Comparative Diving Ecology Across Southern Ocean Marine Predators

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(Quantitative Antarctic Science)
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INSTITUTE FOR MARINE & ANTARCTIC STUDIES

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by any institution. To the best of my knowledge the thesis does not contain any material written or published by another person, except where due reference is made.

Giulia Roncon Date 20/08/2019

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Dedication

To my mum and dad - Chiara and Franco - for their love.

Abstract

The Southern Ocean is home to a great diversity of marine predators (cetaceans, pinnipeds, flying and diving seabirds), many of high conservation value, and all well adapted to exploit their underwater habitats including coastal shelf, sea ice and oceanic zones. Marine divers are particularly interesting for studying the underlying principles related to foraging behavior and diving physiology. Their need to acquire enough food resources (determined by prey distribution, abundance, quality) is balanced against their physiological constraints (e.g., oxygen stores, body mass, diving capacity). This interplay between need and constraint is reflected in what is directly observable, that we can measure, i.e., their diving behavior, by using simple telemetry devices like time-depth recorders. This thesis examines the diving behavior of Southern Ocean marine predators, with a focus in the Indian sector. To do this I use dive datasets available for key Antarctic seal (Antarctic fur *Arctocephalus gazella*; southern elephant *Mirounga leonina*; Weddell *Leptonychotes weddellii*) and penguin (Adélie *Pygoscelis adeliae*; emperor *Aptenodytes forsteri*; king *A. patagonicus*) species.

This thesis is organised into three main chapters as follows: (1) a systematic literature review presenting common approaches for addressing physiological and foraging questions. This is followed by two chapters employing a comparative analytical approach to (2) examine the underlying factors, particularly body mass, that influence diving behavior, and (3) evaluate the dive capacity of air-breathing birds and mammals, and in particular their capacity to adapt their dive behavior when actively foraging.

(1) A systematic literature review synthesizing approaches for addressing physiological and foraging questions. Increasingly sophisticated electronic logging devices record behavioral, physiological and habitat variables, providing insight into the diving physiology and foraging behavior of marine mammals and seabirds. However, a variety of methods have been developed for dive data making comparative studies and syntheses difficult even amongst closely-related species. Adopting a question-driven orientation, I conducted a systematic literature review using dive telemetry data gathered in the Southern Ocean. I focused on the years 2006–2016, as this was a period of considerable study when both well-established

sensors (e.g., time-depth recorders) and newly developed devices (e.g., accelerometers, animal-borne cameras) were employed. I identified key research questions emergent across Southern Ocean species, and explored two major sections focussing on the foraging and physiological inferences obtainable using diving data. Finally, I discuss key emergent areas in which dive telemetry data are being upscaled and more quantitatively integrated with movement and demographic information to link to population level consequences. This work is important because it highlights the benefits of a standardized approach and paves the way for more integrative multi-species meta-analyses.

(2) Investigating diving patterns and body mass scaling within and across six marine predators in the Indian sector of the Southern Ocean. Despite our greatly increased ability to study how marine predators regulate their dive cycle, proximate (e.g. limited oxygen stores, metabolic rate) and ultimate (dive capacity) influences controlling the diving behavior of individuals are still poorly understood. In my comparative analysis of diving data of three penguin and three seal species in the southern Indian Ocean, I examined the influence of body size on dive performance and the interdependencies of dive parameters. Across species, my results support the well-established expectations that dive duration and dive depth are tightly linked, and that mass is an important determinant of dive capacity. However, the body size effect within a species was not the same as the between-species relationship, and more importantly the relationship varied amongst the species. Furthermore, unlike dive depth and duration, post-dive surface intervals were not influenced by body size within a species. This suggests that at the species level dive depth and dive duration are not simply driven by physiological allometry, but probably also by other ecological factors.

Ultimately, my examination of the interdependencies of diving parameters showed support for both between- and within-species effects. These results were more consistent than for the size-based analyses described above, suggesting universal principles to potentially at play.

(3) Behavioral plasticity and observed limits of underwater dive behavior of marine predators during intense foraging. In this chapter, I extend my characterization of the diving capacity of the six Southern Ocean marine predators.

I performed a comparative analysis of relationships between basic dive parameters. Using quantile regressions, I described diving limits of marine vertebrates in terms of these components. I then used a hunting time metric to identify dives as hunting (foraging) or other dives, and observed how diving performance may vary during different levels of activities (foraging vs non-foraging dives; short vs long hunting time dives). My results showed that most marine mammal and seabird species were able to adjust their dive cycle when foraging, generally diving deeper and for longer. Deeper dives corresponded with longer bottom time, but different species displayed different strategies to reduce their transit time. Moreover, most of the species were able to lengthen the duration of their shallower forage dives, but potentially showed less capacity to do so for the deeper, intensive hunting dives. My results quantifying dive limits of Antarctic marine predators showed that their dive plasticity is associated with their taxonomic position, the environmental conditions, and a species' life history traits.

General discussion. This study has provided important new insights into the diving ecology of Southern Ocean marine predators. Assembling high-resolution diving data across various species of marine mammals and seabirds, I developed and applied systematic approaches for dive-based indicators to make inferences about diving behavior, foraging and physiology. These multi-species comparative analysis of dive patterns and performances of Antarctic animals help identify which intrinsic and extinct factors may constrain animals' diving ability. Understanding what determines an animal's dive ability is essential to elucidating its feeding ecology; foraging is a fundamental requirement of all animals and has implications for the distribution, growth and persistence of wild populations. This study has shown how within their morphological and physiological specializations, some species may have considerable plasticity in response to changes in their energetic needs, while others seem to operate at their maximum diving capacity and are thus less likely to have the capacity to increase their foraging effort. The variations in capacity and ability could be used as input into ecological models, and for answering broader ecological questions regarding ecosystem energy flow.

Marine predators have been recognized and monitored as indicators of ecosystem changes in the Southern Ocean for many years. The Southern Ocean is

147 one of the most seasonally dynamic oceans on our planet, and Antarctic marine life
148 has already showed a radical response to a range of climate stressors. Developing
149 an integrated and synthetic view of marine mammals' and seabirds' diving ecology
150 is an important first step to enable the development of predictive models that will
151 improve our understanding of how future climate change will affect this unique
152 biota.
153

Statement of publication and co-authorship

Chapters 2 and 3 comprise manuscripts published or submitted to peer-reviewed journals. The following publications have been produced as part of this thesis:

- Paper 1 (*published*), in Chapter 2: "View from below: inferring behavior and physiology of Southern Ocean marine predators from dive telemetry".

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All authors contributed substantively to writing the manuscript. Author 1 conducted the literature review under the supervision of Authors 2,3,4,5. Candidate was the primary author.

- Paper 2 (*in review*), in Chapter 3: "Investigating diving patterns and body mass scaling within and across six marine predators in the Indian sector of the Southern Ocean".

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Authors 2,3,4,5 designed the study. Author 4 and 5 contributed data. Author 1 compiled and processed all the datasets, and together with Author 2 performed the analyses. Author 1 wrote the first draft of the manuscript, and all authors

contributed equally to the manuscript development.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or *in review*) peer-reviewed manuscripts contributing to this thesis:

Signed

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Chapter 1

General Introduction

Marine mammals and seabirds play an important structuring role in the Southern Ocean marine ecosystem (Goedegebuure et al., 2017). Bio-telemetry technologies have significantly advanced our understanding of the foraging ecology and ecophysiology of these marine species. However, the proximate and ultimate factors that influence the diving behavior of individuals are still poorly understood. The analysis presented in this thesis, which involves six species of marine predators from the Eastern Antarctic sector of the Southern Ocean, utilizes basic diving components to broaden the knowledge of the diving ecology of marine mammal and seabird species. In particular, this study seeks to clarify the following key questions:

(i) What are the best tools and approaches for comparative analysis of diving behavior across and within species that contrast in terms of body size, foraging requirements and phylogeny?

(ii) How do intrinsic factors like body mass and extrinsic factors like prey availability determine the underwater movement for seals and penguins?

(iii) How plastic is the behavior of Southern Ocean marine predators, with particular focus on their range of diving performances?

Diving behavior and physiology

Marine mammals and seabirds undertake a special form of central-place foraging as they must obtain their food at depth yet are obliged to return to the surface to breathe. The depths to which individuals dive, and the amount of time they can spend submerged varies among species, is a function of their physical and physiological adaptations (Kooyman and Ponganis 1998), and their foraging strategy.

When diving, the main physiological challenges encountered by marine predators are the increase in pressure with the resulting mechanical compression of tissue and the lack of *ad libitum* access to oxygen (Kooyman and Ponganis 1998). To cope with these constraints cetaceans and seals have a

flexible rib cage and collapsible lungs, which reduce the effect of pressure that creates a mechanical compression of tissue and gas-filled spaces (Kooyman and Ponganis, 1998). Penguins have decreased their buoyancy by increasing bone density (Ksepka et al., 2015). Moreover, marine mammals and seabirds have also evolved the so-called "dive response" to manage their use of oxygen while diving. When the “dive response” is exhibited, the heart rate drops, the blood perfusion of selected organs is reduced and the body temperature decreases (Butler and Woakes, 2001; Meir and Ponganis, 2010; McDonald and Ponganis, 2014; Wright et al., 2014), resulting in an overall reduction in oxygen consumption.

A dive broadly comprises four phases: a descent phase, the period of active swimming to reach the desired depth (Williams et al., 2000); a bottom phase between the dive descent and ascent (often associated with foraging activity); an ascent phase when the animal makes its way to the surface (Williams et al., 2000); and a post-dive interval or surface phase (PDI) during which the animal re-oxygenates, rests or moves to a new area (Thompson and Fedak, 2001). Marine predators perform a suite of behaviors when hunting (discussed in more detail in Chapter 2), and the analysis of simple dive metrics, such as dive depth, duration and PDI, enable inferences about their foraging preferences (*i.e.*, use of the water column) and diving physiology (*i.e.*, dive limits).

Telemetry and dive data

One of the greatest challenges to understanding the diving and foraging behavior of free-ranging marine animals is observing them while at depth. Historically, the dive capacity of marine predators was investigated using “forced submersion” as in the early experiments on beavers (Irving, 1939), pinnipeds (Bert, 1870) or ducks (Richet, 1899), but such studies were limited in their capacity to elucidate free-living behavior because they were unable to adequately replicate free-ranging conditions such as the effects of pressure.

The first study of diving in a free-ranging animal was by Scholander (1940) on a harpooned fin whale (*Balaenoptera physalus*) in Norway. The first experiments on Southern Ocean predators in 1964 used a pressure gauge and a

clock attached to a Weddell seal (Kooyman, 1966): the first recording lasted 30 minutes. The first study of diving in a foraging seabird (an emperor penguin) followed a few years later (Kooyman et al., 1971).

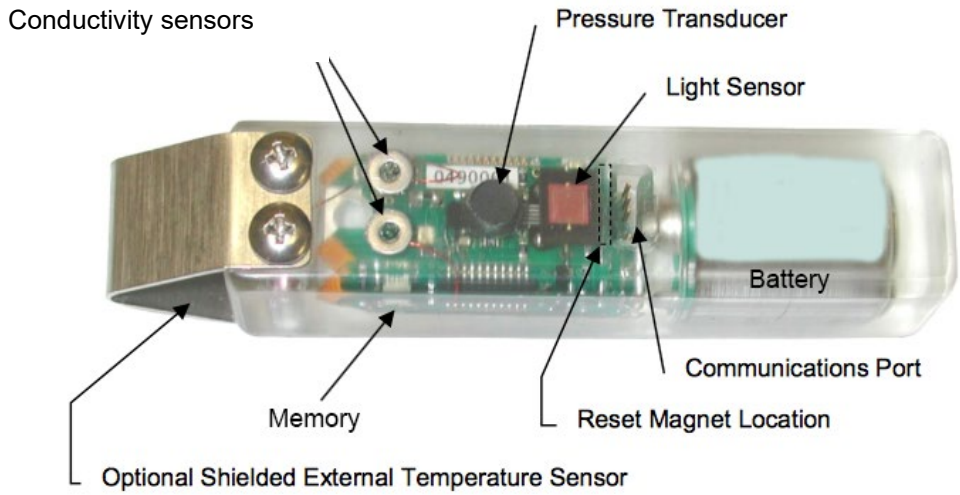

Figure 3. Example of time-depth recorder (TDR): miniaturized pressure sensor recording the depth of a tagged animal as a function of time. Data collected by TDR are stored in an internal memory. Model: TDR-Mk9, Wildlife Computers. The dimensions are 68 mm by 17 mm by 17 mm, weighing 30 g.

More than 50 years after the first dive loggers were deployed, our understanding has been significantly advanced of how taxonomically and ecologically diverse animals manage their dive cycles. For example, thanks to time-depth recorders (TDR, Fig. 3) we now know that Adélie penguins must spend more time at the surface after longer and deeper dives, but in southern elephant seals the duration of a dive does not correlate with the post-dive surface duration (see Chapter 4). A wide variety of analytical approaches have been used to process dive data obtained with data-loggers, and this has made comparative studies and syntheses difficult even amongst closely-related species.

In first part of my thesis, I discuss the tools and approaches addressing key ecological, behavioral and physiological questions. This will pave the way for integrative multi-species analyses that presented in Chapters 3 and 4.

Southern Ocean marine predators

The Southern Ocean (hereafter SO) region is a unique circumpolar biogeographic region, which supports a rich biodiversity with many species of high conservation value (De Broyer and Koubbi, 2014); many of these species are pursuit divers (Trathan and Hill, 2016).

Marine biogeography

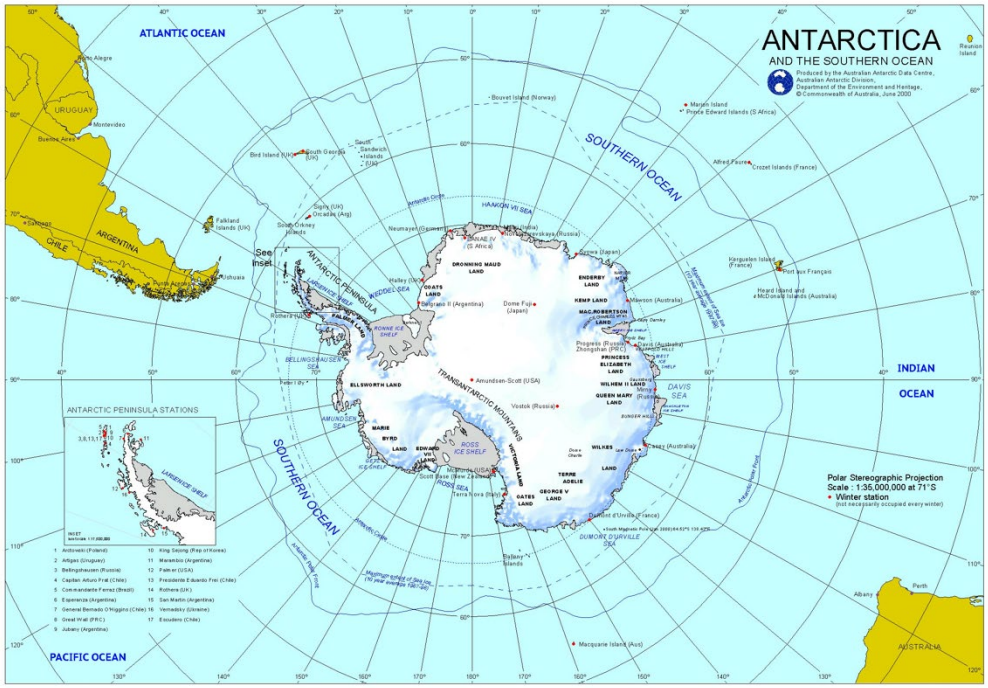

Figure 1. Map of the Southern Ocean and Antarctica. The grey line shows the approximate position of the Antarctic Polar Front. Credits: Australian Antarctic Data Centre, Australian Antarctic division (2000).

The Southern Ocean (south of 40° S) is one of the most remote and dynamic marine systems in the world (Fig. 1). It covers 34.8 million km^2 and comprises three deep oceanic basins (4000–6000 m deep) surrounding the Antarctic continent: Indian-Atlantic basin, Indian-Antarctic basin and Pacific-Antarctic basin (De Broyer and Koubbi, 2014). In the north, these basins are partially connected by a series of ridges that reduce the water flow at the bottom, and in certain areas deflect the surface currents (Garabato et al., 2004). At approximately 1000 m, the continental shelf of the Antarctic continent is deeper than those of all other continents due to the large mass of the ice sheets

(Foldvik et al., 1985).

The SO is a cold ocean. The sea surface temperature ranges from as low as -1.8° C near the Antarctic coast to about 3.5° C at the Antarctic Polar Front (De Broyer and Koubbi, 2014). One of the most dramatic seasonal changes in the Southern Ocean is the distribution of sea ice cover; which ranges from approximately $20x10^{-6}$ km^2 in late winter to $4x10^{-6}$ km^2 in late summer (Comiso and Zwally, 1984). The sea ice provides a resting, breeding and foraging substrate for seals and penguins. It usually reaches its maximum extent is in September and October, and the minimum in February and March. When sea ice forms, the underlying water gets saltier and sinks, mixing the water column and bringing nutrients to the surface (Parkinson and Cavalieri, 2012). When the sea ice thaws, the ocean is exposed again to sunlight. This spurs the photosynthesis of phytoplankton and stimulates its growth (Arrigo et al., 2010). Phytoplankton is an important food source for Antarctic krill (*Euphausia superba*) which in turn plays a major role in the diet of many higher order predators.

The climate of the SO is strongly influenced by wind. The Earth's rotation generates a predominantly easterly flow of wind around the Antarctic continent (Sokolov and Rintoul, 2009), and a westerly wind within the circumpolar belt at 50–60° S; maximum wind strength is concentrated in the region of the Antarctic Circumpolar Current (ACC). In the coastal regions, wind affects the redistribution of snow (Van Lipzig et al., 2004) and is the main driver of the SO circulation. Wind also drives ice-motion which contributes to inter-annual trends in sea ice concentration through both dynamic and thermodynamic effects (Holland and Kwok, 2012).

The SO water masses vary markedly with longitude (Gordon, 1988). The oceanic circulation is divided into the ACC-west wind drift (the only current that encircles the globe), the Antarctic Coastal Current-east drift (near the continent and following the coastline in the direction of the Ross and the Weddell sea), and the Circumpolar Frontal Zones, the most significant of which is the Polar Front that divides the SO into the subantarctic region (north) and the Antarctic region (south) (Deacon, 1977). The various fronts are characterized by variable width, steep gradients in sea-surface temperature,

changes in phytoplankton abundance, zooplankton distribution, pelagic species, weather conditions, and often maximum salinity at the surface (Sciermammano, 1989). Two key features of the SO's circumpolar zonation are: (i) the development of eddies of variable size and duration, where rings of cold and warm water are mixing (Gordon, 1988); and (ii) the formation of regions of long-lived open water (polynyas) as sea ice expands in winter. Polynyas affect Antarctic marine ecosystems in many ways by controlling the biogeochemical fluxes, regulating heat transfer from the oceans to the atmosphere, aiding ice production and the formation of dense shelf water, and influencing spring disintegration of sea ice, phytoplankton and zooplankton production, as well as the distribution of higher trophic animals (Smith and Nelson, 1990).

The Antarctic Intermediate Water masses (AAIW) are high in nutrients including nitrate, phosphate and silicate (El-Sayed and Turner, 1977). SO surface water is rich in oxygen and macro-nutrients but only a small amount of dissolved iron, which is critical for the primary production. The regions with a high concertation of dissolved iron in surface waters are north of the Polar Front, in the Subantarctic Zone, and south of the Antarctic Divergence, near the continent (David and Suacede, 2015). As a result, these areas have the highest production of phytoplankton.

Almost 8,800 species have been described for the SO (Jossart et al., 2015). Its subantarctic and Antarctic regions provide habitats for very large populations of pinnipeds, seabirds and cetaceans, many of which are particularly relevant for our study of the underlying principles related to diving behavior and physiology (Trathan and Hill, 2016). The Southern Ocean fauna is adapted to extreme conditions, resulting in high levels of endemism which makes it potentially vulnerable to effects of climate change, such as ocean warming, ocean acidification, and changes in light or UV exposure (Brierley and Kingsford, 2009).

Pinnipeds

There are seven species of seals in the SO, all with circumpolar distributions (Laws, 1977). These include two species of otariid: Antarctic

(*Arctocephalus gazella*) and Subantarctic fur seals (*A. tropicalis*), and five species of phocid: crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossi)*, southern elephant (*Mirounga leonina*), and Weddell seals (*Leptonychotes weddellii*). These mammals are specialist divers, returning to shore (or sea ice) only to rest, molt or breed. Their distribution during the breeding season depends on the availability of suitable habitats (Siniff, 1991). Ninety five percent of Antarctic fur seals are found at South Georgia, and the remainder at Bouvetøya, Macquarie Island, Crozet Island, the Kerguelen Archipelago, Heard Island and the McDonald Islands, the South Shetland and the South Sandwich Islands (Ropert-Coudert et al., 2014). In contrast, Subantarctic fur seals are generally found in more northerly locations than Antarctic fur seals, especially on Gough Island in the South Atlantic and Île Amsterdam in the southern Indian Ocean. Southern elephant seals predominantly breed and moult on the sandy and shingle coasts of the subantarctic islands. Crabeater, leopard and Ross seals mostly occupy the pack-ice zone (Siniff, 1989), while Weddell seals generally inhabit both pack and fast sea ice. During the non-breeding period, fur, Ross, southern elephant and Weddell seals disperse widely (McCafferty et al., 1998; Arthur et al., 2016; Bornemann et al., 2000), while crabeater and leopard seals are likely to stay in the pack ice zone (Burns et al., 2008; Knox, 1994).

Antarctic seals prey on a wide range of species from Antarctic krill (*Euphausia superba*) to penguins, and consequently their foraging behavior varies among species (Laws, 1984). Crabeater and fur seals utilize the upper portion of the water column, generally foraging at night while resting or swimming at surface during the day (Burns et al., 2004; Lea et al., 2002). Crabeater seals are the true krill specialist, with a diet based 90% on krill and only a small amount of fish and squid (Kooyman, 1981). Weddell, Ross and southern elephant seals feed on fish and cephalopods with marked diurnal diving patterns, which may also change seasonally and with foraging area (Cherel et al., 2008; Hückstädt et al., 2012; Banks et al., 2014). Finally, leopard seals have a diverse diet, and consequently a broad range of foraging strategies, to feed on krill, fish, squid, penguins and other seals (Müller-Schwarze, 1975).

206 Understanding the foraging ecology of Antarctic pinnipeds is essential to
207 elucidating the role of this group of taxa in the SO ecosystem.

208 **Antarctic fur seals** are strongly sexually dimorphic: males grow up to 2 m
209 long and weigh 110–230 kg; their coat is generally dark brown. Females reach
210 up to 1.5 m in length and weigh 40 kg; their coat tends to be grey. Their
211 relatively short flippers are structurally adapted for a semi-aquatic life enabling
212 them to move rapidly on land and at sea (Berta and Churchill, 2012). This
213 species is generally polygynous and forms rookeries on subantarctic islands
214 (Boyd et al., 1998).
215 The deepest dive of an Antarctic Fur Seal was recorded at 354 m, and
216 the longest dive lasting about 11 min (Staniland et al., 2008). The average
217 foraging dive, however, lasts only a couple of minutes and the animals reach a
218 depth of about 30 m (Arthur et al., 2016).

219 **Southern elephant seals** are also strongly sexually dimorphic; males weigh up
220 to 3700 kg and measure 4.5–6.5 m in length. Females weigh 400–800 kg and
221 are 2.5–5 m long (Shirihai and Jarrett, 2006). Elephant seals have a short grey
222 coat and males have an inflatable proboscis (Fig. 2). This species generally
223 breeds in subantarctic locations; males tend to arrive in the colonies earlier than
224 the females and fight for control of harems (De Bruyn et al., 2011).
225 Southern elephant seals dive on average to a maximal depth of 1049 ±
226 315 m (female), and 1170 ± 411 m (male) (Hindell et al., 2016) for up to 20
227 min. The deepest recorded dive reached a little over 2149 m (McIntyre et al.,
228 2010).

229 **Weddell seals** are relatively large, with a short mouth line and similarities in
230 the structure of the nose and whiskers to a cat. Males Weddell seals are slightly
231 smaller than females measuring 2.5–3 m long and weighting 400–660 kg;
232 females reach a length of up to 3.3 m and weigh the same as males. The coat is
233 dark silvery grey with some white. This species has relatively the shortest fore-
234 flippers of all phocids (Shirihai and Jarrett, 2006). Weddell seals congregate at
235 breathing holes in the fast ice only during the moult and breeding time
236 (Stirling, 1969). Weddell seals can dive to ~740 m, and can spend up to 1 h

underwater (Plötz et al., 2002). The longest dives are undertaken when swimming under ice searching for new breathing holes.

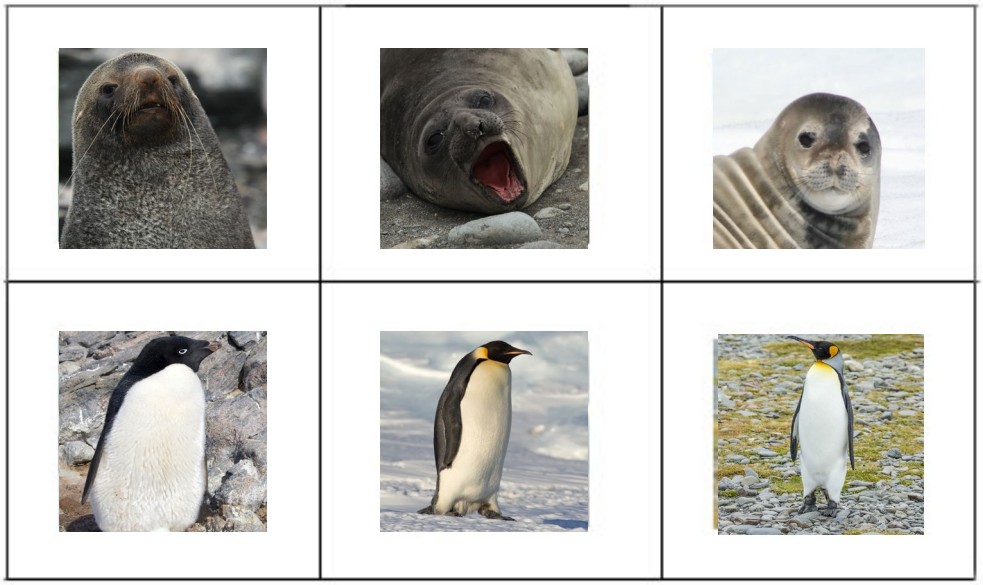

Figure 2. Species of pinnipeds and penguins studied in chapters (3, 4) of this thesis. From top left to bottom right: Antarctic fur seal, southern elephant seal, Weddell seal, Adélie penguin, emperor penguin and king penguin. Photo credit: www.archive.org.

Seabirds

Over 80 non-vagrant species of flying seabirds from nine families in two orders have been recorded in the Southern Ocean (De Broyer and Koubbi, 2014). The majority of flying seabirds belong to the Procellariiformes (*e.g.*, prions, shearwaters, albatrosses, petrels), Charadriiformes (i.e., gulls, skuas, terns) and Suliformes (e.g., cormorants). Most of these birds are extremely wide ranging, travelling hundreds or even thousands of kilometers from the colony during the breeding season to feed on patchily distributed resources that include squids, fish and crustaceans (Woehler, 1997).

Penguins (Sphenisciformes) represent 90% of the Antarctic avian biomass (Woehler and Croxall, 1997). Penguins lost their ability to fly, evolving higher bone density and flipper-like wings to become highly specialized divers (Habib, 2010). In the SO, there are nine species of penguins belonging to three genera: *Aptenodytes* (emperor penguin *A. forsteri,* and king penguin *A. patagonicus*), *Pygoscelis* (Adélie penguin *P. adeliae*, chinstrap penguin *P. antarcticus*, gentoo penguin *P. papua*), *Eudyptes* (macaroni

penguin *E. chrysolophus*, northern *E. moseleyi* and southern *E. chrysocome* rockhopper penguin, royal penguin *E. schlegeli*). Penguins spend a substantial proportion of their time at sea, and when breeding they are most commonly coastal foragers (Wilson and Wilson, 1990). Only four species breed on the coast of the Antarctic continent: Adélie, emperor, chinstrap and gentoo. However, the latter two are mostly found on the islands at the Antarctic Peninsula, and the remaining species (king, macaroni, royal, rockhopper) form colonies only on subantarctic islands (Croxall, 1984). During the non-breeding period (generally in winter, except for emperor penguins), many species undertake extensive migrations. For example, Adélie penguins spend almost 8 months at sea in the pack ice up to 2,790 km from their breeding colonies (Davis et al., 2001).

Crustaceans are the predominant item in the diets of Adélie penguins (Emmerson and Southwell, 2007), but Antarctic krill is replaced by *E. crystallorophias* near the Antarctic coast. Adélie, king and macaroni penguins are generally considered pelagic feeders, while gentoo, rockhopper and chinstrap penguins are benthic feeders that forage close to shore (Denhard et al., 2011). Emperors feed on benthic, bentho-pelagic, and pelagic prey (Roberson et al., 1994).

Adélie penguins are mid-sized penguins: adults measure 70 cm from the tip of their beaks to the tip of their tails and weigh 3–6 kg. Adélie penguins often return to their natal colony to join the breeding population. Parents share the 35 d incubation. Most young penguins are ready to leave their colony to forage independently after two months (Ainley and Schlatter, 1972).

This species can dive as deep as 180 m for about 3 min (Watanuki et al., 1997), although they usually hunt in far shallower waters (~ 18 m) for < 1 min (Cottin et al., 2014).

Emperor penguins are the tallest and heaviest of all penguins: adults are 100 cm tall and weigh 23–45 kg; at the start of the breeding season, males generally weigh more than females. Adults have black dorsal feathers, and white feathers on the belly and ventral side of wings, which tend to become pale yellow on the upper breast. Ear patches are bright yellow (**Fig. 2**) (Borboroglu and

Boersma, 2015). Emperors breed in large colonies on Antarctic fast-ice and incubation lasts 60–68 days. Females lay a single egg in May–June; post-laying females migrate to sea to forage whilemales incubate the egg exclusively until mid-July. Once the chicks hatch, females return to the colony to relieve the males (Stonehouse, 1985).

When foraging, emperor penguins dive for 5–6 min (Wright et al., 2014)); they usually dive to 150–250 m but depths of > 564 m have been recorded (Wienecke et al., 2007).

King penguins are the second tallest penguin species in the world: adults stand up to 100 cm tall and weigh 9–18 kg. King penguins are monogamous and in most populations, they breed only twice in three years between November and March. Incubation duties are shared and last ~54 days. Juveniles fledge in spring/early summer (Stonehouse, 1985). During foraging trips, king penguins can dive repeatedly to > 148 m with a maximum depth of 343 m (Pütz et al., 2005), and a mean dive duration of 4 min.

Aims

The overarching aim of this thesis is to develop a broader understanding of the diving ecology of air-breathing marine predators, filling the gaps in knowledge about animal diving behavior and the biological factors that constrain it.

The main recognized constraint to marine mammals' diving behavior is their ability to store oxygen, which have been extensively discussed in previous published work (Kooyman and Ponganis, 1998; Goldbogen et al., 2013; Balmer et al., 2014; McIntyre, 2014; Hussey et al., 2015). However, there are other factors that can influence dive duration for marine mammals and seabirds and key amongst these is the metabolic rate (MR) - the amount of energy expended by an animal over a specific period of time (Schmidt-Nielsen, 1970). The MR determines how rapidly oxygen stores are depleted and variation in metabolic rate can be due to: evolutionary morphological divergences – marine mammals have increased concentrations of the oxygen-carrying proteins (hemoglobin in blood

and myoglobin in muscle; Kooyman and Ponganis, 1998); size – larger animals having relatively lower metabolic rate than smaller ones (the so-called mouse-elephant curve; Schmidt-Nielsen, 1970); and activity - energetic behaviors such as prey pursuit deplete oxygen stores more rapidly than sedentary behaviors (i.e. resting or transit; Mori, 1999; Kooyman, 1989). The interaction of these three factors is complex and will influence many fundamental aspects of a diving animals' ecology: from foraging preferences (e.g. benthic vs pelagic feeders), hunting strategies (pursuit vs sit-and-wait) and even migration patterns (local vs distant foraging).

Because of the interwoven nature of these factors the best available tool for understanding them is a comparative approach where we contrast diving behaviors among species while simultaneously accounting for body size and activity. Previous reviews (Halsey et al., 2006a; b) have focused on meta-analyses aggregating diving metrics to the species level. This has provided important insights into broad-scale patterns but have not been able to investigate changes at more ecologically relevant scales. What is currently lacking are comparative analyses at the individual animal level, where factors such as body size might be of considerable importance; and the within animal level, where factors such as hunting behavior might come into play.

By reviewing the literature regarding dive data collected across pinnipeds, seabirds and cetaceans in the Southern Ocean, I address the main outstanding questions in the field:

(i) What are the best metrics to measure diving behavior and what are the appropriate tools to use. This is covered in a new review of the diving literature which considers what ecological and physiological insights can be gained from simple time-depth-recorder data and what basic and complex dive metrics can tell us about predators' foraging behavior and physiology.

(ii) To what degree is diving behavior influenced by physiology and body size: do individuals within a species still follow patterns predicted by the mouse-elephant curve? To answer this, I undertake a series of comparative analysis using TDR datasets of three species of seals and three species of penguins tagged in the East Antarctic sector of the SO. Selecting animals that share the same habitat increases

the power of comparison and strengthens the application of my findings.

(iii) To what degree does activity during a dive influence diving behavior? Do all species show the same degree of behavior plasticity? I extend here my comparison to specific dive behavior such as hunting and observe how different species respond to different scenarios.

When completed my thesis will contributes to the existing knowledge on SO marine predators' physiology and behavior, providing a deeper insight into a species ability to adapt to environmental changes (e.g. prey availability). My work has been one of the first attempts to establish a robust treatment of increasingly complex data streams paving the way for more integrative multi-species meta-analyses.

Thesis structure

The thesis has been written as a series of separate manuscripts and consequently some textual overlap occurs between chapters. The thesis consists of three chapters describing aspects of the diving ecology of SO predators, which are brought together and synthesized in a final discussion chapter. Data selected for this Thesis are publically available, they have been recorded in a restricted area of SO region, and they present a different range of taxa in terms of body size, age, and sex. The thesis structure is:

Chapter 2 – Review of dive behavior and physiology
In this review paper, I synthesize the variety of analytical approaches available for individual-based time-depth-record data for questions regarding three key areas:
(i) Diving behavior: I describe the best devices and sensors to quantify diving behavior, and discuss the best dive metrics to analyze the data.
(ii) Foraging behavior: I explain how to use TDR data to infer prey distribution and type, foraging strategies, prey density and quality, prey consumption.
(iii) Diving physiology: I demonstrate how to use TDR data to learn about intrinsic determinants, physiological constraints, and physiological

mechanisms that influence dive behavior.
(iv) Emergent areas in marine telemetry studies: I discuss the integration of dive and location data, and the integration of individual data and demographic and/or population data .

The next two chapters quantify the role of intrinsic factors (e.g., physiology and body mass) in diving behavior. Findings from these analyses allow me to show differences in dive performance and ability of mammals and birds, but also to determine the energetics behind dive behavior and foraging. Foraging is a fundamental requirement of all animals and has implications for their distribution and growth, and the persistence of wild populations (Pyke et al., 1977).

Chapter 3 – Evaluation of relationship between dive behavior and metabolism
Here I investigate patterns in dive cycle management (duration, depth, post-dive surface interval) to evaluate the extent of intrinsic determinants, in particular body mass, of six species of SO predators. I address the following questions:
(i) What is the influence of body mass on dive performance across species?
(ii) Are there interdependencies among diving parameters?

Chapter 4 – Examination of behavioral plasticity
Here I extend my characterization of the diving behavior of a suite of marine predators foraging in the SO region, and examine:
(i) What is an individual's diving performance range in terms of maximum dive duration, maximum dive depth, post-dive duration interval?
(ii) Do species' behaviors vary during foraging and if so, how do penguins and seals adjust their dive cycle?
(iii) Are foraging dives longer, deeper, with longer bottom time and transit time than non-foraging dives? Do foraging dives have a higher energetic cost?

All the findings are drawn together in a final discussion chapter:

Chapter 5 – Final discussion

This discussion provides a summary of the main findings and implications for the field of knowledge with respect to three major themes:
(i) Benefits and limitations of dive-based indicators of physiological capacity;
(ii) Diving ecology of Southern Ocean species;
(iii) A final section which outlines proposed future directions for research in this area.

The contribution of co-authors is outlined in the Statement of Co-authorship at the start of the thesis. A single bibliography is presented at the end of the thesis using the Journal of Animal Ecology referencing style.

Chapter 2

View from below: inferring behavior and physiology of Southern Ocean marine predators from dive telemetry

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Abstract

Air-breathing marine animals, such as seals and seabirds, undertake a special form of central-place foraging as they must obtain their food at depth yet return to the surface to breathe. While telemetry technologies have advanced our understanding of the foraging behavior and physiology of these marine predators, the proximate and ultimate influences controlling the diving behavior of individuals are still poorly understood. Over time, a wide variety of analytical approaches have been developed for dive data obtained via telemetry, making comparative studies and syntheses difficult even amongst closely-related species. Here we review publications using dive telemetry for 24 species (marine mammals and seabirds) in the Southern Ocean in the last decade (2006–2016). We determine the key questions asked, and examine how through the deployment of data loggers these questions are able to be answered. As part of this process we describe the measured and derived dive variables that have been used to make inferences about diving behavior, foraging, and physiology. Adopting a question-driven orientation highlights the benefits of a standardized approach for comparative analyses and the development of models. Ultimately, this should promote robust treatment of increasingly complex data streams, improved alignment across diverse research groups, and also pave the way for more integrative multi-species meta-analyses. Finally, we discuss key emergent areas in which dive telemetry data are being upscaled and more quantitatively integrated with movement and demographic information to link to population level consequences.

Introduction

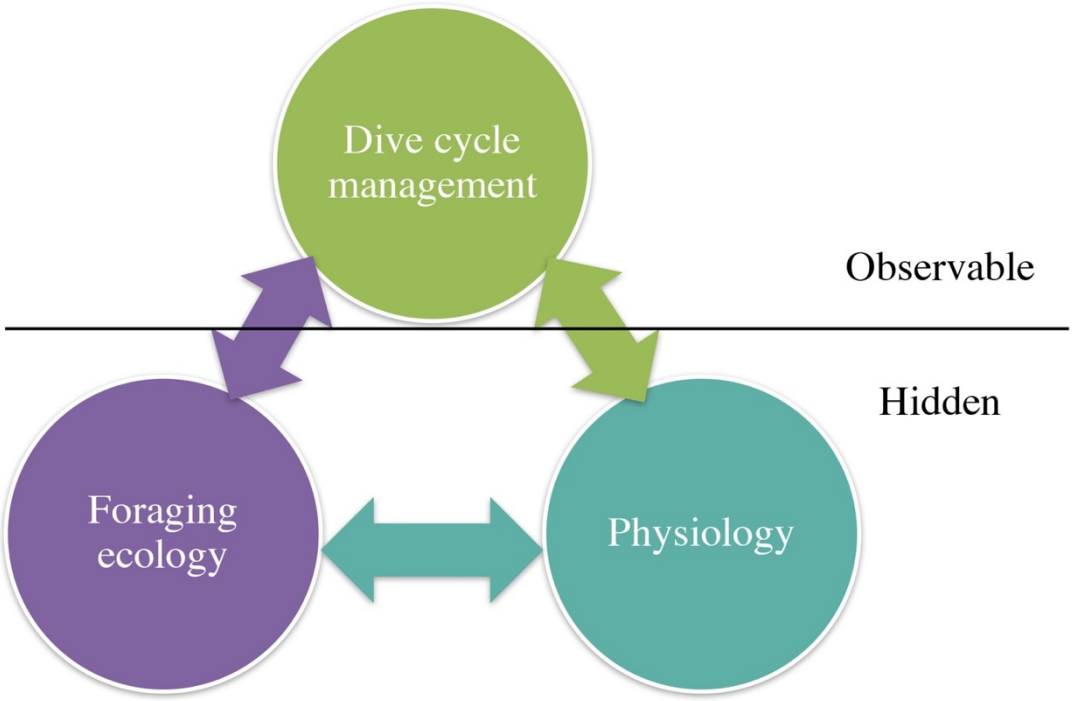
The Southern Ocean (hereafter SO) is a unique circumpolar biogeographic region, supporting a rich biodiversity with many species of high conservation value (De Broyer and Koubbi, 2014b). It is also one of the areas manifesting the most rapid climate-related changes (Larsen et al., 2014). The SO ecosystem supports diverse marine predators, many of which are pursuit divers (Trathan and Hill, 2016) that are particularly interesting for the study of the underlying principles related to foraging behavior and diving physiology. Seven species of seals are endemic to the SO, some breed on land while others use the sea-ice as breeding platform. Toothed whales (parvorder *Odontoceti*) may occupy the SO year-round while in contrast baleen whales (parvorder *Mysticeti*) typically migrate and are present only seasonally. Over 90% of the SO avian biomass comprises penguins (order *Sphenisciformes*) (Woehler and Croxall, 1997) but a large variety of seabirds, the majority of the order Procellariiformes (e.g., prions (genus *Pachytila*), shearwaters (genus *Puffinus*), albatross (family Diomedeidae), petrels (family Procellariidae)) and of the order Charadriiformes (i.e., gulls and terns (family *Laridae*), skuas (family *Stercorariidae*)), visit the Antarctic region during the austral summer. These species are all adapted to the extreme and highly seasonal ocean-ice environment and are likely to respond differently to changing climate and other human-induced influences and activities (Forcada et al., 2008; Constable et al., 2014).

Historically, these highly mobile animals were almost impossible to observe across their range. Today, a multitude of data loggers and sensors provide a broad observational framework for acquiring detailed information about their lives at sea. Information on how animals use the environment in space and time are the central tenants that inform a synthetic overview of ecosystem structure and dynamics (Schick et al., 2013). The demographic performance (e.g., growth rates and reproductive behavior) of these animals provides an integrated measure of overall system function and health (Barbraud and Weimerskirch, 2001). As long-lived species, marine mammals and seabirds can be monitored long-term and act as indicators of ecosystem status across a range of spatiotemporal scales (Schick et al., 2013). Since many of

these species dive to several hundred meters (e.g., elephant seals (genus *Mirounga*, McIntyre et al., 2010) and beaked whales (family Ziphiidae; Tyack et al., 2006), they provide information from the surface to the deep ocean. Quantifying movement and diving behavior can therefore provide information on areas of high and low productivity, how these change over time, and may help provide insights into how animals will respond to global climate change.

Kooyman (1965) was the first to investigate the diving behavior of a Weddell seal (*Leptonychotes weddellii*) using an animal-borne device — a pressure gauge combined with a kitchen timer; the deployment lasted about an hour. This basic time-depth recorder (TDR) recorded for the first time not only dive depth and duration but also ascent and descent rates of the seal. This work revolutionized the study of marine mammals and other marine animals (Kooyman, 2004). From these origins we can now integrate in situ behavior and physical measurements to study direct links, e.g., between the characteristics of the environment (e.g., the water mass a seal uses) and animal behavior (e.g., how deep and long it dives) and performance (e.g., how often it breaths). These linkages can ultimately help to quantify how population growth rates are affected (e.g., Hindell et al., 2017; McMahon et al., 2017).

Diving predators need to acquire sufficient resources which among other factors are determined by prey distribution, abundance, and quality. These need to be balanced against their physiological constraints (e.g., oxygen stores, age/size or sex influencing diving capacity). The interplay between need and constraint is reflected in what is directly observable, and what can be measured, for example, dive behavior using data loggers. How these predators manage their dive cycle structure is the key from which inferences can be made about the “hidden” aspects of foraging and physiology (Fig. 1).



115 **Figure 1**. Diagram showing the interplay between what is directly measured
116 "observable" and can be described using only basic dive parameters i.e., dive behavior
117 and dive cycle management; and what can be inferred combining basic dive metrics
118 into derived parameters, i.e., foraging preferences and ecophysiology, and may be
119 considered "hidden" behavior.
120
121 In our study, we conducted a systematic literature review of
122 publications using dive telemetry in the Southern Ocean with a focus on 2006–
123 2016 (Supplementary Material), as this was a period of considerable study
124 employing both well-established sensors (e.g., time-depth recorders) and
125 emerging techniques (e.g., accelerometry, animal-borne cameras). We searched
126 for peer-reviewed literature, published in English, containing the words: dive
127 data, tag, time-depth recorder, TDR, Southern Ocean, Antarctic, marine
128 mammals, penguins, seabirds, seals, cetaceans, and species names. For

identifying SO birds and mammals, we follow Ropert-Coudert et al. (2014). Most research data is from south of 40° S (De Broyer and Koubbi, 2014a, b), although some species are clearly limited to the Antarctic region (i.e., south of 60° S). This substantial field of telemetry work comprises 218 studies of 24 species, including 10 species of marine mammals and 14 species of seabirds that used a variety of different data loggers and sensors. The full literature database is made available under Supplementary Material.

Where pertinent, we do refer to literature published outside the 2006–2016 time frame, as key studies obviously occurred either before this decade, or studies were conducted on species similar to those included in this review. We do not intend this as a general review of advances in the bio-logging field (see, for example, Halsey et al., 2006a, b, 2007a; Mate et al., 2007; Goldbogen et al., 2013; Balmer et al., 2014; McIntyre, 2014; Ceia and Ramos, 2015; Hussey et al., 2015). Rather we aim to examine the richness of information and insights gained, from relatively simple dive data streams, about the underwater lives of Southern Ocean marine predators. While focusing on mammals or birds only (e.g., Goldbogen et al., 2013; McIntyre, 2014; Carter et al., 2016) would allow a more detailed coverage, it is timely for a more holistic perspective of the Southern Ocean. We hope this review provides a useful synthesis particularly for new researchers commencing Southern Ocean biotelemetry research.

First, we briefly cover the main observational platforms used (devices and sensors), and the general coverage across SO species and geographical areas. Following a basic explanation of diving behavior, we then synthesize the literature by adopting a question-driven approach: exploring the foraging and physiological inferences achievable using dive data. Adopting this approach organizes the insights obtained from dive telemetry under an ecological framework which, we suggest, provides a useful context for aligning the analyses of dive metrics. This perspective might thereby serve to facilitate comparative multi-species analyses and meta-analyses. The scope of the review covers what has been learnt about important SO predators, and particularly how tags, data and analytical methods were used. The review closes with a perspectives section considering the outstanding questions being addressed in

emergent areas.

Observational Platforms

Devices and Sensors

Animal-borne data loggers enable the remote study of various aspects of the biology of free-living animals with regard to behavior, physiology and energetics (Cooke et al., 2004). Data loggers are devices that record information using sensors measuring physical (e.g., light, temperature, or pressure) or physiological properties such as heart rate.

Table 1. Commercially available sensor types for data loggers and their use for marine mammal and seabird research. For further information regarding scales of movement and location errors associated with different positioning sensors see: Bryant (2007), Block et al. 2010), Costa et al. (2010), Patterson et al. (2010), Winship et al. (2012) and references therein.

SENSOR	USE
Time	Activity information: duration, time of the day
Pressure	Activity information: depth reached diving
Accelerometer	Activity information: active swim speed
Speed sensor	Activity information: swim velocity
Wet/dry sensor	Activity information: in/on water
Gyroscope	Activity information: change in direction
Magnetometer	Environmental information, orientation, inertia, position of each sensor relative to the transmitter
Camera	Movie information processed via image processing software

Hydrophone	Sound information
Heart rate	Physiological information as energy expenditure
Stomach or oesophagus temperature	Physiological information as ingestion
Temperature	Environmental information: use of currents
Salinity	Environmental information: ocean circulation
Light	Environmental information, day/night, seasonality
POSITION SENSOR	
Argos transmitter	Local- to meso-scale movement information
GPS (Global Positioning System)	Fine-scale movement information
GLS (Global Location Sensing)	Meso- to basin-scale movement information

Throughout the 1970s and most of the 1980s, TDRs were predominantly archival, needing to be recovered to retrieve the information. Taking into account difficulties often experienced in recapturing a tagged animal, satellite-linked depth recorders (SLDR) were developed (Bengtson et al., 1993). These typically use the Argos satellite system to relay data which, due the system's limited bandwidth, often requires high temporal resolution data to be summarized either into user-defined bins (Fedak et al., 2001, 2002) or greatly simplified time depth profiles (e.g., Photopoulou et al., 2015). Satellite-relayed information offers the only solution to studying animals without prospect of recapture, such as fledglings, non-breeding individuals and/or those not bound to land (or ice) based colonies.

Usage in Southern Ocean Species

From 2006–2016, data loggers were used to study 24 air-breathing

191 species in the SO: 7 pinnipeds, 7 penguins, 3 cetaceans, and 7 flying seabirds.
192 Most studies focused on pinnipeds (44%) and penguins (41%), while studies on
193 flying seabirds and cetaceans accounted for only 6 and 9% of publications,
194 respectively (Table 2). The reasons for this disparity are likely due to
195 differences in the catchability and accessibility of the different species. More
196 than half of the species studied (n = 16) were subantarctic (40–60° S) species
197 and 8 were high Antarctic species (>60° S) (Fig. 2). The sampling effort was
198 greatest in the South Atlantic.

Table 2. Southern Ocean literature review results showing the number of studies conducted by species from 2006–2016. Examples of reported grand mean dive durations (sec) and grand mean depths (m) among individual are given as mean ± SD or range (min – max) as available. Sample sizes are given in brackets. For species with few studies (≤ 5) all references are given here, otherwise the three most recent studies are shown. Abbreviations: nr = numeric value not reported; m = males, f = females, p = pups, j = juveniles. In some case multiple values are given for separate seasons. The full database containing all literature references (n = 218) is made available under Supplementary material S1. * Indicates mean maximum dive depth was reported; **binned data from satellite-linked recorders.

Map ID	Species	No. Studies	Dive duration (sec)	Dive depth (m)	References
1	Antarctic fur seal (AFS) *Arctopcephalus gazella*	28	107 ± 43 97 ± 42 67± 4	31 ± 20 (12) 50 ± 22 (11) 21 ± 2 (5)	Arthur et al. 2016 Viviant et al. 2016 Bestley et al. 2015
2	Subantarctic fur seal (SFS) *A. tropicalis*	3	14 – 18 93 ± 0.5 93 ± 0.5	5 – 13 (78p) 100 ± 0.3 (47)* 40 ± 0.3 (47)	Verrier et al. 2011 Luque et al. 2007a Luque et al. 2008
3	Southern elephant seal (SES) *Mirounga leonina*	47	1103 ± 308 1560 ± 318, 1488 ± 306 1183 ± 326	409 ± 192 (9) 1049 ± 315 (326f), 1170 ± 411 (61m) 334 ± 133 (20)	Le Bras et al. 2016 Hindell et al. 2016 Bestley et al. 2015
4	Leopard seal (LS) *Hydrurga leptonyx*	4	132 ± 74 nr >75% dives <300 (2)** 119 ± 83	17 ± 11 (21) 62 ± 15 (7) 140 ± 8 (1), 108 ± 7 (1) 44 ± 48 (1j)	Krause et al. 2016 Krause et al. 2015 Nordøy and Blix 2009 Kuhn et al. 2006
5	Crabeater seal (CS) *Lobodon carcinophagus*	6	225 ± 23 nr 228	54 ± 27 (13) nr (34) 11 ± 5.3 (34)	Bestley et al. 2015 Friedlaender et al. 2011 Burns et al. 2008

6	Weddell seal (WS) *Leptonychotes weddellii*	12	489 ± 122 1380 ± 0.6 1260 ± 6 600 ± 360	119 ± 38 (18) 511 ± 4 (1), 475 ± 4 (1) 67 ± 54 (1)	Bestley et al. 2015 Heerah et al. 2015 Heerah et al. 2014
7	Ross seal (RS) *Ommatophoca rossii*	1	nr	52–100 (10)	Blix 2007
1	King penguin (KP) *Aptenodytes patagonicus*	22	211 – 248 1 – 495 269.4 ± 62.4 261.6 ± 57.4	95 – 135 (6) 2 – 344.5 (21) 154.8 ± 52.8 (7f), 143.5 ± 45.4 (8m)	Hanuise et al. 2013 Le Vaillant et al. 2013 Le Vaillant et al. 2012
2	Emperor penguin (EP) *Aptenodytes forsteri*	23	222.6 ± 6 282 ± 30 nr	72.3 ± 4.1 (4) 102.9 ± 28.6 (7) 1047.8 ± 108.6 (10)	Wright et al. 2014 Williams et al. 2012 Shiomi et al. 2012
3	Adélie penguin (AD) *Pygoscelis adeliae*	14	56 ± 4 97 ± 38, 78 ± 27 nr	17.3 ± 1.8 (1) nr (14) 43.08 ± 0.1 (65)	Cottin et al. 2014 Watanabe et al. 2013 Ainley et al. 2012
4	Gentoo penguins (GP) *Pygoscelis papua*	6	88 92.3 – 109.6 nr	45.9 (20)* 35.9 – 52.2 (7) 52.7 ± 16.0 (12)	Handley et al. 2015 Lee et al. 2015 Kokubun et al. 2011

5	Chinstrap penguin (CP) *Pygoscelis antarctica*	8	70.5 ± 9 81 ± 13.1 76.7 ± 17.8 62 ± 25 20	29.1 ± 6.6 (20), 37 ± 10.6 (17), 33.9 ± 12.7 (20) 20 ± 14 (31)* 5 (2)*	Kokubun et al. 2015 Blanchet et al. 2013 Mori 2012
6	Macaroni penguin (MP) *Eudyptes chrysolophus*	13	130 ± 11 85 ± 36 40 – 130	48 ± 7 (7) 32 ± 26 (20) 9 – 40 (105)	Whitehead et al. 2016 Blanchet et al. 2013 Hindell et al. 2011
7	Southern rockhooper penguin (SRP) *Eudyptes chrysocome*	4	nr 77.2 ± 3.5 63.2 ± 36.4 71.7 ± 5.5	16 ± 6 (36) 29.7 ± 3.4 (12) 20.6 ± 19.4 (4) 27.1 ± 5.7 (30)	Rosciano et al. 2016 Ludynia et al. 2012 Raya Rey et al. 2009 Pütz et al. 2006
1	Killer whale (KW) *Orcinus orca*	1	294.6 ± 140.4	57.5 ± 112.5 (9)	Reisinger et al. 2015
2	Humback whale (HW) *Megaptera novaeangliae*	12	nr nr nr	18 – 64 (9) 66.1 ± 75.1 (13) 5 – 85 (9)	Friedlaender et al. 2016 Tyson et al. 2016 Friedlaender et al. 2013
3	Antarctic minke whale (MW) *Balaenoptera bonaerensis*	1	84 ± 24	18 ± 5 (2)	Friedlaender et al. 2014

212

213

1	Crozet shags (CRs) *Phalacrocorax melanogenis*	2	nr 371	100 – 110 (12)* 145 (12)*	Cook et al. 2008a Cook et al. 2008b
2	Great shearwaters (GRs) *Puffinus gravis*	1	7.9 ± 8.5	3.3 ± 3.8 (7)	Ronconi et al. 2010
3	Common diving-petrel (CMp) *Pelecanoides urinatrix*	1	10.1 ± 4.1	2.1 ± 0.3 (20)	Navarro et al. 2014
4	White-chinned petrel (WHp) *Procellaria aequinoctialis*	2	4.6 ± 3.9 nr	2.9 ± 2.4 (9) 3.9 ± 1.1 (14)*	Rollinson et al. 2014 Sue-Anne 2012
5	South Georgian diving petrel (SGp) *Pelecanoides georgicus*	1	14.3 ± 4.2	18.1 ± 3.6 (6)	Navarro et al. 2014
6	Kerguelen shag (KEs) *Phalacrocorax verrucosus*	5	< 350 97 87 – 304 nr 321	< 120 23.5 (26) 70 – 80 (15)* 70 – 80 (15)* 108.5 (15)*	Cook et al. 2013 Watanabe et al. 2011 Cook et al. 2010 Cook et al. 2008a Cook et al. 2008b
7	Imperial cormorant (IMc) *Phalacrocorax atriceps*	1	304 – 14	65 – 2 (12)	Quintana et al. 2007

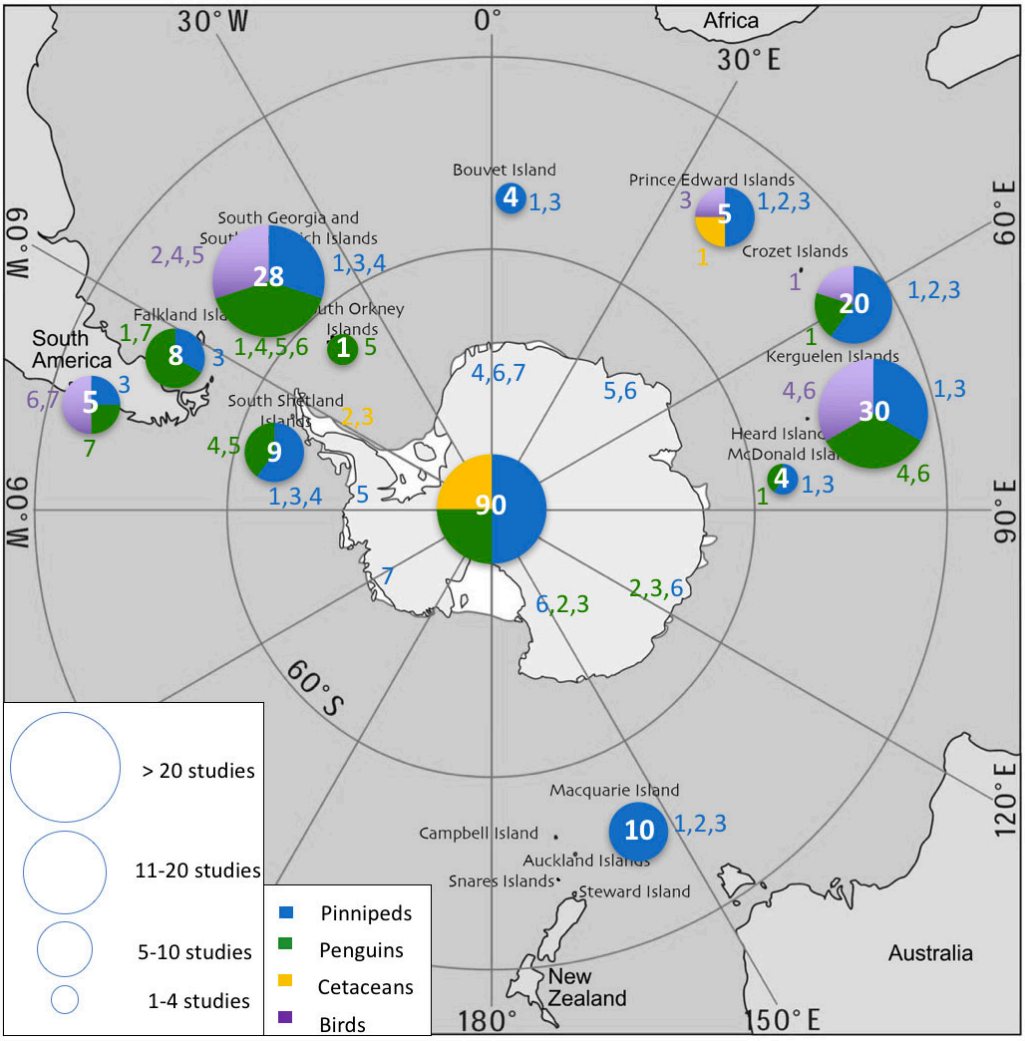


Figure 2. Spatial distribution of sampling effort/data logger deployment in the Southern Ocean during 2006–2016 for each species. Circle size and white number represent the total number of studies carried out in each location. Color-coded numbers correspond to the species cited in **Table 2**. The database containing all literature references is made available under Supplementary Material.

Fourteen of 28 studies on Antarctic fur seals (*Arctocephalus gazella*) took place in the South Georgia region. Southern elephant seals (*Mirounga leonina*) were tagged mostly at breeding colonies on South Georgia, Kerguelen, Crozet, and Prince Edward islands but also at haulouts near Antarctic continental stations. Crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*), and Weddell seals were tagged on or near the continent, especially near the Antarctic Peninsula or near the coast on the sea ice, and occasionally on Subantarctic islands. Access to these dispersed ice-affiliated species remains challenging over large areas of the SO. Some 80% of

studies on Adélie penguins (*Pygoscelis adeliae*) were carried out in Adélie Land. Macaroni penguins (*Eudyptes chrysolophus*) were most commonly tagged at South Georgia and Subantarctic islands within the Indian sector. A few rockhopper penguin (*E. chrysocome*) colonies off Argentina and the Falkland Islands fall within the Southern Ocean (i.e., < 40° S). Chinstrap penguins (*P. antarctica*) were studied at Subantarctic islands including South Georgia, South Orkney (Takahashi et al., 2003), and South Shetland (Croll et al., 2006). Finally, emperor penguins (*Aptenodytes forsteri*) were studied at various colonies along the coast of the Antarctic continent (Wienecke et al., 2007). Albatrosses and diving petrels were studied at South Georgia and the South Orkney Islands (Phillips et al., 2005, 2007; Rollinson et al., 2014). The only site where the diving ability of cormorants (*Phalacrocorax* spp.*)* was studied in the last 10 years is the Crozet archipelago (Cook et al., 2008a, b). For cetaceans, the studies were carried out near the Auckland Islands, the Falkland Islands and in South America, and in the Antarctic Peninsula region.

Cetacean telemetry studies have lagged somewhat behind those of seals and penguins largely due to accessibility, as well as technological issues with tag attachments. These are resolving and beginning to provide valuable longer term tracking datasets (e.g., Reisinger et al., 2015; Weinstein and Friedlaender, 2017). Additionally, the tag design for DTAGs (multisensor archival digital acoustic recording tags, Johnson and Tyack, 2003; Goldbogen et al., 2013) provides some of the most sophisticated diving data achievable for the study of free-living animals, albeit still usually at short time scales (typically a day or so, using suction cup attachments, e.g., Tyson et al., 2016). Taking these developments into account we can expect a maturation of this field and consequent major expansion of these data over the next decade. The study of SO seabirds also largely remains focused on movement studies, often with the addition of simple wet/dry activity sensors (e.g., Phalan et al., 2007). Seabird diving studies continue only in relatively low numbers, but we may similarly expect an increase in future with the ongoing miniaturization of data loggers and sensors.

The Basics of Diving Behavior

Diving behavior occurs at a series of scales: the individual dive scale, the bout scale (being made up of a series of dives) and the trip scale (a trip from land being made up of a series of bouts). Furthermore, diving behavior can vary on different temporal scales (daily, monthly, seasonally) and may also be influenced by the lunar cycle (e.g., Horning and Trillmich, 1999; Biuw et al., 2010; Heerah et al., 2013; Guinet et al., 2014) as expanded in the next section on Foraging Inference.

Each dive can be divided into distinct phases (Fig. 3). The descent phase (DESC) represents a period of active swimming using sequential, large amplitude strokes of flippers, flukes or feet to reach the desired depth (Williams et al., 2000). The bottom phase (BOT) is defined as the period between the dive descent and ascent. Often this is simplified as the time between the first and last recorded depth that is some fraction (e.g., 80%, but also 60–85% depending on the species) of the maximum depth (Austin et al., 2006; Bailleul et al., 2008). Halsey et al. (2007a) proposed the definition as between the first and the last wiggle or step, being deeper than a given proportional depth threshold, assigned per species. The bottom phase is generally assumed to be connected to feeding activity. During the ascent phase (ASC) when the animal returns to the surface, it experiences a decrease in pressure and the re-inflation of the lungs (Williams et al., 2000). The final phase is the post-dive surface interval (PDSI) during which the animal replenishes its oxygen stores before a new dive (Houston, 2011). Time at the surface can also be used for preening, resting, food processing or moving to a new area (traveling or searching) (Thompson and Fedak, 2001). This is a generalized structure of a dive and a useful conceptual framework. However, in reality many dives diverge from this pattern, either having no or a greatly limited bottom phase (“V” and “U” shaped dives), or multiple bottom phases at different depths (Heerah et al., 2014, 2015).

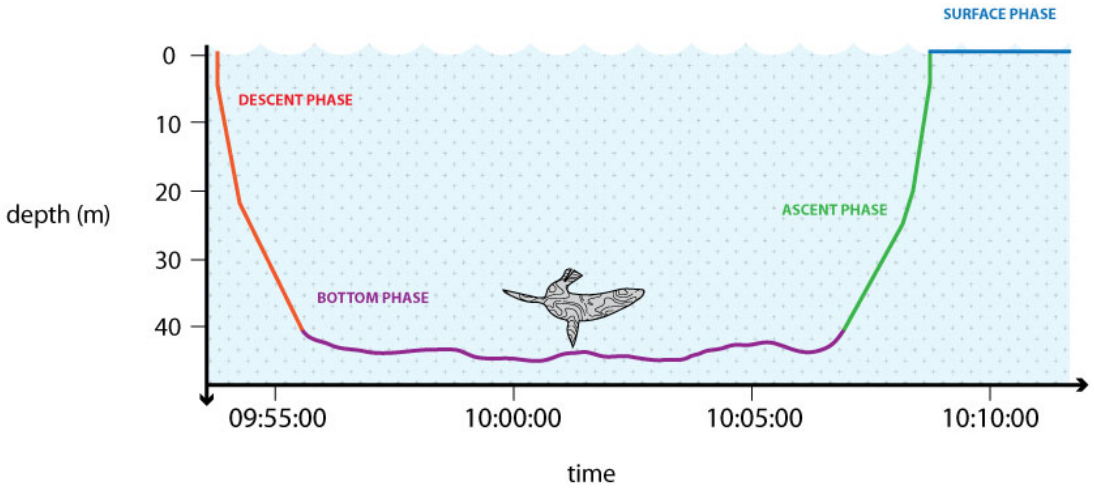


Figure 3. Stylized graphic representation showing a general dive of a marine predator. The diving phases are summarized using different colors: descent phase (red); bottom phase (violet); ascent phase (green); surface phase (blue). Designed by: Charlie Armstrong.

On the basis of their profiles, dives may be classified typically as square dives (DESC = ASC with BOT); V-shaped (DESC = ASC without BOT); skewed right (DESC < ASC) or left dive (DESC > ASC) (Schreer et al., 2001). Among all species and groups, square dives are generally regarded as foraging dives, although Weddell seals may use V-shape dives for feeding (Fuiman et al., 2007). In contrast, left and right skewed dives generally have a different purpose and are usually performed during traveling and searching activities. However, among elephant seals skewed right dives may be linked with food processing (Crocker et al., 1997).

Individual dives often occur in clusters or bouts. Bouts as defined by Boyd and Croxall (1992) are: "a series of four or more dives not separated by a surface period exceeding a few minutes." The end of a bout is derived from the post-dive surface interval of the last dive, but can be difficult to determine. Luque and Guinet (2007b) suggested that employing a maximum likelihood estimation method delivers the most accurate means to determine when a bout has ended. Bout durations and locations can provide information on the spatial scale of prey patches (Mori, 2012), as the animal moves between successive patches (Hooker et al., 2002). Information about bouts can also be used to

make inferences about foraging preferences (e.g., prey type, Elliott et al., 2008), or foraging effort (Della Penna et al., 2015).

A trip comprises the entire time an animal spends at sea from the time it leaves land (or sea ice) to the time it returns; generally, many dive bouts are performed during this period. Depending on the species and breeding status, trips may range from several days to many weeks, and short and long trips may be alternated (e.g., Chaurand and Weimerskirch, 1994; Croxall and Davis, 1999; Luque et al., 2007a; Green et al., 2009a). At the Kerguelen and Crozet islands, rockhopper penguins performed daily trips during the brooding period, but as chicks grew older trip durations increased (Tremblay and Cherel, 2005). For some taxa, such as cetaceans or pack-ice seals, the concept of a trip is not necessarily as well defined but can be regarded as the time spent moving between regions to which they demonstrate some fidelity. For example, Antarctic seal-hunting (B type) killer whales (*Orcinus orca*) from the Antarctic Peninsula make periodic round trips to the South American coasts and back probably for physiological maintenance rather than for feeding or breeding purpose (Durban and Pitman, 2012).

Multiple factors including body condition (e.g., Miller et al., 2012; Richard et al., 2014; Gordine et al., 2015), age (Le Vaillant et al., 2012, 2013), sex (Beck et al., 2003; Baird et al., 2005), life history stage (Schulz and Bowen, 2004; Verrier et al., 2011), and body size (Irvine et al., 2000; Mori, 2002; Navarro et al., 2014) can all influence an animal's diving behavior. An example of how dive capabilities (depth and duration) vary across SO species is presented in Fig. 4. In general, larger seabirds and marine mammals dive longer and deeper than smaller species (Schreer et al., 2001). However, there are exceptions: for example, among petrels and albatrosses, smaller species tend to diver deeper in relation to their body mass than larger species (Prince et al., 1994; Navarro et al., 2014).

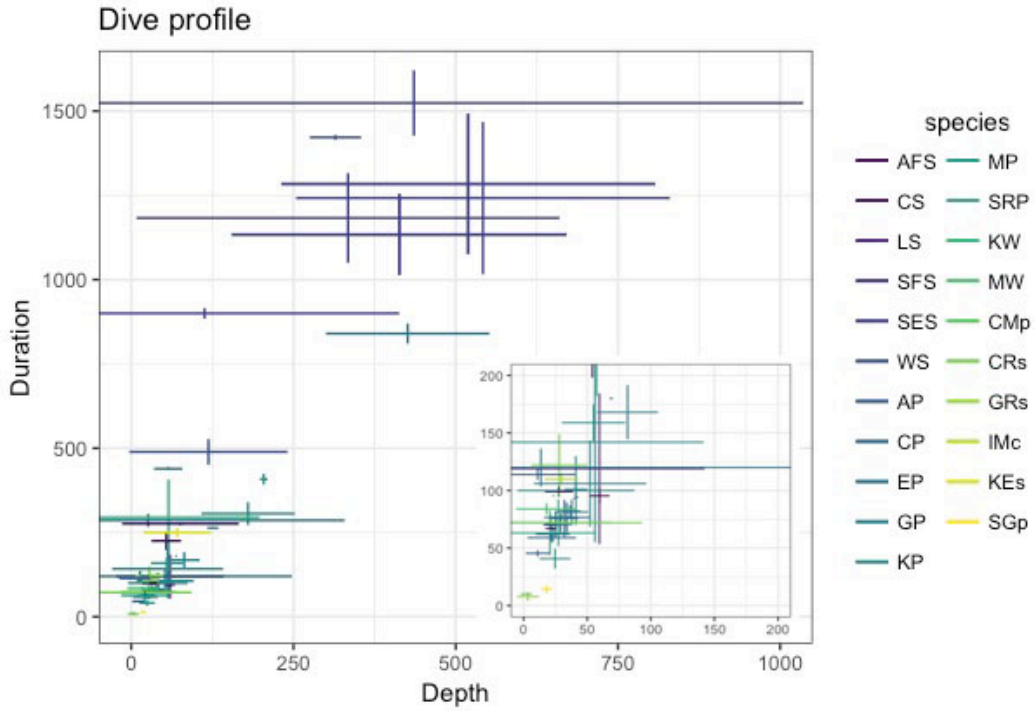


Figure 4. The relationship between dive duration (s) and depth (m) across the most commonly researched SO marine predators described in Table 2 (species abbreviations given in table). Values shown as mean ± SD. Inset panel provides a closer look at shorter (< 100 s) and shallower (< 100 m) dives. Data collected from studies undertaken from 2006–2016 (see Supplementary Material).

Foraging Inference

Southern Ocean predators use diverse habitats and feed on a wide variety of prey. By understanding the diving behavior of these species we are able to address a number of key ecological questions including: What is the distribution of their prey (spatial, vertical, among habitats, and seasonally)? What is their prey type (schooling/individual, benthic, or pelagic)? What are the foraging strategies adopted? What is the prey density (relative abundance) and quality? How much is eaten? Ultimately, integrating these observations can help explain the foraging activity and success for individual animals in time and space, as well as their functional response when facing environmental changes.

Prey Distribution and Type

Marine predators change their diving behavior in relation to the spatial

distribution of their prey (Thompson and Fedak, 2001). Basic information about where prey is located in the water column is obtained from simple dive depth metrics (maximum, mean, daily and seasonal variability, position relative to the ocean floor or other physical features such as seasonal mixed layer depth). Temporal patterns in these metrics can indicate whether prey species migrate vertically over a diurnal (e.g., Robison, 2003) or lunar cycle (e.g., Benoit-Bird et al., 2009). For example, gentoo penguins dive deeper during the day and shallower at night, probably to follow the vertical krill migration (Lee et al., 2015). Similarly, the large number of dives Antarctic fur seals undertake at night may be due to the shallower night time occurrence of a krill patch rather than the quality of the prey patch (Iwata et al., 2012). In general, pelagic foragers tend to dive deeper and longer during the day than at night (e.g., Weddell seals, female southern elephant seals, and Adélie and gentoo penguins; Schreer et al., 2001). Benthic foragers (e.g., blue-eyed shags (*Phalacrocorax atriceps*), male southern elephant seals) in general show little to no diel patterns in maximum depth and duration (Schreer et al., 2001). The depth of benthic dives is clearly determined by the bathymetry of the foraging area. At Signy Island, chinstrap and Adélie penguins hunt the same prey, but foraging chinstraps perform shallower dives than Adélies and feed inshore, while Adélies forage farther offshore (Takahashi et al., 2003). Interpretation of pelagic and benthic foraging behavior clearly requires a spatial context and may be hampered by poorly resolved bathymetry.

The size of prey items consumed by an animal is highly variable and not linearly related to the body size of the predator. For example, some marine predators ingest very large numbers of small prey items at a time (e.g., whales feeding on krill swarms; Kawamura, 1994) while others chase a single large prey item (e.g., Weddell seals eating large lipid-rich toothfish; Ainley and Siniff, 2009). The diet of marine mammals and seabirds has traditionally been studied through of the enumeration of stomach contents and/or scats, and is increasingly approached though methods, such as fatty-acid analyses (Pierce and Boyle, 1991), stable isotope signatures (Cherel et al., 2007; Cherel, 2008) and DNA-based methods (Deagle et al., 2007; McInnes et al., 2016, 2017). Such information may be powerfully integrated with tracking data to provide a

spatial context (e.g., Bailleul et al., 2010; Walters et al., 2014), and dive data may also be used to infer what SO species consume (Hocking et al., 2017).

Dive bout duration and inter-bout intervals can provide a relative indication of the size of prey patches and dispersion of prey types (Boyd and Croxall, 1996; Mori, 1998). Depending on the particular predator and prey combination, a bout may correspond to a single or multiple prey patches. Bout types or structures may be differentiated by combined parameters, such as timing (day/night/dusk), length (short/long), and depth (shallow/deep) (e.g., Boyd et al., 1994; Lea et al., 2002), and can help discriminate the prey item(s) that are being targeted by a predator (e.g., Elliott et al., 2008). Bout duration and timing between bouts can provide information on the temporal distribution of foraging patches (Luque et al., 2008). In a study of provisioning Adélie penguins, Watanuki et al. (2010) found longer dive bouts tended to occur toward the end of foraging trips, and were associated with higher meal mass. Combined information on dive depth distribution and dive bout characteristics (e.g., proportion of dives in a bout, number of dives per bout, bout type) can identify prey as being epipelagic (e.g., surface-swarming krill; Lee et al., 2015), or mesopelagic (e.g., myctophid fish and cephalopod species; Georges et al., 2000), and whether prey are more aggregated (high number of dives per bout) or dispersed (low number of dives per bout) (Lea et al., 2002).

Without ascribing bout structure, Hart et al. (2010) focused on the autocorrelation in raw TDR data (depth and time) as an indicator of the persistence or periodicity of dive behaviors in macaroni penguins. Evidence for foraging flexibility or prey switching may come from high variability and/or temporal (e.g., seasonal) changes in individual dive (Deagle et al., 2007) or bout (Harcourt et al., 2002) characteristics which can be difficult to detect. When animals are large enough, prey selection can be directly observed using miniature cameras mounted on a data logger, as has been done successfully on Antarctic fur seals (Hooker et al., 2002, 2015; Heaslip and Hooker, 2008). Cameras were also deployed on gentoo and Adélie penguins foraging on krill and fishes schooling underneath sea ice (Takahashi et al., 2008; Watanabe and Takahashi, 2013). Using cameras in combination with a number of sensors in Weddell seals, Madden et al. (2015) documented alternative foraging behaviors

(deep anaerobic and shallow aerobic dives) both exploiting the same prey type (Antarctic silverfish (*Pleuragramma antarcticum*)), and hypothesized an energy-saving strategy where the seals were exploiting shallow schools of silverfish. However, animal-borne videos typically represent short observation periods relative to other behavioral records, and efficient image storage and processing methods are currently an active area of research.

Foraging Strategies

Optimal foraging theory (OFT) (Stephens and Krebs, 1986) is a conceptual framework widely employed to examine the strategies animals use to acquire food. Under the OFT framework, animal movement and behaviors are expected to be as efficient as possible. Translated to air-breathing divers, OFT suggests these animals should minimize the costs associated with feeding underwater (e.g., dive transit time, oxygen consumption) and maximize the benefits using some fitness related criterion (e.g., time spent at foraging depths, net energy gain or energy efficiency, load size, prey capture rate) (Kramer, 1988; Houston and Carbone, 1992; Mori, 1998). The most commonly developed dive optimality models are "time allocation models" (Houston, 2011) that seek to optimize the foraging and surfacing time of animals in response to changing conditions, such as prey depth (Mori and Boyd, 2004) or prey encounter rate (Thompson and Fedak, 2001). In the latter case, Thompson and Fedak (2001) investigated the effects of a "giving up" rule to demonstrate cases where a net benefit was obtained by terminating dives that are likely to be unproductive. While this general held true for shallow divers, it was unclear for deep divers such as southern elephant seals. Moreover, in the controlled environment of captive experiments where the model was tested on gray seals (*Halichoerus grypus*), it was not clear if the effect held true in all situations (Sparling et al., 2007).

Time-depth recorders and other bio-logging tools such as accelerometers have allowed OFT models to be developed, and predictions tested, across a wide array of free-ranging marine predators. A non-exhaustive list of applications to SO species include Antarctic fur seals (Mori and Boyd, 2004), southern elephant seals (Gallon et al., 2013), Adélie penguins

(Watanabe et al., 2014), macaroni and gentoo penguins (Mori and Boyd, 2004), king penguins (*A. patagonicus*) (Hanuise et al., 2013), humpback (*Megaptera novaeangliae*) (Tyson et al., 2016) and fin (*Balaenoptera physalus*) whales (Acevedo-Gutiérrez et al., 2002; outside SO). The results of Acevedo-Gutiérrez et al. (2002), who compared observed TDR dive times to those predicted by an OFT model, suggested that the foraging strategies of fin whales are energetically expensive and limit the dive time of these large predators. More recently, Tyson et al. (2016) tested a suite of OFT models for humpback whales foraging at the western Antarctic Peninsula using high-resolution multi-sensor data loggers. They found that the agreement between observed and optimal behaviors varied widely depending on the physiological and behavioral values used to derive optimal predictions, and highlighted the need for an improved understanding of cetacean physiology.

In their seminal paper, Mori et al. (2005) used an optimality framework to derive prey indices from Weddell seal diving profiles, in conjunction with prey richness estimates from animal-borne camera data. The authors generally found positive correlations between these two indices (dive profiles and prey richness), but highlighted the importance of identifying the relationship between the diving behavior of predators and the type of prey they take (see above) in order to estimate prey abundance using diving profiles. Smaller numbers of larger prey are sufficient in terms of energy intake; for example, a single large high-quality items such as Antarctic toothfish (*Dissostichus mawsoni*) delivers possibly more energy per ingestion than smaller prey like Antarctic silverfish which may require several dives to obtain the same amount of biomass comparable to a single toothfish. However, there may be an increased energetic cost when digesting one large prey item whose temperature is much lower than that of the predator's core (see Prey consumption, below).

Dive profiles can also provide more general information on predation strategies, for example whether foraging animals approach their prey from above or below. Using a time-depth-speed logger, Ropert-Coudert et al. (2000) reported steep acceleration events where king penguins swam rapidly upwards mainly during the bottom and early ascent phases of dives. This appears to reflect an upward-looking attack strategy, whereby prey is detected and

approached from below. It is likely that multiple prey approach and capture techniques are employed by individuals, depending on factors, such as light, bioluminescence and seasonal progressions in prey type, and abundance and density. Antarctic marine predators seem to employ active-search hunting rather than ambush (sit-and-wait) strategies, although a passive-gliding approach from above the prey target has been recently documented in elephant seals (Jouma'a et al., 2017). Using time-depth data in conjunction with animal-borne video, Krause et al. (2015) reported novel observations on foraging leopard seals such as unique prey-specific hunting tactics when targeting Antarctic fur seal pups and fishes including stalking, flushing, and ambush behaviors.

Prey Density and Quality

Drawing mainly from the OFT framework, a large research effort has focused on developing indices from diving telemetry data of predators that can provide information on prey quality or density. For example, if animals reduce transit time in a patch, then changes in basic components of the dive, such as descent and ascent rates, might be indicative of patch quality, where rates increase when patch quality is high (Thompson and Fedak, 2001). Steep descent and ascent angles may assist to reduce transit time. In general, deeper dives are associated with steeper angles and higher transit rates, and may be the result of more predictably distributed prey at greater depths, as may be the case over shelf areas (Pütz et al., 2006) or at the base of the mixed layer in oceanic areas (Georges et al., 2000). There is some support for the optimality expectation using in situ measurements of patch quality (as determined from relative body lipid content, high quality areas being indicated from lipid gain): female southern elephant seals from Macquarie Island descended and ascended faster in high-quality patches than in low quality patches (Thums et al., 2013). However, this was not achieved by increasing speed or dive angle, but rather the relative body lipid content was an important predictor of dive behavior (e.g., Thums et al., 2013; Richard et al., 2014; Jouma'a et al., 2015).

Similarly, a straightforward interpretation under an optimality framework might expect maximized time spent at the bottom of a dive to

represent greater prey density and/or quality and enhanced foraging benefit for marine predators. Many indices have been derived to investigate bottom time relationships (Table 3) attempting to account for deeper dives in the water column that necessarily take more time, with less time subsequently to be spent at the bottom. These include dive residuals (Bestley et al., 2015), residual bottom time (Dragon et al., 2012), and residual "first bottom time" (Bailleul et al., 2008). The latter attempts to translate classical first passage time (Fauchald and Tveraa, 2003), widely used to analyse area-restricted search in horizontal movements, into the vertical dimension.

Table 3. Examples of derived dive parameters to investigate diving patterns, foraging behavior, and physiology of SO marine predators.

DERIVED PARAMETERS	QUESTION	EXPLANATION	EXAMPLES OF USAGE
Dive rate or dive frequency	Diving intensity	Number of dives per unit time (e.g., per hour of night or day; per bout; per trip).	Staniland (2008), Antarctic fur seals.
Vertical distance or vertical extent (VD or VE)	Diving intensity	Total vertical distance travelled (m or km) summed or averaged per unit time (per hour, bout, night, 24h etc.). For example: cumulative dive depth x 2 per night divided by night period (units of km h^{-1})	Pütz (2006), southern rockhopper penguins; Zimmer et al. (2008a; 2008b), emperor penguins.
Dive residual	Measure of relative forage effort	Residuals obtained from Linear Mixed Model (random slope and intercept per individual): dive duration ~ dive depth	Bestley et al. (2015) southern elephant, Weddell, Antarctic fur, and crabeater seals.
Residual bottom time (RBT)	Measure of relative forage effort	Residuals from multivariate linear regression: Bottom time ~ maximum dive depth + dive duration	Dragon et al. (2012) southern elephant seals.
Residual first bottom time (rFBT)	Measure of relative forage effort	Modification of the First-Passage Time (FPT) approach using the RBTs described above. The	Bailleul et al. (2008) southern

		variance of the RBTs is calculated within circles of increasing radius (r), as Var(log(t(*r*))), where t(r) is the sum of the absolute values of the RBTs. The spatial scale of most intensive search behavior determined via the maximum peak in variance. Once this scale was determined, the sum of the residuals (not absolute) is calculated within each circle to give rFBT values.	elephant seals.
Wiggles	Foraging behavior	Detected as anomalies in diving profiles: when an animal is spending some time at a particular depth, and travelling up and down while at this depth (zig-zags).	Hanuise et al. (2010) king penguins.
Bottom sinuosity	Foraging behavior	Calculated as the total distance swum in the bottom of the dive divided by the sum of the Euclidean distances from the depth at the beginning of the bottom phase to the maximum depth and from there to the depth at the end of the bottom phase: Bottom sinuosity $=\frac{Bottom\ Distance_{observed}}{Bottom\ Distance_{euclidean}}$	Dragon et al. (2012b) southern elephant seals
Hunting time (HT)	Foraging behavior	Iterative application of a broken stick algorithm to identify the optimum number of segments per dive, and allocation of dive segments as "hunting" or "transit" using a threshold value (0.9) of vertical sinuosity.	Heerah et al. (2014) southern elephant seals and Weddell seals.
Prey encounter events (PEE)	Inference about foraging attempts (prey encounter	Coefficients from a Generalized Linear Mixed Model applied to multiple dive parameters (dive duration, bottom duration, hunting-time,	Labrousse et al. (2015) southern elephant seals.

	but not necessarily capture success)	maximum depth, ascent speed, descent speed of subsequent dive, track sinuosity and horizontal speed) used to predict PEE.	
Proportion of observed dive time to the standard dive time (POS)	Diving behavior optimality	Proportion of observed dive time to the standard dive time, obtained by adopting a rate maximisation model.	Mori (2012) chinstrap penguins
Surface residual	Measure of dive cost	Linear Mixed Model fitted to minimum post-dive surface interval (SI) observed for each (binned) dive duration (random slope and intercept per individual). Residual then calculated as the difference between observed and predicted values: $\log(1+(SI_{obs} - SI_{pred})/SI_{pred})$	Bestley et al. (2015) southern elephant, Weddell, Antarctic fur, and crabeater seals.
Dive efficiency (DE)	Optimal diving	DE = bottom time/ (dive duration + post-dive surface interval)	Lee et al. (2015) gentoo penguins.
Dive:pause ratio	Dive cycle management and time allocation	The ratio of dive duration (time underwater) to time at the surface: $(t + \tau)/s$ where dive duration includes the time spent foraging (t) and the round trip travel time (τ) from the foraging area to the surface.	Houston (2011) seabirds and marine mammals.

Validation with external datasets has not clearly resolved whether longer bottom phases are indicative of higher or lower prey quality or density, and hence foraging success. For example, short-term measurements of head jerks in southern elephant seals using accelerometers suggested increased prey capture attempts with increased bottom durations (Gallon et al., 2013). However, in Antarctic fur seals, the relationship between head jerks and dive metrics — including bottom duration — varied markedly with temporal scale (i.e., dive to all-night scale) (Viviant et al., 2014). In a related study, Viviant et al. (2016)

545 showed Antarctic fur seals adjust their time in the dive bottom phase mainly
546 according to prey patch accessibility (depth) and their physiological constraints
547 (behavioral aerobic dive limit), rather than their prey encounters (mouth-
548 opening events). In king penguins, heart rate loggers showed increased heart
549 rates, and hence energetic costs, associated with shorter dive durations, shorter
550 bottom times, and longer surface durations (Halsey et al., 2007b). Similar
551 patterns in elephant and Weddell seals appear to represent high activity dives in
552 higher quality areas (Bestley et al., 2015). Furthermore, faster descent speeds,
553 shorter dive durations, and reduced bottom times in higher-quality habitat were
554 linked to body condition indices of elephant seals (Thums et al., 2013). Longer
555 dive and bottom durations occurred when patches were of relatively low
556 quality consistent with the predictions of the marginal value theorem (MVT,
557 Charnov, 1976). Qualitative support for the MVT has also been provided for
558 Adélie penguins, with opposing effects of patch-quality on duration at the dive-
559 (positive) and bout- scale (negative), respectively (Watanabe et al., 2014). The
560 way predators balance their dive budgets in terms of transit speed, bottom
561 duration, and surface intervals is likely a function of interacting factors, such as
562 the quality, size, vertical distribution and behavior of the prey, and the optimal
563 approach will be changeable with prey-switching as discussed above. Bottom
564 durations may also differ markedly between habitats — benthic, epipelagic or
565 midwater — with potentially longer bottom phases during benthic dives (e.g.,
566 gentoo penguins, see Kokubun et al., 2010).
567 The complexity of diving depth profiles has been widely investigated to
568 make inferences about feeding activities. In particular, the vertical undulations
569 or “wiggles” — changes in swim direction occurring at depth — are indicators
570 of prey encounter rates or prey capture attempts. These are commonly simply
571 counted (e.g., Bost et al., 2007), although a number of metrics have been
572 developed to evaluate vertical sinuosity of dives (e.g., Dragon et al., 2012) and
573 optimally allocate segments within dives as “hunting” or “transit” time on the
574 basis of sinuosity thresholds (e.g., Heerah et al., 2014, 2015). Validations of
575 such depth variations as feeding proxies have been based on various external
576 measurements including oesophageal temperature (Adélie and king penguins,
577 Bost et al., 2007), stomach temperature (southern elephant seals, Horsburgh et

al., 2008), and accelerometers to detect mouth opening events (king penguins, Hanuise et al., 2010; Antarctic fur seals, Viviant et al., 2014). These studies generally reported good correspondence between dive profile variations and other more direct measures of feeding activity. However, not all vertical undulations are prey encounters, not all encounters have an undulation, and only a proportion of prey encounters result in capture and ingestion. Consequently, in free-living animals it remains difficult to validate the actual success of prey encounters or capture attempts as unsuccessful attempts may still result in ingestion of cold water. Thus, the above mentioned variables ought to be considered mainly as indicators of forage effort rather than forage success.

Prey Consumption

A key question with regard to dynamics of ecosystems is how much food is eaten by marine predators. To obtain actual information on foraging success requires ancillary data to simple dive traces. Short-term direct observations of feeding activity can be obtained with tag-mounted cameras (Mori et al., 2005; Watanabe and Takahashi, 2013). As mentioned briefly above, methods like stomach or esophageal temperature sensors for seabirds (Bost et al., 2007, 2015; Hanuise et al., 2010) and seals (Austin et al., 2006; Horsburgh et al., 2008; Kuhn et al., 2009) can provide information on prey capture attempts; since birds and mammals in the SO have a higher core body temperature than their prey, their stomach temperature drops during ingestion (Wilson et al., 1992). However, unsuccessful attempts may still result in ingestion of cold water and need to be clearly distinguished from successful feeding events. Head or jaw mounted accelerometers and speed sensors have also been used to provide feeding proxies in several seal species (Weddell, Naito et al., 2010; Antarctic fur, Iwata et al., 2012; southern elephant, Gallon et al., 2013; Guinet et al., 2014; Richard et al., 2014; Vacquié-Garcia et al., 2015), and penguins (king, Hanuise et al., 2010; chinstrap and gentoo, Kokubun et al., 2011).

Typically, feeding telemetry delivers smaller sample sizes; the data series are more complex, difficult to obtain and short-term relative to TDR

time-series. Also, issues still remain to be solved on how to keep the sensors in place. Therefore, efforts have been made to develop predictive models from the feeding indices that may be applied across longer dive time-series to estimate prey items from time-depth data alone (e.g., Simeone and Wilson, 2003; Horsburgh et al., 2008; Viviant et al., 2010; Labrousse et al., 2015). For example, Labrousse et al. (2015) developed predictive models for Prey Encounter Events using high-resolution accelerometer data and used these to predict these events for low-resolution dive profiles available over longer periods. Informative variables included ascent speed, maximum depth, bottom time, and horizontal speed (pelagic strategy), compared with just ascent speed and dive duration (demersal strategy).

These modeling approaches may greatly increase the utility of both data types and provide some indicator of feeding activity over whole migration trips. However, information on actual feeding success is available in very few cases for free-living animals. One high-profile example is how buoyancy changes associated with relative lipid content measured from drift dive data in elephant seals (northern, Crocker et al., 1997; Robinson et al., 2010; and southern, Biuw et al., 2003; Bailleul et al., 2007; Thums et al., 2008, 2013; Gordine et al., 2015), with changes in passive vertical drift rates, provide an integrated in situ measure of foraging success. This approach has given insight into the location and characteristics of successful Southern Ocean foraging areas (Biuw et al., 2007; Hindell et al., 2016), and was incorporated into population-level models integrating the physiological and movement ecology of predators (Schick et al., 2013; New et al., 2014). Efforts have been made to validate relationships between descent rates and drift rates (Richard et al., 2014), which represent a promising extension of inference to basic dive profiles and potentially broader application across other species. A recent study on Antarctic fur seals (Jeanniard-du-Dot et al., 2017) incorporated information of prey capture attempts into an energetics framework to estimate foraging efficiency and the consequences for reproductive success (pup growth). Such applications, linking individual foraging behavior with demographic consequences (see also Hiruki-Raring et al., 2012), are important avenues for future biotelemetry research in the Southern Ocean.

Overall, relatively simple dive data streams continue to provide increasingly powerful insights into marine predator foraging. However, when used alone these telemetry data remain largely limited to providing information on effort. Dive metrics cannot confirm success; indeed dive metrics (e.g., residuals: positive and negative from a fitted relationship) may be obtained from an animal that in fact fails to forage at all. Combined usage of TDRs with other devices that provide more direct observations (e.g., accelerometers, miniature cameras, speed turbines, internal sensors), even on a subset of individuals, greatly assists in maximizing inference. In addition, the caveats of inferring from dive data may be alleviated by combining data from different sources, such as isotopes and DNA methods (diet), mass or lipid gain (success), reproductive outputs (energetic costs) thereby achieving a broader perspective on the foraging of Southern Ocean marine predators.

Intrinsic Determinants of Diving — Physiological Inference

The foraging strategies adopted by marine predators are not only dictated by prey abundance and distribution but also by intrinsic factors, such as oxygen stores, metabolism, body size, and age (Kooyman and Ponganis, 1998; Costa, 2007; Ponganis et al., 2009; Ponganis, 2011; Castellini, 2012; Elliott, 2016). Relatively few data have been collected on the at-sea metabolism of marine birds and mammals given the practical difficulties of collecting respiration and activity data in the field. Consequently, much of what is known has been inferred from simple dive data. Information on dive duration and post-dive surface intervals provide valuable insights into diving metabolic rate, and on how animals balance time underwater using oxygen stores with time on the surface replenishing them, i.e., dive cycle management. Determining how these intrinsic factors scale with size, sex or age of the animal are key questions that remain largely unanswered. This section discusses how the use of classic dive data information provides valuable insights into dive energetics and the physiological adaptations of SO marine animals, drawing also upon examples from temperate species in a few cases.

Physiological Determinants and Constraints

Castellini (2012) and Ponganis and Kooyman (2000) reviewed the physiological adaptations among marine mammals and polar seabirds, respectively. We provide a summary here as a base for the following discussion. Many animals dive, but deep divers face a number of challenges, such as the increase in pressure with the resulting mechanical compression of tissue and gas-filled spaces, and the lack of ad libitum access to oxygen (Kooyman and Ponganis, 1998; Costa, 2007; Ponganis, 2011). The former is to some extent dealt with using morphological adaptations, such as flexible rib cages (e.g., Cozzi et al., 2010) and collapsible lungs (e.g., Falke et al., 1985; McDonald and Ponganis, 2012), while the lack of continuous access to oxygen requires a complex suite of physiological adaptations.

A number of adaptations evolved convergently among marine mammals and seabirds to enable deep diving, but there are also important differences, for example with regard to the distribution of oxygen stores in the body and the reliance on anaerobic metabolism (see below). These animals depend on adaptions that increase intrinsic oxygen stores. Body size is one factor which influences both oxygen storage and metabolic rate or oxygen use (e.g., Noren and Williams, 2000). Furthermore, to expand their breath holding capacity, deep divers have large volumes of blood. For example, in Weddell seals about 14% of their body weight is due to blood; this is 63 l for a 450 kg seal, or 140 ml kg^{-1} (Zapol, 1996). In comparison, in human blood makes up only about 7% of body weight (Zapol, 1996). In penguins, the blood volume is less than in seals; emperor penguins comprise about 100 ml blood kg^{-1} body weight (Ponganis et al., 1997a), and for Adélie penguins the value is about 93 ml kg^{-1} (Lenfant et al., 1969).

Oxygen stores are also increased through increased concentrations of the oxygen-carrying proteins hemoglobin (Hb, in blood) and myoglobin (Mb, in muscle). The size of the total oxygen store and the proportions in which it is compartmentalized differ among species. Weddell seals have 26 g 100 ml^{-1} Hb and 5.4 g 100 g^{-1} Mb (Ponganis et al., 1993). In comparison, Adélie penguins 16 g 100 ml^{-1} Hb (Lenfant et al., 1969) and 3.0 g 100 g^{-1} Mb (Weber et al., 1974). Although hemoglobin concentrations in emperor penguins are similar to those of Adélie penguins (18 g 100 ml^{-1}), their Mb concentration is twice as

high (6.4 g 100 g^{-1}) (Ponganis et al., 1997b). The three major compartments are the respiratory and vascular systems and muscles. Generally, marine mammals carry most of their oxygen stores in the blood and muscle tissue, but again there are species specific differences. The percentage distribution of oxygen among Weddell seals (body mass ~ 400 kg) is 66% in blood, 29% in muscle and only 5% is available through the respiratory system. For the smaller Californian sea lions (*Zalophus californianus*) (~35 kg) the values are 45, 34, and 21% for blood, muscle, and respiratory system, respectively (Kooyman and Ponganis, 1998). In comparison, Adélie penguins (~5 kg) store most of their oxygen in the respiratory system (45%), and only 29% in blood and 26% in muscle tissue. The larger emperor penguin (~25 kg) has values more similar to the sea lion with 34 and 47% oxygen in blood and muscle, respectively, and only 19% in the respiratory system (Kooyman and Ponganis, 1998).

The regulation of oxygen use during dives underlies complex physiological processes and depends on a variety of factors, such as dive depth and duration, level of muscle activity (Hindle et al., 2010), and body temperature (Kooyman and Ponganis, 1998). Air-breathing diving vertebrates adjust oxygen consumption through a process known as the "dive response," a process characterized by a drop in heart rates, decreased blood perfusion of organs (except the brain) and a drop in body temperature (Butler and Woakes, 2001); the result is an overall reduction of oxygen consumption. The dive response essentially manages how long an animal can stay submerged, how much oxygen it has available, and the rate at which this oxygen is consumed. Since in deep diving endotherms a great concentration of oxygen is stored in the muscles (see above), the reduction of the blood flow causes a hypoxia facilitating the oxygen dissociation from myoglobin. This mechanism enhances aerobic metabolism in exercising muscles, despite the reduced blood flow during diving (Davis, 2014). If oxygen stores become depleted during a dive, animals can switch to anaerobic metabolism. However, anaerobic production of energy (glycolysis) is less efficient than aerobic pathways as less adenosine triphosphate (ATP, high-energy molecule) is produced and the muscle tissues accumulate lactic acid. Excessive amounts of lactic acid result in metabolic

741 acidosis and consequently severe depression of the heart and the central
742 nervous system (Wildenthal et al., 1968; Siesj, 1988). To remove lactic acid the
743 animal must pay an oxygen debt. This is commonly achieved by spending
744 extended periods at the surface to re-oxygenate tissues (Kooyman et al., 1980)
745 which in turn can reduce foraging time and limit opportunities (Butler, 2006).
746 However, it can be advantageous for individuals to incur such a metabolic debt.
747 The change from aerobic to anaerobic metabolism is determined by the
748 Aerobic Dive Limit (ADL) or diving lactate threshold (DLT), i.e., the time an
749 animal can remain submerged after which there is an increase in the levels of
750 lactate exceed those present when an animal is resting (Butler, 2006). This
751 value has only been measured in freely diving Weddell seals and emperor
752 penguins, for all other species we referred to cADL (calculated aerobic dive
753 limit) i.e. obtained by dividing usable oxygen stores with an estimation of the
754 rate of oxygen consumption during diving (Butler, 2004). Post-dive partial
755 pressures of oxygen in venous blood (PO_2) were measured in free-living
756 Weddell seals and bottlenose dolphins (*Tursiops truncatus*) and ranged from
757 15–20 mmHg (Ridgway et al., 1969; Ponganis et al., 1993) which is less than
758 the values obtained from terrestrial mammals after intense exercise (27–34
759 mmHg; e.g., Taylor et al., 1987). Among free-diving emperor penguins, PO_2
760 levels were < 20 mmHg in 29% of dives and even dropped to 1–6 mmHg at
761 times (Ponganis et al., 2007). Blood oxygen stores were also nearly completely
762 exhausted in northern elephant seals (*M. angustirostris*) in whom venous PO_2
763 was reduced to 2–10 mmHg after dives that lasted > 10 min (Meir et al., 2009).
764 To withstand such extreme levels of hypoxemia various adaptations such as an
765 enlarged density of capillaries are necessary, but these are not yet fully
766 understood (Ponganis et al., 2007). Some species constantly exceed their
767 estimated cADL. In a review of 6 marine predators at South Georgia, all
768 species except Antarctic fur seals (≤ 5%), frequently surpassed their estimated
769 cADL (Boyd and Croxall, 1996). Benthic feeding otariids (e.g., Australian sea
770 lions (*Nephoca cinerea*)) tended to exceed their cADL more often than pelagic
771 foraging species (e.g., Antarctic fur seals, Costa et al., 2004). Female southern
772 elephant seals went beyond their calculated cADL in 40% of dives, in
773 comparison with only 1% in males (Hindell et al., 1992). Emperor (20% of

774 dives, Butler, 2004), king (20% of dives, Kooyman et al., 1992) and gentoo
775 penguins (40–50% of dives, Williams et al., 1992) also regularly exceeded
776 their cADL, as did Macquarie shags (*P. purpurascens*) (e.g., 19% of male
777 dives, Kato et al., 2000) and blue-eyed shags (36% of dives; Boyd and Croxall,
778 1996). The pattern of few anaerobic dives observed among fur seals might be
779 consistent with the maintenance of a high metabolic rate while diving, whereas
780 the bimodality observed in other species suggests fundamentally different
781 strategies may be used to regulate oxygen consumption between short and long
782 dives (Boyd and Croxall, 1996). More recent work has focused on anatomical
783 adaptions and dive capacity (Meir et al., 2008; Ponganis et al. 2009, 2010b;
784 Wright et al., 2014). However, little has been done to empirically determine the
785 ADL for the remaining Southern Ocean species.
786 Longer post-dive surface intervals do not always indicate an oxygen
787 debt. Even after aerobic dives, the time required to re-oxygenate tissues may be
788 longer after extended dives due to the mechanical restrictions of respiration and
789 airway structure. The "dive:pause ratio" measures the ratio of dive duration to
790 time at the surface. Larger ratios indicate that post-dive surface intervals are
791 long relative to the dive, reflecting the relatively greater time required to
792 replenish oxygen stores. Cormorants have to spend more time at the surface
793 after longer dives, resulting in a dive:pause ratio equal to 1 (Lea et al., 1996).
794 Gentoo penguins have a dive:pause ratio for deep dives of 1.2–2.2 and of 0.3–
795 0.4 for shallow dives (Williams et al., 1992).
796 Elephant seals did not have appreciably longer surface intervals even
797 for the longest dives; irrespective of the preceding dive, surface intervals last
798 typically only 2–3 min (Hindell et al., 1992). This was considerably shorter
799 than the 50 min surface intervals made by Weddell seals known to have
800 exceeded their ADL (Kooyman et al., 1980). This provides strong evidence
801 that many, if not all, of the female elephant seal dives that surpassed their
802 cADL were in fact aerobic. Thus, the diving metabolic rate of elephant seals
803 may be less than the allometrically derived estimates of metabolic rate used in
804 the calculation of the cADL. Reduced metabolic rate during diving is a well-
805 known consequence of the dive reflex, and the simple metric of dive depth and
806 PDSI can be used to infer the magnitude of this reduction, at least in aerobic

dives. The estimate of the metabolic rate in emperor penguins, which was relatively low when foraging, could be used to calculate with a better approximation the ADL for this species than the O_2 store data (Nagy et al., 2001). This has implications for energetic models commonly used in ecosystem and fisheries models, as deep diving predators may use less energy than expected from allometric estimations.

Basic diving data (dive and surface duration), along with estimates of total body oxygen stores and metabolic rate, can provide the basis for quantifying dive limits of an individual. These may address fundamental bio-physiology questions for species-specific studies and also be relevant for those focusing on broader ecological questions and ecosystem energy flow studies (Williams et al., 2000). Data loggers can also provide insights into the mechanisms that underpin the dive response. Simple time depth data are insufficient to demonstrate some types of behaviors, but augmentation with an additional sensor (such as velocity from accelerometers) expands the capacity for inference. For example, accelerometers in combination with TDRs revealed that southern elephant and Weddell seals use strategies, such as passive sinking and burst-glide swimming, to reduce their oxygen consumption during diving (Hindell et al., 2000; Williams et al., 2000). Kerguelen shags (*P. verrucosus*) adapt their stroking activity depending on the body buoyancy variation (Cook et al., 2010). A similar mechanism is used by cetaceans (whales, Acevedo-Gutiérrez et al., 2002; dolphins, Williams et al., 2017).

Behavioral Mechanisms as Proxies for Physiological Mechanisms

An animal's buoyancy plays an important role in diving: increased buoyancy provides challenges for animals during descent and is energetically expensive, given that animals require additional work, for example, to maintain their position in the water column (Webb et al., 1998). However, buoyancy varies at a range of temporal scales, firstly within an individual annual cycle (e.g., gestation in elephant seals, Crocker et al., 1997) and also throughout its life as an animal grows and develops different traits (e.g., becoming a dominant male for elephant seals, Galimberti et al., 2007). Buoyancy can, however, also be used as a measure of an animal's body condition because

lipids are less dense than water making fatter animals more buoyant than leaner conspecifics (Miller et al., 2012). Some species perform “drift” dives where they stop swimming and are stationary in the water column. The rate and direction of drift has been related to the animal's total lipid content at that time (Biuw et al., 2003). This means that spatio-temporal dynamics of lipid gain (and loss) can be measured, identifying regions of poor and good foraging. An analysis of elephant seal drift data from many of the major breeding sites indicated that some regions such as the Antarctic Circumpolar Current frontal systems in the Atlantic sector may be better quality habitat than other sectors of the SO. For example, seals from the declining Macquarie Island population had to travel for over a month to reach prime habitats (Biuw et al., 2007). Finer-scale measurements of burst and glide behavior have also been used to measure changes in buoyancy, opening the use of this approach to a wide range of species (Williams et al., 2000; Oliver et al., 2013; Jouma'a et al., 2015).

Tri-axial accelerometers were employed to measure overall dynamic body acceleration (ODBA) which is considered a proxy for energy expended by animals during different diving phases (Wilson et al., 2006; Gleiss et al., 2011). Acceleration is used to measure movement, and since muscle motion involves oxygen consumption, acceleration could be used as a proxy for O_2 consumption itself. When foraging, Magellanic penguins descended faster than they ascended, which means their descent phase was energetically much costlier than their return to the surface (Wilson et al., 2010). Previous studies conducted on cormorants and pinnipeds have shown how ODBA offers a better estimation of energy expenditure than doubly labeled water method (Wilson et al., 2006; Fahlman et al., 2008) or flipper stroke evaluation (Jeanniard-du-Dot et al., 2016). However, ODBA is best used for quantifying energy during individual diving phases only rather than the full foraging trip (Wilson et al., 2010) because it might be affected by animal mass, number of strokes, and the relationship between heart rate and O_2 consumption (e.g., change of heart rate during dive response).

Other sensors can measure an animal's physiology more directly. Heart rate can be measured with externally (Hindell and Lea, 1998; Elmegaard et al., 2016) or subcutaneously (Meir et al., 2008; Wright et al., 2014) mounted

electrodes or acoustic transmitters (Green et al., 2005). Heart rate loggers can demonstrate the degree of bradycardia during diving and anticipatory tachycardia before PSDI (Wright et al., 2014). In elephant seals, heart rates can drop to lower than 10 beats min^{-1}, even during active dives (Andrews et al., 1997). The degree of bradycardia is negatively related to dive duration, so that longer dives have lower heart rates once they pass a certain threshold duration. If the relationship between heart rate and metabolic rate is known, heart rate can be used to estimate metabolic rate during an animal's time at sea (see Green, 2011 for a full review). This approach has been used successfully for several species of penguin (Froget et al., 2002; Green et al., 2005, 2009b; Meir et al., 2008). It requires an initial calibration of the heart rate/metabolic rate relationship, usually in a laboratory, followed by deployment of the heart rate loggers that record heart rate continuously. Based on this approach, the field metabolic rate of macaroni penguins has been estimated to be 9.03 ± 0.39 W kg^{-1}, three times the estimated Basal Metabolic Rate (Green et al., 2002). The utility of using heart rate to measure metabolic rate is hampered by technical issues such as device attachment, as well as the need for the relationship to be calibrated in the lab for each individual (Butler et al., 2004).

In summary, even simple dive data can provide valuable insights into how diving animals manage their oxygen stores and the implications that this has for diving metabolic rate. Nonetheless, more complex data streams are required to address these questions in a fully quantitative way. Additional sensors, such as accelerometers and heart rate recorders, can quantify energy expenditure. However, to obtain accurate estimates laboratory based calibrations are likely to be needed (Green et al., 2007), and the logistic difficulties of doing this in the Antarctic may explain why this has rarely been done on Southern Ocean species. Understanding the underlying mechanisms that control metabolism requires even more specialized equipment, for example to enable serial blood samples to measure oxygen levels (McDonald and Ponganis, 2013). For this work, the isolated hole experimental paradigm is something that is well suited to Antarctic field studies, at least for some species (Ponganis et al., 2010a, 2011), and it is to be hoped that more of this work will be conducted in the future.

Perspectives and Emergent Areas

The aim of this review was to examine the foraging behavior and physiology of marine mammals and seabirds of the SO using data loggers as the main method for collecting the information. The last decade has seen substantial progress in this endeavor, and we now have a solid understanding of these factors for many SO birds and mammals. However, as certain questions are answered, others emerge and a number of key areas are a focus for further work; in this final section we highlight some of these.

Adopting a question-based approach, as we have done in this review, helps to provide a framework so there is a logical flow for how dive analyses may be carried out, depending on the biological or ecological question that is driving the research. Obviously, a massive suite of diving variables is available to be utilized in such analyses, and there is a proliferation of approaches used to infer foraging behavior and diving physiology. Advancements in analytical and statistical approaches, together with generally increasing sample sizes, are providing improved tools for learning more about diving ecology. An excellent example is the now readily accessible software for implementing mixed-effect models (e.g., Wood and Scheipl, 2017; Pinheiro et al., 2018). These enable inferences to be made at the individual level (via the random effects), as well as at the population level (via the fixed effects) while taking account of individual variability. Such techniques provide an appropriate analytical framework for researchers to deal with large, serially (spatially and temporally) correlated, and individual-based datasets, and are increasingly being adopted. Advancements in computationally efficient approaches for fitting models with discrete latent states to time series data, which have been widely used in animal movement modeling (Langrock et al., 2012; Michelot et al., 2016), may similarly promise a step-function in improving capabilities for dive analyses in the near future (e.g., Quick et al., 2017). Finally, hierarchical approaches, enabling information from multiple data sources to be integrated, are also available (Clark, 2007) and present important opportunities particularly for population-level analyses which we return to at the close of this section.

An important research area this review has considered only incidentally is the association of animal diving with the physical environment. This is largely

beyond our scope since the vast majority of telemetry studies investigating how the environment influences the foraging and physiology of Southern Ocean marine predators (i.e., bottom-up processes) do so by integrating spatially-explicit movement (location) data with external habitat information (e.g., from satellite remote sensing, and/or oceanographic models). However, significant advances have been made over the last decade through the *in situ* collection of environmental data by animal-borne sensors, which has opened our eyes to the subsurface environment in a way that is not possible from remotely-sensed data. A prime example is the improved knowledge of how elephant seals use specific water masses and oceanographic features obtained from high-quality temperature-salinity profiles collected onboard tags (e.g., Biuw et al., 2007; Labrousse et al., 2015; Hindell et al., 2016). Other novel approaches include the usage of onboard light-levels (Guinet et al., 2014) to infer bio-optical properties of the water column, including phytoplankton concentrations (Jaud et al., 2012; O'Toole et al., 2014), as well as direct fluorometry measurements (Guinet et al., 2013) to evaluate productivity influences on animal foraging. These clearly demonstrate the benefits gained from collecting environmental information onboard the same tag that is collecting the behavioral (dive) information. The coupling of oceanographic studies with ecological studies is an opportunity that has not reached its full potential yet, but this growing area likely warrants a review in its own right.

Our improved understanding of the at-sea vertical movements, foraging strategies and prey distributions now needs to be placed into a larger population and community context. This has three components. The first upscaling is to combine multiple species-specific studies to obtain community level assessments of diving behavior. This approach is increasingly being adopted in tracking work in the SO (Friedlaender et al., 2011; Thiebot et al., 2012; Raymond et al., 2015; Reisinger et al., 2018) and is providing powerful insights into regions that are of particular ecological significance. However, this only applies to the horizontal dimension (latitude and longitude), and dive studies will enable this approach to move into a third dimension, namely depth (e.g., Hindell et al., 2011). An integrated understanding of how diving animals use the water column will enable us to identify key features, such as the deep scattering layer

(Naito et al., 2013), thermoclines (Bost et al., 2015) and specific water masses (Biuw et al., 2007) that are important to the community of diving predators. This can be matched to highly resolved modern Regional Ocean Models (e.g., Malpress et al., 2017) to estimate how access to prey and foraging efficiencies may change into the future.

Upscaling can also be in a temporal sense. Long time series of diving data sets enable us to address questions of environmental determinants of foraging success and prey distribution (see Trathan et al., 1996; Hindell et al., 2017). Data-logging has the potential to play a key role in ecological monitoring (IMOS reference, Hussey et al., 2015), but this requires long-term funding, which in the past has been difficult to secure for tagging studies.

Better linkage of diving and location data will also lead to better understanding of habitat usage of SO bird and mammals. Describing and modeling of key habitats has been a focus of research for a long time but emerging statistical methods are now able to integrate diving behavior into movement models. For example, Bestley et al. (2015) incorporated several diving indices (dive residual, surface residual) into a state-space movement model to study at-sea foraging behavior. There was a general tendency for the probability of switching into "resident" movement state to be positively associated with shorter dive durations (for a given depth) and longer post-dive surface intervals (for a given dive duration), potentially indicating high energy diving. A growing body of literature demonstrates that simplistic interpretations of optimal foraging theory, based only on horizontal movements, do not directly translate into the vertical dimension in dynamic marine environments. Analyses that incorporate dive data can test more sophisticated models of foraging behavior. Further efforts to integrate multiple data streams (e.g., movement, haulout, diving activity) and thereby represent more realistic movement behaviors (such as at-sea resting) can also lead to improve at-sea activity budgets (Russell et al., 2015; Bestley et al., 2016).

Currently bio-logging studies remain somewhat limited in their scope given that most still focus largely on observations of individual animals that are then extrapolated across the population. This is mainly because instruments are expensive and consequently sample sizes are small. But with increasing

availability of inexpensive GPS loggers, light sensors, and accelerometers it is increasingly possible to achieve large samples. A related question is how many individuals need to be tagged to obtain a population level measure while still minimizing the number of animals that are equipped. Several studies of habitat use have approached this by making cumulative area curves (sequentially increasing the number of animals and calculating the total area used) (Hindell et al., 2003; Arthur et al., 2017). Our new insights into foraging at sea also need to be linked to demography and population level consequences. For many SO species, broad-scale relationships between demographic performance parameters, such as breeding success and recruitment in relation to climate variables (e.g., ice extent and ocean temperature), are well established for some species — Adélie penguins and ice at the western Antarctic Peninsula (Smith et al., 2003), and elephant seals and the Southern Ocean oscillation index (Le Boeuf and Crocker, 2005). But the proximate drivers of these relationships are not clear. Tagging studies have the potential to bridge this gap. For example, the diving behavior of female Antarctic fur seals is linked to prey availability, and forage location; diving activity, diet, and foraging efficiency all change significantly between years as ocean conditions vary (Lea and Dubroca, 2003; Lea et al., 2006). In warmer years, mothers dive deeper and make longer foraging trips. This reduces both maternal and pup body condition, and suppresses pup growth rates (Lea et al., 2006). Increasingly sophisticated approaches are enabling diving behavior to be linked to energetics (Jeanniard-du-Dot et al., 2017) and predator-prey (Hiruki-Raring et al., 2012) frameworks to estimate reproductive consequences at the population level. These expand important research avenues as biotelemetry in the Southern Ocean enters its mature phase. Finally, linking at-sea behavior to demography and population level consequences is now much more feasible, and will provide an advance on traditional individual-based studies, and provide an overarching view of how behavior is linked to population growth and persistence.

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Supplementary material

Materials and methods

Since 1950 nearly 3000 studies investigating diving and foraging behavior of predators in the SO have been carried out. However, the majority of this work was carried out in the decade 2006–2016. Recent advances in telemetry have facilitated this investigation greatly. In our study, we conducted a qualitative literature analysis to gain insights to assess the diving behavior of SO predators based on data obtained through a variety of data loggers and sensors. A systematic literature review was conducted of the last 10 years of published work on the diving telemetry of marine mammals and seabirds of the SO. Online databases such as Google Scholar, Medline, Web of Science, were searched for peer-reviewed literature containing the words: dive data, tag, TDR, Southern Ocean, Antarctic, marine mammals, penguins, seabirds, seals, cetaceans, species name. Publications were only included in the analysis if written in English and published from 2006 to 2016. Furthermore, we only considered studies that employed data loggers designed to measure the underwater behavior within the SO region and on SO species (pinnipeds, cetaceans or seabirds). No fish or turtles were considered in this study. These criteria were chosen to limit the amount of literature to analyze.

For the purpose of the analysis we created a database using the Mendeley Reference Manager (www.mendeley.com). We chose this software over others because of the possibility to search words or full-text in all whole documents added to the library. First we imported all publications that fulfilled out criteria (n = 218) into the database. From each article we collected the following metadata: author and year, species studied, subject (foraging, physiology, energetic, other), location of data logger deployment, aim of the

study, type of data logger used, analysis software used, plots shown and diving variables collected. We entered all metadata into an excel spreadsheet (Microsoft Excel 2010) and identified and synthesised the most commonly used basic dive parameters (dive duration and depth, see Table 2) and derived parameters (see Table 3). Note that not all publications reported all possible dive variables. Based on the publications that reported mean dive duration and depth, we used R software (Ihaka and Gentleman, 1996) to carry out a comparative analysis of the relationship between these two variables for all species (see Fig. 4). Publications were grouped according to the fundamental question being addressed: characterization of the diving behavior as the vertical component of animal movement (30%), foraging as diving activity linked with food research and acquisition (56%), energetics (14%). The latter referred to allocation of energy for maintenance functions, metabolic work, growth, reproduction, and locomotion. From this we examined which variables and methods were used to answer those questions.

Library access

A public access to the review library is available at www.mendeley.com, Mendeley group name: “Supplementary Material: View from below” please email the corresponding author for further details.

Chapter 3

Diving into the Southern Ocean: Investigating dive patterns and body mass scaling within and across multiple marine predators

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Abstract

The diving behavior of marine predators is influenced by their physiology, foraging behavior and the environment. Body mass is generally assumed to be related to diving ability: large body mass confers various benefits such as the ability to dive deeper and for longer. Much of what is known about the diving ability of free-ranging marine mammals and seabirds has been inferred from biotelemetry loggers and earlier meta-analyses have typically summarized diving parameters to a single value per species. Here to examine the effect of body mass on dive behavior, we present comparative analyses from six time-depth recorder datasets for three penguin species and three seal species studied in the southern Indian Ocean. Thus, our dataset encompasses animals of different species, sizes and sex as well as substantial intra-specific size variation which allows us to quantify the effects of size between species, but also within species, and to better understand the relationship drivers.

Our results show that the diving ability of seabirds and marine mammals scales positively with mass between species for dive duration and dive depth. However, this general rule did not hold true within species and for post-dive intervals, suggesting that most of our studied species perform generally aerobic dives given the limits imposed by the chemical processes whereby oxygen and CO_2 are exchanged.

Moreover, our analysis of interdependencies of diving parameters demonstrated both between- and within-species effects, meaning that independently from their mass, individuals may be able to adjust dive behavior to respond to the environmental conditions they experience, but their range of responses is narrower at the within-species level.

Introduction

Making their living within a complex, three-dimensional environment, air-breathing marine predators balance two competing needs: acquiring food resources at depth and oxygen at the surface. Hence, diving seabirds and mammals are well adapted to carefully regulate their dive cycle, maximizing the benefits of time spent underwater (using oxygen stores) and minimizing its cost (Mori, 1998; Mori, 1999). Studying their underwater behavior requires special instruments; among the simplest are time-depth-recorders. From these, fundamental information on dive depth, duration and post-dive interval may be used to investigate diving capacity, and how different species face and solve the constraints, and use opportunities linked to the separation of their essential resources.

One of the principal determinants of diving ability is body mass (Piatt and Nettleship, 1985; Watanuki et al., 1996; Butler and Jones, 1997), particularly for endotherms whose physiological adaptations are tightly linked to respiration and metabolism. Mass directly influences both the ability to store oxygen which in general scales isometrically with mass (Lasiewski and Calder, 1971), and oxygen usage which scales allometrically with an exponent of 0.67 or 0.75 (Butler and Jones, 1982; Noren and Williams, 2000; White and Seymour, 2003). Thus, smaller animals require more energy, and consume more oxygen, to reach the same absolute depth as larger ones (Kooyman, 1989). From a physiological perspective, larger animals have the capacity to dive for longer than smaller ones (the oxygen store/usage hypothesis). However, there are variations to this generality as some species exhibit physiological adaptations specialized for diving, for example, to enhance oxygen storage (e.g., via total blood volume, increased hemoglobin and myoglobin, or differential allocation of oxygen in the blood, muscle and respiratory system), and to reduce oxygen usage (e.g., via reduced diving metabolic rates, tolerance to anaerobic metabolism, energetically efficient movements). Hence, extensive allometric comparative analyses (Boyd and Croxall, 1996; Schreer and Kovacs, 1997; Halsey et al., 2006a, 2006b; Isaac and Carbone, 2010; Gillooly et al., 2016; Hayward et al., 2016) examining the extent to which size is preserved as a fundamental determinant have adopted a phylogenetic approach.

Such high-level comparative diving studies have typically summarized dive characteristics (e.g., dive depth, duration and post-dive interval (PDI)) into a single data point per species (i.e., pooling data from individuals within a species) (Boyd and Croxall, 1996; Schreer and Kovacs, 1997; Watanuki and Burger, 1999; Halsey et al., 2006a, 2006b; Brischoux et al., 2008; Isaac and Carbone, 2010; Gillooly et al., 2016; Hayward et al., 2016).

These studies clearly demonstrate that dive duration is fundamentally related to dive depth, PDI is related to duration, and that in general these parameters scale with mass. Early work from Boyd and Croxall (1996) differentiated between pinnipeds and seabirds and showed a positive relationship between body mass and dive duration. Schreer and Kovacs (1997) extended this across dive duration and depth for a large data set, including turtles and cetaceans, and identified phocid seals and penguins as exceptional divers relative to their masses. More recently, the extensive comparative analysis by Halsey et al. (2006) demonstrated that many diving variables co-vary strongly with body mass, with allometric exponents close to 0.33, showing some support for the oxygen store/usage hypothesis.

In our regional-scale study, we investigate diving patterns and body mass scaling for six air-breathing marine predators that were studied in the Indian sector of the Southern Ocean. We consider information beyond the typical highly summarized level described above by applying mixed-model analyses including data available at the intra-specific level. Adopting this approach should enable a more detailed look into the potential relationship drivers and the relative roles of within-species effects. For example, phenotypically plastic or facultative behavioral responses from between-species effects may reflect higher-order evolutionarily fixed physiological and/or behavioral responses acting on the species group.

The aim of the study is to examine the effect of body mass on dive behavior and the extent to which this is governed by a between-species effect (Table 1), and to explore whether this effect is also expressed at the within-species level. We assess three basic components of dive behavior (dive depth, dive duration and post-dive interval), and additionally consider the inter-dependencies between these three parameters using the same modelling approach. We discuss our findings in the context of expected body mass influences, the biology of our study species, and other factors (environmental, ecological) likely to contribute to shaping marine predators' diving performance.

Materials and Methods

We compiled previously published and contemporary time-depth recorder (TDR) datasets for three penguin and three seal species tagged at various locations within the Indian sector of the Southern Ocean (Supplementary S1). For each species, the TDR datasets used provide measurements for multiple individuals from the same population, within the same region and time period. Raw TDR files were processed using the Wildlife Computer Data Analysis Program, WC-DAP software (v3.0.369.0 5 Jan 2016). The time-depth datasets were

then analyzed with the package diveMove v1.2.6 (Luque, 2007) in R software v3.6.1 (Ihaka and Gentleman 1996; R Development Core Team 2007). The three principal dive parameters dive depth (m), dive duration (s), and post-dive surface interval (s) were investigated in relation to body mass (kg). A natural logarithmic transformation was applied to all data. For the analyses described below, all measurements from the same individual were aggregated into an average value.

We tested the influence of body mass on diving behavior by fitting linear mixed-effect models (LMMs). To test for species-level plasticity, we followed the method described by Van de Pol and Wright (2009) using the technique called 'within-group centring' to distinguish within-species level effects from between-species level effects. This simply involves subtracting the species' mean value from each individual's value $\left(x_{ij} - \underline{x}_j\right)$ where x_{ij} is the x value for individual *i* from species *j*. In the LMMs, the new predictor variable $\left(x_{ij} - \underline{x}_j\right)$ consequently reflects only the within-species variation component, while the species' means $\left(\underline{x}_j\right)$ reflects only the between-species variation component. Working with these two new fixed effects allowed us to model whether the unbiased estimate of either the within-species effect (β_W) or the between-species effect (β_B) is itself significant, as well as whether these two effects (slopes) are statistically different from each other (van de Pol and Wright, 2009). The estimate of $(\beta_B - \beta_W)$ is expected to be close to zero and nonsignificant when the within- and between-individual effects are effectively the same. In the above LMMs, species was included as a random intercept (μ_{0j}), but where we found a significant within-species effect (β_W), and/or $(\beta_B - \beta_W)$ was non-zero (i.e., the within- and between-subject effects were not effectively the same), the degree of between-species variation in within-species slopes around β_W was quantified by adding a random slope (μ_{Wj}) to give a final model:

$$y_{ij} = \left(\beta_0 + \mu_{0j}\right) + \left(\beta_W + \mu_{Wj}\right)\left(x_{ij} - \underline{x}_j\right) + \beta_B \underline{x}_j + \varepsilon_{0ij}$$

Where the intercept term is given by β_0, and the random intercept (μ_{0j}), random slope (μ_{Wj}) and residual error $\left(\varepsilon_{0ij}\right)$ terms are assumed to be normally distributed; for example, μ_{Wj} is assumed to be drawn from a normal distribution with zero mean and between-subject variance $\sigma^2{}_{\mu_{Wj}}$ ((Van de Pol and Wright, 2009, eqn. 4). A likelihood ratio (LR) statistic based on the

restricted maximum likelihood (REML) was used to test between the random-effects structure of the two model forms with/without a random slope μ_{Wj} (Venables and Ripley, 2002).

We applied the same approach to examine the expected dependencies between diving parameters, namely the relationship between dive duration and dive depth, and the relationship between post-surface dive interval and dive duration. This allowed us to examine the extent of species-level plasticity with respect to the fundamental controls of body size, but also with respect to the fundamental constraints on dive-cycle management.

All LMMs were fitted using the R package *nlme* v3.1-141[24]. All data are presented as mean ± s.d. across individual animals, and all parameter estimates refer to mean ± s.e. throughout. For best-fit LMMs, we report marginal R^2 values (R^2_m, for the variance explained only by fixed effects) and conditional R^2 values (R^2_c, based on the variance explained by both fixed and random effects) calculated following Nakagawa and Schielzeth (2013).

165 **Table 1.** Within- and between-species hypotheses examined for diving behavior of marine predators **inthe** Indian sector of the Southern Ocean.
166

Behavioral analyses	Between-species hypothesis	Within-species hypothesis
Body size effects: Diving behavior in relation to body mass	Among air-breathing marine predator species, larger body size confers advantages enabling deeper, longer dives, with subsequently longer post-dive intervals to recover oxygen stores at the surface.	Within species' populations, larger individuals may demonstrate greater diving capacity, and ability to adjust their diving behavior to access deeper waters, with longer dives and subsequent PDIs.
Diving constraints: Dependencies between diving parameters	Among air-breathing marine predator species occupying epi- to meso-pelagic depths, deeper dives fundamentally necessitate longer dive durations and, hence, larger PDI consequences.	Within the range of forage depths generally accessed by a species' population, individuals may adjust dive durations and associated PDIs to adapt to the conditions they experience.

167

Results

High resolution time-depth datasets were available for three pinniped and three penguin species studied in this region: the Antarctic fur (*Arctocephalus gazella*), Weddell (*Leptonychotes weddellii*) and southern elephant (*Mirounga leonina*) seals, and Adélie (*Pygoscelis adeliae*), king (*Aptenodytes patagonicus*) and emperor (*A. forsteri*) penguins. The mean dive depths of the six species spanned the upper epipelagic to mesopelagic, ranging from ~20 m for Adélie penguins, the smallest species examined, to ~500 m for female southern elephant seals (Table 2). Mean dive durations ranged from approximately 1 min for Adélie penguins, to 2–3 min for king and emperor penguins and Antarctic fur seals, to 10 and 30 min for the larger Weddell and elephant seals. Subsequent post-dive intervals at the surface followed similar patterns, but typically with much less variance across species ranging from about 0.5–3 min.

180 **Table 2. Summary of dive variables collated for penguin and seal datasets in the Indian sector of the Southern Ocean.** Data presented as
181 mean ± S.D. across all individuals. PDI = post-dive surface interval.
182

Species	Number of individuals	Number of dives	Depth (m)	Duration (s)	PDI (s)	Mass (kg)
Adélie penguin (*P. adeliae*)	18 (8 F, 10 M)	36,683	22 ± 5	67 ± 8	38 ± 7	4 ± 0.4
King penguin (*A. patagonicus*)	26 (17 F, 9 M)	45,598	67 ± 9	149 ± 20	71 ± 9	10 ± 0.8
Emperor penguin (*A. forsteri*)	14 F	10,253	83 ± 20	196 ± 40	86 ± 30	25 ± 2
Antarctic fur seal (*A. gazelle*)	26 F	37,160	52 ± 9	123 ± 13	63 ± 15	38 ± 4
Weddell seal (*L. weddellii*)	18 F	49,842	191 ± 45	763 ± 123	182 ± 22	369 ± 57
Southern elephant seal (*M. leonina*)	6 F	62,013	508 ± 58	1729 ± 145	136 ± 12	347 ± 40
	6 M	59,363	448 ± 77	1638 ± 259	136 ± 14	613 ± 167
Total/Range	**114**	**300,912**	**22–508**	**67–1729**	**38–182**	**4–613**

183

184 **Body mass relationships**

185 Our LMM results confirmed that body mass effects on dive depth were significant at
186 the between-species-level (Fig. 1a; Table 3) and also identified the within-species and
187 between-species level effects to be statistically different (t = 3.18, p = 0.034). Including
188 between-species variation in within-species slopes around β_W improved the model fit ((1)
189 versus (3), Table 3; likelihood ratio (LR) = 9.95, p = 0.007; estimated $\sigma_{W_j} = 0.51$), indicating
190 a significant degree of plasticity. Best linear unbiased predictors (BLUPs) for the within-
191 species slopes ranged from -0.65–0.59 (ADE:0.16, KP: -0.65, EMP: 0.02, FUR: 0.38, WED:
192 0.59, SES: -0.50), thus showed opposing trends in some cases; hence, the fixed-effect estimate
193 of β_W was close to zero. The between-species effect β_B was estimated at 0.56 ± 0.07 (t = 8.38,
194 p = 0.0011) with the final (best-supported) model explaining 96% of the variance (R^2_M = 0.76,
195 R^2_C = 0.96).

196 The LMM results for dive duration were similar to those reported for depth, again
197 confirming strong body mass effects on dive duration at the between-species-level (Fig. 1b;
198 Table 3) and identifying within- and between-species level effects to be statistically different
199 (t = 4.25, p = 0.013). Significant between-species variation in within-species slopes ((1)
200 versus (3), Table 3; likelihood ratio (LR) = 9.53, p = 0.009; estimated $\sigma_{W_j} = 0.49$) provides
201 some evidence for the existence of variation in phenotypic plasticity and/or behavioral
202 strategies. BLUPs for the within-species slopes ranged from -0.58–0.55 (ADE: 0.20, KP: -
203 0.15, EMP: -0.58, FUR: 0.29, WED: 0.55, SES: -0.31); the between-species effect β_B was
204 estimated at 0.62 ± 0.09 (t = 6.66, p = 0.0026), with the best-supported model explaining 98%
205 of the variance (R^2_M = 0.83, R^2_C = 0.98).

206 The PDI models showed body mass effects on PDI to be significant only at the
207 between-species-level (Fig. 1c, Table 3; estimated β_B = 0.28 ± 0.06, t = 4.43, p = 0.011) and
208 identified the within- and between-species level effects to be effectively the same (t = 1.64, p
209 = 0.18). There wasno evidence for between-species variation in within-species slopes (LR =
210 0.31, p = 0.85). This model explained 87% of the variance (R^2_M = 0.66, R^2_C = 0.87).

Table 3. Result summaries of parameter estimates from the linear mixed models using 'within-group centring' to examine relationships between dive parameters and body mass. The model sequence enables testing of whether (1) the within-species (β_W) and between-species (β_B) effects are significant, (2) the difference ($\beta_B - \beta_W$) between these two effects is significant, and if so (3) whether substantial between-species variation in within-species slopes around β_W warrants the inclusion of a random slope (μ_{Wj}) (see Methods). Model comparison between random effects structures in 1) and 3) is based on likelihood ratio tests (LRTs) using restricted maximum likelihood (REML); shading highlights best-supported model. Table reports the parameter estimates and their approximate standard errors; statistical significance is given for predictor covariates based on the ratios between the estimates and their standard errors, and the associated *p*-value from a *t* distribution. The important significant effects are highlighted in bold and the nonsignificant effects underlined. Random terms are reported as S.D.

Model parameter	Log(depth) v log(mass)	Log(duration) v log(mass)	Log(PDI) v log(mass)
(1) $y_{ij} = \beta_0 + \beta_W(x_{ij} - \underline{x}_j) + \beta_B\underline{x}_j + \mu_{0j} + \varepsilon_{0ij}$			
β_0 (intercept)	2.22 ± 0.48	3.16 ± 0.43	3.21 ± 0.26
β_W (within-species effect)	-0.07 ± 0.15 (p = 0.64)	-0.01 ± 0.10 (p = 0.91)	0.04 ± 0.13 (p = 0.73)
β_B (between-species effect)	**0.53 ± 0.12** (p = 0.01)	**0.61 ± 0.10** (p = 0.004)	**0.28 ± 0.06** (p = 0.011)
$\sigma_{\mu_{0j}}$(random intercept)	0.49	0.44	0.27
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.23	0.16	0.20
(2) $y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_B - \beta_W)\underline{x}_j + \mu_{0j} + \varepsilon_{0ij}$			
β_0 (intercept)	2.22 ± 0.48	3.16 ± 0.43	3.21 ± 0.26
β_W (within-species effect)	-0.07 ± 0.15 (p = 0.64)	-0.01 ± 0.10 (p = 0.91)	0.04 ± 0.13 (p = 0.73)
$(\beta_B - \beta_W)$ (within- versus between-species difference)	**0.60 ± 0.19** (p = 0.034)	**0.62 ± 0.15** (p = 0.013)	0.24 ± 0.15 (p = 0.18)
$\sigma_{\mu_{0j}}$(random intercept)	0.49	0.44	0.27
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.23	0.16	0.20
(3) $y_{ij} = (\beta_0 + \mu_{0j}) + (\beta_W + \mu_{Wj})(x_{ij} - \underline{x}_j) + \beta_B\underline{x}_j + \varepsilon_{0ij}$			
β_0 (intercept)	2.12 ± 0.31	3.12 ± 0.39	3.20 ± 0.25
β_W (within-species effect)	0.10 ± 0.27 (p = 0.71)	0.06 ± 0.24 (p = 0.81)	0.04 ± 0.15 (p = 0.79)
β_B (between-species effect)	**0.56 ± 0.07** (p = 0.0011)	**0.62 ± 0.09** (p = 0.003)	**0.28 ± 0.06** (p = 0.010)

$\sigma_{\mu_{0j}}$(random intercept)	0.46	0.43	0.26
σ_{W_j}(random slope)	0.51	0.49	0.13
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.22	0.15	0.20

219

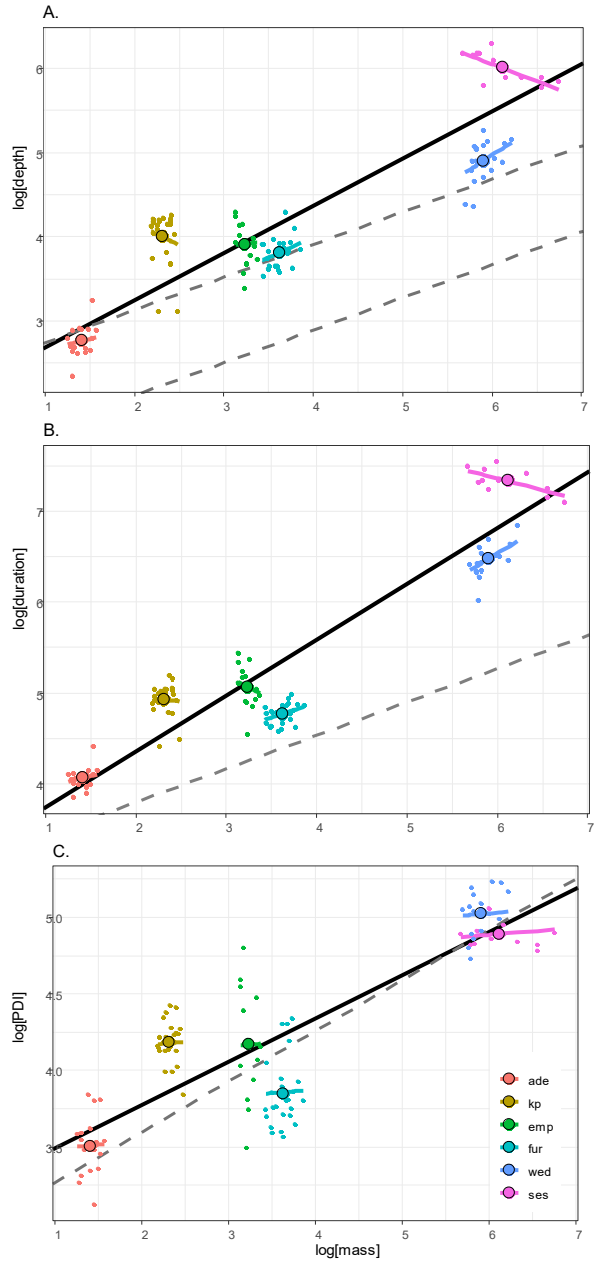

Figure 1. Results from mixed model analyses investigating within- and between species effects on the relationship between three dive parameters and body mass a) dive depth, b) dive duration, and c) post-dive interval (PDI). All variables were natural log-transformed. Full model results are given in Table 3. Colour shows species means (*large circles*) and estimated within-species-level slopes (*lines*), black line represents the between-species-level effect. For a) and b) the LMM results indicated a significant between-species (β_B) effect, and for this to be statistically different from the within-species effect (*i.e.,* $\beta_B - \beta_W$ is non-zero); a random slopes model was supported in both cases indicating substantial between-species variation in within-species slopes around β_W. For c) the LMM results indicated a nonsignificant within-species (β_W) effect, a significant between-species (β_B) effect, and $\beta_B - \beta_W$ to be close zero (i.e. a random intercept only model was supported). For comparative purposes also shown are results from the large-scale analysis of Halsey et al. (2006, *grey dashed lines*). For a) log depth vs log mass, Halsey*, et al.,* [13] reported separate intercepts for birds (log(10.5)) and mammals (log(3.8)), but a common slope of 0.389; b) log duration vs log mass (intercept: log(21.2), slope: 0.368), c) PDI (intercept: log(18.8), slope: 0.331). Species (spp) abbreviations are: ade = Adélie

234 penguins, kp = king penguins, emp = emperor penguins, fur = Antarctic fur seals, wed = Weddell
235 seals, ses = southern elephant seals.
236
237 **Dive parameter relationships**
238 The LMMs examining the relationship between dive duration and depth (Table 4)
239 showed both the within-species effects (β_W = 0.54 ± 0.04, t = 13.65, p < 0.0001) and the
240 between-species effects (β_B = 1.08 ± 0.10, t = 10.43, p = 0.0005) of depth on duration were
241 significant, and that these estimated effects were statistically different (t = 4.84, p = 0.0084).
242 There was no evidence for between-species variation in within-species slopes (LR = 0.27, p =
243 0.87). This model explained 99% of the variance (R^2_M = 0.93, R^2_C = 0.99).
244 The LMMs examining the relationship between post-dive interval and dive duration
245 (Table 4) also showed both the within- (β_W = 0.77 ± 0.11, t = 6.90, p < 0.0001) and between-
246 species (β_B = 0.45 ± 0.08, t = 5.53, p = 0.0052) level effects were significant, but identified
247 the within- and between-species slopes to effectively the same (t = -2.30, p = 0.083). There
248 was no evidence for variation in within-species slopes (LR = 0.49, p = 0.78). This model
249 explained 90% of the variance (R^2_M = 0.74, R^2_C = 0.90).

Table 4. Result summaries reporting parameter estimates from the linear mixed models using 'within-group centring' to examine relationships between dive parameters. Presentation as in Table 3.

Model parameter	Log(duration) v log(depth)	Log(PDI) v log(duration)
(1) $y_{ij} = \beta_0 + \beta_W(x_{ij} - \underline{x}_j) + \beta_B\underline{x}_j + \mu_{0j} + \varepsilon_{0ij}$		
β_0 (intercept)	0.86 ± 0.45	1.79 ± 0.46
β_W (within-species effect)	**0.54** ± **0.04** (p < 0.0001)	**0.77** ± **0.11** (p < 0.0001)
β_B (between-species effect)	**1.08 ± 0.10** (p = 0.0005)	**0.45 ± 0.08** (p = 0.0052)
$\sigma_{\mu_{0j}}$(random intercept)	0.26	0.22
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.10	0.17
(2) $y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_B - \beta_W)\underline{x}_j + \mu_{0j} + \varepsilon_{0ij}$		
β_0 (intercept)	0.86 ± 0.45	1.79 ± 0.46
β_W (within-species effect)	**0.54** ± **0.04** (p < 0.0001)	**0.77** ± **0.11** (p < 0.0001)
$(\beta_B - \beta_W)$ (within- versus between-species difference)	**0.54 ± 0.11** (p = 0.0084)	-0.32 ± 0.14 (p = 0.083)
$\sigma_{\mu_{0j}}$(random intercept)	0.26	0.22
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.10	0.17
(3) $y_{ij} = (\beta_0 + \mu_{0j}) + (\beta_W + \mu_{Wj})(x_{ij} - \underline{x}_j) + \beta_B\underline{x}_j + \varepsilon_{0ij}$		
β_0 (intercept)	0.84 ± 0.44	2.03 ± 0.44
β_W (within-species effect)	**0.55** ± **0.04** (p < 0.0001)	**0.80** ± **0.12** (p < 0.0001)
β_B (between-species effect)	**1.09 ± 0.10** (p = 0.0004)	**0.41 ± 0.08** (p = 0.0065)
$\sigma_{\mu_{0j}}$(random intercept)	0.25	0.22
σ_{W_j}(random slope)	0.02	0.12
$\sigma_{\varepsilon_{0ij}}$(residual error)	0.10	0.17

253

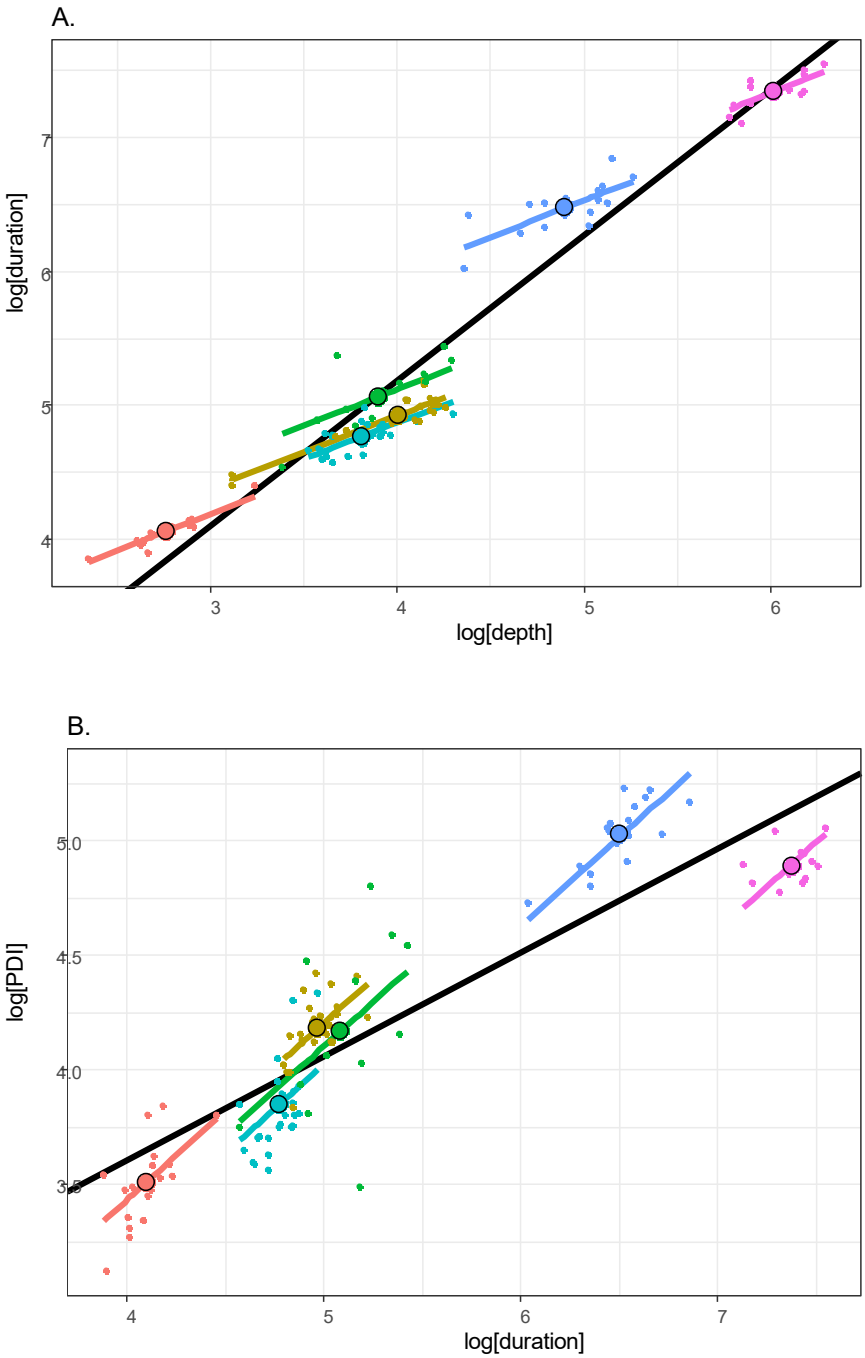

Figure 2. Results from mixed model analyses investigating within- and between species effects on the relationships between dive parameters a) dive duration vs depth, b) post-dive interval (PDI) vs dive duration. Presentation as in Fig. 1, with full model results given in Table 4. For a) and b) the LMM results indicated both a significant within-species (β_W) effect and a significant between-species (β_B) effect. For a) these slopes were statistically different (*i.e.*, $\beta_B - \beta_W$ is non-zero), whereas for b) $\beta_B - \beta_W$ was close zero indicating these slopes were not statistically different. In both cases there was no substantial variation in within-species slopes around β_W (i.e. a random intercept only model was supported).

254

255 **Table 5. Summary of main findings from LMMs** using 'within-group centring' to examine relationships between body mass and diving
256 parameters, and the inter-dependencies between these parameters.

	Between-species effect	**Within-species effect**	**Between- and within-species effect different**	**Between-species variation in within-species effect**	**% Variance explained R^2_M (R^2_C)**
Body size effects					
Depth v Mass	✓	✗	✓	✓	76 (96)
Duration v Mass	✓	✗	✓	✓	83 (98)
PDI v Mass	✓	✗	✗	✗	66 (87)
Dive constraints					
Duration v Depth	✓	✓	✓	✗	93 (99)
PDI v Duration	✓	✓	✗	✗	74 (90)

257

Discussion

Our study compiles a valuable multispecies dataset of six different marine predators of the Southern Ocean that allowed us to explore hypotheses regarding (i) the effect of body size on dive performance, and (ii) the interdependencies of dive parameters. Our results support the well-established expectations that dive performance is tightly linked to species size (Boyd and Croxall, 1996; Schreer and Kovacs, 1997; Halsey et al., 2006a; b); smaller species make shorter, shallower dives with correspondingly shorter surfacing intervals than larger species. This is a result of the allometric relationship between body size and metabolic rate (Schmidt-Nielsen, 1970): smaller animals have relatively higher metabolic rates than larger animals (the so-called "mouse-elephant" curve). However, the slopes for our between-species relationships were considerably higher for dive depth and duration than described by Halsey et al. (2006a). This suggests that, for their size, all six species dive longer for a given depth than expected for average birds or mammals. The species sample examined by Halsey et al. (2006a)included a more diverse range of taxa (ducks and grebes, as well as sea lions and cetaceans) and a wide range of ecotypes (including deep diving specialists and surface-feeding lunge divers) than this study; the authors noted differences in the relationships among some of these groups. Most notably, both the phocid seals and penguins fall above the global relationship. These species are specialist pursuit divers and have adaptations that allow them to maximize the time spent underwater. This is in contrast to animals with a different suite of morphological and physiological adaptations that use other feeding types (e.g., surface lunge feeding of baleen whales (Friedlander et al., 2014).

The influence of body mass on dive performance within a species

Although our study confirmed the universal nature of the relationship of body size and dive performance among species, we found that these relationships did not hold *within* species for dive duration and dive depth (although they did for post-dive surface interval). There was a within-species body size effect different to the between-species relationships. This within-species relationship varied amongst the species. Thus, at the species level, dive depth and dive duration are not simply driven by physiological allometry. For two species, elephant seals and king penguins, the slope of the relationship was negative, indicating that larger individuals made shorter and shallower dives than smaller ones. This suggests there are other factors at play, perhaps ecological in nature. For example, our sample included both male and female elephant seals (males are much larger than females,

Table 2). Males typically feed on benthic prey in relatively shallow shelf waters, while females feed predominantly on mesopelagic prey in the open ocean (Hindell et al., 2016; Green et al., 2020). These very different foraging environments and prey types require different hunting strategies within the species. Age and sex related differences in foraging exist in king penguins. Older birds generally forage more efficiently than younger ones, and older females made shorter trips than males, and also dive deeper (Le Vaillant et al. 2013). In contrast, the two species performing relatively short, shallow dives for their size (Weddell seals and fur seals) the dive depth vs duration relationship had positive slopes. We note though that all our data for fur seals were obtained from females. It would be useful to conduct the analyses on data from males. Overall, the different nature of the intra-specific relationships precludes the use of the global inter-specific relationships to predict dive behavior for individuals within a species.

Unlike dive depth and duration, post-dive surface intervals were not influenced by body size within a species. This suggests that the different dive durations described above are not incurring a physiological cost, or requiring individuals within a species to spend longer periods on the surface to re-oxygenate the storage tissues. One explanation is that individuals operate within their aerobic range and, hence, do not incur an oxygen debt when diving. Several studies have shown that diving animals rarely use anaerobic metabolism when diving, because the resultant oxygen debt leads to a disproportionately long surface interval, and ultimately to a reduced foraging time (Mori, 1999; Kooyman, 1989). However, there were differences among the species in their absolute post-dive surface intervals. For example, king penguins have the longest post-dive surface intervals relative to that expected for their body size, whereas Antarctic fur seals have the shortest. Despite the apparent greater dive effort in the king penguins (demonstrated by the relatively long recovery times), they are still operating within their aerobic capacity. Thus, some species may have physiological and morphological mechanisms that enable them to stay submerged, and that these mechanisms are most developed in deep diving species.

The interdependencies of dive parameters

Our examination of the interdependencies of diving parameters showed support for both between- and within-species effects. These results were more consistent than for the size-based analyses described above, suggesting universal principles may be at play. As expected, all relationships were consistently positive, but within- and between-species the dependency of dive duration upon depth was statistically different; the within-species

slope was essentially half (β_W= 0.55 c.f. β_B= 1.09, Table 4) and, importantly, the same for all species considered here. Hence, individuals remain within the general range of foraging depths of their species, but may adjust dive durations to adapt to the conditions they experience. This result indicates a narrower range of possible responses at the within-species level. Within species, phenotypically plastic or facultative behavioral responses are limited, probably because of some combination of body size, oxygen stores and rate of consumption that fundamentally constrains a species' dive capacity (Kooyman and Ponganis, 1998). This is an important finding as it demonstrates that we cannot use the between-species relationship to predict how individuals respond within a species.

Conversely, our results indicate that PDI can potentially be predicted within a species based either on body size (see above) or on dive duration. While the PDI/duration dependency was important at both the within- and between-species levels, these were not statistically different. This suggests the relationship always scales the same way, inter- and intra-specifically, potentially due to a universality of the laws governing reoxygenation mechanisms. This might relate to either anatomical or physiological mechanisms controlling the rate at which oxygen can return to cells. However, PDI can be difficult to allocate precisely dive-by-dive, and oxygen debts can be deferred. Our data show some noise, and it is possible that a greater sample size would more clearly differentiate these estimated parameters (β_W= 0.77 c.f. β_B= 0.45, Table 4). Nevertheless, our study demonstrates that adopting this approach enables a deeper look into the relative roles of phenotypic plasticity or facultative behavioral responses, as compared with evolutionarily fixed physiological or behavioral responses acting on this species group. While confirming previous findings from comparative analyses on body size, we have illustrated that within species these relationships differ, and highlighted the role of ecological and other influential factors. In particular, our study suggests universal principles to be at play with regard to PDI, probably related to the mechanical processes of reoxygenating blood.

Acknowledgements

We gratefully acknowledge the work of all the researchers, science technical support and field personnel who conducted and supported the fieldwork, upon whose efforts this study was dependent. We also thank the data custodians of the archived satellite tracking and dive data, in particular J. Clarke and L. Emmerson at the Australian Antarctic Division for providing the Adélie penguin data.

Supplementary material

Supplementary S1. Dive telemetry details

We compiled a suite of historical and contemporary time-depth recorder (TDR) datasets collected for six species studied in the Indian sector of the Southern Ocean (Table S1.1, Fig. S1.1). Where possible the datasets also included metadata regarding sex, body mass and/or age of the animals.

Penguin data

- Adélie penguins (n = 19) were fitted with Wildlife Computers (Redmond, WA, USA) Mk7 TDRs (1 s sampling rate) and tracked using Argos platform terminal transmittors (PTTs) in January 2001, 2002, 2003 during guard/créche at Béchervaise Island, Antarctica (62.82° E, 67.58° S). Tracking details can be found in Clarke et al., (2006); however, the TDR data are previously unpublished.
- Incubating king penguins (n = 26) were equipped with Wildlife Computers Mk9 TDRs (2 s sampling rate) and ST-10 satellite trackers from December 2003 to February 2004 at Spit Bay on Heard Island (73.75° E, 53.10° S) (Wienecke and Robertson, 2006).
- Emperor penguins (n = 14) were equipped with Wildlife Computers Mk7 TDRs (5 s sampling rate) during the breeding season between May and October 1993 and 1994 at Auster rookery, East Antarctica (63.82° E, 67.43° S) (Wienecke et al., 2007).

Seal data

- Lactating female Antarctic fur seals (n = 26) were equipped with Wildlife Computers Mk7 and Mk9 TDRs (2 s sampling rate) and PTTs from December 2003 to January 2004 at Spit Bay, Heard Island (73.75° E, 53.10° S) (Frydman and Gales, 2007; Staniland et al., 2010; Hindell et al., 2011).
- Southern elephant seals (n = 12) were equipped with Satellite Relayed Data Loggers Conductivity Temperature Depth (SRDL-CTDs, manufactured by Sea Mammal Research Unit, University of St Andrews) (4 s sampling rate) during February 2012, 2013 and January 2014 near Davis station (77.97° E, 68.58° S), Antarctica, and at the Kerguelen Archipelago (13.70° E , 21.49° S). These data are available from the Australian Integrated Marine Observing System (IMOS, 2017 *online*).

- Female Weddell seals (n = 17) were equipped with SRDL (30 s sampling rate) during late Febraury–March 2011 at Davis station (77.97°E, 68.58°S) Antarctica, as part of the multi-annual IMOS program (IMOS, 2017 *online*).

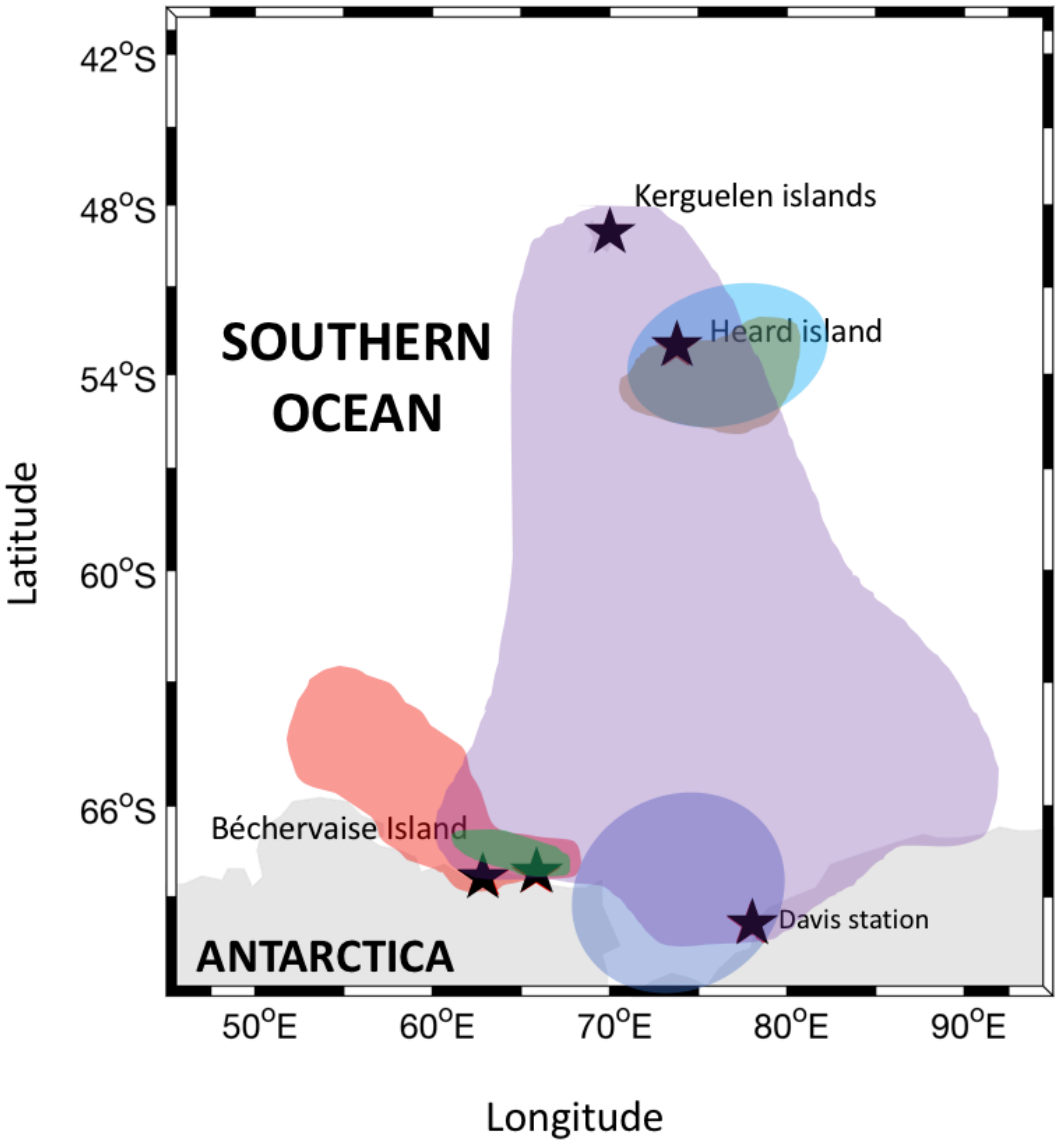

Figure S1.1 Map showing general spatial distribution of diving data compiled in this study. Tagging locations are indicated with a star. Shading indicates species: Adélie (pink), king (brown) and emperor (green) penguins; Antarctic fur (azure), Weddell (blue) and southern elephant (violet) seals. See Table S1.1 for data sources.

Table S1.1. Summary information on the dive data collated for six marine predators from tagging studies in the Indian sector of the Southern Ocean. No. dives indicates the total number of dives available for each species. Species-specific minimum depth and duration thresholds (Table S1.2) were applied prior to further analyses.

Species	Tagging Location	Source	Number of individuals	Number of dives	Sampling frequency (s)	Sampling period (d)
Adélie penguin *P. adeliae*	Béchervaise Island, Antarctica (62.82° E, 67.58° S)	Clarke et al., 2006 (PTT tracking data); TDR data unpubl.	19 (9 F, 11 M)	78,082	1	5 ± 3.8 (0.5 – 12.1)
King penguin *A. patagonicus*	Spit Bay, Heard Island (73.75° E, 53.10° S)	Wienecke and Robertson, 2006	26 (17 F, 9 M)	58,344	2	15 ± 4.77 (7.8 – 27.7)
Emperor penguin *A. forsteri*	Emperor penguins, Auster rookery, Antarctica (63.82° E, 67.43° S)	Wienecke et al., 2007	14 F	12,340	2	16 ± 9.2 (1.4 – 30.2)
Antarctic fur seal *A. gazella*	Spit Bay, Heard Island (73.75° E, 53.10° S)	Frydman and Gales, 2007; Staniland et al., 2010; Hindell et al., 2011	26 F	69,082	2	7 ± 2.46 (5.3 – 13.4)
Weddell seal *L. weddellii*	Davis Station, Antarctica (77.97° E, 68.58° S)	IMOS, 2017; Bestley et al., 2015	17 F	89,563	30	132 ± 63 (37.2 – 285.5)
Southern elephant seal *M. leonina*	Davis Station, Antarctica (77.97° E, 68.58° S)	IMOS, 2017	12 (6 F, 6 M)	131,390	4*	245 ± 60.3 (96.5 – 312.9)

*Indicates original sampling frequency programmed for the Satellite-Relayed-Data-Loggers (SRDLs, manufactured by Sea Mammal Research Unit, University of St Andrews, Scotland, UK). Complete archival records were retrieved for the Southern elephant seal dataset, from recovered tags. Data for the Weddell seals consists of summary records for a randomized subset of individual dives (Photopoulou et al., 2015), including the dive duration, maximum depth and post-dive surface interval for each dive

Chapter 4

Behavioral plasticity and observed limits of underwater dive behavior of marine predators during intense foraging

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Abstract

Data-logger technologies have greatly increased our ability to the study in situ diving behavior of free-ranging marine animals, and time-depth recorders (TDR) have delivered detailed information on dive patterns from many Antarctic marine predators. New analytical methods enable hunting dives to be classified, on the basis of vertical sinuosity, providing the opportunity to investigate how species vary their behavior and characterize the underwater behavioral plasticity across species during intense foraging. Here, I apply a cross-taxa comparative approach using TDR data from three species of seals and three species of penguins (spanning a range of size classes and prey types), to investigate their dive plasticity and to quantify how these animals change dive behavior when foraging. Foraging is a fundamental requirement to all animals, but different species manage differently their dive cycle during such events and not all species showed consistent changes. Notably for Adélie penguins, our approach did not detect significant changes between dive characteristics during non-foraging, low- and high- hunting dives. However, my study provides evidence of how most penguins and seals adjust their dive behavior when foraging and dive longer and deeper. Deeper dives correspond also to longer time at the bottom and this is achieved adjusting their transit time. Finally, due to the energetic cost of intense foraging dives, only few species are able to extend their dive duration and bottom time in these scenarios.

Introduction

To exploit the abundance of food available in the marine environment, aquatic birds and mammals have evolved a suite of morphological, physiological and behavioral adaptations (Schaefer, 1965). To understand the behavioral adaptations different species demonstrate within their marine habitat, research often focuses on marine predators' diving ecology, particularly whilst actively foraging. Three principal factors affect the underwater performances of marine mammals and seabirds: (1) the physical properties of the water (i.e., viscosity, pressure); (2) the lack of access to oxygen, as these species must return to the surface to breathe, and (3) the distribution and abundance of their prey.

Most aquatic species display physical adaptations to maximize their efficiencies underwater, such as a streamlined body; some have greatly reduced the length of their hair (e.g., southern elephant seals) to minimize the viscosity effects of water. Others have maintained long fur and feathers that trap air and help in the ascent phase of a dive (Fish et al., 2002). However, to counteract their positive buoyancy, marine birds like penguins have increased their bones density (Ksepka et al., 2015), and pinnipeds have evolved a flexible rib cage (Cozzi et al., 2010) and collapsible lungs (McDonald and Ponganis, 2012) that also help to deal with the increase in pressure when diving.

Since the time air-breathing animals can spend underwater is limited, all marine mammals and seabirds have physiological adaptations to both increase their capacity to store oxygen as well as minimise the rate of consumption whilst diving. The oxygen consumed during a breath hold dive is stored in three main compartments: the respiratory system, the blood, and the body musculature (Castellini et al., 1992). The total oxygen store and the proportions in which it is compartmentalised differ among species, but in general oxygen stores scale isometrically with body mass (Halsey et al., 2006a). As the rate of oxygen consumption per gram of body mass is much higher in smaller species, body size constrains their dive time (Schmidt-Nielsen, 1970). Consequently, we expect dive duration to be shorter in seabirds than marine mammals, but recent work has shown that some birds can dive deeper and longer than mammals of equivalent mass (Halsey et al., 2006a; Chapter 3). The reason is that lung volumes of birds are 3–5 times bigger than those of mammals, and their respiratory surface area is 15% greater than similarly sized mammals (Maina, 2006). Moreover, birds have a faster metabolism, and oxygen is delivered at higher rates, so the absolute quantity to meet the minimum energetic needs of small species is less than larger ones (Halsey et al., 2006a). Lastly, both seabirds and marine mammals have developed a physiological mechanism — the so called “dive response” —

that allows marine predators to reduce their oxygen consumption when diving. Penguins and seals can switch from aerobic to anaerobic metabolism to overcome the metabolic demand of oxygen when diving, although this is probably relatively rare as it induces an oxygen debt (Roncon et al., 2018).

The diving behavior of marine mammals and seabirds is also determined by the nature of their prey (Boyd et al., 1994). Ecological factors, such as the depth at which prey is found (pelagic/benthic), type of prey species and the prey biology (krill/squid/fish), prey distribution (homogeneous/patchy), all characterise the diving behavior of seals and penguins (Chapter 2). Invoking optimal foraging theory (OFT) (Stephens and Krebs, 1986), marine predators' diving behavior should be as efficient as possible, minimizing the costs associated with feeding underwater (e.g., oxygen consumption, dive transit time) and maximizing its benefits (e.g., net energy gain) (Kramer, 1988; Mori, 1998).

How marine predators manage their dive cycles in response to ecological variability may be observed by evaluating changes in multiple dive parameters, such as descent and ascent rates or dive bottom time, that may be indicative of prey patch quality (Thompson and Fedak, 2001). For example, Thums et al. (2013) demonstrated that female southern elephant seals from Macquarie Island descended and ascended faster in high-quality patches than in low quality patches. Dive data may also provide information about how predators compensate for declining prey abundance by increasing their foraging effort (Harcourt et al., 2001).

Previous studies have shown that species consistently operating near their maximum physiological capacity are less likely to have the ability to increase their foraging effort in response to reductions in prey. For example, probably due to their capacity to exploit a variety of pelagic prey types, Antarctic fur seals are abundant in the Southern Ocean, and draw upon a great energy reserve to pursue prey if it moves deeper (Costa et al., 2006). In comparison, populations of pinnipeds that feed on benthic species are stable or declining, possibly because these animals regularly their aerobic dive limit (hereafter ADL; Kooyman, 1980) switching to anaerobic metabolism to increase their foraging effort (Costa et al., 2004).

As discussed in Chapters 2 and 3, parameters, such as dive duration, depth and post-dive surface interval (hereafter PDI), can be used to describe the basic dive performance of marine predators, and characterise their behavioral plasticity as well as explore which factors may constrain their diving. In the comparative analyses undertaken in the previous chapter, all dives were considered together. But dives may serve many purposes and not all dives are likely to be foraging dives (Crocker et al., 1997). This chapter specifically investigates how seabirds and pinnipeds behave during foraging (hunting) and non-foraging dives, differentiating also between

high- and low-intensity foraging. I investigated the same six marine predator species discussed in previous chapters. To discriminate between "hunting" (hereafter HT) and "non hunting" (no.HT) dives, the hunting time approach developed by Heerah et al. (2014) is utilized.

This chapter builds on the previous (Chapter 3) to:

1. Investigate marine predators' behavioral plasticity in terms of the observed ranges (minimum/maximum) of dive duration, dive depth, and PDI, using a quantile regression approach to identify the observation envelope. Despite their anatomical and physiological constraints, there is still a wide range of diving plasticity among species that could be potentially explained by allometry (Schreer and Kovacs, 1997) and behavioral adaptations.

2. Quantify how seals and penguins change dive behavior when foraging by exploring the following questions:

(i) Do predators vary their dive cycle by potentially diving deeper and longer, and lengthening bottom time when resource distribution may be suboptimal? Marine mammals and seabirds have many different strategies to secure aquatic prey, and according to OFT, we expect them to maximize resource acquisition by adapting their diving patterns.

(ii) Can they respond to environmental fluctuation (e.g., prey distribution) with low and high foraging intensity? These species are expected to dive longer when prey is more plentiful and *vice-versa* (Thompson and Fedak, 2001). But animals operating at the upper edge of their performance are less likely to be able to increase their hunting time in response to reductions in prey (Costa, 2004).

(iii) Is there an increased cost associated with high intensity foraging, requiring longer time at the surface to compensate the oxygen debt? Some species like elephant seals routinely perform very deep benthic dives, and compensate later for their dive effort by spending more time resting once hauled out (Butler and Jones, 1997).

Material and methods

Time-depth recorder (TDR) data

I compiled time-depth recorder (TDR) data for three penguin and three seal species tagged in Eastern Antarctica from 1992 to 2015 (see Supplementary Material S1, Chapter 3 and 4). The raw files were processed using the Wildlife Computer Data Analysis Program, WC-DAP software (v3.0.369.0 05-Jan-2016). For each species, the obtained time-depth datasets were then analysed in the R package *diveMove* v1.2.6 (Luque, 2007) to extract dive parameters, such as maximum dive depth (m), dive duration (s), post-dive surface interval (PDI, s), descent and ascent time (s), and bottom time (s) for each individual dive. The descent and ascent times for

each dive were summed to give overall transit time (s). For the purpose of an across-species comparison, I only considered dives with clearly identifiable descent, bottom, ascent and surface phase. A natural log transformation was applied to all data prior to analyses, and data are presented as mean ± s.d. across individual animals. Note that only high-resolution time-depth recorder (TDR) datasets (sample interval <4 s) were used for this study; for Weddell seals, the dataset of only one individual was available. This was included here as a reference (Supplementary Material S1). Female and male elephant seals were considered separately due to the different diving ecology [Hindell et al., 1991].

Part 1: Marine predators' diving performance range

To visually represent the range of marine predator diving performances, I evaluated the relationships between dive duration and depth, and PDI and dive duration across species using quantile regressions. I used a linear quantile regression analysis (Koenker and Bassett, 1978) because it enables fitting of conditional regressions through a specified quantile (in this case, lower quantile = 2.5%; upper quantile = 97.5%) of a response variable (see Fig.1). As a result, I could determine the observed range of dive behavior and quantify the minimum and maximum edges of these observation envelopes, as reflected in the lower "edge" (red line) and upper "edge" (blue line) of the plot (Fig.1).

I described the distribution of dive data for each case and calculated the slope of each regression line (see Fig. 2). I then compared the slope of lower and upper edges across species and examined these slope values in relation to mass. I also reported the distribution of dive duration data above the calculated ADL (cADL) for all species which was obtained from the literature (Adélie penguins = 110 s, Culik et al., 1994; king penguins = 300 s, Culik et al., 1996; emperor penguins = 480 s, Ponganis et al., 1999; Antarctic fur seals = 245 s, Costa et al., 2001; Weddell seals = 1140 s, Ponganis et al., 1993; southern elephant seals female = 1731 s, Hindell et al., 1992; southern elephant seals male = 2802 s, Hindell et al., 1992).

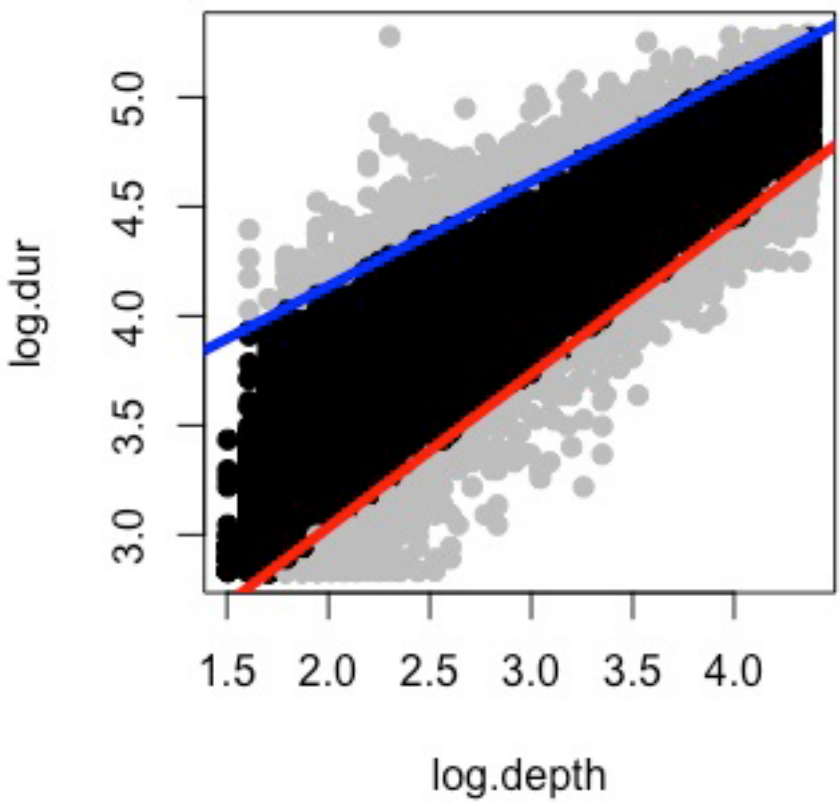

Figure 1. The application of quantile regression analysis on dive data: dive duration vs depth. The results presented here are from a quantile regression on Adélie penguins dive data. The red line shows the lower quantile = 2.5%; the blue line shows the upper quantile = 97.5%.

Part 2: Marine predators' dive plasticity during foraging dives

To investigate dive plasticity during foraging dives, the hunting time method of Heerah et al. (2014) was used to identify likely foraging activity within each dive. This method was originally developed for Weddell seals. Each seal's dive is broken into different segments corresponding to different dive phases, and the vertical sinuosity of the segments is used to infer the behaviors: high-sinuosity segments correspond to "hunting" and less sinuous segments indicates non-hunting activity, such as "transiting" (Heerah et al., 2014). Although all species considered here perform U dives similar to Weddell seals, the threshold of high vertical sinuosity was adapted separately for each species (species thresholds: > 0.9 Weddell, southern elephant and Antarctic fur seals; > 0.7 king and emperor penguins; 0.5 Adélie penguins) to identify "hunting" segments (Heerah et al., 2014). Each dive containing a hunting segment was defined as a foraging dive, and the duration of all hunting segments identified within a dive was summed to obtain total hunting time (s).

Foraging dives were further separated into those with 'low' hunting time (comprising the lower 33% of each species dataset, with quantile applied per individual animal) and 'high' hunting time (representing the upper 33% of each species dataset) dives. These quantiles were selected to retain a high number of individual dive observations (thousands per species) yet discriminate well away from the median (i.e., excludes dives within the 33–66% percentiles). Linear mixed effect models (LMMs, *nlme* package, Pinheiro et al., 2018) were used to investigate the variation of dive parameters in foraging (high and low HT) dives compared to non-foraging (no HT) dives. First, I examined dive depth (m), dive duration (s), bottom duration (s), and transit time (s), taking into account the dependence of these parameters on depth. I also investigated PDI, taking into account the dependence of this parameter on dive duration. 'Individual animal' was included as the random effect (intercept only). Important significant effects were evaluated at $p < 0.001$; a conservative threshold was used given the large sample sizes for models fitted to dive-level data. Note that where LMMs are reported for other species, an equivalent linear model was fitted to the Weddell seal data (see Supplementary Material S1). Male and female southern elephant seals were modelled separately due to their different foraging environments and dive characteristics (Chapter 2 and Table 1). Where I present model predictions (Table 3), the estimate and the 95% confidence intervals associated with the fixed effects are reported.

193 **Table 1. Summary table of dive activity collated for penguin and seal datasets in the Indian sector of the Southern Ocean.** Data given as mean ±
194 S.D. and range across individuals. HT = hunting time. ADL = Aerobic diving limit.

Species	Number of individuals	Number of dives	Percent forage dives	HT (s)	Number of dives >cADL	Percent dives >cADL	Mass (kg)
Adélie penguin *P. adeliae*	16 (8 F, 8 M)	21,115	51 ± 3 14–81	35.7 ± 47.1 20–198.3	3,517	11	4 ± 0.4
King penguin *A. patagonicus*	26 (17 F, 9 M)	36,223	79 ± 1 71–90	38.3 ± 22.8 4.1–134.5	596	1.5	10 ± 0.9
Emperor penguin *A. forsteri*	9 F	5,723	26 ± 6 13–34	65 ± 44.7, 8–250.4	0	0	25 ± 1
Antarctic fur seal *A. gazella*	26 F	35,380	41 ± 45 17–74	78.3 ± 15.1 80–250.7	31	0.07	37 ± 4
Weddell seal *L. weddellii*	1 F	7,241	28	515.2 ± 324.8 60–2,100	3,115	43	379 ± 66
Southern elephant seal *M. leonina* (F)	6	46,282	74 ± 25 61–82	595.1 ± 40.1 148–4,084	27,657	61	346 ± 39
(M)	6	40,396	88 ± 32 67–110	886.1 ± 25.3 146–3,472	2,789	6.7	613 ± 167

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Results

Part 1: Diving ranges

This section describes the range of dive performances ('envelope') observed in the seal and penguin species. Most species performed their dives within the estimated cADL. The proportion of dives exceeding the cADL varied in different species (**Table 1**). For example, female southern elephant and Weddell seals exceeded their published cADL in 61% and 43% of dives, respectively, suggesting these cADL values may be incorrect. In comparison, emperor penguins (0%) and Antarctic fur seals (<1%) rarely if at all exceeded cADL, i.e., they rarely incurred an oxygen debt. This may also reflect how well cADL values have been measured for these two species. King penguins (1.5%) and Adélie penguins: (11%) as well as male southern elephant seals (7%) also generally performed aerobic dives.

All species exhibited relatively pronounced lower and upper edges to the dive duration/depth distribution, which describes how marine species allocate their time when diving **(Fig. 2)**. Here, the lower quantile regression line ('edge') of the dive duration/depth relationship describes the near-minimal duration associated with dives to a particular depth. The upper quantile regression line describes near-maximal dive duration associated with dives to particular depth. (see Table S1**)**. Within these envelopes of observed diving recordings, the density contours (demarcated at 10% intervals to 90%) describe the concentration of dive observations for each species. King penguins, and Weddell and southern elephant seals predominantly performed deep and long dives while Adélie and emperor penguins appeared to be more variable in their dive performance, encompassing a broader envelope from shallower and shorter dives to deeper and longer dives.

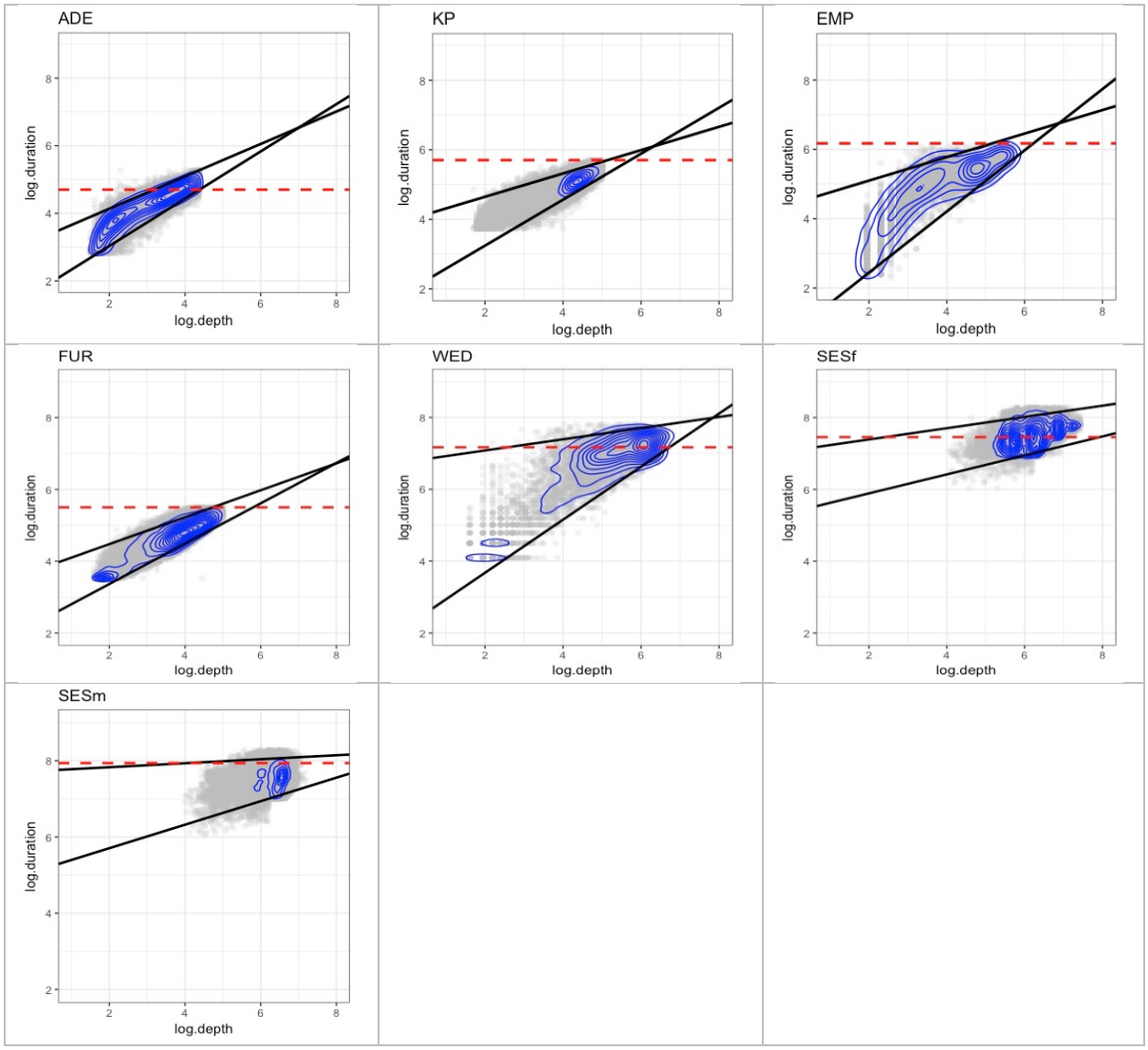


Figure 2. The relationships between dive duration/depth and across species. The results presented here are from a quantile regression (lower= 2.5%, upper= 97.5%). Full details of quantile regression results are given in Table S1**.** Grey dots are data observations. Solid lines show the lower and upper quantile edges. Blue lines show data density contours (demarcated at 10% intervals to 90%). The ADL values (red dashed lines) were obtained from literature. Species abbreviations are: ADE = Adélie penguins, KP = king penguins, EMP = emperor penguins, FUR = Antarctic fur seals, WED = Weddell seals, SESf = female southern elephant seals, SESm = male elephant selas. PDI= post-dive interval.

The quantile regression slopes from Fig. **2** are plotted together for all species in Fig. **4a**. This illustrates the differences in the diving range, ordive envelopes, demonstrated across species. Comparing the smaller species (excluding the phocid seals), Fig. **4a** implies that emperor penguins have the broadest envelopes of possible operation, that is, they show greater variability in duration for a given depth. They perform both shorter and longer dives for a given depth than Antarctic fur seals, king or Adélie penguins. The narrower envelopes observed for these three species largely nestle within that of emperor penguins. The lower edge slope for emperor penguins is also the steepest (m = 0.87 ± 0.004, see Supplementary Materials, **Table S2**). In comparison, southern elephant seals, performed quite steadily and dive duration generally varied less for a given depth.

The duration/depth quantile regression slopes in relation to body mass (**Fig.** 4c) shows that masss is not the sole determinant of dive capacity. However, with the caveat that this is based on only a few species, the upper edge slopes declined somewhat with increasing body mass (linear regression: m = -0.07 ± 0.01, t = -4.67, p = 0.005). The relationship for the lower edge slopes was not statistically significant (m = -0.08 ± 0.04, t = -1.72, p = 0.15).

With regard to the relationship between dive duration and subsequent PDI (**Fig. 3),** the quantile regressions provided less evidence for a clearly defined envelope: when compared across species, these envelopes are not very distinct; a large envelope of performance was observed across all. The density contours show this relationship to be generally less clear with highly variable PDI for a given duration in all species: for example, both male and female southern elephant seals consistently performed long dives with relatively invariant PDIs (spanning only 2–3 mins) (**Fig. 4b**). High variability in PDI was evident for Adélie, king, emperor penguins and particularly Antarctic fur seals (lower edge: m = 1.15 ± 0.01; upper edge: m = 1.02 ± 0.04; Supplementary, **Table S2**). When these relationships were plotted together (**Fig. 4b)** there was no clear pattern across species, nor any indication that body mass influenced the PDI/duration relationships (**Fig. 4d**; linear regression for lower edge: m = -0.07 ± 0.08, t = -0.95, p = 0.39; linear regression for upper edge: m = -0.04 ± 0.08, t = -0.49, p = 0.67).

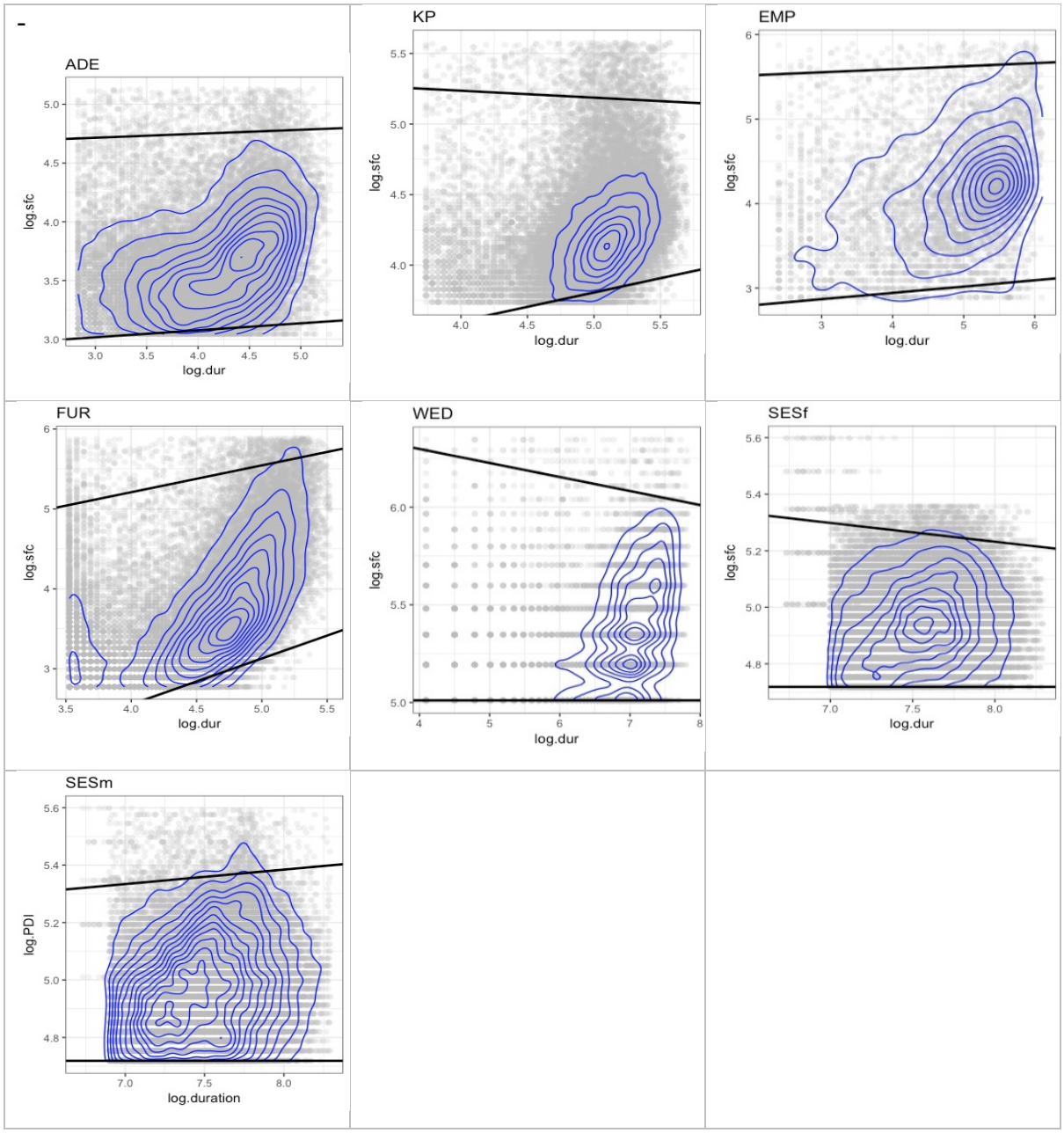


Figure 3. The relationships between PDI/dive duration across species. The results presented here are from a quantile regression (lower = 2.5%, upper = 97.5%). Full details of quantile regression results are given in Table S1**.** Grey dots are data observations. Solid lines show the lower and upper quantile edges. Blue lines show data density contours (demarcated at 10% intervals to 90%). Note axes vary across panels. For species abbreviations see Fig. 2.

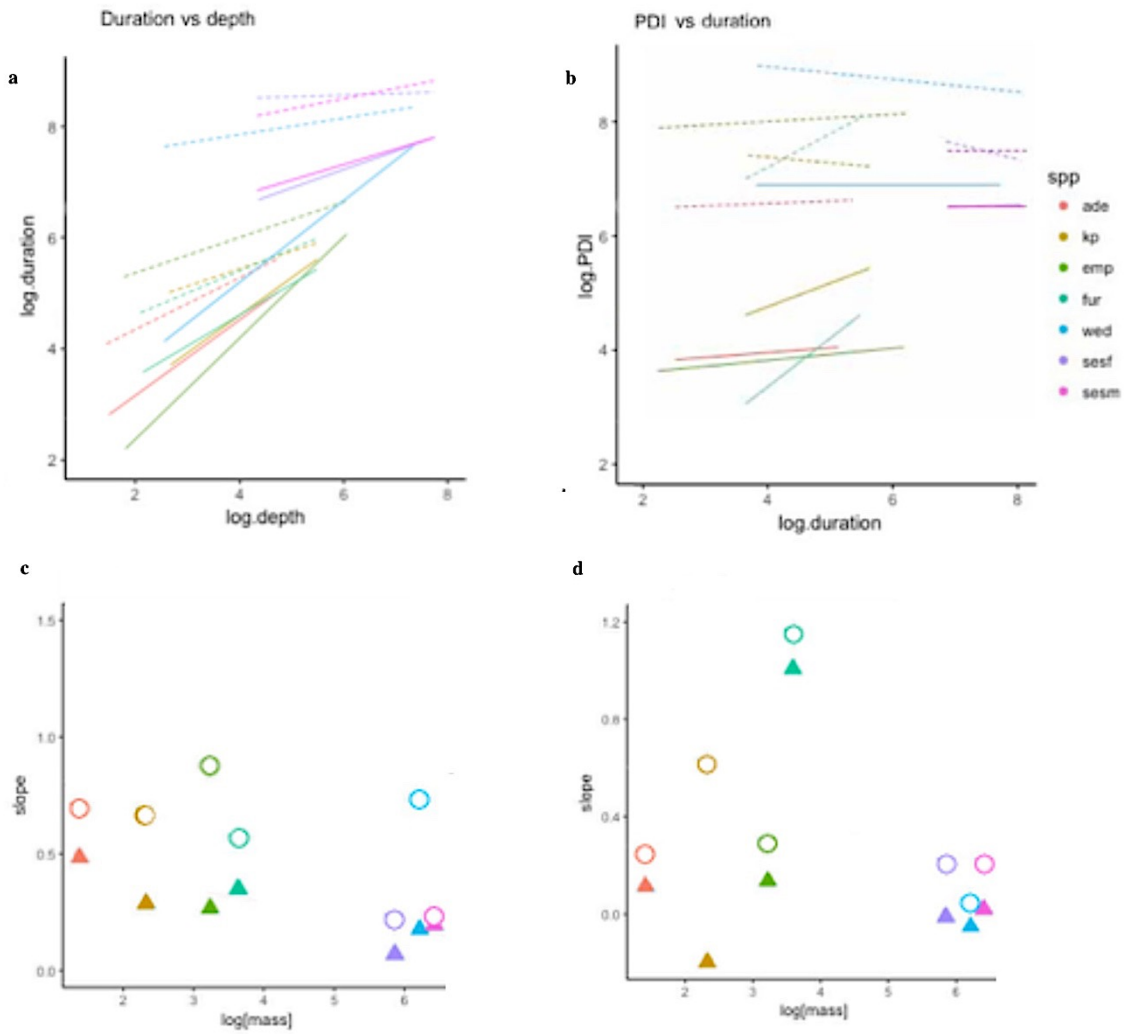
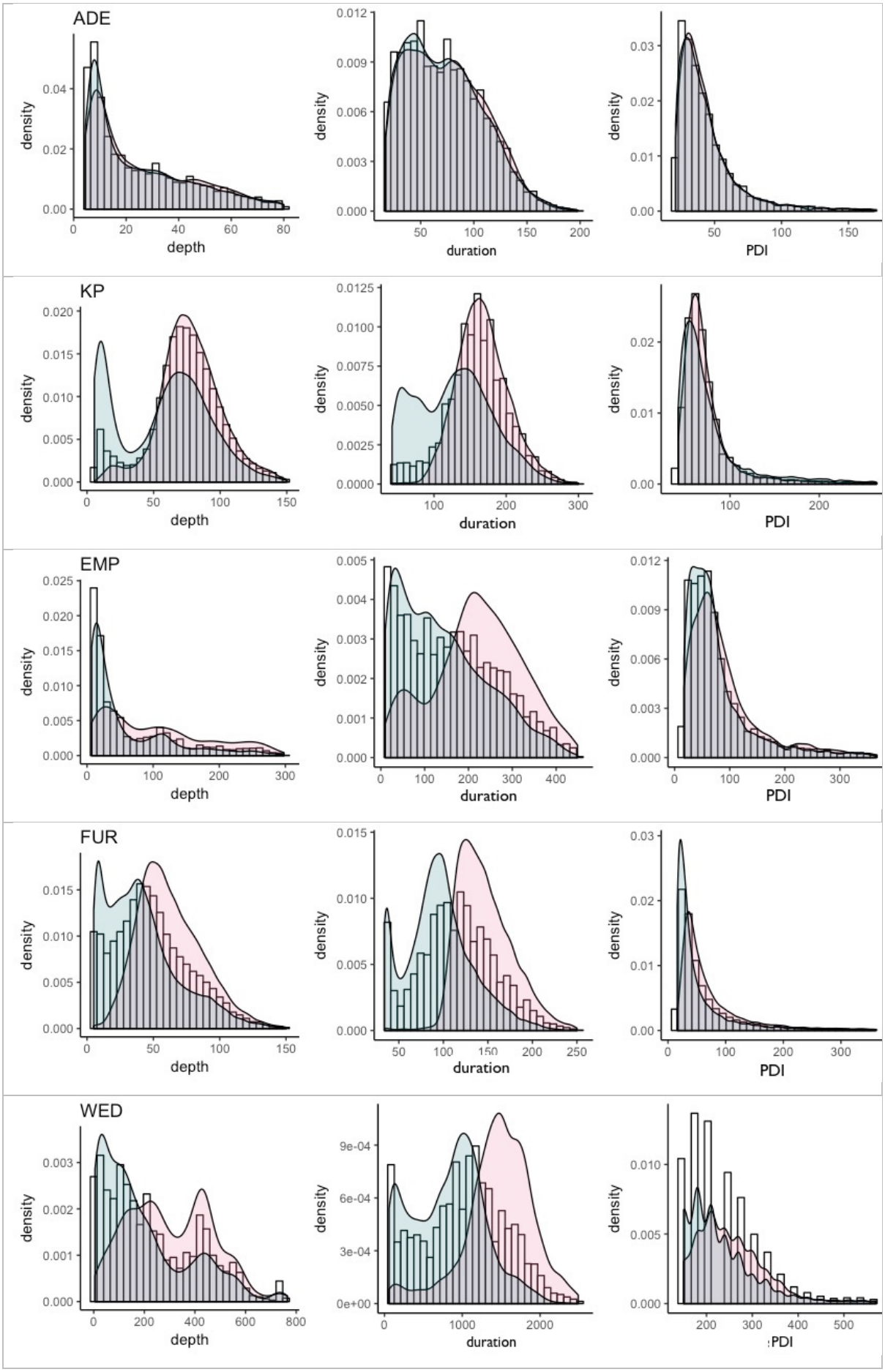


Figure 4. Lower (2.5%) and upper (97.5%) quantile regressions from Fig. 2 and 3 co-plotted for all six seal and penguin species. a) shows the dive duration/depth relationship and b) shows the PDI/duration relationship. Full details of quantile regression results are given in Table S1**.** The regression coefficients (slopes) are plotted against mass for c) duration/depth and d) PDI/duration. In c) and d), triangles correspond to lower quantile slopes; circles correspond to upper quantile slopes (see Fig. 2, 3).

Part 2: Behavioral changes during non-foraging and foraging (high and low hunting time) dives

Across species, the hunting time method identified the majority of dives (60%) as foraging dives, i.e. containing sinuous vertical segments indicative of active hunting. Using this approach, king penguins and southern elephant seals seemed to dive predominantly to forage (king penguins: 79%; southern elephant seals: 74% female, 88% male) (**Table 1**). The average hunting time per dive differed substantially between the six species, ranging from 35.7 ± 47.1 – 886.1 ± 25.3 s (i.e., about 0.5 – 15 min).

The depth distribution of hunting time was apparently deeper in several species (**Fig. 5,** and **Table 2)**. The model results confirmed that high-HT dives were typically deeper than low-HT dives for all species except Adélie penguins, which showed no difference. Differences between no- and low-HT dives were more variable among species; no-HT dives were either slightly shallower (emperor penguins and fur seals), deeper (male SES) or statistically not different (Adélie and king penguins, and female SES) (**Table 2**).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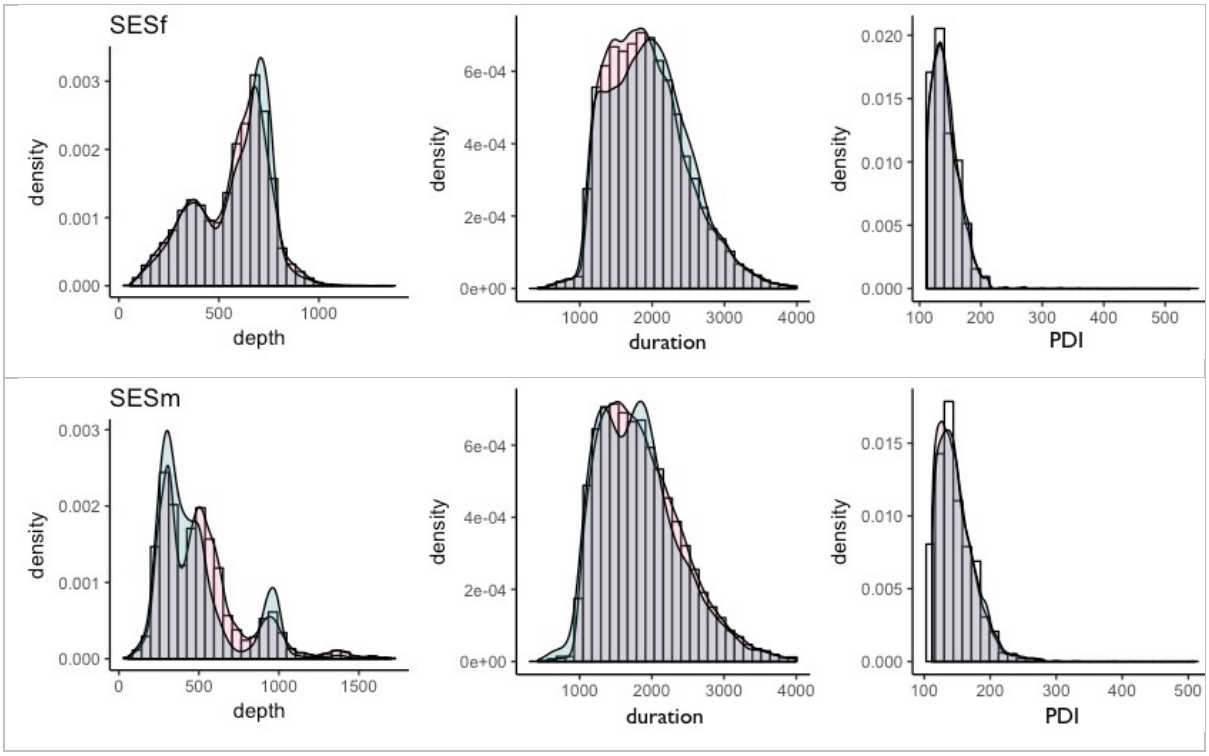

Figure 5. Histogram with density distributions for depth, duration and PDI of dive observations during non-foraging and foraging dives across species. Blue area corresponds to "no-HT" dive distribution, pink area corresponds to "HT" dive distribution, histogram shows all observations. Densities were fitted separately to hunting and no-hunting data. Species abbreviations as in Fig. 2.

Table 2. Summary of models examining depth changes during no-, low- and high-hunting time dives across species. The results showed here are from single factor linear mixed-effect models fit including individual as a random intercept and a temporal autocorrelation term (corAR1) to account for serial non-independence in the time-series data*. Dives (total N = 185,119) were separated as non-foraging (no-HT), low foraging intensity (low-HT) and high foraging intensity (high-HT) for each species (see Methods). Low-HT was the reference level in the predictor variable. Model predictions show mean and 95% CI of dive depth during each different type of dive for each species (predicted values are back-transformed from log-scale). The important significant effects (p <0.001) are highlighted in bold. Note zero probabilities simplify very small values <0.00001.

	Predictor (categorical factor)	**Coefficient (m) ± s.e.**	t	p	**Predicted no-HT**	**Predicted low-HT**	**Predicted high-HT**
Adélie penguin (**N** = 21115 dives, n = 16 individuals)	No-HT	0.015 ± 0.013	-1.12	0.26	16 (13 – 19)	16 (14 – 19)	16 (14 – 19)
	Low-HT	2.79 ± 0.07	37.91	0			
	High-HT	0.006 ± 0.009	0.65	0.51			
King penguin (N = 36223, n = 26)	No-HT	0.014 ± 0.005	3.05	0.0023	52 (46 –59)	52 (46 – 58)	73 (64 – 82)
	Low-HT	3.94 ± 0.06	70.28	0			
	High-HT	**0.34 ± 0.005**	68.36	**0**			
Emperor penguin (N = 5723, n = 9)	No-HT	**-0.18 ± 0.04**	-5.31	**0**	43 (36 – 52)	52 (46 – 58)	78 (66 – 92)
	Low-HT	3.95 ± 0.06	66.63	0			
	High-HT	**0.40 ± 0.02**	16.73	**0**			
Antarctic fur seal (N = 35380, n = 26)	No-HT	**-0.02 ± 0.003**	-6.12	**0**	43 (42 – 44)	44 (43 – 45)	46 (45 – 48)
	Low-HT	3.78 ± 0.01	327.48	0			
	High-HT	**0.06 ± 0.002**	22.01	**0**			
Southern elephant seal (F) (N = 46282, n = 6)	No-HT	0.008 ± 0.005	1.70	0.09	449 (391 – 515)	445 (392 – 506)	465 (406 – 533)
	Low-HT	6.10 ± 0.07	93.55	0			
	High-HT	**0.04 ± 0.004**	10.19	**0**			
Southern elephant seal (M) (N = 40396, n = 6)	No-HT	**0.10 ± 0.004**	23.34	**0**	397 (335 – 471)	361 (307 – 424)	398 (336 – 473)
	Low-HT	5.89 ± 0.08	71.25	0			
	High-HT	**0.10 ± 0.005**	20.90	**0**			

*Note that an equivalent linear model was fit to the Weddell seal data (see Supplementary Material S1).

Following on from the dive range investigation in Part 1, I evaluated the extent to which the relationships in a suite of dive parameters varied when animals forage. Accounting for the dependencies between dive parameters, the LMMs (**Table 3** – **6**) provide insight into how dive performances may change with different levels of activity (i.e., between dives containing no-, low- and high-hunting time).

How does dive duration change when air-breathing marine predators are actively hunting?

Dive duration increased with dive depth in all species; however, not all predators exhibited the same changes in duration during high-, low-, and no-HT dives (**Table 3**, **Fig. 6**). There was no difference in dive duration in Adélie penguins, or the nature of their duration/depth relationship in the three dive types examined. However, in king penguins, fur seals, female and male elephant seals (accounting for the depth dependency) dive durations were consistently longer during high-HT dives than low- or no-HT dives, and in most cases this difference was most pronounced at shallower dive depths (significant negative depth:high-HT interaction term in all cases except for female elephant seals). In contrast, emperor penguins were predicted to dive longer at deeper depths during high-HT dives. Low- and no-HT dives patterns differed across species, but among king penguins, female and male elephant seals dive durations changed more strongly in relation to depth, i.e., varied more strongly during no-HT dives (significant positive depth:no-HT interaction term).

Are longer dive bottom times evident during high-hunting dives?

Results of dive bottom time (**Table 4, Fig. 7**) were generally in accordance with those described above for duration. For Adélie penguins, there was again no differences between dive types. Species with longer dive durations during high-HT dives generally also had longer bottom times (king penguins, fur seals and male elephant seals). Notably, while in most cases bottom times increased during deeper, longer dives, for fur seals bottom time significantly decreased with depth during all dive types.

Do air-breathing marine predators show reduced dive transit times when hunting?

Total dive transit time was positively correlated with dive depth in all species for all dive types (**Table 5**, **Fig. 8**), but predicted changes during no-, low- and high-HT dives varied considerably across species. For example, at shallower dive depths predicted transit

times could be higher (fur seals, emperor penguins and male southern elephant seals) or lower (king penguins) during non-hunting dives, or did not change (Adélie penguins).

Is there an increased cost associated with high-intensity foraging, requiring increased PDI?

Post-dive surface intervals increased with longer dive durations in all cases (Table 6, Fig. 9), but for Adélie and emperor penguins this relationship was statistically not different between low-, no- and high-HT dives. For king penguins, fur seals, male and female elephant seals, PDI increased more strongly with increased dive duration during low-HT dives than predicted during high-HT dives (significant negative duration:high-HT interaction term in all four cases). This indicates that PDIs are more consistent (i.e., vary less with dive duration) during high-HT dives, and can result in shorter PDIs associated with longer dives. This implies that actively foraging animals shortened PDIs, potentially in an effort to return quickly to the forage patch.

Table 3. Results of linear mixed effects models examining dive duration in relation to depth for no-, low- and high-hunting dives. Models are fit separately to each species, see Methods for details of diving parameters and model fitting. Low-HT was the reference level in the dive type predictor variable. The important significant effects ($p < 0.001$) are highlighted in bold. See Fig. 2 for species abbreviation.

Species	Dive variable	Predictor variable	Coefficients		
			Slope (*m*) ± s.e.	*t*	*p*
ADE	Duration	low-HT	2.36 ± 0.030	78.71	0
		log.depth	**0.61 ± 0.008**	**77.71**	**0**
		no-HT	-0.002 ± 0.024	-0.08	0.94
		high-HT	-0.028 ± 0.034	-0.80	0.41
		log.depth*no-HT	0.002 ± 0.008	0.25	0.80
		log.depth*high-HT	0.008 ± 0.011	0.67	0.50
KP	Duration	low-HT	3.21 ± 0.02 0	146.10	0
		log.depth	**0.42 ± 0.004**	**96.51**	**0**
		no-HT	**-0.41 ± 0.020**	**-20.79**	**0**
		high-HT	**0.42 ± 0.030**	**16.50**	**0**
		log.depth*no-HT	**0.09 ± 0.005**	**19.61**	**0**
		log.depth*high-HT	**-0.06 ± 0.006**	**-10.67**	**0**
EMP	Duration	low-HT	3.02 ± 0.100	32.24	0
		log.depth	**0.50 ± 0.020**	**26.76**	**0**
		no-HT	-0.21 ± 0.090	-2.33	0.02
		high-HT	-0.29 ± 0.100	-2.79	0.005
		log.depth*no-HT	0.05 ± 0.020	2.38	0.02
		log.depth*high-HT	**0.10 ± 0.020**	**4.15**	**0**
FUR	Duration	low-HT	3.44 ± 0.030	121.32	0
		log.depth	**0.36 ± 0.006**	**58.35**	**0**
		no-HT	**-0.13 ± 0.030**	**-5.10**	**0**
		high-HT	**0.37 ± 0.030**	**11.98**	**0**
		log.depth*no-HT	0.005 ± 0.006	0.75	0.45
		log.depth*high-HT	**-0.05 ± 0.008**	**-6.71**	**0**
SESf	Duration	low-HT	4.47 ± 0.040	105.04	0
		log.depth	**0.47 ± 0.004**	**104.31**	**0**
		no-HT	**-0.27 ± 0.040**	**-6.87**	**0**
		high-HT	**0.33 ± 0.050**	**6.39**	**0**
		log.depth*no-HT	**0.05 ± 0.006**	**7.08**	**0**
		log.depth*high-HT	-0.02 ± 0.008	-2.66	0.008
SESm	Duration	low-HT	4.03 ± 0.05	88.45	0
		log.depth	**0.52 ± 0.003**	**155.85**	**0**
		no-HT	**-0.64 ± 0.040**	**-16.84**	**0**
		high-HT	**1.96 ± 0.030**	**59.03**	**0**
		log.depth*no-HT	**0.13 ± 0.007**	**20.04**	**0**
		log.depth*high-HT	**-0.26 ± 0.006**	**-46.74**	**0**

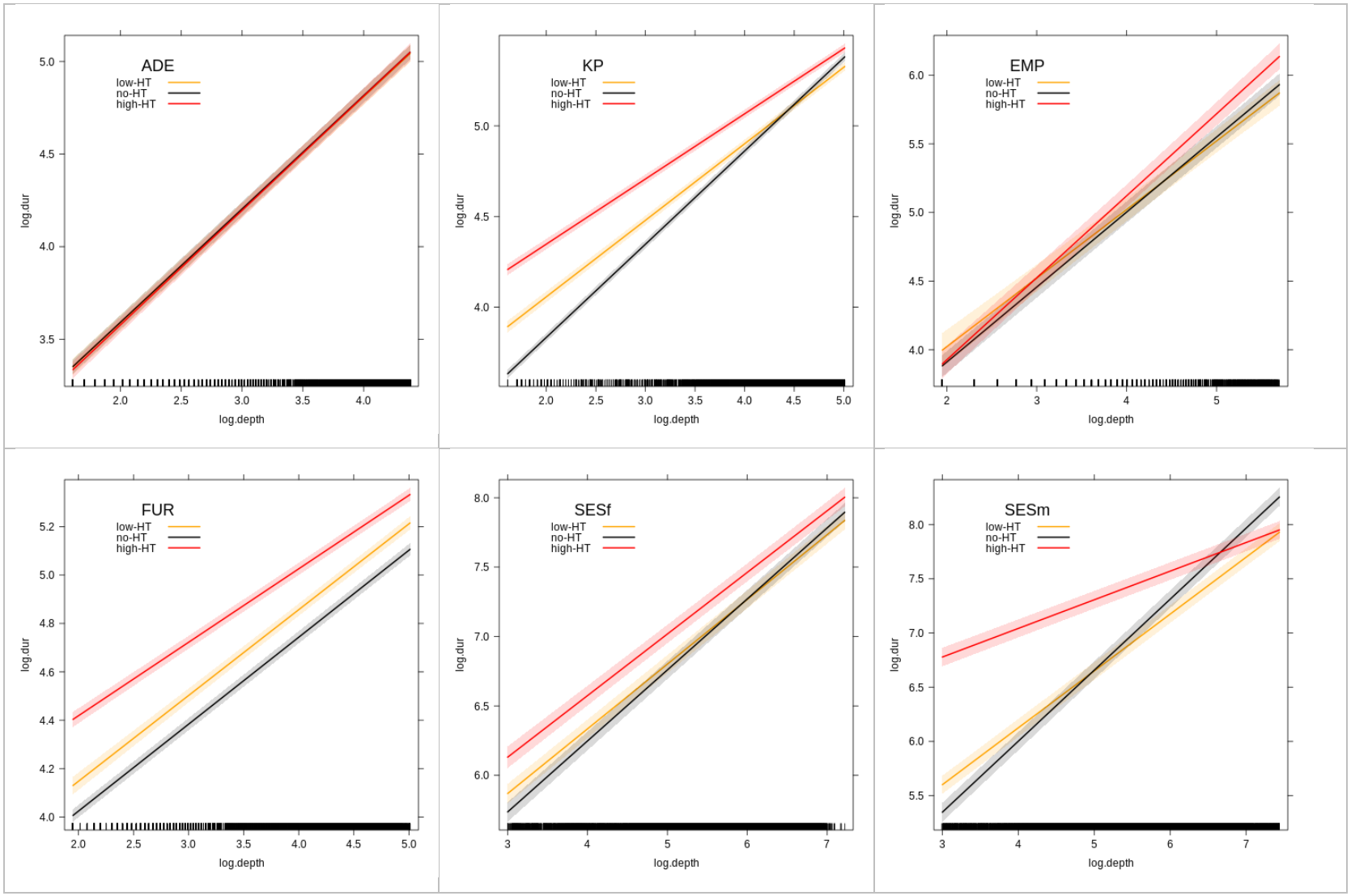
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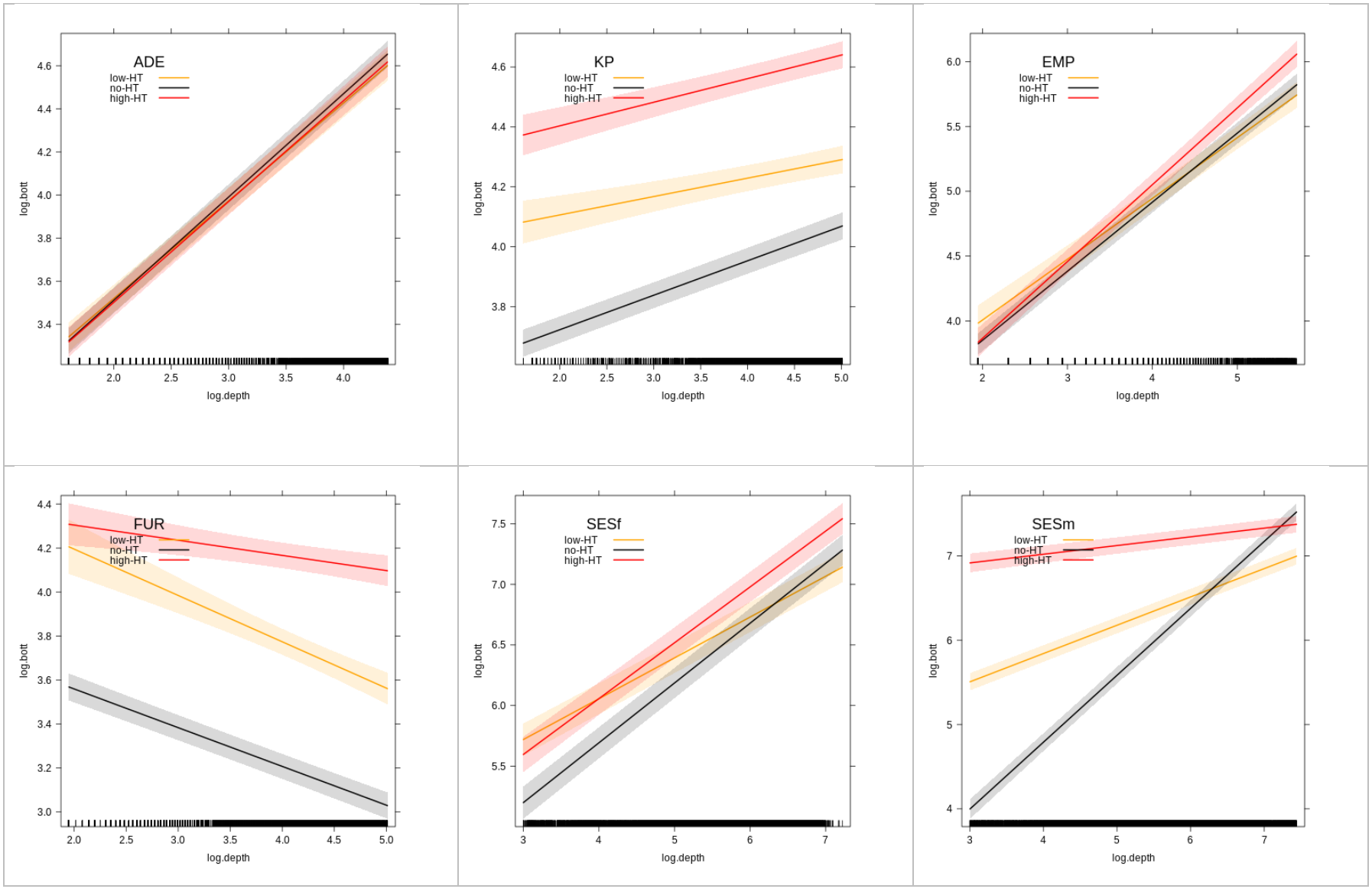
Figure 6. Results from linear mixed effects models examining dive duration in relation to depth for no-, low- and high-hunting dives. Solid lines show the prediction from the linear mixed models fitted separately for each species; shading gives confidence intervals. Full model results are given in Table 3. Species abbreviations are as in Fig. 1.

Table 4. Results of linear mixed effects models examining dive bottom time in relation to depth for no-, low- and high-hunting dives. Results presented as in Table 3.

Species	Dive variable	Predictor variable	Coefficients		
			Slope (*m*) ± s.e.	*t*	*p*
ADE	Bottom time	low-HT	2.61 ± 0.05	58.27	0
		log.depth	0.45 ± 0.01	40.23	**0**
		no-HT	-0.06 ± 0.03	-1.73	0.08
		high-HT	-0.05 ± 0.05	-0.94	0.35
		log.depth*no-HT	0.03 ± 0.01	2.19	0.03
		log.depth*high-HT	0.014 ± 0.01	0.86	0.39
KP	Bottom time	low-HT	3.98 ± 0.05	76.97	0
		log.depth	**0.06 ± 0.01**	**5.57**	**0**
		no-HT	**-0.49 ± 0.05**	**-9.91**	**0**
		high-HT	**0.26 ± 0.06**	**4.14**	**0**
		log.depth*no-HT	**0.05 ± 0.01**	**4.53**	**0**
		log.depth*high-HT	0.02 ± 0.01	1.17	0.24
EMP	Bottom time	low-HT	3.07 ± 0.1	28.98	0
		log.depth	**0.47 ± 0.02**	**21.88**	**0**
		no-HT	-0.28 ± 0.10	-2.81	0.005
		high-HT	-0.39 ± 0.12	-3.24	0.001
		log.depth*no-HT	0.06 ± 0.02	2.83	0.005
		log.depth*high-HT	**0.12 ± 0.03**	**4.57**	**0**
FUR	Bottom time	low-HT	4.62 ± 0.11	42.44	0
		log.depth	**-0.21 ± 0.03**	**-8.35**	**0**
		no-HT	**-0.70 ± 0.11**	**-6.52**	**0**
		high-HT	-0.17 ± 0.13	-1.34	0.17
		log.depth*no-HT	0.03 ± 0.03	1.32	0.19
		log.depth*high-HT	**0.14 ± 0.03**	**4.51**	**0**
SESf	Bottom time	low-HT	4.71 ± 0.08	59.56	0
		log.depth	**0.34 ± 0.008**	**42.86**	**0**
		no-HT	**-0.99 ± 0.07**	**-14.41**	**0**
		high-HT	**-0.50 ± 0.09**	**-5.47**	**0**
		log.depth*no-HT	**0.16 ± 0.01**	**13.92**	**0**
		log.depth*high-HT	**0.12 ± 0.01**	**8.37**	**0**
SESm	Bottom time	low-HT	4.50 ± 0.06	71.73	0
		log.depth	**0.34 ± 0.007**	**48.51**	**0**
		no-HT	**-2.88 ± 0.08**	**-36.61**	**0**
		high-HT	**2.10 ± 0.07**	**30.90**	**0**
		log.depth*no-HT	**0.46 ± 0.01**	**34.22**	**0**
		log.depth*high-HT	**-0.23 ± 0.01**	**-20.30**	**0**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362 **Figure 7. Results from linear mixed effects models examining dive bottom time in relation to dive depth during no-, low- and high-hunting dives.**
363 Results are presented as in Fig. 6.

Table 5. Results of linear mixed effects models examining dive transit time in relation to dive depth for no-, low- and high-hunting dives. Results presented as in Table 3.

Species	Dive variable	Predictor variable	Coefficients		
			Slope (*m*) ± s.e.	*t*	*p*
ADE	Transit time	low-HT	-1.20 ± 0.08	-15.35	0
		log.depth	**1.08 ± 0.03**	**42.37**	**0**
		no-HT	0.07 ± 0.08	0.95	0.34
		high-HT	-0.10 ± 0.11	-0.91	0.36
		log.depth*no-HT	-0.03 ± 0.03	-1.23	0.22
		log.depth*high-HT	0.04 ± 0.04	1.09	0.28
KP	Transit time	low-HT	-0.19 ± 0.05	-4.05	0.0001
		log.depth	**1.04 ± 0.01**	**95.76**	**0**
		no-HT	**-0.60 ± 0.05**	**-12.39**	**0**
		high-HT	-0.05 ± 0.06	-0.77	0.44
		log.depth*no-HT	**0.17 ± 0.01**	**14.28**	**0**
		log.depth*high-HT	0.004 ± 0.01	0.27	0.79
EMP	Transit time	low-HT	-0.41 ± 0.19	-2.23	0.03
		log.depth	**0.60 ± 0.03**	**17.66**	**0**
		no-HT	**0.56 ± 0.16**	**3.49**	**0.0005**
		high-HT	0.43 ± 0.19	2.30	0.02
		log.depth*no-HT	**-0.12 ± 0.04**	**-3.43**	**0.0006**
		log.depth*high-HT	-0.10 ± 0.04	-2.38	0.02
FUR	Transit time	low-HT	1.90 ± 0.030	63.11	0
		log.depth	**0.62 ± 0.007**	**91.92**	**0**
		no-HT	**0.31 ± 0.030**	**10.66**	**0**
		high-HT	0.10 ± 0.030	3.01	0.003
		log.depth*no-HT	**-0.07 ± 0.007**	**-10.11**	**0**
		log.depth*high-HT	-0.02 ± 0.008	-2.03	0.04
SESf	Transit time	low-HT	1.43 ± 0.050	30.83	0
		log.depth	**0.79 ± 0.006**	**127.10**	**0**
		no-HT	0.11 ± 0.050	2.11	0.03
		high-HT	**0.53 ± 0.070**	**7.38**	**0**
		log.depth*no-HT	-0.01 ± 0.009	-1.49	0.14
		log.depth*high-HT	**-0.07 ± 0.010**	**-6.33**	**0**
SESm	Transit time	low-HT	1.06 ± 0.070	14.10	0
		log.depth	**0.86 ± 0.006**	**156.23**	**0**
		no-HT	**0.82 ± 0.060**	**13.03**	**0**
		high-HT	**0.42 ± 0.050**	**7.69**	**0**
		log.depth*no-HT	**-0.10 ± 0.010**	**-9.43**	**0**
		log.depth*high-HT	**-0.0 8± 0.009**	**-8.88**	**0**

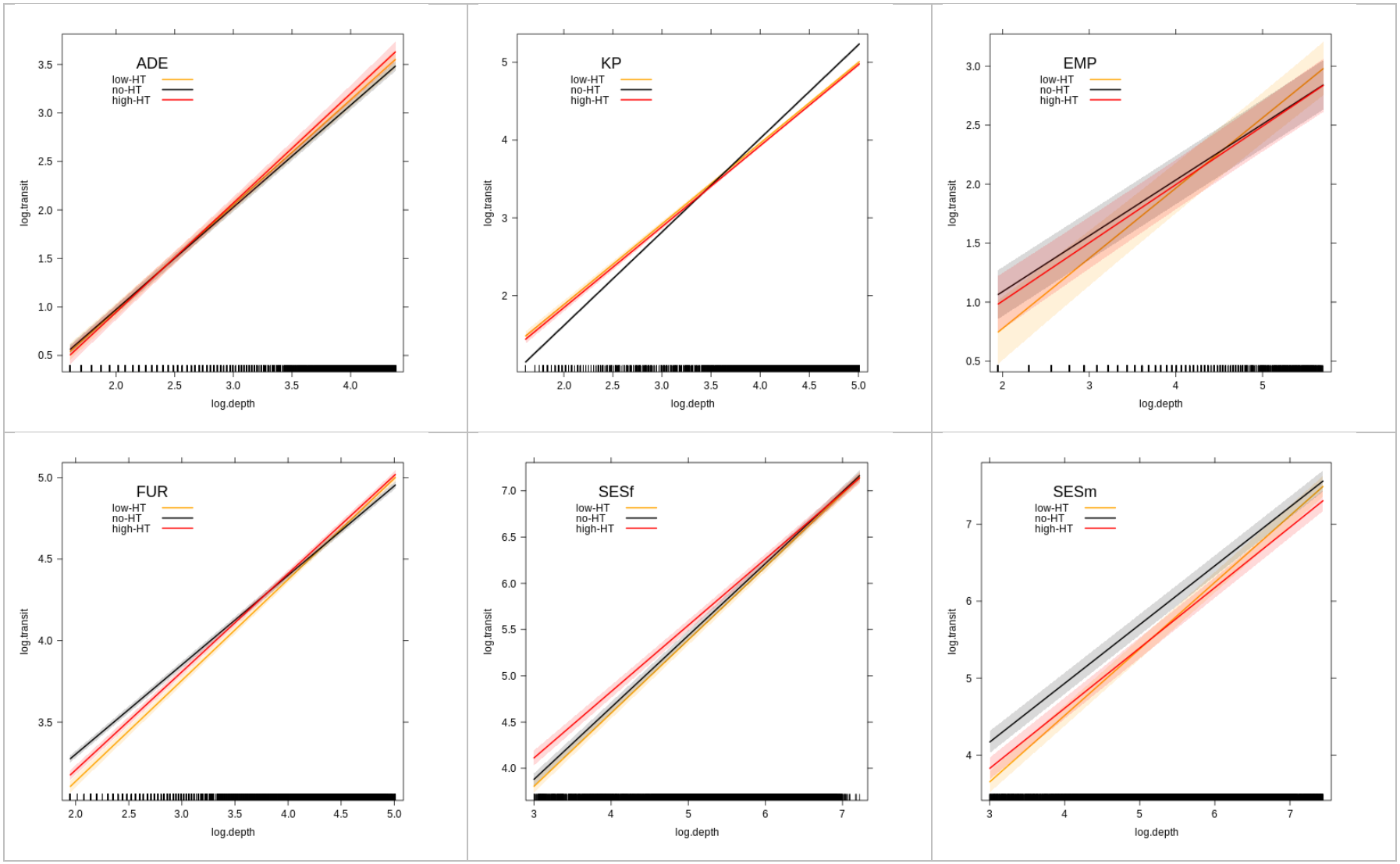

Figure 8. Results from linear mixed effects models examining transit time in relation to dive depth during no-, low- and high-hunting dives.

Results are presented as in **Fig. 6**.

370 **Table 6. Results of linear mixed effects models examining PDI in relation to dive duration for**
371 **no-, low- and high-hunting dives.** Results presented as in Table 3.

Species	Dive variable	Predictor variable	Coefficients		
			Slope (*m*) ± s.e.	*t*	*p*
ADE	PDI	low-HT	2.15 ± 0.20	10.70	0
		log.duration	**0.31 ± 0.04**	**7.25**	**0**
		no-HT	-0.48 ± 0.18	-2.63	0.009
		high-HT	0.11 ± 0.26	0.43	0.66
		log.duration*no-HT	0.12 ± 0.04	2.77	0.006
		log.duration*high-HT	-0.02 ± 0.06	-0.03	0.76
KP	PDI	low-HT	0.90 ± 0.16	5.53	0
		log.duration	**0.67 ± 0.03**	**22.69**	**0**
		no-HT	**0.91 ± 0.16**	**5.72**	**0**
		high-HT	**1.04 ± 0.22**	**4.71**	**0**
		log.duration*no-HT	**-0.16 ± 0.03**	**-4.98**	**0**
		log.duration*high-HT	**-0.23 ± 0.04**	**-5.37**	**0**
EMP	PDI	low-HT	1.42 ± 0.44	3.23	0.001
		log.duration	**0.57 ± 0.08**	**7.25**	**0**
		no-HT	0.84 ± 0.43	1.96	0.05
		high-HT	1.15 ± 0.50	2.30	0.02
		log.duration*no-HT	-0.18 ± 0.08	-2.16	0.03
		log.duration*high-HT	-0.23 ± 0.09	-2.42	0.02
FUR	PDI	low-HT	-8.21 ± 0.28	-29.80	0
		log.duration	**2.52 ± 0.06**	**45.33**	**0**
		no-HT	**2.25 ± 0.28**	**7.96**	**0**
		high-HT	**1.52 ± 0.35**	**4.33**	**0**
		log.duration*no-HT	**-0.44 ± 0.06**	**-7.63**	**0**
		log.duration*high-HT	**-0.36 ± 0.07**	**-5.10**	**0**
SESf	PDI	low-HT	2.17 ± 0.060	34.84	0
		log.duration	**0.36 ± 0.007**	**48.76**	**0**
		no-HT	0.13 ± 0.070	1.79	0.07
		high-HT	**1.16 ± 0.100**	**11.19**	**0**
		log.duration*no-HT	-0.02 ± 0.010	-1.75	0.08
		log.duration*high-HT	**-0.16 ± 0.010**	**-11.19**	**0**
SESm	PDI	low-HT	1.49 ± 0.070	22.04	0
		log.duration	**0.46 ± 0.008**	**55.53**	**0**
		no-HT	**0.75 ± 0.10**	**7.91**	**0**
		high-HT	**2.40 ± 0.11**	**21.10**	**0**
		log.duration*no-HT	**-0.10 ± 0.01**	**-7.71**	**0**
		log.duration*high-HT	**-0.32 ± 0.02**	**-21.13**	**0**

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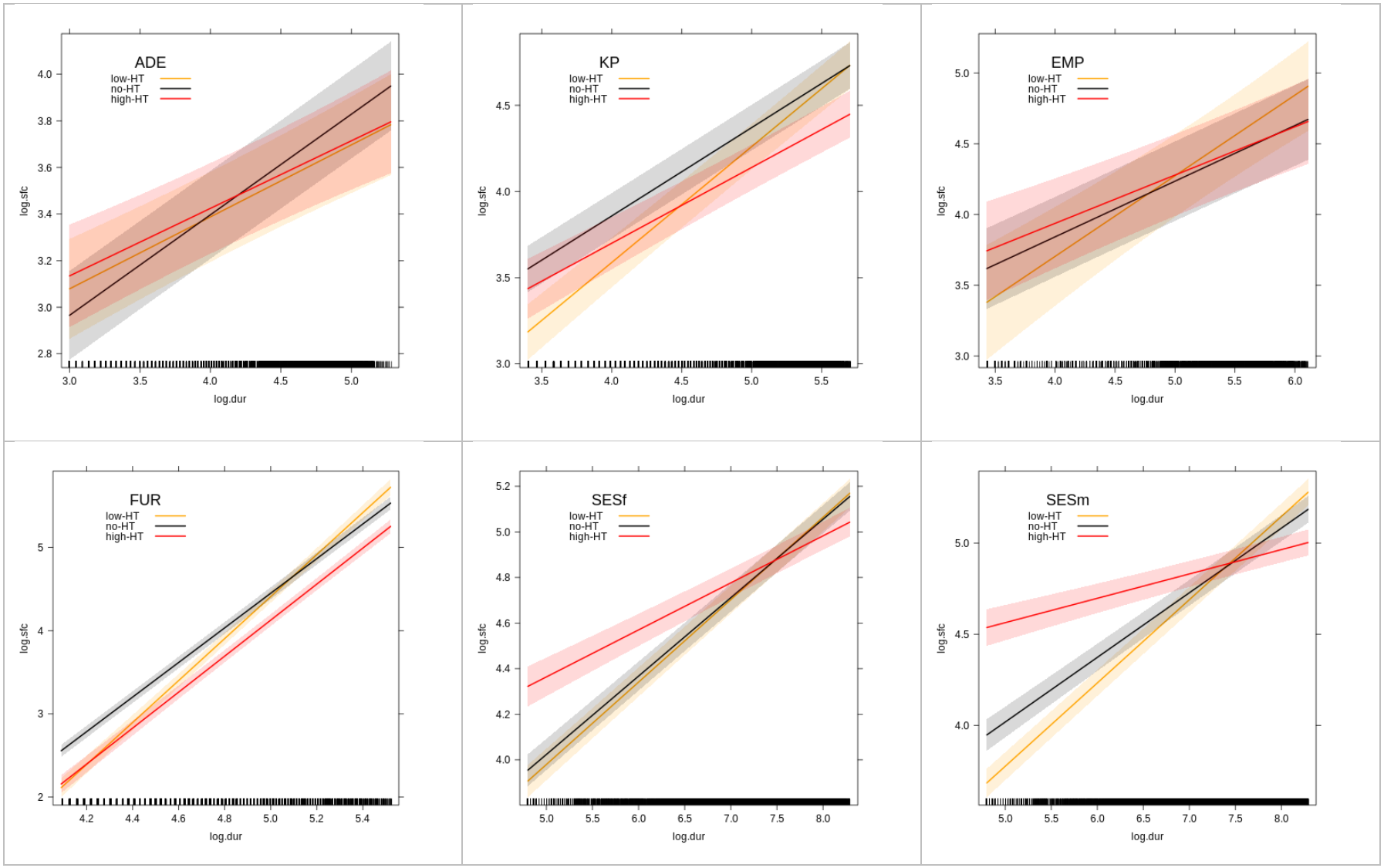

373 **Figure 9. Results from linear mixed effects models examining PDI in relation to dive duration during no-, low- and high-hunting dives.** Results are
374 presented as in **Fig. 6**.

Discussion

Despite the many morphological and physiological specializations for feeding underwater, marine predator diving behavior is constrained by the animal's need to return to the surface to breathe (Boyd, 1997). Within these limits, I observed high levels of variation and plasticity within among East Antarctic seals and penguins.

Part 1: Marine predators' performance range

Across species, seals and penguins perform a wide range of diving behaviors with regard to depth, dive duration and PDI (Table 2). Most species remained well within their cADL while diving (Fig. 2), performing predominantly aerobic dives. Anaerobic dives are costly in terms of oxygen consumption and the longer time spent at the surface to metabolise the lactic acid (Kooyman et al., 1985), which may be the reason why predators tend to remain within their aerobic dive limit. My results agreed with those in previous studies and showed that only a relatively small percentage of dives was anaerobic (Adélie penguins 10%, Culik at al., 1994; king penguins 30%, Culik et al., 1996; emperor penguins 5%, Ponganis et al., 1999; Antarctic fur seals 17%, Costa et al., 2001; Weddell seals 10-20%, Ponganis et al., 1993; southern elephant seals female 44%, southern elephant seals male 1%, Hindell at al. 1992). However, larger species like Weddell seals and southern elephant seals appeared to methodically exceed their cADL suggesting that these species might use other physiological mechanisms that reduce their metabolic rate (Wright and Davis, 2006).

Typically, dive depth was positively related to dive duration so that deeper dives tend to be longer (Fig. 2) in smaller species, such Adélie and emperor penguins; both species performed short and long dives, while southern elephant seals had the capacity to constantly perform very long and deep dives without substantially changing their PDIs (Fig. 3). Butler and Jones (1997) demonstrated that southern elephant seals represent an extreme example of divers, performing continuous long dives at sea and compensating the oxygen debt only during periodical haulout later at the beach. Halsey et al. (2006a) reported that body mass has a greater influence on dive relationships in smaller species (diving shallower and shorter than larger ones) because of the correlation between oxygen stores and body size (Butler and Jones 1982). Dive duration is limited by the physiological adaptations that determine an animal's capacity of storing oxygen, as well as minimising its consumption while swimming. Consequently, similar-sized species like emperor, Antarctic fur seals and king penguins were expected to reach the same depth, and spend the same amount of time underwater. But my results showed that emperor penguins dived deeper and longer than the other two species (Fig. 3). Arthur et al. (2016) noted that Antarctic fur seals change their diving behavior seasonally, swimming shallower and for shorter time during the breeding season. Similarly, king penguin data used here were recorded during the breeding season when these animals generally travel to areas of predictable food resources to maximize their foraging success (Wienecke and Robertson, 2006). Moreover, during winter, the sea-ice extent reduces access to the water preventing

emperor penguins to hunt over the continental shelf. Therefore, emperor penguins foraged at the shelf slope, and dive longer and deeper to reach their prey (Wienecke et al., 2007).

Species dive behavior is also influenced by factors such as the habitat where animals are feeding (benthos vs pelagic), prey assemblages and prey types. Narwhals (*Monodon Monoceros*) and belugas (*Delphinapterus leucas*) are similar in size to southern elephant seals, and have been recorded to dive to similar depths (Laindre et al., 2003; Martin and Smith, 1992); however, these species generally dive within the top 500 m of the water column, and only occasionally dive to < 1000 m. Narwhals and belugas are pelagic feeders hunting predominantly on polar cod (*Boreogadus saida*) which occurs in shallow near shore and deep offshore habitats (>500 m) (Bradstreet, 1982; Marcoux et al., 2012). In contrast, male southern elephant seals are benthic feeders; previously they have been described to continuously dive to the seafloor (McConnell et al., 1996). Sperm whales and beaked whales are also feeding on benthic species, the former spending ~ 75% of their time foraging cephalopods at depth (Whitehead and Weilgart, 1991), and the latter targets high-quality prey near the seafloor (Madsen et al., 2005). Pelagic feeders may also constantly target the same depth. King penguins, for example, specialist consumers of myctophid fish at Falkland Islands (Cherel et al., 2002), are able to dive to > 300 m. However, they usually dive to a depth of 55 ± 16 m where they probably encounter aggregations of their prey particularlyduring twilight hours) (Püttz and Cherel, 2005). Blue-eyed shags at South Georgia, feeding on small crustaceans, tend capture their prey during short, shallow dives (Wanless et al., 1992).

Part 2: Dive plasticity

Air-breathing marine animals find their food resources underwater, and because these are not evenly distributed in space and time, they need to maximize their time underwater while simultaneously minimizing their cost (Houston and Carbone, 1992). Consequently, their diving behavior is a reflection of the strategies used by a given species to search and catch prey (Boyd et al., 1994).

I used the hunting index to discriminate between foraging and non-foraging dives, and found that the majority of dives were performed to forage (**Table 2**). The hunting time method evaluates the vertical sinuosity of each segment of a dive and segments with high sinuosity are identified as hunting phase (Heerah et al., 2014). This method was originally developed on Weddell seals (~ 500 kg) dive data (Heerah et al., 2004), and its usage in the study of smaller species (< 40 kg) did not provide consistent results, especially for Adélie penguins. Adélie penguins are shallow divers and use 'wiggles' as foraging strategy (Bost et al., 2007). Wiggles or undulations, a common dive pattern in penguins (Hanuise et al., 2010), may have missed some foraging events when applying a discrimination method based on the hunting index. In future, different metrics like descent/ascent rate (Gallon et al., 2013; Richard et al., 2014) or speed (Horsburgh et al., 2008; Kokubun et al., 2011; Viviant et al., 2014) should be considered. It is also possible to combine TDR data with other independent source of information, such

as cameras (Hooker et al., 2015; Watanabe and Takahashi, 2013) and/or stomach and esophagial thermometers (Bost et al., 2007; Horsburgh et al., 2008) to confirm foraging events.

In general, most species in this study performed deeper and longer dives when hunting than when not hunting (**Table 3**). I sought to determine whether air-breathing marine predators can extend their performance during intensive foraging dives. Four of the five species examined were able to adjust their foraging behavior during low- and high-hunting dives, prolonging dive times when hunting most intensively; this was most pronounced for the shallow dives. Only one species, the emperor penguin, was able to lengthen dive duration during deep foraging dives (Table 3 and Fig. 6). This species seems to have more capacity to modify behavior in deep divespossibly because emperor penguins are able to recover quickly after long dives, and the decline of lactic acid appears to be more rapid compared to larger species (Ponganis et al., 1997). Other studied species may have a limited capacity to adjust the duration of deep dives possibly due to physiological constraints.

This analysis demonstrated that emperor, king penguins, Antarctic fur, and southern elephant seals are flexible in their diving behavior, and can adjust their behavior to respond to the shifts in prey distribution in the water column (Table 3). Adélie penguins did not make any significant changes, possibly due to their small body size. They may already operate close to their dive limits, and are unable to draw upon a greater energy reserve to pursue prey at deeper depth (Costa, 2004).

Foraging dives had longer bottom times and transit times than non-foraging dives across all species. As expected, longer dives corresponded to longer bottom phases. However, in Antarctic fur seals the increase in depth shortened the duration of the bottom time (Table 4). These animals are generally shallow divers and, as showed in Chapter 3, multiple ecological factors play an important role in determine their dive behavior. Moreover, although positive in all species, the relationship between transit time and depth (Table 5) varied across different activity levels among the taxa. This may reflect the fact that marine predators employ different strategies to minimize their transit time, for example, by diving more vertically or swimming faster at the same angle or a mix of both. This cannot be distinguished in this study as I did not have the swim speed data needed to calculate dive angles. However, my findings concur with those of king penguins from the Crozet Archipelago that increased their swim speed during the bottom and early ascent phases of dives (Ropert-Coudert et al., 2000). Beaked whales also increased their swimming speed when actively hunting to quickly reach the seafloor; they also use the echolocation to search, select and capture the prey item (Madsen et al., 2005). Similarly, harbour seals (*Phoca vitulina*) performed shallower dives at a steeper angle to maximize their time at depth when foraging (Heitmaus et al., 2017), and sperm whales increased their ascent pitch angle when feeding (Watwood et al., 2006).

This comparative analysis demonstrated that diving species have considerable flexibility in their dive behavior. Most species were able to increase their dive effort when foraging except for the small

479 species with constraints related to the allometric relationships of O_2 stores and consumption. However, a
480 greater effort is offset by longer surface intervals. Although this influenced their overall cumulative time
481 at depth in the foraging zone, the differences were relatively slight. In fact, when animals have sufficient
482 oxygen buffers they are able to reduce surface times if needed, or at least reduce the time, which allows
483 them to exploit patchy resources effectively (Table 6). Adélie and emperor penguins did not significantly
484 change their behaviors during no-, low- and high-hunting dives possibly because they may already
485 operate close to their dive limits, and are unable to draw upon a greater energy reserve to pursue prey at
486 deeper (Costa, 2004). For the remaining species, PDI increased mostly with increased dive duration
487 during low-HT dives. This implies that when actively foraging, these animals shortened their PDIs
488 potentially in an effort to return quickly to the forage patch.

489 ## Conclusion

490 This study across a diverse group of seals and penguins provides evidence that some species
491 appear to have more plastic dive behaviors than others and, hence, may be able to respond better to
492 changes in their food resources. Consequently, some seabirds and marine mammal species might be more
493 vulnerable to fluctuations in prey abundance mediated through environmental change. Additionally, this
494 work has provided a deeper insight into what determines marine predators' diving capacity and foraging
495 behavior intrinsically (e.g., taxa, body size, sex) and extrinsically (e.g., prey type and distribution).
496

497 ## *Supplementary Material*

498 ## Supplementary S1. Dive telemetry details

499 We compiled time-depth recorder (TDR) data for three penguin and three seal species tagged in Eastern
500 Antarctica deployed between 1992 - 2015 recording time and dive depth. The datasets might also include
501 metadata regarding sex, body mass and/or age of the animals. Details regarding the datasets for most
502 species are identical to that reported in Chapter 3 - Supplementary Material. However, only one Weddell
503 seal high-resolution TDR dataset was available to be used in this study (details below). Since the hunting
504 time method was originally developed for Weddell seals, we retain this dataset as something akin to a
505 "reference level". While inference cannot be drawn for this species from one individual, it enables some
506 evaluation of the method and its performace across the other species. Note that where LMMs are reported
507 across other species, an equivalent linear model was fit to the Weddell seal data.

508 *Weddell seal*

509 Female Weddell seal (n = 1) equipped with TDR (30 s sampling rate) during late January-November
510 2003 at Davis station (77.97°E, 68.58°S) Antarctica.

Table 2.* Summary of the linear model examining depth changes during no-, low- and high-hunting time dives across species. The results showed here are from single factor linear model fit including individual as a random intercept and a temporal autocorrelation term (corAR1) to account for serial non-independence in the time-series data*. Dives (total N = 7241) were separated as non-foraging (no-HT), low foraging intensity (low-HT) and high foraging intensity (high-HT) for each species (see Methods). Low-HT was the reference level in the predictor variable. Model predictions show mean and 95% CI of dive depth during each different type of dive for each species (predicted values are back-transformed from log-scale). The important significant effects ($p < 0.001$) are highlighted in bold.

	Predictor (categorical factor)	**Coefficient (m) ± s.e.**	***t***	***p***	**Predicted no-HT**	**Predicted low-HT**	**Predicted high-HT**
Weddell seal (N = 7241, n = 1)	No-HT	4.98 ± 0.03	186.29	0	38 (35 – 40)	62 (58 – 66)	195 (191 –199)
	Low-HT	5.67 ± 0.04	147.03	0			
	High-HT	5.56 ± 0.04	148.22	0			

Table 3-6*. Results of linear mixed effects models examining dive duration in relation to depth for no-, low- and high-hunting dives. Models are fit separately to each species, see Methods for details of diving parameters and model fitting. Low-HT was the reference level in the dive type predictor variable. The important significant effects ($p < 0.001$) are highlighted in bold. See Fig.2 for species abbreviation.

Species	**Dive variable**	**Predictor variable**	**Coefficients**		
			Slope (m) ± s.e.	***t***	***p***
WED	Duration	**log.depth**	0.07 ± 0.02	3.10	0.002
		no.HT	4.36 ± 0.03	163.28	0
		low.HT	6.82 ± 0.14	48.55	0
		high.HT	7.34 ± 0.09	74.99	0
		log.depth*no.HT	0.38 ± 0.02	15.22	0
		log.depth*high.HT	-0.05 ± 0.03	-1.62	0.1
	PDI	**log.dur**	0.25 ± 0.16	1.51	0.13
		no.HT	4.70 ± 0.11	42.02	0.004
		low.HT	3.46 ± 1.20	2.87	0
		high.HT	2.53 ± 1.23	2.05	0.04
		log.dur*no.HT	-0.18 ± 0.16	-1.07	0.28
		log.dur*high.HT	0.14 ± 0.23	0.62	0.54
	Bottom time	**log.depth**	-0.12 ± 0.40	-2.95	0.31
		no.HT	4.02 ± 0.05	85.97	0
		low.HT	7.68 ± 0.24	31.28	0
		high.HT	7.82 ± 0.17	45.72	0
		log.depth*no.HT	0.57 ± 0.04	13.10	0
		log.depth*high.HT	0.03 ± 0.05	0.50	0.61
	Transit time	**log.depth**	0.64 ± 0.06	11.29	0
		no.HT	2.89 ± 0.06	46.54	0
		low.HT	1.78 ± 0.33	5.43	0
		high.HT	2.54 ± 0.23	11.16	0
		log.depth*no.HT	-0.22 ± 0.06	-3.73	0.0002
		log.depth*high.HT	-0.12 ± 0.07	-1.71	0.08

Supplementary S2. Performance range

Table S1. The relationships between dive duration/depth and PDI/dive duration across taxonomic groups. The results presented here are from a quantile regression (Lower= 0.025; Upper= 0.0975). The regression was fitted across the complete dataset of each species.

	Lower Quantile Line			Upper Quantile Line		
	Slope (*m*) ± s.e.	***t***	***p***	**Slope (*m*) ± s.e.**	***t***	***p***
Log(duration) v log(depth)						
Adélie penguin (**N** = 21,115 dives; n = 16)	0.70 ± 0.005	125.47	0	0.48 ± 0.004	115.09	0
King penguin (N = 36,223; n = 26)	0.67 ± 0.007	91.33	0	0.34 ±0.005	62.93	0
Emperor penguin (N = 5,723; n = 9)	0.87 ± 0.004	181.72	0	0.33 ± 0.01	25.68	0
Antarctic fur seal (N = 35,380; n = 26)	0.56 ± 0.002	191.21	0	0.38 ± 0.004	82.87	0
Weddell seal (N = 7,241; n = 1)	0.73 ± 0.01	64.33	0	0.16 ± 0.01	13.55	0
Southern elephant seal (F) (N = 46,282; n = 6)	0.22 ± 0.006	34.47	0	0.05 ± 0.006	8.33	0
Southern elephant seal (M) (N = 40,396; n = 6)	0.22 ± 0.003	68.41	0	0.18 ± 0.006	29.19	0
Log(duration) v log(depth)						
Adélie penguin	0.24 ± 0.007	30.47	0	0.10 ± 0.02	6.08	0
King penguin	0.61 ± 0.01	54.95	0	-0.2 ± 0.02	-0.84	0
Emperor penguin	0.29 ± 0.02	17.31	0	0.13 ± 0.02	6.20	0
Antarctic fur seal	1.15 ± 0.01	75.74	0	1.02 ± 0.04	26.88	0
Weddell seal	0.04 ± 0.01	33.59	0	-0.07 ± 0.01	-4.78	0
Southern elephant seal (F)	0.2 ± 0.001	139.78	0	-0.04 ± 0.007	-6.29	0
Southern elephant seal (M)	0.2 ± 0.003	69.28	0	0.03 ± 0.006	5.31	0

Chapter 5

General Discussion

The aim of this thesis was to describe the diving ecology of a suite of Southern Ocean air-breathing vertebrates, and to gain new insights into the processes underlying the diving ability of marine predators. By using high-resolution diving data from six species of marine mammals and seabirds, I developed systematic approaches for dive-based indicators under a framework of ecological questions with emphasis on species' morphology, physiology, and life history. Through a comparative analysis of diving behaviors, I determined how specialist pursuit divers manage their dive cycle during foraging and non-foraging dives and I described which intrinsic and extinct factors may constrain an animal's diving performances.

Here I summarize the major findings of my work in a broader ecological context, in particular with regards to three main areas: (1) benefits and limitations of dive-based indicators to describe marine mammal and penguin dive behavior; (2) diving ecology of SO species; (3) a final section integrating my findings into ecosystem modelling.

Marine predators have been recognized and monitored as indicators of ecosystem changes in the Southern Ocean for many years. Developing an integrated and synthetic view of marine mammals' and seabirds' diving ecology is an important first step to be able to develop predictive models for understanding how future climate change will affect this unique biota.

Benefits and limitations of dive-based indicators

Bio-logging studies have used a range of parameters to describe diving behavior of marine animals offering considerable insights into their underwater exploits (Mate et al., 2007; Goldbogen et al., 2013; McIntyre, 2014; Hussey et al., 2015; Naito, 2016; Carter et al., 2016). Simple depth and time data — although giving a greatly simplified representation of the very complex and dynamic three-dimensional environment that marine animals inhabit (Heerah et al., 2014) — nonetheless are invaluable for quantifying underwater behavior, and my work has used best practise techniques to maximise the insights from these basic time-depth records.

Benefits

Telemetry applications have advanced the understanding of how ecologically and taxonomically diverse animals manage their dive cycles and effectively exploit their three dimensional marine environment by investigating dive behavior in their natural habitat (Halsey et al., 2007a; Lyver et al., 2011; Tyson et al., 2012). Ongoing technological innovation has allowed the miniaturization of logger components (especially data-storage and battery), allowing loggers to be attached to a wide range of

species of diverse sizes and minimized the effect of loggers on animal at-sea performance. This has resulted in new insights on at-sea animal migrations and behavior from a wide range of species (e.g., Davis and Boersma, 1996; Takahashi et al., 2018, van Beest et al., 2018, Burns and Castellini, Schorr et al., 2012, Roncon et al., 2018) that provides the critical information needed to inform long-term conservation and management (Hays et al., 2019; Hindell et al., 2020) and have played a central role in long-term monitoring programs for marine birds and mammals in the SO (Trathan et al., 1996; Hussey et al., 2015; Hindell et al., 2017).

The review of dive telemetry presented in Chapter 2 demonstrated how dive data have been used as a tool to make inferences about foraging behavior and diving physiology of Southern Ocean marine predators in the last decade (2006–2016). I found that predator-prey relationships, abundance of prey and their distribution, and foraging strategies, could be studied using simple (e.g., dive bottom time) and/or derived dive-based indicators (e.g., dive residual or hunting time, see Table 3 - Chapter 2), and how adding sensors to a simple time depth package provides invaluable new insights. For example, Takahashi et al. (2008) combined a depth sensor and camera into one data-logger to confirm how the dive pattern of gentoo penguins at King George Island (Antarctica) was influenced by krill swarms' change from benthic to pelagic habitats. Heerah et al. (2013) described which water masses were used by Weddell seals foraging in winter, using a logger that combined dive depth with environmental variables (i.e., Conductivity Temperature Depth Satellite Relayed Data Loggers or CTD-SRDL).

The analytical Chapters 3 and 4 showed how TDR data can be used to quantify the diving performance and/or dive effort of marine predators across a suite of species and also within species. For example, in Chapter 3, I observed that smaller species make shorter, shallower dives with correspondingly shorter surfacing intervals than larger species, and how rarely penguins and seals exceed their cADL, while generally diving performing predominantly aerobic dives (see Chapter 4). This approach was very useful to estimate diving capacity allowing the comparison between species for understanding the general allometric relationships of diving behavior by knowing what is flexible and what is not. Above all, my analysis demonstrated how robust treatment of dive data, applied across a range of species and utilizing the same basic (Chapter 3) and derived (Chapter 4) parameters, can pave the way for integrative multi-species meta-analyses. The results of my work about the influence of body size on dive ability could be easily integrated and compared with those obtained by Schreer and Kovacs (1997) and Halsey et al. (2006a). However, the slopes I found for between-species relationships were considerably higher for dive depth and duration than described by Halsey et al. (2006a). The species I examined are all specialist pursuit divers, and their behaviors offer great insight into how highly adapted species can maximise the time spent underwater.

Limitations

Acquiring information on SO marine mammals and seabirds is expensive and logistically difficult due the remote locations and adverse conditions, resulting in relatively small samples sizes. Consequently, studies are often limited in their inference by the use of repeated time series of relatively few individuals. Nonetheless, combining multiple small datasets of different species can help to develop comparative analyses and strengthen the interpretations of the results (Chapter 3 and 4). Moreover, it is important to scale up from observations of individual animals to the population level, and analytical and statistical approaches linking dive behavior to demography and population size are developing (Hindell et al., 2003; Nevins, 2004; Frydman and Gales, 2007).

Combining multiple sensors on a data-logger maximizes the behavioral inferences that can be made. However, it is usually still difficult to confirm foraging success (Ancel et al., 1992), as for example parameters such as "wiggle" or "bottom time duration" may not indicate prey encounter or capture (see Chapter 2).

The integration of location and environmental data with diving data has the potential to further the understanding of the foraging ecology of marine species (Hindell et al., 2016). How the environment influences marine predators' foraging has been described in seals (Dracon et al., 2010; O'Toole et al., 2014; Labrousse et al., 2015; Hindell et al., 2016), penguins (Kahl et al., 2010; Rey et al., 2009; Lescroël et al., 2015) and cetaceans (Baumgartner et al., 2003; Hazen et al., 2009; Friedlaender et al., 2014). However, more accurate information of predators' behavior remains crucial to identifying their foraging preferences, habitat selection and spatial population ecology. Once these data are obtained, they might be used as inputs for ecosystem modelling (Langrock et al., 2012) and for identifying critical habitat for marine species that could be designed as Marine Protected Areas (Carter et al., 2016), or evaluating existing MPAs (Patterson et al., 2016).

Regarding the physiological adaptions that enable penguins and seals to hunt underwater, precise estimations of physiological variables (e.g., respiration and hormones) are still needed to quantify energy expenditure and allocation for most marine predators. It is difficult and expensive to obtain these measurements in the field. Despite this, successful field studies have recorded, for example, the heart rate of California sea lions (*Zalophus californianus*) during foraging trips at sea (McDonald and Ponganis, 2013), and the abdominal temperature plus heart rate of macaroni penguins at South Georgia over seasons (Green et al., 2005). As logger technology advances, an increasing number of interesting publications are becoming available in this field (Halsey et al., 2020; Okuyama et al., 2020; Wilson et al., 2020).

Finally, it is necessary for researchers to weigh up the benefits of telemetry studies against their potential effects on reproduction, foraging success, energetics and survival of the sampled individuals (McIntyre, 2014). For example, it is necessary to carefully investigate the best attachment location for the tag, i.e., evaluate whether the attachment causes additional energetic cost to the individual or reduces its

foraging skills. Additional energetic costs are important, especially in smaller species, where mass and size of the tag may limit its usage (Wilson and McMahon, 2006). Also, it is important to consider whether conspecifics might react to tag application, and if its deployment could make the individual more vulnerable to predation (Withey et al., 2001). All these factors need to be considered by researchers and ethic committees that oversee research applications, particularly for species of high conservation concern (Hawkins, 2004; McMahon et al., 2011; Puehringer-Sturmayr et al., 2020).

Diving ecology of Southern Ocean marine predators

The diversity of diving behavior in seabirds and marine mammals has evolved under a combination of factors based on the need of animals to balance their energy budget (Kooyman, 1980). Marine predators differ in the degree of plasticity to which they are able to respond to environmental variability. In chapters 3 and 4, I explored the intrinsic and extrinsic determinants of dive ability to assess behavioral plasticity.

Diving determinants

Metabolic physiology ultimately determines the dive capacity and foraging capabilities of an individual animal (Ponganis, 2015), in particular their available oxygen and energy stores, and the rate at which these are consumed in metabolic processes (Costa, 2004). Marine mammals and seabirds must trade their need to acquire resources with the need to breathe (Kooyman and Ponganis, 1998). Physiological and anatomical modifications of the blood, muscle and respiratory systems allow marine mammals and seabirds to increase oxygen storage, and also to reduce oxygen consumption rates while diving (e.g., the dive response). Since oxygen stores appear to scale isometrically with body mass, larger animals are generally able to dive deeper and for longer than animals of smaller size (Halsey at al., 2006a). However, my analyses in chapters 3 and 4 demonstrated that the trade-off between absolute oxygen stores and relative metabolic rate is solved in different ways by different species according to their life-history. I found that the six species I studied are diving longer for a given depth than expected for average birds or mammals (Chapter 3), showing clearly that body mass is not the sole determinant of dive capacity, and that other traits, such as taxonomy, sex and age, also influence marine predators' diving abilities.

In my work, I have only explored briefly the influence of taxonomy on dive capacity. Major differences in birds' and mammals' adaptations to dive are broadly discussed in the review by Kooyman and Ponganis (1998). Different lung structures and respiration processes allow birds to exchange O_2 and CO_2 quicker compared to mammals, but they consume it more quickly. Penguins carry their oxygen in three stores: the blood, lungs and muscle (Cassandra et al., 2014). Marine mammals store most of their oxygen in muscle and blood having a larger blood volume then penguins, and use it slowly used due to physiological mechanisms like the "diving response". My data showed that Antarctic fur seals and king

penguins behave similarly in terms of dive patterns and performances although they belong to different taxa (Chapter 4). King penguins and Antarctic seals showed similar capacity to extend their hunting time in response to changes in prey distribution.

Another aspect that is only partially considered in my work of diving determinants is the sex of the animal. Female Antarctic fur seals change their foraging strategies during breeding by making short, localized foraging trips to provision their pups (Arthur et al., 2016). In contrast, during winter females disperse more widely, dive for longer and deeper possibly hunting fish and squid (Arthur et al., 2016). Similarly, once they left their partner incubating the egg, travelled to areas of predictable food resources to maximize their foraging success and to ensure fast re-building of body reserves (Wienecke and Robertson, 2006). My TDR data were collected during the breeding season, and it is not surprising that some animals were diving shallower and for shorter time compared to studies that collected dive data during a different time of year (e.g., Arthur et al. 2016; Takashi et al., 2018). Female bearded seals (*Erignathus barbatus*) are limited in their movements while nursing, but when pups reach two months of age, they can easily accompany their mothers having adjusted to longer and deeper dives (Gjertz et al., 2000). Recent studies have shown the diving ability of marine mammals and seabirds is not innate, and new-born animals need to develop their dive capacity in terms of physiological adaptations (e.g., harbor porpoise; Elmegaard et al., 2016) and effectiveness of the movement (e.g., king penguin; Le Vaillant et al., 2013).

Finally, the environment appears to be one of the main influences in shaping diving predators' ability in terms of the feeding niches these groups exploit, the bathymetry of their habitat and degree of dependence on specific prey (for more details see Chapter 2 –4). As an example, male and female elephant seals in my study showed very different hunting behaviors. The explanation for such behavior is found in their feeding ecology. Male elephant seals typically forage on benthic prey in relatively shallow shelf waters, while females feed predominantly on mesopelagic prey in the open ocean (Hindell et al., 2016). Takahashi et al. (2003) confirmed that the depth of benthic dives is clearly determined by the bathymetry of the foraging area. At Signy Island, where chinstrap and Adélie penguins hunt the same prey, chinstraps perform shallower dives than Adélies while feeding inshore, while Adélies forage farther offshore (Takahashi et al., 2003).

Behavioral plasticity

Although the effects of some life-history traits are fixed, marine species also show flexible foraging behaviors that vary depending on environmental conditions (Waugh and Weimerskirch, 2003). Behavioral plasticity maximizes the energy gain of an individual, but it has also implications for the performance of a whole population (Croxall et al., 1999). How deep and how much time marine predators spend underwater is closely linked to the feeding strategies they adopt and their foraging preferences. Blue whales (*Balaenoptera musculus*) and the fin whales (*B. physalus*) perform dives short for their size

due to the high feeding cost of hunting euphausiids which disperse very quickly (Acevedo-Gutiérrez et al., 2002). Lunge-feeding behavior limits these whales to shallow dives and reduces their dive duration.

My study showed that penguins and seals appear to be able to vary their dive performance when foraging, but only few species are able to extend their hunting time during intense foraging dives (see Chapter 4 - Part 3). Four of the species were able to adjust their foraging behavior during short and long hunting dives, making relatively long dives when hunting most intensively. Only one species, the emperor penguin, was able to lengthen its dive duration during active deep foraging dives with long hunting time. The behavior of Adélie penguins did not significantly change during short or longer hunting time dives (Chapter 4). My results confirm what has been described in previous studies (e.g., Costa, 2004; Halsey et al., 2006a; Zimmer et al., 2008b) showing that diving behavior is a reflection of the strategies used by the predators to search and catch their prey (Boyd et al., 1994). Living in a dynamic marine environment, air-breathing predators should be adaptable to accommodate changes in prey distribution and abundance (Boyd, 1994). Generalist feeders like harbour seals change their foraging behavior according to the area and availability of clupeids and sandeels (Pierce et al., 1991), and gentoo penguins changed their diet and foraging habits (benthic to pelagic) in different years in response to changes in prey abundance (Miller et al., 2009). Even Adélie penguins, considered specialist feeders hunting predominantly on krill, switch their diet to fish and squid across years and seasons in response to climate change (Emslie et al., 1998). Species that are not capable of adjusting their behavior are more vulnerable to change due to their inability to acquire sufficient resources, and are likely to face declines in population numbers and breeding success. Oedekoven et al. (2001) demonstrated that different species of seabirds responded to changes in prey distribution in central California from 1985 to 1994: during that period, upwelling of cool, nutrient-rich water had declined and so did the numbers of shallow-diving shearwaters and auklets, while deep-diving murres did not. The number of sooty shearwaters (*Puffinus griseus*) decreased after 1988 as this species changed the migration route avoiding the California Current and moved through the central part of North Pacific Ocean in response to the prey availability; murres simply adjusted their foraging strategies switching their diet from rockfish and squid to anchovies inshore. Cassin's auklet (*Ptychoramphus aleuticus*) that are strictly depend on zooplankton, were not able to change prey and this affected negatively their breeding success (Oedekoven et al., 2001).

Future perspectives

Using predators as marine system indicators

Earth's climate is changing rapidly, and it has warmed at the rate of 1.5° C yr^{-1} (Intergovernmental Panel on Climate Change (IPCC), 2019). The general warming of the Earth's surface is manifesting in the marine environment as an increase in global sea surface temperature, height of the sea level and changes in ocean circulation and nutrients availability (IPCC, 2015). This has interfered with many ecological and physiological processes causing a distributional shift in nutrient availability,

prey and organizational assemblages, and consequently biological interactions of species. Melting of snow and ice have increased the global mean sea level by 1.7 mm yr^{-1} in the last century (1901–2010) (IPPC, 2007) causing habitat loss and gain and shifts in species distribution and abundance (Constable et al., 2014). Furthermore, marine communities face changes in ocean circulation patterns and increases in the magnitude and frequency of freshwater incursions, altering the nutrients profile of marine environments (Hays et al., 2016). Moreover, there is a widespread concern for the exploitation of the precious living resources of the Southern Ocean, which has led to an organized effort to manage and conserve this marine ecosystem (Constable, 2004).

One of the central problems in the management of the Southern Ocean ecosystem is the assessment of actual and potential impacts on the system by various threats (e.g., harvesting regime). Fluctuations in prey availability may be reflected in the responses of the primary and secondary predators of krill, and there is evidence that trends in bird and seal populations in the southern Indian Ocean are indicators of system shifts (Weimerskirch et al., 2003). Marine mammals and seabirds occupy the upper-trophic level, and some demographic and behavioral variables integrate changes in the prey they rely upon (Moore, 2008). For these reasons, they are used as "sentinels" for the assessment of ecosystem changes, and long-term monitoring programs have been established in the Southern Ocean to quantify temporal and spatial variation that may reflect changes in the prey base (Reid and Croxall, 2001; Reid et al., 2005; Trathan et al., 2015). The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) represents a significant milestone in monitoring marine predator species and fish stocks. Many species variables, such as growth, reproduction, and behavior, are flexible parameters that change in response to factors such as prey availability. For this reason, a number of species of seals and penguins have been designated as CCAMLR Ecosystem Monitoring Program (CEMP) species, and several locations have been selected as CEMP Network Sites for monitoring programs. Additionally, because penguins are meso-level predators and feed also on krill, the Scientific Committee on Antarctic Research (SCAR) has collected information on the status and population trends of Southern Ocean penguins since 1980. The Australian Antarctic Division has developed a long-term monitoring program on Adélie penguins at Béchervaise Island (67°35' S, 62°48' E), East Antarctica, to evaluate how changes in the Antarctic environment might affect these bio-indicators.

Linking dive data with energetics

For many marine species, the relationships between demographic performance and environmental variability (e.g., ice extent) have not been established yet. However, as demonstrated by previous biotelemetry studies (Smith et al., 2003; Le Boeuf and Crocker, 2005), dive data have the potential to link at-sea behavior to demography and population level consequences, and provide insights on how dive behavior is linked to population growth and persistence (Lea and Dubroca, 2003; Lea et al., 2006). This gap can be filled linking dive data to energetics, which provides a method to quantitatively assess the

effort animals spend acquiring resources, as well as how they allocate those resources (Halsey, 2011). An "efficient" dive provides energy for maintenance functions, growth, reproduction and metabolic work.

One way to assess energy requirements in animals is to accurately measure total metabolic rate (Kooyman, 1985), but due to the environment in which they live, a limited amount of data has been collected on the metabolism of Southern Ocean marine predators. Nevertheless, since the primary energetic cost faced by diving animals is influenced by locomotor movements, data loggers offer a great tool to investigate animal dive cycle management and the energy expenditure during dives (Halsey et al., 2006b). As presented in my work, simple dive variables have been used to estimate how much energy, has been used by different species when diving in term of oxygen consumption. Parameters like "post-dive interval" can be used as a measure of dive cost, based on the fact that divers should maximize time spent underwater, and minimize their transit time and subsequent surface recovery time (Kramer, 1988). All my species showed an increase of post-dive surface intervals with longer dive durations (Chapter 4), but the interval variation was less consistent during intense foraging dives with long hunting times, potentially implying a higher energetic cost for this level of activity. Similarly, Acevedo-Gutiérrez et al. (2002) used TDR data to demonstrate how lunge-feeding in whales is highly costly by measuring the time needed by these animals to recover at the surface after a dive. Speed data have also been used as proxy for energy expended, since muscle motion involves oxygen consumption (Gleiss et al., 2011). Moreover, TDR data may provide measurements of animal energetics in the field over long periods, and even during particular time of the year such as the breeding season.

The calculation of energetic cost and its integration into different behavior categories like foraging, travelling, breeding is the basis to obtain time-activity budgets (Fort et al., 2011). Energetic activity budgets are critical for determining the overall ecology of marine predators, as well as quantifying the effects of environmental variation on their energy needs and prey requirements. Since energy budgets can be derived from time-activity information, my findings could easily be integrated into energetics studies offering a deeper understanding of how foraging behavior is linked with dive metabolism, as well as the constrains and determinants imposed by marine predators' physiology, morphology and other life history traits.

Integrate dive data into ecosystem modelling

The SO ecosystem is experiencing significant environmental changes (IPCC, 2019). Due to the size and complexity of this marine ecosystem, it is particularly difficult to forecast how climate change will affect marine life (Hoegh-Guldberg and Bruno, 2010). To produce such forecasts, ecology needs to become more predictive and needs to develop the capacity to understand how ecological systems will behave in the future (Marguire, 1975). To do so, we must better our understanding of what we can forecast and how individual behavior determines interactions within and between species (Dietze, 2017).

SO marine predators may have an important indicator role because marine predators' foraging areas are likely to shift and change in size, presenting both accessibility and availability issues (Lambert et al., 2014). Combining dive data with remotely sensed oceanographic data has allowed the investigation of the effects of environmental factors on animals (Bailleul et al., 2007; Heerah et al., 2013). For example, elephant seals change from transit to foraging mode when they move into new water masses (Bestley et al., 2015). Additionally, as shown by my work, dive data offer an integrated understanding of how diving animals use the water column and forage, but also how changes in dive behavior could be related to environmental variation (e.g., prey distribution and abundance). Previous studies evaluating the relationship between air-breathing vertebrate behavior and climate have demonstrated that marine species responded by exploring new foraging grounds and switching prey species (Boyd, 1994; Oedekoven et al., 2001; Miller at al., 2009), changing their distribution (Guinet et al., 1996; Alonzo et al., 2003; Trivelpiece et al., 2011) and modifying the length and timing of migrations (Scheinin et al., 2011; Bailleul et al., 2012; Ramp et al., 2015).

With regard to the factors limiting diving behavior for SO species, my work suggests that different species respond differently to changes in food resources, depending on their degree of plasticity. These differences in behavior may help to define which species are more 'sensitive' because of their limited capacity to adjust their behavior. This will identify which species are the best sentinels for certain locations or ecosystems (e.g., krill abundance; Reid et al., 2005) and which parameters should be measured in the monitored species to reflect the change. Furthermore, the integration of my results on diving behavior and energetic costs (derived indirectly from time-activity data) could be used to implement ecosystem energy flow models (Williams et al., 2000), and/or to correct and increase the accuracy of Regional Ocean Models (Malpress et al., 2017) that estimate how access to prey and foraging efficiencies may change into the future.

Finally, the ongoing development of telemetry instrumentation and statistical techniques to analyze the data will enable better assessments of the diving ecology of SO species. As multi-year and even multi-decadal time-series of observations build, it will be possible to move from individual-based results to broader-scale population dynamics, and to predict how Southern Ocean specialists respond to environmental variability. As ecosystem approaches to management are becoming increasingly important, we need a broader understanding of the links between species and the effect of environmental conditions on these interactions.

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