MARINE MAMMALS OF THE SOUTHERN OCEAN

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Marine mammals are a conspicuous faunal element of the Southern Ocean ecosystem and have evolved specialized life history patterns to live there. Six species of pinnipeds inhabit the Southern Ocean, including five species of true seals (family Phocidae) and one species of eared seal (family Otariidae). It is a critical feeding ground for many cetaceans: 15 species of cetaceans, including 6 species of baleen whales, Mysticeti, and 8 species of toothed whales, Odontoceti, inhabit the Southern Ocean. Climate, substrate and prey availability are the key factors controlling breeding distributions. A unique reproductive pattern has evolved in the true seals, Phocidae, that enables them to inhabit and breed in the extensive ice regions of the Southern Ocean. While exerting strong direct influences on distribution, changes in the physical properties of the environment, most likely have strong indirect effects on both the quality and quantity of breeding substrate, the nature of foraging habitat, or on distribution and abundance of potential prey. The occurrence and extent of seasonal ice also plays a role in determining the distribution and abundance of marine mammals. This chapter provides an overview of the biology of marine mammals found in the Southern Ocean.

1. INTRODUCTION

Diverse life history patterns have evolved in marine mammals allowing them to accommodate the extreme fluctuations in the physical and biological environment of the Southern Ocean. As they are long lived animals, they must be able to withstand variations in food resources over large spatial and temporal scales. Marine mammals, as endotherms with high metabolic rates, are dominant consumers of zooplankton biomass and may significantly influence the community structure of the Southern Ocean [Laws, 1977]. One estimate of CO₂ production by marine mammals and birds suggests that they may play an important role in the Southern Ocean carbon cycle [Huntley *et al.*, 1991]. Six species of pinnipeds inhabit the Southern Ocean, including five species of true seals (family Phocidae) and one species of eared seal (family Otariidae). The high productivity of the Southern Ocean is reflected in estimates that it contains nearly 50% of the world's seal population and 80% of the world's biomass of pinnipeds [Laws, 1984]. It is a critical feeding ground for many cetaceans: 15 species of cetaceans, including 6 species of baleen or mysticete whales and 8 species or subspecies of toothed or odontocete whales inhabit the Southern Ocean. In this chapter we provide a general overview of the biology of marine mammals of the Southern Ocean and where possible provide suggestions for new research.

The abundance of marine mammals was thought to be related to the Southern Ocean's high productivity and short food chain, which insured that a high proportion of the fixed carbon was available to the top predators [Laws, 1977; Ever-

son, 1984]. However, recent information indicates that the primary production of the Southern Ocean is significantly lower [Smith, 1991] and food webs are considerably more complex than originally thought [Murphy *et al.*, 1988; Pridde *et al.*, 1992]. Marine mammals likely rely on regional patches of high productivity resulting from localized sources of nutrient influx associated with upwelling regions, bottom topography, divergence zones or the sea ice edge [Ainley and DeMaster, 1990]. Marine mammal populations are patchy and their numbers are good predictors of areas of high prey abundance.

While a wealth of information exists for many species during the breeding season, our knowledge of the general biology, feeding ecology and migratory patterns during the non-breeding season is limited. Such information is especially lacking for cetaceans due to their pelagic nature. Application of new technologies such as satellite telemetry, recoverable data loggers, molecular markers, acoustic tracking and remote sensing, combined with dedicated research vessels, holds significant promise to increase our understanding of the ecology and biology of Southern Ocean marine mammals. These new tools have already provided significant insights into the lives of a few species of marine mammals during the winter, while at-sea and underwater [Costa, 1993a; Boyd, 1993]. For example, data are accumulating to suggest that marine mammals rely on oceanographic features, such as frontal systems, thermocline depth, and bathymetry to concentrate or aggregate prey, which may be necessary to enable effective predation [Hui, 1979, 1985; Winn *et al.*, 1986; Reilly, 1990; Ainley and De Master, 1990; Boyd and Arnborn, 1991; Mate *et al.*, 1992; van Franeker,

Fig. 1. Weddell seal resting on the fast ice in McMurdo Sound. (Photo by D. Costa)

1992; Whitehead *et al.*, 1992; Kenney *et al.*, 1995]. It is also clear that the occurrence and extent of seasonal ice plays a direct role in determining the distribution and abundance of marine mammals. The importance of sea ice extends beyond providing some marine mammals with a substrate for breeding and hauling out or as a physical barrier to others. Sea ice is an important physical oceanographic feature that is associated with regional high primary production, which supports abundant populations of Antarctic krill.

2. PINNIPEDS

The biology of Antarctic seals has been reviewed by a number of authors [Bonner and Laws, 1964; Laws, 1964; Øritsland, 1970; Ray, 1970; Laws, 1984; Siniff, 1991]. Six out of 19 pinniped genera worldwide are present in the Southern Ocean [Laws, 1984], and one species of seal, the crabeater seal (*Lobodon carcinophagus*) is thought to be so abundant that its population comprises over half of the pinniped numbers worldwide [Laws, 1977]. Four species of Antarctic seals make their living on the pack-ice region surrounding the Antarctic continent: the crabeater seal, the Ross seal (*Ommatophoca rossi*), the leopard seal (*Hydrurga leptonyx*), and the Weddell seal (*Leptonychotes weddellii*) (Figure 1). One other true seal species, the southern elephant seal (*Mirounga leonina*), as well as an eared seal, the Antarctic fur seal (*Arctocephalus gazella*), are generally found somewhat further to the north using land as a haul-out site for reproduction instead of ice, but are known to forage in waters south of the Antarctic convergence into the marginal ice zone (Figure 2).

2.1. Pinniped Reproductive Biology

A unique reproductive pattern has evolved in phocid seals that enables them to inhabit and breed in the extensive ice

regions of the Arctic and Antarctic. Although we know little about the breeding biology of Ross, leopard and crabeater seals we can make some predictions based on the patterns observed for other seals. Phocid seals can use ice, which is ephemeral, as a breeding substrate because they have a significantly shortened period of pup dependency. This insures that the pup is weaned prior to the break up or disappearance of the ice [Stirling, 1975, 1983]. Thus seals reproducing on unstable, unpredictable pack ice have the shortest lactation interval and fastest growth rates (this may apply to crabeater, Ross and leopard seals), whereas seals breeding on more stable fast ice have a longer pup dependency period and slower growth rates (e.g., Weddell seal).

Many phocid mothers remain on the rookery or ice floe continuously from the birth of their pup until it is weaned, and milk must be produced from body reserves stored prior to parturition. However, by breeding on stable fast ice, Weddell seals have more time to nurse their pups and can augment their maternal energy budget by feeding during lactation since prey are directly below the pupping site [Testa *et al.*, 1989]. Such short duration feeding trips are insufficient to supply the energy to support the growth rate observed for Weddell seal pups. Therefore, most of the energy and materials supplied to the pup must be derived from maternal body reserves [Costa, 1993b; Testa *et al.*, 1989].

Island-breeding elephant seals have a lactation interval intermediate between fast and pack ice breeding polar seals [Kovacs and Lavigne, 1986]. Elephant seals feed far offshore, often thousands of kilometers away from their pupping islands [Hindell *et al.*, 1991; McConnell *et al.*, 1992] and therefore cannot feed during lactation because the food resources are too distant. A shortened lactation period insures that the greatest proportion of maternal nutrients and energy go into milk production and not to maternal maintenance metabolism [Fedak and Anderson, 1982; Costa, 1991b, 1993].

Fig. 2. Antarctic fur seal female and her suckling pup on Bird Island, South Georgia, South Atlantic. (Photo by D. Costa).

The distribution of Otariids (sea lions and fur seals) is limited in the Southern Ocean due to the considerably longer period of pup dependency. Otariid breeding rookeries are restricted to seasonally ice free islands predominately in the sub-Antarctic region. In contrast to phocids, otariid mothers remain with their pups only during the first week or so following birth and thus return to sea to feed intermittently returning to suckle their pup which remains on the rookery [Bonner, 1984]. Depending on the species, otariids spend between 1 to 7 days feeding at sea, and then 1 to 3 days ashore suckling their pups [Gentry *et al.*, 1986a]. This period of intermittent suckling on the rookery and feeding at sea lasts approximately 4 months in the polar fur seals (Antarctic, *Arctocephalus gazella*, and northern, *Callorhinus ursinus*) [Bowen, 1991].

Lactation allows pinnipeds to concentrate the energy content of their milk independent of prey type or breeding pattern, and compensates for differences in the length of the breeding season [Costa, 1991a]. By increasing the fat content of their milk, pinnipeds increase the rate of energy transfer to their offspring and thus offset the shortened reproductive interval [Ofstedal, 1987]. The total energy delivered to polar pinniped offspring is similar to that delivered to temperate pinnipeds [Costa, 1991b].

2.2. Pinniped Distribution and Abundance

Climate, substrate and prey availability are key factors controlling breeding distributions. Changes in the physical properties of the environment, while exerting strong direct influences on distribution, most likely have strong indirect effects on both the quality and quantity of breeding substrate, the nature of foraging habitat, and on distribution and abundance of potential prey [Croxall, 1992]. Pinnipeds are distributed in circumpolar latitudinal zones, except where distribution is affected by the Antarctic Peninsula and Scotia arc, which extends the breeding distribution of some high latitude species northwards and of some lower latitude species southwards [Laws, 1984]. The greatest number of seals occupy the pack-ice region. The distribution of ice-breeding seals may be most strongly influenced by the effects of the nature and extent of ice on the availability of breeding sites with suitable access to water for mating and feeding. The four species that occupy the pack-ice region have become specialized in terms of habitats and their utilization so that little ecological overlap exists [Siniff, 1991]. Elephant seals and fur seals, while not directly affected by the ice, are influenced by the effects of ice on prey populations which originate in areas of seasonal ice-cover. Estimations of population sizes have been hampered by use of vessels of opportunity. Researchers have had only limited control of their survey tracks with minimal helicopter time. Therefore data from relatively small survey areas (totaling around 10,500 km²) must be extrapolated to much larger areas, totaling approximately 3 million km² [Gilbert and Erickson, 1977].

Fig. 3. Maxillary dentition's of six Antarctic seals and one sub-Antarctic species. Inset, enlarged diagram of opposed jaws to show sieve (J, jaw; G, gumline) [from Laws, 1984].

This introduces the possibility of dramatic errors in population estimates if survey areas do not accurately reflect overall distributions. The best population estimates are based on investigations utilizing ice-breakers [Erickson *et al.*, 1971; Siniff *et al.*, 1970; Gilbert and Erickson, 1977].

2.3. Crabeater Seal

The crabeater seal is usually found near the outer edge of the pack-ice region with highest numbers seen in summer [Laws, 1984]. Gilbert and Erickson [1977] suggested that this is related to availability of food, with krill being more abundant near the ice edge. The crabeater seal population on the pack-ice was estimated at between 15 and 30 million and has been believed to be increasing in numbers [Laws, 1977; Laws, 1984]. However, more recent data suggest that abundance may have declined somewhat recently [Erickson and Hanson, 1990]. It has been suggested that these apparent declines may be the result of earlier surveys having been carried out in regions of high seal abundance. Based on population estimates from 1968-1973, approximately 9% of the total crabeater population was associated with pack-ice in the Amundsen-Bellingshausen Sea. Due to the nature of the limited surveys that have been carried out to date any conclusions about absolute numbers or population trends of crabeater seals is premature. There are plans by a number of nations to carry out more extensive surveys of crabeater and other pack ice seals [Anonymous, 1995].

The crabeater seal feeds almost exclusively on Antarctic krill (*Euphasia superba*) [Øritsland, 1977; Laws, 1984]. To facilitate capture of krill, they have special lobed teeth that aid in removing the small krill from seawater (Figure 3).

Fig. 4. Examples of the four types of dives identified in crabeater seals during March 1986. Each dive is plotted from time-depth recorder data, which were obtained every 10 seconds [from Bengston and Stewart, 1992].

The great abundance of crabeater seals coupled with their extreme dietary and habitat specialization (pack ice) is ecologically unusual and merits further examination [Anonymous, 1995]. Laws [1977] reported a decline in the age of first reproduction in a sample of 750 crabeater seals taken for dog food in Marguerite Bay, West Antarctic Peninsula. This decline was correlated with the opening of the area west of the Antarctic Peninsula to whaling in 1955. Age of first reproduction was determined from tooth cementum layers. For the period 1934-37 and mid 1940's to 1955, the age of 1st reproduction was about 4.0 years, by 1965 it had declined to 3 years and by 1970 to 2.5 years. Such a decline in the age of first reproduction is indicative of a population responding to an increased food supply or reduced density dependence. As they no longer take crabeater seals for dog food, more recent data are not available for comparison. It would be instructive to have data on recent crabeater seal reproductive parameters, since there has been no whaling in the Southern Ocean in recent years.

The killer whale (*Orcinus orca*) and leopard seal both prey on crabeater seals. Killer whales prey on crabeater seals from all age classes while the leopard seal preys mostly on

newly-weaned or juvenile animals [Siniff and Bengston, 1977; Laws, 1984; Siniff, 1991]. Leopard seal predation has most likely had an important effect on the evolution of the life-histories of crabeater seals, with an unusually high proportion (25-83%) of individuals exhibiting leopard seal scars [Condy, 1976; Siniff and Bengston, 1977; Siniff, 1982].

Recent data on the diving behavior of crabeater seals obtained using recoverable time-depth recorders indicates that they have a preference for diving and presumably feeding during darkness and haul out during daylight [Bengston and Stewart, 1992]. Their dives were relatively shallow (89% with a depth less than 40 m) with most (90%) being less than 5 minutes in duration. The deepest dive was to 430 m and the longest dive lasted 10.8 minutes. They observed four distinct dive patterns (Figure 4). Type I dives were quite shallow and thought to be associated with horizontal movement through sea ice. Type II and III dives were similar and were thought to be feeding dives. Type II dives are shallow and thought to occur during the most favorable period of krill feeding (at night), whereas Type III dives appeared to occur during the transitional periods of light level with a progressive change in the depth of the dives. Finally Type IV dives were speculated to be associated with navigation or orientation. As the sea ice environment is very noisy, it was suggested that the seals could be going to depth to listen for others seals, to hear navigational cues or to locate new krill swarms. These behaviors appear to be optimal for predation on krill, if krill use vision to avoid predation. We must be careful not to extrapolate too much from this single study as the behavior of only 6 animals was studied during the single month of March. However, it provides a glimpse of what could be achieved if data derived from dive recorders are coupled with data on krill behavior and distribution over multiple seasons.

2.4. Leopard Seal

Leopard seals are usually observed in the summer as solitary animals [Erickson et al., 1971; Gilbert, 1974], with higher densities near the pack-ice edge, like the crabeater seal [Laws, 1984]. Population size was estimated at between 220,00 and 440,000 in 1984 [Laws, 1984].

Leopard seals prey on a variety of warm-blooded animals, as well as fish, cephalopods, and Antarctic krill [Siniff and Stone, 1985; Siniff, 1991]. Newly-weaned crabeater seals are an important prey during December and January [Siniff and Stone, 1985]. Predation on penguin colonies in late January and February is extensive and well documented [Laws, 1981; Siniff and Stone, 1985]. Krill becomes the most important prey item during the winter [Lowry et al., 1988; Siniff and Stone, 1985], comprising up to 60% of the total yearly diet. Data suggest that the breeding season of leopard seals is much later in the summer than that of pack-ice seals and that delayed implantation might not exist in this species [Siniff and Stone, 1985]. It was hypothesized that these

differences might be related to the leopard seal's generalist feeding strategy, resulting in a less tightly synchronized breeding period. As an apex predator with a large and dispersed feeding range, leopard seal breeding behavior may have parallels to that observed for terrestrial non-social carnivores like cats. Like cats, leopard seals may have a breeding system that maximizes successful reproduction when encounters between mates are infrequent.

2.5. Weddell Seal

The Weddell seal is distributed primarily on nearshore fast-ice. It is the most studied of the pack-ice seals, since it utilizes pack-ice habitats that are close to the continent and sometimes close to research bases. In spring, the Weddell seal forms pupping colonies on the fast-ice along annual tide cracks and broken ice, which enables the maintenance of haul-out ice holes [Stirling, 1971; Siniff *et al.*, 1977; Kooyman, 1981]. Several females may share a single ice hole and exhibit fidelity to a colony from one year to the next. This is most likely possible due to the predictability of the fast-ice, in marked contrast to the unstable pack-ice on which the remaining ice-breeding seals pup. After breeding, the seals move into the pack-ice and somewhat away from the continent [Siniff, 1991]. Individuals are nearly always solitary on the pack-ice, but overall densities are most likely higher near the coast or fast-ice [Laws, 1984]. The Weddell seal population has been estimated at 800,000 individuals and is thought to be stable [Laws, 1984], except for decreases at some colonies associated with human harvesting [Siniff, 1991].

Weddell seals feed primarily on a variety of fish species, especially the Antarctic cod (*Dissostichus mawsoni*) and the Antarctic silverfish (*Pleuragramma antarcticum*) [Øritsland, 1977], as well as cephalopods and other invertebrates. Analysis based on stomach contents and fecal sampling have suggested spatial and temporal variation in Weddell seal prey items. For example, Antarctic cod is an important food resource in McMurdo sound in December, while small nototheniid fish, like the Antarctic silverfish, crustaceans and cephalopods are most prevalent in November, January, and February [Testa *et al.*, 1985]. The physiology and diving behavior of Weddell seals has been studied extensively [Kooyman, 1981, 1989]. Weddell seals are relatively deep and long duration divers, with 200-400 m feeding dives of less than 15 minutes in duration being common.

Predation on Weddell seals is rare as predators access is limited by the seals proximity to shore. Testa and Siniff [1987] concluded that predation by killer whales and leopard seals, as the ice breaks up in spring and summer, had little influence on Weddell seal distribution. In contrast to crabeater seals, Weddell seals have a high juvenile survival due to a lack of predation in the fast ice yet have a limited adult survival. As Weddell seals age, their specially modified front incisors, which are used to maintain ice holes to breathe, wear and they lose their ability to maintain breathing holes,

and thus die at an earlier age than do crabeater seals [Laws, 1977].

2.6. Ross Seal

The Ross seal is the rarest and least studied of the Antarctic seals. They are primarily observed as solitary individuals with the highest numbers being associated with larger ice floes [Gilbert and Erickson, 1977]. Breeding appears to occur in November and December [Laws, 1984] but this period of the animal's life-history is virtually unstudied. Ross seals have a wide distribution, being observed in all pack-ice regions surrounding the continent, but are never very abundant in any one area [Siniff, 1991]. Collections of this species have suggested that it feeds primarily on cephalopods [Øritsland, 1977]. The large eyes of Ross seals and stomach content analysis and have led some researchers to speculate that they may feed at depths in excess of several hundred meters [Laws, 1984]. While the reasons for the rarity of the Ross seal are not known, it has been suggested that, as a cephalopod-feeding specialist, it might not be abundant due to a scarcity of cephalopods within the pack-ice environment for much of the year [Siniff, 1991].

2.7. Southern Elephant Seals

Although the breeding distribution of elephant seals is more closely associated with sub-Antarctic and temperate islands, recent investigations have demonstrated that the species is widely distributed at sea during the post-breeding and post-molt foraging migrations. Recent developments in the application of microcomputer data-loggers for studying at-sea behavior have yielded a more detailed picture of the foraging and diving behavior of this species. Southern elephant seals dive continuously, day and night, for the entire trip to sea which lasts between 2 to 8 months. Females who have just completed lactation depart and forage at sea for 10 weeks, return to molt, and then depart for a 8 month foraging trip during which gestation occurs. While at sea they spend 90% of their time underwater, with dives averaging 20 minutes (maximum dives of up to 2 hours) followed by surface intervals of less than 4 minutes. Their diving patterns follow a diurnal cycle with the deepest dives occurring during the day and shallowest at night. Modal dive depths are 300-600 m with a maximum reported dive depth of 1430 m [Slip *et al.*, 1994].

Southern elephant seals from Macquarie Island carried time-depth recorders which also measured temperature [Hindell *et al.*, 1991]. The daily sea temperature/depth profiles were matched with detailed oceanographic temperature data for the Southern Ocean to estimate foraging location. Although there were important differences in foraging location between the sexes, the primary foraging areas of the instrumented adult animals were located in the cold Antarctic waters. Data from 5 post-breeding males suggested three

Fig. 5. Map of the South Atlantic showing the movements of three post-breeding female southern elephant seals in relation to the continental shelf. Seals 1, 2 and 3 were tracked for 70, 17 and 20 days providing an average of 9.3, 3.5, and 6.2 valid locations per day [from McConnell *et al.*, 1992].

foraging regions close to the Antarctic continent. Subsequent data from satellite telemetry were consistent with estimations from depth/temperature profiles [Slip *et al.*, 1994]. A study on southern elephant seals used a time-depth recorder that incorporated data on water column temperature [Boyd and Arnborn, 1991]. This elephant seal was observed to rapidly descend to the discontinuity between cold surface water and the warmer deep water. The animal spent a substantial amount of its time (57%) at or near the thermocline indicating the likelihood that it was foraging there. Further, the structure of the water mass indicated that the animal was foraging south of the Antarctic Polar Front. Ultimately marine mammal distribution, abundance and behavior is related to the oceanographic factors that either aggregate or otherwise determine prey distribution. Our understanding of this relationship is limited and is thus a fertile area for investigation.

Although the diving pattern of southern elephant seals has been well described using recoverable time depths recorders [Hindell *et al.*, 1991; Boyd and Arnborn, 1991], until recently there was little information on specific foraging locations. Using ARGOS linked satellite tags, McConnell *et al.* [1992] recorded diving and traveling patterns of elephant seal females tagged at South Georgia Island in the South Atlantic (Figure 5). Regardless of the direction of travel, all animals traversed deep water prior to the initiation of "foraging" dives, apparently in an effort to feed in areas associated with hydrographic features where prey might be concentrated. One female swam southwest 1845 km in 23 days to Livingston Island, where she hauled out for 18 hours, and then traveled an additional 805 km to the southwest following the

continental shelf margin of the Antarctic Peninsula to a location of an underwater canyon 110 km west of Adelaide Island. Once there she initiated a series of dives to the bottom (300–400 m) which were consistent with presumed feeding. Prolonged transits to important foraging areas (associated with the Antarctic Polar Front, continental shelf or ice edge) are consistent with estimates inferred from sea surface temperature measurements for elephant seals tagged on Macquarie Island [Hindell *et al.*, 1991].

Elephant seal physiology and reproductive biology are ideally suited for utilization of distant prey resources [Costa, 1993b]. These satellite data suggest that utilization of distant prey resources associated with relocatable hydrographic and geomorphological features, such as the Antarctic Polar Front and the continental shelf where prey is reliably concentrated [Comiso *et al.*, 1993], is a more optimal foraging pattern than looking for prey patches nearer the breeding site [McConnell *et al.*, 1992]. However, recent data, acquired using light sensor geolocation determinations with southern elephant seals foraging from Patagonia, Argentina, suggests that animals from this population forage due east of the colony in the South Atlantic Ocean, not near, in or south of the Antarctic Polar Front [Campagna *et al.*, 1995]. This rookery is also the only one to show significant population increases, while most stocks associated with sub-tropical islands are declining [Laws, 1994]. The total population estimate of southern elephant seals in 1990 was 664,000 [Laws, 1994]. As over two-thirds of this population are from stocks associated with South Georgia or Macquarie Island, it is possible that a significant proportion of the adult population is foraging in cold Antarctic waters.

Elephant seals' large size, high energy storage capacity, low at-sea energy expenditure, and ability to fast while breeding, may enable them to utilize foraging areas distant from breeding grounds, where prey is associated with reliable oceanographic features [Costa, 1991; Le Boeuf *et al.*, 1993]. Analysis of stomach contents have suggested that elephant seals feed predominantly on cephalopods [Clark and Macleod, 1982], although some records of diving behavior have suggested feeding on benthic or demersal prey [Fedak, 1994].

2.8. Antarctic Fur Seal

Over 95% of Antarctic fur seals haul out to breed on South Georgia Island, with very small populations occurring elsewhere [Doidge *et al.*, 1986]. The breeding range of this species is restricted to islands south of the Antarctic Convergence and north of about 65°S [Bonner, 1981]. Antarctic fur seals have made a dramatic comeback from near extinction due to human exploitation. Mean annual population growth rate was 16.8% between 1958 and 1972 [Payne, 1977]. Since this period of population expansion, the annual increase has declined to 9.8% between 1976 and 1990 [Boyd,

1993]. Total population size was estimated at around 1.5 million seals [Boyd, 1993].

Antarctic fur seals feed primarily on krill, particularly *Euphasia superba* [Doidge and Croxall, 1985]. This prey preference has played an important role in the rapid recovery of fur seals, as until recently (1983-84) the population has not been food limited in the summer [Doidge et al., 1984; Costa et al., 1989; Croxall et al., 1988]. During winter at South Georgia, mainly adult and sub-adult fur seals ate only krill (28%), krill and fish (35%), or only fish (37%) [Reid, 1995]. Fur seals are tied to shore for breeding and rely on the availability of nearby prey resources to produce milk to provision the young. Female fur seals must optimize the time they spend feeding at-sea to the time spent nursing the pup onshore [Costa et al., 1989; Costa, 1991a,b; Lunn et al., 1993]. Movements into the Southern Ocean for foraging can be estimated from diving behavior and assumed swimming speeds [Kooyman et al., 1986]. These calculations suggest a maximum range from the breeding colony of 150 km from the continental shelf, for a 4- or 5-day foraging trip from South Georgia Island. Whereas, VHF transmitters used to track a radio-tagged fur seal foraging from Seal Island indicated a maximum distance of 240 km [Bengston et al., 1991]. Although we have considerable information about this species during the summer breeding season, almost nothing is known about its distribution and foraging ecology in the Southern Ocean during the winter months.

Coordination of data on diving pattern with information on prey species indicates that prey size, behavior, and energy content influence the foraging pattern [Costa, 1991a,b]. Fur seals made most (75%) of their dives at night and these were consistently shallower (dive depth <30 m) than dives during the daytime (mostly 40-75 m) [Croxall et al., 1985; Boyd and Croxall, 1992]. This pattern closely followed the vertical distribution of krill, which during daylight hours was below a depth of 50 m and at night was present in substantial quantities above 50 m. 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 depths, since this is when krill are most efficiently obtained.

The almost total dependence on krill as a food resource during the breeding season results in a tight coupling of the reproductive success of Antarctic fur seals with local krill availability. In the winter and summer of 1983, oceanographic anomalies reduced krill biomass, resulting in very poor reproductive performance of krill-eating penguins, albatrosses, and fur seals [Croxall et al., 1988b]. By the next summer krill were again abundant, and off-spring production and survival for seabirds and seals were typical of average values for 1975-86. Similar 'poor krill' years occurred in 90/91 and 93/94. Data on the energetics of female fur seals foraging during a year when krill availability was low (1983/84) versus a more normal season (1984/85) provide information on how female at-sea energy expenditure changed in

relation to food availability [Costa et al., 1989]. Female fur seals apparently stay at sea long enough to replenish their own reserves expended while fasting ashore and to acquire enough nutrients for milk production. In 1983-84, these needs apparently required foraging trips of twice normal duration. Interestingly, there was no difference in the mean costs of foraging between seasons (1983/84), suggesting that female fur seals were working near maximal rates during both seasons. The at-sea energy expenditure of individual fur seal females was quite variable within seasons indicating substantial variation in the effort of individual females during any given season. This is noteworthy since several females carried out trips of normal duration even during krill poor years [Costa et al., 1989]. Such variation in individual foraging costs may be related to individual differences in diving pattern. Boyd et al. [1994] found that some fur seals exhibited foraging patterns that emphasized shallow rather than deep diving bouts, while others showed the opposite tendency. One of the most intensive examinations of the foraging behavior of a marine mammal to date, recorded the behavior of 75 individual females over 5 reproductive seasons and provides insight into how females modify their foraging activities in response to changes in prey availability [Boyd et al., 1994]. During a period of poor krill availability (1990/91) females increased the time spent foraging, increased the amount of activity while at sea and a greater proportion of their dives were deeper. Interestingly, the worst reproductive performance was observed in seasons after El Niño events (1977/78, 1983/84, 1990/91). Although Boyd et al. [1994] were able to measure differences in foraging activity between seasons it appears that the ability of Antarctic fur seal females to substantially modify their foraging intensity may be limited compared to other fur seals and sea lions. Antarctic fur seals feeding on krill possess one of the highest at-sea metabolic rates and they spend considerably more of their time at-sea diving than other species examined to date [Costa et al., 1989; Costa, 1991]. In response to variations in local prey resources other fur seal and sea lions may choose different prey or may have greater flexibility in their time-activity budgets than do Antarctic fur seals. If Antarctic fur seals normally operate closer to their metabolic maximum than other fur seals, they may not be able to sufficiently modify their foraging intensity to preclude increasing trip duration during years when prey resources are depleted. Measurements of foraging behavior and energetics in locations or times of year where fur seal females feed on other prey (i.e., Seal Island where late in the season females may feed on fish) would provide insight into this question. Regardless of the interpretation, all of these studies support the concept that foraging trip duration is a sensitive index of local resource conditions in lactating Antarctic fur seals.

Variation in trip duration has profound effects on the rate of milk delivery and thus growth rate of suckling pups. Measurements of milk intake during a resource poor year

Fig. 6. Relationship between estimates of growth rates of male (closed circles) and female (open circles) pups at Main Bay and mean duration of foraging trips of females at a nearby study beach at Bird Island, South Georgia. Numbers above the symbols are the last two digits of the austral summer [from Lunn *et al.*, 1993].

(1983/83) compared to a resource normal year (1984/85) were quite variable but indicated that on average females delivered similar amounts of milk to their pups independent of time spent foraging at-sea. In resource poor years, females made fewer visits to their pups and thus pups received less milk and exhibited significantly lower growth rates [Costa and Croxall, 1988]. Analysis of long term data on duration of female foraging trips, growth rate, and weaning mass and pup survival of Antarctic fur seals measured over the period 1976-87 showed considerable variation associated with variations in krill availability [Croxall *et al.*, 1988]. Lunn and Boyd [1993] found that the effects of a varying food supply extend beyond one breeding season. Following a season of poor prey availability, females gave birth later in the breeding season and fewer pups were born. Lunn *et al.* [1993] examined the relationship between maternal characteristics (trip duration, number of trips) and pup growth rate and weaning mass. They found that there was no relationship between maternal characteristics and pup growth when prey resources were locally abundant. However, during years when resources were less available, mean foraging trip duration was negatively correlated with pup growth. From data on pup growth rate collected over a 20 year period they found periodic fluctuations in pup growth that coincided with periods of low food availability (Figure 6). Finally, Boyd and Roberts [1993] examined the variation in thickness of growth layers in the dentine of fur seal teeth and found that this provided a retrospective look at fur seal responses

to annual variations in prey availability. There was a high correlation between the thickness of annual dentine layers and the Southern Oscillation Index (SOI) (Figure 7). The dentine layers were thinnest during 1968/69, 1983/84 and thickest during 1976/77, 1981/82, 1984/85. The years with thin dentine layers corresponded to periods of low krill availability, and thick dentine layers years with high krill availability. This technique could be used to examine periodic fluctuations in krill availability in other places or time periods where teeth can be obtained. As fur seals were harvested over many years and skulls and teeth are often kept in museums or other repositories, there is a potential to use this technique to examine long time periods over large geographic areas.

2.9. Periodic Fluctuations in Phocid Populations

In contrast to the fur seals described above, seals are somewhat buffered from short term fluctuations in prey availability due to their unique reproductive pattern. In phocids, reproductive performance (maternal investment) during a given season reflects prey availability over the preceding year and represents the mothers' foraging activities over a much larger spatial and temporal scale than is the case for otariids [Stewart and Lavigne, 1982, Costa, 1993b, Trillmich and Ono, 1993]. It follows that the weaning mass of a phocid pup is an indicator of their mothers' foraging success over the previous year. The subsequent post-weaning survival of the pup is related to both its weaning mass (energy reserves provided by the mother) and the resources available to the pup after weaning. Variability in the numbers of individuals in ice-seal cohorts should provide an index of fluctuations in prey availability that correlate with oceanographic events on the scale of the maternal foraging range or foraging range of the weaned pup. Unfortunately, we know little about the foraging range of female seals prior to parturition and essentially nothing about the foraging range of weaned seal pups. Nonetheless, three of the pack-ice breeding seals have exhibited quasi-cyclic fluctuations in population processes. Strong cohorts are evident in the age structure of crabeater seals in the Antarctic peninsula at 4 or 5 year intervals [Bengston and Laws, 1985]. There is a seasonal cycle in the occurrence of leopard seals on sub-Antarctic islands which is probably related to the proximity of the pack-ice edge [Rounsevell and Eberhard, 1980]. The extent of the northward movement seems to be cyclic, with the largest numbers appearing at Macquarie Island every 4-5 years [Rounsevell, 1988]. Reproductive rate in Weddell seals at McMurdo exhibit 4-6 year fluctuations [Testa and Siniff, 1987]. Testa *et al.* [1991] compared these patterns to the SOI, a measure of the strength of El Niño-Southern Oscillation events. All three data sets exhibited some level of cyclic behavior with an approximate periodicity of 5 years. Weddell seals were generally in phase with SOI. Leopard seals were in phase with the SOI throughout the 1960's, but

Fig. 7. Mean ($\pm$ S.E) variation in the depth of annual dentine layers in teeth from that expected based on a linear model of declining layer depth fitted to the data for each tooth (solid line). Also shown is the Darwin-Tahiti sea level pressure anomalies or Southern Oscillation Index (SOI), expressed as a six month mean (dashed line). [from Boyd and Roberts, 1993]

the SOI subsequently proceeded the leopard seal pattern by about a quarter cycle. Associations between crabeater seals and SOI were more complicated, but suggested some similarities with the other data sets. These findings are significant in that they suggest large-scale oceanographic processes may dramatically impact population processes of ice-breeding seals and may be an important factor in the regulation of top predator populations in the Antarctic [Croxall and Rothery, 1991; Testa et al., 1991]. Obviously, there is a need to understand what oceanographic events are responsible for these fluctuations and to what geographic and time scale seals are responding.

3. CETACEANS

Much of what we know about cetacean distribution and biology comes from the whaling industry and observations from ship-based platforms of opportunity. Cetacean species occurring in the Southern Ocean are more widely distributed and none are exclusive to the region. An overview of their biology was presented by Brown and Lockyer [1984]. Of the six species of mysticete whales, five are rorquals (family Balaenopteridae) found in separate populations in both the northern and southern hemispheres, with the remaining species being the southern right whale (family Blaeuinae). The Balaenopteridae undergo extensive latitudinal migrations as does, to a lesser extent, the southern right whale. Only eight

of the 42 odontocete species found in the southern hemisphere frequent the waters south of the Antarctic convergence [Nishiwaki, 1977].

3.1. Mysticeti

Mysticete whales are highly migratory and thus are seasonally abundant in the Southern Ocean. All five species of rorquals or balaenopterid whales breed in warm, temperate, sub-tropical or tropical waters in winter and feed in cold temperate and polar waters in summer. It is believed that most if not all of the food requirements of these whales are met during the brief summer feeding season. This includes the energy required to give birth and suckle the calf until the mother returns to the summer feeding grounds with the calf the following season. These species feed on krill, *Euphasia superba*, and other planktonic crustaceans which are primarily concentrated in Antarctic and cold temperate waters in the southern hemisphere. During non-feeding periods, whales obtain energy from fat reserves laid down in the summer. The most extensively studied species is the humpback whale (*Megaptera novaeangliae*), in terms of seasonal distribution and migratory patterns. There is clear temporal segregation of different age classes and sexes, with the different classes becoming intermixed on the Antarctic feeding grounds [Brown and Lockyer, 1984]. Blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales are seen at all longi-

Fig. 8. Comparison of the zones occupied by selected species of krill and marine mammals from the Antarctic Continent northward. Range presented is the approximate average latitudinal range. Shaded area indicates higher densities [modified from Laws, 1977].

tudes but appear to concentrate in specific areas. Sei whales (*Balaenoptera borealis*) also move into the Southern ocean to feed. This migration begins slightly later than blue or fin whales and does not progress as deeply into the high latitudes [Budylenko, 1978]. Minke whales (*Balaenoptera acutorostrata*) exhibit a circumpolar distribution in the Southern Ocean during summer, with concentrations in the Atlantic, Indian, and southwest Pacific sectors [Arsenev, 1960; Ohsumi, 1970; Brown and Lockyer, 1984]. Most individuals are south of the Antarctic convergence with highest densities close to the ice-edge. The pygmy blue whale (*Balaenoptera musculus breviceauda*) does not move very deeply into Antarctic waters and is generally found north of the Antarctic convergence between 40°S and 55°S latitude [Ichihara, 1966].

The migration of southern right whales is considerably less extensive, with mating in the southwest Pacific as far south as Campbell Island. Stocks in the southeast Atlantic and southwest Indian Oceans breed in winter in latitudes between 20°S and 30°S. Southern right whales appear to be distributed primarily between 40° and 50°S latitude in the summer, and are rarely seen south of the Antarctic convergence [Omura et al., 1969].

3.2. Odontocetes

Nishiwaki [1977] described the approximate southern boundaries of odontocetes in Antarctic waters. Little information is available about the biology of these species. Juvenile and female sperm whales (*Physeter macrocephalus*) do not generally move south of the sub-tropical convergence,

or below 45-50°S in the southwest Pacific and Indian Oceans, yet adult males can occur south of this limit. Arnoux's beaked whale (*Berardius arnuxii*) and the southern bottlenose whale (*Hyperoodon planifrons*) both have circumpolar distributions and have been found at latitudes as high as the ice edge [Brown and Lockyer, 1984]. The killer whale (*Orcinus orca*) is found throughout Antarctic waters. Killer whales prey on seals and penguins, and their distribution is therefore affected by seasonal abundance of elephant seals and penguins associated with sub-Antarctic islands [Condy et al., 1978].

Published records of pelagic sightings of the remaining Southern Ocean odontocetes, Commerson's dolphin (*Cephalorhynchus commersonii*); hourglass dolphin (*Lagenorhynchus cruciger*); long-finned pilot whale (*Globicephala maculata*); and spectacled porpoise (*Phocoena diotrica*), in Antarctic waters are more rare and summarized by Brown and Lockyer [1984]. Commerson's dolphin has been observed from South Georgia and Kerguelen Island. The hourglass dolphin has a circumpolar distribution in Antarctic waters. The long-finned pilot whale is rarely seen but specimens have been collected at Kerguelen Island. Very few records of the spectacled porpoise exist. Baker [1977] suggests a circumpolar sub-Antarctic distribution for this species.

4. ECOLOGICAL SEPARATION OF MARINE MAMMALS

Breeding behavior, geographical distribution, foraging behavior, diving ability, and habitat preferences all contribute to the ecological separation of the previously discussed species (Figure 8). The degree of ecological separation appears to be quite high among the seal species discussed, with resultant reduced competition. Differences in habitat preferences (fast-ice, pack-ice, or land), and foraging depths (shallow vs. deep divers) contribute to three-dimensional separation. This separation is also related to prey choices. Shallow divers (crabeater, leopard, and fur seals) are for the most part krill-feeders. While deep-divers (Weddell, elephant, and Ross seals) feed for the most part on fish and squid. Within these groups, differential preferences and geographical separation further reduce competition. Despite these factors there is still significant overlap, particularly between crabeater and leopard seals.

All baleen whales foraging south of the Antarctic Convergence are in potential competition with seals and penguins for krill. This interspecies competition is reduced considerably by variation in peak arrival times and the degree of penetration into polar waters. Blue whales arrive in December and tend to feed on first year krill (20 to 30 mm), around one month in advance of fin whales, which tend to feed on second-year krill (30 to 40 mm) [Figure 8; Laws, 1977; Lockyer, 1981]. Peak arrival of sei whales occurs three months later in March and sei whales feed predomi-

nately on copepods, such as *Calanus tonsus*, *Calanus similimus*, *Drepanopus pectinatus*, *Euphausia valentini*, *Euphausia superba* and *Parathemisto gaudicahudi*, [Laws, 1977]. Minke whales move much further south than any of the other species and they tend to feed on even smaller krill (10-20 mm) [Laws, 1977; Masaki, 1977; Masaki and Yamura, 1978]. Blue and minke whales have been observed feeding on *Euphausia crystallorophias* over the continental shelf [Laws, 1977]. Humpback, blue and fin whales are farther north, but south of the Antarctic Convergence. Sei and southern right whales are usually found north of the Antarctic Convergence. As most of these data were derived from research carried out in association with commercial whaling, there is little recent information. However, application of satellite telemetry and acoustic tracking methods could significantly improve our understanding of the foraging ecology of Southern Ocean whales.

Similarly, other vertebrates and invertebrates which feed on krill are also in potential competition. Therefore, krill-eating seals might be in competition with baleen whales and penguins. However, it is likely that the size of the krill patch utilized and its distance from shore is distinct for the pinnipeds, penguins and cetaceans. For example, during the breeding season birds and fur seals have a limited foraging range since they must return to feed their young waiting onshore. Breeding sites are therefore limited to islands or continental regions with a oceanographic regime that ensures an abundant and predictable supply of krill throughout the breeding season [Croll *et al.*, submitted]. Furthermore, since these animals are long lived and show high degrees of site fidelity, krill availability must be reliable over time scale of many years to decades. The patch size is important because the absolute food requirements of birds, fur seals, seals and cetaceans is very different. For example, breeding adult Chinstrap, Adélie or Gentoo penguins consume between 130 and 160 kg during the breeding season, whereas a female fur seal must consume 917 kg of krill, whereas a blue whale consumes this much krill in a day [Croll, submitted]. It then follows that a penguin can feed on smaller krill patches than a fur seal and a fur seal can utilize considerably smaller krill patches than would be required by a blue whale. An additional ecological separation exists when we consider that krill-eating seals tend to be associated with the pack-ice, while baleen whales and penguins are more northerly distributed, feed away from the pack-ice and forage at different depths [Laws, 1984]. Fish and squid eating groups, like penguins and odontocetes, might compete with elephant, Ross, and Weddell seals.

5. FUTURE RESEARCH OPPORTUNITIES

An area that has received little attention with respect to southern ocean whales is the role of their low frequency vocalizations (blue and fin whales produce calls around 20

Hz with energy up to 100 Hz) [Cummings and Thompson, 1971; Scheville and Watkins, 1972; Watkins, 1981; Edds, 1982]. Low frequency sounds travel tremendous distances in the ocean, and, therefore, any animal that produces a low frequency signal can be heard from considerable distances. A typical low frequency blue whale vocalization could allow a whale to "communicate" to another whale, or receive information about its environment on an ocean basin scale [Costa, 1993a]. It is possible that these calls are used to locate oceanographic features such as bottom topography or density gradients that concentrate prey or even to locate large prey swarms. Researchers have used the sounds made by whales to track and/or assess the populations of bowhead, minke, fin, blue, and sperm whales [Clark *et al.*, 1986; Nishimura and Conlon, 1993; Leaper *et al.*, 1992]. The low frequency characteristics and duration of many baleen whale calls make their calls ideal for tracking with large aperture hydrophone arrays [McDonald *et al.*, 1995]. Since individual animals may have unique characteristics or signatures to their calls, we should be able to follow the acoustic behavior of individuals. For example, Chris Clark of Cornell University and Lt. Chuck Gagnon of the U.S. Navy tracked the movements of a single blue whale around Bermuda Island for 43 days covering over 1700 km [Nishimura and Conlon, 1993]. Unfortunately, the bottom mounted hydrophone arrays that were used in this study do not exist in the Southern Ocean. However, smaller scale hydrophone arrays, as have been used to track bowhead whales in the Arctic and Weddell seals in the Antarctic, could be employed or long aperture arrays could be towed behind research vessels to attain this information. Such approaches could provide significant information on ocean scale movements of whales, insights into how marine mammals use low frequency signals, and how they respond to acoustic disturbances in their environment.

Recoverable data loggers, satellite tags, molecular probes and acoustic tracking methods are providing an unprecedented insight into the open ocean ecology and population structure of marine mammals [Wartzok *et al.*, 1992a,b; Clark *et al.*, 1986; Spiesberger and Fristrup, 1990; Costa, 1993a; Amos, 1993; Boness *et al.*, 1993; Hoelzel, 1993]. However, proper interpretation of these data will require incorporation of information on ocean structure and prey distribution. Although marine mammals have been observed in association with oceanographic features such as bottom topography, frontal systems, and thermocline depth [Hui, 1979, 1985; Winn *et al.*, 1986; Reilly, 1990; Ainley and DeMaster, 1990; Mullin *et al.*, 1991; Boyd and Arnborn, 1991; Mate *et al.*, 1992; van Franeker, 1992; Whitehead *et al.*, 1992; Kenney *et al.*, 1995], this association is not well understood. A better understanding would be achieved if we knew what aspects of ocean structure are correlated with specific behaviors and the level of dependence of marine mammals on these oceanographic features to concentrate prey. It would also be valuable to know how marine mammals locate their prey, the

foraging strategies employed and how marine mammals optimize these strategies to respond seasonal and annual fluctuations in prey.

A large multinational 5 year effort to study Antarctic Pack Ice Seals as indicators of environmental change and contributors to carbon flux is currently being planned [Anonymous, 1995]. This program was initiated by the SCAR Group of Specialists on Seals to promote studies on the status of Antarctic pack ice seal populations and the role they play in Antarctic marine ecosystems. In the case of the large whales it would be interesting to know if they use low frequency sound to locate the prey or the oceanographic features that concentrate them. A promising approach would be to coordinate data collected with satellite tags and/or recoverable data loggers on the physical environment (e.g., ambient acoustic environment, water temperature and salinity profiles) with simultaneous collection of data on behavior (diving pattern, swim speed, physiological status, etc.). Such information could then be integrated with satellite remote sensing observations of large-scale oceanographic features such as squirts, jets, warm core rings, eddies, etc. [Comiso et al., 1993]. Simultaneous measurements of marine mammal diving behavior and prey distribution using active acoustic methods [Peiper and Holliday, 1984; Greene and Wiebe, 1990; Macaulay et al., 1995; Croll et al., submitted] would provide information on prey abundance and distribution, which would give considerable insight into the foraging strategies employed by marine mammals. A variety of new tools are providing an unique opportunity to understand the ecology and biology of marine mammals in the context of the biological and physical oceanographic of the Southern Ocean.

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