Cambridge University Press
978-0-521-76555-8 - Diving Physiology of Marine Mammals and Seabirds
Paul J. Ponganis
Excerpt
More information

1 Diving behavior

Diving physiology is best interpreted in light of behavior. Therefore, this first chapter is an overview of the diving behavior of marine mammals and seabirds. Prior to Kooyman's development of the first time–depth recorder in the 1960s (Kooyman, 1965, 1968), reviews of diving behavior primarily cited (a) dive depths and durations of harpooned whales, (b) depths at which carcasses were found entangled in nets or cables, and (c) even average time until last movement during forced submersion (Andersen, 1966, Harrison and Kooyman, 1968, Kooyman and Andersen, 1968, Piatt and Nettleship, 1985, Schorger, 1947). However, the development of microprocessor-based data loggers and satellite transmitters over the past three decades has now allowed documentation of remarkable diving behaviors in many marine species. Amazingly, at the time of this writing, a depth recorder has been deployed on every pinniped species. The number of studies is now so extensive that, even with today's internet search engines, it is difficult to be sure that every investigation has been found, especially in regard to maximum dive depths and durations. One excellent source of such information for readers is on the internet, Penguiness Book (http://penguinessbook.scarmarbin.be/index.php), a website created and maintained by Drs. Yan Rupert-Coudert and Akiko Kato.

The tables in this chapter list both common and maximum dive depths and durations that had been published at the time of writing. As future studies will increase the size of the data base as well as the range of diving environments encountered, these values, especially the maximum dive durations and depths, will undoubtedly change. Nonetheless, these data, especially the common dive durations and depths, provide a background to (a) appreciate differences in the dive performance, breath-hold capacities, and ecology of various species; (b) understand the role of physiological adaptations underlying such dive behaviors; and (c) evaluate differences between dives and physiological responses under experimental conditions versus those in the wild.

In addition to review of the depths and durations of dives in marine mammals and seabirds, this chapter will also highlight recent advances in documentation of underwater behaviors with the advent of more sophisticated dive recorders. We are only beginning to glimpse how these animals function and thrive in an underwater world hidden from our view. From a biologist's perspective, these are indeed exciting times.

When reviewing these dive behaviors, readers should remember that physiology ultimately underlies the dive capacity and foraging capabilities of a given species. All marine mammals and diving birds are potentially faced with alterations in prey availability and prey distribution due to overfishing, pollution, and climate change. Consequently, how an animal dives and how close it pushes itself to its physiological limits during foraging activity are important topics. While it is true that understanding diving physiology does not directly "save" a species, it does help provide a rational basis for arguments to (a) regulate the fishing industry and pollution, (b) create marine sanctuaries, and (c) limit greenhouse gas emissions to decrease global warming.

Systematics, evolution, and foraging ecology of marine mammals and seabirds are not included in this chapter. Those topics could easily constitute another book. For such details, readers are referred to several texts and reviews (Berta *et al.*, 2006, Castellini and Mellish, 2015, Croxall, 1987, Davis and Darby, 1990, Perrin *et al.*, 2009, Reynolds and Rommel, 1999, Ridgway and Harrison, 1981–1998, Schreiber and Burger, 2002, Sibley and Monroe Jr., 1990).

1.1 Marine mammals

Marine mammals are composed of representatives from four mammalian orders, Pinnipedia, Cetacea, Sirenia, and Carnivora. The pinnipeds, which has also been classified as a suborder of the Carnivora, consist of the phocids (true or earless seals), otariids (eared seals – the fur seals and sea lions), and odobenids (walruses). The cetaceans are divided into the odontocetes (toothed whales) and mysticetes (baleen whales), while the sirenians include the manatees (three species) and dugongs (one species). Marine carnivore species include the polar bear (*Ursus maritimus*), sea otter (*Enhydra lutris*), and several other marine otters. After review of dive behaviors in each of these mammalian orders, this section on marine mammals will conclude with brief mention of the diving abilities of several aquatic mammals.

1.1.1 Pinnipeds: phocids

Although routine dive durations and depths of many phocid seals are less than 10–15 min and 100 m, almost all of these seals are capable of occasional exceptional dives of 25–30-min duration and greater than 300-m depth (Table 1.1). Both the routine and extreme dives are quite a physiological accomplishment in terms of breath-hold duration and pressure tolerance. However, it is the large phocid seals that are the longest-duration and deepest divers among the pinnipeds (Table 1.1). These include Weddell seals (*Leptonychotes weddellii*), hooded seals (*Cystophora cristata*), and northern and southern elephant seals (*Mirounga angustirostris*, *M. leonina*). Routine dive durations are up to 30 min, and common depths are 400–600 m. The southern elephant seal currently holds the record for the deepest (2388 m) and longest (120 min) dives of any pinniped (Hindell *et al.*, 1992, Costa et al., 2010).

Table 1.1 Dive characteristics of phocid pinnipeds.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Harbor seal *Phoca vitulina*	<10	35	5–100	481	A
Spotted seal *P. largha*	<10	–	<100	–	B
Harp seal *P. groenlandica*	2–15	>15	50–300	568	C
Ringed seal *P. hispida*	<10	>50	20–100	500	D
Baikal seal *P. sibirica*	2–6	>40	5–50	324	E
Caspian seal *P. caspica*	1	<4	<50	>200	F
Hawaiian monk seal *Monachus schauinslandi*	5–15	>20	20–450	>500	G
Mediterranean monk seal *M. monachus*	5–10	18	10–80	123	H
Grey seal *Halichoerus grypus*	1–8	32	10–120	436	I
Ribbon seal *Histriophoca fasciata*	–	–	200–600	>600	J
Bearded seal *Erignathus barbatus*	1–6	19	10–60	480	K
Hooded seal *Cystophora cristata*	5–25	>52	100–600	>1016	L
Crabeater seal *Lobodon carcinophagus*	5	24	90	713	M
Ross seal *Ommatophoca rossii*	5–15	>20	100–300	792	N
Leopard seal *Hydrurga leptonyx*	<5	15	10–50	304	O
Weddell seal *Leptonychotes weddellii*	10–15	96	150–400	904	P
Northern elephant seal *Mirounga angustirostris*	15–30	119	200–600	1735	Q
Southern elephant seal *Mirounga leonina*	20–29	120	269–552	2388	R

References: A: Bowen *et al.*, 1999, Eguchi and Harvey, 2005, Lesage *et al.*, 1999; B: Lowry *et al.*, 1994; C: Folkow *et al.*, 2004, Lydersen and Kovacs, 1993; D: Born *et al.*, 2004, Gjertz *et al.*, 2000a, Kelly and Wartzok, 1996;, E: Stewart *et al.*, 1996, Watanabe *et al.*, 2004, 2006; F: Miyazaki, 2001; G: Parrish *et al.*, 2002; H: Dendrinos *et al.*, 2007, Gazo and Acuilar, 2005, Kirac *et al.*, 2002; I: Beck *et al.*, 2003, Goulet *et al.*, 2001, Thompson and Fedak, 1993, Thompson *et al.*, 1991; J: London *et al.*, 2014; K: Gjertz *et al.*, 2000b, Krafft *et al.*, 2000; L: Folkow and Blix, 1999; M: Burns *et al.*, 2004; N: Blix and Nordoy, 2007; O: Nordoy and Blix, 2009; P: Castellini *et al.*, 1992a, Heerah *et al.*, 2013, Schreer and Testa, 1996; Q: Le Boeuf *et al.*, 1988, Robinson *et al.*, 2012, Stewart and DeLong, 1995; R: Bennett *et al.*, 2001, Costa *et al.*, 2010; Hindell *et al.*, 1991).

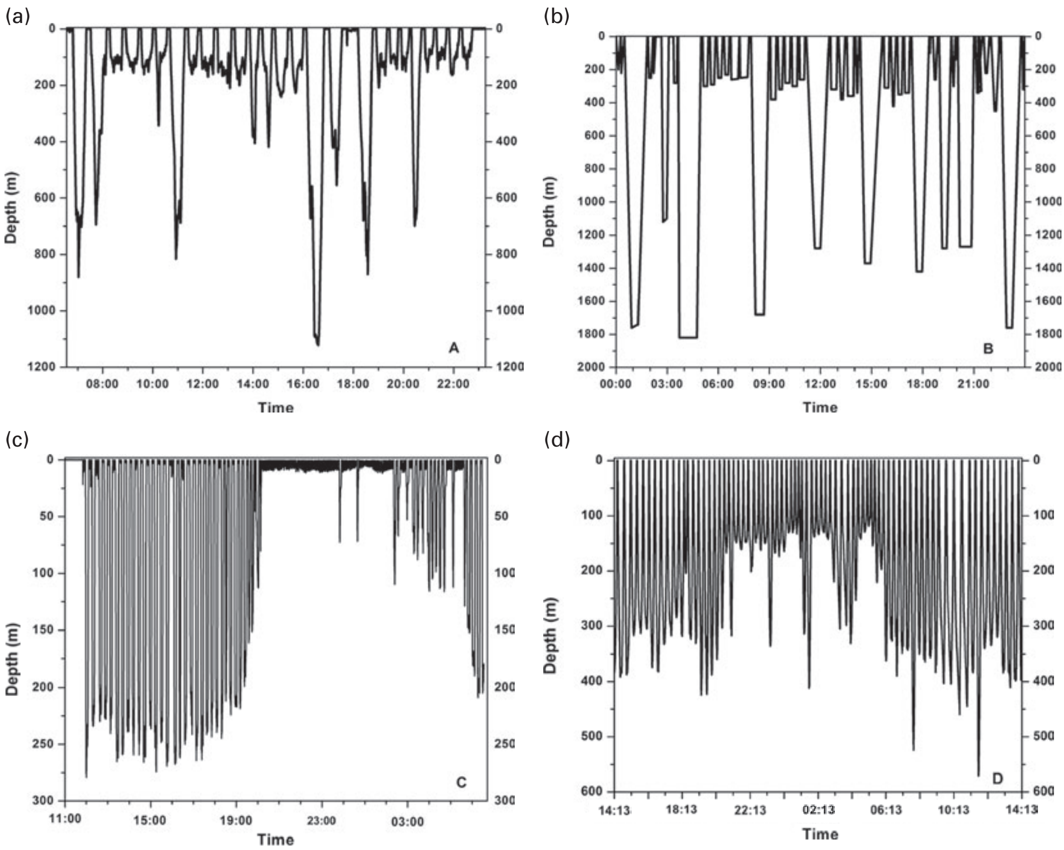

Figure 1.1 Representative 15–24-hour dive activity profiles of marine mammals and seabirds. **(a)** Sperm whale (*Physeter macrocephalus*) in the Bleik Canyon near Andenes, Norway, 2011 (courtesy of P.O. Miller, unpublished data). **(b)** Cuvier's beaked whale (*Ziphius cavirostris*), adapted from Schorr *et al.*, 2014. **(c)** Fin whale (*Balaenoptera physalus*), adapted from Goldbogen *et al.*, 2006, data courtesy of J. Goldbogen. **(d)** Juvenile northern elephant seal (*Mirounga angustirostris*), adapted from data of Meir *et al.*, 2009.

Weddell seals dive in bouts, with long rest periods on the sea ice between bouts (Kooyman, 1981, Kooyman *et al.*, 1980). Harbor seals (*Phoca vitulina*) and many other phocid seals also haul out regularly between foraging trips (Thompson *et al.*, 1989, 1991). This interrupted pattern of diving contrasts with that in northern/southern elephant seals and hooded seals (see Fig. 1.1). During the several-month-long trips of these three species to sea, the animals are underwater 80–90% of the time (Folkow and Blix, 1999, Hindell *et al.*, 1991, Le Boeuf *et al.*, 1988). Surface intervals are less than a few minutes. Accordingly, these species have been termed "surfacers," in contrast to the Weddell seal, which has been considered a "diver" (Kramer, 1988). Although this surfacer–diver concept was developed in regard to foraging ecology, the distinction between surfacers and divers also has implications for diving physiology.

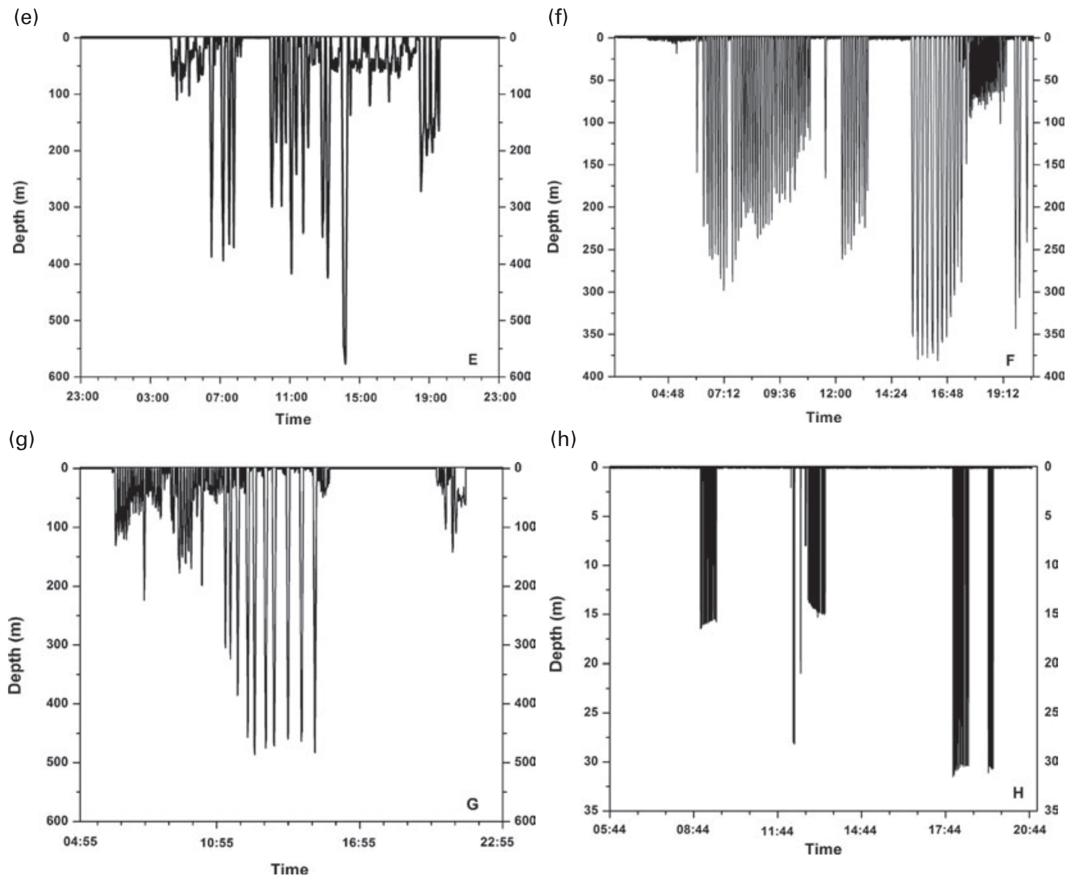

Figure 1.1 (*cont.*) **(e)** Weddell seal (Leptonychotes weddellii) in the Ross Sea, 2011 (courtesy of K. Goetz and D. Costa, unpublished data). **(f)** California sea lion (Zalophus californianus), adapted from data of McDonald and Ponganis, 2014. **(g)** Emperor penguin (*Aptenodytes forsteri*), adapted from data of Sato *et al.*, 2011. Last dive is the longest reported dive of an emperor penguin. **(h)** European shag (*Phalacrocorax aristotelis*), adapted from Sato *et al.*, 2008, data courtesy of K. Sato.

A surfacer such as the elephant seal, which goes to sea for 2–7 months, at times gaining an average of 1 kg of body mass per day (Le Boeuf *et al.*, 1988, Robinson *et al.*, 2012), must forage, process food, build up fat reserves, recover from long dives, and probably sleep all while holding its breath at depth underwater. It is remarkable that even after a two-hour dive, a southern elephant seal continued to make 30-min dives with short surface intervals for five hours, and then resumed serial one-hour dives after that (Hindell *et al.*, 1992). There was no prolonged surface recovery period. In contrast, after a 45-min dive, a Weddell seal spent nearly 70 min of the next two hours at the surface (Kooyman *et al.*, 1980). And, even without long dives, Weddell seals typically dive for only about 12 hours of the day (Castellini *et al.*, 1992a, Kooyman *et al.*, 1980).

Partitioning of the metabolic demands of travel, foraging, and digestion into different dive types may play a significant role in the continuous dive behavior of a surfacer such as the elephant seal. In the gray seal (*Halichoerus grypus*), a diver which routinely hauls out (Thompson *et al.*, 1991), the cost of digestion can be delayed until rest or haul-out periods (Sparling *et al.*, 2007). That option to process food at the surface does not occur in elephant seals. However, intensive research on the dive behavior of elephant seals has revealed several distinct dive profiles, including V-shaped dives (transit), active flat-bottom dives (benthic feeding), active bottom dives (pelagic feeding), and drift dives (dives with prolonged periods with no flipper strokes) (Crocker *et al.*, 1997, Hindell *et al.*, 1991, Le Boeuf *et al.*, 1993, Mitani *et al.*, 2010, Robinson *et al.*, 2012). Drift drives, considered to be rest dives because of the lack of stroking activity, have received much attention and have been proposed as periods of sleep as well as food processing. Changes in drift rates in such dives throughout a trip to sea have been used to identify the times and locations of increases in body buoyancy (fat deposition) and hence successful foraging by elephant seals (Biuw *et al.*, 2003, Robinson *et al.*, 2010). Partitioning of energy demands in different dive types so that dives are energetically similar in cost in elephant seals is supported by similar rates of blood oxygen depletion during those different dive types (Meir *et al.*, 2013).

Further documentation of foraging behavior, prey ingestion, and prey identification during foraging dives are being developed with use of stomach temperature sensors, jaw motion sensors, three-dimensional dive profile reconstructions, and digital/video cameras (Davis *et al.*, 1999, Horsburgh *et al.*, 2008, Kuhn *et al.*, 2009, Liebsch *et al.*, 2007, Naito *et al.*, 2013, Parrish *et al.*, 2002, Suzuki *et al.*, 2009, Ydesen et al., 2014). Such studies should yield insight into the time partitioning of energy demands of surfacers and, hence, into their ability to dive continuously.

1.1.2 Pinnipeds: otariids

Investigations of diving behavior in the otariids have primarily been conducted on lactating females during maternal foraging trips to sea. Such studies take advantage of a natural behavior – the regular return of lactating females from foraging trips to nurse their pups. Observation of this behavior in northern fur seals (*Callorhinus ursinus*) by Gentry in the early 1970s led to his collaboration with Kooyman to develop a longer-duration time–depth recorder and to their eventual documentation of dive behavior in six otariid species distributed from Alaska to the Antarctic and from the Galapagos to South Africa (Gentry and Kooyman, 1986, Kooyman *et al.*, 1976b). Since that time, every otariid species has been studied (Table 1.2).

In general, the fur seals and sea lions have not been considered as good divers as the phocid seals. The dives of otariids are shorter and shallower than those of phocid seals, with most dives less than four-min duration and less than 100 m in depth. However, at least some otariids do regularly perform deep dives. Even in the earliest

Table 1.2 Dive characteristics of otariid pinnipeds.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Northern fur seal *Callorhinus ursinus*	2	10	65	256	A
Antarctic fur seal *Arctocephalus gazella*	<2	11	30	240	B
Sub-Antarctic fur seal *A. tropicalis*	<2	7	10–30	208	C
South African fur seal *A. pusillus pusillus*	2	8	45	204	D
Australian fur seal *A. pusillus doriferus*	2–4	9	65–85	164	E
New Zealand fur seal *A. forsteri*	2–3	11	30–75	274	F
Galapagos fur seal *A. galapagoensis*	<2	5	26	115	D
Juan Fernandez fur seal *A. philippii*	2–4	–	<10	90	G
Guadalupe fur seal *A. townsendi*	2–3	18	10–20	130	H
South American fur seal *A. australis*	2–4	7	20–60	170	I
California sea lion *Zalophus californianus*	2	16	62	>482	J
New Zealand sea lion *Phocarctos hookeri*	4	20	123	597	K
Australian sea lion *Neophoca cinerea*	3–4	9	60	200	L
Southern sea lion *Otaria flavescens*	2–4	8	20–40	243	M
Steller sea lion *Eumetopias jubata*	<2	8	9–24	452	N
Galapagos sea lion *Zalophus wollebaeki*	3–6	11	50–150	387	O

References: A: Gentry *et al.*, 1986, Ponganis *et al.*, 1992a, Sterling and Ream, 2004; B: Boyd and Croxall, 1992, Kooyman *et al.*, 1986; C: Georges *et al.*, 2000a, 2000b; D: Horning and Trillmich, 1997, Kooyman and Trillmich, 1986; E: Arnould and Hindell, 2001; F: Mattlin *et al.*, 1998; G: Francis *et al.*, 1998; H: Gallo-Reynoso *et al.*, 2008, Lander *et al.*, 2000; I: Trillmich *et al.*, 1986; J: Feldkamp *et al.*, 1989, Melin *et al.*, 2008; K: Chilvers *et al.*, 2006; Gales and Mattlin, 1997; L: Costa *et al.*, 2001, Fowler *et al.*, 2006; M: Thompson *et al.*, 1998, Werner and Campagna, 1995; N: Merrick and Loughlin, 1997, Pitcher *et al.*, 2004; O: Villegas-Amtmann and Costa, 2010, Villegas-Amtmann *et al.*, 2008).

studies of northern fur seals, dive depths clustered at 50–60 m and 175 m, and individual fur seals were classified as shallow, deep, or mixed divers, dependent on their dive profiles (Gentry *et al.*, 1986). And although initial studies found that most dives of California sea lions (*Zalophus californianus*) and Galapagos sea lions

(*Zalophus wollebaeki*) were shallow (<100 m) (Feldkamp *et al.*, 1989, Kooyman and Trillmich, 1986), later investigations of these species in other locations have documented dives in the 400-m depth range (McDonald and Ponganis, 2013, Melin *et al.*, 2008, Villegas-Amtmann and Costa, 2010). Although such deep dives in Galapagos and California sea lions are a small percentage of all dives, performance of such dives, especially serial deep dives as in the California sea lion, demonstrate the physiological capacity of these animals. The deepest diving otariid is the benthic-feeding New Zealand sea lion (*Phocarctos hookeri*), which can dive as deep as 600 m and as long as 20 min (Chilvers, 2008). In regard to the surface–diver classification, otariids are divers, often not diving for about 50% of their time at sea, and, if some individuals do continuously dive while in the water, they regularly haul out onto land during their foraging trips (Thompson *et al.*, 1998).

1.1.3 Pinnipeds: odobenids

The walrus (*Odobenus rosmarus*), the lone member of the Odobenidae, is difficult to study due to both size and accessibility. Typically, these animals dive for 4–6 min, with a maximum of 24 min during underwater territorial displays and during foraging activity (Born and Knutsen, 1997, Gjertz *et al.*, 2001, Jay *et al.*, 2001, Nowicki *et al.*, 1997, Wiig *et al.*, 1993). Depths of dives are 30–70 m in range.

1.1.4 Cetaceans

The ability to document cetacean diving behavior began with the pioneering radio telemetry research of Evans on dolphins, and Watkins and Schevill on whales (Evans, 1971, Watkins, 1978, 1979, Watkins and Schevill, 1977, Watkins and Tyack, 1991). Miniaturization of recorders/transmitters and refinement of attachment techniques, including suction cups and percutaneous darts, have since allowed application to a wide variety of species (Andrews *et al.*, 2008, Balmer *et al.*, 2014, Baird, 1998, Hooker and Baird, 2001, Johnson and Tyack, 2003, Mate *et al.*, 2007). In particular, Johnson and Tyack's development of the DTAG, an archival recorder specifically designed to examine behavioral responses of marine mammals to sound, has been a significant breakthrough in at-sea cetacean behavioral research. Data from DTAGs have allowed detailed analyses of depth profiles, orientation, stroking, echolocation signals, prey capture, and foraging efficiency in sperm whales (*Physeter macrocephalus*) and beaked whales (family: Ziphiidae) (Johnson *et al.*, 2004, 2006, Madsen *et al.*, 2002, 2005, 2007, Miller *et al.*, 2004b, 2004c, Tyack *et al.*, 2006, Watwood *et al.*, 2006, Zimmer *et al.*, 2003).

Among the cetaceans, the most notable dive depths and durations are those of the large toothed whales, specifically sperm whales and beaked whales (Baird *et al.*, 2008, Hooker and Baird, 1999, Schorr *et al.*, 2014, Tyack *et al.*, 2006, Watkins *et al.*, 1993) (Table 1.3). Routine depths and durations range from 400 to 800 m and 40 to 60 min, respectively, with maximum depths and durations greater than 2000 m and 120 min. Currently, in 2015, Cuvier's beaked whale (*Ziphius cavirostris*) holds the record for any mammal for the

Table 1.3 Dive characteristics of some odontocete cetaceans.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Harbor porpoise *Phocoena phocoena*	1	5	14–40	226	A
Finless porpoise *Neophocoena phocoenoides*	2	–	<25	–	B
Dall's porpoise *Phocoenoides dalli*	2–4	–	<70	94	C
Bottlenose dolphin *Tursiops truncatus*	1	8	20	>500	D
Spotted dolphin *Stenella attenuata, S. frontalis*	1–2	5	20–60	213	E
Spinner dolphin *S. longirostris*	<4	–	–	–	F
Common dolphin *Delphinus delphis*	–	5	30–60	280	G
Dusky dolphin *Lagenorhynchus obscurus*	–	–	50–65	130	H
Atlantic white-sided dolphin *L. acutus*	<1	1	–	–	I
Pacific white-sided dolphin *L. obliquidens*	–	6	–	215	J
Risso's dolphin *Grampus griseus*	<50	>400	–	–	K
Pilot whale *Globicephala* sp.	5–15	21	100–800	1019	L
Narwhal (*Monodon monoceros*)	1–15	26	150–500	>1000	M
Beluga whale *Delphinapterus leucas*	9–16	23	50–350	647	N
False killer whale *Pseudoorca crassidens*	5–12	15	50–650	650	O
Killer whale *Orcinus orca*	2–5	–	–	265	P
N. bottlenosed whale *Hyperoodon ampullatus*	40	70	800	1483	Q
Cuvier's beaked whale *Ziphius cavirostris*	58–70	138	1070–1334	2992	R
Baird's beaked whale *Berardius bairdii*	10–45	65	100–1500	1777	S
Arnoux's beaked whale *Berardius arnuxii*	10–45	>70	–	–	T
Blainville's beaked whale *Mesoplodon densirostris*	47–55	84	835–1099	1599	U

Table 1.3 (*cont.*)

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Sperm whale *Physeter macrocephalus*	40–60	138	400–900	2250	V

References: A: Otani *et al.*, 1998, Westgate *et al.*, 1995; B: Akamatsu *et al.*, 2010; C: Hanson and Baird, 1998, Jefferson, 1987; D: Klatsky *et al.*, 2007, Mate *et al.*, 1995, Ridgway, 1986; E: Baird *et al.*, 2001, Davis *et al.*, 1996, Scott and Chivers, 2009; F: Norris and Dohl, 1980; G: Evans, 1971, Ridgway, 1986; H: Benoit-Bird *et al.*, 2004; I: Mate *et al.*, 1994; J: Hall, 1970, Ridgway, 1986; K: Wells *et al.*, 2009; L: Aguilar de Soto *et al.*, 2008, Baird *et al.*, 2002, Heide-Jorgensen *et al.*, 2002, Nawojchik *et al.*, 2003; M: Heide-Jorgensen and Dietz, 1995, Laidre *et al.*, 2002; N: Martin and Smith, 1992, 1999, Ridgway *et al.*, 1984; O: Minamikawa *et al.*, 2013; P: Baird *et al.*, 2006a; Q: Hooker and Baird, 1999; R: Baird *et al.*, 2008, Schorr *et al.*, 2014, Tyack *et al.*, 2006; S: Minamikawa *et al.*, 2007; T: Hobson and Martin, 1996, Ponganis *et al.*, 1995; U: Baird *et al.*, 2008, Tyack *et al.*, 2006; V: Jaquet *et al.*, 2000, Norris and Harvey, 1972, Papastavrou *et al.*, 1989, Watkins *et al.*, 1993, Watwood *et al.*, 2006.

Table 1.4 Dive characteristics of some mysticete whales.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Humpback whale *Megaptera novaeanglieae*	4–8	–	23–118	~160	A
Blue whale *Balaenoptera musculus*	5–10	–	180–200	–	B
Fin whale *Balaenoptera physalus*	3–8	12	<100	470	C
Minke whale *Balaenoptera acutorostrata*, *B. bonaerensis*	<5	9	<50	105	D
Bryde's whale *Balaenoptera brydei*	5	9	40–200	292	E
Right whale *Eubalaena glacialis*	12	–	120	–	F
Bowhead whale *Balaena mysticetus*	≤1–15	63	<16–100	487	G
Gray whale *Eschrictius robustus*	2–5	13	<30	–	H

References: A: Witteveen *et al.*, 2008; B: Croll *et al.*, 1998; C: Panigada *et al.*, 1999; D: Friedlaender *et al.*, 2014, Stockin *et al.*, 2001; E: Alves *et al.*, 2010; F: Baumgartner and Mate, 2003; G: Krutzikowsky and Mate, 2000, Laidre *et al.*, 2007; H: Stelle *et al.*, 2008, Stewart *et al.*, 2001, Woodward and Winn, 2006, Würsig *et al.*, 1986).