VARIABILITY IN POPULATION TRENDS, LIFE HISTORY CHARACTERISTICS, AND MILK COMPOSITION OF NORTHERN FUR SEALS IN ALASKA

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ABSTRACT

The northern fur seal population on the Pribilof Islands has been declining since the 1960s and is now less than 30% of its former size. Chapter 1 examines factors that might cause a population to decrease to such an extent and concludes that only nutritional limitation caused by climate change or commercial fisheries, predation by killer whales, or a combination of factors that includes conditions in the North Pacific during the winter were possible explanations. Chapter 2 reports the seasonal patterns in proximate composition of fur seal milk between St. Paul Island (one of the Pribilof Islands) and Bogoslof Island (an increasing population) to understand the energy requirements of lactation and the energetics of pup growth and body condition at weaning. Factors that caused variability in milk composition included days postpartum, time ashore, individual phenotype, island and preceding trip duration. Average milk lipid increased from 45.5±0.7% to 53.8±1.0% at St. Paul and from 45.8±0.7% to 57.3±0.8% at Bogoslof between July and October, while average milk protein remained relatively stable ranging between 10.0% and 10.5%. The lipid content of northern fur seal milk near peak lactation is the highest reported among otariid seals and among the highest known for all mammals.

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DEDICATION

To my husband David Hayden and our son Beckett who make life and the work I love doing more meaningful.

INTRODUCTION

The northern fur seal population on the Pribilof Islands has been declining since the 1960s and is now less than 30% of its former size (Towell et al., 2006). Other species of marine mammals have also experienced population declines in the Bering Sea and Aleutian Islands region in this time. For example, the western stock of Steller sea lions collapsed by over 80% in the 1970s-1990s and are still declining in the central and western Aleutian Islands (Braham et al., 1980, Merrick et al., 1987, NMFS, 1992, NMFS, 1995, NMFS, 2007), harbor seals collapsed by up to 85% in the 1970s-1980s but are now recovering slowly in some areas (Pitcher, 1990, Frost et al., 1999, Small, 2003, Ver Hoef and Frost, 2003, Small et al., 2008), and the sea otter population in the Aleutian Islands collapsed by about 85% in the 1980s-1990s (Estes et al., 1998, Doroff, 2003). The reason for each of these declines may or may not be linked. The sea otter declines were most likely caused by killer whale predation (Estes et al., 1998), but the reason, or reasons, for declines of the other species remain unknown.

In Chapter 1 I review the potential causes of the decline of northern fur seals on the Pribilof Islands in the context of other important changes to the ecosystem since the middle 20th century. The factors I review include commercial harvests, subsistence harvests, bycatch in commercial fisheries, entanglement in fishing gear, direct shootings, disease, contaminants, nutritional limitation due to fisheries competition or climate change, predation, conditions during the winter and multiple causes. I conclude by summarizing questions that still need to be addressed and that provide guidance for future research.

Chapter 2 reports on the proximate composition of northern fur seal milk on St. Paul Island (Pribilof Islands) and Bogoslof Island, as part of a larger study called Consequences of Fur Seal Foraging Strategies (COFFS). COFFS investigated factors that may be contributing to differing population trajectories of northern fur seals in the Bering Sea by comparing numerous aspects of fur seal biology at St. Paul and Bogoslof, a smaller northern fur seal rookery site located approximately 200 miles south of the

Pribilofs that has been experiencing exponential growth (R^2=0.91) since its establishment more than 30 years ago (Lloyd et al., 1980, NMFS, 2007). The Pribilofs are located on the Bering Sea continental shelf, whereas Bogoslof is located off the Aleutian Islands chain in the deep ocean domain. These two rookeries offer a natural setting to compare aspects of the biology of fur seals in two populations in contrasting ecoregions and with divergent population trajectories.

The objectives of the COFFS study were to 1) determine the consequences of female foraging strategies to the growth of pups and to the physiological condition of pups and females near the time of weaning, i.e., determine if adult female fur seals at the Pribilofs are less able to raise robust pups than those at Bogoslof; and 2) determine if conditions in the North Pacific during the winter and spring could be differentially affecting adult females breeding at the Pribilofs compared to Bogoslof. Individual females and their pups were followed over the breeding season between July and October during 2005 and 2006 to determine female foraging trip locations, distances and durations, attendance patterns, diets, and milk delivery rates; pup growth rates; and the physiological condition of females and pups near the time of weaning. Females were also instrumented with satellite transmitters at the end of the breeding season to record winter movements, and attempts were made to recapture the same females upon their return to the rookery sites in the spring to assess their condition.

Knowledge of milk composition is essential for understanding the energy requirements of lactation and the energetics of pup growth and body condition at weaning. My study was unique because it compared the milk composition of females from two contrasting populations in longitudinal studies over most of the lactation period. It examined multiple variables—location, year, time ashore, days postpartum, foraging trip duration, maternal mass and pup gender—to determine potential sources of temporal and spatial variability in milk composition. Understanding how these factors affect milk composition and provisioning gives us insight into differences in pup growth, development and survival and adds to our ability to know if nutritional limitation could be causing or contributing to the population decline on the Pribilofs.

CHAPTER 1

Northern fur seal history and status in the Bering Sea: using current knowledge as a guide to prioritize future investigations[1]

Abstract

The northern fur seal (*Callorhinus ursinus*) population on the Pribilof Islands has declined by more than 70% over the past 50 years and the reasons remain unexplained. Here I examine the factors that have the potential to cause a population decline of this magnitude and compare them to the factors that may be affecting other pinniped and sea otter species that are also experiencing population declines in the Bering Sea and Aleutian Islands. I also make comparisons to a rapidly growing population of northern fur seals on Bogoslof Island, located in the basin domain of the Bering Sea close to the Aleutian Islands. The Bering Sea ecosystem has been an area of great change due to human and natural causes for multiple centuries and it is difficult to determine "normal" population levels and population fluctuations of fur seals or many other species, or past environmental conditions because the area was not monitored well until comparatively recently. Nevertheless, I draw some conclusions from the available literature and data. Factors such as diseases, parasites, subsistence harvests, direct shootings and bycatch have likely affected fur seals in the past and during this current decline, but they could not cause a reduction of this magnitude without being detected. Factors that were important to consider in the past and should continue to be monitored, but are probably not currently issues in the current population decline, include entanglement and contaminants. The factors that could cause a population to fall to the level seen in northern fur seals on the Pribilof Islands are nutritional limitation, due to climate change or fisheries competition; predation; or a combination of factors that include conditions in the North Pacific during the winter. In the end I list several questions and make recommendations about areas of research that need to be addressed in the future.

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[1] Hayden, A.B. Northern fur seal history and status in the Bering Sea: using current knowledge as a guide to prioritize future investigations. Prepared as a report for the Pollock Conservation Cooperative Research Center.

Introduction

Northern fur seals (*Callorhinus ursinus*) breed at six locations in the United States and Russia for four months during the summer each year. St. Paul Island (St. Paul, Pribilof Islands) supports the largest number of fur seals and, along with St. George Island (St. George, Pribilof Islands), which also has large rookeries, is located in the heart of the Bering Sea, a valuable and highly productive fisheries region. The Pribilof Islands (Pribilofs) population of fur seals has been decreasing for over 50 years (Towell et al., 2006); however, fur seals are not the only species of marine mammals to undergo a substantial decline in the region. The western stock of Steller sea lions (*Eumetopias jubatus)* collapsed by over 80% in the 1970s-1990s and is still declining in the central and western Aleutian Islands (Braham et al., 1980, Merrick et al., 1987, NMFS, 1992, NMFS, 1995, NMFS, 2007), harbor seals (*Phoca vitulina*) collapsed by up to 85% in the 1970s-1980s but are now recovering slowly in some areas (Pitcher, 1990, Frost et al., 1999, Small, 2003, Ver Hoef and Frost, 2003, Small et al., 2008), and the sea otter (*Enhydra lutris*) population in the Aleutian Islands collapsed by about 85% in the 1980s-1990s (Estes et al., 1998, Doroff, 2003). The reason, or reasons, for each of these declines may or may not be linked. The sea otter declines were most likely caused by killer whale predation (Estes et al., 1998) but the reason, or reasons, for declines of the other species remain unknown.

Because multiple species have experienced large decreases in population size in the region of the Bering Sea and Aleutian islands, there is a heightened need to understand what may be causing the ongoing decline of northern fur seals. Northern fur seals have been a species of interest for centuries, and particularly since the discovery of rookeries on the Pribilofs in 1786 and 1787 (Bancroft, 1886). Initially, they were highly valued for their furs and were harvested in huge numbers for profit, which led historically to two major population declines (Roppel and Davey, 1965). More recently, the economic value has faded and none are harvested for furs, but the importance of fisheries and ecosystem productivity has emerged as conservation concerns for the population.

This chapter reviews the potential causes of the current fur seal decline on the Pribilofs in the context of other important changes to the ecosystem since the middle 20th century and summarizes research questions that still need to be addressed.

Background

Northern fur seals inhabit the waters of the Bering Sea, the Sea of Okhotsk, and the North Pacific Ocean from California to Japan. They breed at six locations each summer – The Pribilofs in the eastern Bering Sea, Bogoslof Island (Bogoslof) in the eastern Aleutian Islands, San Miguel Island off of southern California, and the Commander Islands, Robben Island and Kuril Islands in Russia (Figure 1.1) (Kenyon and Wilke, 1953, Gentry, 1998). During the winter, northern fur seals migrate south from the rookery sites and remain pelagic for about 8 months (Ream et al., 2005) (Figure 1.2). Females typically travel the farthest south: for example, females from the Pribilofs travel to the North Pacific Transition Zone, the Pacific Northwest and the shelf edge off of California (Ream et al., 2005). Males do not migrate as far south (Kajimura, 1984, Biggs, 1990, Loughlin et al., 1999) and juveniles depart with the females but appear to scatter in many directions and have less predictable migration patterns than the adults (Lea et al., 2009).

Northern fur seals have a similar reproductive strategy to other otariid seals. They have a harem system in which males arrive first, in June, to establish territories. Usually only the largest males, which are typically between 7 and 11 years old, are able to defend the prime territories and fast throughout the critical period when copulation occurs (Johnson, 1968, Vladimirov, 1987). Females arrive in early July and give birth within 1-2 days. Females remain on shore fasting and nursing their newborn pups for a short perinatal period of about 1 week. After the perinatal period, females begin alternating between feeding trips to sea to acquire the energy needed for lactation, and nursing trips to shore to feed their pups. This pattern continues for about 4 months. In late October to early November, females depart and pups are abruptly weaned and embark on their first migration in which they must learn to forage and survive on their own. The last fur seals typically depart by mid to late November. Although this type of breeding strategy is similar to other otariids, there is one significant difference. Northern fur seal pups are weaned earlier than all other otariid species, except the Antarctic fur seal, so they need to acquire the needed nutrients for growth and development in a shorter amount of time.

Northern fur seals have experienced two known population declines before the present stock reduction and these declines occurred throughout their range. The first decline, which occurred in the late 1700s and early 1800s, was the result of overharvesting at the summer rookery sites (Jordan, 1898, Kenyon et al., 1954, Roppel and Davey, 1965). The second decline, which occurred between the end of the 1800s and the beginning of the 1900s, was the result of unmanaged pelagic harvesting during the summer and winter periods (Kenyon et al., 1954, Lander and Kajimura, 1982). In both cases, once the reason for the decline was determined and regulations were made to minimize the effect to the stock, population numbers increased (Roppel and Davey, 1965). In fact, after the North Pacific Fur Seal Convention of 1911 when the United States, Russia, Japan, and England signed a treaty to ban pelagic harvesting, fur seal numbers grew steadily for approximately 40 years and reached what some have suggested were pristine levels of 1,500,000 to 3,000,000 animals (Kenyon et al., 1954, Lander, 1980, Lander and Kajimura, 1982).

The current decline on the Pribilofs began soon after a female harvest was implemented in 1956 (Figure 1.3). Managers believed that the population had reached its peak level by the late 1940s and as a consequence, female reproductive success and the number of animals available for commercial harvest each year were decreasing because of density dependent depression of productivity (Roppel and Davey, 1965, York and Hartley, 1981). In an effort to increase productivity of the herd, and to increase harvest numbers, a plan to reduce the estimated 1,200,000 females to about 800,000 was implemented (Roppel and Davey, 1965). By the end of the harvest in 1968, the fur seal population was clearly in decline (York and Hartley, 1981). To determine if the harvest alone explained the population trajectory, a modeling study was undertaken using the total number of animals taken in the commercial harvest and in a scientific pelagic harvest between 1958-1974, and the best known vital rates and estimated changes in pup production through the 1970s (York and Hartley, 1981). The study concluded that 70% of the population decline that was evident between the end of the female harvest in 1968 and 1979 could be explained by the reduced number of females and their pup's potential recruitment in the population. There are two things to note about this conclusion. First, a substantial portion (30%) of the decline could not be explained by the loss of females to the harvest. Second, the continuing, overall decline might not have been as severe in the 1970s had the female harvest not occurred. These observations thus raise the question of whether multiple causes could have contributed to the overall population decline since the late 1950s.

Trends based on direct counts of pups (Figure 1.3) indicate that the population on St. Paul showed some signs of recovery after the termination of the female harvest, but reversed course in the mid 1970s, stabilized briefly in the 1980s, then continued to decline in the 1990s and through this century (Towell et al., 2006). At St. George, however, the population has experienced an essentially monotonic decline since the inception of the female harvest (Towell et al., 2006). The only other fur seal population decline in Alaska that we have a good historic record for, to compare trends, is the one that occurred on the Pribilofs between the late 1800s and the early 1900s due to unregulated pelagic harvesting. Many females were taken at that time, yet recovery began immediately once regulations were implemented. Why was there a continued decline after the end of the female harvest of 1956-1968, after the end of the scientific pelagic harvest of 1958-1974, and after the end of all commercial harvests on St. George in 1974 and on St. Paul in 1984? And of particular note, why has the herd on Bogoslof, nearby in the eastern Aleutian Is., been in exponential growth since it was founded in the mid 1970s?

There are a number of factors in the Bering Sea and the North Pacific Ocean that might cause a population to change in size. Long-term climate warming and events such as the Pacific Decadal Oscillation (PDO) and El Nino Southern Oscillation (ENSO) have documented effects on ecosystems that could alter overall productivity and prey availability to fur seals (Polovina et al., 1995, Francis et al., 1998, Anderson and Piatt, 1999, Bailey, 2000, Hare and Mantua, 2000, Hollowed et al., 2001, Chavez et al., 2003, Overland and Stabeno, 2004, Coyle et al., 2011, Mueter et al., 2011). Commercial fishing pressures in the Bering Sea since the 1950s have removed prey of fur seals and, along with industrial whaling in the 1950s and 1960s, have changed predator-prey relationships (Bakkala et al., 1987, Alverson, 1992, Merrick, 1997, Springer et al., 2003). Direct killings are known to have driven populations down in the past, and entanglement in discarded fishing nets and other marine debris was common in the 1970s (Jordan, 1898, Kenyon et al., 1954, Roppel and Davey, 1965, Fowler, 1987). Contaminants and diseases have also been implicated as factors, as has predation (Beckmen, 1999, Beckmen et al., 1999, Springer et al., 2003, DeLong, 2007). However, the northern fur seal is a long-lived species and individuals only need to reproduce successfully once during their lifetime to maintain stable populations. It is natural and expected to have more productive and less productive years over time. But what factor, or factors, could be great enough to cause the northern fur seal population on the Pribilofs to decline by more than 70% over the past 50 years?

Direct Mortality by Humans

Commercial and subsistence harvests

The harvesting of northern fur seals on the Pribilofs for commercial purposes began once fur seals were discovered on St. George in 1786 and on St. Paul in 1787. Historic population changes due to overharvesting and management protections are discussed in the background section above. In short, past commercial harvests are known to have decreased population numbers; however, populations recovered once management decisions were made to protect the herds. An interesting aspect of the current population decline is that when commercial harvests were concluded on St.

George in 1976 and on St. Paul in 1984 the population did not recover. This would suggest that the problem is not solely due to commercial harvesting.

Subsistence harvests have occurred since man came into contact with northern fur seals. For example, there is archeological evidence that suggests humans were hunting and eating northern fur seals as far back as the middle to late Holocene (~1200-1800 years BP) (Burton et al., 2001, Newsome et al., 2007). Before the Pribilofs were discovered, it is also known that the Aleuts that inhabited the Aleutian Islands hunted fur seals as they migrated north and south through the numerous passes (Jordan, 1898). When the Pribilofs were discovered, subsistence harvests became more regular but management increased to minimize the impact. In recent years, very low numbers have been taken for subsistence purposes. Takes on St. Paul were reduced from 1591 in 1996 to 522 in 2003 (Zavadil, 2008). Efforts have also been made to eliminate the collection of females and adult males (Zavadil, 2008). This very low rate of subsistence harvesting represents less than 0.1% of the northern fur seal stock on the Pribilofs and can not account for the 5.2% per year decline that has occurred between 1998-2008 (Towell et al., 2006, Allen and Angliss, 2010) .

Bycatch in commercial fisheries and entanglement in fishing gear and debris

Incidental takes in fishing gear occur occasionally and are difficult to avoid because of the overlapping interest of fur seals and commercial fishermen in fish resources. Since the implementation of the Marine Mammal Protection Act in 1972 and the Magnuson Stevens Fishery Conservation and Management Act of 1977 (MFCMA), efforts were made to record the number of incidental takes that occurred within the 200-mile fishery conservation zone of United States waters (Loughlin et al., 1983). Early foreign high seas driftnet and gillnet fisheries had the highest incidents of marine mammal bycatch. For instance, total takes from the high sea driftnet fishery were estimated at 5,200 in 1991 (Perez and Loughlin, 1991, Larntz and Garrott, 1993) and takes from the Japanese high seas salmon gillnet fishery were estimated between 100-1,000 a year from 1975 to 1981 (Jones, 1980, Jones, 1981). These fisheries no longer operate and so have not had an impact on the northern fur seal stock in recent years. In the past, the groundfish fisheries of the Bering Sea and Gulf of Alaska had the highest incidents of marine mammal bycatch (Loughlin et al., 1983), but estimates of mortality remain very low and are unlikely to be the cause of the current population decline (Ferrero et al., 2000). Recent estimates suggest that as few as two northern fur seals are injured or killed by fishery-related incidental catch each year (Perez, 2006, Allen and Angliss, 2010). It is likely that there are other unreported incidents; however, given the large stock of fur seals, these takes would not be large enough to adversely affect population levels (Allen and Angliss, 2010).

Entanglement in floating debris is thought to have increased fur seal mortality and/or reduced reproductive success in the 1970s. Objects wrapped around fur seal necks, shoulders and flippers were observed at a greater frequency following the mid-1960s increase in fishing effort in the North Pacific and Bering Sea and when plastic materials, which float and do not rot, started being used to pack trawl nets (Fowler, 1987). Estimates suggest that the world's fishing fleet dumped about 135,400 tons of plastic fishing gear and 23,600 tons of synthetic packing material into the ocean in 1975 alone (Derraik, 2002). The observed rates of entanglement were typically less than 1% (Fowler and Ragen, 1990), but some estimates suggested that young animals might have been more highly affected, lost at sea, and thus not observed (Fowler, 1987). The work that Fowler and others did to determine the contribution of entanglement to the population decline during the 1970s and 1980s was inconclusive (Fowler, 1982, Fowler, 1987, Feldkamp et al., 1989, Fowler et al., 1989). Since that time, large-scale efforts have been made to clean up fishing and packing materials that could cause entanglement. There also have been efforts to educate fishermen and the public about the problem and reduce the amount of dumping. Entanglement still occurs on the Pribilofs and at other rookery sites but the frequency has been substantially reduced (Fowler et al., 1989, Zavadil et al., 2007).

Direct shootings

Direct shooting of northern fur seals probably occurred. It's known that shootings of Steller sea lions occurred regularly and were legal before the passage of the Marine Mammal Protection Act in 1972. Between 1972 and 1990, it was still legal to shoot Steller sea lions and other marine mammals that were destroying fishing gear or causing a threat to human life. It was only after 1990 that it became illegal to discharge a firearm near a marine mammal. It is difficult to assess the impact of legal and illegal shootings now because no records were kept; however, the number of Steller sea lion takes could have been significant before 1972 and could have contributed to their population decline in the 1970s (Allen and Angliss, 2010). In contrast, northern fur seals tend to be less visible and less of a nuisance to fishermen than Steller sea lions, so it is unlikely that shooting has contributed to the continuing decline in recent decades.

Disease

A number of diseases have been recorded in northern fur seals over time, but the only significant infection that is known to have caused repeated large numbers of deaths is the hookworm parasite (*Uncinaria lucasi*). Lucas (1899) first recognized hookworm in the northern fur seal in 1896 and Olsen and Lyons (1965) conducted a complete analysis of the parasite's lifecycle in 1965. The parasite has been found in the soil at rookeries, and it is believed that adult fur seals are infected through their pulmonary system and pups are infected through milk transferred from the mother during nursing (Olsen and Lyons, 1965). The cause of death from hookworm infection can vary. Pups that were infected with hookworm on the Pribilofs usually died from anemia, whereas recently infected pups on San Miguel Island died from secondary bacterial infections (DeLong, 2007).

From the time of its discovery until the early 1980s, the hookworm parasite was responsible for a substantial number of northern fur seal pup deaths on the Pribilofs (DeLong, 2007). For example, 56% of the 1727 pup deaths that were examined in 1957 were caused by hookworm, compared to just 0.6% of the 2735 pup deaths examined in the 1980s (DeLong, 2007). Currently, however, the main hookworm problems exist on San Miguel Island and the Commander Islands, but not on the Pribilof, Kuril or Robben islands. Hookworm infection has not been assessed on Bogoslof. There is some debate about what factors drive hookworm infection rates, but the two leading possibilities are density dependence and substrate use (DeLong, 2007). The decreased incidence of hookworm infection on the Pribilofs, for instance, could be the result of the declining population or because soil and grassy areas where hookworms have been found are no longer being utilized. In either case, fur seal deaths from hookworm infection have been decreasing and are unlikely to be responsible for the present decline.

Other parasites and diseases that have been studied in northern fur seals are mites, namatodes (*Dipetalonema odendhali*), *Salmonella enteritidis*, *Pseudomonas aeruginosa*, *Acinetobacter lwoffii*, *Staphylococcus* sp., *Leptospirosis* and fungal infections (Smith et al., 1977, Keyes et al., 1979, Keyes et al., 1980, Burd et al., 1990, NMML, 1998). However, these outbreaks have not been ongoing or severe enough to cause a long-term population decline like that on the Pribilofs. There is some debate about whether other factors may weaken the fur seal immune system allowing viruses, bacteria and parasites to have an advantage, but that would mean that the disease is the secondary effect and the primary cause still needs to be determined.

Contaminants

Organochlorines are one of the primary contaminants found in the marine system. They include pesticides such as DDT, endocrine disruptors such as endosulfan, polychlorinated biphenyls (PCBs) such as coolants and flame retardants, and chloromethanes, which are precursors to substances like silicone. Organochlorines are slowly metabolized and tend to accumulate in long-lived species that are high in the food chain (known as biomagnification). Because they are lipophilic, they can bind to milk fat and be transferred to the offspring of mammals during lactation. Northern fur seals have high levels of organochlorines compared to other arctic marine mammals because they migrate south during the winter and feed in areas off the coasts of California and Japan that have historically had high contaminant levels (Bacon et al., 1992, Tanabe et al., 1994, Krahn et al., 1997, Loughlin et al., 2002). Females of reproductive age have slightly reduced levels compared to males and juveniles because they transfer contaminants to their pups during lactation – first born pups receive the highest levels of contaminants because of the accumulation in females in the 4-5 years before first reproduction (Beckmen, 1999, Beckmen et al., 1999).

The possible effects of high or chronic exposure to synthetic contaminants have been studied in a number of marine mammal species, but it has been difficult to confirm direct cause and effect relationships. Chronic exposure may impair the immune response (Ross et al., 1995, De Swart et al., 1996, Beckmen, 1999), and there is evidence that high PCB levels can cause reproductive failure (DeLong et al., 1973, Reijnders, 1986). High organochlorine levels in first born northern fur seal pups have been related to poor lymphoproliferative responses as well as to lowered serum retinol and thyroxine (Beckmen, 1999). It is unclear, however, if these factors translate to reduced post-weaning survival. It is well known that first born pups are often born at a lower birth weight and smaller size, but a relationship between those factors and contaminant levels has not been found (Beckmen, 1999). Additional work is needed to determine if the effects of organochlorines decrease the rate of survival for first year pups. However, it is unlikely that Organochlorines affected the fur seal population on the Pribilofs but did not affect the fur seal populations at other rookery locations.

Mercury is the primary heavy metal of concern in the marine environment. It is found in several forms, organic and inorganic, but all have the potential to become highly toxic methylmercury (Beijer and Jernelov, 1979). The most common natural sources are volcanic activity and leaching of mercuric sulfide (cinnabar). Anthropogenic sources include the combustion of fossil fuels, particularly in coal-fired powered plants, mining and the disposal of batteries and fluorescent lights. Mercury levels in the environment have increased by up to 5% since the beginning of the industrial era and mercury and its compounds have no known biological function and their presence in an organism is undesirable and potentially hazardous (Clarkson, 1993). Methylmercury has a high absorption rate, a large distribution throughout the body, can cross the blood brain barrier affecting the central nervous system, is slowly metabolized, and has a low excretion rate (Jugo, 1979). Methylmercury is especially dangerous to young animals because it is absorbed at a higher rate during development. Although most forms of mercury are not lipid soluble, methylmercury can be transferred to offspring transplacentally and through the proteins in milk (Jugo, 1979). There is typically a latent affect after poisoning so the effects of a toxic dose may not be immediately apparent.

Methylmercury bioaccumulates in the marine environment (Beijer and Jernelov, 1979), and northern fur seals have very high levels of mercury compared to other marine mammal species (Anas, 1974, Noda et al., 1995, Beckmen et al., 2002). It is still not known, however, if high mercury levels in marine mammals lead to lower survival. In fact, it has been suggested that the dietary element selenium, which is also found at high levels in northern fur seals, may protect against the toxic effects of mercury (Carty and Malone, 1979, Ikemoto et al., 2004). Further work is needed to understand how selenium may protect against the toxic effects of mercury and to determine if mercury contamination causes higher mortality or reduced fitness in marine mammals. It is unlikely that mercury is causing the population decline on the Pribilofs. There is no evidence to suggest that the fur seals from the Pribilofs have higher concentrations of mercury than other fur seal populations that are stable or growing.

Nutritional Limitation

Nutritional limitation is caused when the net energy obtained from foraging decreases to a point that is detrimental to an animal. This can be caused by decreases in the quantity or quality of the food that is available or by increases in the amount of energy that is expended to obtain food and maintain physiological condition. Climate change and commercial fisheries are the two leading factors that have the potential to cause nutritional limitation in northern fur seals. Nutritional limitation can lead to decreases in growth rates, pregnancy rates, and reproductive success and to increases in mortality through disease, predation, and starvation. To be able to assess how climate change and fisheries may have impacted fur seals over time, it is important to understand the potential effects to the ecosystem and how these effects may influence the diet and foraging patterns of fur seals. Northern fur seals breed at northern rookery sites in the summer and migrate south where they remain pelagic during the winter, so both areas are important to assess when trying to understand possible nutritional impacts.

Climate change

Climate change generally means a change in atmospheric conditions over time. There are natural examples of climate change such as El Nino, which occurs on an episodic basis. There are also long-term climate trends that cause persistent shifts in ecosystems such as the ice ages and inter ice age periods. Anthropogenic causes of climate change in the past century, through the release of carbon dioxide and other greenhouse gasses, is the leading theory for global warming (IPCC, 2007), but this has been hotly debated in recent years (IPCC, 2007, Akasofu, 2010).

Climate change affects a broad range of ocean processes. On a physical level it can affect ocean temperatures and in Arctic regions seasonal sea ice dynamics; the timing, location and strength of circulation patterns; spring stratification and the strength and depth of the pycnocline; and the frequency and intensity of storms, all of which can influence the timing and amount of primary production and the distribution, behavior and abundance of forage species and higher trophic level organisms (Francis et al., 1998, Wyllie-Echeverria and Wooster, 1998, Napp and Hunt, 2001, Stabeno et al., 2001, Hunt et al., 2002, , Schumacher et al., 2003, Mizobata and Saitoh, 2004, Overland and Stabeno, 2004, Bond and Overland, 2005, Grebmeier et al., 2006, Mueter et al., 2006, Hunt et al., 2008, Mueter and Litzow, 2008, Hollowed et al., 2012, Stabeno et al., 2012) Ultimately, these changes affect how energy flows through an ecosystem. Change is part of any marine system and species adapt to the range of conditions common in their habitat; however, if shifts become too unpredictable or exceed tolerable ranges, as is now occurring with increasing frequency (Hansen et al., 2012), species can be negatively impacted. One of the concerns about rapid climate change, such as global warming, is that species do not have enough time to adapt to the changes that are outside the natural range of variability.

Two types of climate change that have been studied in depth in recent years are regime shifts and global warming. Regime shifts, which appear to persist for about 12 to 30 years, are characterized by a stepwise change in a number of physical and biological features (Ebbesmeyer et al., 1991, Francis and Hare, 1994, Graham, 1994, Francis et al., 1998, McGowan et al., 1998). These features include atmospheric pressure, air temperature, sea surface temperature, ocean circulation patterns, ice cover, and zooplankton, jellyfish and fish recruitment, and catch amounts. Indices such as the Southern Oscillation Index (SOI), the PDO, the Aleutian Low Pressure Index (ALPI) and the North Pacific Index (NPI) are commonly studied to determine when regime shifts occur. It is believed that regime shifts occurred in the Bering Sea and North Pacific in 1925, 1947, 1977, 1989 and possibly 1998 (Mantua et al., 1997, Minobe, 1997, Beamish et al., 1999, Hare et al., 1999, Overland et al., 1999, Hare and Mantua, 2000, McFarlane et al., 2000, Benson and Trites, 2002). A distinctive regime shift, which changed the climate from predominantly cool to warm, occurred in winter of 1976-1977 and was the only one that was apparent in all indices.

Long-term global warming differs from a regime shift because it is not a step change that occurs in one year, and changes so far have been unidirectional. The Intergovernmental Panel on Climate Change (IPCC) has stated that a warming climate is unequivocal and it provides evidence of increases in the average global air and ocean temperatures, as well as widespread melting of snow and ice (IPCC, 2007). Climate warming has led to glaciers retreating, permafrost melting, sea ice shrinking, sea level rising, and extreme weather events that have changed in frequency and/or intensity (IPCC, 2007). As a result ecosystems are being altered. In the Arctic the effects of global warming are amplified because of open water formation efficiency, ice and snow surface albedo feedback, and possibly rapid increases in ocean heat being transported to the Arctic (Overpeck et al., 1997, Holland et al., 2006). The IPCC reports that temperature increases in the Arctic are almost twice the global average. In the Bering Sea, temperature increases through 2005 resulted in less sea ice and impacts to the ecosystem (Grebmeier et al., 2006, Mueter and Litzow, 2008).

A decrease in the extent and duration of winter sea ice coverage in the Bering Sea directly impacts the extent of the cold pool, which is dense cold bottom water that remains on the middle shelf through the summer because it is below the surface mixed layer and little affected by tidal mixing (Barnes and Thompson, 1938, Wyllie-Echeverria and Wooster, 1998). The edge of the cold pool represents the southern boundary of the arctic ecosystem and the northern boundary of the subarctic ecosystem (Mueter and Litzow, 2008). Between the early 1980s and mid 2000s, the southern boundary shifted northward by about 230 km (Mueter and Litzow, 2008). Although a northward shift such as that would be expected to result in a northward shift in the arctic and subarctic fish communities, it appears to not be that simple. The way species are responding to the changing conditions is variable so new community combinations are being built (Mueter et al., 2009). Additional factors such as the frequency and intensity of winter storms (Stabeno et al., 2001), patterns of cross-shelf advection (Rosenkranz et al., 1998, Bond and Harrison, 2000, Zheng and Kruse, 2006), and the timing of the spring algal bloom (Niebauer et al., 1995) are also affected by climate change and may play a role in the new community reorganization.

Because northern fur seals migrate into the North Pacific Ocean during the winter, we are also interested in how climate change may have affected that region. Many studies that focus on climate change in the North Pacific have studied the region's response to two major large scale climate phenomena – the ENSO and the PDO (Mantua et al., 1997). Francis et al. (1998) provide a very good overview of the effects of these two climate events in the Northeast Pacific. Physical changes in the wind stress can alter horizontal and vertical water flow and the depth of the surface mixed layer (Polovina et al., 1995, Francis et al., 1998). In addition, air heat exchange and oceanic fronts and other mesoscale features can be affected (Latif and Barnett, 1994, Francis et al., 1998). These physical effects lead to changes in primary production that include the timing of blooms and the composition, concentration and distribution of phytoplankton species (Brodeur and Ware, 1992, Polovina et al., 1995, Roemmich and McGowan, 1995). Lower trophic level changes such as these have an effect on higher trophic level species like fish, marine mammals and sea birds (Beamish, 1993, Beamish and Bouillon, 1993, Hollowed and Wooster, 1995, Mantua et al., 1997, Anderson and Piatt, 1999, McFarlane et al., 2000). The pronounced climate regime shift in the North Pacific in 1976-77, when sea surface temperature changed from cold to warm, caused a deepening of the winter and spring mixed layer in the subtropical domain and the central transition zone, which lead to an overall increase in pelagic productivity in this nutrient limited region (Polovina et al., 1995). In the Gulf of Alaska, the intensification of the Aleutian Low after 1977 led to a shoaling of the mixed layer depth but also higher pelagic productivity in this light limited region (Brodeur and Ware, 1992, Polovina et al., 1995). There has been less work done on the possible effects of a general warming, but it appears that it may lead to increased storm frequency and intensity (Salathe, 2006), as well as primary production patterns similar to a warm regime. The extent to which these factors may affect northern fur seals is discussed below.

Fisheries

The Bering Sea is a very productive region and its resources have supported a number of fisheries over the centuries. Subsistence harvests, although generally small, affecting only local resources and having minimal impact on larger fish stocks, have occurred since humans moved into the region (Burton et al., 2001, Newsome et al., 2007, Zavadil, 2008). Commercial fisheries for species such as Pacific herring (*Clupea pallasii*), Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*) and salmon (*Oncorhynchus spp.*) began in the early 20th century but it was not until after

World War II (WWII) that commercial fishing went through a period of expansive growth (SAFE report, 2012).

The technologies that were developed during WWII gave birth to a whole new scale of fishing. The development of Loran, radar and echosounders assisted in safe navigation, position finding and fish locating; the development of strong and lightweight synthetic fibers allowed for larger nets; improved propulsion made ships faster and more powerful; and refrigeration allowed larger catches to be made at greater distances without fish perishing (Bailey, 2011). Small fishing fleets that primarily targeted coastal fish species became diverse high tech fleets of small and large vessels that could fish demersal, pelagic and anadromous fish and shellfish species that inhabited regions previously not accessible. Japanese, Soviet and U.S. fisheries for salmon, herring, yellowfin sole, halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) grew throughout the 1950s and 1960s, and after these fish stocks declined in the late 1960s and early 1970s, other fish species were targeted (SAFE report, 2012). The walleye pollock (*Theragra chalcogramma*) fishery, which began in 1964, expanded to become the largest fishery in the eastern Bering Sea, peaking between 1970 and 1975 with catches ranging from 1.3 to 1.9 million tonnes (SAFE report, 2012). Although management of marine mammal harvests had been implemented earlier, foreign fisheries, and the bycatch associated with these fisheries, remained unregulated beyond 12 miles of the Alaska coast until 1977 (Witherell and Pautzke, 1997).

The first large scale commercial harvests for marine mammals—sea otters and fur seals—started in the 18th century and commercial whaling began around 1845 (Roppel and Davey, 1965). Following World War II, Japan and Russia turned intensively to whaling in the North Pacific and Bering Sea, depleting stocks of all the great whales to fractions of their former abundance before they were all fully protected over the course of the following three decades (Springer et al. 2003). Finfish and whale fisheries led to huge biomass removals between the 1950s and the late 1970s from the eastern Bering Sea, which likely resulted in a reorganization of the ecosystem.

Management regulations to protect fishery resources and set priorities for US citizens were finally implemented in 1977 with the passage of the MFCMA. This meant that foreign fleets, which could fish freely beyond 12 miles of the Alaska coast, would have to conduct their operations under the approval of the US federal government. Joint venture operations, in which domestic catcher vessels delivered their catch to foreign processing ships, were established in the period between 1977 and 1988 in an effort to transfer fishing technology and experience to domestic fishermen (Witherell and Pautzke, 1997). By 1988, foreign fisheries were phased out entirely.

Currently, the National Marine Fisheries Service (NMFS), the Alaska Department of Fish and Game (ADFG), and the International Pacific Halibut Commission (IPHC) manage the fishing stocks of the eastern Bering Sea. NMFS monitors and manages the groundfish fishery. They define three categories of fishes: target species, which are designated as fish that have commercial importance and are managed on their own biological merits; prohibited species, which are to be avoided and if caught have to be returned to the sea immediately with minimal injury; and forage fish, which are to be avoided and allowable bycatch and commercial exchange are limited (SAFE report, 2012) (Table 1.1). ADFG monitors and manages the fisheries for species such as herring and salmon in Alaska waters. The commercial fisheries for herring and salmon primarily use only purse seiners and gillnetters. Trawling is only allowed for herring on a small scale in Prince William Sound and around Kodiak and trolling is allowed for salmon in Southeast Alaska. The Pacific halibut fishery is managed by IPHC and is limited to hook and line capture. Total allowable catch limits are established annually for each of these species. These management efforts allowed earlier exploited stocks to recover and targeted species to be harvested at more sustainable levels.

The fishery resources of the eastern Bering Sea are now fairly well managed; however, there is one region of the Bering Sea that is outside the exclusive economic zone (EEZ) of the bordering countries. It is the only international fishing zone left in the Bering Sea, it is located in the deep water of the Aleutian Basin, and it is referred to as the "Donut Hole" (Bailey, 2011). Japanese scientists began reporting the presence of large quantities of pollock there in the mid-late 1970s, by the mid-late 1980s foreign vessels were intensively fishing there, and by 1987 the high seas pollock catch exceeded that within the EEZ (SAFE report, 2012). Fishing in the Donut Hole peaked in 1989 and then declined sharply (SAFE report, 2012). A fishing moratorium was enacted in 1993 and only trace amounts of pollock have been found in the Aleutian Basin by resource assessment fisheries since (SAFE report, 2012). In the U. S. portion of the Bering Sea there are three pollock stocks identified for management purposes – the eastern Bering Sea stock (EBS), which is comprised of pollock from the EBS shelf; the Aleutian Islands stock, encompassing the Aleutian Island region; and the Central Bering Sea/Bogoslof Island stock, which includes pollock from the Aleutian Basin and Bogoslof regions (SAFE report, 2012). There is likely some dispersal between these three stocks but the extent is unknown (SAFE report, 2012). Bailey (2011) defined the loss of fish in Aleutian Basin, due to overfishing in the Donut Hole, as a collapse of the fishery in that area. After 20 years the pollock population still has not recovered.

Ecosystem change relating to climate change and fisheries

There is little debate that both the effects of climate change and the effects of large-scale biomass removals by commercial fisheries have the potential to alter entire ecosystems; however, it is difficult to determine which may have had more of an impact on the northern fur seal population in the eastern Bering Sea, if any. Coincidentally, both a pronounced climate change event and the first large scale management regulations to protect fisheries resources in the eastern Bering Sea occurred during the same year in 1977. Some researchers believe that important forage fish species may have had higher stock levels before the 1977 regime shift, whereas pollock and certain other groundfish species did better after (Anderson and Piatt, 1999, Sinclair et al., 2008). However, the effects of fisheries have also been implicated in the apparent shift from a diverse ecosystem that supported high levels of forage fish to one with large populations of pollock and other groundfish species. For instance, the large-scale removals of species like herring, yellowfin sole, and Pacific Ocean perch, which began in the 1950s and increased through the early 1970s, could have led to a shift in the ecosystem that benefited pollock. Another hypothesis suggests that the shift occurred earlier with the removal of baleen whales, fishes and some pinnipeds. Reduced populations of baleen whales, Pacific herring, and Pacific ocean perch could have resulted in the release of 1.36-2.81 million mt of euphausiid and calanoid copepod prey to other consumers, and the removal of fur seals could have decreased predation on young pollock (Merrick, 1997). Increases in pollock and other predatory fish could have directly or indirectly reduced populations of other forage fish that might have been important to fur seals.

The Bering Sea ecosystem has clearly undergone significant change due to natural and human causes over the past few centuries. In many ways it is difficult to determine the cause and effect of certain processes because of the limited knowledge about the ecosystem prior to the late 1970s. To determine the possible effects of these changes on top predators, like the northern fur seal, perhaps it is best to examine if and how their diets and foraging strategies have changed.

Is there evidence that nutritional limitation is affecting northern fur seals?

Bottom up forces, commercial fisheries, habitat characteristics and the biogeography of forage species can affect fur seal energy expenditures and acquisitions in summer and winter by altering the abundance and/or distribution of prey resources and thus foraging behaviors such as trip distance, trip duration, dive depth and diet. In many ways these factors are related, so foraging trip duration and diet will be used as indicators of change for this discussion. During the summer, trip duration is important because it represents the time that a female needs to gain the required energy for lactation. The trip duration also represents the amount of time that a pup remains on shore fasting, and translates to the number of times a pup is fed before weaning, so it has the potential to directly affect growth and condition, and ultimately the probability of survival. Diet data are important because they provide insight into changes in quantity and quality of the prey that might otherwise be undetectable. Plus, from a management perspective, they give critical information about what resources are important to preserve.

Foraging trip duration

Northern fur seals exhibit varying foraging trip lengths across their range. Females from Bogoslof took foraging trips that averaged 2.2 days (Springer et al., 2010) and females from Medney Island took foraging trips that averaged 3.5 days (Vladimirov, 1983). This contrasts with females from St. Paul that took longer foraging trips that averaged 6.5 days (Springer et al., 2010). Each of these rookery sites is located at similar latitudes but is surrounded by different physical features. Bogoslof is an oceanic island and females forage in the surrounding deep ocean domain on abundant mesopelagic prey (Ream et al., 2000). Medney Island also is near the oceanic domain, in the Commander Islands, and females have ready access to deep ocean resources there as well. In contrast, the Pribilofs are located in the shallow middle continental shelf domain and females must travel farther to the deep basin and continental shelf edge, as well as to on-shelf foraging locations (Robson et al., 2004). Thus, rookery location, and its proximity to food resources, appears to be an important factor in the length of the foraging trip, but other factors such as prey composition, or quality, and prey availability are also important to consider. Studies of Antarctic fur seals have been able to link prey composition and availability to trip duration (Costa et al., 1989, Boyd et al., 1994).

Because of the relationship between foraging trip duration and prey distribution, composition and availability, a logical question to ask is if foraging trip duration has changed over time on the Pribilofs. An increase in trip duration would indicate that fur seals have had to forage for longer periods of time to meet their energy demands. A number of studies have examined trip duration in lactating females (Tables 1.2 and 1.3), but an increasing trend over the entire period of population decline is not distinguishable (Bartholomew and Hoel, 1953, Peterson, 1965, Kooyman et al., 1976, Gentry and Holt, 1986, Gentry et al., 1986, Loughlin et al., 1987, Gentry, 1998, Goebel, 2002, Robson et al., 2004).

It is important to note that there are differences in methodology between the studies that examined trip duration and this complicates a direct comparison between results. For example, early studies were based on observation and later studies used instrumentation. Two issues arise from this difference: observers could overestimate trip length if each female was not sighted on the day of her return; and instruments, especially the larger early models, created drag because of their size and the way they were attached, which could add additional energy demands to an animal, potentially lengthening foraging times. Another issue has to do with when the data were collected during the breeding season. Some studies followed animals for an entire season, from July to November, and other studies followed animals for shorter lengths of time. Trip duration has been shown to change over the length of the breeding season in Antarctic fur seals (McCafferty et al., 1998), so trip duration results can differ greatly depending on the length of time an animal is studied and when during the breeding season the study occurred.

Nevertheless, some conclusions have been drawn from the data that are available. Sterling (2009) combined the diet data from fur seal stomachs, gastrointestinal (GI) tracts, scats and spews, examined the relationship to trip duration data and pollock stock size, and found that adult female mean trip duration on St. Paul decreased with higher numbers of age 1-5 pollock. Gentry (1998) examined the attendance patterns of lactating females from St. George between 1974 and 1985 and found that trip lengths were longer between 1974-1978 than they were between 1979-1985. More specifically, he examined the variability that occurred between each year and also was able to relate it to pollock stock size (Gentry, 1998). Baker (1992) examined the nursing lines in teeth collected from harvested 3 year-old males between 1949 and 1981 and was able to relate the number of nursing lines to foraging trip duration. Foraging trips were shorter during the female harvest when the competition for resources was reduced and they were shorter during years when the 2 year old pollock stock size was larger (Baker, 1992).

Pollock are the primary prey resource for fur seals that forage on the shelf in the eastern Bering Sea (Goebel, 2002, Zeppelin and Ream, 2007, Sterling, 2009). It seems logical that forces that affect the distribution and abundance of pollock would directly impact fur seals. But what about fur seals that forage in other regions and on different prey resources? For instance, females from the northern rookeries on St. Paul typically forage on the shelf to the north of the Pribilofs and are known to consume primarily pollock (Goebel, 2002, Robson et al., 2004, Zeppelin and Ream, 2007). However, many females from the southern rookeries on St. Paul forage at and beyond the shelf break to the west and consume mostly mesopelagic species like squid, bathylagids and myctophids (Goebel, 2002, Robson et al., 2004, Zeppelin and Ream, 2007, Sinclair et al., 2008). Females from Bogoslof forage in the deep ocean domain directly offshore from the island and they also consume those same mesopelagic species (Sinclair et al., 1994). If prey type alone dictated foraging duration then females from Bogoslof and females from the southern rookeries on St. Paul would have similar foraging trip durations and this is not the case—females from Bogoslof take significantly shorter foraging trips (Springer et al., 2010). This suggests that distance from prey resources is a more important factor. This has implications when considering climate warming and the possibility of a redistribution of prey species.

Diet

Another factor that has been studied to a great extent is whether the quality of available prey has changed. High fat prey such as herring and capelin (*Mallotus villosus*) provide more calories per mass than low fat prey such as pollock. In theory, a predator could obtain its energy needs faster, while expending less energy, when eating high fat prey. There have been several studies that have suggested that the diet of fur seals foraging from the Pribilofs changed around the time of the 1976-77 regime shift (Sinclair et al., 1994, Hunt et al., 2002, Sinclair et al., 2008). Sinclair et al. (1994) concluded that changes in northern fur seal diet in the eastern Bering Sea were the result of climate-mediated shifts in fish communities. They compared diet information from pelagic studies made between 1960 and 1974 to collections made in 1981, 1982, and 1985. In the earlier studies, walleye pollock, Pacific herring, capelin, Atka mackeral (*Pleurogrammus monopterygius*), gonatid squid and northern smoothtongue (*Leuroglossus schmidti*) were reported to be the principal prey of northern fur seals in the eastern Bering Sea (Scheffer, 1950, Wilke and Kenyon, 1952, Wilke and Kenyon, 1957, Fiscus et al., 1964, Fiscus and Kajimura, 1965, Fiscus et al., 1965, Kajimura, 1984, Perez and Biggs, 1986). In the later years, pollock, Atka mackeral, gonatid squid and northern smoothtongue were common in diets, but it was claimed that there was an absence of high fat capelin and herring.

In the most recent northern fur seal diet analysis, Sinclair et al. (2008) added scat samples from 1987-2000 and data about seabird diets to the fur seal stomach and GI tract data that were previously analyzed. Results from the 2008 study supported the earlier findings made by Sinclair et al. (1994) with one addition. Greenland turbot (*Reinhardtius hippoglossoides*) was added to capelin and herring as missing from fur seal diets after the regime shift. If correct, these results suggest that northern fur seals consumed a diet that included more high quality forage fish before the 1976-1977 regime shift than they did after. However, there has been some debate about whether these conclusions were a true reflection of a change in capelin and herring distribution and abundance, or the result of variation in the locations where fur seals were collected.

Sterling (2009) examined the same fur seal diet records as Sinclair et al. (2008), but came to different conclusions. Sterling (2009) was concerned about spatial sampling biases because fishes are not uniformly distributed in the Bering Sea, and 70% of the fur seals were collected around Unimak Pass and in the basin domain during the 1960s, compared to approximately 81% that were collected on the eastern Bering Sea shelf in the 1970s and 1980s. Therefore, he filtered the scientific pelagic records from 1960-1985 to include only collections from the eastern Bering Sea shelf domain. Sinclair et al. (2008) in contrast, combined data that were collected from a much broader area that included Unimak Pass, the basin domain, and the eastern Bering Sea shelf domain. As a result, Sterling (2009) did not find evidence of a reduction in capelin and Pacific herring in the diet of fur seals that was associated with the 1976-77 regime shift, which supported the work of Fritz and Hinckley (2005), who previously found no evidence that forage fish dominated the Bering Sea ecosystem prior to the 1976/77 regime shift.

Whether changes in diet have occurred during the winter in the North Pacific is difficult to know. All available diet data from the North Pacific were obtained from pelagic harvests conducted between 1896 and 1985, but survey locations and timing differed depending on the year of study (Jordan, 1898, Scheffer, 1950, Kenyon and Wilke, 1953, Wilke and Kenyon, 1954, Wada, 1971, Fiscus, 1982, Antonelis and Perez, 1984, Kajimura, 1984, Perez and Biggs, 1986, Sinclair et al., 1994). And, there is little if any information on diets since the mid-1980s. In general, we know that fur seals typically follow the complimentary water movement of the Alaska gyre and North Pacific Current and forage in areas associated with eddies, the subarctic-subtropical transition zone and along the continental shelf edge during the winter (Ream et al., 2005). While in the North Pacific, they consume prey such as northern anchovies (*Engraulis mordax*), Pacific whiting (hake, *Merluccius productus*), squid, saury (*Cololabis saira*), rockfish (*Sebastes spp.*), salmon, capelin, sandlance (*Ammodytes hexapterus*) and herring. To assess how winter diets may have changed it may be more revealing to understand if these prey stocks have varied over time.

As noted above, after the 1976/77 climate change there was a deepening of the winter and spring mixed layer depth in the subtropical and transition zones, which lead to an increase in overall productivity, and a shoaling of the mixed layer depth in the Gulf of Alaska and an increase in productivity there as well. A number of reports have documented salmon being low in the Gulf of Alaska before this regime shift and increasing after (Beamish and Bouillon, 1993, Hare and Francis, 1995, Mantua et al., 1997, Hare et al., 1999, McFarlane et al., 2000, Irvine and Fukuwaka, 2011). Hake also appear to have increased in the warm regime (Bailey, 1981). Northern anchovy and

Pacific sardines (*Sardinops sagax*) have opposite relationships to climate change (Chavez et al., 2003). Anchovies were below average between 1977 and 1989, whereas sardines were above average (Noakes and Beamish, 2009). Pollock also seemed to do well after the regime shift, but herring appeared to have lower population numbers (Noakes and Beamish, 2009). In short, some prey species were more abundant in the cold regime, while others were more abundant in the warm regime. Northern fur seals eat a variety of prey species so it is difficult to assess how these changes in species composition, without knowledge of foraging energy expenditures related to each prey type, might affect net energy gains.

Winter prey availability and energetics

Another factor may have had more of an impact on winter foraging energetics than prey composition—global warming may be increasing storm frequency and intensity in the North Pacific (Salathe, 2006). The overwintering survival of females and pups depends on finding predictable and abundant prey resources while avoiding predation. Adult females are usually pregnant during the winter migration period, so have increased energy demands. However, pups are especially vulnerable because they are not experienced foragers, they have greater thermoregulation demands because of their smaller size, and they are not able to dive as deep as females to find prey (Lea et al., 2009). Prey resources are often found around eddies and in coastal upwelling areas; however, storms have the ability to disrupt productive areas and disperse prey assemblages from the surface mixed layer (Sterling, 2009). There is evidence that fur seals transit quickly through storm zones because of the lack of prey (Sterling, 2009). Furthermore, because of their small size, pups would be expected to be less able to physically cope with high winds and turbulent seas. If increased storm frequency and intensity are affecting prey availability and increasing energy demands, female reproductive success, as well as female and pup survival, could be impacted.

Is there evidence that different foraging strategies are related to survival and reproduction?

If climate change or competition from fisheries were negatively impacting northern fur seals in summer and causing the Pribilof Island population to decline, we would expect to see evidence in a few key areas. We would expect to see a difference in foraging strategies between pre-decline and post-decline populations. We would also expect to see differences in pup growth, development and possibly survival. There does not appear to be a clear difference in foraging trip duration between pre-decline and post-decline periods, but there are smaller scale variations that seem to be related to the distribution and abundance of pollock and other prey. Sterling (2009) found that in years when age 1-5 pollock were estimated to be above average, not only were fur seal foraging trip durations shorter, but they also had a higher occurrence of pollock in their diets and pups weighed more. Another recent study found that at Bogoslof, where the population is increasing and females make relatively short foraging trips for prey, pups are weaned at significantly heavier weights than pups from St. Paul (Springer et al., 2010). This may confer an advantage to Bogoslof pups in winter, since they appear to migrate to the same dispersed locations as pups from St. Paul (Lea et al., 2009). In addition, male pups were not larger than female pups at weaning on St. Paul, as they were on Bogoslof and as reported in other pinniped species (Arnould et al., 1996, Ono and Boness, 1996, Boltnev et al., 1998, Guinet et al., 2000, Springer et al., 2010). This could be evidence that pup growth and development on St. Paul decreased compared to healthy populations. Together, these studies suggest that prey distribution and abundance can affect pup growth and development, which has been linked to pup survival.

There is no known evidence of starvation or increased susceptibility to disease due to malnutrition on the Pribilofs (NMFS, 2007). Evidence is not available or is inconclusive in other areas that are important for assessing changes in survival and reproductive success. Studies have been made to determine pregnancy rates and evaluate whether they have changed on the Pribilofs but conclusions have not been reported yet (Adams et al., 2007, NMFS, 2007).

Predation

The primary natural predator of the northern fur seal in the Bering Sea is the transient killer whale (*Orcinus orca*). There are three killer whale ecotypes: resident killer whales that primarily eat fish and squid, transient killer whales that consume marine mammals, and offshore killer whales, whose foraging habits are largely unknown but are thought to eat fish, including sharks (Ford et al., 2011). Although killer whale foraging events are rarely seen, there has been documentation of killer whales consuming fur seals in the Bering Sea since the late 1800s (Jordan, 1898, Hanna, 1922, Matkin et al., 2007, Newman and Springer, 2008). Transient killer whales have been seen hunting and preying on fur seals in areas where fur seals concentrate, for example Unimak Pass, a bottle neck that fur seals need to pass through on the their northward migration back to summer rookery sites from winter foraging (Matkin et al., 2007). At St. Paul, Newman and Springer (2008) recorded transient killer whale vocalizations during 19 of the 22 days that recordings were made in the summer of 2006. It is clear that killer whales prey on northern fur seals and that females that make longer foraging trips are more exposed to this threat. Young animals that are more buoyant and have not developed the physiological capacity to dive as deeply as adults may be at a greater risk as well. Whether predation from killer whales is responsible for the population decline of the northern fur seal is still being hotly debated.

The Sequential Megafaunal Collapse theory posits that the declines of harbor seals, Steller sea lions, northern fur seals, and sea otters in the Aleutian Islands and Bering Sea are due to increased killer whale predation, which was caused by the post-World War II overharvesting of great whales in the Bering Sea and North Pacific (Springer et al., 2003). This theory is based on a few basic concepts: great whales were important prey of killer whales in this region; after the demise of the great whales, killer whales broadened their diets to include greater numbers of other marine mammals; top-down forcing, especially by large vertebrate consumers, is an important process in ecology; there is a lack of compelling evidence and mechanistic explanations for the hypothesis that bottom-up forces caused the pinniped and sea otter declines; and demographic/energetic models demonstrate how vulnerable pinniped and sea otter populations would be to a relatively small change in the diet of transient killer whales (Springer et al., 2003, Williams et al., 2004, Springer et al., 2008, Estes et al., 2009). In short, the overall implication is that after the great whale harvests occurred, killer whales needed to consume more of other prey to meet their high-energy demands. Pinnipeds and sea otters were an abundant food source in the Aleutian Islands and Bering Sea so they were consumed at a higher rate, which lead to the declines in their abundance.

The primary arguments against this theory are that the great whales (fin, sperm, sei and humpback whales) that were left in the Bering Sea and Aleutian Islands during the 1950s and 1960s were rarely attacked or eaten by killer whales (DeMaster et al., 2006, Mizroch and Rice, 2006), the multispecies collapse was not sequential (DeMaster et al., 2006, Wade et al., 2007), the timing of the collapse was inconsistent with the timing of the great whale depletions (Wade et al., 2007), and other areas where great whales were removed do not have the same trends in pinniped and sea otter populations (Trites et al., 2007). To each of these arguments Springer et al. (2008) and Estes et al. (2009) made convincing rebuttals. For instance, they present further references and evidence to show that great whales were and still are prey to killer whales; they reworked the statistical analysis conducted by DeMaster et al. (2006) and Wade et al. (2007) and showed that the collapse was in fact sequential; they discussed factors such as scavenging of great whale carcasses (Whitehead and Reeves, 2005) that could have led to a lag in the timing between the great whale depletions and the pinniped and sea otter population declines; and they discussed the ecological differences between regions where great whales were harvested that could have caused divergent pinniped and sea otter population trends.

Regardless of whether the specifics of the Sequential Megafaunal Collapse theory are found to be correct or incorrect, top down pressures from predation are important to consider when understanding the impacts to an ecosystem or to a specific population from radical changes in community structure. The northern fur seal population on the Pribilofs has been declining now for over 50 years. The further the population is reduced, the more of an effect predation could have. We still know very little about transient killer whales in the Bering Sea and Aleutian Island regions and there is still much to learn about the ecosystem dynamics of that region.

Multiple Causes

A number of researchers have hypothesized that there may have been more than one cause to have sustained the population decline of northern fur seal on the Pribilofs for over half a century. For instance, it is likely that the female harvest was a factor in the initial decline but research has shown that approximately 30% was possibly being caused by another factor such as commercial fisheries or entanglement in fishing gear (York and Hartley, 1981, Fowler et al., 1989). Currently, theories about fisheries and bottom up processes, which cause nutritional limitation, and theories about predation are the two leading hypotheses for the population decline.

There are three combinations of factors that have a high likelihood of being problematic. First, climate change could be causing changes in forage fish recruitment and distribution, which may not be accounted for in management models. This could lead to large fisheries having more of an impact on top-predators, such as the northern fur seal, than expected. Second, the long foraging trips that females from the Pribilofs need to make to obtain their prey that is distributed farther due to fisheries effects, climate change, or simply the biogeography of prey populations may expose them to more predation pressure. Third, bottom up forces in the Bering Sea that may be limiting energy acquisition, coupled with increased storm frequency in the North Pacific that may be causing dispersal of fur seal prey to deeper depths (Mackas et al., 2005) or raising the energetic cost of coping with inclement weather, could be creating an environment where fur seals are nutritionally limited in the summer and in the winter. The first two combinations have not been investigated but the third scenario describing the combination of effects from limited resources in the Bering Sea and North Pacific has been discussed by Sterling (2009).

Conclusions

The northern fur seal is a long-lived species and individuals need to reproduce successfully only once during their lifetime for population levels to remain stable. It is natural and expected to have more productive and less productive years. Fur seal have evolved life history strategies that provide a buffer to certain variability in climate so within a range of ecosystem conditions the population should not be dramatically affected. What has happened in the past 50 or more years that is different enough to cause the fur seal population from the Pribilofs to fall by more than 70% and not show signs of stabilization or recovery? And why has the population on Bogoslof increased exponentially during the same time period?

These are not easy questions to answer, clearly, since they have not been answered despite considerable attention and research. The fact is that the Bering Sea ecosystem has been an area of great change due to human and natural causes for longer than the northern fur seal population has been declining. It is difficult to determine "normal" population levels, "normal" population fluctuations or past environmental conditions because the area was not monitored well until comparatively recently.

A number of the factors discussed above are likely to not be responsible for a decline of this magnitude. Diseases and parasites have affected fur seal populations before and during this current population decline, but it is unlikely that significant effects of disease(s) could have lasted this long without being detected. Subsistence harvests, while ongoing, are too small to cause a population decline of this size for so many years. Commercial fur seal harvests have caused population declines in the past, but they have not been conducted since 1976 on St. George and 1984 on St. Paul, so they are no longer a concern. The female harvest in 1956-1968 apparently precipitated the initial recent decline, but was not responsible for the continuing trend. Direct shootings, while an important factor to consider in the Steller sea lion decline, likely were not an issue in the northern fur seal decline because northern fur seals are rarely seen at sea away from rookeries and are less of a nuisance to fisherman than Steller sea lions.

Other factors that were important to consider in the past, but are probably not issues in the current population decline, include entanglement in fishing gear and debris and contaminants. Entanglement was high in the 1970s and may have contributed to some of the early decline, but it is unlikely that it is still causing high mortality rates because of the extensive cleanup efforts and education programs that were conducted. Contaminants such as organochlorines and mercury are known to be high in northern fur seals, but negative effects due to contaminant loads have not been established. In addition, contaminant loads would likely be similar at Bogoslof and the Pribilofs, so if they were having a negative effect on fur seals the population on Bogoslof would not be growing.

The factors that could cause a population decline of the magnitude seen in northern fur seals on the Pribilofs are nutritional limitation, predation or a combination of factors. Nutritional limitation could be caused either by climate change or by commercial fisheries. Climate change can alter ocean temperature, the timing, location and strength of circulation patterns, the frequency and intensity of storms, spring stratification and the strength and depth of the pycnocline, all of which can directly or indirectly affect fish distributions and abundances. There have been a large number of publications that have examined how climate change is affecting the resources of the Bering Sea, and while important discoveries are continually being made, there are still many unexplained consequences. The interactions of the biotic and abiotic factors of the Bering Sea ecosystem are complex so, for example, instead of seeing a simple northward movement of species because of climate warming, species are responding to changing conditions in variable ways and new community combinations are being built. How, or if, this is affecting fur seals is still unclear. One hypothesis is that prey quality changed from one high in forage fish before the 1976-77 regime shift to one dominated by pollock after; however, there is debate about whether a shift in species composition occurred in the Bering Sea and, more importantly, it is clear that pollock was an important prey species for the fur seal well before the 1970s. Northern fur seals eat a variety of prey which should buffer them against effects of changes in distribution and abundance of individual species (Sinclair et al., 1994, Zeppelin and Ream, 2007).

Climate change can affect fish community composition, distribution and abundance but so can large biomass removals by commercial fisheries. In fact, deciphering which ecosystem changes are the result of commercial fisheries compared to climate change can be difficult. For instance, a hypothesis proposed by Merrick (1997) suggests that the removal of baleen whales, Pacific herring, Pacific Ocean perch and northern fur seals could have caused the increase in pollock biomass in the 1970s that others have attributed to climate change. One thing is clear—commercial fisheries and climate change have both had an effect on the Bering Sea ecosystem.

The female harvest that began in 1956 was started because it was believed that the population had reached a plateau and the number of young animals available to harvest had decreased (Roppel and Davey, 1965, York and Hartley, 1981). This suggests that the fur seal population had reached the carrying capacity of the ecosystem; however, this may not have been the result of the population reaching historic population levels. Instead, it could have been caused by changes in the ecosystem that lowered the carrying capacity of the region. The modeling work conducted by York and Hartley (1981) concluded that only 70% of the decline evident between 1968 and 1979 could be explained by the female harvest. This could this mean that competition with commercial fisheries for prey resources was affecting the fur seal population earlier in the 1950s, as well as through the 1960s and 1970s.

Japanese fisheries for salmon, yellowfin sole, halibut and sablefish, as well as Soviet and U.S. fisheries for herring began in the early–mid 1950s in the Bering Sea.

These fisheries grew throughout the 1960s, and other species like Pacific Ocean perch also started being targeted. By the early 1970s, stocks of most of these species were depleted and pollock started being fished in higher numbers. Regulations on foreign fisheries, and the fish bycatch associated with them, were not implemented until 1977. The biomass removed by the commercial fishing industry between the end of WWII and the passage of the MFCMA in 1977 could have decreased the prey available to northern fur seals during the initial years of their population decline.

After the passage of the MFCMA targeted species started being managed on their own biological merits, stocks that were severely depleted were designated as prohibited, and bycatch was monitored and limited (SAFE report, 2012). These regulations should have reduced the amount of competition for fish and squid resources between commercial fisheries and northern fur seals. And, in fact, the population on St. Paul stabilized briefly in the mid 1980s, which could have been the result of increased prey availability, but ultimately the population continued to decline. Could the pollock fishery that continued on the eastern Bering Sea shelf have decreased prey availability to female fur seals? It is possible, but females from the southern rookeries on St. Paul and St. George consume other species including squid, bathylagids, and myctophids and these rookeries also declined. Could the unregulated pollock fishery in the Donut Hole, which was being intensively fished in the mid-late 1980s, have continued the northern fur seal population decline? Female fur seals from the Pribilofs forage for pollock mainly on the shelf, and the basin pollock are considered a different stock. Juvenile fur seals are known to forage farther from the Pribilofs, sometimes foraging in the basin, so decreases in pollock in that region could have increased juvenile competition for female prey resources (Sterling and Ream, 2004). This, however, is purely conjecture. There is little evidence to show that fur seals from the Pribilofs consumed pollock from the Aleutian Basin region. This leaves some question about whether population declines that occurred after the 1970s were the result of commercial fishing competition there.

The first confirmed identification of northern fur seals on Bogoslof occurred in 1976 and the first pups were observed in 1980 (Lloyd et al. 1980). This means that the population on Bogoslof did not exist when unregulated foreign fisheries were operating up to 12 nm offshore in the Bering Sea. Since then, however, the population on Bogoslof has grown exponentially. What is different between Bogoslof and the Pribilofs that could be causing these divergent population trajectories? Bogoslof is located in the deep ocean domain near the Aleutian Islands and fur seals that breed there forage close to the island and consume mostly mesopelagic prey (Ream et al., 2000). In comparison, the Pribilofs are located on the eastern Bering Sea shelf and fur seals from the northern rookeries forage on the shelf and consume mostly pollock, whereas many fur seals from the southern rookeries forage at the shelf break and consume mostly mesopelagic species similar to those consumed by Bogoslof fur seals (Goebel, 2002, Robson et al., 2004, Zeppelin and Ream, 2007, Sinclair et al., 2008). Although there are differences in where the islands are located and in the diets of the fur seals, the factors that appear to have the greatest effect on pup growth and development are the differences in foraging trip distance and duration. Female fur seals from St. Paul need to travel approximately two times farther and approximately three times longer to forage (Springer et al., 2010). This means that pups remain on shore fasting three times longer on St. Paul. Pups from Bogoslof spend less time fasting and feed more frequently. As a result, pups from Bogoslof are weaned at a significantly greater mass than pups from St. Paul and they may have a greater chance of survival (Springer et al., 2010).

A number of studies have hypothesized that there is a relationship between the pollock stock size and the foraging duration of female fur seals from the Pribilofs (Baker, 1992, Gentry, 1998, Sterling, 2009). Sterling (2009), found that there was a relationship between the pollock stock size and pup mass. There are still a number of factors that need to be researched further to determine if pollock stock size actually affects reproductive success. To date, we have evidence that pup mass may be associated with survival during the first year in other pinniped species (Boltnev et al., 1998, Beauplet et al., 2005), and there is some evidence that pup growth and development was limited on St. Paul because female and male pups did not differ in mass at weaning as observed in other fur seal species (Sterling, 2009). If fluctuations in the pollock stock affect fur seal reproductive success on the Pribilofs, commercial fisheries, climate change or a combination of the two could have caused the continued population decline since the 1980s.

Steller sea lions, harbor seals and sea otters have also experienced population declines in the Bering Sea and Aleutian Islands. It is not entirely clear if these declines are related, but it is important to consider that they may be. The foraging and life history strategies of each of these species differ, however, so direct comparisons are not straightforward. Female Steller sea lions, for instance, make foraging trips of generally less than 2-3 days during the breeding season. Northern fur seals at the Pribilofs make foraging trips that can last as long as 10 days and they commonly forage farther from rookery sites. In addition, Steller sea lions, harbor seals and sea otters remain in Alaska and continue to haul out on land during the eight months of winter, whereas northern fur seals migrate into the North Pacific and remain pelagic. Steller sea lions have declined significantly on Bogoslof and show no sign of recovery, whereas the northern fur seal population has increased exponentially over the same time period. The two primary causes of nutritional limitation, commercial fisheries and climate change, could have affected each of these species but the mechanism likely would have been different in each case.

The one theory that can explain all of the pinniped and sea otter declines in the Bering Sea and Aleutian Islands is predation. Although killer whale predation is the most probable cause for the sea otter decline, and killer whale predation has been documented in northern fur seals, Steller sea lions and harbors seals, there is still debate about whether predation is responsible for the overall declines of each of these species. Why, for instance, is the Steller sea lion population on Bogoslof affected by killer whale predation but the fur seal population is not? It could be because sea lions are being preyed upon in another location before or after they are on Bogoslof, or are being preyed upon in winter when the fur seals are gone. If predation is the cause, why are the fur seals on St. Paul declining but the fur seals from Bogoslof are not? Fur seals from St. Paul take longer foraging trips than fur seals from Bogoslof, so perhaps they are exposed to more predation, but there is still limited evidence to support this theory.

Because of the difficulty in producing convincing evidence that any one of the above factors alone could have caused the northern fur seal population decline, it is important to consider that more than one of the factors could have had an effect. If the female harvest of northern fur seals is not responsible for the entire population decline in the 1960s and early 1970s, then the effect of the commercial fishing industry, through entanglement and competition for prey resources, may have contributed to the initial decline. After management regulations started being implemented in 1977, other factors could have had more of an influence. For instance, climate change could have affected prey distribution and abundance in the Bering Sea after the 1977 regime shift, or perhaps killer whale predation started having an effect because of the reduced fur seal population size. Increased storm frequency and intensity due to climate change in the North Pacific could have tipped the energetic balance for fur seals, reducing survival. In this case, Bogoslof females may be exposed to the same decrease in prey availability in the North Pacific, if there was a decrease, but resources around Bogoslof in summer may be high enough to counter the effects by enabling both females and pups to be in better physiological condition than those at the Pribilofs at the time of migration. Each of these theories is plausible and should be examined further.

Recommendations

1. Monitoring and education programs that were established to reduce the effects of entanglement in fishing gear and debris should be continued so that it does not affect fur seal and other marine mammal populations in the future.
2. Although it is unlikely that northern fur seals population decline on the Pribilof Islands is being caused by contaminants, research in this area should continue so that the effects of high levels of organochlorines and mercury on fur seals and other marine mammals are better understood.

3. Further research and discussion should be conducted to examine the effects of the foreign commercial fishery on the northern fur seal population in the 1950s, 1960s and 1970s.
4. For the targeted fish species that northern fur seals consume, surveys should continue and include regions important to the seals. Knowledge about forage fish species that do not have a direct survey and squid species that are caught opportunistically needs to be increased. Although of no commercial value, mesopelagic forage species such as bathylagids, myctophids, and squids have very high ecological value.
5. Fur seal vital rates and causes of mortality must be better documented.
6. The possible effects of reduced numbers of pollock on fur seals in the international waters of the Aleutian Basin (the Donut Hole) should be examined further.
7. Longitudinal studies of pups from Bogoslof and the Pribilofs should be undertaken to determine how mass and body condition at birth and weaning affect survival and eventual reproductive success.
8. A study that compares the foraging behavior, reproductive success, and winter movements of northern fur seals and Steller sea lions on Bogoslof would help in understanding why these two species that breed on the same island are experiencing divergent population trends.
9. Further research into the transient killer whale population and its effects on marine mammals is needed.
10. Further examination of the combined effects of factors such as commercial fisheries, climate change, predation, and prey availability and environmental conditions in winter should be conducted.

Figures and Tables

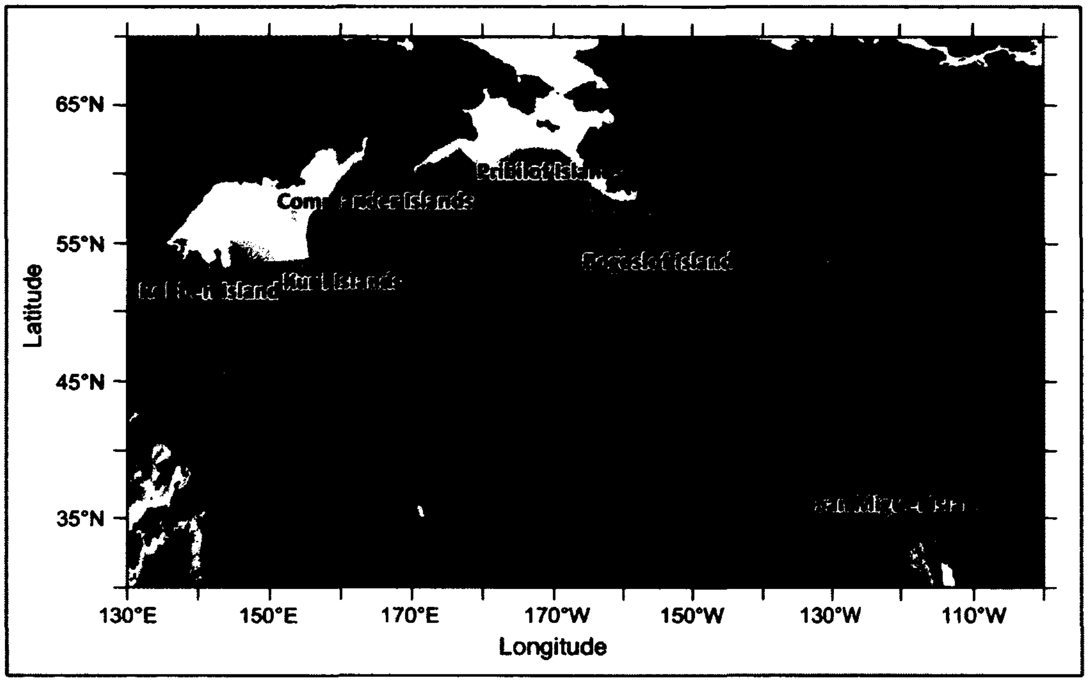

Figure 1.1. Northern fur seal range in the North Pacific and the six locations where they breed. The blue circles represent the relative size of the population at each location. The Pribilof Islands now support approximately 50% of the total population (Sterling pers. com.)

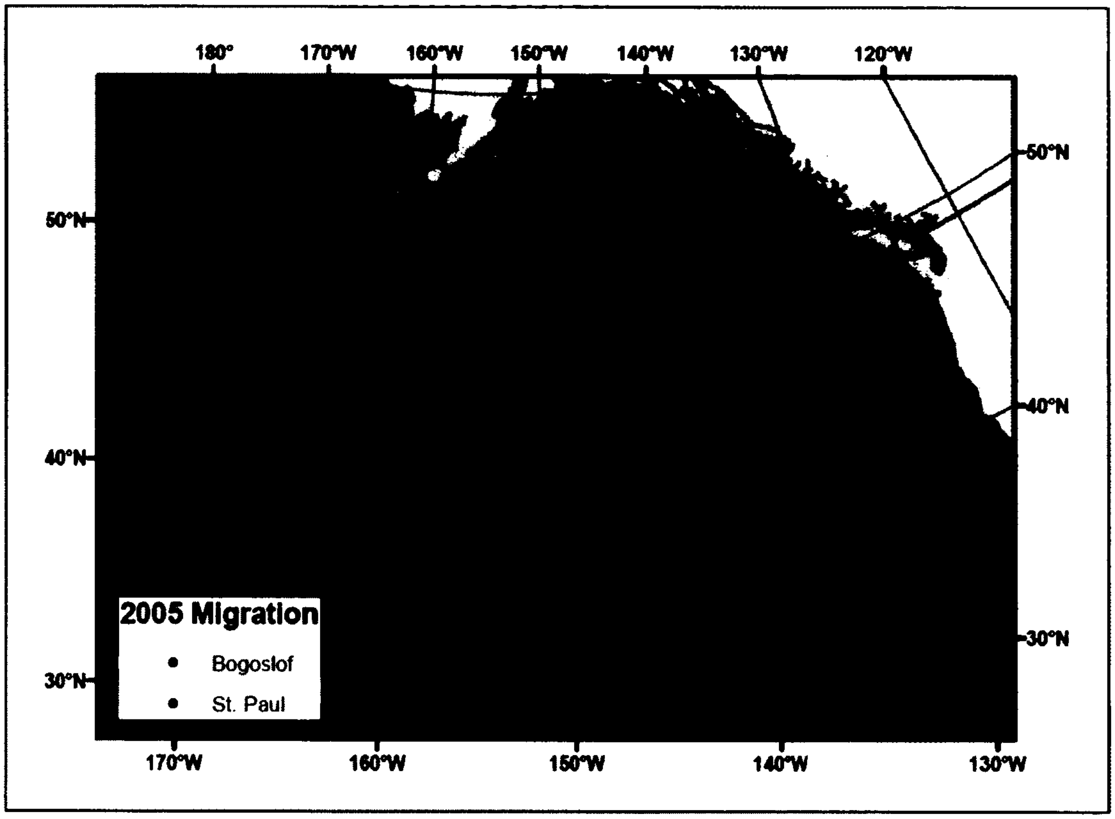

Figure 1.2. An example of the northern fur seal winter migration routes. These track lines were recorded with satellite transmitters and the analysis of the data is being completed and published by the National Marine Mammal Laboratory. The movements of females from St. Paul, one of the Pribilof Islands, and Bogoslof are represented here (Springer et al. 2010).

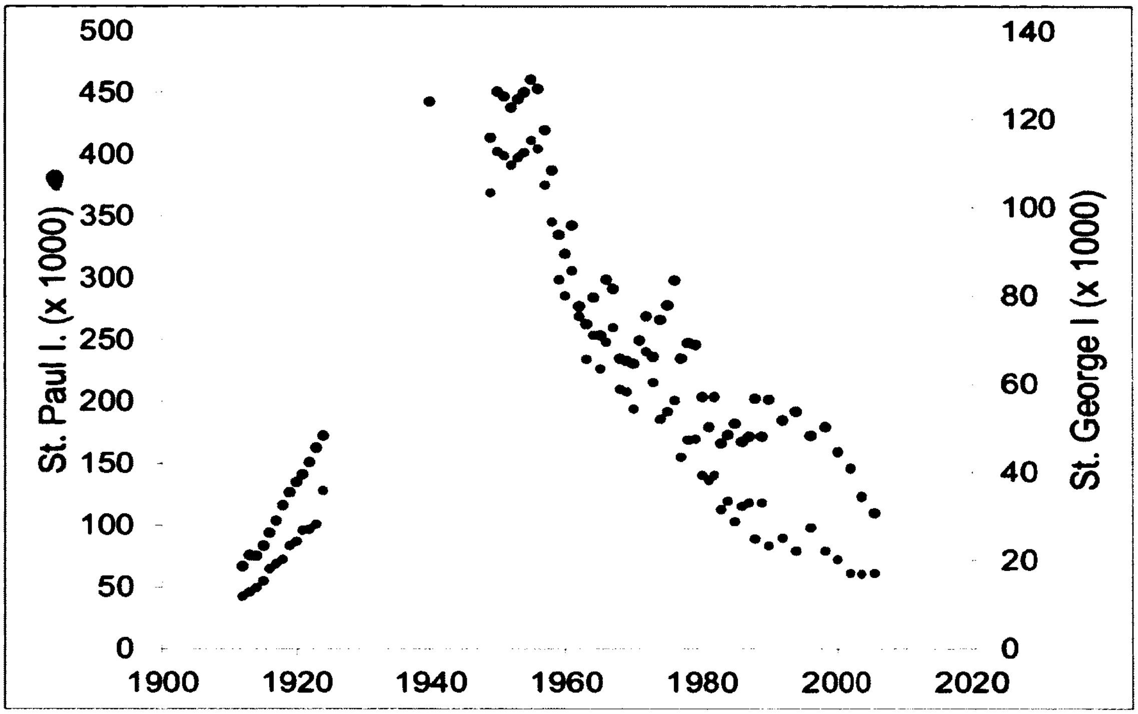

Figure 1.3. Pup production on the Pribilof Islands, St. Paul and St. George.

Table 1.1. Targeted, protected and forage species as defined by the NMFS Bering Sea groundfish fishery.

Target species	Walleye pollock Pacific cod Sable fish Yellowfin sole Greenland turbot Arrowtooth flounder Northern rock sole Flathead sole Alaska plaice Other flatfish assemblage Pacific ocean perch Northern rockfish Shortraker rockfish Blackspotted/Rougheye rockfish assemblage Other rockfish assemblage Atka mackerel Squid assemblage Shark assemblage Skate assemblage Sculpin assemblage Octopus assemblage
Prohibited species	Pacific halibut Pacific herring Pacific salmon Steelhead trout King crab Tanner crab
Forage species	Osmeridae (eulachon, capelin, and other spelt) Myctophidae (lanternfish) Bathylagidae (deep-sea smelts) Ammodytidae (Pacific sand lance) Pholidae (gunnels) Stichaeidae (pricklebacks, warbonnets, eelblennys, cockscombs, and shannys) Gonostomatidae (bristlemouths, lightfishes, and anglemouths) Euphausiacea (krill)

Table 1.2. Studies that examined trip duration in northern fur seals at St. Paul Island. TDR stands for Time Depth Recorder.

Reference	Study years	Rookery	Time observed	No. females observed	Method	Average trip length (days)
Bartholomew and Hoel 1953	1951	Kitovi	Jun - Aug	12	Observation	7.2
Peterson 1965	1962	Kitovi	Jul - Oct	146	Observation	9.7
Peterson 1965	1963	Kitovi	Jul - Oct	85	Observation	8.0
Gentry and Holt 1986	1976	Kitovi	Jul - Nov	11	Observation	8.5
Gentry and Holt 1986	1977	Kitovi	Jul - Nov	26	Observation	7.1
Loughlin et al 1987	1984	Zapadni Reef	Jul - Aug	40	Radio transmitters	5.9
Goebel 2002	1995	Reef, Vostochni, Tolstoy	Jul - Nov	32	Radio transmitter	6.6
Robson et al. 2004	1995	Reef, Tolstoi, Vostochnoi, Polovina Cliffs	1-2 trips	21	TDR	8.8
Robson et al. 2004	1996	Reef, Vostochni	1-2 trips	31	TDR	8.0
Ream et al (unpub)	2005-2006	Reef, Vostochni	Jul - Nov	~40	TDR	6.5

Table 1.3. Studies that examined trip duration in northern fur seals at St. George Island. TDR stands for Time Depth Recorder.

Author	Study years	Rookery	Time observed	No. females observed	Method	Average trip length (days)
Gentry and Holt 1986	1974	East	Jul – Nov	11	Observation	5.7
Gentry and Holt 1986	1975	East	Jul – Nov	16	Observation	5.8
Gentry and Holt 1986	1976	East	Jul – Nov	6	Observation	6.4
Gentry and Holt 1986	1977	East	Jul – Nov	15	Observation	5.7
Gentry and Holt 1986	1976	Zapadni	Jul – Nov	31	Observation	6.1
Gentry and Holt 1986	1977	Zapadni	Jul - Nov	20	Observation	6.1
Gentry et al. 1986	1980 and 1982	East Reef	Jul	7	Early TDR (big)	7.5
Gentry 1998	1974-1978	Zapadni, East Reef	Jul - Aug	-	Observation	5.6
Gentry 1998	1979-1985	Zapadni, East Reef	Jul - Aug	-	Observation	4.4
Goebel 2002	1996	North, Staraya Artil, Zapadni	Jul - Nov	36	Radio transmitter	6.0
Robson et al. 2004	1995	North, Staraya, East, Zapadni/ South	1-2 trips	20	TDR	8.6
Robson et al. 2004	1996	North, Staraya, East, Zapadni/ South	1-2 trips	25	TDR	7.5

References

ADAMS, G. P., TESTA, J. W., GOERTZ, C. E. C., REAM, R. R. & STERLING, J. T. 2007. Ultrasonographic characterization of reproductive anatomy and early embryonic detection in the northern fur seal (*Callorhinus ursinus*) in the field. *Marine Mammal Science,* 23, 445-452.

AKASOFU, S. 2010. On the recovery from the little ice age. *Natural Science,* 2, 1211-1224.

ALLEN, B. M. & ANGLISS, R. P. 2010. Alaska Marine Mammal Stock Assessments, 2010. *NOAA Technical Memorandum NMFS-AFSC-223*

ALVERSON, D. L. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Review in Aquatic Sciences,* 6, 203-256.

ANAS, R. E. 1974. Heavy metals in the northern fur seal, *Callorhinus ursinus*, and harbor seal, *Phoca vitulina richardi*. *Fisheries Bulletin,* 72, 133-137.

ANDERSON, P. J. & PIATT, J. F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series,* 189, 117-123.

ANTONELIS, G. A. & PEREZ, M. A. 1984. Estimated annual food consumption by northern fur seals in the California current. *CalCOFI report,* XXV, 135-145.

ARNOULD, J. P. Y., BOYD, I. L. & SOCHA, D. G. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Canadian Journal of Zoology,* 74, 254-266.

BACON, C. E., JARMAN, W. M. & COSTA, D. P. 1992. Organochlorine and polychlorinated biphenyl levels in pinniped milk from the Arctic, the Antarctic, California and Australia. *Chemosphere,* 24, 779-791.

BAILEY, K. M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. *Marine Ecology Progress Series,* 6, 1-9.

BAILEY, K. M. 2000. Shifting control of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Marine Ecology Progress Series,* 198, 215-224.

BAILEY, K. M. 2011. An empty donut hole: the great collapse of a North American fishery. *Ecology and Society,* 16, 1-28.

BAKER, J. D. 1992. The feeding cycles of northern fur seals. *Alaska Fisheries Science Center Quarterly Report,* Jan-Mar 1992, 1-4.

BAKKALA, R. G., WESPESTAD, V. G. & LOW, L. 1987. Historical trends in abundance and current condition of walleye pollock in the Eastern Bering Sea. *Fisheries Research,* 5, 199-215.

BANCROFT, H. H. 1886. *History of Alaska 1730-1885,* San Francisco, A.L. Bancroft and Company.

BARNES, C. A. & THOMPSON, T. G. 1938. Physical and chemical investigations in the Bering Sea and portions of the North Pacific Ocean. *University of Washington Publications in Oceanography,* 3, 35-79.

BARTHOLOMEW, G. A. J. & HOEL, P. G. 1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. *Journal of Mammalogy,* 34, 417-436.

BEAMISH, R. J. 1993. Climate and exceptional fish production off the West coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 2270-2291.

BEAMISH, R. J. & BOUILLON, D. R. 1993. Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 1002-1016.

BEAMISH, R. J., NOAKES, D. J., MCFARLANE, G. A., KLYASHTORIN, L., IVANOV, V. V. & KURASHOV, V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences,* 56, 516-526.

BEAUPLET, G., BARBRAUD, C., CHAMBELLANT, M. & GUINET, C. 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology,* 74, 1160-1172.

BECKMEN, K. B. 1999. *Blood organochlorines, immune function and health of free ranging northern fur seal pups (Callorhinus ursinus).* PhD, University of Alaska Fairbanks.

BECKMEN, K. B., DUFFY, L. K., ZHANG, X. & PITCHER, K. W. 2002. Mercury concentrations in the fur of Steller sea lions and northern fur seals from Alaska. *Marine Pollution Bulletin,* 44, 1130-1135.

BECKMEN, K. B., YLITALO, G. M., TOWELL, R. G., KRAHN, M. M., O'HARA, T. & BLAKE, J. E. 1999. Factors affecting organochlorine contamination concentration in milk and blood of northern fur seal (*Callorhinus ursinus*) dams and pups from St. George Island Alaska. *The Science of the Total Environment,* 231, 183-200.

BEIJER, K. & JERNELOV, A. 1979. Methylation of mercury in aqautic environments. *In:* NRIAGU, J. O. (ed.) *The Biochemistry of Mercury in the Environment.* Amsterdam: Elsevier/North-Holland Biomedical Press.

BENSON, A. J. & TRITES, A. W. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries,* 3, 95-113.

BIGGS, M. A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off Western North America. *Canadian Technical Report of Fisheries and Aquatic Science.* Nanaimo, British Columbia: Pacific Biological Station.

BOLTNEV, A. I., YORK, A. E. & ANTONELIS, G. A. 1998. Northern fur seal young: interrelationships amoung birth size, growth and survival. *Canadian Journal of Zoology,* 76, 843-854.

BOND, N. A. & HARRISON, D. E. 2000. The Pacific Decadal Oscillation, air-sea interaction and central north Pacific winter atmospheric regimes. *Geophysical Research Letters,* 27, 731-734.

BOND, N. A. & OVERLAND, J. E. 2005. The importance of episodic weather events to the ecosystem of the Bering Sea shelf. *Fisheries Oceanography,* 14, 97-111.

BOYD, I. L., ARNOULD, J. P. Y., BARTON, T. & CROXALL, J. P. 1994. Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology,* 63, 703-713.

BRAHAM, H. W., EVERITT, R. D. & RUGH, D. J. 1980. Northern sea lion population decline in the eastern Aleutian Islands. *Journal of Wildlife Management,* 44, 25-33.

BRODEUR, R. D. & WARE, D. M. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fisheries Oceanography,* 1, 33-38.

BURD, M. A., HARVEY, J. T. & ANTONELIS, G. A. 1990. Enteric bacterial pathogens associated with northern fur seal pups on the Pribilof Islands and at Medley Island, U.S.S.R. *In:* KAJIMURA, H. & SINCLAIR, E. H. (eds.). *Fur seal investigations, 1990.* NOAA, AFSC, US Department of Commerce.

BURTON, R. K., SNODGRASS, J. J., GIFFORD-GONZALEZ, D., GUILDERSON, T., BROWN, T. & KOCH, P. L. 2001. Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna. *Oecologia,* 128, 107-115.

CARTY, A. J. & MALONE, S. F. 1979. The chemistry of mercury in biological systems. *In:* NRIAGU, J. O. (ed.) *The Biochemistry of Mercury in the Environment.* Amsterdam: Elsevier/North-Holland Biomedical Press.

CHAVEZ, F. P., RYAN, J., LLUCH-COTA, S. E. & NIQUEN, M. C. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science,* 299, 217-221.

CLARKSON, T. W. 1993. Mercury: major issues in environmental health. *Environmental Health Perspectives,* 100, 31-38.

COSTA, D. P., CROXALL, J. P. & DUCK, C. D. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology,* 70, 596-606.

COYLE, K. O., EISNER, L. B., MUETER, F. J., PINCHUK, A. I., JANOUT, M. A., CIECIEL, K. D., FARLEY, E. V. & ANDREWS, A. G. 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. *Fisheries Oceanography,* 20, 139-156.

DE SWART, R. L., ROSS, P. S., VOS, J. G. & OSTERHAUS, A. D. M. E. 1996. Impaired immunity in harbour seals (*Phoca vitulina*) exposed to bioaccumulated environmental contaminants: review of long term feeding study. *Environmental Health Perspectives* 104, 823-828.

DELONG, R. L. 2007. The dynamics of hookworm disease in northern fur seals. *Alaska Fisheries Science Center Quarterly Report,* April, May, June, 1-5.

DELONG, R. L., GILMARTIN, W. G. & SIMPSON, J. G. 1973. Births in California sea lions: association with high organochlorine pollutant residue levels. *Science,* 181, 1168-1170.

DEMASTER, D. P., TRITES, A. W., CLAPHAM, P., MIZROCH, S., WADE, P., SMALL, R. J. & VER HOEF, J. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. *Progress in Oceanography,* 68, 329-342.

DERRAIK, J. G. B. 2002. The pollution of the marine environment by plastic debris: A review. *Marine Pollution Bulletin,* 44, 842-852.

DOROFF, A. M. 2003. Sea otter population declines in the Aleutian Archipelago. *Journal of Mammalogy,* 84, 55-64.

EBBESMEYER, C. C., CAYAN, D. R., MCLAIN, D. R., NICHOLS, F. H., PETERSON, D. H. & REDMOND, K. T. 1991. 1976 step in the pacific climate: fourty environmental changes between 1968-1975 and 1977-1984. *In:* Seventh Annual Pacific Climate Workshop, 1990. California Department of Water Resources.

ESTES, J. A., DOAK, D. F., SPRINGER, A. M., WILLIAMS, T. M. & VAN VLIET, G. B. 2009. Trend data do support the sequential nature of pinniped and sea otter declines in the North Pacidic Ocean, but does it really matter? *Marine Mammal Science,* 25, 748-754.

ESTES, J. A., TINKER, M. T., WILLIAMS, T. M. & DOAK, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science,* 282, 473-476.

FELDKAMP, S. D., COSTA, D. P. & DEKREY, G. K. 1989. Energetic and behavioral effects of net entanglement on juvenile northern fur seals, *Callorhinus ursinus. Fishery Bulletin,* 87, 85-94.

FERRERO, R. C., DEMASTER, D. P., HILL, P. S., MUTO, M. M. & LOPEZ, A. L. 2000. Alaska Marine Mammal Stock Assessments. US Department of Commerce, NOAA, NMFS, AFSC, AK.

FISCUS, C. H. 1982. Predation by marine mammals on squids of the eastern North Pacific Ocean and the Bering Sea. *Marine Fisheries Review,* 44, 1-10.

FISCUS, C. H., BAINES, G. A. & KAJIMURA, H. 1965. Pelagic fur seal investigations, 1965. *U.S. Fish and Wildlife Service Special Scientific Report NMFS-AFSC-489.*

FISCUS, C. H., BAINES, G. A. & WILKE, F. 1964. Pelagic fur seal investigations, Alaska waters 1964. *U.S. Fish and Wildlife Service Special Scientific Report NMFS-AFSC-475.*

FISCUS, C. H. & KAJIMURA, H. 1965. Pelagic fur seal investigations, 1965. *U.S. Fish and Wildlife Service Special Scientific Report NMFS-AFSC-522.*

FORD, J. K. B., ELLIS, G. M., MATKIN, C. O., WETKLO, M. H., BARRETT-LENNARD, L. G. & WITHLER, R. E. 2011. Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology,* 11, 213-224.

FOWLER, C. W. 1982. Interactions of northern fur seals and commercial fisheries. *Transaction of the 47th North American Wildlife and Natural Resources Conference.*

FOWLER, C. W. 1987. Marine debris and northern fur seals: a case study. *Marine Pollution Bulletin,* 18, 326-335.

FOWLER, C. W., MERRICK, R. & BAKER, J. D. 1989. Studies of the population level effects of entanglement on northern fur seals. *Proceedings of the second international conference on marine debris,* NOAA-TM-NMFS-SWFSC-154, 453-474.

FOWLER, C. W. & RAGEN, T. J. 1990. Entanglement studies, St. Paul Island, 1989; Juvenile male roundups. *In:* NWAFS processed report 90-06.

FRANCIS, R. C. & HARE, S. R. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fisheries Oceanography,* 3, 279-291.

FRANCIS, R. C., HARE, S. R., HOLLOWED, A. B. & WOOSTER, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystem of the NE Pacific. *Fisheries Oceanography,* 7, 1-21.

FRITZ, L. W. & HINCKLEY, S. 2005. A critical review of the regime shift - "Junk Food" - nutritional stress hypothesis for the decline of the western stock of Steller sea lion. *Marine Mammal Science,* 21, 476-518.

FROST, K. J., LOWRY, L. F. & VER HOEF, J. M. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Marine Mammal Science,* 15, 494-506.

GENTRY, R. L. 1998. *Behavior and Ecology of the northern fur seal,* Princeton, NJ, Princeton University Press.

GENTRY, R. L. & HOLT, J. R. 1986. Attendance behavior of northern fur seals. *In:* GENTRY, R. L. & KOOYMAN, G. L. (eds.) *Fur Seals: Maternal Strategies on Land and at Sea.* Princeton, NJ.: Princeton University Press.

GENTRY, R. L., KOOYMAN, G. L. & GOEBEL, M. E. 1986. Feeding and diving behavior of northern fur seals *In:* GENTRY, R. L. & KOOYMAN, G. L. (eds.) *Fur seals: Maternal strategies on land and at sea.* Princeton, NJ.: Princeton University Press.

GOEBEL, M. E. 2002. *Northern fur seal lactation, attendance and reproductive success in two years of contrasting oceanography.* Ph.D. dissertation, University of California, Santa Cruz.

GRAHAM, N. E. 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: observations and model results. *Climate Dynamics,* 10, 135-162.

GREBMEIER, J. M., OVERLAND, J. E., MOORE, S. E., FARLEY, E. V., CARMACK, E. C., COOPER, L. W., FREY, K. E., HELLE, J. H., MCLAUGHLIN, F. A. & MCNUTT, S. L. 2006. A major ecosystem shift in the northern Bering Sea. *Science,* 311, 1461-1463.

GUINET, C., LEA, M.-A. & GOLDSWORTHY, S. D. 2000. Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands. *Canadian Journal of Zoology,* 78, 476-483.

HANNA, G. D. 1922. What becomes of the fur seals. *Science,* 55, 505-507.

HANSEN, J., SATO, M. & RUEDY, R. 2012. Perception of climate change. *Proceedings of the National Academies of Science,* doi:10.1073/pnsa.1205276109.

HARE, S. R. & FRANCIS, R. C. 1995. Climate change and salmon production in the Northeast Pacific Ocean. *In:* BEAMISH, R. J. (ed.) *Climate Change and Northern Fish Populations.* Canadian Special Publication of Fisheries and Aquatic Sciences.

HARE, S. R. & MANTUA, N. J. 2000. Empirical evidence for North Pacific regime shifts in the 1977 and 1989. *Progress in Oceanography,* 47, 103-145.

HARE, S. R., MANTUA, N. J. & FRANCIS, R. C. 1999. Inverse production regimes:Alaska and West coast Pacific salmon. *Fisheries,* 24, 6-14.

HOLLAND, M. M., BITZ, C. M. & TREMBLAY, B. 2006. Future abrupt reduction in the summer Arctic sea ice. *Geophysical Research Letters* 33, 1-5.

HOLLOWED, A. B., BARBEAUX, S. J., COKELET, E. D., FARLEY, E., KOTWICKI, S., RESSLER, P. H., SPITAL, C. & WILSON, C. D. 2012. Effects of climate variation on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. *Deep-Sea Research II,* 65-70, 230-250.

HOLLOWED, A. B., HALL, A. J. & WOOSTER, W. S. 2001. Pacific basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography,* 49, 257-282.

HOLLOWED, A. B. & WOOSTER, W. S. 1995. Decadal-scale variation in the eastern subarctic Pacific: II Response of Northeast Pacific fish stocks. *In:* BEAMISH, R. J. (ed.) *Climate Change and Northern Fur Seal Populations.* Canadian Journal of Fisheries and Aquatic Sciences.

HUNT, G. L. J., STABENO, P. J., STROM, S. & NAPP, J. M. 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof domain. *Deep-Sea Research II,* 55, 1919-1944.

HUNT, G. L. J., STABENO, P., WALTERS, G., SINCLAIR, E., BRODEUR, R. D., NAPP, J. M. & BOND, N. A. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research II,* 49, 5821-5853.

IKEMOTO, T., KUNITO, T., TANAKA, H., BABA, N., MIYAZAKI, N. & TANABE, S. 2004. Detoxification mechanism of heavy metals in marine mammals and seabirds: Interaction of selenium with mercury, silver, copper, zinc, and cadmium in liver. *Achives of Environmental Contamination and Toxocology,* 47, 402-413.

IPCC 2007. *Climate change 2007: The physical science basis.,* Cambridge, Cambridge University Press.

IRVINE, J. R. & FUKUWAKA, M. 2011. Pacific salmon abundance trends and climate change. *ICES Journal of Marine Science* 68, 1122-1130.

JOHNSON, A. M. 1968. Annual mortality of territorial male fur seals and its management significance. *Journal of Wildlife Management* 32, 94-99.

JONES, L. L. 1980. Estimates of the incidental take of northern fur seals in Japanese salmon gillnets in the North Pacific 1975-1979. *Background paper submitted to the 23rd annual meeting of the standing scientific committee of the North Pacific Fur Seal Commission.*

JONES, L. L. 1981. Incidental take of northern fur seals in Japanese salmon gillnets in the North Pacific Ocean 1980. *Background paper submitted to the 24th annual meeting of the standing scientific committee of the North Pacific Fur Seal Commission.*

JORDAN, D. S. 1898. *The fur seals and fur-seal islands of the North Pacific Ocean,* U.S. Govt. Printing Office, Washington D.C.

JUGO, S. 1979. The chemistry of mercury in biological systems. *In:* NRIAGU, J. O. (ed.) *The Biochemistry of Mercury in the Environment.* Amsterdam: Elsevier/North-Holland Biomedical Press.

KAJIMURA, H. 1984. Opportunistic feeding of the northern fur seal, Callorhinus ursinus, in the Eastern North Pacific Ocean and Eastern Bering Sea. *NOAA Technical Report NMFS-SSRF-779.*

KENYON, K. W., SCHEFFER, V. B. & CHAPMAN, D. G. 1954. A population study of the Alaska fur seal herd. *U.S. Fish and Wildlife Service Special Scientific Report,* 12, 77.

KENYON, K. W. & WILKE, F. 1953. Migration of the northern fur seal, *Callorhinus ursinus. Journal of Mammalogy,* 34, 86-98.

KEYES, M. KIM, K. C., DAILEY, M. D. & VEDROS, N. A. 1980. Veterinary medical services and research *In:* KOZLOFF, P. (ed.). *Fur seal investigations 1980* NMFS, NOAA, US Department of Commerce.

KEYES, M., STROUD, R. & KIM, K. C. 1979. Veterinary medical services and reseach. *In:* KOZLOFF, P. (ed.). *Fur seal investigations 1979.* NMFS, NOAA, US Department of Commerce.

KOOYMAN, G. L., GENTRY, R. L. & URQUHART, D. L. 1976. Northern fur seal diving behavior: A new approach to its study. *Science,* 193, 411-412.

KRAHN, M. M., BECKER, P. R., TILBURY, K. L. & STEIN, J. E. 1997. Organochlorine contaminants in blubber of four seal species: integrating biomonitoring and specimen banking. *Chemosphere,* 34, 2109-2121.

LANDER, R. H. 1980. Summary of northern fur seal data and collection procedures *Land Data of the United States and Soviet Union.* Seattle: Alaska Fisheries Science Center.

LANDER, R. H. & KAJIMURA, H. 1982. Status of northern fur seals. *Mammals in the Seas.* Food and Agriculture Organization. United Nations, Rome.

LARNTZ, K. & GARROTT, R. 1993. Analysis of 1991 bycatch of selected mammal species in the North Pacific neon squid driftnet fishery. *Final contract report prepared for the NMFS.*

LATIF, M. & BARNETT, T. P. 1994. Causes of decadal climate variability over the North Pacific and North America. *Science,* 226, 634-637.

LEA, M., JOHNSON, D., REAM, R. R., STERLING, J. T., MELIN, S. & GELATT, T. S. 2009. Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters,* 5, 252-257.

LLOYD, D. S., MCROY, C. P. & DAY, R. H. 1980. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslof Island, southeastern Bering Sea. *Arctic,* 34, 318-320.

LOUGHLIN, T. R., BENGSTON, J. L. & MERRICK, R. L. 1987. Characteristics of feeding trips of female fur seals. *Canadian Journal of Zoology,* 65, 2079-2084.

LOUGHLIN, T. R., CASTELLINI, M. A. & YLITALO, G. 2002. Spatial aspects of organochlorine contamination in northern fur seal tissues. *Marine Pollution Bulletin,* 44, 1024-1034.

LOUGHLIN, T. R., CONSIGLIERI, L., DELONG, R. L. & ACTOR, A. T. 1983. Incidental catch of marine mammals by foreign fishing vessels, 1978-1981. *Marine Fisheries Review,* 45, 44-49.

LOUGHLIN, T. R., INGRAHAM, W. J., BABA, N. & ROBSON, B. W. 1999. Use of a surface-current model and satellite telemetry to assess marine mammal movements in the Bering Sea. *In:* LOUGHLIN, T. R. & OHTANI, K. (eds.) *Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and A Synopsis of Research on the Bering Sea.* Fairbanks, Alaska: University of Alaska, Sea Grant.

LUCAS, F. A. 1899. The causes of mortality among seals. *In:* JORDAN, D. S. (ed.) *The Fur Seals and Fur Seal Islands of the North Pacific. Part 3.* Washington DC: US Government Printing Office.

MACKAS, D. L., TSURUMI, M., GALBRAITH, M. D. & YELLAND, D. R. 2005. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: II. Mechanisms of eddy colonization by and retention of offshore species. *Deep-Sea Research II,* 52, 1011-1035.

MANTUA, N. J., HARE, S. R., ZHANG, Y., WALLACE, J. M. & FRANCIS, R. C. 1997. A pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society,* 78, 1069-1079.

MATKIN, C. O., BARRETT-LENNARD, L. G., YURK, H., ELLIFRIT, D. & TRITES, A. W. 2007. Ecotype variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska. *Fishery Bulletin,* 105, 74-87.

MCCAFFERTY, D. J., BOYD, I. L., WALKER, T. R. & TAYLOR, R. I. 1998. Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology Progress Series,* 166, 285-299.

MCFARLANE, G. A., KING, J. R. & BEAMISH, R. J. 2000. Have there been recent changes in climate? Ask the fish. *Progress in Oceanography,* 47, 147-169.

MCGOWAN, J. A., CAYAN, D. R. & DORMAN, L. M. 1998. Climate-ocean variability and ecosystem response in the Northeastern Pacific. *Science,* 281, 210-217.

MERRICK, R. L. 1997. Current and historical roles of apex predators in the Bering Sea ecosystem. *Journal of Northwestern Atlantic Fishery Science,* 22, 343-355.

MERRICK, R. L., LOUGHLIN, T. R. & CALKINS, D. G. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus,* in 1956-1986. *Fishery Bulletin,* 85, 351-365.

MINOBE, S. 1997. A 50-70 year climatic oscillation over the North Pacific and North America. *Geophysical Research Letters,* 24, 683-686.

MIZOBATA, K. & SAITOH, S. 2004. Variability of Bering Sea eddies and primary production along the shelf edge during 1998-2000 using satellite multisensor remote sensing. *Journal of Marine Systems,* 50, 101-111.

MIZROCH, S. A. & RICE, S. W. 2006. Have North Pacific killer whales switched prey species in response to depletion of the great whale population? *Marine Ecology Progress Series,* 310, 235-246.

MUETER, F. J., BOND, N. A., IANELLI, J. N. & HOLLOWED, A. B. 2011. Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under climate change. *ICES Journal of Marine Science,* 68, 1284-1296.

MUETER, F. J., BROMS, C., DRINKWATER, K. F., FRIEDLAND, K. D., HARE, J. H., HUNT, G. L. J., MELLE, W. & TAYLOR, M. 2009. Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. *Progress in Oceanography,* 81, 93-110.

MUETER, F. J., LADD, C., PALMER, M. C. & NORCROSS, B. L. 2006. Bottom-up and top-down control of walleye pollock (*Theragra chalcogramma*) on the eastern Bering Sea shelf. *Progress in Oceanography,* 68, 152-183.

MUETER, F. J. & LITZOW, M. A. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications,* 18, 309-320.

NAPP, J. M. & HUNT, G. L. J. 2001. Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and biology. *Fisheries Oceanography,* 10, 61-68.

NEWMAN, K. & SPRINGER, A. M. 2008. Nocturnal activity by mammal-eating killer whlaes at a predation hot spot in the Bering Sea. *Marine Mammal Science,* 24, 990-999.

NEWSOME, S. D., ETNIER, M. A., GIFFORD-GONZALEZ, D., PHILLIPS, D. L., VAN TUINEN, M., HADLY, E. A., COSTA, D. P., KENNETT, D. J., GUILDERSON, T. P. & KOCH, P. L. 2007. The shifing baseline of northern fur seal ecology in the northeast Pacific Ocean. *Proceedings of the National Academy of Sciences of the United States of America,* 104, 9709-0714.

NIEBAUER, H. J., ALEXANDER, V. & HENRICHS, S. M. 1995. A time-series study of the spring bloom at the Bering Sea ice edge I. Physical processes, chlorophyll and nutrient chemistry. *Continental Shelf Research,* 15, 1859-1877.

NMFS 1992. Recovery plan for the Steller sea lion (*Eumetopias jubatus*). Steller sea lion recovery team for the National Marine Fisheries Service, Silver Spring, MD.

NMFS 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*). The National Marine Fisheries Service, Alaska Fisheries Science Center. Seattle, WA.

NMFS 2007. Conservation plan for the Eastern Pacific stock of northern fur seals (*Callorhinus ursinus*). National Marine Fisheries Service, Juneau, AK.

NMML 1998. Incidence of fungal infections of the palage in northern fur seals during 1998. *In:* ROBSON, B. W. (ed.). *Fur Seal Investigations 1998*. AFSC, NOAA, US Department of Commerce.

NOAKES, D. J. & BEAMISH, R. J. 2009. Synchrony of marine fish catches and climate and ocean regime shifts in the North Pacific Ocean. *Marine and Coastal Fisheries* 1, 155-168.

NODA, K., ICHIHASHI, H., LOUGHLIN, T. R., BABA, N., KIYOTA, M. & TATSUKAWA, R. 1995. Distribution of heavy metals in muscle, liver, and kidney of northern fur seal (*Callorhinus ursinus*) caught off Sanriku, Japan and from the Pribilof Islands, Alaska. *Environmental Pollution,* 99, 51-59.

OLSEN, O. W. & LYONS, E. T. 1965. Life cycle of *Unicinaria lucasi* stiles, 1901 (Nematoda:Ancylostomatidae) of fur seals, *Callorhinus ursinus* Linn., on the Pribilof Islands, Alaska. *The Journal of Parasitology,* 51, 689-700.

ONO, K. A. & BONESS, D. J. 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behavioral Ecology and Sociobiology,* 38, 31-41.

OVERPECK, J., HUGHEN, K., HARDY, D., BRADLEY, R., CASE, R., DOUGLAS, M., FINNEY, B., GAJEWSKI, K., JACOBY, G. C., JENNINGS, A., LAMOUREUX, S., LASCA, A., MACDONALD, G., MOORE, J., RETELLE, M., SMITH, S., WOLFE, A. & ZIELINSKI, G. 1997. Environmental change of the last four centuries. *Science,* 278, 1251-1256.

OVERLAND, J. E., ADAMS, J. M. & BOND, N. A. 1999. Decadal variability of the Aleutian Low and its relation to high-latitude circulation. *Journal of Climate,* 12, 1542-1548.

OVERLAND, J. E. & STABENO, P. J. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem. *EOS,* 85, 309-316.

PEREZ, M. A. 2006. Analysis of marine mammal bycatch data from the trawl, longline, and pot groundfish fisheries of Alaska, 1998-2004, defined by geographic area, gear type, and target groundfish catch species. *NOAA Technical Memorandum NMFS-AFSC-167.*

PEREZ, M. A. & BIGGS, M. A. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western north America. *Fishery Bulletin,* 84, 957-971.

PEREZ, M. A. & LOUGHLIN, T. R. 1991. Incidental catch of marine mammals by foreign-directed and joint venture fishing vessels in the US EEZ of the North Pacific, 1973-1988. *NOAA Tchnical Report NMFS-104*

PETERSON, R. S. 1965. *Behavior of the northern fur seal.* Ph.D., John Hopkins University.

PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science,* 6, 121-134.

POLOVINA, J. J., MITCHUM, G. T. & EVANS, G. T. 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific. *Deep-Sea Research I,* 42, 1701-1716.

REAM, R. R., BAKER, J. D. & TOWELL, R. G. 2000. Foraging ecology and population growth of northern fur seals on Bogoslof Island, Alaska. *Marine Mammals of the Holarctic Regions.* Archangelsk, Pravada Severa.

REAM, R. R., STERLING, J. T. & LOUGHLIN, T. R. 2005. Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research II* 52, 823-843.

REIJNDERS, P. J. H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters *Nature,* 324, 456-457.

ROBSON, B. W., GOEBEL, M. E., BAKER, J. D., REAM, R. R., LOUGHLIN, T. R., FRANCIS, R. C., ANTONELIS, G. A. & COSTA, D. P. 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology,* 82, 20-29.

ROEMMICH, D. & MCGOWAN, J. A. 1995. Climatic warming and the decline of zooplankton in the California Current. *Science,* 267, 1324-1326.

ROPPEL, A. Y. & DAVEY, S. P. 1965. Evolution of fur seal management on the Pribilof Islands. *Journal of Wildlife Management,* 29, 448-463.

ROSENKRANZ, G. E., TYLER, A. V., KRUSE, G. H. & NIEBAUER, H. J. 1998. Relationship between wind and year class strength of tanner crabs in the Southeastern Bering Sea. *Alaska Fishery Research Bulletin,* 5, 18-24.

ROSS, P. S., DE SWART, R. L., REIJNDERS, P. J. H., LOVEREN, H. V., VOS, J. G. & OSTERHAUS, A. D. M. E. 1995. Contaminant-related suppression of delayed-type hypersensitivity and antibody responses in harbor seals fed herring from the Baltic Sea. *Environmental Health Perspectives,* 103, 162-167.

SAFE REPORT 2012. Stock assessment and fisheries evaluation report for the groundfish resources of the Bering Sea/Aleutian Island region. Compiled by the planning team for the groundfish fisheries of the Bering Sea and Aleutian Islands, Anchorage, AK.: North Pacific Fisheries Management Council.

SALATHE, E. P. J. 2006. Influences of a shift in North Pacific storm tracks on western North American precipitation under global warming. *Geophysical research letters,* 33, 1-4.

SCHEFFER, V. B. 1950. Growth layers on the teeth of pinnipedia as an indication of age. *Science,* 112, 309-311.

SCHUMACHER, J. D., BOND, N. A., BRODEUR, R. D., LIVINGSTON, P. A., NAPP, J. M. & STABENO, P. J. 2003. Climate change in the southeastern Bering Sea and some consequences for biota. *In:* HEMPLER, G. & SHERMAN, H. A. (ed.) *Large Marine Ecosystems of the World - Trends in Exploitation, Protection and Research.* Amsterdam, Netherlands: Elsevier.

SINCLAIR, E. H., LOUGHLIN, T. R. & PEARCY, W. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. *Fishery Bulletin,* 92, 144-156.

SINCLAIR, E. H., VLIETSTRA, L. S., JOHNSON, D. S., ZEPPELIN, T. K., BYRD, G. V., SPRINGER, A. M., REAM, R. R. & HUNT, G. L. J. 2008. Patterns in prey use among fur seals and seabirds in the Pribilof Islands. *Deep-Sea Research II,* 55, 1897-1918.

SMALL, R. J. 2003. Trends in abundance of Alaska harbor seals, 1983-2001. *Marine Mammal Science,* 19, 344-362.

SMALL, R. J., BOVENG, P. L., BYRD, G. V. & WITHROW, D. E. 2008. Harbor seal population decline in the Aleutian Archipelago. *Marine Mammal Science,* 24, 845-863.

SMITH, A. W., BROWN, R. J., SKILLING, D. E., BRAY, H. L. & KEYES, M. C. 1977. Naturally-occurring Leptospirosis in northern fur seals (*Callorhinus ursinus*). *Journal of Wildlife Diseases,* 13, 144-148.

SPRINGER, A. M., ESTES, J. A., VAN VLIET, G. B., WILLIAMS, T. M., DOAK, D. F. & DANNER, E. M. 2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: a reply to critics of Springer et al. 2003. *Marine Mammal Science,* 24, 414-442.

SPRINGER, A. M., ESTES, J. A., VAN VLIET, G. B., WILLIAMS, T. M., DOAK, D. F., DANNER, E. M., FORNEY, K. A. & PFISTER, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences,* 100, 12223-12228.

SPRINGER, A. M., REAM, R. R. & IVERSON, S. J. 2010. Seasonal foraging strategies and consequences for northern fur seals at colonies with opposite population trends - year 2. *North Pacific Research Board Project Final Report.*

STABENO, P. J., BOND, N. A., KACHEL, N. B. & SCHUMACHER, J. D. 2001. On the temporal variability of the physicial environment over the south-eastern Bering Sea. *Fisheries Oceanography,* 10, 81-89.

STABENO, P. J., FARLEY, E. V., KACHEL, N. B., MOORE, S., MORDY, C. W., NAPP, J. M., OVERLAND, J. E., PINCHUK, A. I. & SIGLER, M. F. 2012. A comparison of the physics of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem. *Deep-Sea Research II,* 65-70, 14-30.

STERLING, J. T. 2009. *Northern fur seal foraging behaviors, food webs, and interactions with oceanographic features in the eastern Bering Sea.* Ph.D. Dissertation, University of Washington.

STERLING, J. T. & REAM, R. R. 2004. At-sea behavior of juvenile male northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Zoology,* 82, 1621-1637.

TANABE, S., SUNG, J., CHOI, D., BABA, N., KIYOTA, M., YOSHIDA, K. & TATSUKAWA, R. 1994. Persistent organochlorine residues in northern fur seal from the Pacific coast of Japan since 1971. *Environmental Pollution,* 85, 305-314.

TOWELL, R. G., REAM, R. R. & YORK, A. E. 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. *Marine Mammal Science,* 22, 486-491.

TRITES, A. W., DEECKE, V. B., GREGR, E. J., FORD, J. K. B. & OLESIUK, P. F. 2007. Killer whales, whaling, and sequential megafaunal collapse in the North Pacific: a comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. *Marine Mammal Science,* 23, 751-765.

VER HOEF, J. M. & FROST, K. J. 2003. A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environmental and Ecological Statistics,* 10, 201-219.

VLADIMIROV, V. A. 1983. On reproductive biology of sea bear females on the Urilye rookery (Mednyi Island). *Biulleten' Moskovskogo Obshchestvo ispytatelei prirody. Otdel Biologicheskii.* In Russian with English subtitles ed.

VLADIMIROV, V. A. 1987. Age Specific reproductive behavior of northern fur seals on the Commander Islands. *In:* CROXALL, J. P. & GENTRY, R. L. (eds.) *Status, Biology, and Ecology of Fur Seals: Proceedings of an International Symposium and Workshop.* Cambridge, England.

WADA, K. 1971. Food and feeding habit of northern fur seals along the coast of Sanriku. *Bulletin of Tokai Regulatory Fisheries Research Laboratory,* 64, 1-37.

WADE, P. R., BURKANOV, V. N., DAHLHEIM, M. E., FRIDAY, N. A., FRITZ, L. W., LOUGHLIN, T. R., MIZROCH, S. A., MUTO, M. M. & RICE, D. W. 2007. Killer whales and marine mammal trends in the North Pacific - a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. *Marine Mammal Science,* 23, 766-802.

WHITEHEAD, H. & REEVES, R. 2005. Killer whales and whaling: the scavenging hypothesis. *Biology Letters,* 1, 415-418.

WILKE, F. & KENYON, K. W. 1952. Notes on the food of fur seal, sea lion, and harbor porpoise. *The Journal of Wildlife Management,* 16, 396-397.

WILKE, F. & KENYON, K. W. 1954. Migration and food of the northern fur seal. *Nineteenth North American Wildlife Conference Procedings,* 19, 430-441.

WILKE, F. & KENYON, K. W. 1957. The food of fur seals in the Eastern Bering Sea. *The Journal of Wildlife Management,* 21, 237-238.

WILLIAMS, T. M., ESTES, J. A., DOAK, D. F. & SPRINGER, A. M. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology,* 85, 3373-3384.

WITHERELL, D. & PAUTZKE, C. 1997. A brief history of bycatch management measures for eastern Bering Sea groundfish fisheries. *Marine Fisheries Review,* 59, 15-22.

WYLLIE-ECHEVERRIA, T. & WOOSTER, W. S. 1998. Year-to-year variation in Bering Sea ice cover and some consequences for fish distributions. *Fisheries Oceanography,* 7, 159-170.

YORK, A. E. & HARTLEY, J. R. 1981. Pup production following harvest of female northern fur seals *Canadian Journal of Fisheries and Aquatic Sciences,* 38, 84-90.

ZAVADIL, P. A. 2008. Subsistence fur seal harvest on St. Paul Island. . *Memorandum for the record, December 7, 2008.* St. Paul Island, Pribilof Islands, Alaska: Aleut Community of St. Paul Island, Tribal Government, Ecosystem Conservation Office

ZAVADIL, P. A., ROBSON, B. W., LESTENKOF, A. D., HOLSER, R. & MALAVANSKY, A. 2007. Northern fur seal entanglement studies on the Pribilof Islands in 2006. *available online:* *http://doc.nprb.org/web/research/research%20pubs/outside_publications/733_entanglement.pdf.*

ZEPPELIN, T. K. & REAM, R. R. 2007. Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska. *Journal of Zoology,* 270, 565-576.

ZHENG, J. & KRUSE, G. H. 2006. Recruitment variation of Eastern Bering Sea crabs: climate-forcing or top-down effects? *Progress in Oceanography,* 68, 184-204.

CHAPTER 2

Proximate composition of northern fur seal milk: sources of variability and comparisons between rookeries in the Bering Sea with opposing foraging strategies[1]

Abstract

Knowledge of the composition of northern fur seal (*Callorhinus ursinus*) milk is needed to examine the energetics of pup growth and body condition at weaning, two necessary factors in evaluating the possible reasons for divergent population trends of fur seals on the Pribilof Islands (continental shelf, declining population) and Bogoslof Island (Aleutian Islands, deep basin, growing population), Alaska. In this study milk samples were collected from female fur seals at St. Paul Island (Pribilofs) and Bogoslof Island in 2005 and 2006 during the perinatal period in early July and again near the end of the breeding season in October, approximately three-fourths through the lactation period. Island and rookery (representing divergent foraging/nursing patterns), year, time ashore, days postpartum, preceding foraging trip duration, female mass, July milk composition, and milk withdrawal volume were used as potential independent variables in multivariate regression analyses to identify sources of variability in milk composition. There was no difference in the composition of perinatal milk from females at the two islands in July (lipid ~ 46%, protein ~ 10%, and energy ~ 21 kJ/g; $p \geq 0.18$). In October, the factors island, time ashore, days postpartum, preceding trip duration, and July milk composition explained variability in milk lipid and the factors time ashore, days postpartum, and July milk composition explained the variability in milk energy content. In October, lipid content averaged 53.8±1.0% at St. Paul Island and 57.3±0.8% at Bogoslof Island ($p < 0.01$) and energy content averaged 24.0±0.4 kJ/g at St. Paul Island and 25.2±0.3 kJ/g at Bogoslof Island ($p = 0.11$). On average milk lipid content increased 22% from July to

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October, protein remained relatively stable with averages ranging between 10.0% and 10.5%, and total energy content increased by 20%. The lipid content of northern fur seal milk near peak lactation is the highest reported among otariid seals and is comparable to the highest known for phocid seals, making it among the highest known for all mammals. This is consistent with the short lactation length and long foraging trip durations typical in northern fur seals.

Introduction

The northern fur seal (*Callorhinus ursinus*) population on the Pribilof Islands (Pribilofs), Alaska, has been declining since the 1960s and is now less than 30% of its former size (Towell et al., 2006). There have been two known historic population declines before the present one; the first in the late 1700s and early 1800s due to summer overharvesting at the rookeries, and the second in the late 1800s and early 1900s due to a year round unregulated pelagic harvest (Roppel and Davey, 1965). However, in both cases when regulations on harvests were implemented the population recovered. What is unusual about the current decline is that there is no known explanation, and efforts to reduce possible causes, such as eliminating commercial harvesting and reducing entanglement in fishing debris, have been ineffective. Currently, the three leading hypotheses for the ongoing decline are nutritional limitation in the Bering Sea, predation, and/or conditions in the North Pacific where fur seals spend the winter (Springer et al., 2003, Sinclair et al., 2008, Sterling, 2009).

Bogoslof Island (Bogoslof), a small rookery located approximately 200 miles south of the Pribilofs, has been experiencing exponential growth (R^2=0.91) since its establishment more than 30 years ago (Lloyd et al., 1980, NMFS, 2007). Bogoslof and the Pribilofs differ in several ways. The Pribilofs are located on the Bering Sea continental shelf, whereas Bogoslof is located off the Aleutian Islands chain in the deep ocean domain. Females from the Pribilofs typically make 5-9 day foraging trips to provision their pups, whereas females from Bogoslof make 1-2 day foraging trips (Ream et al., 2000, Robson et al., 2004). Females from the Pribilofs also travel about 2-3 times farther than females from Bogoslof to find food (Ream et al., 2000, Robson et al., 2004). There is a separation of foraging habitat among rookery sites on the Pribilofs but not on Bogoslof, diets on St. Paul Island (St. Paul, one of the Pribilof Islands) differ based on where females forage, and diets at St. Paul differ from diets at Bogoslof (Ream et al., 2000, Robson et al., 2004, Zeppelin and Ream, 2007). These differences can have implications for individuals as well as populations.

Lactation is the most energetically demanding period in the life cycle of female mammals and factors that affect energy acquisition, prior to and/or during the lactation period, affect provisioning to offspring (Oftedal, 1984, Iverson, 2007). Milk is the primary source of energy and nutrients that mammalian neonates receive before they are weaned. Milk composition, milk output, frequency of nursing, and length of lactation all affect how much energy a neonate receives over the lactation period and this varies in a variety of ways among species and to a lesser extent among individuals. Otariid seals (fur seals and sea lions) generally store a limited amount of energy as fat in a layer of blubber prior to giving birth to a single pup on land. These energy reserves allow females to remain on shore for an approximate one-week perinatal period after the pup is born but they are not sufficient to support a female and pup through the entire lactation period such as in phocid seals. Because of the spatial and temporal separation between land breeding sites and marine prey resources, otariid seals begin alternating between foraging trips to sea and nursing trips to shore to feed their pups for the remaining lactation period until weaning.

The lactation length of northern fur seals is approximately 4 months, during which time females must deliver enough energy to their pups for growth and survival and the transition to nutritional independence. The differences in female foraging strategies between St. Paul and Bogoslof should affect rates and/or quality of energy delivery to pups. For example, the longer foraging trips of females from St. Paul result in longer periods of fasting by pups between meals than at Bogoslof (Springer et al., 2010). St. Paul females also feed their pups fewer times over the entire lactation period compared to females at Bogoslof (Springer et al., 2010). These factors can have consequences to a pup's growth profile and condition at weaning which may affect their likelihood of survival.

In order to assess factors that may be contributing to differing population trajectories of northern fur seals in the Bering Sea, a study was undertaken to assess the lactation strategies of fur seals at Bogoslof and St. Paul. Two components central to understanding the energetics of lactation are accurate information on the milk composition of individual females and the potential sources of variability. Based on previous studies of milk composition in northern fur seals and other orariids, it has variously been proposed that days postpartum, foraging trip duration, time ashore, maternal diet, and maternal mass may affect milk composition and overall energy transfer to pups (Oftedal, 1984, Costa and Gentry, 1986, Trillmich and Lechner, 1986, Arnould and Boyd, 1995a, Arnould and Hindell, 1999, Goldsworthy and Crowley, 1999, Georges et al., 2001, Goebel, 2002). Although some of these factors have been included based on an understanding of the variables that affect the regulation of milk composition in mammals (e.g. days postpartum), others do not (e.g., maternal mass or diet; Oftedal and Iverson, 1995), but continue to be explored in the literature. Our study compared the milk composition of females from two contrasting populations and examined multiple variables that might contribute to individual variation. Knowledge about what factors affect provisioning can provide insight into differences in pup growth, development and survival and ultimately add to our understanding about the potential causes of the divergent population trends of fur seals in the Bering Sea.

Methods

Study area

This study was conducted in 2005 and 2006 at St. Paul Island, located in the middle shelf domain of the eastern Bering Sea (57°07'17"N, 170°16'24"W); and Bogoslof Island, located in the deep ocean basin off the eastern Aleutian Islands

(53°55'37"N, 168°02'03"W) (Figure 2.1). Collections on St. Paul were made at Vostochni rookery, located on the north end of the island, and Reef rookery, located on the southeastern tip of the island (Figure 2.2). Adult female fur seals at Vostochni forage to the north on the shallow continental shelf, whereas females at Reef tend to forage to the west near the continental shelf edge and in the basin, as well as to the east on the southeastern shelf—there is almost no overlap in the foraging areas of females from the two rookeries (Robson et al., 2004). Fur seals were sampled from two adjacent sites on Bogoslof, but separation of foraging habitat was not distinguishable (R. Ream pers. comm.).

Capture and sampling

The same protocols for animal captures and sample collections were followed at both study locations in 2005 and 2006. Females were captured and restrained following the techniques of Gentry and Holt (1982). Modifications to minimize the handling stress to animals were made in 2006. Specifically, females and pups were held in large boxes with holes or in large kennels instead of on restraint boards. All females had white vibrissae indicating that they were at least 7 years of age (Scheffer, 1962).

The first samples were collected in July, during the approximate one-week perinatal period, when pups were about 24-72 hours old. The identification of a pup of this age was based on the presence of a fresh umbilicus. A minimum period of 24 hours was allowed to pass before capture so that there was sufficient time for the mother-pup bond to form. Upon capture, females were administered an intramuscular dose of 0.25 ml oxytocin to facilitate milk let-down. Milk samples were collected by manual expression and ranged from 0.2-26 ml in volume. Mother and pup were weighed to the nearest 0.5 kg and VHS (Advanced Telemetry Systems) and satellite linked transmitters (MK9, Wildlife Computers) were attached to the back (between the shoulder blades) of the female using epoxy prior to release to monitor time ashore and trip duration. Mother and pup were released together. Milk samples were frozen shortly after collection and stored until analysis could be completed.

The same females that were sampled in July were recaptured in October of the same year; this was approximately 90 days postpartum and within approximately 35 days of when pups are typically weaned. Two different sets of females were studied in 2005 and 2006. Milk samples were collected on Bogoslof from 19 females in 2005 and 20 females in 2006 and on St. Paul from 21 females in 2005 and 19 females in 2006. A slightly reduced number of females was sampled in October (17 in 2005 and 19 in 2006 on Bogoslof; 16 in 2005 and 16 in 2006 on St. Paul), as not all females could be recaptured.

Laboratory analysis

Laboratory analysis of the milk was conducted at the University of Alaska Fairbanks and at Dalhousie University. Samples were thawed and homogenized before each analysis. Dry matter was determined using forced air convection drying of a 1 g subsample at 100°C for 5 hours. Lipid content was measured from a separate 1 g subsample using the Roese-Gottlieb method (Cunniff, 1995). Total nitrogen (TN) was measured from a 0.1 g subsample on a LECO truSpec CN analyzer and crude protein was determined by using the conversion factor TN x 6.38 (Cunniff, 1995). Duplicate samples were analyzed for each milk constituent and additional samples were analyzed if the difference between the first two samples was greater than 10%. Carbohydrate was not measured because it generally represents less than 1% of the total mass of pinniped milk (Oftedal et al., 1987). Gross energy was calculated using energy density values for lipid (39.8 KJ/g) and protein (23.9 KJ/g) (Kleiber, 1975).

Statistical analysis

Student's t-tests and linear regression analysis were used to explore the basic relationships between the variables, and multiple regression analysis was used to determine which variables, when assessed together, were predictors of milk composition. The dependent variables lipid %, protein % and energy content were analyzed separately. Dry Matter includes lipid and protein, and water is inversely related to dry matter, so neither of these dependent variables was included in the analyses. The independent variables that were used in the multiple regression analysis of July milk data were island, rookery, year (i.e., representing divergent foraging/nursing strategies or potential environmental perturbations), female mass (variously assumed to relate to milk composition in previous studies), and milk sample volume. The independent variables that were used in the October analysis were island, rookery, year, days postpartum, preceding trip duration, female time ashore since the last foraging bout (time ashore), female mass, individual July milk composition, and milk sample volume. To improve the precision of the multiple regression model, backward elimination was used to remove variables that were not significant. The lipid % values for one female from Bogoslof in July and one female from Bogoslof in October were determined to be outliers through casewise analysis of the residuals. Outliers were classified when the individual residual was more than three times the standard deviation of the residuals. Only females that had data for each of the independent variables were used in this analysis (July lipid % N=76, protein % N=71, water % N=71, and energy content N=70; October lipid % N=57, protein % N=56, water % N=54, and energy content N=51)

Paired t-tests and linear regression analyses were used to assess the differences between July and October milk samples. Only samples from females that were captured from both times were used in this analysis. Three females from Bogoslof were determined to be outliers using casewise analysis of the residuals. A total of 65 samples were used in the analysis of lipid % and 57 samples were used in the analysis of protein % and energy content (KJ/g).

Results

Rookeries – St. Paul

An initial multiple regression analysis determined that rookery location on St. Paul was not a predictor of milk lipid % (p=0.83), protein % (p=0.77), or energy content (p=0.88) in July, or milk lipid % (p=0.32), protein % (p=0.99), or energy content (p=0.50) in October. Because of this, Vostochni and Reef rookeries were grouped together as single samples from St. Paul for July and October.

July

There was high variability in the milk composition between females in July—dry matter ranged from 47.0% to 66.7% (CV = 7.3), lipid ranged from 33.3% to 54.3% (CV = 9.1), protein content ranged from 7.7% to 13.0% (CV = 10.7), and energy content ranged from 16.7 KJ/g to 24.3 KJ/g (CV = 7.9). The average milk composition was 57.2% dry matter, 45.7% lipid, 10.2% protein, and 20.6 KJ/g energy. None of the independent variables tested had an effect on milk composition (Table 2.1).

October

As in July, we found high overall variability between females in October—dry matter ranged from 49.5% to 76.6% (CV = 8.0), lipid ranged from 38.5% to 66.3% (CV = 10.0), protein content ranged from 8.3% to 13.4% (CV = 11.5), and energy content ranged from 17.7 KJ/g to 28.5 KJ/g (CV = 8.6). The average milk composition was 67.6% dry matter, 55.6% lipid, 10.3% protein, and 24.7 KJ/g energy.

The independent variables island, time ashore, days postpartum, preceding trip duration and July value were determined to be predictors of October lipid and the variables time ashore, days postpartum, and July value were predictors of October energy content (Table 2.2). The variables year, female mass, and milk volume were not predictors of milk composition, so they were removed from the analysis using backward elimination (for year lipid p=0.92, protein p=0.30, and energy p=0.57; for female mass lipid p=0.48, protein p=0.17, and energy p=0.62; for milk volume lipid p=0.92, protein p=0.09 and energy content p= 0.99). None of the independent variables were related to protein % so the following analyses only include the dependent variables lipid % and energy content.

Island was a predictor of milk lipid so comparisons of milk composition were made between Bogoslof and St. Paul (Table 2.2). The average milk composition for each island in July and October is listed in Table 2.3. Milk composition differed between the two islands by 4% in dry matter, 7% in lipid, 5% in protein and 5% in energy content.

Time ashore predicted milk lipid % and energy content in October (Table 2.2) and the effect of time ashore on milk lipid % was the same at each island (the slopes of the regression lines from the two islands were not significantly different, $p=0.95$) so the data were combined to estimate the change per hour ashore (Figure 2.3). If we assume that the rate of change was linear, milk lipid decreased by approximately 0.29% per hour and energy content decreased 0.12 KJ/g per hour during a shore visit. However, the rate of change does not appear to be linear over the entire shore visit. During the first 10 hours, milk lipid ranged between 50.0% and 66.3% but a linear relationship was not apparent ($R^2<0.01$, $p=0.98$). When assessing only samples collected after 10 hours, milk lipid decreased by approximately 0.31% per hour and energy content decreases 0.13 KJ/g per hour ($R^2=0.3$, $p<0.01$).

Days postpartum also predicted milk lipid % and energy content (Table 2.2). Figure 2.4 illustrates the change in lipid, protein and energy content between July and October. The 21.6% change in lipid and the 19.8% change in energy content were significant ($p<0.01$) but the 2.6% change in protein was not ($p = 0.22$). If we assume that there was a continuous increase in milk lipid % and energy content between the July and October sampling periods in this study, lipid would have increased by approximately 0.11% per day and energy content would have increased by approximately 0.04 KJ/g per day. Efforts were made to collect samples at the same number of days postpartum at each location and during each year; however, samples from Bogoslof were collected at an average of 94 days postpartum in 2005, which was significantly later than samples that were collected at an average of 87 days postpartum on Bogosof in 2006 ($p<0.01$), 89 days postpartum on St Paul in 2005 ($p=0.03$) and 89 days postpartum on St. Paul in 2006 ($p<0.01$).

July milk lipid % predicted October milk lipid % and July energy content predicted October energy content (Table 2.2). In general, individuals that had milk with higher lipid % in July also had higher lipid % in October (Figure 2.5). There were four exceptions to this trend – one female from Bogoslof and three females from St. Paul had milk that decreased slightly in lipid between July and October; however, when the October values were adjusted for time ashore all female milk increased in lipid % between July and October.

Discussion

Comparing northern fur seal milk composition results between studies and species

The lipid content of northern fur seal milk that we sampled in October at an average of 90 days postpartum, approximately three-fourths through the lactation period, is the highest known among otariid seals, where meaningful comparisons can be made, and is comparable to the highest reported for phocid seals (Table 2.4). If, as Goebel (2002) reported, the average lipid content of northern fur seal milk increases through at least 108 days of the lactation period, then it is possible that lipid content would reach even higher peak values than those recorded in this study.

Lipid is the most variable constituent of milk and ranges from just 0.2% in the black rhinoceros to around 60% in some phocid seals (Iverson, 2007). In general, the most dilute milks are produced by species that nurse frequently and on demand such as the odd-toed ungulates, primates and some even-toed ungulates; and the most concentrated milks are produced by species that nurse infrequently and on a scheduled basis such as the lagomorphs, some rodents and some carnivores (Oftedal, 1984, Iverson, 2007). Pinnipeds likely evolved to have very high milk lipid content because their foraging habitat is spatially and temporally separated from their land breeding sites on land or ice. Female otariid seals make foraging trips during lactation that range in length from 1-10 days, whereas female phocid seals typically fast on shore. The highly concentrated milk in pinnipeds enables females to transfer the required energy to pups to meet all of their physiological requirements over short intervals.

Comparison of our data on milk composition to data from past studies on northern fur seals and other pinniped species can be problematic for a number of reasons. Several northern fur seal milk composition studies have been conducted since the 1960s (Table 2.5), but sampling, analysis, and reporting methodologies varied. Sample size was very small in at least one early study (Ashworth et al., 1966), and in another the milk was removed from the mammary glands of dead adult females (Dosako et al., 1983), which can lead to the inclusion of blood in the sample (Oftedal, 1984). Costa and Gentry (1986) collected samples directly from females and had a relatively large sample size, but they only covered the first half of the 4-month lactation period so results did not include higher lipid content milk that is produced later in the season. Costa and Gentry (1986) also derived milk protein content by subtraction from lipid, water, and ash, which is known to compound errors from other measurements and to overestimate protein content (Goebel 2002). The study conducted by Goebel (2002) had a large sample size, included milk from nearly the entire lactation period, and used comparable methods to measure milk composition, but reported only an average milk composition for the entire lactation period. Goebel (2002) did report coefficients for regressions of lipid and energy content versus days postpartum. According to those equations, at 90 days postpartum (the average number of days among our females in October), average milk lipid content would be 57.5% and energy content would be 24.6 KJ/g. These values are close to our results from Bogoslof (57.3% lipid and 25.2 KJ/g energy) and comparable to our results from St. Paul (53.8 % lipid and 24.0 KJ/g) and overall (55.6 % lipid and 24.7 KJ/g).

Because milk composition does change during lactation, comparisons to and among other species of pinnipeds are likewise difficult. In northern fur seals and Antarctic fur seals (*Arctocephalus gazella*) that breed in the sub-polar regions, milk fat and energy content increase during at least 90% of the 4-month lactation period, so peak levels likely occur just before pups are weaned (Arnould and Boyd, 1995a, Goebel, 2002). In more temperate otariid species like the subantarctic fur seal (*Arctocephalus tropicalis*) and the Australian fur seal (*Arctocephalus pusillus doriferus*) that have lactation periods of between 10 and 11 months, milk fat and energy content increase until a peak and then decrease when pups begin to supplement their diets by foraging on their own (Arnould and Hindell, 1999, Georges et al., 2001). Peak lactation in phocid seals is easier to assess than in otariids because they have much shorter lactation periods, averaging from 4 to 28 days, and their milk typically increases in fat and energy content to a peak and then asymptotes (Riedman and Ortiz, 1979, Oftedal et al., 1988, Iverson et al., 1993, Lang et al., 2005). Table 2.6 lists a number of otariid studies that simply averaged milk composition over a range of lactation phases and did not report peak lactation levels. Other sources of variability were also not accounted for so comparisons between these studies are problematic.

Accounting for sources of variability in milk composition in this study

Time ashore

During the first 10 hours that a female was on shore in October milk did not change significantly in composition. After 10 hours, milk lipid decreased at an average rate of 0.31% per hour and energy content decreased at an average rate of 0.13 KJ/g per hour. Two previous studies on the Pribilofs of northern fur seal milk reported similar results - Costa and Gentry (1986) reported that lipid decreased by 6.5% over the 1-2 day nursing bout (~0.14% to 0.27% per hour), and Goebel (2002) reported a 0.16% per hour decrease. A decrease in lipid and energy content during time ashore has also been measured in Antarctic fur seals (Arnould and Boyd, 1995a, Goldsworthy and Crowley, 1999), subantarctic fur seals (Goldsworthy and Crowley, 1999, Georges et al., 2001), and Juan Fernandez fur seals (*Arctocephalus philippii*) (Ochoa-Acuna et al., 1999). In contrast, no change in milk composition was detected in the two species of sea lions that have been studied for the effect of time ashore (Oftedal et al., 1987, Kretzmann et al., 1991, Gales et al., 1996).

Protein % did not change during the time that females were on shore, but it has been reported to change in other fur seal species. In our study, the average protein % of milk ranged from 10.0-10.5 % throughout a stay on shore (Table 2.6), which was comparable to the average protein of 10.8% reported by Goebel (2002). Other fur seal studies that measured nitrogen directly to calculate protein content, as we did, reported declines during shore stays from 12.8% to 8.8% in Antarctic fur seals (Arnould and Boyd, 1995a), 13.4% to 10.7% in subantarctic fur seals (Georges et al., 2001), and 13.2% to 11.0% in Juan Fernandez fur seals (Ochoa-Acuna et al., 1999). The length of time ashore varies in each of these species: northern fur seals stay on shore for approximately 1-3 days (Gentry and Holt, 1986, Goebel, 2002), Antarctic fur seals stay on shore for approximately 1-2 days (Doidge et al., 1986, Boyd et al., 1991), subantarctic fur seals stay onshore for approximately 4 days (Georges and Guinet, 2000) and Juan Fernandez fur seals stay onshore for an average of 5.3 days (Francis et al., 1998). It is possible that longer shore visits result in decreases in milk protein %, but the lengths of shore visits by Antarctic fur seals are very similar to those of northern fur seals and results after just 2-3 days in subantarctic fur seals showed significant decreases in protein %.

Because time ashore is a sampling bias, results from samples collected after 10 hours were normalized using the average rate of decrease in lipid and energy content listed above. Normalized October results were higher than the previously reported milk composition results for northern fur seals and were as high as the highest reported for phocid seals. The average normalized milk lipid was 59.8% and energy content was 26.4 KJ/g. Protein % was not normalized because it was not affected by time ashore in this study. Time ashore is known to also affect milk composition during the July perinatal period. Costa and Gentry (1986) found that the milk of northern fur seals decreased in lipid by 15% (from 46.3% to 39.6%) and Arnould and Boyd (1995a) found that the milk of Antarctic fur seals decreased in lipid by 13% (from 40.8% to 35.6%) over the perinatal period. In the current study, the change in milk composition during the perinatal period was not assessed because samples were only collected once in July, approximately 24-72 hours postpartum. There were attempts, however, to collect animals close to the same time and it is unlikely that females were collected later than 72 hours postpartum or near the end of the approximate one-week perinatal period.

There are three leading theories for why milk composition changes during shore visits in fur seals. First, it is possible that the initial high lipid and energy content milk is produced solely from the energy that females acquire during their foraging trip to sea, and decreases in lipid and energy content are the result of increasingly more milk being produced from the females' fat reserves. Georges et al (2001) support this theory with evidence from fatty acid analysis of milk at different times during a shore visit. The second theory is that females have evolved to produce higher energy milk at the beginning of the shore visit to compensate for the period in which pups were left fasting (Georges and Guinet, 2000, Georges et al., 2001). Decreases in milk quality over the shore visit, in this case, would be associated with the pup's reduced need for energy with successive feedings. The third theory is that the milk fed to a pup when a female first returns to shore is more concentrated because it is what was stored in the mammary gland during the foraging trip (Arnould and Boyd, 1995b). In this case, more concentrated milk enables the female to store more energy per volume for the initial feeding.

Because the rate of decrease in milk lipid and energy content is fairly constant over time and among females, either the second and/or the third theory are likely responsible for the change in milk composition over the time a female is on shore. Change with time ashore is likely an adaptation that allows females to provide the highest amount of energy to the pup upon arrival from foraging while at the same time conserving her own fat reserves, which are not extensive due to the fur seal strategy of insulating with fur rather than blubber. If it were caused by a shift from producing milk from prey consumed during a foraging bout to producing milk from fat reserves, one would expect higher variability in the rate of decline during a shore visit.

Days postpartum

Milk composition changes in all mammal species over the course of lactation, although the degree of change differs between phylogenetic groups (Oftedal, 1984). Like other mammals, northern fur seals produce colostrum during the perinatal period. There is an abrupt transition time when females begin to alternate between foraging trips to sea and nursing trips to shore, and when milk fat and energy content appear to increase until near to the end of the lactation period (Goebel, 2002). The end of lactation occurs somewhere between late October to early November, approximately 125 days postpartum (Gentry and Holt, 1986). In this study between the July perinatal period and October, lipid increased by an average 23.4% and energy content increased by an average of 20.5% on Bogoslof; and lipid increased by an average of 19.8% and energy content increased by an average of 19.0% on St. Paul. Protein content did not change significantly over the sampling period, which was expected because it did not change in previous northern fur seal studies (Costa and Gentry, 1986, Goebel, 2002).

Studies that examined milk composition over time in other otariid and phocid seals generally reported increases in lipid and energy content until peak lactation, with little change in protein. Milk lipid and energy content appear to increase throughout the four month lactation period in Antarctic fur seals (Arnould and Boyd, 1995a) and generally increase midway through lactation and decrease in late lactation in temperate species like the subantarctic fur seal (Georges et al., 2001), Australian fur seals (Arnould and Hindell, 1999) and Australian sea lion (*Neophoca cinerea*) (Gales et al., 1996). Lipid and energy content of the milk also tend to increase to peak levels in mid-lactation and then asymptote throughout late lactation in phocid species like the grey seal (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*); however, there are individual variations (Iverson et al., 1993, Lang et al., 2005).

The results from two otariid studies differed from the above trends in milk composition. Kretzmann et al. (1991) found high variability in the milk lipid % of Australian sea lions and did not detect a change over the lactation period even though samples were collected up to 125 days postpartum, and Trillmich and Lechner (1986) found a decrease in the lipid and energy content of Galapagos fur seal (*Arctocephalus galapagoensis*) milk during their study period. In the first case, Kretzmann et al. (1991) did not account for the variable time ashore, whereas in a subsequent study conducted by Gales et al. (1996) time ashore was accounted for and increases in milk lipid % between early and mid-lactation were reported. In the second case, Trillmich and Lechner (1986) used a small sample size (n=19) and only examined milk composition for the first 30 days of a 2+ year lactation period. There is evidence that milk lipid and energy content can decrease during the perinatal fast and that it could take at least three weeks for them to rebound to levels recorded immediately postpartum (Costa and Gentry, 1986, Arnould and Boyd, 1995a).

Hypotheses for why milk lipid and energy content increase over the lactation period have been discussed in previous studies. Two theories are that they increase with improvements in female mass and body condition or with increases in trip duration (Trillmich and Lechner, 1986, Arnould and Boyd, 1995a, Arnould and Hindell, 1999 Georges and Guinet, 2000,). These theories, however, assume that milk composition can change in relationship to environmental influences on female physiology, which is unlikely because proximate composition is largely a function of phylogeny and genetic regulation (Iverson, 2007). Environmental influences typically alter milk output instead of composition (Iverson, 2007). It seems more likely that the increases in milk lipid and energy content have evolved due to the increasing energy needs of the growing pup and the development of the digestive system. Decreases do not occur until pups are capable of supplementing their diets by foraging on their own.

Island effect

There was a significant difference in milk composition between St. Paul and Bogoslof in October (lipid % $p<0.01$) indicating that there may be factor(s) that differ between the two islands that have the potential to alter mammary function. These results differ from two previous studies that examined milk composition at multiple locations. Goldsworthy and Crowley (1999) compared the milk composition of Antarctic fur seals that breed on South Georgia Island and Macquarie Island and found no significant difference between the two locations, and Adams (2000) compared the milk composition of Steller sea lions (*Eumetopias jubatus*) from five widely spaced rookery sites in Alaska

(Lowrie, Fish, Chirikof, Seguam and Yunaska Islands) and also found no statistical difference between locations.

This raises the question of what factors contributed to the difference in milk composition between Bogoslof and St. Paul. Factors that are known to differ between the two locations include foraging habitat, diet, dive type, trip duration, trip distance and time ashore (Goebel et al., 1991, Springer et al., 2010). The differences in foraging habitat between the two locations in this study are important because they suggest that the seals may be consuming different prey species, but there is no evidence that diet affects milk composition in otariids. Previous studies of milk composition in cows and humans have concluded that milk fat remains at near normal levels regardless of the nutritional status of the mother (Jenness, 1974, Jensen, 1989). Diets that are inadequate in fat or energy lead to a mobilization of the mother's body stores to produce milk of normal fat content (Jensen, 1989). Goebel (2002) studied the dive type of northern fur seals at the Pribilofs, which can be used as a proxy for diet, and found no relationship to milk composition. Furthermore, in this study, females from Vostochni and Reef rookeries foraged in different habitats (on shelf at Vostochni compared to primarily the shelf break and off the shelf at Reef), and likely consumed different prey, yet milk composition did not differ between rookery sites. The one factor that differs between islands and may be related to milk composition is foraging trip duration. This factor and its possible affects on milk composition are discussed further in the next section.

Foraging trip duration

When considering central place foraging theory, it has been predicted that females that travel farther to find food would make fewer trips and return with greater amounts of energy per trip compared to females traveling shorter distances (Orians and Pearson, 1977). And, indeed, preceding trip duration has been linked to otariid milk composition in previous studies through both inter-specific and intra-specific comparisons. From inter-specific comparisons, it was hypothesized that one of the evolutionary factors that led to higher milk fat in some otariids compared to others is the longer length of time that females of some species need to forage to provision their pups (Trillmich and Lechner, 1986) - lipid rich milk compensates for the longer periods that pups are on shore fasting (Costa and Gentry, 1986). Georges et al. (2001) suggested that the higher lipid content in milk of Antarctic fur seals, subantarctic fur seals, and Juan Fernandez fur seals compared to Galapagos fur seals is because the former make longer foraging trips. The results from the Arnould and Hindell (1999) study of Australian fur seal milk composition support this. However, it those comparisons may be misleading because only the average milk composition values were used to assess inter-specific differences, and the Galapagos fur seal milk composition data are problematic because they are for just the first 30 days of the 2+ year lactation period. In addition, other variables such as time ashore were not accounted for, also discussed above, so there may be less of a difference between species than originally thought.

Two otariid studies reported intra-specific relationships between trip duration and milk composition - Arnould and Boyd (1995b) and Arnould and Hindell (1999). The first study examined the milk composition of 16 female Antarctic fur seals during two months in mid-lactation and found that there was a positive relationship between milk lipid and protein and trip duration (Arnould and Boyd, 1995b). The second study examined the milk composition of seven female Australian fur seals throughout lactation and found that milk lipid was positively related to trip duration. However, neither of these studies accounted for stage of lactation. In addition, Arnould and Boyd (1995b) did not account for time ashore. Arnould and Hindell (1999) tried to limit the variance associated with time ashore by capturing females within the first 6 hours of their return. We know these variables are important when assessing milk composition.

This study found that preceding trip duration was negatively related to milk lipid % ($p=0.04$). This is opposite to what would be expected when considering central place foraging theory and it is opposite to all otariid studies that have reported a relationship between trip duration and milk composition. A negative relationship between trip duration and milk composition could be explained by the affect that long intervals between nursing bouts may have on mammary function. Lang et al. (2005) found evidence in harbor seals of a feedback mechanism that initiates mammary gland involution and a reduction in lipid content of milk after prolonged intervals between suckling. If St. Paul females forage near a threshold limit, because of poor prey availability, such a process may occur. However, Lang et al. (2005) also found that milk lipid percent increased to previous levels after nursing was reestablished. The milk composition of individual females over their time on shore was not examined in this study so it was not possible to detect a reversal of involution. However, the time ashore data that were available suggest that there was only a decrease in milk lipid with time ashore, not an increase which would be associated with the reversal of involution. Northern fur seals and other otariid seals have evolved to tolerate multiple day foraging trips and the foraging trip durations reported in this study are not unusually long compared to past studies. The question of whether mammary gland involution begins on longer foraging trips needs further research.

July value in the October analysis

The July value, which refers to a female's milk composition in July, was included in the October analysis to account for high individual variation. It is thought that nutrient partitioning by the mammary gland is tightly controlled within individual females and that variation between females is related more to physiological capacity than to factors such as resource availability, body condition or body size (Lang et al., 2009). Our results support that interpretation in the following ways: 1) there was no relationship between milk composition and female mass; 2) females that had milk with a higher lipid and energy content in July typically had milk with a higher lipid and energy content in October. Together, these findings suggest that individual variability is an important factor to consider when studying milk composition over the lactation period, and is critical to evaluating variability in pup growth and condition at weaning.

Summary

The northern fur seal population on the Pribilofs has been declining for over 50 years, but the cause has not been determined. In contrast, the population on Bogoslof has been increasing exponentially since it was founded in the mid-1970s. This work was part of a larger study conducted to investigate underlying factors that might be responsible for the contrasting trajectories. Accurate information on milk composition of the seals across lactation was necessary for models of pup growth and condition comparing the two populations.

Despite considerable variability in milk composition between individual females in both July and October, on average the lipid content increased by approximately 22% overall during the portion of the lactation period our study covered (approximately three-fourths). The lipid content near peak lactation is the highest reported among otariid seals and lipid content normalized for time ashore is as high as the highest known for phocid seals, making it among the highest known for all mammals.

The lipid content of the milk produced by females at Bogoslof was higher compared to the milk produced by females at St. Paul in October. There are a number of variables that differ between the two islands, but foraging trip duration is the only factor that also had an effect on milk composition in this study. The average trip duration for females from St. Paul was 6.5 days compared to 2.2 days for Bogoslof females. If the females in this study were foraging close to their physiological threshold on St. Paul Island, it is possible that changes in mammary function occurred. Lang et al. (2005) found evidence in harbor seals of a feedback mechanism that initiates mammary gland involution and a reduction in lipid content of milk after prolonged intervals between suckling. However, Lang et al. (2005) also found that milk lipid percent increased to previous levels after nursing was reestablished. This study did not examine the milk composition of individual females over the time on shore so it was not possible to detect a reversal of involution, if involution had begun. In fact, the time ashore data suggest that there was only a decrease in milk lipid with time ashore. Northern fur seals and other otariid species have adapted to making long foraging trips, but at St. Paul might be near a threshold of initiation of involution. Future research is needed to understand how otariid seals are able to produce high-lipid milk during multiple day foraging trips and to gain knowledge about when involution begins.

Past inter- and intra-species comparisons of pinniped milk composition are generally difficult, because studies of otariid milk composition often averaged results from early, mid and/or late lactation, whereas phocid studies typically reported only values at peak lactation. For the first time, this study used only milk composition data at or near peak lactation values for northern fur seals, other otariids where available, and phocids to compare milk composition. The results suggest that at least northern, Antarctic, subantarctic and Australian fur seals all have milk comparable in composition to milk of phocid seals.

Figures and Tables

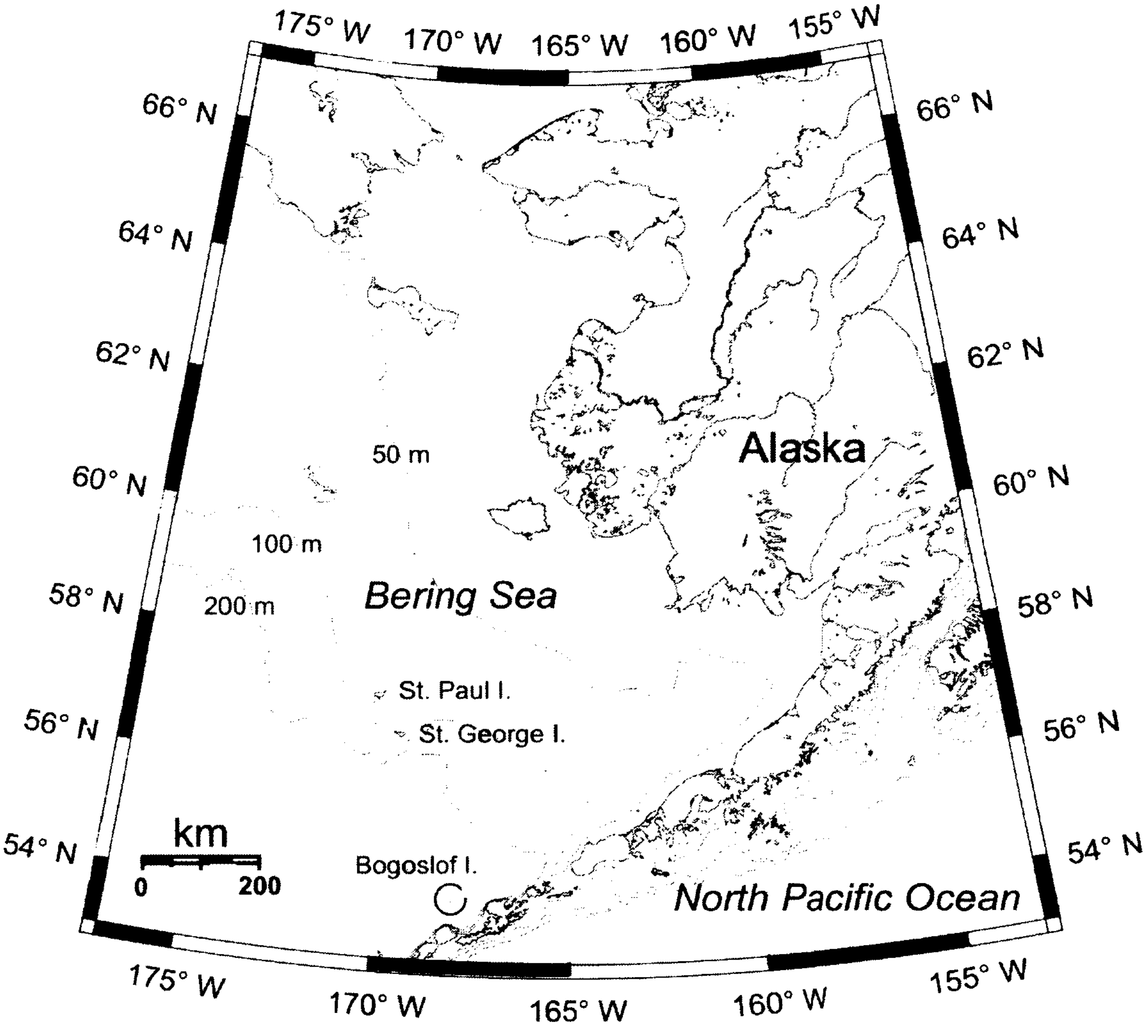

Figure 2.1. Location of the Pribilof Islands (St. Paul Island and St. George Island) and Bogoslof Island in the Bering Sea.

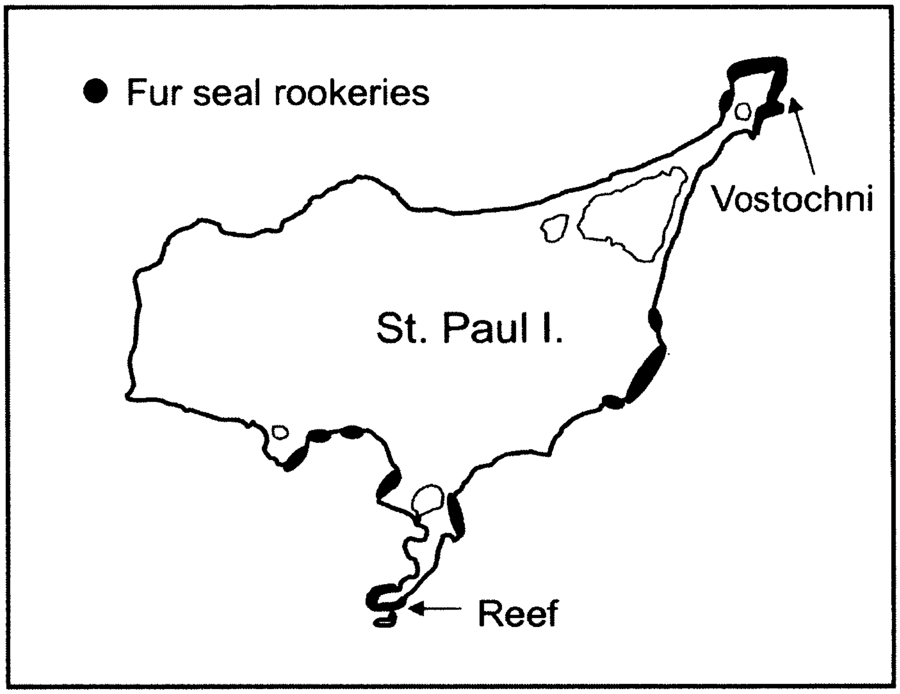

Figure 2.2. Locations of Vostochni and Reef northern fur seal rookeries on St. Paul Island.

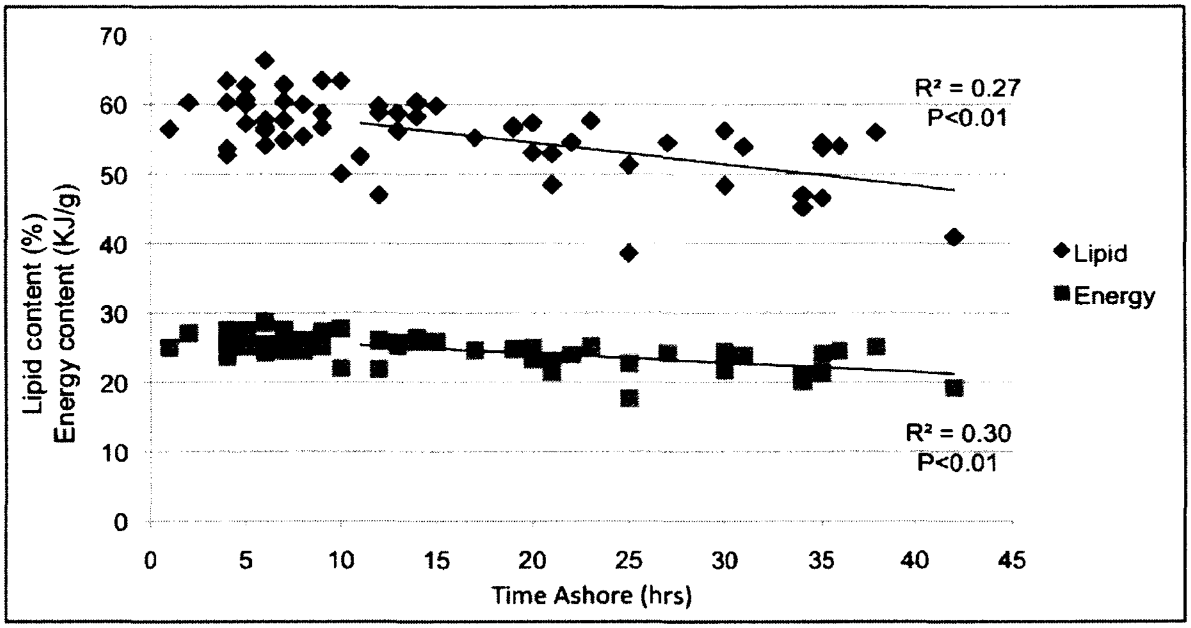

Figure 2.3. Relationship of milk lipid and energy content to time ashore of northern fur seals at Bogoslof Island and St. Paul Island combined. There was no detectable change in milk lipid or energy content until after 10 hours. The rate of change after 10 hours was 0.31% per hour in lipid and 0.13 KJ/g per hour in energy.

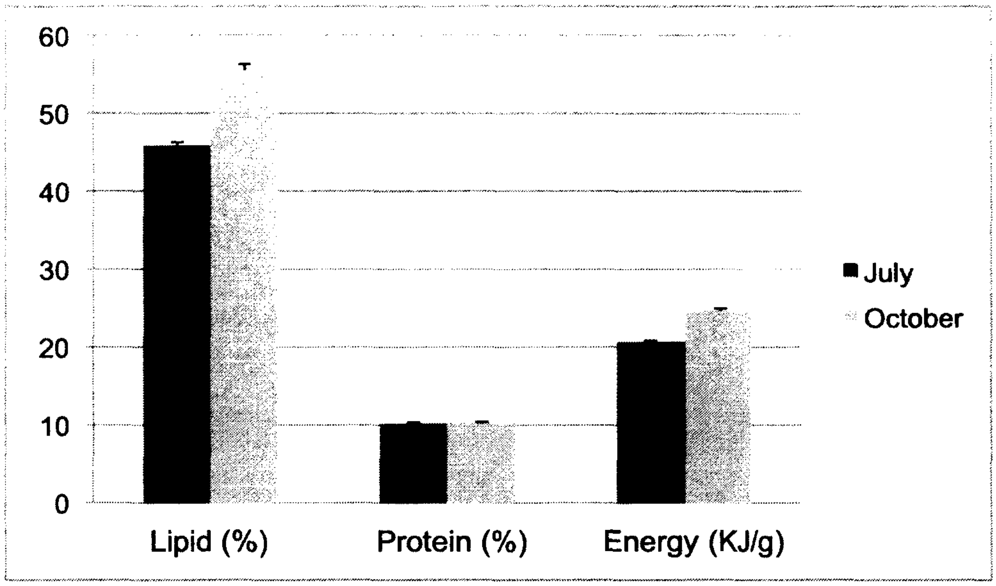

Figure 2.4. Change in the average lipid, protein and energy content between July (approximately 2 days postpartum) and October (approximately 90 days postpartum). There was a significant change in lipid ($p<0.01$) and energy content ($p<0.01$) but not in protein content ($p=0.22$).

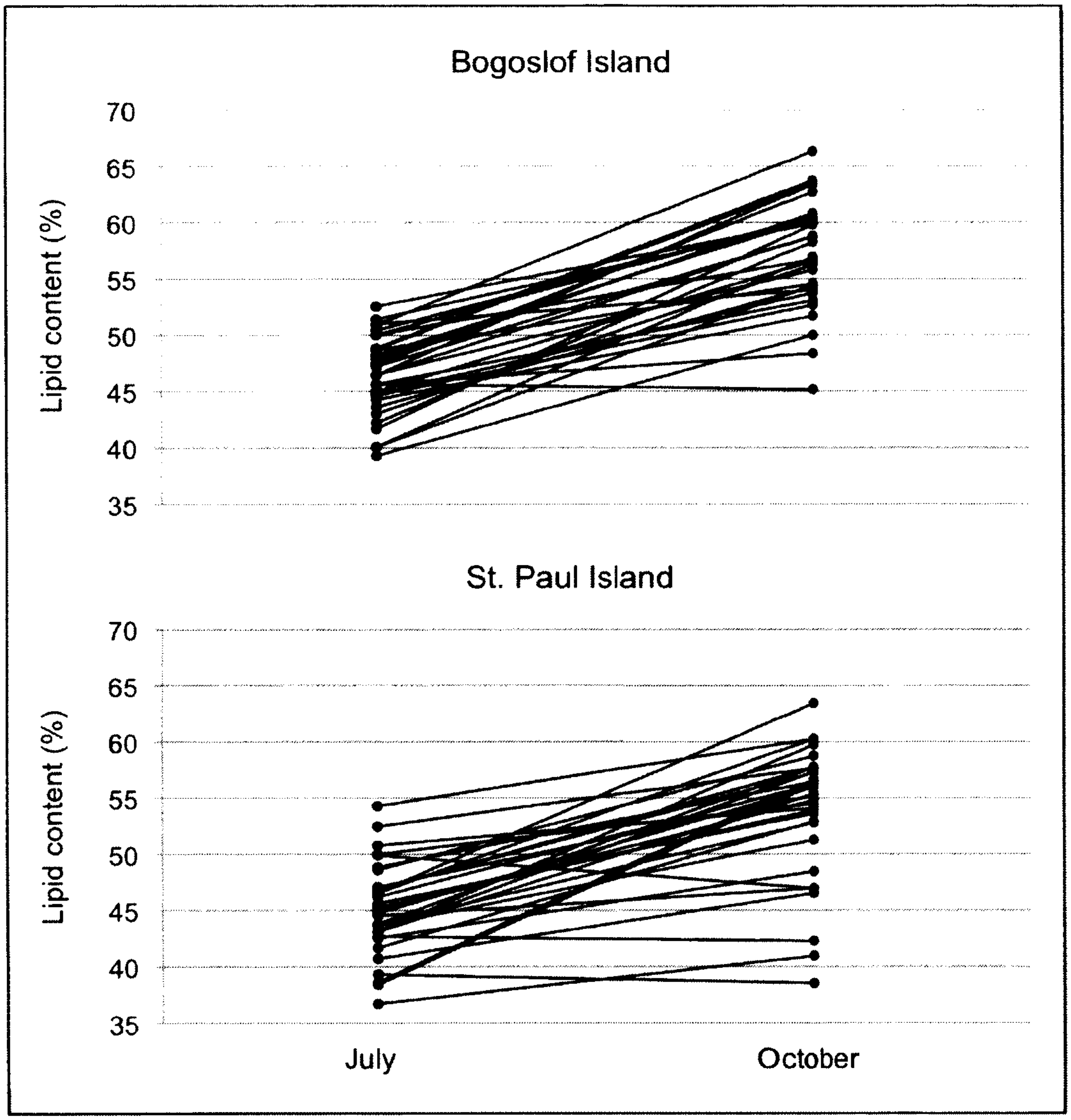

Figure 2.5. Variability between individual female northern fur seals from Bogoslof and St. Paul Islands in the change in milk lipid content between July and October.

Table 2.1. Probability values (p) generated from multiple regression analysis of northern fur seal milk composition data from Bogoslof Island and St. Paul Island in July. The dependent variables were protein, lipid and energy content and the independent variables were island, year, female mass (Kg), and milk sample volume (ml).

	Island	**Year**	**Female Mass (Kg)**	**Milk Volume (ml)**
Lipid %	0.80	0.82	0.87	0.90
Protein %	0.18	0.96	0.27	0.86
Energy content (KJ/g)	0.46	0.58	0.52	0.80

Table 2.2. Probability values (p) generated from multiple regression analysis of northern fur seal milk composition data from Bogoslof Island and St. Paul Island in October. The dependent variables were lipid, energy and protein content and the independent variables were island, time ashore, days postpartum, preceding trip duration, and July value (protein %, lipid % or energy content). Significant values are listed in bold.

	Island	**Time Ashore (hrs)**	**Days Post Partum**	**Preceding Trip Duration (days)**	**July value**
Lipid %	**<0.01**	**<0.01**	**<0.01**	**0.04**	**<0.01**
Protein %	0.12	0.52	0.22	0.48	0.31
Energy Content (KJ/g)	0.11	**<0.01**	**<0.01**	0.22	**<0.01**

Table 2.3. The means and standard errors for dry matter, lipid, protein and energy content of northern fur seal milk from Bogoslof Island and St. Paul Island in July and October. There was no difference between the two islands in July (lipid p=0.80, protein p= 0.18 and energy p=0.46), but there was in October lipid % (p<0.01). October protein and energy content were not different between the two islands (protein p=0.12, energy p=0.11).

	Mean Dry Matter %	SE	Mean Lipid %	SE	Mean Protein %	SE	Mean Energy Content (KJ/g)	SE
Bogoslof July	57.7	0.7	45.8	0.7	10.3	0.2	20.8	0.3
Bogoslof October	68.8	0.9	57.3	0.8	10.0	0.2	25.2	0.3
St. Paul July	56.9	0.7	45.5	0.7	10.0	0.2	20.5	0.3
St. Paul October	66.2	1.0	53.8	1.0	10.5	0.2	24.0	0.4

Table 2.4. The milk lipid and protein content for otariid and phocid seals from studies with comparable data. All data were collected at or near peak lactation. (1. current study, 2. Arnould and Boyd, 1995a, 3. Arnould and Hindell, 1999, 4. Georges et al., 2001, 5. Iverson et al., 1993, 6. Lang et al., 2005, 7. Oftedal et al., 1988, 8. Le Boeuf and Ortiz, 1977, 9. Carlini et al., 1994)

#	Species	Sample size	Lipid %	Protein %	Approximate length of lactation
1	Northern fur seal	68	55.6	10.3	4 months
2	Antarctic fur seal	8	52.7	14.0	4 months
3	Australian fur seal	89	50.0	10.4	11 months
4	Subantarctic fur seal	14	52.3	11.5	10 months
5	Grey seal	42	59.8	9.2	16 days
6	Harbor seal	71	50.2	9.0	28 days
7	Hooded seal	22	61.0	4.9	4 days
8	Northern elephant seal	9	54.4	9.0	28 days
9	Southern elephant seal	46	43.2	10.2	24 days

Table 2.5. Comparison of the milk composition results from all previous northern fur seal studies.

Reference	Sample size	Lipid %	Water %	Protein %	Energy KJ/g
Goebel 2002	189	49.1	37.6	10.8	22.1
Costa and Gentry 1986	58	41.5	44.4	14.2	19.9
Dosako et al. 1983	?	45.6	39.0	12.4	21.1
Ashworth et al. 1966	5	53.3	34.7	9.6	23.5

Table 2.6. The average reported milk composition of otariid species in studies that did not account for peak lactation or other variability. (1. Trillmich and Lechner, 1986, 2. Figueroa-Carranza, 1994, 3. Ochoa-Acuna et al., 1999, 4. Ponce de Leon, 1984, 5. Oftedal et al., 1987, 6. Werner et al., 1996, 7. Adams, 2000)

#	Species	Sample size	Lipid %	Protein %	Phase of lactation	Time sampled (postpartum)	Approximate length of lactation
1	Galapagos fur seal	19	29.4	12.1	Early	1-30 days	24+ months
2	Guadalupe fur seal	14	43.2	9.9	Early - mid	1-60 days	8-9 months
3	Juan Fernandez fur seal	44	41.4	11.9	Early, mid	~1 and ~90 days	7-10 months
4	South American fur seal	11	44.3	10.5	Mid	~150 days	6-12 months
5	California sea lion	12	43.7	8.9	Early – mid	1-60 days	12-24 months
6	Southern sea lion	10	33.5	10.8	Early	1-20 days	12+ months
7	Steller sea lion	51	21.6	9.3	Early	1-30 days	12 + months

References

ADAMS, T. C. 2000. *Foraging differences and early maternal investment in adult female Alaskan Steller sea lions (Eumetopias jubatus).* Ph.D. dissertation, Texas A&M University.

ARNOULD, J. P. Y. & BOYD, I. L. 1995a. Inter- and intra-annual variation in milk composition in Antarctic fur seals (*Arctocephalus gazella*). *Physiological Zoology,* 68, 1164-1180.

ARNOULD, J. P. Y. & BOYD, I. L. 1995b. Temporal patterns of milk production in Antarctic fur seals (*Arctocephalus gazella*). *Journal of Zoology London,* 237, 1-12.

ARNOULD, J. P. Y. & HINDELL, M. A. 1999. The composition of Australian fur seal (*Arctocephalus pusillus doriferus*) milk throughout lactation. *Physiological and Biochemical Zoology,* 72, 605-612.

ASHWORTH, U. S., RAMAIAH, G. D. & KEYES, M. C. 1966. Species difference in the composition of milk with special reference to the northern fur seal. *Journal of Dairy Science,* 49, 1206-1211.

BOYD, I. L., LUNN, N. J. & BARTON, T. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology,* 60, 577-592.

CARLINI, A. R., MARQUEZ, M. E. I., SOAVE, G., VERGANI, D. F. & RONAYNE DE FERRER, P. A. 1994. Southern elephant seal, *Mirounga leonina*: composition of milk during lactation. *Polar Biology,* 14, 37-42.

COSTA, D. P. & GENTRY, R. L. 1986. Free-ranging energetics of northern fur seals. *In:* GENTRY, R. L. & KOOYMAN, G. L. (eds.) *Fur seals: Maternal Strategies on Land and at Sea.* Princeton, N.J.: Princeton University Press.

CUNNIFF, P. 1995. *Official methods of analysis of the Association of Official Analytical Chemists International, 16th edition,* Arlington, VA: AOAC Intl.

DOIDGE, D. W., MCCANN, T. S. & CROXALL, J. P. 1986. Attendance behavior of Antarctic fur seals. *In:* GENTRY, R. L. & KOOYMAN, G. L. (eds.) *Fur seals: Maternal strategies on Land and at Sea.* Princeton, NJ: Princeton University Press.

DOSAKO, S., TANEYA, S., KIMURA, T., OHMORI, K., DAIKOKU, H., SUZUKI, N., SAWA, J., KANO, K. & KATAYAMA, S. 1983. Milk of northern fur seal: composition, especially carbohydrate and protein. *Journal of Dairy Science,* 66, 2076-2083.

FIGUEROA-CARRANZA, A. 1994. *Early lactation and attendance behavior of the Guadalupe fur seal females, (Arctocephalus townsendi).* MS, University of California, Santa Cruz.

FRANCIS, J. M., BONESS, D. J. & OCHOA-ACUNA, H. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. *Marine Mammal Science,* 14, 552-574.

GALES, N. J., COSTA, D. P. & KRETZMANN, M. 1996. Proximate composition of Australian sea lion milk throughout the entire supra-annual lactation period. *Australian Journal of Zoology,* 44, 651-657.

GENTRY, R. L. & HOLT, J. R. 1982. Equipment and techniques for handling northern fur seals. *NOAA Technical Report. NMFS SSRF-758.*

GENTRY, R. L. & HOLT, J. R. 1986. Attendance behavior of northern fur seals. *In:* GENTRY, R. L. & KOOYMAN, G. L. (eds.) *Fur Seals: Maternal Strategies on Land and at Sea.* Princeton, NJ.: Princeton University Press.

GEORGES, J., GROSCOLAS, R., GUINET, C. & ROBIN, J. 2001. Milking strategy in subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: evidence from changes in milk composition. *Physiological and Biochemical Zoology,* 74, 548-559.

GEORGES, J. & GUINET, C. 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology,* 81, 295-308.

GOEBEL, M. E. 2002. *Northern fur seal lactation, attendance and reproductive success in two years of contrasting oceanography.* Ph.D. dissertation, University of California, Santa Cruz.

GOEBEL, M. E., BENGSTON, J. L., DELONG, R. L., GENTRY, R. L. & LOUGHLIN, T. R. 1991. Diving patterns and foraging locations of female northern fur seals. *Fisheries Bulletin,* 89, 171-179.

GOLDSWORTHY, S. D. & CROWLEY, H. M. 1999. The composition of the milk of Antarctic (*Arctocephalus gazella*) and subantarctic (*A. tropicalis)* fur seals at Macquarie Island. *Australian Journal of Zoology,* 47, 593-603.

IVERSON, S. J. 2007. Milk composition and lactation strategies across mammalian taxa: implications for hand-rearing neonates. *Proceedings of the Nutrition Advisory Group. Seventh Conference on Zoo and Wildlife Nutrition,* 1-7.

IVERSON, S. J., BOWEN, W. D., BONESS, D. J. & OFTEDAL, O. T. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology,* 66, 61-88.

JENNESS, R. 1974. The composition of milks *In:* LARSON, B. L. & SMITH, V. R. (eds.) *Lactation: A Comprehensive Treatise.* New York, NY: Academic Press.

JENSEN, R. G. 1989. *The lipids of human milk,* Boca Raton, FL., CRC Press Inc.

KLEIBER, M. 1975. *The fire of life,* New York, NY., Robert E. Krieger, Publishing Co. Inc.

KRETZMANN, M. B., COSTA, D. P. & HIGGINS, L. V. 1991. Milk composition of Australian sea lions *Neophoca cinerea:* variability in lipid content. *Canadian Journal of Zoology,* 69, 2556-2561.

LANG, G. M., IVERSON, R. L. & BOWEN, W. D. 2005. Individual variation in milk composition over lactation in harbour seals (*Phoca vitulina*) and the potential consequences of intermittent attendance. *Canadian Journal of Zoology,* 83, 1525-1531.

LANG, S. L. C., IVERSON, S. J. & BOWEN, W. D. 2009. Repeatability in lactation performance and the consequences for maternal reproductive success in gray seals. *Ecology,* 90, 2513-2523.

LE BOEUF, B. J. & ORTIZ, C. L. 1977. Composition of elephant seal milk. *Journal of Mammalogy,* 58, 683-685.

LLOYD, D. S., MCROY, C. P. & DAY, R. H. 1980. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslof Island, southeastern Bering Sea. *Arctic,* 34, 318-320.

NMFS 2007. Conservation plan for the Eastern Pacific stock of northern fur seals (*Callorhinus ursinus*). National Marine Fisheries Service, Juneau, AK.

OCHOA-ACUNA, H., FRANCIS, J. M. & OFTEDAL, O. T. 1999. Influence of long intersuckling interval on composition of milk in the Juan Fernandez fur seal, *Arctocephalus philippii. Journal of Mammalogy,* 80, 758-767.

OFTEDAL, O. T. 1984. Milk composition, milk yield, and energy output at peak lactation: a comparative review. *Symposium of Zoological Society London,* 51, 33-85.

OFTEDAL, O. T., BONESS, D. J. & BOWEN, W. D. 1988. The composition of hooded seal (*Cystophora cristata*) milk: an adaptation for postnatal fattening. *Canadian Journal of Zoology,* 66, 318-322.

OFTEDAL, O. T. & IVERSON, S. J. 1995. Phylogenetic variation in the gross composition of milks. *In:* JENSEN, R. G. (ed.) *Handbook of Milk Composition.* Orlando, FL: Academic Press.

OFTEDAL, O. T., IVERSON, S. J. & BONESS, D. J. 1987. Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex, growth and predicted maintenance requirements. *Physiological Zoology,* 60, 560-575.

ORIANS, G. H. & PEARSON, N. E. 1977. On the theory of central place foraging *In:* HORN, D. J., STAIRS, G. R. & MITCHELL, R. D. (eds.) *Analysis of Ecological Systems.* Columbus, OH: Ohio State University Press.

PONCE DE LEON, A. 1984. Lactancia y composicion cuantitativa de la leche del lobo fino sudamericano *Arctocephalus australis* (Zimmerman, 1786). *Anales industria lobera y pesquera del estado, Montevideo, Uruguay.*

REAM, R. R., BAKER, J. D. & TOWELL, R. G. 2000. Foraging ecology and population growth of northern fur seals on Bogoslof Island, Alaska. *Marine Mammals of the Holarctic Regions.* Archangelsk, Pravada Severa.

RIEDMAN, M. & ORTIZ, C. L. 1979. Changes in milk composition during lactation in the northern elephant seal. *Physiological Zoology,* 52, 240-249.

ROBSON, B. W., GOEBEL, M. E., BAKER, J. D., REAM, R. R., LOUGHLIN, T. R., FRANCIS, R. C., ANTONELIS, G. A. & COSTA, D. P. 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology,* 82, 20-29.

ROPPEL, A. Y. & DAVEY, S. P. 1965. Evolution of fur seal management on the Pribilof Islands. *Journal of Wildlife Management,* 29, 448-463.

SCHEFFER, V. B. 1962. Pelage and surface topography of the northern fur seals *U.S. Fish and Wildlife Service North American Fauna,* 64, 1-206.

SINCLAIR, E. H., VLIETSTRA, L. S., JOHNSON, D. S., ZEPPELIN, T. K., BYRD, G. V., SPRINGER, A. M., REAM, R. R. & HUNT, G. L. J. 2008. Patterns in prey use among fur seals and seabirds in the Pribilof Islands. *Deep-Sea Research II,* 55, 1897-1918.

SPRINGER, A. M., ESTES, J. A., VAN VLIET, G. B., WILLIAMS, T. M., DOAK, D. F., DANNER, E. M., FORNEY, K. A. & PFISTER, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences,* 100, 12223-12228.

SPRINGER, A. M., REAM, R. R. & IVERSON, S. J. 2010. Seasonal foraging strategies and consequences for northern fur seals at colonies with opposite population trends - year 2. *North Pacific Research Board Project Final Report.*

STERLING, J. T. 2009. *Northern fur seal foraging behaviors, food webs, and interactions with oceanographic features in the eastern Bering Sea.* Ph.D. Dissertation, University of Washington.

TOWELL, R. G., REAM, R. R. & YORK, A. E. 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. *Marine Mammal Science,* 22, 486-491.

TRILLMICH, F. & LECHNER, E. 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). *Journal of Zoology London,* 209, 271-277.

WERNER, R., FIGUEROA-CARRANZA, A. & ORTIZ, C. L. 1996. Composition and energy content of milk from Southern sea lions (*Otaria flavescens*). *Marine Mammal Science,* 12, 313-317.

ZEPPELIN, T. K. & REAM, R. R. 2007. Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska. *Journal of Zoology,* 270, 565-576.

CONCLUSIONS

What is causing the northern fur seal population decline on the Pribilof Islands? This is the big picture question that the project Consequences of Fur Seal Foraging Strategies (COFFS) assessed. The two chapters from this thesis contributed to this larger study.

Chapter 1 reviewed the potential causes of the current population decline on the Pribilofs in the context of other important changes to the ecosystem since the middle 20th century and summarized research questions that still need to be addressed. Factors such as diseases, parasites, subsistence harvests, direct shootings and bycatch likely had small effects on fur seals in the past and during this current population decline, but they could not have caused a reduction of this magnitude without being detected. Factors that were important to consider in the past and that should continue to be monitored, but are probably not issues in the current decline, include entanglement and contaminants. The factors that could cause a population to decrease to the current level seen on the Pribilofs are nutritional limitation due to climate change or fisheries competition, predation, or a combination of those causes that also includes conditions in the North Pacific during the winter. Until we have a better understanding of fur seal vital rates, effects of fisheries and environmental change on fur seal prey fields and diets, and sources and levels of fur seal mortality, particularly predation mortality, it is unlikely that definitive answers will be achieved.

The milk composition results from Chapter 2 provide information necessary to calculate how much energy pups from St. Paul and Bogoslof receive during the nursing period, and were part of a broader assessment by COFFS of whether nutritional limitation could be causing the northern fur seal population decline on St. Paul. There was no difference in milk composition between islands in July shortly after pups were born but there was a 7% difference in October that may be related to trip duration. Females that make the longest foraging trips may begin mammary gland involution similar to what is known to occur in harbor seals (Lang et al 2005). However, otariids have evolved a lactation strategy that includes extended periods of foraging away from the neonate. There is little evidence to suggest that the foraging trips recorded in this study were unusually long and there is no evidence to suggest that a reversal of involution occurred once suckling was reestablished. Future research is needed to understand when involution begins in otariids.

On average milk lipid content increased by approximately 22% between July and October, from about 33% to about 54%. The northern fur seal milk produced in October near peak lactation has the highest lipid content known among otariid seals and is comparable to the milk composition of phocid seals, making it among the highest known for all mammals. This has important implications when considering evolutionary biology. There must be an adaptive advantage to producing milk with such a high energy density. Fur seals have a short lactation period relative to other otariids, and they make multiday foraging trips while their pups fast on shore. These factors result in less time for females to transfer the necessary energy for growth and development. Higher milk fat increases the rate of energy transfer so pups can develop faster, tolerate periods of extended fasting, and leave the rookeries at weaning with sufficient fat reserves to survive until they are proficient at capturing prey on their own.

There was large variability in the milk lipid content between individual females in both July and October, and in general females with higher values in July also had higher values in October. These longitudinal data on milk composition, coupled with data on female foraging trip durations, will allow a detailed evaluation of the energetics of pup growth and condition near weaning that likely affects survival during their first winter.

The COFFS project found that females from St. Paul travel approximately two times farther and leave their pups fasting on shore for approximately three times longer than females from Bogoslof. Trip duration has been found to be an indicator of the proximity and availability of prey, so these findings suggest that females from St. Paul need to exert more energy to find food than females from Bogoslof. Longer foraging trips have a direct consequence to the pups because they are left on shore fasting for longer and are not fed as often. In addition, if the beginning stages of involution occur in females that make longer foraging trips, pups that are already fed less often, will experience additional reductions in provisioning.

References

BRAHAM, H. W., EVERITT, R. D. & RUGH, D. J. 1980. Northern sea lion population decline in the eastern Aleutian Islands. *Journal of Wildlife Management,* 44, 25-33.

DOROFF, A. M. 2003. Sea otter population declines in the Aleutian Archipelago. *Journal of Mammalogy,* 84, 55-64.

ESTES, J. A., TINKER, M. T., WILLIAMS, T. M. & DOAK, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science,* 282, 473-476.

FROST, K. J., LOWRY, L. F. & VER HOEF, J. M. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Marine Mammal Science,* 15, 494-506.

LANG, G. M., IVERSON, R. L. & BOWEN, W. D. 2005. Individual variation in milk composition over lactation in harbour seals (*Phoca vitulina*) and the potential consequences of intermittent attendance. *Canadian Journal of Zoology,* 83, 1525-1531.

LLOYD, D. S., MCROY, C. P. & DAY, R. H. 1980. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslof Island, southeastern Bering Sea. *Arctic,* 34, 318-320.

MERRICK, R. L., LOUGHLIN, T. R. & CALKINS, D. G. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in 1956-1986. *Fishery Bulletin,* 85, 351-365.

NMFS 1992. Recovery plan for the Steller sea lion (*Eumetopias jubatus*). Steller sea lion recovery team for the National Marine Fisheries Service, Silver Spring, MD.

NMFS 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*). The National Marine Fisheries Service, Alaska Fisheries Science Center. Seattle, WA.

NMFS 2007. Conservation plan for the Eastern Pacific stock of northern fur seals (*Callorhinus ursinus*). National Marine Fisheries Service, Juneau, AK.

PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science,* 6, 121-134.

SMALL, R. J. 2003. Trends in abundance of Alaska harbor seals, 1983-2001. *Marine Mammal Science,* 19, 344-362.

SMALL, R. J., BOVENG, P. L., BYRD, G. V. & WITHROW, D. E. 2008. Harbor seal population decline in the Aleutian Archipelago. *Marine Mammal Science,* 24, 845-863.

TOWELL, R. G., REAM, R. R. & YORK, A. E. 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. *Marine Mammal Science,* 22, 486-491.

VER HOEF, J. M. & FROST, K. J. 2003. A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environmental and Ecological Statistics,* 10, 201-219.