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A Tale of Two Stocks: Studies of Northern Fur Seals Breeding at the Northern and Southern Extent of the Range

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This is a tale of two stocks of northern fur seals (*Callorhinus ursinus***): the Eastern Pacific stock and the San Miguel Island stock. The Eastern Pacific stock breeds mostly on the Pribilof Islands, Alaska, at the northern extent of the breeding range in the Bering Sea Large Marine Ecosystem (Fig. 1). This stock was listed as depleted in 1988 under the Marine Mammal Protection Act of 1972, but not all populations within the stock boundaries display similar population trends. Within the Eastern Pacific stock, the Pribilof Islands population, historically the largest breeding population in the world, has declined dramatically over the past 20 years, whereas a new breeding population at Bogoslof Island has increased exponentially since its discovery in 1980. In contrast, the San Miguel Island stock, which breeds mostly on San Miguel Island, California, at the southern extent of the breeding range in the California Current Large Marine Ecosystem (Fig. 1), is not listed as depleted because it has increased or been stable since its discovery in 1968.**

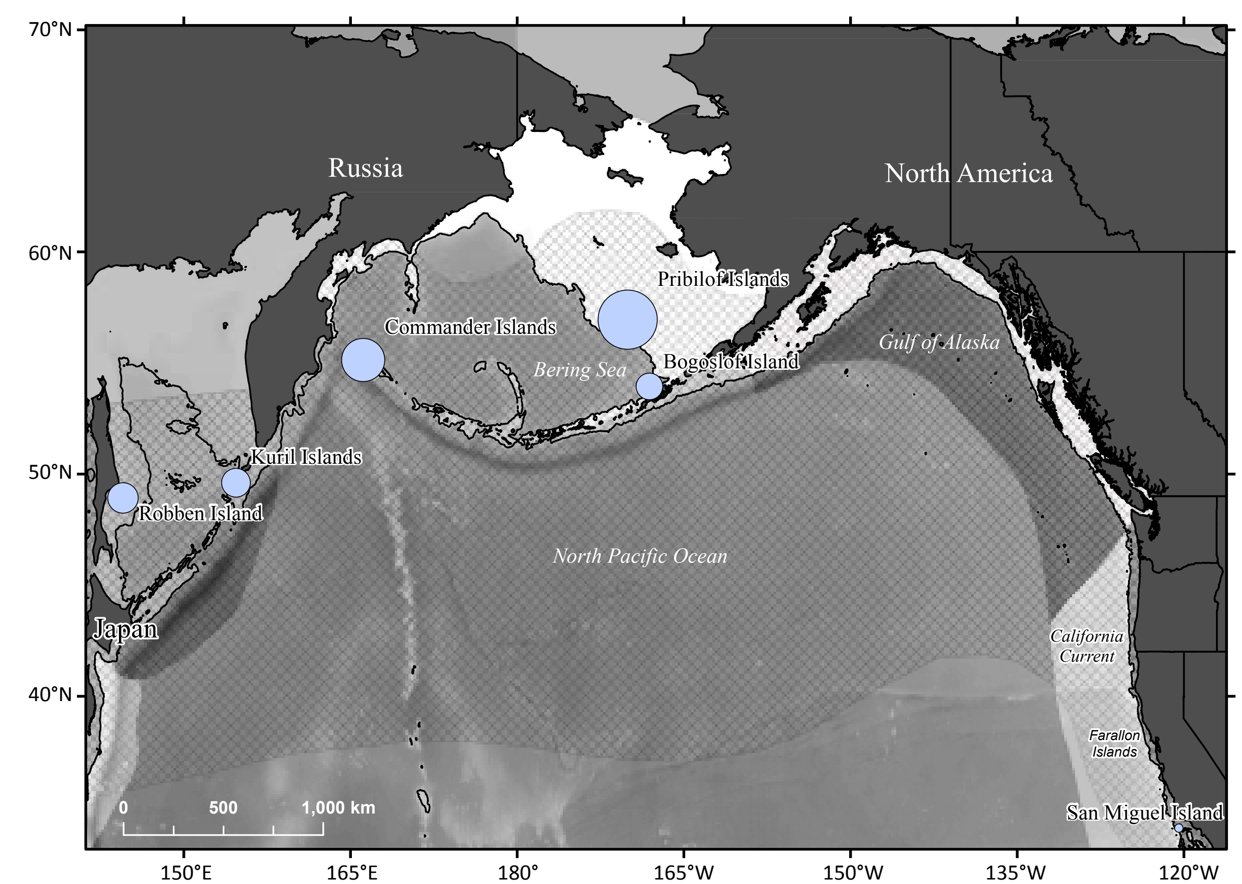

Figure 1. Breeding sites and range of northern fur seals. Breeding sites are indicated by circles and the size of the circles represents the relative size of the population. Range is depicted by hatching.

Photo 1. Northern fur seal breeding group at Bogoslof Island, Alaska. Adult male is in the center surrounded by smaller adult females and black pups.

Over the past 20 years, the San Miguel and Bogoslof Island fur seal populations have thrived while the Pribilof Island population has declined. It is unclear why annual pup production continues to decrease at the Pribilof Islands, but it is likely related to declines in the health, survival, or reproduction of fur seals breeding there. Survival and reproduction of Pribilof Islands fur seals may be affected by factors such as climate shifts in the North Pacific Ocean that alter migratory or foraging patterns, alterations in available prey, new or increased interactions with commercial fisheries that increase mortality rates, or an increase in predation levels. The increase in pup production at Bogoslof and San Miguel Islands is likely influenced by immigration of animals from the Pribilof Islands; however, the movement of animals to Bogoslof and San Miguel Islands cannot solely account for the magnitude of declines documented at the Pribilof Islands.

The U.S. Northern Fur Seal Conservation Plan describes research and actions to be taken to restore the Eastern Pacific stock to a healthy population level. One of its aims is to quantify environmental effects on foraging behaviors and identify essential habitat during the annual cycle of northern fur seals throughout the species' range. To do this, the National Marine Mammal Laboratory's (NMML) Alaska and California Current Ecosystem Programs have taken a collaborative approach in their investigations of the Eastern Pacific and San Miguel Island stocks since the 1970s. The goal is to better understand the interplay between the stocks' biophysical environment, diet, foraging behavior and, ultimately, population dynamics. Comparing the two stocks could help identify ecological drivers of the divergent population trends within and between stocks. This article compares the history of the two stocks and highlights NMML's research investigating population dynamics, foraging behaviors of adult females and their diet.

Natural History of Northern Fur Seals

The expansive range of northern fur seals covers seven different marine ecosystems (Kuroshio Current, Oyashio Current, West Bering Sea, East Bering Sea, Gulf of Alaska, California Current, and North Pacific Ocean). For 6 months of the year (mid-November to mid-May) fur seals are usually solitary and remain at sea migrating throughout the North Pacific Ocean. Most fur seals return to land once a year for the summer reproductive season (mid-May to mid-November) and form dense breeding aggregations on islands in Russia, Alaska, and California (Fig. 1). Northern fur seals have a polygynous breeding system. Adult males compete for access to breeding females by defending land territories. This has given rise to pronounced sexual size dimorphism with males up to 5 times the size of females. Adult males arrive at the colonies and set up territories in mid-May or early June and remain on land and fast for up to 3 months while defending their territories. Females aggregate in the territories for protection from other males and often breed with the territorial male, though not always (Photo 1).

Pregnant adult females arrive throughout June or July and give birth to single pups within 2 days after arriving ashore. Females remain ashore with their pups for up to 8 days and then breed before beginning a series of feeding trips to sea, alternated with nursing visits ashore throughout the 4-month lactation period. Feeding trips may last more than 10 days and nursing visits up to 2 days. While the mother is away, the pup remains ashore and fasts. Weaning is relatively abrupt with the female or pup departing from the colony and not returning.

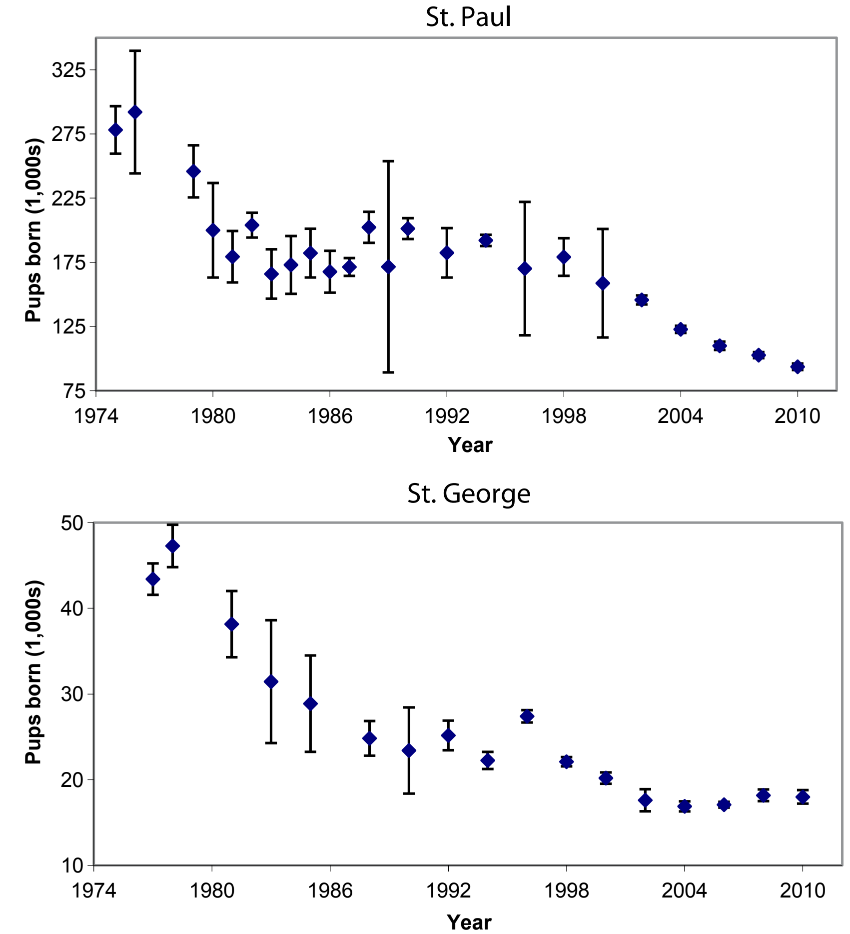

Figure 2. Estimated number of northern fur seal pups born (± 95% confidence intervals) on the Pribilof Islands (St. Paul and St. George), Alaska, 1975 to 2010.

Once weaned, the pups spend up to 3 years traveling the North Pacific Ocean, remaining almost exclusively at sea. Historically, about 50% of the pups have died in their first year. Some yearlings and 2-year-olds return to the colonies, but most remain at sea; thus, little is known about the juvenile life stage.

Females become reproductive at 3 or 4 years of age and are reproductive for most of their life span, which averages about 26 years. Males reach sexual maturity between 5 and 7 years of age and begin defending territories between 7 and 9 years of age. Breeding males have shorter life spans than females because of the energetic cost of fighting and fasting during the breeding season.

Despite a high affinity of both female and male northern fur seals to return to their natal sites to breed, there is very little genetic differentiation between stocks throughout their range. The only evidence of genetic differentiation is weak differences between the Russian populations and the Eastern Pacific stock. Northern fur seals from the San Miguel Island stock are not genetically distinct from those from either Russia or the Eastern Pacific stock. This is not surprising given that San Miguel Island was colonized by animals from throughout the range only 60 years ago – so only 12 generations have been born at San Miguel Island, leaving relatively little time for genetic differentiation to occur among the populations. In contrast, the Pribilof Islands were colonized by fur seals approximately 10,000 years ago following the Wisconsin glaciations. The genetic structure of the Pribilof Islands population indicates that it expanded initially but then experienced a dramatic decline, a result of intensive commercial harvesting between the late 18th and early 20th centuries. With the regulation of commercial harvesting after 1911, the Pribilof Islands population underwent another expansion increasing to almost 2.0 million animals by the late 1940s. Interestingly, even with the dramatic decline from commercial harvesting, there is no evidence of reduced genetic diversity in the population, suggesting that the worldwide population level of northern fur seals has remained large enough to maintain genetic variability at high levels throughout the range.

The Fall of the Eastern Pacific Stock

The Eastern Pacific stock of northern fur seals has been exploited on and around the Pribilof Islands (St. George and St. Paul) since their discovery by Russian fur hunters in 1786. There have been three distinct periods of commercial exploitation and management of the Eastern Pacific stock: Russian harvest, U.S. government lease, and U.S. government management. Two periods of severe depletion in the Pribilof herds took place under Russian ownership, but restrictive killing and protection of females enabled the population to recover. Unregulated harvests commenced in 1867 immediately after the purchase of the Alaskan territory by the United States. The Alaska Commercial Company was granted a 20-year lease beginning in 1870 and harvested nearly 100,000 animals annually. During this period, pelagic sealing accelerated and, due to the high composition of females killed by this practice, severely depleted the Pribilof Islands population of northern fur seals by the early 20th century. The North Pacific Fur Seal Convention of 1911, a treaty agreed upon by England, Japan, Russia, and the United States, subsequently protected fur seals from pelagic sealing and raids on the breeding islands and led to the development of scientific research programs investigating the population dynamics and biology of the northern fur seal. Following the cessation of pelagic sealing and the commencement of restrictive harvest practices on the Pribilof Islands, fur seals recovered and numbered about 2.0 million animals during the late 1940s.

In 1956, the United States government implemented a northern fur seal herd reduction program which removed more than 300,000 females over a 10-year period. The purpose was to increase productivity of the herd by reducing the number of females; the reasoning for the reduction program was that females would reproduce at younger ages and produce more pups if there was less competition among fur seals for resources. However, pup production rates did not increase as expected but instead declined due to removals of females with the highest reproductive value. The program ceased in 1968. The signing of the Interim Convention on Conservation of North Pacific Fur Seals by the United States, Japan, England, and Russia in 1957 expanded scientific research programs that had been initiated under the 1911 treaty on the biology and life history of northern fur seals. Pelagic sampling of fur seals was conducted collaboratively by all treaty countries from 1958 through the 1970s to study northern fur seal distribution, feeding habits, reproduction, and survival. Juvenile male fur seals were commercially harvested on the Pribilof Islands until 1984 and currently are harvested in small numbers for subsistence needs of the Aleut people.

Despite cessation of the herd reduction program in 1968, pup production on the Pribilof Islands has exhibited an overall declining trend, with a period of stabilization in the late 1980s (Fig. 2). Pup production continues to decline in the absence of heavy commercial harvesting pressure.

Photo 2. Polovina Cliffs rookery on St. Paul Island, Alaska in 1940 (top) and 2004 (bottom) taken from the same vantage point.

Specifically, from 1998 to 2010, pup production on St. Paul Island decreased 5.46% (SE = 0.32, P< 0.01) annually, while on St. George Island it declined 2.90% (SE = 0.69, P = 0.03) annually. Overall, pup production on the Pribilof Islands has decreased 4.90% (SE = 0.36, P < 0.01) annually since 1998 (Photo 2).

The recent decline in pup production at the Pribilof Islands decreased their contribution to the worldwide abundance of northern fur seals (Fig. 3). The Pribilof Islands population accounted for approximately 74% of the worldwide population in 1992. Since then, fur seal abundance at the Pribilof Islands dropped 46%, and recent estimates from other colonies indicate that the Pribilof Islands now account for approximately 45% of the worldwide population, with a decline in worldwide abundance of 10% to a total of roughly 1.18 million animals.

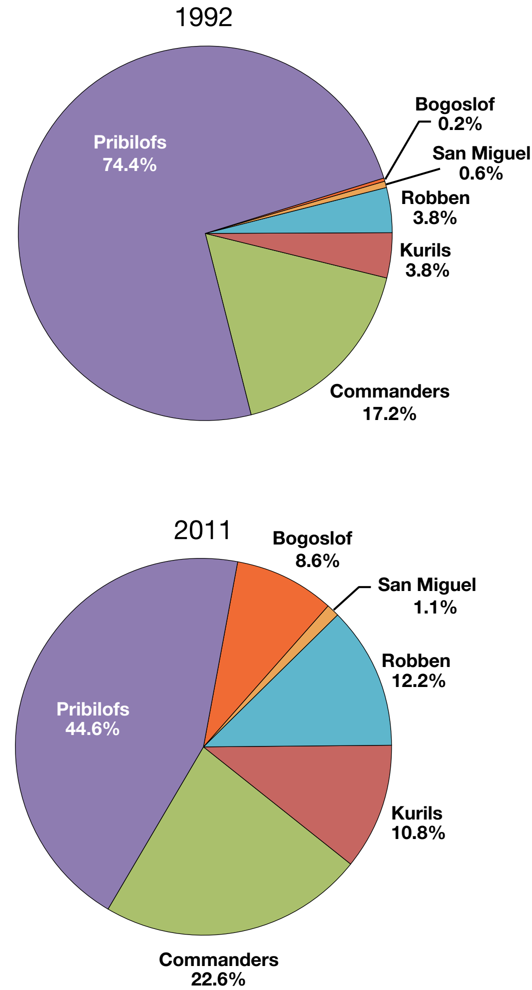

Figure 3. Estimated contribution of the breeding islands to worldwide abundance of northern fur seals in 1992 and 2011.

In contrast with the decline observed at the Pribilof Islands, fur seal numbers at a new location at Bogoslof Island have increased dramatically in recent years. Located approximately 74 km west of Dutch Harbor, Alaska, Bogoslof Island was formed by a series of volcanic eruptions in the late 18th century. Since pups were first observed there in 1980, pup production has increased at an annual rate of 38.2% (SE = 2.60, P < 0.01) through 2011, and at an annual rate of 11.7% (SE = 0.90, P < 0.01) from 1997 to 2011 (Fig. 4). Pup production on Bogoslof Island, estimated to be 22,905 (SE = 921.5) in 2011, has surpassed recent estimates for St. George Island.

The Rise of the San Miguel Island Stock

The San Miguel Island stock of northern fur seals has quite a different history from the Eastern Pacific stock. Once considered part of the Eastern Pacific stock, breeding fur seals at San Miguel Island and the Farallon Islands, California, were reclassified in 1992 as their own distinct stock due to their disparate population trends, continuous geographic distribution but geographic separation during the breeding season from the Eastern Pacific stock, and high natal site fidelity. Evidence of northern fur seals on San Miguel Island, located 46 km offshore in southern California, dates back to the island's occupation by Chumash Indians 12,000 years ago. Northern fur seal remains have been recovered from Chumash kitchen middens, but it is unknown if the animals bred on San Miguel Island or used it only as a hauling ground. There is some confusion about the history of commercial sealing of this stock because it was not considered distinct from the Guadalupe fur seal (*Arctocephalus townsendi*) until 1897, more than 40 years after most of the fur seals had been extirpated from the California Channel Islands. Furthermore, a large historical breeding population was likely located at the Farallon Islands, 43 km west of San Francisco Bay. Heavy commercial harvesting during the summer breeding season extirpated this population in the 1800s.

Northern fur seals recolonized San Miguel Island sometime in the 1950s and were first documented there in 1961 in photographs taken by George Silk, a photographer for Time-Life books. In 1968, biologists surveyed the northern fur seal population at San Miguel Island and identified 100 females, 36 pups, and 1 adult male at Adams Cove on the southwest end of the island where they shared space with California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*) (Photo 3). In 1972, another breeding population was discovered on Castle Rock, a small offshore rock 2 km northeast of Adams Cove.

Evidence that the San Miguel population was founded by a mixture of animals from Pribilof Islands and Russian fur seals is based on identification of individuals by flipper tags deployed in these populations as part of the collaborative fur seal research that stemmed from the Interim Convention on Conservation of North Pacific Fur Seals of 1957. The tags uniquely identified individual animals to their birth or breeding sites. Tagging studies have been a cornerstone of fur seal population studies throughout the range; tagging studies of Russian and Pribilof Islands populations conducted from the 1940s to the 1970s provided the first comprehensive information on behavior, survival, reproduction, and movements of fur seals. Large-scale tagging programs conducted by NMML for the Eastern Pacific stock ceased in 1968. The need for recent information on survival and reproductive rates of the Eastern Pacific stock to better understand the current population decline led to the initiation of a new large-scale tagging program of pups and adult females in 2009. Fur seal pups at San Miguel Island have been tagged since 1975. Comparisons of the survival rates between the Eastern Pacific stock and the San Miguel Island stock determined from the tagging studies may provide insights into the role of survival and reproductive rates in the decline of the Pribilof Islands population.

Unlike the Eastern Pacific stock, the primary factors influencing the population dynamics for the San Miguel Island stock are fairly well known. The small size of the Adams Cove and Castle Rock populations allows for all the pups to be counted; NMML

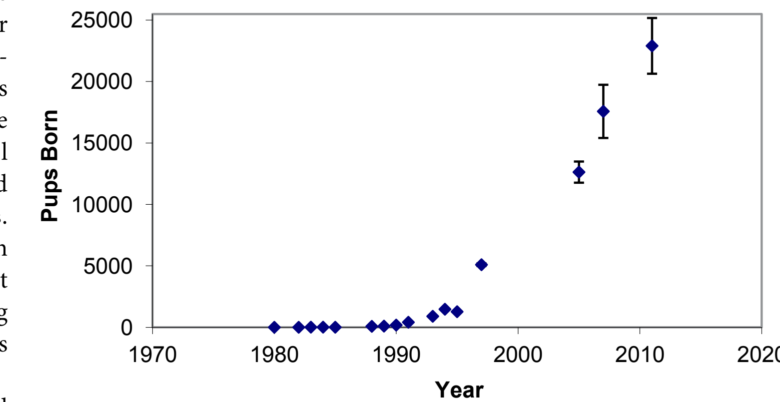

Figure 4. The numbers of Northern fur seal pups born on Bogoslof Island, Alaska, 1980-2011. Error bars are approximate 95% confidence intervals.

Photo 3. Adams Cove northern fur seal herd at San Miguel Island, California, and an interaction between a northern fur seal bull (black) and California sea lion bull (brown). The fur seal herd is intermixed with a California sea lion breeding herd.

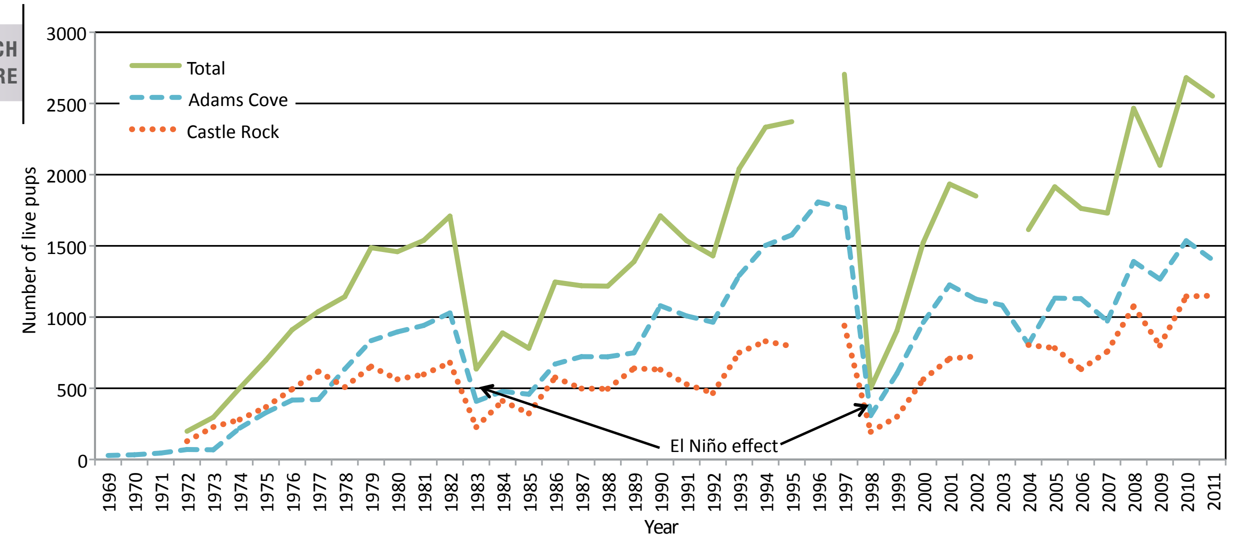

Figure 5. Number of live pups counted in July each year from 1969 to 2011 at Adams Cove (dashed blue), Castle Rock (dotted orange), and total for both rookeries (solid green).

biologists have counted live pups at San Miguel Island in July of each year and estimated the population size since 1968. The San Miguel pup counts cycle with periods of rapid increase followed by significant declines related to El Niño events (Fig. 5). In the California Current ecosystem, El Niño conditions produce changes in the marine environment that result in redistribution and reduced availability of prey to adult and juvenile fur seals that affect survival and reproduction. The strong El Niño events of 1982-83 and 1997-98 reduced the pup births on San Miguel Island by 63% and 81%, respectively. Over a 7-year period following 1983, the number of pup births slowly increased to reach pre-1983 levels in 1990. The slow recovery of pup production indicated that fewer animals were alive to produce pups following El Niño and, therefore, that a significant number of juveniles and adults also had died as a result of El Niño. The recovery from the 1998 decline has been even slower, but interpretation of the recovery is complicated by the emergence of hookworm disease in the San Miguel Island stock in the early 1990s. Hookworm disease has killed up to half of fur seal pups born since 1990 and in the early 2000s emerged as the primary cause of mortality for pups. Even so, the overall population trend for the San Miguel Island stock has generally increased or been stable throughout the last 20 years, likely due in part to immigration from populations from Alaska and Russia. The San Miguel stock, with a current population of about 10,000 animals, currently represents less than 1% of the worldwide northern fur seal population.

After more than a 150-year absence, northern fur seals returned to the Farallon Islands in the 1970s, and in 1996 the first pups were observed there. In 2011, a minimum of 180 live pups was counted in August. Many of the individuals recolonizing the Farallon Islands have tags that identify them as animals born at San Miguel Island, indicating that immigration from the San Miguel population is an important factor in the Farallon Islands population growth. However, not all the animals observed at the Farallon Islands are tagged, and it is possible that some are immigrants from Alaska or Russia.

Broad-scale Foraging Patterns

The National Marine Mammal Laboratory's approach to identifying essential habitat of northern fur seals and quantifying environmental effects on foraging behaviors includes describing age- and sex-specific broad-scale foraging patterns within the Eastern Pacific and San Miguel Island stocks as well as examining individual dive depths in relation to fine-scale biophysical measurements obtained from advanced oceanographic instruments. The research explores variability in foraging patterns within and among seasons (summer and winter) and among years. The goal is to identify environmental factors that influence foraging behavior and the possible consequences to population health, condition, reproduction, or survivorship.

In 2006, NMML researchers deployed satellite-linked telemetry instruments on lactating adult female fur seals at St. Paul, Bogoslof, and San Miguel Islands during the summer breeding season and prior to the winter migration to compare patterns in foraging behavior among the populations and relate them to divergent population trends. The foraging habitat surrounding each of the three islands consists of three oceanographic domains: continental shelf (<200 m), slope (200-1,000 m), and offshore (>1,000 m). Bogoslof and San Miguel Islands have little shelf habitat available around the islands, whereas St. Paul Island is located on the large Bering Sea continental shelf. The oceanographic domains support different prey assemblages and give rise to foraging behaviors that vary within and among the islands. Satellite telemetry instruments were glued to the fur between the shoulders (Photo 4) and provided location information on the animals while at sea or on land for up to 8 months. In addition, some of these satellite transmitters deployed on Alaska animals during the winter also provided information on the seals diving behavior, which can identify important foraging grounds.

Breeding Season

During the summer breeding season, average foraging trip durations (2.7 days) and average maximum foraging trip distances (51.6 km) were shortest for Bogoslof Island females (n=20), which primarily fed offshore, close to the island (Fig. 6). Females from St. Paul Island (n=20) mostly fed in geographically distinct areas from those at Bogoslof Island and exploited shelf and offshore habitats. Their average foraging trips were longer in duration (6.5 days) and in average maximum distance (293 km) than Bogoslof Island females'. Females at San Miguel Island (n=8) had the longest average foraging trip duration (12.5 days) and greatest average maximum distance (341 km) among the colonies.

Migration

Adult females departed the islands in November and began their winter migration. Thirteen of 19 females instrumented at Bogoslof (n=9) and St. Paul (n=10) Islands traveled from the Bering Sea, through the Aleutian passes, into the Gulf of Alaska, and into the North Pacific Ocean (Fig. 6). Of the 13 adult females that were tracked from Alaska, 5 were monitored for more than 90 days, and each ventured into the California Current ecosystem. They remained there and in the Gulf of Alaska ecosystem for 5-6 months foraging along the western slope of the continental shelf break and west into pelagic waters. By June, only one animal was still being tracked, and this female had departed the California Current and Gulf of Alaska ecosystems and was travelling towards her original departure site in Alaska. In contrast to the long distances travelled by the Alaska females, all nine females from San Miguel remained in the California Current and simply shifted their distribution farther offshore and northward compared to their summer foraging range but exploited similar continental shelf break and offshore habitats (Fig. 6). They spent little time in transit and spent most of their time feeding. None of the instruments on San Miguel animals functioned long enough to capture the full migration, but three females tracked into April began moving southward from northern California toward San Miguel Island and presumably returned to the island for breeding in June or July. There was considerable overlap between the San Miguel and Alaska female migration distributions in the California Current ecosystem – which highlights this region as an important winter foraging habitat for both the Eastern Pacific and San Miguel Island stocks.

Photo 4. Adult northern fur seal female with satellite telemetry device (yellow), dive recorder (yellow/green), and identification flipper tag. Instruments are glued to the fur and fall off when the animal molts in the autumn. Flipper tag is retained for several years.

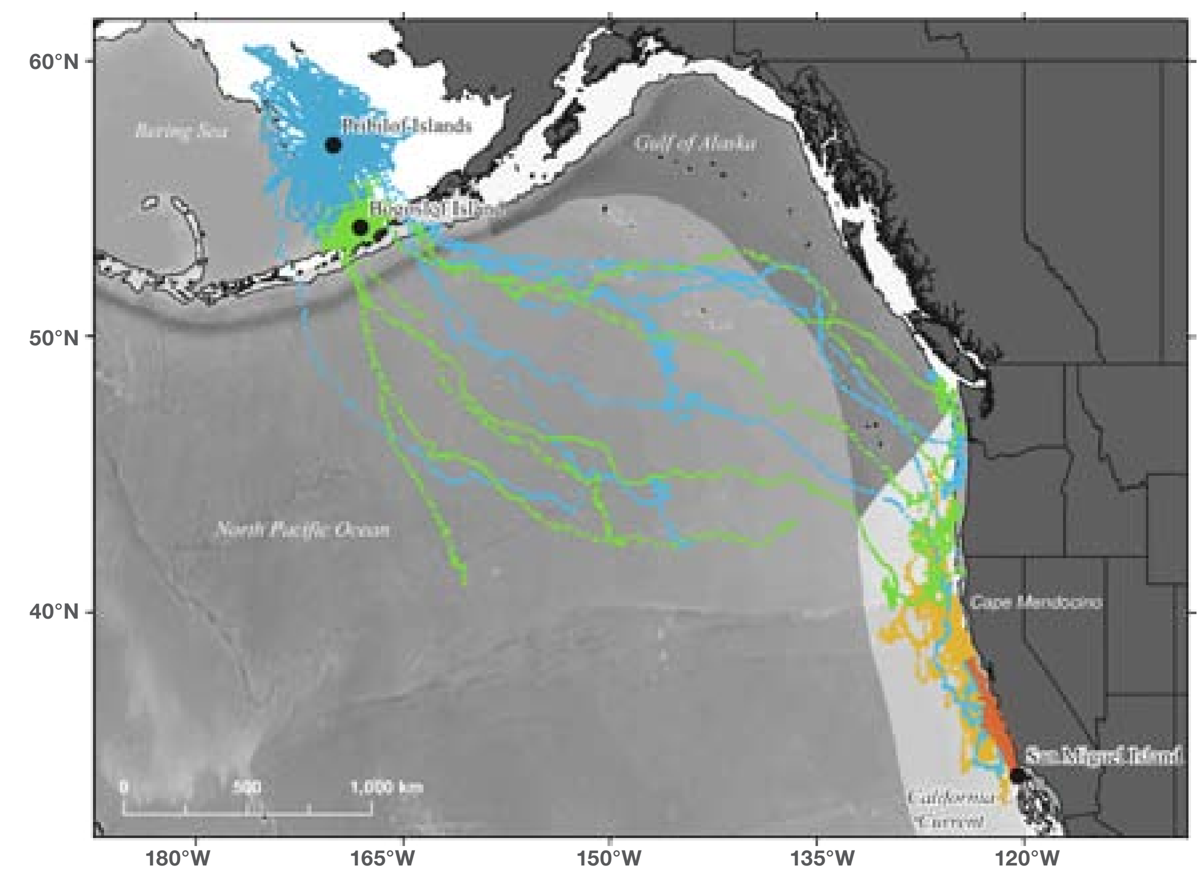

Figure 6. Foraging distribution of northern fur seals instrumented at St. Paul and Bogoslof Islands, Alaska, and San Miguel Island, California, in 2006. Summer movements were centered around the colonies at all sites with little overlap between St. Paul (blue) and Bogoslof (green) islands and no overlap between the Alaska sites and San Miguel Island (red). Alaskan animals migrated across the North Pacific Ocean during the winter, whereas San Miguel (yellow) animals remained in the California Current.

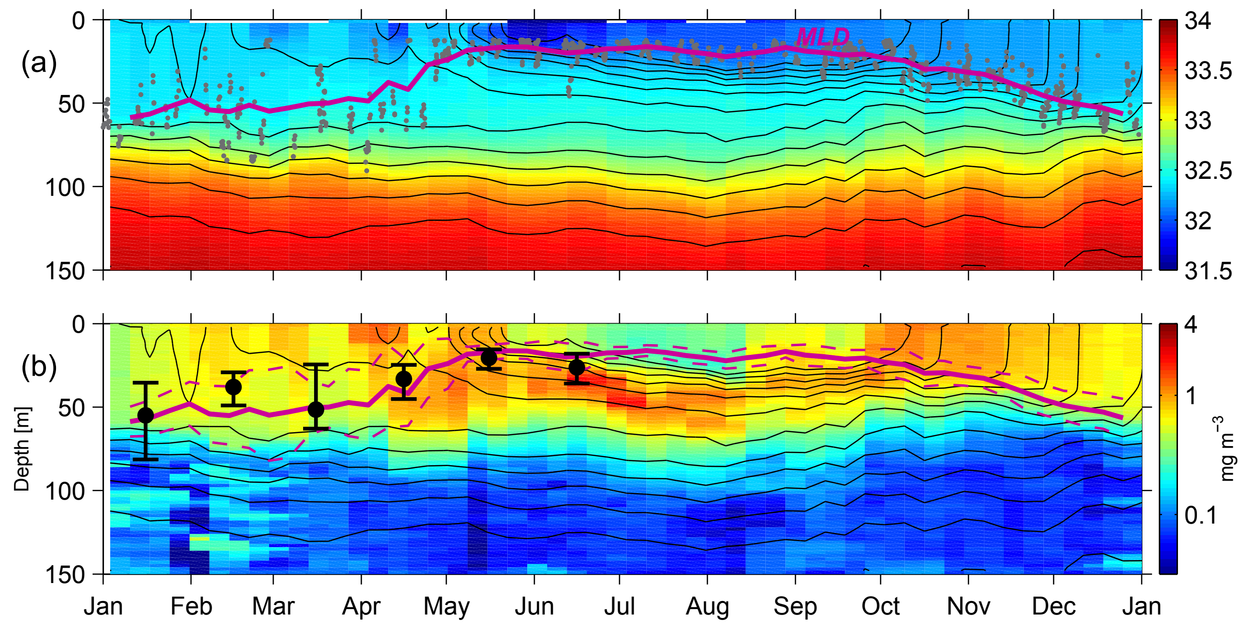

Figure 7. Average annual cycle of (a) salinity and (b) Chlorophyll a, 60-80 km off the Washington coast shelf break, taken from 2003-09 Washington coast Seaglider observations (see Fig. 8 for region). In each panel, average annual cycle of density (σ_t) is contoured in intervals of 0.2 kg m^{-3}. Mixed Layer Depths (MLD) calculated from individual glider casts are indicated by grey dots in panel (a), with the mean in solid magenta; in panel (b), individual casts are not shown and instead dashed magenta lines indicate ±1 standard deviation of the MLD within each bin over all years. In panel (b), black circles plotted in the middle of each month indicate median adult female northern fur seal daytime diving depths during that month. Whiskers denote 1st and 3rd quartiles.

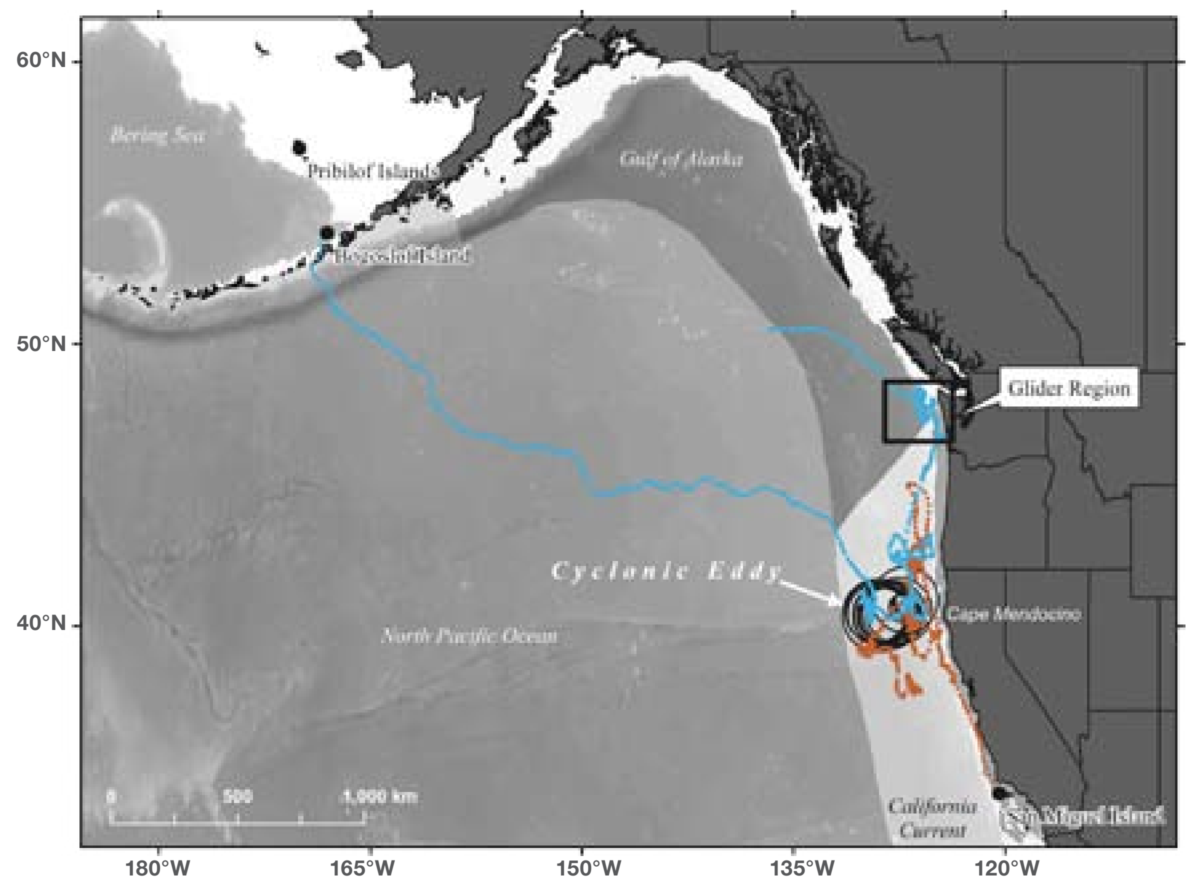

Figure 8. Satellite tracks of two adult female northern fur seals instrumented at Bogoslof Island (blue) and San Miguel Island (red) during winter migration 2006/2007, and the track of a cyclonic eddy present between January and March 2007 (black circles). Both females arrived at the eddy in January and were associated with it until March when the Bogoslof female began to move northward and the San Miguel female began moving southward. Box indicates area surveyed by Washington coast Seaglider Project (data presented in Figs. 7 and 9).

Small-scale Foraging Patterns

The National Marine Mammal Laboratory's collaboration with the University of Washington Applied Physics Laboratory and School of Oceanography also has described northern fur seal foraging patterns on a smaller spatial scale that reflect seasonal, mesoscale, and fine-scale oceanographic variability in the California Current ecosystem. The seasonal features of the California Current ecosystem are important factors affecting the density, distribution, and abundance of fur seal prey during the winter. Integration of remotely sensed oceanographic environmental data off the Washington coast, obtained from surveys conducted using an autonomous underwater vehicle (Washington Coast Seaglider survey), were combined with northern fur seal diving and movement patterns to demonstrate the interplay between northern fur seal behavior and the mixed-layer depth (MLD), eddies, wind-driven coastal upwelling, and seasonal ocean production. For example, seasonal changes in fur seal diving depths from deeper to shallower corresponds well with seasonal shoaling of the surface MLD and initiation of the spring chlorophyll bloom (Fig. 7). As adult females from Alaska arrive to the California Current in January their diving depths are deeper and more variable compared to diving depths in May and June (Fig. 7).

Mesoscale variability such as coastal jets and eddies also affects the movement behavior of both San Miguel Island and Alaska fur seals. The animals' distributions overlap during the winter, and they tend to forage along steep oceanographic gradients both horizontally and vertically (Figs. 6 and 7). Eddies form in the California Current ecosystem and can persist for several months to a year and promote production and aggregation of zooplankton and northern fur seal prey species such as fish and squid. Biophysical interactions between eddies and fur seals generally occur along eddy edges (Fig. 8). Presumably, eddy physical structure promotes good foraging opportunities for northern fur seals, which may partially explain why the distant Alaska migrants travel to the California Current ecosystem during the winter months and why the San Miguel Island fur seals remain resident.

Furthermore, broad-scale wind patterns can cause alterations in fine-scale biophysical structure, which ultimately affects fur seal movement and diving behavior (Fig. 9). For example, a shift in the dominant wind direction (Fig. 9(d)) is associated with coastal upwelling and advection of nutrients westward and can promote a strong surface and subsurface chlorophyll bloom (Fig. 9(a), (b)). Fur seals responded to increased ocean productivity with a shift in movement from transitory to searching behavior and remained within 50 km from the continental shelf break in an area of high production (Fig. 9(a), (c)). Fine-scale vertical variability and the surface chlorophyll bloom indicate a shoaling of the MLD close to the continental shelf break (~ 20m depth; Fig. 9(b)). Fur seal diving depths, both during the daytime (white triangles; Fig. 9(b)) and nighttime (black triangles; Fig. 9(b)) were shallow and aggregated around the MLD, reflecting the depth and distribution of their prey. Thus, the spatial and temporal integration of fur seal behavior with seasonal, mesoscale, and fine-scale biophysical structures highlights important linkages between atmospheric patterns, ocean production, and fur seal prey.

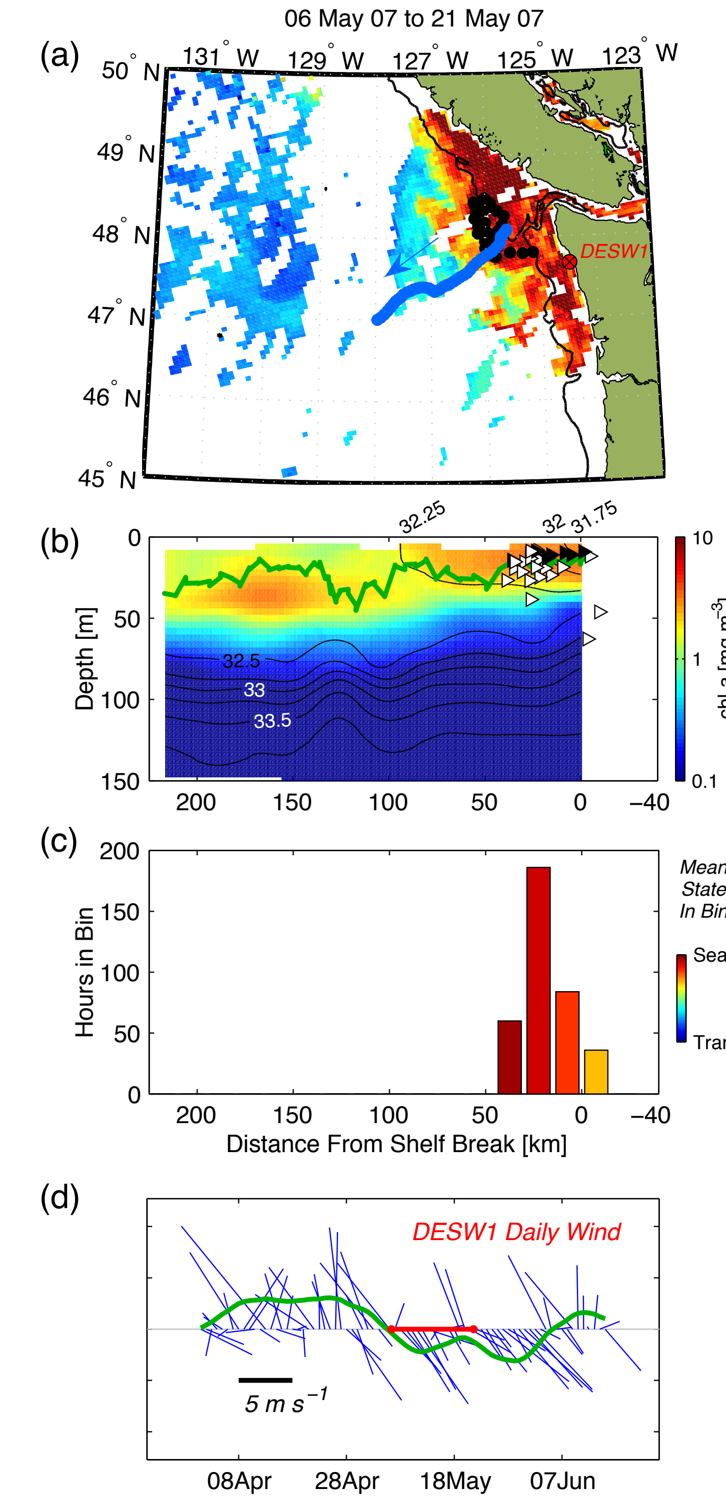

Figure 9. Movement and dive behavior of an adult female northern fur seal in relation to surface chlorophyll a (a), subsurface salinity and chlorophyll a (b), distance from the continental shelf break (c) and spring winds (d) in the California Current. Subsurface salinity and chlorophyll a measurements (b) were obtained along the Washington coast Seaglider survey line shown as blue dots in (a). Black dots in (a) indicate fur seal locations and the black and white triangles in (b) represent the average dive depth for each 6 hour period during nighttime and daytime periods, respectively. Movement behavior was determined as either searching or transitory and this behavior relative to the continental shelf break is shown in (c). The behavior of this fur seal switched to a searching behavior just as the spring winds switched to a northwesterly direction (d), causing upwelling and a chlorophyll bloom (a). In addition, the seal's dive behavior intensified and was aggregated at the mixed-layer depth (MLD) (b).

Diet Differences Within and Between Stocks

Diet samples are collected within each stock to monitor how diet changes over time in relation to the diverse prey and marine habitats available to northern fur seals during the summer breeding season and winter migration. The research employs multiple techniques including stable isotope analysis and scat (feces) collection, which provide a more comprehensive view of the diet by encapsulating both small and large spatial and temporal scales of seal foraging. The goal is to determine if seal diets can help explain the divergent population trends observed within and between the two stocks.

Scat analysis involves the identification of prey hard parts (e.g., fish bones and cephalopod beaks) found in samples and is useful for providing information on specific prey taxa consumed. Stable isotope analysis is based on the premise that the stable isotope composition of a consumer's diet is reflected in its tissues and that each tissue assimilates diet at different temporal scales due to dissimilar isotopic turnover rates within each tissue. For fur seals, plasma represents the diet integrated about 1-2 weeks prior to collection (i.e., foraging trip); red blood cells (RBCs) represent the previous month or two (i.e., breeding season); and fur represents diet from the breeding season and, to a lesser extent, the previous winter migration. The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of the fur seal tissues indicate foraging location and trophic level, respectively. Values of $\delta^{13}C$ increase from high to middle latitudes, offshore to nearshore, and pelagic to benthic environments; $\delta^{15}N$ values increase with each trophic level.

The goal is to determine if seal diets can help explain the divergent population trends observed within and between the two stocks.

Table 1. Percent frequency of occurrence (%FO > 5%) of prey taxa retrieved from northern fur seal fecal samples collected at Bogoslof Island (BI, 2007), San Miguel Island (SMI), and two rookeries on St. Paul Island (SPI) in 2006. n **represents the number of samples that had identifiable prey remains. Bold numbers indicate prey taxa with %FO > 10%.**

Prey taxa	SPI Reef	SPI Vostochni	BI	SMI
	(n = 28)	(n = 74)	(n = 41)	(n = 27)
Northern anchovy				**92.6**
Northern smoothtongue			**73.2**	
Walleye pollock	**89.3**	**68.9**	9.8	
Pacific hake				**55.6**
Pacific sardine				**51.9**
Market squid				**22.2**
Gonatid squid	3.6	5.4	**73.2**	3.7
Clupea harengus	**14.3**	27.0		
Pacific salmon	**17.9**	**18.9**		
Gadid spp.	3.6	**25.7**	2.4	
Myctophid spp.	**10.7**		**17.1**	3.7
Atka mackerel	**14.3**	6.8	2.4	
Rockfish				7.4
Pacific sand lance		5.4		
Three-spine stickleback		5.4		
Irish lord		5.4		
Sculpin				3.7

Diet studies were conducted at the same locations as the satellite telemetry studies: St. Paul Island in the Pribilof Islands, Bogoslof Island, and San Miguel Island. Scat analysis revealed that relatively few prey taxa had high occurrences (found in >10% of scats) at each location (Table 1). Prey identified from scats at each site was associated with a specific oceanographic domain. At St. Paul Island, scats from two different areas had different primary prey taxa; Vostochni Rookery on the northeast side of the island had highest occurrences of on-shelf species (e.g., walleye pollock, Pacific herring, Pacific sand lance) and Reef Rookery on the south side of the island had high occurrences of both on-shelf (e.g., walleye pollock, Pacific herring) and off-shelf species (e.g., myctophids). Bogoslof Island was characterized by high occurrences of off-shelf prey (e.g., gonatid squid and northern smoothtongue), whereas San Miguel Island had high occurrences of on-shelf schooling prey (e.g., northern anchovy, Pacific hake, Pacific sardine, rockfishes, and market squid).

Plasma and RBC $\delta^{13}C$ values were different at each island (San Miguel Island > St. Paul Island > Bogoslof Island; Fig. 10). These results corresponded with scat analyses and reflected the geographic differences in the prey assemblages around each island during the breeding season. All tissues collected from animals at San Miguel Island were more $\delta^{13}C$-enriched than those collected from animals at Alaska locations, likely due to latitudinal isotopic differences (Fig. 10). There were some similarities (San Miguel Island and Vostochni Rookery at St. Paul Island) and differences (San Miguel Island and Vostochni Rookery, St. Paul>Reef Rookery, St. Paul Island >Bogoslof Island) in plasma and RBC $\delta^{15}N$ values among islands (Fig. 10). This pattern indicates that individuals that feed on prey in relatively nearshore or on-shelf waters were feeding at a higher trophic level compared to those feeding in off-shelf, pelagic areas. Fur $\delta^{15}N$ values followed this same pattern.

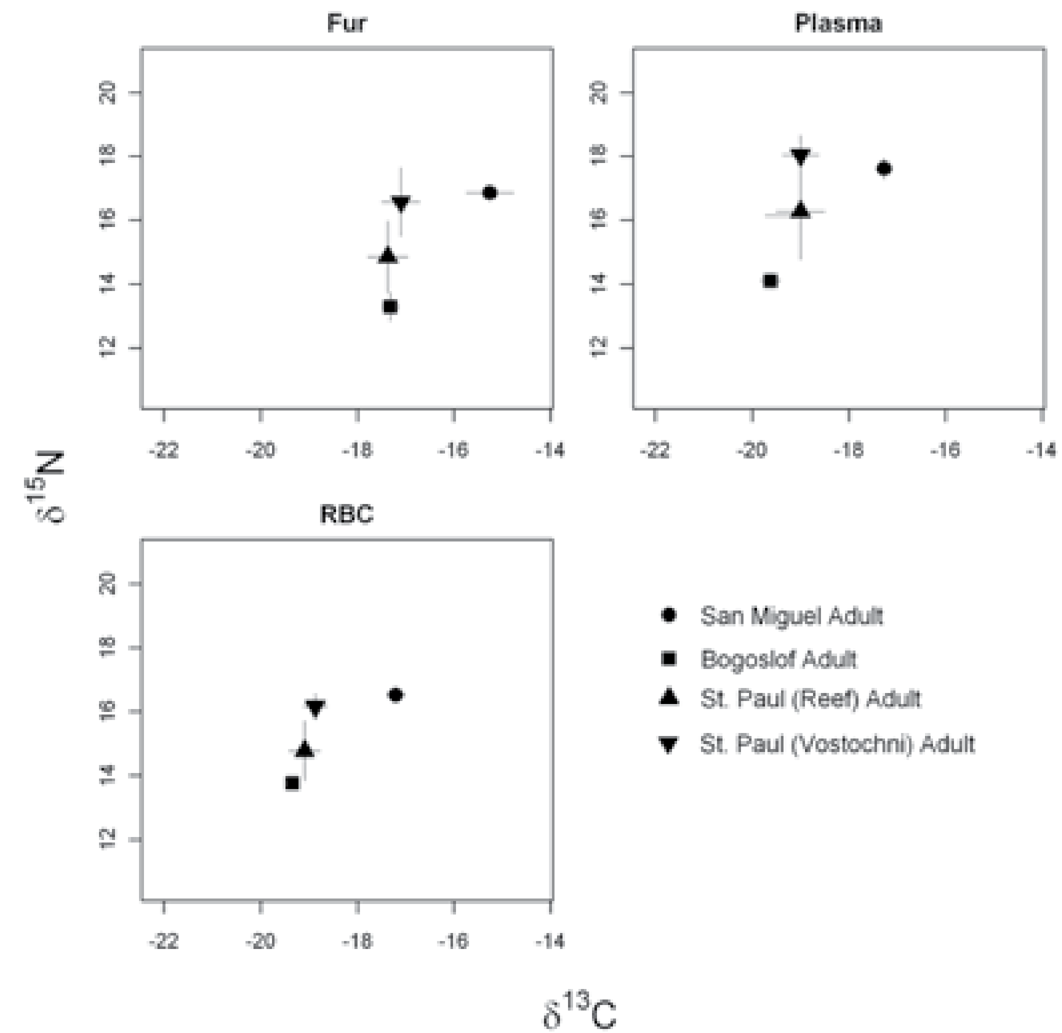

Figure 10. The relationship between mean $\delta^{13}C$ and $\delta^{15}N$ of tissues collected from adult female northern fur seals at Bogoslof Island (in 2007), San Miguel Island, and two rookeries on St. Paul Island (Vostochni, Reef) in 2006. Error bars represent ± 1 SD. RBC: red blood cells.

Apart from a few discrepancies (e.g., at San Miguel Island scat diet data indicated on-shelf foraging; however, telemetry data indicated slope/off-shore feeding), the diet data corroborate the movement patterns from our satellite telemetry studies. Fur $\delta^{13}C$ values were similar among the Alaska populations, suggesting that Alaska fur seals migrate to the same general areas during winter to feed. These individuals had lower $\delta^{13}C$ values compared to their counterparts at San Miguel Island, indicating that during part of the fur growth, these animals were feeding in different oceanic domains. The satellite data support this finding; between molting periods, San Miguel Island females feed exclusively in the California Current ecosystem whereas Alaska female fur seals only spend 3-4 months in this ecosystem and the rest of the year in the North Pacific Ocean and Bering Sea.

Future Directions

The Northern Fur Seal Conservation Plan describes the importance of comparative studies across the range of northern fur seals to better understand ecological processes that affect fur seal population dynamics. As our research demonstrates, there are similarities in foraging behavior among the populations in the two stocks, but it is the differences among them that should help to explain the divergent population trends. Future studies will focus on connecting foraging behavior and oceanographic features to demographic parameters throughout the range with the goal of identifying what is driving the decline of the Eastern Pacific stock.

Additional Reading:

National Marine Fisheries Service. 2007. Conservation Plan for the Eastern Pacific stock of Northern fur seal (*Callorhinus ursinus*). U.S. Dept. of Commerce, NMFS, Protected Resources Division, Alaska Region. Available at http://www.fakr.noaa.gov/protectedresources/seals/fur/cplan/final1207.pdf.

Zeppelin, T.K. and A.J. Orr. 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. Marine Ecology Progress Series 409:241-253.