

Chapter 2

When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids



Daniel P. Costa and Ana M. Valenzuela-Toro

Abstract Otariids exhibit a semiaquatic lifestyle, feeding in the water and breeding and resting on land. Fur seals and sea lions, the two groups of otariids, exhibit an overall income breeding system where the females alternate between trips to the foraging grounds and periods at the breeding colony to feed the pup. How far and how long lactating females can be away from their foraging trips is ultimately dictated by ecological and physiological tradeoffs. In this chapter, we examine the interrelations between behavior and physiology and how they enable or constrain the reproductive, foraging biology, and life history of otariids. For example, income breeding limits otariid females to forage near their reproductive colonies, which constrains them to inhabit highly productive oceanographic regions. Further, as sea lions are larger than fur seals they are capable of deeper and longer dives. As a result, fur seals tend to feed closer to the surface in the epipelagic regions, while sea lions tend to forage in deeper environments on benthic, epipelagic and mesopelagic prey. We review the patterns of resource acquisition and allocation, including an examination of the energetics of reproduction, milk composition, foraging behavior, and differences between fur seals and sea lions. Further, we assess how these factors may have led to their current distribution and demographic trends during the last decades. We finish by discussing how these physiological and ecological tradeoffs would have influenced the evolutionary history of otariids in the deep time.

Keywords Foraging ecology · Otariids · Energetics · Diving behavior · Reproduction · Life histories

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2.1 Introduction

The origin of the amphibious lifestyle of pinnipeds occurred at a time when coastal upwelling intensified (White et al. 1992), resulting in an abundant, diverse marine food resource for which there was likely decreased competition from other endothermic tetrapods (Vermeij and Dudley 2000; Lipps and Mitchell 1976). For pinnipeds, the necessity to return to land to mate and provision their young required a separation of feeding from breeding in both time and space (Bartholomew 1970; Cassini 1999). In response, otariids evolved a modified “income breeding” system (Costa 1991b; Costa 1991a; Schulz and Bowen 2005; Stephens et al. 2009). Under this strategy, production of milk is supported by many short foraging bouts across a prolonged lactation period (Fig. 2.1). The need to return to the colony to suckle the pup limits the amount of time a lactating otariid mother can forage at sea and thus constrains her to foraging on resources that are relatively close to the breeding colony (Costa 1993; Boyd 1998; Trillmich and Weissing 2006; Houston et al. 2007; Stephens et al. 2014). As a result, reproductive success in otariids is closely connected to the abundance and availability of local prey, creating a strong linkage between local environmental fluctuations (e.g. El Niño events) and population status (Trillmich et al. 1991; Costa 2008).

In the sections that follow, we examine how the interdependency between the requirement to provision the pup on shore with the need to forage at sea fundamentally constrains the reproductive pattern of otariids. This fundamental life-history constraint results in some common patterns that vary across the ecological conditions of the different habitats. We examine (1) the energetic challenges of income breeding, (2) the connection between habitat diversity and diversity of foraging patterns and breeding systems; (3) the origins and evolutionary implications of this reproductive strategy; and (4) future directions for research into otariid reproductive and foraging energetics.

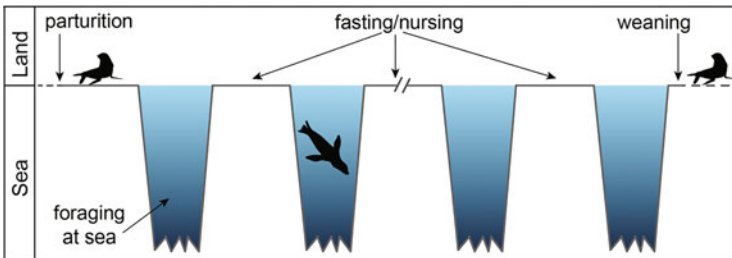


Fig. 2.1 Otariids are income breeders that make intermitted trips foraging at sea and then returning to their pups onshore

2.2 Energetics of Growth, Reproduction and an Amphibious Lifestyle

Growth and reproduction require an animal to acquire more energy and nutrients than are necessary to support vital maintenance. In most mammals, males do not invest energy in parental care of the offspring; instead the cost of reproduction is associated with finding and maintaining access to estrous females and with inseminating as many females as possible. Specifically, in male otariids, reproductive success is associated with large body size. Thus, there is a substantial investment in growth, as large body size confers an advantage in fighting, dominance and territory maintenance as large animals can fast longer, allowing them to maintain their harem longer (Bartholomew 1970; Cassini 1999). The larger size of males is apparent at birth and is maintained throughout life (Payne 1979; Mattlin 1981; Costa and Gentry 1986; Trillmich 1986; Oftedal et al. 1987; Costa et al. 1988; Higgins et al. 1988; Ono and Boness 1996; Georges and Guinet 2001; Weise and Costa 2007). However, in some species (e.g. Guadalupe, *Arctocephalus townsendi*; Juan Fernandez, *A. philippii* and Galapagos, *A. galapagoensis* fur seals and California sea lions, *Zalophus californianus*), the physiological need to access cool water in warmer climates reduces the advantage of large body size (relative heat loss decrease along with increasing body size), thus sexual size dimorphism is reduced in those species that maintain harems in water, or that need access to water (Gentry 1973; Boness and Francis 1991).

For female mammals, reproductive costs are associated with investment in offspring growth through gestation and lactation. Gestation costs come in the form of the energy contained in fetal tissues, as well as the energy to fuel the metabolic processes associated with gestation—also known as the “heat of gestation” (Brody 1945). After a relatively long gestation period, otariid pups are born larger (representing 3.5%–16.5% of the maternal body size) than terrestrial carnivores (0.5%–3%), which is consistent with giving birth to a highly precocial pup. Nevertheless, their lactation duration is comparable to other carnivores (Costa and Maresh 2017). Lactation costs come in the form of the energy and nutrients contained in milk, as well as the energy to fuel milk synthesis. Among pinnipeds, otariids exhibit an income breeding system. Under this strategy, the energy and nutrients required for milk production are obtained during intermittent bouts of foraging, interspersed between shore visits to suckle the pup. For example, female California sea lions can make 50 trips to sea during an 11-month lactation period, typically spending ~3 days foraging within 85 km of their breeding colonies (Kuhn and Costa 2014) (Fig. 2.2).

The shortest lactation durations are 4 months and are found in the Antarctic (*Arctocephalus gazella*) and northern (*Callorhinus ursinus*) fur seals, which inhabit high latitudes. Most otariids have a lactation period of about 11 months. The longest lactation periods are found in Australian sea lions (*Neophoca cinerea*) and Galapagos fur seals. Those species have lactation durations of 17.5 months (Higgins and Gass 1993) and 2–3 years (Trillmich 1990), respectively. These prolonged lactation durations are thought to be associated with a less productive benthic ecosystem in Australia (Costa and Gales 2003) and the highly seasonal and unpredictable nature of prey resources in the Galapagos (Trillmich 1990). Thus,

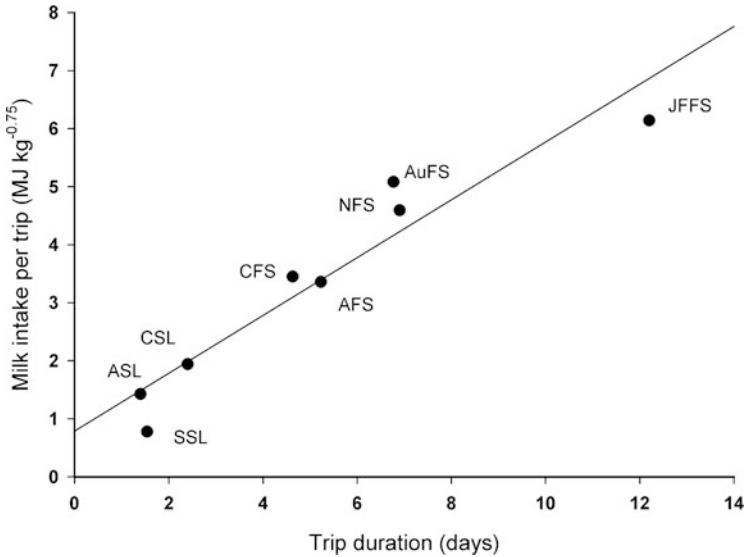


Fig. 2.2 The amount of milk energy delivered to the pup per shore visit relative to the time spent at sea foraging is presented for 8 otariids. Milk energy delivery rates were normalized for differences in female body mass^{-0.75}. Data are for Australian sea lion (ASL) Costa unpublished, California sea lion (CSL) (Oftedal et al. 1987), Steller sea lion (SSL) (Higgins et al. 1988), Antarctic fur seal (AFS) (Arnould and Boyd 1995), Cape fur seal (CFS) (Gamel et al. 2005), Australian fur seal (AuFS) (Arnould and Hindell 2002), and Juan Fernandez Fur Seal (JFFS) (Ochoa-Acuña 1995) and northern fur seal (NFS) (Costa and Gentry 1986)

the income breeding strategy couples reproductive success with local prey abundance (Costa 1993; Boyd 1998), creating a strong link between local environmental fluctuations and population status (e.g. El Niño events) (Trillmich et al. 1991; Costa 2008). As a result, income breeders tend to be limited to breeding in highly productive regions (Costa 1993), and the few species that breed in less productive regions compensate with longer lactation periods. Abbreviations: AFS, Antarctic fur seals; AuFS, Australian fur seals; CFS, Cape fur seals; GFS, JFFS, Juan Fernandez fur seals; NFS, northern fur seals; ASL, Australian sea lions; CSL, California sea lions; SSL, Steller sea lions.

2.2.1 Tradeoffs in Time on Land and at Sea

In otariids, the timing and pattern of maternal investment are optimized in response to their different habitats. Sea lions tend to forage nearshore and make shorter trips (e.g. Steller sea lions, *Eumetopias jubatus*: ~ 2 days, Australian sea lions: ~2 days, southern sea lions, *Otaria flavescens*: 1.6 days, on average) than fur seals that forage further offshore and make longer trips (e.g. northern fur seals: 7.4 days, Juan Fernandez fur seals: 12.3 days, subantarctic fur seals, *A. tropicalis*: 16 days,

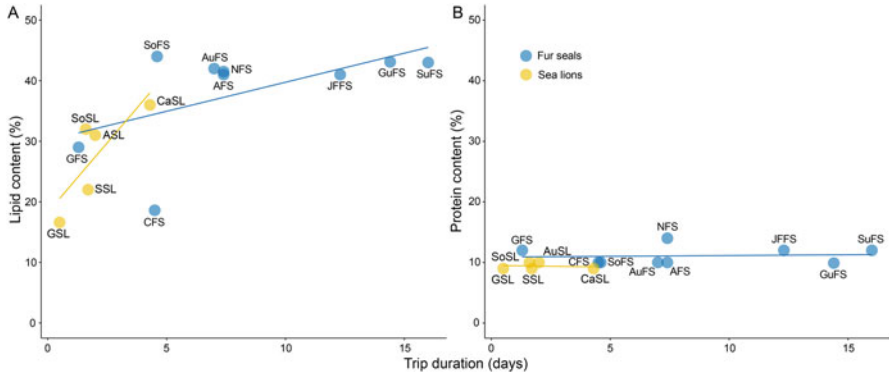


Fig. 2.3 Lipid (a) and protein (b) content of maternal milk in species of fur seals (blue) and sea lions (yellow). Abbreviations: AFS Antarctic fur seals, AuFS Australian fur seals, CFS Cape fur seals, GFS Galapagos fur seals, GuFS Guadalupe fur seals, JFFS Juan Fernandez fur seals, NFS northern fur seals, SoFS South American fur seals, SuFS SubAntarctic fur seals, ASL Australian sea lions, CaSL California sea lions, GSL Galapagos sea lions, SoSL South American sea lions, SSL Steller sea lions

Antarctic fur seals: 7.4 days, on average) (Gentry and Holt 1986; Ono et al. 1987; Boyd et al. 1991; Higgins and Gass 1993; Georges and Guinet 2000; Milette and Trites 2003; Soto et al. 2006). This is even observed within a species as northern fur seals at San Miguel Island where the shelf break is only 2 km away make 3.8 day foraging trips, compared to 7.1–9.8 day foraging trips on the Pribilof Islands where the shelf break is 115 km (Gentry 1998). Such a pattern follows central place foraging theory, which predicts that the optimal strategy is to make longer trips when prey is distant from the central place (reproductive colony) and shorter trips when prey is nearby (Orians and Pearson 1977). Further, as females have longer foraging trips, it is optimal to provide more milk energy to the offspring per shore visit. This is not only more efficient; it also allows otariid mothers to provide similar amounts of energy while making fewer visits. Indeed, empirical data show that those species that make longer trips to sea provide proportionally more milk energy to their pups during their shore visit (Fig. 2.2). The ability to provide more milk energy over a short shore visit is made possible by the high fat content of their milk, which ranges between ~20% and 45% (Fig. 2.3a). In contrast, terrestrial mammals produce milk relatively low in fat. For example, cows and humans produce milk containing 4% and 8% fat, respectively. Nevertheless, there is a disadvantage to an elevated milk fat content, as it is associated with a reciprocal decrease in water content, with no corresponding change in protein content (Fig. 2.3b). Therefore, the protein-to-energy ratio of pinniped milk is lowest in the most energy-dense milk. While pups provisioned with high fat milk receive sufficient energy to fuel their metabolism, they receive relatively less protein that is essential for lean body growth. The issue of how a young pup who is still developing its physiological competence can maintain water balance when they receive relatively less water (as the milk they ingest is so lipid rich) remains unknown.

2.2.2 *Diving Physiology and Capacity*

Despite their external similarities, fur seals and sea lions differ in their morphology, physiology, foraging ecology, and life history (Arnould and Costa 2006). For instance, insulation in fur seals is mainly provided by a dense and impermeable fur coat (with an underfur layer), whereas in sea lions, insulation relies on a thick blubber layer (Liwanag et al. 2012a; Liwanag et al. 2012b). While blubber maintains its insulating quality with depth, the insulation of fur seals declines as the seal dives as the air contained in fur compresses (Repenning 1976). Furthermore, just as in sea otters, an air layer would add buoyancy that may require more effort during the descent phase of the dive.

Body size also differs between these groups, as sea lions are larger than fur seals, which results in differences in their physiology and foraging ecology. The larger body size of sea lions facilitates longer and deeper dives (Ponganis 2016). Thus, while sea lions tend to dive deeper and longer often foraging at or near the benthos on the continental shelf, fur seals tend to exploit the upper reaches (epipelagic) of the water column often offshore (Table 2.1 and Fig. 2.4) (Villegas-Amtmann et al. 2013). Diving capacity is, in part, controlled by body size, as the metabolic rate (oxygen demand) scales to body mass^{0.75} while oxygen stores (supply) scale with body mass^{1.0}. Therefore, larger animals have a lower mass-specific metabolism for a relatively constant proportion of oxygen storage capacity (Ponganis 2016). All things being equal, large animals should be able to dive longer and deeper than small ones based on body size alone (dive ability scales with body mass^{0.25}). This pattern holds when we compare sea lions to fur seals, as sea lions are, in general, larger and are more capable divers than fur seals (Fig. 2.4). However, if we just compare sea lions, we find the largest sea lion species, the southern and Steller sea lions, make the shortest-shallowest dives (Hückstädt et al. 2016) while the smallest, the Galapagos sea lion makes the longest dives (Figs. 2.5 and 2.6) (Villegas-Amtmann and Costa 2010). The exceptional diving ability of Galapagos sea lions is made possible by having the highest oxygen storage capacity (greater blood volume and muscle myoglobin) of any otariid, equal to that of many deep diving phocids (Villegas-Amtmann and Costa 2010).

Different foraging patterns require different physiological capabilities as deeper dives are also longer. In air breathing vertebrates, the primary determinant of dive duration is the aerobic dive limit, which is determined by the animals' oxygen stores coupled with the rate at which oxygen is utilized (Ponganis 2016). The oxygen storage capacity of mesopelagic and benthic divers (e.g. sea lions) is higher, enabling them to make longer dives compared to epipelagic foragers (e.g. fur seals) who have relatively lower oxygen stores and consequently shorter dives (Fig. 2.5). Greater oxygen stores are achieved by a synergistic effect between increases in hematocrit (proportion of red blood cells in whole blood), blood volume, and muscle myoglobin concentration (Ponganis 2016). Nevertheless, there is a tradeoff as an elevated hematocrit also increases blood viscosity, reducing the ability of blood to transport oxygen optimally (Hedrick and Duffield 1991). As otariids exhibit highly aerobic

Table 2.1 Summary of life-history attributes of otariid species. Average values are presented

Common name	Scientific name	Population trend	Mean dive depth (m)	Mean dive duration (min)	Trip duration (days)
Antarctic fur seal	<i>Arctocephalus gazella</i>	Stable/ Increasing	53.0	1.6	7.4
Australian fur seal	<i>Arctocephalus pusillus doriferus</i>	Stable/ Increasing	58.0	2.9	7.0
Cape/Brown fur seal	<i>Arctocephalus pusillus pusillus</i>	Increasing	74.0	2.5	4.5
Galapagos fur seal	<i>Arctocephalus galapagoensis</i>	Declining	26	N/I	1.3
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	Increasing	17	N/I	14.4
Juan Fernandez fur seal	<i>Arctocephalus philippii</i>	Increasing	26.4	1.8	12.3
New Zealand fur seal	<i>Arctocephalus forsteri</i>	Increasing	33.3	1.5	~7
Northern fur seal	<i>Callorhinus ursinus</i>	Declining	18.3	1.0	7.4
South American fur seal	<i>Arctocephalus australis</i>	Declining	61	2.1	4.6
Subantarctic fur seal	<i>Arctocephalus tropicalis</i>	Stable/ Increasing	39.7	1.6	16
Australian sea lion	<i>Neophoca cinerea</i>	Stable	61.0	3.3	< 2
California sea lion	<i>Zalophus californianus</i>	Increasing	58.2	2.2	4.3
Galapagos sea lion	<i>Zalophus wollebaeki</i>	Declining	97.4	3.7	0.5
New Zealand sea lion	<i>Phocarcos hookeri</i>	Declining	117.1	3.4	1.7
South American sea lion	<i>Otaria flavescens</i>	Declining	21.7	2.0	1.6
Steller sea lion	<i>Eumetopias jubatus</i>	Declining	29.6	1.8	1.7

Common name	Dominant Foraging behavior	Body length males (m)	Body length females (m)	Body mass males (kg)	Body mass females (kg)	Reference
Antarctic fur seal	Epipelagic	1.8	1.3	165	39.3	1, 8, 20, 28
Australian fur seal	Benthic	2.2	1.6	289	77	1, 7, 27
Cape/Brown fur seal	Epipelagic	2.2	1.4	229	54	1, 14, 25

(continued)

Table 2.1 (continued)

Common name	Dominant Foraging behavior	Body length males (m)	Body length females (m)	Body mass males (kg)	Body mass females (kg)	Reference
Galapagos fur seal	Epipelagic	1.6	1.2	64	28.9	1, 5, 11, 20
Guadalupe fur seal	Epipelagic	2.2	1.5	165	49.1	1, 2, 9
Juan Fernandez fur seal	Epipelagic	2.0	1.4	142.1	48.1	1, 4, 10
New Zealand fur seal	Epipelagic	2.0	1.3	150	38.1	1, 3, 7, 20
Northern fur seal	Epipelagic	2.1	1.5	270	41.4	1, 19, 20, 29
South American fur seal	Epipelagic	2	<1.5	125	41.7	1, 6, 19, 20
Subantarctic fur seal	Epipelagic	1.8	1.4	117.5	49.6	1, 13, 20, 30, 31
Australian sea lion	Benthic	2.2	1.6	215	80	1, 7, 20, 26
California sea lion	Epipelagic/ Mesopelagic/ Benthic	2.5	1.6	523	84	1, 16, 23
Galapagos sea lion	Epipelagic/ Mesopelagic/ Benthic	NI	1.6	200	77	1, 17, 22
New Zealand sea lion	Mesopelagic/ Benthic	2.4	1.9	375	112	1, 12, 15, 24, 26
South American sea lion	Benthic	2.4	1.8	325	131	1, 15, 24
Steller sea lion	Benthic	3.3	2.5	1000	275	1, 18, 20, 21

NI no information

References: ⁽¹⁾ Kovacs et al. (2012), ⁽²⁾ Gallo-Reynoso et al. (2008), ⁽³⁾ Harcourt et al. (2001), ⁽⁴⁾ Francis et al. (1998), ⁽⁵⁾ Kooyman and Trillmich (1986), ⁽⁶⁾ Baylis et al. (2018), ⁽⁷⁾ Kirkwood and Goldsworthy (2013), ⁽⁸⁾ Hofmeyr (2016), ⁽⁹⁾ Aurioles-Gamboa (2015a), ⁽¹⁰⁾ Aurioles-Gamboa (2015b), ⁽¹¹⁾ Trillmich (2015), ⁽¹²⁾ Chilvers (2015), ⁽¹³⁾ Hofmeyr (2015a), ⁽¹⁴⁾ Hofmeyr (2015b), ⁽¹⁵⁾ Cárdenas-Alayza et al. (2016a), ⁽¹⁶⁾ Aurioles-Gamboa and Hernández-Camacho (2015), ⁽¹⁷⁾ Gelatt and Sweeney (2016), ⁽¹⁸⁾ Gelatt et al. (2015), ⁽¹⁹⁾ Cárdenas-Alayza et al. (2016b), ⁽²⁰⁾ Schulz and Bowen (2004), ⁽²¹⁾ Rehberg et al. (2009), ⁽²²⁾ Villegas-Amtmann and Costa (unpublished data), ⁽²³⁾ McHuron and Costa (unpublished data), ⁽²⁴⁾ Hückstädt and Costa (unpublished data), ⁽²⁵⁾ Kirkman et al. (2019), ⁽²⁶⁾ Costa (unpublished data), ⁽²⁷⁾ Arnould and Hindell (2001), ⁽²⁸⁾ Lea et al. (2002), ⁽²⁹⁾ Kuhn et al. (2014), ⁽³⁰⁾ Georges and Guinet (2000), ⁽³¹⁾ Luque et al. (2007)

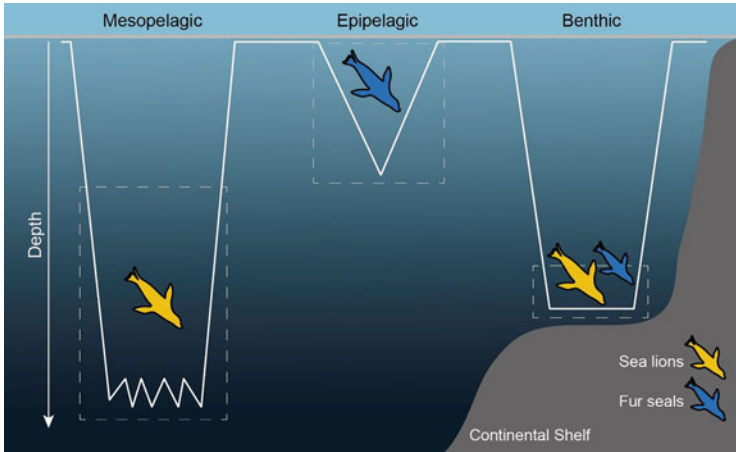


Fig. 2.4 General marine foraging patterns exhibited by otariids. Note that there are some exceptions to this classification, including California sea lions which also exhibit epipelagic foraging. The dashed boxes represent the potential area where they are likely able to search and capture prey. The relative size of fur seals and sea lions is not in scale. Modified from Costa et al. (2006) and Gallagher et al. (2015)

energetic foraging behavior, their hematocrit is lower than phocids but is optimal for maximizing oxygen delivery while maintaining elevated blood oxygen stores. Diving behavior and physiological capacity also vary within a species; for instance, individuals of Galapagos sea lions that make longer-deeper dives also have greater oxygen stores than those that make shorter-shallower dives (Villegas-Amtmann and Costa 2010). Further, the oxygen stores of California sea lions increase as they undergo seasonal increases in dive depth and duration (Villegas-Amtmann et al. 2012). Variation of oxygen stores within a species suggests that oxygen stores are plastic and may increase in response to periodic or prolonged bouts of hypoxia as a “training effect”.

In most cases, for most species, individual sea lions that dive longer also exhibit greater post-dive surface intervals (Fig. 2.7). Due to the need to maximize bottom time searching and/or pursuing prey, mesopelagic and benthic foraging otariids appear to be working closer to their physiological limits, often exceeding their aerobic dive limit (Costa and Gales 2000, 2003; Costa et al. 2000a, 2004). Because these deep diving species are already working at or near their maximum physiological capacity, they may have a limited ability to further increase their dive duration and/or foraging effort in order to respond to changes in their environment and resource limitations. Therefore, benthic-foraging species might be particularly sensitive to changes in their habitat resulting from climate change or interactions with fisheries, which remove the larger size classes of fish upon which they depend (Chilvers and Wilkinson 2009). In fact, species such as Australian and New Zealand sea lions, which specialize on benthic or demersal prey, have endangered populations, while the California sea lion, a generalist that feeds on prey

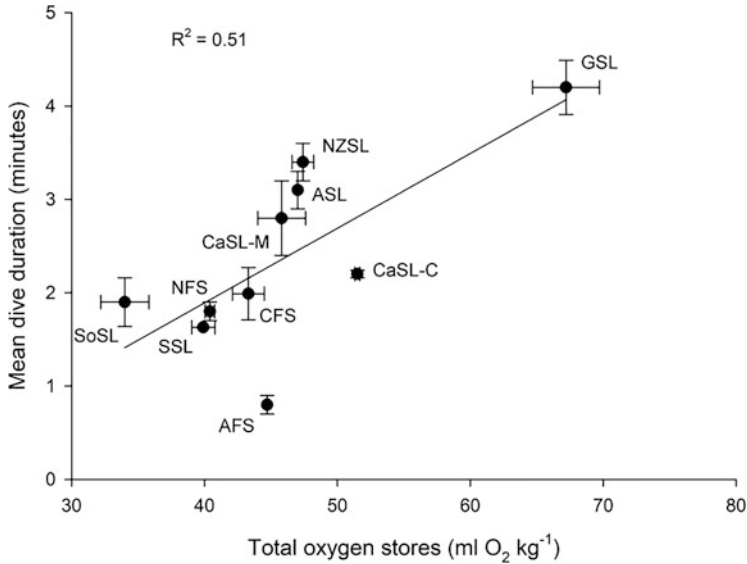


Fig. 2.5 The mean dive duration (mean \pm se) is plotted as a function of the total oxygen stores (mean \pm se) for South American sea lions (SoSL), Australian sea lions (ASL), California sea lions from Mexico (CaSL-M), California sea lions from California (CaSL-C), Antarctic fur seals (AFS), Cape fur seals (CFS), New Zealand sea lions (NZSL), Galapagos sea lions (GSL), Steller sea lions (SSL), and northern fur seals (NFS). O₂ stores and dive duration data were measured in the same individuals for ASL, NZSL, CaSL-M, SoSL, AFS, GSL and CFS. Data are from Riet-Sapriza et al. (2013), Costa et al. (1998, 2001), Costa and Gales (2000), Kuhn and Costa (2014), Villegas-Amtmann and Costa (2010), Weise and Costa (2007), Richmond et al. (2006), Rehberg et al. (2009), Shero et al. (2012), Hückstädt et al. (2016), and Kirkman et al. (2019)

throughout the water column, is now thriving and has recovered from previous exploitation (Chilvers and Meyer 2017; Hamer et al. 2013; Laake et al. 2018; Costa et al. 2006).

Further, the pressure imposed by fisheries would present an even more significant challenge for juvenile sea lions and fur seals as they are smaller, have less experience and are still acquiring their oxygen stores (Fowler et al. 2007b; Weise and Costa 2007; Shero et al. 2012). Not surprisingly, juvenile sea lions and fur seals make significantly shorter and typically shallower dives compared to adults (Loughlin et al. 2003; Pitcher et al. 2005; Fowler et al. 2006; Jeglinski et al. 2012; Leung et al. 2014) and they forage in different areas or within a restricted region of the same habitat as adults (Fowler et al. 2007a; Jeglinski et al. 2013; Hückstädt et al. 2014; McHuron et al. 2018a; Salton et al. 2019; Zeppelin et al. 2019). These factors make juveniles more susceptible to resource limitations in general and particularly so for benthic-foraging species, and are likely associated with the low recruitment in these declining populations (Costa et al. 2004; Arnould and Costa 2006).

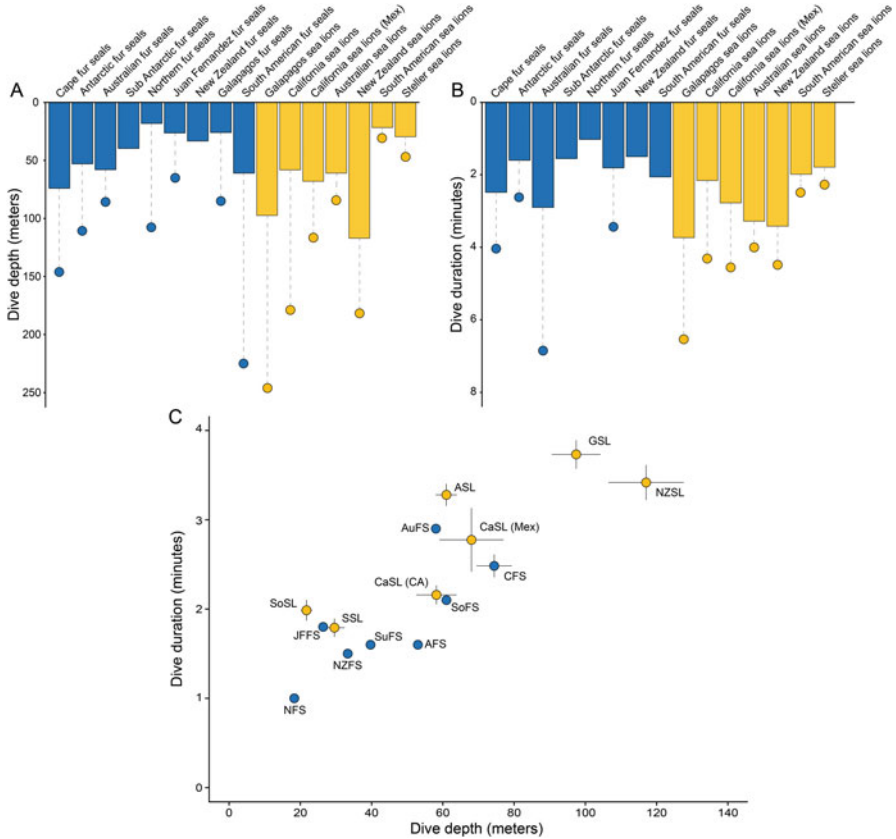


Fig. 2.6 Mean dive depth (a) and mean dive duration (b) for species of fur seals (blue) and sea lions (yellow). Dots represent the maximum values for dive depth and dive duration, respectively. (c) Plot showing the maximum dive duration as a function of diving depth for selected species of otariids. Abbreviations: AFS Antarctic fur seals, AuFS Australian fur seals, CFS Cape fur seals, GFS Galapagos fur seals, GuFS Guadalupe fur seals, JFFS Juan Fernandez fur seals, NFS northern fur seals, SoFS South American fur seals, SuFS SubAntarctic fur seals, ASL Australian sea lions, CaSL California sea lions, GSL Galapagos sea lions, SoSL South American sea lions, SSL Steller sea lions. Data are from Kirkman et al. (2019), Rehberg et al. (2009), Riet-Sapirza et al. (2013), Villegas-Amtmann and Costa (2010), Villegas-Amtmann et al. (2012), Costa and Gales (2000), Hückstädt et al. (2016), Costa et al. (2001), Kuhn and Costa (2014), and Baylis et al. (2016, 2018)

2.2.3 Field Metabolic Rates

Field metabolic rate (FMR) measures an animal’s total energy expenditure after all constituent costs are supported, and provide insight into the energetic strategies used by marine mammals (Costa 2008). Several approaches have been used to study the FMR of animals at sea and onshore. Time budget analysis sums the daily metabolic

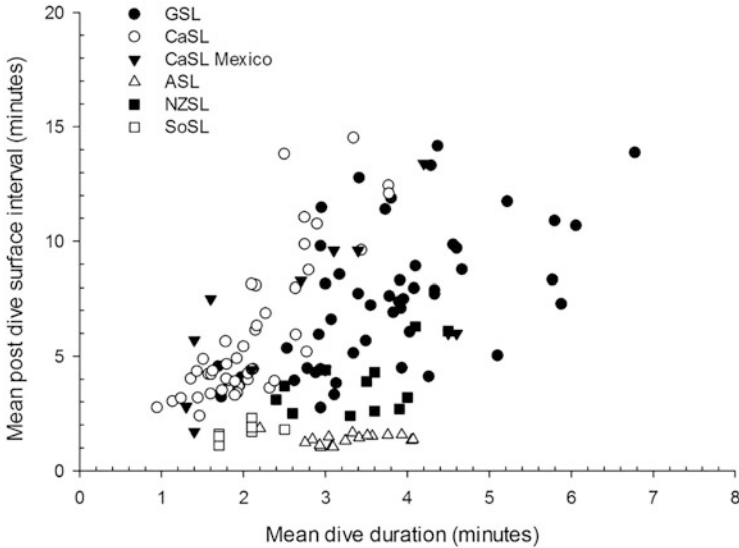


Fig. 2.7 Each point of the figure is the mean post dive surface as a function of the mean dive duration for that individual. Dive data are for individual Southern sea lions (SSL), Australian sea lions (AuSL), California sea lions in Mexico (CaSL-M), California sea lions in California (CaSL), New Zealand sea lion (NZSL) and for Galapagos sea lions (GSL). Data are from Riet-Sapriza et al. (2013), Villegas-Amtmann and Costa (2010), Villegas-Amtmann et al. (2012), Costa and Gales (2000), Hückstädt et al. (2016), Kirkman et al. (2019), Costa et al. (2001), and Kuhn and Costa (2014)

costs associated with various activities (Williams et al. 2004, 2007). Other methods rely on predictive relationships between FMR and physiological variables such as heart rate or ventilation rate, between FMR and changes in body mass and composition, or between FMR and bio-mechanical power (Young et al. 2011; Fahlman et al. 2013; Maresh et al. 2015). The breeding system of otariids where mothers periodically forage at sea and return to the pup on shore facilitates measurements of female foraging behavior and energy expenditure. Measurements of FMR using the doubly labelled water method have taken advantage of the need for the mother to return to her pup onshore, as this facilitates the likelihood of recovering instruments and getting final blood samples required for FMR measurements. Thus, FMR measurements using doubly-labelled water have been carried out on a number of species, including northern, Antarctic, and Galapagos fur seals and California, Galapagos, Australian, and New Zealand sea lions (Costa and Gentry 1986; Costa et al. 1989; Costa and Gales 2000, 2003; Jeanniard-du-Dot et al. 2017a, b, c; Fowler et al. 2007b; McDonald et al. 2012; McHuron et al. 2017b, 2019; Arnould et al. 1996). These studies indicate that otariids have an expensive lifestyle, expending energy at ~ 6 times the predicted basal metabolic rate. Such a high field metabolic rate is consistent with a fast pace of life, where a high rate of energy expenditure is associated with a high rate of prey energy acquisition (Schmitz and Lavigne 1984;

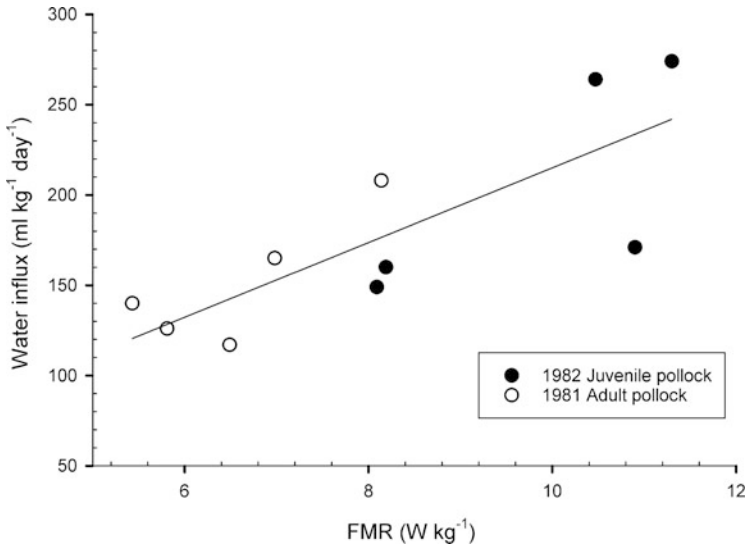


Fig. 2.8 Plot of FMR as a function of water influx of northern fur seal females foraging between two seasons (Costa and Gentry 1986). Fur seals in 1981 (open circles) were feeding primarily on adult pollock and during 1982 (solid circles) they were feeding on 0 age pollock (Sinclair et al. 1996)

Wright et al. 2018), which in turns enables a greater investment of energy into reproduction. This is in marked contrast to the lower field metabolic rate (1.5-3 times) predicted for elephant (*Mirounga* spp.) and Weddell seals (*Leptonychotes weddellii*), phocids which also have a slower pace of life (Maresh et al. 2015).

FMRs are quite variable between and within species and are associated with year-to-year changes in both the abundance and availability of prey (Costa 2008). For example, California sea lions significantly increased their foraging effort in response to reductions in prey availability during the 1983 El Niño event (see below for more insights on the El Niño events). Foraging effort also varies with the type of prey consumed. In fact, northern fur seals, foraging on mature pollock (*Theragra chalcogramma*) during 1981, had lower metabolic rates than fur seals feeding predominately on juvenile pollock during 1982 (Fig. 2.8). Further, the importance of the thermal environment on field metabolic rate can also be seen in Galapagos fur seals and sea lions, which due to the warm equatorial climate, have substantially reduced field metabolic rates compared to other otariids (Trillmich and Kooyman 2001; Villegas-Amtmann et al. 2017).

2.3 Habitat Diversity, Foraging Patterns and Reproductive Strategies

Otariids occupy a wide range of habitats in the Pacific, South Atlantic and Southern Oceans, but are completely absent from the North Atlantic Ocean, which is consistent with both the historical and paleontological records of this family (Berta et al. 2018) (Fig. 2.9). They breed on predator-free islands and, in some cases, mainland colonies from the equatorial regions of the Galapagos to the sub-polar regions of the Antarctic and the Bering Sea. In contrast to true seals and walruses (see Miller and Kochnev, Chap. 22), otariids do not breed on ice. However, some species like Antarctic fur seals often haul out on ice floes to rest (Fig. 2.10). Within these regions, their distribution is limited to highly productive habitats, mostly associated with upwelling systems (Fig. 2.9). This distributional pattern results from the physiological constraints associated with income breeding, an energetically expensive strategy that requires abundant and predictable prey resources relatively near the colony (Costa 1993; Boyd 1998; Trillmich and Weissing 2006; Stephens et al. 2014).

2.3.1 Foraging Behavior Relative to Habitats and Energetics

Different habitats are associated with three distinct marine foraging patterns: epipelagic, where animals forage in the upper water column between 0 and 200 m;

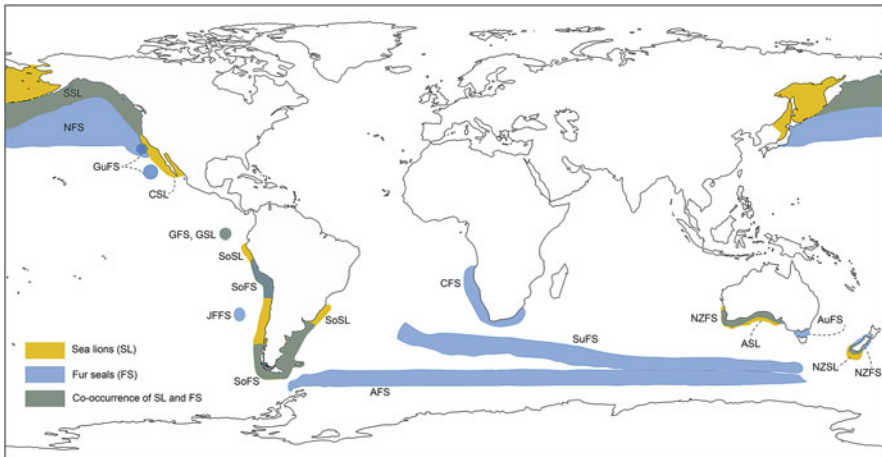


Fig. 2.9 Primary geographic distribution of Otariids around the globe. Abbreviations: AFS Antarctic fur seals, AuFS Australian fur seals, ASL Australian sea lions, CFS Cape fur seals, CSL California sea lions, GFS Galapagos fur seals, GuFS Guadalupe fur seals, GSL Galapagos sea lions, JFFS Juan Fernandez fur seals, NFS Northern fur seals, NZFS New Zealand fur seals, NZSL New Zealand sea lions, SoFS, South American fur seals, SoSL, South American sea lions, SuFS Sub Antarctic fur seals, SSL Steller sea lions



Fig. 2.10 Male Antarctic fur seal resting on an ice flow in the Antarctic Peninsula. Photo by Dan Costa

mesopelagic, where animals forage deeper between 200 and 1000 m, and benthic, where animals forage at or near the bottom of the seafloor (Costa et al. 2001, 2004, 2006; Arnould and Costa 2006) (Fig. 2.4). Benthic and mesopelagic dives are generally longer as animals must transit to depth before they can begin searching and pursuing prey and, once the prey has been captured or pursuit discontinued, they must then transit back to the surface (Fig. 2.4). As epipelagic dives are shallow, animals may initiate searching and pursuit at or near the surface or soon after the dive commences within little or no transit phase. Thus, epipelagic dives can be shorter than either mesopelagic or benthic dives as a greater proportion of the dive is spent searching or pursuing prey. Furthermore, these foraging strategies also affect the diet as epipelagic foragers can capture numerous small prey per dive, whereas benthic foragers tend to pursue single large prey per dive, and mesopelagic foragers pursue many small or a few large prey per dive (Costa 1988, 1991a, 1993; Volpov et al. 2016).

The tradeoffs associated with these different diving patterns have been examined using optimality models (Carbone and Houston 1996; Houston et al. 2003; Foo et al. 2016) and show that large prey and/or energy dense prey are preferred unless small or energy poor prey is considerably more abundant/available. However, there is an upper threshold that is determined by the animals' digestive physiology when they can no longer forage as they are satiated and require time to process the ingested prey (Rosen and Trites 2004). Marine mammals have a long gut compared to terrestrial carnivores, and this may increase their capacity to process and absorb nutrients, increasing foraging efficiency (Williams and Yeates 2004; Williams et al. 2001). The occurrence of these foraging and diving patterns varies widely across the

otariids (Table 2.1 and Fig. 2.4). Nevertheless, behavioral plasticity has been recognized in some species including Galapagos sea lions which exhibit all three foraging patterns (Villegas-Amtmann et al. 2008). Other species like Australian sea lions forage primarily at or near the benthos (Costa and Gales 2003), while New Zealand (*Phocartos hookeri*) sea lions, the deepest diving sea lion, forage in both the mesopelagic and benthic regions (Chilvers et al. 2006; Chilvers 2017).

Foraging patterns also vary with habitat and colony location. For example, Antarctic fur seal females feed primarily on krill around the Antarctic Peninsula (Osman et al. 2004) and South Georgia. However, at Kerguelen and Heard Islands, they forage deeper primarily on fish (Lea et al. 2008; Staniland et al. 2010). Dives are shallower when feeding on small prey, such as krill, compared to larger prey such as fish, which are larger and energetically more beneficial (Staniland et al. 2010). Similarly, female California sea lions foraging in the Southern California Bight are generalists foraging epipelagically on a variety of fish and squid (McHuron et al. 2016, 2018b). Still, in the Sea of Cortez (= Gulf of California), they forage both in the epipelagic and mesopelagic zones (Villegas-Amtmann et al. 2011).

Furthermore, benthic foraging species regularly undertake dive durations exceeding their calculated aerobic dive limit (cADL), whereas the epipelagic foraging species rarely dive longer than their cADL (Costa et al. 1999, 2004). Thus, benthic species might have a lower capacity to increase foraging effort in times of nutritional stress than epipelagic species. This reduced capacity or resilience to change could result in reductions in reproductive output, offspring growth, and survival (Arnould and Costa 2006). This pattern is supported by the lower reproductive rate observed in the Australian fur seals (*A. pusillus doriferus*) (and benthic feeding sea lions) compared to the epipelagic conspecific South African fur seal (*A. pusillus pusillus*) and California sea lions. Indeed, the difference between the mean birth rate of all benthic ($61.7 \pm 4.0\%$) and epipelagic ($79.1 \pm 1.1\%$) foragers approached significance ($t^2 = 4.15$, $P = 0.053$). The low reproductive rate of Australian fur seals may explain their very slow recovery from commercial sealing in comparison to the rapid recovery of the conspecific South African fur seals, which is now the most numerous otariid. Similarly, California sea lions were hunted prior to their protection under the Marine Mammal Protection Act of 1972 and have since recovered, unlike anything observed in *benthic* foraging sea lions (Laake et al. 2018).

2.3.2 Consequences for Population Dynamics

Associated with these divergent trends of *epipelagic* and *benthic* foraging behavior are differences in the population dynamics of sea lions and fur seals. All species of otariid seals throughout the world were subject to extensive and, in most cases, excessive hunting pressure during the eighteenth and nineteenth centuries (Wickens and York 1997) (Crespo, Chap. 24). By the late 1800s, however, most species were protected or were subject to sustainable harvests. Despite this protection, populations of the various sea lion species have experienced minimal recovery and, in some

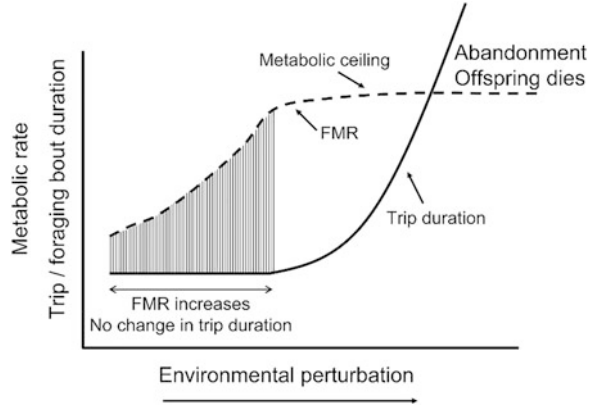
cases, are declining, whereas many fur seal species have recovered or are recovering (Wickens and York 1997; Costa et al. 2006; Kovacs et al. 2012). This suggests that there may be life-history consequences associated with the different foraging modes, which influence population dynamics (i.e., specific foraging mode may be more efficient?).

2.3.3 *Role of Food Availability*

The impact of environmental variability on marine mammal populations is best documented by their response to variations to the El Niño Southern Oscillation (ENSO). ENSO events are characterized by a reduction in upwelling favorable winds along the West Coasts of North and South America and teleconnections to other regions, including the Southern Ocean (Murphy et al. 2007; Clarke 2014). Among the changes that occur are the deepening of the thermocline depth and associated reductions in primary production due to the loss of upwelling. Most notable are the 1983 and 1998 ENSO events, where pinnipeds along the west coasts of North and South America faced significant reductions in prey availability, leading to increased foraging times, reduced prey captures rates, reduced pup growth rates, lower weaning weights, increased pup mortality, and in some cases reduced adult survival (Trillmich and Limberger 1985; Trillmich and Ono 1991; Boyd and Roberts 1993; Melin et al. 2012; Sielfeld et al. 2018). The impact of the 1983 and 1998 ENSO events on pup production in California sea lions is a remarkable example (Laake et al. 2018). Pup production significantly declined during the 1983 ENSO event and took almost a decade to recover to pre-ENSO values. This contrasts with the 1998 ENSO event, where although pup production declined during that event, it returned to near normal levels the following year. The difference is likely due to the mortality of both pups and breeding females during the 1983 ENSO event compared to just a loss of pups during the 1998 ENSO event. While the two events were of similar intensity, the 1983 event was of longer duration. There are also multidecadal trends such as the Pacific Decadal Oscillation, which is likened to a longer-term ENSO event on the order of 10–20 years of warm vs. cold water regimes (Mestas-Nunez and Miller 2006; Pennington et al. 2006) that are also associated with changes in community composition (Chavez et al. 2003). These longer-term variations in climate have been suggested as a factor affecting the decline of Steller sea lions (Rodionov et al. 2005).

Successful reproduction by otariids requires a foraging pattern that optimizes the amount of time spent feeding at-sea with the amount of milk energy delivered to the pup waiting at the rookery. Studies of females with dependent young show that as food resources decrease, mothers first respond by increasing the intensity of their foraging effort, and if this is insufficient, by increasing the time spent at-sea. Females might be able to capture more prey by increasing the diving frequency and/or the time spent in foraging bouts (also resulting in decreased resting time) (Boyd 1996). In addition, females could increase the time at sea, allowing more foraging time and

Fig. 2.11 A conceptual model of how a female otariid should respond to environmental perturbation that causes a reduction in prey availability. The dashed line represents FMR and the solid line is trip duration. From Costa (2008)



greater travel distances. For example, during a warm water event, lactating California sea lions traveled a mean of 117 ± 27 se km away from the colony compared to a mean of 68 ± 6.9 se km during normal years (Kuhn and Costa 2014). Attempts to increase foraging effort or intensity would be preferred, as longer foraging trips increase the time between visits to the pup. As trip durations increase, a greater proportion of the pup's energy budget is directed to maintenance rather than growth resulting in slower pup growth (Costa 2008, 2012) (Fig. 2.11). Some species are already working at their maximum capability and have little if any ability to increase their effort without negatively impacting pup growth (Costa et al. 2000b; McHuron et al. 2019). However, success averaged over a series of foraging events is more important than the success over a single foraging trip. This is supported by the observation that weaning mass of northern fur seals was not linked to success over an individual foraging trip (Goebel 2002).

2.4 Evolutionary Implications of Otariid Foraging Patterns

Pinnipeds have a globally distributed and well represented fossil record (Valenzuela-Toro and Pyenson 2019; Berta et al. 2018); however, their macroevolutionary history and ecological transitions, including the evolution of reproductive and foraging strategies, have been comparatively understudied. To date, our knowledge of pinniped reproductive strategies comes primarily from comparative morphology of fossils, including aspects of skull morphology and size (Cullen et al. 2014). Thus, it has been inferred that basal pinnipeds, such as *Enaliarctos*, known from the late Oligocene to early Miocene (~25 million years ago) of the eastern North Pacific (Berta et al. 1989), were sexually dimorphic. This attribute suggests that a polygynous breeding system was the ancestral state for the group (Wyss 1994; Cullen et al. 2014). These small fur seal-like sized early carnivores (150–170 cm) (Churchill et al. 2015) most likely made short trips to feed in the coastal ocean during a period when

there was increased upwelling of cold nutrient rich water (White et al. 1992). Enhanced upwelling increased all levels of biological productivity (Lipps and Mitchell 1976), making prey species more available. In such systems, endothermic tetrapod predators would have faced reduced competition for the now abundant prey (Vermeij and Dudley 2000). Like all mammals, *Enaliarctos* and other basal pinnipeds would have high constant body temperature, which given an inferred relatively dense coat of fur, could be maintained even in cold water. As endotherms, these early pinnipeds would have maintained an elevated body temperature with a high aerobic metabolism that, in turn, allowed their muscles to perform optimally even when operating in cold water, similar to extant otariids. Considering that upwelled water is cold, the muscles of ectothermic prey are not as efficient and would thus be susceptible to predation from the faster, more efficient endothermic predators (Cairns et al. 2008; Grady et al. 2019). Therefore, the congruence of abundant prey and the predatory advantage of air-breathing endothermy would make it possible for these early pinnipeds to successfully inhabit coastal marine environments. As these taxa evolved, they diverged into different lineages, including the modern Otariidae as well as the morphologically and ecologically derived Phocidae and Odobenidae and the extinct seal-like taxa, Desmatophocidae. Subsequent transformations of their foraging and diving skills would allow them to forage further and deeper offshore, reducing competition with coexisting coastal nearshore marine mammals. Foraging further away from the colony would have resulted in an increase in the duration of their foraging trips along with a consequent decrease in their number and frequency. In this regard, increased milk lipid content in some groups (e.g. phocids and fur seals) would have facilitated rapid milk energy transfer, decreasing the time females needed to spend with their pups onshore.

Otariids were constrained to remain in the North Pacific Ocean until the Central American Seaway closed as it presented an ecological barrier to an income breeding otariid given their foraging and reproductive pattern are tightly linked in space and time to highly productive upwelling regions (Briscoe et al. 2017, 2018). Once the seaway closed during the late Pliocene (between 3 and 4 million years ago; Duque-Caro 1990; Hoorn and Flantua 2015; Montes et al. 2015; Kirby et al. 2008) oceanographic conditions, including the expansion of coastal upwelling conditions in the Southeast Pacific (Ibaraki 1997) developed. This would have allowed otariids to cross the equator into the Southern Hemisphere (Churchill et al. 2014). Once they invaded the South Eastern Pacific, otariids would have once again encountered an eastern boundary current with upwelling conditions that favored their energy expensive life history. It is interesting that before the closure of the Central American Seaway, there were several fossil phocids in the Southern Hemisphere during the Miocene and Pliocene (Valenzuela-Toro et al. 2013). This shows that phocid seals were able to disperse into the Southern Hemisphere before the Central American Seaway closed, probably because they had evolved a capital breeding system that allowed a spatial and temporal separation of feeding from breeding, increasing their dispersal capability (Costa 1993).

Once otariids dispersed into the Southern Hemisphere their more energy intensive lifestyle could take advantage of the highly productive upwelling regions as the

reproductive output (total energy invested in offspring) is greater for species with higher metabolic rates and or that have a faster pace of life (Hennemann 1983; Schmitz and Lavigne 1984; Dmitriew 2011; Wright et al. 2018). It then follows that otariids with a high metabolic rate and thus a faster pace of life could obtain and invest more resources into reproduction and therefore were able to outcompete phocids who, as capital breeders, have a more economical lifestyle and slower pace of life. Other factors such as local and global changes in sea level and subsequent suitable habitat transformations might also play a role in this faunal turnover; however, new fossil findings are required to resolve this issue. Finally, the lack of otariids in the North Atlantic is consistent with the presence of an ecological barrier in the form of the equatorial region between the Gulf of Mexico and the Mediterranean Sea, preventing their dispersal in this region along with their dispersal into the Southern Hemisphere. Further, the orientation of land masses also prevents favorable cold-water oceanographic conditions that would facilitate the expansion of otariids from the South Atlantic across the equator into the North Atlantic.

2.5 Future Directions

While we have acquired a significant amount of information on the reproductive and foraging biology and energetics of otariids, considerable gaps remain. Most of the research has been carried out on tractable species such as Antarctic and Galapagos fur seals and Australian and New Zealand sea lions. The difficulty of accessing mothers and pups on rocky shorelines and their skittish nature has limited measurements on some of the most common species of otariids, such as Steller and California sea lions.

For most species, we lack fundamental bioenergetics measurements, such as prey assimilation efficiencies and metabolic rates. We also lack data on the birth mass, weaning mass, growth rate, and lactation duration. Milk intake and milk composition data have only been completed on a few species, and milk intake over the entire lactation interval has only been completed on Antarctic, Australian and northern fur seals. We have only scratched the surface of the physiological adaptations that allow otariid pups to rapidly process lipid-rich milk. Such data are critical to parametrize models that predict how environmental disturbance will affect behavior and ultimately, population dynamics (Costa 2012; McHuron et al. 2017a; Pirota et al. 2018). The broad distribution of otariids presents a compelling argument that income breeding, as typified by otariids, is a more successful life history pattern than capital breeding, as exemplified in phocids. This appears to be the case, at least when prey is abundant. Further comparisons between different species in different habitats would help elucidate the eco-evolutionary dynamics that drove the emergence of the costs and benefits of these very different reproductive strategies. Integration of paleontological and neontological knowledge would help elucidate the ecological transitions, including the origin of the reproductive strategies and changes in the foraging ecology along the evolutionary history of otariids, and pinnipeds in general. A better

understanding of the energetic constraints of different foraging patterns would allow better prediction on how changing ocean conditions and anthropogenic disturbance will affect otariid populations (McHuron et al. 2017a; Pirootta et al. 2018).

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