

# Pinnipeds with proportionally wider aortic bulbs make longer dives

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## Abstract

The enlarged size of the aortic bulb is thought to enhance the ability of marine mammals to remain underwater for extended periods. However, a convincing link between aortic bulb size and diving capacity has not been established. Using new and existing data, we examined the relationships between body size, maximum and routine dive duration, and aortic bulb size of pinnipeds. Comparisons among seven species of pinnipeds showed that the diameter of the aortic bulb increases allometrically with body mass (aortic bulb diameter =  $0.58 \times \text{body mass}^{0.41}$ ). We also found a linear relationship between routine dive duration and relative aortic bulb diameter (routine dive duration =  $0.20 \times \text{relative aortic bulb diameter} - 3.30$ ), but no apparent relationship with maximum dive duration. Our results indicate that relative aortic bulb diameter influences diving capacity, providing further evidence that the aortic bulb is an adaptation to diving. Specifically, the relative diameter of the aortic bulb partially determines how long pinnipeds can routinely remain underwater. This has implications for the ability of different species of marine mammals to adapt to projected environmental changes and effectively forage or evade threats in altered habitats.

## KEYWORDS

allometry, aortic bulb, body mass, dive duration, diving capacity, pinniped, scaling

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## 1 | INTRODUCTION

The fundamental ability of marine mammals to breath-hold dive for extended durations is underpinned by anatomical and physiological adaptations. Together, these adaptations set the upper limit for how long a marine mammal can stay underwater on a single breath. This, in turn, determines important aspects of their ecology and biology. To predict how marine mammals will respond to environmental changes that may require them to dive for longer durations (e.g., changes in prey and predator distributions, increased anthropogenic threats such as vessel traffic and manmade noise), it is important to understand what physiological adaptations they have and what limitations these adaptations impose on diving.

Not all marine mammals exhibit the same diving capacity (e.g., routine or maximum dive duration) (Favilla & Costa, 2020; Ponganis, 2015), nor experience the same level of physiological response to diving (e.g., degree of bradycardia) (Blix & Folkow, 1983; Butler, 1982; Butler & Jones, 1982, 1997; Kooyman et al., 1981; Kooyman & Ponganis, 1998). While there is a general trend for larger species to dive longer and deeper (Halsey et al., 2003), it is unclear what physical adaptations permit some species to have greater diving capacity independent of overall body mass scaling.

The aortic bulb—a balloon-shaped enlargement of the ascending aorta—has been recognized as an anatomical adaptation of some pinniped species since as early as 1838 (Figure 1; Burow, 1838). This structure is thought to maintain constant blood flow when heart rates are low during diving (via the Windkessel effect; Blix et al., 2016; Drabek, 1975; Elsner et al., 1966; van Nie, 1985; Shadwick & Gosline, 1995), and decrease myocardial work by reducing cardiac afterload (Campbell et al., 1981).

Aortic bulb size is expected to contribute to diving capacity because it has the potential to set the lower limit on heart rate. Attaining lower diving heart rates allows for greater peripheral vasoconstriction and therefore a greater capacity for oxygen conservation, which can prolong a dive (Irving, 1939). The aortic bulb stores blood ejected from the left ventricle during systole and pushes it into circulation during diastole via elastic rebound of the arterial wall. A larger aortic bulb has the capacity to hold a greater volume of blood which can, in theory, supply a constant blood



**FIGURE 1** Lateral view of the ascending aorta of a gray seal (*Halichoerus grypus*). Dissected heart muscle attached to the proximal ascending aorta is visible near the bottom of the image. The narrow, proximal part of the vessel is referred to as the base of the aorta which then expands to form the aortic bulb.

flow over a longer interbeat interval, thereby facilitating a lower heart rate than a smaller aortic bulb. A lower diving heart rate is accompanied by greater total peripheral resistance meaning that blood flow to the peripheral tissues will be reduced and more oxygen stored in blood will be available for the brain and heart. As such, larger aortic bulbs should contribute to greater diving capacity.

In addition to the aortic bulb's role in facilitating vasoconstriction, simulations show that the presence of an aortic bulb reduces myocardial work (Campbell et al., 1981). Specifically, the presence of an aortic bulb reduces peak systolic blood pressure in the diving state (by decreasing the resistance the left ventricle is pumping against), with the greatest decrease in blood pressure occurring when aortic bulb diameter is largest. Hearts that do less work consume less oxygen, which can further prolong a dive.

At its core, the adaptive value of having an aortic bulb to enhance diving capacity is based on simple geometry—a larger aortic bulb has the potential to accommodate a greater volume of blood than could a narrower, more cylindrical blood vessel (assuming the compliance of the vessel wall is equal). Despite the proposed benefits, a convincing link between aortic bulb size and diving capacity has not been established. In a comparison of phocid seal aorta morphology, Drabek (1975) suggested that species with relatively larger aortic bulbs are capable of longer dives. Blix et al. (2016) disputed this claim, noting a lack of correlation between absolute aortic bulb size and diving capacity—and instead suggested that aortic bulb size should be related to stroke volume and therefore lean body mass, rather than relative diving ability.

A distinct aortic bulb has been described in pinnipeds (Blix et al., 2016; Burow, 1838; Drabek, 1975; Drabek & Burns, 2002; King, 1977; King & Harrison, 1961; Murie, 1874; Smodlaka et al., 2009; van Nie, 1985), while in cetaceans the walls of the aorta have been noted to be thicker and more compliant than expected (Mompeó et al., 2020, 2022; Shadwick & Gosline, 1994). Due to the paucity of data on cetacean aortas, and the anatomical differences between the pinniped and cetacean aorta, we only focused on the pinniped aortic bulb. Previous comparisons of aortic bulb size among pinnipeds have proven challenging because measurements have been made in relatively few individuals and different metrics have been reported for different species. Furthermore, the focus of these investigations has been the absolute diameter of the aortic bulb which is expected to increase with body size. As such, it has been difficult to isolate changes in aortic bulb diameter due to body size and those which may be a mass-independent adaptation to diving.

To investigate how the ascending aorta of marine mammals relates to diving ability, it would be ideal to observe how this structure responds to changes in heart rate, blood pressure, and stroke volume in an actively diving marine mammal. Unfortunately, these data are not available for any species of marine mammal. We therefore used existing measurements of aortic diameter from excised tissues and ultrasound in vivo images under the assumption that these two measurement techniques provide similar results.

To address whether the aortic bulb is an adaptation to diving, we compiled published values of aortic bulb diameter, body mass, and dive duration for seven species of pinnipeds and modeled the relationships among them. We focused on relative aortic bulb diameter as opposed to absolute diameter to account for differences in body size. The objectives of our study were thus to determine how the diameter of the aortic bulb relates to routine and maximum dive duration, and whether any underlying relationship is simply a factor of body size or is an independent adaptation to increased diving capacity.

## 2 | METHODS

### 2.1 | Interspecific aortic bulb comparisons

We collected aortic bulb measurements from seven species of pinnipeds to investigate trends with body size and dive behavior. Data for five of these species were from previously published studies, while data for Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) were acquired as part of a broader study of cardiac

function in these species (Storlund et al., 2024). Measurements for crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*), harbor (*Phoca vitulina vitulina*), and Weddell (*Leptonychotes weddellii*) seals were made on excised tissue, whereas measurements from Steller sea lions and northern fur seals were made using transesophageal ultrasound while the animals were anaesthetized with isoflurane anesthesia both before and after they received atropine. Where aortic bulb circumferences were reported (i.e., Rhode et al., 1986), we calculated aortic bulb diameter. Most studies reported body mass except in the case of harbor seals where we estimated body mass from provided heart mass according to the mammalian scaling equation: heart mass (g) = 6.0 × body mass (kg)<sup>0.98</sup> (Prothero, 1979), and a leopard seal where we used the average adult body mass from Costa et al. (2020). Subadult animals were excluded from the comparison of aortic bulb diameter and body mass using a cut-off of 50 kg for harbor seals, 175 kg for Steller sea lions, and 280 kg for Weddell seals. All other measurements were from adults. Routine and maximum dive durations were extracted from Favilla and Costa (2020) and the references therein. Table 1 includes the data used for the body mass analysis, and Table 2 includes the data used for the dive duration analyses.

To evaluate relationships between the diameter of the aortic bulb and dive duration, we needed to calculate a dimensionless index that would account for differences in body mass among species. The most relevant parameter to standardize to body mass would be resting stroke volume, but we did not have those measurements. Instead, we used the diameter of the base of the aorta as a proxy because aortic dimensions are correlated to both body mass (Günther & Léon de la Barra, 1966) and stroke volume (Sahlén et al., 2016). Such standardizations using the base of the aorta had already been done for Antarctic seals by Drabek (1975). We termed the index the relative aortic bulb diameter and examined it in six pinniped species from published values or our own calculations. Harbor seals could not be included in the comparisons of relative aortic bulb diameter and dive duration because no measurements of the base of the aorta were available for this species. Relative aortic bulb diameter was calculated as the percent increase in the size of the aortic bulb over the size of the base of the aorta using the formula previously used by Drabek (1975):

$$\frac{\text{aortic bulb diameter} - \text{base diameter}}{\text{base diameter}} \times 100\%$$

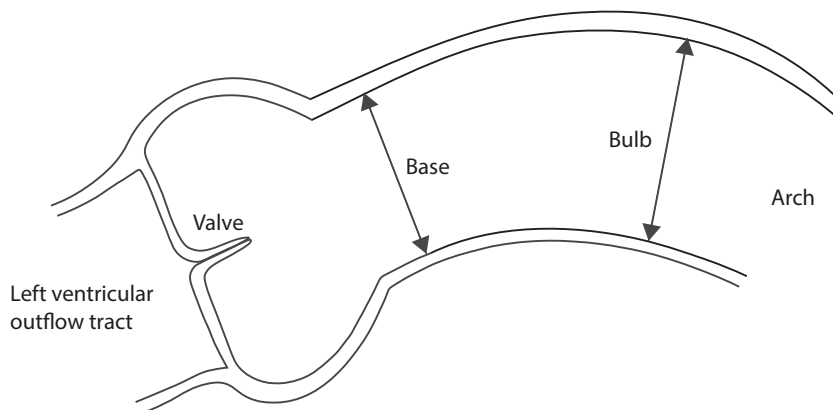
**TABLE 1** Pinniped aortic bulb and body mass measurements and data sources.

Species	Body mass (kg)	Aortic bulb inner diameter (cm)	Source
Crabeater seal ( <i>Lobodon carcinophaga</i> )	180	4.53	Drabek (1975)
Harbor seal ( <i>Phoca vitulina vitulina</i> )	73.4	3.32	van Nie (1985)
Leopard seal ( <i>Hydrurga leptonyx</i> )	389 <sup>a</sup>	5.16	Drabek (1975)
Northern fur seal ( <i>Callorhinus ursinus</i> )	34.6	2.44	Storlund et al. (2024)
Ross seal ( <i>Ommatophoca rossii</i> )	180	5.48	Drabek (1975)
Steller sea lion ( <i>Eumetopias jubatus</i> )	202.4	5.82	Storlund et al. (2024)
Weddell seal ( <i>Leptonychotes weddellii</i> )	397.3	8.13	Drabek (1975); Rhode et al. (1986)

<sup>a</sup>Body mass for the leopard seal was taken from Costa et al. (2020) because it was not available in Drabek (1975).

**TABLE 2** Pinniped relative aortic bulb diameters, dive durations, and data sources. Routine and maximum dive durations were extracted from Favilla and Costa (2020) and the references therein.

Species	Relative aortic bulb diameter (%)	Routine dive duration (min)	Maximum dive duration (min)	Source
Crabeater seal ( <i>Lobodon carcinophaga</i> )	49.5	5	24	Drabek (1975)
Leopard seal ( <i>Hydrurga leptonyx</i> )	33.0	3.8	15	Drabek (1975)
Northern fur seal ( <i>Callorhinus ursinus</i> )	25.3	2.2	10	Storlund et al. (2024)
Ross seal ( <i>Ommatophoca rossii</i> )	52.0	6.44	20	Drabek (1975)
Steller sea lion ( <i>Eumetopias jubatus</i> )	22.6	2	8	Storlund et al. (2024)
Weddell seal ( <i>Leptonychotes weddellii</i> )	72.5	13	96	Drabek (1975)



**FIGURE 2** Illustration of a pinniped ascending aorta. Internal diameters were measured at the base of the aorta and the aortic bulb as shown.

(Figure 2). In this case, aortic bulb diameter refers to the maximum diameter of the aortic bulb in its uninflated state for excised tissues and its mid-systolic state for ultrasound measurements. For Antarctic seals, we used the calculated percent increase in aortic bulb diameter reported in Drabek (1975) rather than calculating percent increase ourselves using the grouped averages for base and bulb diameters. For Steller sea lions and northern fur seals, we calculated relative aortic bulb diameter using the measurement of the ascending aorta as the “base” as this was the narrowest diameter measured proximal to the heart and is assumed to be comparable to the base measurement reported by Drabek (1975).

## 2.2 | Statistical analysis

All analyses were performed in R (R Core Team, 2022) and R Studio (RStudio Team, 2022). We plotted the effects of body mass, routine dive duration, and maximum dive duration on the maximum and relative diameter of the aortic bulb to assess existing relationships. Where no relationship was visually apparent, no further analysis was performed

on the data.  $\log_{10}$ -transformations were used to linearize the data when an exponential relationship was identified. Linear models were fit to test the effects of body mass on aortic bulb diameter, and relative aortic bulb diameter on routine dive duration. The resulting parameter estimates are reported with 95% confidence intervals (CIs). The assumptions of linear regression were assessed using nonconstant variance score test (car package) (Fox & Weisberg, 2019) and the Shapiro–Wilk normality test. Results were considered statistically significant when  $p < .05$ .

### 3 | RESULTS

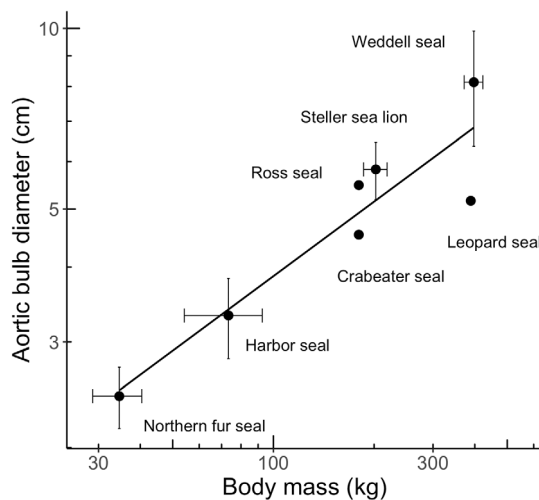
Aortic bulb diameter, relative aortic bulb diameter, and dive durations for seven pinniped species are listed in Tables 1 and 2. The results showed that larger pinnipeds generally have larger aortic bulbs (Figure 3). Despite allometrically scaling with body mass, aortic bulb diameter did not correlate to routine dive duration. Similarly, routine dive duration did not correlate to body mass.

In contrast to the absolute diameter of the aortic bulb, relative aortic bulb diameter showed no relationship with body mass indicating it is likely a mass-independent measure of aortic diameter.

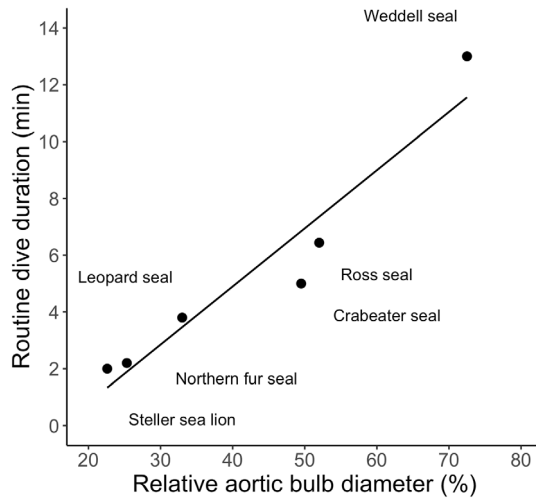
Routine dive duration increased linearly with relative aortic bulb diameter (Figure 4). In other words, species with larger aortic bulbs relative to the diameter of the base of the aorta dive for longer durations. In contrast, the relationship between maximum dive duration and relative aortic bulb diameter was unclear (Figure 5). In this limited data set, the Weddell seal stood out for having a longer maximum dive duration than predicted based on relative aortic bulb diameter.

### 4 | DISCUSSION

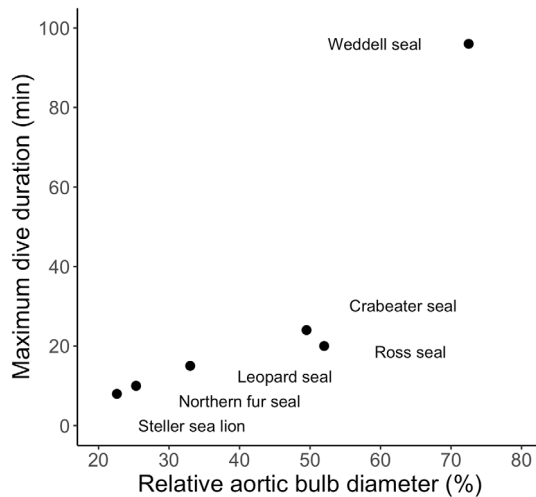
Our comparative analysis among pinnipeds supports the contention that the diving capacity of marine mammals is enhanced by the diameter of their aortic bulbs independent of body size. Most notably, we found that the mean dive durations of six species of pinnipeds increases as the relative diameter of the aortic bulb increases.



**FIGURE 3** Aortic bulb diameter scales with body mass in pinnipeds ( $t = 5.37$ ,  $p = .003$ ). The fitted regression model was: aortic bulb diameter =  $0.58 \times \text{body mass}^{0.41 \pm 0.20}$  (allometric scaling exponent estimate  $\pm 95\%$  CI). The overall regression was statistically significant (adjusted  $R^2 = 0.82$ ,  $F_{1,5} = 28.79$ ,  $p = .003$ ). Horizontal error bars are the standard deviations of mean body mass and vertical error bars are the standard deviations of the average aortic bulb diameter. Note the  $\log_{10}$  scales on both axes.



**FIGURE 4** Pinnipeds with relatively larger aortic bulbs routinely dive for longer durations ( $t = 6.62$ ,  $p = .003$ ). The fitted regression model was: routine dive duration =  $0.20 (\pm 0.09) \times$  relative aortic bulb diameter – 3.30 ( $\pm 3.95$ ) (parameter estimate  $\pm 95\%$  CI). The overall regression was statistically significant (adjusted  $R^2 = 0.90$ ,  $F_{1,4} = 43.78$ ,  $p = .003$ ).



**FIGURE 5** Maximum dive duration increases with relative aortic bulb diameter. Visual assessment suggests that there are factors other than aortic bulb diameter that influence maximum dive duration. No linear or curvilinear fit is provided because it is unclear what relationship best describes the data when considering the strong influence that the Weddell seal data point would have on the model.

#### 4.1 | Aortic bulb diameter scales with body size

We found that the maximum diameter of the aortic bulb is determined by body size with a scaling exponent of  $0.41 \pm 0.02$  (Figure 3). Relating aortic bulb diameter to body size emphasizes the overall importance of the aortic bulb to blood circulation in marine mammals, as these results indicate that aortic bulb diameter has been selected for over evolutionary time. Allometric scaling with body size is an indication that the aortic bulb, despite being an

enlargement when compared to the ascending aorta of other species (Storlund et al., 2024), is appropriately sized for the routine hemodynamics (blood pressure, volume, flow) it experiences.

The precise reason for the increase in aortic bulb diameter with mass is uncertain. As stroke volume also increases with body size (He et al., 2023; Stahl, 1967), it has been suggested that the absolute size of the aortic bulb may be matched to stroke volume, as has previously been found intraspecifically in hooded seals (*Cystophora cristata*; Blix et al., 2016) and Steller sea lions (*Eumetopias jubatus*; Storlund et al., 2024). This makes sense because the ascending aorta needs to be able to accommodate the volume of blood ejected from the left ventricle to prevent detrimental increases in blood pressure. In pinnipeds this is especially important during diving when peripheral resistance is high (Blix et al., 2016).

Determining what drives the relationship between body mass and the maximum diameter of the aortic bulb helps to explain how this structure evolved and how it impacts circulation in pinnipeds. Unfortunately, we were unable to assess this relationship on an interspecific basis because stroke volumes are not available for all the species included in our comparison. Although stroke volume can be estimated from scaling equations (He et al., 2023; Stahl, 1967), it is problematic to compare these estimates to aortic bulb diameter because both variables have a known relationship to body mass. Future efforts should focus on measuring body mass, stroke volume, and aortic bulb dimensions and capacitance at systolic and diastolic pressures within individuals so that direct comparisons can be made.

Care should be taken in applying the relationship between body mass and aortic bulb diameter beyond the data range. For example, applying the scaling equation for pinnipeds to large cetaceans estimates that a blue whale (*Balaenoptera musculus*) weighing 70,000 kg would have an aortic diameter of 57.8 cm and a fin whale (*Balaenoptera physalus*) weighing 35,000 kg would have an aortic diameter of 43.4 cm. However, the actual external diameter of the aorta has been measured as 28.0 cm in blue whales (Black-Schaffer et al., 1965) and 27.9 cm in fin whales (Shadwick & Gosline, 1994).

Considering the geometric relationship between length and volume, we expected the scaling exponent for pinnipeds to be  $1/3$  but instead found that it was 0.41—halfway between  $1/3$  and  $1/2$ . This positive allometry may explain why the equation we report for pinnipeds greatly overestimates aortic bulb maximum diameter in blue whales and fin whales. As our analysis of pinnipeds is over a relatively narrow range of body masses (34.6–397.3 kg), it is unknown if including a larger range of body masses would result in the expected geometric scalar of  $1/3$  rather than  $1/2$ . Further aorta measurements along with estimates of body size from cetaceans will provide the data needed to determine if separate equations are needed to explain the relationship between aorta and body size in different groups of marine mammals, or if there is a single equation that applies to all species.

Among the species included in our study, there was no apparent evidence that larger species of pinnipeds with larger aortic bulbs dive for longer durations. With only seven species to compare, we may not have had the statistical power to detect the expected relationship between body mass and routine dive duration (Halsey et al., 2003). Conversely, our results may correctly demonstrate that there is no relationship between the maximum diameter of the aortic bulb and diving capacity. One of the reasons is that the aortic bulb must always function regardless of whether a pinniped is on land or in water. Therefore, its absolute size might not reflect a specific aspect of diving physiology, as shown in our results and those of Blix et al. (2016). However, this finding does not preclude there being a relationship between aortic bulb size and diving.

## 4.2 | Dive duration increases with relative aortic bulb diameter

The underlying relationship between absolute aortic bulb diameter and body mass makes it difficult to assess the degree to which it contributes to diving capacity. Therefore, we used Drabek's (1975) measure of relative aortic bulb diameter which is independent of body mass, by expressing maximum aortic bulb diameter as a proportion of the vessel base. We found that species with relatively larger aortic bulbs, such as the Weddell seal, routinely dive for



longer durations than species that have relatively smaller aortic bulbs (Figure 4). For every 10% increase in relative aortic bulb diameter, routine dive duration increased by 2 min. Thus, our results support Drabek's (1975) claim that relative aortic bulb diameter correlates with dive behavior.

Relative aortic bulb diameter appears to be evolutionarily selected to optimize routine dive duration. In theory, having a relatively larger aortic bulb would extend dive duration by allowing for lower heart rates, which would in turn allow for greater vasoconstriction and enhanced oxygen conservation. Lower diving heart rates will also contribute to prolonging dive duration simply by reducing the total number of times the heart muscle contracts. For example, the Weddell seal heart is estimated to consume 112.5 ml of oxygen per minute at rest (Davis & Kanatous, 1999). Based on a resting heart rate of 51.6 beats per minute (Zapol et al., 1979), this would result in an energy savings of 2.2 ml of oxygen per minute for every heartbeat per minute decrease achieved while diving. Overall, blood flow to the peripheral tissues would be reduced, less oxygen would be consumed by the heart, and therefore more oxygen stored in blood would be available for the brain and other critical oxygen-dependent tissues.

We hoped to directly evaluate the relationship between relative aortic bulb diameter and diving heart rate, but routine diving heart rates from the pinnipeds included in our aortic bulb comparison were not available. However, greater insights can be gained into the relationship between relative aortic bulb diameter and diving heart as underwater heart rate monitoring technology advances. For now, our data confirm that relative aortic bulb diameter correlates to diving capacity but do not identify the mechanism (e.g., allow for lower heart rates, reduced myocardial work) by which this structure helps conserve oxygen during diving.

We also observed that phocid seals had larger relative aortic bulb diameters than otariids (Figure 4). Phocids typically dive deeper and for longer durations than otariids, so this finding lends further support to the idea that species with larger relative aortic bulb diameters have greater diving capacities. It is interesting that, despite having different styles of diving, the same linear relationship between routine dive duration and relative aortic bulb diameter fits both phocids and otariids.

In contrast to routine dive duration, we found that the relative diameter of the aortic bulb of pinnipeds does not demonstrate a clear linear relationship with maximum dive duration (although the data does not allow us to test for any underlying curvilinear relationship because there are not enough data points from seals that dive for long durations). In other words, it may be that selection for aortic bulb diameter only acts on routine activity, and that the relative diameter of the aortic bulb does not set the upper limit on dive duration. Pinnipeds are capable of increasing dive duration by other means, namely total body oxygen stores and anaerobic metabolism (Butler & Jones, 1982, 1997; Kooyman et al., 1981), independent of aortic bulb diameter. This is most evident in Weddell seals, which have a maximum dive duration of 96 minutes (Heerah et al., 2013) that is almost seven times longer than their routine dive time. Recognizing that some species can dive for longer than expected based on their relative aortic bulb diameter is important when considering anatomical limitations to diving and their impacts on dive behavior.

Relative aortic bulb diameter can be used to partially explain similarities in routine dive behavior in size dimorphic pinniped species such as the northern fur seal and Steller sea lion. Both species routinely dive for about two minutes (Gentry et al., 1986; Gerlinsky et al., 2013; Merrick & Loughlin, 1997) despite adult female Steller sea lions weighing about six times more than northern fur seals (~200 kg compared to ~35 kg). Despite the difference in body mass, the relative aortic bulb size in both species was similar (Figure 4). In fact, relative aortic bulb diameter was 2.7% greater in northern fur seals than in Steller sea lions even though they are considerably smaller. It is unclear whether relative aortic bulb diameter is smaller than expected in Steller sea lions, larger than expected in northern fur seals, or some combination of the two. Further investigation of relative aortic bulb diameter is needed to sufficiently address this question.

The mechanism by which relative aortic bulb diameter influences diving capacity remains uncertain. Further investigation should reveal how this structure relates to its function and create opportunities for assessing cardiovascular contributions to diving capacity.

### 4.3 | Possible effects of measurement techniques

In this study, we assumed that measurements obtained using ultrasound are comparable to those obtained ex vivo. We recognize that the pressurized state of the aorta in vivo may cause measurements to be larger than ex vivo measurements, and that the process of fixation can also alter dimensions (Ito et al., 2022). That said, comparisons of ultrasound and ex vivo measurements of aortic diameters in mice have shown good agreement (Ibrahim et al., 2022; Sawada et al., 2019), suggesting that it is fair to compare aortic diameters measured using these two different techniques.

### 4.4 | Conclusions

Our comparative analyses provide evidence that the aortic bulb contributes to diving capacity—specifically routine dive duration—and highlights the importance of this structure in pinnipeds. We therefore conclude that the aortic bulb is an adaptation to diving.

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#### AUTHOR CONTRIBUTIONS

**Rhea Louise Storlund:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – original draft; writing – review and editing. **David Rosen:** Funding acquisition; supervision; writing – review and editing. **Andrew Trites:** Funding acquisition; supervision; writing – review and editing.

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