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Reproductive and Foraging Energetics of High Latitude Penguins, Albatrosses and Pinnipeds: Implications for Life History Patterns[1]

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SYNOPSIS. Pinnipeds and seabirds feed at sea, but are tied to shore to rear their young. Such a fundamental life history constraint should lead to convergent adaptations in foraging and reproductive ecology. However, intrinsic differences in mammalian and avian reproductive biology may limit the potential for convergence. In this paper I examine both reproductive and foraging energetics of pinnipeds and seabirds. This is done in an attempt to identify traits that might be considered convergent adaptations to life in the marine environment and to show how divergent life history patterns are optimal for different reasons. From this analysis we find that seabirds invest a greater total amount of energy and protein into the offspring than pinnipeds, but this comes at the cost of making more trips to sea. Whereas pinnipeds forage in a manner more consistent with the predictions of central place foraging theory and exhibit a greater ability to compensate to the shortened breeding season typical of high latitude environments.

INTRODUCTION

Having secondarily returned to the marine habitat, seabirds and pinnipeds face similar constraints on provisioning their young. Since initially their offspring cannot follow them to sea, the parents must leave their young ashore while they feed at sea. Given that the two groups share such a fundamental life history constraint one might expect convergent adaptations to this lifestyle. However, the intrinsic differences between avian oviparous or mammalian viviparous reproduction may result in different solutions to the problem of marine feeding and terrestrial reproduction. In this paper I examine both reproductive and foraging energetics of pinnipeds and seabirds using the comparative approach, in an attempt to identify traits that might be considered convergent adaptations to life in the marine environment. Otariids (fur seals and sea lions) and penguins are ideal for such comparisons, since they utilize similar marine resources and often breed sympatrically. Although the similarities are greatest between penguins and fur seals, I will also include comparisons with albatrosses and phocids (true seals). Inclusion of albatrosses allows comparison between swimmers and flyers. In the southern hemisphere, albatrosses breed sympatrically with penguins and fur seals, often feeding on the same prey, and their body masses fall within the mass range for penguins. Phocid seals are included because, like otariids, they are diving mammals tied to shore for parturition. However, they have solved the problem of marine feeding and terrestrial parturition in a different manner and thus demonstrate the flexibility of mammalian reproductive biology.

REPRODUCTIVE PATTERNS OF PINNIPEDS AND PENGUINS

The Pinnipedia is composed of three families, the Otariidae, the Phocidae and the Odobenidae. Each of these possesses a rather distinctive reproductive pattern (see Bonner, 1984; Kovacs and Lavigne, 1986; Oftedal et al., 1987*a*; Anderson and Fedak, 1987). In this paper I will deal only with the Otariidae, the eared seals (seal lions and fur seals), and the Phocidae, or earless seals ("true seals"). In both groups, young are conceived during the previous reproductive season and the embryo undergoes a period of delayed implantation that usually lasts two to three months. Actual foetal development then occurs over a 9 month period. During this time the mother is free

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to feed at sea yet, for many of the otariids, she may be simultaneously suckling the pup of the year.

The major difference between otariid and phocid reproductive biology comes after parturition. Most phocid mothers give birth to a pup and stay onshore continuously, suckling the pup until weaning. During lactation the mother does not feed and milk is produced from body reserves stored prior to parturition. Weaning is abrupt and occurs after a minimum of 4 days of nursing (in the hooded seal, Bowen *et al.*, 1985) to a maximum of approximately 5 weeks (in the Weddell seal, Kaufman *et al.*, 1975). In many species the pup remains on or near the rookery fasting until it develops its feeding and diving skills.

In contrast to phocids, otariid mothers remain with their pups only during the first week following parturition. After this initial perinatal period the female returns to sea to feed, intermittently returning to suckle her pup onshore. Depending on the species, the mother spends between 1 and 7 days feeding at sea, then returns to her pup, which has been fasting onshore, and suckles it for 1 to 3 days. This period of intermittent onshore suckling and offshore feeding lasts from a minimum of 4 months in the polar fur seals (Antarctic, *Arctocephalus gazella,* and Northern, *Callorhinus ursinus*) to up to 3 years in the equatorial Galapagos fur seal (*A. galapagoensis*) (Gentry *et al.*, 1986*a*). The remaining otariids are temperate and, in these species, pups are usually weaned within a year of birth. In all pinniped species, male parental investment is non-existent and twins are exceptionally rare.

In comparison to pinnipeds, avian young are conceived during the reproductive season, after a short courtship period. In penguins the female produces an egg within 2 to 3 weeks of copulation. The female then goes to sea to feed while the male takes the first incubation shift (see Croxall, 1984 for review). The emperor penguin, *Aptenodytes forsteri,* is an extreme case where the male is responsible for the entire incubation period (Stonehouse, 1953). More commonly, incubation duties are more equally shared, as in the gentoo, *Pygoscelis papua,* or little, *Eudyptula minor,* penguins (Croxall, 1984; Stahel and Gales, 1987). Upon hatching the parents take turns brooding the young and going to sea to forage for themselves and the hatchling. Once the chick can thermoregulate on its own and is safe from predation, it is left on the rookery thereby freeing both parents to feed and provision the chick. Chicks are fledged from a low of 60% of adult size in emperor penguins to approximately 104% of adult size in gentoo penguins (Stonehouse, 1953; Trivelpiece *et al.,* 1988). After fledging, the chick is completely independent and must learn to feed on its own. Albatrosses follow a similar pattern except that incubation and fledgling periods are longer and chicks are fledged at 120–130% of adult body mass (Croxall, 1984).

In order to elucidate differences in the reproductive energetics of pinnipeds and seabirds, I will examine both onshore and at sea components. Onshore comparisons will be limited to differences in the rates of parental provisioning in both the biomass and quantity of energy delivered per visit, and the total energy and material invested in the offspring over the reproductive period. This comparison will show that the pattern of onshore provisioning of seabird and pinniped young is quite different and that this difference is due to lactation. Lactation provides greater flexibility in the timing and patterning of offspring provisioning. Such flexibility allows pinnipeds to wean their pups at a constant relative size even in the shortened breeding season, typical of high latitudes. Provisioning of penguin and albatross young appears to be limited by the quality of their prey and the mechanical limitations of carrying unprocessed prey. In contrast to pinnipeds, the shortened high latitude reproductive season results in penguin young being fledged at a lower relative body mass. However, penguins and albatrosses are able to invest more energy and protein in their offspring relative to body parental mass than pinnipeds. Finally, I will show that penguins and pinnipeds show considerable convergence in their foraging behavior and energy expenditure offshore. Foraging pattern is influenced more by the size of the prey and depth of occurrence rather than the taxonomic origin of the predator.

OFFSPRING PROVISIONING

Seabird data

Data on food provided to seabird young are straightforward to obtain compared to pinnipeds. Most researchers have weighed the chick before and after a meal, either by employing automatic weighing devices under the nests (Prince and Walton, 1984; Ricketts and Prince, 1984) or by removing the chick and weighing it before and after a meal (Adams and Klages, 1987). Other investigators have removed the stomach contents of returning adults by stomach lavage (Wilson, 1984; Gales, 1987). Once collected, the composition of the diet fed to the chick can be assessed, and its energy and nutritional content estimated. In this review, I will use data collected over the entire breeding season for gentoo, chinstrap and adelie penguins at King George Island (Trivelpiece *et al.*, 1988), and those measured for peak loads delivered during representative feeding trips for emperor, king, jackass, macaroni and little penguins (Offredo and Ridoux, 1986; Adams and Klages, 1987; Cooper, 1977; Croxall *et al.*, 1988*b*; Gales, 1987) and gray headed (*Diomedea melanophris*), black browed (*D. chrysostoma*) and wandering (*D. exulans*) albatrosses (Pennycuick *et al.*, 1984).

Pinniped data

Measurement of the provisioning rates of suckling pups is considerably more difficult than it is for seabirds. Even so, pinnipeds offer a unique system among mammals since, in many species, milk is the sole source of material and energy. Furthermore, lactation tends to be a discrete interval that in many pinnipeds species is easily quantified.

Two methods have been used to estimate milk intake of pinniped young. The first method calculates the milk intake necessary to meet the pup's estimated energy metabolism and measured growth over the lactation interval. This method has been used to estimate milk intake over the entire lactation interval for harp seals, *Phoca groenlandica* (Stewart and Lavigne, 1984), gray seals, *Halichoerus grypus* (Fedak and Anderson, 1982; Anderson and Fedak, 1987) and hooded seals, *Cystophora cristata* (Bowen *et al.*, 1987). The other method measures milk consumption of suckling pups by following the decline of either tritiated or deuterium labeled water (Costa, 1987; Oftedal and Iverson, 1987). This method has been used to measure milk intake in northern elephant seals, *Mirounga angustirostris,* (Ortiz *et al.*, 1984; Costa *et al.*, 1986), northern fur seals, *Callorhinus ursinus* (Costa and Gentry, 1986), California sea lions, *Zalophus californianus* (Oftedal *et al.*, 1987*b*), Weddell seals, *Leptonychotes weddelli* (Tedman and Green, 1987), Steller sea lions, *Eumatopias jubatus* (Higgins *et al.*, 1988) and Antarctic fur seals, *Arctocephalus gazella* (Costa and Croxall, 1988). In this method milk water intake is measured from the difference between total water influx determined with labeled water and the oxidative water produced from the pup's maintenance metabolism. Milk consumption is then calculated from the milk water content. This procedure requires that the pup obtain all of its exogenous water from its mother's milk. In all of the above studies, other water sources were negligible. Furthermore, validation studies have found no significant difference between measured amounts of milk fed to 8 northern fur seal pups and that estimated from the isotope water dilution method (Costa, 1987).

Energy provisioning as a function of adult mass

One problem with comparisons of energy intake is the influence of body size as a variable (Calder, 1984). For example, body mass varies from the 1 kg little penguin to the 32 kg emperor penguin (Table 1a) and, within the pinnipeds, it varies from the 27 kg female Galapagos fur seal and to the 504 kg female northern elephant seal (Table 1b). The effect of body size on provisioning rates can be assessed by plotting the amount of energy delivered to the young per visit by a parent against adult body mass. These data are plotted in Figure 1 using a log--log plot to accommodate

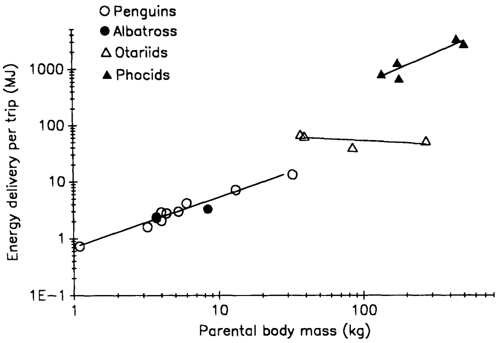

FIG. 1. Energy delivered to the offspring per visit onshore is plotted against parental body mass for penguins (open circles), albatrosses (solid circles), otariids (fur seals and sea lions, open triangles) and phocids (earless seals, solid triangles). Lines are the best fit linear regression for each group.

the large range of body mass and energy delivery. The most striking pattern to emerge from this plot is that avian provisioning rates are highly correlated with body mass, whereas no such relationship exists for otariids. If we further examine a plot of energy delivery per trip as a function of body mass for seabirds alone, we find that body mass accounts for most of the variability in energy delivery per trip (penguin data: linear regression $r^2 = 0.98$, $P < 0.01$, $n = 9$). Energy delivery is also independent of locomotory mode employed, since soaring albatrosses and swimming penguins essentially fall on the same regression line. This is surprising since we would expect an aerodynamic limitation on the mass carried by albatrosses that would not exist for penguins. It would be interesting to determine if this relationship holds for smaller procellariforms as well. Regardless, the data imply that, at least for penguins and albatrosses, the amount of food energy delivered to the chick is a constant proportion of adult body mass. This is not surprising if we consider that a bird's foraging ability has a mechanical limitation imposed by the size of its stomach. This is consistent with the observation that gut mass varies linearly with body mass in birds (gut mass [kg] = $0.098\ M^{1.0}$ [kg] Calder, 1984). Assuming that gut capacity is a function of gut mass, it follows that peak prey energy delivery to the chick should scale directly with adult body mass. Another important variable is the energy density of the prey and this will be discussed later.

In contrast to seabirds there is no correlation between energy delivery per visit and body mass in otariids ($r = 0.535$, $n = 4$, $P > 0.1$), but there is an excellent correlation with body mass and energy delivery in phocids ($r = 0.924$, $n = 5$, $P < 0.05$). However, these phocid seals make only one trip onshore to suckle their pups, thus the energy delivered in one trip is also the total energy invested in the offspring. Therefore, for some phocids we can also conclude that the total energy invested in the offspring is highly correlated with adult female body mass. Unlike the energy delivery per trip, the total energy invested over the entire lactation interval scales with body mass for otariids as well as for phocids.

Energy provisioning and trip duration

If body mass does not predict energy delivery per feeding visit to the offspring in otariids, then some other variable such as trip duration may. After normalizing the data for differences in parental body mass a correlation exists between trip duration and energy delivery per trip for otariid mothers ($r = 0.934$, $n = 4$, $P < 0.10$), but not for seabirds or phocids (penguins: $r = 0.407$, $n = 8$, $P > 0.10$) (Fig. 2).

The relationship between trip duration and energy delivery for otariids is consistent with the predictions of central place foraging theory (Orians and Pearson, 1977). This theory predicts the optimal behavior of animals foraging at varying distances from a central place, such as a nest or rookery. For example, when foraging a long distance from the rookery a parent should make few trips of long duration and return with a greater quantity of energy per trip. In contrast, parents feeding close to the rookery (nearshore) should make many short trips, with a comparatively lower energy return per trip. This is consistent with the pinniped data plotted in Figure 2. Otariids like the Steller sea lion, make trips of relatively short duration (36 hr), feed nearshore and thus travel short distances to the feeding grounds, whereas northern fur seals feed 100 km offshore

TABLE 1a. *For each seabird the parental mass, the amount of food and energy fed to the chick per visit onshore are given along with data on mean foraging trip duration.**

	Parental mass kg	Food fed to chick per trip			Time at sea hr	Fledging	
		g	MJ	MJ/kg		Age days	Mass % adult mass
Little penguin	1.1	143	0.73	0.67	12	56	100 (1)(3)
Jackass penguin	3.2	228	1.60	0.50	9	73	77 (6)(1)
Chinstrap penguin	4.0	629	2.89	0.72	16.7	52	89 (2)
Adelie penguin	4.4	607	2.79	0.64	24	52	79 (2)
Gentoo penguin	5.3	635	3.00	0.57	12.5	72	104 (2)
Macaroni penguin	4.0	448	2.06	0.52	24	62	68 (1)(9)
King penguin	13.1	1,650	7.20	0.55	96	350	90 (5)(11)
Emperor penguin	32.6	2,820	13.4	0.41	72	170	60 (1)(8)(7)
Grey headed albatross	3.7	600	2.27	0.61	24	141	124 (1)(4)(10)
Black browed albatross	3.7	570	2.41	0.65	24	116	132 (1)(4)(10)
Wandering albatross	8.4	920	3.32	0.40	72	278	132 (1)(4)

* Data on age and relative mass of chicks at fledging is given for comparison. Numbers in parentheses refer to the source of the data as follows: (1) Croxall, 1984, (2) Trivelpiece *et al.*, 1988, (3) Gales, 1987, (4) Pennycuick *et al.*, 1984, (5) Adams and Klages, 1987, (6) Cooper, 1977, (7) Stonehouse, 1953, (8) Offredo and Ridoux, 1986, (9) Croxall *et al.*, 1988*b*, (10) Prince, 1985, (11) Adams, 1987.

and make trips of 7 days duration (Loughlin *et al.*, 1987). As predicted by the model, Steller sea lions deliver considerably smaller amounts of milk (0.2 MJ/kg) per visit to their pup than northern fur seals (1.9 MJ/kg) (Table 1a). Such optimization of foraging behavior is also consistent with the proximity of the phocid data to the extrapolated otariid regression line (Fig. 2). In this case phocid seals are an extreme example of an offshore feeder or a predator that feeds on a highly dispersed prey resource, where the optimal solution is to make only one trip per reproductive event. Thus these phocids have essentially separated feeding from onshore lactation. This has the advantage that phocid seals are not limited by the amount of time it takes to get to the foraging grounds or how long they may remain once they find an optimal patch.

TABLE 1b. *For each pinniped the maternal mass, mass and energy of milk consumed by her pup per shore visit is given along with data on the mean foraging trip duration.**

	Maternal mass kg	Milk fed to pup per trip			Time at sea hr	Weaning		Milk fat %
		g	MJ	MJ/kg		Age days	Mass % maternal	
Galapagos fur seal	27	n.a.	n.a.	n.a.	12	800	52–59	25 (1)
Antarctic fur seal	39	3,600	63.7	1.6	120	117	44–52	40 (2)(11)
Northern fur seal	37	3,460	68.9	1.9	142	125	32–38	51 (3)(12)
South African fur seal	57	n.a.	n.a.	n.a.	70	310	37–44	19 (1)
Galapagos sea lion	80	n.a.	n.a.	n.a.	12	341	?	18 (1)
Australian sea lion	84	n.a.	n.a.	n.a.	57	550	?	25 (17)
California sea lion	85	2,800	39.9	0.5	96	300?	40–52	32 (4)(13)
Steller sea lion	273	4,420	52.1	0.2	37	330?		24 (5)
Harp seal	135	39,700	808	6.0		12	25	52 (6)(14)(16)
Grey seal	174		1,274	7.3		18	26	52 (15)(16)
Hooded seal	179	34,100	678	3.8		4	23	61.4 (8)(7)
Weddell seal	447	159,300	3,320	7.4		43	24	53.6 (9)(16)
Northern elephant seal	504	149,800	2,700	5.4		28	26	54.4 (10)

* Data on age and relative mass of pup at weaning is given for comparison. Numbers in parentheses refer to the source of the data as follows: (1) Gentry *et al.*, 1986*a*, (2) Costa and Croxall, 1988, (3) Costa and Gentry, 1986, (4) Oftedal *et al.*, 1987*b*, (5) Higgins *et al.*, 1988, (6) Stewart and Lavigne, 1984, (7) Oftedal *et al.*, 1988, (8) Bowen *et al.*, 1985, 1987, (9) Tedman and Green, 1987, (10) Costa *et al.*, 1986*a*, (11) Doidge *et al.*, 1986, (12) Gentry and Holt, 1986, (13) weaning mass, Worthy and Costa, unpublished data, (14) Oftedal *et al.*, 1987*a*, (15) Fedak and Anderson, 1982, (16) Kovacs and Lavigne, 1986, (17) Costa, Kretzmann, Thorson and Higgins, unpublished data.

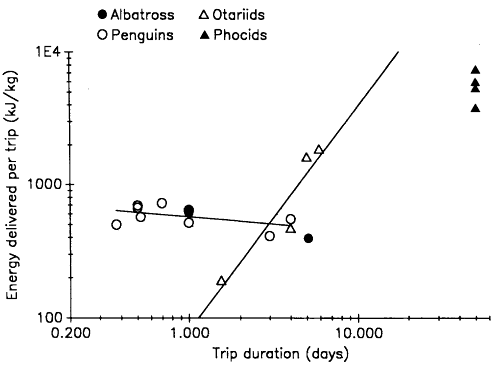

FIG. 2. The amount of energy delivered per visit onshore corrected for parental mass is plotted against the duration of a foraging trip for penguins (open circles), albatrosses (solid circles), otariids (open triangles) and phocids (solid triangles). Trip duration for phocids was arbitrarily chosen, since good data are not available.

More importantly, this reproductive pattern may allow them to utilize a more dispersed or patchy food resource. For example, since the entire cost of lactation is spread out over many months at sea, northern elephant seal females need only increase their daily food intake by 12% (Costa *et al.*, 1986*a*). In contrast, Perez and Mooney (1986) estimate that lactating northern fur seal females have a food intake 1.6 times non-lactating levels. It may be that the increased food intake of lactating fur seals (and probably otariids in general) can only be sustained in the highly productive waters characteristic of upwelling environments. The lack of a truly tropical otariid or penguin may be related to the lower production of these warmer waters. The Galapagos fur seal and Galapagos penguin are not truly tropical species since they exist in a highly productive equatorial upwelling region. In contrast, laysan albatrosses and monk seals do exist in a truly tropical, warm water, non-upwelling environment. It may be that otariids and penguins have a reproductive pattern that is optimal for prey that is concentrated and predictable, whereas phocids and albatrosses may have a reproductive pattern that is better suited for prey that is dispersed and unpredictable.

It is the long distance foraging ability of phocid seals and albatrosses that may allow them to utilize a more dispersed food base. In this respect it is the albatrosses' great aerial ability that enables them to cover thousands of square kilometers of feeding habitat in a short time, and then return to the chick. Whereas, the inability of phocids to cover great distances quickly may have forced them to forgo alternating between feeding and suckling the young onshore. Instead phocids may rely on the separation of feeding from lactation to allow them to utilize a highly dispersed food resource.

Advantages of mammalian lactation

What enables pinnipeds to optimize their foraging behavior according to the predictions of central place foraging, while penguins and albatrosses apparently cannot? The answer is that mammalian lactation enables pinnipeds to process and concentrate the material fed to the young, independent of the mechanical limitations of the stomach, differences in prey quality, or variations in distance or time spent away from the rookery (Pond, 1977). A penguin feeding on krill or squid is not capable of concentrating the energy density of the prey fed to the chick. However, pinnipeds such as the California sea lion which feeds on fish, the Antarctic fur seal which feeds on krill, the northern fur seal which feeds on fish or squid and the hooded seal which feeds on fish, provision their offspring with milk of significantly greater energy density than that of the prey consumed. Alternatively, since an avian equivalent to lactation apparently exists in some cases, the presence of a second parent feeding the young may preclude the necessity to further process the material fed to the offspring. For example, fasting male emperor penguins provide recently hatched young with a limited crop secretion. Similarly, increases in the energy density of the material fed to the young occurs in the smaller procellariforms by the production of stomach lipids.

The high energy density of pinniped milk is due to the milk's higher lipid content (Bonner, 1984; Oftedal *et al.*, 1987*a*). However, since there is no corresponding increase in the protein or other components of the milk, the protein to energy ratio of pinniped milk is lowest in the most energy dense milk (Fig. 3). This implies that pinniped young have less protein available to them than seabird chicks.

It has been suggested that the energy rich stomach oil of procellariform birds is a method of concentrating the energy content of the material fed to the chick. However, this may only be of importance to the smaller procelliforms. Prince (1980) found that in gray headed and black browed albatrosses the liquid fraction of the diet fed to chicks in many cases is low in lipid and thus may be energetically unimportant. Furthermore, lipid content is related to the diet and the duration of the foraging trip (Prince, 1980). The longer the bird is at sea the greater the time for digestion and production of stomach lipids. (The higher the lipid content of the prey, the greater the lipid content of the liquid fraction of the diet.)

Limitation of avian provisioning

Since albatrosses and penguins do not concentrate the material fed to their offspring they can only compensate by feeding them higher quality prey, lengthening the fledgling period or fledging the young at a smaller size. The limitation of feeding unaltered prey to the offspring is exemplified by Prince's (1985) work on sympatrically breeding gray headed and black browed albatrosses, which fledge chicks of similar body mass (124%–132% of adult mass), exhibit equivalent trip durations (24 hr) and meal sizes (660 g), but feed on prey with different energy densities. Black browed albatrosses feed on krill (40%), fish (39%) and some squid (21%), with an overall energy density of 4.02 kJ/g. Gray headed albatrosses feed mostly on squid (49%), fish (35%) and some krill (16%), which has an overall energy density of 3.79 kJ/g. Since gray headed albatrosses feed on a diet of lesser energy density their energy return (2,272 kJ/trip) is lower than that of the black browed albatrosses (2,410 kJ/trip). Therefore, over the same time interval gray headed albatross chicks receive less energy than black browed albatross chicks. Gray headed albatross chicks adjust for the reduced energy delivery by growing slower and fledging after 141 days compared to 116 days for black browed albatross chicks (Prince, 1980, 1985). Furthermore, interspecific differences in growth rate have both a dietary and genetic basis as determined by chick cross fostering experiments (Ricketts and Prince, 1981).

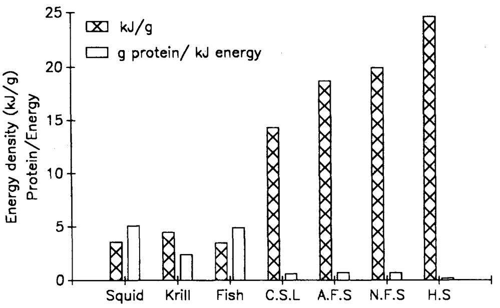

FIG. 3. The energy density of squid, notothaenid fish, krill and milk of California sea lions (C.S.L.), Antarctic fur seal (A.F.S.), northern fur seal (N.F.S.) and hooded seal (H.S.) are given along with the ratio of protein to energy for these items (Clarke, 1980).

Variations in milk composition

In contrast to seabirds, pinnipeds are able to optimize food delivery to their young, in a manner consistent with the predictions of central place foraging theory by adjusting milk composition in response to differences in trip duration. Lipid and therefore energy content of the milk of otariids has been shown to increase as trip duration increases (Trillmich and Lechner, 1986). Recently, Trillmich (personal communication) found that data on milk lipid content of Galapagos fur seal females making long feeding trips (3–4 day) also fit this regression, which suggests that this relationship is applicable within as well as between species. Such a pattern has only been described for otariids, however, data for phocid seals can be included if we consider that they are making one extremely long foraging trip. Incorporating phocid milk composition data and a larger data set for otariids we find species that make short foraging trips have lipid-poor milk (low energy density), whereas species that make long foraging trips produce lipid-rich milk (high energy density) (Fig. 4). It is likely that phocid milk is as lipid rich as is possible and that an asymptote is reached between milk fat content and trip duration.

Correlations of milk fat content and trip

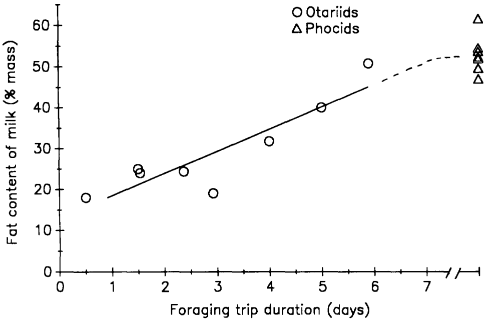

FIG. 4. The fat content (% wet mass) of otariid (circles) is plotted against the duration of a foraging trip. Data on milk fat content of phocid milk are provided for comparison. Phocid seals make one very long foraging trip of unknown duration.

duration are confounded by the fact that otariid females with short trip durations are low latitude species and those with long trip durations are high latitude species. Furthermore, high latitude species have shorter lactation periods than low latitude species (Oftedal *et al.*, 1987*a*). We might expect that females with short lactation intervals have higher milk fat content to allow delivery of a greater amount of milk energy in a shorter interval. Consistent with this prediction, there is a clear pattern between milk fat content and the amount of time the female spends onshore with her pup (Fig. 5). Notice that the hooded seal with the shortest lactation interval has the highest milk fat content of any pinniped (Oftedal *et al.*, 1988) and that the milk fat content of the two polar otariids (Antarctic and northern fur seals) have milk fat contents that are almost equivalent to phocid levels. However, this relationship is not linear and other factors may become important as time available for suckling increases.

The increased energy density of pinniped milk does have a tradeoff in that it may limit the amount of protein or other essential nutrients available to the offspring. This is because the increased energy content of pinniped milk is achieved by increases in milk lipid content with negligible changes in its protein content. Thus the young are provided with more than enough energy to fuel metabolism, but may be limited in their ability to grow. In fact, most of the postnatal growth of phocid seals is due to the accumulation of adipose tissue stored as blubber, with little growth in lean tissue (Bryden, 1968; Worthy and Lavigne, 1983; Costa *et al.*, 1986*a*). For example, at birth northern elephant seal and harp seal pups are born almost without fat and upon weaning are composed of approximately 50% lipid (Worthy and Lavigne, 1983; Ortiz *et al.*, 1984).

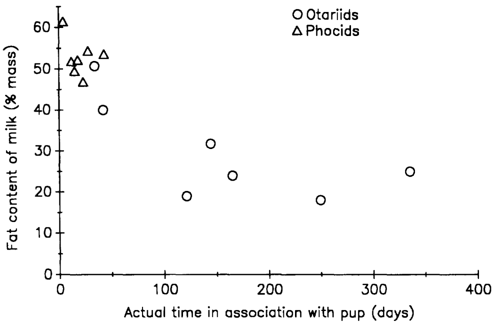

FIG. 5. Milk fat content (% wet mass) of otariids (circles) and phocids (triangles) is plotted against the time spent by the mother with her pup onshore.

Total investment in offspring

So far we have examined the amounts of energy invested in the offspring per foraging trip, but this is only part of the story. Of ultimate importance is the total energy and material invested in the offspring. Penguins and some pinnipeds provide a good system to estimate total parental investment, because the investment period is brief; in most cases, the young are completely dependent upon parental provisioning until they are fledged or weaned and the transition from dependence to independence is abrupt. Trivelpiece *et al.* (1988) recently determined total parental investment in adelie, chinstrap and gentoo penguins. Total parental investment has been reported for a variety of phocid seals, including harp (Stewart and Lavigne, 1984), gray (Fedak and Anderson, 1982; Anderson and Fedak, 1987), hooded (Bowen *et al.*, 1987), Weddell (Tedman and Green, 1987) and elephant seals (Ortiz *et al.*, 1984; Costa *et al.*, 1986*a*), but only portions of the investment interval have been measured in otariids such as northern (Costa and Gentry, 1986) and Antarctic fur seals (Costa and Croxall, 1988), California

TABLE 2. *The data on parental mass, period of parental investment, mean milk consumption of the pup per day of lactation used to calculate total parental investment in terms of energy and protein are given for each pinniped.**

				Total parental investment in offspring			
				Energy		Protein	
	Parental mass kg	Investment duration days	Milk energy MJ/day	MJ	MJ/kg	kg	g/kg
Harp seal	135	12	67.3	810	6	3.2	2 (2)
Gray seal	174	18	70.8	1,270	7	6.4	37 (3)
Hooded seal	179	4	203.0	680	4	1.4	1 (5)
N. elephant seal	504	28	96.3	2,700	5	18.0	36 (4)
Weddell seal	447	45	73.7	3,320	7	14.2	32 (6)
Antarctic fur seal	39	117	10.5	1,240	31	7.6	192 (7)
Northern fur seal	37	125	8.6	830	22	5.9	159 (1)
California sea lion	85	300	10.2	3,050	36	17.2	202 (8)
Stellar sea lion	273	330	21.0	6,930	26	55.8	204 (10)
Adelie penguin	4.4	52		157	52	4.8	1,595 (9)
Chinstrap penguin	4.0	52		240	85	7.6	2,686 (9)
Gentoo penguin	5.3	72		487	140	15.5	4,454 (9)

* Data on parental mass, fledgling duration and total energy and protein invested by both parents in the offspring are given. Numbers in parentheses are the sources for the data as follows: (1) Costa and Gentry, 1986, (2) Stewart and Lavigne, 1984, (3) Fedak and Anderson, 1982, (4) Costa *et al.*, 1986*a*, (5) Bowen *et al.*, 1985, 1987, (6) Tedman and Green, 1987, (7) Costa and Croxall, 1988, (8) Oftedal *et al.*, 1987*a*, *b*, (9) Trivelpiece *et al.*, 1988, (10) Higgins *et al.*, 1988.

(Oftedal *et al.*, 1987*b*), and Steller (Higgins *et al.*, 1988) sea lions. Total investment is difficult to measure in otariids because rates of milk ingestion may increase and the composition of the milk may change as the pups get older (Costa and Gentry, 1986; Oftedal *et al.*, 1987*a*). Furthermore, in some cases weaning is gradual and pups may begin to feed on their own prior to weaning. However, for comparison, we can roughly estimate the total energy and material invested by these otariid mothers if we multiply mean daily milk intake by the length of the lactation period (Table 2).

Comparison of the total investment into penguin or pinniped offspring shows that penguins provide more energy and protein relative to their body mass than either pinniped family, and that otariids invest more energy and protein in their offspring than phocids (Figs. 6, 7). The greater investment is reflected by the offspring becoming independent at a higher relative body mass in penguins (91% of adult mass at fledging) with otariids intermediate (46% of adult mass at weaning) and phocids the lowest (25% of adult body mass at weaning) (Table 1). However, the difference in parental investment between otariids and penguins disappears if we consider that two adults feed the young in penguins. If we compensate for two parents by dividing the fledgling mass by the mass of two adults we get a fledgling mass to adult mass ratio (46%) identical to that of otariids. It appears that the penguin and otariid strategy promote lean growth early, whereas phocids defer lean growth until after weaning. Lastly, it is important to consider that this analysis only compares the energy provided to the offspring and does not include the cost of acquiring and processing it.

Effect of latitude on total investment in penguins

Total energy investment and fledgling mass are not correlated with adult body mass in penguins, but rather with breeding latitude. In high latitude species, the energy investment is limited by the length of the breeding season. For example, adelie penguins, which breed the furthest south of any penguin species, have compensated for the very short Antarctic summer by reducing the fledging period to 52 days and breeding earlier in the austral summer. Since they are constrained by the mechanical limitations to carry food to the offspring, the shortened breeding season results in lower total energy delivery to the chick, resulting in a fledging mass of only

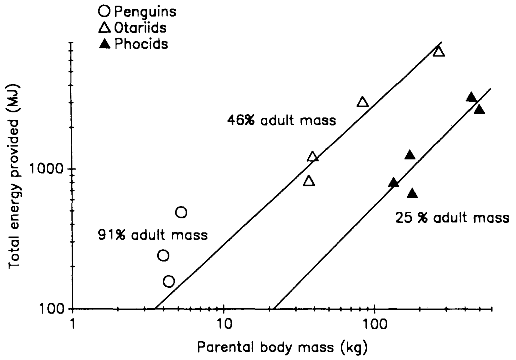

FIG. 6. The total energy invested by the parent(s) into the offspring is plotted as a function of adult body mass of penguins (open circles) or maternal mass in otariids (open triangles) and phocids (solid triangles). Penguins are fledged at 91% of adult body mass, otariids at 46% and phocids at 25% of maternal mass. However, if we correct for provisioning by two adults in penguins the fledgling mass of penguins becomes 46% of the combined adult mass. The two regression lines are least squares linear fit for the otariid and phocid data.

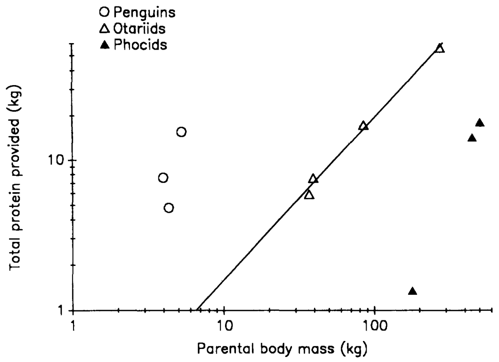

FIG. 7. The total protein invested by the parent(s) into the offspring is plotted as a function of adult body mass in penguins (open circles) or maternal mass in otariids (open triangles) and phocids (solid triangles). The single regression line is the least squares linear fit for the otariid data.

79% of adult mass. The chinstrap penguin breeds in the more moderate Antarctic peninsula area, has a breeding season that starts later in the austral summer, but is of equivalent duration. Since they breed later when krill is apparently more available they provide more total energy to their offspring and fledge them at 89% of adult mass. Finally, gentoo penguins, which have a sub-antarctic distribution, fledge their young after 72 days, and have the greatest total energy investment of the three species, fledge their young at 104% of adult mass (Trivelpiece *et al.,* 1988).

Effect of latitude on total investment in pinnipeds

Unlike penguins, both otariids and phocids are capable of accommodating to latitudinal differences in the length of the reproductive season. For example, otariids and phocids invest a total amount of energy in their young, which is a surprisingly constant proportion of adult body mass for each group, and is independent of latitude or the length of the breeding season. Even though the two polar otariids, the northern and Antarctic fur seal, have shorter reproductive seasons (4 months) than the temperate Steller and California sea lions (10–11 months), the energy invested per kg of maternal body mass is quite similar (Fig. 8). A similar pattern exists for phocids (Kovacs and Lavigne, 1986). Even though the duration of lactation is considerably shorter in arctic breeding species such as the hooded (4 days) and harp seal (12 days), the total energy delivered to the offspring is quite similar to that for the longer lactation intervals of the sub-arctic gray seal (18 days), temperate elephant seal (28 days), and Antarctic Weddell seal (45 days) (Table 2). This ability to compensate for differences in the length of breeding

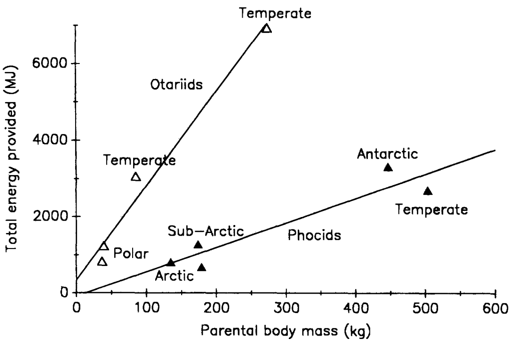

FIG. 8. The total energy invested by female pinnipeds in their pups is plotted as a function of maternal mass in otariids (open triangles) and phocids (solid triangles). The two regression lines are the least squares linear fit for the otariid and phocid data. Latitudinal gradients are given for each group. High latitude species have shorter lactation periods than low latitude species.

season without modifications in total energy investment is made possible by lactation, which, as discussed earlier, allows pinnipeds to act as optimal central place foragers. It is interesting to note that the timing of the breeding season appears to be genetically fixed. For example, small populations of Antarctic and northern fur seals breed in temperate habitats but wean their pups at four months of age, while sympatric otariids wean their pups at one year of age (Kerley, 1985).

FORAGING BEHAVIOR

The previous discussion on parental provisioning leads one to believe that there are many more differences than similarities in the reproductive ecology of avian and mammalian marine predators. However, I have only discussed what happens once the food energy is obtained and have not explored how these groups compare with respect to their prey-specific foraging behaviors and costs of foraging. I will show that with respect to foraging behavior and energetics, pinnipeds and penguins are quite similar.

Foraging behavior data

The diving patterns of free-ranging animals have been measured in a variety of ways from using small dye-filled capillary tubes (Kooyman *et al.*, 1971; Montague, 1984; Lishman and Croxall, 1983) to larger and more expensive devices which employ a variety of analog and digital electronic, and photomechanical transducers (Kooyman *et al.*, 1976; Kooyman *et al.*, 1983*a*; Wilson and Bain, 1984; Hill, 1986). Some of these devices are limited to collecting data on the relative number and depth of dives only (Kooyman *et al.*, 1982; Wilson and Bain, 1984; Croxall *et al.*, 1988) whereas larger instruments can obtain a complete accounting of how the animal spends its time at sea (Kooyman *et al.*, 1980; Kooyman, 1981; Le Boeuf *et al.*, 1986; Le Boeuf *et al.*, 1988; Trillmich *et al.*, 1986; Gentry *et al.*, 1986*b*; Kooyman and Gentry, 1986; Croxall *et al.*, 1985; Kooyman *et al.*, 1986; Kooyman and Trillmich, 1986*a*; Feldkamp *et al.*, 1989; Kooyman and Trillmich, 1986*b*). The results of these studies with respect to maximum diving depth are summarized in Figure 9.

Several general patterns on maximum dive depth become apparent in Figure 9. First, phocid seals, and in particular elephant seals, are exceptional among all groups in their deep diving ability. Second, with the exception of the Hooker's sea lion, otariids and penguins are quite similar in the maximum diving depths reported. Third, the larger the mass of the animal, the greater their dive time and thus the deeper their diving ability. This observation is not new and is explained by a more efficient utilization of stored oxygen with increasing body mass (Kooyman *et al.*, 1983*b*; Gentry *et al.*, 1986*a*). If larger animals can dive deeper than smaller animals it is interesting that so many pinnipeds, which are larger than penguins, dive to such shallow depths (Fig. 9).

One might expect Antarctic fur seals to be capable of reaching the depths achieved by the similar sized northern fur seal. This implies that in some cases diving animals may rarely reach their potential maximum diving depth. Obviously a variety of factors regarding prey type, including behavior, energy content and size, influence the cost and benefit of pursuing prey at different depths.

A complete analysis of foraging behavior requires an examination of diving behavior as a function of prey type. Data of this type are available for a few species, but they suggest that otariids and penguins exhibit strikingly similar foraging behaviors, which will be discussed below.

Single species krill predators

Many Antarctic marine mammals and seabirds prey upon krill and several of these do so exclusively. Unfortunately detailed studies of foraging behavior exist only for king (Kooyman *et al.*, 1982), gentoo and macaroni penguins (Croxall *et al.*, 1988*b*) and Antarctic fur seals (Croxall *et al.*, 1985; Kooyman *et al.*, 1986). Of these, only macaroni penguins, Antarctic fur seals and crabeater seals are exclusively krill predators (Laws, 1984; Croxall and Pilcher, 1984; Croxall *et al.*, 1988*b*). The most complete analysis of foraging behavior was car-

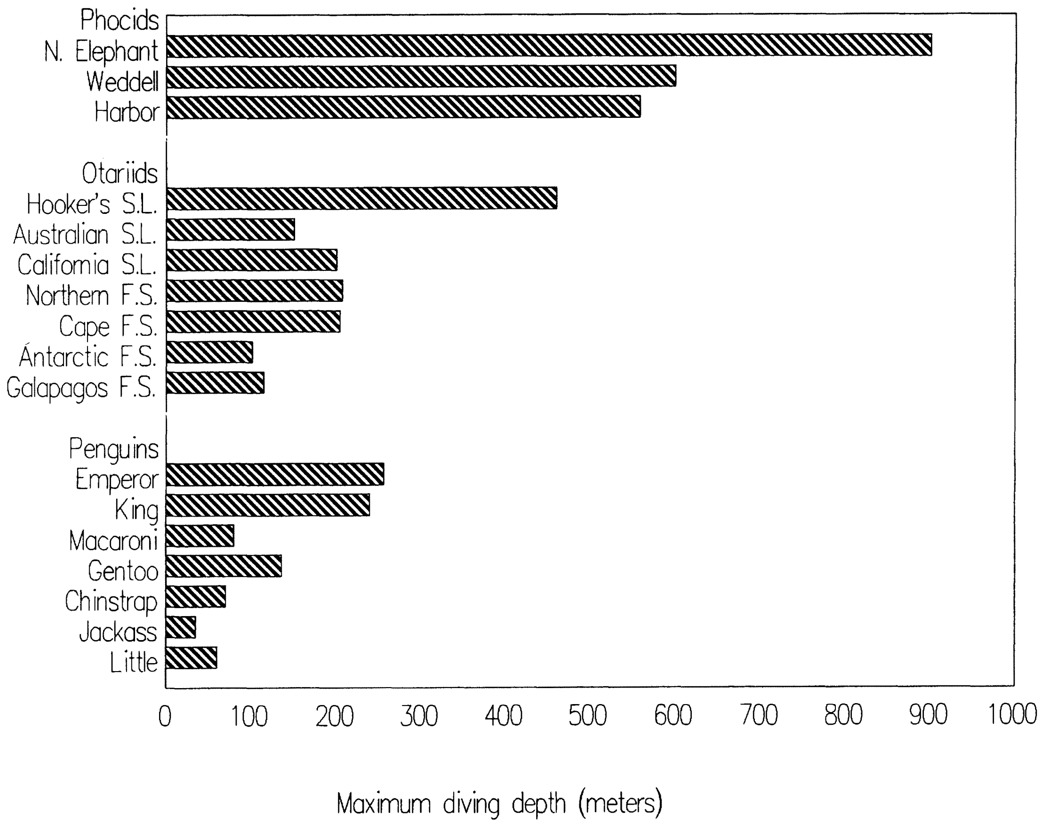

FIG. 9. Maximum diving depth for 10 pinnipeds and 7 penguins. Data are from little penguin, Montague, 1984; jackass penguin, Wilson and Bain, 1984; chinstrap penguin, Lishman and Croxall, 1983; gentoo and macaroni penguins, Croxall *et al.*, 1988*b*; king penguin, Kooyman *et al.*, 1982; emperor penguin, Kooyman *et al.*, 1971; Galapagos fur seal, Kooyman and Trillmich, 1986*a*; Antarctic fur seal, Kooyman *et al.*, 1986; cape fur seal, Kooyman and Gentry, 1986; northern fur seal, Gentry *et al.*, 1986; California sea lion, Feldkamp *et al.*, 1989; Australian sea lion, Costa, Thorson and Kretzmann, unpublished; Hooker's sea lion, Gentry *et al.*, 1987; harbor seal, Kolb and Norris, 1982; Weddell seal, Kooyman, 1981; northern elephant seal, Le Boeuf *et al.*, 1988.

ried out on Antarctic fur seals (Croxall *et al.*, 1985). These investigators found that fur seals made most (75%) of their dives at night and that these dives were consistently shallower (dive depth <30 m) than dives during the daytime (mostly 40–75 m). This pattern closely followed the vertical distribution of krill, which during daylight hours was below a depth of 50 m and was present at night in substantial quantities above 50 m. Furthermore, they found that even though more than 40% of the krill was below 75 m depth at any time of day, fur seal dives seldom (3%) exceeded this depth. They concluded that krill are captured only from shallow waters, since this is when they are most efficiently consumed. Less complete data available for other krill predators such as macaroni, chinstrap and gentoo penguins suggest that the same pattern exists for them as well (Croxall *et al.*, 1988*b*). A possible exception is the crabeater seal, which apparently pursues krill deeper (Bengston, unpublished data). However, this may not be unexpected given the greater diving capability of phocid seals (Fig. 9).

Further data on gentoo penguins support the concept that it is only economical to forage upon krill when they are shallow. When preying upon fish, 59% of their dives were to 54–136 m, whereas when preying upon krill 77% of their dives were shallower than 54 m (Croxall *et al.*, 1988*b*). Gentoo penguins could pursue krill to deeper depths, but they apparently choose not to.

Such a pattern indicates that prey type influences foraging efficiency. The major differences between fish as a prey resource and krill is that fish are larger. Croxall *et al.* (1988*b*) estimated that in order to meet their energy requirements gentoo penguins would only have to obtain 1 fish every third dive compared with 15–50 krill every dive. They concluded that prey size and therefore energy payoff is the important component determining or limiting dive pattern. Their analysis supports the hypothesis that due to the small size and low energy content of krill, hunting individual krill is only efficient for penguins and fur seals when krill are shallow.

Dive patterns of multispecies predators

The diving pattern of gentoo penguins indicates that different prey species have different behavioral optima. Like gentoo penguins, female northern fur seals exhibit two distinct diving patterns that are specific to the type of prey consumed. Gentry *et al.* (1986*b*) found that during a foraging trip, fur seals exhibited one of the following patterns: those composed exclusively of deep dives, having a mean depth of 185 m, those composed exclusively of shallow dives with a mean depth of 50–60 m, and those with a mixture of both deep and shallow dives. Deep diving fur seals did not exhibit diurnal fluctuations in dive depth, implying that they were feeding on demersal or benthic species. However, shallow divers exhibited a striking diurnal fluctuation in diving pattern quite similar to that observed for krill feeding species. Recent data suggests that these deep diving seals are feeding on demersal fish such as pollock on the Bering Sea Shelf, whereas shallow diving seals feed on vertically migrating squid over deep water beyond the Bering Sea Shelf (Loughlin *et al.*, 1987). Like krill, squid are available throughout the day, and comparable to krill predators, northern fur seals wait for squid to move into shallow water before preying on them. Finally, analogous to gentoo penguins, northern fur seals pursue fish, with 4 times the energy value of squid, to considerably deeper depths than when diving for squid (Costa, 1988). A summary of the data available on prey type and dive depth are summarized in Table 3 for a variety of fur seals and penguins. When combined with estimates of the number of prey that must be captured per dive to meet the predator's energy expenditure, the data suggest a relationship between the number of prey taken and dive depth. Deep divers take prey that is large which only requires the capture of a few individuals per dive. Conversely when small prey are taken, many individuals must be captured per dive and these dives appear to be limited to shallow depths. For example, it has been estimated that to meet their energy requirements, deep-diving king penguins need only capture 1 squid every tenth dive, whereas shallow diving Antarctic fur seals need to capture 70 krill every dive (Kooyman *et al.*, 1982; Gentry *et al.*, 1986*a*)!

This suggests that deep diving is only economical when the predator is foraging on large prey which can supply a significant fraction of the energy requirement with each dive. In contrast, predation on small prey, where many individuals must be captured per dive, is limited to shallow depths. The terms shallow and deep are relative to the diving capability of the predator. For example, shallow to an elephant seal may be 300 m, whereas shallow to a northern fur seal is 30 m.

TABLE 3. *Measured diving depths of predators and the prey type known or thought to be consumed on those dives.**

	Diving depth m	Prey type	# prey consumed per dive
Gentoo penguin	<80	Krill	15
	<136	Fish	0.3
Macaroni penguin	<80	Krill	6
King penguin	<245	Squid	0.1
Antarctic fur seal	<65	Krill	70
Northern fur seal	>100	Fish	1.3
	<100	Squid	5

* The number of prey captured per dive was estimated from data on energy content and the size of consumed prey, the total number of dives made during a foraging trip and the energy expended over that trip. For king penguins prey intake was estimated from water influx. Data on gentoo and macaroni penguins are from Croxall *et al.*, 1988*b*, data on Antarctic and northern fur seals are from Gentry *et al.*, 1986 and data for king penguins are from Kooyman *et al.*, 1982.

What constraints may be associated with depth that account for these different foraging strategies? First, let us examine a hypothetical predator making deep and shallow dives of equivalent duration, on which oxygen is utilized at the same rate, and in which no anaerobic debt is incurred. Incurring an anaerobic debt results in a disproportionate increase in surface interval (Kooyman *et al.*, 1980). A diagram of these diving patterns suggests that shallow dives use relatively little time in transit, which leaves proportionately more time to search for or pursue prey (Fig. 10A). Alternatively, as a deep diver spends relatively more time in transit getting to the foraging depth, it has proportionately less time remaining to search for or pursue prey, and fewer prey can be obtained per dive. Given that the same amount of time is spent per dive it would be prudent to always pursue prey of greater size and energy content. Likewise, if dives are of the same duration and catch rate, but result in the capture of prey with different energy contents, more dives would be required when pursuing the prey of lower energy content. One could also use an argument that is similar to central place foraging theory, where the central place is the surface of the water. Shallow dives have short transit times thus suggesting that the optimal solution is to make many short dives with a lower premium on energy return per dive. For deep dives where transit time is long, few dives of long duration with a high energy return per dive would be favored.

An additional model again holds the oxygen stores as constant but proposes that the rate of oxygen utilization is a function of the animal's swimming or search and pursuit speed (Fig. 10B). A fast swimming animal would utilize its oxygen stores faster and would thus be limited to shallow dives or "spiked" dives with minimal bottom time. A slow swimming animal would utilize oxygen more slowly and thus could make dives of long duration. It is likely that the pursuit of many small prey requires fast and agile swimming with high rates of oxygen utilization. Such a high rate of O_2 utilization would constrain the predator to short dives. However, for a shallow diving predator this may not be a serious constraint since transit time to foraging depth is brief. In this case since transit time is relatively low, most of the dive would be spent in pursuit and acquisition of prey. For deep dives, however, the opposite is true. If a deep diver were to swim fast, most, if not all, of the oxygen stores might be utilized in transit to depth, with little left over for the search and pursuit of prey. Such a situation probably results in the "spiked" dives seen in many diving pinnipeds (Gentry *et al.*, 1986*a*; Le Boeuf *et al.*, 1988). Since some searching and pursuit of prey may be desirable at depth, an alternative would be to reduce oxygen consumption and swim slowly. This would allow greater bottom time at depth but might limit the predator to obtaining slow moving prey or prey that is only encountered occasionally. If this were the case the predator would have to pursue prey that was of large size and high energy content. Flat bottom dives consistent with this behavior have been observed for deep diving northern elephant seals (Le Boeuf *et al.*, 1988), Hooker's sea lions (Gentry, personal communication) and Australian sea lions (Costa *et al.*, unpublished data). A corollary of this pattern would be to limit the pursuit phase to slow methodical swimming at least until the prey has been spotted. Switching to a rapid high energy swim speed would result in rapid utilization of oxygen which could limit the dive to a single capture before O_2 stores were depleted. If deep divers can only capture a few individuals per dive, then in order to maintain energy balance they must pursue prey that contain a greater amount of energy per capture.

FORAGING ENERGETICS

The preceding discussion on foraging behavior of penguins and pinnipeds suggests that these predators face similar constraints. In this section I will examine how these predators compare with respect to the metabolic expenditure associated with foraging. Given the different foraging behaviors listed above it is likely that each dive pattern is associated with a different cost (Costa, 1988). Unfortunately, such data

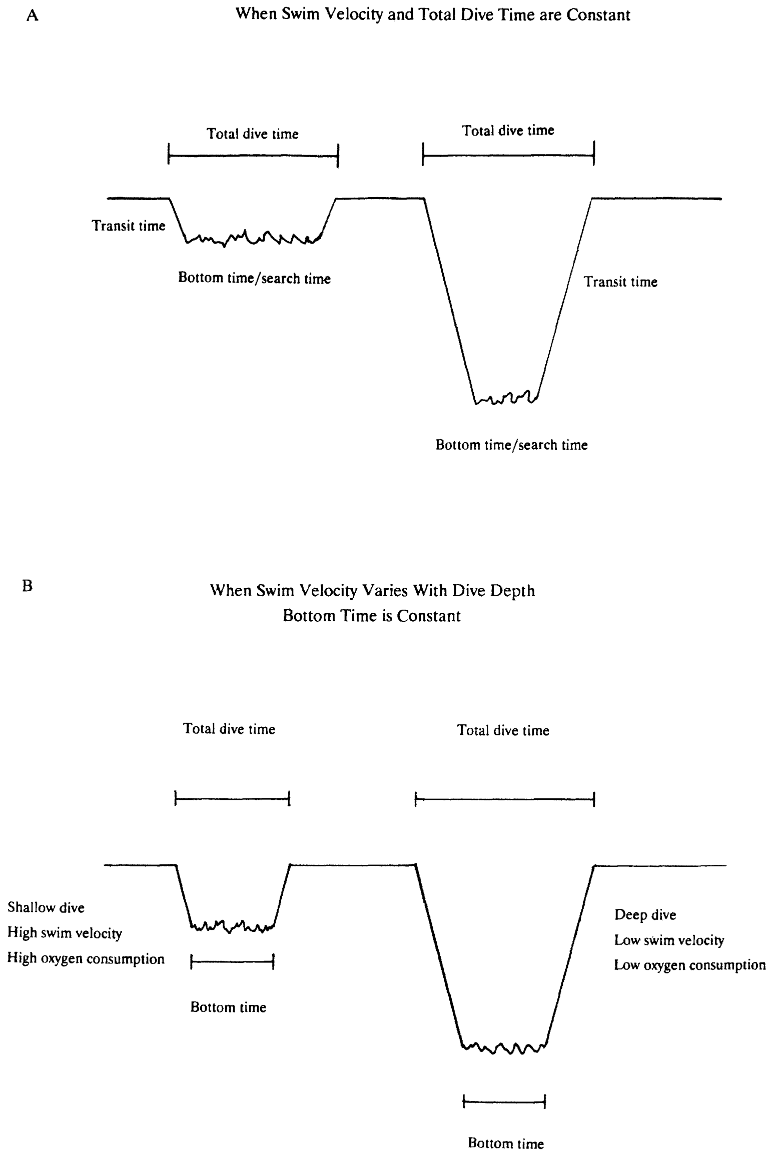

FIG. 10. A. Schematic representation of the diving pattern of a deep and shallow diving predator when oxygen utilization is constant and total dive durations are equivalent. B. Diving pattern where the rate of oxygen utilization is greater for shallow dives than for deep dives. In this case total dive duration is not constant.

are not available. However, data are available on the energy consumption while at sea for a few of these marine predators. Energy expenditure of free-ranging animals has been measured using the oxygen-18 doubly-labeled water method. In this technique, known amounts of tritium and oxygen-18 labeled water are injected into an animal. The oxygen-18 water equilibrates with both the CO_2 and water pools, and declines as a function of water influx and CO_2 production, whereas, tritiated water equilibrates only with the water pool and dilutes as a function of water influx. As CO_2 is produced by metabolism only oxygen-18 labeled water is diluted. There-

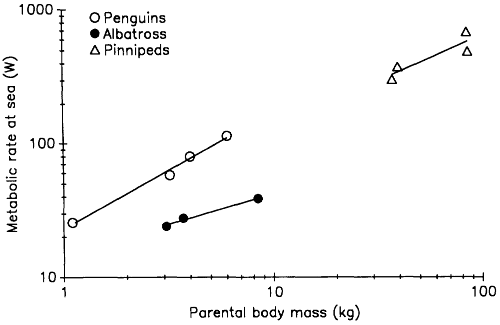

FIG. 11. Metabolic rates at sea determined with the O-18 doubly-labeled water method are plotted as a function of body mass for little (Costa *et al.*, 1988), jackass (Nagy *et al.*, 1984), macaroni and gentoo (Davis *et al.*, 1989) penguins, grey headed (Costa and Prince, 1987), wandering (Adams *et al.*, 1987) and laysan (Pettit *et al.*, 1988) albatrosses, northern (Costa and Gentry, 1986) and Antarctic (Costa *et al.*, 1989) fur seals and Australian (Costa, unpublished data) and California sea lions (Costa *et al.*, 1990).

fore, the difference between oxygen-18 turnover and tritiated water turnover is a measure of the animal's CO_2 production. A complete discussion of these methods and their inherent errors can be found in Lifson and McClintock (1966), Nagy (1980), Nagy and Costa (1980), Schoeller and van Santen (1982) and Costa (1987).

This approach has yielded data on the at sea metabolism of macaroni, gentoo (Davis *et al.*, 1989), jackass (Nagy *et al.*, 1984) and little penguins (Costa *et al.*, 1986*b*; Costa *et al.*, 1988), gray headed (Costa and Prince, 1987), laysan (Pettit *et al.*, 1988) and wandering albatrosses (Adams *et al.*, 1987), as well as northern (Costa and Gentry, 1986), Galapagos (Trillmich and Kooyman, unpublished data) and Antarctic fur seals (Costa *et al.*, 1989) and Australian (Costa, unpublished data) and California sea lions (Costa *et al.*, 1989). Unfortunately data are not yet available for phocid seals. Of interest is the observation that the metabolic rates of swimming and diving penguins and fur seals and sea lions are more similar to each other than to those of soaring and gliding albatrosses (Fig. 11). This is a striking example of the low cost of dynamic soaring flight (Costa and Prince, 1987) compared to the high cost of swimming and diving, at least for the species studied to date. Also these data show that like foraging behavior, the energy expenditure while at sea is surprisingly similar for penguins, fur seals and sea lions. The slightly elevated metabolic rate of birds is to be expected since they normally sustain higher metabolic rates than mammals (Bartholomew, 1982).

SUMMARY AND CONCLUSIONS

Given the similarities and differences between pinniped and seabird (penguins and albatrosses) reproductive energetics and behavior, the goal of present investigations is to show how divergent life history patterns are optimal for different reasons. For example, absolute differences in body size may have a profound influence on the pattern that produces optimal results. Larger animals have greater energy reserves, which are used at a slower rate (Calder, 1984). In this context penguins are smaller than pinnipeds with the largest, the 32 kg emperor penguin, just overlapping the mass of the smallest pinniped, the 27 kg Galapagos fur seal.

Another potential difference between these groups is in their tolerance to variations in food supply. Croxall *et al.* (1989) recently reported on over 10 years of monitoring data on inter-annual variation in reproductive performance of gentoo and macaroni penguins, wandering, black browed and gray headed albatrosses and Antarctic fur seals on Bird Island South Georgia, South Atlantic. They found that krill predators, such as gentoo and macaroni penguins and black browed albatrosses, exhibited extreme interannual fluctuations in fledgling success. However, variation in reproductive performance of the exclusively krill consuming Antarctic fur seal was considerably less than that exhibited by the avian krill consumers. The most severe example was during the austral summer 1983–84 when krill was exceptionally scarce. During this season all of the krill consuming avian predators, including gray headed and black browed albatrosses, gentoo and macaroni penguins, failed to fledge their young. In contrast, even though pup survival declined from the norm of 84% there was still good success of 68% in the exclusively krill-consuming

Antarctic fur seal during 1983–84 season. These data imply that fur seals have a greater resistance to variations in food supply, which may be related to the differences in mammalian and avian reproduction discussed earlier.

Given the constraints of avian and mammalian reproductive patterns we can summarize the advantages and disadvantages of seabirds, otariids and phocids as follows. Seabird provisioning allows a greater overall investment of energy and protein into the offspring. This in turn allows the young to be fledged at a high relative body mass, which may confer greater juvenile survival. However, this increased provisioning rate results in more trips to sea, which may expose the adults and chicks to greater predation pressure. A disadvantage of the avian pattern is that it is more affected by the shorter breeding season of high latitudes, and thus fledgling success is more sensitive to variations in prey availability.

In contrast, otariids provide the young with less mass specific total energy and protein than seabirds, but more than phocid seals. This allows them to wean their young at a relative mass that is intermediate between seabirds and phocids. Lactation allows pinnipeds to forage in a manner that more closely follows the predictions of central place foraging theory, which results in a pattern of parental investment that is less affected by the short high latitude breeding season. Lastly, otariids show greater buffering to fluctuations in prey resources than do seabirds.

Phocid seals possess the shortest period of parental investment, which is made necessary by their habit of fasting during lactation. Such a pattern has been considered the result of breeding on unstable ice (Stirling, 1983). However, utilization of patchy, or highly dispersed prey resources may have forced phocids to forgo a lactation pattern that alternates between feeding at sea and suckling the pup onshore. The phocid reproductive pattern may allow utilization of such a resource by acquiring and storing all of the material and energy needed to successfully rear the young in advance of parturition so they can then fast during lactation. Once attained, such a breeding pattern may have enabled phocids to secondarily inhabit seasonally variable environments like unstable ice. However, fasting while lactating places a limit on the total amount of energy and protein that can be invested in the young, which results in the smallest relative mass at weaning and the shortest period of parental care.

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