Cardiovascular physiology in dolphins and other cetaceans

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Abstract

The cardiovascular system in cetaceans follows the general mammalian model but is custom designed for individual species. Notable features include (a) a compliant, elastic ascending aorta and aortic arch, (b) the retia mirabilia, (c) venous plexuses in the head and tracheo-bronchial tree, (d) prominent epidural veins, (e) diaphragmatic caval slings, and (f) thermoregulatory plexuses. During high-speed surface and sub-surface swimming of more active porpoises and dolphins, high heart rates, enlarged hearts, and higher affinities of hemoglobin for oxygen (O_2) are postulated to maximize lung-to-muscle O_2 transport just as during exercise of terrestrial mammals. However, during dives, the cardiovascular dive response (bradycardia and vasoconstriction) is variable and serves to regulate the depletion of O_2 stores according to the nature of a given dive. Depth, dive duration, exercise, lung volume reflexes, and cognitive control have all been postulated to influence heart rate during the dive.

This chapter examines the anatomy and physiology of the cardiovascular system of the bottlenose dolphin (*Tursiops truncatus*), with comparison to other cetaceans and with particular emphasis on cardiovascular responses during diving. After review of basic cardiovascular structure and function in these animals, we focus on the nature of the cardiovascular dive response (the decrease in heart rate [bradycardia] and increase in peripheral vasoconstriction associated with the breath hold). Here, we also consider neuroregulation of the dive response during the dive, the effect of the dive response on oxygen (O_2) store management during the dive, and the effects of sustained high heart rates during the postdive surface interval. We do not review the contributions of the cardiovascular system to respiratory gas exchange and thermoregulation as these topics are addressed in other chapters. As one of the primary functions of the cardiovascular system is blood O_2 transport from the lungs to tissues, we conclude with a consideration of hemoglobin (Hb) and the O_2-Hb dissociation curve in cetaceans.

Cardiovascular anatomy and function

Heart—Anatomy

The hearts of bottlenose dolphins and other cetaceans follow the four-chamber mammalian design. Blood returns from the body via the anterior and posterior venae cavae into the right atrium and then enters the right ventricle from where it is pumped via the pulmonary artery to the lungs for gas exchange. Blood returns from the lungs through the pulmonary veins to the left atrium and enters the left ventricle from which it is pumped into the aorta and out to body organs and tissues. The valves of the heart (tricuspid, pulmonary, mitral, and aortic) are also characteristics of mammals. The foramen ovale and ductus arteriosus, essential components of the fetal circulation, both close after birth as in other mammals (Slijper, 1961, 1962).

In contrast to terrestrial mammals, but similar to seals, the cetacean heart is dorso-ventrally flattened and broad (Race et al., 1959; Truex et al., 1961; Slijper, 1962; Rowlatt and Gaskin, 1975; Rowlatt, 1981; Ochrymowych and Lambertsen, 1984; Bisaillon et al., 1987; Tarpley et al., 1993; Drabek and Burns, 2002). Although the heart can be almost
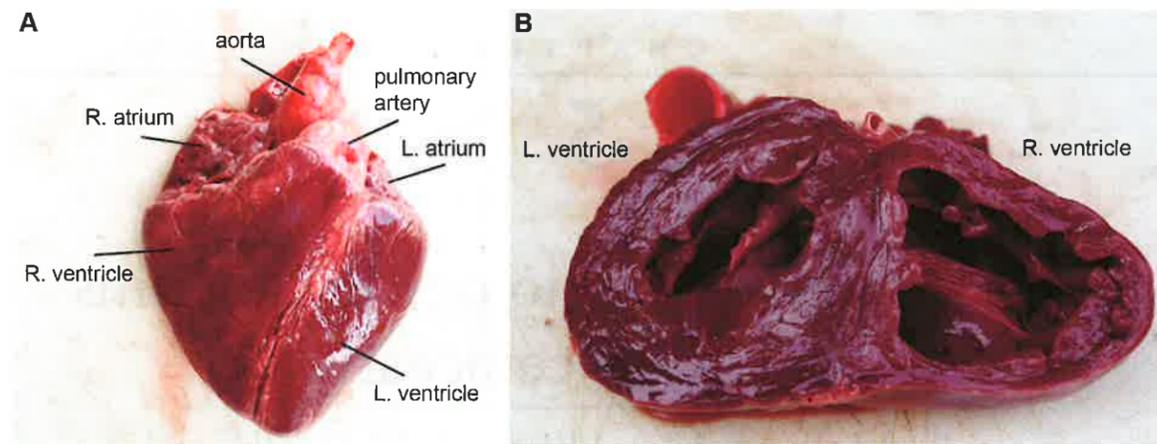
FIG. 1   Heart of the harbor porpoise (*Phocoena phocoena*). (A) Ventral view of the four-chambered heart, pulmonary artery, and aorta. (B) Cross section of the heart at the level of the ventricles. The thicker-walled left ventricle weighs about twice as much as the right ventricle (Rowlatt and Gaskin, 1975). *With permission from Robin Dunkin.*

oval in deeper divers and in larger cetacean species, the hearts of dolphins and porpoises have the more typical triangular shape of many mammals (Fig. 1). The endocardium (inner surface) of the ventricles of the bottlenose dolphin has been reported to be thicker and more elastic than in other mammals (Simpson and Gardner, 1972). The multiple anastomoses between the right and left coronary arterial trees that have been observed in several cetacean species are absent in the bottlenose dolphin (Race et al., 1959; Truex et al., 1961; Sommer et al., 1968; Cave, 1977; Ochrymowych and Lambertsen, 1984; Bisaillon et al., 1988; Picco et al., 2020). Such coronary anastomoses also do not occur in the harbor porpoise (*Phocoena phocoena*) (Rowlatt and Gaskin, 1975). The coronary arterial interconnections in deep divers such as the sperm whale (*Physeter macrocephalus*) are thought to optimize blood flow and O_2 delivery to the heart during long dives.

The Purkinje fibers are specialized, rapidly conducting cells of the cardiac electrical conduction system located beneath the endocardium of the ventricles. These fibers allow for uniform contraction of the ventricular walls, and they have been noted to be large in bottlenose dolphins, as well as other cetaceans (White and Kerr, 1915–1917; Simpson and Gardner, 1972; Pfeiffer, 1990; James et al., 1995; Ono et al., 2009; Aoki et al., 2017). The activation pattern and possibly the distribution pattern of these fibers in the ventricular walls have been postulated to contribute to the shape and duration of the electrocardiogram (ECG) signal in cetaceans (King et al., 1953; Kanwisher and Senft, 1960; Hamlin and Scher, 1961; Hamlin et al., 1970, 1972; Rowlatt and Gaskin, 1975; Meijler et al., 1992; Harms et al., 2013; Storlund et al., 2021). This type B ECG pattern, which is found in ungulates and pinnipeds in addition to cetaceans, contrasts with the type A pattern of primates, cats, and dogs. It has also been reported that Purkinje-like fibers, Todd fibers, occur in the atrial wall of the white-beaked dolphin (*Lagenorhynchus albirostris*) (Van Nie, 1987). It was postulated that such fast-conducting fibers might facilitate transmission of electrical signals from the atrium to the ventricle, and allow for rapid transitions between slow heart rates during dives and fast heart rates at the surface.

The position of the heart in the cetacean thorax is more rostral than in other mammals (Cozzi et al., 2017). The heart is just caudal to the axillary line between the foreflippers, essentially at the cranial end of the thorax. The heart lies ventral to the lungs and along the sternum. The shape and position of the heart have been postulated to accommodate better the compression of the chest by hydrostatic pressure at depth and/or to allow for a very convex, rostral curvature of the diaphragm during rapid exhalations at the surface (Drabek, 1975; Slijper, 1962; Cozzi et al., 2017).

Heart size

The relative size of the heart of the bottlenose dolphin, about 0.5% of body mass (Ridgway and Johnston, 1966; Ridgway and Kohin, 1995; Turner et al., 2006), is characteristic of most mammals and other cetaceans (Tables 1 and 2). A relative heart mass of 0.93% for the bottlenose dolphin (Slijper, 1962) has often been cited in the literature; however, it appears this measurement was from a single juvenile dolphin (Sergeant and Brodie, 1969). Based upon the results and sample sizes from the four studies for bottlenose dolphins in Table 1, a relative heart mass near 0.5% appears to be the most accurate number.

TABLE 1   Relative heart masses (M_H/M_B) of dolphins and porpoises, expressed as percentage (%) of body mass.

Species	M_H/M_B (%) Mean	M_H/M_B (%) Range	n	Reference
Bottlenose dolphin *Tursiops truncatus*	0.54	0.54–0.56	4	Ridgway and Johnston (1966)
	0.45	0.35–0.61	20	Ridgway and Kohin (1995)
	0.55		36	Turner et al. (2006)
	0.56 Female 0.64 Male		8 11	Mallette et al. (2016)
	0.51		50	Sergeant (1969)
	0.5		1	Irving et al. (1941a)
	0.93		1	Slijper (1962)
Indo-Pacific bottlenose dolphin *Tursiops aduncus*	0.6		131	Plon et al. (2012)
Pacific white-sided dolphin *Lagenorhynchus obliquidens*	0.85	0.70–0.92	5	Ridgway and Johnston (1966)
	0.75	0.72–0.78	4	Ridgway and Kohin (1995)
	0.72	0.67–0.84	5	Ponganis et al. (2022)
Peale's dolphin *Lagenorhynchus australis*	1.14		1	Goodall et al. (1997)
Dall's porpoise *Phocoenoides dalli*	1.31	1.25–1.34	4	Ridgway and Johnston (1966)
	0.99	0.57–1.34	35	Ridgway and Kohin (1995)
	0.89	0.68–1.20	36	Ponganis et al. (2022)
Northern right whale dolphin *Lissodelphis borealis*	0.82	0.70–0.93	4	Ponganis et al. (2022)
Harbor porpoise *Phocoena phocoena*	0.50 Female 0.53 Male		20 20	Rowlatt and Gaskin (1975)
	0.69 Female 0.69 Male		44 8	McLellan et al. (2002)
	0.8		97	Lockyer et al. (2003)
	0.84	0.65–1.22	27	Sergeant (1969)
Spotted dolphin *Stenella attenuata*	0.42	0.37–0.51	11	Perrin and Roberts (1972)
Spinner dolphin *Stenella longirostris*	0.46	0.37–0.52	6	Perrin and Roberts (1972)
Striped dolphin *Stenella coeruleoalba*	0.85	0.62–1.15	11	Miyazaki et al. (1981)
Indo-Pacific humpback dolphin *Sousa chinensis*	0.52		350	Plon et al. (2012)
Long-beaked common dolphin *Delphinus capensis*	0.62		308	Plon et al. (2012)
Common dolphin *Delphinus delphis*	0.48		50	Sergeant (1969)
Rough-toothed dolphin *Steno bredanensis*		0.5–0.8	15	Miyazaki and Perrin (1994)

TABLE 1 Relative heart masses (M_H/M_B) of dolphins and porpoises, expressed as percentage (%) of body mass—cont'd

Species	M_H/M_B (%) Mean	M_H/M_B (%) Range	n	Reference
Francisciana dolphin	0.61 Female		16	Weber Rosas et al. (2007)
Pontoporia blainvillei	0.61 Male		21	
	0.51 Female	0.49–0.52	5	Kamiya and Yamasaki (1974)
	0.49 Male	0.48–0.49	2	
Guiana dolphin	0.56 Female		12	Weber Rosas et al. (2007)
Sotalia guianensis	0.62 Male		12	
Tucuxi	0.45 Female		6	Da Silva and Best (1994)
Sotalia fluviatilis	0.43 Male		5	
Amazon River dolphin	0.35 Female	0.24–0.47	4	Best and Da Silva (1989)
Inia geoffrensis	0.33 Male	0.29–0.37	5	
Ganges River dolphin	0.26 Female	0.24–0.28	2	Kamiya and Yamasaki (1974)
Platanista gangetica	0.24 Male	0.22–0.25	2	

Most mammals are typically in the 0.6% range with more athletic species such as dogs, horses, and antelopes in the 0.8%–1.2% range (Schneider et al., 1964; Snow, 1985; Woodall, 1992; Williams et al., 2015a). Exceptional greyhounds and racehorses have values as high as 1.7%–2% (Poole and Erickson, 2011). High values of 1.19%–1.55% also occur in smaller, mammals with high resting metabolic rates, such as bats, shrews, and Arctic hares (Bishop, 1997). Sloths have among the lowest (0.24%) relative heart masses reported in mammals (Bishop, 1997). In other marine mammals, typical relative heart masses are 0.5%–0.8%, 0.73%, and 0.3% in pinnipeds (seals, furs seals, and walrus), sea otters, and manatees, respectively (Crile and Quiring, 1940; Bryden, 1972; Morejohn et al., 1975; Bisaillon, 1982; Drabek and Burns, 2002). Abbreviations: M_B, body mass; M_H, heart mass; n, sample size.
Based on supplemental files of Ponganis et al. (2022).

TABLE 2 Relative heart masses (M_H/M_B) of larger odontocetes and baleen whales, expressed as percentage (%) of body mass.

Species	M_H/M_B (%) Mean	M_H/M_B (%) Range	n	Reference
Beluga	0.56	0.56–0.57	2	Crile and Quiring (1940)
Delphinapterus leucas				
	0.57	0.37–0.69	20	Sergeant and Brodie (1969)
Narwhal	0.59 Female	0.54–0.65	4	Hay and Mansfield (1989)
Monodon monoceros	0.51 Male	0.48–0.57	3	
Long-finned pilot whale		0.50–0.59[a]		Bloch et al. (1993), Cowan (1966),
Globicephala melas		0.39–0.45[a]		Bloch et al. (1993), Lockyer (1993)
	0.44		1	Sergeant and Brodie (1969)
Killer whale	0.64	0.50–0.73	3	Sergeant (1969)
Orcinus orca				
Pygmy sperm whale	0.33		1	Sergeant (1969)
Kogia breviceps				
Sperm whale	0.38		25	McAlpine (1985)
Physeter macrocephalus				
	0.34			Slijper (1962)
	0.47		1	Race et al. (1959)
	0.32		1	Quiring (1943)
Baird's beaked whale	0.63		1	Sergeant (1969)
Berardius bairdii				
Sei whale	0.52		27	McAlpine (1985)
Balaenoptera borealis				

TABLE 2 Relative heart masses (M_H/M_B) of larger odontocetes and baleen whales, expressed as percentage (%) of body mass—cont'd

Species	M_H/M_B (%) Mean	M_H/M_B (%) Range	n	Reference
	0.40	0.34–0.49	17	Sergeant (1969)
Fin whale	0.52		33	McAlpine (1985)
Balaenoptera physalus				
	0.55			Slijper (1962)
	0.4			Nishiwaki (1950)
	0.64		1	Quiring (1943)
Blue whale	0.55			Slijper (1962)
Balaenoptera musculus				
Minke whale	0.5			Slijper (1962)
Balaenoptera acutorostrata				
Bryde's whale	0.46	0.23–0.68	20	Sergeant (1969)
Balaenoptera brydei				
Humpback whale	0.5			Slijper (1962)
Megaptera novaeangliae				
	0.50	0.45–0.56	3	Quiring (1943)
Pacific right whale	0.56	0.43–0.73	6	Omura et al. (1969)
Eubalaena sieboldii				
Bowhead whale	0.6	0.3–1.2	9	Tarpley et al. (1993)
Balaena mysticetus				
Gray whale	0.55		1	Sergeant (1969)
Eschrichtius robustus				

Most values for these larger cetaceans are at the lower end of the typical mammalian range (see Table 1 legend). Abbreviations: M_B, body mass; M_H, heart mass; n, sample size.
[a] Estimates for pilot whales were based on measurements of heart mass and body length (Cowan, 1966) and two different body length-body mass relationships (Bloch et al., 1993; Lockyer, 1993).

Although heart mass scales allometrically over a wide range of body masses in mammals (Brody, 1945; Stahl, 1967), other factors such as metabolic demand (including aerobic exercise capacity and thermoregulation) can contribute to relative heart masses that are larger than the typical 0.5%–0.6% value of most mammals (Bishop, 1997; Williams et al., 2015a). Common mammalian examples of more athletic species with larger relative heart masses (0.8%–1.2%) include dogs, horses, and antelopes (Schneider et al., 1964; Snow, 1985; Woodall, 1992). Even higher relative heart masses of 1.2%–1.5% occur in smaller mammals, such as bats, shrews, and Arctic hares, which have high metabolic rates due to size, activities, and/or a cold environment (Bishop, 1997). As far as we know, the highest relative heart masses in mammals are 1.7%–2% in the most elite greyhounds and racehorses (Poole and Erickson, 2011).

In regard to the range of relative heart masses in cetaceans, the relative heart masses of bottlenose dolphins, Pacific white-sided dolphins (Lagenorhynchus obliquidens), and Dall's porpoises (Phocoenoides dalli), three species of similar body mass, were 0.45%–0.55%, 0.75%–0.86%, and 0.99%–1.31% (Ridgway and Johnston, 1966; Ridgway and Kohin, 1995; Turner et al., 2006). In other words, for a Dall's porpoise and bottlenose dolphin of the same body mass, the heart of the Dall's porpoise is about twice as large as that of the dolphin. Based on the higher swim speeds, larger muscle mass, thinner blubber layer, and suspected deeper-diving activity of Dall's porpoises, Ridgway and Johnston (1966) suggested that a relatively larger heart in Dall's porpoises supported a higher metabolic rate and faster/more efficient gas exchange and restoration of larger blood and muscle O_2 stores.

Given the data in Tables 1 and 2 and the positive correlation of aerobic exercise capacity and maximal O_2 consumption with relative heart mass (Bishop, 1997; Williams et al., 2015a), Dall's porpoise is, by far, the most "elite" athlete among the cetaceans. This species would be predicted to be capable of prolonged, elevated aerobic activity, similar to that of many horses and dogs, although probably less than the most elite racehorses and greyhounds. As suggested by Ridgway and Johnston (1966) and Williams et al. (2015a), enlarged hearts appear to occur in those cetacean species with high-speed, intense surface-swimming activities. Certainly, Dall's porpoise fits this picture with its high surface

swim speeds and "rooster tailing" through the water, as well as with its stocky build, and increased muscle mass, blood volume, Hb concentration, and Hb-O_2 affinity (Ridgway, 1966; Ridgway and Johnston, 1966; Horvath et al., 1968; Jefferson, 1987, 1988). The larger relative heart masses of the striped dolphin (*Stenella coeruleoalba*) and Pacific white-sided dolphin (Table 1), although lower than that of Dall's porpoise, also stand out among cetaceans, and suggest that they too are capable of sustained, intense aerobic activity.

The harbor porpoise is a cetacean with high resting and field metabolic rates (Kanwisher and Sundnes, 1965; Rojano-Doñate et al., 2018). It is among the smallest of cetaceans, lives in cold waters, and has exceptionally high foraging rates (Wisniewska et al., 2016). A larger relative heart mass (0.7%–0.8%, Table 1) is consistent with the higher metabolic rate and thermoregulatory requirements of this small-bodied species. One study had lower (0.5%) relative heart mass values; it is unclear if the heart preservation technique, body weight estimation formula, or differences in body mass composition (blubber thickness) may have accounted for this difference. Heart size also varies with physiological condition, such as athletic training or pregnancy (Hill and Olson, 2008; Savu et al., 2012). It should not be surprising that the highest relative heart masses (0.86%) in harbor porpoises were reported in pregnant animals (McLellan et al., 2002). Again, these findings support Ridgway and Johnston's original suggestion that relatively larger hearts in some cetaceans support higher metabolic demands, whether those elevations in metabolic rate are due to high swim speeds, deep dives, or thermoregulatory needs. At the other end of the spectrum, the Ganges River dolphin (*Platanista gangetica*) has a relative heart mass of 0.25%, similar to those of manatees and sloths, and about half that of the bottlenose dolphin (Table 1). On the basis of its small relative heart size, this small river dolphin would be expected to have the lowest metabolic demands and smallest aerobic exercise capacity among the cetacean species in Tables 1 and 2.

Exceptionally, large relative heart masses do not occur in many deep-diving cetaceans, such as the beluga (*Delphinapterus leucas*), Baird's beaked whale (*Berardius bairdii*), and sperm whale (Table 2) or even in the long-finned pilot whale (*Globicephala melas*), which has been postulated to have a high-diving metabolic rate due to high transit swim speeds (Aoki et al., 2017). Apparently, an increase in relative heart mass is not essential in all species either to meet metabolic demand during the dive or to allow for rapid, efficient gas exchange at the surface between dives. Indeed, heart rate, pulmonary blood flow, and lung ventilation requirements after the dive are probably most dependent on the magnitude of O_2 depletion and carbon dioxide (CO_2) accumulation during the dive. These requirements, in turn, are dependent on dive duration, dive metabolic rate, and the size of blood and muscle oxygen stores (i.e., blood volume, Hb concentration, muscle mass, and myoglobin concentration).

It is also important to remember that body composition (% blubber, % muscle, and blood volume) varies among these many species and can even vary seasonally within a species (fasting, migration, and location). These differences in body composition and body mass may contribute to differences in overall metabolic needs and relative heart masses. The sperm whale is a good example; its relative heart mass is low, near 0.3% (Table 2). This whale may either be an exceptionally efficient swimmer, and/or its size, low muscle mass (22%–30% of body mass), high blubber content (33%–40% of body mass), and large spermaceti organ (~6%–7% of body mass) may result in a relatively low mass-specific metabolic demand (Omura, 1950; Lockyer, 1976, 1991; Clarke, 1978). The technical difficulty of accurate total body weight determinations in large whales may also contribute to inaccuracy.

Returning to consideration of the bottlenose dolphin's unremarkable relative heart mass of 0.5%, and the relationship of aerobic exercise capacity to relative heart mass, the aerobic scope (the ratio of maximum O_2 consumption to resting O_2 consumption) of the bottlenose dolphin would be expected to be "typical" of most mammals. Namely, as in most "typical" mammals, maximum O_2 consumption would be about 12 × the allometrically predicted resting O_2 consumption, and far less than the 30-fold increase observed in elite mammalian athletes such as horses and dogs (Taylor et al., 1987). Indeed, maximum O_2 consumption rates of two exercising bottlenose dolphins were 7–11 × the allometrically predicted resting O_2 consumption rate (Williams et al., 1993).

Hemodynamics: Cardiac output and stroke volume

The design and size of the heart in combination with heart rate are prime determinants of the ability of the heart to pump blood throughout the body. Cardiac output, the flow rate at which blood is pumped to the body, is determined by heart rate and stroke volume (the volume of blood ejected from the heart during a heartbeat) (Hellsten and Nyberg, 2016). In comparative physiology, these indices of cardiac function are often expressed relative to body mass, i.e., cardiac output in $mL\,kg^{-1}\,s^{-1}$, and stroke volume in $mL\,kg^{-1}$. In the bottlenose dolphin, based on a relative heart mass typical of most mammals, the cardiac output and stroke volume of the heart should be in the range expected for a mammal of its size.

There have been few measurements of cardiac output and stroke volume in dolphins (Sommer et al., 1968; Miedler et al., 2015; Fahlman et al., 2019, 2020b). As outlined in Table 3, stroke volumes of anesthetized bottlenose dolphins and

TABLE 3 Cardiac outputs (CO) and stroke volumes (SV) of bottlenose dolphins.

Animal	Condition	HR (beats min^{-1}) (measured)	CO (mL kg^{-1} s^{-1}) (measured)	SV (mL kg^{-1}) (measured)	CO (mL kg^{-1} s^{-1}) (allometric)	SV (mL kg^{-1}) (allometric)	Reference
Dolphin 175 kg (mean)	At rest	41	0.5	0.8	1.1	0.9	Miedler et al. (2015)
	1-min postexercise	84	1.7	1.3			
Dolphin 169 kg (mean)	Apnea at rest (spontaneous)	44	0.8	1.1	1.1	0.9	Fahlman et al. (2019)
	Postapneas (stationary)	78	1.8	1.3			
Dolphin 80 kg	First anesthesia	84	1.1	1.1	1.3	0.8	Sommer et al. (1968)
Dolphin 80 kg	Second anesthesia	120	1.1	0.6	1.3	0.8	Sommer et al. (1968)
Dolphin 70 kg	Anesthesia	110	0.8	0.4	1.3	0.8	Sommer et al. (1968)
Dolphin 114 kg	Anesthesia	140	1.8	0.8	1.2	0.8	Sommer et al. (1968)
Beluga 162 kg	Apnea at rest (spontaneous)	38	1.9	3.1	1.2	0.8	Fahlman et al. (2020b)
False killer whale 520 kg	Apnea at rest (spontaneous)	29	0.6	1.2	0.9	0.9	Fahlman et al. (2020b)
Human 70 kg	At rest	80	1.2	0.9	1.3	0.8	Sommer et al. (1968)
Pony 171 kg (mean)	At rest	39	1.5	2.4	1.1	0.9	Taylor et al. (1987)
	At $\dot{V}_{O2max}$	215	8.9	2.5			

Data were collected at rest, after 1.5-min exercise sessions, after stationary apneas at the surface, and during anesthesia. The allometrically predicted values at rest are also provided for each dolphin. Data for a young beluga and an adult false killer whale are also included (Fahlman et al., 2020b). To facilitate comparison to terrestrial mammals, corresponding values are provided for humans and horses. Measurements were made with different techniques: echocardiography (Miedler et al., 2015; Fahlman et al., 2019), indocyanine green dilution (Sommer et al., 1968), and the Fick technique (Taylor et al., 1987). In the awake dolphins, CO and SV reported by the authors in the table were from early apnea when heart rates (HR) were constant because both HR and SV varied with respirations. For example, the highest individual postapneic CO was 2.6 mL kg^{-1} s^{-1} with a stroke volume of 1.8 mL kg^{-1} (Fahlman et al., 2019). In dolphins at rest and under anesthesia, and in humans, the measured SVs were close to allometrically predicted values (Holt et al., 1968) as would be expected since relative heart mass is about 0.5%, the typical value for most mammals (Table 1). In contrast, COs in dolphins during anesthesia and rest periods were less than, although, often close to predicted values (Stahl, 1967) because of the time of measurement during apnea, and especially, during anesthesia, because of potential effects of the anesthetic, body positioning (out of water also), and effects of positive pressure ventilation. COs in dolphins after exercise or after surface breath holds were above the allometrically predicted value. In contrast to the dolphins and humans, CO and SV of ponies were greater than predicted allometrically. This is attributed to the larger relative heart masses (0.8%–1.2%) of most horses (Snow, 1985). In contrast to the variability of SV with breathing in dolphins, SV remains constant in the pony (Taylor et al., 1987) even when exercising at maximum oxygen consumption ($\dot{V}_{O2max}$). CO and SV have not been measured in dolphins during surface swimming or during dives to depth. Additional data are now also available from a beluga and a false killer whale. The large SV of the beluga was attributed to the size of the heart in this young animal. In adult belugas, however, relative heart mass is similar to that of bottlenose dolphins (Table 2).

dolphins at rest are close to those predicted by allometric equations (Holt et al., 1968). This is expected since the allometric equations are based on large numbers of mammals, and, as reviewed earlier, the relative heart mass of the bottlenose dolphin is typical of most mammals (Table 1).

In the awake dolphins (Miedler et al., 2015; Fahlman et al., 2019), both heart rate and stroke volume increased with respirations and decreased during the breath hold. To report data at a constant heart rate, the cardiac outputs and stroke volumes summarized by the authors were measured during early apnea. Consequently, cardiac outputs measured in early apneas of dolphins (Table 3) can be less than the allometrically predicted value since the allometric equations are based on continuously breathing mammals in a steady state with relatively stable heart rates both during and between respirations (Stahl, 1967; Fahlman et al., 2020b). In contrast to the resting state, cardiac outputs and stroke volumes of the dolphins after exercise or long breath holds were elevated above the allometrically predicted resting values (Table 3). For the sake of comparison, it should also be noted that the pony has a resting cardiac output and

stroke volume that are greater than calculated by allometric equations (Table 3). This is again consistent with heart size; as reviewed earlier, most horses have a relative heart size about twice the typical mammalian value (Crile and Quiring, 1940; Snow, 1985).

The change in stroke volume with respirations in the dolphin is not unexpected. Apneic-to-eupneic changes in stroke volume occur in seals (Ponganis et al., 1990). Changes in stroke volume can also occur during exercise in some mammals, including humans (Åstrand et al., 1964; Vella and Robergs, 2005). In contrast, stroke volume in the horse remains constant (Table 3), even with exercise at maximum O_2 consumption (Taylor et al., 1987). Stroke volume can vary because of changes in venous return and optimal filling of the heart, and to changes in the contractility of ventricular muscle (sympathetic nervous system activation) (Hellsten and Nyberg, 2016). Overall, although studies are limited, the cardiac output and stroke volume of the heart of the bottlenose dolphin at rest are as predicted for a mammal of its size. From the available data, it is expected that increased heart rates during surface swims or during surface intervals between dives will also be associated with increased stroke volumes.

Hemodynamics: Heart function and blood pressure

Investigation of cardiac physiology and hemodynamics in the dolphin has only been conducted in one cardiac catheterization study in which the bottlenose dolphins were under anesthesia (Sommer et al., 1968). As the authors remarked, positive pressure ventilation, anesthetic drug side effects, body position, out-of-water effects on the body, and even occult disease may have affected results. The so-called filling pressures of the heart (right atrial pressure, left atrial pressure, and pulmonary capillary wedge pressure) were occasionally equivalent to human values but were often elevated, possibly secondary to the mode of ventilation (per the authors). In addition, mean pulmonary artery pressures were high, up to $4\times$ the human reference values, while mean aortic pressures were about $1.5 \times$ the human value (Sommer et al., 1968). With the available data, pulmonary vascular resistance and systemic vascular resistance, indices of the impedance or afterload that the right and left ventricles must work against, can be calculated (Kaplan, 1979; Kwan et al., 2019). In both cases, the values in the anesthetized dolphins were extreme, with pulmonary vascular resistance as high as 679 dynes s cm^{-5} (upper normal limit in humans: 250), and systemic vascular resistance as high as 2570 dynes s cm^{-5} (upper normal limit in humans: 1200) (Kaplan, 1979; Kwan et al., 2019). However, despite the high vascular resistances, most cardiac output measurements were equivalent to or greater than the predicted resting level (Table 3). From the perspective of cardiac function, that is remarkable. Clearly, further hemodynamic investigation of dolphins in the awake state would benefit our understanding of the roles of intracardiac, pulmonary artery, and systemic arterial pressures in cardiac function of these animals.

The vasculature

The arterial and venous systems of the bottlenose dolphin and other cetaceans are remarkable for many features (see Fig. 2). Readers are referred to the literature for detailed descriptions and excellent overviews of vascular anatomy (Slijper, 1962; Rommel et al., 2006; Costidis and Rommel, 2012, 2016b; Cozzi et al., 2017). Most studies have focused

FIG. 2   Cervical and thoracic retia mirabilia of the bottlenose dolphin, *Tursiops truncatus*. Branches of the brachiocephalic trunk, internal thoracic arteries, and intercostal arteries extend from the aorta to form interbranching arterial networks of the retia, which eventually enter the intervertebral canal to form the spinal meningeal arteries, the major blood supply to the brain. The internal carotid artery is vestigial. The external carotid artery extends to tissues associated with the lower jaw and rostrum. For review, see Cozzi et al. (2017). *Illustration by Uko Gorter.*
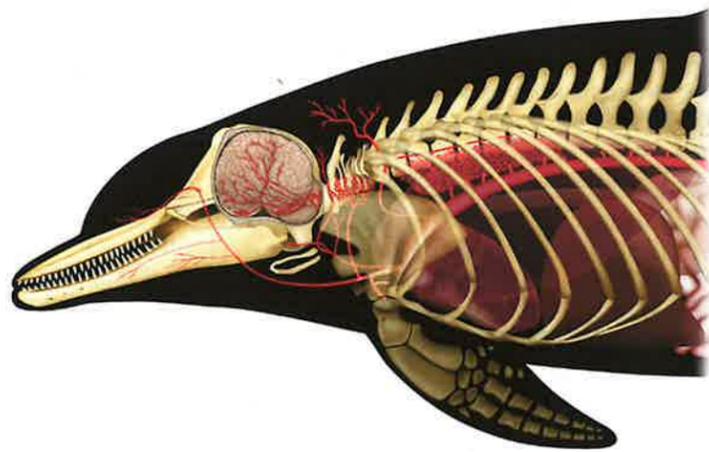
on the systemic arterial and venous systems. As far as we know, anatomical features of the pulmonary arteries and veins have not been extensively examined.

However, the pulmonary vasculature has some unique features. In contrast to terrestrial mammals, the septae of the lung's alveoli in cetaceans have a double capillary bed, one on each side of the septal wall (for review, see Piscitelli et al., 2013). In addition, there are occasional transeptal anastomoses between the pulmonary artery and vein (Piscitelli et al., 2013). Lastly, smooth muscle sphincters have been observed around pulmonary veins in the lungs of cetaceans, including the bottlenose dolphin (Slijper, 1962; Simpson and Gardner, 1972). Interestingly, sphincters around branches of the portal vein within the liver have been noted in bottlenose dolphins and several other, although not all, cetaceans (Slijper, 1962; Simpson and Gardner, 1972; Hilton and Gaskin, 1978). The function of these sphincters is unknown. Pulmonary vein sphincters have the potential to affect flow in the transeptal pulmonary arterio-venous anastomoses mentioned above and to contribute to postulated regulation of ventilation-perfusion matching in the dolphin lung during dives (Garcia Párraga et al., 2018).

Major structural features of the arterial system in cetaceans include (a) modifications of the compliance and elasticity of the ascending aorta, aortic arch, and distal aorta; (b) the thoracic and vertebral retia mirabilia that form the major blood supply to the brain; (c) the presence of both a countercurrent arrangement of arteries and veins, as well as superficial arterio-venous anastomoses in the flippers, fluke, and dorsal fin for thermoregulation (Scholander and Schevill, 1955; Elsner et al., 1974, 2004; Plön et al., 2019); and (d) intra-abdominal countercurrent vascular networks for thermoregulation of reproductive organs (Rommel et al., 1992, 1993, 1994; Pabst et al., 1995).

The venous system is notable for extensive venous plexuses in the head and in the tracheal/bronchial walls, the presence of large veins (epidural veins) within the posterior vertebral canal, and the presence of a diaphragmatic muscular sling or sphincter around the posterior vena cava (Slijper, 1962; Cozzi et al., 2005; Ninomiya et al., 2005; Costidis and Rommel, 2012; Lillie et al., 2018). The spleen, which can function as a large storage organ for red blood cells in some seals, is small in the bottlenose dolphin and other cetaceans (Slijper, 1958, 1962; Castellini and Castellini, 1993; Haldiman and Tarpley, 1993; E Silva et al., 2014). In this chapter, we review the aorta and the retia, briefly consider the venous plexuses and epidural veins, and conclude with the hemodynamics of blood flow in the posterior vena cava during fluking. Thermoregulation and the associated design/function of more peripheral vascular networks are examined in Chapter 3: Thermoregulation.

Aorta

The aorta and its tributaries, in addition to acting as a vascular conduit, contribute to the regulation of the magnitude and distribution of blood flow to organs and tissues, to management of blood pressure, and to optimization of the function of the heart. As we will review later, during the bradycardia (decreased heart rate) and decreased cardiac output of the dive response, it is the contraction of smooth muscle in arterial walls that constricts arteries, maintains blood pressure, and regulates peripheral blood flow (Irving, 1938; Scholander, 1940; Irving et al., 1941b; Grinnell et al., 1942). Equally important are the structure and biomechanical properties of the aorta that facilitate cardiac function and blood flow during the long pauses between the slow heart beats of intense dive responses (Drabek, 1977; Rhode et al., 1986; Shadwick and Gosline, 1994). Modifications of the aorta occur not only in cetaceans but also in pinnipeds. A highly compliant, elastic expansion of the ascending aorta, the so-called aortic bulb, is especially prominent in deep-diving seals (Drabek, 1975; Drabek and Burns, 2002).

Before consideration of the aorta in bottlenose dolphins and other odontocetes, we first review the anatomy of the aorta in baleen whales. The fin whale (*Balaenoptera physalus*) is a good example because of the anatomical and biomechanical studies of Shadwick and Gosline (Shadwick and Gosline, 1994; Gosline and Shadwick, 1996; Shadwick, 1999), and because of the Krogh Principle that, for a given problem or question, there will be an animal in which it is best studied (Krogh, 1929). The large body size of baleen whales in combination with the dive response should result in exceptionally low heart rates during dives and in optimal design of the aorta to support cardiac function and blood flow under those conditions.

Shadwick and Gosline found that the fin whale had an enlarged, highly compliant, and elastic aortic arch. In comparison with the thoracic aorta, the arch had a higher elastin to collagen ratio, larger diameter, and a different arrangement of lamellar units (layers of elastin, collagen, and smooth muscle). The thoracic and abdominal sections of the aorta were rigid (Shadwick and Gosline, 1994; Lillie et al., 2013). Shadwick and Gosline hypothesized that the arch acted as an elastic reservoir (windkessel) to maintain blood pressure and flow during the pause between heart beats (diastole, the relaxation phase of the heartbeat). During ventricular contraction (systole, the ejection phase of the heartbeat), the compliant arch expands to accommodate the stroke volume of the heart, and then, during diastole, it gradually contracts due to its elastic fibers to maintain blood pressure and peripheral flow. In the presence of widespread

vasoconstriction at low heart rates, the compliant aortic arch also serves to decrease the workload and O_2 consumption of the heart. In addition, because coronary blood flow only occurs during diastole, maintenance of diastolic blood pressure is especially important for perfusion of the coronary arteries. An enlarged ascending aorta or aortic arch has also been found in three other baleen whales, the minke whale (*Balaenoptera acutorostrata*, Ochrymowych and Lambertsen, 1984), the bowhead whale (*Balaena mysticetus*, Tarpley et al., 1997; Castellini and Ponganis, 2020), and the gray whale (*Eschrichtius robustus*, Elsner et al., 1966a). Enlargement of the ascending aorta is absent or only slightly increased in Bryde's whale (*Balaenoptera brydei*, Melnikov, 1994, 1997).

Based upon the wavelengths of pressure waves generated by the heart at different heart rates, Shadwick and Gosline have also postulated that the dimensions and biomechanical properties of the arch and of the rigid descending aorta of the fin whale decrease aortic impedance and allow for a more efficient circulation during the higher heart rates of the surface period. The aortic impedance is decreased through the destructive interference of outgoing and reflected pressure waves at the higher heart rates expected in the fin whale at the surface (above 20 beats min^{-1} (bpm)). Recently, documented heart rates in the blue whale (*Balaenoptera musculus*) support these hypotheses on the function of the aortic arch in baleen whales (Goldbogen et al., 2019).

Such quantitative biomechanical studies of the ascending aorta and aortic arch have not been performed in odontocetes. An expansion of the ascending aorta has been mentioned in summary reports of smaller to medium-size odontocetes, including Pacific bottlenose dolphins, pilot whales, and Cuvier's beaked whale (*Ziphius cavirostris*) (Elsner et al., 1966a). Ridgway also reported enlargements of the aorta in every cetacean he dissected or necropsied (Ridgway, 1972).

However, no aortic dilatation was observed in dissections of harbor porpoises or in angiographic studies of Atlantic bottlenose dolphins (Viamonte et al., 1968; Rowlatt and Gaskin, 1975). Viamonte et al. reported that the only aortic dilatation observed was associated with the sinuses of Valsalva in the aortic root. These three sinuses (spaces) bulge outward as they extend from the bases of the aortic valve leaflets to the aortic wall; the ostia (openings) of the right and left coronary artery are located in two of the sinuses. Typically, in humans, the diameter of the aorta at this level is about 1.5 × that of the aortic valve (Campens et al., 2014). In the Atlantic bottlenose dolphin, based on echocardiographic measurements of the diameters of the ascending aorta and aortic valve, the ascending aorta is also about 1.5 × the diameter of the aortic valve (Chetboul et al., 2012; Miedler et al., 2015; Fahlman et al., 2019, 2020b). Melnikov (1997) also reported that the ascending aorta was not enlarged in Dall's porpoise, the Pacific white-sided dolphin, and the spinner dolphin. In view of all these findings, it appears that any dilatation of the ascending aorta of the Atlantic bottlenose dolphin is not especially prominent. Despite the lack of significant enlargement, the ascending aorta of bottlenose dolphins has been described as elastic and thickened (Simpson and Gardner, 1972), which would support some function as an elastic reservoir.

Enlargement of the ascending aorta in odontocetes has also been suggested to be proportional to diving capacity (Galantsev, 1991) (Ridgway, personal communication). Enlargements of the ascending aorta have been reported or mentioned in deeper-diving odontocetes, including sperm whales (Melnikov, 1997), pilot whales (Jackson, 1845; Elsner et al., 1966a), and Cuvier's beaked whale (Elsner et al., 1966a; Díaz-Delgado et al., 2016). Certainly, the plastic cast of the ascending aorta of the beluga appears quite prominent in Vogl and Fisher's monograph on retia in the beluga and narwhal (*Monodon monoceros*) (Vogl and Fisher, 1982). In the sperm whale, Melnikov (1997) described the ascending aorta as a bulbous expansion. He found that the diameter of the ascending aorta was 1.5 × the diameter of the aorta at the level of the coronary ostia (i.e., the sinuses of Valsalva) and that large diameter was actually on the aortic arch after the take-off of the right brachiocephalic trunk. So, there is definite evidence of enlargement of the ascending aorta in some deep-diving odontocetes. There are also reports of high elastin content in the ascending aorta of a beluga (Simpson and Gardner, 1972) and higher elastin/collagen ratios in the proximal versus distal aorta in three delphinid species (Mompeó et al., 2020). In conclusion, although aortic structure and biomechanical properties have not been examined as extensively in odontocetes as in mysticetes, we suspect that a compliant, elastic ascending aorta exists even in the bottlenose dolphin and that the elastic reservoir—windkessel function is more developed in deeper, longer-duration divers, and, especially, in larger animals with baseline slow heart rates due to large body mass. Furthermore, anatomic and biomechanical research is needed to evaluate the hypothesis of an aortic arch windkessel in odontocetes and determine how blood pressure and flow are maintained during the long pauses between slow heartbeats.

Retia mirabilia

A rete mirabile ("wonderful net") has been described as the extension of a single artery into multiple branches that eventually coalesce back into a single artery (Cozzi et al., 2017). It is a complex structure (Figs. 2 and 3) that can be associated with a corresponding network of interbranching veins, and it is not exclusive to cetaceans. In the bottlenose dolphin, the largest rete mirabile is the thoracospinal rete. It is primarily arterial and extends from the aorta via

FIG. 3   Thoracic rete mirabile of the common dolphin, *Delphinus delphis*. In this view of the dorsal surface of the thoracic cavity, the rete mirabile is visible between the ribs, extending from the vertebral column toward the periphery. Most of the thoracic aorta had been removed; a transected segment remained attached to the vertebrae near the diaphragmatic end of the thorax. *Credit: P. Ponganis.*

intercostal and dorsal thoracic arteries into the intervertebral canal where it continues cranially to form the spinal meningeal arteries and the primary blood supply to the brain (Galliano et al., 1966; Nagel et al., 1968; Viamonte et al., 1968; McFarland et al., 1979). In the bottlenose dolphin, this rete extends the entire length of the thorax into the skull (Fig. 2). In the literature, the thoracospinal rete complex is also often described as two retia, the thoracic rete and the spinal rete. In addition, there is a contiguous, more cranial segment, the cervical rete (see Fig. 2).

Thoracospinal retia also occur in other cetaceans and are primarily composed of arterial blood vessels. Slijper (1962) described these retia to be most extensive in dolphins and sperm whales. Melnikov (1997) considered the thoracospinal rete of the sperm whale to be the most well-developed among cetaceans; it begins in the midlumbar region. In contrast, the rete was less developed in ziphiids and rorqual whales; in these whales, it only begins in the mid-thorax region (Slijper, 1962). The anatomy of the thoracospinal rete is exceptionally well described in the narwhal and beluga (Vogl and Fisher, 1981a,b, 1982; Vogl et al., 1981). In these two monodontids, the thoracospinal rete forms the blood supply to both the brain and spinal cord, is predominantly arterial and associated with fat, and has muscular arterial walls, but is poorly innervated. The cervical rete of the bowhead whale also appears to be primarily arterial (Pfeiffer and Kinkead, 1990). For detailed descriptions of vascular supply and structure of the thoracospinal retia, readers are referred to McFarland et al. (1979), Vogl and Fisher (1982), Melnikov (1997), and Costidis and Rommel (2016a,b). Excellent overview summaries are provided in Rommel et al. (2006) and Cozzi et al. (2017). In summary, the major anatomical features of the thoracospinal retia mirabilia in cetaceans are that the retia are predominantly arterial, not well-innervated, embedded in fat and are the primary blood supply to the brain.

The thoracospinal rete has been postulated to have many different functions, including windkessel functions, engorgement to prevent "lung squeeze" at depth, thermoregulation, and modification of the composition of blood, including the trapping of air bubbles (Slijper, 1962; Hui, 1975; Vogl and Fisher, 1982). One effect of the rete is a dampening of the pulse pressure in the spinal meningeal artery; mean blood pressure was the same as in the aorta, but there was no systolic peak or diastolic trough in the pressure profile (Nagel et al., 1968). Although blood flow in the spinal meningeal artery was nonpulsatile in that study, blood does, nonetheless, flow to the brain, and, in fact, blood flow can even selectively decrease in one cerebral hemisphere versus the other during unihemispheric sleep in dolphins (Ridgway et al., 2006).

Recent hypotheses on the function of the thoracospinal rete have included nitrogen absorption, a supplemental blood storage function, and dampening of venous pressure waves in the large veins (epidural veins) within the vertebral canals of cetaceans. In an investigation of the harbor porpoise thoracospinal rete (Blix et al., 2013), it was found that arteries in the central portion of the rete became quite thin-walled and were, as in other species, embedded in fat. Based on the fivefold greater solubility of nitrogen in fat than in water and the thin walls of the retial vessels, the authors postulated that the fat acted as a localized nitrogen sink to lower elevations of blood nitrogen during dives and minimize the risk of decompression sickness. We also note that lowering of high nitrogen levels in the blood supply to the brain could also minimize the risk of nitrogen narcosis during dives.

In another recent study, a numerical model was constructed for heart rate, stroke volume, and cardiac output during dives in bottlenose dolphins (Bonato et al., 2019). For heart rates less than 10 bpm, the model resulted in a cardiac output that was too low to support adequate blood flow to the brain and heart, the two most O_2-dependent organs in

the body. On this basis, it was suggested that transfer of blood from the spinal rete could supplement blood flow to adequate levels during the severe bradycardia. The model, of course, is subject to assumptions about stroke volumes and heart rates during the dives and is dependent on the postulated transfer of intra-abdominal pressures to the thorax to compress thoracic vessels and propel additional blood from the rete to the brain. In addition, as far as we know, a heart rate of less than 10 bpm has not been reported in a bottlenose dolphin, either during trained dives in a tank as long as 4.5 min, or during dives at sea to as deep as 210 m and almost 6-min duration (Elsner et al., 1966b; Ridgway, 1986; Williams et al., 1999; Houser et al., 2010; Noren et al., 2012).

A third paper that will be reviewed later in the chapter modeled changes in intra-abdominal pressure and venous pressure profiles due to fluking (Lillie et al., 2018). In that study, it was postulated that the spinal rete may protect the brain against pressure oscillations in the epidural veins within the vertebral canal. These hypotheses have been further developed in a more recent paper (Lillie et al., 2022).

Other retia of variable size and structure have been described throughout the cetacean body, including an ophthalmic rete, and retia in the pterygoid sinus, in mandibular fat pads, in the nasal plug/passages of the head, in the neck, along the esophagus, within the thorax, in the lumbar region (between the lumbar vertebrae and the hypaxial muscles), and in the pelvis (Slijper, 1962; McFarland et al., 1979; Vogl and Fisher, 1982; Melnikov, 1997; Piscitelli et al., 2010; Costidis and Rommel, 2012; Ninomiya et al., 2014; Costidis and Rommel, 2016b). Many of these retia, such as the ophthalmic rete, are also associated with complex venous networks (plexuses) and are probably involved in thermoregulation. In addition, in the head, it has been suggested that these vascular networks may (a) allow for gas exchange and nitrogen absorption from blood into associated fat in pterygoid sinus and mandibular fat, (b) affect acoustic properties of the intermandibular fat body, (c) engorge to prevent barotrauma in the pterygoid air sinus and nasal passages, and (d) engorge in the nasal plug to promote sealing of the plug in the blowhole during a dive (Costidis and Rommel, 2012, 2016a,b). In the abdominal cavity, extensive arterial and venous networks are associated with the uterus/ovaries and the testes in odontocetes ranging from bottlenose dolphins to sperm whales (Rommel et al., 1992, 1993; Melnikov, 1997). These vascular networks associated with the reproductive organs often consist of parallel arteries associated with veins or venous plexuses in a countercurrent flow arrangement that can contribute to thermoregulation. See Section "Thermal effects of exercise and diving," and Fig. 10 in Chapter 3 for further review of these structures.

Venous plexuses and epidural veins

Extensive venous plexuses throughout the body, including those described in the prior paragraph, have long been noted in many cetaceans, including the bottlenose dolphin (Slijper, 1962). As already mentioned, many of these venous networks, dependent on their anatomy and location, may contribute to thermoregulation with influx of cooler blood from the skin and appendages, and efflux of heat away from central organs (see Chapter 3 for further review). Engorgement of large venous plexuses at depth is also an important mechanism for baroprotection in the cranial air sinuses (see prior paragraph) and in the middle ear (Sassu and Cozzi, 2007). The increase in venous volume decreases the fixed volume within a rigid bony cavity and allows for compression of air to smaller volumes without mechanical disruption of tissues.

Venous plexuses are also considered to play a role in baroprotection in the respiratory system with transfer of peripheral blood into the thorax and allowance of greater compression of air volume without associated tissue damage. It has been proposed that engorgement of the large submucosal venous plexuses found in the tracheae and bronchi of cetaceans contribute to such baroprotection (Slijper, 1962; Leith, 1989; Cozzi et al., 2005; Ninomiya et al., 2005; Davenport et al., 2009, 2013). The extensive development of the thoracic rete within the thorax in deep-diving cetaceans also raises the possibility that these structures, although arterial, may contribute to baroprotection (Slijper, 1962; Melnikov, 1997). Volume of the intrathoracic retial tissue of deeper-diving kogiid whales is twice that in the bottlenose dolphin (Piscitelli et al., 2010). In addition, in a modeling study of the fin whale, the estimated volume of blood in the rete was adequate for pressure equilibration (Lillie et al., 2013). Another structure that may contribute to the equilibration of pressure by engorgement within the thorax is the pericardial venous plexus (Harrison and Tomlinson, 1956; Piscitelli et al., 2013).

In seals, there are large hepatic sinuses that can store blood and that empty into the vena cava (Harrison and Tomlinson, 1956; Elsner et al., 1964). From available anatomical studies, cetaceans do not appear to have these large hepatic sinuses (Harrison and Tomlinson, 1956; Barnett et al., 1958; Slijper, 1962). In the northern elephant seal, for example, the posterior vena cava and hepatic sinuses can store up to 20% of the blood volume (Elsner et al., 1964). Slijper (1962) did report that the hepatic veins were enlarged in odontocetes, but not in mysticetes. The relative size of these hepatic veins and their role in blood storage in cetaceans is unclear. Recently, large central veins and vascular sinuses have been observed in the liver tissue of several odontocete species, including the bottlenose dolphin
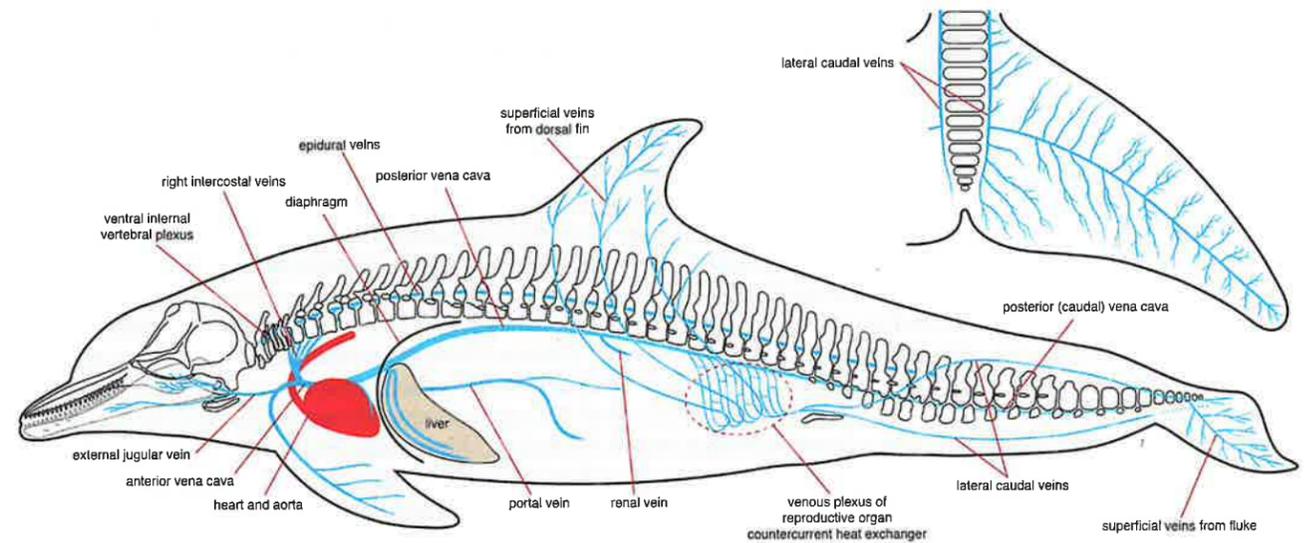
FIG. 4   Venous anatomy in the bottlenose dolphin. The major components of the venous system include the anterior and posterior venae cavae, the paired epidural veins inside the vertebral canal, countercurrent heat exchangers (see Chapter 3: Thermoregulation) in the dorsal fin, flippers, and fluke and around the reproductive organs, and venous plexuses of the head and abdomen (partially illustrated). The anterior vena cava receives venous inflow from the epidural veins via the large intercostal veins, and from the cranial plexi, and central veins from heat exchangers in the flippers and dorsal fin. The epidural veins receive inflow from the brain and dorsal musculature. There are small communicating veins (not illustrated) in the lumbar region between the epidural veins and posterior vena cava. The posterior vena cava receives input from the kidneys, muscle, multiple abdominal structures, including the hepatic veins, and various venous plexi associated with countercurrent heat exchangers in the fluke and in the abdomen. Posterior to the renal vein, the vena cava is paired and has two channels. The posterior vena cava travels inside a diaphragmatic sling as it enters the thorax through the caval hiatus. The portal vein conducts blood from the gastrointestinal tract, spleen, pancreas, and gall bladder to the liver. The upper right insert is a schematic diagram of the superficial venous network of the fluke. Flow through superficial veins in the fluke and dorsal fin returns cooled blood to the abdomen via the lumbo-caudal venous plexus and then into the abdominal heat exchangers around the reproductive organs. Central veins from the fin and fluke heat exchangers (not illustrated) return warm blood more directly to the vena cava. See Harrison and Tomlinson (1956), Rommel et al. (1992, 1993, 1994, 2006), and Lillie et al. (2018) for detailed reviews. *Modified from Harrison and Tomlinson (1956), Rommel et al. (1992, 1993, 1994, 2006), and Lillie et al. (2018) and suggestions from S.A. Rommel, A.M. Costidis, and D.A. Pabst. Illustration by Uko Gorter.*

(Cozzi et al., 2017). The portal vein sphincters described earlier in this section were also seen. These authors have suggested that there may be complex regulation of liver blood flow in these animals during diving. Furthermore, investigation would be beneficial.

Another striking feature of the cetacean venous system is the presence of large epidural veins located ventral to the spinal cord inside the vertebral canal (Harrison and Tomlinson, 1956; Slijper, 1962). These veins are valveless and communicate with the anterior and posterior venae cavae via intercostal and lumbar veins (Fig. 4). In the anterior portion of the vertebral canal, a venous rete drains blood from the brain and eventually links with the epidural veins in the mid-thorax region to empty into the anterior vena cava (Harrison and Tomlinson, 1956). Posteriorly, the epidural veins receive blood from the dorsal musculature through small veins that enter the vertebral canal through the ligamentum flavum (the dorsal ligament between adjacent vertebrae). Blood from the tail fluke does not drain into the epidural veins; rather, blood drains from the tail either via lateral veins beneath the skin or the chevron veins at the bases of the vertebrae into the vena cava. Readers are again referred to Chapter 3 for further review.

The volume of the vasculature within the vertebral canal is markedly increased in deeper-diving cetaceans (Rowlands et al., 2021). In beaked whales, extreme deep divers, vascular volume was 22–35 times greater than spinal cord volume in contrast to the 6–10-fold value in shallower diving dolphins. Remarkably, vascular volume in Cuvier's beaked whale occupied 96% of the volume of the vertebral canal.

Posterior vena caval hemodynamics during fluking

In seals, a striated muscle sphincter around the posterior vena cava at the level of the diaphragm is considered to regulate venous return to the heart (Elsner et al., 1971; Ronald et al., 1977). Such a distinct sphincter around the vena cava does not occur in cetaceans, but there have been observations of diaphragmatic "slings" at the caval hiatus (the opening in the diaphragm through which the vena cava travels, Fig. 4), reports of sphincter-like arrangements of

muscle in the diaphragm around the caval hiatus, as well as mention of the absence of a sphincter (Harrison and Tomlinson, 1956; Slijper, 1962; Rowlatt and Gaskin, 1975; Hilton and Gaskin, 1978). This question of a diaphragmatic sphincter in cetaceans led to a recent examination of sphincters in cetaceans and to investigation of the role of such sphincters in the hemodynamics of the posterior vena cava (Lillie et al., 2018).

Lillie et al. (2018) found that diaphragmatic sphincters (annular or V-shaped arrangements of muscle fibers around the caval hiatus) existed in all seven cetacean species examined (harbor porpoise, Dall's porpoise, Pacific white-sided dolphin, beluga, killer whale (*Orcinus orca*), fin whale, and minke whale). In addition, there did not appear to be any structural differences in the sphincters among the odontocetes. This was not expected as the authors had hypothesized that higher intra-abdominal pressures during fluking in faster-swimming cetaceans would require more well-developed sphincters to prevent surges or oscillations in venous return to the heart.

Previously, the authors had found that faster swimmers such as Dall's porpoises, Pacific white-sided dolphins, and harbor porpoises had higher diaphragmatic subserosal collagen contents than the slower cetacean species, and that pinnipeds lacked such collagen in their diaphragms (Lillie et al., 2017). From the correlation of diaphragm collagen content with swim speed, they hypothesized that this increase in collagen content reinforced the diaphragm against deformation due to high intra-abdominal pressures generated by fluking. Pinnipeds, on the other hand, lacked collagen because they did not experience elevated intra-abdominal pressures since they did not fluke. Even in phocid seals, the lateral movements of hindflippers would not generate the intra-abdominal pressures developed in cetaceans, by compression of the abdominal cavity during fluking.

These findings led to new hypotheses as to (a) posterior vena caval hemodynamics during fluking, (b) the function of the diaphragmatic sphincter in cetaceans, (c) another role for the intravertebral rete, and (d) differences in the function of the diaphragmatic sphincter in cetaceans versus phocid seals. Basically, the authors examined and modeled how elevations in intra-abdominal pressure during fluking might influence posterior vena caval inflow into the thorax, as well as retrograde flow from the posterior vena cava through the lumbar communicating veins into the epidural veins.

In a hemodynamic model of vena caval blood flow into the thorax, blood flow into the thorax oscillated with each stroke of the tail if intra-abdominal pressure was low (Fig. 5). The return of blood to the heart was irregular with a surge

of blood with each stroke. Under these conditions, transient contractions of a caval sphincter could minimize surges into the thorax, providing a more constant return of blood to the heart. However, if increased intra-abdominal pressure (time 0, Fig. 5) occurred with fluking, compression of the intra-abdominal segment of the vena cava dampened the flow oscillations into the thorax. At first glance, this might seem to obviate the need for a diaphragmatic sphincter to regulate venous return to the heart under these conditions. However, there was a large surge of blood flow into the thorax at the initial increase in intra-abdominal pressure (time 0, Fig. 5), and it is this surge that the authors postulate the sphincter contraction can regulate to control blood flow into the thorax. Hence, a diaphragmatic sphincter is present in all cetaceans regardless of swim speed and diaphragm collagen contents. However, the sphincter need not be more developed in faster-swimming species because high intra-abdominal pressure minimizes any surge of flow into the thorax. Equally significant at the onset of the elevated intra-abdominal pressure (time 0, Fig. 5) was the retrograde surge of blood out of the vena cava into the epidural veins and toward the brain. The authors postulate that any retrograde blood flow or pressure oscillations experienced by the brain are minimized by the small size of the lumbar communicating veins and, importantly, by the retia.

In contrast to cetaceans, pinnipeds do not fluke, yet the phocid seals, especially, have well-developed vena caval sphincters. In addition, as reviewed earlier, the phocids can store blood, which sometimes can be completely oxygenated (Meir et al., 2009), in their large hepatic sinuses and posterior venae cavae. So, in phocids in contrast to cetaceans, Lillie et al. (2018) postulated that intra-abdominal pressures may fluctuate with lateral undulations of the hindflippers, but that such intra-abdominal pressures were low, and not elevated. Under those conditions, there would be a continual oscillation in flow into the thorax that could be minimized by transient contractions of a sphincter. In phocids, regulation of venous return to the heart with a vena caval sphincter is postulated not only to optimize cardiac filling from the large venous reservoir behind the diaphragm but also to meter out the large blood O_2 store contained in the hepatic sinuses and posterior venae cavae.
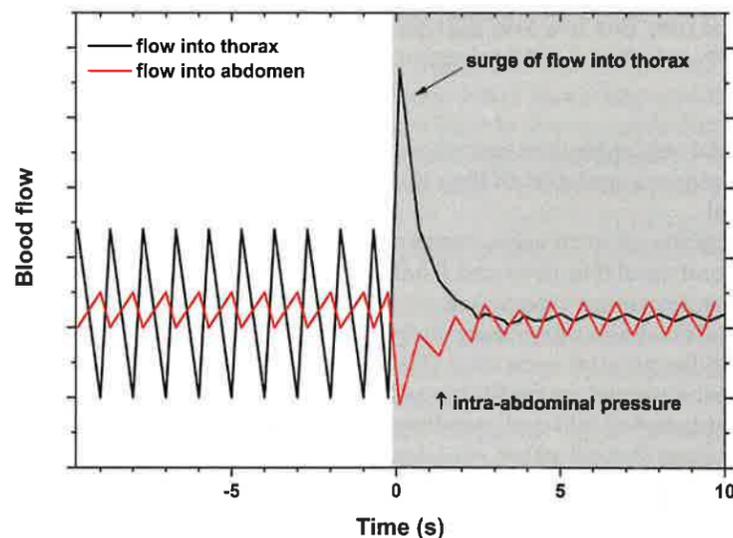

FIG. 5 Hypothesized effect of increased intra-abdominal pressure on vena caval blood flow entering the abdomen from the periphery and exiting the abdomen into the thorax. In the model, fluking is continuous, and intra-abdominal pressure and vena caval blood flow into the thorax oscillate due to fluking if intra-abdominal pressures are low. A caval sphincter could minimize oscillations in venous return to the heart under these conditions. If greater intra-abdominal pressures occur during fluking (time 0), the intra-abdominal segment of the vena cava will compress and dampen the flow oscillations into the thorax. This process has been described as a vascular waterfall or Starling resistor effect. Blood flow into the thorax and heart would be more constant at the higher intra-abdominal pressure even without a sphincter. However, at the onset of an increase in intra-abdominal pressure, there is a transient forward surge of flow into the thorax, and also a backward surge out of the abdomen, most probably into the epidural veins. Here again, a diaphragmatic caval sphincter could minimize this transient forward surge, preventing overdistention of the heart. In regard to retrograde flow into epidural veins, the communicating veins between the vena cava and epidural veins are small, thus offering resistance to such flow. In addition, the spinal/cranial retia mirabilia may protect against any pulsatility or transient retrograde surge of blood via the epidural veins toward the brain. *Modified from Lillie et al. (2018).*

Cardiovascular function during diving

In this section, we first review the cardiovascular dive response and examine the heart rate profiles of some cetaceans during dives. We conclude with consideration of the implications of these heart rate profiles for peripheral blood flow, O_2 store management, and respiratory gas uptake, distribution, and removal during dives.

The dive response

The cardiovascular dive response, which consists of the bradycardia (decreased heart rate) and peripheral vasoconstriction associated with the breath hold, underlies diving physiology and the management of O_2 stores during dives (Ponganis et al., 2011). This response results in the redistribution of blood flow to organs and tissues and the conservation of the blood O_2 store (Scholander, 1940; Irving et al., 1941b; Scholander et al., 1942; Elsner et al., 1966a). In forcibly submerged seals, the dive response was extreme with blood flow essentially restricted to the brain and heart (Scholander, 1940; Scholander et al., 1942; Zapol et al., 1979; Blix et al., 1983). However, in free-diving seals, the bradycardia was often less intense and variable, with the preservation of digestive, renal, and hepatic function during aerobic dives (Jones et al., 1973; Davis et al., 1983; Thompson and Fedak, 1993; Andrews et al., 1997; Davis, 2014).

The intensity and pattern of heart rate reduction may be influenced by many potential factors, including exercise, depth, lung volume changes, and volitional control. Readers are referred to several recent papers and reviews for consideration of the neuroregulation and neuropathways involved in the dive response (Davis and Williams, 2012; Panneton, 2013; Williams et al., 2015b; Elmegaard et al., 2016, 2019; Ponganis et al., 2017; Kaczmarek et al., 2018; Panneton and Gan, 2020; Fahlman et al., 2020a). Because of the complexity of peripheral blood flow measurements, heart rate has often been used as an index of the intensity of the dive response in free-diving and free-swimming animals.

Early studies of heart rates in small- and medium-sized cetaceans

Some of the earliest heart rate studies in cetaceans were conducted with long break-away ECG leads and a benchtop recorder in free-swimming dolphins and porpoises (Scholander, 1940; Irving et al., 1941a). In fragmentary heart rate records, Irving and Scholander observed that both the intensity and pattern of bradycardia were variable during short

dives of bottlenose dolphins, but that the reduction in heart rate was minimal in rapidly breathing, surface-swimming harbor porpoises.

In the early 1960s, Elsner and coworkers applied the long ECG lead technique to a Pacific bottlenose dolphin and found that apneic heart rates during spontaneous swimming ranged between 40 and 60 bpm, about a 50% reduction from heart rates associated with breathing (eupnea) (Elsner et al., 1966b). During a trained, stationary, 4.7-min dive, heart rate declined to about 10 bpm, gradually rose to about 30 bpm by the end of the dive, and reached 120 bpm during rapid postdive respirations with minimal decreases in heart rate during the short apneic intervals between breaths.

During the 1960s–70s, Ridgway and Kanwisher utilized both the long ECG lead approach and underwater telemetry to examine heart rate in a variety of species during rest (with slow respiratory rates) and during shallow swimming/dives (Kanwisher and Sundnes, 1965; Ridgway, 1972, 1986; Kanwisher and Ridgway, 1983). They documented that, under these conditions, the oscillation in heart rate occurred with every breath (respiratory arrhythmia) and that the change in heart rate was similar to that reported by Elsner et al. (1966b). Regardless of breath-hold duration, heart rate decreased during apnea by about 50% from the faster heart rate (tachycardia) during eupnea. It was also noted again that after longer dives, the postdive tachycardia was higher and remained high throughout the rapid respiratory cycles until exhaled CO_2 levels returned to baseline. Species included killer whales, pilot whales, belugas, bottlenose dolphins, common dolphins, Pacific white-sided dolphins, Dall's porpoises, harbor porpoises, and Amazon River dolphins (Spencer et al., 1967; Ridgway, 1972). Among mysticetes, a respiratory arrhythmia heart rate pattern was documented in a young gray whale much later with use of a Holter monitor (Ponganis and Kooyman, 1999).

Characteristics of the respiratory arrhythmia heart rate profile in dolphins have been examined in recent post–breath hold investigations of trained animals. These studies suggested that the peak heart rate and magnitude of the respiratory arrhythmia after the breath hold may be related to respiratory rate and other respiratory variables, including tidal volume (Cauture et al., 2019; Blawas et al., 2021a). Similar to heart rate at rest, the peak and minimum heart rates of the respiratory arrhythmia were inversely related to body mass (Blawas et al., 2021b).

Heart rate profiles during diving

Advances in biologging technology have now allowed the documentation of heart profiles during trained and natural dives in several cetacean species. In more recent studies of cetaceans under managed care, the general heart rate profile described above has been confirmed in bottlenose dolphins, Risso's dolphins (*Grampus griseus*), harbor porpoises, killer whales, belugas, and pilot whales during trained stationary breath holds and spontaneous dives of three to 4-min duration, as well as in bottlenose dolphins during trained dives at sea (Williams et al., 1999, 2015b; Noren et al., 2004, 2012; Houser et al., 2010; Davis and Williams, 2012; Elmegaard et al., 2016; Suzuki et al., 2017; McDonald et al., 2018; Bickett et al., 2019; Aoki et al., 2021; Blawas et al., 2021a). Application of the equipment and techniques developed with animals under managed care has now allowed initial investigations of heart rates of wild cetaceans at sea in three species: the narwhal, harbor porpoise, and blue whale (Williams et al., 2017; Goldbogen et al., 2019; McDonald et al., 2021).

During a dive, heart rate is, of course, dependent on body mass, as well as on the nature of a given dive. Heart rate at rest declines as body mass increases (Stahl, 1967). This relationship was reflected in the range of dive heart rate profiles for cetaceans ranging from a 54 kg harbor porpoise to a 70,000 kg blue whale in Fig. 6. In addition to body mass, dive heart rates vary among and within dives because of a variety of factors, including dive duration and depth, dive function (foraging, travel or sleep), locomotory activity, changes in dive expectations, and stressors (Davis and Williams, 2012; Noren et al., 2012; Williams et al., 2015b, 2017; Elmegaard et al., 2016, 2019; Goldbogen et al., 2019; Fahlman et al., 2020a).

Most of what we know about the factors that regulate of heart rate during dives of cetaceans is from trained animals, primarily bottlenose dolphins. Exercise is one such factor. In deeper dives, trained bottlenose dolphins exhibited heart rate profiles that were similar to profiles observed in diving seals and sea lions: rapidly decreasing from predive values of 100–120 beats min^{-1} to lows of 20–30 beats min^{-1}, before increasing again as the dolphin started ascent (Williams et al., 1999; Houser et al., 2010) (Fig. 7). Based on the similarity to heart rate profiles previously documented in shallow, stationary dives (Elsner et al., 1966b), Williams et al. (1999) concluded that the dive response during deep dives dominated over the typical mammalian exercise response of increased heart rate and muscle blood flow.

However, more recently, a correlation between stroke rate and heart rate in short shallow dives led to the hypothesis that bottlenose dolphins exhibit an exercise modulated dive heart rate response (Davis and Williams, 2012; Noren et al., 2012; Williams et al., 2015b). Trained harbor porpoises also exhibited an exercise modulated heart rate response
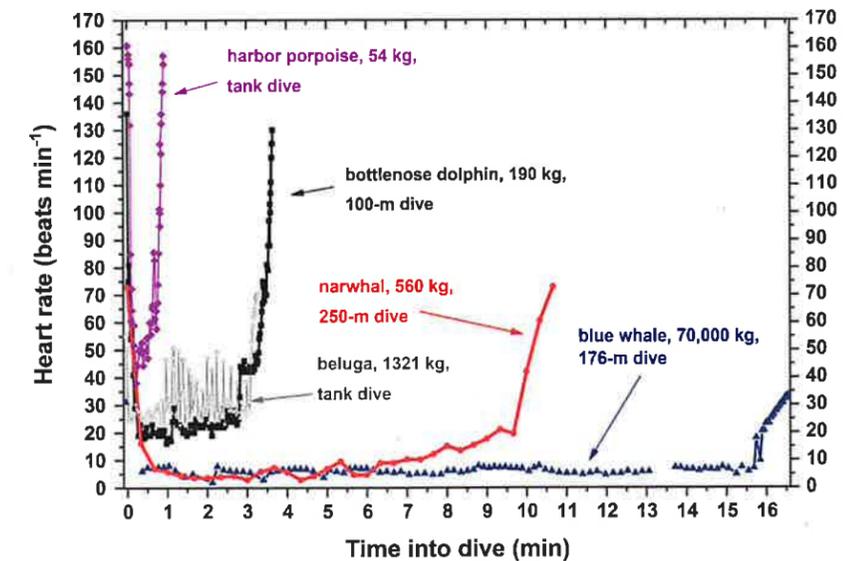
FIG. 6   Heart rate profiles of five cetaceans during spontaneous dives. The common features of the dive heart rate profile include the overall pattern, the variability in beat-to-beat heart rates, and the general effects of body mass on heart rate. Heart rate typically decreases during descent to a level determined by the nature of a dive and then increases during ascent. Pre- and postdive heart rates are elevated and are higher in smaller animals due to the allometric relationship of body mass and heart rate. The intensity and pattern of the bradycardia during the bottom phase of the dive are a function of both the nature of the dive and body mass. For instance, it is expected that heart rate of a beluga during a deep, long dive would be much slower and probably less variable than a shallow, leisurely dive in a tank. *Modified from McDonald et al. (2018), Houser et al. (2010), Bickett et al. (2019), Williams et al. (2017), and Goldbogen et al. (2019).*

during dives that varied in duration and activity (McDonald et al., 2018). The exercise modulated dive response has been proposed to be key to maximizing aerobic dive duration through the efficient balancing of blood and muscle O_2 store depletion (Davis and Kanatous, 1999; Davis and Williams, 2012; Davis, 2014; Williams et al., 2015a,b). In this model, increased heart rates associated with increased stroke rates have been postulated to increase muscle blood flow and O_2 delivery, thus supplementing and prolonging aerobic metabolism in exercising muscle and potentially resulting in simultaneous depletion of blood and muscle O_2 stores.

Measurements of heart rates in wild cetaceans have demonstrated that exercise modulation of heart rate is probably variable and, again, dependent on the nature of a dive (Figs. 6 and 8). In narwhals, heart rate was extremely low and did not correlate with stroke rate during dives immediately postrelease (Williams et al., 2017). In contrast, during dives several hours after release, heart rate was higher (though still low) and it correlated with stroke rate. In the shallow-diving harbor porpoise (Fig. 8), the bradycardia was moderate, relatively stable, and appeared independent of dive type, dive duration, and activity (McDonald et al., 2021). In these spontaneously diving, foraging, and highly active animals, heart rate was not linked with activity. In a blue whale (Fig. 8), heart rates were consistently below allometrically predicted resting heart rates in both foraging and nonforaging dives (Goldbogen et al., 2019). However, heart rate did transiently increase during feeding lunges, consistent with an increase in heart rate because of exercise. These three investigations are a beginning. Furthermore, evaluation of the regulation of heart rate in cetaceans at sea and better understanding of the role of the cardiovascular response in foraging ecology and stress responses require more research and further advances in technology.

Heart rate profiles during postdive intervals and during high-speed surface travel

We have already mentioned that the typical apneic decline in heart rate during slow breathing at rest did not occur during the rapid breathing of the immediate postdive period of the bottlenose dolphin or during the rapid breathing of a fast surface-swimming harbor porpoise. Sustained high heart rates presumably optimize gas exchange during these conditions of high respiratory activity (Fahlman et al., 2018).

As illustrated in Fig. 7A and B, high heart rates were maintained during surface intervals between serial 100-m dives of a trained bottlenose dolphin while diving heart rates declined to about 20 bpm (Houser et al., 2010). After the dive
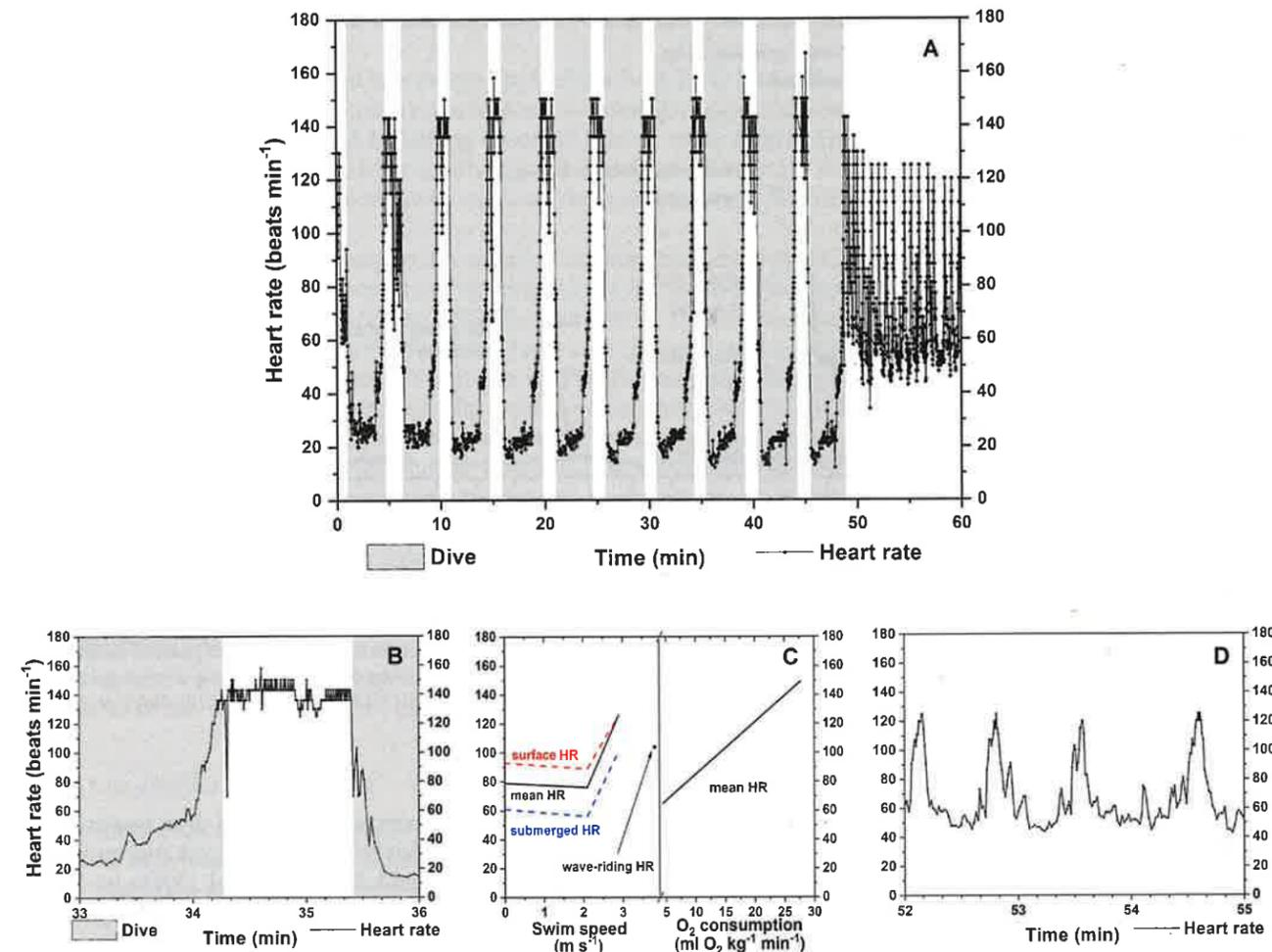
FIG. 7   Heart rates in the bottlenose dolphin. (A) Heart rate profiles of a bottlenose dolphin during serial trained dives to 100-m depth and during the post-dive-bout period when the dolphin underwent ultrasound exams while beached. Heart rate was 140–150 beats min^{-1} (bpm) during surface intervals between dives, reached 30–40 bpm during the bottom phases of the dives, and demonstrated a consistent increase during ascent. (B) 3-min heart rate profile from A illustrates the variability in heart rate both during the dives and during the surface interval. However, despite respirations during the surface interval, the typical respiratory sinus arrhythmia (elevated heart rate with inspiration, decreased heart rate during the breath hold) was not evident. Heart rate remained high throughout the surface interval. (C) During surface swimming of a bottlenose dolphin, the difference in heart rate between inspiration and the breath hold (sinus arrhythmia) gradually disappeared as swim speed increased. Both surface and submerged heart rates increased with swim speed and merged at the highest swim speeds. Heart rate increased with exertion in exercise studies. At maximum oxygen consumption, heart rate was 140 bpm, similar to that during surface intervals between dives (A, B). During wave-riding, heart rate was lower at higher speeds, consistent with a lower metabolic rate during wave-riding. (D) 3-min heart rate profile during post-dive-bout period in A demonstrated a typical sinus arrhythmia pattern associated with breathing in contrast to that during the surface intervals between dives. *Modified from Houser et al. (2010) and Williams et al. (1992, 1993).*

session, similar to the earlier observations of Elsner and Ridgway, eupneic and apneic heart rates gradually declined, and the typical 50% difference between apneic and eupneic heart rate returned (Fig. 7A and D). Sustained high heart rates during surface intervals between dives have also been documented in the harbor porpoise, one of the smallest cetaceans, and in the blue whale, the largest (McDonald et al., 2018, 2021; Goldbogen et al., 2019).

In addition to Scholander's early observations in the harbor porpoise, current evidence also indicates that high heart rates are maintained during high-speed surface travel of dolphins. Elevated eupneic and apneic heart rates merged in trained bottlenose dolphins both during high-speed surface swimming at sea and during maximal exercise studies where dolphins swam against a load cell (Fig. 7C) (Williams et al., 1992, 1993). In contrast to diving, the physiology of exercise during high-speed surface travel of dolphins and porpoises appears more similar to that of terrestrial
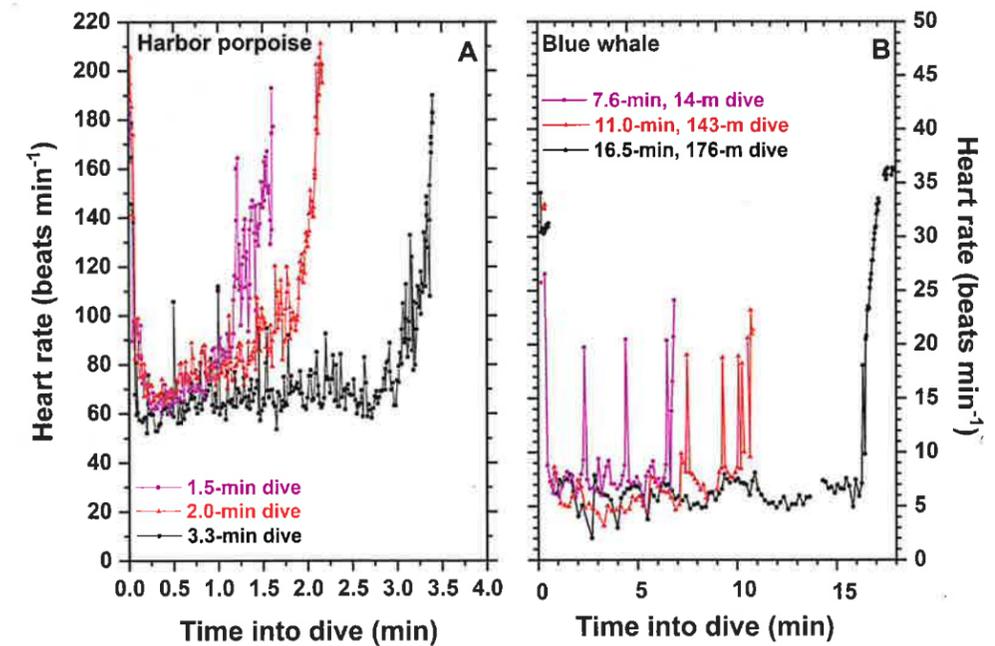
FIG. 8   Harbor porpoise and blue whale heart rates during dives at sea. Heart rate in diving cetaceans is affected by both body mass and the nature of a dive as evidenced by these heart rate profiles of one of the smallest porpoises and the largest whale. (A) Heart rate in the harbor porpoise ranges from 50 to 80 beats min^{-1} (bpm) during the bottom phase of the dive and is near 190–220 bpm while at the surface. (B) In contrast, in the blue whale, heart rate is typically 2–10 bpm during the dive and reaches 25–35 bpm on the surface. There is considerable variation in heart rate in both species during the dive, often including abrupt one to three-beat oscillations in heart rate. Feeding lunges in blue whales were typically associated with transient increases in heart rate of two to five bpm (most evident in the longest dive). All dives were associated with an increase in heart rate during ascent. Gaps in the blue whale heart rate profiles were secondary to artifact in the ECG record. *Modified from McDonald et al. (2021) and Goldbogen et al. (2019).*

mammals (Taylor et al., 1987) with maximization of O_2 transport from lungs to muscle supported by high heart rates and respiratory rates. The increased heart masses of faster-swimming species, and even the increased affinities of Hb for O_2 in the faster species are consistent with this hypothesis (Ridgway and Johnston, 1966; Horvath et al., 1968).

Heart rate and oxygen store management

Review of the role of heart rate and the dive response in O_2 store management and diving physiology must take into consideration the species and type of dive performed. The bottlenose dolphin and many shallow-diving odontocetes have larger lung masses (possibly a greater respiratory O_2 store) than deeper-diving species (Piscitelli et al., 2010). From available data, the coastal form of the bottlenose dolphin also has a lower Hb content, smaller blood volume, lower myoglobin concentration, and smaller relative muscle mass (Ridgway and Johnston, 1966; Mallette et al., 2016; Pabst et al., 2016). Based on (a) the coastal bottlenose dolphin's lower mass-specific O_2 store with a greater percentage of O_2 in the lungs, and (b) its predominant shallow (<20 m) diving (above the expected depth of alveolar collapse and lack of pulmonary gas exchange (Ridgway and Howard, 1979; Mate et al., 1995)), a less intense bradycardia and greater transport of O_2 from the lung to muscle would be expected during shallow dives and subsurface swims. Indeed, the very low exhaled lung O_2 fractions of a bottlenose dolphin trained to actively swim between divers at 20-m depth, as well as the elevated heart rates during trained underwater swims at shallow depths, suggest that this is the case (Ridgway et al., 1969; Noren et al., 2012). On the other hand, during deep dives near or below the depth of alveolar collapse, one would expect a more intense bradycardia, decreased muscle blood flow, and greater reliance on myoglobin-bound O_2 stores in muscle. This is again supported by the lower heart rates during deeper dives of bottlenose dolphins (Williams et al., 1999; Houser et al., 2010).

Different heart rate profiles will affect cardiac output and degree of peripheral vasoconstriction during different types of dives. These changes in the magnitude and distribution of blood flow will not only affect O_2 store management but will also affect the uptake and distribution of other respiratory gases (CO_2, nitrogen). Readers are referred to Chapter 6: Respiratory physiology in the dolphin and other whales and Chapter 7: Diving physiology in dolphins and human for further review of respiratory and diving physiology.

Blood O_2 transport

One of the primary functions of the cardiovascular system is the transport of O_2 to tissues. The higher the blood O_2 content is, the greater the delivery of O_2 to the periphery with every heartbeat is. Here, we review the primary determinants of blood O_2 content, hemoglobin (Hb) concentration, and the oxygen-hemoglobin (O_2-Hb) dissociation curve. Compared with the Hb-bound O_2, the amount of dissolved O_2 is quite low. Readers are referred to Chapter 6 for the details of the uptake and distribution of respiratory gases.

Hemoglobin concentration

Hemoglobin concentrations in bottlenose dolphins ranged from about 14–15 g dL^{-1} in coastal forms to 18.5 g dL^{-1} in deeper diving, offshore forms (Ridgway and Johnston, 1966; Duffield et al., 1983). For comparison, human standard values are 12–16 g dL^{-1} (Dominelli et al., 2021). In general, Hb concentrations were higher in cetaceans that dive deeper and/or that have higher metabolic rates whether because of higher routine swim speeds, foraging activity, or thermoregulatory demand (Ridgway and Johnston, 1966). Although available data are limited and sometimes conflicting (Table 4), the highest values (20–23 g dL^{-1}) among odontocetes occurred in documented or suspected deep-diving

TABLE 4 Hemoglobin concentration ([Hb]) and P_{50} (partial pressure of O_2 at which Hb is 50% saturated) in dolphins and other cetaceans.

Species	[Hb] (g dL^{-1})	P_{50} (mmHg)	Reference
Bottlenose dolphin (coastal) *Tursiops truncatus*	14.4	24.6, 26.8	Horvath et al. (1968), Ridgway and Johnston (1966), Lenfant (1969)
Bottlenose dolphin (offshore) *Tursiops truncatus gilli*	18.5	26.0	Duffield et al. (1983), Lenfant (1969)
Common dolphin *Delphinus delphis*	18	21.6	Horvath et al. (1968), Sharp et al. (2014)
Pacific white-sided dolphin *Lagenorhynchus obliquidens*	17.0	20.2, 24.8	Horvath et al. (1968), Lenfant (1969), Ridgway and Johnston (1966)
Dall's porpoise *Phocoenoides dalli*	20.3	19.1	Horvath et al. (1968), Ridgway and Johnston (1966)
Beluga *Delphinapterus leucas*	20.9–23.0	24.2	Choy et al. (2019), Dhindsa et al. (1974), Ridgway et al. (1984)
Harbor porpoise *Phocoena phocoena*	19, 20	24.5	Green and Redfield (1933), Koopman et al. (1999), Reed et al. (2000)
Amazon dolphin *Inia geoffrensis*	14.3	25	Lenfant (1969)
Sperm whale *Physeter macrocephalus*	15.1–15.8, 22	26.5	Lenfant (1969), Green and Redfield (1933), Tawara (1950)
Gray whale *Eschrichtius robustus*	14.0	30.0	Lenfant (1969)
Risso's dolphin *Grampus griseus*	21.4,	30.5	Lenfant (1969)
Killer whale *Orcinus orca*	16.0–18.0	30.7, 25.2	Dhindsa et al. (1974), Lenfant et al. (1968), Ridgway (1972)
Pilot whale *Globicephala macrorhynchus, G. melas*	15.1–16.5, 19.6	31	Lenfant (1969), Medway and Moldovan (1966), Ridgway et al. (1970), Velten et al. (2013)
Rough-toothed dolphin *Steno bredanensis*	13.7–15.5		Manire et al. (2018)
Yangtze finless porpoise *Neophocaena asiaeorientalis*	14.3–17.1		Nabi et al. (2017)

TABLE 4 Hemoglobin concentration ([Hb]) and P_{50} (partial pressure of O_2 at which Hb is 50% saturated) in dolphins and other cetaceans—cont'd

Species	[Hb] (g dL^{-1})	P_{50} (mmHg)	Reference
Spotted dolphin *Stenella attenuata*	17		St. Aubin et al. (2013)
Spinner dolphin *Stenella longirostris*	18		Suarez et al. (2019)
Commerson's dolphin *Cephalorhynchus commersoni*	18		Hedrick and Duffield (1991)
Fraser's dolphin *Lagenodelphis hosei*	20.2–22.1		Clark et al. (2002), Rhinehart et al. (1995)
Striped dolphin *Stenella coeruleoalba*	20.9		Gales (1992)
Narwhal *Monodon monoceros*	22.5		Vogl and Fisher (1982)
Beaked whale *Mesoplodon* sp.	22.9		Velten et al. (2013)
Blue whale *Balaenoptera musculus*	9.6		Laurie (1933)
Fin whale *Balaenoptera physalus*	9.6		Laurie (1933)
Sei whale *Balaenoptera borealis*	15.6		Tawara (1950)
Bowhead whale *Balaena mysticetus*	20.5		Castellini et al. (2006)

Note: 1 mm Hg = 0.133 kPa.

species such as beaked whales, sperm whales, narwhals, belugas, Dall's porpoises, Risso's dolphins, Fraser's dolphins (*Lagenodelphis hosei*), and striped dolphins. The high Hb content of the harbor porpoise has been attributed to its small size and thermoregulatory metabolic demands. Hemoglobin concentration in pilot whales, relatively active deep divers (Aguilar De Soto et al., 2008; Aoki et al., 2017), was high in one study but was similar to that of the coastal bottlenose dolphin in three other studies (Table 4). In comparison, much higher Hb concentrations (25–27 g dL^{-1}) have been reported in some phocid seals (Ponganis, 2011).

Relatively, low Hb concentrations of 10–15 g dL^{-1} have been reported in several species of rorqual whales, while bowhead whale Hb content was near 20 g dL^{-1} (see Table 4). Very few data were available for mysticetes. However, these differences in Hb concentrations between rorquals and the bowhead paralleled similar differences in the concentrations of muscle myoglobin, the other major O_2-binding protein in the body (Tawara, 1950; Lawrie, 1953; Hochachka and Foreman, 1993; Noren and Williams, 2000; Cartwright et al., 2016).

O_2-Hb dissociation curves

A single Hb molecule can bind up to four O_2 molecules; at full saturation of Hb, there are 1.34 mL O_2 g^{-1} Hb in blood (Dominelli et al., 2021). The sigmoidally shaped O_2-Hb dissociation curve reveals the degree of Hb saturation as a function of the partial pressure of O_2 (P_{O_2}) in blood (Fig. 8). The P_{50} (P_{O_2} at which Hb is 50% saturated) is an index of the affinity of Hb for O_2; as affinity increases, the P_{50} decreases (Dominelli et al., 2021). The O_2 affinity of Hb can reversibly change as a function of blood temperature, CO_2, and pH, as well as by changes in intracellular organophosphates (Storz, 2016). Hemoglobin's affinity for O_2 decreases with increased temperature or acidity, and increases with lowered temperature and alkalosis. Thus, the O_2-Hb dissociation curve can shift to the left (increased affinity, lower P_{50}) or to the right (decreased affinity, higher P_{50}). Decreased Hb-O_2 affinity promotes the release of O_2 from Hb in the periphery, while increased affinity enhances uptake of O_2 by Hb in the lung. In many mammals and birds exposed to chronic
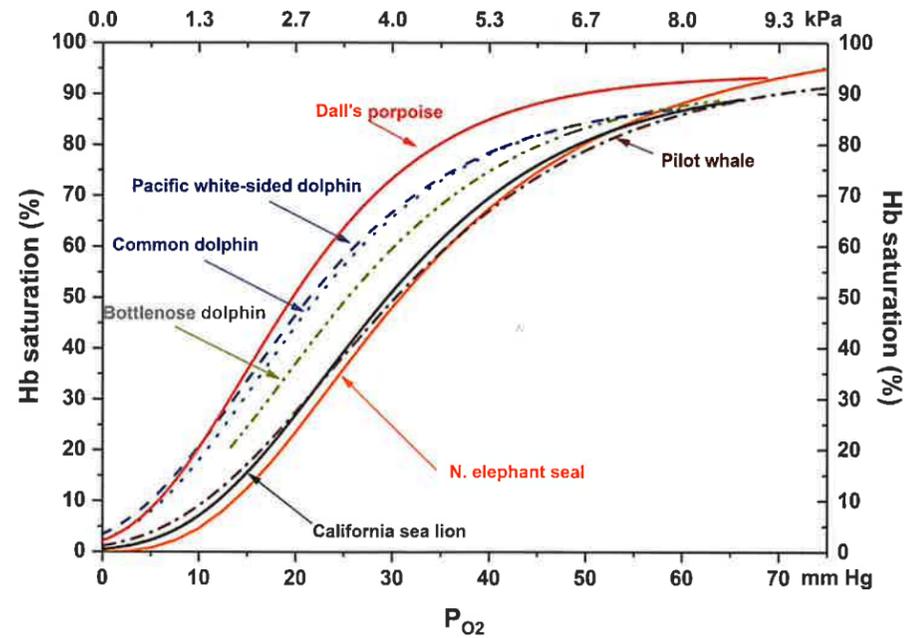
FIG. 9 Increased hemoglobin-oxygen (Hb-O_2) affinities in four small pelagic cetaceans. Increased affinities of Hb for O_2 in the dolphins and porpoises are indicated by the left shift of their oxygen-hemoglobin (O_2-Hb) dissociation curves relative to those of the pilot whale, the sea lion, and the premier pinniped diver, the elephant seal (Horvath et al., 1968; Lenfant, 1969; Meir et al., 2009; McDonald and Ponganis, 2013). See Table 4 for a comparison of oxygen affinities of Hb of other cetaceans. Abbreviations: *Hb*, hemoglobin; P_{O_2}, partial pressure of O_2. *Modified from Horvath et al. (1968), Lenfant (1969), McDonald and Ponganis (2013), and Meir et al. (2009).*

hypoxia (i.e., high altitude or burrows), Hb-O_2 affinity is elevated secondary to genetic mutations and changes in the primary structure of Hb (Storz et al., 2010; Storz, 2016; Storz and Scott, 2019).

Relative to other cetaceans, humans, and several pinnipeds, Hb-O_2 affinity is markedly increased (P_{50} decreased) in several small, fast-swimming pelagic cetaceans (see Table 4, Fig. 9). The P_{50} was 19–22 mmHg (2.53–2.93 kPa) in Dall's porpoise, the Pacific white-sided dolphin, and the common dolphin (Horvath et al., 1968). The P_{50} of the bottlenose dolphin (24 mmHg, 3.20 kPa) was intermediate, but still less than the standard value of 27 mmHg (3.60 kPa) in humans (Dominelli et al., 2021) and less than the P_{50}s of sea lions and elephant seals (see Fig. 9). In larger dolphins and whales, the P_{50} was equivalent or greater than that in the bottlenose dolphin and sometimes even greater than in humans (see Table 4, Fig. 8). In other words, in contrast to the relationship of Hb affinity and body mass in terrestrial mammals (Schmidt-Neilsen and Larimer, 1958; Lahiri, 1975; Snyder, 1983), the affinity of Hb was less in the larger whales than in the smaller dolphin species. In the only study of Hb-O_2 affinity in a beaked whale, the O_2 affinities of isolated Hb fractions were considered slightly higher than in human Hb; P_{50} values were not specifically reported (Vedvick and Itano, 1976).

Increased Hb-O_2 affinity is considered advantageous in hypoxic situations in that it enhances blood O_2 uptake in the lung and increases Hb saturation at low P_{O_2} values (Dominelli et al., 2021). Shifts in Hb-O_2 affinity due to changes in pH, CO_2, and temperature in the periphery contribute to adequate O_2 delivery (Schumacker et al., 1985, 1987; Dominelli et al., 2021). The range of Hb-O_2 affinities in marine mammals, including deep divers, suggests that an elevation in Hb-O_2 affinity as high as in Dall's porpoise is not essential to diving capacity.

It has been suggested that elevated Hb-O_2 affinity facilitates O_2 uptake from the relatively large lung O_2 stores of shallow-diving dolphins and porpoises (Snyder, 1983). In addition to a role during shallow dives, the increased Hb-O_2 affinity may also be important in facilitating O_2 uptake during the rapid subsurface swimming activities of Dall's porpoise and other small pelagic dolphins.

Summary

The design of the cardiovascular system in cetaceans follows the general mammalian model but is modified according to the needs of a given species. Remarkable structures, developed to varying degrees in different species, include

(a) a compliant, elastic ascending aorta and aortic arch; (b) the retia mirabilia; (c) venous plexuses in the head and tracheo-bronchial tree; (d) prominent epidural veins; (e) diaphragmatic caval slings; and (f) thermoregulatory plexuses. During high-speed surface and subsurface swimming of more active porpoises and dolphins, high heart rates, enlarged hearts, and higher Hb-O_2 affinities are postulated to maximize lung-to-muscle O_2 transport just as during exercise of terrestrial mammals. However, during dives, the cardiovascular dive response (bradycardia and vasoconstriction) is variable and serves to regulate the depletion of O_2 stores according to the nature of a given dive. Depth, dive duration, exercise, lung volume reflexes, and cognitive control have all been postulated to influence heart rate during the dive.

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