NORTH PACIFIC RESEARCH BOARD PROJECT FINAL REPORT

Seasonal Foraging Strategies and Consequences for Northern Fur Seals at Colonies with Opposite Population Trends – Year 2 (COFFS)

NPRB Project 524 Final Report

Alan M. Springer[1], Rolf R. Ream[2] and Sara J. Iverson[3]

[1]Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775. (907) 474-6313, ams@ims.uaf.edu

[2]National Marine Mammal Laboratory, National Marine Fisheries Service, 7600 Sand Point Way NE, Bldg. 4, Seattle, WA 98115

[3]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

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ABSTRACT

The abundance of northern fur seals at the Pribilof Islands, which accounts for the majority of the world population, has fallen by nearly 80% in the past five decades. The cause since the mid 1970s is unknown. In contrast, fur seals have increased exponentially in the past three decades at Bogoslof I. in the eastern Aleutian Is., where oceanographic conditions differ substantially—the Pribilofs lie on the shallow continental shelf, whereas Bogoslof lies in the deep oceanic basin. We compared foraging strategies of adult females in the two regions and the consequences to the growth and condition of mothers and pups during the lactation period to identify factors important to the divergent population trends. The physical condition of females upon arrival from wintering grounds in the N. Pacific, where they spend eight months each year, was somewhat different between Bogoslof and St. Paul, indicating variable foraging opportunities during winter/spring or differing foraging strategies: spring diets of females at St. Paul were notably different than at Bogoslof in 2006. The composition of fall diets of seals differed in both species composition and levels between Bogoslof and St. Paul, and between Reef and Vostochni rookeries at St. Paul, although the aggregate energy index values of the various diets were quite similar. However, females at the Pribilof rookeries foraged 2.3 times farther and 2.9 times longer between nursing periods than seals at Bogoslof, reducing milk delivery rates to pups at St. Paul compared to Bogoslof. Pups at St. Paul grew slower and attained less weight before weaning than those at Bogoslof, and females at St. Paul lost condition during summer, whereas females at Bogoslof did not. If weaning weight of pups is proportional to milk delivery throughout lactation and to post-weaning survival, and if female condition at the end of lactation is proportional to the energetic expense of foraging and to their survival or reproductive success, then the differences we observed could be contributing to the contrasting population trends.

KEY WORDS

Northern fur seal, *Callorhinus ursinus*, Bering Sea, Pribilof Islands, Bogoslof Island, foraging strategy, satellite tracking, female physiology, pup growth

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STUDY CHRONOLOGY

This project was Year 2 of a study that began in 2005 as Project 414 under the same title. A final report for Project 414 was submitted to NPRB in March 2006. Progress reports for this project (514) were submitted to NPRB on June 25, 2006 (Jan-Jun 2006), January 15, 2007 (Jun-Dec 2006), and February 15, 2008 (Jun-Dec 2007).

INTRODUCTION

One of the most striking ecological changes in Alaska in the past 40 years has been the collapse of populations of sea otters *Enhydra lutra* and three species of pinnipeds—harbor seals *Phoca vitulina*, Steller sea lions *Eumetopias jubatus*, and northern fur seals *Callorhinus ursinus*—in the central-western Gulf of Alaska, Aleutian Islands, and Bering Sea (southwest Alaska). The phenomenon is now commonly known as the Sequential Megafaunal Collapse (Springer et al. 2003), the exact nature and cause(s) of which remain unresolved, but have been the subject of heated debate for several years (Estes et al. 1998, Springer et al. 2003, 2008, Trites et al. 2007, Wade et al. 2007, DeMaster et al. 2006, Mizrock and Rice 2006, Williams et al. 2004). The abundances of harbor seals, sea lions, and sea otters declined precipitously over short intervals and have now more or less stabilized, with some areas showing evidence of increasing trends recently and other areas still in decline (Merrick et al. 1987, Pitcher 1990, Doroff et al. 2003, Small et al. 2003, Jemison et al. 2006, Fritz et al. 2008, J. Estes unpubl. data, US Fish and Wildlife Service unpubl. data). Unlike these patterns, the abundance of fur seals on the Pribilof Islands in the Bering Sea, once home to some 74% of the total world population, has been in a less steep decline but over a much longer period than the others, is still falling at an alarming rate, and is now only about 20% of its peak size (Gentry 1998, Loughlin et al. 1994, Angliss and Outlaw 2006, Towell et al. 2006). Another important contrast between fur seals and the other species is that their abundance on Bogoslof Island in the eastern Aleutian Islands, the only other rookery of fur seals in Alaska, has been increasing exponentially during the past 30 years, whereas there were no similar examples of population growth for any of the other species within this overall range of southwest Alaska during this time.

The contrast between the population trajectories of fur seals on the Pribilofs and Bogoslof mirrored that between certain species of fish-eating (piscivorous) seabirds at the two locations, which also experienced declines at the Pribilofs but increases at Bogoslof and at Buldir Island in the western Aleutians in the 1970s-1980s (Dragoo et al. 2007). Thus, there were clear, opposing, signals from two distinct ecoregions of the Bering Sea—the shallow continental shelf where the Pribilofs lie, and the deep ocean basin where Bogoslof lies.

These juxtapositions provided unique opportunities to probe the workings of the ecosystem. We aimed to compare fundamental elements of fur seal foraging strategies (e.g., diet, foraging range and region, and attendance patterns) during the summer lactation period at those two locations, and assess the consequences of those strategies to the fitness of adult females and their pups. We believed that such comparisons of strategies and consequences would inform us about the importance of habitat quality in the Bering Sea to fur seal population dynamics.

However, habitat quality in the Bering Sea is just one element in the fur seal equation. A second element is that adult females and juveniles spend considerably more time away from the Bering Sea each year than in it—roughly eight months between breeding seasons are spent in various regions of the open N. Pacific Ocean south of the Aleutians. Thus, conditions in the Bering Sea may be less important to individuals and populations than conditions experienced elsewhere during winter prior to parturition. Longitudinal studies of individual fitness through complete annual cycles, which we undertook and report on here, further informed us about the importance of conditions in the Bering Sea compared to conditions in the N. Pacific.

These concepts of habitat quality as factors in fur seal population dynamics have as their underpinning the idea that bottom-up processes important to biomass yield at all levels of the food web are also responsible for standing stock sizes. However, there are other elements of possible importance to stock size, including predation, disease, disturbance at rookeries, and other anthropogenic effects such as entanglement in marine debris. Failure to find support for habitat quality as a principal explanation for lower fitness of mothers and/or offspring and thus a potential contribution to declining abundance of fur seals at the Pribilofs could implicate other factors as more important causes.

These observations and ideas led to the following two working hypotheses:

Prey availability and quality are lower on the continental shelf than in the basin of the Bering Sea.

> Prey availability could be a function of physical oceanographic features, food web productivity, or effects of commercial fisheries. Prey quality is likely determined more by habitat type and condition (e.g., relatively warmer or cooler, depending on variable physical forcing as characterized by the PDO) and associated community structure.

Or alternately:

Food web productivity in the N. Pacific is insufficient to support fur seals in winter-spring, which is causing their decline at rookeries on the Pribilofs.

If females returning to the Bering Sea are in poor condition, this may drive declines in the population as a whole. Differences in trends between the two islands could thus be related to other factors or unexplained shifts in distribution within the Bering Sea population.

Failure to find support for either of these propositions could implicate other factors as causes of fur seal declines.

OBJECTIVES

Our objectives were framed as predictions based on the two working hypotheses:

- Adult female fur seals at the Pribilofs are less able to raise robust pups to the age of weaning than those at Bogoslof. Therefore, at the Pribilofs:
  - Foraging distances from rookeries are greater
  - Foraging times are longer
  - Diet quality and/or quantity is poorer
  - Milk delivery rates are lower
  - Growth rates of pups are slower
  - Weights of pups near weaning are lower
  - Percent body fat of pups near weaning is lower
  - Body condition indices of females in late lactation are lower

- Conditions in the North Pacific during the winter/spring will not differentially affect females breeding at the Pribilofs compared to Bogoslof. Therefore:
  - There will be no difference in the physiological condition of female seals at the Pribilofs compared to Bogoslof when they first arrive at the rookeries in the summer.
  - The body condition of individual females returning to St. Paul will not be affected by the location in the N. Pacific where they over winter.

METHODS

Study area

Our study was undertaken at St. Paul Island, one of the two large islands in the Pribilof Island group, and at Bogoslof Island in the eastern Aleutians (Fig. 1). The majority of the world's population of fur seals breeds on St. Paul, and although numbers are growing rapidly on Bogoslof they are still only about 10% of those on St. Paul I. (Angliss and Outlaw 2006). We sampled animals at two of the several discrete rookeries on St. Paul I., Vostochni and Reef rookeries (Fig. 2), and at Bogoslof.

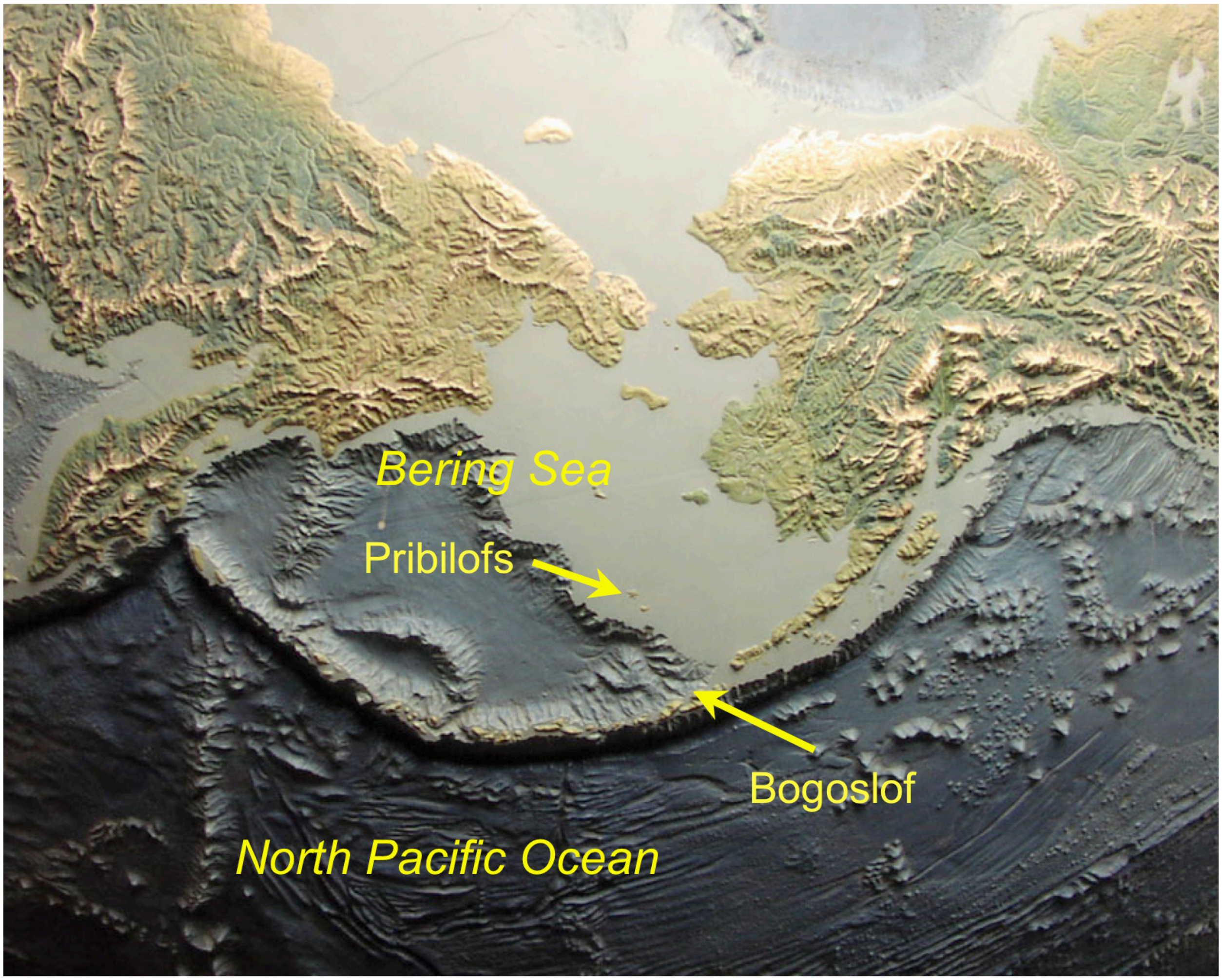


Figure 1. Location of the Pribilof Is. and Bogoslof I. in the eastern Bering Sea.

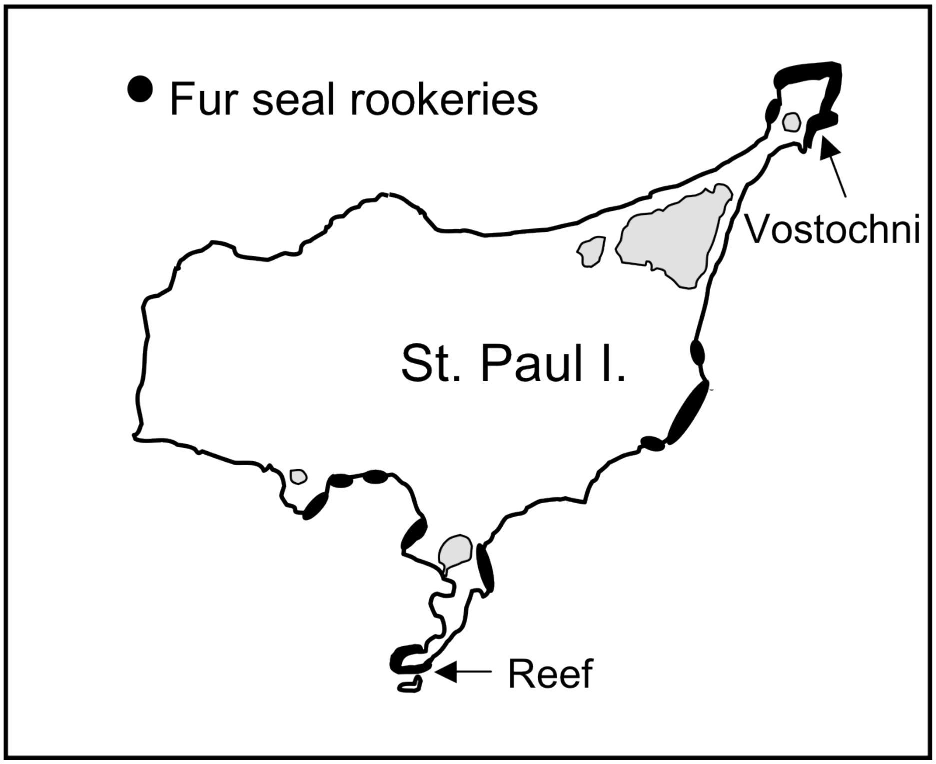


Figure 2. Locations of Reef and Vostochni rookeries at St. Paul I.

Pre-winter tagging

In Phase 1 of this study (Banks et al. 2006), 20 adult females that had recently molted were captured and restrained following the techniques of Gentry and Holt (1982) at St. Paul in early November 2004. A blood sample was collected from the rear flipper as near as possible to the time of capture for measurement of background isotope levels. Females were weighed to the nearest 0.5 kg, measured to the nearest 0.5 cm (length and girth), and given a precisely weighed dose (at $1\ g \cdot kg^{-1}$) of 99.8% deuterium oxide (D_2O; Sigma Aldrich) by gastric intubation to determine total body water (TBW) and body composition. Blood samples (5-10 cc) were collected at 1.5 h and 2 h following isotope administration for measurement of isotope concentration and to confirm equilibration. Satellite transmitters (Kiwisat 101 PTT, Sirtrack Ltd.) were attached to their pelage with 10 Minute® Epoxy (Devcon) to assess winter foraging areas. Females were given uniquely numbered tags (Allflex Global Medium, Allflex USA, Inc.) in the fore flippers for identification. Prior to the final blood sampling, females were administered an IM dose of oxytocin to facilitate milk let-down and a milk sample was collected by manual expression for analysis of proximate and fatty acid (FA) composition. A blubber biopsy was taken from the neck region of the female using a 6 mm sterile biopsy punch according to Kirsch et al. (2000) to be used to determine FA composition and eventually dietary sources of onboard energy reserves. Females were then released.

Pre-winter tagging at St. Paul in 2004 and 2005 occurred in early November. Pre-winter tagging at Bogoslof occurred in mid to late October 2005 only at the time of the recapture of mothers and pups. The sampling protocol in 2005 was modified from 2004 by substituting an IM administration of a precisely weighed quantity of tritiated water (^3H_2O) for the D_2O to determine female body composition. We also used an updated model of satellite transmitters (Kiwisat 202 PTT, Sirtrack Ltd.) in 2005.

Perinatal sampling

Twenty females with newborn pups were identified by the presence of a fresh umbilicus on the pup. At the Pribilofs in 2005 and 2006 and at Bogoslof in 2006, these were the females that were tagged the previous fall, with the addition of new females (as needed to replace those that did not return or were not found) to make a sample size of 20. At Bogoslof in 2005, these were simply 20 mother-pup pairs with known parturition dates. At 1-2 days postpartum, pairs were captured according to Goebel (2002). A blood sample was collected from the flipper of both female and pup for measurement of background isotope levels. Female and pup were weighed to the nearest 0.1 kg and given isotopically labeled water to determine TBW and body composition, and milk intake in pups. Females were injected with ^3H_2O. Pups were first intubated to remove and discard any milk in their stomachs (which delays equilibration) and then given D_2O (at 3 $g\cdot kg^{-1}$). Female and pup were kept together but not allowed to suckle during a 2-hour equilibration period. Blood samples were collected at 1.5 and 2 hrs following isotope administration for measurement of isotope concentration and to confirm equilibration.

Prior to the final blood sampling, females were administered oxytocin and a milk sample was collected. Immediately prior to release, a full-depth blubber biopsy was taken. Females were instrumented with satellite transmitters to determine summer foraging areas, time-depth recorders (MK9 TDR, Wildlife Computers) to assess foraging effort, and VHF transmitters (MM420, Advanced Telemetry Systems, Inc) to monitor attendance patterns during the sampling period and to locate individuals on the rookery. Any new females were given a uniquely numbered tag in the fore flipper and pups were given a unique mark with commercial hair-bleach. Female and pup were released and observed to make sure that the mother-pup bond was intact.

Daily observations using VHF were made of the rookery to determine when the female ended her perinatal suckling period and departed to sea. The pup was then briefly captured to obtain a body mass measurement and blood sample for D_2O analysis.

All samples (blood, milk, and blubber) were stored in a cooler on ice during collection periods in the field. Upon return to the field laboratory, blood samples were centrifuged and serum collected into cryovials and frozen. Milk samples were stored frozen and blubber biopsies were placed in a glass vial containing chloroform with 0.01% BHT and stored frozen until analysis.

Mid-lactation sampling

At approximately 3 months postpartum (3/4 way through the lactation period) in both years, the same mother-pup pairs were captured and restrained following the techniques of Gentry and Holt (1982). Instruments (PTT, TDR, VHF) were removed from the females at this time. All other procedures were repeated as described above with the exception that pups were administered D_2O at 1 $g \cdot kg^{-1}$ to measure equilibration levels only. We used pup growth rate and body condition as a proxy for overall milk intake rates to avoid continual and long-term recaptures of mother-pup pairs throughout lactation.

Prey sampling

Prey commonly taken by fur seals in the Bering Sea were obtained from the NMFS groundfish trawl surveys, the NMFS BASIS program, and other cruises of opportunity. In addition to the prey FA database acquired under this and another NPRB grant to us (Project 320), prey data from the Bering Sea and western Gulf of Alaska we acquired with support from other funding sources were also used (S. Iverson, A. Springer, and S. Wang unpubl. data). Once collected, prey samples were frozen until they were returned to the lab for processing.

Laboratory analyses and interpretation

Tagging data

Female foraging areas during the winter migration and the summer lactation period were determined from satellite telemetry data. Locations were calculated by Service Argos Inc., and filtered iteratively based on Argos location quality rankings, time sampling/transmission intervals and maximum swim speed, similar to methods described by Robson et al. (2004) and Ream et al. (2005). Foraging patterns during the summer lactation period were determined using data from TDRs, in combination with the satellite telemetry data. Distinct foraging trips were first identified for individual females and then the number of foraging trips, number of trips per week deployed, mean trip durations, and proportion of time spent at sea was calculated for comparison of females among rookeries. Maternal attendance patterns were used to compare shore (nursing visit) durations with foraging trip durations of females among rookeries. We assessed variability between islands, between years, and between two rookeries on opposite sides of St. Paul Island (based on expected differences in foraging behavior among rookeries as observed by Robson et al. (2004), Sterling and Ream (2004), and Zeppelin and Ream (2006).

Body composition and milk intake

Serum samples were distilled using the method of Ortiz et al. (1978) and counted for ^3H activity using a Beckman LS 5000CE scintillation counter, or distilled using the method of Oftedal and Iverson (1987) and analyzed for D_2O concentration on a Thermo Electron Corp. Nicolet Avatar 370 DTGS spectrophotometer with a BaF2 0.10 mm EZ fill cell, using gravimetrically prepared standards and distilled water as reference, and with spectra collected and processed using EZ OMNIC and TQ Analyst software.

Isotope dilution space was converted to total body water (TBW) using the equation derived by Bowen & Iverson (1998). TBW was then used to calculate total body fat (TBF) and total body protein (TBP) content using the equations of Arnould et al. (1996).

All milks were analyzed for proximate composition: dry matter, by both freeze drying and by forced convection drying to compare methods; protein, by nitrogen analysis on a LECO TruSpec CN analyzer and using previously derived conversion factors for milk protein (Oftedal and Iverson 1995); and total fat by the Roese-Gottlieb procedure for milks (AOAC). Milk intake of pups during the perinatal period will be determined according to Oftedal and Iverson (1987) and Iverson et al. (1993).

Fatty acid analyses and QFASA

Lipids were quantitatively extracted from blubber, milk, and prey (after recording length and mass of each whole prey) according to Iverson et al. (2001). FA methyl esters were prepared, identified, and analyzed according to Iverson et al. (1997, 2001, 2002) using temperature-programmed gas liquid chromatography on a Varian Capillary FID gas chromatograph fitted with a 30m x 0.25 mm id. column coated with 50% cyanopropyl polysiloxane (0.25µ film thickness; Agilent Technologies DB-23; Palo Alto, CA) and linked to a computerized integration system (Varian Galaxie software). Qualitative differences and variation in diets were evaluated from milk and blubber FA signatures of females after winter foraging (North Pacific) and again after summer foraging (Bering Sea).

Diets were estimated using quantitative fatty acid signature analysis (QFASA) of female blubber samples according to Iverson et al. (2004) using the prey databases available from this and other studies in the Bering Sea and western Gulf of Alaska (see above). Since calibration coefficients, which account for metabolic effects on lipid deposition in predators (see Iverson et al. 2004 for a detailed description of calibration coefficients), were not available for northern fur seals, we used those recently determined for another otariid, the Steller sea lion (Tollit et al. 2006; D. Tollit and S. Iverson unpubl. data). Given the closely related nature of otariids and the fact that calibration coefficients from all pinniped species analyzed to date are quite similar, these were considered to be most appropriate. We tested FA sets that previously have been used successfully and found that all produced similar diet estimates, and thus used the set that included most dietary FAs. Results are reported for prey species that were present in diets at levels $\geq$ 5% mass after correcting FA signature estimates for lipid content. An energy index was calculated to scale the energetic value of diets by multiplying the mass percent contribution of each prey species by the percent lipid of that species and then summing these values across species for each female. Given that fat contributes most of the calories in prey, and certainly accounts for the greatest differences in caloric content among species, this relative index was used since protein levels were not available. Turnover times of FAs in fur seal blubber are not known for any season, but we expect that our estimates represent diets integrated over intervals of approximately two to four weeks, rather than four to six weeks previously determined (e.g., Iverson et al. 2004; Nordstrom et al. 2008; Wang et al. 2010). That is, we expected that especially during the lactation period, the rapidity with which fur seal females acquire energy stores and then dump them into milk during suckling intervals should lead to a relatively rapid turnover of FAs.

RESULTS

Female wintering locations in the N. Pacific

In November 2004, 20 adult female fur seals were captured and instrumented with satellite transmitters at two St Paul I. rookeries – 10 from Reef and10 from Vostochni. This sampling was repeated at St. Paul Island in November 2005, and 20 additional females were also instrumented at Bogoslof Island in October 2005. Tracking began immediately and continued through the winter migration periods. Adult females instrumented in the fall of 2005 were characterized by notably short tracking durations; nearly half of the satellite tags deployed at St. Paul (50%) and Bogoslof (45%) stopped transmitting before January 1st, 2006. By comparison, less than 6% of tags deployed at St. Paul in 2004 stopped transmitting before January 1st, 2005. We suspect that instrument failure (rather than variable molt patterns or animal mortality) was responsible for the early termination of transmissions. By March, females that were still being tracked were spread out across the North Pacific from the coast of Washington (deep, off-shelf waters), westward to the transition region of the west-central North Pacific Ocean (37°N, 176 °W). Adult female fur seals instrumented during the fall of 2005 at St. Paul and Bogoslof used the same regions of the North Pacific during the winter migration (Fig. 3). For animals that were tracked to a destination region during the 2005 winter migration, or for which we were able to determine the probable destination region based on transit patterns, six of 13 females from Bogoslof and nine of 13 females from St. Paul were using the transition region or other open ocean habitat. The remaining animals were using habitat off the coast of Washington, Oregon, and British Columbia, Canada. The proportion of animals using coastal or open ocean habitat did not differ between years (£q^2 < 1.418, P = 0.234).

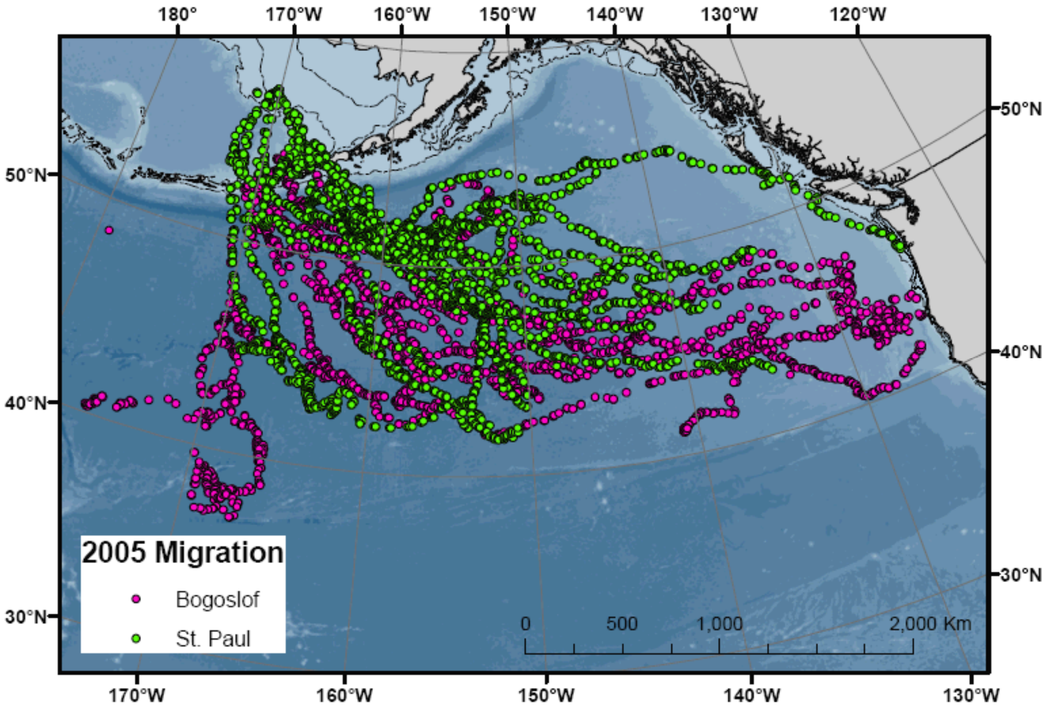


Figure 3. Satellite locations of adult female northern fur seals from St. Paul I. and Bogoslof I. during the 2005 winter migration into the North Pacific Ocean.

Transit routes and habitat use during the winter migration were also similar between years for adult females instrumented at St. Paul I. in the fall of 2004 and 2005 (Fig. 4). For animals that were tracked to a destination region during the 2004 winter migration, or for which we were able to determine the probable destination region based on transit patterns, 11 of 16 females from St. Paul were using the transition region or other open ocean habitat. The remaining animals were using habitat off the coast of Washington, Oregon, California, and British Columbia, Canada. The proportion of animals from St. Paul Island using coastal or open ocean habitat was not differ between years (£q^2 < 0.001, P = 0.978).

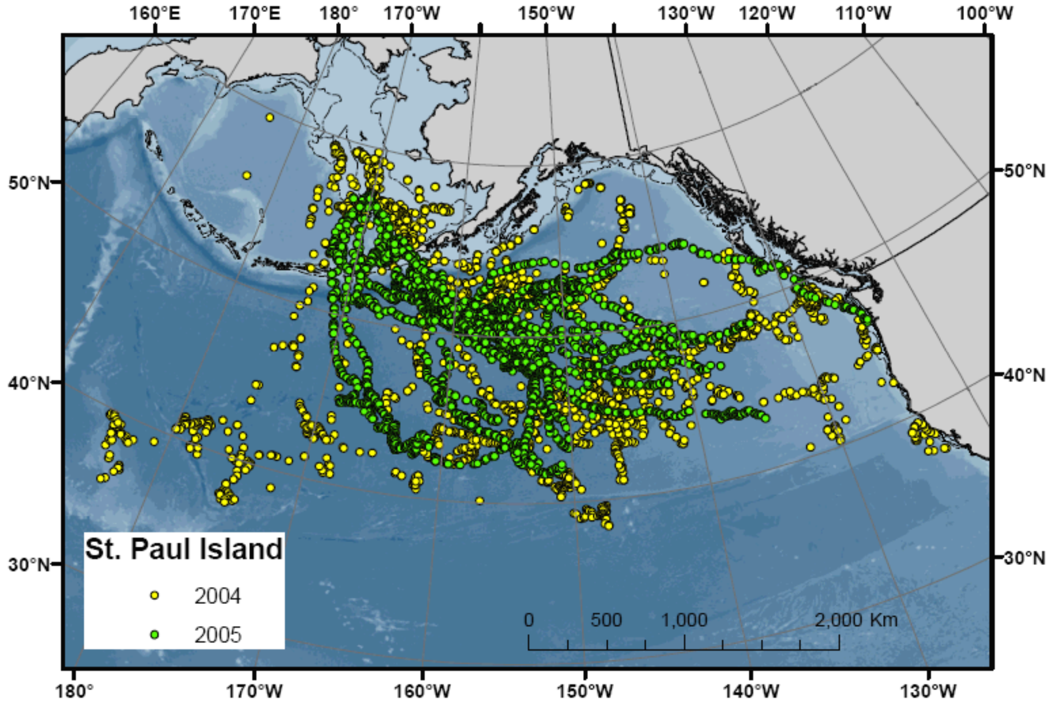


Figure 4. Satellite locations of adult female northern fur seals from St. Paul I. during the 2004 and 2005 winter migration into the North Pacific Ocean.

Female foraging distribution during the breeding season in the Bering Sea

Satellite transmitters were deployed on adult female fur seals 1-2 days postpartum in July and removed in October to determine foraging strategies during the summer breeding season in the Bering Sea. Twenty females from St. Paul I. (10 from Vostochni rookery and 10 from Reef rookery), and 20 females from Bogoslof I. were instrumented during each study year and tracking began immediately. There were three distinct foraging areas that were utilized by the female fur seals in our study (Fig. 5). Females from Vostochni rookery traveled north of St. Paul, foraging entirely over the continental shelf. Females from Reef rookery foraged to the south of St. Paul around the shelf break. Females from Bogoslof I. foraged in deep water a relatively short distance from the island, and in all directions.

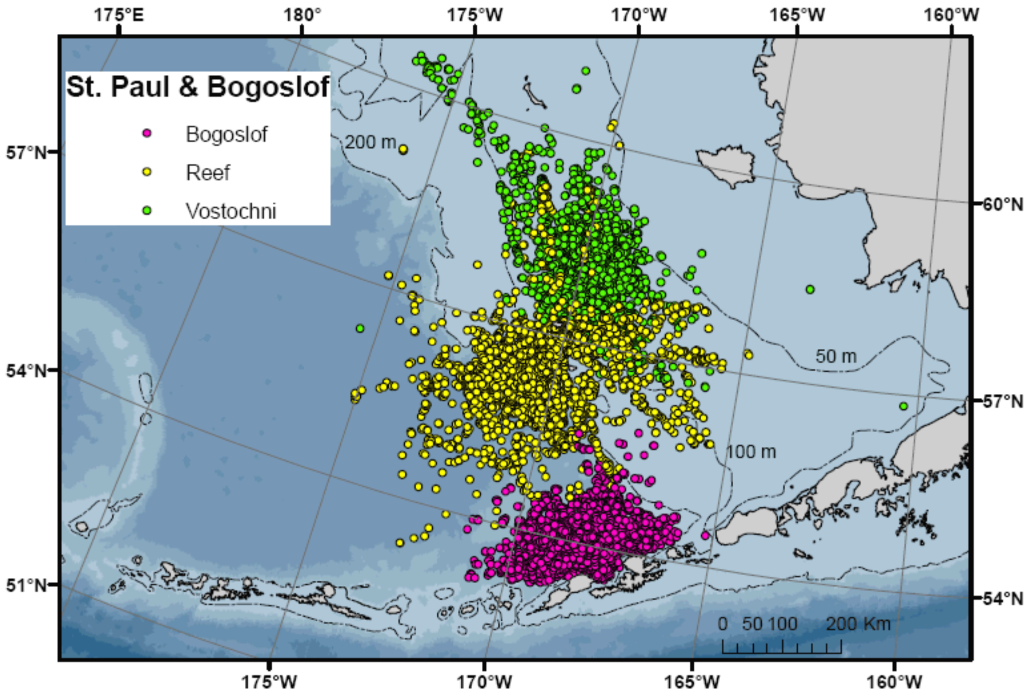


Figure 5. Satellite locations of adult female northern fur seals in the Bering Sea during 2005 and 2006 summer foraging trips from St. Paul I. (Reef and Vostochni rookeries) and Bogoslof I.

Foraging trips of individuals from Reef rookery were relatively variable in direction of travel and use of habitat domains (Fig. 6). Though these females tended to feed to the south of St. Paul, the direction of travel was not consistent among individuals and they used habitat on the continental shelf, at the shelf break, and in deep oceanic waters. Females from Reef rookery used similar habitat, however, during 2005 and 2006. Foraging trips of females from Vostochni rookery were concentrated to the north and northeast of St. Paul (Fig. 7). During 2006, foraging trips of females from Vostochni were located further to the west than during 2005. Foraging patterns of adult females from Bogoslof Island were similar between years (Fig. 8).

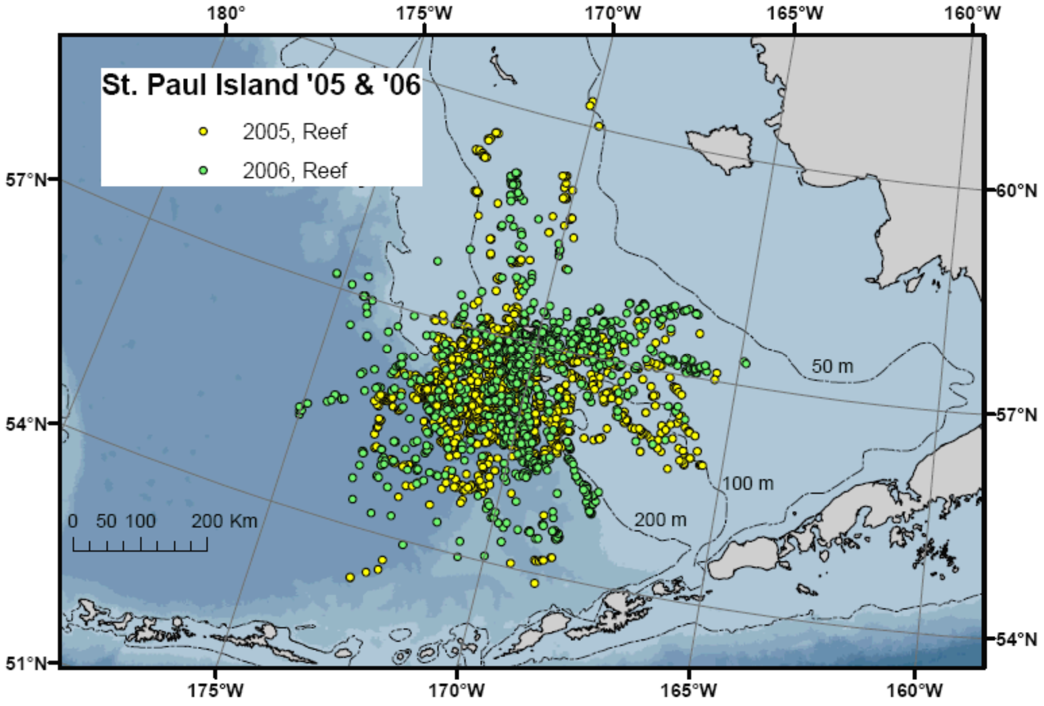


Figure 6. Satellite locations of adult female northern fur seals in the Bering Sea during 2005 and 2006 summer foraging trips from Reef rookery on St. Paul I.

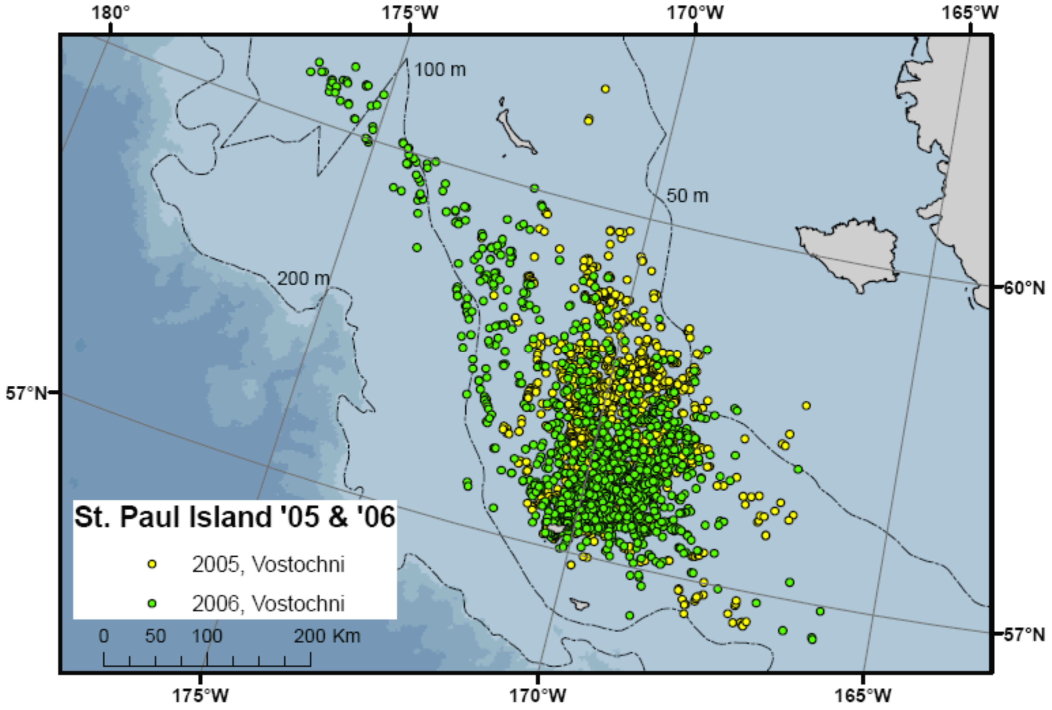


Figure 7. Satellite locations of adult female northern fur seals in the Bering Sea during 2005 and 2006 summer foraging trips from Vostochni rookery on St. Paul I.

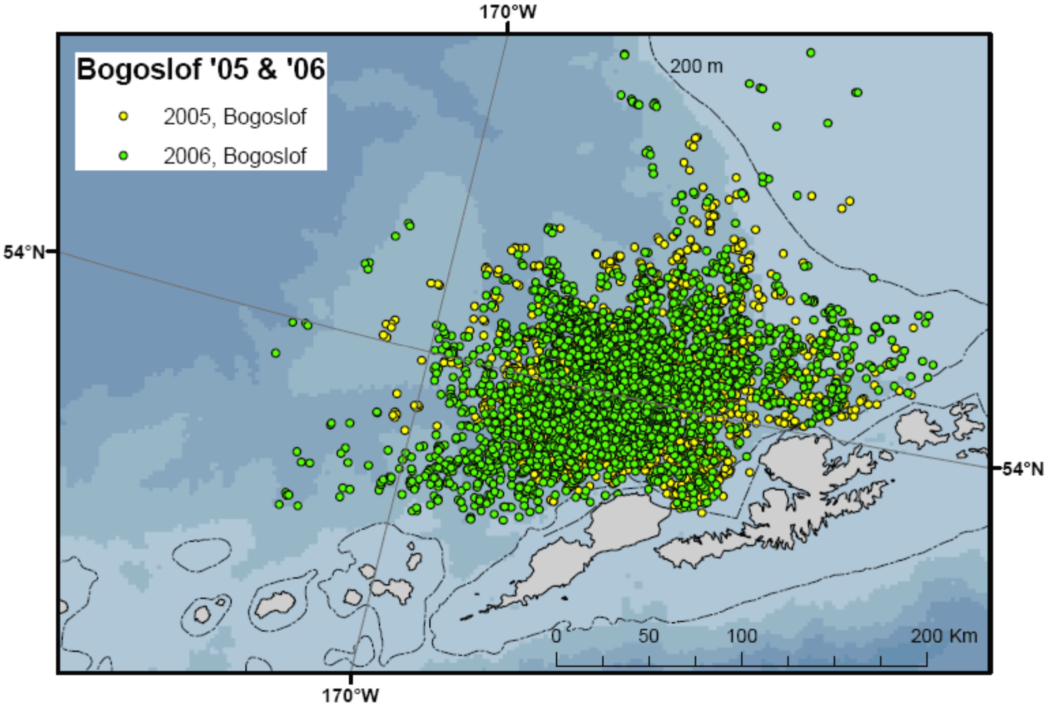


Figure 8. Satellite locations of adult female northern fur seals in the Bering Sea during 2005 and 2006 summer foraging trips from Bogoslof I.

Qualitative evaluation of female diet differences between islands, seasons and years

The 18 FAs that exhibited the greatest average variance, abundance, and reflection of diet in both milk and blubber samples (Table 1) were used in all discriminant analyses and transformed prior to analysis, according to Budge et al. (2002) and Iverson et al. (2002). Analysis of milk FAs from both 2005 and 2006 revealed relatively minor variation among females between Bogoslof and St. Paul in July at parturition, after winter foraging in the N. Pacific, although some variation with year was apparent (Fig. 9). In contrast, there were substantial differences near the end of three months of foraging from their respective breeding grounds in the Bering Sea. This variation was most apparent in the FAs that are particularly indicative of dietary differences in North Pacific/Bering Sea prey (e.g., Iverson et al. 1997, 2002, 2007, see Table 1). Discriminant analysis correctly classified 87% of milks to season and island. Season was clearly and entirely separated on the first discriminant function, with island/year being largely separated on the second function, especially in October (Fig. 9). The greatest misclassifications occurred among the perinatal milks, especially within years, indicating substantial overlap in FA signatures of females arriving at both islands. In contrast, only three females out of 72 were misclassified to island during the period of foraging from both islands during lactation in the Bering Sea.

Table 1. Seleceted Fatty Acids (mass %) in Fur Seal Milk and Blubber (18 FAs used in Discriminant Analyses)

MILKS

Fatty Acid	**BogJul05** n=19	**BogJul06** n=20	**BogOct05** n=19	**BogOct06** n=19
14:0	4.85 ± 0.08	5.18 ± 0.08	4.87 ± 0.06	5.11 ± 0.08
16:0	18.89 ± 0.24	19.58 ± 0.28	21.32 ± 0.37	21.87 ± 0.19
16:1n-7	4.75 ± 0.06	5.00 ± 0.09	4.97 ± 0.05	5.34 ± 0.10
18:0	1.69 ± 0.04	1.73 ± 0.05	2.42 ± 0.07	2.54 ± 0.06
18:1n-9	22.54 ± 0.50	23.41 ± 0.45	20.09 ± 0.51	21.94 ± 0.33
18:1n-7	3.53 ± 0.09	3.72 ± 0.09	5.68 ± 0.13	5.39 ± 0.10
18:2n-6	1.61 ± 0.03	1.64 ± 0.04	1.07 ± 0.02	1.08 ± 0.03
18:3n-3	0.79 ± 0.02	0.81 ± 0.03	0.57 ± 0.01	0.56 ± 0.02
18:4n-3	0.78 ± 0.04	0.73 ± 0.04	0.95 ± 0.06	0.74 ± 0.03
20:1n-11	3.54 ± 0.17	3.49 ± 0.14	2.53 ± 0.32	2.66 ± 0.13
20:1n-9	3.01 ± 0.12	2.85 ± 0.13	3.37 ± 0.13	3.46 ± 0.14
20:4n-6	0.88 ± 0.02	0.76 ± 0.03	0.53 ± 0.01	0.37 ± 0.01
20:4n-3	1.74 ± 0.07	1.61 ± 0.06	1.15 ± 0.02	1.05 ± 0.02
20:5n-3	5.93 ± 0.15	6.27 ± 0.16	9.75 ± 0.35	9.15 ± 0.22
22:1n-11	2.39 ± 0.12	1.73 ± 0.10	1.77 ± 0.20	2.01 ± 0.14
22:1n-9	0.52 ± 0.01	0.38 ± 0.02	0.55 ± 0.03	0.52 ± 0.03
22:5n-3	2.34 ± 0.08	2.18 ± 0.09	2.31 ± 0.07	2.16 ± 0.05
22:6n-3	7.55 ± 0.20	8.24 ± 0.35	6.75 ± 0.25	6.12 ± 0.32

BLUBBERS

Fatty Acid	**BogJul05** n=18	**BogJul06** n=19	**BogOct05** n=19	**BogOct06** n=17
14:0	4.32 ± 0.12	4.39 ± 0.09	4.71 ± 0.09	4.79 ± 0.12
16:0	12.66 ± 0.19	14.08 ± 0.38	14.87 ± 0.50	12.40 ± 0.38
16:1n-7	3.46 ± 0.16	3.57 ± 0.21	4.04 ± 0.18	3.99 ± 0.28
18:0	3.23 ± 0.11	3.56 ± 0.15	3.57 ± 0.12	3.46 ± 0.14
18:1n-9	21.93 ± 0.70	22.22 ± 0.48	20.65 ± 0.39	19.11 ± 0.81
18:1n-7	2.86 ± 0.11	3.57 ± 0.26	5.02 ± 0.14	3.77 ± 0.21
18:2n-6	1.42 ± 0.03	1.32 ± 0.04	1.06 ± 0.02	1.13 ± 0.05
18:3n-3	0.60 ± 0.02	0.53 ± 0.02	0.42 ± 0.01	0.45 ± 0.03
18:4n-3	0.87 ± 0.08	0.77 ± 0.04	0.87 ± 0.06	0.94 ± 0.09
20:1n-11	6.23 ± 0.35	5.61 ± 0.28	6.48 ± 0.57	8.59 ± 0.74
20:1n-9	5.60 ± 0.33	6.01 ± 0.52	6.07 ± 0.26	5.22 ± 0.44
20:4n-6	0.67 ± 0.02	0.62 ± 0.03	0.44 ± 0.02	0.48 ± 0.04
20:4n-3	0.98 ± 0.05	0.89 ± 0.04	0.74 ± 0.02	0.74 ± 0.05
20:5n-3	2.76 ± 0.17	3.10 ± 0.22	4.09 ± 0.16	3.63 ± 0.29
22:1n-11	4.78 ± 0.40	4.43 ± 0.26	4.44 ± 0.36	5.73 ± 0.49
22:1n-9	0.90 ± 0.04	0.95 ± 0.07	1.18 ± 0.06	0.97 ± 0.06
22:5n-3	3.25 ± 0.13	3.05 ± 0.15	2.69 ± 0.08	3.22 ± 0.15
22:6n-3	12.43 ± 0.44	10.84 ± 0.68	8.14 ± 0.34	10.70 ± 0.54

Table 1. Seleceted Fatty Acids (mass %) in Fur Seal Milk and Blubber (18 FAs used in Discriminant Analyses)

MILKS

	StPJul05	**StPJul06**	**StPOct05**	**StPOct06**
Fatty Acid	n=20	n=20	n=17	n=17
14:0	4.95 ± 0.10	5.30 ± 0.14	5.36 ± 0.15	5.56 ± 0.25
16:0	17.66 ± 0.28	17.93 ± 0.26	16.06 ± 0.41	17.12 ± 0.41
16:1n-7	5.37 ± 0.12	5.60 ± 0.13	6.14 ± 0.24	7.25 ± 0.64
18:0	1.64 ± 0.03	1.68 ± 0.03	1.94 ± 0.06	1.97 ± 0.08
18:1n-9	22.51 ± 0.56	23.68 ± 0.58	15.91 ± 0.62	18.80 ± 1.02
18:1n-7	3.65 ± 0.10	3.67 ± 0.10	4.56 ± 0.17	5.15 ± 0.31
18:2n-6	1.60 ± 0.04	1.69 ± 0.03	0.99 ± 0.04	1.29 ± 0.07
18:3n-3	0.78 ± 0.02	0.87 ± 0.03	0.54 ± 0.04	0.63 ± 0.04
18:4n-3	0.86 ± 0.04	0.84 ± 0.06	1.25 ± 0.12	1.02 ± 0.11
20:1n-11	3.68 ± 0.13	3.49 ± 0.18	6.35 ± 0.45	5.02 ± 0.64
20:1n-9	2.62 ± 0.10	2.56 ± 0.12	2.55 ± 0.14	2.28 ± 0.16
20:4n-6	0.82 ± 0.02	0.76 ± 0.02	0.52 ± 0.02	0.39 ± 0.01
20:4n-3	1.72 ± 0.06	1.68 ± 0.06	0.99 ± 0.06	1.00 ± 0.07
20:5n-3	6.39 ± 0.19	6.64 ± 0.26	8.67 ± 0.20	8.84 ± 0.33
22:1n-11	2.02 ± 0.11	1.64 ± 0.13	3.57 ± 0.36	2.75 ± 0.39
22:1n-9	0.46 ± 0.02	0.34 ± 0.02	0.45 ± 0.04	0.36 ± 0.04
22:5n-3	2.66 ± 0.09	2.54 ± 0.09	2.85 ± 0.12	2.73 ± 0.11
22:6n-3	7.95 ± 0.23	8.60 ± 0.23	9.48 ± 0.37	8.04 ± 0.39

BLUBBERS

	StPJul05	**StPJul06**	**StPOct05**	**StPOct06**
Fatty Acid	n=13	n=19	n=16	n=17
14:0	4.28 ± 0.12	4.36 ± 0.07	4.93 ± 0.04	5.30 ± 0.09
16:0	12.93 ± 0.26	12.45 ± 0.27	16.34 ± 0.19	12.61 ± 0.28
16:1n-7	3.38 ± 0.20	3.52 ± 0.12	4.00 ± 0.12	5.32 ± 0.35
18:0	3.42 ± 0.20	2.60 ± 0.11	3.78 ± 0.08	3.02 ± 0.18
18:1n-9	21.75 ± 0.77	20.99 ± 0.37	21.40 ± 0.24	20.24 ± 0.45
18:1n-7	3.04 ± 0.27	4.34 ± 0.21	4.85 ± 0.10	4.89 ± 0.22
18:2n-6	1.40 ± 0.04	1.31 ± 0.03	1.03 ± 0.01	1.20 ± 0.06
18:3n-3	0.61 ± 0.03	0.68 ± 0.02	0.42 ± 0.01	0.41 ± 0.02
18:4n-3	0.77 ± 0.06	0.79 ± 0.03	0.76 ± 0.01	0.88 ± 0.04
20:1n-11	4.92 ± 0.41	2.39 ± 0.55	6.00 ± 0.24	6.28 ± 0.76
20:1n-9	6.29 ± 0.76	7.41 ± 0.44	5.99 ± 0.14	5.44 ± 0.57
20:4n-6	0.74 ± 0.03	0.60 ± 0.03	0.36 ± 0.01	0.33 ± 0.01
20:4n-3	0.98 ± 0.04	0.95 ± 0.03	0.75 ± 0.02	0.60 ± 0.04
20:5n-3	3.06 ± 0.23	3.14 ± 0.19	4.45 ± 0.19	4.12 ± 0.22
22:1n-11	3.67 ± 0.28	2.93 ± 0.26	4.79 ± 0.23	4.93 ± 0.33
22:1n-9	0.99 ± 0.14	1.59 ± 0.12	1.22 ± 0.04	1.40 ± 0.24
22:5n-3	3.35 ± 0.28	3.26 ± 0.14	2.44 ± 0.04	3.05 ± 0.15
22:6n-3	13.21 ± 0.92	13.47 ± 0.55	7.07 ± 0.14	9.17 ± 0.24

Given the known foraging differences between females at the two St. Paul rookeries during lactation (Fig. 5), we examined potential separations of females at St. Paul by their milk FAs. Consistent with the above findings (Fig. 9), there was little indication of foraging differences upon arrival from the North Pacific (July), at either of the two St. Paul rookeries (Reef versus Vostochni), but a clear distinction of females foraging in October in the Bering Sea from Vostochni in 2006 compared to 2005 or to Reef females in either year (Fig. 10).

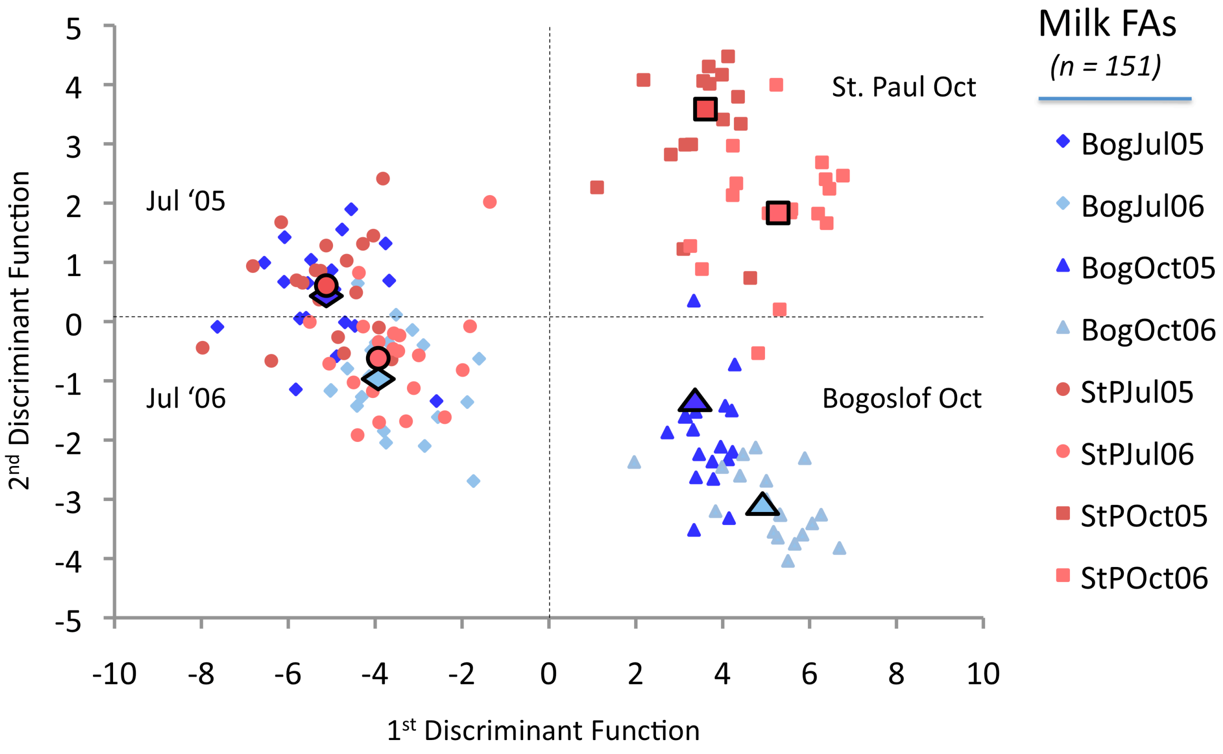


Figure 9. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal milk FAs collected in 2005 and 2006 at Bogoslof I. and St. Paul I. These first two functions accounted for 82.3% of the variance in the discriminant analysis. Milks were separated with 86.8% of original grouped cases, and 74.8% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0005, $p < 0.001$). Samples sizes: BogJul05 (n = 19), BogJul06 (n = 20), BogOct05 (n = 19), BogOct06 (n = 19), StPJul05 (n = 20), StPJul06 (n = 20), StPOct05 (n = 17), StPOct06 (n = 17).

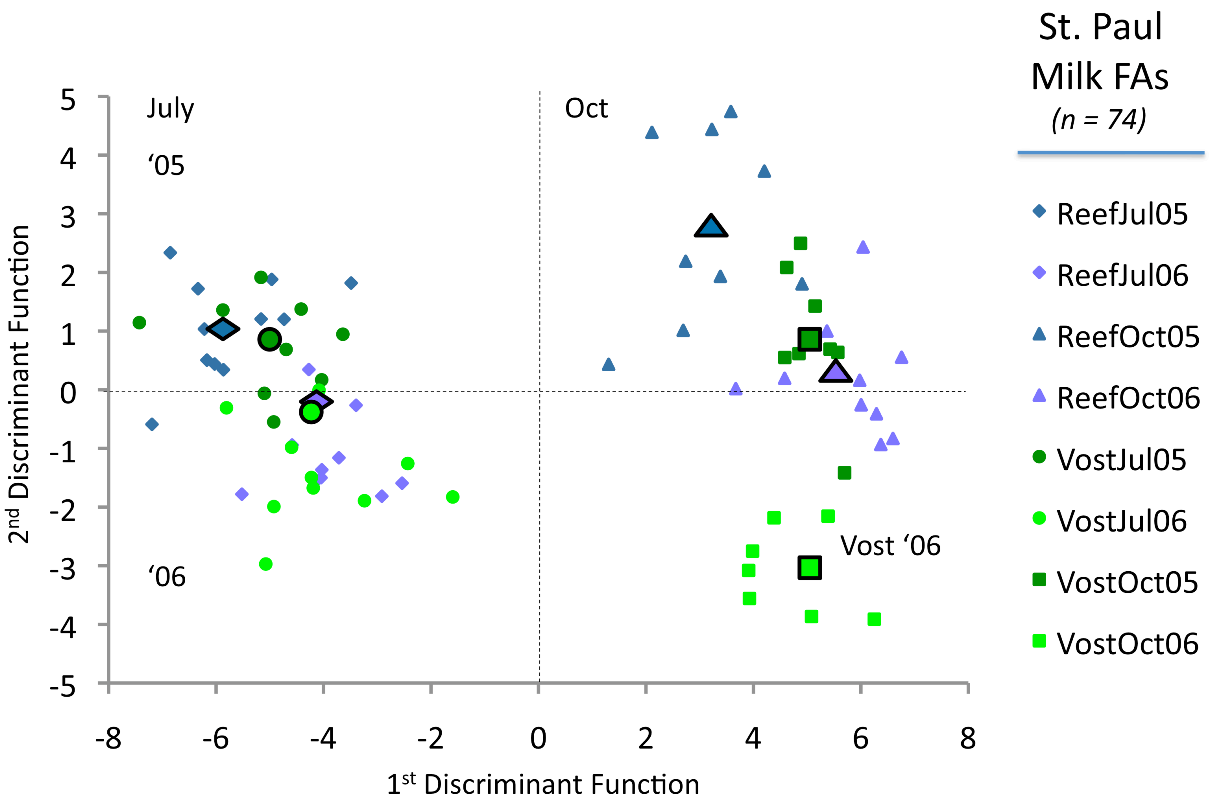


Figure 10. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal milk FAs collected in 2005 and 2006 at St. Paul I., split by the south (Reef) and north (Vostochni) rookeries. These first two functions accounted for 85.3% of the variance in the discriminant analysis. Milks were separated with 86.5% of original grouped cases, and 52.7% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0006, $p < 0.001$). Samples sizes: ReefJul05 (n = 11), ReefJul06 (n = 10), ReefOct05 (n = 9), ReefOct06 (n = 10), VostJul05 (n = 9), VostJul06 (n = 10), VostOct05 (n = 8), VostOct06 (n = 7).

Although blubber FAs generally tracked the same kinds of differences and changes observed in milk FAs, there was broader overlap among females in October after three months of foraging in the Bering Sea (Fig. 11), demonstrated by a lower overall classification success of 68%. However, the separation of females between the two rookeries at St. Paul during lactation by blubber FAs was far more clearly distinguished than using milk FAs, with a classification success of 91% (Fig. 12). Season and year were the clearest drivers of this separation. In all cases, annual variation was apparent.

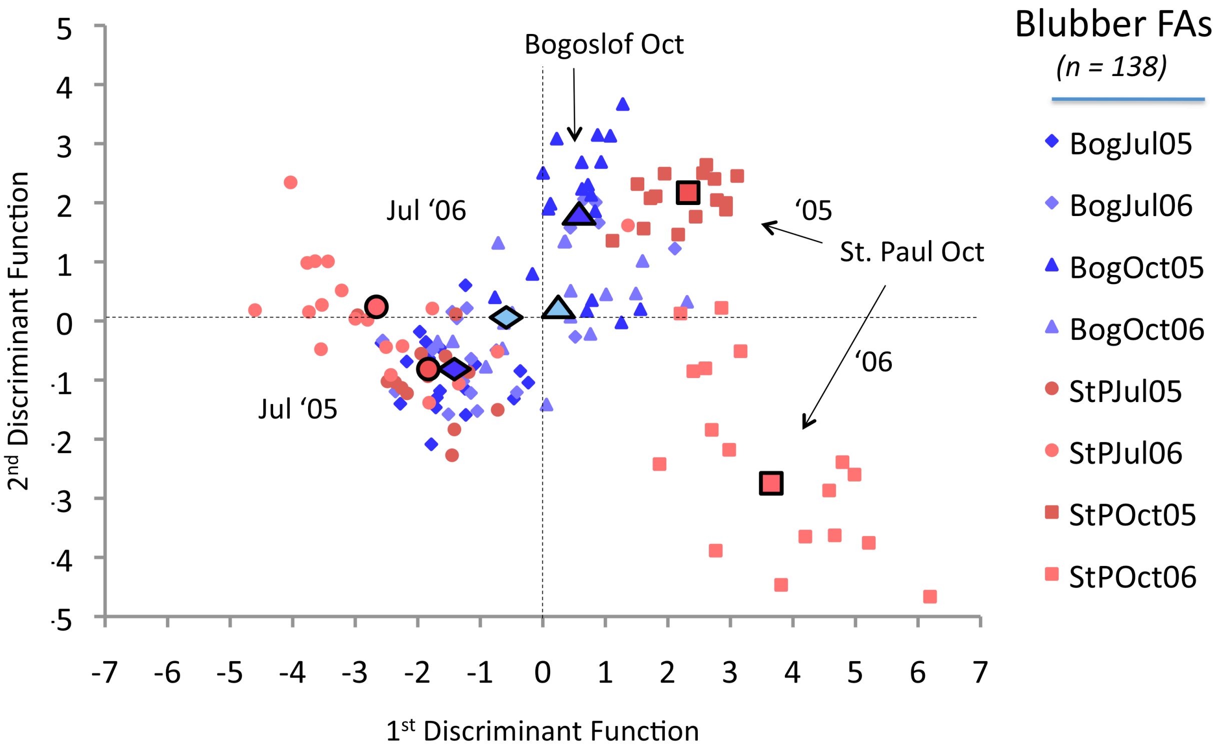


Figure 11. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal blubber FAs collected in 2005 and 2006 at Bogoslof I. and St. Paul I. These first two functions accounted for 67.3% of the variance in the discriminant analysis. Blubbers were separated with 68.1% of original grouped cases, and 55.1% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0083, $p < 0.001$). Samples sizes: BogJul05 (n = 18), BogJul06 (n = 19), BogOct05 (n = 19), BogOct06 (n = 17), StPJul05 (n = 13), StPJul06 (n = 19), StPOct05 (n = 16), StPOct06 (n = 17).

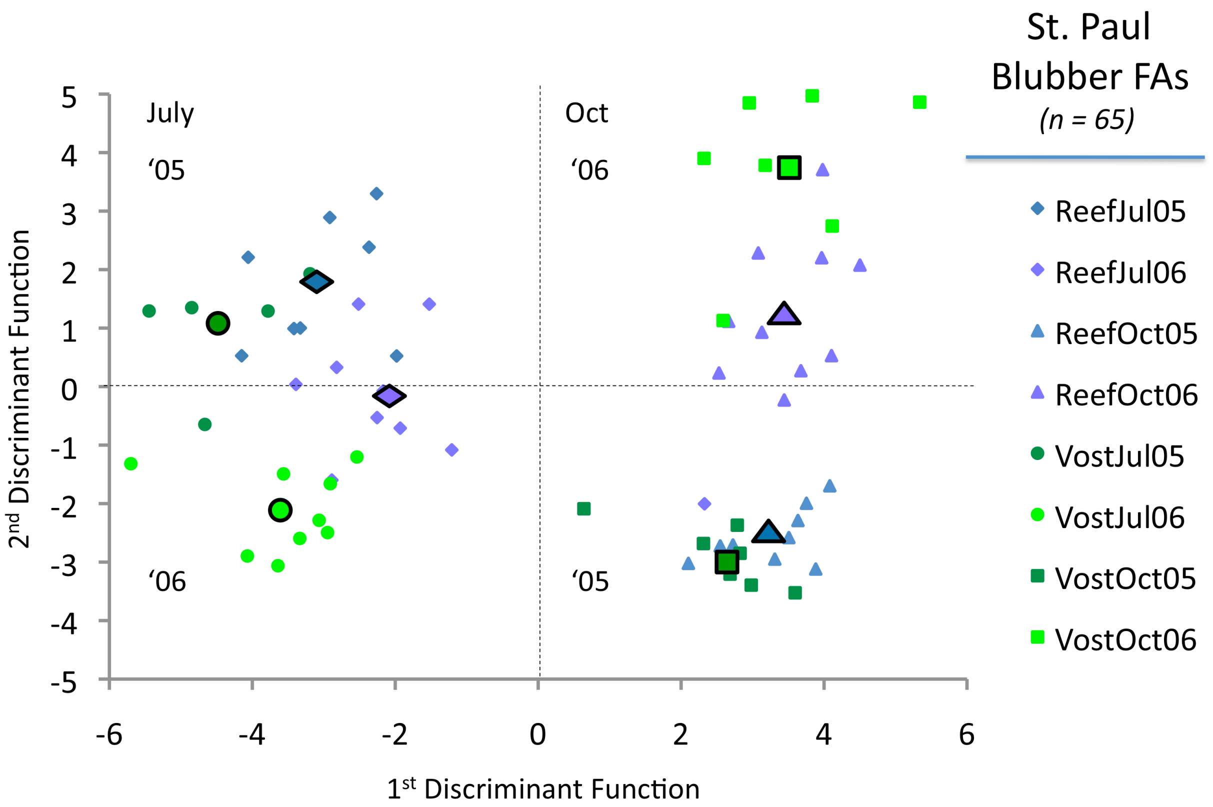


Figure 12. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal blubber FAs collected in 2005 and 2006 at St. Paul I., split by the south (Reef) and north (Vostochni) rookeries. These first two functions accounted for 77.4 % of the variance in the discriminant analysis. Blubbers were separated with 90.8% of original grouped cases, and 46.2% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0006, $p < 0.001$). Samples sizes: ReefJul05 ($n = 8$), ReefJul06 ($n = 10$), ReefOct05 ($n = 9$), ReefOct06 ($n = 10$), VostJul05 ($n = 5$), VostJul06 ($n = 9$), VostOct05 ($n = 7$), VostOct06 ($n = 7$).

Finally, milk and blubber FAs should provide different information on female diets, especially in terms of the time frame of integration of dietary history, thus we would not expect milk and blubber FAs from the same females to be identical. This was clearly borne out in the analyses of milks and blubbers from the same females at each of the islands (Figs. 13 and 14). At both Bogoslof and St. Paul, milk and blubber were separated on the first discriminant function. Nevertheless, on the second function, seasons were separated out similarly using either milk or blubber FAs, but more clearly at St. Paul than at Bogoslof (94% and 83% overall classification success, respectively), mostly due to the extensive overlap at Bogoslof of blubber FAs in both seasons and years in comparison to milk FAs (Fig. 13).

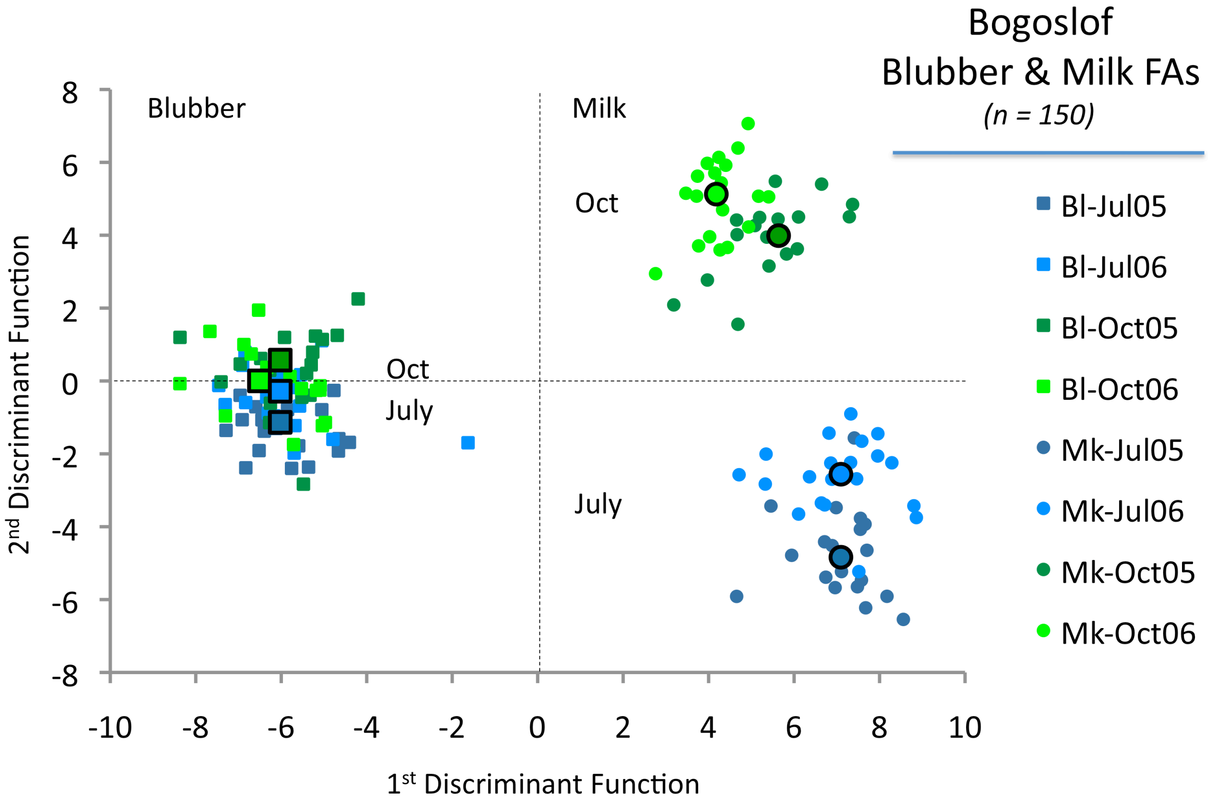


Figure 13. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal blubber milk and FAs collected in 2005 and 2006 at Bogoslof I. These first two functions accounted for 91.9% of the variance in the discriminant analysis. Overall blubbers and milks were separated with 82.7% of original grouped cases, and 70.7% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0001, $p < 0.001$). Samples sizes: Bl-Jul05 (n = 18), Bl-Jul06 (n = 19), Bl-Oct05 (n = 19), Bl-Oct06 (n = 17), Mk-Jul05 (n = 19), Mk-Jul06 (n = 20), Mk-Oct05 (n = 19), Mk-Oct06 (n = 19).

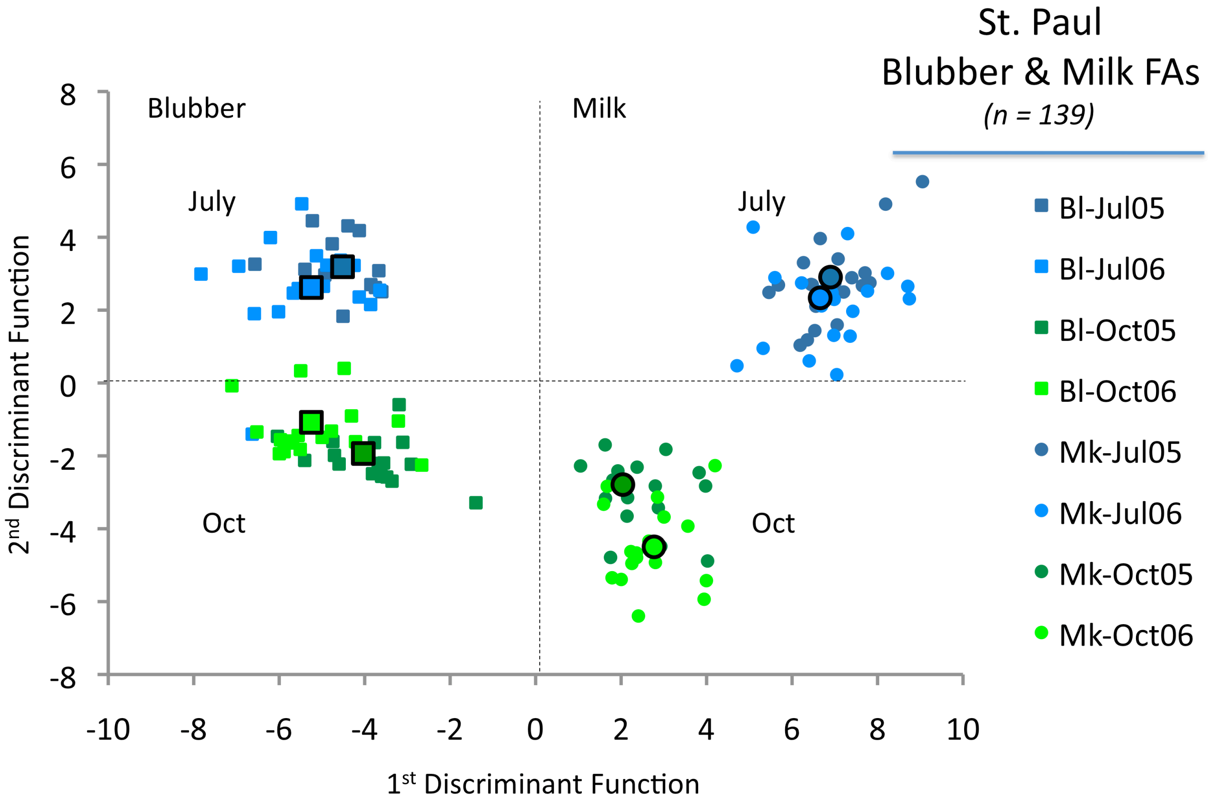
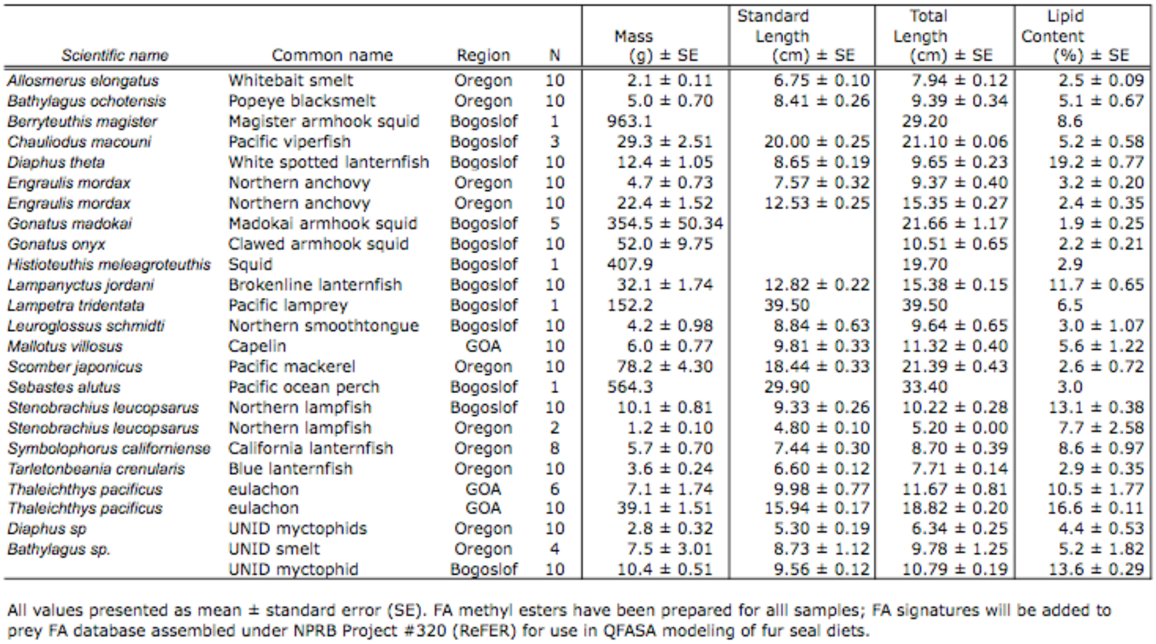


Figure 14. Discriminant scores and group centroids (within group mean for each discriminant function) for the first and second (of 7 significant) discriminant functions for northern fur seal blubber milk and FAs collected in 2005 and 2006 at St. Paul I. These first two functions accounted for 84.4% of the variance in the discriminant analysis. Overall blubbers and milks were separated with 93.5% of original grouped cases, and 85.6% of cross-validated grouped cases, correctly classified (Wilk's Lambda 0.0001, $p < 0.001$). Samples sizes: Bl-Jul05 (n = 13), Bl-Jul06 (n = 19), Bl-Oct05 (n = 16), Bl-Oct06 (n = 17), Mk-Jul05 (n = 20), Mk-Jul06 (n = 20), Mk-Oct05 (n = 17), Mk-Oct06 (n = 17).

Prey samples collected under this grant have been analyzed for total fat content (Table 2). The FA signatures of these and the additional prey collected under separate funding were combined with specific prey previously contained in the prey database established for seabirds (NPRB project #320), which are also relevant to modeling fur seal diets.

Table 2. Collection data and fat content of initial prey assembled for the QFASA prey database funded by this grant.



Scientific name	Common name	Region	N	Mass (g) ± SE	Standard Length (cm) ± SE	Total Length (cm) ± SE	Lipid Content (%) ± SE
Allosmerus elongatus	Whitebait smelt	Oregon	10	2.1 ± 0.11	6.75 ± 0.10	7.94 ± 0.12	2.5 ± 0.09
Bathylagus ochotensis	Popeye blacksmelt	Oregon	10	5.0 ± 0.70	8.41 ± 0.26	9.39 ± 0.34	5.1 ± 0.67
Berryteuthis magister	Magister armhook squid	Bogoslof	1	963.1		29.20	8.6
Chauliodus macouni	Pacific viperfish	Bogoslof	3	29.3 ± 2.51	20.00 ± 0.25	21.10 ± 0.06	5.2 ± 0.58
Diaphus theta	White spotted lanternfish	Bogoslof	10	12.4 ± 1.05	8.65 ± 0.19	9.65 ± 0.23	19.2 ± 0.77
Engraulis mordax	Northern anchovy	Oregon	10	4.7 ± 0.73	7.57 ± 0.32	9.37 ± 0.40	3.2 ± 0.20
Engraulis mordax	Northern anchovy	Oregon	10	22.4 ± 1.52	12.53 ± 0.25	15.35 ± 0.27	2.4 ± 0.35
Gonatus madokai	Madokai armhook squid	Bogoslof	5	354.5 ± 50.34		21.66 ± 1.17	1.9 ± 0.25
Gonatus onyx	Clawed armhook squid	Bogoslof	10	52.0 ± 9.75		10.51 ± 0.65	2.2 ± 0.21
Histioteuthis meleagroteuthis	Squid	Bogoslof	1	407.9		19.70	2.9
Lampanyctus jordani	Brokenline lanternfish	Bogoslof	10	32.1 ± 1.74	12.82 ± 0.22	15.38 ± 0.15	11.7 ± 0.65
Lampetra tridentata	Pacific lamprey	Bogoslof	1	152.2	39.50	39.50	6.5
Leuroglossus schmidti	Northern smoothtongue	Bogoslof	10	4.2 ± 0.98	8.84 ± 0.63	9.64 ± 0.65	3.0 ± 1.07
Mallotus villosus	Capelin	GOA	10	6.0 ± 0.77	9.81 ± 0.33	11.32 ± 0.40	5.6 ± 1.22
Scomber japonicus	Pacific mackerel	Oregon	10	78.2 ± 4.30	18.44 ± 0.33	21.39 ± 0.43	2.6 ± 0.72
Sebastes alutus	Pacific ocean perch	Bogoslof	1	564.3	29.90	33.40	3.0
Stenobrachius leucopsarus	Northern lampfish	Bogoslof	10	10.1 ± 0.81	9.33 ± 0.26	10.22 ± 0.28	13.1 ± 0.38
Stenobrachius leucopsarus	Northern lampfish	Oregon	2	1.2 ± 0.10	4.80 ± 0.10	5.20 ± 0.00	7.7 ± 2.58
Symbolophorus californiense	California lanternfish	Oregon	8	5.7 ± 0.70	7.44 ± 0.30	8.70 ± 0.39	8.6 ± 0.97
Tarletonbeania crenularis	Blue lanternfish	Oregon	10	3.6 ± 0.24	6.60 ± 0.12	7.71 ± 0.14	2.9 ± 0.35
Thaleichthys pacificus	eulachon	GOA	6	7.1 ± 1.74	9.98 ± 0.77	11.67 ± 0.81	10.5 ± 1.77
Thaleichthys pacificus	eulachon	GOA	10	39.1 ± 1.51	15.94 ± 0.17	18.82 ± 0.20	16.6 ± 0.11
Diaphus sp	UNID myctophids	Oregon	10	2.8 ± 0.32	5.30 ± 0.19	6.34 ± 0.25	4.4 ± 0.53
Bathylagus sp.	UNID smelt	Oregon	4	7.5 ± 3.01	8.73 ± 1.12	9.78 ± 1.25	5.2 ± 1.82
	UNID myctophid	Bogoslof	10	10.4 ± 0.51	9.56 ± 0.12	10.79 ± 0.19	13.6 ± 0.29

All values presented as mean ± standard error (SE). FA methyl esters have been prepared for alll samples; FA signatures will be added to prey FA database assembled under NPRB Project #320 (ReFER) for use in QFASA modeling of fur seal diets.

Quantitative evaluation of female diet differences between islands, seasons and years

Diets of females in spring were similar between Bogoslof and St. Paul in 2005 and were dominated by northern smoothtongue (Figs. 15, 16). Spring diets at Bogoslof in 2006 were similar to those in 2005, however females at St. Paul in 2006 had fed on substantially more salmon and lesser amounts of smoothtongue and most of the other species compared to 2005. Despite high frequencies of occurrence of many species, the quantitative contributions to diets were comparatively small for most of them except smoothtongue and salmon, and smaller yet when scaled by the energy index.

Female diets in fall at Bogoslof were dominated still by northern smoothtongue in both years, which was consistent with their foraging distributions in the basin domain (Fig. 17). The mix of other species in fall diets differed from those in spring.

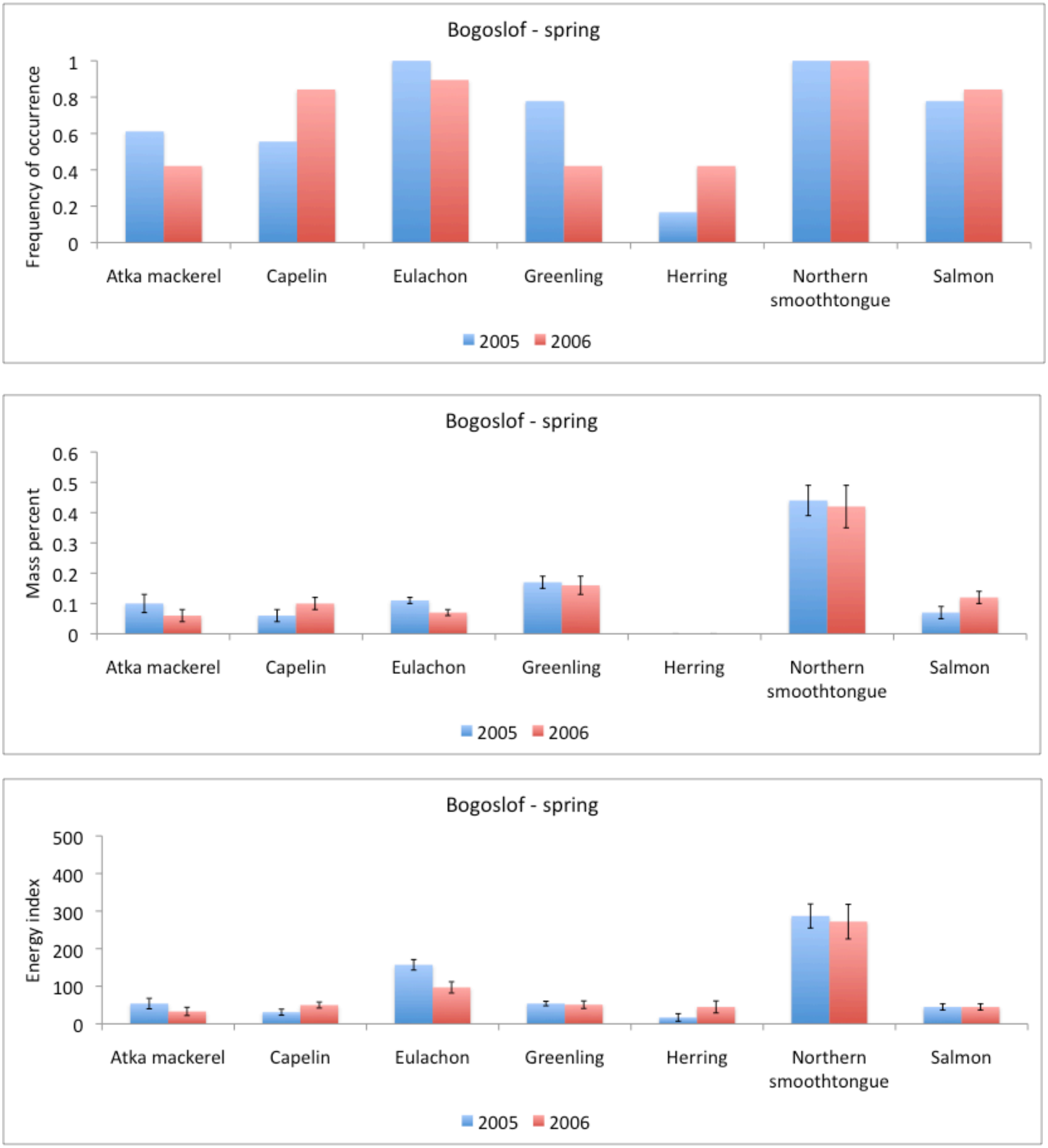


Figure 15. Diets of female northern fur seals at Bogoslof I. in spring 2005 and 2006. Error bars are standard errors of the means. See methods for explanation of energy index.

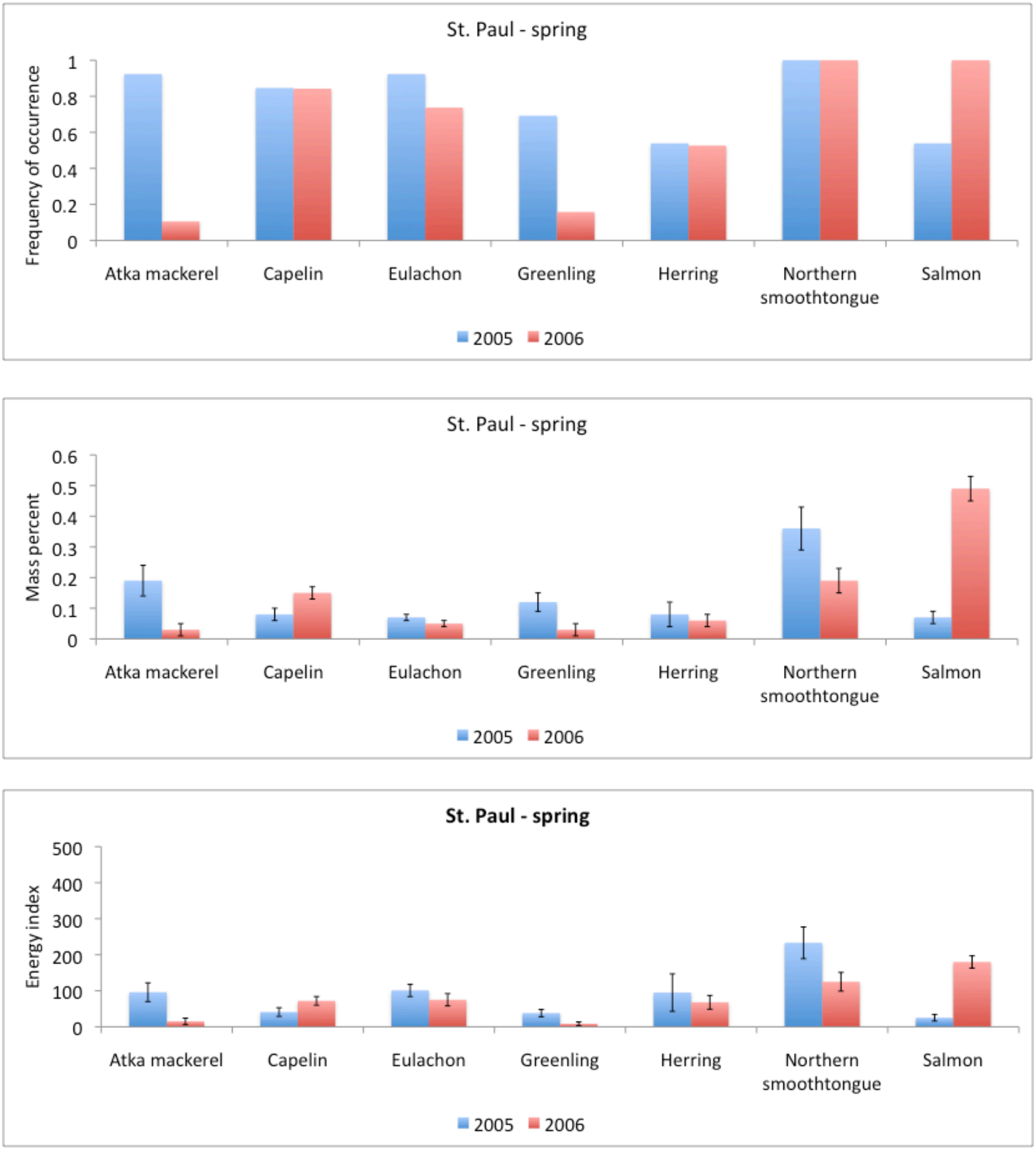


Figure 16. Diets of female northern fur seals at St. Paul I. in spring 2005 and 2006. Error bars are standard errors of the means. See methods for explanation of energy index.

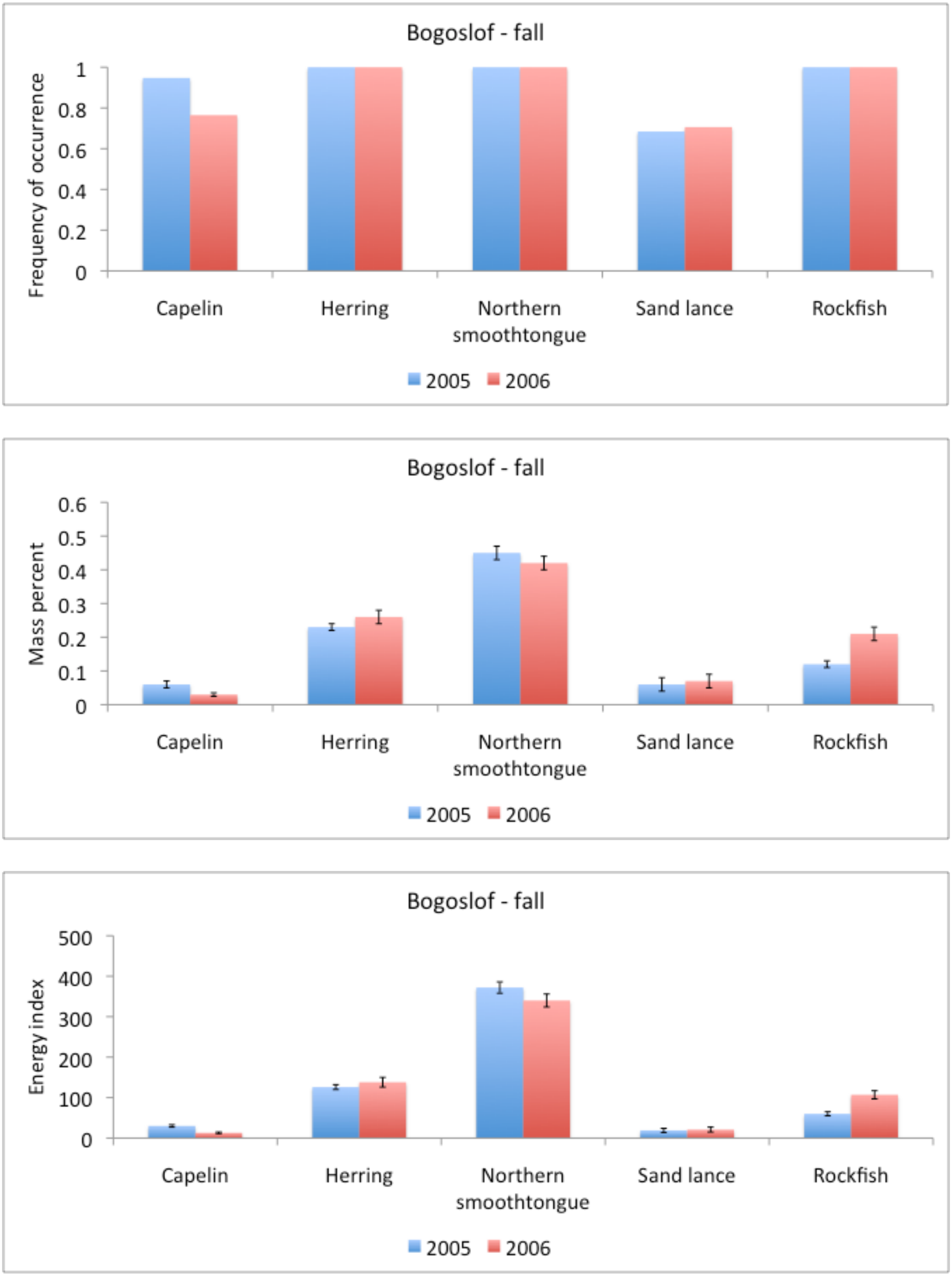


Figure 17. Diets of female northern fur seals at Bogoslof I. in fall 2005 and 2006. Error bars are standard errors of the means. See methods for explanation of energy index.

Foraging distributions at Reef rookery on St. Paul varied between years, in that females foraged in a mixture of habitats, including the outer shelf domain, the shelf edge, and the basin west of the Pribilofs, as well as the much shallower middle shelf domain east and southeast of the Pribilofs: hence, diets of females foraging in the deeper regions would be expected to differ from those foraging in shallower regions. Therefore, to assess fall diets at Reef, females were stratified based on the amount of time they spent foraging in deeper and shallower regions in September, a period of four weeks before they were sampled that corresponded to the likely maximum time over which QFASA diet estimates were integrated. Two groups were defined by summing the total hours spent in the outer plus basin domains for each female and then dividing them into two equal groups, with one half composed of females with lower total times in the outer shelf and basin domains (shallow) and the other half composed of females with greater total times in the deeper regions (deep; Fig. 18). In 2005 there was little difference in time spent in

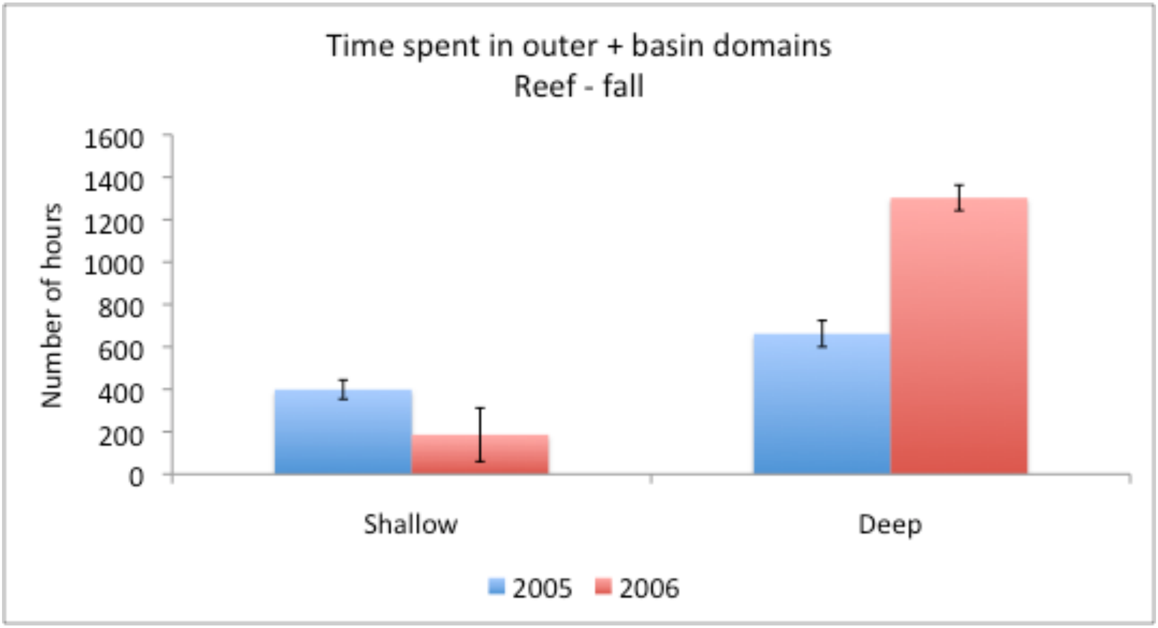
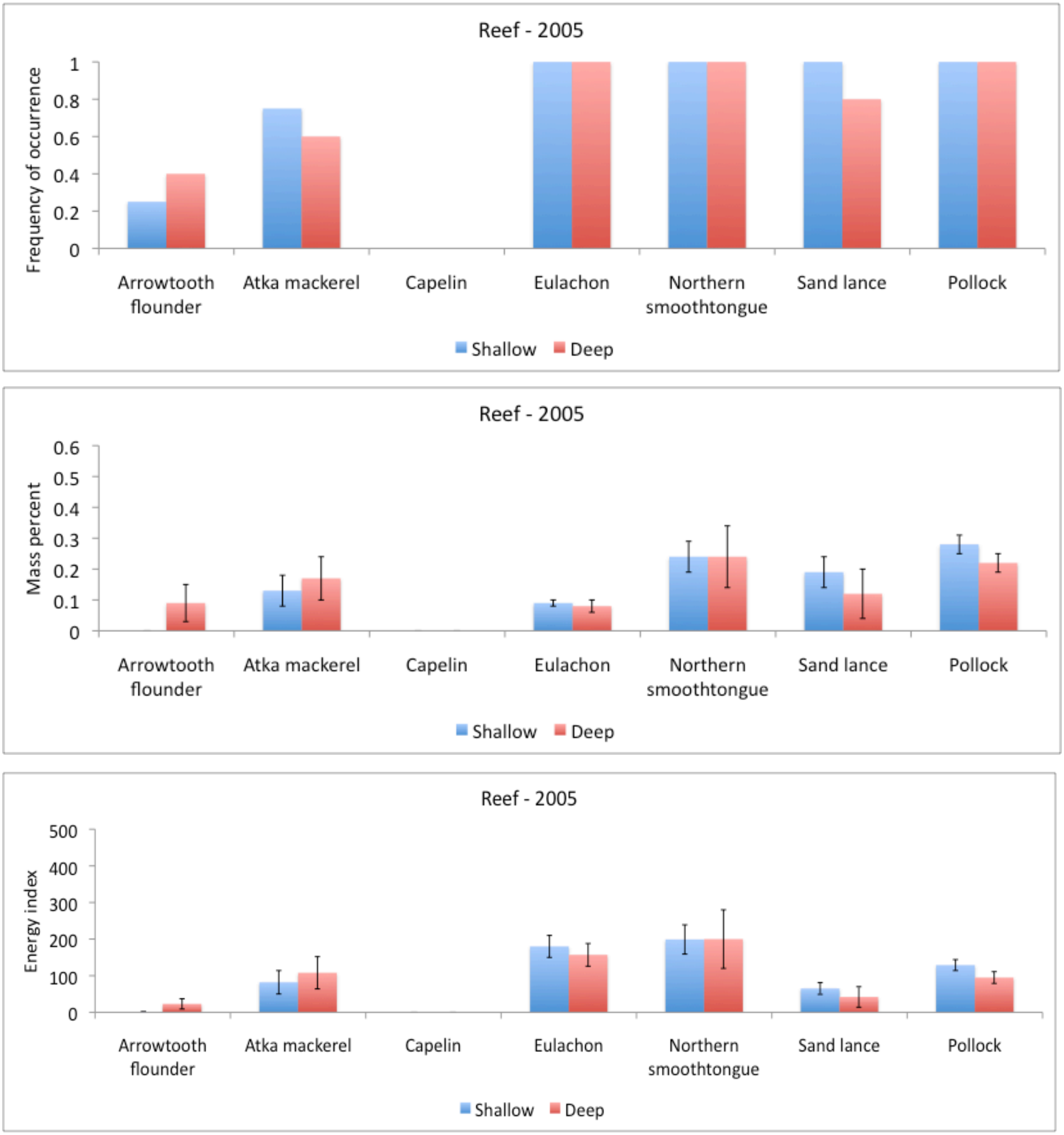


Figure 18. Proportion of time spent foraging by female northern fur seals at Reef rookery, St. Paul I., in the outer plus basin domains in fall 2005 and 2006. Error bars are standard errors of the means.

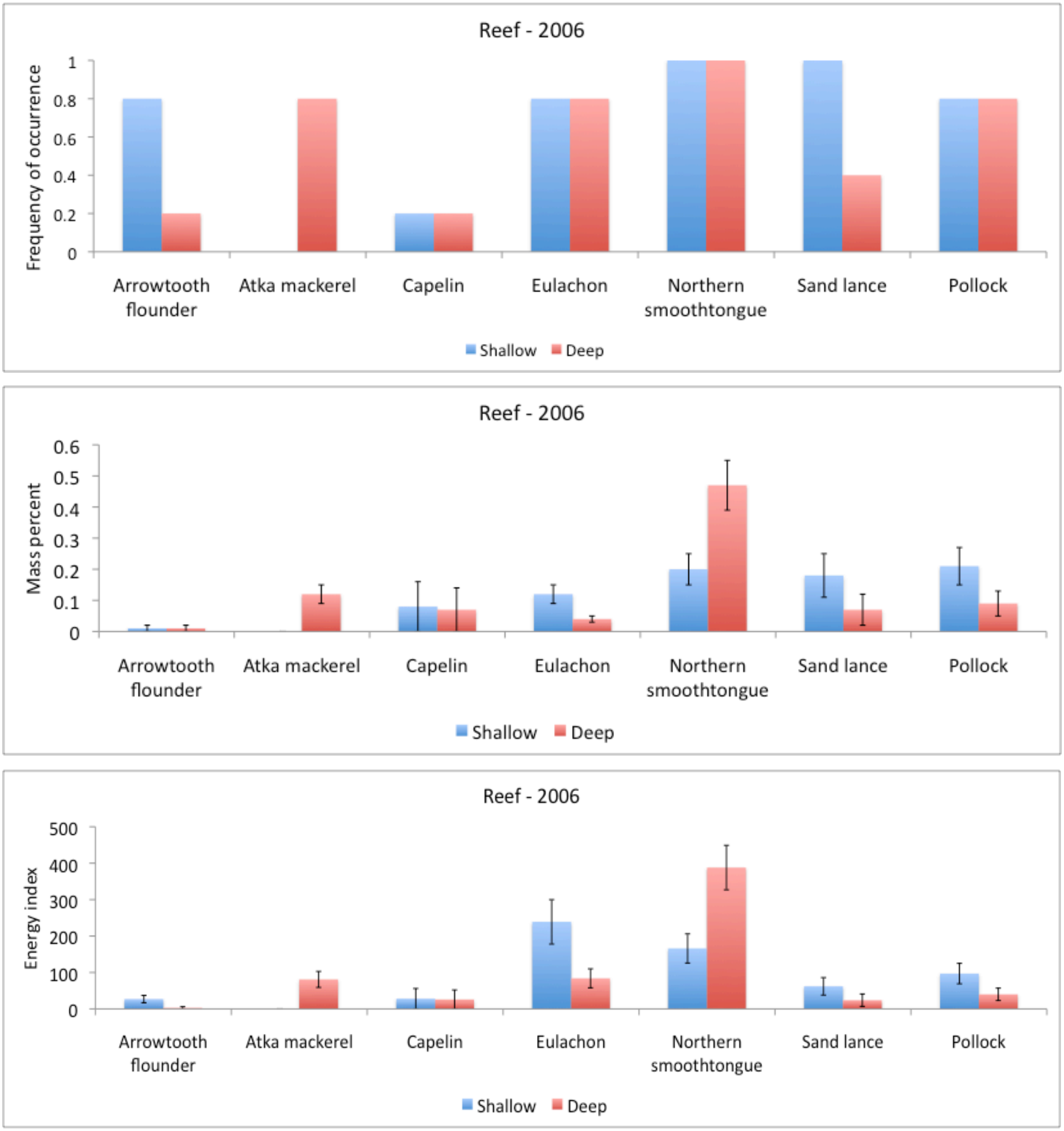
shallow versus deep habitats, but in 2006 there was a large difference, with half of the females foraging much more in shallower waters and half foraging much more in deeper waters. The mix of prey was similar between groups and between years (Fig. 19), however the proportions of individual species varied considerably in 2006 corresponding to the great geographical and depth divergence in foraging locations of the two groups: Atka mackerel and northern smoothtongue were much more important in diets of females that foraged predominantly in deep water, whereas eulachon, pollock, and sand lance were much more important in diets of females that foraged in shallower water.

The foraging distribution of females from Vostochni rookery on St. Paul was consistent between years and was concentrated in the shallow middle shelf domain north of St. Paul. Diets of females at Vostochni were notably different than those at Reef or Bogoslof —Vostochni diets were dominated by herring in both years, particularly in 2006, and by pollock in 2005 (Fig. 20). Although lamprey was of relatively little importance in diets based on mass percent, it was of highest importance based on the energy index because of its very high lipid content.

Despite variability between islands, ecoregions, and years in the mix of forage species consumed and in proportions of each, the aggregate energy index values of the spring and fall diets exhibited little variability between islands or years (Fig. 21).


Reef - 2005
Frequency of occurrence
1
0.8
0.6
0.4
0.2
0
Arrowtooth flounder
Atka mackerel
Capelin
Eulachon
Northern smoothtongue
Sand lance
Pollock
Shallow
Deep
Reef - 2005
Mass percent
0.6
0.5
0.4
0.3
0.2
0.1
0
Arrowtooth flounder
Atka mackerel
Capelin
Eulachon
Northern smoothtongue
Sand lance
Pollock
Shallow
Deep
Reef - 2005
Energy index
500
400
300
200
100
0
Arrowtooth flounder
Atka mackerel
Capelin
Eulachon
Northern smoothtongue
Sand lance
Pollock
Shallow
Deep

(A)



(B)

Figure 19 A&B. Diets of female northern fur seals at Reef rookery, St. Paul I., in fall 2005 and 2006. All herring were small (< 110 mm), and all pollock were adult. Error bars are standard errors of the means. See methods for explanation of energy index.

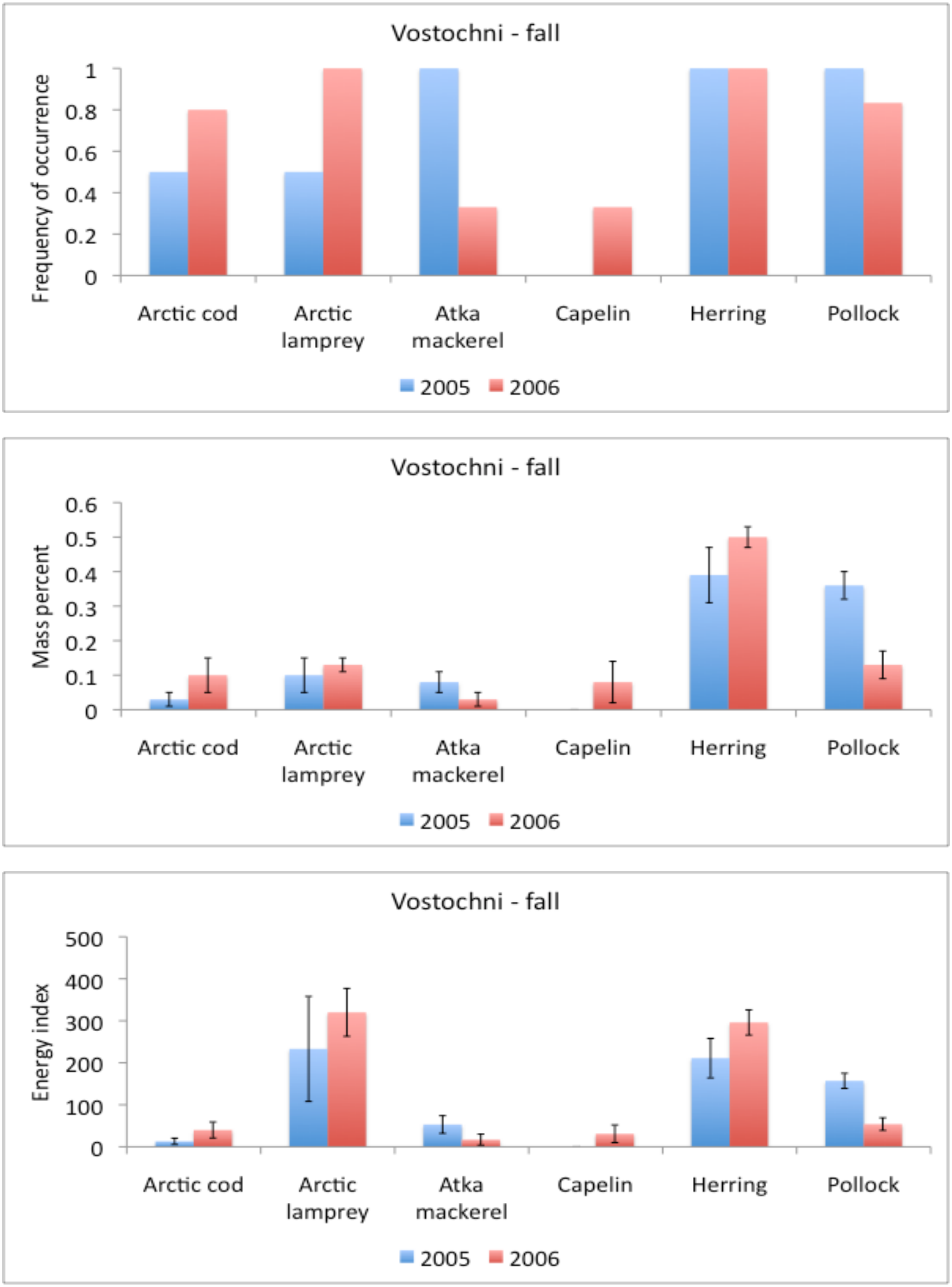


Figure 20. Diets of female northern fur seals at Vostochni rookery, St. Paul I., in fall 2005 and 2006. Large herring were > 110 mm. Error bars are standard errors of the means.

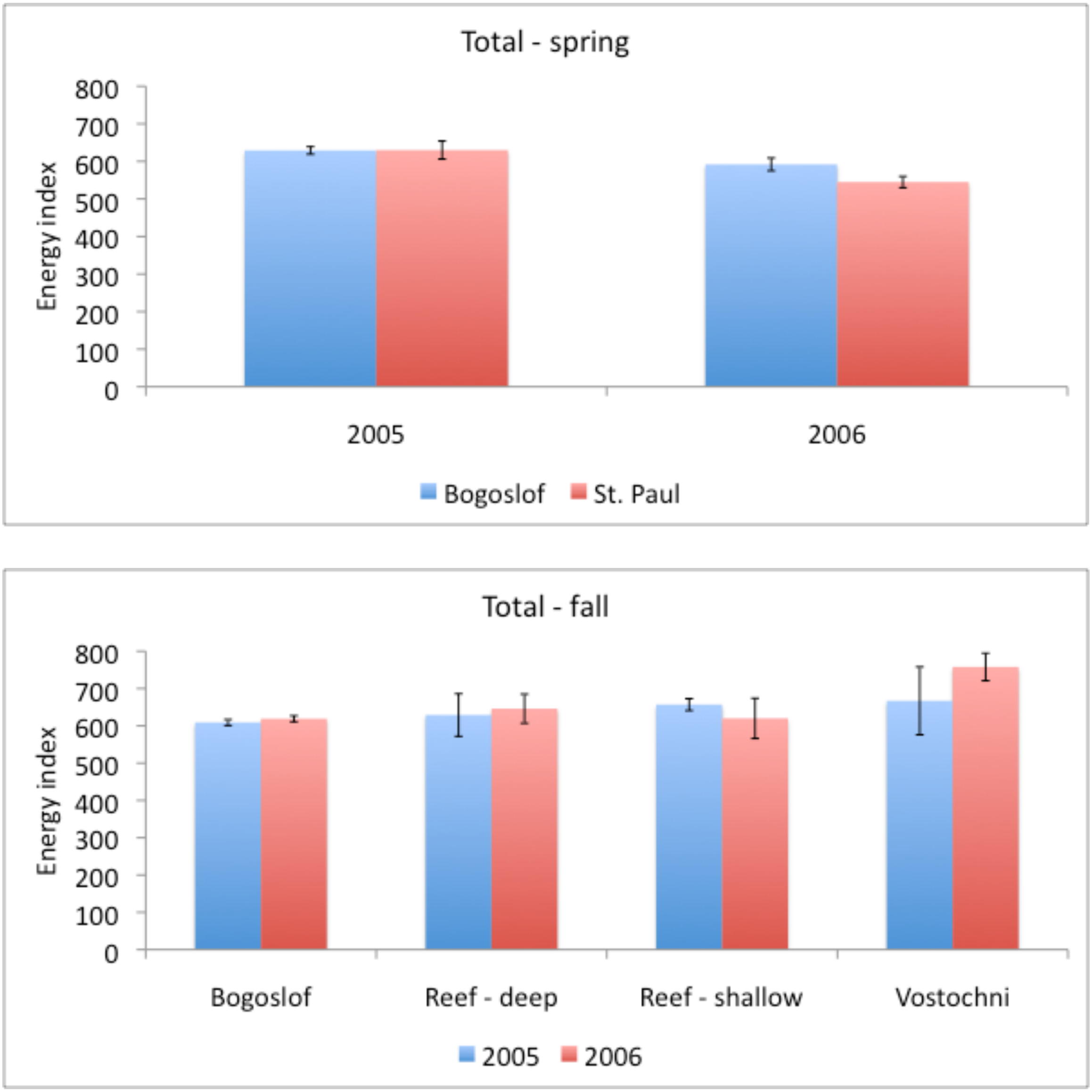


Figure 21. Aggregate energy index values of diets of female northern fur seals at Bogoslof I. and St. Paul I. in 2005 and 2006. Error bars are standard errors of the means.

Female foraging trip and maternal attendance patterns

Deployment duration (the time from initial capture until recapture) for adult female northern fur seals was similar at both islands for both years (Table 3). The total number and rate (trips/week) of foraging trips was greater at Bogoslof than St. Paul during each year and for both years combined (all $P < 0.001$). Despite the higher foraging trip intensity, females from Bogoslof spent only 66.5% of their time at sea on foraging trips over the two summer seasons while females from St. Paul spent 79.4% of their time on foraging trips. The total number of foraging trips was similar between years at both St. Paul ($P = 0.69$)

and Bogoslof (P = 0.18). The foraging trip rate was also similar between years at both St. Paul (P = 0.42) and Bogoslof (P = 0.51). Between the two rookeries on St. Paul Island, the total number and rate of foraging trips were similar in 2005 (P = 0.14; P = 0.12), but females at Reef rookery made fewer trips and had a lower rate of foraging trips than females at Vostochni rookery during 2006 (P = 0.018; P = 0.047) and for both years combined (P = 0.005; P = 0.011). The total number and rate of foraging trips was similar between years at both Reef (P = 0.83; P = 0.86) and Vostochni (P = 0.34; p =0.25) rookeries.

Table 3. Adult female northern fur seal mean instrument deployment duration, mean number of foraging trips, number of foraging trips per week, and percent of time spent at sea during the 2005 and 2006 summers in the Bering Sea. Standard deviations of the means are shown in parentheses.

Island *Rookery*	Year	N	Deployment duration (d)	Number of Trips	Trips/Week	Time at sea (%)
Bogoslof	2005	18	82.6 (6.1)	27.7 (6.1)	2.4 (0.5)	65.9 (3.0)
St. Paul	2005	17	82.0 (10.2)	10.2 (2.1)	0.9 (0.2)	80.0 (2.4)
Reef		*9*	*81.0 (5.7)*	*9.4 (2.2)*	*0.8 (0.2)*	*81.2 (2.4)*
Vostochni		*8*	*83.2 (14.1)*	*11.0 (1.9)*	*0.9 (0.1)*	*78.7 (3.0)*
Bogoslof	2006	15	78.1 (4.2)	24.5 (7.6)	2.2 (0.7)	67.3 (4.5)
St. Paul	2006	14	79.7 (4.3)	10.5 (2.4)	0.9 (0.2)	78.8 (4.2)
Reef		*8*	*78.5 (4.4)*	*9.3 (1.4)*	*0.8 (0.1)*	*78.2 (4.7)*
Vostochni		*6*	*81.2 (4.0)*	*12.2 (2.6)*	*1.1 (0.2)*	*79.2 (3.8)*

Adult female maximum foraging trip distances were greater at St. Paul than at Bogoslof during both years and for both years combined (all P < 0.001). The maximum female foraging trip distance averaged 293 km from St. Paul Island over the two years, and was 2.3 times greater in distance than the average maximum distance of 128 km from Bogoslof Island (Fig. 22). Between years, the maximum foraging trip distance was similar at St. Paul (P = 0.53), but was greater in 2006 than in 2005 at Bogoslof (P = 0.043). Between St. Paul Island rookeries, the maximum foraging trip distances were similar during 2005 (P = 0.90), 2006 (P = 0.27), and for both years combined (P = 0.40). There were also no differences between years at either Reef rookery (P = 0.99) or Vostochni rookery (P = 0.48).

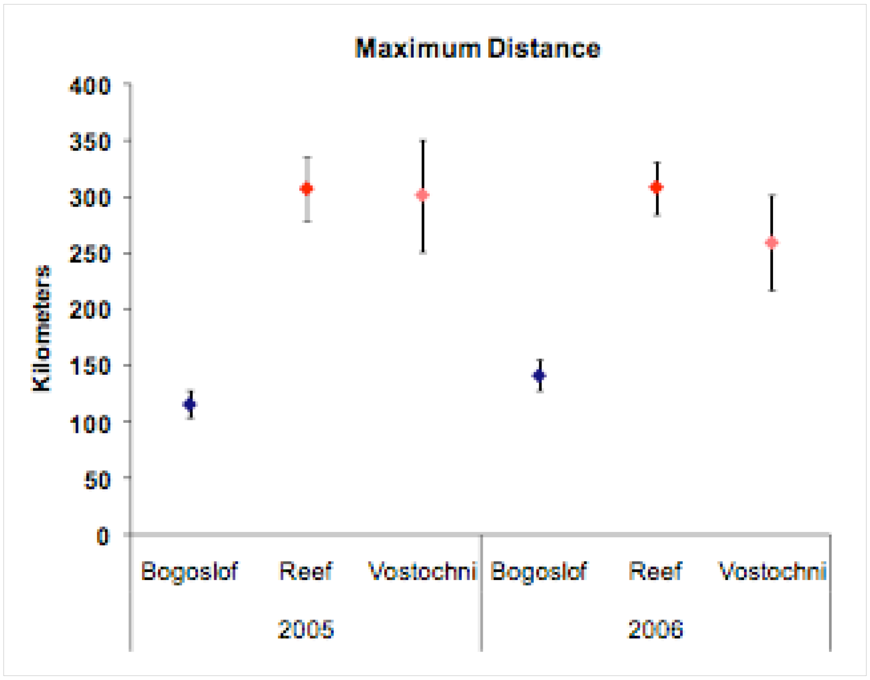


Figure 22. Mean maximum foraging trip distance (with 95% confidence intervals) for adult female northern fur seals from Bogoslof I. and St. Paul I. (Reef and Vostochni rookeries) during 2005 and 2006.

Adult female foraging trip durations were greater at St. Paul than Bogoslof during 2005 and 2006, and for both years combined (all $P < 0.001$). Overall, mean foraging trip durations were 2.9 times greater on St. Paul (6.5 days) than Bogoslof (2.2 days; Fig. 23). Foraging trip durations were similar between years on both islands (St. Paul, $P = 0.49$; Bogoslof, $P = 0.22$). Between St. Paul Island rookeries, foraging trip durations were similar during 2006 ($P = 0.16$), but were greater at Reef during 2005 ($P = 0.046$) and for both years combined ($P = 0.015$). Foraging trip durations were similar between years at both Reef rookery ($P = 0.58$) and Vostochni rookery ($P = 0.53$).

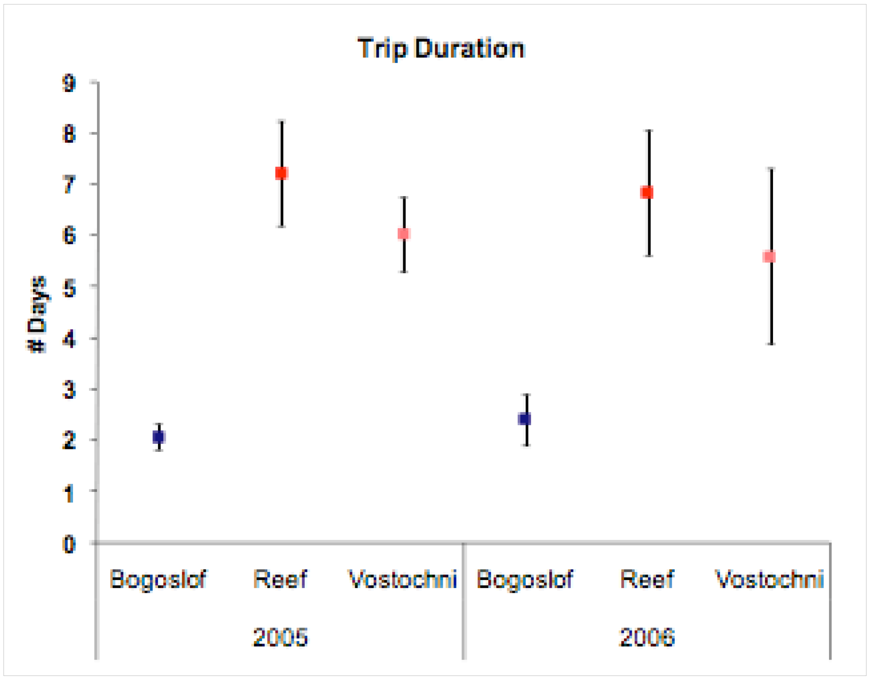


Figure 23. Mean foraging trip duration (with 95% confidence intervals) for adult female northern fur seals from Bogoslof I. and St. Paul I. (Reef and Vostochni rookeries) during 2005 and 2006.

Maternal visit (shore) durations of adult females were greater at St. Paul than Bogoslof during both years and for both years combined (all $P < 0.001$; Fig. 24). Overall, the mean maternal visit was 1.8 days at St. Paul during the two years, and only 1.1 days at Bogoslof. Shore durations were similar between years on both St. Paul ($P = 0.82$) and Bogoslof ($P = 0.46$). Between St. Paul Island rookeries shore durations were similar during 2005 ($P = 0.58$), but were shorter at Vostochni during 2006 ($P = 0.015$), and for both years combined ($P = 0.025$). Shore durations were also similar between years at Reef ($P = 0.27$) and Vostochni ($P = 0.096$) rookeries.

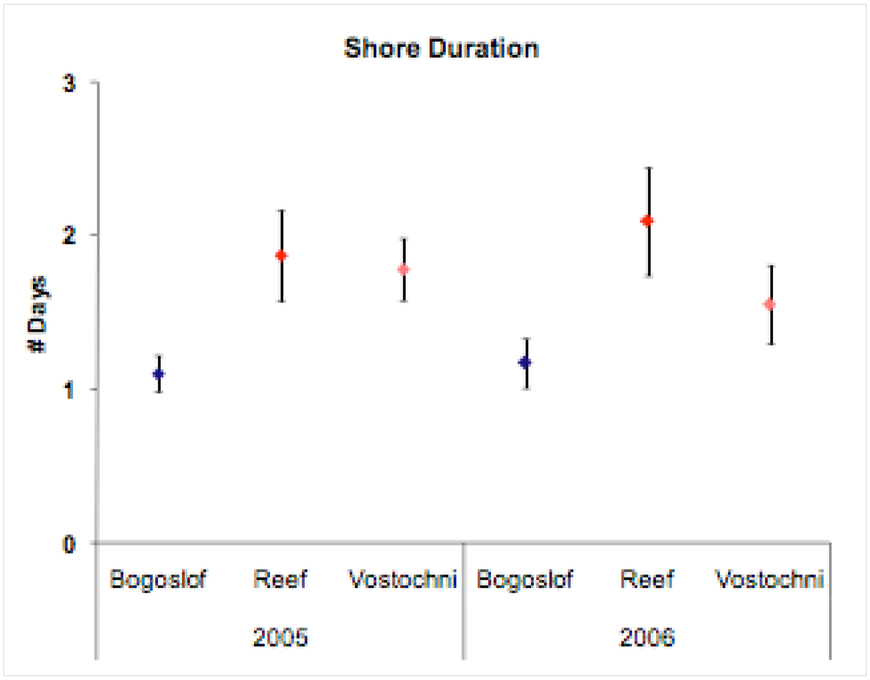


Figure 24. Mean shore (maternal visit) duration (with 95% confidence intervals) for adult female northern fur seals from Bogoslof I. and St. Paul I. (Reef and Vostochni rookeries) during 2005 and 2006.

Female body condition over lactation

Female mass

There were no inter-annual differences in the mass of females captured at St. Paul or Bogoslof in July or October either year (ANOVA P = 0.065, Fig. 25, Table 4). Females at St. Paul were larger than those at Bogoslof in July 2005, but not in October 2005 or at either time in 2006. Females lost mass during July-October in both years at both locations (Fig. 26). The rate of mass loss averaged least at Bogoslof in 2005, although it was not significantly different than in 2006 at Bogoslof or either year at St. Paul (ANOVA P = 0.44, Fig. 26).

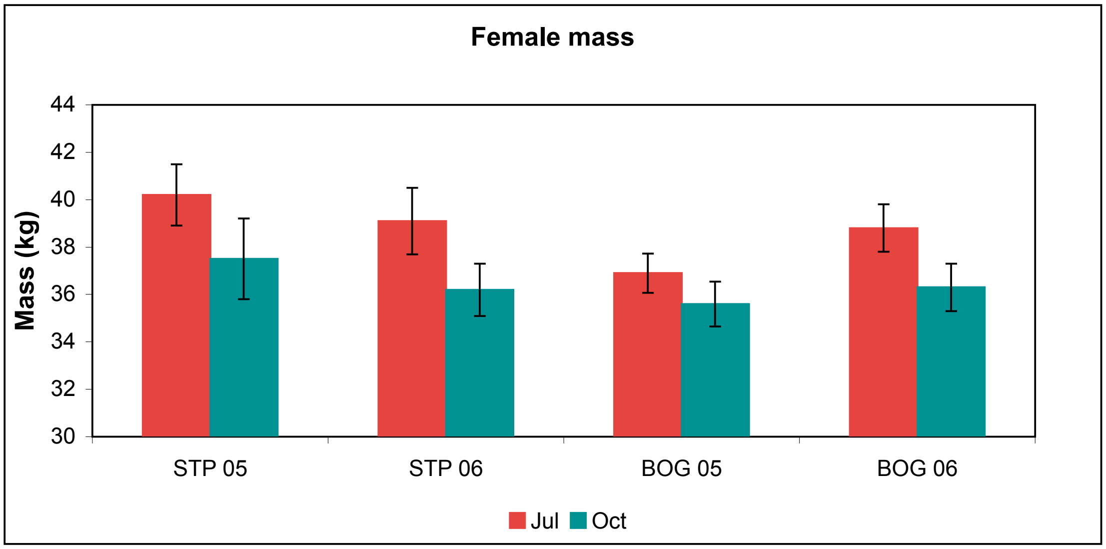


Figure 25. Mass of female northern fur seals (±SE) captured in July and again in October 2005 and 2006 at St. Paul I. and Bogoslof I. STP = St. Paul I., BOG = Bogoslof I., 05 = 2005, 06 = 2006.

Table 4. T-test probabilities for female northern fur seal mass comparisons in Figure 25. Paired 2-sample for intra-annual means by location; 2-sample for all others. STP = St. Paul I., BOG = Bogoslof I., 05 = 2005, 06 = 2006.

	STP Oct 05	STP Jul 06	STP Oct 06	BOG Jul 05	BOG Oct 05	BOG Jul 06	BOG Oct 06
STP Jul 05	0.009	0.56	-	0.03	-	-	-
STP Oct 05	-	-	0.51	-	0.31	-	-
STP Jul 06	-	-	0.007	-	-	0.88	-
STP Oct 06	-	-	-	-	-	-	0.92
BOG Jul 05	-	-	-	-	0.021	0.14	-
BOG Oct 05	-	-	-	-	-	-	0.62
BOG Jul 06	-	-	-	-	-	-	<0.001

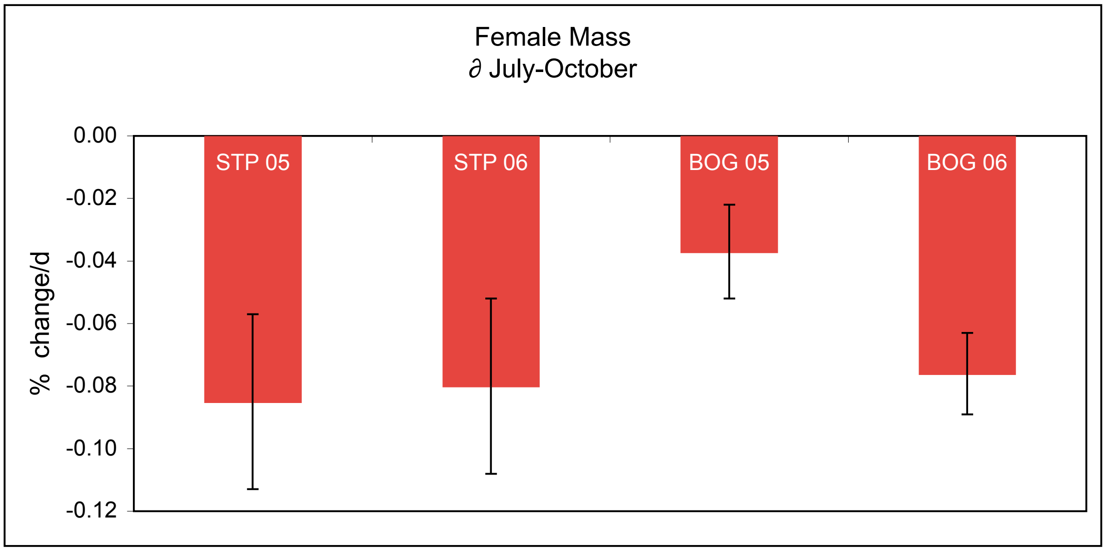


Figure 26. Rate of change in mass (±SE) of female northern fur seals captured in July and again in October 2005 and 2006 at St. Paul I. and Bogoslof I. STP = St. Paul I., BOG = Bogoslof I., 05 = 2005, 06 = 2006.

Female total body lipid

Total body lipid (TBL) of females at St. Paul was higher than TBL of females at Bogoslof in July 2005 and 2006, but lower in October of 2006: there was no difference between islands in October 2005 (ANOVA $P < 0.001$, Fig. 27). TBL of females declined between July and October in 2005 and 2006 at St. Paul, but did not differ significantly in either year at Bogoslof. The rate of change in TBL between July and October did not differ between years at either island, but was negative at St. Paul and positive at Bogoslof and significantly different between the islands both years
(Fig. 28, $P < 0.001$).

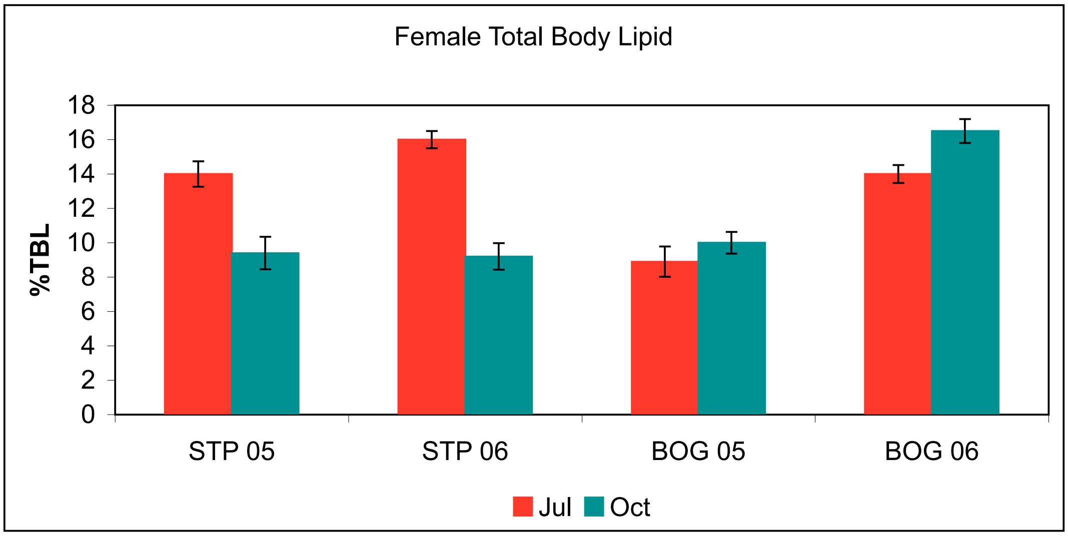


Figure 27. Total body lipid (±SE) as a percentage of mass of female northern fur seals in 2005 and 2006. STP = St. Paul I., BOG = Bogoslof I., 05 = 2005, 06 = 2006.

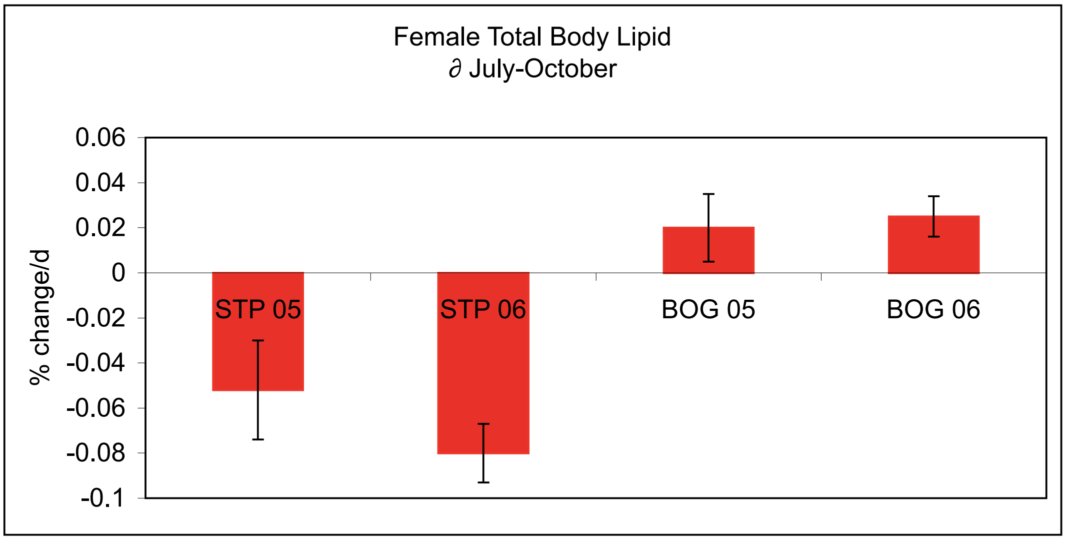
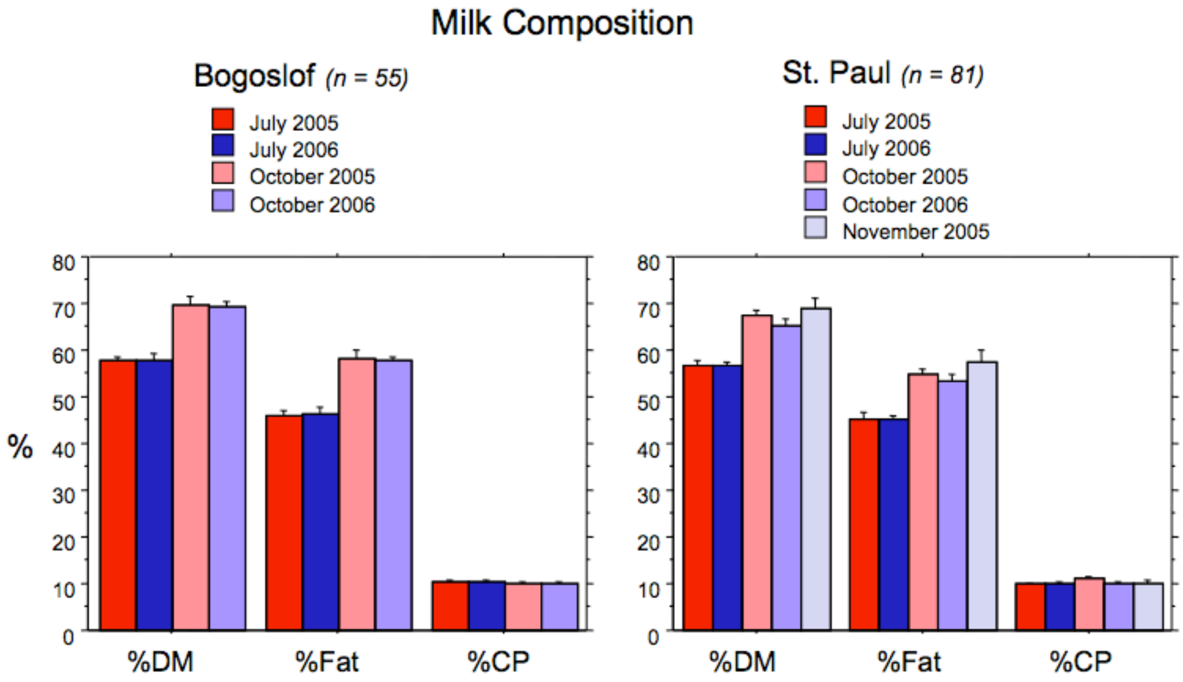


Figure 28. Rate of change (±SE) in total body lipid of female northern fur seals captured in July and again in October 2005 and 2006 at St. Paul I. and Bogoslof I. STP = St. Paul I., BOG = Bogoslof I., 05 = 2005, 06 = 2006.

Female milk composition

The proximate composition of fur seal milk changed over lactation from perinatal to mid and late lactation (Fig. 29).



ANOVA
<u>St. Paul alone</u>: July different than October and November ($p < 0.001$), October vs November (ns)

<u>Bogoslof and St. Paul – July and October</u>:
%DM: season ($p < 0.001$), year (ns), island ($p = 0.014$)
%Fat: season ($p < 0.001$), year (ns), island ($p = 0.006$)
%CP: season *x* island ($p = 0.030$)

Figure 29. Proximate composition of northern fur seal milk during the perinatal period (1-2 days postpartum, July), mid-late lactation (October) and near weaning (St. Paul I. only, November). Bars are mean ± SEM for dry matter content (%DM), fat content (%Fat), and crude protein content (%CP). Overall, DM and fat content significantly increased from July to October and were higher in females at Bogoslof I. *v* St. Paul I. in October. There were no differences between years.

In order to appropriately test for changes within individual females, we removed November samples (which were unpaired females) and used repeated measures ANOVA for females that we were able to sample in both July and October. The large changes in milk composition were attributed to total dry matter and fat content. Dry matter increased similarly within all females with season ($P < 0.001$), averaging 58.3 ± 0.91% and 56.1 ± 0.80% in July, and 69.4 ± 1.19% and 65.6 ± 1.12% in October at Bogoslof and St. Paul, respectively. Fat averaged 46.8 ± 0.88% and 44.7 ± 0.76% in July and 57.9 ± 1.08% and 53.4 ± 1.11% in October at Bogoslof and St. Paul, respectively. Significant differences in both dry matter and fat were found between islands in October ($P = 0.02$ and $P = 0.008$, respectively). The changes that occurred within individuals are clearly illustrated in fat content (Fig. 30).

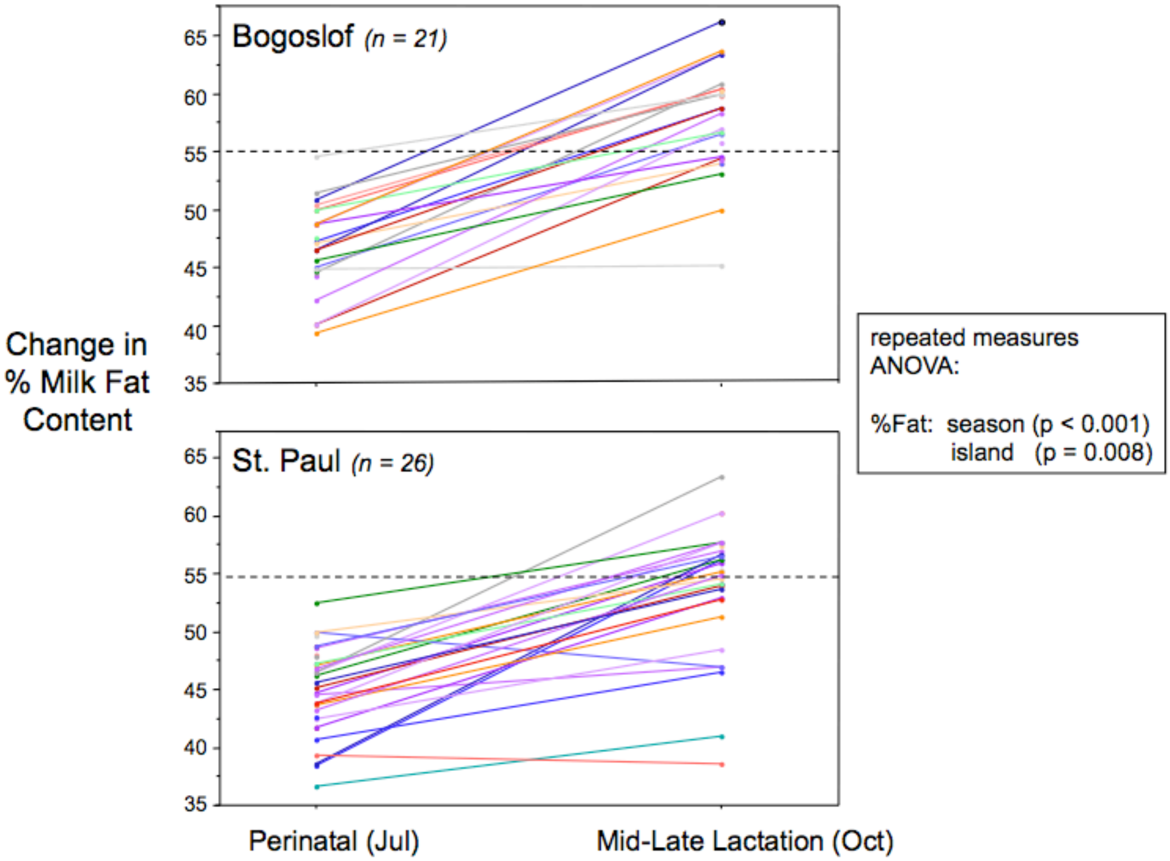


Figure 30. Changes in milk fat content within individual northern fur seal females over lactation at Bogoslof I. and St. Paul I. in 2005 and 2006.

Protein remained consistent throughout lactation and at both islands, averaging 10.1 ± 0.15% in July and 10.4 ± 0.15% in October. As expected, variation in fat content explained > 98% of the variation in estimated energy content, which overall averaged 20.3 ± 0.24 MJ/kg in July and 24.2 ± 0.33 MJ/kg in October.

Pup mass, growth rates, and percentage body lipid during the perinatal period and subsequent duration of lactation: indices of milk delivery rates

Intra-island comparisons – St. Paul

We found no differences between male or female pups at Reef rookery compared to Vostochni rookery at St. Paul in 2005 ($P \geq 0.35$) in birth mass, defined as mass when pups were first captured and which was generally within one to two days postpartum; perinatal mass, defined as mass at the end of the perinatal period; October mass, defined as mass at recapture in October; perinatal growth, defined as growth rate (kg/d) during the perinatal period; and nursing growth, defined as growth rate between the end of the perinatal period and the October weighing. Female October mass and nursing growth rate were greater at Vostochni than at Reef in 2006 (P = 0.01), and male perinatal growth rate was lower at Vostochni (P = 0.02; Figs. 31 and 32). Because there were no differences in 2005, and few, but not consistent differences in 2006, we combined the data from the two rookeries at St. Paul for comparisons between years and between St. Paul and Bogoslof. The two locations at Bogoslof where we captured seals were close together (within ~200m) with no evidence for segregation of foraging areas, such as at St. Paul. Therefore, comparisons between them were not undertaken.

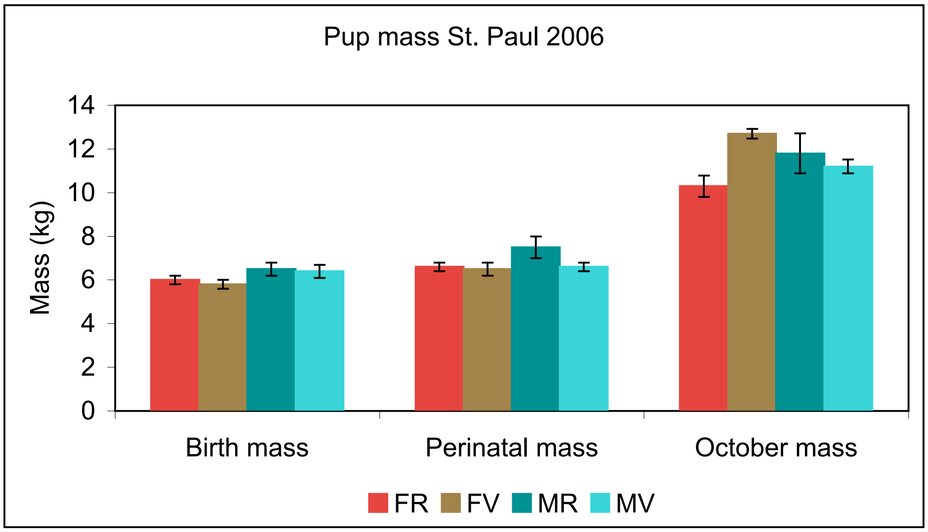


Figure 31. Northern fur seal pup masses (±SE) at two rookeries at St. Paul I. in 2006. FR = Female Reef, FV = Female Vostochni, MR = Male Reef, MV = Male Vostochni. Sample sizes Birth and Perinatal: FR = 6, FV = 5, MR = 4, MV = 5. Sample sizes October: FR = 6, FV = 3, MR = 4, MV = 3.

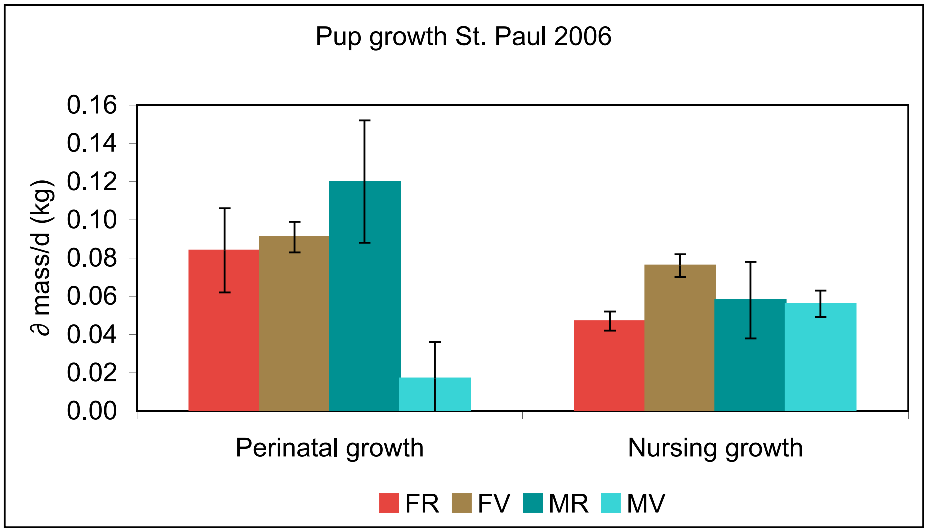


Figure 32. Northern fur seal pup growth rates (±SE) at two rookeries at St. Paul I. in 2006. FR = Female Reef, FV = Female Vostochni, MR = Male Reef, MV = Male Vostochni. Sample sizes Perinatal: FR = 6, FV = 5, MR = 4, MV = 5. Sample sizes Nursing: FR = 6, FV = 3, MR = 4, MV = 3

Female-male comparisons – St. Paul and Bogoslof

Birth mass of male pups was greater than that of female pups at both islands and in both years (ANOVA $P < 0.0001$, Fig. 33, Table 5). Perinatal mass of males averaged heavier than that of females, although the difference was significant only at St. Paul in 2005 and Bogoslof in 2006 (ANOVA $P < 0.0005$, Fig. 33, Table 5). October mass of males also averaged heavier than females at both islands in both years, but was significant only at Bogoslof (ANOVA $P < 0.0001$, Fig. 33, Table 5).

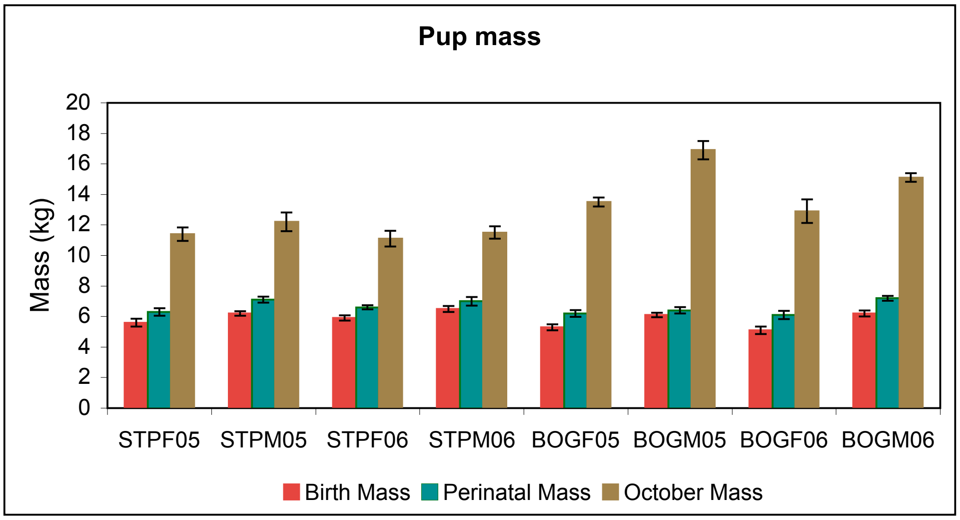


Figure 33. Mass (±SE) of northern fur seal pups at St. Paul I. and Bogoslof I. in 2005 and 2006. STP = St. Paul, BOG = Bogoslof, F = female, M = male, 05 = 2005, 06 = 2006. Sample sizes Birth and Perinatal: STPF05 = 8, STPM05 = 12, STPF06 = 11, STPM = 9, BOGF05 = 10, BOGM05 = 10, BOGF06 = 8, BOGM06 = 12. Sample sizes October: STPF05 = 7, STPM05 = 9, STPF06 = 11, STPM06 = 9, BOGF05 = 10, BOGM05 = 8, BOGF06 = 7, BOGM06 = 10

Perinatal growth rates of males and females differed only at Bogoslof in 2005, when females grew about 4 times faster (ANOVA P = 0.0016, Fig. 34, Table 5). Growth rates during the nursing period did not differ between males and females at St. Paul, but males grew faster than females at Bogoslof in both years (ANOVA P < 0.0001, Fig. 35, Table 5).

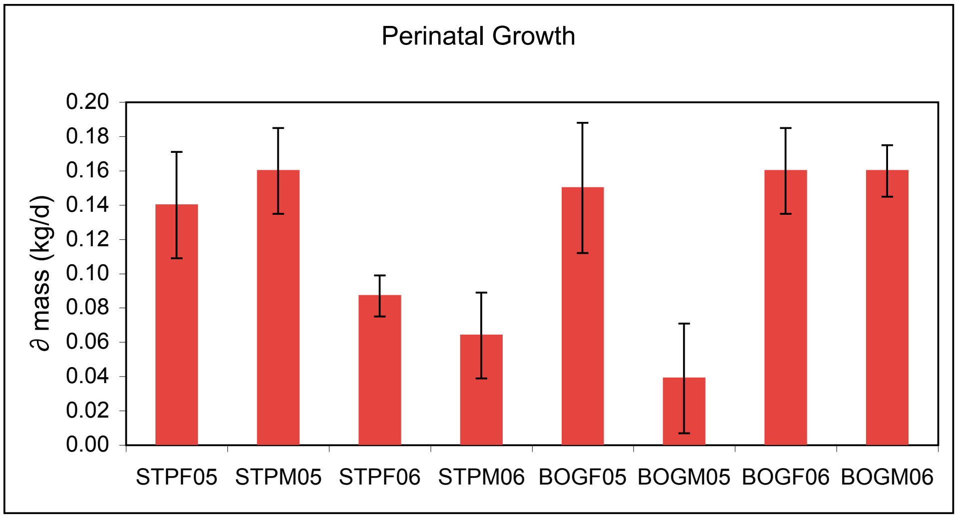


Figure 34. Growth rate of northern fur seal pups during the perinatal period at St. Paul I. and Bogoslof I. in 2005 and 2006. STP = St. Paul, BOG = Bogoslof, F = female, M = male, 05 = 2005, 06 = 2006. Sample sizes: STPF05 = 8, STPM05 = 12, STPF06 = 11, STPM = 9, BOGF05 = 10, BOGM05 = 10, BOGF06 = 8, BOGM06 = 12.

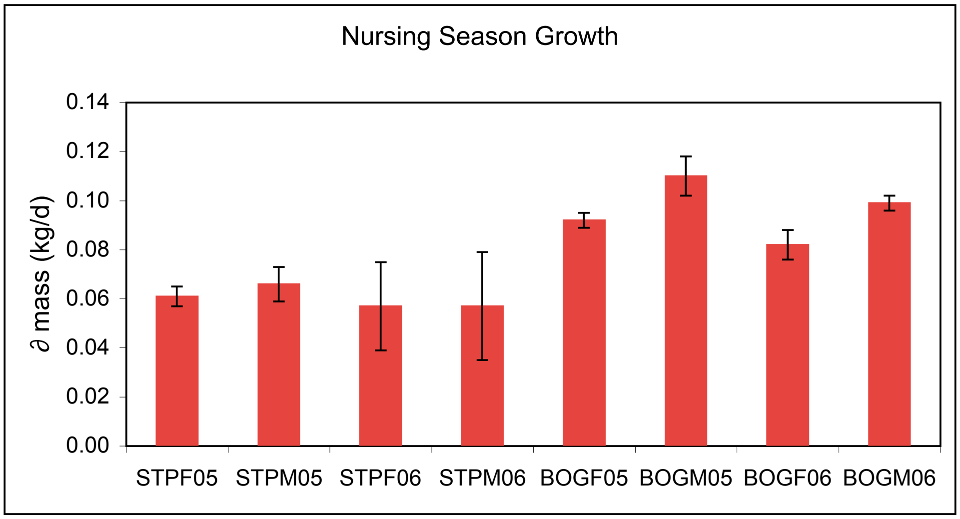


Figure 35. Growth rates of northern fur seal pups from the end of the perinatal Period until recapture in October at St. Paul I. and Bogoslof I. in 2005 and 2006. STP = St. Paul, BOG = Bogoslof, F = female, M = male, 05 = 2005, 06 = 2006. Sample sizes: STPF05 = 7, STPM05 = 9, STPF06 = 11, STPM06 = 9, BOGF05 = 10, BOGM05 = 8, BOGF06 = 7, BOGM06 = 10.

Table 5. T-test probabilities for northern fur seal pup mass and growth rate comparisons shown in Figures 33, 34, and 35. STP (St. Paul I.), BOG (Bogoslof I.), F (female), M (male).

	STP F 05	STP M 05	P
Birth mass (kg)	5.6	6.2	0.032
Perinatal mass (kg)	6.3	7.1	0.016
October mass (kg)	11.4	12.2	0.29
Perinatal growth (∂ mass/d)	0.14	0.16	0.57
Nursing growth (∂ mass/day)	0.061	0.066	0.62
	STP F 06	STP M 06	P
Birth mass (kg)	5.9	6.5	0.039
Perinatal mass (kg)	6.6	7.0	0.17
October mass (kg)	11.1	11.5	0.55
Perinatal growth (∂ mass/d)	0.087	0.064	0.38
Nursing growth (∂ mass/day)	0.057	0.057	0.98
	BOG F 05	BOG M 05	P
Birth mass (kg)	5.3	6.1	0.002
Perinatal mass (kg)	6.2	6.4	0.43
October mass (kg)	13.5	16.9	<0.001
Perinatal growth (∂ mass/d)	0.15	0.039	0.037
Nursing growth (∂ mass/day)	0.092	0.11	0.016
	BOG F 06	BOG M 06	P
Birth mass (kg)	5.1	6.2	0.003
Perinatal mass (kg)	6.1	7.2	0.002
October mass (kg)	12.9	15.1	0.007
Perinatal growth (∂ mass/d)	0.159	0.164	0.85
Nursing growth (∂ mass/day)	0.082	0.099	0.017
	STP F 05	STP F 06	P
Birth mass (kg)	5.6	5.9	0.33
Perinatal mass (kg)	6.3	6.6	0.36
October mass (kg)	11.4	11.6	0.69
Perinatal growth (∂ mass/d)	0.14	0.087	0.090
Nursing growth (∂ mass/day)	0.061	0.057	0.59
	STP M 05	STP M 06	P
Birth mass (kg)	6.2	6.5	0.36
Perinatal mass (kg)	7.1	7.0	0.65
October mass (kg)	12.2	11.5	0.35
Perinatal growth (∂ mass/d)	0.16	0.064	0.012
Nursing growth (∂ mass/day)	0.066	0.057	0.43
	BOG F 05	BOG F 06	P
Birth mass (kg)	5.3	5.1	0.61
Perinatal mass (kg)	6.2	6.1	0.85
October mass (kg)	13.5	12.9	0.44
Perinatal growth (∂ mass/d)	0.15	0.159	0.87
Nursing growth (∂ mass/day)	0.092	0.082	0.15

	BOG M 05	BOG M 06	P
Birth mass (kg)	6.2	6.2	0.90
Perinatal mass (kg)	6.4	7.2	0.008
October mass (kg)	16.9	15.1	0.010
Perinatal growth (∂ mass/d)	0.039	0.164	0.001
Nursing growth (∂ mass/day)	0.11	0.099	0.12
	STP F 05	BOG F 05	P
Birth mass (kg)	5.6	5.2	0.27
Perinatal mass (kg)	6.2	6.2	0.67
October mass (kg)	11.4	13.5	< 0.001
Perinatal growth (∂ mass/d)	0.14	0.15	0.87
Nursing growth (∂ mass/day)	0.061	0.092	< 0.001
	STP M 05	BOG M 05	P
Birth mass (kg)	6.2	6.1	0.57
Perinatal mass (kg)	7.1	6.4	0.02
October mass (kg)	12.2	16.9	< 0.001
Perinatal growth (∂ mass/d)	0.16	0.039	0.005
Nursing growth (∂ mass/day)	0.066	0.11	< 0.001
	STP F 06	BOG F 06	P
Birth mass (kg)	5.9	5.1	0.013
Perinatal mass (kg)	6.6	6.1	0.12
October mass (kg)	11.1	12.9	0.057
Perinatal growth (∂ mass/d)	0.087	0.159	0.012
Nursing growth (∂ mass/day)	0.057	0.082	0.013
	STP M 06	BOG M 06	P
Birth mass (kg)	6.5	6.2	0.26
Perinatal mass (kg)	7.0	7.2	0.52
October mass (kg)	11.5	15.1	<0.001
Perinatal growth (∂ mass/d)	0.064	0.164	0.002
Nursing growth (∂ mass/day)	0.057	0.099	<0.001

The percent total body lipid (TBL) of neonatal pups (Fig. 36) was not different between sexes or between St. Paul and Bogoslof in either 2005 or 2006 (ANOVA $p = 0.23$). TBL in October differed only for males at Bogoslof in 2005, which were fatter than any other group ($p \leq 0.005$)

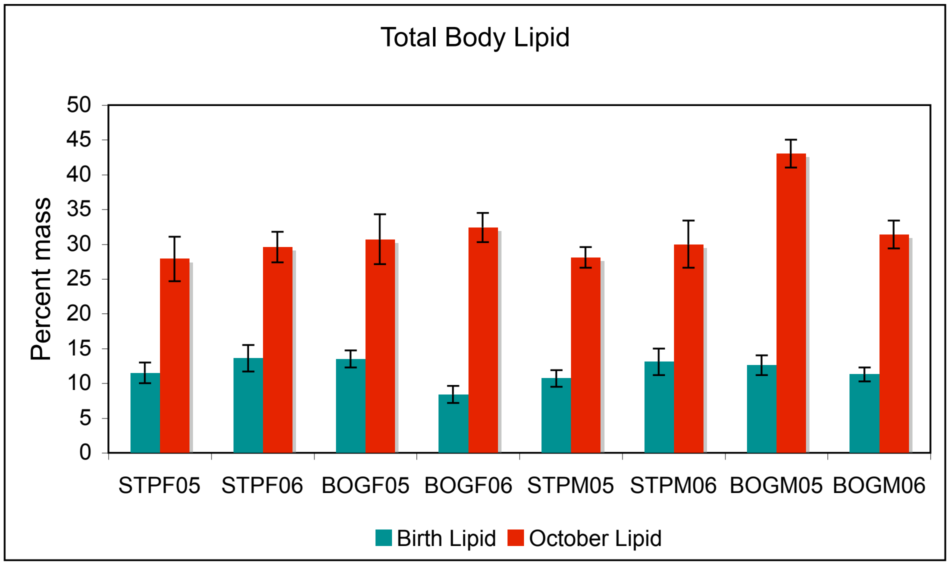


Figure 36. Percent total body lipid of northern fur seal pups at birth and in October at St. Paul I. and Bogoslof I. in 2005 and 2006. STP = St. Paul, BOG = Bogoslof, F = female, M = male, J = July, O = October, 05 = 2005, 06 = 2006. Sample sizes: STPFJ05 = 8, STPM05 = 12, STPFJ06 = 10, STPMJ06 = 9, BOGFJ05 = 9, BOGMJ05 = 9, BOGFJ06 = 8, BOGMJ06 = 10, STPFO05 = 5, STPMO05 = 8, STPFO06 = 8, STPMO06 = 7, BOGFO05 = 8, BOGMO05 = 9, BOGFO06 = 5, BOGMO06 = 8.

Inter-annual comparisons – St. Paul and Bogoslof

The only difference between years in mass or growth rate of pups at St. Paul was for perinatal growth of both males and females, which was greater in 2005 than in 2006: although perinatal growth of females in 2005 averaged 60% greater than in 2006, the difference was not significant (Fig. 35, Table 5). There were no differences in any of the five parameters between years for females at Bogoslof, but for males perinatal mass and growth were greater in 2006, whereas October mass was greater in 2005: nursing growth averaged higher in 2005, as it did for females, but neither difference was significant (Fig. 37, Table 5). Although interannual differences in birth TBL were not significant between years at either island, there was a consistent interannual pattern: both females and males averaged fatter in 2006 at St. Paul, but averaged thinner in 2006 at Bogoslof (Fig. 36). In October males at Bogoslof were much fatter in 2005 than in 2006.

Inter-island comparisons – St. Paul v Bogoslof

Birth mass of pups averaged higher on St. Paul than Bogoslof in both years, but was significant only for females in 2006. Perinatal mass differed between islands only for males in 2005, which were heavier at St. Paul: females at St. Paul were on average 8% heavier than at Bogoslof in 2006 but the difference was not significant (Fig. 33, Table 5). Perinatal growth rates of female pups did not differ between islands in 2005, but were much greater for males at St. Paul (Fig. 34, Table 5). In 2006, perinatal growth of both males and females was much greater at Bogoslof. Growth rates of both sexes in both years were greater during the nursing period at Bogoslof than at St. Paul (Fig. 35, Table 5), and thus the October masses were as well. Female pups grew 31%-33% faster during the nursing period and were 14%-16% heavier in October at Bogoslof than at St. Paul, and male pups grew 34%-43% faster and were 26%-28% heavier at Bogoslof. Nevertheless, TBL differed only at Bogoslof in 2005, when males were much fatter (Fig. 36).

Determinants of pup growth

Milk energy output/intake is the most significant predictor of offspring growth and weaning mass in pinnipeds (e.g., Iverson et al. 1993, Schulz and Bowen 2005). Thus, pup growth rate in northern fur seals will be a function of milk composition (and thus milk energy content) and milk output by the female/milk intake by the pup. Despite the reasonably wide variation among females in milk fat and energy content (i.e., 37-55% fat and 16.5-23.6 MJ/kg in July, and 38-66% fat and 17.4-28.2 MJ/kg in October), pup growth rates were not significantly related to milk fat or energy content ($P > 0.3$) across females, although the trend was positive. Instead, the large differences in growth rates between Bogoslof and St. Paul were explained primarily by overall differences in female attendance patterns (see Figs. 23 and 24). When the overall differences between islands in these patterns were expressed on an individual female basis, the effects on pup growth rate were clearly evident (Fig. 37). The primary drivers of this relationship were the extended foraging trip durations of females at St. Paul, which in fact showed almost no overlap with females at Bogoslof. Within females at Bogoslof alone, there was no relationship between foraging trip duration and pup growth ($P = 0.257$). However, within females at St. Paul alone, the relationship remained significant ($P < 0.001$), with females that had shorter trip durations able to achieve similar pup growth rates as those on Bogoslof (Fig. 37).

Interestingly, females with longer trip durations also had longer suckling durations on shore (Fig. 38). This was true both across all females from both islands, as well as within females from each individual island (Bogoslof, $P < 0.001$; St. Paul, $P = 0.002$), although the relationship at Bogoslof was tighter. Nevertheless, this apparent compensation for longer foraging trips did not mitigate the dominant effects of the trip lengths themselves, as the ratio of trip duration to shore duration was still far greater in females at St. Paul compared to Bogoslof, resulting in reduced pup growth rates (Fig. 39).

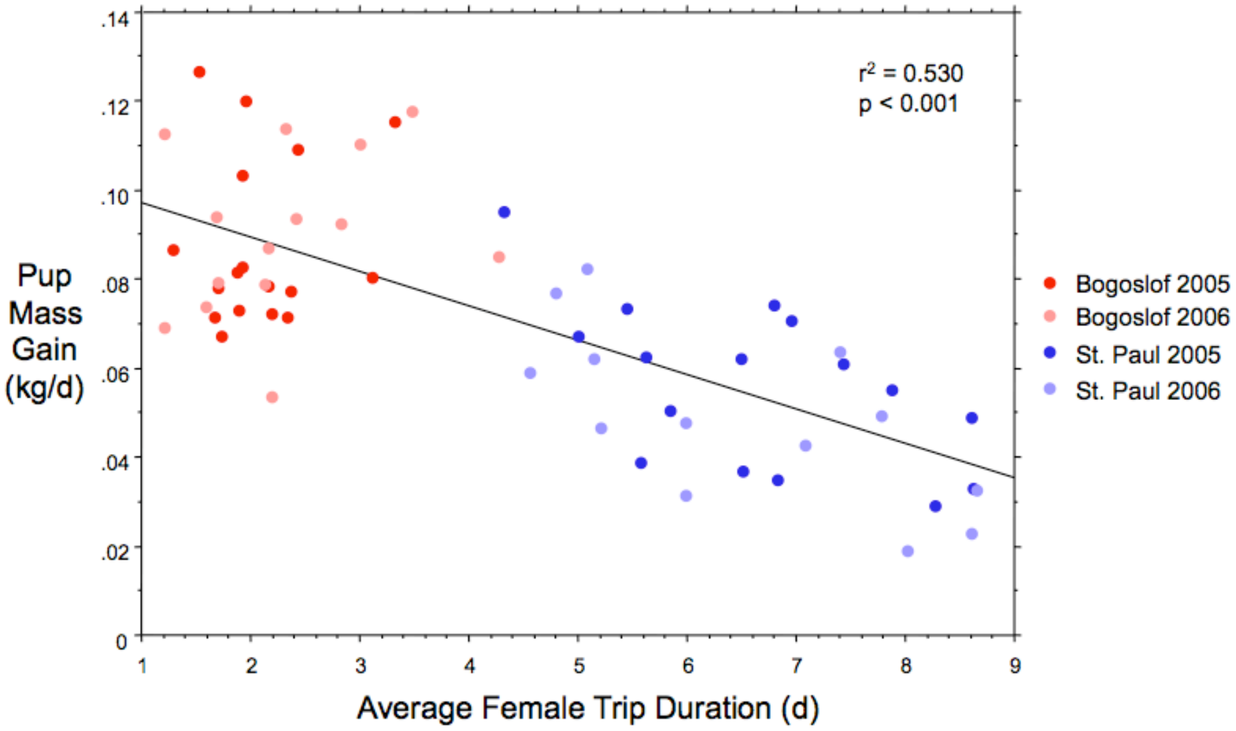


Figure 37. The relationship of northern fur seal daily pup mass gain (from female perinatal departure to recapture in October) to average foraging trip duration of their mothers during the same period at Bogoslof I. and St. Paul I. in 2005 and 2006.

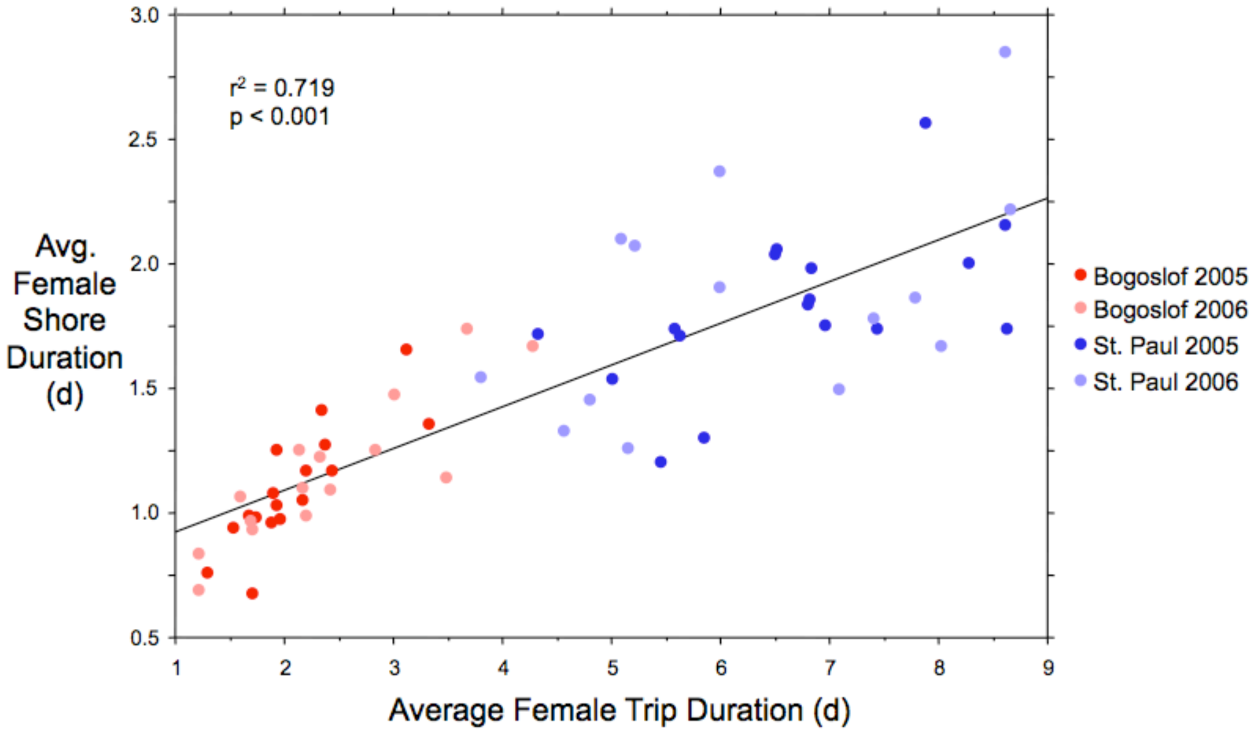


Figure 38. The relationship of average shore duration to average foraging trip duration throughout the lactation period in female northern fur seals from Bogoslof I. and St. Paul I. in 2005 and 2006.

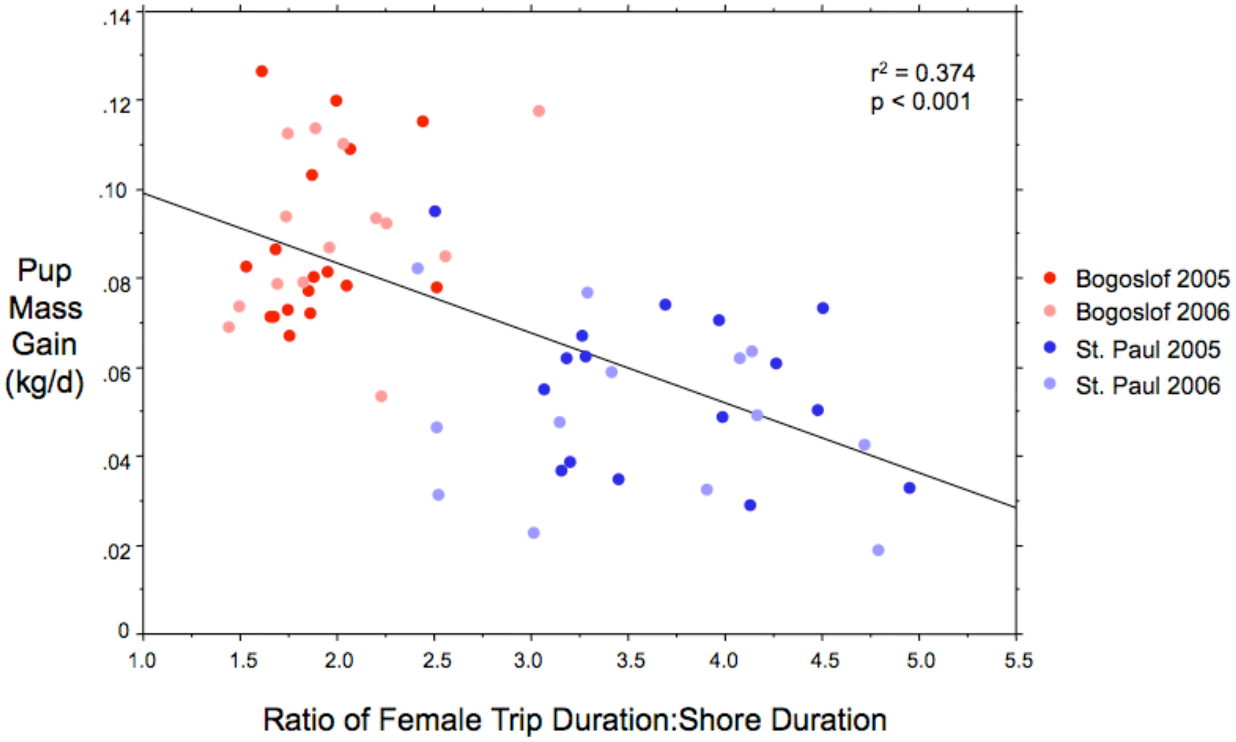


Figure 39. The relationship of northern fur seal daily pup mass gain over the lactation period (from female perinatal departure to recapture in October) to the ratio of average foraging trip duration:shore duration of their mothers during the same period at Bogoslof I. and St. Paul I. in 2005 and 2006.

DISCUSSION

Winter migration and consequences in the North Pacific Ocean

Migration

The migration of northern fur seals from the Pribilof Is. has previously been described from extensive pelagic collections of seals but, because these collections were concentrated near the coast, the descriptions give an incomplete picture of their winter distribution (Kenyon and Wilke, 1953, Lander and Kajimura 1982, Bigg, 1990). Moreover, once the animals were killed, there was no means to determine if the specific habitats selected by the seals may have differentially affected their condition. Ream et al. (2005) used satellite telemetry to track fur seals throughout their migrations. Though the sample size was much smaller than the current study, they were able to determine winter foraging areas for most of the fur seals, and found that thirty percent of the animals were using the subarctic–subtropical transition region of the central North Pacific. This unexpected finding was even more evident during the tracking we conducted in 2004 and 2005. In fact, 62% of the animals appeared to be using the transition region or other open ocean habitat as their winter foraging destination.

The tracking durations were considerably shorter for animals instrumented in 2005, and this limited the number of animals we could compare. Nearly half of the satellite tags deployed in 2005 stopped transmitting by January 1, 2006, compared to 6% of those that were deployed in the fall of 2004. None of the animals instrumented by Ream et al. (2005) stopped transmitting before January 1. We suspect that instrument failure (due to a bad batch of instrument components rather than variable molt patterns or animal mortality) was responsible for the truncated results. For animals that we were able to determine actual or probable destination regions, habitat use and travel routes were similar between St. Paul and Bogoslof, suggesting that these populations experience comparable environmental conditions and foraging opportunities during their migration into the North Pacific Ocean. Habitat use was also similar between 2005 and 2006 for adult females migrating from St. Paul Island.

Female body condition in July

The average sizes (mass) of female fur seals we captured in July at St. Paul and Bogoslof were nearly the same, except that in 2005 Bogoslof females were somewhat smaller than those at St. Paul. This is more likely a consequence of sampling bias rather than a reflection of population differences. However, TBL of females at St. Paul was higher than at Bogoslof in July of both years, indicating that there may have been differences in winter-spring foraging patterns or migration routes of seals at the two islands that were not apparent based on the satellite tracking data alone. The differences were not great and likely of little significance to the fitness of mothers at the time of parturition.

Summer foraging strategies and consequences in the Bering Sea

Foraging strategies

Adult female fur seals with dependent young at St. Paul I. had dramatically different summer foraging strategies in the Bering Sea than those at Bogoslof I. during the two years of this study. Females from Bogoslof I. foraged in deep water a relatively short distance from the island and in all directions during the summers of 2005 and 2006. Consistent with the findings of Robson et al. (2004) and Call et al. (2008), females from Vostochni and Reef rookeries on St. Paul Island used distinct habitats, foraging in opposite directions from the island with minimal overlap. Females from Vostochni rookery traveled to the north of St. Paul, and foraged nearly entirely in the middle domain of continental shelf. Females from Reef rookery traveled to the west, east, and southeast of St. Paul, and used habitat on the continental shelf, at the shelf break, and in deep oceanic water. Compared to females from Vostochni rookery, the Reef females exhibited more variability in route choice and habitat use among individuals. Adult females from Reef rookery had been shown to use predictable foraging habitat, with little variability in foraging direction among individuals, during tracking studies conducted in the mid-1990s (Robson et al. 2004). Research carried out by Call et al. (2008) during the summer of 2004, however, found that Reef females had less fidelity to foraging areas than Vostochni females. The variable foraging pattern of the Reef females was associated with mass loss in the individuals; Call et al. (2008) suggested that this variability in foraging habitat might have been due to poor or changing conditions in the habitat encountered by these animals.

Maximum foraging trip distances and trip durations were 2.3 and 2.9 times greater, respectively, for St. Paul females than for Bogoslof females. Maximum foraging trip distances of adult females from St. Paul did not differ between years and averaged 293 km, while the maximum foraging trip distance from Bogoslof was greater in 2006 (141 km) than in 2005(116 km) and averaged 128 km. Mean foraging trip durations were 6.5 days on St. Paul and 2.2 days on Bogoslof, and were similar between years on both islands. As a result of these differences, St. Paul females spent 79% of their time at sea on foraging trips, while Bogoslof females spent only 66% of their time at sea.

Foraging trip durations appear to have decreased at St. Paul Island since the mid-1990s; mean trip duration was 8.8 days in 1995 and 8.0 days in 1996 (Robson et al. 2004). Differences in methods prevent appropriate comparison of St. Paul Island maximum foraging trip distances from the mid-1990s to the current study. Between St. Paul Island rookeries, the maximum foraging trip distances did not differ during either 2005 or 2006. Trip durations, however, were greater at Reef rookery than at Vostochni rookery during 2005 (Reef, 7.2 days; Vostochni, 6.0 days), and for both years combined (Reef, 7.0 days; Vostochni, 5.8 days). This suggests that Vostochni rookery females may have had an easier time locating prey resources, perhaps at more predictable areas, than females at Reef rookery during 2005. Similar patterns were observed at the two rookeries in 2004; mean foraging trip duration was 7.6 days at Reef rookery and 6.6 days at Vostochni rookery (Call et al. 2008)

The duration of northern fur seal female shore visits is determined by pup demand for milk (Gentry and Holt 1986). Similar to other otariids, northern fur seal shore visits have been reported to average 2.0-2.1 days and are the least variable component of maternal attendance patterns (Gentry 1998). Uniformity of shore visit duration among colonies also has been reported, even when the colonies differ in foraging habitat and availability of prey resources (factors that influence foraging trip duration) (Gentry 1998). However, we found differences even between the two rookeries on St. Paul, with Vostochni having shorter duration of shore visits during 2006 (Vostochni, 1.5 days; Reef, 2.1 days), and for both years combined (Vostochni, 1.7 days; Reef, 2.0 days). More importantly though, the duration of maternal visits to shore at Bogoslof was notably short compared to St. Paul, and was also substantially shorter than the duration of shore visits previously reported for the species. Overall, the mean maternal visit lasted 1.8

days at St. Paul during the two years, but only 1.1 days at Bogoslof. Gentry (1998) also suggested that environmental changes could affect variability in duration of visits to shore. However, the duration of shore visits at Bogoslof were nearly identical in 2005 (1.1 days) and 2006 (1.2 days).

Given the sizable difference in duration of shore visits between islands, it is likely that adult females at Bogoslof have adapted a different maternal attendance strategy (short trip duration/short visit duration) than that used by adult females at St. Paul (long trip duration/long visit duration). An alternate strategy such as this may have developed in response to a reliable abundance of nearby prey. By spending less time on foraging trips to sea, the adult females minimize the likelihood of their pups starving to death. However, it also requires that the females are able to build up their energy stores quickly and efficiently deliver large quantities of milk to their pups.

Qualitative evaluation of female diet differences between islands, seasons and years

Milk and blubber FA results were entirely consistent with the data obtained from female foraging locations and differences both during the winter migration in the North Pacific and during foraging from the breeding grounds in the Bering Sea. In carnivores, including pinnipeds, milk FAs are derived almost entirely from FAs in diet when feeding or from FAs mobilized from adipose tissue stores when fasting - indeed, given the regulatory processes of the mammary gland, when females are actively feeding, FAs consumed in diet are deposited first into the mammary gland over all other tissues, including adipose tissue and blubber (Iverson 1993). Thus, when female fur seals arrive on the breeding grounds in July (i.e., during the perinatal fast) milk FAs will be derived primarily from the FAs that the female has stored in blubber prior to parturition—that is, reflecting the end of foraging in the North Pacific. Although it might be possible that some milk FAs might arise from feeding just prior to arriving at the rookery, this is not likely to contribute substantially, as the hormonal signal for active milk production, prolactin, does not occur until parturition. Milk secreted subsequently during foraging trips should instead reflect primarily FA input from the immediate diet (Iverson and Oftedal 1995, Iverson 1993, Iverson et al. 1997).

Thus, if female diet differs before versus during lactation, then we would expect to detect changes in milk FA composition. This was clearly demonstrated in fur seal females (Figs. 9, 11, 13, 14). The extensive overlap in milk FA signatures of females at both islands immediately after parturition in July was consistent with the extensive overlap in foraging locations and likely diet of females (from both islands) throughout the North Pacific (Fig. 3). In contrast, the almost total separation of milk FA signatures after foraging during the lactation period (Fig. 9) was consistent with the high degree of separation of foraging locations and habitats in the Bering Sea (Fig. 5). Blubber FAs exhibited similar trends but generally with somewhat greater overlap (Fig. 11). In contrast to milk, blubber FAs will reflect a much longer-term integration of dietary intake by the female (e.g., weeks to months). In addition, milk

FAs may also be somewhat influenced by uptake patterns of the mammary gland. Hence it was not surprising to find clear distinction between milk and blubber FAs from females at both islands. Nevertheless, both revealed the same patterns of differentiation with season and year (Figs. 13 and 14).

These results indicate that females from the two islands were not only making use of prey resources in vastly differing proximity to the breeding grounds (short foraging trips from Bogoslof, long trips from St. Paul), but also that prey types in the two regions likely differed, as FA signatures of a given prey species will not vary substantially by location within this overall Bering Sea region and certainly not to the degree to cause such large differences in milk FA signatures (e.g., Iverson et al. 2002, Iverson and Springer unpubl. data). In addition to island and year differences, milk and blubber FA patterns and differences (Figs. 10 and 12) were also consistent with the observed differences in foraging patterns of females at St. Paul from the two rookeries.

Quantitative evaluation of female diet differences between islands, seasons and years

Our estimates of diet based on FAs are not entirely comparable to earlier estimates based on scats and stomach contents because of inherent biases of each method. Particularly, scat and stomach content estimates tend to overestimate prey with robust hard parts. In contrast, QFASA estimates of diet integrate intake over a longer period of time (weeks to months) and provide quantitative proportions of prey intake, but are unlikely to record rare occurrences of prey consumption. However, perhaps most importantly, previous diet studies (using scats and stomachs) occurred in prior decades and regimes of climate, fisheries, and ecosystem state, such that the proportions of prey consumed in 2005 and 2006 may well be different than before (Sinclair et al. 2008).

Spring diets of females at Bogoslof and St. Paul were similar, suggesting similar migratory and foraging behavior as they returned to the Bering Sea from wintering areas in the North Pacific. This was consistent with satellite tracks of females departing the islands in the fall showing extensive overlap in the winter months (e.g., Figs. 3, 4). The only exception was the amount of salmon detected in diets of Reef females in 2006, and we cannot at present evaluate its significance.

The suite of forage species in diets of females in fall at the three rookeries were consistent with expectations of what they might be based on known patterns in the distribution of their primary forage species and previous studies of fur seal diets in the Bering Sea (Jordan 1899, Kajimura 1984, Perez and Bigg 1986, Sinclair et al. 1994, Antonelis et al. 1997, Mecklenburg et al. 2002, Zeppelin and Ream 2006). Females at Bogoslof foraged in the deep Aleutian Basin primarily on northern smoothtongue, one of the most abundant species in this ecoregion (Sinclair et al. 1999) and one known to be important in fur seal diets, as well as high in fat. Females at Reef rookery on St. Paul also foraged on northern smoothtongue, with consumption highest among females that spent the greatest amount of time in deep water of the outer domain, shelf edge, and basin west of St. Paul. Reef females that foraged more over the shallow shelf consumed lesser amounts of smoothtongue and greater amounts of eulachon, pollock, and sand lance. Females at Vostochni rookery, which foraged entirely in the shallow middle domain north of St. Paul fed predominantly on herring and pollock, although they obtained most energy from lamprey owing to its extremely high fat content.

Interannual differences in diets at Bogoslof were minor. An assessment of interannual differences in diet at Reef is difficult because of the movements of females among deeper and shallower regions of the eastern Bering Sea in the two years, and the effect of prey availability and thus diet. The suite of prey species consumed between years was similar, except that capelin was not consumed in 2005. In contrast, there were conspicuous differences in diets of females at Vostochni between 2005 and 2006, with the contribution of herring approximately 30% higher and the contribution of pollock approximately 65% lower in 2006 and, as at Reef, with capelin occurring in diets only in 2006.

The explanation for the change between years in diets at Vostochni, and of capelin in diets at Reef, is probably related to the marked cooling of the Bering Sea in 2006, the presence of a more extensive cold pool on the middle shelf compared to 2005, and the effect that likely had on the distribution of forage species (Brodeur et al. 1999, Wyllie-Echeverria and Ohtani 1999). For example, pollock tend to avoid cold water and are displaced off the middle shelf in years of extensive cold pool development, whereas herring are not so affected and in fact are typically found in October in just the region of the middle shelf where females from Vostochni were foraging (Wespestad 1983). Capelin favor colder waters than pollock as well. Deeper waters of the eastern shelf and Aleutian Basin, where Bogoslof and Reef females foraged, are not affected by the cold pool, which is confined primarily to the middle shelf, and interannal differences in the thermal environment of relevance to fish distribution are much less.

Despite differences in diets of females at the three rookeries, including differences between deep and shallow foraging females at Reef, the aggregate energy index values of all diets were quite similar. This is significant in how we interpret the consequences of female foraging strategies. That is, if the energetic value of mixed diets is not different between rookeries or years, then it is clearly the extreme differences in foraging distances and time away from pups of females at Bogoslof (short) compared to St. Paul (long), and thus on female energetic costs and milk delivery rates to pups, which explain the significant differences in female body condition and pup growth rates between locations.

Female body condition in October

Changes in %TBL of females at the two islands during summer were opposite, decreasing in both years at St. Paul but increasing in both years at Bogoslof: differences between years were not significant. This is consistent with our general prediction that foraging conditions at Bogoslof are better than at St.

Paul. It further suggests that whatever interannual variability there might have been between 2005 and 2006 in prey resources in the oceanic and shelf habitats, it was not significant to the females' energy budgets. The opposite trends in change in mass and TBL of females at Bogoslof (decreasing mass with increasing percent TBL) are not well understood at this time. It might be explained if *percent* TBL increased but *total* TBL did not because they were losing mass via water and/or protein.

Female milk composition

Our results demonstrated that northern fur seal milk contains extremely high fat and energy content, reaching levels as high as 54% fat and 23.6 MJ/kg in July and 66% fat and 28.2 MJ/kg in October. These levels match or even exceed those found in the highest milk fats measured in phocid seals at peak lactation (i.e., averaging 60% fat in hooded seals *Cystophora cristata* and grey seals *Halichoerus grypus*; Oftedal et al. 1988, Iverson et al. 1993). These levels appear to be the highest peak levels recorded in an otariid and are consistent with this species living at high latitude and having a relatively brief and fixed lactation length compared to many other otariids (e.g., Schulz and Bowen 2004, 2005). Protein levels remained consistent throughout lactation, averaging about 10%, which is typical for most pinniped and carnivore milks.

The finding of a significant difference in milk fat content in October between Bogoslof and St. Paul females (58% vs. 53%) was surprising. In mammals, females are phylogenetically constrained by species in their mammary physiology and general pattern of nutrient transfer to offspring, but particularly in their milk composition. That is, the proximate composition of milk is a species characteristic with little influence by such factors as maternal plane of nutrition or diet (reviewed in Iverson 1993; Oftedal and Iverson 1995). Regulatory mechanisms govern the production of a species' milk regardless of environmental influences (except for disease states). Nevertheless, lactation cannot continue without sufficient metabolic substrates for synthesis, and thus levels of milk *production*, that is milk output, can be greatly influenced by nutrient availability. On a low plane of nutrition, milk output rather than milk composition is altered. However, recent studies have also shown that even within species, there is significant heritability in traits of milk composition, with inherent differences attributed to individual females (Lang et al. 2009). To this end, there are several possible explanations to account for the greater levels of peak milk fat in females at Bogoslof *v* St. Paul. First, although not statistically significant, there was a trend that the same females at Bogoslof had somewhat higher levels of milk fat in July than at St. Paul (47% vs. 45%). Thus, assuming that milk composition is primarily characteristic of individuals in fur seals, it could be that the females we happened to sample at Bogoslof were already predisposed to having higher fat contents at peak lactation. Alternatively, the differences may be related to trip duration in relation to mammary function in otariids, which remains very poorly understood. If St. Paul females are foraging near the limits of their foraging duration because of poor food proximity/availability, there could be a temporary feedback occurring within the gland that results in lower milk fat contents in the females that are gone the longest. Otariids clearly have a very modified feedback system compared to that found in other mammals. Nevertheless, there must come a point where feedback does begin—that is, at some point prolonged absence from suckling may trigger the gland to begin even temporary involution (the process of mammary shut down; Wilde et al. 1999). Unfortunately, there have been no studies of milk composition/mammary gland function in an otariid that may be operating at the extreme limits of its foraging duration. However, a similar effect from extended suckling separation has been demonstrated in the harbor seal *Phoca vitulina*, which although a phocid, adopts a foraging strategy early to mid-way through lactation (Lang et al. 2005). If indeed this were the case, as with harbor seal pups, northern fur seal pups at St. Paul may face a double insult: that is, not only is a long trip duration associated with reduced milk energy transfer (Fig. 39) because of reduced suckling opportunity and long fasting times, but it may also be associated with a reduced milk energy transfer when females do return because of some potential (albeit temporary) lowering of function (Lang et al. 2005).

Pup growth rates and body condition: indices of milk delivery rates

Growth rates of pups at the two rookeries at St. Paul were similar, as they should be since the foraging trip durations of their mothers also were similar, albeit somewhat greater at Reef—pup growth is primarily constrained by nursing frequency.

Male pups tended to be heavier than female pups at both St. Paul and Bogoslof. There were no consistent differences in perinatal growth rates between males and females at either island, or in nursing period growth at St. Paul, whereas nursing period growth of males was higher than that of females at Bogoslof in both years. Male pinniped pups typically do grow faster than female pups (e.g., Guinet et al. 1999), so the observations we made suggest that pup growth is more constrained at St. Paul than at Bogoslof.

This is not to say, however, that pup growth is not constrained at Bogoslof, as suggested by the greater perinatal growth rates of males in 2006 than in 2005. Likewise, perinatal growth at St. Paul varied between years, tending to be greater in 2005 than in 2006, or just the opposite of Bogoslof. The opposing patterns in interannual growth are consistent with other behaviors in shelf and basin ecosystems as described for seabirds n the Pribilofs and Aleutian Islands (Dragoo et al. 2007, Kitaysky et al. 2008). At this time, it is not clear what factors caused this variability in growth rates of pups during the perinatal period.

Differences between islands in growth rates of pups during the extended nursing period (Fig. 35) were consistent with our expectations—female and male pups grew much faster at Bogoslof than at St.

Paul in both 2005 and 2006. Despite the differences between 2005 and 2006 in foraging patterns of females at St. Paul, it was of no significance to the growth of pups, since trip durations did not change.

Although pups of both sexes gained more mass at Bogoslof than at St. Paul in both years, only males at Bogoslof in 2005 were significantly fatter in October (Fig. 36). This suggests that foraging conditions at Bogoslof in 2005 were particularly good.

The large differences in growth rates and mid to late lactation pup body masses were primarily explained by differences in the relative foraging trip durations of their mothers (Fig. 37). In general, the otariid pattern of lactation has been described as energetically expensive (e.g., Iverson et al. 2006). That is, due to the constraints faced by the female of giving birth and suckling their young on land, but needing to feed at sea at such an energetically expensive time, compounded by the inability of females to store sufficient body energy supplies (as blubber) to support lactation while fasting, females must alternate suckling with foraging, resulting in intermittent milk delivery to the pup and resulting in slow mass gain. Although fur seals produce milk that is very high in fat and energy (Fig. 30), every time the mother leaves to forage, the pup must fast, loosing a substantial portion of the energy it just gained from nursing. This yo-yo pattern of energy intake and loss results in extremely slow growth rates comprised more of lean tissue than fat. However, there is clearly a continuum of maternal effects on this pattern, as demonstrated by our results.

On average, female fur seals were similar in mass at parturition at both Bogoslof and St. Paul, as were birth masses, TBL of their pups, and pup growth during the 6-9 d perinatal period, indicating that initial capital stored prior to parturition was not a constraint for females. These similarities were supported by the foraging overlap of females prior to arrival on the rookeries (Figs. 3 and 10). However, during the remainder of the lactation period, females at St. Paul had to forage substantially farther and longer on trips from the rookery than those at Bogoslof. Thus, maternal attendance at Bogoslof was greater, resulting in more frequent milk delivery and far greater pup mass gain/d. Consequently, pups near weaning were heavier, but generally not fatter at Bogoslof than those at St. Paul. It is unknown if the difference in size alone would confer different probabilities for survival for these offspring.

CONCLUSIONS

We hypothesized that conditions in the North Pacific during winter/spring do not differentially affect females breeding at St. Paul compared to Bogoslof, and we predicted that there would be no difference in the physiological condition of females when they arrived at the two islands in July. This prediction might have been incorrect—although there was no obvious difference in wintering locations based on satellite data, in July of both years total body lipid of females was higher at St. Paul than at Bogoslof. This might suggest that there was some variation in foraging conditions on the wintering grounds or along the migration routes of seals from the two islands during later spring (when most tags had fallen off): although FA data and QFASA estimates indicate extensive overlap in their spring diets, the possibility remains that seals encountered different quantities of individual prey species as suggested by the abundance of salmon in spring diets of females at St. Paul in 2006. Alternatively, the difference in body condition in July might reflect somewhat different foraging/energetic strategies in winter/spring that females from the two islands have adopted in anticipation of summer foraging conditions in their respective habitats. That is, females at St. Paul might gain more mass in winter/spring in anticipation of more energetically costly foraging conditions on the continental shelf than females at Bogoslof. Females at Bogoslof must work much less to forage in the basin due to the proximity of prey, thus affording them the energetic luxury of not needing to arrive on the rookery with lipid reserves as great as those that females must arrive with at St. Paul. Whether these differences lead to differential survival or fitness of females at the two islands is not known.

As we predicted, adult female fur seals foraged farther from rookeries at St. Paul than at Bogoslof, their foraging times were longer, and thus milk delivery rates (opportunities) to their pups were lower. Foraging trip distances and durations were likely determined by the distribution and abundance of forage species. Diets of seals differed between St. Paul and Bogoslof, between Reef and Vostochni rookeries at St. Paul, and between shallow and deep foraging females at Reef, yet the energetic value of the various diets, as scaled by the aggregate energy index, did not. In each case, a mixture of both lower and higher fat prey were consumed by seals, resulting in diets with similar energy contents. The longer foraging trips of females at both rookeries on St. Paul led to slower growth rates of pups there, resulting in lower body mass at weaning, than for pups at Bogoslof. Nevertheless, pups at St. Paul were as fat as those at Bogoslof, except for the case of males at Bogoslof in 2005. Thus, as hypothesized, it appears that adult female fur seals at the Pribilofs are not able to raise pups to the age of weaning that are as robust as those at Bogoslof, based on body size alone, but this is not so clear based on the percentage of total body lipid. It remains to be determined in future studies whether this leads to differential survival of pups from the two islands once they depart in fall.

PUBLICATIONS

Most of the physiological work reported here forms the basis of the graduate research of A. Banks, and results will be reported in scientific journals as she prepares her dissertation.

In Whole

None

In Part

Newman, K. and Springer, A.M. 2008. Nocturnal activity by marine mammal eating killer whales at a predation hot spot in the Bering Sea. Marine Mammal Science 24:990-999.

OUTREACH

Web page developed

None

Exhibits/demonstration project developed

None

Conference presentations

Iverson, S.J. and Lang, S.L.C. 2008. Physiological consequences of nutrient provisioning rates for offspring and mothers among capital- and income-breeding pinnipeds. Comparative Nutrition Society 7th Biennial Symposium, August 2008.

Iverson, S.J. and Bowen, W.D. 2008. What top predators can tell us about temperate and Arctic marine ecosystems: grey seals, polar bears and fur seals. Invited plenary talk: Canadian Society of Zoologists Annual Meeting, May 2008.

Iverson, S.J., Ream, R.R., Springer, A.M., Sterling, J., Banks, A., Towel, R., Fadely, B.S. 2008. Consequences of Fur Seal Foraging Strategies (COFFS): Relationships to Opposing Population Trends, Interannual Variability, and Reproductive Performance in the Bering Sea. Alaska Marine Science Symposium, Anchorage, AK, January 2008.

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Iverson, S.J. 2007. Physiological consequences of nutrient provisioning rates for offspring and mothers among income- and capital-breeding marine mammals. Invited talk: Canadian Society of Zoologists Annual Meeting, May 2007.

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Springer, A. Northern fur seal research in the Bering Sea, September 2006, Forum of Alaska Marine Issues series, Marine Advisory Program (UAF), Dutch Harbor, AK.

Springer, A. and Iverson, S. Overview of NPRB seabird (REFER) and fur seal (COFFS) research, July 2005, St. Paul I. community presentation.

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Banks, A. Consequences of fur seal foraging strategies, March 2006, Rasmuson Foundation annual meeting, Anchorage, AK.

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Fadely, B. 2006. 2006. Steller sea lion and northern fur seal research. Presentation at North Pacific Universities Marine Mammal Research Consortium Annual Meeting, Vancouver, B.C., Canada.

Fadely, B. 2006. National Marine Mammal Laboratory Alaska Ecosystems Program: Steller sea lions and northern fur seals. Presentation at NOAA Fisheries Alaska Fisheries Science Center Habitat and Ecological Processes Research Program Planning Meeting, Seattle, WA.

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Presentations in Schools (K-12, undergraduate)

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Sterling, J.T. 2006. Overview of COFFS research on St. Paul and Bogoslof Islands, Presentation to the St. Paul school, St. Paul Island, Alaska, October 2006.

Sterling, J.T. 2008. Northern fur seal research on St. George Island and in the Bering Sea. Presentation to the St. George school, St. George Island, Alaska, August 2008.

Press Articles (Newspaper/Journal/Newsletter)

None

Factsheets Produced

None

Video Produced

In production by NOAA's Ocean Media Center, who needed (and obtained) additional footage during the summer of 2008.

Radio/Television Interviews.

None

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