PHILOSOPHICAL TRANSACTIONS B

Fur seals do, but sea lions don't – cross taxa insights into exhalation during ascent from dives

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Summary

Management of gases during diving is not well understood across marine mammal species. Prior to diving, phocid (true) seals generally exhale, a behaviour thought to assist with prevention of decompression sickness. Otariid seals (fur seals and sea lions) have a greater reliance on their lung oxygen stores, and inhale prior to diving. One otariid, the Antarctic fur seal (*Arctocephalus gazella*), then exhales during the final 50-85% of the return to the surface, which may prevent another gas management issue: shallow-water blackout. Here we compare data collected from animal-attached tags (video cameras, hydrophones, and conductivity sensors) deployed on a suite of otariid seal species to examine the ubiquity of ascent exhalations for this group. We find evidence for ascent exhalations across four fur seal species, but that such exhalations are absent for three sea lion species. Fur seals and sea lions are no longer genetically separated into distinct subfamilies, but are morphologically distinguished by the thick underfur layer of fur seals. Together with their smaller size and energetic dives, we suggest their air-filled fur might underlie the need to perform these exhalations, although whether to reduce buoyancy and ascent speed, for the avoidance of shallow-water blackout or to prevent other cardiovascular management issues in their diving remains unclear.

Glossary

Apnoea – cessation of breathing
Barotrauma – physical damage caused by pressure difference between a gas space and its surroundings
Baroreceptor – stretch receptor detecting changes in blood pressure
Bradycardia – reduction in heart rate
Diastole – phase of the heartbeat when the heart muscle relaxes and the chambers fill with blood
Hypoxia – deprivation of oxygen supply at tissue level
Hypoxemia – oxygen deficiency in arterial blood
Syncope – transient loss of consciousness and muscle strength

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Tachycardia – increase in heart rate
Vasoconstriction – constriction of blood vessels
Vasomotor – actions upon a blood vessel which alter its diameter

Introduction

The dual constraints for diving, air-breathing vertebrates are the ability to maintain aerobic metabolism during apnoea, and the need to avoid physiological trauma caused by the effects of changing pressure. To achieve a longer underwater (aerobic) breath-hold duration, animals maximise their oxygen stores and minimise the rate of oxygen consumption, both of which extend their aerobic dive limit (ADL) – the maximum breath-hold possible without anaerobic respiration [1-3]. However, for diving mammals, air stores are subject to the effects of increasing pressure with depth (Boyle's Law).

All marine mammals have reinforced airways which allow a graded compression-collapse of the alveoli at depth [4, 5]. This reduces gas absorption at depth such that there is no further absorption when deeper than the depth of alveolar collapse. For deep-diving marine mammals, this reduces the utility of lung oxygen stores, and most oxygen tends to be stored in the blood and muscle [6, 7]. However, in some shallower-diving species the lungs are a significant source of oxygen during a dive. Under pressure at depths shallower than alveolar collapse this can pose a risk because of the high partial pressures of gases in the lungs at depth. Nitrogen (in addition to oxygen) in the lungs is absorbed into the blood at high partial pressures, and upon ascent this can come out of solution and cause decompression sickness (DCS) and gas bubble disease (GBD). Acute DCS and GBD are rarely observed [8], but there is some evidence of probable chronic, asymptomatic bubble formation [9, 10].

Estimates of oxygen stores and their variation between species rely on several assumptions [6, 11-13]. For the lungs it is usually assumed that diving lung volume is a fraction (~50% for pinnipeds, 100% for cetaceans) of the lung capacity (0.1[body mass]$^{0.96}$). For the blood, it is assumed that oxygen stores are based on blood volume, haemoglobin concentration and haemoglobin oxygen binding capacity. For muscle, it is assumed that oxygen stores are based on estimated muscle mass, myoglobin concentration and myoglobin oxygen binding capacity. Such calculations show that the magnitude and distribution of these oxygen stores varies quite substantially among taxonomic groups. Within the pinnipeds, phocids and otariids have markedly different oxygen storage strategies. Both have large muscle oxygen stores representing approximately 30-35% of total body oxygen, but otariid seals (19% lung, 47% blood) rely more on their lung oxygen stores and less on their blood oxygen stores compared with phocid seals (5% lung, 60-65% blood) [6, 7]. In fact, differences in oxygen stores are likely to be even greater than these body oxygen store calculations suggest, because of these assumptions, particularly for lung oxygen stores. In fact both static respiratory variables (such as anatomy) and dynamic respiratory variables (such as differences in behaviour) vary between species [14]. For instance, lung capacity is lower for deep-diving species than the standard allometric prediction above [15]. Furthermore, diving lung volume is that inhaled immediately prior to diving, and seal species differ markedly in this. Phocid seals are thought to exhale while otariid seals are thought to inhale prior to diving, rendering the assumption that diving lung volume is 50% of lung capacity for both unlikely to be accurate [16, 17].

The observation that Antarctic fur seals (*Arctocephalus gazella*) dive upon full inhalation and then exhale continuously during the last 50-85% of ascent from all dives was novel and surprising [18]. This behaviour is counter-intuitive both in terms of increasing the risk of decompression sickness (by reducing the potential for nitrogen to be removed from the blood during ascent) and in terms of losing buoyancy that would otherwise help with ascent. However, for species which rely on lung oxygen during the dive, it seems that the lung air is no longer a particularly useful oxygen store during ascent [6, 19, 20]. Hooker et al. [18] suggested that this behaviour might be needed for species which inhale prior to diving and which have particularly energetic dives. The combination of high energy expenditure resulting in low blood oxygen, combined with lung re-expansion and potential reversal of the oxygen gradient on ascent could lead to hypoxic syncope (herein called black-out). Ascent exhalations would not be expected in phocid seals, which dive after exhalation and therefore dive on relatively low lung volumes. Indeed, Weddell seals have only once been observed to exhale during ascent, despite hundreds of observed dives [7]. Similarly, harbour seals (*Phoca vitulina*) and monk seals (*Neomonachus schauinslandi*) have carried Crittercam video camera tags and acoustic tags and no ascent exhalations have been observed [21-23].

If all otariid seals are indeed inhalation divers, and sea lions and fur seals show similar diving behaviour and morphology, we would expect all otariids to perform ascent exhalations. In this paper, we examine evidence for and against the presence of ascent exhalations in four fur seal species and three sea lion species. We consider similarities and differences between morphology and behaviour of these species, and explore hypotheses underlying gas management that might help to explain observations.

Methods

We used several sources of data and video to monitor the presence/absence of exhalations in as many otariid species as possible. While no specific logger has been developed to test for the presence of ascent exhalations, these were detected in Antarctic fur seals using three types of animal-borne instruments: inductive-cell conductivity sensors, video recorders and acoustic recorders (Table 1; [18]). We used the same types of instruments here. Conductivity measurements were obtained using a conductivity and temperature datalogger (ACT-HR, Alec Electronics, Japan) deployed alongside a time-depth recorder (TDR Mk7 or Mk9, Wildlife Computers, USA). Conductivity was measured using an inductive-cell sensor that measured the rate of decay of an electromagnetic field (ca. 3 cm around the sensor, for details see [24]). Conductivity, together with temperature, was used to calculate water salinity [24]. Anomalies caused by air bubbles around the sensor cause the conductivity/salinity measurements to drop dramatically (see [18]). Video recordings were obtained with a National Geographic Crittercam system [25, 26] using either colour or black and white video, or with a Video and Data Recorder (VDR) [27, 28]. In some cases, sound was recorded with a hydrophone simultaneously with the video recordings.

Instruments were deployed on seals of several otariid species for a single foraging trip (generally ~5-10 days; Table 2). Animals were captured using standard methods for each species. Subantarctic fur seals (*Arctocephalus tropicalis*) were captured with a hoop net and were physically restrained, but other species were anaesthetized. Instruments were attached either directly or were cable-tied to webbing which was attached with adhesive to the fur on the dorsal midline of the seal immediately posterior to the scapulae, using double component, quick setting epoxy resin. Upon return from the foraging trip, seals were recaptured and the devices were removed either by cutting cable ties and leaving a small piece of webbing attached to the fur or by careful clipping of the fur to remove the tag. At each of the deployments and retrievals, the restrained seals were released within 30 min of capture.

Results

Results were clear for all species except the northern fur seal (*Callorhinus ursinus*) for which one set of results was ambiguous (Table 2).

Antarctic fur seal male – Instrument problems limited the data and video collected. Of more than 50 dives, exhalations were common despite relatively shallow depth (maximum dive depth was less than 50 m and most dives were less than 20 m). The acoustic record from these dives showed continuous and increasing volume of exhaled bubbles heard for 16 sec before surfacing. The camera footage also showed bubbles, but due to the camera mount being quite high on the animal's head, these bubbles were at times easier to detect acoustically than visually (Figure 1a, b; electronic supplementary material, movie S1).

Subantarctic fur seals – ACT-HR loggers were deployed on two female subantarctic fur seals at a low-density breeding colony on Marion Island in April/May 2008. Recordings were from austral winter deployments (late April to early August), and showed clear deviations in conductivity/salinity measurements in the latter half of 412 dive ascents (Figure 2), indicative of ascent exhalations.

Australian fur seals – Video recordings were obtained from 26 female Australian fur seals (*Arctocephalus pusillus doriferus*). Three different camera systems were used: Crittercam (41.2 hours, 18 animals), CATS (18 hours, 5 animals) and BBC cameras (22.3 hours, 3 animals). Crittercam studies used a 40 m depth trigger, but other systems recorded continuously. Over 1772 foraging dives were recorded showing clear evidence of ascent exhalations (figure 1c, d; electronic supplementary material, movie S2). On 80m dives, bubbles were released during ascent from around 60m.

Northern fur seals – Two female northern fur seals were instrumented with Crittercams in the Kuril Islands, eastern Russia. Bubbles were visible in 72 of 174 videos from one animal and from 152 of 196 videos from the other (Figure 1e, f). There were some problems with recording protocols resulting in lack of light in some recordings and an error in the operation of the onboard A-D converter, corrupting the pressure transducer data. Dive records were therefore unavailable alongside the video recordings, and so we were unable to examine the depth trajectory for these. However, some ascents to the surface were clear (as the seal swam continuously toward the backlit surface), and ascent exhalations could be seen for approximately 20 sec prior to surfacing (see electronic supplementary material, movie S3). Some dives in daytime (light) conditions were clearly benthic and were followed by ascent exhalation.

Deployment of an ACT-HR logger on St George Island, Alaska was more ambiguous in identifying whether this seal was performing ascent exhalations. Only 32 dives deeper than 30 m were recorded, and discontinuities in the conductivity record were observed only at relatively shallow depths (Figure 2), contrasting with observations for Antarctic fur seals [18] or subantarctic fur seals (Figure 2).

New Zealand sea lion – Crittercam video recordings were obtained for five female New Zealand sea lions (*Phocarctos hookeri*), resulting in a total of 14h 56 min of footage. For three animals the camera used a depth trigger and recorded 193 dives. For two animals, the camera was duty-cycled (one recorded for 15 min, the other for 9 min) and 38 complete ascents to surface, lasting up to 2 min duration, were recorded. There was no evidence of ascent exhalations from dives in any of this footage, although for some near surface ventilation dives the seals could be seen to begin exhalation in the second before the animal broke the surface.

Steller sea lion - Three female Steller sea lions (*Eumetopias jubatus*) were instrumented with VDR cameras and recorded 713 dives (duration 3.1 ± 1.2 min and depth 56 ± 44 m; max depth 200 m) in the Kuril Islands, eastern Russia. There were two peaks in the distribution of dive depths, with 65% of dives < 50 m and 24% between 100-150 m. There were no ascent exhalations during ascents from either deep or shallow dives.

Australian sea lion - Two female Australian sea lions (*Neophoca cinerea*) were instrumented with Crittercam video cameras, resulting in 8.2h of footage. Neither animal showed any sign of ascent exhalations.

Discussion

Although ascent exhalations have been reported for female Antarctic fur seals [7, 18], they have not previously been investigated for males or for other otariid species. This paper is the first to document the prevalence of this behaviour across both sexes of Antarctic fur seals and across multiple fur seal species (Figures 1 and 2). Importantly, we also show that ascent exhalation does not appear to occur in sea lion species (Table 2). We examine the potential factors that might lead to this difference between otherwise similar species, in order to explore the likely function of these exhalations.

Phylogeny
Data presented here show ascent exhalations for four of the nine extant fur seal species. Eight of the fur seals are in the genus *Arctocephalus*, and the other is in the genus *Callorhinus*. Results were similar across all Arctocephaline fur seals investigated, showing ascent exhalations during every ascent (Figure 1). Results for northern fur seals were a little less clear. Crittercam records from northern fur seals in Russia clearly show exhalation for 20 sec prior to surfacing (electronic supplementary material, movie S3). However, ACT-HR deployment on a northern fur seal in Alaska did not show clear exhalations (although only 32 dives were recorded, Figure 2). Acoustic records have previously been collected from four northern fur seals in St Paul, Alaska, but the effective frequency bandwidth was <800 Hz [29], and so not sufficient to detect bubbles which are generally >1kHz in audible frequency (Table 1).

Data for three of the five extant sea lions (each a different genus) suggest that these species do not perform ascent exhalations. This apparent difference between fur seals and sea lions is somewhat surprising since these groupings are not monophyletic. In fact, the dated molecular supertree for all pinniped species suggests that *C. ursinus* is a sister species to all remaining otariids, with neither the

sea lions nor *Arctocephalus* species forming a separate clade [30]. The five sea lion genera were positioned basally to the various *Arctocephalus* species, with the exception of *Phocarctos*, which nested within *Arctocephalus* [30]. Thus, the behavioural differences observed here do not seem to fit with what is known about phylogeny of these species. We therefore look instead at other possibilities.

Mass, Metabolic Rate and Diving Behaviour
Sea lions generally have greater mass than fur seals (between 2-6 times the mass; Table 3), although there is some overlap (e.g., Australian fur seals are not all that dissimilar in size to Australian sea lions; and male Antarctic fur seals are larger than female Australian sea lions), and so size alone does not seem to be responsible for the absence of exhalations in sea lions. For the species we examine here, there do not appear to be major differences in their published dive behaviour (Table 3). Although sea lions have the capacity to perform longer, deeper dives, there is generally much overlap in their diving behaviour and some sea lion species perform short, shallow dives while some fur seal species perform long, deep dives (Table 3). Previous comparisons between fur seals and sea lions have also suggested little difference in diving behaviour [31]. These comparisons are slightly problematic, however, due to different criteria used in definition of 'dives', differences in diving effort between species, and methods of analyses used [31]. Sympatric studies of Steller sea lions and northern fur seals in Russia conformed to expectations that fur seals perform shallower (epipelagic) dives and sea lions perform longer, deeper (near shore benthic) dives [32].

Several studies investigated field metabolic rates in these species (Table 3). In general fur seals have higher metabolic rates than sea lions although there is much overlap. A comparative study of captive Australian otariids suggested that Australian sea lions, Australian fur seals and New Zealand fur seals had similar metabolic rates [33]. However, measurements of metabolic rate may also be exercise dependent, as there appears to be as much as fivefold variation in diving metabolic rate during short dives of the Steller sea lion [34].

The calculated aerobic dive limit (cADL) is a measure of the estimated oxygen stores for an animal divided by its metabolic rate. Comparisons of diving behaviour and cADL suggested that the benthic diving behaviour of Australian fur seals, Australian sea lions and New Zealand sea lions in deep water causes these species to exceed their cADL and use a greater proportion of their oxygen stores during dives than do the epi/mesopelagic foraging dives of Antarctic fur seals and California sea lions which dive well within their cADL ([35], Table 3). However, this does not appear to explain our observations – since Australian fur seals, which exceed their cADL, perform exhalations in the same manner as Antarctic fur seals which dive within their cADL. It is tempting to question the ambiguity around ascent exhalations in northern fur seals in Alaska in terms of whether these might have been pelagic dives? Indeed, the seal instrumented in Alaska performed only shallow dives (<30m). However, for Antarctic and subantarctic fur seals, exhalations are seen even for pelagic dives to such shallow depths ([18], Figure 2).

Barotrauma and avoidance of alveolar rupture
It has been suggested that the distribution of air in the lungs might be a concern during ascent from dives [36]. Human divers use the mantra "never hold your breath when scuba diving". This is particularly dangerous for divers with a lung full of pressurised air which can expand beyond lung capacity during ascent if not exhaled. Free-divers do not have the same concern since they retain their initial air volume (i.e. it matches their lung capacity). However, non-uniform expansion of collapsed lungs or a minor airway obstruction could potentially cause some alveoli to overinflate and rupture. This may have been what happened to a human free-diver, who ultimately suffered a cerebrovascular accident (stroke) [7]. However, he ascended at 5 m/s which is much faster than is observed for marine mammal diving. In general, fur seals and sea lions appear to dive in very similar ways and to show similar behaviour and movements underwater, so it is not clear that any risk during lung reinflation should be any greater for fur seals than for sea lions.

Pulmonary volume and cardiovascular changes during diving
The most striking morphological difference between these two groups which are otherwise remarkably similar is the presence of a thick underfur layer in the pelage of fur seals. Fur seals have a dense waterproof fur which traps air against the body when submerged [37]. Compared to sea lions, fur seals have greater fur density (430 ± 110 hairs/mm for fur seals compared to 20 ± 10 hairs/mm for sea lions), longer guard hairs, longer underhairs, and elongated scalar patterning on both guard and underhairs allowing them to lock together and maintain a relatively still air layer against the skin [37]. Fur seals use the air layer trapped between these fur layers as their primary

means of thermoregulation, and use their homogeneous blubber layer primarily for energy storage, whereas sea lions have a stratified blubber layer and use the outer layer of their blubber for thermal insulation and the inner layer for energy storage [38]. This could have various consequences. There could be implications of the difference in buoyancy between fur seals and sea lions caused by the buoyant layer of air in the fur of fur seals. Fur seals might need to expend more energy during descent to counter this high surface buoyancy with energetic ramifications for diving behaviour. Alternatively the additional buoyancy during ascent could be problematic, and fur seals might lose buoyancy during ascent to control rate of ascent/maneuverability. This could even help to avoid barotrauma as detailed above. Alternatively, there could be thermal insulation differences, particularly at depth. The layer of air trapped in the fur will be very much compressed at depth resulting in reduced insulation and which might only be partially offset by an increased metabolic rate during diving. We examine current knowledge of diving physiology for otariid seals in order to explore these possibilities.

Recent work on California sea lions (*Zalophus californianus*) provides much additional insight into their diving behaviour, and the transport and sequestration of oxygen for this species. California sea lions have reduced stroke rates during descent with prolonged glides during much of the descent for deeper dives, despite their increased lung air volume [39]. In contrast, stroke rates of Antarctic fur seals and northern fur seals [29, 40], and thrusting intensity for Antarctic fur seals were greater on descent than on ascent from dives ([18], SK Hooker 2002, unpublished data), likely related to the additional buoyancy their air-filled fur in addition to lung air provides.

The extent of bradycardia may be related to energy expenditure in descent. Diving California sea lions were able to lower their heart rates more extensively than Antarctic fur seals. California sea lion heart rate reduced to on average 55bpm for dives less than 3 min in duration and to 40 bpm (minimum 11 bpm) for dives longer than 5 min [41]. Antarctic fur seals reduced heart rate only to approx. 70-100 bpm during dives [42]. It may be that fur seals, which need to overcome their high buoyancy during descent, require higher heart-rates to facilitate their increased energy expenditure. Heart-rate ashore may also be higher for Antarctic fur seals (109 bpm for time ashore [42]) compared to California sea lions (54bpm [41]), although the latter were recorded resting motionless, while the former were in an active busy colony. However, Australian fur seals decreased heart-rate <40bpm for benthic dives >300s duration (JPY Arnould 2008, unpublished data), which questions any link between fur seal ascent observations and lack of heart-rate reduction.

Unlike Antarctic fur seals which had a constant diving lung volume [18], arterial oxygen partial pressure measurements showed that lung collapse depth for California sea lions (160-260m) varied in relation to dive depth, suggesting an increased air volume for deeper dives [43]. When sea lions dived below their lung collapse depth, they preserved a pulmonary oxygen reservoir that was accessed again during initial ascent to boost their blood oxygen [43]. In other words, if these sea lions had exhaled during ascent, this oxygen reservoir would not have been available to them. Further work looking at venous oxygen profiles in California sea lions showed arterialization of venous blood before and possibly during shallow dives, likely via arteriovenous (a-v) shunts in the peripheral vasculature [44, 45]. This maintains highly oxygenated blood in the anterior vena cava throughout much of the dive [45] compared to decreasing oxygenation in the posterior vena cava [39, 44]. Whether similar mechanisms are found for fur seals is not known, and we wonder whether different thermal properties of the fur of fur seals might impact their use of peripheral vasculature.

Potential physiological benefits of ascent exhalations
In their original description of ascent exhalations, Hooker et al. [18] speculated that these might function to mitigate against shallow-water blackout. By preventing lung gas re-expansion and recruitment of the alveoli on ascent, these seals would prevent any reversal of oxygen diffusion from the pulmonary capillaries into the lung that might lead to hypoxemia and cerebral hypoxia [6]. Recent measurements for California sea lions [39, 41, 43-45] showing their gliding on descent, more pronounced bradycardia, venous oxygen store, and high end-of-dive arterial haemoglobin saturations suggest minimal risk for shallow-water blackout in sea lions. A phocid seal, the harbour seal, has also shown a high tolerance to hypoxia [46]. Such data are not yet available for a fur seal, so their tolerance to hypoxia and risk of shallow-water blackout remain open questions.

Active-swimming from depth is seen in our video recordings for both fur seals and sea lions, and this will cause a suite of dynamic, physiologically complex afferent signalling which triggers cardiovascular responses in order to maintain optimal blood flow in high-priority tissues, such as the brain. Depth- and apnoeic-dependant changes in gas tensions may affect vascular resistance and

distribution of systemic flow [43, 44]. Additional demands of exercise will increase the need for perfusion [47]. Pronounced non-linear changes in lung volume also cause mechanical effects to which the cardiovascular system responds. As such, there are many simultaneous inputs to the nervous system which will be both peripherally and centrally integrated causing cardiovascular response patterns which may themselves also cause additional modulating feedback.

The physical changes in lung volume itself are likely to be important. Upper airway receptors such as pulmonary stretch receptors as well as arterial chemoreceptors and intra/extrathoracic arterial baroreceptors will provide ample physiological signalling to initiate cardiac and vasomotor reflexes, and will also modify the effectiveness of incoming impulses from other cardiovascular receptors. Exhalation on ascent might then be beneficial to reduce such signals. Pulmonary stretch receptors in the airways respond to changes in both lung volume and rate of volume change, reflexively causing tachycardia [47], and probably also vasodilation (otherwise arterial blood pressure would increase). This reduction in systemic vascular resistance could increase the rate of oxygen depletion as heart-rate increases, as appears to be seen for California sea lions [45].

Depletion of arterial blood oxygen during a dive and decrease in oxygen tension with ascent should cause stimulation of the arterial chemoreceptors (carotid bodies). The cardiac response to stimulation of the carotid bodies (in seals) during diving without changes in lung volume is a marked bradycardia [48]. Yet ascent is commonly associated with elevation of heart-rate towards pre-diving levels (tachycardia). Thus the carotid body bradycardia/vasoconstriction response appears to be masked as arterial gas tension reduces [49]. This may be due to insensitivity (refractoriness) of the central vasomotor neurons associated with excitation of the pulmonary stretch receptors [50, 51]. Indeed, studies of non-diving animals have highlighted the increased refractoriness that pulmonary stretch receptor excitation can have on chemoreception with a proportional increasing effect with lung inflation [52]. Therefore, as depth decreases, re-inflation of the lungs would override arterial chemoreceptors, systemic vascular resistance is reduced and rate of oxygen depletion would increase. The observed heart-rate increase during ascent of Antarctic fur seal dives [42] occurs despite reduced pulmonary stretch receptor activity (since ascent exhalations reduce lung reinflation), and is therefore contrary to expectations, but may be modulated by additional factors such as exercise during ascent.

There is also the potential that baroreceptor signalling is overridden during ascent. During lung inflation, cardiac vagal motoneurons become partially or wholly insensitive to incoming baroreceptor impulse traffic [52-54]. As depth-dependant changes during ascent will significantly and non-linearly affect intrathoracic pressure, failure to appropriately regulate arterial and venous blood pressure [55] could also impact tissue-specific perfusion and metabolic regulation. Changes in intrathoracic pressure contribute to alterations in transmural pressure in all large intrathoracic viscera - particularly the low-pressure areas in the thorax and high-pressure areas of the left ventricle, especially during the period of diastole. As intrathoracic pressure becomes more negative there is a movement of blood toward the thorax as the pressure gradient between the peripheral veins and the right atrium increases. Blood flow into the chest is thus accelerated, with the additional blood coming from the large intrathoracic veins. Increased venous return must be compensated by elevated heart rate, stroke volume, and reduced systemic vascular resistance in order to avoid elevated arterial pressure. If atrial and arterial baroreceptor signalling is overridden by pulmonary stretch receptors, there could hypothetically be a situation where blood pressure is not optimally regulated. Furthermore, prolonged or rapid excessive emptying of the large extrathoracic veins could collapse these veins particularly at the point of entry into the thorax. The implications of any combination of these phenomena may not be without consequence, and could affect the arterial and venous systems as well as tissue-specific haemodynamic regulation. If appropriate integrated regulation of systemic vascular resistance (to reduce oxygen depletion) and/or regulation of blood pressure during lung reinflation is of concern to fur seals, then ascent exhalations could help to facilitate this by reducing some of the dynamic cardiovascular and respiratory signalling, and potentially facilitating better autonomic regulation.

Further work
Understanding regulation of blood flow and gas dynamics in free-ranging marine mammals is extremely challenging. The primary difficulty has been limitation in available technologies to measure cardiovascular variables. Heart rate/ECG recording is now becoming more widely available and additional detail for other fur seal and sea lion species would certainly be useful to help understand haemodynamics. The combination of heart-rate with accelerometry and acoustic sampling would enable examination of work effort (stroke rate) and heart-rate coincident with

ascent exhalations. P_{O_2} electrodes can be highly informative and have been used successfully on California sea lions, but maintaining a sensor intravenously in a highly manoeuvrable animal is problematic and data collection is often hampered by logistical and technical factors [45]. Recent developments in optical technologies, some of which are wearable, may also provide tools to allow external measurements of cardiovascular regulation. Continuous-wave near-infrared spectroscopy (CW-NIRS) has been tested on both diving seals and humans [56, 57]. CW-NIRS provides high-resolution data on relative measures of the concentration of oxyhaemoglobin and deoxyhaemoglobin, the dynamics of which allow various measures of haemodynamic changes. For example, calculation of total haemoglobin can be used as a proxy for changes in blood volume and calculation of relative haemoglobin difference can be used as a proxy of oxygenation changes while removing the effect of changes in blood volume. Diffuse correlation spectroscopy (DCS) and broadband CW-NIRS, which are currently only static technologies, can also provide measures of blood flow, intracranial pressure and metabolic rate changes.

Although we have discussed this issue here in terms of comparisons between otariid seals, cetaceans and sea otters also dive on inhalation, and sea otters (*Enhydra lutris*) have air-filled fur. No ascent exhalations have been observed in underwater video observations for these species (e.g., [58-60]), although their physiology, particularly for cetaceans, may be unique and it is possible that their alveolar and perhaps also their caval sphincters could play a role in stabilising arterial, venous and cerebral responses.

Much of our understanding about diving physiology to date has come from only a handful of the more easily-studied marine mammal species. The observations presented here highlight the need for caution in inferring common physiological responses across species. We have shown that two related groups of seals show a dramatically different approach to their otherwise similar diving behaviour. Whether this is caused by their differences in size, fur, buoyancy or thermoregulation costs is not yet clear. The most parsimonious explanation may be that of buoyancy reduction to avoid overly rapid ascent, although many questions remain – in particular, the consequences of this behaviour on their gas management and cardiovascular and respiratory signalling. We look forward to further work that might help provide the answer to this physiological puzzle.

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Additional Information

Tables

Table 1. Biologging methods for detection of ascent exhalations, and potential problems causing mis-classification of bubble presence/absence.

	Available biologging devices	Detection	Potential problems
Conductivity sensor	ACT-HR (Alec Instruments)	Data record drops to zero caused by interference of bubbles in EM field.	Tag placed high on head/neck may not record bubbles which stream around neck and down back.
Video camera	Venus (Wild Insight Ltd) Crittercam (National Geographic) VDR (Video and Data Recorder, Pisces Design, San Diego) CATS (Customised Animal Tracking Solutions)	Visible bubbles (some cameras include audio)	Field of view potentially limited, and forward facing camera high on neck might miss bubbles.
Acoustic sensor	D-tag Acousonde^{TM} tags (Greenridge Sciences Ltd)	Audible bubbles	Requires sampling at approx. 2-6kHz [18]

Table 2. Ascent exhalations examined in otariid seal species. Biologging equipment was deployed for a single trip, from female (♀) and male (♂) seals. Maximum depth and duration are presented for these data, unless indicated by ~ showing typical values for this species and location.

	Location	Sex	Year	Biologging equipment	#	# dives	Max depth (m)	Max duration (min)	Ascent exhalation present
Fur seals									
Antarctic fur seal *Arctocephalus gazella*	South Georgia, Antarctic	♂	2006-07	VDR	1	>50	50	3	✔
Subantarctic fur seal *A. tropicalis*	Marion Island	♀	2008	ACT-HR logger and TDR	2	412	93	3.4	✔
Australian fur seal *A. pusillus doriferus*	Bass Strait, SE Australia	♀	2008	Crittercam videocamera	18	1772	~85 [a]	~3.7 [a]	✔
		♀	2015-19	CATS camera	5	n/a	~85 [a]	~3.7 [a]	✔
		♀	2017	BBC camera	3	n/a	~85 [a]	~3.7 [a]	✔
Northern fur seal *Callorhinus ursinus*	St George Island, Alaska	♀	2005	ACT-HR logger and TDR	1	32	58	3.4	Near surface (~10m) on 19 dives
	Kuril Islands, eastern Russia	♀	2007	Crittercam videocamera	2	227	~102 [b]	~3.8 [b]	✔
Sea lions									
New Zealand sea lion *Phocarctos hookeri*	Auckland Islands, New Zealand	♀	1997	Crittercam videocamera with acoustic	5	231	n/a	7.2	✘
Steller sea lion *Eumetopias jubatus*	Kuril Islands, eastern Russia	♀	2008	VDR	3	713	200	6-7	✘
Australian sea lion *Neophoca cinerea*	S. Australia	♀	2008/09	Crittercam videocamera	2	n/a	~103 [c]	~7.5 [c]	✘

[a] [61]; [b] [32]; [c] [62]

Table 3. Typical body size and dive characteristics of otariid species recorded here. All results are presented for females unless specified as male (♂).

Species and general citation	Typical Length (m)	Mass (kg)	Typical depth (m)	Max dive depth (m)	Typical duration (min)	cADL	Field metabolic rate ($mlO_2kg^{-1}min^{-1}$) (method*)
Fur seals							
Antarctic fur seal [63]	1.4	22-51	20-50	181	1.3	1.6 [35]	29.6 (DLW) [11]
Antarctic fur seal ♂ [63]	2.0	122-159	50	100	n/a	n/a	n/a
Subantarctic fur seal [64]	1.2	24-43	46	194	1.8	n/a	n/a
Australian fur seal [61]	1.4	67-93	58	89	2.9	1.7 [35]	15.95 (resp) [33]
Northern fur seal [65]	1.5	~43	68	168	2.2	2.6 [69]	36.8 (resp) [71]
Sea lions							
NZ sea lion [66]	2	91-148	125	470	3.4	2.3 [35]	20.3 (DLW) [11]
Steller sea lion [67]	2.9	~200	24	>250	2	3.0 [70]	12.6 (resp) [70]
Australian sea lion [68]	1.8	83-147	61	105	3.3	2.3 [35]	14.25 (resp) [33]

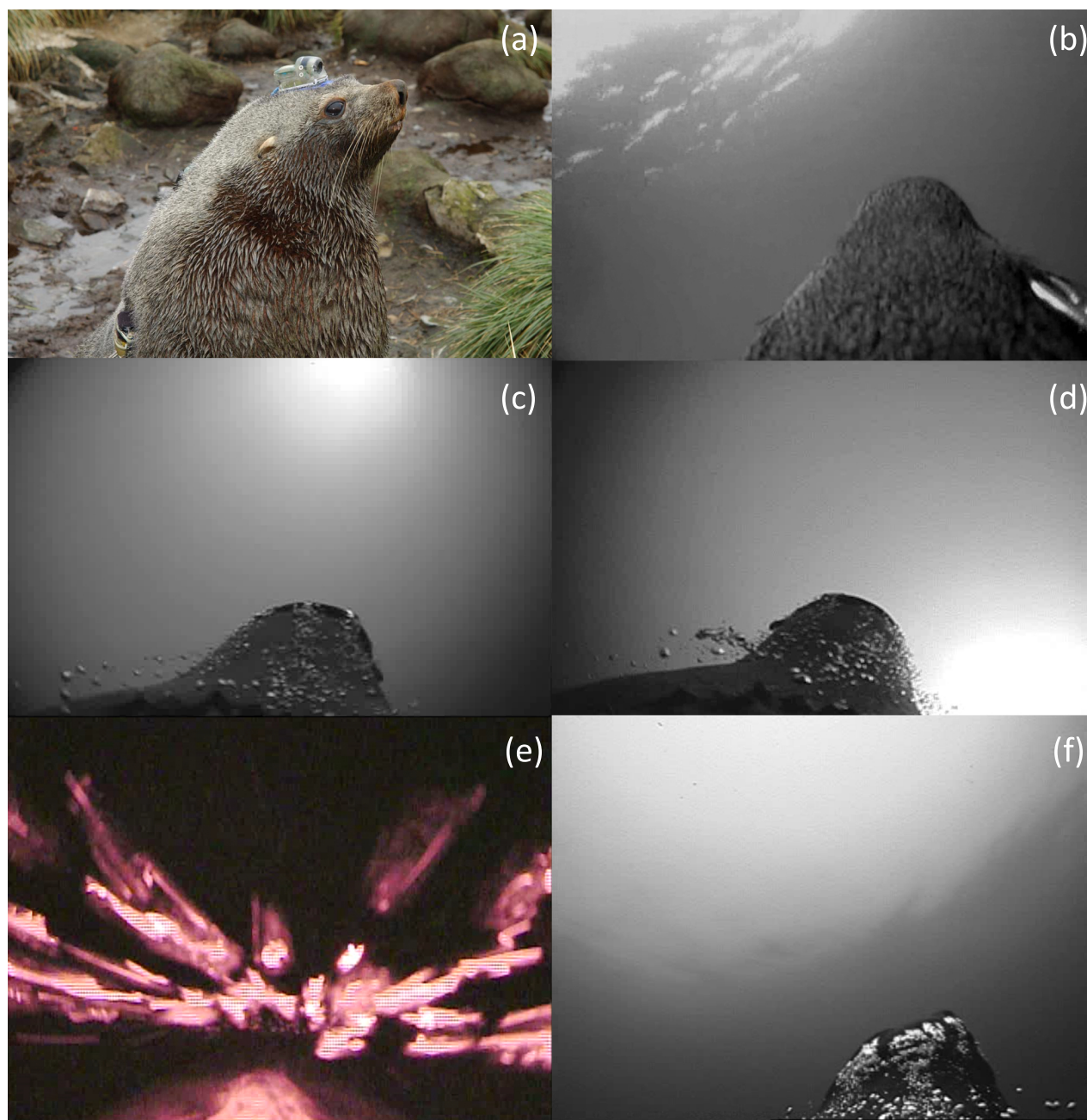*Method: doubly labelled water (DLW), respirometry (resp)

Figures

Figure 1. (a, b) Video and data recorder setup and observations for male Antarctic fur seal, (c, d) Crittercam observations from two female Australian fur seals, (e, f) Crittercam observations from two female northern fur seals; (e) shows recording in low light conditions.
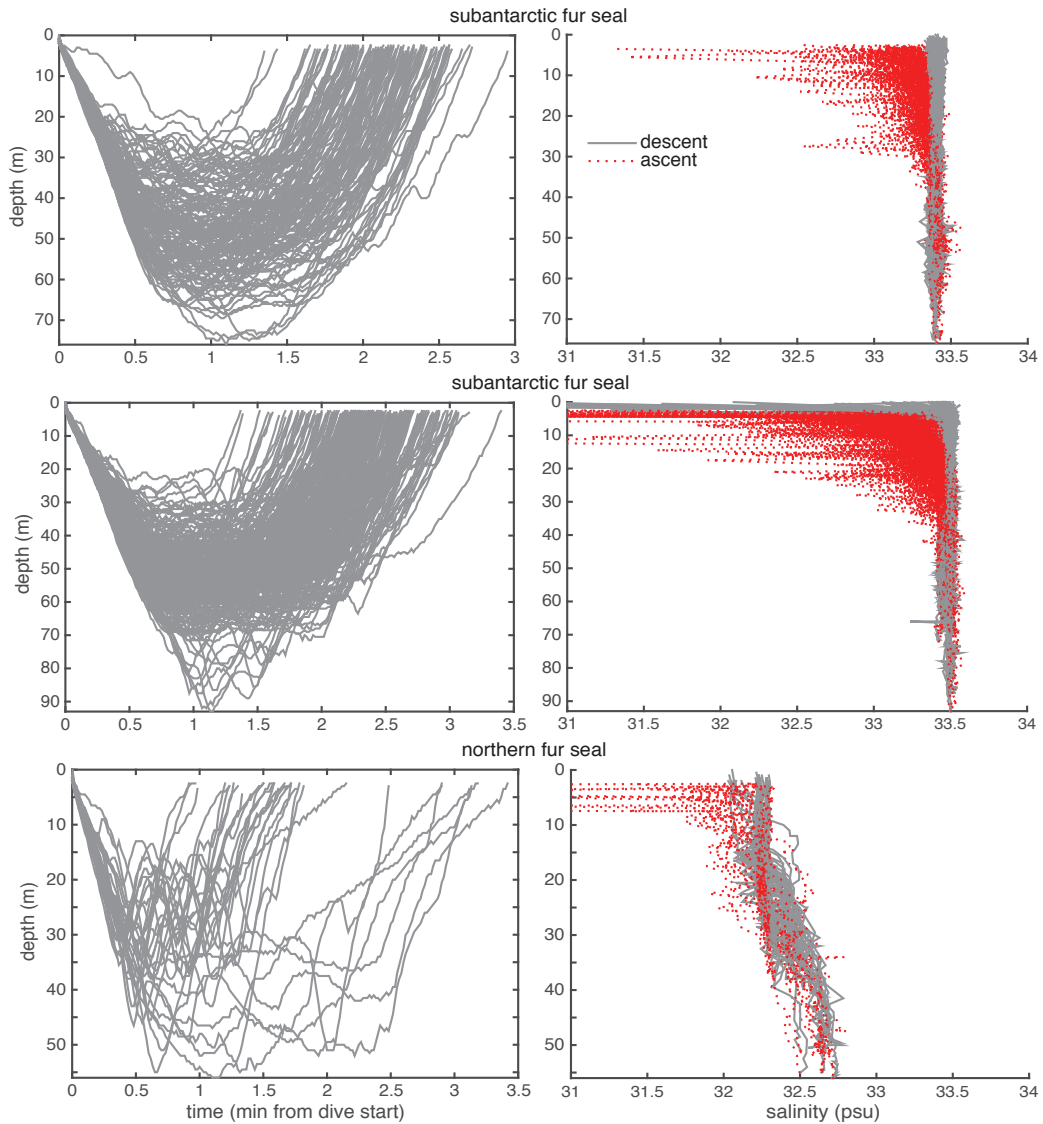
Figure 2. Dives over 30 m depth are plotted (a) as depth-time profiles for each seal with (b) corresponding depth-salinity recorded during descent (solid grey) and ascent (dotted red) for these dives. The two upper plots show dives of subantarctic fur seals (n = 143 dives, n=269 dives), while the lower plot shows dives of one northern fur seal (n=32 dives).

Supplementary material

Movie 1. Male Antarctic fur seal, South Georgia, 2007. Short dive on krill.
Movie 2. Australian fur seal dive, Bass Strait, Australia, 2013. 134 sec foraging dive includes octopus capture.
Movie 3. Northern fur seal dive, Kuril Is. Dive portion from benthos to surface (44s).