The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? [☆]

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Abstract

Many diving seabirds and marine mammals have been found to regularly exceed their theoretical aerobic dive limit (TADL). No animals have been found to dive for durations that are consistently shorter than their TADL. We attached time–depth recorders to 7 blue whales and 15 fin whales (family Balaenopteridae). The diving behavior of both species was similar, and we distinguished between foraging and traveling dives. Foraging dives in both species were deeper, longer in duration and distinguished by a series of vertical excursions where lunge feeding presumably occurred. Foraging blue whales lunged 2.4 (± 1.13) times per dive, with a maximum of six times and average vertical excursion of 30.2 (± 10.04) m. Foraging fin whales lunged 1.7 (± 0.88) times per dive, with a maximum of eight times and average vertical excursion of 21.2 (± 4.35) m. The maximum rate of ascent of lunges was higher than the maximum rate of descent in both species, indicating that feeding lunges occurred on ascent. Foraging dives were deeper and longer than non-feeding dives in both species. On average, blue whales dived to 140.0 (± 46.01) m and 7.8 (± 1.89) min when foraging, and 67.6 (± 51.46) m and 4.9 (± 2.53) min when not foraging. Fin whales dived to 97.9 (± 32.59) m and 6.3 (± 1.53) min when foraging and to 59.3 (± 29.67) m and 4.2 (± 1.67) min when not foraging. The longest dives recorded for both species, 14.7 min for blue whales and 16.9 min for fin whales, were considerably shorter than the TADL of 31.2 and 28.6 min, respectively. An allometric comparison of seven families diving to an average depth of 80–150 m showed a significant relationship between body mass and dive duration once Balaenopteridae whales, with a mean dive duration of 6.8 min, were excluded from the analysis. Thus, the short dive durations of blue whales and fin whales cannot be explained by the shallow distribution of their prey. We propose instead that short duration diving in large whales results from either: (1) dispersal behavior of prey; or (2) a high energetic cost of foraging. © 2001 Elsevier Science Inc. All rights reserved.

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1. Introduction

Blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) are the largest animals on earth. In the Southern Hemisphere, adult blue whales average 24.7 m in length and 92 671 kg, while fin whales average 21.2 m in length and 52 584 kg (Nishiwaki, 1950). As with the rest of baleen whales, the two species feed by filtering prey through baleen plates that hang from the roof of the mouth. However, rorquals, of which blue whales and fin whales are members, capture their prey by lunge feeding. During a lunge, they capture food by swimming rapidly at a prey school and opening the mouth to engulf large quantities of water and schooling or otherwise aggregated prey as the tongue moves backward and downward (Kawamura, 1980; Lambertsen, 1983). Blue whales feed almost exclusively on euphausiid crustaceans while fin whales feed on planktonic crustaceans, including euphausiids and pelagic shoaling fishes (Kawamura, 1980). Due to their large size, baleen whales require large concentrations of food (Brodie et al., 1978; Macaulay et al., 1995; Wishner et al., 1995). Croll et al. (2001) found that blue whales feed on euphausiid concentrations at least two orders of magnitude greater than the average density of euphausiids within the vicinity of the foraging area.

If an animal makes an aerobic dive, it must return to the surface before its O_2 reserves are exhausted (Houston and Carbone, 1992; Boyd, 1997). Thus larger animals should dive for longer durations than smaller animals since oxygen stores increase and mass-specific metabolic rates decrease with increasing body size (Costa, 1991). This relationship between mass specific oxygen stores and diving metabolic rates has led to the development of the concept of the aerobic dive limit (Kooyman et al., 1980). The aerobic dive limit (ADL) is defined as 'the maximum breath-hold that is possible without an increase in the blood lactic acid concentration during or after a dive'. The theoretical aerobic dive limit (TADL) is calculated by estimating the O_2 stores and diving metabolic rate of a species, usually based upon body mass (Kooyman, 1989). While Boyd and Croxall (1996) and Boyd (1997) have found that many seabirds and some pinnipeds routinely exceed this limit, few field-based studies have described diving behavior where dive duration is consistently less than the calculated TADL.

Baleen whales dive to shallower depths and for shorter periods than would be predicted from an allometric consideration of their body size (Schreer and Kovacs, 1997). This has been explained as a consequence of prey being found in relatively shallow waters (Schreer and Kovacs, 1997). In a general sense, theoretical models support this explanation, but such arguments have never been applied to the largest diving animals (blue and fin whales) using field measurements of diving behavior. Recent studies have measured the depth distribution of the euphausiid prey of large whales in the Mediterranean Sea and the coast of California. These studies have shown that dense euphausiid concentrations that are important in the diet of blue and fin whales are typically found at depths exceeding 100 m (Sardou et al., 1996; Croll et al., 1998, 2001). Furthermore, if blue and fin whales dive for short periods of time because their prey is located at shallow depths, the allometric relationship between body size and dive duration predicts that their dive durations should be longer than that of species that are smaller in size yet diving to a similar depth. Here we: (1) describe the foraging and non-foraging dive behavior of blue whales and fin whales; (2) relate body mass and dive duration of several families of divers in which individuals dive to depths close to 100–150 m; and (3) calculate the TADL of blue whales and fin whales and compare it to field measurements of their dive durations.

2. Materials and methods

2.1. Data collection

The diving behavior of 7 blue whales and 15 fin whales was measured between 1995 and 1999 using attached time–depth recorder packages (Tables 1 and 2). Recorders remained attached for 5.7 ± S.D. 3.10 h in blue whales and 12.6 ± S.D. 7.10 h in fin whales. Whales were tagged in Bahia de La Paz, Mexico (24°30′N, 110°30′W); Bahia de Loreto, Mexico (25°42′N, 111°09′W); Monterey Bay, USA (35°34′N, 112°00′W) and the Channel Islands, USA (34°00′N, 120°30′W).

The tags and methodology employed to attach them are described in Croll et al. (1998). Briefly, tags were attached to the dorsal surface of the whale 2–3 m caudal of the blowhole using a

Table 1
Maximum depth and duration of dive tagged blue whales

Whale ID	Location and date		Dive depth (m)	Dive time (min)	Maximum descent rate of dive (m s^{-1})	Maximum ascent rate of dive (m s^{-1})	Maximum descent rate of lunge (m s^{-1})	Maximum ascent rate of lunge (m s^{-1})
Bluefred	La Paz	$x =$	129.6	7.9	2.5	2.3	1.9	2.6
	Mexico	S.D. $=$	4.99	1.32	0.74	0.47	0.95	1.23
	3 May 1995	$n =$	27	27	27	27	23	23
Cedar	Channel	$x =$	57.5	4.0	1.7	1.8	1.3	2.1
	Islands, USA	S.D. $=$	31.21	1.88	0.43	0.88	0.64	0.84
	9 July 1996	$n =$	22	22	22	22	3	3
Vanesa	Channel	$x =$	150.2	8.7	2.7	1.9	1.2	1.6
	Islands, USA	S.D. $=$	67.75	3.92	1.20	0.76	0.42	0.68
	13 July 1996	$n =$	12	12	12	12	7	7
Casper	Channel	$x =$	71.2	5.1	2.0	1.7	1.2	2.0
	Islands, USA	S.D. $=$	65.04	2.21	0.66	0.81	0.64	1.23
	19 July 1996	$n =$	52	52	52	52	11	11
Torrey	Channel	$x =$	80.3	4.5	2.3	3.0	1.7	3.5
	Islands, USA	S.D. $=$	46.58	2.94	0.67	1.23	0.56	0.97
	26 July 1996	$n =$	80	80	80	80	45	45
Blue2	Monterey	$x =$	145.6	8.5	2.3	2.0	1.5	3.3
	Bay, USA	S.D. $=$	37.36	1.55	0.63	0.53	0.38	0.76
	19 July 1996	$n =$	14	14	14	14	13	13
Bootsie	Monterey	$x =$	172.8	8.3	2.5	1.9	1.3	2.0
	Bay, USA	S.D. $=$	14.72	1.44	0.41	0.59	0.54	0.64
	22 August 1996	$n =$	24	24	24	24	19	19
Average		$x =$	113.1	6.6	2.2	2.1	1.5	2.4
of median		S.D. $=$	64.35	2.26	0.38	0.52	0.38	0.93
		$n =$	7	7	7	7	7	7

compound crossbow. They were deployed from a small skiff (< 7 m). Each tag had three components: (1) a Wildlife Computers (Redmond, Washington) Mk 5 time/depth/temperature recording device (TDR); (2) a VHF radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) to track the tagged whale; and (3) a radio activated release mechanism (Jamie Stamps, Livermore, California). Time, depth and temperature were logged at 1-s intervals. Upon tagging each whale was followed in a 15-m vessel at a distance of 100–200 m. The behavior of each tagged whale was observed and recorded every surface interval. We recorded location, direction of movement and proximity of conspecifics. Once the tag was released from the whale, we localized it with the directional VHF system.

2.2. Data analysis

Dive data were analyzed using software provided by the TDR manufacturer (Dive Analysis, Wildlife Computers). We considered each individual whale an independent observation and calculated median values for dive parameters for individual whales. These median values were then averaged across whales to produce mean values for each species. In order to exclude surface respiration activity, we defined a dive as a submergence that exceeded 20 m in depth. We report dive depth as the maximum depth that a whale reached during a dive. We calculated maximum rates of ascent and descent when whales were lunging (defined below) and when they were traveling to and from the surface. We refer to the rates of travel to and from the surface as rates of ascent and descent of the dive. These rates were measured in m s^{-1} and are likely underestimates because we assumed that whales ascended or descended directly. Visual inspection of the dive profile revealed that whales often made a series of ascending and descending vertical excursions exceeding 8 m during the dive. We defined each excursion as a foraging lunge and estimated the number of lunges for each dive. Croll et al. (1998) simultaneously measured euphausiid densities and

Table 2
Maximum depth and duration of dive tagged fin whales

Whale ID	Location and date		Dive depth (m)	Dive time (min)	Maximum descent rate of dive (m s^{-1})	Maximum ascent rate of dive (m s^{-1})	Maximum descent rate of lunge (m s^{-1})	Maximum ascent rate of lunge (m s^{-1})
Finwhale	La Paz	$x =$	128.7	7.4	2.5	2.2	1.1	1.6
	Mexico	S.D. =	15.10	1.58	0.49	0.37	0.43	0.76
	2 May 1995	$n =$	31	31	31	31	29	29
Fred01	Loreto	$x =$	122.8	7.9	2.3	1.9	1.5	2.1
	Mexico	S.D. =	45.74	2.96	1.00	0.61	0.47	0.70
	9 April 1996	$n =$	43	43	43	43	22	22
Freedom	Loreto	$x =$	43.3	5.0	2.0	1.6	2.5	2.3
	Mexico	S.D. =	38.25	2.09	0.64	0.44	0.71	1.06
	10 April 1996	$n =$	33	33	33	33	2	2
Friend	Loreto	$x =$	93.9	4.4	2.3	2.1	1.6	1.6
	Mexico	S.D. =	45.62	1.79	0.57	0.51	0.58	0.75
	11 April 1996	$n =$	52	52	52	52	29	29
Raven	Loreto	$x =$	85.7	7.9	1.8	1.4	1.4	2.1
	Mexico	S.D. =	38.74	2.73	0.67	0.61	1.60	2.09
	13 April 1996	$n =$	83	83	83	83	35	35
Luna	Loreto	$x =$	65.8	6.2	1.9	1.2	1.3	2.1
	Mexico	S.D. =	43.28	1.51	0.70	0.47	0.21	0.88
	14 April 1996	$n =$	32	32	32	32	4	4
Althea	La Paz	$x =$	66.5	4.3	1.8	1.8	1.4	2.3
	Mexico	S.D. =	37.71	2.30	0.60	0.54	1.30	1.62
	30 April 1996	$n =$	86	86	86	86	33	33
King	La Paz	$x =$	114.4	5.7	1.8	2.1	1.0	1.8
	Mexico	S.D. =	41.41	1.37	0.43	0.63	0.51	0.58
	1 May 1996	$n =$	36	36	36	36	22	22
Maya	Channel	$x =$	91.6	5.1	2.6	2.0	2.0	2.2
	Islands, USA	S.D. =	76.24	2.39	1.31	0.99	0.86	1.14
	21 September 1997	$n =$	73	73	73	73	51	51
Grace	Channel	$x =$	75.8	6.7	1.9	1.3	1.1	1.7
	Islands, USA	S.D. =	64.76	2.98	0.89	0.64	0.64	1.01
	5 October 1997	$n =$	113	113	113	113	48	48
Correc-aminos	Loreto	$x =$	77.1	3.5	2.1	2.0	1.4	2.0
	Mexico	S.D. =	49.76	1.45	0.50	0.58	0.45	0.49
	22 March 1999	$n =$	180	180	180	180	45	45
Spanky	Loreto	$x =$	84.3	5.7	1.9	1.7	1.3	1.6
	Mexico	S.D. =	62.10	2.22	0.40	0.64	0.38	0.45
	29 March 1999	$n =$	139	139	139	139	41	41
Loreta	La Paz	$x =$	61.9	3.9	2.3	1.6	1.4	1.5
	Mexico	S.D. =	14.60	1.13	0.49	0.49	0.48	0.46
	8 April 1999	$n =$	98	98	98	98	38	38
Pappy	La Paz	$x =$	72.1	3.9	2.1	1.8	1.4	1.2
	Mexico	S.D. =	36.29	1.49	0.67	0.61	0.48	0.30
	12 April 1999	$n =$	50	50	50	50	12	12
Lorenzo	La Paz	$x =$	79.4	4.2	2.5	2.1	1.2	1.7
	Mexico	S.D. =	38.81	1.85	0.77	0.58	0.39	0.65
	13 April 1999	$n =$	103	103	103	103	48	48
Average of median		$x =$	78.1	5.5	2.0	1.7	1.4	1.7
		S.D. =	32.08	1.58	0.17	0.37	0.46	0.37
		$n =$	15	15	15	15	15	15

whale diving, and found such vertical excursions occurred in regions of densely aggregated euphausiids.

2.2.1. Dive behavior

Whales were considered to be foraging if the profile of time vs. depth showed one or more

lunges during the dive (Figs. 1a and 2a), and non-foraging if no lunges were recorded (Fig. 1b and Fig. 2b). Thus, non-foraging dives were defined as dives in which the whale dove directly to depth and returned to the surface without spending time at depth (Figs. 1b and 2b). As a result, we excluded dives in which the whale might have lunged horizontally. We compared dive depth and dive duration between foraging and non-foraging dives of individual whales with a paired-sample t-test (Zar, 1996). Because we conducted two dif-ferent tests, significance was assessed at $P = 0.03$. We also compared the speed of ascent and descent of lunges between foraging and non-foraging whales with a paired-sample t-test (Zar, 1996).

2.2.2. Dive duration vs. body mass

To examine allometric relationship between dive duration and body mass across taxonomic groups of divers, we averaged the dive durations of species belonging to the same family. We only analyzed studies in which the species dove to a
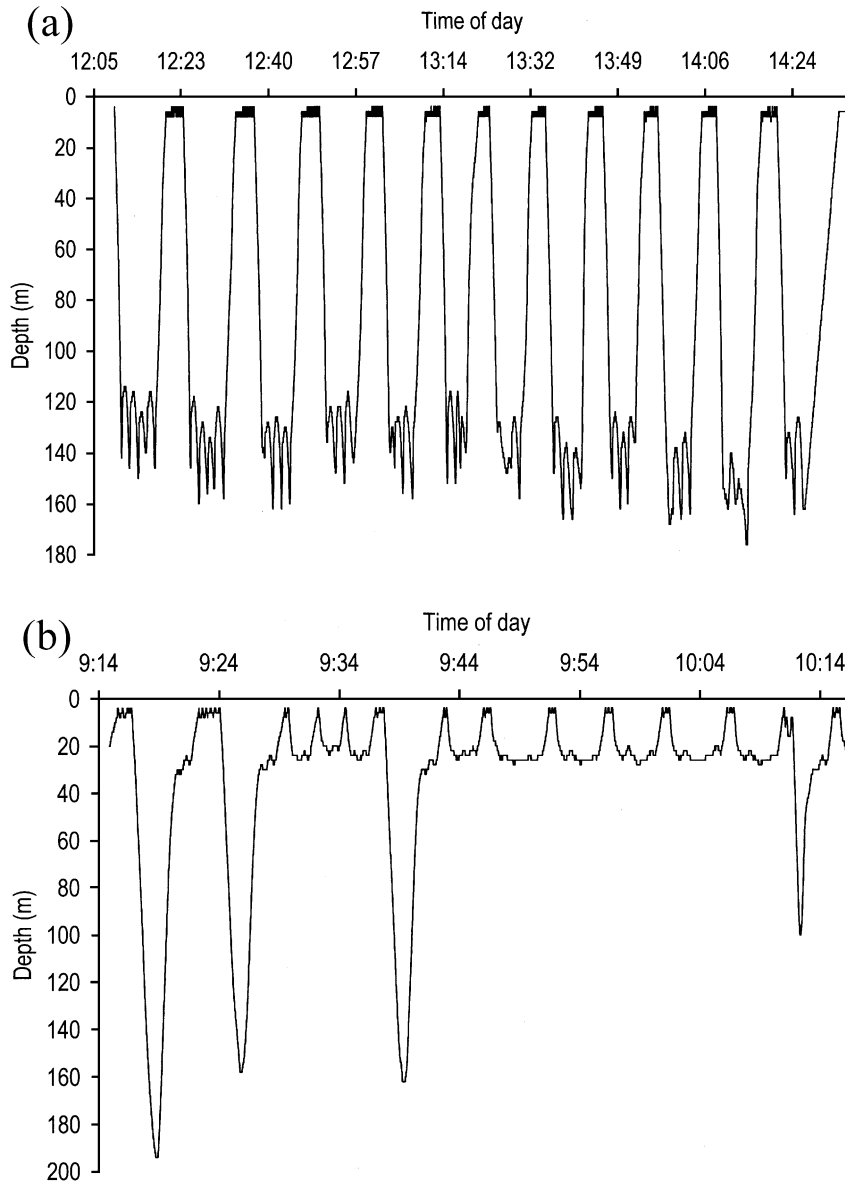

Fig. 1. (a) A series of foraging dives made by a blue whale. The spikes at the bottom of the dive are interpreted as lunges. (b) A series of non-foraging dives made by a blue whale.
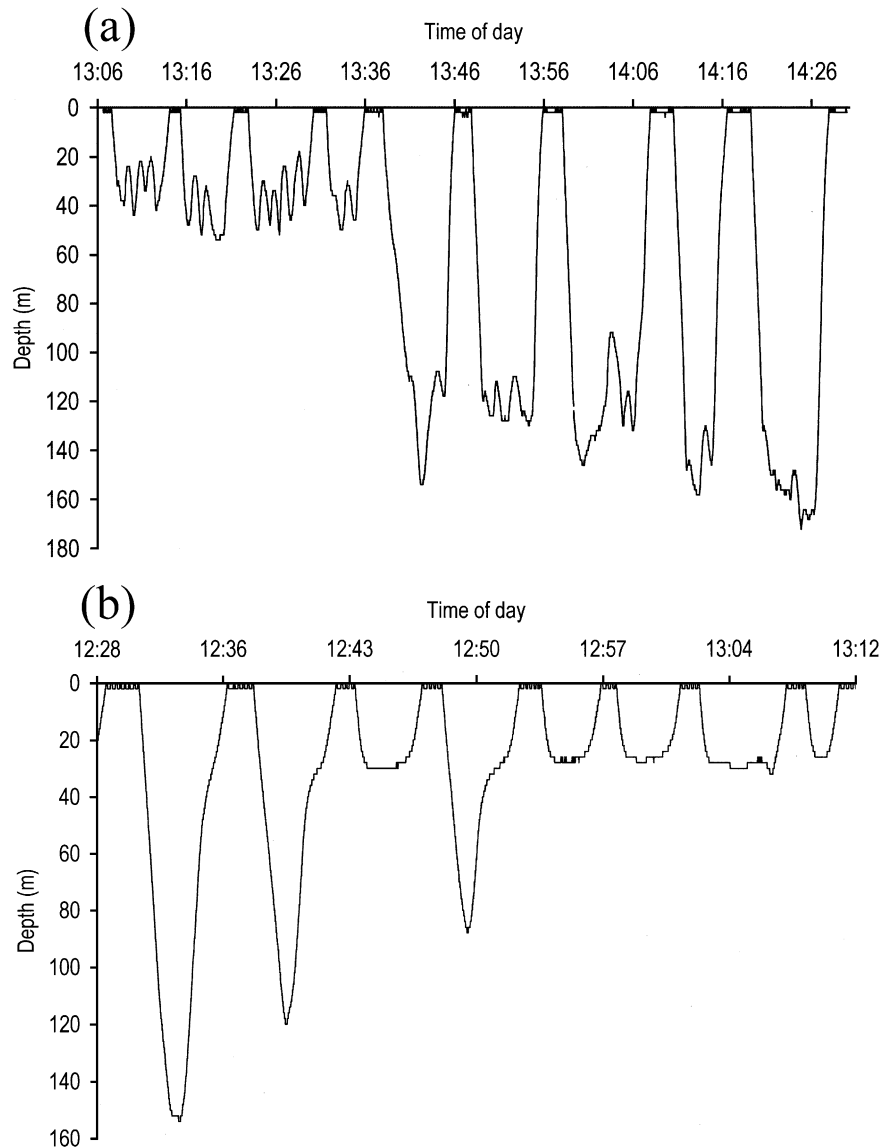
Fig. 2. (a) A series of foraging dives made by a fin whale. The spikes at the bottom of the dive are interpreted as lunges. (b) A series of non-foraging dives made by a fin whale.

depth of 80–150 m to ensure that differences in the duration of the dive were not related to differences in the depth of the dive. A regression of body mass and dive duration was conducted between the following families: Spheniscidae; Otariidae; Phocidae; Ziphiidae; Monodontidae; Balaenidae; and Balaenopteridae (average masses of species from Table 3).

2.2.3. Theoretical aerobic dive limit (TADL)

We compared dive durations with calculated TADLs (Boyd and Croxall, 1996). The TADLs of

blue whales and fin whales were calculated following the methodology described by Kooyman (1989). We estimated oxygen stores based on published values from other marine mammals (Table 4) and the methodology of Shaffer et al. (1997). Basal metabolic rate was calculated from the allometric equation of Kleiber (1961) and we utilized $4 \times BMR$ as an estimate of diving metabolic rate when foraging underwater following the convention of Boyd and Croxall (1996). At least some marine mammals, including blue whales, extend their aerobic dive duration by gliding underwater

Table 3
The duration of dive of animals that dove on average to 80−150 m (Fig. 5)

Family	Species	Body[a] mass (kg)	Mean dive time (min)	Mean dive depth (m)	N[k]	Reference for weight	Reference for dive
Spheniscidae	*Pygoscelis papua*	6	2.8[f]	100[f]	7	Dunning, 1993	Williams et al., 1992
Spheniscidae	*Aptenodytes patagonicus*	13	4.1	125	1	Kooyman et al., 1992	Kooyman et al., 1992
Spheniscidae	*Aptenodytes forsteri*	27[b]	4.1[f]	100[f]	5	Kooyman and Kooyman, 1995	Kooyman and Kooyman, 1995
Otariidae	*Arctocephalus forsteri*	39[c]	3.4	96	4	Wilkens and York, 1997	Mattlin et al., 1998
Otariidae	*Callorhinus ursinus*	39[c]	2.8	99	1	Wilkens and York, 1997	Gentry et al., 1986
Phocidae	*Phoca hispida*	80[b]	6.2[g]	106[g]	1	Kelly and Wartzok, 1996	Kelly and Wartzok, 1996
Otariidae	*Zalophus californianus*	111	2.8	98	1	Odell, 1981	Feldkamp et al., 1989
Otariidae	*Phocarctos hookeri*	115[b]	3.9	123	14	Gales and Mattlin, 1997	Gales and Mattlin, 1997
Phocidae	*Leptonychotes weddellii*	355[d]	8.3	118	24	Castellini et al., 1992	Schreer and Testa, 1996
Monodontidae	*Delphinapterus leucas*	956	11.4	150−350	3	Brodie, 1989	Martin and Smith, 1992
Phocidae	*Mirounga leonina*	1771	16.1	110	3	Ling and Bryden, 1981	Campagna et al., 1999
Phocidae	*Mirounga angustirostris*	1814	16.3	109	1	Deutsch et al., 1994	DeLong and Stewart, 1991
Ziphiidae	*Hyperoodon ampullatus*	3500	11.2	166	2	Benjaminsen and Christensen, 1979	Hooker and Baird, 1999
Balaenidae	*Balaena mysticetus*	48 250[e]	23[f,h]	100	1	Lockyer, 1976	Krutzikowsky and Mate, 2000
Balaenidae	*Balaena glacialis*	72 960	11.5[i]	134	?	Omura et al., 1969	Goodyear, 1995
Balaenopteridae	*Megaptera novaeangliae*	29 900	8.2	101−120[j]	?	Nishiwaki, 1950	Dolphin, 1988
Balaenopteridae	*Balaenoptera physalus*	56 288	5.5	78	15	Nishiwaki, 1950	This study
Balaenopteridae	*Balaenoptera musculus*	100 393	6.6	113	7	Nishiwaki, 1950	This study

[a] Most values are not from the tagged animals, mass from literature. If sex of diver was not disclosed, we report female mass.
[b] Data from tagged individuals.
[c] Pregnant females.
[d] Masses of females and males ($n = 5$).
[e] Based on body mass−length equations for right whales. The mean length of 14.6 m comes from Nerini et al., 1984 (photogrammetric data).
[f] Based on regression equations of duration and depth of dive.
[g] Median values.
[h] Only significant regressions with $R^2 > 0.25$.
[i] Mean of range.
[j] Based on echosounder recordings.
[k] Number of different individuals from which diving data were collected.

Table 4
Values used in calculating the theoretical aerobic dive limit (TADL) of blue whales and fin whales

	Unit	Computational	Blue whales	Fin whales	Reference
(1) Body mass (BM)	kg		92 671	52 584	Nishiwaki, 1950
(2) O$_2$ Stores					
Lunges					
Total lung capacity (TLC)	1	$0.1 \times (BM^{0.96})$	5865	3404	Kooyman, 1989
Diving lung volume (DLV)	1	$0.75 \times TLC$	4399	2553	Goforth, 1986
Total O$_2$ in lungs	1	$0.15 \times DLV$	660	383	Kooyman, 1973
Muscle					
Muscle mass	%BM		39.4	45.6	Nishiwaki, 1950
Muscle mass	kg		36 549	23 978.3	
Myoglobin (Mb)	g	$34\ g\ kg^{-1}$	1 242 681	815 262	Noren, 1997
O$_2$ combining capacity	$1\ g^{-1}$ Mb		0.0013	0.0013	Kooyman, 1989
Total O$_2$ in muscle	1		1665	1092	
Blood					
Blood volume (BV)	1	$0.127\ l\ kg - 1$	11 769	6678	Ridgway et al., 1984
Arterial volume	1	$0.33 \times BV$	3884	2204	Lenfant et al., 1970
Venous volume	1	$0.67 \times BV$	7885	4474	Lenfant et al., 1970
Arterial haemoglobin (A Hb)	g	$209\ g\ l^{-1}$	811 723	460 593	Ridgway et al., 1984
Venous haemoglobin (V Hb)	g	$209\ g\ l^{-1}$	1 648 043	935 144	Ridgway et al., 1984
O$_2$	$1\ g^{-1}$ Hb		0.0013	0.0013	Kooyman, 1989
Combining capacity					
Arterial blood O$_2$	1	95% saturation	1033	586	Kooyman, 1989
Venous blood O$_2$	1	75% saturation	1656	940	Kooyman, 1989
Total O$_2$ in blood	1		2690	1526	
Body O$_2$ stores	1		5015	3002	
(3) Metabolic rate					
Basal metabolicrate (BMR)	$J\ s^{-1}$		18 659	12 157	Kleiber, 1961
BMR	$1\ O_2\ min^{-1}$		55.7	36.3	
Diving metabolic rate (DMR)	$1\ O_2\ min^{-1}$	$4 \times BMR$	222.8	145.2	Boyd and Croxall, 1996
DMR — gliding savings	$1\ O_2\ min^{-1}$	DMR — 27.8%	160.9	104.8	Williams et al., 2000
(4) TADL	min		31.2	28.6	

(Williams et al., 2000). The reduction in oxygen consumption due to this behavior averages 27.8% in Weddell seals (*Leptonychotes weddellii*), the only species in which this reduction has been calculated (Williams et al., 2000). We assumed a similar reduction in recovery oxygen consumption for blue whales and fin whales (Table 4).

3. Results

We recorded 231 dives from seven tagged blue whales (Table 1). The maximum dive depth was 204 m and the maximum duration was 14.7 min. We recorded 1152 dives from 15 tagged fin whales (Table 2). The maximum dive depth was 316 m and the maximum duration of a dive was 16.9 min.

3.1. Dive behavior

Foraging dives were deeper and longer than non-feeding dives in both blue and fin whales (Figs. 2 and 3). Blue whales dove to $140.0 \pm$ S.D. 46.01 m when foraging and to $67.6 \pm$ S.D. 51.46 m when not foraging (paired *t*-test: $t_6 = 3.25$; $P = 0.017$; Fig. 3a). They dove for $7.8 \pm$ S.D. 1.89 min when foraging and for $4.9 \pm$ S.D. 2.53 min when not foraging (paired *t*-test: $t_6 = 2.91$; $P = 0.027$; Fig. 3b). Fin whales dove to $97.9 \pm$ S.D. 32.59 m when foraging and to $59.3 \pm$ S.D. 29.67 m when not foraging (paired *t*-test: $t_{14} = 4.46$, $P < 0.001$; Fig. 4a). They dove for $6.3 \pm$ S.D. 1.53 min when foraging and for $4.2 \pm$ S.D. 1.67 min when not foraging (paired *t*-test: $t_{14} = 8.22$; $P < 0.001$; Fig. 4b).

Foraging blue whales lunged $2.4 \pm$ S.D. 1.13

times per dive, with a maximum of six lunges; foraging fin whales lunged $1.7 \pm$ S.D. 0.88 times per dive, with a maximum of eight lunges ($n = 7$ blue whales and 15 fin whales). Vertical excursions during lunges averaged $30.2 \pm$ S.D. 10.04 m in blue whales and $21.2 \pm$ S.D. 4.35 m in fin whales ($n = 7$ blue whales and 15 fin whales). The maximum rate of ascent of lunges was greater than the maximum rate of descent (paired *t*-test; blue whales: $t_6 = 2.95$; $P = 0.026$; Table 1; fin whales: $t_{14} = 2.80$; $P = 0.014$; Table 2).

3.2. Dive duration vs. body mass

There was no relationship between dive duration and body mass in the seven taxonomic families analyzed ($r^2 = 0.34$; $F_{1,5} = 4.14$; $P = 0.097$; Fig. 5). If we exclude the family Balaenopteridae from the regression, the relationship becomes significant ($r^2 = 0.90$; $F_{1,4} = 44.48$, $P = 0.003$).
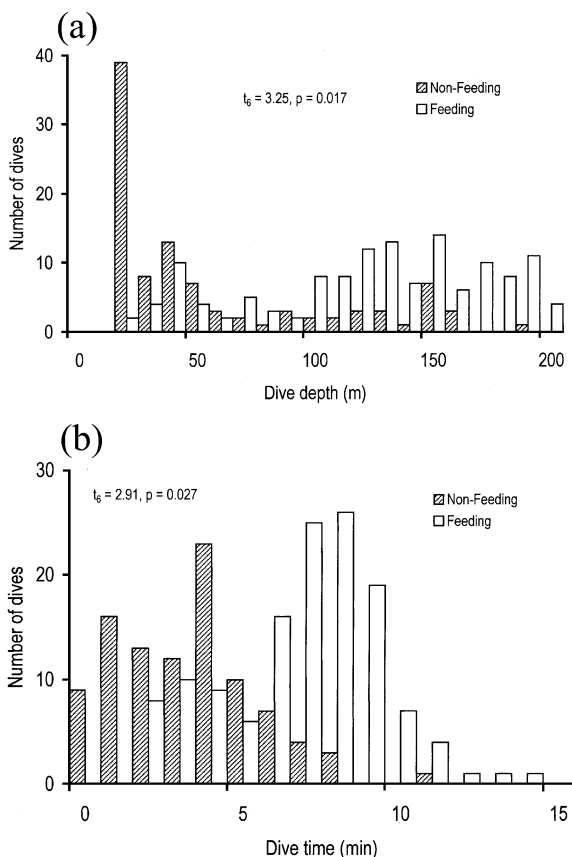

Fig. 3. (a) Frequency distribution of depth of dive in blue whales relative to behavior. (b) Frequency distribution of duration of dive in blue whales relative to behavior.
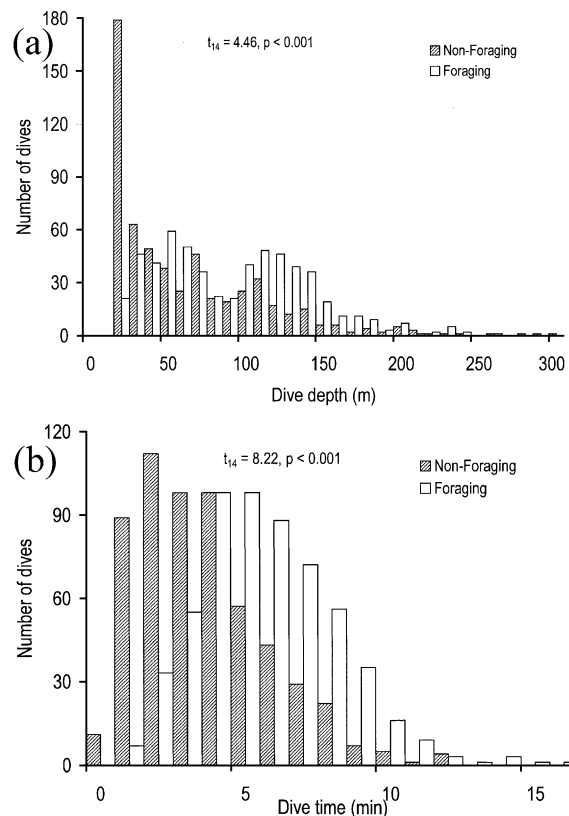

Fig. 4. (a) Frequency distribution of depth of dive in fin whales relative to behavior. (b) Frequency distribution of duration of dive in fin whales relative to behavior.

3.3. Theoretical aerobic dive limit (TADL)

Dive duration as a proportion of the TADL followed a unimodal distribution in both blue whales and fin whales (Fig. 6a,b). The median dive duration represented 19 and 17% of the TADL in blue whales and fin whales, respectively. The longest dive observed represented 47% of the TADL in blue whales and 59% in fin whales.

4. Discussion

Foraging dives were longer and deeper than non-foraging dives in both blue and fin whales (Figs. 3–6). The depth of foraging dives we measured was related to the depth at which prey were concentrated (Croll et al., 1998). Our data also indicate that blue whales and fin whales fed mostly at depth and rarely at the surface, which highlights the importance of remote-sensing techniques in understanding the behavior of whales.
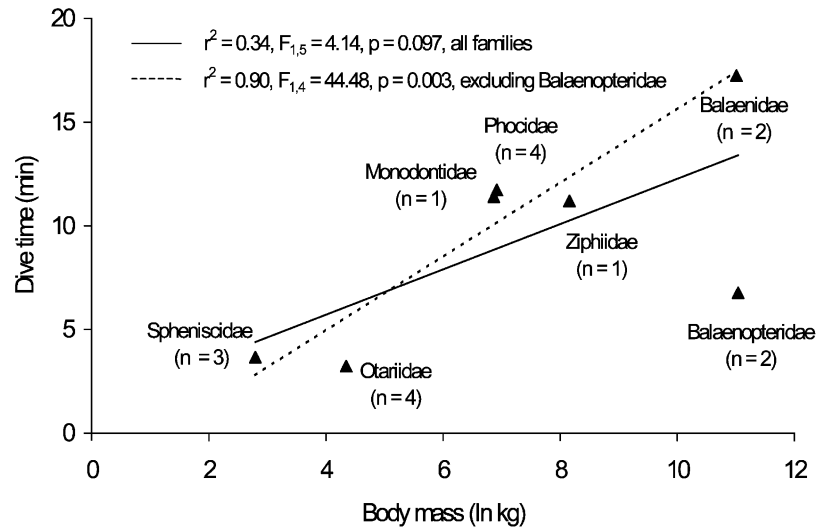
Fig. 5. The relationship between body mass and dive duration of animals diving to an average depth of 80–150 m. Fitted curve: $y = 1.348 + x\,1.091$. Fitted curve excluding Balaenopteridae: $y = -2.183 + x\,1.785$. Values and references are listed in Table 3.

The higher rates of ascent vs. descent during lunges suggest that prey capture takes place during the ascending portion of the lunge. Under this scenario, whales may perform several foraging lunges during an individual dive and whales close their mouths and expel water during the descending portion of the lunge (with little need for fast swimming during descent). This framework is also consistent with observations of blue whales gliding during the descent part of a lunge (Williams et al., 2000).

Blue whales and fin whales did not dive for long durations. The maximum dive durations we recorded for blue whales and fin whales (14.7 and 16.9 min, respectively) are similar to those reported in the literature: blue whales 16.4–26.9 min (Donovan, 1984; Strong, 1990; Lagerquist et al., 2000); fin whales 12.6–25.9 min (Strong, 1990; Panigada et al., 1999). Unlike all species of diver studied to date, blue and fin whales never exceeded their TADL of 31.2 and 28.6 min, respectively. Anecdotal evidence indicates that blue whales and fin whales are able to dive for as long as 50 and 30 min, respectively (Leatherwood et al., 1982). However these appear to be cases in which whales found themselves in life-threatening situations (Leatherwood et al., 1982). In contrast, most seabirds and some pinniped species regularly exceed their TADL (Boyd and Croxall, 1996; Boyd, 1997). Even species that usually dive below their TADL, such as the Antarctic fur seal

(*Arctocephalus gazella*), occasionally exceed this limit (Boyd and Croxall, 1996).

Why do Balaenopteridae whales dive for durations so much less than their TADL? Comparisons of dive depth with the reported depth distribution of prey does not support the hypothesis that Balaenopteridae whales dive for short durations due to the shallow distribution of their prey. The euphausiid prey of fin and blue whales in the California Current is generally found at depths exceeding 100 m (Croll et al., 1998, 2001). Two possibilities may explain the short duration of dives in comparison with the TADL for rorquals: (1) dispersal of prey during foraging lunges leads to sub-optimal densities of prey during the course of a foraging dive; or (2) we have underestimated the metabolic cost of foraging lunges in our calculation of TADL. We believe that a high cost of lunging is the most likely explanation because hydroacoustic measurement of euphausiid densities in the presence of foraging whales do not indicate reduced prey densities (Croll et al., 1998). Furthermore, the rapid swimming necessary for successful lunge feeding is likely energetically costly and thus, would deplete oxygen stores and reduce dive duration (Costa, 1991). A similar explanation has been proposed to explain foraging dives in Antarctic fur seals, which appear to dive with a high metabolic rate (Boyd et al., 1995) and rarely exceed their TADL (Boyd and Croxall, 1996). The argument that lunging is a costly be-
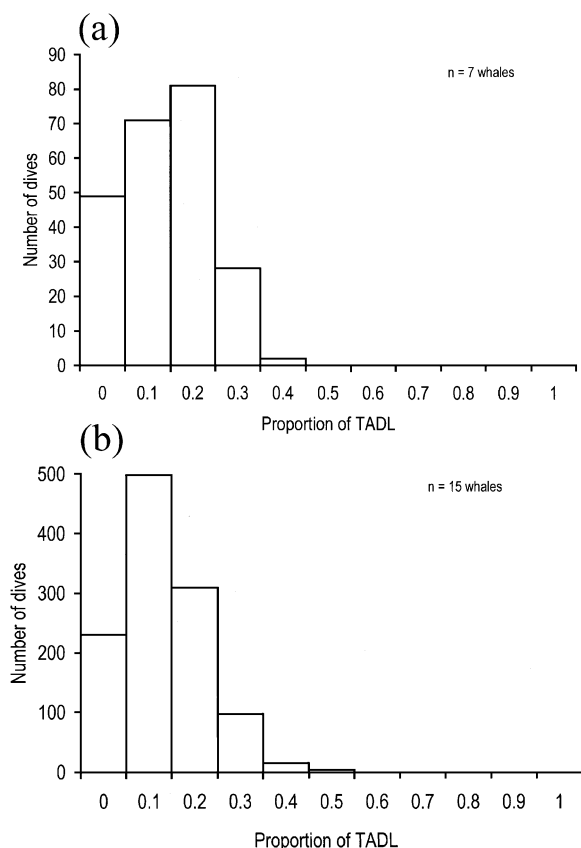
Fig. 6. (a) Frequency distribution of duration of dive in blue whales relative to the theoretical aerobic dive limit (TADL). (b) Frequency distribution of duration of dive in fin whales relative to TADL.

havior would also explain the discrepancies between rorquals and right whales when diving at similar depths (Fig. 5). Right whales move slowly while skimming small planktonic prey through the water column (Pivorunas, 1979). The speed of right whales at depth averages 0.7 m s^{-1} (Goodyear, 1995) and foraging dives in bowhead whales last longer than 30 min (Würsig and Clark, 1993). We hypothesize that whereas foraging costs are low in right whales, allowing them to forage for longer periods underwater on more dispersed prey, they are high in Balaenopteridae whales, forcing them to forage for relatively short periods.

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