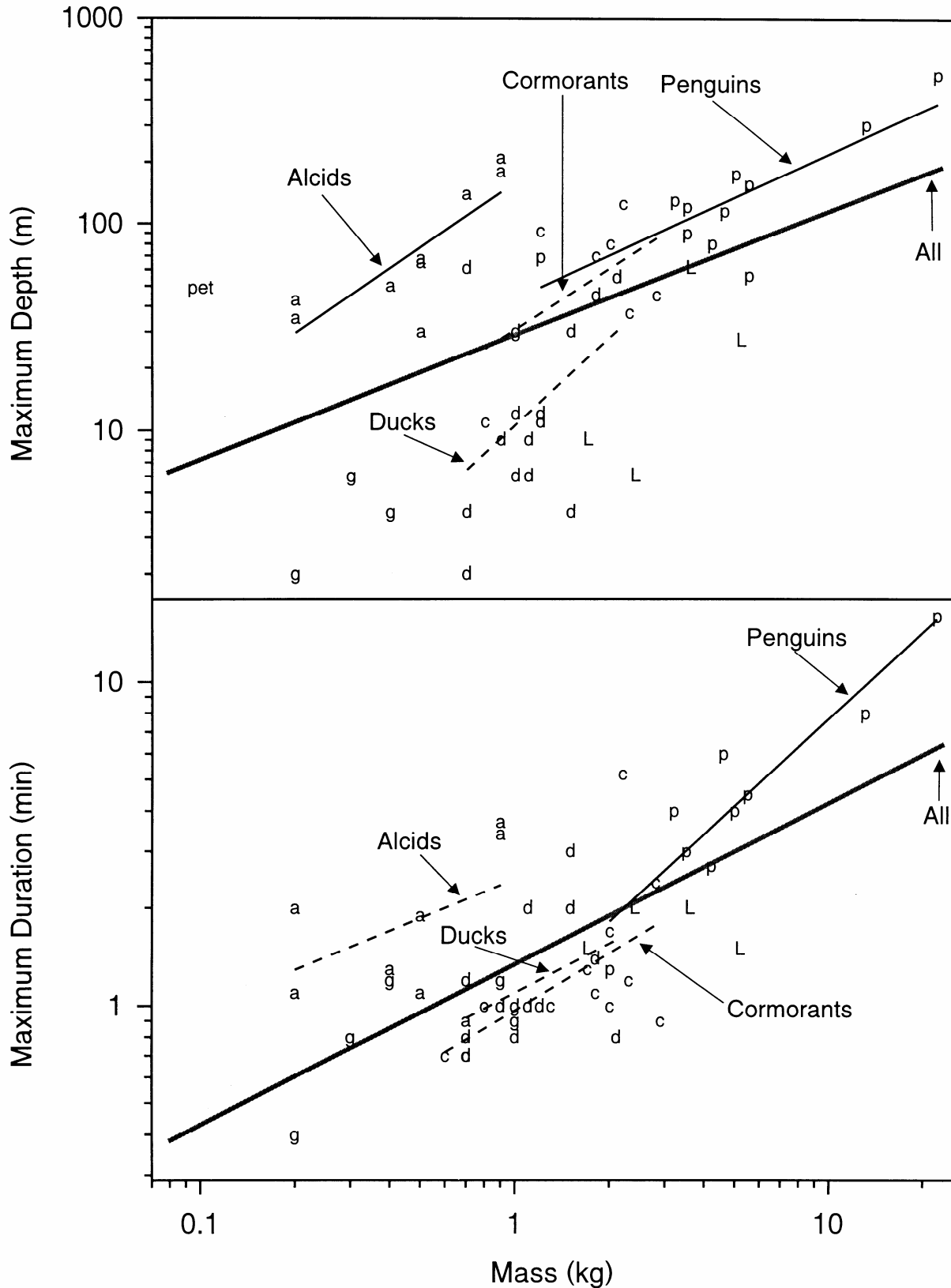


Table 3. Allometric relationships between \log_{10} diving capacity (maximum depth (m) and duration (min)) and \log_{10} body mass (M_b (kg)) for various families of diving birds.

Group	n^a	Regression equation ^b	r^c	r^2	p
All	51	Max. depth = $28.84 M_b^{0.60}$	0.48	0.23	<0.001
	54	Max. duration = $1.35 M_b^{0.50}$	0.69	0.48	<0.001
Penguins	11	Max. depth = $42.66 M_b^{0.71}$	0.81	0.66	0.003
	9	Max. duration = $0.98 M_b^{0.90}$	0.93	0.86	<0.001
Alcids	9	Max. depth = $158.49 M_b^{1.04}$	0.81	0.66	0.008
	9	Max. duration = $2.14 M_b^{0.37}$	0.40	0.16	0.283
Cormorants	7	Max. depth = $30.90 M_b^{0.99}$	0.53	0.28	0.223
	12	Max. duration = $0.98 M_b^{0.59}$	0.56	0.31	0.059
Ducks	15	Max. depth = $10.72 M_b^{1.41}$	0.45	0.20	0.093
	14	Max. duration = $1.10 M_b^{0.51}$	0.41	0.17	0.143

^aNumber of maximum depth or duration observations.

^bY intercepts for diving capacity were calculated for a mass of 1, since \log_{10} of 1 = 0.

^cPearson's correlation coefficient.

Overall

The diving depths and durations attained by diving vertebrates are related to body mass. Fifty and 71% percent of the variability (r^2) observed in depth and duration, respectively, was attributed to mass. However, there was considerable scatter of depth and duration values around the regression lines (Fig. 1), indicating that factors other than mass also affect the diving capacities of these animals. Diving capacities recorded for cetaceans and flying birds were highly variable. For both cetacean suborders, this may reflect the range of methods used for data collection. Variability among flying birds may represent the inappropriateness of lumping several different bird families into one group, as well as differences in feeding ecology, methods of data collection, and locations of study sites.

Comparisons of diving capacity with mass for marine mammals and birds indicated that maximum diving depth and duration increased faster with increasing mass for birds than for marine mammals. However, when the shallow- and short-diving mysticete cetaceans were excluded from the comparisons, there were no discernible differences in the diving capacities of these two groups relative to mass. This suggests that similar physiological and ecological factors affect the diving behavior of these two groups.

The relationships between diving capacity and mass found here were generally in agreement with interspecific comparisons previously made. Burger (1991) found a similar relationship in that larger alcids and penguins had greater maximum diving depths than smaller species. This was not surprising, as that study and this work used much of the same data. The relationship between diving duration and mass for cormorants in Cooper's (1986) study was stronger than that found here (for birds diving in water more than 2 m deep). However, Cooper had much larger sample sizes, using values recorded for the same species at different locations as separate observations. Irving (1939) suggested that the exceptional diving capacities of large whales may be due to their large size, but his comparative analysis showed a different result. In contrast to the results here, Irving found that breath-hold endurance data acquired experimentally from diving animals ranging in size from 0.6 kg (muskrats (*Ondatra zibethicus*)) to 100 kg (seals) demonstrated no rela-

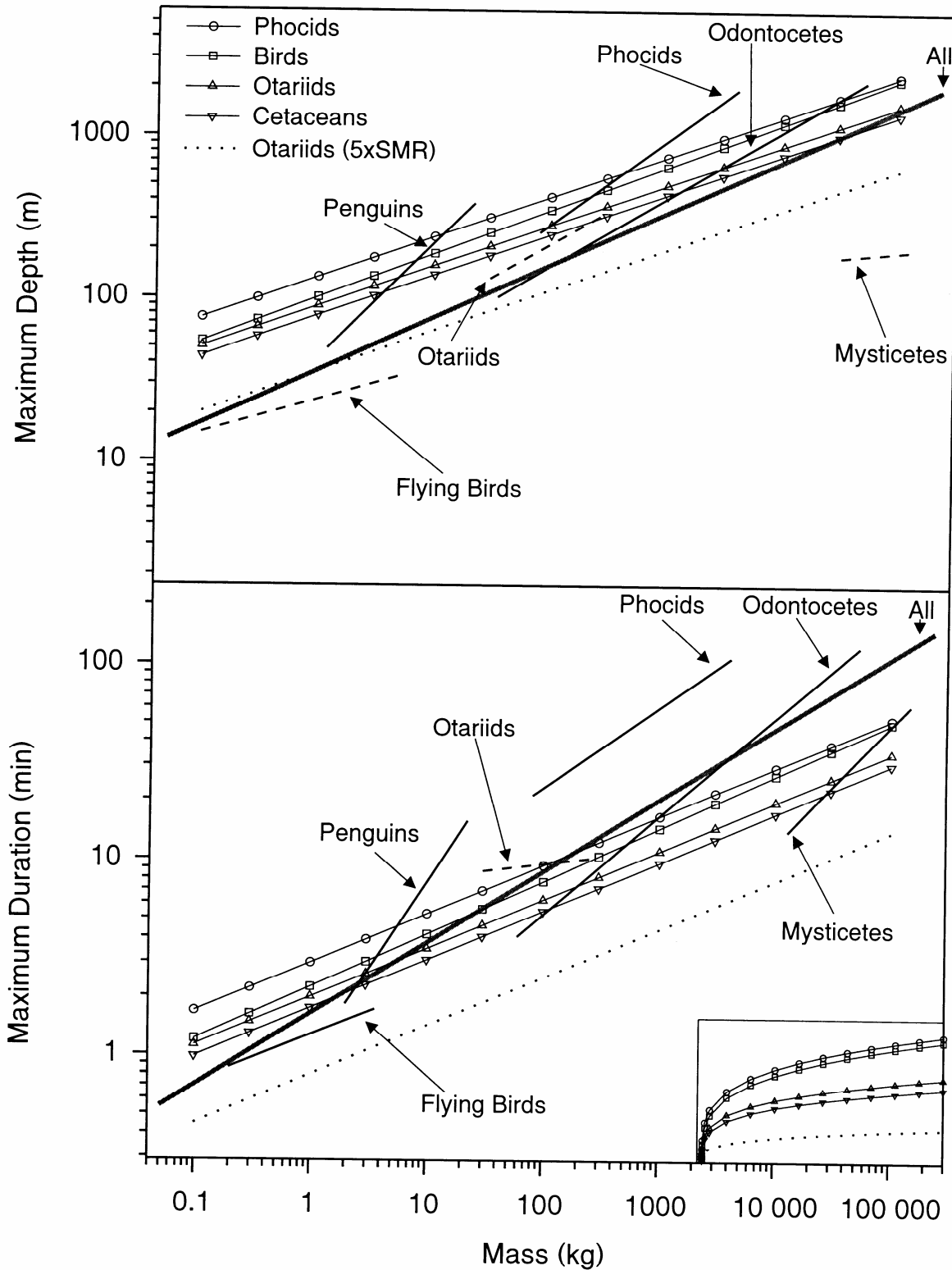
tionship between endurance and size. However, Irving usually recorded dive duration during forced submersion, which can often give considerably different results from those obtained under natural conditions.

Predicted versus observed

The various predicted relationships generally overlapped the overall observed lines for vertebrates (Fig. 3); however, the rates at which predicted diving capacity increased with mass were generally lower than for those calculated from the observed data. This may be due to underestimation of many of the flying birds' observed diving capacities, causing the slopes of the overall lines to be steeper. It may also be due to an overestimation of the swimming speeds of smaller divers. Smaller divers would not be expected to swim as fast as larger ones because drag increases with surface area (L^2), while power increases with muscle volume (L^3). This can be seen in little penguins (*Eudyptula minor*) (Baudinette and Gill 1985) and pochard (*Aythya ferina*) and tufted ducks (*Aythya fuligula*) (Carbone 1995; C. Carbone, personal communication), which have estimated cruising-swim speeds of $0.7-0.8 \text{ m} \cdot \text{s}^{-1}$. If the smaller divers swim more slowly, their predicted maximum depths would be less, and consequently the slope of the predicted relationship would be greater (i.e., more similar to the observed relationship). Lastly, since the predictive models developed here incorporated only aerobic metabolism and not anaerobic metabolism (which is important when maximum capacities are considered), the rates of increase may have been underestimated. This is substantiated by the results of Hudson and Jones (1986) and the calculations of Hochachka and Somero (1984), who found that in ducks, the rate of increase in maximum diving time relative to mass during forced submersion is higher when anaerobic + aerobic metabolism is considered compared with just aerobic modes.

The fact that anaerobic metabolism was not incorporated into the predictive models may also explain why many of the observed capacities (at least in terms of duration) were above predicted levels for the corresponding groups. Mysticete cetaceans and flying birds were exceptions, probably as a result of the methods used to record their behavior, the locations of the studies, or the ecological niches occupied by

Fig. 3. Relationships between \log_{10} predicted diving capacity (maximum depth and duration) and \log_{10} body mass for birds, phocids, otariids, and cetaceans overlaid on the regression lines calculated for observed data from Fig. 1 (solid lines denote significant results and broken lines nonsignificant results). Predicted maximum diving duration was approximated by the calculated ADL. The lines with symbols represent predicted diving capacities. Diving metabolic rates were assumed to be $2 \times \text{SMR}$ for all groups. The dotted lines represent a second set of predicted diving capacities for otariids, using diving metabolic rates equal to $5 \times \text{SMR}$. The small graph at the bottom right shows the various predicted lines on a linear scale.



these animals. For depth, observed relationships generally fell close to predicted values; however, had anaerobic metabolism been included in the models, most of the observed values would have fallen below predicted relationships. This would be expected, since the observed relationships only represent minimum diving capacities.

Finally, it must be noted that these predictive models are quite crude and rely on many assumptions. If any of the parameters (diving metabolic rate, oxygen stores, or cruising speed) were changed, the relationships would change markedly (e.g., the difference between otariid diving capacity calculated with diving MR equal to 2 or $5 \times$ SMR). Many studies have found considerably higher estimates for swimming MRs, ranging from 4 to $10 \times$ SMR (e.g., Nagy et al. 1984; Chappell et al. 1993; Costa 1993), and others have estimated much slower cruising-swim speeds, $0.7-0.8 \text{ m} \cdot \text{s}^{-1}$ (e.g., Baudinette and Gill 1985; Carbone 1995).

Cetaceans

Cetaceans range dramatically in size, from small river dolphins (e.g., franciscana (*Pontoporia blainvillei*) weighing 34 kg) to the largest animals to have ever lived (i.e., blue whales weighing 145 000 kg and up to 33 m in length) (Jefferson et al. 1993). Mysticetes had the largest mean body mass in this study (55 000 kg), followed by odontocetes (3200 kg), phocids (610 kg), marine turtles (140 kg), otariids (94 kg), penguins (6.1 kg), and flying birds (1.3 kg). On the basis of body size it would be expected that mysticete and odontocete cetaceans should be able to dive longer and deeper than all other groups because they can store more oxygen and have lower mass-specific metabolic rates. Even though the sperm whale (*Physeter catodon*) is one of the longest and deepest divers in this study (138 min and 3000 m; Clarke 1976; Watkins et al. 1985), as well as being one of the largest animals (51 700 kg; Jefferson et al. 1993), both odontocete and mysticete cetaceans were surpassed by the considerably smaller phocids in average diving capacity. Further, the plots of duration and depth versus mass (Fig. 1) showed that mysticetes always fell below the overall regression lines for both maximum duration and depth. These plots and the regression comparisons also suggest that if penguins were as large as mysticetes or even odontocetes, they would dive much longer and deeper. The plots for predicted diving capacity (Fig. 3) also support this suggestion. It is interesting to note that a 80-kg human (holding their breath) fits well within the overall regression lines, with a maximum depth of 125 m using a weighted sled (Matthews 1996) and a duration of 13.5 min anchored in a pool after hyperventilating with oxygen (McFarlan and McWhirter 1990). The duration record without supplementary oxygen was 5.5 min (Lavigne and Kovacs 1988). However, these amazing feats were accomplished under highly artificial conditions.

There are three possible reasons why cetaceans do not dive as long and as deep as would be expected: (1) this order may have physiological and morphological limitations relative to some of the other groups, (2) the methods used to measure their diving behavior may underestimate their capacity, or (3) cetaceans may exploit resources that are located at lesser depths than some of the other groups and therefore may not need to dive as deep or for as long. The first explanation seems unlikely, since several cetaceans have

exceptional diving capacities (e.g., sperm whales and bottle-nose whales (*Hyperoodon* sp.)). However, considering total body oxygen stores, cetaceans have available considerably less oxygen per unit mass than either penguins or phocids (Kooyman 1989), which would limit their potential diving capacity (see Fig. 3 for a schematic representation of this concept).

Some of the cetaceans, specifically the mysticetes, seem to have even more limited diving capacities than would be predicted from oxygen stores. This is perhaps where data-collection methods and feeding ecology greatly affect observed diving capacity. Unlike most of the pinniped and penguin diving data, which have been collected using modern depth and duration recorders, much of the cetacean data were inferred from feeding ecology or simply observed directly. Although these methods have provided considerable insight into the behavior of cetaceans and other groups, they are far less accurate. Depth and duration recorders allow thousands of dives ($>50\,000$; Hindell et al. 1991; Schreer and Testa 1995, 1996) for individual species to be recorded over extended periods of time (>8 months; Testa 1994; Schreer and Testa 1996), while much of the cetacean data were single records or just a few observations collected on one or a few occasions. Also, although probable feeding depths give a potential maximum depth for an animal, these values are probably better estimates of mean diving depth. In many studies using depth recorders, it has been found that a species has preferred depths that are associated with preferred prey, but that the maximum depths reached by the species far exceed these depths (e.g., Hindell et al. 1991; Prince and Jones 1992; Schreer and Testa 1996). Therefore, many of the values representing cetacean diving capacity are probably underestimates.

The shallow maximum depths and short maximum durations observed among the mysticetes may also be an accurate reflection of their feeding ecology. Many of the largest animals in this study (e.g., blue whales, bowhead whales (*Balaena mysticetus*), fin whales (*Balaenoptera physalus*), and right whales (*Eubalaena* sp.)) feed primarily on planktonic or micronektonic crustaceans or small pelagic fish (Gaskin 1982) usually found between 100 and 500 m (Parsons et al. 1984). The relatively shallow depths of the mysticetes' prey eliminates their need to dive to great depths. Also, since it takes less time to reach these depths, dive durations do not need to be as great for the animals to forage efficiently (i.e., net energy gain). However, since surfacing takes away from foraging time, dive duration should be maximized for increased efficiency. This may explain why maximum duration is more closely correlated with mass than maximum depth in mysticetes ($r = 0.84$ vs. 0.07). It must be noted that this argument is only valid when dives are shorter than the ADL so as not to cause an increase in plasma lactate concentration and a consequent increase in surface clearance time. To complicate this issue even further, Kramer (1988) and Houston and Carbone (1992) argue that surface time increases with diving time even before the ADL, because of diminishing returns in oxygen loading (i.e., it takes longer to load the last few millilitres of oxygen prior to achieving maximum loading), and that this also influences the duration of dives.

Marked differences in feeding ecology may also explain

the differences in observed diving capacity for the two cetacean groups. That is, mysticetes feed on prey at relatively shallow depths, while odontocetes feed on prey such as fish and squid, which live at greater depths (Gaskin 1982).

Pinnipeds

Diving behavior of pinnipeds as a group could be predicted with reasonable accuracy on the basis of body mass, although some differences were displayed between families. Phocid diving capacity was significantly correlated with mass, while that of otariids was not. Additionally, observations of phocids generally fell above the overall vertebrate line, while otariids generally fell nearer to this line, indicating that phocids dive deeper and longer relative to body mass than otariids do. The mass-adjusted mean durations for these two groups also support this conclusion, with phocids diving for significantly longer. Phocids are generally larger than otariids, so it would be expected that they would dive deeper and longer. However, they seem to excel in diving capacity more than expected, based solely on this criterion. Phocids have higher concentrations of hemoglobin for a given blood volume and more myoglobin per unit of muscle than otariids, which allows them to store more oxygen and hence dive deeper and longer (Snyder 1983; Kooyman 1989; Reed et al. 1994). Phocids also have lower metabolic rates while diving, in part because of slower swim speeds (Kooyman 1988b; Costa 1993), which decreases their rate of oxygen consumption. This can be seen in Fig. 3, with phocids ($2 \times$ SMR) having considerably higher predicted diving capacities relative to mass than otariids ($5 \times$ SMR).

The comparisons of observed data are preliminary in that the available data do not include large otariids. Most studies of otariid diving behavior have focused on females (e.g., Gentry and Kooyman 1986), which are considerably smaller than males. The inclusion of males may increase the observed similarity between otariids and phocids. This suggestion is substantiated by the depth values from the larger species (e.g., California (*Zalophus californianus californianus*), Hooker's (*Phocarctos hookeri*), and Steller sea lions (*Eumetopias jubatus*)), all of which fit well with the lower end of the phocid line.

The otariid duration data are a bit more difficult to interpret. Perhaps their higher swim speeds allow them to reach depths comparable to those of the smaller phocids, but their physiological limitations (less stored oxygen and higher metabolic rates) prevent them from staying submerged as long. It has also been suggested that the distribution of prey (Feldkamp et al. 1989) and foraging economics (Gentry et al. 1986a) may be primary factors determining observed diving capacity in otariids. That is, the observed maximums do not reflect true capacity. Their smaller size and physiological limitations relative to phocids may make it more economical for them to forage on prey that are smaller, live at shallower depths, and are perhaps easier to catch, while phocids can exploit larger, more energy-rich prey at greater depths. This would explain their more limited observed diving capacity relative to phocids, as well as the lack of any relationship between diving capacity and mass.

The walrus (*Odobenus rosmarus*) is a good example of how ecology can strongly affect diving behavior. It is the third largest pinniped in this study, but one of the shallowest

and shortest divers. It is thought that walrus may be able to dive to greater depths than the maximums recorded, but have little reason to do so because of the abundance of their benthic prey in shallow waters (Fay and Burns 1988).

Birds

Penguins dive deeper than flying birds (when all flying birds are pooled into one group), and their diving duration increases more rapidly with increasing mass than that of flying birds (i.e., greater mass-adjusted depth and steeper slope for duration versus mass). However, the equations for penguins were strongly affected by the exceptional depths and durations recorded for emperor (*Aptenodytes forsteri*) and king penguins. Penguin diving capacities had the highest correlations with mass of all the groups examined, indicating that mass is an excellent predictive tool for penguin diving behavior. Some of the differences in diving capacity between penguins and flying birds are likely due to differences in data-collection methods. Like the cetacean data, much of the flying bird data were manually observed over short periods of time, while most of the penguin data were collected by depth or duration recorders, providing more accurate estimates. Also, lumping all flying birds into one group is perhaps inappropriate and may be a primary reason for the weak and nonsignificant relationships.

The separate analysis of just the bird data provided more insight into avian diving capacities. Ducks appear to be relatively poor divers, but this may simply be due to the methods of data collection or the shallow inshore water of many of the study sites, resulting in shorter, shallower dives (e.g., Dewar 1924). Alcids, unlike the other flying bird families, showed a strong correlation between maximum dive depth and mass. The results also indicated that not only do alcids dive deeper and longer than cormorants and ducks, but in agreement with Burger (1991), if they were as big as penguins, they would be able to dive deeper. This is surprising, as it would be expected that penguins would be more capable divers than flying birds because of their more highly evolved "aquatic" body morphology and concomitant loss of flight. If the exceptional depths of common and thick-billed murres are excluded, most of the alcid depths fit well with the extension of the penguin depth line. It has been suggested that large, wing-propelled diving/flying birds (i.e., larger alcids) may be approaching the threshold at which a further increase in size would result in a flightless condition (Stonehouse 1975; Piatt and Nettleship 1985). Stonehouse (1975) estimated that wing-propelled diving birds can retain the ability to fly only if they weigh less than 1 kg. Since some alcids may be nearing this condition, it would be expected that their diving capacities would be similar to those of smaller penguins. This can be seen by splitting the birds into predominantly wing-propelled (alcids, penguins, and petrels) and predominantly foot-propelled (ducks, cormorants, grebes, and loons) categories. The values for wing-propelled diving birds are located almost entirely above the overall bird lines for depth and duration versus mass, while almost all of the values for foot-propelled birds lie below these lines. This could indicate that wing propulsion is a more highly evolved or adaptive characteristic of an aquatic life-style, although the great depths achieved by several of the foot-propelled cormorants challenge this conclusion.

Marine turtles

Although there were too few turtle observations to allow allometric equations to be calculated, it is obvious that these animals are exceptional divers. Other reptiles and amphibians were not included in this study because many of these animals can reduce their metabolic rates to such low levels that they can stay submerged for days, weeks, and even longer (Butler and Jones 1982). The temperature and oxygen tension of the water also affect the ability of these animals to stay submerged (Butler and Jones 1982). Therefore mass-specific relationships comparable to those of mammals and birds, which have much higher metabolic rates even when at rest, would not be expected. Marine turtles were included in this study for the sake of interest and because they have maximum depth and duration values within the ranges of those found for mammals and birds. However, since these animals also have the ability to undergo extended submergences at low temperature (e.g., many weeks for green turtles (*Chelonia mydas*), and loggerhead turtles (*Caretta caretta*), during winter; Butler and Jones 1982), comparisons are very tentative. Like most marine mammals, marine turtles are able to lower their metabolic rate (within certain organs) when diving (Hochachka and Somero 1984), decreasing oxygen utilization and increasing potential diving duration. In marine mammals this results in hypometabolism in comparison with exercising levels, but still above those for resting. However, turtles can lower their overall metabolism below resting levels, in part because of lower body temperatures (Hochachka and Somero 1984; Kooyman 1989). Additionally, marine turtles excel in their ability to metabolize anaerobically (Hochachka and Somero 1984; Kooyman 1989). Marine turtles have large glycogen stores in their tissues as well as having efficient fermentation pathways (Hochachka and Somero 1984), which increases their potential for long-duration, and therefore deep, dives. Along with these adaptations, marine turtles may have an evolutionary advantage for diving in that they have relatively smaller and less complex brains than mammals (Robin 1973). The smaller brain size decreases oxygen utilization, and the lack of complexity may allow marine turtles to tolerate longer periods of anoxia (Robin 1973; Hochachka and Somero 1984). Both of these characteristics would increase potential diving capacity.

Interspecifically, the diving capacities of air-breathing vertebrates are strongly influenced by body mass, although this relationship was not always present when smaller taxonomic groups were analyzed. Differences among groups, as well as the lack of relationships in some groups, could often be explained by such factors as the various ecological niches these groups exploit or the methods used to record their behavior. The addition of data from work currently being conducted and future work on diving behavior of air-breathing vertebrates will undoubtedly improve our understanding of the relationships explored in a preliminary fashion in this paper. Better comparative data bases are likely to provide stronger relationships among some groups of diving vertebrates and provide clearer explanations of observed variance in others. Also, additional data may allow interspecific allometric analyses to be conducted using mean dive values or perhaps dive shapes (e.g., Hindell et al. 1991; Schreer and Testa 1995, 1996), which may better represent the natural diving behavior of air-breathing vertebrates.

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References

- Aschoff, S., and Pohl, H. 1970. Rhythmic variation in energy metabolism. *Fed. Proc.* **29**: 1541–1552.
- Baker, A.N. 1981. The southern right whale dolphin, *Lissodelphis peronii* (Lacépède) in Australian waters. *Natl. Mus. N.Z. Rec.* **2**: 17–34.
- Baudinette, R.V., and Gill, P. 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *J. Comp. Physiol. B*, **155**: 373–380.
- Bengtson, J.L., and Stewart, B.S. 1992. Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biol.* **12**: 635–644.
- Bengtson, J.L., Croll, D.A., and Goebel, M.E. 1993. Diving behaviour of chinstrap penguins at Seal Island. *Antarct. Sci.* **5**: 9–15.
- Benjaminsen, T., and Christensen, I. 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Forster). In *Behavior of marine mammals*. Vol. 3. Cetaceans. Edited by H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 143–164.
- Boersma, P.D. 1976. An ecological and behavioral study of the Galapagos penguin. *Living Bird*, **15**: 43–93.
- Bower, C.A., and Henderson, R.S. 1972. Project deep ops: deep object recovery with pilot and killer whales. Tech. Pap. No. 306, Naval Undersea Center, San Diego.
- Boyd, I.L., and Croxall, J.P. 1992. Diving behaviour of lactating Antarctic fur seals. *Can. J. Zool.* **70**: 919–928.
- Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Board Can.* **22**: 1491–1497.
- Burger, A.E. 1991. Maximum diving depth and underwater foraging in alcids and penguins. *Can. Wildl. Serv. Occas. Pap.* No. 68. pp. 9–15.
- Burger, A.E., and Powell, D.W. 1990. Diving depths and diet of Cassin's Auklet at Reef Island, British Columbia. *Can. J. Zool.* **68**: 1572–1577.
- Burger, A.E., and Simpson, M. 1986. Diving depths of Atlantic puffins and common murre. *Auk*, **103**: 828–830.
- Burger, A.E., and Wilson, R.P. 1988. Capillary-tube depth gauges for diving animals: an assessment of their accuracy and applicability. *J. Field Ornithol.* **59**: 345–354.
- Butler, P.J., and Jones, D.R. 1982. The comparative physiology of diving in vertebrates. In *Advances in comparative physiology and biochemistry*. Edited by O. Lowenstein. Academic Press, New York. pp. 179–364.
- Carbone, C. 1995. Guidelines for estimating the feeding performance of diving birds. *Wildfowl*, **46**: 119–128.
- Carbone, C., de Leeuw, J.J., and Houston, A.I. 1996. Adjustments in the diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways? *Anim. Behav.* **51**: 1257–1268.
- Castellini, M.A. 1991. The biology of diving mammals: behavioral, physiological, and biochemical limits. In *Advances in comparative and environmental physiology*. Vol. 8. Edited by R. Gilles. Springer-Verlag, Berlin. pp. 105–134.

- Castellini, M.A., Davis, R.W., and Kooyman, G.L. 1992a. Annual cycles of diving behavior and ecology of the Weddell seal. *Bull. Scripps Inst. Oceanogr. Univ. Calif.* **28**.
- Castellini, M.A., Kooyman, G.L., and Ponganis, P.J. 1992b. Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* **165**: 181–194.
- Chappell, M.A., Shoemaker, V.H., Janes, D.N., Maloney, S.K., and Bucher, T.L. 1993. Energetics of foraging in breeding Adélie penguins. *Ecology*, **74**: 2450–2461.
- Clarke, M.R. 1976. Observations on sperm whale diving. *J. Mar. Biol. Assoc. U.K.* **56**: 809–810.
- Cody, M.L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. *Ecology*, **54**: 31–44.
- Cooper, J. 1985. Biology of the bank cormorant, Part 3. Foraging behaviour. *Ostrich*, **56**: 86–95.
- Cooper, J. 1986. Diving patterns of cormorants Phalacrocoracidae. *Ibis*, **128**: 562–570.
- Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symp. Zool. Soc. Lond. No. 66*. pp. 293–314.
- Costa, D.P., Thorson, P.H., and Kretzman, M. 1989. Diving and foraging energetics of the Australian sea lion, *Neophoca cinerea*. *Am. Zool.* **29**: 71A. [Abstr.]
- Cramp, S., and Simmons, K.E.L. 1977. Handbook of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Vol. 1. Oxford University Press, Oxford.
- Croll, D.A., Gaston, A.J., Burger, A.E., and Konnoff, D. 1992. Foraging behavior and physiological adaptation for diving in thick-billed murre. *Ecology*, **73**: 344–356.
- Croxall, J.P., Naito, Y., Kato, A., Rothery, P., and Briggs, D.R. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *J. Zool. (Lond.)*, **225**: 171–199.
- Croxall, J.P., Briggs, D.R., Kato, A., Naito, Y., Watanuki, Y., and Williams, T.D. 1993. Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J. Zool. (Lond.)*, **230**: 31–47.
- Cruikshank, R.A., and Brown, S.G. 1981. Recent observations and some historical records of southern right-whale dolphins *Lissodelphis peronii*. *Fish. Bull. S. Afr.* **15**: 109–121.
- Cummings, W.C. 1985. Bryde's whale—*Balaenoptera edeni* Anderson, 1878. In *Handbook of marine mammals*. Vol. 3. The Sireniacs and baleen whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 137–154.
- del Hoyo, J., Elliot, A., and Sargatal, J. 1992. Handbook of the birds of the world. Vol. 1. Lynx Edicions, Barcelona.
- DeLong, R.L., and Stewart, B.S. 1991. Diving patterns of northern elephant seal bulls. *Mar. Mammal Sci.* **7**: 369–384.
- Dewar, J.M. 1924. The bird as a diver. Witherby and Co., London.
- Dolphin, W.F. 1988. Foraging dive patterns of humpback whales, *Megaptera novaeangliae*, in southeast Alaska: a cost-benefit analysis. *Can. J. Zool.* **66**: 2432–2441.
- Dow, D.D. 1964. Diving times of wintering water birds. *Auk*, **81**: 556–558.
- Duffy, D.C. 1983. The foraging ecology of Peruvian seabirds. *Auk*, **100**: 800–810.
- Eckert, S.A., Nellis, D.W., Eckert, K.L., and Kooyman, G.L. 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during interesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. *Herpetologica*, **42**: 381–388.
- Eckert, S.A., Eckert, K.L., Ponganis, P., and Kooyman, G.L. 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* **67**: 2834–2840.
- Eliassen, E. 1960. Cardiovascular responses to submersion asphyxia in avian divers. *Univ. Bergen Mat. Naturvitensk. Ser. 2*: 1–100.
- Evans, W.E. 1971. Orientation behavior of delphinids: radio telemetric studies. *Ann. N.Y. Acad. Sci.* **188**: 142–160.
- Evans, W.E. 1974. Telemetry of temperature and depth data from a free ranging yearling California gray whale, *Eschrichtius robustus*. *Mar. Fish. Rev.* **36**: 52–58.
- Fay, F.H., and Burns, J.J. 1988. Maximum feeding depth of walrus. *Arctic*, **41**: 239–240.
- Feldkamp, S.D., DeLong, R.L., and Antonelis, G.A. 1989. Diving patterns of California sea lions, *Zalophus californianus*. *Can. J. Zool.* **67**: 872–883.
- Fitch, J.E., and Brownell, R.L., Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Board. Can.* **25**: 2561–2574.
- Folkow, L.P., and Blix, A.S. 1995. Distribution and diving behaviour of hooded seals. In *Whales, Seals, Fish, and Man: Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, November 29 – December 1, 1994*. Edited by A.S. Blix, L. Walløe, and Ø. Ulltang. Elsevier, Amsterdam. pp. 193–202.
- Forbes, L.S., and Sealy, S.G. 1988. Diving behaviour of male and female western grebes. *Can. J. Zool.* **66**: 2695–2698.
- Frost, K.J., Lowry, L.F., Davis, R., and Suydam, R.S. 1993. Movements and behavior of satellite tagged spotted seals in the Bering and Chukchi Seas. In *Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, Tex., November 11–15, 1993*. p. 50. [Abstr.]
- Gales, N.J. and Mattlin, R.H. 1995. Summer diving behaviour of female New Zealand seal lions: the deepest diving otariid. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Fla., December 14–18, 1995*. p. 41. [Abstr.]
- Gallo-Reynoso, J.P., Le Boeuf, B.J., and Figueroa, A.L. 1995. Track, location, duration and diving behavior during foraging trips of Guadalupe fur seal females. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Fla., December 14–18, 1995*. p. 41. [Abstr.]
- Gambell, R. 1985. Sei whale—*Balaenoptera borealis* Lesson, 1828. In *Handbook of marine mammals*. Vol. 3. The sireniacs and baleen whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 155–170.
- Gaskin, D.E. 1982. The ecology of whales and dolphins. Heinemann, London.
- Gentry, R.L., and Kooyman, G.L. 1986. Fur seals. Maternal strategies on land and at sea. Princeton University Press, Princeton, N.J.
- Gentry, R.L., Costa, D.P., Croxall, J.P., David, J.H.M., Davis, R.W., Kooyman, G.L., Majluf, P., McCann, T.S., and Trillmich, F. 1986a. Synthesis and conclusions. In *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 220–264.
- Gentry, R.L., Kooyman, G.L., and Goebel, M.E. 1986b. Feeding and diving behavior of northern fur seals. In *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 61–78.
- Gentry, R.L., Roberts, W.E., and Cawthorn, M.W. 1987. Diving behavior of the Hooker's sea lion. In *Abstracts from the Seventh Biennial Conference on the Biology of Marine Mammals, Miami, Fla., December 5–9, 1987*. p. 10. [Abstr.]
- Goodyear, J.D. 1995. Dive behavior, and the question of food limitation in right whales. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Fla., December 14–18, 1995*. p. 46. [Abstr.]
- Greenewalt, C.H. 1975. The flight of birds. The significant dimensions, their departure from the requirements of dimensional similarity, and the effect on flight aerodynamics of that departure. *Trans. Am. Philos. Soc.* **65**: 1–67.

- Guyot, I. 1988. Relationships between the shag feeding areas and human fishing activities in Corsica (Mediterranean Sea). In *Seabird Food and Feeding Ecology: Proceedings of the 3rd International Conference of the Seabird Group*, Cambridge, England, February 1988. Edited by M.L. Tasker. Royal Society for the Protection of Birds, Sandy, Bedfordshire, England. pp. 22–23.
- Hall, J.D. 1970. Conditioning Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, for open ocean release. Tech. Publ. No. 200, Naval Undersea Center, San Diego.
- Hammill, M.O., Kovacs, K., and Lydersen, C. 1993. Postbreeding movements of western Atlantic grey seals as revealed by satellite telemetry. In *Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals*, Galveston, Tex., November 11–15, 1993. p. 57. [Abstr.]
- Harrison, R.J., and Kooyman, G.L. 1971. Diving in marine mammals. In *Oxford Biology Readers No. 6*. Edited by J.J. Head. Carolina Biological Supply Co., Burlington. pp. 1–16.
- Harvey, J.T., and Mate, B.R. 1984. Dive characteristics and movements of radio-tagged gray whales in San Ignacio Lagoon, Baja California Sur, Mexico. In *The gray whale*. Edited by M.L. Jones, S.L. Swartz, and S. Leatherwood. Academic Press, Orlando. pp. 561–575.
- Heide-Jørgensen, M.P., and Dietz, R. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals*, Orlando, Fla., December 14–18, 1995. p. 52. [Abstr.]
- Heyning, J.E. 1989. Cuvier's beaked whales—*Ziphius cavirostris* G. Cuvier, 1823. In *Handbook of marine mammals*. Vol. 4. River dolphins and the larger toothed whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 289–308.
- Hindell, M.A., Slip, D.J., and Burton, H.R. 1991. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.* **39**: 595–619.
- Hobson, R.P., and Martin, A.R. 1996. Behaviour and dive times of Arnoux's beaked whales, *Berardius arnuxii*, at narrow leads in fast ice. *Can. J. Zool.* **74**: 388–393.
- Hochachka, P.W., and Somero, G.N. 1984. *Biochemical adaptation*. Princeton University Press, Princeton, N.J.
- Hohn, A., Scott, M., Westgate, A., Nicolas, J., and Whitaker, B. 1995. Radiotracking of a rehabilitated pygmy sperm whale. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals*, Orlando, Fla., December 14–18, 1995. p. 55. [Abstr.]
- Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**: 255–265.
- Hudson, D.M., and Jones, D.R. 1986. The influence of body mass on the endurance to restrained submergence in the Pekin duck. *J. Exp. Biol.* **120**: 351–367.
- Irving, L. 1939. Respiration in diving mammals. *Physiol. Rev.* **19**: 112–134.
- Jefferson, T.A., Leatherwood, S., and Webber, M.A. 1993. *FAO species identification guide: marine mammals of the world*. Food and Agriculture Organization, Rome.
- Jerison, H.J. 1970. Gross brain indices and the analysis of fossil endocasts. In *Advances in primatology*. Vol. 1. The primate brain. Edited by C.R. Noback and W. Montagna. Appleton–Century–Crofts, New York. pp. 225–244.
- Johnsgard, P.A. 1987. *Diving birds of North America*. University of Nebraska Press, Lincoln.
- Jury, J.A. 1986. Razorbill swimming at depth of 140 m. *Br. Birds*, **79**: 339.
- Katona, S.K., Rough, V., and Richardson, D.T. 1993. A field guide to whales, porpoises, and seals from Cape Cod to Newfoundland. 4th ed. Smithsonian Institution Press, Washington, D.C.
- Kelly, B.P., and Wartzok, D. 1996. Ringed seal diving behavior in the breeding season. *Can. J. Zool.* **74**: 1547–1555.
- Kenyon, K.W. 1981. Sea otter *Enhydra lutris*. In *Handbook of marine mammals*. Vol. 1. The walruses, sea lions, fur seals and sea otters. Academic Press, New York. pp. 209–223.
- Kleiber, M. 1961. *The fire of life. An introduction to animal energetics*. John Wiley and Sons, New York.
- Kooyman, G.L. 1981. *Weddell seal: consummate diver*. Cambridge University Press, New York.
- Kooyman, G.L. 1988a. Pressure and the diver. *Can. J. Zool.* **66**: 84–88.
- Kooyman, G.L. 1988b. Diving physiology. Marine mammals. In *Comparative pulmonary physiology: current concepts*. Edited by S.F. Woods. Marcel Dekker, New York. pp. 721–734.
- Kooyman, G.L. 1989. *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
- Kooyman, G.L., and Gentry, R.L. 1986. Diving behavior of South African fur seals. In *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 142–152.
- Kooyman, G.L., and Kooyman, T.G. 1995. Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor*, **97**: 536–549.
- Kooyman, G.L., and Ponganis, P.J. 1990. Behavior and physiology of diving in emperor and king penguins. In *Penguin biology*. Edited by L.S. Davis and J.T. Darby. Academic Press, San Diego.
- Kooyman, G.L., and Trillmich, F. 1986a. Diving behavior of Galapagos fur seals. In *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 186–195.
- Kooyman, G.L., and Trillmich, F. 1986b. Diving behavior of Galapagos sea lions. In *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 209–219.
- Kooyman, G.L., Kerem, D.H., Campbell, W.B., and Wright, J.J. 1973. Pulmonary gas exchange in freely diving Weddell seals. *Respir. Physiol.* **17**: 283–290.
- Kooyman, G.L., Billups, J.O., and Farwell, W.D. 1983a. Two recently developed recorders for monitoring diving activity of marine birds and mammals. In *Experimental biology at sea*. Edited by A.G. MacDonald and I.G. Priede. Academic Press, London. pp. 197–214.
- Kooyman, G.L., Castellini, M.A., Davis, R.W., and Maue, R.E. 1983b. Aerobic diving limits of immature Weddell seals. *J. Comp. Physiol. B*, **151**: 171–174.
- Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V., and Kooyman, C.A. 1992. Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* **62**: 143–163.
- Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**: 89–94.
- Krutzikowsky, G.K., and Mate, B.R. 1995. Dive behavior of individual bowhead whales (*Balaena mysticetus*) monitored by satellite radio-telemetry. In *Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals*, Orlando, Fla., December 14–18, 1995. p. 64. [Abstr.]
- Landis, C.J. 1965. New high pressure research animal? *Undersea Technol.* **6**: 21.
- Lavigne, D.M., and Kovacs, K.M. 1988. *Harps and hoods*. University of Waterloo Press, Waterloo, Ont.
- Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J., and Hickie, J.P. 1986. Metabolic rates of seals and whales. *Can. J. Zool.* **64**: 279–284.

- Leatherwood, S., and Walker, W.A. 1979. The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern North Pacific. In *Behavior of marine mammals*. Vol. 3. Cetaceans. Edited by H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 85–141.
- Le Boeuf, B.J. 1994. Variation in the diving pattern of northern elephant seals with age, mass, sex, and reproductive condition. In *Elephant seals: population ecology, behavior, and physiology*. Edited by B.J. Le Boeuf and R.M. Laws. University of California Press, Berkeley. pp. 237–252.
- Le Boeuf, B.J., Naito, Y., Huntley, A.C., and Asaga, T. 1989. Prolonged, continuous, deep diving by northern elephant seals. *Can. J. Zool.* **67**: 2514–2519.
- Lumsden, W.H.R., and Hadow, A.J. 1946. The food of the shag (*Phalacrocorax aristotelis*) in the Clyde Sea area. *J. Anim. Ecol.* **15**: 35–42.
- Marsh, H., Lloze, R., Heinsohn, G.E., and Kasuya, T. 1989. Irrawaddy dolphin—*Orcaella brevirostris* (Gray, 1866). In *Handbook of marine mammals*. Vol. 4. River dolphins and the larger toothed whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 101–118.
- Matthews, P. 1996. The Guinness book of records. Guinness Publishing Ltd., Enfield, Middlesex, England.
- Mattlin, R.H. 1993. Seasonal diving behaviour of the New Zealand fur seal, *Arctocephalus forsteri*. In *Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals*, Galveston, Tex., November 11–15, 1993. p. 74. [Abstr.]
- McFarlan, D., and McWhirter, N.D. 1990. Guinness book of world records. Bantam Books, New York.
- Medonca, M.T., and Pritchard, P.C.H. 1986. Offshore movements of post-nesting Kemp's ridley sea turtles (*Lepidochelys kempi*). *Herpetologica*, **42**: 373–381.
- Melin, S.R., De Long, R.L., Thomason, J.R., and Valesquez, D.E. 1993. Foraging behavior of female California sea lions at San Miguel Island, California: winter 1992 and 1993. In *Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals*, Galveston, Tex., November 11–15, 1993. p. 76. [Abstr.]
- Miyazaki, N., and Perrin, W.F. 1994. Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). In *Handbook of marine mammals*. Vol. 5. The first book of dolphins. Edited by S.H. Ridgway and S.R. Harrison. Academic Press. San Diego. pp. 1–21.
- Montague, T.L. 1985. A maximum dive recorder for little penguins. *Emu*, **85**: 264–267.
- Morejohn, G.V. 1979. The natural history of Dall's porpoise in the North Pacific Ocean. In *Behavior of marine mammals*. Vol. 3. Cetaceans. Edited by H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 45–83.
- Nagy, K.A., Siegfried, W.R., and Wilson, R.P. 1984. Energy utilization by free-ranging jackass penguins. *Spheniscus demersus*. *Ecology*, **65**: 1648–1655.
- Naito, Y., Asaga, T., and Ohshima, Y. 1990. Diving behavior of Adélie penguins determined by time–depth recorder. *Condor*, **92**: 582–586.
- Newby, T.C. 1975. A sea otter (*Enhydra lutris*) food dive record. *Murrelet*, **56**: 7.
- Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. *Ornis. Scand.* **3**: 55–78.
- Nishiwaki, M., and Marsh, H. 1985. Dugong—*Dugong dugon*. In *Handbook of marine mammals*. Vol. 3. The sirenians and baleen whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 1–31.
- Nordøy, E.S., Folkow, L., and Blix, A.S. 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biol.* **15**: 261–268.
- Orr, T., and Aurióles-Gamboa, D. 1995. Foraging characteristics and activity patterns of California sea lions (*Zalophus californianus*) on Los Islotes, Bay of La Paz, B.C.S., Mexico. Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Fla. p. 85. [Abstr.]
- Parsons, T.R., Takahashi, M., and Hargrave, B. 1984. Biological oceanographic processes. 3rd ed. Pergamon Press, Elmsford, N.Y.
- Pastukhov, V.D. 1969. Some results of observations on the Baikal seal under experimental conditions. *Morsk. Mlekopitayushchie*, **1**: 105–110. [Translation No. 3544 by the National Marine Fisheries Service.]
- Peixun, C. 1989. Baiji—*Lipotes vexillifer* Miller, 1918. In *Handbook of marine mammals*. Vol. 4. River dolphins and the larger toothed whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 25–43.
- Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, New York.
- Piatt, J.F., and Nettleship, D.N. 1985. Diving depths of four alcids. *Auk*, **102**: 293–297.
- Prince, P.A., and Harris, M.P. 1988. Food and feeding ecology of breeding Atlantic alcids and penguins. *Proc. Int. Ornithol. Congr.* **19**: 1195–1204.
- Prince, P.A., and Jones, M. 1992. Maximum dive depths attained by South Georgia diving petrel *Pelecanoides georgicus* at Bird Island, South Georgia. *Antarct. Sci.* **4**: 433–434.
- Pritchard, P.C.H. 1979. Encyclopedia of turtles. T.F.H. Publications, Neptune, N.J.
- Reed, J.Z., Butler, P.J., and Fedak, M.A. 1994. The metabolic characteristics of the locomotory muscles of grey seal (*Halichoerus grypus*), harbour seals (*Phoca vitulina*) and Antarctic fur seals (*Arctocephalus gazella*). *J. Exp. Biol.* **194**: 33–46.
- Reeves, R.R., and Brownell, R.L., Jr. 1989. Susu—*Platanista gangetica* (Roxburgh, 1801) and *Platanista minor* Owen, 1853. In *Handbook of marine mammals*. Vol. 4. River dolphins and the larger toothed whales. Edited by S.H. Ridgway and S.R. Harrison. Academic Press, London. pp. 69–99.
- Ridgway, S.H. 1986. Diving by cetaceans. In *Diving in animals and man*. Edited by A.O. Brubakk, J.W. Kanwisher, and G. Sundness. The Royal Norwegian Society of Science and Letters, Trondheim. pp. 33–62.
- Robin, E.D. 1973. The evolutionary advantages of being stupid. *Perspect. Biol. Med.* **16**: 369–380.
- Robinson, B., and Craddock, J. 1983. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. *Fish. Bull.* **81**: 283–289.
- Sage, B.L. 1971. A study of white-billed divers in Arctic Alaska. *Br. Birds*, **64**: 519–528.
- Schmidt-Nielsen, K. 1984. *Scaling: Why is animal size so important?* Cambridge University Press, New York.
- Schmidt-Nielsen, K. 1990. *Animal physiology: adaptation and environment*. Cambridge University Press. New York.
- Scholander, P.F. 1940. Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skr.* **22**: 1–131.
- Schorger, A.W. 1947. The deep diving of the loon and the old-squaw and its mechanism. *Wilson Bull.* **59**: 151–159.
- Schreer, J.F., and Testa, J.W. 1995. Statistical classification of diving behavior. *Mar. Mammal Sci.* **11**: 85–93.
- Schreer, J.F., and Testa, J.W. 1996. Classification of Weddell seal diving behavior. *Mar. Mammal Sci.* **12**: 227–250.
- Scolaro, J.A., and Suburo, A.M. 1991. Maximum diving depths of the Magellanic penguin. *J. Field Ornithol.* **62**: 204–210.
- Scott, M.D., Chivers, S.J., Olson, R.J., and Lindsay, R.J. 1993.

- Radiotracking of spotted dolphins associated with tuna in the eastern tropical Pacific. *In* Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, Tex., November 11–15, 1993. p. 97. [Abstr.]
- Seddon, P.J., and van Heezik, Y. 1990. Diving depths of the yellow-eyed penguin *Megadyptes antipodes*. *Emu*, **90**: 53–57.
- Snyder, G.K. 1983. Respiratory adaptations in diving mammals. *Respir. Physiol.* **54**: 269–294.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W.H. Freeman and Co., New York.
- Soma, M. 1985. Radio biotelemetry system applied to migratory study of turtle. *J. Fac. Mar. Sci. Technol. Tokai Univ.* **21**: 47–56.
- Stahl, W.R. 1965. Organ weights in primates and other mammals. *Science (Washington, D.C.)*, **150**: 1039–1042.
- Stewart, B.S., Leatherwood, S., and Yochem, P.K. 1989. Harbor seal tracking and telemetry by satellite. *Mar. Mammal Sci.* **5**: 361–375.
- Stonehouse, B. 1975. Introduction: the Spheniscidae. *In* The biology of penguins. *Edited by* B. Stonehouse. Macmillan Press, London. pp. 1–15.
- SYSTAT. 1992. SYSTAT for Windows: statistics. Vol. 5. SYSTAT, Inc. Evanston, Ill.
- Testa, J.W. 1994. Overwinter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the SW Ross Sea, Antarctica. *Can. J. Zool.* **72**: 1700–1710.
- Thompson, D., Hammond, P.S., Nicholas, K.S., and Fedak, M.A. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool. (Lond.)*, **224**: 223–232.
- Tinker, S.W. 1988. *Whales of the world*. E.J. Brill, Leiden.
- Trillmich, F., Kooyman, G.L., Majluf, P., and Sanchez-Griñan, M. 1986. Attendance and diving behavior of South American fur seals during El Niño in 1983. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 153–167.
- Tucker, V.A. 1973. Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* **58**: 689–709.
- Wanless, S., Morris, J.A., and Harris, M.P. 1988. Diving behaviour of guillemot *Uria aalge*, puffin *Fratercula arctica* and razorbill *Alca torda* as shown by radio-telemetry. *J. Zool. (Lond.)*, **216**: 73–81.
- Watanuki, Y., Kato, A., and Naito, Y. 1996. Diving performance of male and female Japanese cormorants. *Can. J. Zool.* **74**: 1098–1109.
- Watkins, W.A., and Tyack, P. 1991. Reaction of sperm whales (*Physeter catodon*) to tagging with implanted sonar transponder and radio tags. *Mar. Mammal Sci.* **7**: 409–413.
- Watkins, W.A., Moore, K.E., and Tyack, P. 1985. Investigations of sperm whale acoustic behaviors in the southeast Caribbean. *Cetology*, **49**: 1–15.
- Watkins, W.A., Tyack, P., Moore, K., and Notarbartolo-di-Sciara, G. 1987. *Steno bredanensis* in the Mediterranean Sea. *Mar. Mammal Sci.* **3**: 78–82.
- Watkins, W.A., Daher, M.A., Fristrup, K.M., Howald, T.J., and di Sciara, G.N. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mammal Sci.* **9**: 55–67.
- Werner, R., and Campagna, C. 1993. Diving behavior of southern sea lions in Patagonia. *In* Abstracts from the Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, Tex., November 11–15, 1993. p. 112. [Abstr.]
- Westgate, A.J., Read, A.J., Berggren, P., Koopman, H.N., and Gaskin, D.E. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Can. J. Fish. Aquat. Sci.* **52**: 1064–1073.
- Whitehead, M.D. 1989. Maximum diving depths of the Adelic penguin, *Pygoscelis adeliae*, during the chick rearing period, in Prydz Bay, Antarctica. *Polar Biol.* **9**: 329–332.
- Wiig, Ø., Gjertz, I., Griffiths, D., and Lydersen, C. 1993. Diving patterns of an Atlantic walrus *Odobenus rosmarus rosmarus* near Svalbard. *Polar Biol.* **13**: 71–72.
- Williams, A.J., and Cooper, J. 1983. The crowned cormorant: breeding biology, diet and offspring-reduction strategy. *Ostrich*, **54**: 213–219.
- Williams, T.D., Briggs, D.R., Croxall, J.P., Naito, Y., and Kato, A. 1992. Diving patterns and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *J. Zool. (Lond.)*, **227**: 211–230.
- Williams, T.M., Friedl, W.A., and Haun, J.E. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* **179**: 31–46.
- Wilson, R.P. 1985. The jackass penguin (*Spheniscus demersus*) as a pelagic predator. *Mar. Ecol. Prog. Ser.* **25**: 219–227.
- Wilson, R.P., and Wilson, M.-P.T. 1990. Foraging ecology of breeding *Spheniscus* penguins. *In* Penguin biology. *Edited by* L.S. Davis and J.T. Darby. Academic Press, San Diego. pp. 181–206.
- Worthy, G.A.J., and Davis, R.W. 1995. Diving behavior and movement patterns of an Atlantic spotted dolphin (*Stenella frontalis*) obtained by satellite telemetry. *In* Abstracts from the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Fla., December 14–18, 1995. p. 124. [Abstr.]
- Würsig, B., Wells, R.S., Norris, K.S., and Würsig, M. 1994. A spinner dolphin's day. *In* The Hawaiian spinner dolphin. *Edited by* K.S. Norris, B. Würsig, R.S. Wells, and M. Würsig. University of California Press, Berkeley. pp. 65–102.