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Foraging capacities, behaviours and strategies of otariids and odobenids

Tiphaine Jeanniard-du-Dot ^{1,2} and Christophe Guinet²

Abstract: Fur seals, sea lions and walruses are breath-hold divers that rely on swimming at depth to feed at sea. As their diving capacities are more limited than phocids, otariids and odobenids are geographically constrained to highly productive environments and relatively shallow dive depths. They are also mostly coastal species, central place foragers with relatively limited foraging ranges. Diving patterns and strategies are diverse among the otariid group – although fur seals tend to be more pelagic and sea lions more benthic divers –, and driven by extrinsic factors such as the type of habitat they occupy, environmental factors, intra- or inter-specific density-dependent competition, predation risk and the behavior of the prey they feed on; as well as intrinsic factors such as age, sex, reproduction status, size and experience. There are usually several foraging strategies present within a species, and individuals tend to specialize to one of these strategies, with a degree of adaptability to changing conditions possible. Diving behaviors and strategies define the feeding success and foraging efficiency of individuals, and as such their capacities to successfully survive and reproduce in their environment. The diversity of these behaviors within otariid and odobenid populations are likely evolutionary stable strategies that provide a buffer under changing environmental conditions.

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1. Introduction

Accurately determining dive behavior and underwater foraging of marine predators, including fur seals, sea lions and walrus (Fig. 1) is inherently difficult as they cannot be directly observed in the open oceans, and yet it is essential to determine, explain, and predict their foraging success, the use of prey resources in their environment, as well as their consequences on energetics and fitness (Costa et al. 1989, Boyd 2002, Austin et al. 2006, Bost et al. 2007, New et al. 2014). However, technological advancements in the field of bio-logging and bio-telemetry, i.e. archival and satellite-transmitting devices attached to animals while they go at sea, has made it possible to collect information on these diving behaviors at an increasingly fine scale.

The first bio-loggers used on marine mammals were time-depth recorders (TDR) that recorded low resolution 2D dive patterns over a relatively short period of time (Kooyman 1965). Nowadays, new and miniaturized sensors, as well as improved processing capacities, large memory capabilities and battery life allows marine mammal scientists to record data about dive behavior and foraging success at a much finer scale and for up to several months. For example, tri-axial accelerometers, magnetometers or gyroscopes, recording data at 20Hz, allow reconstruction of 3D underwater tracks of the animals. They can also provide indirect indices of swimming effort, feeding attempts and foraging success (Viviant et al. 2014, Jeanniard du Dot et al. 2016b, Ladds et al. 2017b). The field of bio-logging is in rapid development (the International Bio-logging Society was born in 2015 <https://www.bio-logging.net>). Currently, most loggers deployed on otariids incorporate pressure, temperature and light sensors. More recently other types of sensors

(passive or active acoustics, salinity etc...) have allowed scientists to study animal behavior in relation to their immediate environment. This has shed light on the links between foraging behavior, feeding success and the oceanographic conditions.

Biologging-based studies of otariid diving behavior have exponentially increased over the last 30 years (McIntyre 2014). Some species have been intensely studied: Antarctic fur seals (*Arctocephalus gazella*), northern fur seals (*Callorhinus ursinus*), followed by New Zealand sea lions (*Phocarctos hookeri*), Steller sea lions (*Eumatopias jubatus*), and California sea lions (*Zalophus californianus*). On the other end of the spectrum, there is little information on dive behavior of Juan Fernandez fur seals (*Arctocephalus phillippii phillippii*) (Francis et al. 1998), Guadalupe fur seals (*Arctocephalus phillippii townsendi*) (Gallo-Reynoso et al. 2008) or South American Sea Lions (*Otaria flavescens*) (Werner & Campagna 1995, Mueller 2004). In addition, a majority of studies have focused on diving behavior of adult lactating females during the breeding season when they become central place foragers. Significantly less information is available for males or juveniles, even though efforts have been made to start bridging these gaps (Boyd et al. 1998, Baylis et al. 2017, Knox et al. 2018, Salton et al. 2019). Consequently, general knowledge of diving behavior of otariids and odobenids is inherently biased towards the taxa, season, and sex/age groups from which we have the most information.

Fur seals and sea lions are mostly coastal species, especially during breeding season, and their yearly movements can cover little variation in habitat use (Australian sea lion) to thousands of km for those with a pelagic phase (northern and Antarctic fur seals during their 8-month migration). Their distribution is concentrated in areas of high productivity, mostly in temperate to sub-polar latitudes, or near areas with cold upwellings for more tropical species (i.e. Humboldt or Cromwell current, Fig. 2). This pattern is a consequence of their relatively expensive lifestyle and their

subsequent needs for high feeding rates to balance their energy budget (Boyd 2002). As fur seals and sea lions travel and rest at the surface of the ocean, the main purpose of their diving is to feed at depth. Intrinsic factors such as phylogeny, sex, size, age, experience and reproductive status, as well as extrinsic factors including habitat characteristics, environmental factors, intra- or inter-specific density-dependent competition, predation pressure, food web structure and the distribution and behavior of the prey they feed upon, all influence diving behavior in otariids (Schoener 1974, Gentry & Kooyman 1986, Boyd 1996, Harcourt et al. 2002, Jeglinski et al. 2012, Benoit-Bird et al. 2013, Leung et al. 2014). Ultimately, these factors will shape the foraging efficiency of animals, i.e. the cost/benefit ratio of their foraging at sea and hence their body condition, survival and reproductive success and the resulting trends in population.

This chapter focuses on diving and foraging activities of fur seals and sea lions as a group – and to a lesser extent the walrus –, emphasizing phylogenetic similarities or differences between them or with the other major pinniped family, the phocidae. We look at how otariid diving is limited by physiological capacities, what diving strategies they display in the wild and what biological or environmental factors affect them. Finally, we discuss how diving patterns and strategies can be used to assess and understand foraging energetics and efficiency and ultimately how it shapes the capacity of fur seals and sea lions to survive and reproduce successfully in their environment.

2. Morphological and physiological diving capacities of fur seals and sea lions

Diving behavior of fur seals and sea lions is constrained by their overall capacity to balance the energetic costs of moving effectively through water, a medium ~ 800 times denser than air and 25 times more heat conducive, while on a limited oxygen supply during apnea. The quantity of oxygen

available in the body and the rate at which it is consumed (and carbon dioxide produced) by metabolic processes during a dive controls how long animals can remain underwater, given their total oxygen stores. Fur seals and sea lions have developed morphological and physiological adaptations to simultaneously decrease the costs of exercising underwater or diving metabolic rate and increase the magnitude of body oxygen stores and transport. Combined, these adaptations allow fur seals and sea lions to prolong the time spent at depth to forage, and so is essential to understanding diving behavior and foraging efficiencies of eared seals.

Morphologically, otariids have streamlined body shapes that highly reduce the drag created by, and thus the energetic cost of, moving through water (Fig. 3). Their body shape presents with an average fineness ratio (~ 5.5 , compared to walrus *O. rosmarus* with a fineness ratio ~ 1 for example) and a position of the maximum diameter of their body (shoulders area at $\sim 40\%$ of the total body length) close to the optimum for minimal drag given the body volume (Feldkamp 1987). Unlike phocids and odobenids who use caudal propulsion and lateral or vertical oscillations of their rear appendages to move through water, fur seals and sea lions use their pectoral flippers for propulsion in a 4-phase stroke pattern creating a horizontal thrust and vertical lift with little to no resulting distortion of the body (Feldkamp 1987). Otariid fore-flippers are hydrofoil-shaped and dorso-ventrally compressed which reduces pressure drag and improves lift during propulsion underwater (Fig. 3). Fore-flipper propulsion also offers high maneuverability at depth, as well as great speed and turning angle. These adaptations insure efficient mechanical performance for swimming underwater at a much reduced energetic cost of swimming at depth (at optimum speed) compared to terrestrial mammals of similar sizes (Costa & Williams 1999). Other particularities of otariids amongst marine mammals are their limited fat content (especially in fur seals) and their diving with inflated lungs, which both affect buoyancy and thus energetic costs of diving.

In addition to their morphology, fur seal and sea lion physiology has evolved to adapt to breath-hold diving. They possess a series of physiological adaptations which decrease the rate at which body oxygen stores are depleted underwater to prolong dive duration. These physiological adjustments are ubiquitous amongst marine mammals – although not to the same extent – and are together called the ‘dive response’ (Davis 2014). It mostly involves a peripheral vasoconstriction and a decrease in heart rate (bradycardia) compared to ‘resting’ heart rates in response to asphyxia (diving heart rates decreasing to ~ 25 - 50% compared to eupneic levels, Ponganis 2015). Together these adjustments reduce the perfusion of blood to ‘non-essential’ organs – while maintaining adequate blood pressure and cardiac output to the heart and the brain – thereby limiting the overall rate of oxygen consumption. Free-ranging mammals (i.e. non-controlled and unrestrained conditions) show a wide range of physiological plasticity while diving and the extent of the ‘dive response’ cardiovascular adjustments is usually greater in longer dives (i.e. requiring greater conservation of O₂)(Andrews et al. 1997).

Diving physiology has mostly been studied in deep diving phocid species, and few studies have measured these responses in the shallow and shorter-diver otariids – mostly California sea lions, Steller sea lions and Antarctic fur seals (Andrews et al. 1997, Boyd et al. 1999, Hindle et al. 2010). Nevertheless, similar responses have been found in California sea lions who show extreme bradycardia to the same extent as the deepest diving phocid seals during very long dives (McDonald & Ponganis 2014). In pelagic, shallow diving fur seals, however, the extent of these adjustments is not always as pronounced (Fig. 4). Even during long dives, heart rate is reduced by only ~ 33% of surface resting heart rate in Antarctic fur seals compared to up to 75% in other pinnipeds (Boyd et al. 1999). Interestingly, while California sea lion show intense bradycardia in deep dives, the profile of heart rate decrease is slower than typical of phocid seals. This might be

due to otariids inhaling before diving and so gas exchange continues underwater, while phocid seals exhale before diving (Hooker et al. 2005, McDonald & Ponganis 2014).

In addition to oxygen conservation mechanisms, oxygen stores in otariids are primarily located in the lungs, blood and muscles, and depends on their volume/mass as well as on hemoglobin (Hb) and myoglobin (Mb) concentrations in the body (Ponganis 2015). However, amongst pinnipeds, otariids have more limited diving capacities (shallower dive depths, shorter dive durations on average) than comparably sized phocids, which as a group possess larger oxygen stores relative to their mass than similar size otariids (Table 2, t-test $p = 0.01$). This results from a lower Hb concentration despite relatively similar blood volumes ($p = 0.008$) and arguably similar O_2 affinity (Qvist et al. 1981, Kooyman 1989, Meir et al. 2009, McDonald & Ponganis 2013) as well as lower Mb concentration ($p = 0.001$). Together, blood and muscles represent ~ 75 - 90% of oxygen storage in fur seal and sea lions' body (Ponganis 2015), and the remaining ~ 10 - 25% reside in the lungs compared to only ~ 3 - 10 % in phocids. The 6-fold higher proportion of oxygen in otariids' lungs compared to blood – 1 : 2.5 in otariids vs 1 : 12 in phocids – indicates substantial differences in diving strategy (Hooker et al. 2005).

Interestingly, total O_2 stores have a scaling factor of 1 with body mass while metabolic rate a scaling factor of 0.75 (Costa 1993). This means that breath-hold diving capacities increase with body size for a given mass-specific O_2 store (Fig.5). Consequently, larger sea lions and fur seals should have greater diving capacities than smaller ones (Baylis et al. 2015b). Alternatively, smaller animals should increase their mass-specific O_2 stores to maintain similar diving capacities as larger ones. This was observed intra-specifically among females in South American sea lions (Hückstädt et al. 2016), as well as in California sea lions where females compensated for their smaller body sizes and thus lower absolute oxygen stores, by having higher mass-specific O_2 stores compared

to the larger males (Weise & Costa 2007). Similarly, the Galapagos sea lion is the smallest of all sea lion species (60 - 95 kg for females, Villegas-Amtmann et al. 2017), yet has the highest mass-specific oxygen stores (74 ml O₂ / kg, Villegas-Amtmann & Costa 2010) – and thus greatest diving capacities –, while the lowest mass-specific O₂ store is found in Steller sea lion (40 ml O₂ / kg, Richmond et al. 2006), the largest of otariids (150 - 300 kg for females, Calkins et al. 1998) (Fig. 5).

The time required to consume O₂ stores via aerobic metabolism while diving is thought to be the major determinant of diving performance (Boyd & Croxall 1996, Costa et al. 2004). The aerobic dive limit (ADL) is defined as the maximum dive duration before blood lactic acid levels rise, because of an increase in anaerobic metabolism. When seals exceed this aerobic threshold, the relative post-dive surface interval increases greatly as extra time is necessary to clear lactic acid accumulated during the previous dive (Burns 1999, Horning 2012) resulting in a disproportionate increase in surface time and a decrease in foraging efficiency.

To overcome the technical difficulties of measuring blood lactate in free-ranging seals, two indirect estimates have been widely used in eared seal studies. Based on observations that most dives in wild seals are shorter than the measured ADL (Kooyman et al. 1980, Kooyman et al. 1983), the behavioral aerobic dive limit (ADL_B), has been estimated as the dive duration below which 95–97% of dives occur and after which surface intervals begin to disproportionately increase (Burns & Castellini 1996, Hindle et al. 2011). Alternatively, the calculated aerobic dive limit (ADL_C) represents the total O₂ stores divided by the diving metabolic rate (Costa et al. 2004), (Fig. 6).

Since its first mention in the 1980s (Kooyman et al. 1983), ADL has become a fundamental concept in the interpretation of diving physiology, diving behavior, and more widely foraging

ecology of diving animals. Irrespective of the differences due to the ADL estimation method (2.0 min ADL_B versus 1.6 min ADL_C in Antarctic fur seals (Costa et al. 2004, Viviant et al. 2016); 2.3 min ADL in captive California sea lions versus 2.7 - 3.8 min ADL_C in wild counterparts (Ponganis et al. 1997, Costa et al. 2004)), there is a wide variation in ADL between species of eared seals from 1.3-1.7 min in South American sea lions and Australian fur seals (Costa et al. 2004, Hückstädt et al. 2016) to 3.2 min in Galapagos fur seals (Horning 2012) – and 10.5-14.8 min for walruses (Wiig et al. 1993, Noren et al. 2015)(Table 1).

More interestingly, the difference in tendencies to exceed ADL between otariid species appears to depend on their foraging ecology (pelagic versus benthic divers) rather than their phylogeny (fur seals versus sea lions). Benthic fur seals and sea lions divers tend to exceed their ADL more often than pelagic divers (Costa & Gales 2000, Costa et al. 2004, Hückstädt et al. 2016). For example, benthic Australian sea lions exceed their ADL_C in almost 80% of their dives (Costa & Gales 2003), – likely to maximize time on the sea floor –, while the pelagic Antarctic fur seal only surpass it in ~ 16% of their dives (Viviant et al. 2016).

ADL should also not be considered a fixed unalterable threshold (See Costa and Toro, this volume). In California and South American sea lions, exposure to different habitats and geographical locations dramatically altered individual ADL and overall diving physiology (Hückstädt et al. 2016). Shallow epipelagic California sea lions from San Nicholas island had an ADL of 2.7 min compared to 3.8 min for deeper mesopelagic counterparts off Los Islotes (Costa et al. 2004), while benthic South American sea lions in Southern Chile had greater mass-specific O_2 stores than shallow diver counterparts in Uruguay (Hückstädt et al. 2016). This ‘training effect’ or ‘local adaptation’ from greater hypoxic exposure indicates that the physiology of fur seals and sea lions can be adjusted and improved to a certain extent depending on the ecological conditions

to which they are routinely exposed. Consequently, diving behavior and overall foraging efficiency result not only from physiological constraints and capacities outlined above but from a complex interaction between genetics, physiology and the environment.

3. Diving strategies of fur seals and sea lions

Diving strategies are diverse among the otariid group and can be classified as epi-/meso-pelagic (i.e. within the water column) or benthic (on the seafloor) (see also Costa and Toro, this volume). Pelagic divers typically perform bouts of short shallow dives (10 – 60 m depth for 0.5 – 3.0 min) with a diurnal variation in dive depths (greater at dawn and dusk and shallow at night) that reflect the circadian migration of their prey to the surface. They spent 20 – 35% of their time at sea diving. On the other hand, benthic divers forage mostly on continental shelf areas perform relatively deep and long dives with no obvious diurnal pattern (25 – 400 m depth for 1.5 – 7.0 min on average) with long periods at the bottom of their dive. They invest 50 – 60% of their time at sea diving, performing 10 – 20 dives/h with bottom time representing 45 – 55% of each dive (Werner & Campagna 1995, Thompson et al. 1998, Costa & Gales 2000, Costa & Gales 2003) (Fig. 7 & Table 1). The maximization of bottom time for deeper dives can be achieved by faster descent rates through ‘burst and glide’ transit without an increase in swimming costs (Crocker et al. 2001). The deepest diving otariid is thought to be the benthic-feeding New Zealand sea lion, which can dive as deep as 600 m and as long as 20 min (Chilvers 2008b, Chilvers this volume), although recent studies have shown that the Galapagos sea lion can also perform dives within this range despite its smaller size (Villegas-Amtmann et al. 2017, Costa and Toro this volume).

It is generally recognized that fur seals are nocturnal epi-/meso-pelagic divers, while most sea lions – and walruses – are benthic divers. This general pelagic/benthic distinction is thought to result from a difference in insulation capacity and/or in size between taxa (Arnould & Costa 2006). Fur

seals are indeed overall smaller (25 to 80 kg for females, Table 1) with consequently lower diving capacities, and rely on a layer of air trapped in their very dense fur for thermoregulation. On the other hand, sea lions are larger (70 – 300 kg for females, Table 1) with concomitant greater diving capacities and rely on a blubber layer for insulation. This taxon-derived dichotomy in diving strategy is however not entirely so clear cut. Australian fur seals are exclusive benthic divers (Kirkwood and McIntosh this volume) while California sea lions are epi/meso-pelagic divers (Weise et al. 2010, Kuhn & Costa 2014, Costa and Toro this volume).

In addition, as the number of bio-logging studies increases and more individuals of different sex/age are tracked repeatedly over time, our understanding of intra-individuals / inter-populations variability gets refined. Several species of fur seals and sea lions seem to employ more than one of these diving strategies (Arnould & Hindell 2001, Chilvers & Wilkinson 2009, Kuhn et al. 2010b, Villegas-Amtmann et al. 2013, Baylis et al. 2015b). For example, northern fur seal females display epipelagic or benthic or mixed strategies when foraging in the Bering sea (Gentry et al. 1986, Kuhn et al. 2010a, Jeanniard du Dot et al. 2018) (Fig. 7& Table 1). On the other hand, adult female southern sea lions breeding in northern Patagonia or the Falklands (Werner & Campagna 1995, Baylis et al. 2015b), New Zealand sea lions (Chilvers & Wilkinson 2009) and Galapagos sea lions (Villegas-Amtmann et al. 2008) have all been reported to show a pelagic strategy in tracked animals, (Mattlin et al. 1998). Rarely have three foraging patterns (epipelagic, mesopelagic and benthic) been found in one species, with the exception of sea lions from the *Zalophus* genus (California and Galapagos sea lions) that seem to have high behavioral flexibility (Villegas-Amtmann et al. 2008, Villegas-Amtmann et al. 2011, McHuron et al. 2016).

Individuals from the same species have a wide range of diving behaviors at their disposal likely driven by both intrinsic and extrinsic circumstances. Age, sex, and size can affect diving behavior.

Younger animals are ontogenetically limited in their diving capacities and dive shallower than adults (Horning & Trillmich 1997, Baylis et al. 2005, Fowler et al. 2006, Verrier et al. 2011), while larger adult individuals have greater diving capacities than smaller ones as mentioned earlier (Boyd et al. 1998, Lea et al. 2006, Baylis et al. 2015b). There is also evidence that males have a very different foraging ecology compared to females in Antarctic and New Zealand fur seal males for example, but not necessarily in others species (Fea et al. 1999, Staniland & Robinson 2008, Kernaleguen et al. 2015, Drago et al. 2016, de Albernaz et al. 2017). Alternatively, variation in diving strategies can be attributed to habitat characteristics, targeted prey type, behavior or prey availability in these habitats, and competition or predation pressure (Chilvers & Wilkinson 2009, Baylis et al. 2015b, Arthur et al. 2016, Paez-Rosas et al. 2017, Jeanniard du Dot et al. 2018). For example, Galapagos sea lions foraging west of the archipelago displayed pelagic diving and fed on mesopelagic fish such as the Galapagos sardine (*Opisthonema berlangai*), while females foraging benthically south west of the Galapagos archipelago preyed upon larger fish from the Serranidae and Scorpenidae families in deep areas with rocky substrates (Villegas-Amtmann et al. 2017).

While several diving strategies exist amongst fur seal and sea lion species, it appears that adult individuals tend to remain faithful to specific diving strategies. A high degree of specialization was for example observed in female New Zealand sea lions (both within and between years, Chilvers 2008a, Chilvers 2008b, Chilvers 2017), Australian sea lions (Lowther et al. 2013), Australian fur seals (Kernaléguen et al. 2015) and Antarctic fur seals (Arthur et al. 2015), although it is less clear for New Zealand fur seals and California sea lions (Melin et al. 2008, Kuhn & Costa 2014, McHuron et al. 2016). Individual specialization is expected to occur more frequently in generalist top marine predators with a wide range of potential prey as it provides the ecological

opportunity for different strategies to occur (Araújo et al. 2011), and when competition for resources is strong. This can be the case for breeding females nursing their offspring. As central place foragers, they are constrained to forage within limited areas around the breeding grounds and experience stronger intraspecific competition for resources, resulting in foraging niche segregation. Foraging niche segregation also occurs inter-specifically for sympatric otariid species such as Galapagos sea lions and Galapagos fur seals, New Zealand fur seals and Australian fur seals, and southern sea lions and South American fur seals with one of the two species being benthic and the other pelagic foragers.

It is difficult to know whether different diving strategies within a population have recently emerged as a result of changes in habitat characteristics or have been retained over time as Evolutionary Stable Strategies (Hines 1987). Regardless, they entail different trade-offs in terms of risks and benefits. Benthic foragers dive deeper for longer periods of time which results in animals surpassing their ADL more frequently with likely greater overall energy expenditure (Costa et al. 2004). However, one of the benefits of preying upon benthic prey is that they tend to be evenly distributed, predictable, relatively large and overall less susceptible to acute environmental changes or events such as El Niño (Miller & Sydeman 2004). By contrast, pelagic divers perform short and shallow dives rarely exceeding ADL, and prey upon small size fish that occur in high densities when they find them. However, mesopelagic prey tend to be patchily distributed, less predictable and more sensitive to oceanographic perturbations (Boyd 1996, Harcourt et al. 2002). Consequently, the different strategies might be more or less beneficial depending upon annual environmental conditions, and the existence of diversity in diving behaviors and strategies within population provides a buffer for species occupying changeable habitats (Villegas-Amtmann et al. 2008, Lowther et al. 2012, McHuron et al. 2016).

An essential component of understanding these diving strategies and the trade-offs they entail is to estimate the energetic costs associated with them. Studies on northern and Antarctic fur seals, and on Galapagos, Australian and New Zealand sea lions that simultaneously measured field metabolic rates and foraging strategies in otariids show that energy expenditures of foraging otariids are influenced by the variability of their behaviors at sea, i.e. their time-activity budget comprised of diving, traveling, and resting (Arnould et al. 1996, Costa & Gales 2000, Jeanniard du Dot et al. 2017b). Diving was found to be the most energetically expensive activity at sea in free-ranging northern and Antarctic fur seals (however, see Arnould et al. (1996)), in semi-captive Steller sea lions and others (Butler et al. 1995, Goundie et al. 2015, Jeanniard du Dot et al. 2017b), and deeper dives more costly than shallower dives of similar duration (Halsey et al. 2006). In addition, the most energetically efficient pattern of diving resides in sequences or bouts of multiple dives close to the ADL with short surface intervals (Goundie et al. 2015).

Consequently, benthic divers that dive deeper, for longer, and that overall exceed their ADL more often than pelagic divers, should have greater rates of energy expenditure at sea. It is, however, difficult to make definite conclusions about the relative energetic costs of each strategy in free ranging studies. First, fur seals and sea lions all seem to operate within a narrow range of FMR (6.25 – 7.05 W/kg, Table 1) with the exception of the deep diving Galapagos sea lions (4.08 W/kg, closer to the 3.36 W/kg of walruses) (Arnould et al. 1996, Costa & Gales 2000, Costa & Gales 2003, Acquarone et al. 2006, Jeanniard du Dot et al. 2017a, Villegas-Amtmann et al. 2017, Jeanniard du Dot et al. 2018). Second, finer patterns of field energy expenditures are not always consistent between and within otariids. Galapagos and California sea lions show a slight decrease in FMR when their time spent diving increases (Hurley & Costa 2001, Villegas-Amtmann et al. 2017). Deep diving New Zealand Sea lions experience lower FMR than shallow diving

conspecifics (Costa & Gales 2000), whereas deep diving and shallow diving northern fur seals and California sea lions have similar FMR (Jeanniard du Dot et al. 2018, McHuron et al. 2018).

Otariids can adapt to different foraging habitat and/or environmental changes either behaviorally or physiologically. They tend to increase their time at sea rather than their FMR in poor foraging conditions (Trillmich 1990, Boyd 1999) (noting that foraging trip duration does not appear to impact FMR either in northern fur seals and New Zealand sea lions, Costa & Gales 2000, Jeanniard du Dot et al. 2018). Pelagic divers that forage at night on prey with a circadian migration pattern are limited in the opportunities to increase their diving effort in years of poor foraging conditions, as prey are not accessible to them during daylight. They have to respond by increasing their total time at sea. Deeper divers, or divers with more flexible foraging strategies such as California sea lions, can access prey during the day and increase their diving effort locally without the need to extend their total time at sea. Nevertheless, even for the few species that can increase their FMR, total metabolic changes remain limited. The overall low metabolic plasticity indicates that fur seals and sea lions most probably operate close to their metabolic ceiling with important implications for the scope of their adaptive capacities to environmental changes (Costa & Gales 2000, Costa & Gales 2003, Arnould & Costa 2006, Ladds et al. 2017c, Villegas-Amtmann et al. 2017).

4. Dive metrics to infer behaviours and energetics

Unlike phocids who travel and sleep underwater, fur seals and sea lions transit and rest at the surface of the ocean. The function of their diving is thus mainly to find and access patchily distributed prey resources in a three dimensional and dynamic environment. Ecologists have long attempted to transpose dive profiles into foraging behaviors, as well as use dive metrics – such as dive duration, maximum dive depth, surface interval duration, bottom duration, 2D dive shape,

time-at-depth, ascent and descent rates, residuals of dive depth-duration models indicative of longer than average dives for a given depth, etc. – to quantify and predict energetic costs of diving and feeding success. The relationship between dive shape and behavior may however not be consistent between species, age classes or life history stages (Kuhn et al. 2009a, Carter et al. 2016). More recently with high resolution datasets, different methods have emerged to partition and quantify time-activity budgets, foraging efforts and diving activities: the vertical area-restricted search, the vertical sinuosity at the bottom of dives, the vertical velocity used in hidden Markov models or behavioral state-space models for example (Joy et al. 2015, Arthur et al. 2016, Heerah et al. 2017) (Fig. 8). It is important to keep in mind however, that the application and the accuracy of each of these methods and metrics depend on the resolution of the data and the temporal scale of analysis (Carter et al. 2016) as well as the minimum depth taken into account to define a dive. This parameter varies widely between studies (2 to 6 m minimum dive to define a dive, see Table 1) and induces significant variations in the mean diving depth and the percentage of time spent diving.

In addition, inferring tri-dimensional behaviors from two-dimensional information is inherently subjective as 2D dive profiles do not account for lateral displacement – or lack thereof – while underwater at a given depth (Harcourt et al. 2000). The development of new sensors such as tri-axial accelerometers and magnetometers have provided means to derive dive profile of animals in 3D (Fig. 9, 10), as well as their body position in the water column, pitch, roll and yaw angles, as well as relative swimming effort (Fig. 10), and detailed behaviors using varied methods for example spectral analyses of tri-axial acceleration with unsupervised signal categorization (using available ethographer software, Battaile et al. 2015), classification tree algorithms (Jeanniard du Dot et al. 2017b), or random forest models (Ladds et al. 2016). This new but complex information

has shown that pinniped foraging behavior can be varied and complex and that 2D profiles used on their own may be overly simplistic (Davis et al. 1999, Harcourt et al. 2000, Simpkins et al. 2001, Hindell et al. 2002).

In addition, without direct validation, it remains unclear whether any of these dive and behavioral characteristics can be used to differentiate successful from unsuccessful foraging in diving pinnipeds. Stomach temperature pills (Kuhn & Costa 2006, Kuhn et al. 2009b) and head- or back-mounted accelerometers have been combined with TDR and video data to identify prey capture attempts in several fur seal and sea lion species (Fig. 11, and see Fig. 7 for example at sea) (Viviant et al. 2010, Volpov et al. 2016). The combination of dive profiles with these new indices of feeding attempts or events have provided opportunities to ground-truth time-at-depth dive metrics as indicators of foraging behaviors and success (Sala et al. 2011). For example, (Viviant et al. 2016) deployed accelerometers (measuring jaw-openings as a proxy for prey capture attempts) in conjunction with TDRs in Antarctic fur seals to test dive metrics including bottom duration, ascent and descent rates and maximum dive depth as predictors of foraging success. They concluded that the metrics to best predict foraging success depends on the timescale considered (from single dives, to bout or to nights).

Dynamic tri-axial acceleration metrics such as ODBA or VeDBA (Overall – or Vectorial – dynamic body acceleration) were hypothesized to be directly related to metabolic rate in free ranging animals (Gleiss et al. 2011). While studies have shown promising relationships between metabolic rate and ODBA on terrestrial animals (Halsey et al. 2009), this relationship is more controversial in captive or wild fur seals and sea lions (Fahlman et al. 2008, Dalton et al. 2014, Ladds et al. 2017a). In Antarctic and northern fur seals, ODBA did not correlate with doubly-labeled water measures of field metabolic rates over a full foraging trip at sea (Jeanniard du Dot

et al. 2016a). This was argued to be due, amongst other reasons, to the difference in time-activity budgets between individuals by the authors, but it was later shown that relationships between ODBA/VeDBA and energy expenditure metrics was likely found significant due to a ‘time trap’, i.e. time being inherently conflated into the 2 tested variables (Halsey 2017, Ladds et al. 2017a). Whether or not ODBA/VeDBA can accurately measure field metabolic rate in free-ranging fur seals and sea lions, dynamic acceleration can certainly provide a relative index of swimming effort underwater between phases of dives, between dives, and over total foraging trips for a given individual (Miller et al. 2012). This refines the scale at which changes in swimming effort during dives can be estimated to an unprecedented level.

In addition to using dive profiles, ecologists have built theoretical frameworks to infer foraging efficiency in diving animals. These models were specifically adapted to diving animals from the Optimal Foraging Theory (OFT, MacArthur & Pianka 1966) taking into account the physiological needs to regularly return to breath at the surface of the water, i.e. leave the prey patch. OFT stipulates that natural selection favors animals that forage more efficiently, with foraging efficiency defined as the ratio of energy gained to energy expended to acquire food per unit of time. Consequently, individuals should maximize rate of energy intake while minimizing the rate of energy expenditure associated with prey searching, capture and handling, and thus concentrate their time in areas of successful feeding. Given this and the previously mentioned assumption that most foraging occurs during the bottom phase of dives, Optimal Diving models hypothesized that divers should maximize their time at the bottom phase, i.e. at the feeding depth, effectively increasing the probability of capturing prey while minimizing the time and energy spent traveling from and to the surface (descent and ascent phase), as well as the time recovering at the surface after the dive (post-dive surface interval) (Kramer 1988, Houston & Carbone 1992, Thompson et

al. 1993). Within this framework, foraging success should thus increase with dive duration, bottom phase duration and dive frequency.

This was however not verified for wild benthic diving Australian fur seals regularly diving at the fairly constant benthos of the oceans. Neither bottom duration nor post-dive surface intervals were indicative of whether prey capture attempts occurred during dives, while descent rate was the best predictor of successful feeding dives (Volpov et al. 2016). In Australian and Antarctic fur seals, bottom time duration was not the best predictor of successful foraging which rather depended on the temporal scale at which the analyses occurred from single dives, to bout, nights etc. (Iwata et al. 2015, Foo et al. 2016, Viviant et al. 2016). This highlights the importance of the time scale and initial research question since predictors of foraging success for a particular dive bout may not perform as well when applied across an entire foraging trip.

The distribution, accessibility and quality/density of prey patches, the level of competition for a given prey patch, as well as the physiological needs, capacities or degree of plasticity of diving animals are likely to influence their foraging strategies. Adding inferences about prey patch density and quality in the decision making process of diving seals (Marginal Value Theorem. Charnov 1976), (Thompson & Fedak 2001) hypothesized that individuals should terminate a dive earlier (i.e. shorter dive and bottom durations) when there are no prey present or prey density is low, but that the benefit of early dive termination is reduced for deeper dives. These assumptions are however not clearly validated in wild otariids either. Antarctic fur seal females increased their foraging effort by diving more and spending more time searching for prey at the bottom of dives in poor-quality patches (Mori & Boyd 2004, Viviant et al. 2014). Similarly, Australian fur seals decreased bottom duration with increasing prey encounter rate at the scale of a dive, possibly to come back to the surface to consume larger prey items, but not at the scale of a bout (Foo et al.

2016). It is however interesting to note that Antarctic fur seals did tend to dive and forage at a depth shallower than the depth with the highest rate of prey capture attempts (Viviant et al. 2016) in accordance with Mori's model (1998) that postulates that if species are physically capable of reaching depths of highest prey densities, they will tend to dive at depths slightly shallower than the maximum prey density as a trade-off with physiological constraints of diving. This indicates that species favor foraging efficiency (i.e. the net energy gain taking into account diving costs) rather than just maximizing prey intake.

The wide breadth of these results highlights the complexity of the decision making process of fur seals and sea lions in the wild. They modify their dive behavior based on real-time evaluation of prey encounter rates during a given dive (especially if the first prey encounter occurs early in the dive, Foo et al. 2016), or during several preceding dives (Iwata et al. 2015, Viviant et al. 2016, Volpov et al. 2016) all while within their physiological constraints. Information gathered at any point in the foraging experience is thus essential in the multifactorial decision making process, and current theoretical foraging models using dive metrics only may be too simplistic to accurately represent such a complex ecological system.

To conclude, there is no doubt that dive-related data are a powerful resource to assess underwater behavior and quantify foraging efficiency in animals which cannot be observed directly. This is particularly relevant given the new types of data accessible from a wide range of additional sensors. However, these data should be used with a clear understanding of their limitations given the wide diversity of behaviors and the complexity of factors affecting the decision making process of individual animals even within the single otariid taxon itself.

5. Conclusion - Impacts of diving strategies on fitness and population trends

The identification and behavioral characterization of foraging strategies is an important first step towards understanding the energetics consequences of the variability in foraging behaviors in fur seals and sea lions. In a population of Antarctic fur seal with a single foraging strategy, the time lactating females spend ashore was positively correlated with pup weaning mass (Doidge & Croxall 1989, Lunn et al. 1994); and mothers with diving patterns yielding a greater foraging efficiency during their trips at sea produced heavier pups more likely to survive during their first year at sea (Jeanniard du Dot et al. 2017a). Consequently, the resulting foraging efficiency ultimately impacts survival and reproductive capacities of individuals and the trend of their population both intra- and inter-specifically.

It has been suggested that the benthic feeding strategy inherently results in a higher foraging cost for likely similar energy gain (thus lower foraging efficiency) (Costa et al. 2004) and benthic foragers usually exhibit smaller population sizes and lower population growth rates compared with those that feed in the water column (Arnould & Costa 2006). In Northern fur seals and California sea lions, the pelagic strategy offers greater foraging efficiency than the benthic strategy, but females often have to travel further and spend more time at sea away from their pup to reach their foraging ground (McHuron et al. 2016, Jeanniard du Dot et al. 2018). Pup growth rates of benthic and pelagic females could not be measured in these two studies so it is difficult to tease apart what strategy would be more beneficial, if any. However, the population of northern fur seals from Bogoslof island, a breeding ground where only the pelagic diving strategy exists, is increasing while the Pribilof Island breeding population where both the pelagic and benthic strategies can be

seen has been decreasing by 3.5% per year for the last 20 years (Muto et al. 2018). Similarly, adult female southern sea lions in northern Patagonia feeding on ‘offshore’ pelagic prey had higher pup growth rates than females with an ‘inshore’ benthic prey diet (in this particular study year, Dragon et al. 2010). South American sea lions which have only a benthic feeding strategy in Uruguay are decreasing, while the population in the Falklands where some individuals display limited pelagic feeding is showing signs of recovery (Baylis et al. 2015a). Beyond the benthic/pelagic dichotomy, the deeper dive depths of Antarctic fur seals breeding on Heard Island compared to fur seals from Bird Island is hypothesized to be a reason for their low population growth rates and limited population recovery (Staniland et al. 2010). All these studies indicate that behavioral decisions related to diving and foraging affect pup growth and survival for income-breeding species, and shape population trends and structure.

Despite evidence that pelagic strategies seem to lead to higher population growth rates than benthic ones, the fact that diverging strategies are retained and co-exist within and between populations indicates that they have valuable benefits on the evolution time-scale. While the benthic diving strategy may inhibit rapid population growth compared to pelagic feeding, benthic prey are more predictable and stable and so benthic strategies may buffer populations during times of drastic environmental change (see also Costa and Toro this volume). Given that our oceans are now facing major biochemical, biological and trophic alteration of marine ecosystems, there is a growing need to understand which factors influence long-term persistence of different strategies within and between species and hence what the broader implications of foraging decisions are over evolutionary time.

Figures



Figure 1: Example of sea lions and fur seals of the family otariidae (A. Steller sea lion, *Eumetopias jubatus*, and B. Antarctic fur seals *Arctocephalus gazella*), and walrus (C.

Odobenus rosmarus) of the family odobenidae. (Picture credits: A, B Tiphaine Jeanniard du Dot, C Brian Battaile)

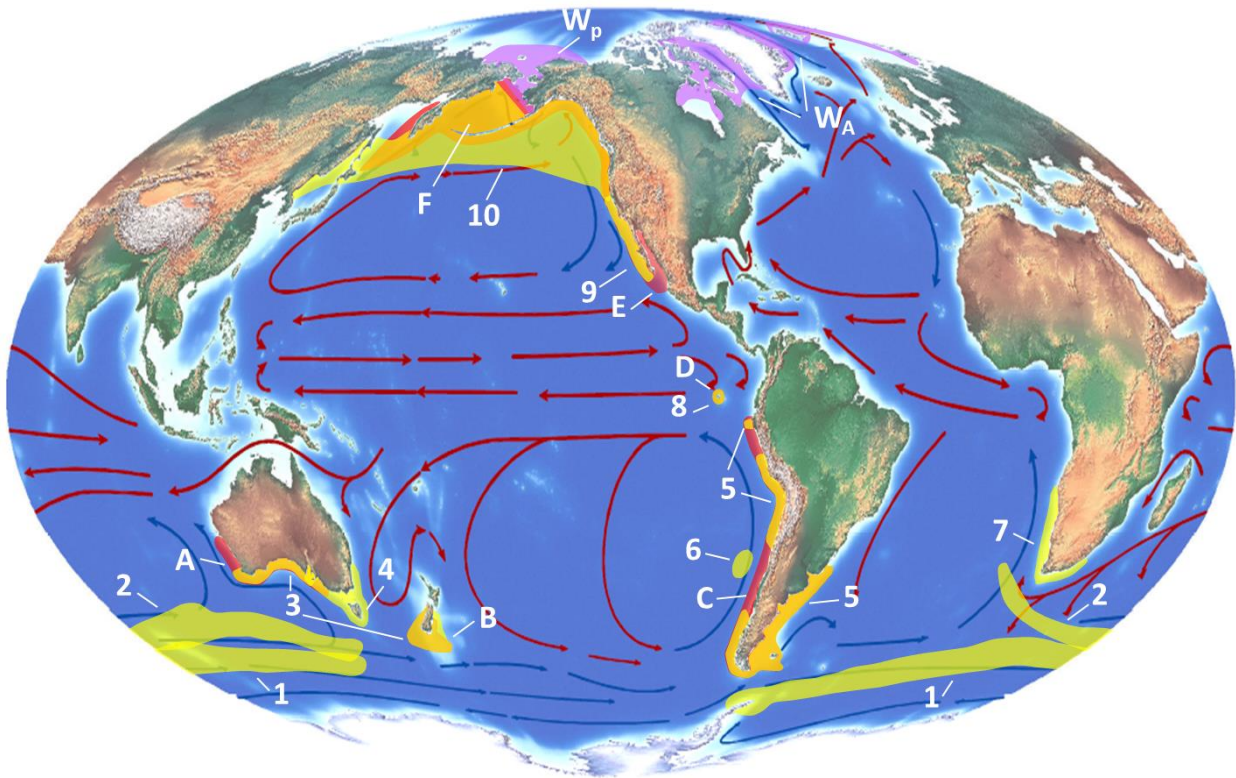


Figure 2: Distribution of otariid and odobenid species worldwide. Fur seals species are shown in yellow and with numbers; sea lion species in red (with overlap between sympatric species resulting in orange) and in single letters, and walruses in purple and double letters. Otariid species are distributed worldwide in areas of cold ocean currents (blue arrows) or upwellings rather than warm ocean currents (red arrows). Legends corresponding to numbers and letters are as follow:

- 1- Antarctic fur seals – *Arctocephalus gazella*
- 2- Sub-Antarctic fur seals – *Arctocephalus tropicalis*
- 3- New Zealand fur seals – *Arctocephalus forsteri*
- 4- Australian fur seals – *Arctocephalus pusillus doriferus*
- 5- South American fur seals – *Arctocephalus australis*
- 6- Juan Fernandez fur seals – *Arctocephalus philippii*
- 7- Cape fur seals – *Arctocephalus pusillus pusillus*
- 8- Galapagos fur seals – *Arctocephalus galapagoensis*
- 9- Guadalupe fur seals – *Arctocephalus townsendi*
- 10- Northern fur seals – *Callorhinus ursinus*
- A- Australian sea lions – *Neophoca cinerea*
- B- New Zealand (Hooker’s) sea lions – *Phocarcots hookeri*
- C- South American sea lions – *Otaria flavescens*
- D- Galapagos sea lions – *Zalophus californianus wollebaeki*
- E- California sea lions – *Zalophus californianus californianus*

F- Steller sea lions – *Eumetopias jubatus*

W_P- Pacific walruses – *Odobenus rosmarus divergens*

W_A- Atlantic walruses – *Odobenus rosmarus rosmarus*

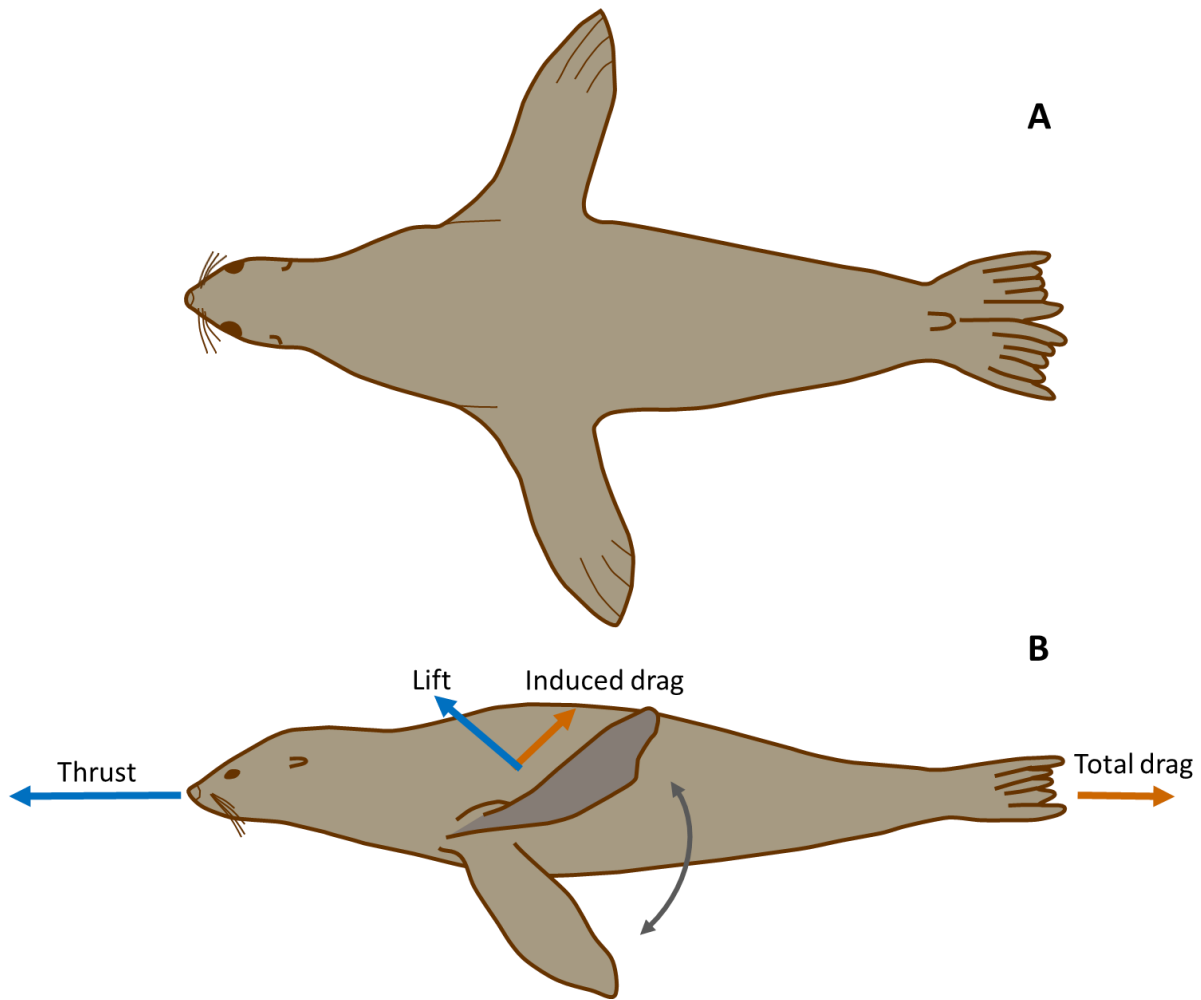


Figure 3: Morphological features of otariids with a view from above (A) or from the side (B). Notice the streamline body shape closely resembling a technical body of revolution designed to minimize drag underwater. The hydrofoil-shape fore-flippers are used for propulsion in a 4-phase stroke pattern and delivers a forward thrust and lift movement with little to no resulting distortion of this streamlined body shape (B).

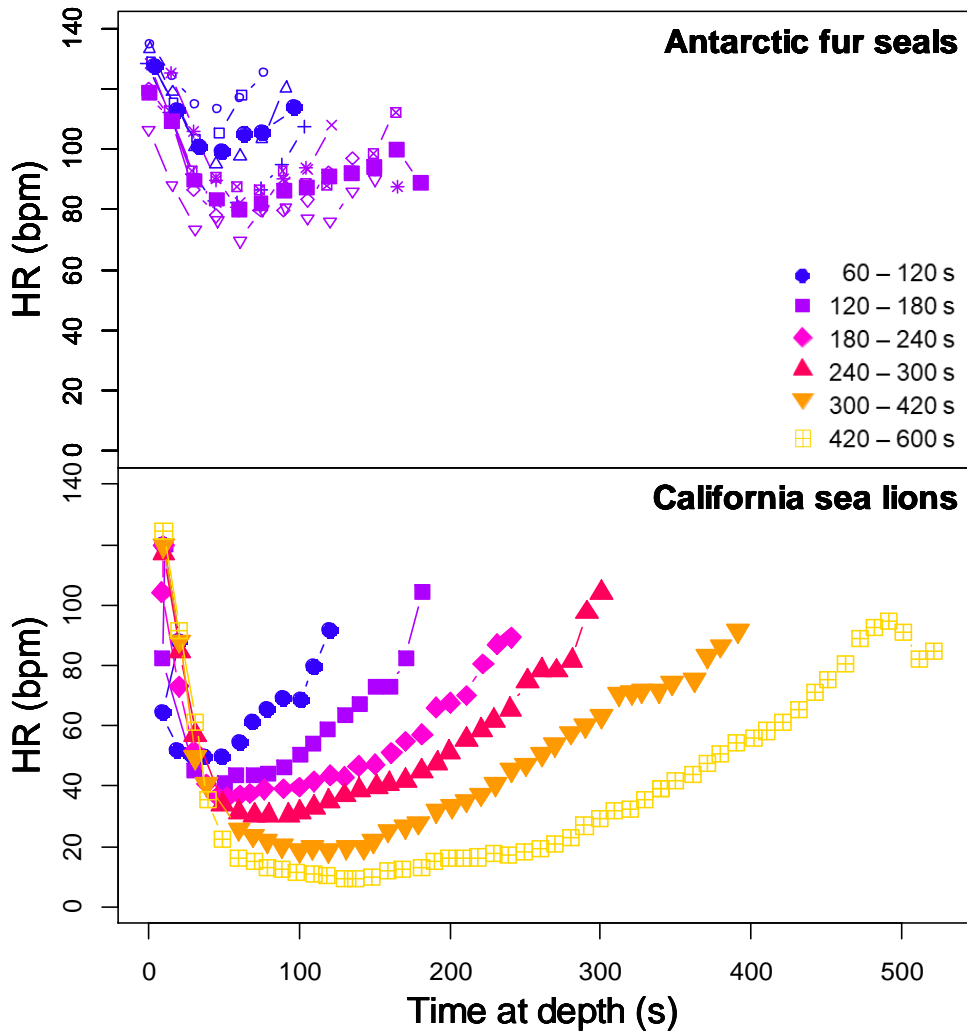


Figure 4: Changes in heart rate (bpm) measured in free-ranging epipelagic Antarctic fur seals (upper graph, data from Boyd et al. 1999) and mesopelagic California sea lions (lower graph, data from McDonald & Ponganis 2014) during dives of various durations (see colour-coded legend). For easier comparison, the dives of Antarctic fur seals lasting between 60 to 120 s (in blue open symbols) and between 120 and 180 s (in purple open symbols) were averaged (closed symbols) to match the time bins for California sea lions.

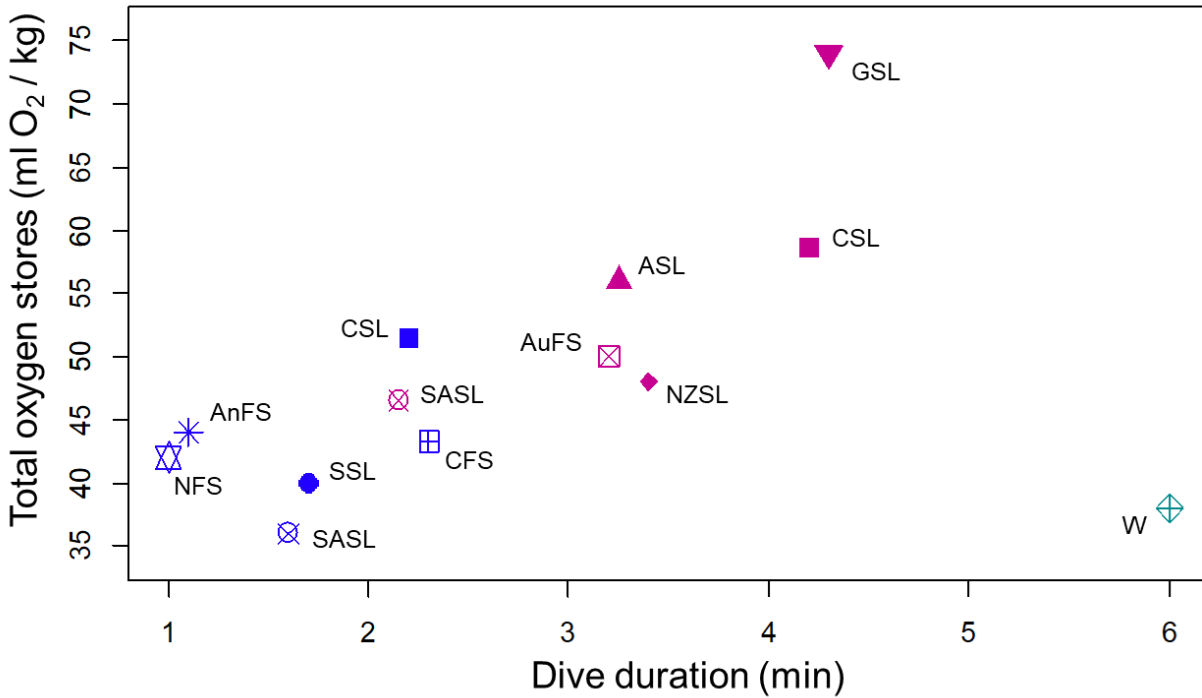


Fig 5: Mass-specific total oxygen stores (ml O₂ / kg) related to dive duration (min) in 8 otariid species, as well as the walrus for comparison. Different symbols indicate the species (NFS northern fur seal, AnFS Antarctic fur seal, SSL Steller sea lion, SASL South American sea lions, CFS Cape fur seal, CSL California sea lion, AuFS Australian fur seal, NZSL New Zealand sea lion, ASL, Australian sea lion, GSL Galapagos sea lion, and W Walrus). The symbol color indicates epi/mesopelagic otariid species in blue and benthic species in pink, with the walrus shown in green. California sea lions and South American sea lions are shown twice as shallow epipelagic and mesopelagic/benthic strategies are displayed in the population. Total oxygen store data from Lenfant et al. (1970), Costa et al. (1998), Costa et al. (2001), Richmond et al. (2006), Weise and Costa (2007), Fowler et al. (2007), Villegas-Amtmann and Costa (2010), Ponganis (2011) and dive duration data from Kuhn and Costa (2014), Costa and Gales (2003), Costa and Gales (2000), Villegas-Amtmann et al. (2017), Jeanniard du Dot et al. (2018), Georges et al. (2000), Gjertz et al. (2001). Australian fur seal and meso/benthic California sea lion data are taken from Costa et al. (2004), South American sea lion data from Hückstädt et al. (2016), and Cape fur seal data from Kirkman et al. (2019).

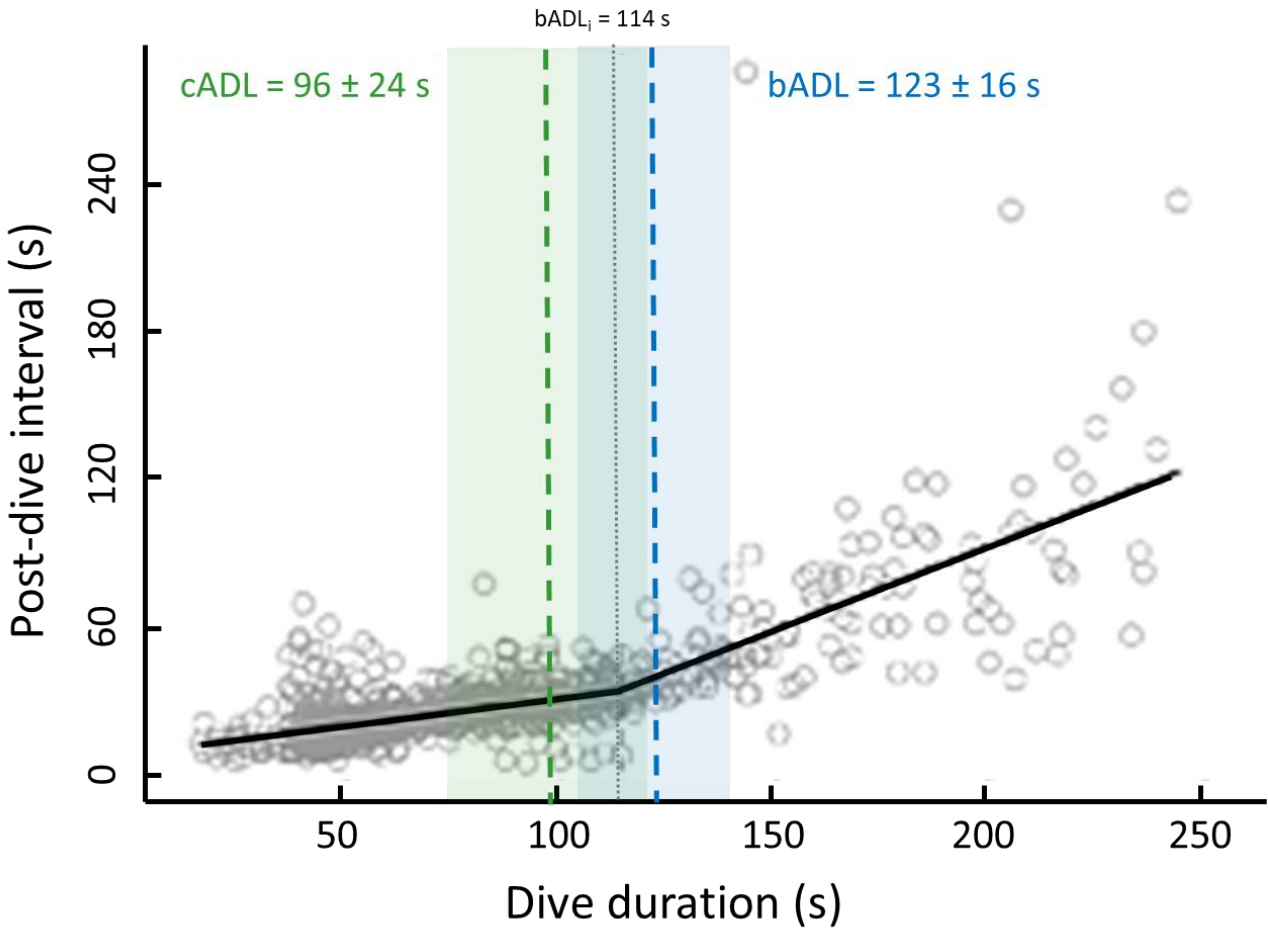


Figure 6: Example of post-dive interval durations (s) as a function of dive duration (s) of a female Antarctic fur seal during a foraging trip at sea used to determine, via broken-line models (solid black lines), the individual behavioral aerobic dive limit (bADL, dotted grey line, data from Viviant et al. 2016). For comparison, the average (\pm SD) bADL for 11 Antarctic fur seal females in Viviant et al. (2016) is shown in blue dashed line and shaded area, and the average (\pm SD) calculated aerobic dive limit (cADL) for 15 Antarctic fur seal females in Costa et al. (2004) is shown in green dashed line and shaded area.

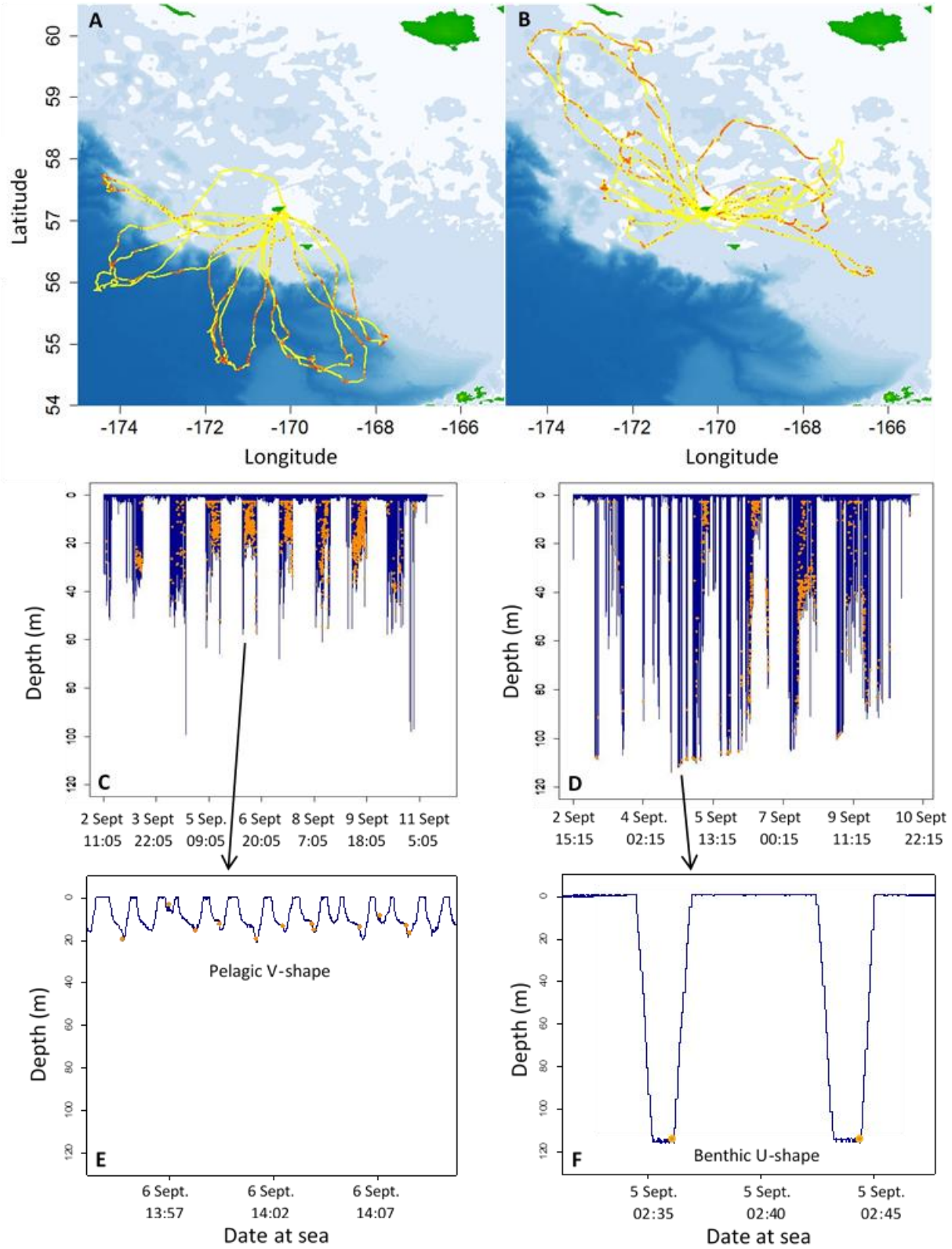


Figure 7: Foraging tracks (A,B) and dive profiles over a full foraging trip (C,D), and a 5-min period of diving (E,F) for lactating northern fur seals from Reef Rookery on St. Paul Island in the

Bering Sea in 2011. Fur seals foraged either pelagically off the shelf in oceanic waters where bathymetry reaches 3000 m, (left panels, n = 8) or benthically on the shallow (~ 100m deep) shelf in neritic waters (right panels, n = 12). Notice that pelagic divers display a typical circadian diving cycle (only at night, shallow at night and deeper at dawn and dusk, C), while benthic divers dive night and day at similar depths (D). Orange dots show spatial distribution of prey capture attempts in Panels A and B (with yellow representing no prey capture attempt) and distribution of prey capture attempts over time and depth profiles in Panels C–F. Figure from Jeanniard du Dot et al. (2018).

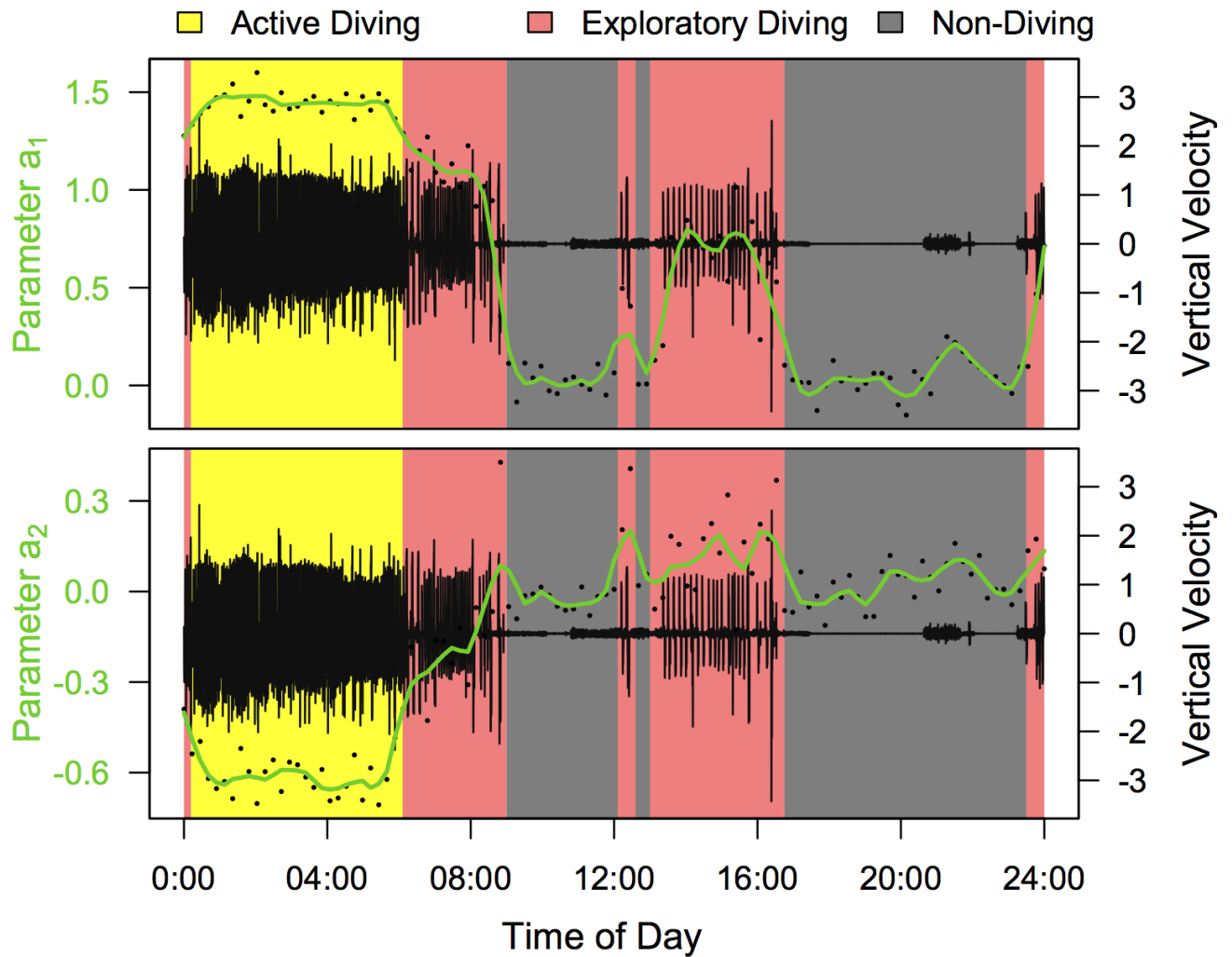


Figure 8: Foraging behaviours of a northern fur seal female breeding on St Paul Island, in the Bering sea during the breeding season 2006 inferred from a behavioural state-space model (results from model parameters a_1 and a_2 are shown with the green lines and original estimates with black dots), based on time series of vertical velocity (black lines). The yellow, pink and grey blocks correspond to active diving, exploratory diving, and non-diving, respectively (as diagnosed from values of a_1 and a_2 from the model). Figure from Joy et al. (2015).

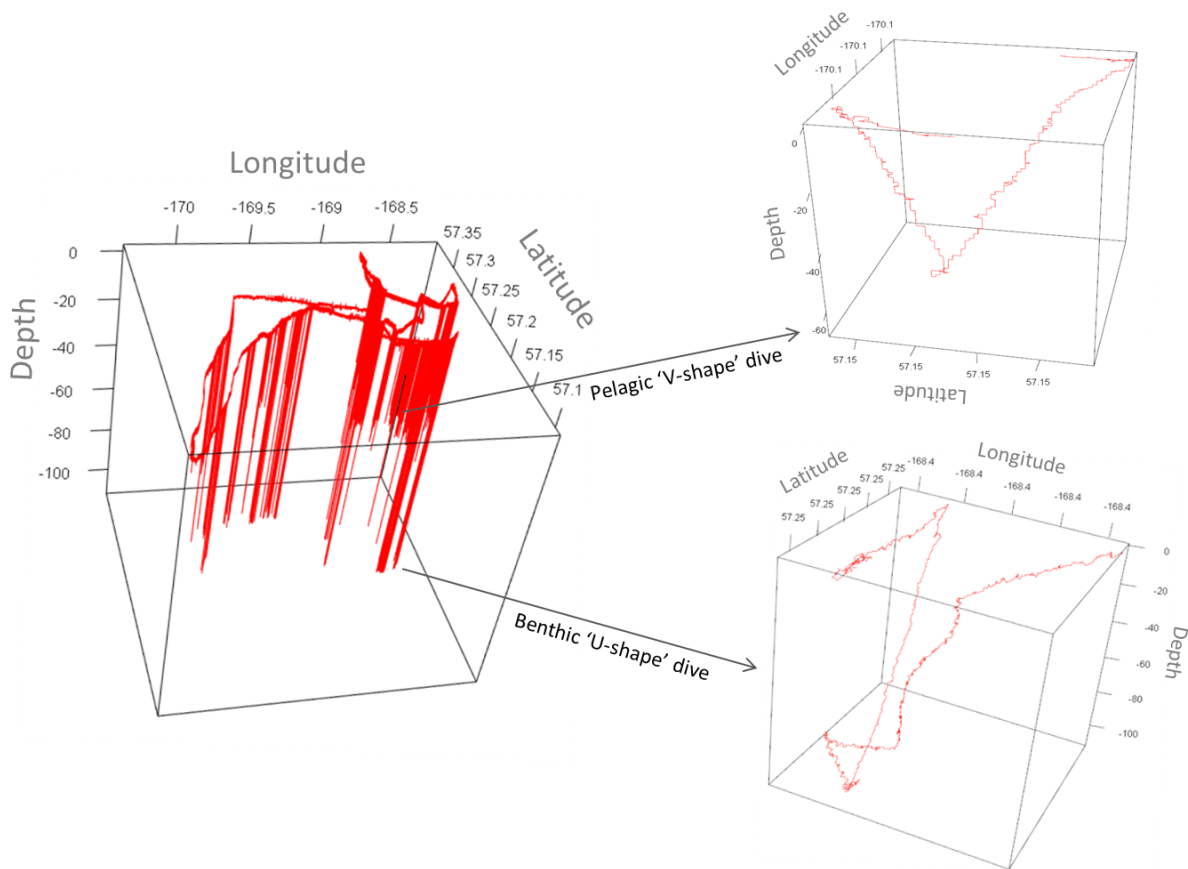


Figure 9: Example of the 3D track of a foraging trip at sea from a female northern fur seal from St. Paul Island reconstructed using tri-axial acceleration, dive depths and GPS data from high-resolution bilogger (and using package TrackReconstruction in R colored by depth). Detailed 3D paths during a benthic (typically classified as U-shape in 2D) and a pelagic (typically classified as V-shape in 2D) are shown as examples.

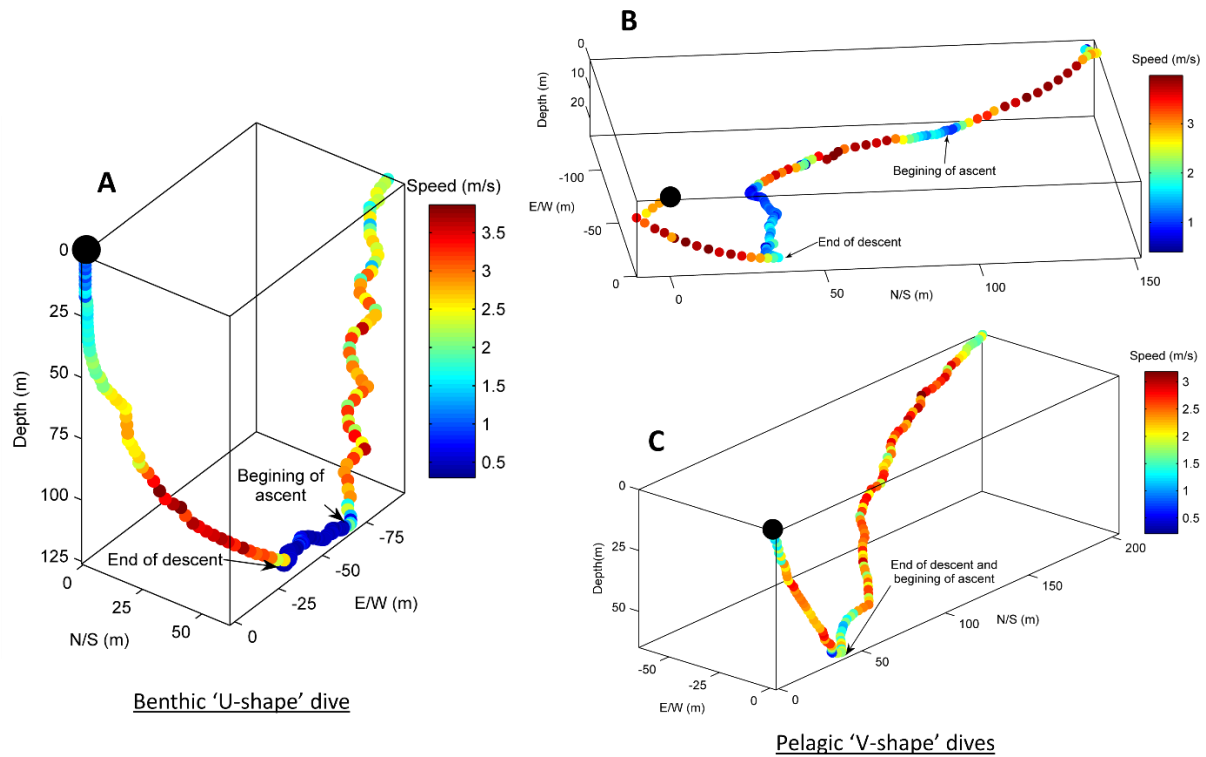


Figure 10: Example of dives performed by a female Steller sea lion from Lovushki Island, Russia, displayed in 3D, color-coded by swim speed and with the black dots representing the beginning of the dives. Graph A shows a typical benthic 'U-shape' dive with steep descent and ascent angles. The animal speeds up from surface to bottom of the dive, likely due to buoyancy-driven gliding strategy, displays a slow swimming speed at the benthos before barrel-rolling back to the surface (as observed in several species of otariids), slowing down towards the end of the ascent. Graphs B and C illustrate pelagic dives with more moderate descent and ascent angles. Graph B shows a dive where changes in swim speed are typical of a prey chase behavior. Graph C illustrates a typical pelagic 'V-shape' dive with a smaller range of swim speeds displayed. Figures from Olivier (2015).

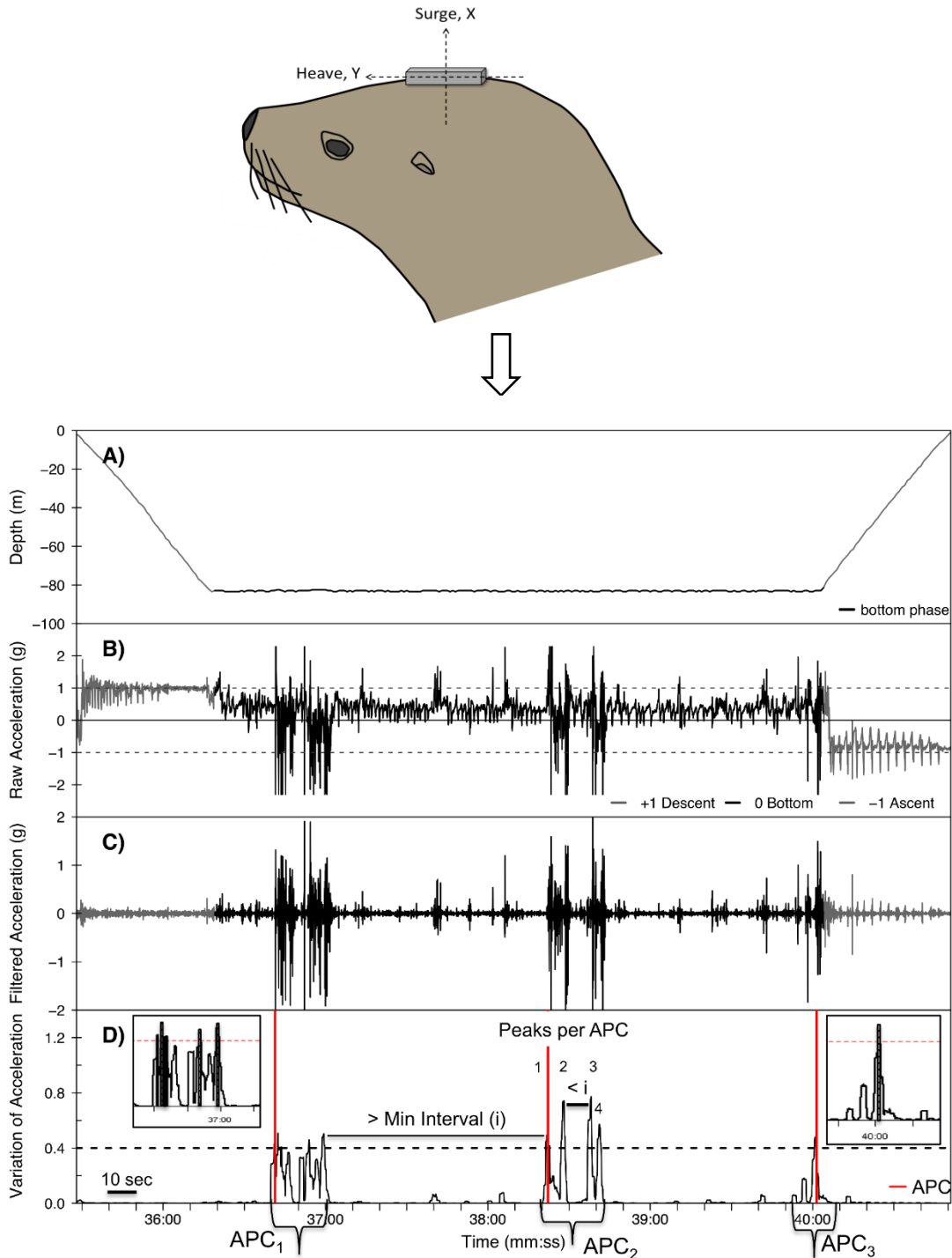


Figure 11: Example of otariid equipped with a head accelerometer showing the surge (X) and heave (Y) axes, and the process of identification of attempted prey captures (APC) from the recorded signal of depth and acceleration. Dive depth for a single dive is shown in panel A, and raw surge acceleration (in g) in panel B. Head movements were isolated from body movements with a 3 Hz high-pass filter (panel C) and variance of acceleration (g^2) was calculated for each individual dive (panel D). Peaks in variance of acceleration above a variance threshold and

within a minimum time interval (i) were used to estimate attempted prey capture (APC, panel D). Figure from Volpov et al. (2015).

Tables

Table 1: See other file

Table 2: Average oxygen carrying capacities of otariids compared to phocid seals. Species used in calculating these averages are indicated in footnote below.

	Otariids	Phocids
Mass-specific total oxygen stores (ml O ₂ / kg)	49.3 ± 11.0 ¹	69.6 ± 16.4 ²
Hb concentration (g Hb / dl blood)	17.8 ± 2.3 ¹	22.9 ± 3.3 ²
Mb concentration (g Mb / 100g muscle)	3.7 ± 1.2 ¹	6.5 ± 1.7 ²
Oxygen affinity, P ₅₀ (mmHg)	28 ± 2 ³	26.9 ± 1.2 ⁴ / 30.5 ± 1.2 ₅

Values used to calculate these means can be found in Lenfant et al. (1970), Costa et al. (1998), Costa et al. (2001), Richmond et al. (2006), Fowler et al. (2007), Weise and Costa (2007), Villegas-Amtmann and Costa (2010), Hückstädt et al. (2016), Kirkman et al. (2019), Qvist et al. (1981), Kooyman (1989), Meir et al. (2009) and McDonald and Ponganis (2013). Values for phocids can be found in Table 4.2, 4.7 and 4.10 in Ponganis (2015). Values for the walrus *O. rosmarus* are 38 ml O₂ / kg, 16 g Hb / dl blood, and 3 g Mb / 100g muscle (Lenfant et al. 1970).

¹ *Z. californianus*, *Z. wollebaeki*, *E. jubatus*, *N. cinerea*, *C. ursinus*, *A. gazella*, *A. pusillus pusillus*, *O. byronia*

² *P. vitulina*, *P. groenlandica*, *P. hispida*, *P. sibirica*, *L. carcinophagus*, *L. weddellii*, *H. leptonyx*, *H. grypus*, *H. fasciata*, *C. cristata*, *M. angustirostris*

³ *Z. californianus*

⁴ *L. weddellii*

⁵ *M. leonina*

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