Northern fur seals: Why have they declined?

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Abstract

A high mortality of juvenile and adult female northern fur seals (*Callorhinus ursinus*) is believed to be responsible for the most recent decline of the Pribilof population which began in the early 1970s. The two most likely explanations for the high mortality rates are related to 1) commercial fishing of major fur seal prey species in the Bering Sea and Gulf of Alaska, and 2) entrapment of seals in lost and discarded fishing gear. A review of the entanglement hypothesis found many of the assertions made about the extent of entanglement mortality were poorly supported by the available data and were inconsistent with the dynamics of other pinniped populations. The build up of commercial fishing is consistent with the timing of the fur seal decline, but studies of growth (lengths and weights of pups, subadults and adults) and the duration of foraging trips by lactating mothers suggest per capita increases in food abundance. These fur seal observations suggest food resources in the spring are sufficient to meet the needs of the currently low population as the seals migrate north through the coastal waters of British Columbia and Alaska. However, the data are also consistent with the view that per capita fish abundance is insufficient for young fur seals during the fall migration as the seals swim south through the Aleutian archipelago. It is hypothesized that reduced food availability for young fur seals in the Gulf of Alaska during this stage of the seal's life cycle creates a bottleneck for the entire population, which can account for the decline of the Pribilof herd. This possibility is supported by the sharp decline in numbers of Steller sea lions and harbour seals along the Alaskan panhandle.

Introduction

The Pribilof population of northern fur seals (*Callorhinus ursinus*), breeding on the islands of St Paul and St George, is believed to have numbered 3 million animals when Alaska was purchased in 1867 (Lander and Kajimura 1982). But excessive harvests on land, combined with inefficient hunting of seals at sea, subsequently reduced the population, such that by 1910, only 200 000 to 300 000 seals remained (Kenyon *et al.*, 1954; Lander and Kajimura 1982).

A moratorium on pelagic hunting and a carefully regulated harvest of subadult males on land reversed the downward trend of the Pribilof fur seal (Fig. 1; Roppel 1984; Scheffer *et al.*, 1984). However, population growth slowed during the 1940s as the population approached 1.5 million animals (Kenyon *et al.*, 1954; Lander and Kajimura 1982). Biologists believed the reduced rate of population growth was due to reduced rates of reproduction (Kenyon *et al.*, 1954) and lower juvenile survival (Chapman 1961; NPFSC 1962) arising from competition for limited food around the Pribilof Islands. They felt the herd would be more productive and would produce a larger male harvest if the population were smaller (Nagasaki 1961; Chapman 1961). Thus, 315 000 females were killed between 1956 and 1968 (Lander 1980a).

There has been a long-term downward trend in the size of the Pribilof population since the mid 1950s (Fig. 1). On St George Island, pup production has declined by 6% per year since 1973 (York 1990). On St Paul, pup production declined 7% per year from 1975 to 1983, and has shown no significant trend since 1984 (York 1990).

Mathematical models conclude that commercial harvesting of females and a series of years of poor juvenile survival rates can explain the population decline from 1950 to 1970 (Eberhardt 1981; York and Hartley 1981; Trites and Larkin 1989). The most recent decline, 1975 to 1984, appears to be due to a high mortality of juveniles and adult females (Trites and Larkin 1989). The mortality of adult females may have increased by 2–5% beginning in the mid 1970s. Mortality of juveniles (birth to age 2 years) increased in 1971 and appears to have maintained a constant elevated level of about 70% ever since (Trites 1989). The failure of the Pribilof population to recover since the mid 1980s may be due to high rates of juvenile mortality.

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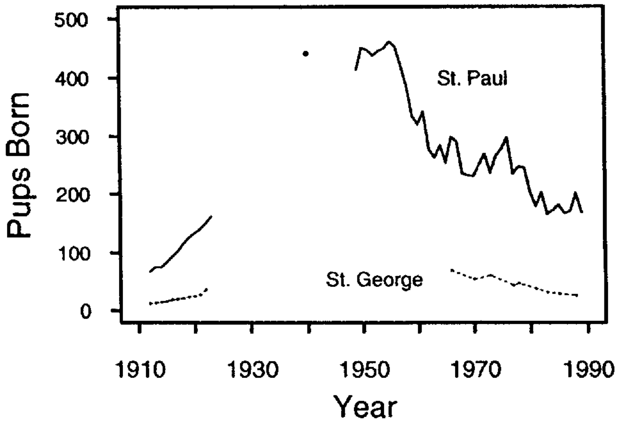

Figure 1. Numbers of fur seal pups born on St Paul and St George islands from 1911 to 1989 (in thousands). The data are an index of population abundance and are taken from Lander (1980a), Trites (1989), Antonelis *et al.* (1990), and York and Antonelis (1990).

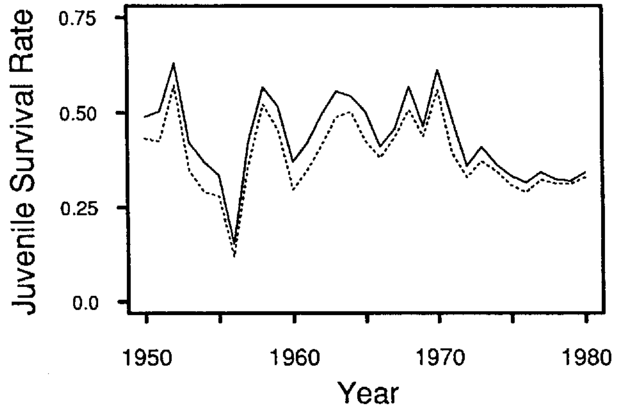

Figure 2. Survival rates of juvenile male northern fur seals from birth till their return to land 2 years later (dashed line) and from weaning (age 4 months) until 2 y (solid line). From Trites (1989).

Simulation results indicate that the size of the northern fur seal population can remain stable when 40% of the juveniles survive their first two years of life (Trites and Larkin 1989). Estimates of juvenile survival rates varied considerably from 1950 to 1970 (Fig. 2). However, since 1971 the expected natural variation in juvenile survival rates has been virtually absent. This might indicate a response to exogenous factors.

The two most likely explanations for the increases in fur seal mortality rates are commercial overfishing of fur seal food in the Bering Sea and Gulf of Alaska, and increased mortality caused by entrapment in lost and discarded fishing debris. The entanglement hypothesis has received considerable attention over the past decade, but has never been critically evaluated, while the reduced food hypothesis has generally been dismissed as the cause of the fur seal decline (see Fowler 1986).

In this review I re-assess these two hypotheses and present a third, the 'bottleneck hypothesis', which is a refinement of the food hypothesis. I show how this new hypothesis is consistent with the available fur seal data as well as with the condition of other pinniped species breeding in the Bering Sea and Gulf of Alaska. I conclude by outlining some directions for future research that may offer further insight into the dynamics of the Pribilof fur seal.

Entanglement-Related Mortality

Commercial fishing might be contributing to the decline of the population through the accumulation of lost and discarded fishing debris at sea which is entrapping and killing fur seals. Since the 1930s, small numbers of fur seals have been observed in the commercial male harvest with bits of netting around their necks and shoulders (Scheffer 1950; Fiscus and Kozloff 1972). The incidence of entangled males in the harvest increased during the 1960s and 1970s as commercial fisheries expanded in the Bering Sea. This was also during the same period of time that the fishing industry switched to synthetic fibers which did not sink or rot (Uchida 1985).

The observed rate of entanglement over the past three decades has been low, but variable. Less than 1% of the male fur seals taken in the commercial harvest on St Paul Island from 1967 to 1985 were entangled in debris (Scordino and Fisher 1983; Scordino 1985; Fowler 1987). The average has been about 0.40% or 104 individuals per year based on the average annual harvest of 26 000 seals from 1967–81. The incidence of entanglement went from a low of 0.15% in 1967 to a high of 0.72% in 1975. The rate of observed entanglement dropped sharply in 1976 and was relatively stable at 0.41% until 1986. The estimated entanglement rate in 1988 and 1989 was approximately 0.30% (Fowler and Ragen 1990). Two-thirds of the debris observed on seals ashore is trawl net fragments. The remaining third is mostly packing bands (Fowler 1987).

Northern fur seals have a high probability of encountering floating debris while feeding and migrating. Ocean surveys indicate that a seal migrating 8000 km will encounter 3 to 14 pieces of trawl debris over the course of a year (Fowler 1987). The mesh size of 30% of this debris is of sufficient size to entrap a seal and cause death from strangulation, starvation, infection, severed carotid arteries, drowning, or combined effects (Fowler 1987). Few fur seals are observed to die in actively fished trawl gear (Loughlin *et al.*, 1983), but many are believed to be victims of discarded floating debris.

Fowler (1985a,b, 1987) attributed the decline of the Pribilof population to a high mortality of young animals caused by debris entanglement. He estimated that 15.5% of fur seals became entangled in their first few months at sea and subsequently died. This mortality estimate $[0.003/(0.20*0.46^3)=0.155]$ was extrapolated from the proportion of 3 y olds in the harvest entangled in small net fragments (0.003), the proportion of pelagic debris consisting of small net fragments (0.20), and the probability of an entangled animal surviving for 3 years (0.46^3).

Field observations and correlations between entanglement rates and population parameters (survival rates, bull counts and pup estimates) have been put forward in support of the entanglement hypothesis (Fowler 1985a,b, 1987). However, a number of questions might be raised.

In support of the entanglement hypothesis, Fowler (1985a) found a correlation between the mean change in pup numbers and the rate of entanglement 6 years earlier, thereby suggesting that young females died at sea from entanglement and did not mature to breeding age. The 6-year lag was justified as the time required for a female pup to reach sexual maturity. However, studies of reproductive biology indicate that some females begin reproducing as early as 3 years-old with the most substantial contribution of a year class to production beginning at age 5 and continuing through to age 13 (Lander 1981; Trites 1990). Simulation studies further indicate that the mortality of young females could not by itself explain the drop in pup production observed from the mid 1970s to the mid 1980s (Trites and Larkin 1989). Thus the 6-year lag seems to be an unlikely explanation for the correlation.

Another tenet of the entanglement hypothesis is that young fur seals are more susceptible to entanglement than older animals. This is based on the age composition of entangled versus non-entangled males in the 1982 harvest, and is supported by captive studies (Fowler 1985a, 1987). The captive studies showed 'younger animals (mostly females) become entangled more often than older males' (Fowler 1985a, p. 298). But the entanglement study done at Izo Mito Oceanarium in Japan by Yoshida *et al.* (1985) only used 22 animals, of which 2 were young (1 male and 1 female) and 20 were adults (2 males and 18 females). The fact that both of the young and seven of the adult females became entangled is not significant. The sample size and age composition are invalid to support an inference concerning differential mortality of young.

Fowler (1985a) further reported that the age distribution of entangled males was significantly different in 1982 from the age distribution of animals harvested with no debris. There were more entangled males aged 2, 4, 5, and 6 years old than expected, but fewer 3 year olds. However, this difference in age distribution is biased by the inclusion of the entangled 6 year olds. Most of the 6 year olds were killed because of the debris on them, even though they exceeded the size limits imposed on the harvest[1] (Scordino and Fisher 1983). Possibly some of the 5 year olds also fall into this category.

Using the data contained in Fowler (1985a), I tested the hypothesis that more young were entangled than older seals by comparing the frequency of entangled and unentangled 2 year olds harvested on St Paul with pooled samples of older animals (ages 3+4 and 3+4+5). In both cases the results were not significant when tested with the log-likelihood ratio or G test corrected for continuity (respectively $G_c=3.22$, $0.05<P<0.10$; $G_c=2.71$, $0.05<P<0.10$). If younger seals are not entangled more frequently than older seals, the mortality estimate associated with entanglement (15.5% of pups, Fowler 1985a) may be suspect.

All of the annual estimates of entanglement rates are for immature males only and tend to be biased upward. For many years the total number of entangled males in the harvest also included all those individuals killed for humane reasons, even though they exceeded the upper length limit of the commercial harvest (Scordino and Fisher 1983). There is also evidence that some of the entangled seals observed on land later escape from their debris (Scordino 1985, NPFSC 1985).

The male rates of entanglement may not apply equally to females. Observations of fur seals on the Pribilofs suggest less entanglement of breeding females than young males in the harvest (Bigg 1979a). Perhaps this is because fewer entangled females make it back to the rookeries or because much of the debris carried by the seals comes from the Bering Sea (Fowler 1982; Merrell 1980) where males spend proportionally more time than females during the pelagic phase of their life cycle; or perhaps the effect of female entanglement mortality is not large enough to be detected.

In view of the preceding difficulties, the conclusions drawn from the entanglement data require further investigation. No doubt large numbers of fur seals are dying unnecessarily in lost and discarded fishing gear. But it is unlikely that entanglement is causing the decline of the Pribilof population.

Commercial Fisheries

A second way that commercial fishing might be contributing to the decline of the fur seal population is by reducing the seal's food base, thereby causing starvation, reduced growth and lower productivity. Fish are caught commercially in four regions of the North Pacific Ocean: A. the eastern Bering Sea, B. the international waters of the Bering Sea, the 'donut

[1]only subadults males shorter than a specified length (tip of nose to base of tail) could be killed for commercial purposes.

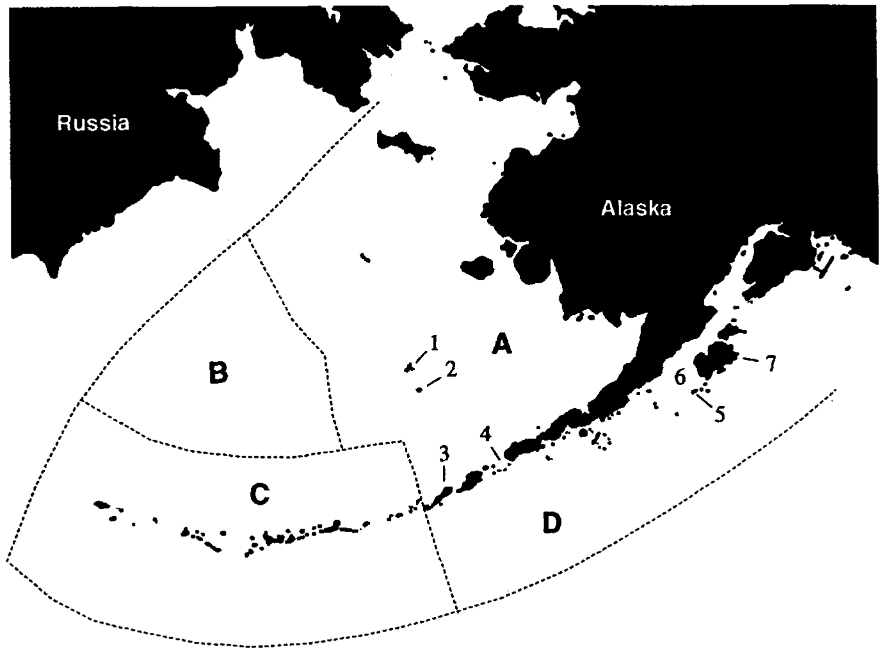

Figure 3. Four major fishing regions in the Bering Sea and Gulf of Alaska: *A*. eastern Bering Sea, *B*. the 'donut hole', *C*. Aleutian Islands region, and *D*. the Gulf of Alaska. Also identified are the Pribilof Islands (1. St Paul and 2. St George), 3. Bogoslof Island, 4. Unimak Pass, 5. Tugidak Island, 6. Shelikof Strait and 7. Kodiak Island.

hole', C. the Aleutian Islands region, and D. the Gulf of Alaska (see Fig. 3).

The first major commercial groundfish fishery in the Gulf of Alaska targeted Pacific Ocean perch (*Sebastes alutus*) in 1958 (see Fig. 4 and reviews by Megrey and Wespestad 1990, and Alverson 1991). The size of the catch rose quickly through the early 1960s until the resource was depleted (Bakkala *et al.*, 1981). The fishery then began targeting walleye pollock (*Theragra chalcogramma*). As happened with perch, the catch of pollock rose gradually through to 1980 when a large spawning aggregation was discovered in Shelikof Strait, west of Kodiak Island. Over the next 5 years the spawning aggregation was heavily exploited and the fishery peaked and collapsed. Some speculate that this spawning aggregation may have been the bulk of mature pollock in the Gulf of Alaska (see Lloyd and Davis 1989).

In the eastern Bering Sea (henceforth referred to as simply the Bering Sea), the commercial groundfish fishery targeted yellowfin sole (*Limanda aspera*) from 1954–61 until the stock declined due to overfishing (Bakkala *et al.*, 1979). At its peak in 1961, the total catch was 0.6 million metric tons (mt). As the yellowfin sole declined, the fishery moved to walleye pollock. The amount of pollock caught rose quickly through the late 1960s, peaking at 1.8 million mt in 1972 (Fig. 4). Since quotas were imposed in 1977, the pollock catch has slowly risen from 1.0 to 1.4 million mt y^{-1}, and currently represents about 78% of the groundfish catch in the Bering Sea (OCSEAP 1987; Bakkala and Low 1985; Ito and Balsiger 1983).

Catches of pollock in the Aleutian Islands region began in the 1980s near Bogoslof Island and Unimak Pass (Wespestad and Traynor 1990), but the amount of fish caught in the Aleutian region is small compared to the Bering Sea fishery. In recent years, a new pollock fishery has developed in the international waters (the 'donut hole'). The catch from this unregulated area is huge and exceeds the amount of fish caught in the Bering Sea (Wespestad and Traynor 1990). Concern has been expressed that this large reservoir of fish may be a mixture of several stocks including the Aleutian region and Bering Sea (Okada 1986; Hinkley 1987; Lloyd and Davis 1989; Wespestad and Traynor 1990).

The pollock fishery, like most fin-fisheries, appear to be sustained by one or two strong year classes that have occurred about once every eight years over the past three decades (Fig. 5). The large fluctuations in year class strength is believed to be related to starvation, predation and the transport of larvae to unfavourable nursery areas (Bailey *et al.*, 1986; Bakkala 1989), which may be a function of water temperature and solar activity (Bulatov 1989).

In contrast to the pollock fishery, which is currently the largest single species fishery in the world, commercial catches of pelagic species in the Bering Sea and Gulf of Alaska are small (OCSEAP 1987). In recent times, the largest pelagic fishery in the Gulf of Alaska targeted Pacific herring (*Clupea harengus*

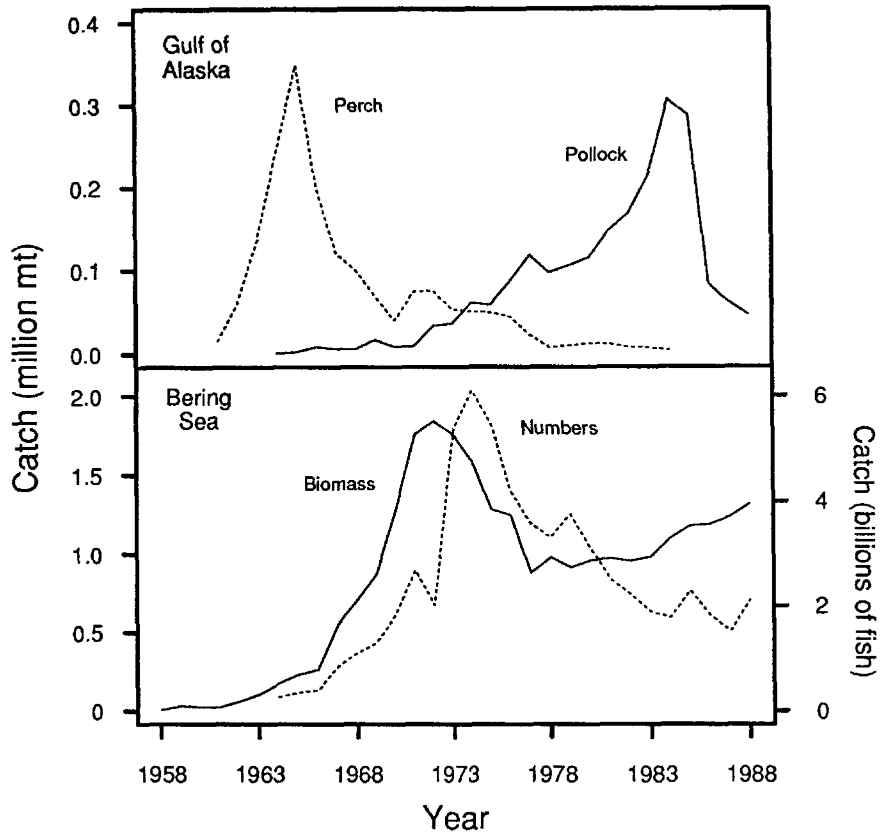

Figure 4. Commercial catch of walleye pollock and Pacific ocean perch in the Gulf of Alaska and Bering Sea. The biomass of perch and pollock shown in the top panel are from OCSEAP (1987) and Megrey (1989). In the bottom panel, the biomass and numbers of pollock caught are from Wespestad and Traynor (1990).

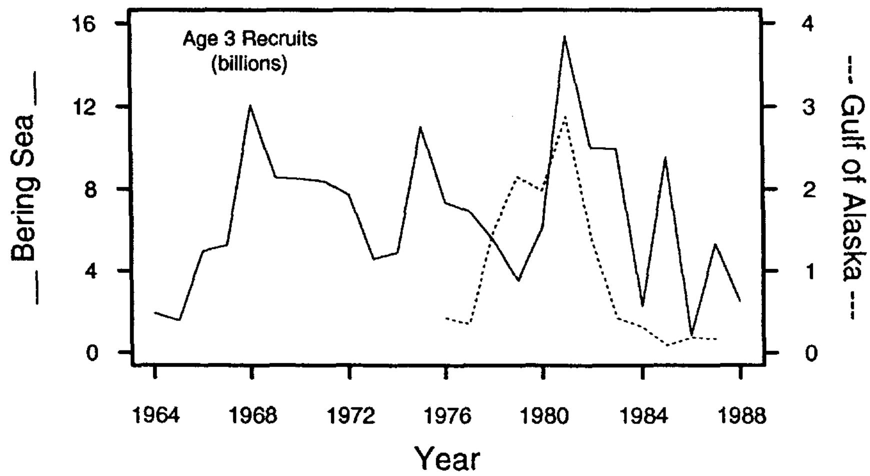

Figure 5. Estimated numbers of 3 year old walleye pollock in the eastern Bering Sea (solid line) and Gulf of Alaska (dashed line). Data are in billions of fish and are from Lloyd and Davis (1989) and Wespestad and Traynor (1990).

pallasi), peaking at 0.13 million mt in 1970. Catches since 1971 have been low, suggesting the stock is depleted (Skrade 1980). New fisheries may be developed to catch other pelagic species that are currently under-exploited in the North Pacific. Some candidates are Capelin (*Mallotus villosus*), Sandlance

Table 1. Abundance and seal diet composition estimates for major fish species in the Bering Sea and Gulf of Alaska. The maximum annual commercial catch and estimated equilibrium biomass of the fish stocks are in metric tons [from Laevastu and Livingston 1980]. The proportion of the fur seal diet consisting of each species from July to September was determined by the percent modified volume method and represents the diet in 1960, 1962, 1968 (Gulf of Alaska) and in 1960, 1962–64, 1968, 1973–74 (Bering Sea) [from Perez and Bigg 1981].

			% of Fur Seal Diet	
Species	Equilibrium Biomass	Maximum Annual Catch	Bering Sea	Gulf of Alaska
Walleye Pollock	9 210 000	1 800 000	38.1	0.8
Cottids (Sculpins, . . .)	4 120 000	—	0.0	0.0
Capelin, Sandlance, other smelts	3 500 000	—	19.0	42.2
Flatfish (Yellow fin sole, . . .)	2 120 000	900 000	0.9	<0.1
Pacific Herring	1 970 000	132 000	4.5	18.4
Pacific Ocean Perch	1 630 000	628 000	<0.1	<0.1
Squids	1 270 000	—	34.1	8.7
Atka Mackerel	1 127 000	28 000	1.5	5.7
Sablefish (Blackcod)	130 000	20 000	0.3	16.5
Salmonids	—	—	1.5	7.6

(*Ammodytes hexapterus*), Mackerel (*Scomber japonicus*), Pomfret (*Brama japonica*), Grenadiers (Macrouridae), and squids (Trumble 1973).

Fur Seal Diet

Northern fur seals feed primarily on herring, capelin, sandlance, sablefish, pollock and squid in the northeast Pacific Ocean (Kajimura 1985; Perez and Bigg 1981, 1986). As the seals migrate northward through the Gulf of Alaska and into the Bering Sea their diet switches from primarily capelin, herring and sablefish (*Anoplopoma fimbria*) to pollock and squid (Table 1). They appear to feed opportunistically upon the most abundant schools of small fishes. Unfortunately, there is no information about the diet of fur seals after they leave the Pribilof Islands and migrate southward into the Gulf of Alaska (November to January); and nothing is known about the diets of juveniles after weaning.

Pollock is an important component of the marine ecosystem in the Bering Sea and Gulf of Alaska (Springer 1992). Not only is it the most abundant species (Table 1), but it also makes up a substantial part of the diets of other organisms (Table 2) such as fish (older pollock, Pacific cod *Gadus macrocephalus*, Pacific halibut *Hippoglossus stenolepis*, Greenland turbot *Reinhardtius hippoglossoides* and sablefish), seabirds (cormorants, kittiwakes, puffins and murres) and marine mammals (some toothed and baleen whales, northern fur seals, Steller sea lions *Eumetopias jubatus* and harbour seals *Phoca vitulina richardsi*). Given that humans are now the largest consumer of pollock (Table 2), it is logical to suspect that commercial fishing may be contributing to the decline of the Pribilof fur seal. Unfortunately the interaction between fur seals and fisheries, as with all marine mammals, is poorly documented, making it difficult to draw firm conclusions (Lowry *et al.*, 1979; Lowry 1982; Lowry and Frost 1985; Swartzman and Haar 1985; Gulland 1987).

Marine mammals clearly consume substantial amounts of fish and invertebrates. In 1981, when marine mammal populations were larger than present, the consumption by eight species of pinnipeds in the eastern Bering Sea and Aleutian area was estimated at just over 2 million mt, of which fur seals consumed 0.48 million (McAlister 1981). The consumption of pollock by all marine mammals was estimated at 1.13 million mt, which was almost equivalent to the commercial catch (Laevastu and Larkins 1981). Walleye pollock is the principal food of fur seals in the eastern Bering Sea. In 1972, fur seals were thought to have consumed the equivalent of 15% of the commercial pollock catch (Sanger 1974, cited by Lander and Kajimura 1982). In 1973, pollock contributed about 85% of the total food volume of stomachs examined from around the Pribilof Islands (Kajimura 1984). Pollock is less important in the seals' diet in the Gulf of Alaska where capelin, sandlance, herring and sablefish predominate (see Table 1).

A Depleted Food Base?

Information about the availability of food for fur seals is scant. Of the few studies conducted on feeding success and energetic status, most do not appear to support the contention that fur seal food resources have been depleted. For example, two studies on

Table 2. Estimated annual consumption of walleye pollock in the eastern Bering Sea. Several known consumers of pollock are not shown because no estimates of their consumption are available. Note also that the estimates may not be strictly comparable because they are derived by different investigators, in different years and months. From Lloyd and Davis (1989).

	Pollock Consumption		
Consumer	Metric Tons	Dominant Age Classes	Reference
Pollock (cannibalism)	2 695 900	ages 0 and 1	Dwyer *et al.* (1987)
Humans (fishery)	1 200 000	ages 2+	NPFMC (1988)
Pacific cod	968 400	broad range	Livingston *et al.* (1986)
Seabirds	272 000	ages 0 and 1	Kajimura and Fowler (1984) Hunt *et al.* (1981)
Other fish	147 800	broad range	Livingston *et al.* (1986)
Northern fur seals	133 000	ages 1 and 2	Livingston and Dwyer (1986) Frost and Lowry (1986)
Northern sea lions	123 800	broad range	Perez and McAlister (1988) Frost and Lowry (1986)
Harbour seals	81 600	ages 1–3	Ashwell-Erickson and Elsner (1981) Frost and Lowry (1986)

lactating females showed a decrease in the length of feeding trips since the 1960s (Gentry *et al.*, 1977; Gentry and Holt 1986; Loughlin *et al.*, 1987). Similarly, the weight of pups at 2 months and the survival of pups on land have increased in recent years as the Pribilof population declined (Fowler 1985b, 1990; Trites 1990). Growth curves for adults and immature seals also indicate increased growth rates as do the weights of teeth and lengths of 3 y old males harvested each year (Bigg 1979b; Baker and Fowler 1990; Trites 1990; Trites and Bigg 1992). All of these positive changes presumably reflect better per capita feeding conditions.

The apparent signs of well being in the fur seal population are explained in a number of ways. One is that fur seals are switching to other prey species not commercially exploited (stomach samples have identified 53 different species of fish and 10 species of squid in the fur seal diet: Kajimura 1984). Another is that the food base of the seal has been increased by fishing. Fur seals and commercial fisheries generally select fish of different sizes (Salveson and Alton 1976). In the case of pollock, it is hypothesized that fishing reduces the numbers of cannibalistic adults, thereby increasing the number of juvenile pollock that can be eaten by fur seals (Swartzman and Haar 1980; Livingston 1989).

Despite the apparent lack of evidence for food reduction, there are reasons to remain sceptical. For example, with regards to the hypothesis that the pollock fishery has increased the abundance of fur seal prey, there does not appear to be any relationship between the number of adult pollock (i.e. cannibalism) and the recruitment success of pollock (Bakkala 1989). Furthermore, the data on size and survival rates of pups and the length of their mother's feeding trips does not mean that fish stocks in fur seal feeding areas are abundant. Instead the findings only imply there is sufficient food to meet the needs of the reduced fur seal population. Increases in the size of subadult males and mature females may simply reflect reduced intraspecific competition. In other words, per capita food availability may have increased or remained stable, even though biomass of prey stocks may have decreased. Competition among fur seals for food presumably dropped as the seal population declined through the 1970s and 80s because high mortality of young between the ages of weaning and 2 y reduced population density (Trites and Larkin 1989). Furthermore nothing is known about the availability or 'quality' of prey available to recently weaned pups (Perez and Bigg 1981; Antonelis and Perez 1984), nor even where these juveniles migrate and feed. It is this gap in knowledge that may contain the explanation for the decline of the Pribilof population.

The Bottleneck Hypothesis

The studies of growth (lengths and weights of pups, subadults and adults) and the duration of foraging trips by lactating mothers suggest per capita increases in food abundance during the summer months near the Pribilof Islands and during the spring as the seals migrate north through the coastal waters of British Columbia and Alaska. But the studies say nothing about per capita fish abundance during the fall migration as the seals swim south through the eastern Aleutian Archipelago. It is therefore possible that food availability near the Aleutian Archipelago may be insufficient during the fall migration. Large numbers of young fur seals may starve after passing into the Gulf of Alaska, thereby creating a bottleneck for the entire Pribilof population.

Fur seal pups leave the Pribilof Islands shortly after weaning in early to mid November (Bartholomew and Hoel 1953; Peterson 1968; Bigg 1990; Ragen 1990). The first stage of their solitary migration follows along the edge of the continental shelf towards the passes through the Aleutian archipelago. In 1989, pups swam the 420 km distance from St Paul to Unimak Pass in an average of 10 days at a rate of 42 km day^{-1} (Ragen 1990). The pups' mothers spent about 6 days in the Bering Sea and swam an average of 68 km day^{-1}. Thus most pups enter the Gulf of Alaska from late November to early December. In 1989, pups swam through Unimak Pass and many other passes further west, dispersing over a much wider area than adult females (Ragen 1990). The highest frequency of pups was noted in Akutan Pass (next to Unimak Pass).

Groundfish are concentrated along the shelf break in the Bering Sea during the winter months (Favorite and Laevastu 1981). The same phenomenon probably occurs in the Gulf of Alaska and would enhance the ability of all seals, including inexperienced pups, to capture prey. However, the actual density of fish encountered is unlikely to be constant and will probably depend upon the prevailing environmental conditions and the extent of earlier removals by commercial fisheries. Different age classes of fur seals will respond differently to changes in the number of prey available to them. Young fur seals (juveniles and subadults) are likely to be more sensitive to changes in their food supply than the older fur seals. For example, older animals can swim faster than a pup (Ragen 1990) and can presumably sustain themselves for longer periods of time when faced with temporary shortages of food. However pups, being much smaller and less experienced than adults, have lower body reserves to maintain their body temperature in the cold north Pacific waters and would be more likely to succumb if food was scarce.

Baker and Fowler (1990) note that changes observed in growth before weaning and after age 2 y do not support the theory that resources vital to recently weaned pups are scarce. They argue that negative changes should have been registered on the teeth and in the lengths of subadults to indicate food shortages. The fact that they were not however, does not reflect food abundance, but rather how seals grow. Data from the pelagic collections (Lander 1980b) show that fur seals of all ages and sexes lose length and body mass from July to March (Trites 1990). Growth only occurs during a brief 1 to 3 month period as the seals migrate northward in the spring towards the Pribilof Islands (Trites 1990). Although there are no data for seals between weaning and 1 y, it is unlikely that their growth pattern differs significantly from that of older animals. Thus, given that seals do not grow during their southward migration, there is no reason for severe food shortages during the winter to be reflected in overall growth rates, because seals do not grow during this period of time.

Young could starve during their first winter without there being any sign of this in terms of reduced growth or size of the survivors captured in subsequent months or years. This phenomenon is termed 'catch-up growth' (Tanner 1990). Tanner writes 'the power to stabilize and return to a predetermined growth curve after being pushed, so to speak, off trajectory persists throughout the whole period of growth and is seen in the response of young animals to illness or starvation. During starvation an animal's growth slows down, but when feeding begins again its velocity increases to above normal for its age of maturity. Unless the starvation has been prolonged or has occurred very early in life[2], the original growth curve is caught up to and then once again followed.' Tanner goes on to give examples of children between the ages of 1 and 6 years that were starved for periods of 6 months to 5 years and experienced growth retardation. With improved nutrition, growth velocity increased and the original curve was attained. In some cases the growth period was extended and maturity was delayed, but in the end complete catch-up was achieved.

Conditions experienced over a period of weeks during the southward migration through the northern Gulf of Alaska (Aleutians region and waters to the south) may have created a bottleneck for the Pribilof fur seal population. The young that survive and get through find sufficient food further south to complete their migration. The high mortality of young caused by food shortages at this stage of their life cycle lowers the population density thereby reducing competition among this age group during their return northward migration in the spring. This would account for the increases in body growth recorded in recent years.

The supposed shortage of food probably occurs in the Gulf of Alaska or as the pups pass through the Aleutian archipelago and enter the Gulf. Increasing weights of 2 month old pups and the shorter lengths of feeding trips by lactating females imply there is sufficient food near the Pribilof Islands to meet the current needs of the reduced population (Trites 1990). Similarly, the positive growth rates of subadults sampled from January to July suggests adequate food supplies along the coasts of British Columbia and Alaska during the spring (Trites 1990). Nothing is known though about food availability from

[2]early in utero.

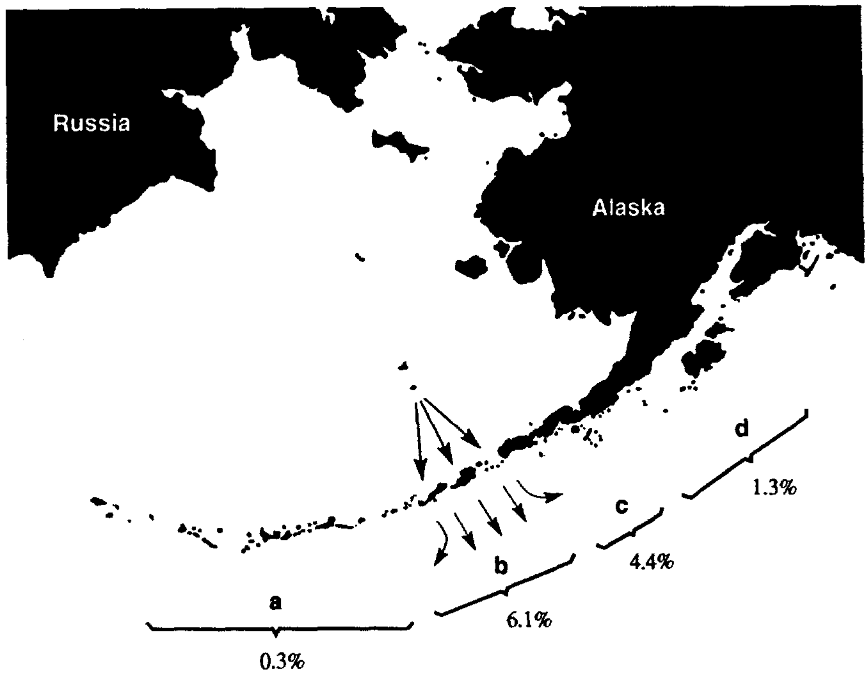

Figure 6. Annual rate of decline in numbers of Steller sea lions in the Gulf of Alaska and southern Bering Sea. Hauling sites were grouped into four regions: *a.* central Aleutian Islands, *b.* eastern Aleutian Islands, *c.* western Gulf of Alaska and *d.* central Gulf of Alaska. The arrows indicate the major migratory route of juvenile fur seals in the fall. Sea lion data are from Merrick *et al.* 1987.

November to December as the seals pass through the Aleutian chain and enter the Gulf of Alaska. But there is information from studies of harbour seals and Steller sea lions to implicate the Aleutian Islands and the Gulf of Alaska as the key areas for further investigation.

Decline of Other Species

In the late 1950s there were about 140 000 Steller sea lions living and breeding in the northern Gulf of Alaska (Merrick *et al.*, 1987). But by 1989 fewer than 50% of the total population remained (Loughlin *et al.*, 1992). The biggest decline occurred in the eastern Aleutians region (79%), followed by the western Gulf to the east (73%), and the central Gulf (31%) still further to the east (see Figs. 6 and 7). To the west, the decline in the central Aleutian islands was much smaller (8%), while in southern Alaska there has been virtually no change in sea lion numbers (Merrick *et al.*, 1987; Loughlin and Merrick 1989).

The decline of the Steller sea lions probably occurred over two periods, the early 1970s, and 1977 to present, and may have been caused, at least in part, by reduced prey abundance (Merrick *et al.*, 1987; Calkins and Goodwin 1988; Loughlin and Merrick 1989). Adult females and yearlings tend to stay in the Gulf of Alaska throughout the year and are therefore dependent upon local prey stocks (R. Merrick, pers. comm.). Yearlings, more than any other age group, are likely to be particularly vulnerable to reductions in food abundance, which can retard growth and lower survival and reproductive potential.

Calkins and Goodwin (1988) found that sea lions were significantly smaller (length, weight and girth) in the 1980s than in the 1970s. They believed this was caused by poor nutrition and suggested that the primary food base had changed. One speculation is that the sea lion diet may have switched from high caloric herring to the less nutritious pollock (Alverson 1991). Currently, the single most important prey item is pollock, but it has been difficult to connect the commercial pollock catch with the decline in sea lion abundance. Although correlations support the notion that yearlings are affected by changes in prey stocks, it has not yet been possible to statistically support or refute the commercial fishery hypothesis (Loughlin and Merrick 1989). Part of the difficulty in assessing the role of commercial fisheries in the seal decline is incomplete data combined with the confounding influence of large and variable pollock recruitment.

One of the largest concentrations of harbour seals in the world used to occur on Tugidak Island (see Fig. 3). In 1956 there were about 17 000 seals counted (Mathisen and Lopp 1963). But, in 1976 only 12 000 were counted (Pitcher 1990). By 1988 the population had declined a further 85% as shown in Fig. 7

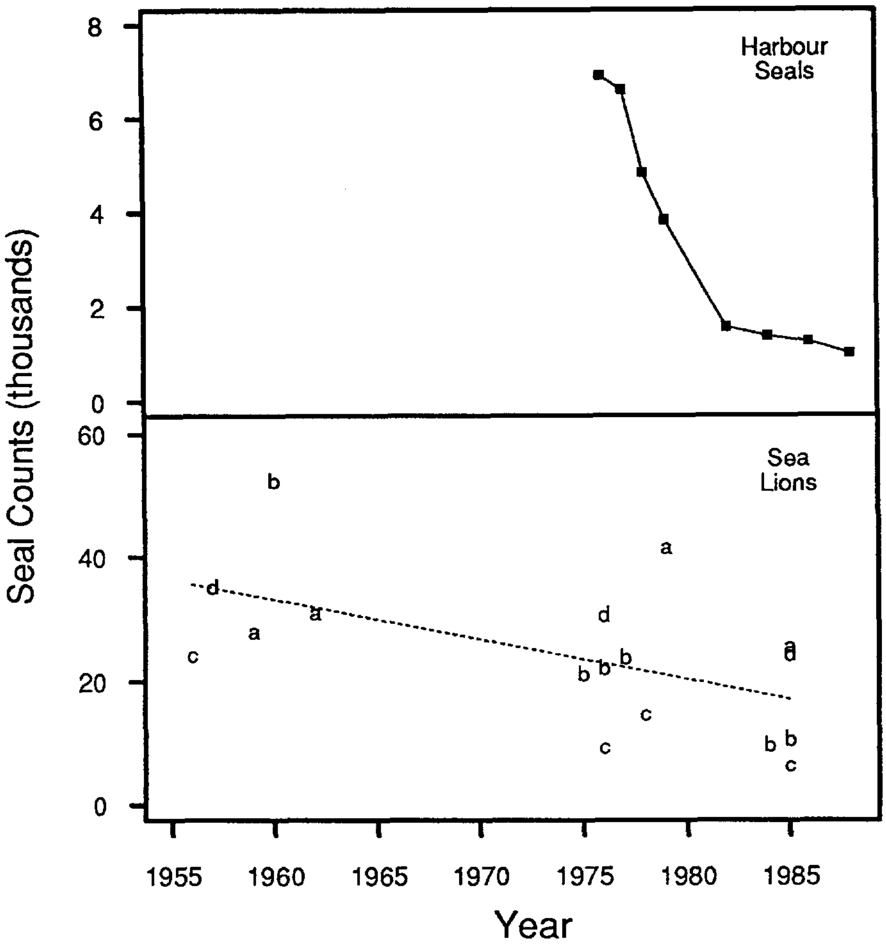

Figure 7. Decline in the numbers of harbour seals and Steller sea lions in the Gulf of Alaska. The top panel shows the counts of harbour seals on the southwestern side of Tugidak Island hauling area during the molting period (data from Pitcher 1990). The sea lion counts in the bottom panel were made in four regions of the Gulf of Alaska in spring and summer. The letters identify the region as shown in Fig. 6 (data from Merrick *et al.* 1987). The linear regression indicates a significant decline in sea lion abundance ($r^2 = 0.32$, $F_{1,15} = 6.96$, $P = 0.02$).

(Pitcher 1990). From 1976 to 1979, the population dropped 19% per year, then slowed to 7% from 1982–88 (Pitcher 1990). There is no clear reason for this decline. Disease could have been a factor, but no reports of mass die-offs of harbour seals have been reported in this region. Nor have there ever been observations of seals entangled in fishing debris on Tugidak Island (Pitcher 1990). Pitcher expresses doubt that the decline was caused by a reduction of the food base by commercial fishing because the seal decline was underway before the largest catches of pollock were made (compare Figs. 4 and 7). However the harbour seal decline could be related to the effects of poor pollock recruitment that occurred at this time (Fig. 5), combined with the collapse of the Pacific ocean perch stock and build up of commercial pollock catches (Fig. 4).

The decline in harbour seal numbers on Tugidak Island is not an isolated case. Limited data from other regions of Alaska also indicate population declines have occurred since the mid 1970s in the southeastern Bering Sea and Prince William Sound (Pitcher 1990). This is in contrast to the relatively stable populations in southeast Alaska (Pitcher 1990).

Some species of seabirds are also heavily dependent upon pollock in the Bering Sea and Gulf of Alaska. As with fur seals, harbour seals and sea lions, some seabirds are also in decline. The best data are from the Pribilof Islands (Fig. 8) and show declines since 1976 in the numbers of murres and kittiwakes breeding here. The decline in the numbers of birds that depend upon pollock is thought to reflect a reduction in the Bering Sea carrying capacity (Springer and Byrd 1989).

All of the declining species in the Gulf of Alaska and Bering Sea depend to some extent on pollock in their diet (Springer 1992). In contrast, the abundance

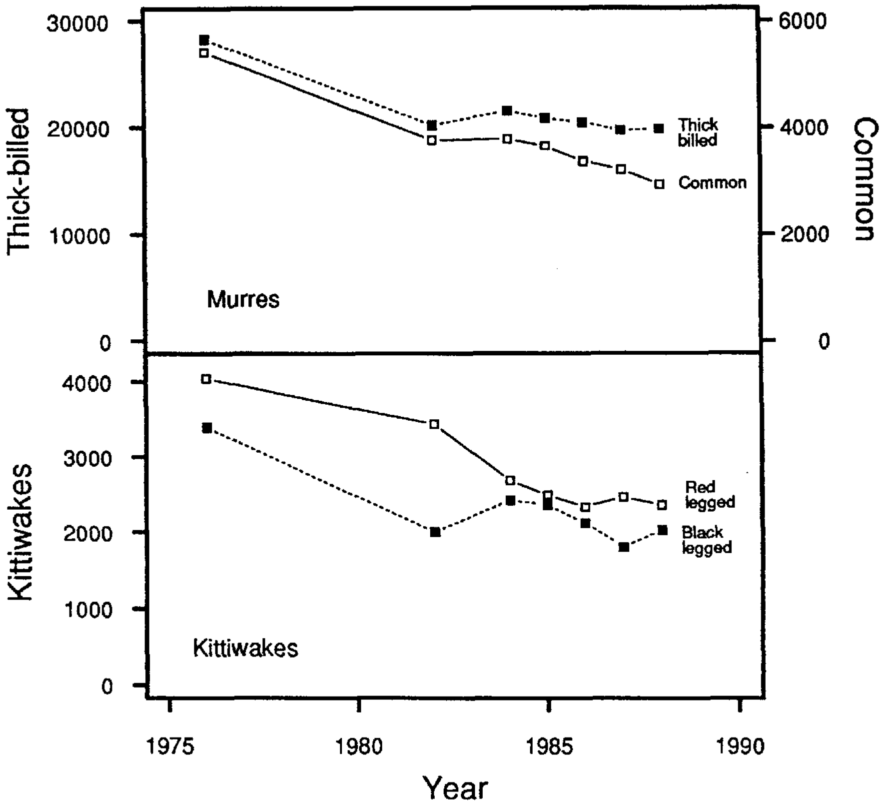

Figure 8. Counts of kittiwakes and murres on census plots on the Pribilof Islands (data from Dragoo *et al.* 1989).

of other species, such as Pacific cod and planktivore birds (Least, Crested and Parakeet Auklets), that compete with pollock for common prey have been increasing (Springer 1992).

Future Research

Major changes have occurred and are continuing to occur in the Bering Sea and Gulf of Alaska. The available evidence suggests that the food base for some marine mammals and seabirds has been substantially reduced in recent times by the combined effects of commercial catches and natural fluctuations in the environment that affect fish distribution and year class strength. The indication from the increasing biomass and decreasing numbers of pollock caught in the Bering Sea since 1977 is that pollock are declining and may be currently overfished (see Fig. 4). An additional consideration is the impact that cannibalistic adult pollock might be having on pollock recruitment (see Table 2). In the worst case scenario, these factors could lead to the collapse of pollock stocks and put those species that depend upon them in greater peril.

The available evidence suggests that the decline of the Pribilof fur seal is primarily related to a reduced food base, not entanglement. Of course it can always be argued that most animals that become entangled die at sea, and are not observed at haulout sites. I do not dispute this, nor do I reject the notion that entanglement is contributing to the decline and can impede population growth. But it has not yet been demonstrated that entanglement mortality is the principal factor causing the decline of the Pribilof population. Furthermore the entanglement hypothesis is inconsistent with observations of other pinniped populations. For example, the Antarctic fur seal population on South Georgia is increasing despite experiencing entanglement rates comparable to those reported for northern fur seals on the Pribilof Islands (Croxall *et al.*, 1990). Similarly, Russian populations of northern fur seals breeding on the Commander Islands are increasing, yet estimated entanglement rates are similar to those on the Pribilofs (V. Vladimirov, pers. comm.). Elsewhere in the North Pacific Ocean, populations of California sea lions, northern elephant seals and harbour seals are increasing. In British Columbia, harbour seals are increasing at an annual rate of 12% per year, while Steller sea lion numbers have remained relatively constant (M. Bigg, pers. comm.). The same is true for Steller sea lions and harbour seals in southeast Alaska (L. Lowry, pers. comm.). Only in the Bering Sea and in the Aleutian archipelago are pinniped populations declining.

The decline of Pribilof fur seals and other pinnipeds from the Aleutian archipelago strongly suggests that food, and the lack thereof, is the proximate factor in the population declines. Changes in prey abundance may be a natural phenomenon and/or may be related to localized, large commercial fish catches. The intensity of commercial fisheries in and near the Aleutian passes used by the pups should be given further consideration. Depending upon the timing of migration and the timing of fishing, the removal of a large number of fish near the passes could have a large impact on pups and not show up in the gross fish catch statistics for the region.

There is an urgent need to gather more information about the extent of entanglement and possible changes in the fur seal's food base. Future research can take several avenues to address these concerns. One approach is to make inquiries among fishermen and others who might be in the northern Gulf of Alaska when fur seals are migrating southward, and who might have useful observations to contribute. A second cost effective approach is to combine the efforts of the subsistence harvest with a concentrated research effort on a few selected rookeries and haulout areas.

Most discussions of the Pribilof fur seal refer to the total St George or St Paul Island population, whereas data are actually available for many years from as many as 34 distinct haulout sites and 14 rookeries. The research efforts that are now spread thinly over the entire island population might be better spent by intensively studying 4 of the 14 rookeries. These rookeries could be identified by time series analysis, should be representative of others, and should be free of mitigating factors that could confound generalizing the results of studies conducted on them. Two of the areas should be controls while the others are subjected to a concentrated subsistence harvest. Samples of pups in all four areas should be weighed and sexed with half of them being tagged and the other half ear clipped. Subadult seals can be driven[3] from all four areas, but killed from only two so that all animals can be inspected for tags and indications of entanglement. All harvested animals ought to be aged and measured for length and weight, while entangled animals are captured, tagged and released. Blood samples could be taken to monitor the incidence of disease, while attaching radio and light-weight satellite tags to some pups would enable the fur seal migration to be tracked so that feeding areas and place of death can be identified.

The results of this kind of proposed research have several benefits. The first is that it concentrates limited monitoring resources and makes full use of the animals killed by the subsistence harvest. The second benefit is that further information about the extent of entanglement mortality and the availability of food for lactating females and subadult males is gathered. Changes in food abundance should produce changes between years and among year classes in the size and growth of fur seals which would be recorded at birth and later when harvested. Changes in the survival of juveniles and subadults can be detected from the tagging studies done on all four areas. Driving all animals from the haulouts provides further information on the rate of entanglement and mortality of observed entangled animals. Other benefits of the proposed research include examining the effect of harvesting and gaining further insight into density dependent changes. The informaion to be gained from a concentrated research effort is urgently required to understand and monitor the current status of the Pribilof fur seal and to make much needed predictions of future population trends. This information cannot be gained quickly, but requires a carefully planned long term research effort.

[3]The act of surrounding and forcing groups of seals to move on land from one location to another.

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