

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/228328880>

The relationship between reproductive and foraging energetics and the evolution of Pinnipedia

Chapter · January 1993

CITATIONS

110

READS

157

1 author:



Daniel P Costa

University of California, Santa Cruz

535 PUBLICATIONS 16,483 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Energy expenditure of free-ranging birds [View project](#)



MEOP: Marine Animals Exploring the Oceans Pole to Pole [View project](#)

All content following this page was uploaded by [Daniel P Costa](#) on 29 May 2014.

The user has requested enhancement of the downloaded file.

The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia

Daniel P. COSTA

*Department of Biology
and the Institute of Marine Science
University of California
Santa Cruz, CA 95064, USA*

Synopsis

Marine feeding and terrestrial parturition are fundamental components of the life history of the Pinnipedia and present a series of trade-offs between the conflicting needs to feed the pup ashore and to maximize energy acquisition at sea. The Otariidae, eared seals, and the Phocidae, earless seals, have evolved different solutions to this problem. The phocids are capable of storing what is required for the entire lactation interval, whereas otariids must feed during the lactation interval. The evolution of these different patterns is related to co-variant traits such as metabolic rate, energy and oxygen storage capacity and body size. The interaction of these traits sets wider or narrower limits to such parameters as dive duration, duration of lactation, fasting ability, efficiency and amount of maternal investment and rate of prey energy acquisition. These factors may have been important in the evolution of the different life-history patterns of otariids and phocids. The phocid breeding pattern is quite economical, but one that limits the total nutrient and energy investment in the pup. In contrast, the otariid breeding pattern is quite expensive, but it allows the mother to provide more energy and nutrients to her pup. However, the separation of lactation from feeding may have enabled phocids to utilize a patchy, low-production, highly dispersed or distant prey resource as well as an unstable breeding substrate.

Introduction

Life-history patterns evolve in response to trade-offs between beneficial traits and the deleterious traits that are often linked to them (Brodie 1975; Stearns 1983, 1989; Read & Harvey 1989). Two fundamental components of the life history of the Pinnipedia, marine feeding and terrestrial parturition, offer an excellent example of such a series of trade-offs. The initial utilization of the marine environment by pinnipeds occurred at a time

when coastal upwelling was at a cyclic high and thus presented an abundant, diverse and essentially untapped food resource (Lipps & Mitchell 1976). However, the need to return to shore to feed the young required a spatial and/or temporal separation of feeding from lactation (Bartholomew 1970). The ideal solution required a balance between the conflicting demands of optimal provisioning of the pup on shore and the need to maximize energy acquisition at sea. Within the Pinnipedia the Otariidae, the eared seals (sea lions and fur seals), and the Phocidae, or earless seals ('true seals') exhibit strikingly different solutions to this apparent conflict (Bonner 1984; Kovacs & Lavigne 1986; Oftedal, Boness & Tedman 1987; Bowen 1991). All conceive young during the previous reproductive season and exhibit a period of delayed implantation that usually lasts two to three months. Actual foetal development occurs over a nine-month period, while the mother feeds at sea, continuously in the case of phocids, or intermittently in the case of many of the otariids, which have not yet weaned their pups. Phocid mothers remain on or near the rookery continuously from the birth of their pup until it is weaned; milk is produced from body reserves stored prior to parturition. Although some phocids, most notably harbour (*Phoca vitulina*), ringed (*Phoca hispida*) and Weddell (*Leptonychotes weddelli*) seals, feed during lactation, most of the maternal investment is derived from body stores (Testa, Hill & Siniff 1989). Weaning is abrupt and occurs after a minimum of four days of nursing (hooded seal, *Cystophora cristata*: Bowen, Oftedal & Boness 1985) to a maximum of six to seven weeks (Weddell seal: Kaufman, Siniff & Reichle 1975; Thomas & DeMaster 1983).

In contrast, otariid mothers only stay with their pups for the first week or so after parturition and then periodically go to sea to feed, intermittently returning to suckle their pup on the rookery (Bonner 1984). Feeding trips vary from one to seven days, depending on the species, and shore visits to the pup, which has been fasting, last one to three days (Gentry, Costa *et al.* 1986). The age at which the pups are weaned varies from a minimum of four months in the sub-polar fur seals (Antarctic, *Arctocephalus gazella*, and northern, *Callorhinus ursinus*) to up to three years in the equatorial Galapagos fur seal (*A. galapagoensis*) (Gentry, Costa *et al.* 1986). The remaining otariids occur in temperate latitudes. In these species, pups are usually weaned within a year of birth (Gentry, Costa *et al.* 1986), although weaning age can vary both within and between species as a function of seasonal and site-specific variations in environmental conditions (Trillmich 1990). In summary, most phocids are capable of storing what is required for the entire lactation period, whereas all otariids feed during lactation.

Adaptation to marine feeding and terrestrial parturition has resulted in different reproductive strategies in otariids and phocids that reflect trade-offs between traits that have different optima in different marine environ-

ments. Traits such as metabolic rate and oxygen storage capacity co-vary with body size in ways that determine dive duration and the rate and ability to acquire prey (Costa 1991a, b). The relationship between metabolic rate, body energy and nutrient stores determines how long and how efficiently the mother can feed her pup while she is fasting. This paper will examine the interaction between these traits in an attempt to illustrate how they have influenced or even driven the evolution of the Pinnipedia and their ability to inhabit different oceanic regimes.

Maternal body mass

Body mass has a profound influence on the evolution of life-history patterns (Ralls 1976; Peters 1983; Lindstedt & Boyce 1985; Elgar & Harvey 1987; Read & Harvey 1989; Millar & Hickling 1990); it is therefore appropriate to examine body mass trends in otariids and phocids. A summary of maternal body mass for all extant phocids and otariids indicates that otariid females (mean = 80 kg; median = 55 kg) are significantly smaller than phocid females (mean = 229 kg; median = 141 kg). In fact the majority of otariid females are smaller than 100 kg, whereas phocid females are predominantly larger than 100 kg (Appendix). The following sections will explore what factors favour large body size in phocid females and smaller body size in otariid females.

Acquisition of maternal resources

Relationship to foraging ecology

It has been proposed that the phocid breeding pattern, in which most, if not all, of the nutrients and energy necessary to rear the young successfully are acquired and stored in advance of parturition, is quite economical (Costa, Le Boeuf *et al.* 1986). In contrast, otariids have an expensive reproductive pattern that relies on food resources immediately offshore and requires many trips between the foraging grounds and the rookery (Costa 1991a, b). For example, lactating northern fur seal females consume 80% more food than non-lactating females (Perez & Mooney 1986). Northern elephant seal females need only to increase their daily food intake by 12% because the acquisition of the energy necessary to cover the entire cost of lactation is spread over many months at sea (Costa, Le Boeuf *et al.* 1986).

It may be that the increased energy requirements of lactating fur seals (and probably otariid mothers in general) can only be sustained in highly productive areas such as upwelling regions. Otariids have a reproductive pattern that is optimal for prey that is concentrated and predictable, whereas some phocids have a reproductive pattern better suited for dispersed or unpredictable prey or prey that is located at great distances

from the rookery. The long-distance foraging ability of these phocids, which would allow them to utilize a more dispersed or distant food resource, is achieved by reducing the importance of feeding during lactation. However, fasting during lactation places a limit on the duration of investment and this limits the total amount of energy that a phocid mother can invest in her pup (Costa 1991a).

Foraging energetics

Do data on rates of energy intake and expenditure support the hypothesis that the costs of foraging are low in phocids and higher in otariids? Direct measurements on four species of otariids indicate that, while at sea, otariids exhibit metabolic rates that are 4.8–7.3 times the predicted basal metabolic rate (BMR) (Costa & Gentry 1986; Costa, Croxall & Duck 1989; Costa, Kretzmann & Thorson 1989; Costa, Antonelis & DeLong 1991). Comparable measurements are not available for phocids. However, estimates of the diving metabolic rate of elephant seals suggest that they expend 1.3 times the predicted BMR while diving (Le Boeuf, Costa *et al.* 1988). Similarly, oxygen consumption measurements of Weddell seals diving from a restricted ice-hole indicate that they expend 1.5 to 3 times BMR while diving (Kooyman, Kerem *et al.* 1973).

Diving behaviour

What are the implications of such different metabolic rates for the diving and therefore foraging capability of pinnipeds? Phocids are exceptional divers with respect to their long and deep dive patterns. Otariid dives are shallow and brief (Fig. 1). What allows phocids to make such long deep dives and what restricts otariids to such short and therefore shallow dives? The maximum depth of a dive is directly proportional to its duration, since the deeper an animal dives the farther it must travel. Although animals can increase the duration of individual dives by using anaerobic metabolism, it is more efficient to rely on aerobic metabolism (Kooyman, Wahrenbrock *et al.* 1980; Kooyman, Castellini *et al.* 1983; Kooyman 1989). This maximum dive limit has been defined as the aerobic dive limit (ADL) and can be calculated from the total oxygen store (l oxygen) divided by the rate of oxygen utilization ($\text{ml oxygen} \cdot \text{min}^{-1}$; Kooyman 1985).

The greater diving ability of phocids is not unexpected since they can store $60 \text{ ml oxygen} \cdot \text{kg}^{-1}$ body mass compared to $40 \text{ ml oxygen} \cdot \text{kg}^{-1}$ body mass for otariids (Kooyman 1985). However, this only accounts for a 50% increase in dive duration, while phocids dive ten times longer than otariids (Fig. 2). This can be explained by the difference in metabolism at sea; the rate measured in otariids is greater than that estimated for phocids. A comparison of the importance of oxygen stores and metabolic rate in

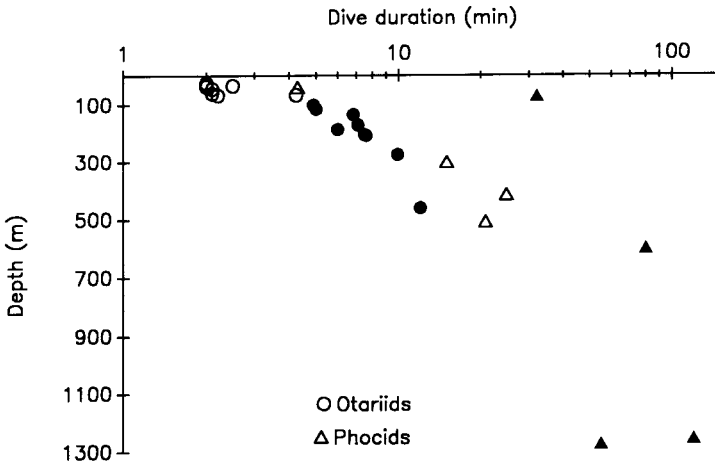


Fig. 1. Maximum (solid symbols) and mean (open symbols) dive duration is plotted as a function of dive depth for eight otariids and four phocids. Data are from Galapagos, Antarctic, Cape and northern fur seals (Gentry, Costa *et al.* 1986); California sea lion (Feldkamp *et al.* 1989); Australian sea lion (Costa, Kretzmann *et al.* 1989); Hooker's sea lion (Gentry, Roberts *et al.* 1987); Weddell seal (Kooyman 1981; M. A. Castellini pers. comm.); northern elephant seal (Le Boeuf, Costa *et al.* 1988 and unpubl. data); grey seal (Thompson *et al.* 1991); southern elephant seal (Hindell *et al.* 1991).

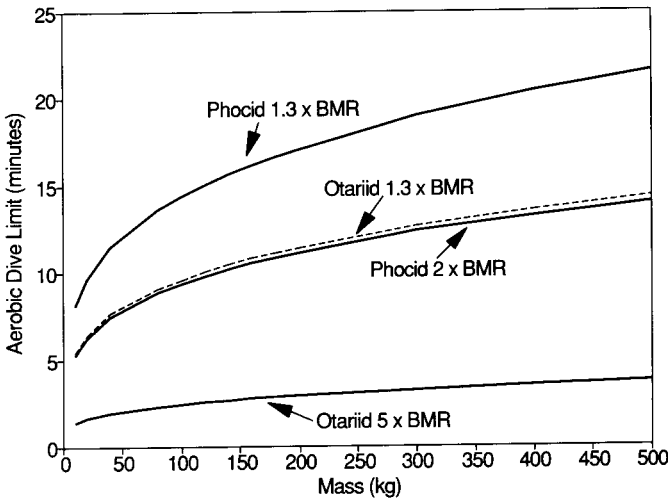


Fig. 2. The variation in aerobic dive limit as a function of body mass was calculated for a phocid seal operating at 1.3 and 2 × BMR and an otariid operating at 1.3 and 5 × BMR. Oxygen stores were assumed to be 60 ml oxygen·kg⁻¹ for a phocid and 40 ml oxygen·kg⁻¹ for an otariid (Kooyman 1985).

determining ADL as a function of body mass can be seen in Fig. 2. Variation in ADL due to body oxygen stores alone can be seen by comparing the lines predicted for both groups at 1.3 times BMR. Although differences between otariid and phocid oxygen storage capacity have a significant effect on ADL, differences in at-sea metabolism have a greater impact (Fig. 2). Also notice that ADL varies with body mass (Fig. 2). This is because metabolic rate scales to body mass^{0.75} whereas oxygen storage capacity scales to mass^{1.0}. Thus larger mammals have a lower mass-specific metabolism for a relatively constant proportion of oxygen storage capacity (Kooyman, Castellini *et al.* 1983; Gentry, Costa *et al.* 1986; Kooyman 1989). Large mammals should be able to dive longer and therefore deeper than small ones. This suggests that, from differences in body size alone, phocids as a group should be better divers than otariids.

It is interesting that the influence of body size on ADL decreases as the metabolic rate increases. This implies that with respect to diving ability (ADL) the advantage of large size is less in otariids because their metabolism is higher (Fig. 2). There may even be an advantage to small body size, since although small animals have a higher mass-specific metabolism their absolute food energy requirements are lower (Peters 1983; Millar & Hickling 1990) (Fig. 3). These differences have implications for the evolution of optimal body size in the Pinnipedia. Large body size would be favoured in phocids because it confers the benefits of increased diving capability. In otariids, on the other hand, smaller size would be favoured, because they gain more from reductions in absolute energy requirements than from minimal increases in dive duration resulting from greater mass.

Observations of travelling behaviour are consistent with the economical life-style of phocids and the costly life-style of otariids. Otariids typically travel at the surface, porpoising, while phocids use stereotypic travelling dives that are more cost-effective (Gentry, Costa *et al.* 1986; Feldkamp, DeLong & Antonelis 1989; Le Boeuf, Naito *et al.* 1992). Although surface swimming is more costly than sub-surface swimming (Vogel 1981) it is likely to be faster and may therefore reduce the time otariid mothers spend in transit between the foraging grounds and the rookery. This is a more expensive strategy but it may be optimal when resources are abundant as in offshore upwelling regions.

Differences in the cost and efficiency of foraging

How do these different diving patterns and energy expenditures affect the ability of pinnipeds to obtain prey and the efficiency with which they acquire energy? Differences in dive performance for a sea lion, a fur seal and an elephant seal are presented in Table 1. Although elephant seals obtain more prey energy per dive than either northern fur seals or California sea

Table 1. Dive rate and duration, rate of prey energy acquired, energy expenditure and metabolic rate of two otariids and a phocid are summarized. Data on prey intake were estimated from water influx and metabolic rate of the sea lion and fur seals from 0–18 doubly-labelled water measurements (Costa & Gentry 1986; Costa 1988; Costa, Antonelis *et al.* 1991). Metabolic rate of northern elephant seal was estimated from dive behaviour (Le Boeuf, Costa *et al.* 1988)

	Mass kg	Dive rate n/d	Dive duration min	Energy acquisition		Energy expended		Ratio of acquired/ expended	Metabolic rate FMR/BMR
				kj/dive	kj/min	kj/dive	kj/min		
Northern elephant seal (prey: squid)	350	65	19.2	1770	92	403	21	4	1.3
California sea lion (prey: fish)	85	202	2.0	224	112	52	26	4	4.8
Northern fur seal (prey: squid)	37	38	2.1	853	406	38	18	23	6.0

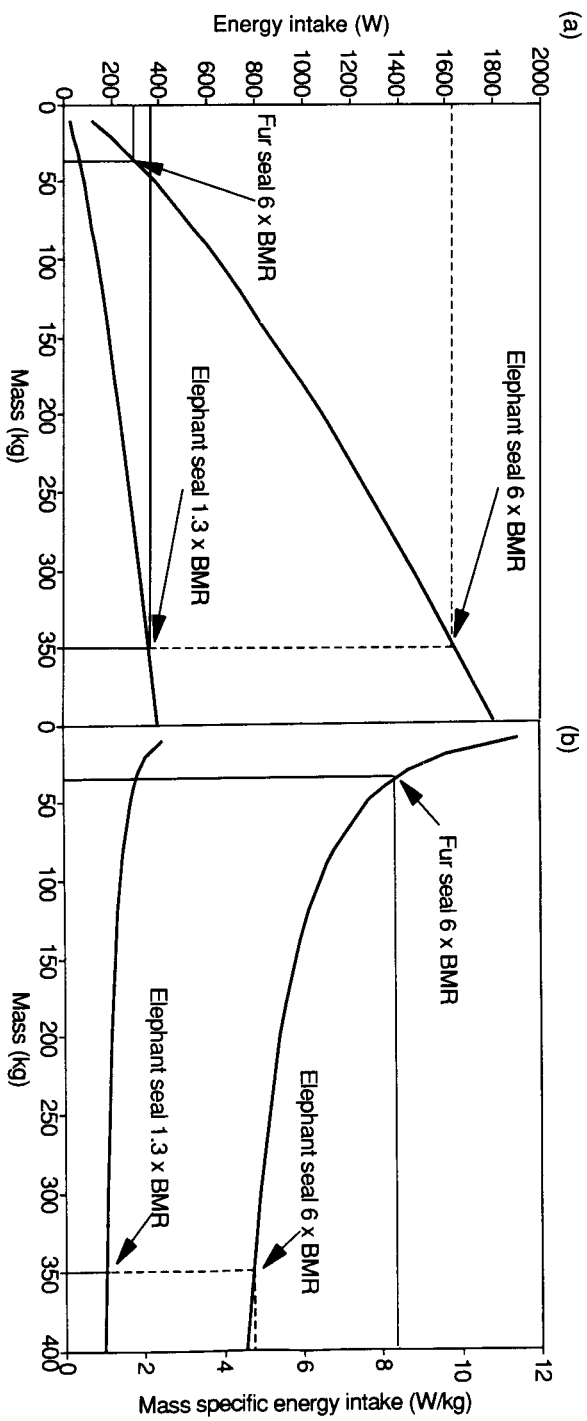


Fig. 3. (a) The total energy requirement of a smaller (37 kg) fur seal working at 6 x BMR is less than that of a larger elephant seal (350 kg) operating at 1.3 or 6 x BMR. The actual energy requirement of an elephant seal is likely to be that needed when operating at 1.3 x BMR; whereas (b) the mass-specific energy requirement of a smaller fur seal operating at 6 x BMR is higher than that of the larger elephant seal operating at either 6 or 1.3 x BMR.

lions, they take more time to do it, and acquire less energy per unit time (Table 1). However, the ratio of energy acquired to energy expended is the same for the sea lion and the elephant seal, but is significantly greater for the fur seal. These data imply that a high metabolic rate may be advantageous in achieving a high rate of energy acquisition. There is a cost to this strategy, however, in terms of the animal's absolute energy requirements. For example, even though the elephant seal is ten times larger than the fur seal and four times larger than the sea lion, its absolute energy expenditure is almost identical and accordingly its absolute energy intake is equivalent to that of the sea lion and only one quarter that of the fur seal. If these species are representative, this analysis suggests that phocids expend less energy to obtain a similar amount of prey, which may enable them to subsist on a poorer or more dispersed prey resource than otariids require. One may consider otariids to be energy maximizers, that is, they maximize the net rate of prey energy intake irrespective of the cost (i.e. a high metabolic rate). In the right environment, like upwelling zones, this strategy is successful because it allows a greater net rate of prey energy intake (as shown by the fur seal data in Table 1). In contrast, phocids maximize the efficiency of prey energy intake. Phocids can maximize the efficiency of prey acquisition because they can take considerably longer foraging trips than otariids. One result of maximizing the efficiency of energy gain is that it either requires or enables a lower metabolic rate while diving (as shown in the elephant seal data in Table 1). A lower diving metabolic rate enables longer and thus deeper dives, which potentially opens up a new or different prey resource to phocids that would not be available to otariids. Alternatively, utilization of a deep prey resource may promote the development of a lower diving metabolic rate, which limits prey acquisition, thus in turn affecting the phocid breeding strategy. However, the dramatic performance of northern fur seals also suggests that in the right circumstances otariids may be able to make better use of resources when prey is plentiful. Such an interpretation of the data in Table 1 is consistent with the hypothesis that the phocid breeding pattern is economical.

Comparisons with terrestrial vertebrates

There are a number of examples where higher rates of energy expenditure allow a greater acquisition of energy. For example, a series of investigations of the foraging and reproductive energetics of predatory lizards show that those which employ a more costly, highly active, widely foraging behaviour expend more energy but in so doing acquire proportionately more energy than lizards that utilize a more economical, sit-and-wait foraging behaviour (Anderson & Karasov 1981; Karasov & Anderson 1984; Nagy, Huey & Bennett 1984; Anderson & Karasov 1988). These investigations also show

that widely foraging predators are able to devote more energy to reproduction than the sit-and-wait predators. Similarly, McNab (1980, 1984, 1986) argues that mammals reproduce as fast as their metabolic rates allow. That is, mammals with high metabolic rates are able to invest more energy in reproduction than animals with low metabolic rates. Such a pattern holds true when marine mammals are included in this analysis (Schmitz & Lavigne 1984). These arguments are consistent with the hypothesis that otariids expend more energy foraging but get more for their effort than phocids. There must be sufficient resources available to support such an expensive life-style, but this is likely to be the case in the upwelling environments that otariids typically inhabit (Repenning & Tedford 1977; King 1983). The ultimate advantage and/or cost of these divergent life-history patterns lies in differences in reproductive success and pup production. Unfortunately, such data are not available.

Allocation of maternal resources

The role of metabolic overhead

If the phocid reproductive pattern is a derived trait that facilitates exploitation of resources that would not otherwise be available, what factors shape this pattern? Analogous to dive duration, the ability of the female to remain ashore fasting, while providing milk to her pup, is related to the size of her energy and nutrient reserves and the rate at which she utilizes them. In this case the optimal solution is to maximize the amount of energy and nutrients provided to the pup and to minimize the amount expended on herself. Fedak & Anderson (1982) coined the term 'metabolic overhead' to define the amount of energy the female expends on herself while ashore suckling her pup. Metabolic overhead can be reduced in two ways. The first is to increase the rate of milk energy transfer and thereby reduce the time spent ashore with the pup. The second is to reduce maternal maintenance metabolism and thus increase the relative amount of maternal reserves that are available for milk production. Apparently phocid mothers apply both strategies. For example, relative to otariids, phocids have a very short lactation interval that is facilitated by a rapid transfer of milk energy made possible by producing a lipid-rich milk (Bonner 1984; Oftedal, Boness & Tedman 1987; Costa 1991a). The extreme is the hooded seal, which lactates for only four days, producing milk that is 64% lipid (Oftedal, Boness & Bowen 1988).

The relationship between metabolic overhead, milk production and lactation duration was modelled with data from northern elephant seals (Fig. 4). In this model the total amount of energy available for maternal investment was assumed to be constant, and metabolic overhead was calculated for each lactation duration. Milk production was calculated as

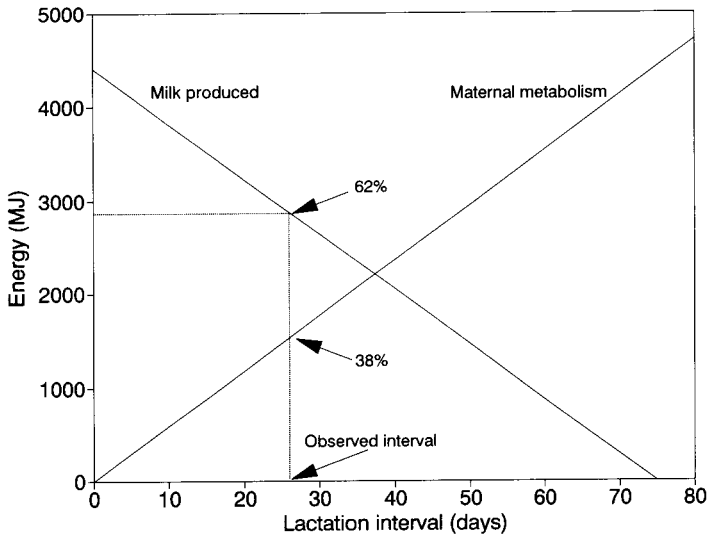


Fig. 4. Maintenance metabolism (as measured using the 0–18 doubly-labelled water method) and milk production data were taken from nine northern elephant seal mother-pup pairs (see Costa, Le Boeuf *et al.* 1986; D. P. Costa & B. J. Le Boeuf unpubl.) and were used to model changes in the energy budget as lactation duration varied. Actual data are shown by the vertical line starting at the abscissa marked as the observed lactation interval (26.4 days) where 38% of the energy went to maternal maintenance metabolism and 62% to pup milk intake. Total energy available for lactation (4400 MJ) was assumed to be the sum of the energy expended on maintenance (1670 MJ) and the milk energy provided to the pup (2730 MJ). Milk production was calculated for each time point as the difference between total energy available and maternal maintenance (4400 MJ – (lactation duration \cdot 63.3 MJ/d)).

the proportion of maternal resources remaining after the cost of the metabolic overhead was met for a given lactation duration. Not surprisingly, the net amount of energy utilized for maternal maintenance increases with increasing lactation duration as the energy available for milk production steadily decreases (Fig. 4).

The effect of size on fasting duration

Metabolic overhead can also be reduced by attaining larger body mass and it also varies non-linearly with mass. Over an equivalent lactation period small pinnipeds experience a higher metabolic overhead than large ones (Costa 1991a). This is because female maintenance metabolism scales as $\text{mass}^{0.75}$, whereas energy stores scale as $\text{mass}^{1.0}$ or as $\text{mass}^{1.19}$ (Calder 1984; Lindstedt & Boyce 1985; Millar & Hickling 1990). Again using the data presented in Fig. 4, we can determine the proportion of total energy that would be available for mothers of different body mass. This analysis

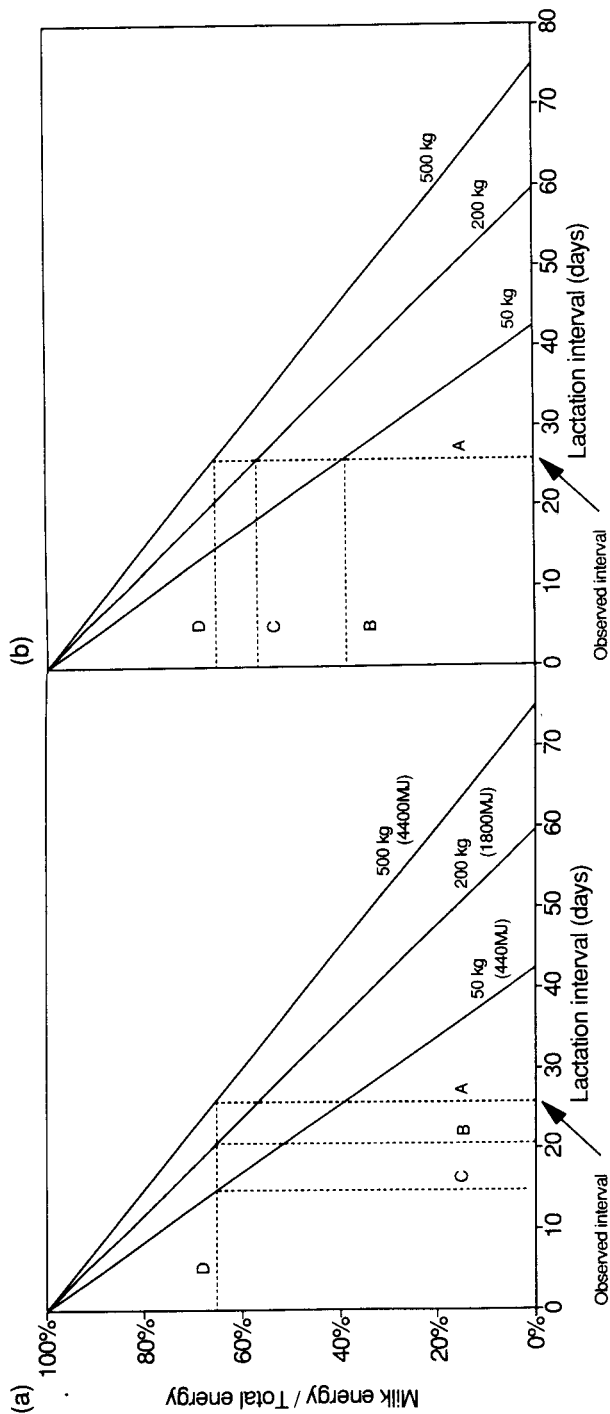


Fig. 5. The data presented in Fig. 4 were used to model how the relative energy budgets of 50-, 200- and 500-kg female northern elephant seals would vary as a function of maternal mass. Numbers in parenthesis are the total energy available for lactation and were calculated as a constant proportion of maternal body mass (8.8 MJ/kg) whereas maintenance metabolism was calculated as lactation duration in days times the daily maternal maintenance metabolism given as $0.560 \text{ kg}^{0.75}$. (a) The lactation duration necessary to be able to devote 62% of the available energy to milk production regardless of body size. A 62% level of maternal investment in milk energy is shown by dotted line D and the lactation interval necessary to achieve this is shown as dotted lines C for a 50-kg female, B for a 200-kg female and A for a 500-kg female. (b) The reduction in milk production necessary to achieve this is shown as dotted line C for a 50-kg female, B for a 200-kg female and A for a 500-kg female. A 26-day lactation interval is shown as dotted line A and the energy available for milk production for a 50-kg female is given by dotted line B, for a 200-kg female by dotted line C and for a 500-kg female by dotted line D.

shows that over the same lactation period a small female has less energy available for milk production than a large female, owing to the increased metabolic overhead (Fig. 5b). However, a small female can reduce her metabolic overhead by reducing the duration of lactation (Fig. 5a). The relationship between lactation duration, body mass and the proportion of total energy available for milk production, for a given lactation interval, is summarized in Fig. 6. Here we find that the greatest increase in the proportion of energy made available for milk production is achieved by reducing lactation duration, whereas body size becomes increasingly important when the duration of lactation is long. The validity of this analysis can be seen by a comparison of lactation duration and body size for 12 phocid females (Fig. 7). We see that lactation is shortest for small females that fast during lactation and that the longest lactations are observed in females that are able to supplement their energy budget by feeding during lactation.

Are otariids placed at a significant disadvantage by their small body mass? Utilizing equivalent data for a representative otariid, the northern fur seal, we can make a similar model (Fig. 8). Here again we see that short shore visits make the greatest proportion of maternal energy available for milk production. However, the advantage of large body size is minimal, especially over the two-day or shorter shore visit typical of otariids.

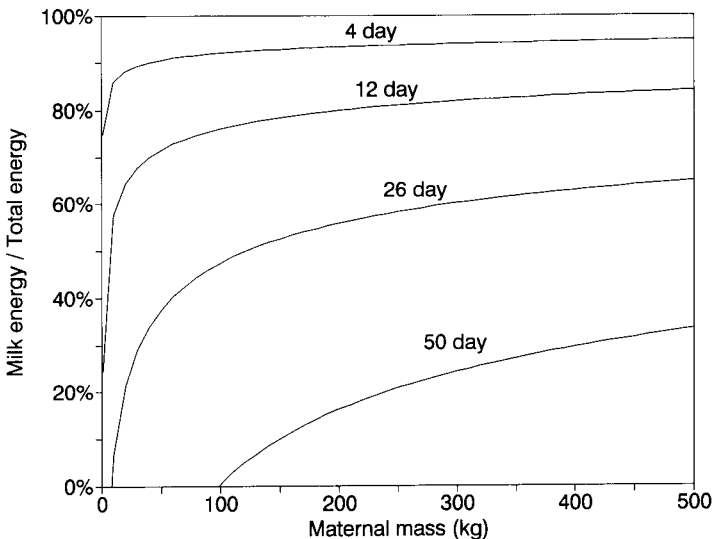


Fig. 6. The variation in the relative amount of energy available for milk production as a function of maternal body mass is estimated for hypothetical elephant seal females with lactation durations of 4, 12, 26 and 50 days. The model uses the data and methods described in Figs 4 and 5.

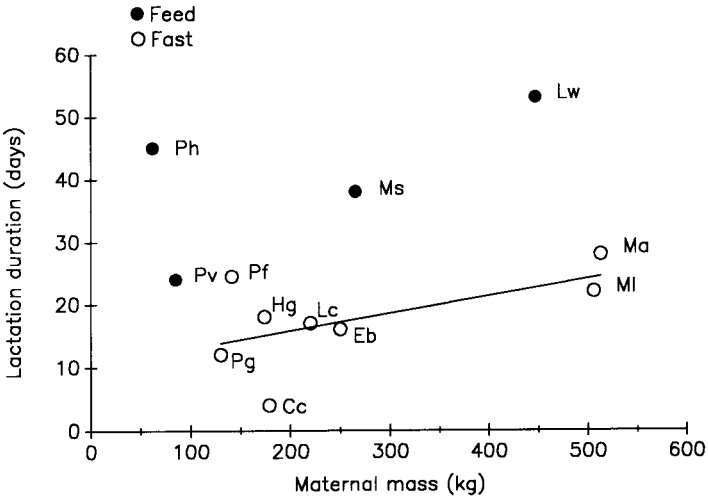


Fig. 7. Lactation duration is plotted as a function of maternal body mass for phocids. Solid symbols denote females that are known to do some feeding during lactation; open symbols denote females that fast. Cc = *Cystophora cristata*, Eb = *Erignathus barbatus*, Hg = *Halichoerus grypus*, Lc = *Lobodon carcinophagus*, Lw = *Leptonychotes weddelli*, Ma = *Mirounga angustirostris*, MI = *Mirounga leonina*, Ms = *Monachus schauinslandi*, Pf = *Phoca fasciata*, Pg = *Phoca groenlandica*, Ph = *Phoca hispida*, Pv = *Phoca vitulina*. Data from Appendix.

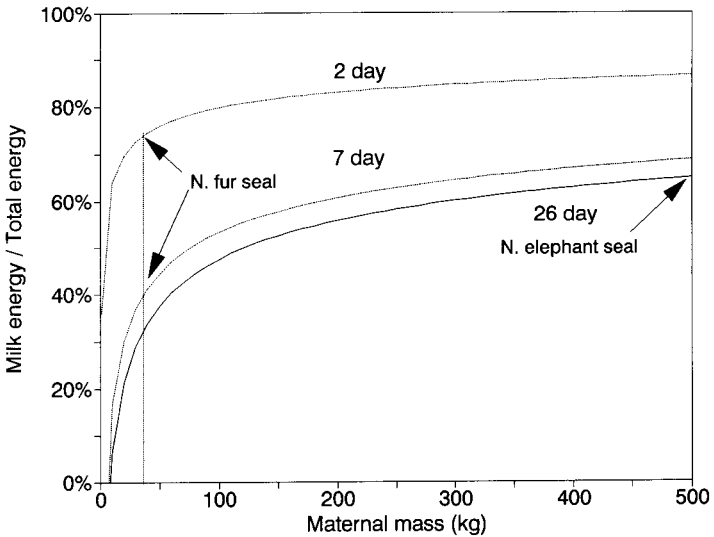


Fig. 8. The effect of body mass on the theoretical proportion of milk energy to total energy expended over lactation for northern fur seal and northern elephant seal females. Northern fur seal females remain ashore for 7 days immediately after parturition and thereafter stay ashore for 2 days after feeding, whereas the entire lactation period lasts 26 days in northern elephant seals. Data derived from Costa, Le Boeuf *et al.* (1986) and D. P. Costa & B. J. Le Boeuf (unpubl.) for elephant seals and from Costa & Gentry (1986) for fur seals.

size (Barnes 1987). This trend is consistent with the importance of large body size in enabling separation of feeding from lactation, a fundamental component of the phocid breeding pattern (Fig. 9a). Once separation of foraging and lactation was achieved these ancestral phocids could inhabit and reproduce in non-upwelling environments like the Hawaiian Islands or the Caribbean. This would represent a transition between the desmatophocines and the monachine groups. This is consistent with the Hawaiian monk seal being a Pacific Ocean relic of the early phocid lineage (Wyss 1989). Ancestral monk seals could then pass through the Central American Seaway, and establish breeding populations in the Caribbean, because their life-history pattern allowed utilization of highly dispersed prey or environments of lower productivity. Otariids, however, either could not venture through the seaway or could not reproduce in the Caribbean owing to the lack of pronounced upwelling regimes. Once in the Atlantic, phocids could easily move north and south as they would have no competition from otariids. Upon reaching the high latitudes, the attenuated lactation interval would have pre-adapted them to breeding on unstable substrates such as ice. Once ice breeding was initiated, the lactation interval would be further shortened as they expanded their range to pack ice (following the arguments of Stirling 1975, 1983).

This paper has highlighted generalized features in the evolution of life-history patterns in the Pinnipedia. Deviations from the broad patterns delineated here are to be expected since individual species adapt to specific pressures or specialized habitats. It is hoped that such a broad examination of pinniped life-history patterns will help to further stimulate research into this area. Research into species that do not fit the model is especially warranted as it will test the ideas presented here as well as provide insight into reasons for divergence from the 'typical' phocid or otariid pattern.

Acknowledgements

This work was supported by grants from the Office of Naval Research (N 0014-91-MD24G40) and the Biological Oceanography Program of the National Science Foundation (OCE 9018626). Many of the ideas presented here are the distillation of numerous conversations with colleagues who have freely shared their ideas and in so doing have stimulated my thinking in this area. I would especially like to thank D. Boness, J. Croxall, M. Fedak, S. Feldkamp, R. Gentry, B. J. Le Boeuf, G. Kooyman, K. Nagy and F. Trillmich. Special thanks go to Dave Lavigne who opened my eyes to pinniped monophyly and the possibility that desmatophocids were ancestral phocids.

References

- Anderson, R. A. & Karasov, W. H. (1981). Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* **49**: 67–72.
- Anderson, R. A. & Karasov, W. H. (1988). Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecol. Monogr.* **58**: 79–110.
- Barnes, L. G. (1987). An early Miocene pinniped of the genus *Desmatophoca* (Mammalia: Otariidae) from Washington. *Contr. Sci. Los Angeles* No. 382: 1–20.
- Bartholomew, G. A. (1970). A model for the evolution of pinniped polygyny. *Evolution, Lancaster, Pa* **24**: 546–559.
- Berta, A., Ray, C. E. & Wyss, A. R. (1989). Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science* **244**: 60–62.
- Bonner, W. N. (1984). Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symp. zool. Soc. Lond.* No. 51: 253–272.
- Bowen, W. D. (1991). Behavioural ecology of pinniped neonates. In *The behaviour of pinnipeds*: 66–127. (Ed. Renouf, D.). Chapman and Hall, London etc.
- Bowen, W. D., Oftedal, O. T. & Boness, D. J. (1985). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Can. J. Zool.* **63**: 2841–2846.
- Brodie, P. F. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology* **56**: 152–161.
- Calder, W. A. (1984). *Size, function and life history*. Harvard University Press, Cambridge, Mass. & London.
- Costa, D. P. (1988). Assessment of the impact of the California sea lion and northern elephant seal on commercial fisheries. In *California Sea Grant: biennial report of completed projects 1984–86*: 36–43. California Sea Grant College Program, University of California, La Jolla. Publication # R-CSCP-024.
- Costa, D. P. (1991a). Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In *The behaviour of pinnipeds*: 300–344. (Ed. Renouf, D.). Chapman and Hall, London etc.
- Costa, D. P. (1991b). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am. Zool.* **31**: 111–130.
- Costa, D. P., Antonelis, G. P. & DeLong, R. (1991). Effects of El Niño on the foraging energetics of the California sea lion. In *Pinnipeds and El Niño: responses to environmental stress*: 156–165. (Eds Trillmich, F. & Ono, K.). Springer-Verlag, Berlin. (*Ecol. Stud.* **88**.)
- Costa, D. P., Croxall, J. P. & Duck, C. D. (1989). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**: 596–606.
- Costa, D. P. & Gentry, R. L. (1986). Free-ranging energetics of northern fur seals. In *Fur seals: maternal strategies on land and at sea*: 79–101. (Eds Gentry, R. L. & Kooyman, G. L.). Princeton University Press, Princeton, N. J.

- Costa, D. P., Kretzmann, M. & Thorson, P. H. (1989). Diving pattern and energetics of the Australian sea lion, *Neophoca cinerea*. *Am. Zool.* **29**: 71A.
- Costa, D. P., Le Boeuf, B. J., Huntley, A. C. & Ortiz, C. L. (1986). The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *J. Zool., Lond.* **209**: 21–33.
- Elgar, M. A. & Harvey, P. H. (1987). Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecol.* **1**: 25–36.
- Fedak, M. A. & Anderson, S. S. (1982). The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *J. Zool., Lond.* **198**: 473–479.
- Feldkamp, S. D., DeLong, R. L. & Antonelis, G. A. (1989). Diving patterns of California sea lions, *Zalophus californianus*. *Can. J. Zool.* **67**: 872–883.
- Gentry, R. L., Costa, D. P., Croxall, J. P., David, J. H. M., Davis, R. W., Kooyman, G. L., Majluf, P., McCann, T. S. & Trillmich, F. (1986). Synthesis and conclusions. In *Fur seals: maternal strategies on land and at sea*: 229–264. (Eds Gentry, R. L. & Kooyman, G. L.). Princeton University Press, Princeton.
- Gentry, R. L. & Kooyman, G. L. (Eds) (1986). *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton.
- Gentry, R. L., Roberts, W. E. & Cawthorn, M. W. (1987). Diving behavior of the Hooker's sea lion. *Abstr. bienn. Conf. Biol. mar. Mammals 7*. Society for Marine Mammalogy. Unpublished.
- Hindell, M. A., Slip, D. J. & Burton, H. R. (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.* **39**: 595–619.
- Karasov, W. H. & Anderson, R. A. (1984). Interhabitat differences in energy acquisition and expenditure in a lizard. *Ecology* **65**: 235–247.
- Kaufman, G. W., Siniff, D. B. & Reichle, R. (1975). Colony behavior of Weddell seals, *Leptonychotes weddelli*, at Hutton Cliffs, Antarctica. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **169**: 228–246.
- King, J. E. (1983). *Seals of the world*. (2nd edn). British Museum (Natural History), London & Oxford University Press, Oxford. (*Publs Br. Mus. nat. Hist.* No. 868: 1–240.)
- Kooyman, G. L. (1981). *Weddell seal: consummate diver*. Cambridge University Press, Cambridge, London & New York.
- Kooyman, G. L. (1985). Physiology without restraint in diving mammals. *Mar. Mamm. Sci.* **1**: 166–178.
- Kooyman, G. L. (1989). *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin & London.
- Kooyman, G. L., Castellini, M. A., Davis, R. W. & Maue, R. A. (1983). Aerobic diving limits of immature Weddell seals. *J. comp. Physiol. (B)* **151**: 171–174.
- Kooyman, G. L., Kerem, D. H., Campbell, W. B. & Wright, J. J. (1973). Pulmonary gas exchange in freely diving Weddell seals. *Respir. Physiol.* **17**: 283–290.
- Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W. & Sinnett, E. E. (1980). Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. comp. Physiol. (B)* **138**: 335–346.

- Kovacs, K. M. & Lavigne, D. M. (1986). Maternal investment and neonatal growth in phocid seals. *J. Anim. Ecol.* **55**: 1035–1051.
- Le Boeuf, B. J., Costa, D. P., Huntley, A. C. & Feldkamp, S. D. (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* **66**: 446–458.
- Le Boeuf, B. J., Naito, Y., Asaga, T., Crocker, D. & Costa, D. P. (1992). Swim velocity and dive patterns in a northern elephant seal, *Mirounga angustirostris*. *Can. J. Zool.* **70**: 786–795.
- Lindstedt, S. L. & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**: 873–878.
- Lipps, J. H. & Mitchell, E. (1976). Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology* **2**: 147–155.
- McNab, B. K. (1980). Food habits, energetics, and the population biology of mammals. *Am. Nat.* **116**: 106–124.
- McNab, B. K. (1984). Basal metabolic rate and the intrinsic rate of increase: an empirical and theoretical re-examination. Commentary. *Oecologia* **64**: 423–424.
- McNab, B. K. (1986). The influence of food habitats on the energetics of eutherian mammals. *Ecol. Monogr.* **56**: 1–19.
- Millar, J. S. & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Funct. Ecol.* **4**: 5–12.
- Nagy, K. A., Huey, R. B. & Bennett, A. F. (1984). Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology* **65**: 588–596.
- Oftedal, O. T., Boness, D. J. & Bowen, W. D. (1988). The composition of hooded seal (*Cystophora cristata*) milk: an adaptation for postnatal fattening. *Can. J. Zool.* **66**: 318–322.
- Oftedal, O. T., Boness, D. J. & Tedman, R. A. (1987). The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Curr. Mammal.* **1**: 175–245.
- Perez, M. A. & Mooney, E. E. (1986). Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus*. *Fish. Bull. U.S. Fish Wildl. Serv.* **84**: 371–381.
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press, Cambridge, London etc.
- Ralls, C. M. (1976). Mammals in which females are larger than males. *Q. Rev. Biol.* **51**: 245–276.
- Read, A. F. & Harvey, P. H. (1989). Life history differences among the eutherian radiations. *J. Zool., Lond.* **219**: 329–353.
- Repenning, C. A. & Ray, C. E. (1977). The origin of the Hawaiian monk seal. *Proc. biol. Soc. Wash.* **89**: 667–688.
- Repenning, C. A., Ray, C. E. & Grigorescu, D. (1979). Pinniped biogeography. In *Historical biogeography, plate tectonics, and the changing environment*: 357–369. (Eds Gray, J. & Boucot, J.). Oregon State Univ. Press, Corvallis.
- Repenning, C. A. & Tedford, R. H. (1977). Otarioid seals of the Neogene. *Prof. Pap. U.S. geol. Surv.* No. 992: 1–93.
- Schmitz, O. J. & Lavigne, D. M. (1984). Intrinsic rate of increase, body size, and specific metabolic rate in marine mammals. *Oecologia* **62**: 305–309.
- Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* **41**: 173–187.

- Stearns, S. C. (1989). Trade-offs in life history evolution. *Funct. Ecol.* 3: 259–268.
- Stirling, I. (1975). Factors affecting the evolution of social behaviour in the Pinnipedia. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 169: 205–212.
- Stirling, I. (1983). The evolution of mating systems in pinnipeds. *Spec. Publ. Am. Soc. Mammal.* No. 7: 489–527.
- Testa, J. W., Hill, S. E. B. & Siniff, D. B. (1989). Diving behavior and maternal investment in Weddell seals (*Leptonychotes weddelli*). *Mar. Mamm. Sci.* 5: 399–405.
- Thomas, J. A. & DeMaster, D. P. (1983). Diel haul-out patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. *Can. J. Zool.* 61: 2084–2086.
- Thompson, D., Hammond, P. S., Nicholas, K. S. & Fedak, M. A. (1991). Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool., Lond.* 224: 223–232.
- Trillmich, F. (1990). The behavioral ecology of maternal effort in fur seals and sea lions. *Behaviour* 114: 3–20.
- Vogel, S. (1981). *Life in moving fluids*. Willard Grant Press, Boston.
- Wyss, A. R. (1987). The walrus auditory region and the monophyly of pinnipeds. *Am. Mus. Novit.* No. 2871: 1–31.
- Wyss, A. R. (1988). Evidence from flipper structure for a single origin of pinnipeds. *Nature, Lond.* 334: 427–428.
- Wyss, A. R. (1989). Flippers and pinniped phylogeny: has the problem of convergence been overrated? *Mar. Mammal Sci.* 5: 343–360.

Appendix

Maternal mass and lactation interval are summarized for all extant phocids and otariids. Data are from Bonner (1984); Kovacs & Lavigne (1986); Gentry & Kooyman (1986); Oftedal, Boness & Tedman (1987); Bowen (1991); Costa (1991a).

Phocid species	Maternal mass (kg)	Lactation duration (days)	Feeds while lactating	Breeding substrate
Caspian seal, <i>Phoca caspica</i>	55	20–25	?	Fast ice
Baikal seal, <i>P. siberica</i>	94	60–75	Yes	Fast ice lairs
Ring seal, <i>P. hispida</i>	62	41–48	Yes	Fast ice lairs
Harbour seal, <i>P. vitulina</i>	85	24	Yes	Land
Spotted seal, <i>P. largha</i>	86	14–21	?	Pack ice
Harp seal, <i>P. groenlandica</i>	130	12	No	Pack ice
Ribbon seal, <i>P. fasciata</i>	141	21–28	?	Pack ice
Grey seal, <i>Halichoerus grypus</i>	174	18	No	Land and ice
Hooded seal, <i>Cystophora cristata</i>	179	4	No	Pack ice
Ross seal, <i>Ommatophoca rossi</i>	186	30	?	Pack ice
Crabeater seal, <i>Lobodon carcinophagus</i>	220	17	Probably not	Pack ice

Appendix (cont.)

Phocid species	Maternal mass (kg)	Lactation duration (days)	Feeds while lactating	Breeding substrate
Bearded seal, <i>Erignathus barbatus</i>	250	12–18	Probably not	Pack ice
Hawaiian monk seal, <i>Monachus schauinslandi</i>	265	39–41	No	Land
Mediterranean monk seal, <i>M. monachus</i>	275	42–49	Yes	Land, caves
Weddell seal, <i>Leptonychotes weddelli</i>	447	53	Yes	Fast ice
Leopard seal, <i>Hydrurga leptonyx</i>	450	30	?	Pack ice
Southern elephant seal, <i>Mirounga leonina</i>	506	22	No	Land
Northern elephant seal, <i>M. angustirostris</i>	513	26	No	Land
Mean	229			
Median	141			

Otaviid species	Maternal mass (kg)	Lactation duration (days)
Galapagos fur seal, <i>Arctocephalus galapagoensis</i>	27	720
New Zealand fur seal, <i>A. forsteri</i>	35	300–365
Northern fur seal, <i>Callorhinus ursinus</i>	37	118
Antarctic fur seal, <i>A. gazella</i>	39	117
Juan Fernandez fur seal, <i>A. philippii</i>	40	300–365?
South American fur seal, <i>A. australis</i>	55	300–365
Guadalupe fur seal, <i>A. townsendi</i>	45	300–365?
Sub-Antarctic fur seal, <i>A. tropicalis</i>	36	300–330
South African fur seal, <i>A. pusillus</i>	57	300–330
Galapagos sea lion, <i>Z. c. wolfebaeki</i>	80	180–365
Australian sea lion, <i>Neophoca cinerea</i>	82	532
California sea lion, <i>Zalophus californianus</i>	85	300–365
South American sea lion, <i>Otaria flavescens</i>	121	360
Hooker's sea lion, <i>Phocarcotus hookeri</i>	183	365
Steller's sea lion, <i>Eumetopias jubatus</i>	273	300–365
Mean	80	
Median	55	