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).

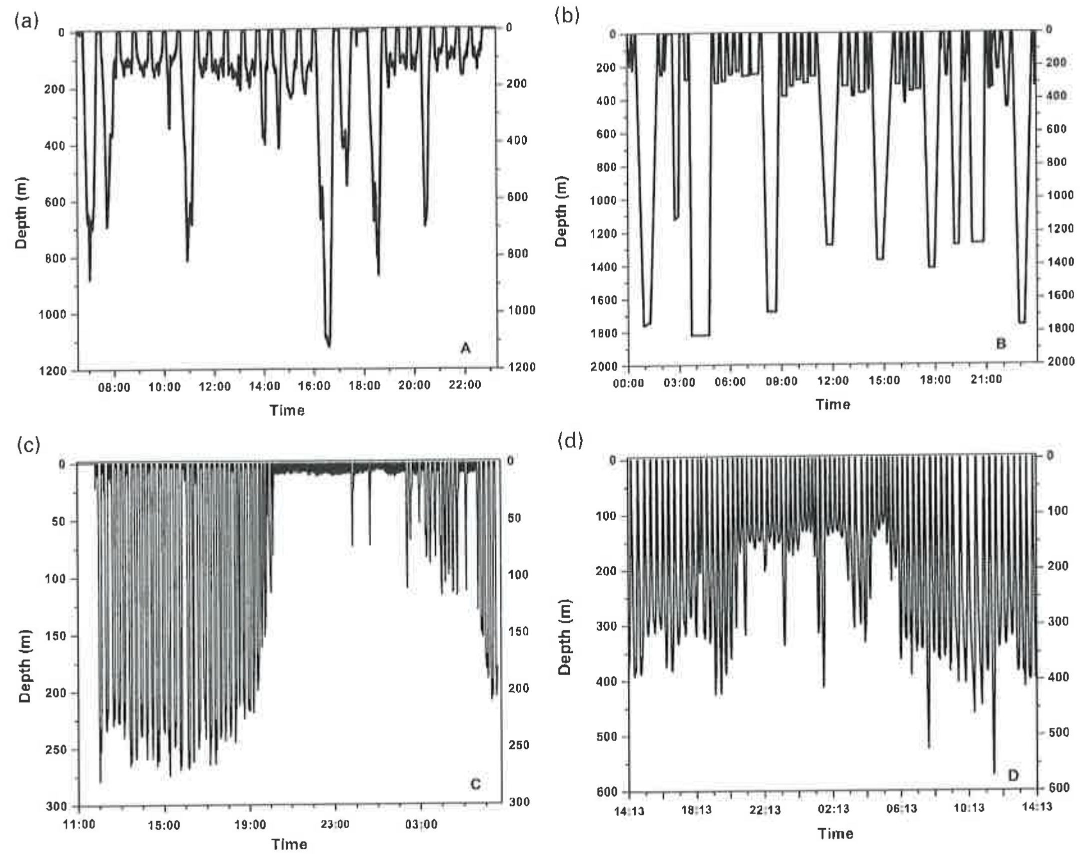

Figure 1.1 Representative 15–24-hour dive activity profiles of marine mammals and seabirds. **(a)** Sperm whale (*Physeter macrocephalus*) in the Bleik Canyon near Andenes, Norway, 2011 (courtesy of P.O. Miller, unpublished data). **(b)** Cuvier's beaked whale (*Ziphius cavirostris*), adapted from Schorr *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.

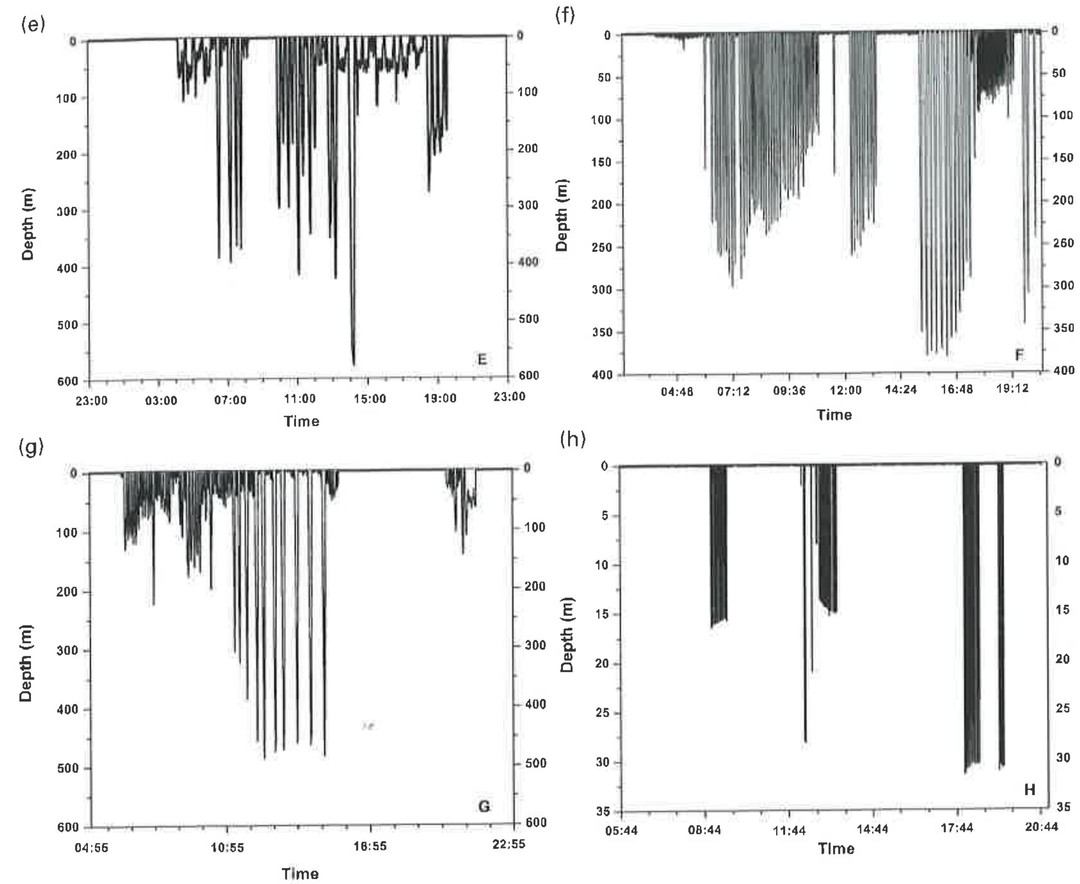

Figure 1.1 (*cont.*) **(e)** Weddell seal (Leptonychotes weddellii) in the Ross Sea, 2011 (courtesy of K. Goetz and D. Costa, unpublished data). **(f)** California sea lion (Zalophus californianus), adapted from data of McDonald and Ponganis, 2014. **(g)** Emperor penguin (*Aptenodytes forsteri*), adapted 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).

longest (137.5 min) and deepest (2992 m) dives (Schorr *et al.*, 2014). Pilot whales (*Globicephala* sp.), narwhals (*Monodon monceros*), beluga whales (*Delphinapterus leucas*), and false killer whales (*Pseudoorca crassidens*) are also deep divers, although dive durations are usually less than 20 min (Table 1.3).

The well-known bottlenose dolphin (*Tursiops truncatus*) was considered to typically dive for fewer than 5 min to shallow depths <20 m (Mate *et al.*, 1995). But, again, more recent studies of bottlenose dolphins in other locations have revealed regular dives to near 500-m depth (Klatsky *et al.*, 2007). Such deep dives are consistent with trained, open-water dives of Atlantic bottlenose dolphins (*Tursiops truncatus*), and Pacific bottlenose dolphins (*Tursiops gillii*) to 390 m and 535 m, respectively, with durations of 7.5 to 8 min (Ridgway, 1986). Dives of pelagic spotted dolphins (*Stenella attenuata*) are up to five min in duration, and can be as deep as 200 m (Mate *et al.*, 1995, Scott and Chivers, 2009). Documentation of the dive behavior of other dolphins and porpoises, as well as the mysticete whales, has been limited due to difficulties in capture or recorder deployment/attachment. In some cases, as for river dolphins and gray whales (*Eschrictius robustus*), only visual observations are primarily available for estimation of dive durations. River dolphins usually dive for fewer than 2 min, although dives as long as 8 min have been reported in Ganges River dolphins (*Platanista gangetica*) and Irawaddy dolphins (*Orcaella brevirostris*) (Bashir *et al.*, 2013, Edwards and Schnell, 2001, Renjun *et al.*, 1994, Stacey and Hvenegaard, 2002). In general, the baleen whales have dive durations under 10 min; they too, however, can reach depths of 200 m (Croll *et al.*, 1998, Friedlaender *et al.*, 2014, Witteveen *et al.*, 2008).

Classification of cetaceans as surfacers or divers depends on the species. Data are limited due to lack of long-term deployments of dive recorders, but currently available evidence indicates that sperm whales and beaked whales should be considered surfacers. Similar to the elephant seal, 80–90% of the day they are submerged below 10-m depth (Hooker *et al.*, 2012, Watkins *et al.*, 1999). Surface periods of Cuvier's beaked whale averaged less than two minutes (Schorr *et al.*, 2014). However, killer whales (*Orcinus orca*) and pilot whales should be classified as divers as they have been reported to spend almost 70–80% of their time within 10 m of the surface (Hooker *et al.*, 2012). Hanging or logging at the surface has been observed in some baleen whales and beluga whales, but the percentage time at the surface is unknown (Lyamin *et al.*, 2000, Sjare and Smith, 1986). Similarly, the percentage of time that some dolphin species may swim apparently asleep in shallow water is also not known (Lyamin *et al.*, 2008, Norris and Dohl, 1980, Wursig and Wursig, 1980).

1.1.5 Sirenians

Manatees (*Trichechus* sp.) and dugongs (*Dugong dugon*) usually dive for 2–3 min (Chilvers *et al.*, 2004, Gallivan and Best, 1980, Gallivan *et al.*, 1986, Marsh *et al.*, 1978, Reynolds III, 1981, Reynolds III and Odell, 1991). Maximum dive depths of these herbivorous mammals are about 12 m.

1.1.6 Marine carnivores

The polar bear, perhaps the most famous and certainly the largest of marine carnivores, is an excellent swimmer (Stirling, 1974). Most dives are less than 0.5 min; the longest reported dive is 3.2 min (Dyck and Romberg, 2007, Stirling and van Meurs, 2015). Most dives of sea otters are 1–3 min in duration and less than 30 m in depth (Ralls *et al.*, 1995, Tinker *et al.*, 2007, Yeates *et al.*, 2007). Dive durations of other otters such as the Eurasian otter (*Lutra lutra*) are usually less than 1 min (Conroy and Jenkins, 1986, Nolet *et al.*, 1993).

1.1.7 Aquatic mammals

Among aquatic animals, the muskrat (*Ondatra zibethicus*) has been perhaps the most frequent subject of physiological investigations. Dive durations of the muskrat are usually less than 2 min, although exploratory and alarm dives can be as long as 4 min (MacArthur *et al.*, 2001). Beavers (*Castor canadensis*), another research subject, usually dive for less than 2 min, but have been observed to stay underwater as long as 15 min at rest (Irving and Orr, 1935, Tevis, 1950). The Eurasian beaver performs dives as long as 4.9 min and as deep 4.2 m (Graf *et al.*, 2014) The platypus (*Ornithorhynchus anatinus*) usually dives for less than 2 min duration and to depths of less than 10 m (Bethge *et al.*, 2003). One of the smallest mammalian divers, the star-nosed mole (40–60 g, *Condylura cristata*) makes 10-sec dives with a reported maximum dive duration of 47 sec (McIntyre *et al.*, 2002). The capybara (*Hydrochaeris hydrochaeris*), a South American aquatic rodent, usually dives for less than 30 sec, although it has been reported to dive for several minutes (Creed, 2004).

1.2 Seabirds

Diving seabirds are composed of members from several avian orders, Procellariiformes, Charadriiformes, Pelecaniformes, and Sphenisciformes. The Procellariiformes (tube noses) include diving petrels, storm petrels, fulmars, prions, shearwaters, other petrels, and albatrosses. The family, Alcidae, comprises the diving seabirds of the Charadiformes, an order which also includes gulls, skuas, skimmers, and terns. The alcids include murres, little auks, razorbills, true guillemots, two groups of murrelets, puffins, auklets, and the extinct great auk (*Pinguinus impennis*). Cormorants (shags), gannets, and boobies are the accomplished divers of the order, Pelicaniformes; this order also includes pelicans, frigatebirds, and tropicbirds. Penguins comprise the Sphenisciformes.

Documentation of the diving activities of many seabirds has been limited by recorder size, flight requirements, and body size. Dive durations of many of the smaller alcids have only been determined by observation or surface radio transmissions, while diving

Table 1.5 Dive characteristics of the Procellariiformes.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Common diving petrel *Pelecanoides urinatrix*	<1	–	<50	64	A
Peruvian diving petrel *Pelecanoides garnotii*	–	–	<40	83	B
S. Georgian diving petrel *Pelecanoides georgicus*	–	–	<40	49	C
Antarctic prion *Pachyptila desolata*	–	–	<5	7	D
Slender-billed petrel (thin-billed prion) *Pachyptila belcheri*	–	–	5	7	E
Blue petrel *Halobaena caerulea*	–	–	5	6	E
Bulwer's petrel *Bulweria bulwerii*	–	–	3	5	F
Northern fulmar *Fulmarus glacialis*	<0.1	0.1	<1	<3	G
Westland petrel *Procellaria westlandica*	–	–	3	<8	H
White-chinned petrel *Procellaria aequincotialis*	<0.1	0.1	<10	13	I
Monteiro's storm petrel *Oceanodroma monteiroi*	–	–	<1	<2	J
Audubon's shearwater *Puffinus lherminieri*	–	–	<30	35	K
Balearic shearwater *Puffinus mauretanicus*	<0.5	1.1	<10	26	L
Black-vented shearwater *Puffinus opisthomelas*	–	–	<40	52	M
Flesh-footed shearwater *Puffinus carneipes*	–	–	<10	67	N
Short-tailed shearwater *Puffinus tenuirostris*	–	–	<60	71	O
Sooty shearwater *Puffinus griseus*	–	–	<40	70	P
Wedge-tailed shearwater *Puffinus pacificus*	–	–	<50	66	K
Barolo shearwater *Puffinus baroli*			<20	23	Q
Streaked shearwater *Calonectris leucomelas*	–	–	–	5	R
Black-browed albatross *Thalassarche melanophris*	<0.1	0.2	<4	4.5	S
Grey-headed albatross *Thalassarche chrysostoma*	<0.1	0.2	<5	6.5	T

Table 1.5 (*cont.*)

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Shy albatross *Thalassarche cauta*	<0.2	0.3	<5	7.4	U
Light-mantled albatross *Phoebetria palpebrata*	–	–	<8	12.4	V
Wandering albatross *Diomedea exulans*	–	–	<0.5	0.6	V

References: A: Bocher *et al.*, 2000a, 2000b, Chastel, 1994, Ryan and Nel, 1999; B: Zavlaga and Jahncke, 1997; C: Bocher *et al.*, 2000a, Prince and Jones, 1992; D: Cherel *et al.*, 2002; E: Chastel and Bried, 1996; F: Mougin and Mougin, 2000; G: Garthe and Furness, 2001; H: Freeman *et al.*, 1997; I: Huin, 1994; J: Bried, 2005; K: Burger, 2001; L: Aguilar *et al.*, 2003; M: Keitt *et al.*, 2001; N: Rayner *et al.*, 2011; O: Weimerskirch and Cherel, 1998; P: Shaffer *et al.*, 2006, 2009, Weimerskirch and Sagar, 1995; Q: Neves *et al.*, 2012; R: Oka, 1994; S: Prince *et al.*, 1994, Sakamoto *et al.*, 2009; T: Huin and Prince, 1997, Prince *et al.*, 1994; U: Hedd *et al.*, 1997; V: Prince *et al.*, 1994.

depths of most procellariforms have been determined only with capillary depth gauges. Consequently, there are only limited observations on many of the species in Tables 1.5 (Procellariiformes) and 1.10 (other aquatic birds).

The miniaturization of electronic dive recorders, and conduct of studies on many seabird species, have been pioneered by Naito and colleagues at Japan's National Institute of Polar Research and the University of Tokyo (Croxall et al., 1991, 1993, Kato *et al.*, 1992, 2003, Kuroki *et al.*, 2003, Ropert-Coudert *et al.*, 2004a, Watanuki *et al.*, 1996, Williams *et al.*, 1992b). Their international collaborations have provided much of the data in Tables 1.6–1.9. Despite size limitations, more advanced recorders have also been developed for analysis of behavior and activity during diving of seabirds. These recorders and techniques include velocity meters, accelerometers, three-dimensional dive profile reconstructions, stomach and esophageal temperature recorders, beak angle detectors, and digital/video cameras (Charrassin *et al.*, 2001, Ponganis *et al.*, 2000, Sato *et al.*, 2002, 2007, Shiomi *et al.*, 2012, Takahashi *et al.*, 2004a, 2004b, 2008, Watanabe *et al.*, 2011, Wilson *et al.*, 1992a, 1995, 2002b). In addition to documenting behavior during the dive, such applications have also provided insight into foraging ecology, biomechanics, and even diving physiology (Sato *et al.*, 2002, 2009, 2011, Watanabe and Takahashi, 2013, Watanabe *et al.*, 2012, Watanuki *et al.*, 2006, 2008, Wilson *et al.*, 2010).

1.2.1 Procellariiform seabirds

Among Procellariiformes (Table 1.5), the diving petrels and shearwaters appear to be the best divers, reaching depths of 60–70 m. These birds plunge dive and use winged

Table 1.6 Dive characteristics of alcids.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Atlantic puffin *Fratercula arctica*	<1	1.9	10–40	68	A
Rhinoceros auklet *Cerorhinca monocerata*	<1	2.5	10–30	60	B
Cassin's auklet *Ptychoramphus aleuticus*	<1	1.2	10–20	43	C
Common murre (common guillemot) *Uria aalge*	<2	3.4	20–50	138	D
Thick-billed murre (Brunnich's guillemot) *Uria lomvia*	<2	4.1	10–60	210	E
Little auk (Dovekie) *Alle alle*	<1	1.5	8–12	27	F
Razorbill *Alca torda*	<1	–	15–30	140	G
Pigeon guillemot *Cepphus columba*	<2	2.4	10–40	45	H
Xantu's murrelet *Synthliboramphus hypoleucus*	<1	–	–	–	I
Marbled murrelet *Brachyramphus marmoratus*	<1	1.9	–	–	J

References: A: Burger and Simpson, 1986, Wanless *et al.*, 1988; B: Burger *et al.*, 1993, Kuroki *et al.*, 2003; C: Ainley *et al.*, 1990, Burger and Powell, 1990; D: Burger and Simpson, 1986, Tremblay *et al.*, 2003, Wanless *et al.*, 1988; E: Croll *et al.*, 1992a, Elliott *et al.*, 2007; F: Brown *et al.*, 2012, Falk *et al.*, 2000, Harding *et al.*, 2009; G: Benvenuti *et al.*, 2001; Jury, 1986; H: Clowater and Burger, 1994; I: Hamilton *et al.*, 2005; J: Henkel *et al.*, 2004, Jodice and Collopy, 1999, Thoresen, 1989.

propulsion, although shearwaters can also use their legs for underwater locomotion (Brown *et al.*, 1978). The depths are impressive, given that diving petrels weigh only 100–150 g (Chastel, 1994, Prince and Jones, 1992). Prions and other petrels appear confined to shallow depths (<10 m) while the occasional dives of albatrosses are also shallow. The southern giant petrel (*Macronectes giganticus*) has also been observed to dive and feed on submerged carrion in shallow water (Van Den Hoff and Newbery, 2006).

1.2.2 Charadriiform seabirds

The diving behaviors of the alcids have been more extensively studied than those of the Procellariiformes. Dive durations of the wing-propelled alcids are usually less than 1–2 min and less than 60 m in depth (Table 1.6). The 1-kg murres are the best divers

Table 1.7 Dive characteristics of cormorants and shags.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Antarctic shag *Phalacrocorax bransfieldensis*	<2	5.4	10–70	113	A
Cape cormorant *Phalacrocorax capensis*	<1	1.2	10–20	34	B
Crozet shag *Phalacrocorax melanogenis*	1–2	6.2	< 40	145	C
Great cormorant *Phalacrocorax carbo*	<1	2.5	<10	33	D
Japanese cormorant *Phalacrocorax capillatus*	<1	2.4	<20	45	E
King cormorant *Phalacrocorax albiventer*	1–3	5.1	<40	109	F
European shag *Phalacrocorax aristotelis*	<1	2.7	<40	61	G
Blue-eyed shag *Phalacrocorax atriceps*	2–4	6.3	10–80	125	H
Flightless cormorant *Phalacrocorax harrisi*	<2	3.3	<15	73	I

References: A: Casaux, 2004, Casaux and Barrera-Oro, 2006, Casaux *et al.*, 2001; B: Ryan *et al.*, 2010; C: Tremblay *et al.*, 2005; D: Grémillet *et al.*, 1999, Kato *et al.*, 2006; E: Watanuki *et al.*, 1996; F: Kato *et al.*, 2000; G: Wanless *et al.*, 1993, 1997, 1999; H: Croxall et al., 1991, Wanless and Harris, 1993, Wanless *et al.*, 1992; I: Wilson et al., 2008).

among the group, with remarkable maximal dive durations and depths near 3–4 min and 138–210 m. Puffins, auklets, and the razor bill (*Alca torda*) have slightly shallower routine depths and shorter dive durations (Table 1.6).

1.2.3 Pelecaniform seabirds

Cormorants and shags of the Pelecaniformes order are foot-propelled divers with some maximum dive depths and durations that are equally or perhaps more impressive than those of murres (Table 1.7). Both the Crozet shag (*Phalacrocorax melanogenis*) and blue-eyed shag (*Phalacrocorax atriceps*), about 2–2.5 kg in weight, have maximum dive durations greater than 6 min and maximum depths greater than 125 m (see Table 1.7 for references). The diving performances of the Antarctic shag (*Phalacrocorax bransfieldensis*) and king cormorant (*Phalacrocorax albiventer*) are only slightly less.

Boobies and gannets are short-duration (<1 min) plunge divers that primarily reach depths less than 20 m (Table 1.8). Although not studied extensively, pelicans appear limited to near-surface activities. Darters or anhingas are foot-propelled,

Table 1.8 Dive characteristics of the Pelecaniformes, excluding cormorants and shags (Phalacrocoracidae). All are marine birds except the African darter.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Peruvian pelican *Pelecanus thagus*	<0.1	–	–	–	A
Blue-footed booby *Sula nebouxii*	<0.3	0.6	<8	22	B
Peruvian booby *Sula variegata*	0.1	<0.3	<5	10	C
Red-footed booby *Sula sula*	<0.1	<0.2	<7	10	D
Cape gannet *Morus capensis*	0.1	0.5	<5	13	E
Northern gannet *Morus bassanus*	<0.3	0.7	<15	34	F
Red-tailed tropic bird *Phaethon rubricauda*	–	–	<7	13	G
African Darter *Anhinga rufa*	<1.5	1.8	–	–	H

References: A: Duffy, 1983; B: Zavalaga *et al.*, 2007; C: Duffy, 1983, Ludynia *et al.*, 2010; D: LeCorre, 1997, Weimerskirch *et al.*, 2005; E: Grémillet *et al.*, 2004, Ropert-Coudert *et al.*, 2004a, 2004b; F: Brierley and Fernandes, 2001, Lewis *et al.*, 2002, Ropert-Coudert *et al.*, 2009; G: LeCorre, 1997; H: Ryan, 2007.

shallow-diving, freshwater members of the Pelecaniformes, but are in a separate family (Anhingidae) from the cormorants and shags (Phalacrocoracidae).

1.2.4 Penguins

Penguins (order: Sphenisciformes) have a broad range of diving behaviors (Table 1.9). Routine dive depths and durations of many penguin species with smaller body masses are less than 60 m and 2 min, respectively. These values and even the maximum values of those penguin species are equivalent to the dive data for murres and the deeper-diving cormorant species. The gentoo penguin (*Pygoscelis papua*) appears to be the best diver among the pygoscelid and other smaller-bodied penguin species, with routine dive depths greater than 80 m and regular dive durations of three or more minutes (see Table 1.9). The largest-bodied penguins, king (*Aptenodytes pagagonicus*) and emperor (*A. forsteri*) penguins, are the most accomplished avian divers. The 12-kg king penguin routinely makes dives of 3–6-min duration, with most maximum depths near 300 m, while 25-kg emperor penguins have regular dives as long as 10 min and as deep as 400 and even 500 m (see Table 1.9). Although 400–500-m deep dives of emperor penguins form a small percentage of all the dives during a

Table 1.9 Dive characteristics of penguins.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Galapagos penguin *Spheniscus mendiculus*	<1	3.2	<6	52	A
Magellanic penguin *S. magellanicus*	1–2	4.6	<60	97	B
Humboldt penguin *S. humboldti*	<1	2.8	<20	54	C
African penguin *S. demersus*	1–2	2.3	20–80	130	D
Little penguin *Eudyptula minor*	<1–1.5	1.5	<10	69	E
Yellow-eyed penguin *Megadyptes antipodes*	1–2	–	10–30	56	F
Royal penguin *Eudyptes schlegeli*	1–3	7.5	<10–60	226	G
N. rockhopper penguin *E. chrysocome moseleyi*	<1–1.5	3.2	<10–40	168	H
S. rockhopper penguin *E. chrysocome filholi*	1–2	11	<10–60	113	I
Macaroni penguin *E. chrysolophus*	1–2	4	20–35	113	J
Adélie penguin *Pygoscelis adeliae*	1–2	5.9	10–40	180	K
Chinstrap penguin *P. anarcticus*	1–2	3.6	10–40	179	L
Gentoo Penguin *P. papua*	1–3	9.1	10–100	225	M
King penguin *Aptenodytes patagonicus*	2–6	9.2	<100–250	343	N
Emperor penguin *A. forsteri*	<5–10	27.6	<100–400	564	O

References: A: Boersma, 1976, Mills, 2000, Steinfurth *et al.*, 2008; B: Peters *et al.*, 1998, Walker and Boersma, 2003; C: Culik *et al.*, 2000, Luna-Jorquera and Culik, 1999; D: Petersen *et al.*, 2006, Wilson, 1985, Wilson and Wilson, 1990; E: Bethge *et al.*, 1997, Gales *et al.*, 1990, Montague, 1985, Ropert-Coudert *et al.*, 2003, 2006; F: Seddon and Vanheezik, 1990; G: Hull, 2000; H: Cherel *et al.*, 1999, Tremblay and Cherel, 2003; Tremblay *et al.*, 1997; I: Hull, 2000, Schiavani and Rey, 2004, Tremblay and Cherel, 2000, Wilson et al., 1997a; J: Boyd and Croxall, 1996, Croxall *et al.*, 1993, Green *et al.*, 1998, 2003; K: Chappell *et al.*, 1993, Norman and Ward, 1993, Watanuki *et al.*, 1997; L: Bengtson *et al.*, 1993, Miller and Trivelpiece, 2008, Takahashi *et al.*, 2003, Wilson and Peters, 1999; M: Lescroel and Bost, 2005, Robinson and Hindell, 1996, Williams *et al.*, 1992b; N: Charrassin and Bost, 2001, Kooyman *et al.*, 1992a, Pütz and Cherel, 2005, Pütz *et al.*, 1998; O: Kirkwood and Robertson, 1997, Kooyman and Kooyman, 1995, Rodary *et al.*, 2000, Sato *et al.*, 2011, Wienecke *et al.*, 2007.

foraging trip to sea, the emperor penguins in the Ross Sea do regularly perform such deep dives (Kooyman and Kooyman, 1995, Sato *et al.*, 2011). The frequency of these dives is much lower for emperor penguins in other areas of Antarctica (Wienecke *et al.*, 2007).

Table 1.10 Dive characteristics of other aquatic birds.

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Common loon *Gavia immer*	<1.5	2	–	55	A
Australasian grebe *Tachybaptus novaehollandiae*	<0.5	–	–	–	B
Least grebe *Tachybaptus dominicus*	<0.5	–	–	–	C
Great crested grebe *Podiceps cristatus*	<1	–	–	–	D
Red-necked grebe *Podiceps grisegena*	<0.6	–	–	–	E
Horned grebe *Podiceps auritus*	<0.6	–	–	–	F
Hoary-headed grebe *Poliocephalus poliocephalus*	<0.5	–	–	–	G
New Zealand dabchick *Poliocephalus rufopectus*	<0.5	<1.0	–	–	H
Pie-billed grebe *Podilymbus podiceps*	<0.5	–	–	–	C
Western grebe *Aechmophorus occidentalis*	<0.5	<1.1	–	–	I
Common goldeneye *Bucephala clangula*	<0.5	–	–	–	J
Common scoter *Melanitta nigra*	<1.0	–	–	–	K
Long-tailed duck *Clangula hyemilis*	–	–	–	60	L
Common eider *Somateria mollissima*	<1.0	1.3	<6	9	M
Common pochard *Aythya ferina*	<0.3	–	–	–	N
Tufted duck *Aythya fuligula*	<0.5	0.8	–	–	O
Lesser scaup *Aythya affinis*	<0.5	–	–	–	P
Red-headed duck *Aythya americana*	<0.5	–	–	–	Q
Canvasback duck *Aythya valisineria*	<0.5	–	–	–	R

Table 1.10 (*cont.*)

Species	Duration (min)		Depth (m)		Reference
	Common	Max	Common	Max	
Mallard (pekin) duck *Anas platyrhynchos*	<0.1	<0.2	–	–	S
American coot *Fulica americana*	<0.1	–	–	–	T
Dipper *Cinclus mexicantis*	<0.5	0.5	<1.0	6.0	U

References: A: Nocera and Burgess, 2002, Schorger, 1947; B: Ropert-Coudert and Kato, 2009; C: Jenni and Gambs, 1974; D: Ulenaers *et al.*, 1992; E: Simmins, 1969; F: Dow, 1964, Ladhams, 1968; G: Ropert-Coudert and Kato, 2009; H: Edgar, 1962; I: Forbes and Sealy, 1988; J: Heintzelman, 1963; K: Kaiser *et al.*, 2006; L: Schorger, 1947; M: Guillemette *et al.*, 2004, Ron and Guillemette, 1991; N: Butler and Woakes, 1979; O: Butler and Woakes, 1979, 1982, Stephenson *et al.*, 1989b; P: Stephenson, 1994; Q: Furilla and Jones, 1987b; R: Woodin and Stephenson, 1998; S: Furilla and Jones, 1987a; T: Batulis and Bongiorno, 1972; U: Murrish, 1970.

In terms of the surfacer–diver classification, penguins are best considered divers. King penguins, for example, spend only about 40% of time at sea diving during their 5–10-day foraging trips (Pütz and Cherel, 2005, Pütz *et al.*, 1998). In contrast to the continuous diving activity of a surfacer such as the elephant seal, after the longest reported dive (27.6 min) of an emperor penguin, the bird required 6 min to stand up from the prone position on the sea ice, another 20 min to begin to walk, and a total of 8.4 hours before it began to dive (Sato *et al.*, 2011). During foraging trips to sea during the chick-nurturing period, emperor penguins spend 20–40% of their time out of the water on the sea ice (Watanabe *et al.*, 2012).

1.2.5 Other aquatic birds

The last table in this chapter reviews known diving behavior of other aquatic birds. Although many of these birds are freshwater rather than marine species, they are included both for comparison and because many diving physiology studies have been conducted on ducks. Although they are members of different avian orders, the loons, grebes, and ducks are all foot-propelled swimmers. Eiders also use their wings. As of this writing, the diving of grebes and loons has been little studied. Loons, however, have been caught in nets as deep as 55 m and observed to dive for as long as 2 min (see Table 1.10). Such diving performance is probably comparable to those of diving petrels and shearwaters, boobies and gannets, some of the smaller alcids, and even the smallest-bodied penguin species.

Examination of the diving behaviors of different duck species has been primarily limited to observation, often in experimental aquaria (Table 1.10). In general, the best divers among the ducks are considered to be the diving ducks (pochards, and scaups including the genus *Aythya*, and stiff-tailed ducks), and the sea ducks (multiple species including eiders, scoters, goldeneyes, mergansers, smews, the harlequin duck (*Histrionicus histrionicus*), and the long-tailed duck (*Clangula hyemilis*)). The long-tailed duck has been caught in nets at 60 m depth (Schorger, 1947). Otherwise, the known diving depths and durations of diving ducks and sea ducks are shallow and short (<1 min). The dabbling ducks (primarily members of the genus *Anas*, including teals, pintails, mallards, and shovelers) are not considered divers.

The distinction between diving and dabbling ducks is important because diving physiology studies have been conducted on both types of ducks and some physiological responses to breath-holding are distinct between the two groups (Furilla and Jones, 1987a). Consequently, in reviewing physiological findings in ducks, it is important to always remember whether the subject species is a diver or a dabbler.