Biology of the Ringed Seal (*Phoca hispida*) in Alaska, 1960–2010

Final Report to:

National Marine Fisheries Service

Lori Quakenbush
John Citta
and
Justin Crawford

Arctic Marine Mammal Program
Alaska Department of Fish and Game
1300 College Road, Fairbanks, AK 99701

March 2011

EXECUTIVE SUMMARY

The Alaska Department of Fish and Game (ADF&G) has been monitoring the health and status of ringed seals (*Phoca hispida*) in Alaska since 1960 by collecting information and samples from the Alaska Native subsistence harvest. This monitoring program is especially important because agencies are unable to overcome the logistical and sampling constraints necessary to estimate seal abundance in remote, ice covered waters. As such, reliable estimates of ringed seal abundance or population trend are lacking. Retrospective data analyses from this monitoring program allow us to examine how parameters that affect population size and status may vary in time and how current conditions compare with past conditions. Parameters we monitor that are indicative of population health or status include growth rate, body condition, diet, age distribution, sex ratio, age of maturation, and pregnancy rate. Since 2000, ADF&G has also conducted surveys for local knowledge and hunter preferences and analyzed tissue samples for contaminants and disease. All of these collections rely on the cooperation of coastal subsistence communities. Villages that have participated in the sampling program span the region from Hooper Bay in the Bering Sea to Kaktovik in the Beaufort Sea, including islands in the Bering Sea; an area that encompasses most of the range of ringed seals in Alaska.

Local knowledge—Hunter questionnaires are used to evaluate seal availability for harvest and hunter bias in the samples so that we can determine whether changes are due to hunter behavior or related to the seal population itself. Responses to hunter questionnaires from five participating villages did not indicate decreases in ringed seal numbers (availability) at any location. The majority of respondents from all villages reported that ringed seals were found in the same areas as in the past and hunting occurred at the same time as in the past.

Diet—Using stomach contents from 1,555 ringed seals collected between 1960 and 2009, we identified 155 different fish and invertebrate prey of which 99 were common. Using percent frequency of occurrence, fish were consumed significantly more frequently (4.1 times) during the 2000s than during the 1960s and 1970s. Too few data were available for analysis in the 1980s and 1990s. The increase in general fish consumption over time was strongly correlated (Pearson correlation) with changes in the consumption of cod from the Family Gadidae (r = 0.67), suggesting changes in the consumption of Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), and to a lesser extent walleye Pollock (*Theragra chalcogramma*) were likely responsible for variations we observed among all fish. Ringed seals have also consumed significantly more Pacific herring (*Clupea harangus*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and prickleback (Stichaeidae), including eelblenny (*Lumpenus* spp.) in the 2000s than in the 1960s and 1970s ($P < 0.01$).

In general, invertebrates were consumed less frequently in the 2000s (66%) than during the 1960s and 1970s (89%; $P < 0.01$). Too few data were available for analysis in the 1980s and 1990s. Although invertebrates were consumed less frequently in the 2000s, the diversity (D) of invertebrate species consumed recently was somewhat greater (D = 0.26) than during the 1960s and 1970s (D = 0.29), based on Simpson's Diversity Index. The decrease in general invertebrate consumption over time was strongly correlated with crustacean (r = 0.96) and shrimp consumption (r = 0.58), suggesting decreases in their consumption were likely responsible for the decrease observed among all invertebrates.

Contaminants—Liver (n = 35) and kidney (n = 12) tissues from ringed seals collected during 2003 and 2007 were analyzed for concentrations of potentially toxic elements such as arsenic, cadmium, mercury, and lead. Concentrations of these elements in ringed seals in Alaska were lower than for ringed seals in Canada, Greenland, and Russia. Within Alaska, ringed seals had the second lowest concentrations of cadmium and mercury of the four species of ice seals in our studies (only spotted seals were lower) and lead levels were very low in all ringed seals analyzed. Blubber (n = 35) and liver (n = 26) tissues were analyzed for persistent organochlorine compounds and compared to bearded, spotted, and ribbon seals in Alaska, ringed seals had the lowest levels of total CHL (chlordanes), and the second lowest of HCH (hexachlorocyclohexane), DDT (dichlorodiphenyltrichloroethane), and PCB (polychlorinated biphenyls) in our studies. Ringed seals in our study also had lower levels of these compounds than ringed seals in Canada, Norway, and Russia.

Disease—Antibodies for *Brucella*, phocine herpesvirus, phocine and canine distemper, *Leptospira*, and *Toxoplasma*, were detected in ringed seals at levels below or similar to the past. Screening for toxic algae detected domoic and saxitoxin at very low levels in four and six of 34 individual ringed seals, respectively.

Growth rates—We analyzed growth rate using length at age data for 1,610 seals ≥1 years old and 543 pups. Seals were identified as being longer or shorter than expected, given their age, and were then classified by birth year. For seals ≥1 year of age, individuals born after 1976 were larger than expected in 20 of 23 sample years. We fit von Bertalanffy growth curves to age-at-length data. Seals harvested before and after 1976 reached similar asymptotic (maximum) lengths; however, seals harvested after 1976 grew at a faster rate. For example, at age 1, seals born after 1976 were an average of 1.7 cm longer than seals born in 1976 or earlier. This affect was greatest at 6 years of age, when seals born after 1976 were an average of 6.2 cm longer. By age 25, the affect had diminished to an average of only 2.8 cm. Growth rates for pups were lowest in 1961 and 2005. Pups were shorter than expected, given their date of harvest, in six of ten (60%) sample years between 1960 and 1979. In contrast, pups were shorter than expected in only three of nine (33%) sample years between 2000 and 2009. Too few data were available for analysis in the 1980s and 1990s.

Body condition—We examined patterns in sternal blubber thickness using linear models to control for covariates, such as time of year, for 147 pups, 215 subadults, and 189 adults collected between 1971 and 2010. Pups had less blubber than expected in 1971 and 1976; since 2002, blubber thickness of pups has been average. Adults and subadults also had less blubber than expected in 1971, but more than expected in 1978. Since 2002, blubber thickness of adults and subadults has been average.

Age distributions—We analyzed age at harvest for 528 ringed seals harvested in the 1960s, 4,694 in the 1970s, and 727 in the 2000s. Too few data were available for analysis in the 1980s and 1990s. A much greater proportion of pups were identified in the 2000s (56%) than in the 1960s (14%; P <0.01) and 1970s (23%; P <0.01). On average, ringed seals harvested in the 1960s were older than those harvested in the 1970s, and seals harvested in the 1970s were older than those harvested in the 2000s.

Sex ratios—Sex ratios were generally male biased. However, the patterns were not consistent through time or by age class. The shifts in the sex ratios were driven by an increase in the proportion of adult males (ages 5 and older; $P < 0.01$) harvested in the 1960s and 2000s. Too few data were available for analysis in the 1980s and 1990s.

Age at maturity and pregnancy rate—Sexual maturity was determined by examining reproductive tracts of 690 female ringed seals; 47 harvested between 1965 and 1975, 84 in 1976, 196 in 1977, 162 in 1978, 81 between 1979 and 1984, and 120 between 1999 and 2010. The average age of maturity varied significantly in time. Average age of maturity was 5.3 years of age between 1965 and 1975 and increased to 6.4 in 1976 and 6.5 in 1977 ($P < 0.05$). In 1978, the average age of maturity significantly decreased to 5.0 years of age ($P < 0.05$). Age at maturity rose to 5.9 years from 1979 to 1984. Since 1999, however, the average age of maturity has been the lowest observed (3.2 yrs), and is significantly lower than all other years ($P < 0.05$).

Female reproductive tracts were analyzed for percent pregnant at harvest. The decades with the lowest percentage was the 1960s (76.8%) and the 1980s (76.2%). The 1970s had the highest percentage at 89.1% and the 2000s were next highest at 79.5%. Too few data were available for analysis in the 1990s.

Conclusions—These data span five decades and include time periods well before changes in sea ice or other factors attributed to global climate change were present. Our analyses show that ringed seals have been positively and negatively affected by past and current conditions. Currently, however, ringed seals are growing faster, have average blubber thickness, are maturing at the youngest age to date (indicating females are in a positive nutritional state allowing them to grow faster and become mature at an earlier age), and have the second highest pregnancy rate to date. Current environmental conditions have not had a negative effect on any of these factors. In addition, there are more pups in the harvest now. Because age ratios are proportional, a higher proportion of pups in the sample may indicate that adult survival is decreasing or that reproduction is increasing. Based upon other information, however, it is most likely that reproduction has increased. For example, growth rate, age of maturation, pregnancy rate, and blubber thickness are average or better than expected, and hunter responses to questionnaires indicate that ringed seal numbers have not decreased. The high proportion of pups in the harvest also indicates that pups are surviving long enough to be harvested (*i.e.*, pups survive to weaning). Sex ratios are currently male biased; however, this is probably not a concern as it corresponds to a period with high pregnancy rates and increasing numbers of pups. Levels of contaminants in ringed seals harvested in Alaska are lower than levels reported in Canada, Europe, and Russia, and the prevalence of diseases has remained stable.

The results from this long-term program demonstrate its ability to monitor and detect changes in parameters that are useful for monitoring population status when estimating the population size is not possible. Parameters that determine the status of the ringed seal population in the Bering, Chukchi, and Beaufort seas have been more favorable throughout the 2000s than during the 1960s and 1970s.

INTRODUCTION

In Alaska, the ringed seal (*Phoca hispida* or *Pusa hispida*) is one of four species of seals that are associated with sea ice during some portion of the year. The other ice-associated species are the bearded seal (*Erignathus barbatus*), the spotted seal (*Phoca largha*) and the ribbon seal (*Histriophoca fasciata*). Ringed seals have the widest distribution, which includes the Bering, Chukchi, and Beaufort seas near Alaska but they are also found throughout the Arctic, including Canada, Greenland, Svalbard, and Russia, and in freshwater lakes in Europe (Frost and Lowry 1981). Ringed seals feed on a variety of fish and invertebrates in the water column. They are the most ice adapted of the arctic phocids and maintain breathing holes and subniviean lairs in shorefast ice where the adults breed and pups are born in March and April. Pups are weaned after 5–7 weeks (Frost and Lowry 1981). Although ringed seal distribution is strongly correlated with the presence of sea ice all year, during the open-water season, ringed seals occur in ice-free waters of the Beaufort, Chukchi, and Bering seas (Burns *et al*. 1981).

Population estimates for ringed seals are difficult to obtain due to problems related to conducting surveys over large areas of ice-covered waters far from shore and the lack of correction factors for seals under the ice. Aerial surveys of nearshore areas in the 1980s (Frost *et al*. 1988) and 1990s (Moulton *et al*. 2002, Bengtson *et al*. 2005) resulted in several minimum estimates that indicated the population of ringed seals in Alaskan waters is more than one million individuals and the population throughout the Arctic is on the order of several million. There are no current estimates of abundance or trend.

Ringed seals are currently being considered for listing as threatened under the Endangered Species Act due to concerns that climate change may alter sea ice habitat (50 CFR 223 Vol. 75, No. 237:77476–77495). Sea ice is changing in thickness, persistence, and distribution (Rigor and Wallace 2004, Comiso 2006, Serreze *et al.* 2007, Stroeve *et al*. 2008). Evidence also indicates that oceanographic conditions have been changing in the Bering and Chukchi seas (Niebauer 1980, 1983, 1988; Trenberth 1990; Ebbesmeyer *et al.* 1991; Grebmeier *et al.* 2006a; Bluhm and Gradinger 2008), which suggests changes in the ecosystem may be occurring as well.

The Alaska Department of Fish and Game (ADF&G) has collected information and samples from the Alaska Native subsistence harvest of all ice seal species, including ringed seals, for more than 40 years in order to monitor the health and status of the population in the absence of reliable population estimates and trends. Retrospective analyses of these samples and measurements provide evidence of current population status by evaluating changes in population parameters, such as body condition, the growth rate of individuals, diet, age distribution and sex ratio of the harvest, age of maturation, and pregnancy rate. Since 2000, ADF&G has also used surveys to collect information on local knowledge and assessed contaminant levels and disease rates. Participating villages span the region from Hooper Bay in the Bering Sea to Kaktovik in the Beaufort Sea, including islands in the Bering Sea (Fig. 1), thereby encompassing virtually the entire range of ringed seals in Alaska.

In this report we analyze results from ringed seal measurements and samples collected between 1960 and 2010 in order to evaluate how growth rates, body condition, diet, age

distribution, sex ratio, and productivity have changed over time. The purpose of this report is to make unpublished data, collected by ADF&G, available for researchers, managers, subsistence hunters, and others with an interest in the status of ringed seals in Alaska.

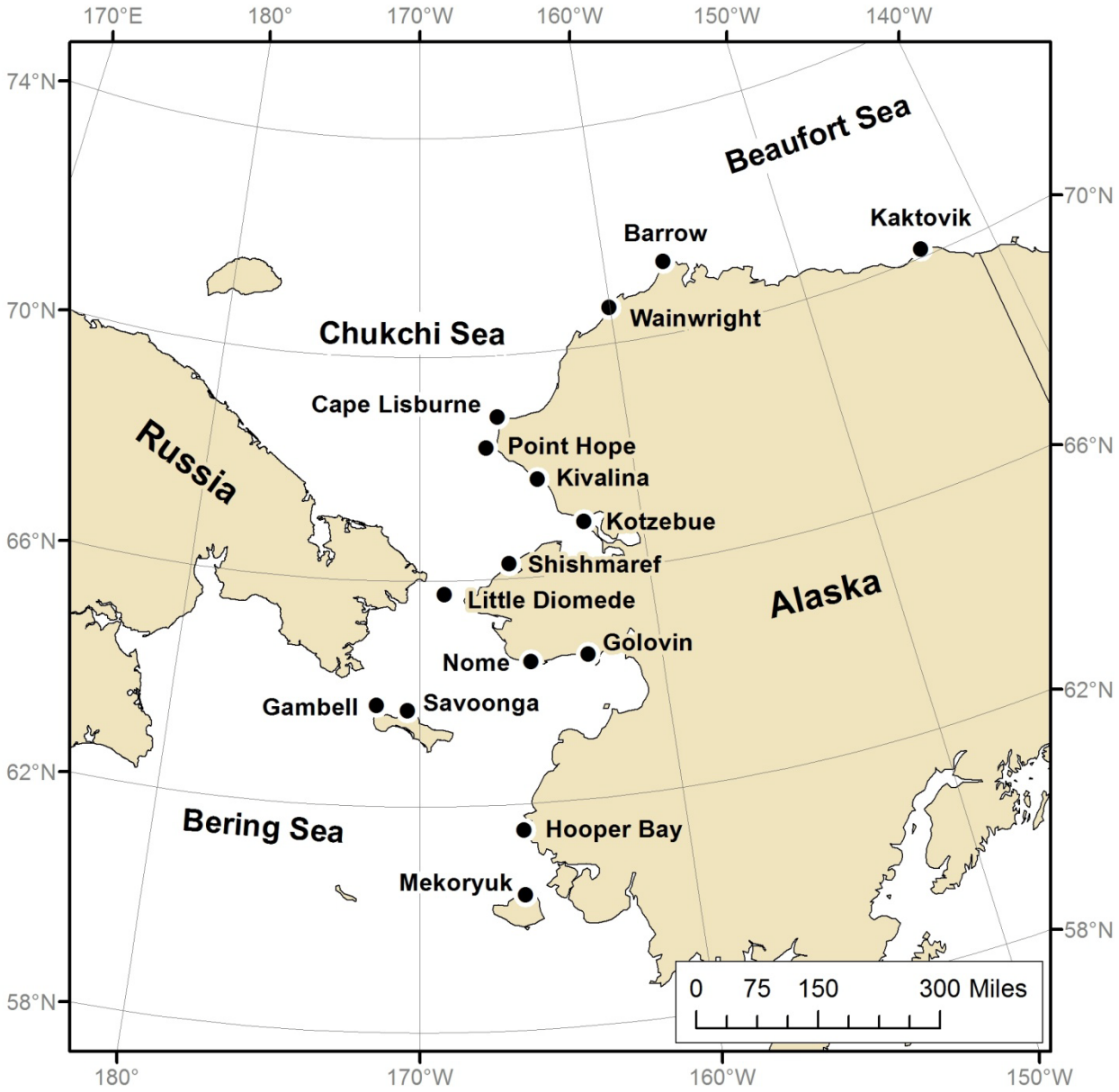

Figure 1. Collection locations.

METHODS

Sampling years

Ringed seals from the subsistence harvest were sampled between 1960 and 2010; however, sampling effort and opportunity were not consistent. The majority of ringed seals sampled were harvested during two time periods, 1960–1979 (1960s and 1970s) and 1998–2010 (2000s; Fig. 2). Ringed seals were also collected on scientific cruises in 1968, 1972, and 1976–1979 (n = 47) and were included in our analyses as appropriate. Age class distributions of ringed seals collected during cruises were significantly different from ringed seals harvested by subsistence hunters during the same decade (P = 0.02), therefore cruise data were included where age distribution was not important. Cruise data were included in analyses of diet, age at maturation, and pregnancy rate, but not in age at harvest. We were able to include data from 429 ringed seals harvested near Point Hope as part of the Cape Thomson, Project Chariot study (1960–1961; Wilimovsky and Wolfe 1966). In addition to the summary information presented by Johnson *et al*. (1966) we acquired copies of original datasheets from that study, which included data collected using methods consistent with ours. For each analysis, the sample size of seals used differed slightly as not all measurements or samples were collected for each seal.

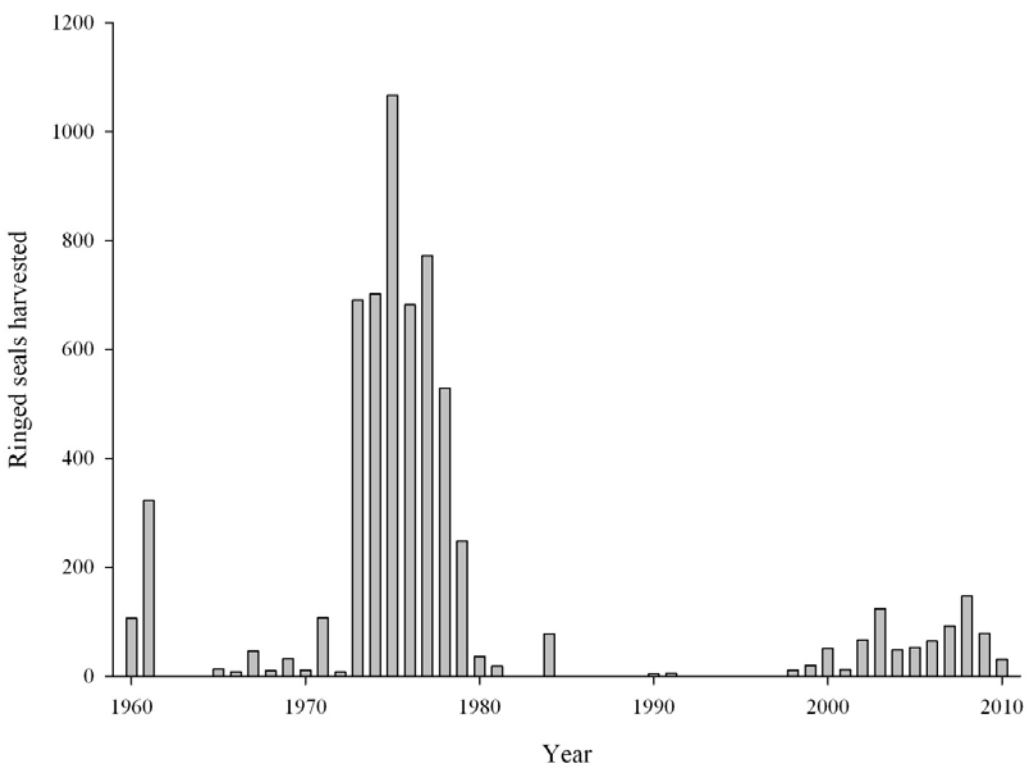

Figure 2. Number of ringed seals sampled in Alaska, by year, for which ages were known, 1960–2010. Sample sizes differed slightly for each analysis, as not all measurements or samples were collected for each seal. Although sample sizes differ by analysis, this figure illustrates the general distribution of samples by year.

Local knowledge

Harvest data require careful interpretation, as hunters may not randomly sample seals throughout their range. For example, changing preferences of hunters may confound the interpretation of seal distribution or age structure. Hunters may also have local knowledge that corroborates or aids the interpretation of data from the biomonitoring program. Hence, discussions with hunters are critical for understanding how to interpret results of data collected from the harvest. In collaboration with the Subsistence Division at ADF&G, we developed a questionnaire to collect information from villages participating in the bio-monitoring project. Questions were designed to determine the importance of the different seal species, whether changes had occurred in seal numbers, seal distribution, seal health, harvest methods, harvest timing, and local conditions. We used the responses to help us understand seal hunting practices and to identify topics that may need further investigation. The results help us understand whether changes observed in our sample collections are due to changes in seal availability or changes in harvest methods or preferences. Results obtained from the questionnaires were not intended to be definitive as they do not represent all or even the majority of the hunters from each community; however, majority responses give us a reasonable indication of hunter activity and preferences.

Collection and handling of specimens

Biological information collected included location, date harvested, date sampled, species, sex, standard length, blubber thickness, and axillary girth. Standard length measured along a straight line from nose to tip of tail with seals on their backs (American Society of Mammalogists 1967). Blubber thickness was measured through a small incision to the sternum midway between the front flippers and axillary girth was measured with a soft tape placed under the foreflippers at the level of the axillae (McLaren 1958). Samples collected included one of the mandibles, the female reproductive tract, the whole stomach, and liver, kidney, blubber, and skin tissue. Samples were frozen in the field and shipped to ADF&G in Fairbanks for processing.

Age determination

For specimens collected in the 1960s and 1970s, ages were determined by counting the number of growth bands or ridges on claws (McLaren 1958, Burns 1969) and by counting cementum layers within decalcified sections of canine teeth (Hewer 1960, Mansfield and Fisher 1960, Burns 1969, Stewart *et al.* 1996). After 2000, all ages were determined by counting cementum layers within sectioned teeth. We refer to ages determined via claws as “claw ages” and ages determined via teeth as “tooth ages.” Ages determined with claws are known to be biased low for older age classes, because claws wear over time; however, McLaren (1958) found that seals could be reliably aged by counting growth bands on claws until seals were at least nine years of age. After age nine, claw wear removes growth bands and only minimum age can be determined. When both claws and teeth were sampled, we relied on tooth ages. Some analyses are expected to be sensitive to the proportion of older seals (*e.g.*, growth rates and age distributions) so we repeated these analyses with and without claw ages to ensure that the inclusion of claw ages did not bias results.

Stomach content analysis

We investigated stomach contents of ringed seals from 1961–2009 to determine if the frequency of prey items has changed over time. Stomachs from ringed seals harvested by Alaskan Natives and during scientific cruises were collected, frozen, and shipped to ADF&G offices in Fairbanks. Stomach were thawed in the laboratory and the contents were rinsed with freshwater through two sieves with mesh sizes of 1.0 mm and 0.5 mm and prey items were indentified to the lowest taxonomic level and weighed to the nearest 0.1 g.

To provide an overall description of ringed seal diet, we first calculated the frequency of occurrence (FO) for each prey taxa, *i*. FO_i is calculated as the number of stomachs that contains prey taxa *i*, divided by the number of stomachs with contents (*i.e.*, we did not include empty stomachs in the calculation). Because FO_i is a proportion, it mediates the effect of large differences in samples size between collection periods (Sinclair *et al*. 2008). To make direct comparisons over time, prey items sampled were grouped by taxa and compared by decade. We used Pearson Correlation Coefficients in SAS (Version 9.2; PROC CORR, SAS Institute Inc., Cary, NC, USA) to examine correlations among annual FO values for all prey items across all time periods and within each time period. Due to biases in digestion time, volume measurements were not considered representative of the true volume of prey consumed and were not analyzed.

In order to determine whether ringed seal diet had changed over time, we used logistic regression (Ramsey and Schafer 2002) to calculate odds ratios and test for differences in the presence (0 = absent, 1 = present) of prey species in stomachs containing prey. Variables of interest included time period (1961–1984 or 1998–2009), sex, region (Bering or Chukchi sea), season (winter: November–May; open water or summer: June–October), and age class (pup: <1, subadult: 1–4 or adult: ≥5). We used odds ratios to assess the strength of an association between an explanatory variable and the presence of a prey item. A prey item that occurred more frequently in the 2000s than during the 1960s and 1970s would have an OR >1.0; this change would be expressed as a multiplicative increase in the odds of occurrence from one time period to another (*e.g.*, a prey item that occurred 2.5 times as often in the 2000s than during the 1960s and 1970s would have an odds ratio of 2.5). Models were fit using SAS software (PROC LOGISTIC) and the best model was selected using a backward elimination procedure that sequentially eliminated statistically non-significant variables (P >0.05) until only statistically significant variables remained (P >0.05).

To examine the occurrence of prey items relative to other prey items, we also calculated their relative occurrence (RO). RO_i is calculated as the number of stomachs that contains a prey taxa *i* (*e.g.*, fish), divided by the cumulative number of fish taxa identified in all ringed seal stomachs. For example, assume five stomachs contained fish and that sculpin were found in all five stomachs and cod, sand lance, and flatfish were each found in only one stomach. Hence, there were eight fish occurrences of four fish taxa. Using RO, cod, sand lance, and flatfish were each one of eight fish occurrences (1/8 or 12.5%) and sculpin represented five of eight fish occurrences (5/8 or 62.5%). Whereas, using FO, cod, sand lance, and flatfish each occurred in 1 of 5 (20%) stomachs and sculpin occurred in 5 of 5 (100%) stomachs. The use of RO allows us to assess the diversity of taxa consumed by ringed seals and does not treat each prey item in isolation. RO was calculated each time period for five fish taxa (rainbow smelt, cod, sculpin,

flatfish, and sand lance) and we evaluated differences in RO ratios by decade using chi-squared statistics using SAS software (PROC FREQ).

We also used the Simpson's Diversity Index (*D*) to further evaluate the diversity of fish and invertebrate taxa identified in ringed seal diets for each time period (Simpson 1949). We calculated *D* in two ways: first using the total count of all fish identified (*i.e.* the sum of all fish identified from each fish group; range: 0–1,150), then using the occurrence of fish (*i.e.* only the presence of a fish taxa) in seal stomachs. The index is calculated as:

$$D = \frac{\sum_{i=1}^{S} n_i (n_i - 1)}{N(N-1)},$$

where:

S is the number of fish (or invertebrate) taxa considered,

n_i is the number of prey taxa i counted in all stomachs (totals) or the number of stomachs that contained prey taxa i (occurrences), and

N is the sum of all individual prey items identified (total) or the cumulative number of prey taxa identified in all stomachs (occurrences).

For invertebrate prey, we only used counts of prey item occurrences due to our concern that digestion processes bias counts of invertebrate prey. We considered index values close to zero to represent more diverse or heterogeneous diets and values near 1 to be more homogeneous.

Contaminants

Tissue preparation—Ringed seal samples collected in 2003–2007 were analyzed for contaminants. Liver and blubber tissue were clean-sampled at ADF&G following protocols established by the National Institute of Standards and Technology (Becker *et al*. 1991) and organochlorine contaminants were quantified by TDI – Brooks International, Inc., B&B Laboratories, Inc., College Station, TX. Subsamples of liver tissue analyzed for organochlorines were analyzed for trace metals by LET laboratories in Columbia, MI. Individual seals were selected for contaminants testing only if liver, kidney, and blubber tissue were available in quantities required for testing after clean sampling each tissue. A tooth was also required so that age could be related to results.

Trace metals and other elements—Liver, kidney, and muscle tissues were analyzed for trace metals. Samples were homogenized with a meat grinder. An aliquot of approximately 100 g was weighed and freeze-dried and then further homogenized using a blender prior to extraction. Percent moisture was calculated by comparing the weight of the wet sample with the weight of the dry samples before a 0.5 g sample was extracted and digested in a microwave wet ash procedure using, H_2O_2, and HCl. Microwave digestion was used for all metals except As and Se.

Samples analyzed for As and Se were digested using magnesium dry ash digestion methods. This method uses methanol, HNO_3, HCl, and heat for digestion. After digestion As and Se were analyzed using Hydride Generation AA. Calibration was done at 0, 1.0, 5.0, and 15.0 ppb and the QC check was 10.0 and a known reference sample. The 5.00 ppb standard was checked every tenth sample and if the value differed by >5% from 5.00 the instrument was recalibrated. If the value was >10% different from 5.00 the last 10 samples were re-analyzed. Pb was analyzed using Graphite Furnace AA. Calibration was done at 0 and 1.0 ppb and then 3–5 standards were run to check the calibration. All other metals were analyzed using ICP on a Perkin-Elmer 4300 DV.

For total mercury, a 10 ml aliquot was removed immediately after dilution, HCl was added and concentrations were determined using Cold Vapor AA. Calibration was done at 0, 1.0, 5.0, and 30.0 ppb and the QC checks were 10.0, 20.0, and a known reference sample. The 5.00 ppb standard was checked every tenth sample and if the value differed by >5% from 5.00 the instrument was recalibrated. If the value was >10% different from 5.00 the last 10 samples were rerun.

For analysis of methyl mercury (MeHg), liver samples were delivered frozen to the University of Alaska Wildlife Toxicology Laboratory in Fairbanks. Samples were freeze-dried before extraction to eliminate water and aid in the extraction process. Extraction of MeHg was initiated by the addition of 10 g 25% KOH in methanol and left overnight at room temperature (25ºC). The extraction procedure was continued over 24 hours with the addition of 15.6 g of methanol. The extraction process was complete when all tissues were solubilized in the KOH in methanol solution. Extracts were analyzed for MeHg using cold vapor atomic fluorescence spectrometry (CVAFS) using the BrooksRand Model III detection system (Seattle, WA) and following procedures modified from Woshner *et al*. (2001a and b), Dehn *et al*. (2005, 2006) and Method 1630 (EPA-821-R-01-020, 2001). In short, 0.05–1.00 mL of the extract was added to 100 mL of ultrapure water, adjusted to pH 4-5 with acetic acid buffer. Methylated forms of mercury in the sample were ethylated with a solution of 1.0% sodium tetraethyl borate ($NaBEt_4$) in 2% KOH in a closed bubbler for 20 minutes. Methyl ethyl mercury was subsequently separated from the solution by purging with nitrogen (N_2) gas onto Tenax® speciation traps. The methyl ethyl mercury was thermally desorbed from the traps and traveled via inert argon gas through a gas chromatography (GC) column heated to 105ºC that further isolated the mercury species of interest. Mercury forms were next heated to 750ºC with a pyrolytic coil that converted all organic mercury to elemental forms (Hg II), which can be detected by CVAFS. Three peaks emerge during the detection run, with the second (representing methyl ethyl mercury forms) used for calculation of MeHg in the sample. The amount of MeHg in each sample was compared to a 6 point calibration curve (calibration coefficient = 0.07; RSD = 14.3%), calculated using Mercury Guru software (version 3.0.48; BrooksRand, Seattle, WA), and converted to ppb wet weight (ww). All samples were performed in duplicate with a coefficient of variation <18%. The detection limit for the sample run was 25 pg and recovery of quality control samples ranged from 88 to 136%.

Organochlorines—Liver and blubber tissues were analyzed for organochlorines (*e.g.*, PCBs and pesticides). Tissue samples were homogenized using a stainless steel blender with titanium blades. Aliquots of approximately 15 g of wet tissue were chemically dried using Hydromatix® and extracted with 100% dichloromethane using a Dionex Accelerated Solvent Extractor (ASE200) operated at 100°C and 2,000 psi. The extracts were reduced to 3 mL by

evaporative solvent reduction. A 100 μL aliquot is removed and weighed to determine lipid weight. The remaining sample portion was purified using alumina/silica gel column chromatography and gel permeation column (GPC)/high performance liquid chromatography (HPLC). After HPLC purification, the eluents were reduced to 0.5 mL and analyzed for PCBs and pesticides by either gas chromatography/mass spectrometry (GC/MS) or gas chromatography/electron capture detector (GC/ECD).

A GC/ECD, coupled to two capillary columns, was used to resolve and detect chlorinated hydrocarbons (polychlorinated biphenyls and pesticides) in tissues. Samples were injected into a temperature-programmed GC/ECD, operated in splitless mode. The capillary columns were DB-5 (30 m x 0.25 mm ID and 25 μm film thickness) and DB-17HT (30 m x 0.25 mm ID and 0.15 μm film thickness). The DB-17HT column is used for analyte confirmation. A data acquisition system continuously acquired and stored all data for quantitation. This method is capable of producing data at parts-per billion and parts-per trillion concentrations. The surrogate spiking solution includes 4,4'-dibromooctaflurobiphenyl (DBOFB), 2,2',4,5',6 pentachlorobiphenyl (PCB 103), and 2,2',3,3',4,5,5'6 octachlorobiphenyl (PCB 198). Surrogate solution (100 μL) is added to all samples and quality control samples prior to extraction. Surrogate compounds are resolved from, but elute in close proximity to, the analytes of interest. The recovery of PCB 103 is used to correct analyte concentrations. Spikes, duplicates, and blanks were analyzed for quality control with each batch of 20 samples or less.

Disease

We collected blood from ringed seals harvested near Point Hope, Kotzebue, Shishmaref, and Little Diomede Island, between 1998 and 2010. We tested serum for antibodies to four diseases known to affect phocids; *Brucella* spp., phocine herpesvirus-1 (PhHV-1), phocine herpesvirus-2 (PhHV-2), and phocine distemper virus (PDV). *Brucella* is known to cause reproductive problems in marine mammals, including placental infections and abortion (*e.g.*, Miller *et al.*1999). Zarnke *et al.* (2006) identified *Brucella* in harbor seals, in Alaska. PhHV-1 usually affects pups and immunocompromised or diseased adults (Zarnke *et al.*1997). In contrast to PhHV-1, PhHV-2 is not known to cause disease in phocids, however its antibodies have been detected in all the phocids within Alaskan waters (Zarnke *et al.*1997, Zarnke *et al.*2006). PDV is a morbillivirus known to cause large die-offs. PDV infected seals exhibit symptoms of respiratory distress and the most common post-mortem finding is pneumonia (Kennedy 1998). In Alaska, PDV has previously been identified in harbor seals (Zarnke *et al.*1997).

Blood collected from harvested seals was allowed to clot before being centrifuged and serum was transferred to sterile cryovials. The cryovials were stored at –20°C for several weeks and then at –40°C for several months before shipping to the Oklahoma Animal Disease Diagnostic Laboratory (OADDL) in Stillwater, OK for testing. For *Brucella*, serum was screened for antibodies by using the standard card agglutination test (SCA). Samples that tested positive were retested using SCA, particle concentration fluorescence immunoassay, *Brucella* buffered antigen standard plate agglutination test, complement fixation test, standard plate test, and Rivanol test (MacMillan 1992). For PDV, PhHV-1, and -2, serum was tested for the

presence of antibodies by using the microplate virus neutralization test (Saliki and Lehenbauer 2001). Threshold titers of ≥8 were considered positive.

In addition to testing blood for antibodies to bacteria, viruses, and parasitic protozoans, we also tested intestinal material for domoic acid and saxitoxin produced by the ingestion of toxic algae, and we tested tongue tissue for the nematode *Trichinella*. Digestion assays using PCR were used to isolate two species of *Trichinella* (*T. nativa* and *T. spiralis*).

Morphometrics

Analysis of growth rates—We examined standard length (cm) of ringed seals between 1961 and 2010 to determine if length varied by seal cohort. For seals ≥1 year of age, we first calculated the average length for each age class. Seals were classified into year classes for ages 1 through 14. Because there are relatively few seals in each year class >15 years of age, we pooled seals older than 14 years of age into a single age class. We subtracted the seal's age from the year of harvest to determine the birth year. For each birth year, we then calculated residual growth as the length of a seal minus the average length of seals given that year age. We then looked for years or strings of years associated with seals that were long (or short), given their age at harvest.

By linking residual growth with the birth year of seals, this approach assumes the length of seals is more dependent upon events that occur early in life than later in life. For example, we are assuming that a year with poor foraging conditions or a short nursing period will affect pups and one year old seals more than eight or nine year old seals. We believe this is reasonable, as ringed seals attain approximately 50% of their body length within approximately the first three years of age (McLaren 1958, Frost and Lowry 1981).

However, for seals that are harvested after their birth year (*i.e.*, non-pups), discrete perturbations in growth will have an integrative effect. For example, consider a series of years characterized by good foraging conditions that were followed by a single poor year. Although, the effect of this poor year on growth would be most discernable in pups born within that year, we would also expect to see decreased growth in seals born prior to that year. As such, a year with poor foraging would cause the largest perturbation in pup growth, followed by smaller perturbations in older seals.

Seals less than one year of age (pups) were analyzed separately. Methods for calculating the residual growth of pups were similar for that of seals ≥1 year of age, except pups were classified by harvest month instead of year age. Hence, when calculating residuals of pup length, we accounted for the month in which the pup was harvested and assumed that all seals were born on 1 April. Although we are standardizing residuals by month, a limitation of this approach is that parturition dates and growth rates are confounded. Hence, differences in the length of pups by year could be due to shifts in the average date of parturition and not changes in the actual growth rate of pups. For example, if parturition occurs late in a given year, this will result in pups that are short given their month age.

Asymptotic growth models—For seals ≥1 year of age, we also described growth with asymptotic growth curves. Age-at-length data was fit with a generalized von Bertalanffy growth curve (*e.g.*, Schnute 1981, McLaren 1993). The model is:

$$L_x = L_\infty \left(1 - e^{-a(x-x_0)}\right)^b,$$

where:

L_x is the standard length of harvested individuals,
L_∞ length at infinite age (*i.e.*, asymptotic length),
a and b are rate parameters that define the rate at which growth approaches asymptotic length,
x is the empirical age of individuals, determined by teeth and/or claws, and
x_0 is an adjustment for where the curve crosses the x-axis. Because of prenatal growth, individuals are not length 0 at birth.

L_x and x are vectors of empirical data, from harvested seals; L_{inf}, a, and b are estimated parameters. McLaren (1993) recommends setting x_0 to a constant, rather than estimating x_0 from the growth curve. We follow McLaren's (1993) recommendation for ringed seals from the Bering and Chukchi seas and use -0.61 years for x_0. We also followed McLaren's recommendation and only included seals one year of age or older. Seals less than one year of age are analyzed elsewhere in this document. To account for the time of year seals were sampled, we assumed that all seals were born on 1 April. Growth of seals is rapid during the first few years of age; by adjusting the seal age to account for a spring birth date, we account for the fact that seals nearing a birthday will generally have a length closer to that of the next year age than the last year age.

We estimated L_{inf}, a, and b within a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulations and Gibbs sampling (Congdon 2003, Gelman *et al*. 2004) in WinBugs (Speigelhalter *et al*. 2003). Bayesian methods use simulations to describe the probability distribution of a parameter, such as L_{inf}, given the data (Gelman *et al*. 2004). Typically, when using MCMC sampling, a set number of initial iterations are discarded (*i.e.*, the 'burn-in') to remove the effect of initial values on the posterior distribution. We used Raftery and Lewis's diagnostic (Raftery and Lewis 1995), as calculated by Package CODA (available at: http://cran.r-project.org/web/packages/coda) in R, to estimate the required 'burn-in' and to determine how many iterations are required to completely describe the posterior distribution. Iterations had high levels of autocorrelation; this results in large number of iterations being necessary to accurately estimate the posterior distribution. In effect, more iterations are needed to 'fill in' the posterior distribution and yield consistent parameter estimates. We ran four simulations (*i.e.*, 'chains') 200,000 iterations each and discarded the first 10,000 iterations of each chain for the 'burn-in'.

We compared four models that represented competing hypotheses for how growth rates of seals may have changed through time or by harvest location. We used the pattern of growth residuals to guide us in specifying time periods for comparison. The residual analysis indicated that seals harvested after 1977 were larger than those harvested prior to 1977 (see RESULTS). Hence, one model estimated growth curves specific to these two time periods (*i.e.*, prior to 1977

and after 1977). McLaren (1993) reported that ringed seals are longer in the Bering Sea (standard length = 137.1 cm) than in the Chukchi Sea (standard length = 120.9 cm). Hence, the second model assumed different growth parameters for the Bering and Chukchi seas. The third model partitioned growth parameters by sex (male or female). McLaren (1993) found that male ringed seals were larger than female ringed seals; however, this relationship was not statistically significant. The final model assumed that all growth parameters were constant. Since 1980, few older female seals have been harvested and this prevented fitting models where sex interacted with time or location. Furthermore, most seals sampled in the Bering Sea were sampled in the 1970s, so we could not fit models where sampling location interacted with sex or time.

Models were compared using Deviance Information Criterion (DIC; Spiegelhalter *et al*. 2002). DIC is equal to the -2 log likelihood of the model, calculated with the posterior means of the model parameters, plus 2 times the effective number of parameters. DIC are used for model selection in a similar fashion as Akaike Information Criterion (Burnham and Anderson 2002); models greater than 4 DIC units from the best approximating model are considered to have little statistical support.

Body condition—We used sternal blubber thickness as an index for body condition because we did not have enough ancillary data (*e.g.*, axillary girth or standard length) to calculate indices of body condition that are more correlated with the true blubber content of a seal (*e.g.*, Parsons 1977, Ryg *et al.* 1990*a*, Gales and Renouf 1994, Arnould 1995). We examined blubber thickness using linear models with covariates to account for known patterns of variability in blubber thickness. We focused on seals sampled in May, June, and July, as these months had samples in most years. Covariates were tested for significance using Type III sums of squares and dropped from the model, one-at-a-time, if significance was $P > 0.05$. For seals $\geq$1 year of age, we examined the effect of month (May, June, or July), age class (subadult or adult), standard length (cm), standard length squared, and the interaction between age class and standard length. Subadults seals were 1 to 4 years of age; adults were 5 years of age and older. Month was included because seals are expected to gain and lose mass seasonally (Ryg *et al*. 1990b). An examination of blubber thickness for all months indicated that blubber thickness increased with standard length in spring and summer, but not in winter. We speculate that the cost of molting and breeding are largely fixed costs. If these costs are fixed, we would expect bigger seals, with longer standard length, to lose less blubber during the breeding season. Because we are comparing the months of May, June, and July, we included standard length as a covariate. To account for possible curvilinear effects, standard length squared was included. Subadults, most of which are not of breeding age, may require less blubber than adults seals during these months. Hence, we also included the interaction of age class and standard length to allow the relationship between standard length and blubber thickness to vary by age class. The residuals of this model were then grouped by time period to identify time periods during when seals had thicker than average blubber given their length, sex, age class, or harvest month.

Similar methods were used for pups (<1 year of age). For pups, we examined the effect of month (May, June, or July) and standard length (cm). The length of pups generally increases by month while average blubber thickness decreases. For pups, we are assuming that length is related to parturition date or age; by controlling for length, we remove variability due to variation in parturition dates. If poor foraging conditions lead to seals that grow more slowly, but

maintain constant blubber thickness, controlling for length may mask changes in blubber thickness. The residuals of this model were then grouped by time period to identify time periods when seals had thicker than average blubber given their length or harvest month.

Population parameters

Age distribution—If harvest is an unbiased sample of the population, we can approximate the age distribution of the population by calculating the proportion of the harvest that falls into age categories. We assigned seals to one of three age categories; pups were <1 year of age, subadults were 1 to 4 years of age, and adults were ≥5 years of age, and then calculated the proportion of the harvest that fell into each age class on an annual basis. Seals collected during research cruises in the 1970s (n = 47) were omitted from the analysis of age distributions because their distribution of age classes included a higher proportion of adults and pups than the subsistence harvest (χ^2 = 7.61; P = 0.02).

Mean age of harvest—We estimated mean age of ringed seals harvested during 1960–2010. To isolate the effect of including pups in our calculations, we estimated mean age both including and excluding pups. If hunters harvested ringed seals randomly with respect to age, differences in mean harvest ages may represent actual changes in the age structure of the ringed seal population. We tested mean age, including and excluding pups, for differences among decades using SAS software (PROC GENMOD). Data were modeled with a gamma error distribution and a log link to account for skewness in the data (Garlich-Miller *et al*. 2006). We considered variables statistically significant at the level of $\alpha = 0.05$.

Sex ratios—We evaluated differences in sex ratios of ringed seals harvested during 1960–2010. Models were fit using PROC LOGISTIC in SAS. Data were modeled with a binomial error distribution and a logit link. Variables of interest included decade (1960s, 1970s, and 2000s), sex, region (Bering and Chukchi seas), season (winter: November–May; open water: June–October), age class (pups: <1; subadults: 1–4; adults ≥5) and all two-way interactions. The best model was selected using a backward elimination procedure. In general, seal hunters do not target a specific sex of ringed seal, therefore the sex of each harvested seal should not be subject to hunter bias, and therefore a change in the sex ratio of ringed seals over time may represent a change in the population structure. However, hunters avoid adult male ringed seals in the spring when they are in rut because of their strong smell (Hardy *et al*. 1991, Ryg *et al*. 1992). While this is a form of hunter bias, we expect this behavior to be consistent over time.

Age at maturity and pregnancy rate—Reproductive tracts collected in the 1960s, 1970s, and 2000s were evaluated for sexual maturity (*i.e.*, whether ovulation had occurred) and reproductive condition (i.*e.*, pregnant, not pregnant) by sectioning ovaries, identifying *corpora lutea* and *corpora albicantia*, and examining the condition of uterine horns (McLaren 1958, Johnson *et al.* 1966, Smith 1973). We defined age at sexual maturity as the age at which the first ovulation occurred (McLaren 1958, Tikhomirov 1966, Smith 1973). Due to the delay between conception and implantation in pinnipeds (Harrison and Kooyman 1968) there are several months where pregnancy cannot be determined by the presence of a fetus. The presence of a *corpora lutea* indicates that the female ovulated but pregnancy cannot be confirmed during this time period. We considered all females with a *corpora lutea* that were harvested from May to

September to be pregnant. Because each ovulation does not result in a pregnancy, the pregnancy rate will be inflated.

We estimated the average age of maturity as the age at which 50% of sampled seals are mature. Average age of maturity was estimated using a generalized linear model with a probit link function and a binomial error distribution (*e.g*., Trippel and Harvey 1991) using PROC PROBIT in SAS (SAS Institute Inc. 2009). Like logistic regression, probit regression is designed to analyze data limited to two outcomes (*i.e*., binomial) and these two methods yield very similar parameter estimates. Probit regression is commonly used to estimate lethal doses for medical or pesticide studies and the average lethal dose (LD50) is analogous to the average age of maturation in our analysis. We chose to work with probit regression as these methods for estimating and comparing lethal doses is well described (*e.g*., Trippel and Harvey 1991, Wheeler *et al*. 2006, Robertson *et al*. 2007). Seals that had not ovulated were classified as immature; seals that had ovulated at least once were classified as mature. The accuracy of estimating age at maturity is largely dependent upon how many seals are sampled within age classes of intermediate maturity status (*e.g*., DeMaster 1978), where the proportion of mature seals is greater than zero, but less than one. Within our sample, intermediate maturity status was generally observed between three and seven years of age. For analysis, we pooled years within which fewer than 20 seals were sampled within this age range (Table 1). As such, seals were pooled into one of six groups; 1965–1975, 1976, 1977, 1978, 1979–1984, and 1999–2010. For each time period, model fit was assessed using a log-likelihood chi-square test. Estimates of the average age of maturation were statistically compared using the ratio test of Robertson *et al*. (2007, pages 27–29) at the level of $P = 0.05$.

RESULTS

Local knowledge

A total of 176 questionnaires were analyzed from five Bering and Chukchi sea villages. Responses did not indicate decreases in ringed seal population abundance at any location except for Hooper Bay where just over half (53%) of the respondents thought there were fewer ringed seals now, 38% thought the population was the same, and 9% thought there were more now (Table 2). The majority of respondents from all villages reported that ringed seals were found in the same locations as in the past. The timing of hunting had not changed for ringed seals in any village. Although the majority of Point Hope, Gambell, and Hooper Bay hunters reported preferences for certain types of ringed seals their preferences were highly variable. Some preferred big seals for more meat and oil, others liked small seals for tender meat, ease of handling, and because they are less likely to smell (referring to adult males in rut). There were also preferences for males because they are bigger and have more meat and oil and preferences for females because they are more tender. The majority of hunters in Shishmaref and Diomede that did not target specific types of ringed seals did not have a preference because all seals are food and taste good. Others said that they catch what they see and that they cannot tell the difference.

Table 1. Sample sizes (*n*) for female ringed seals between 3 and 8 years of age with complete reproductive data. Seals were pooled into 1 of 6 groups for analysis. Years with >20 seals 3–8 years of age were analyzed without pooling.

Year	***n* (all seals)**	***n* (3–8 years of age)**	**Pooling group**
1965	1	1	1965–1975
1966	1	0	1965–1975
1967	7	1	1965–1975
1968	2	1	1965–1975
1969	15	6	1965–1975
1970	1	1	1965–1975
1972	1	1	1965–1975
1973	3	1	1965–1975
1975	16	8	1965–1975
1976	84	26	1976
1977	196	49	1977
1978	162	38	1978
1979	35	10	1979–1984
1980	15	0	1979–1984
1981	7	0	1979–1984
1984	24	11	1979–1984
1999	2	1	1999–2010
2000	13	2	1999–2010
2002	5	1	1999–2010
2003	18	2	1999–2010
2004	4	0	1999–2010
2005	7	0	1999–2010
2006	9	0	1999–2010
2007	28	3	1999–2010
2008	22	1	1999–2010
2009	5	1	1999–2010
2010	7	2	1999–2010
Total	**690**	**167**	

Table 2. Summary of selected local knowledge questions regarding seal harvest. Numbers are the percentage of respondents answering in the affirmative to selected questions. Responses of "don't know" are not included in this table.

		Location				
		Point Hope	**Diomede**	**Shishmaref**	**Gambell**	**Hooper Bay**
Species	**Question**	*n* = 16	*n* = 29	*n* = 14	*n* = 44	*n* = 73
Ringed	Have numbers remained the same?	31	55	43	63	38
	Have numbers decreased?	31	40	36	22	53
	Have numbers increased?	13	5	7	14	9
	Are seals found in the same areas?	73	87	85	84	60
	Does the hunt occur at the same time?	71	89	71	88	79
	Do you try for certain types of this seal?	86	44	36	56	61
	What is the hunting season?	Jan–Aug	Sept–Jun	Jun; Sept–Nov	Aug–May	Sept–May
Bearded	Have numbers remained the same?	56	70	64	75	60
	Have numbers decreased?	19	15	7	6	29
	Have numbers increased?	13	15	21	19	11
	Are seals found in the same areas?	100	74	92	83	56
	Does the hunt occur at the same time?	100	97	71	98	84
	Do you try for certain types of this seal?	56	42	50	43	70
	What is the hunting season?	May–Jun	Sept–Jun	May–Jun	Year round	Aug–Jun
Spotted	Have numbers remained the same?	56	65	36	62	46
	Have numbers decreased?	13	26	36	26	24
	Have numbers increased?	0	9	21	12	30
	Are seals found in the same areas?	100	92	85	75	69
	Does the hunt occur at the same time?	94	100	100	98	83
	Do you try for certain types of this seal?	44	26	31	55	62
	What is the hunting season?	May–Aug	Year round	Jun; Sept–Nov	Year round	Year round
Ribbon	Have numbers remained the same?	15	50	40	67	25
	Have numbers decreased?	23	33	0	21	70
	Have numbers increased?	0	17	0	13	5
	Are seals found in the same areas?	55	82	43	77	44
	Does the hunt occur at the same time?	89	95	80	83	81
	Do you try for certain types of this seal?	0	22	33	52	53
	What is the hunting season?	May–Jun	Apr–Jun; Oct	May–Jun; Oct–Nov	May–Jun; Nov	Year round

Diet

In the 1960s, 1970s, and early 1980s, stomachs from 1,300 ringed seals were examined and 1,080 (83%) contained prey items (Fig. 3); 247 were from the Bering Sea and 834 were from the Chukchi Sea. Samples from the Bering Sea came from eight villages (219) and four research cruises (28). Samples from the Chukchi Sea were from ten villages, the most were from Shishmaref (449). Three stomachs were collected from Kivalina as part of the Project Chariot investigation (1960–1961) near Cape Thompson (Wilimovsky and Wolfe 1966). Stomachs were collected during the spring-summer (739) and fall (342) subsistence harvests. Between 1998 and 2009, stomachs from 589 ringed seals were examined and 475 (81%) contained prey items (Fig. 3); 266 were from five villages in the Bering Sea and 209 were from four villages in the Chukchi Sea. Stomachs were collected during the spring-summer (99) and fall (376) subsistence harvests. No ringed seal stomachs with contents were collected in 1962–1968, 1972, 1973, 1982, 1983 and 1985–1997 (Fig. 3).

We identified 155 different prey taxa in 1,556 ringed seals sampled. The most common prey taxa and their frequency of occurrence (%FO) are presented in Table 3. There was no significant difference in occurrence of prey in the diets of males and females; therefore, sexes were pooled for all diet analyses.

Fishes— Fish prey were commonly consumed by ringed seals within both time periods (annual %FO range: 72–100%; Fig. 4), but more frequently during the 2000s (93%) than during the 1960s and 1970s (82%; Table 3). Specifically, ringed seals were 4.1 times more likely to consume fish in the 2000s than during the 1960s and 1970s. We were able to identify significant increases in occurrence for fifteen fish taxa (*i.e.*, genera or species; Table 3). Fish were also consumed more frequently in the Chukchi Sea than the Bering Sea and in winter than summer (Table 4). The average number of fish consumed per ringed seal was also higher in the 2000s ($\bar{x}$ = 42.6; *SE* = 3.2; range: 0–619) than in the 1960s and 1970s ($\bar{x}$ = 32.8; *SE* = 2.7; range: 0–1,550; U = 181422.50; $P < 0.01$). Changes in general fish consumption over time were strongly correlated with changes in consumption of species from the Family Gadidae (r = 0.67), suggesting changes in cod consumption were likely responsible for differences we observed among all fish.

Currently ringed seals are consuming a greater diversity of fish than they did in the 1960s and 1970s. In the 1960s and 1970s, the diet was dominated by three species or taxa: Arctic cod (*Boreogadus saida*; 42%), saffron cod (*Eleginus glacialis*; 37%), and sculpin spp. (Cottidae; 13%). Whereas, in the 2000s, there are five dominant species or taxa; the original three: Arctic cod (61%), saffron cod (46%), and sculpin (15%); plus rainbow smelt (*Osmerus mordax*; 27%) and walleye pollock (*Theragra chalcogramma*; 15%).

Of the dominant taxa in the 1960s, the occurrence of Arctic cod increased from 39 to 59% in the Bering Sea and from 43 to 63% in the Chukchi Sea. In contrast, the occurrence of saffron cod has remained stable in the Bering Sea (35 and 31%), but increased from 38 to 65% in the Chukchi Sea. Walleye pollock was rarely consumed (<1%) in both the Bering and Chukchi seas, but has become commonly consumed in the Bering Sea (26%; Table 4). Sculpin from the Family Cottidae, were identified in <20% of stomachs from both time periods (Table 4; Fig. 4). Of sculpin, the genus *Myoxocephalus* was consumed most frequently; the occurrence of

Myoxocephalus increased in the Bering Sea ($P < 0.01$), but remained constant in the Chukchi Sea ($P = 0.68$; Table 4).

Of the two fish taxa that became frequently consumed in the 2000s, rainbow smelt is being consumed more frequently in the Chukchi Sea than the Bering (Table 4), and more frequently in the winter than summer (Table 4). In contrast, walleye pollock, the other new taxa, is being consumed more frequently in the Bering Sea than the Chukchi Sea (Table 4).

In general, fish were found more commonly in the stomachs of adults and subadults than pups. Across all taxa of fish, adults (88%; $P = 0.01$) and subadults (85%; $P < 0.01$) were ~2.4 times more likely to consume fish than pups (77%); however here was no evidence that consumption of fish varied between adults and subadults ($P = 0.17$). This pattern was generally true for cod, sculpin, and flatfish. Interestingly, this pattern was different for rainbow smelt; subadults consumed more rainbow smelt (15%) than pups (10%; $P < 0.01$), which consumed more than adults (8%; $P < 0.01$).

In addition to examining %FO, we investigated changes in diet by calculating Simpson's Diversity Indexes for the total number of fish identified (*i.e.*, the sum of individual fish prey items) and also for the occurrence of taxa (*i.e.*, the cumulative sum of fish taxa identified in all stomachs). We also calculated the relative occurrence (RO), defined as the number of stomachs that contains a prey category *i* (*e.g.*, fish), divided by the cumulative number of fish taxa identified in all ringed seal stomachs (See METHODS). Simpson's Diversity Index showed that ringed seals consumed a greater diversity of fish species (total counts: $D = 0.78$; occurrences: $D = 0.31$) in the 2000s than during the 1960s and 1970s (total counts: $D = 0.89$; occurrences: $D = 0.48$). The diet of ringed seals was dominated by five fish taxa throughout both time periods (Fig. 5). The RO of rainbow smelt increased from 3% in the 1960s and 1970s to approximately 19% in the 2000s (Fig. 6). Although cod and sculpin were consumed more frequently during the 2000s than the 1960s and 1970s (Table 3), their relative occurrence decreased proportionally in response to the addition of rainbow smelt (walleye pollock is part of the cod proportion).

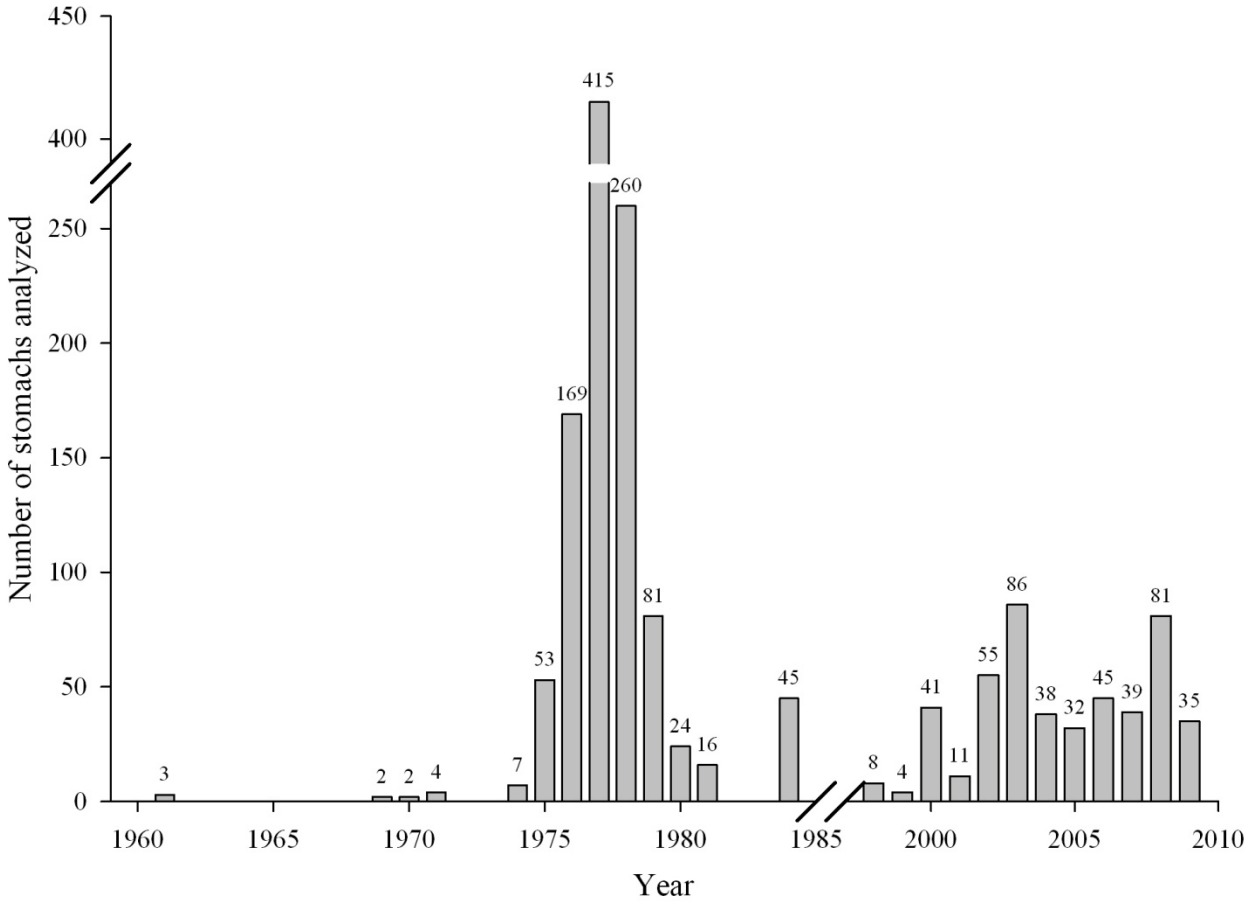

Figure 3. Number of stomachs from ringed seals harvested in Alaska, 1961–1984 and 1998–2009 that contained prey. No stomachs were analyzed in 1962–1968, 1972, 1973, 1982, and 1983.

Table 3. Percent frequency of occurrence (%FO$_i$) of prey identified from ringed seal stomachs collected in Alaska, 1961–2009. Highlighted rows are discussed in text.

	Time period	**1961–1984**	**1998–2009**
Prey (*i*)	***n***	1,081	475
All Fish *		81.59	93.05
Pacific herring (*Clupea pallasi*) *		3.70	5.68
Smelt (*Osmerus mordax*) *		2.41	26.74
Capelin (*Mallotus villosus*) *		0.65	7.37
Eelpout (*Lycodes* spp.)		1.02	1.05
Pacific sand lance (*Ammodytes hexapterus*) *		5.09	9.47
All Cod (Gadidae) *		66.60	83.58
Arctic cod (*Boreogadus saida*) *		42.09	60.63
Saffron cod (*Eleginus gracilis*) *		37.00	46.11
Walleye pollock (*Theragra chalcogramma*) *		0.09	14.53
All Sculpin (Cottidae) *		12.67	14.95
Gymnocanthus spp. *		1.20	5.26
Arctic staghorn sculpin (*Gymnocanthus tricuspis*) *		0.00	5.26
Myoxocephalus spp. *		3.70	7.79
All Snailfish (Liparidae)		1.39	1.68
All Pricklebacks (Stichaeidae) *		1.11	4.00
Eelblenny (*Lumpenus* spp.) *		0.74	3.16
Slender eelblenny (*Lumpenus fabricii*)		0.09	1.89
Ninespine stickleback (*Pungitius pungitius*)		1.30	1.68
All Flatfish (Pleuronectidae) *		4.35	6.32
Yellowfin sole (*Limanda aspera*) *		0.09	2.74
Longhead dab (*Limanda proboscidea*)		0.00	1.47
Arctic flounder (*Pleuronectes glacialis*)		1.48	0.00
Alaska plaice (*Pleuronectes quadrituberculatus*)		0.37	0.84
All Invertebrates *		88.62	66.11
Polychaeta		2.31	1.89
All Mollusca *		1.02	8.42
Gastropoda *		0.37	2.53
Bivalvia *		0.56	6.74
Cephalopoda *		0.37	1.89
Squid		0.28	0.21
Octopus (Octopodia)		0.09	0.84
All Crustacean *		88.44	62.53
All Copepods		3.15	0.00
All Mysidacea *		47.09	12.63
Mysidae *		46.62	12.21
Mysis spp. *		20.35	1.26
Mysis littoralis *		11.84	0.00
Neomysis spp. *		32.93	10.32
Neomysis rayii *		32.38	9.26
Diastylis spp. (Cumacean)		0.46	0.42
All Isopoda		4.63	2.53
Saduria entomon		4.26	1.26
All Amphipoda *		54.49	30.95
Ampeliscidae *		9.62	5.89
Ampelisca spp. *		8.51	2.74
Ampelisca macrocephalus		2.13	0.00
Bybils spp.		1.20	1.47
Atylus spp.		2.04	0.84
Eusirus spp.		1.20	0.00

Rhacotropis spp.	2.31	0.00
Melitidae *	0.56	2.53
Melita spp.	0.56	2.11
Gammaridae *	21.92	7.79
Gammarus spp. *	18.32	4.63
Gammarus wilkitzkii *	13.88	0.00
Gammaracanthus loricatus	1.39	0.00
Weyprechtia spp. *	2.13	0.21
Weyprechtia pinguis	1.76	0.00
Ischyroceridae	0.65	0.21
Anonyx spp. *	15.26	6.95
Anonyx nugax *	15.17	2.32
Onisimus spp. *	7.49	2.11
Oedicerotidae *	5.27	0.42
Acanthostepheia spp. *	5.18	0.21
Acanthostepheia behringiensis	1.39	0.00
Hyperiidae *	25.44	10.53
Parathemisto libellula *	23.22	10.53
All Euphausiidae *	9.07	8.42
Thysanoessa spp. *	7.77	3.79
Thysanoessa raschi	2.50	2.53
All Decapods *	66.51	45.05
All Shrimp *	66.42	44.42
Hippolytidae *	30.62	7.16
Spirontocaris spp.	1.57	0.21
Lebbeus spp.	1.30	0.42
Eualus spp. *	29.42	4.21
Eualus fabricii	2.87	0.00
Eualus gaimardi *	25.44	2.95
Pandalidae *	28.03	13.26
Pandalus spp. *	27.66	10.53
Pandalus goniurus *	25.53	6.74
Pandalus hypsinotus	2.31	0.21
Crangonidae *	37.65	18.95
Crangon spp. *	24.98	10.32
Crangon dalli	1.39	0.21
Crangon alaskensis *	20.81	7.37
Sclerocrangon boreas	2.68	0.21
Argis spp. *	11.01	2.53
Argis lar *	9.53	1.47
Sabinea septemcarinata	1.30	0.00
All Crab *	0.74	2.95
Paguridae	0.19	0.42
Brachyura	0.56	0.84
Hyas lyratus	0.28	0.42
Chionoecetes opilio	0.09	0.63
All Echiuridae *	7.96	7.16
All Echinodermata	0.37	0.21
All Urochordata	0.19	0.42

* Significant difference in the occurrence of the prey item among time periods ($P < 0.05$).

Table 4. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of fish prey identified from ringed seal stomachs collected in Alaska, 1961–2009. Highlighted rows are discussed in text.

	Region				Season			
	Bering		Chukchi		Spring-Summer		Fall-Winter	
Time period	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**
Prey (*i*) ***n***	247	266	834	209	739	99	342	376
All Fish [ab]	74.49	91.35	83.69	95.22	77.54	87.88	90.35	94.40
Pacific herring (*Clupea pallasi*) [a]	1.62	1.13	4.32	11.48	3.11	2.02	4.97	6.67
Smelt (*Osmerus mordax*) [abc]	5.26	19.55	1.56	35.89	0.95	12.12	5.56	30.67
Capelin (*Mallotus villosus*) [bd]	0.40	6.39	0.72	8.61	0.81	2.02	0.29	8.80
Eelpout (*Lycodes* spp.)	-	1.88	1.32	-	0.54	-	2.05	1.33
Pacific sand lance (*Ammodytes hexapterus*) [ac]	3.24	12.03	5.64	6.22	4.33	9.09	6.73	9.60
All Cod (Gadidae) [b]	60.32	83.08	68.47	84.21	62.92	75.76	74.56	85.60
Arctic cod (*Boreogadus saida*) [bd]	38.46	58.65	43.17	63.16	30.18	58.59	67.84	61.07
Saffron cod (*Eleginus glacialis*) [abc]	35.22	31.20	37.53	65.07	43.30	25.25	23.39	51.73
Walleye pollock (*Theragra chalcogramma*) [a]	0.40	25.56	-	0.48	0.14	18.18	-	13.60
All Sculpin (Cottidae) [abd]	16.19	19.55	11.63	9.09	9.20	17.17	20.18	14.40
Gymnocanthus spp. [a]	2.43	8.65	0.84	0.96	0.81	6.06	2.05	5.07
Arctic staghorn sculpin (*Gymnocanthus tricuspis*) [a]	-	8.65	-	0.96	-	6.06	-	5.07
Myoxocephalus spp. [ac]	3.24	10.90	3.84	3.83	3.92	9.09	3.22	7.47
All Snailfish (Liparidae) [b]	0.81	3.01	1.56	-	0.41	1.01	3.51	1.87
All Pricklebacks (Stichaeidae)	1.21	5.64	1.08	1.91	1.08	3.03	1.17	4.27
Eelblenny (*Lumpenus* spp.)	0.40	4.14	0.84	1.91	0.68	3.03	0.88	3.20
Slender eelblenny (*Lumpenus fabricii*)	-	2.63	0.12	0.96	0.14	3.03	-	1.60
Ninespine stickleback (*Pungitius pungitius*) [a]	4.05	2.63	0.48	0.48	1.08	1.01	1.75	1.87
All Flatfish (Pleuronectidae) [abd]	0.40	4.89	5.52	8.13	6.09	4.04	0.58	6.93
Yellowfin sole (*Limanda aspera*) [a]	-	0.75	0.12	5.26	0.14	1.01	-	3.20
Longhead dab (*Limanda proboscidea*)	-	1.13	-	1.91	-	1.01	-	1.60
Arctic flounder (*Pleuronectes glacialis*)	-	-	1.92	-	2.17	-	-	-
Alaska plaice (*Pleuronectes quadrituberculatus*)	-	1.50	0.48	-	0.54	1.01	-	0.80

[a] Significant difference in the occurrence of the prey item between regions ($P < 0.05$).
[b] Significant difference in the occurrence of the prey item between seasons ($P < 0.05$).
[c] Significant difference in the occurrence of the prey item between regions and time periods: Interaction Time period × Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and time periods: Interaction Time period × Season ($P < 0.05$).

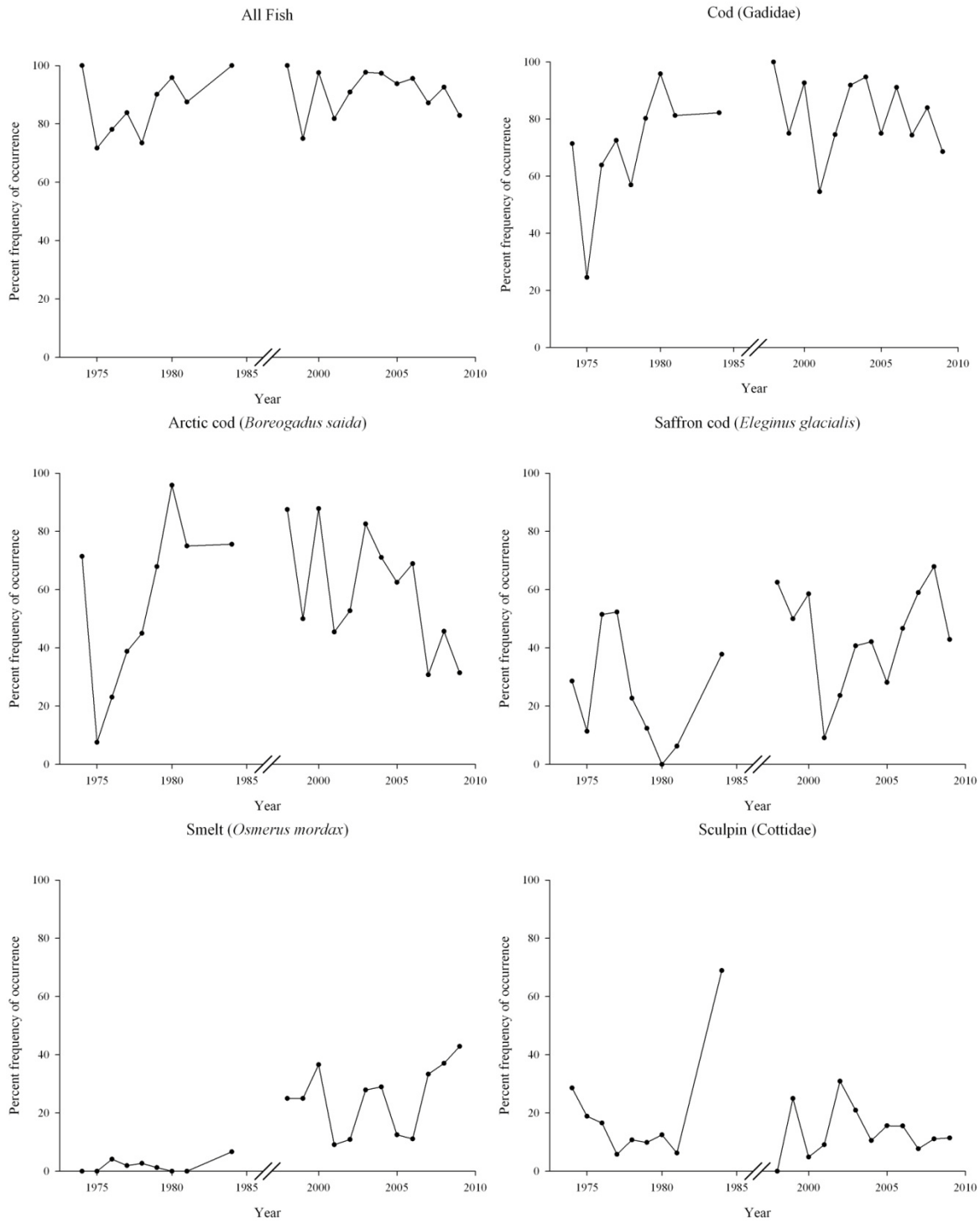

Figure 4. Yearly patterns in percent frequency of occurrence (%FO_i) of primary fish prey identified from stomachs of ringed seals harvested in Alaska, 1974–1984 and 1998–2009. Stomachs sampled before 1974 were omitted because sample sizes were small (n <5). No stomachs were analyzed in 1982 and 1983.

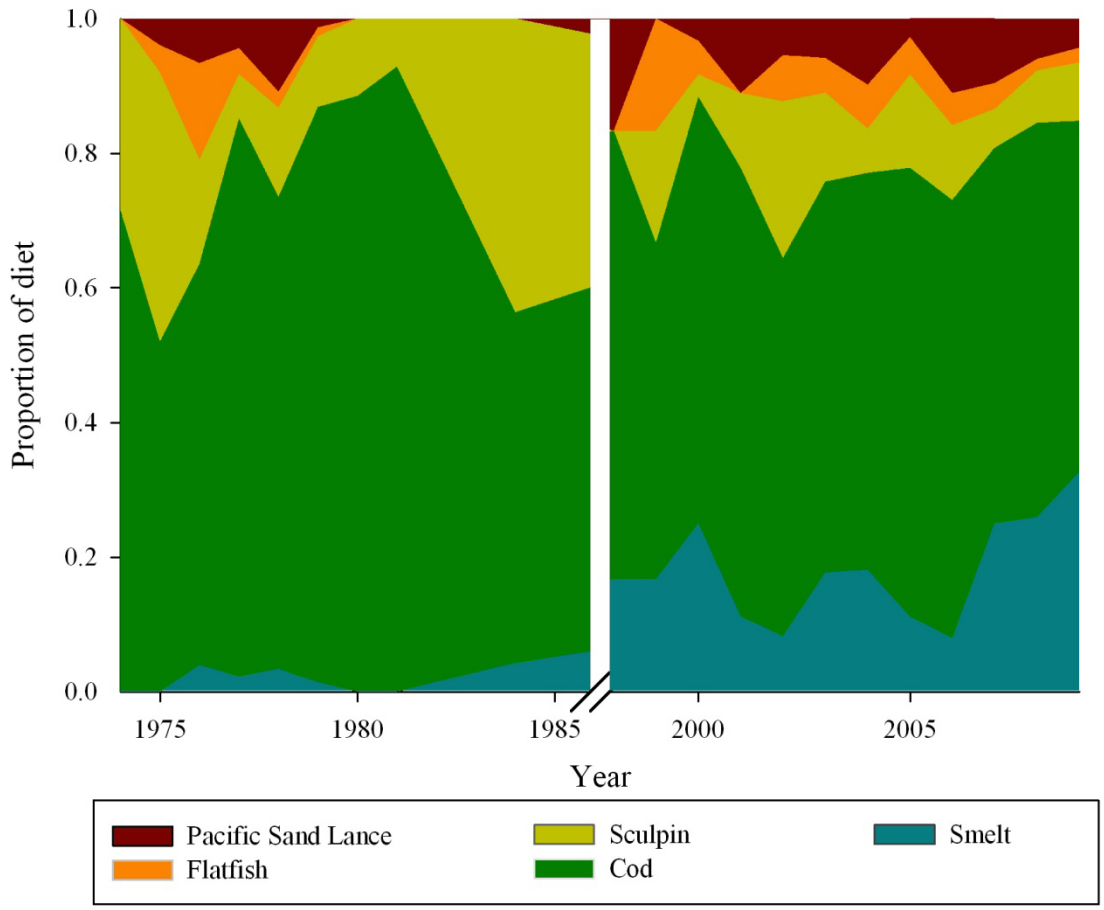

Figure 5. Yearly patterns in relative occurrence (RO) of fish prey identified in the stomachs of ringed seals harvested in Alaska, 1974–1984 and 1998–2009. Sample sizes of seals sampled prior to 1974 were too small to include with this comparison. No stomachs were analyzed in 1982 and 1983.

Invertebrates—Invertebrate prey items were commonly consumed by ringed seals within both time periods (annual %FO range: 49–100%; Fig. 6.). However, we found more stomachs with invertebrates in the 1960s and 1970s (89%) than during the 2000s (66%; Table 3). We identified a total of 103 invertebrate taxa. Of 56 commonly identified taxa, 30 significantly declined between time periods (Table 3). Within the early time period, all invertebrates were consumed more frequently in the Chukchi Sea than in the Bering Sea; however, the opposite was true for the later period (Table 5). However, there were differences among specific invertebrate groups (Tables 6 and 7).

Prey items predominantly came from three Orders of the Class Crustacea: Mysidacea, Amphipoda, and Decapoda. Decapods were the most dominant class accounting for 66% in the early time period and 44% recently. Predominant decapod prey items came from three families of shrimp (Hippolytidae, Pandalidae, and Crangonidae). Within Hippolytidae, the genus *Eualus* was most common, declining from 29 to 4% between time periods (Table 3). For Pandalidae, the genus Pandalus was most common and declined from 28 to 11%. For Crangonidae, Crangon

and Argis were the dominant genera, declining from 25 to 10% and 11 to 2%, respectively. All Shrimp were consumed more frequently in the Bering Sea than the Chukchi Sea during both time periods (Table 7). Changes in shrimp consumption over time were correlated with changes in consumption of shrimp from the Family Crangonidae (r = 0.56).

Amphipods were consumed by 54% of ringed seals in the early time period and 31% recently (Table 3; annual %FO range: 6–100%; Fig. 6). Predominant amphipod prey items came from the taxonomic suborders of Ampeliscidae, Gammaridae and Hyperiidae (Table 3). Within Ampeliscidae two genera, *Ampelisca* and *Bybils*, were represented. Occurrence in *Ampelisca* declined from 9 to 3%, while the occurrence of *Bybilis* remained low in both time periods (1 and 2%). Within Gammaridae two genera, *Gammarus* and *Anonyx*, were identified. *Gammarus* declined from 18 to 5% and *Anonyx* declined from 15 to 7%. Seals consumed amphipods of the genus *Gammarus* more frequently in the Chukchi Sea than in the Bering Sea during the early time period (Table 6), but amphipods of the genus *Anonyx* were consumed more frequently in the Bering Sea. The only species identified within the suborder Hyperiidae was *Parathemisto libellula*; this species declined from 23 to 10% (Table 3); however, *P. libellua* did not decline as much in the Chukchi Sea (15%) as in the Bering Sea (7%; Table 6). During both periods it was consumed more in the winter than summer. Overall amphipod consumption was correlated with changes in *Parathemisto libellula* consumption (r = 0.52).

Mysids were commonly identified in ringed seal stomachs (annual %FO range: 0–100%; Fig. 6). Two genera, *Mysis* and *Neomysis*, were identified. Mysidacea were consumed more frequently in the 1960s and 1970s (47%) than during the 2000s (13%; Table 3). Seals consumed mysids more frequently in the Chukchi Sea than in the Bering Sea and more in summer than winter (Table 5).

Consumption of crustaceans varied by seal age class. Adult and subadult seals consumed crustaceans ~2 times more frequently than pups, but there was no evidence that consumption of crustaceans varied between adults and subadults (P = 0.10). Changes in the occurrences of crustaceans over time were correlated with changes in shrimp consumption (r = 0.60) and changes in general invertebrate consumption over time were strongly correlated with changes in crustaceans (r = 0.96).

Although mollusks were infrequently consumed by ringed seals (Table 3), they were one of the few invertebrate prey items consumed less frequently in the 1960s and 1970s (1%) than during the 2000s (8%). Changes in mollusk consumption over time were correlated with changes in gastropod (r = 0.55) and bivalve consumption (r = 0.86). Ringed seals consumed more clams in the 2000s (7%) than during the 1960s and 1970s (<1%; Table 3). Clams were also consumed more frequently in the Bering Sea than in the Chukchi Sea (Table 5).

In addition to examining %FO, we investigated changes in diet by calculating Simpson's Diversity Indexes for the occurrence of taxa (*i.e.*, the cumulative sum of invertebrate taxa identified in all stomachs; See METHODS). Although invertebrates were consumed less frequently in the 2000s, ringed seals consumed a similar diversity of invertebrate species in the 2000s (D = 0.26) than during the 1960s and 1970s (D = 0.29) based on Simpson's Diversity Index for occurrences of prey items.

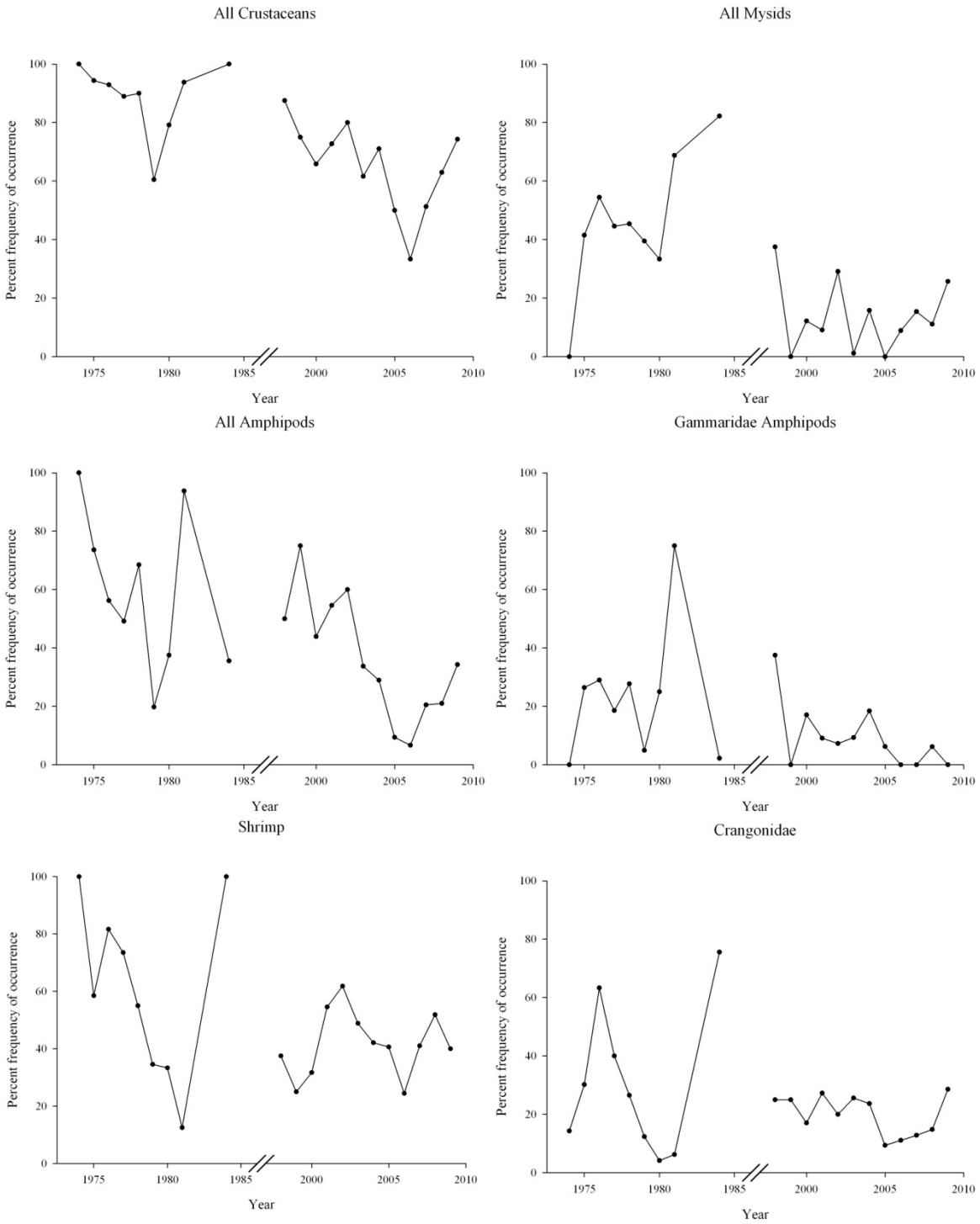

Figure 6. Yearly patterns in percent frequency of occurrence (%FO_i) of primary invertebrate prey identified from stomachs of ringed seals harvested in Alaska, 1974–2009. Stomachs sampled before 1974 were omitted because sample sizes were small (n < 5). No stomachs were analyzed in 1982 and 1983.

Table 5. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of invertebrate (polychaetes, mollusks, cephalopods, copepods, and mysids) prey identified from ringed seal stomachs collected in Alaska, 1961–2009. Highlighted rows are discussed in text.

		Region				Season			
		Bering		Chukchi		Spring-Summer		Fall-Winter	
	Time period	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**
Prey (*i*)	***n***	247	266	834	209	739	99	342	376
All Invertebrates [abcd]		84.62	71.05	89.81	59.81	91.47	67.68	82.46	65.87
Polychaeta		1.21	3.38	2.64	-	2.57	5.05	1.75	1.07
All Mollusca [a]		1.21	13.16	0.96	2.39	0.95	16.16	1.17	6.40
Gastropoda [a]		0.40	4.51	0.36	-	0.14	5.05	0.88	1.87
Bivalvia [a]		0.81	10.15	0.48	2.39	0.68	13.13	0.29	5.07
Cephalopoda [bd]		-	3.38	0.48	-	0.14	5.05	0.88	1.07
Squid		-	0.38	0.36	-	0.14	1.01	0.58	-
Octopus (Octopodia)		-	1.50	0.12	-	-	4.04	0.29	-
All Crustacean [abcd]		84.21	65.79	89.69	58.37	91.34	61.62	82.16	62.93
All Copepods		4.05	-	2.88	-	2.57	-	4.39	-
All Mysidacea [ab]		40.89	10.90	48.92	14.83	51.15	13.13	38.30	12.53
Mysidae [ab]		40.08	10.90	48.56	13.88	50.61	13.13	38.01	12.00
Mysis spp. [b]		21.05	1.88	20.14	0.48	22.19	3.03	16.37	0.80
Mysis littoralis [b]		14.98	-	10.91	-	15.56	-	3.80	-
Neomysis spp. [ab]		23.48	8.27	35.73	12.92	37.35	10.10	23.39	10.40
Neomysis rayii [ab]		22.67	7.52	35.25	11.48	36.67	9.09	23.10	9.33
Diastylis spp. (Cumacean)		-	0.75	0.60	-	0.68	2.02	-	-
All Isopoda [ab]		-	4.14	6.00	0.48	6.36	7.07	0.88	1.33
Saduria entomon [ab]		-	2.26	5.52	-	5.82	4.04	0.88	0.53

[a] Significant difference in the occurrence of the prey item between regions ($P < 0.05$).
[b] Significant difference in the occurrence of the prey item between seasons ($P < 0.05$).
[c] Significant difference in the occurrence of the prey item between regions and time periods: Interaction Time period × Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and time periods: Interaction Time period × Season ($P < 0.05$).

Table 6. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of invertebrate (amphipods and euphausiids) prey identified from ringed seal stomachs collected in Alaska, 1961–2009. Highlighted rows are discussed in text.

		Region				Season			
		Bering		Chukchi		Spring-Summer		Fall-Winter	
	Time period	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**
Prey (*i*)	***n***	247	266	834	209	739	99	342	376
All Amphipoda [ac]		53.44	35.34	54.80	25.36	53.04	27.27	57.60	32.00
Ampeliscidae [ab]		14.98	10.53	8.03	-	6.22	6.06	16.96	5.87
Ampelisca spp. [ab]		10.12	4.89	8.03	-	4.87	3.03	16.37	2.67
Ampelisca macrocephalus		2.43	-	2.04	-	1.49	-	3.51	-
Bybils spp.		5.26	2.63	-	-	1.49	3.03	0.58	1.07
Atylus spp.		2.02	1.13	2.04	0.48	2.57	1.01	0.88	0.80
Eusirus spp.		2.02	-	0.96	-	0.54	-	2.63	-
Rhacotropis spp. [a]		7.69	-	0.72	-	2.44	-	2.05	-
Melitidae [a]		1.62	3.38	0.24	1.44	0.68	4.04	0.29	2.13
Melita spp. [a]		1.62	2.63	0.24	1.44	0.68	3.03	0.29	1.87
Gammaridae [abcd]		14.57	8.65	24.10	6.70	26.52	5.05	11.99	8.53
Gammarus spp. [abcd]		9.72	5.64	20.86	3.35	24.09	4.04	5.85	4.80
Gammarus wilkitzkii [ab]		6.88	-	15.95	-	18.54	-	3.80	-
Gammaracanthus loricatus		-	-	1.80	-	1.35	-	1.46	-
Weyprechtia spp.		2.02	0.38	2.16	-	2.30	1.01	1.75	-
Weyprechtia pinguis		2.02	-	1.68	-	2.17	-	0.88	-
Ischyroceridae [a]		2.02	0.38	0.24	-	0.81	1.01	0.29	-
Anonyx spp. [ac]		27.53	12.03	11.63	0.48	15.70	10.10	14.33	6.13
Anonyx nugax [a]		27.53	3.76	11.51	0.48	15.56	4.04	14.33	1.87
Onisimus spp. [a]		3.24	0.38	8.75	4.31	8.66	-	4.97	2.67
Oedicerotidae [b]		3.64	0.75	5.76	-	3.65	-	8.77	0.53
Acanthostepheia spp. [b]		3.64	0.38	5.64	-	3.52	-	8.77	0.27
Acanthostepheia behringiensis		1.21	-	1.44	-	1.49	-	1.17	-
Hyperiidae [abc]		28.34	7.14	24.58	14.83	19.62	2.02	38.01	12.80
Parathemisto libellula [abc]		26.72	7.14	22.18	14.83	16.78	2.02	37.13	12.80
All Euphausiidae [abd]		7.29	4.14	9.59	13.88	11.50	1.01	3.80	10.40
Thysanoessa spp. [abc]		6.07	1.13	8.27	7.18	10.15	-	2.63	4.80
Thysanoessa raschi [ac]		2.43	0.75	2.52	4.78	3.52	-	0.29	3.20

[a] Significant difference in the occurrence of the prey item between regions ($P < 0.05$).
[b] Significant difference in the occurrence of the prey item between seasons ($P < 0.05$).
[c] Significant difference in the occurrence of the prey item between regions and time periods: Interaction Time period × Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and time periods: Interaction Time period × Season ($P < 0.05$).

Table 7. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of invertebrate (shrimp, crabs, echiurids, echinoderms, urochordates) prey identified from ringed seal stomachs collected in Alaska, 1961–2009. Highlighted rows are discussed in text.

		Region				Season			
		Bering		Chukchi		Spring-Summer		Fall-Winter	
	Time period	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**	**1961–1984**	**1998–2009**
Prey (*i*)	***n***	247	266	834	209	739	99	342	376
All Decapods [abd]		72.47	46.62	64.75	43.06	74.29	46.46	49.71	44.80
All Shrimp [abd]		72.47	45.86	64.63	42.58	74.15	45.45	49.71	44.27
Hippolytidae [abc]		38.87	12.03	28.18	0.96	35.32	15.15	20.47	5.07
Spirontocaris spp.		2.83	0.38	1.20	-	1.62	-	1.46	0.27
Lebbeus spp. [a]		4.05	0.75	0.48	-	1.49	1.01	0.88	0.27
Eualus spp. [ab]		36.03	6.77	27.46	0.96	34.10	9.09	19.30	2.93
Eualus fabricii [ab]		9.72	-	0.84	-	3.25	-	2.05	-
Eualus gaimardi [ab]		29.15	5.26	24.34	-	30.99	8.08	13.45	1.60
Pandalidae [b]		30.36	15.04	27.34	11.00	32.07	15.15	19.30	12.80
Pandalus spp. [b]		29.96	12.03	26.98	8.61	31.80	13.13	18.71	9.87
Pandalus goniurus [b]		22.67	8.27	26.38	4.78	30.18	8.08	15.50	6.40
Pandalus hypsinotus [ab]		9.72	-	0.12	0.48	0.54	-	6.14	0.27
Crangonidae [bd]		30.77	16.17	39.69	22.49	43.03	14.14	26.02	20.27
Crangon spp. [abd]		9.72	7.14	29.50	14.35	32.88	10.10	7.89	10.40
Crangon dalli		0.81	0.38	1.56	-	1.49	1.01	1.17	-
Crangon alaskensis [abd]		6.07	5.26	25.18	10.05	28.69	7.07	3.80	7.47
Sclerocrangon boreas		2.83	0.38	2.64	-	2.84	-	2.34	0.27
Argis spp. [a]		15.79	4.14	9.59	0.48	9.20	1.01	14.91	2.93
Argis lar [a]		10.93	2.26	9.11	0.48	7.85	1.01	13.16	1.60
Sabinea septemcarinata		2.02	-	1.08	-	1.08	-	1.75	-
All Crab [abd]		2.02	4.51	0.36	0.96	0.68	9.09	0.88	1.33
Paguridae		0.81	0.38	-	0.48	0.14	1.01	0.29	0.27
Brachyura [a]		1.21	1.50	0.36	-	0.68	3.03	0.29	0.27
Hyas lyratus		1.21	0.75	-	-	0.41	1.01	-	0.27
Chionoecetes opilio		-	1.13	0.12	-	0.14	3.03	-	-
All Echiuridae [abcd]		1.21	10.53	9.95	2.87	10.55	9.09	2.34	6.67
All Echinodermata		-	0.38	0.48	-	-	1.01	1.17	-
All Urochordata		0.81	0.38	-	0.48	0.27	1.01	-	0.27

[a] Significant difference in the occurrence of the prey item between regions ($P < 0.05$).
[b] Significant difference in the occurrence of the prey item between seasons ($P < 0.05$).
[c] Significant difference in the occurrence of the prey item between regions and time periods: Interaction Time period × Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and time periods: Interaction Time period × Season ($P < 0.05$).

Contaminants

Metals and other elements—Concentrations of 19 trace elements were quantified in liver (n = 35) and kidney (n = 12) tissue of ringed seals. Some elements are essential nutrients (*e.g.*, copper (Cu), iron, magnesium (Mg), manganese (Mn), selenium (Se), and zinc (Zn)), while others are potentially toxic at high levels (arsenic (As), cadmium (Cd), mercury (Hg), lead (Pb)). The highest concentrations of all elements were found in liver tissue, except for Cd with was highest in kidney tissue (Table 8). Geometric means for potentially toxic elements were 0.04 ppm for Pb, 0.66 ppm for As, 1.62 ppm for Cd, and 1.32 ppm for total Hg. Liver had higher concentrations of all elements except for Cd, which was higher in kidney.

In addition to total Hg (THg), a more toxic form called methyl mercury (MeHg) was analyzed in liver tissue of seven ringed seals (three females and four males) ranging in age from 2–19 years old ($\bar{x}$ = 9.29, SD = 5.91). When MeHg was expressed as a percentage of THg the values ranged from 2.9–14.3% (geometric mean = 6.88, arithmetic mean = 8.07, SD = 4.66). Females had higher geometric (8.96%) and arithmetic means (10.44%) than males (gmean = 5.64%, amean = 6.30%). Females were also older on average (10.7 years) than males (8.3 years).

Organochlorines—Concentrations of organochlorines (OC) were summarized in the blubber (n = 35) and liver (n = 26) of ringed seals sampled during 2003–2007. We examined four compounds of hexachlorocyclohexane (HCH; Alpha-HCH, Beta-HCH, Delta-HCH, and Gamma-HCH), seven compounds of chlordane (CHL; Heptachlor, Heptachlor-Epoxide, Oxychlordane, Alpha-Chlordane, Gamma-Chlordane, Trans-Nonachlor, and Cis-Nonachlor), six compounds of dichlorodiphenyltrichloroethane (DDT;2,4'-DDD; 4,4'-DDD; 2.4'-DDE; 4,4'-DDE; 2,4'-DDT; and 4,4'-DDT), and 84 congener and congener groups of polychlorinated biphenyls (PCB) in both blubber and liver tissues.

In general, OC concentrations in blubber tissue were an order of magnitude higher than in liver. The relationship among the compounds differed slightly between blubber and liver with ΣHCH < ΣCHL < ΣDDT < ΣPCB in blubber (Table 9). As with blubber tissue, the lowest levels of ΣHCH and the highest levels of ΣPCB were observed in liver tissue; however, ΣDDT was lower than ΣCHL (Table 9).

Of the six compounds composing ΣDDT in blubber tissue, the most dominant compound detected was 4,4' DDE (90.0%). The geometric mean sum of DDTs (ΣDDT = Σ2,4'- and 4,4'-DDD and DDE and DDT) was 126.3 ng/g wet wt.

Of the 84 PCB congener and congener groups, four made up the more than half (54.7%) of the ΣPCBs in blubber (Table 10). They were, in decreasing dominance, 153/132 (21.1%), 101/90 (12.8%), 138/160 (12.2%), and 99 (8.6%). In liver, the five compounds with the highest concentrations accounted for 39.7% of the ΣPCBs (Table 11). Congener 109/90 was dominant and accounted for 10.7% of the ΣPCBs. The other dominant compounds, in decreasing order, were 18 (7.8%), 138/160 (7.3%), 153/132 (7.2%), and 66 (6.7%).

Table 8. Geometric mean (Gmean), arithmetic mean (Amean) and range of concentrations (µg/g wet wt = ppm) of selected elements in liver (*n* = 35) and kidney (*n* = 12) of ringed seals harvested in Alaska, 2003–2007. The tissue with the highest value for each element is in bold. Elements that were not detected during analysis are denoted by nd. Some essential elements and those where information is not available to biologically evaluate concentrations are not included.

	As	**Cd**	**Cu**	**THg**	**Mg**	**Mn**	**Pb**	**Se**	**Zn**
Liver									
Gmean	**0.66**	1.62	**9.52**	**1.32**	**220.31**	**4.61**	**0.04**	**3.00**	**39.01**
Amean	**0.77**	2.62	**11.59**	**2.45**	**220.69**	**4.76**	**0.04**	**3.74**	**43.64**
Range	**0.10–1.85**	0.17–20.80	**2.89–60.33**	**0.14–12.88**	**185.6–255.3**	**2.62–7.72**	**0.03–0.12**	**0.95–12.64**	**0.48–67.39**
Kidney									
Gmean	0.46	**3.75**	5.65	0.28	148.27	1.28	nd	2.82	29.48
Amean	0.52	**5.94**	5.93	0.34	148.98	1.29	nd	2.86	29.84
Range	0.17–0.95	**0.91–18.73**	3.47–10.33	0.09–0.82	128.4–177.3	0.95–1.60	nd	2.24–3.50	21.61–39.75

Table 9. Geometric mean and range (ng/g or ppb wet wt) of concentrations for total organochlorines by chemical category in blubber (*n* = 35) and liver (*n* = 26) from ringed seals harvested in Alaska, 2003–2007. Contaminants that were not detected during analysis are denoted by nd.

	Compound			
	∑ HCH	**∑ CHL**	**∑ DDT**	**∑ PCB**
Blubber				
Gmean	51.47	98.02	126.28	273.66
Range	(17.16–150.21)	(23.50–341.82)	(18.72–627.59)	(61.10–908.28)
Liver				
Gmean	1.04	4.46	2.49	10.72
Range	(nd–12.02)	(1.33–18.87)	(0.53–13.42)	(3.51–174.88)

Table 10. Geometric mean and range (ng/g or ppb wet wt) of concentrations of dominant PCB congeners in blubber (*n* = 35) from ringed seals harvested in Alaska, 2003–2007.

	Dominant PCB Congeners			
	153/132	**101/90**	**138/160**	**99**
Blubber				
Gmean	57.79	35.10	33.32	23.53
Range	9.61–330.08	6.12–131.15	11.06–118.72	5.23–79.77
% of total	21.12	12.83	12.18	8.60

Table 11. Arithmetic mean and range (ng/g or ppb wet wt) of concentrations of dominant PCB congeners in liver (*n* = 26) from ringed seals harvested in Alaska, 2003–2007. Congeners that were not detected during analysis are denoted by nd.

	Dominant PCB Congeners				
	101/90	**18**	**138/160**	**153/132**	**66**
Liver					
Amean	2.05	1.50	1.40	1.37	1.28
Range	nd–22.66	nd–29.55	nd–4.93	nd–3.66	nd–25.97
% of total	10.70	7.83	7.31	7.15	6.68

Disease

We identified *Brucella* antibodies (*i.e.*, evidence of exposure but no infection) in 6.4% (3 of 47) and PhHV-1 antibodies in 16.7% (14 of 84) of ringed seals that were sera tested (Table 12). We found no antibodies for PhHV-2 in 5 individuals and no antibodies for CDV or PDV in 82 individuals. We found antibodies to four of six *Leptospira* species we tested for. *Leptospira bratislava* had the highest prevalence at 27.8%, *L. icterrohemorrhagiae* was next at 20.8%, and *L. grippotyphosa* and *L. hardjo* each had a low prevalence at 1.4% (Table 12). We did identify Toxoplasma in 5.0% (4 of 80) ringed seals tested. Ringed seal tongue tissue was tested for the parasite *Trichinella* but none were found to be positive (*n* = 58).

Stomach or intestinal contents of 34 ringed seals (three harvested in 2007, six in 2008, and 25 in 2009) were tested for toxic algae (domoic acid and saxitoxin). The ringed seals tested were harvested in Point Hope, Shishmaref, Diomede, Gambell, Savoonga, and Hooper Bay. Four ringed seals had levels of domoic acid above the detection limit of 4 ng/ml and six had levels of saxitoxin above the same detection limit. Domoic acid concentrations ranged from 4.1 to 31.1 ng/ml and saxitoxin ranged from 5.2 to 13.8 ng/ml, which were all far below (by 500–1000 times) the regulatory limit for domoic acid in shellfish tissue tested for human consumption. Only one ringed seal contained both toxins. The ringed seal with the highest level of domoic acid was from Diomede, as was the one with the highest level of saxitoxin.

Table 12. Serum antibody prevalence for 12 disease agents in ringed seals harvested near Point Hope, Kotzebue, Little Diomede, and Shishmaref, Alaska, 2003–2010.

Disease Agent	**Antibody prevalence** **No. positive/No. tested (%)**
Brucella spp.	3/47 (6.4)
Canine distemper virus	0/82 (0)
Phocine distemper virus	0/82 (0)
Phocine herpesvirus-1	14/84 (16.7)
Phocine herpesvirus-2	0/5(0)
Leptospira bratislava	20/72 (27.8)
Leptospira canicola	0/72 (0)
Leptospira grippotyphosa	1/72 (1.4)
Leptospira hardjo	1/72 (1.4)
Leptospira icterrohemorrhagiae	15/72 (20.8)
Leptospira pomona	0/72 (0)
Toxoplasma spp.	4/80 (5.0)

Morphometrics

Growth rates—Our analyses of standard length included 1,610 seals one year of age or older (Fig. 7) and 543 pups (Fig. 8). The birth year of these seals ≥1 year of age ranged from 1933 to 2009 and the birth year of pups ranged from 1961 to 2010.

Some ringed seals were aged by counting claw annuli. Claw annuli wear away over time, leading to a count of age that is biased low in seals >9 years old (McLaren 1958). To avoid a negative bias in estimated age, researches generally used claws to only age younger seals. Forty-four of 396 seals were aged using claws in the 1960s, 386 of 881 in the 1970s, and 16 of 97 in the 1980s. All 188 seals sampled in the 2000s were aged with teeth. In general, length-at-age was similar for seals aged with teeth and claws (Figs. 9a and 9b) so we included claw ages in our analyses.

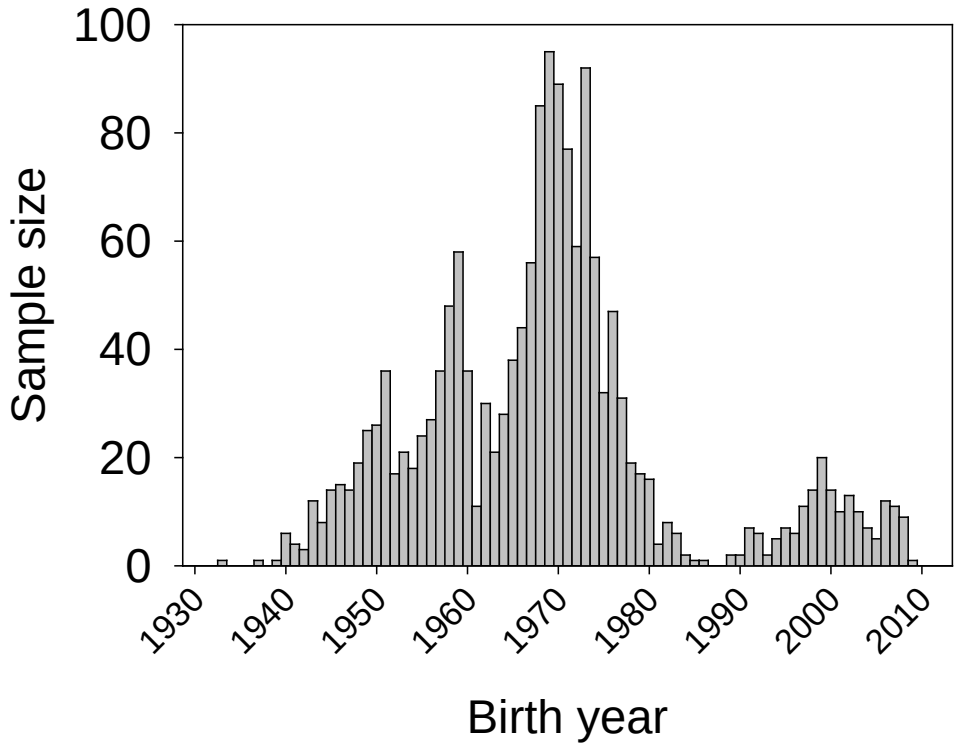

Figure 7. Distribution of ringed seals ≥1 year of age by birth year. A total of 1,610 seals were used to analyze growth rates.

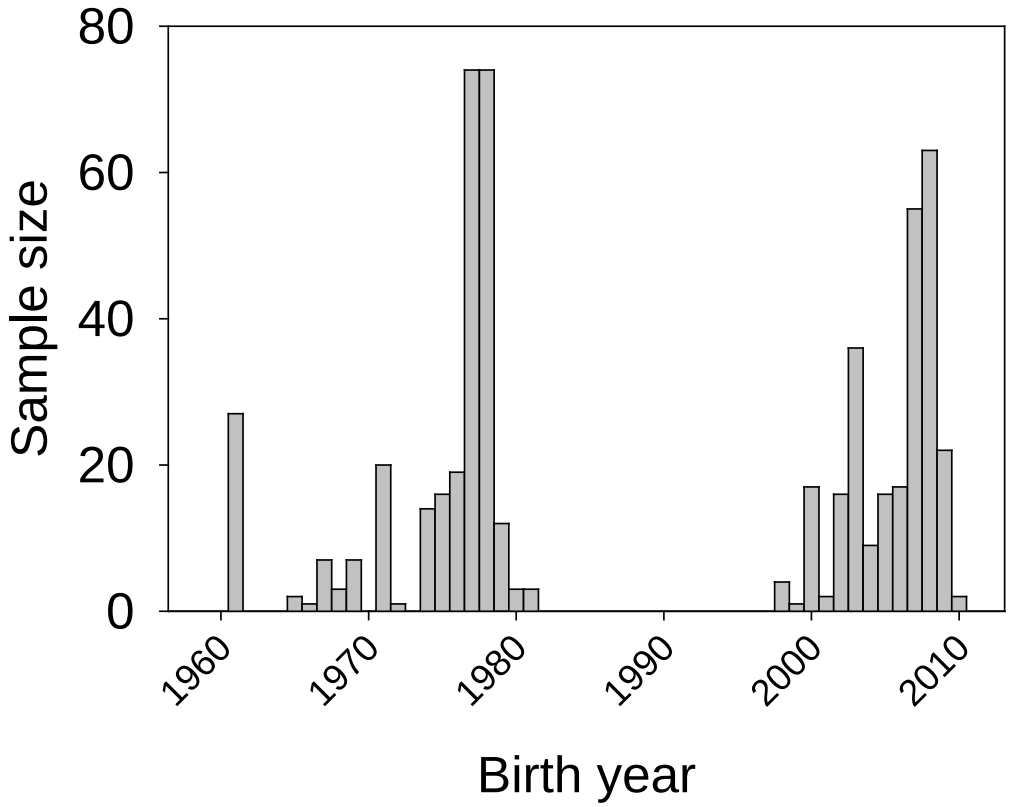

Figure 8. Distribution of 543 ringed seal pups plotted by birth year that were used to analyze growth rates.

For seals ≥1 year of age, averaged residuals ranged from -6.2 cm in 1961 to 19.3 in 2005. In general, seals born after 1977 tended to be larger (*i.e.*, have positive residuals) than seals born before 1977 (Fig. 10). Larger standard errors were present after 1980; this is partially due to smaller sample sizes, but may also be due to more sampling error or greater environmental variability. Two abrupt declines in residuals are apparent. One occurred in 1961 and was preceded by a gradual decline in residual values. The other occurred between 1974 and 1976 and forms an abrupt 3-year decline in residual values. Because of the integrative nature of assigning growth to the birth year, it is likely that the perturbation occurred sometime between 1974 and 1977, but the timing and duration of this event is uncertain.

The best approximating model of seal growth indicated that seals grew differently between 1977 and 2009 than between 1940 and 1976. This model was 38 DIC units better than the model that partitioned growth rate parameters by sex, 62.9 DIC units better than the model that portioned growth rate parameters by sampling location (Bering vs. Chukchi), and 80.1 DIC units better than a model that assumed growth rate parameters were constant.

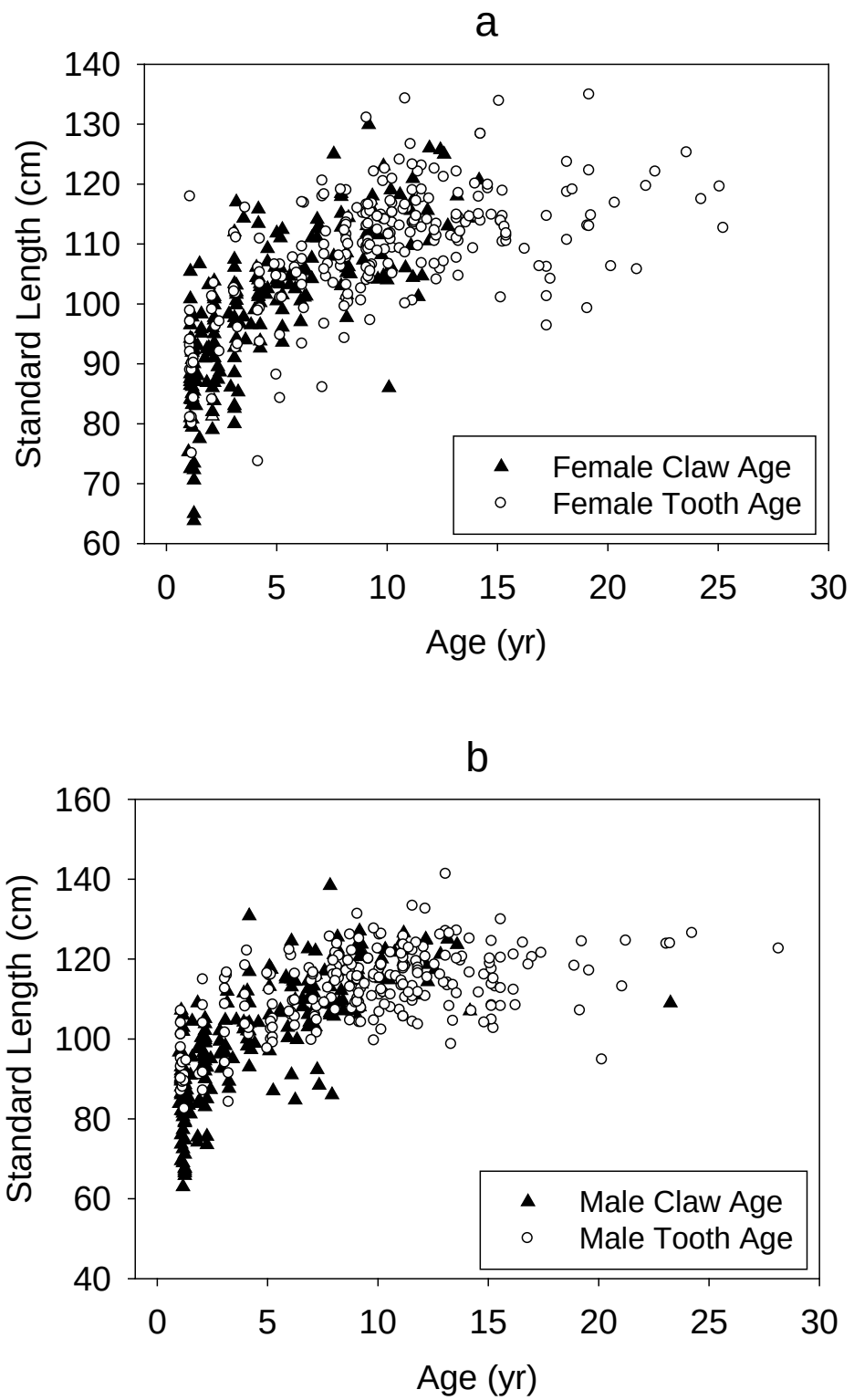

Figure 9. Standard length (cm) of (a) male ringed seals and (b) female ringed seals by age, as determined by counting claw annuli (triangles) or counting dentine/cementum layers in teeth (circles).

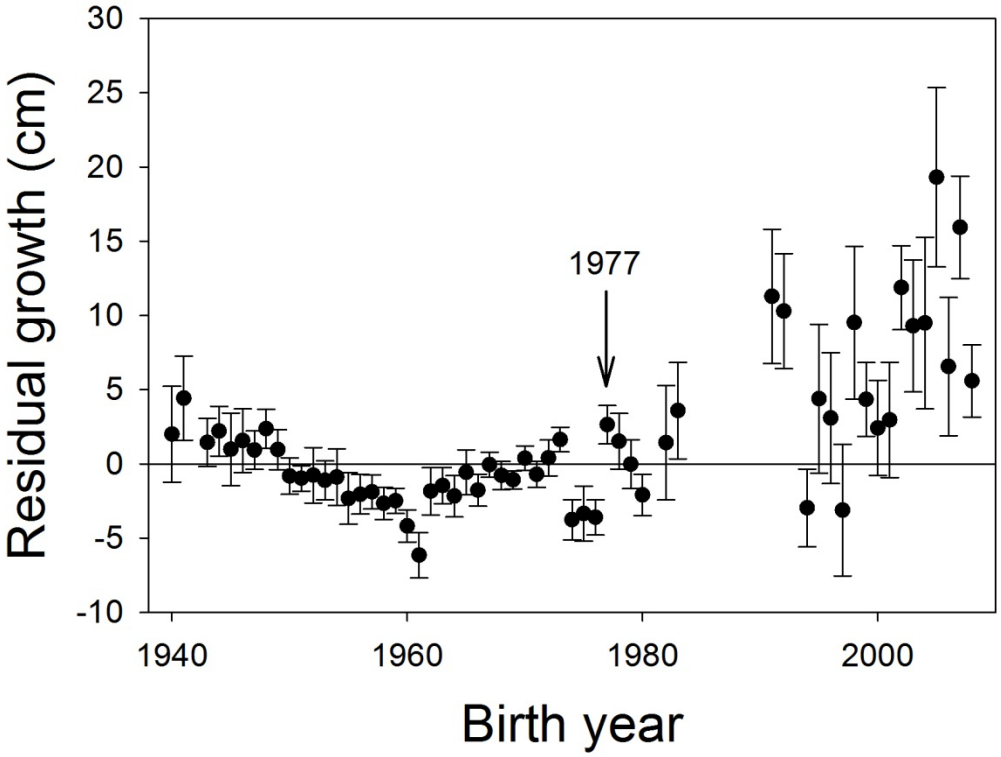

Figure 10. Residual growth of ringed seals ≥1 year of age by birth year.

The best approximating model indicated that asymptotic length was slightly less in seals born prior to 1977 (asymptotic length = 121.8 cm; 95% CL = 119.4–124.9) than seals born on or after 1977 (asymptotic length = 123.6 cm; 95% CL = 120.1–128.0; Fig. 11a). However, the major difference in growth was not in asymptotic length, but how fast seals reached asymptotic length (Fig. 11b). At age 1, seals born on or after 1977 were an average of 1.7 cm longer than seals born prior to 1977. This affect was greatest at 6 years of age, when seals born on or after 1977 were an average of 6.2 cm longer. By age 25, the affect had diminished to an average of only 2.8 cm.

Although the models with sex-specific or location-specific growth rate parameters were not supported, the estimates from these models are of biological interest. Asymptotic length was estimated to be virtually identical for both males (121.4 cm, *SD* = 1.2) and females (121.5 cm, *SD* = 3.4). Likewise, asymptotic length of ringed seals was almost identical for seals harvested in the Bering (119.8 cm, *SD* = 2.3) and Chukchi (121.1, *SD* = 1.3) seas.

For pups, averaged residual growth ranged from -9.5 cm in 1961 to 11.4 cm in 2004 (Fig. 12). The longest string of years with negative residuals occurred from 1975 to 1978 (4 years). However, the two years with the lowest growth rates occurred in 1961 and 2005. Six of ten (60%) sample years have negative residuals between 1960 and 1979. In contrast, only three of nine (33%) sample years have negative residuals between 2000 and 2009.

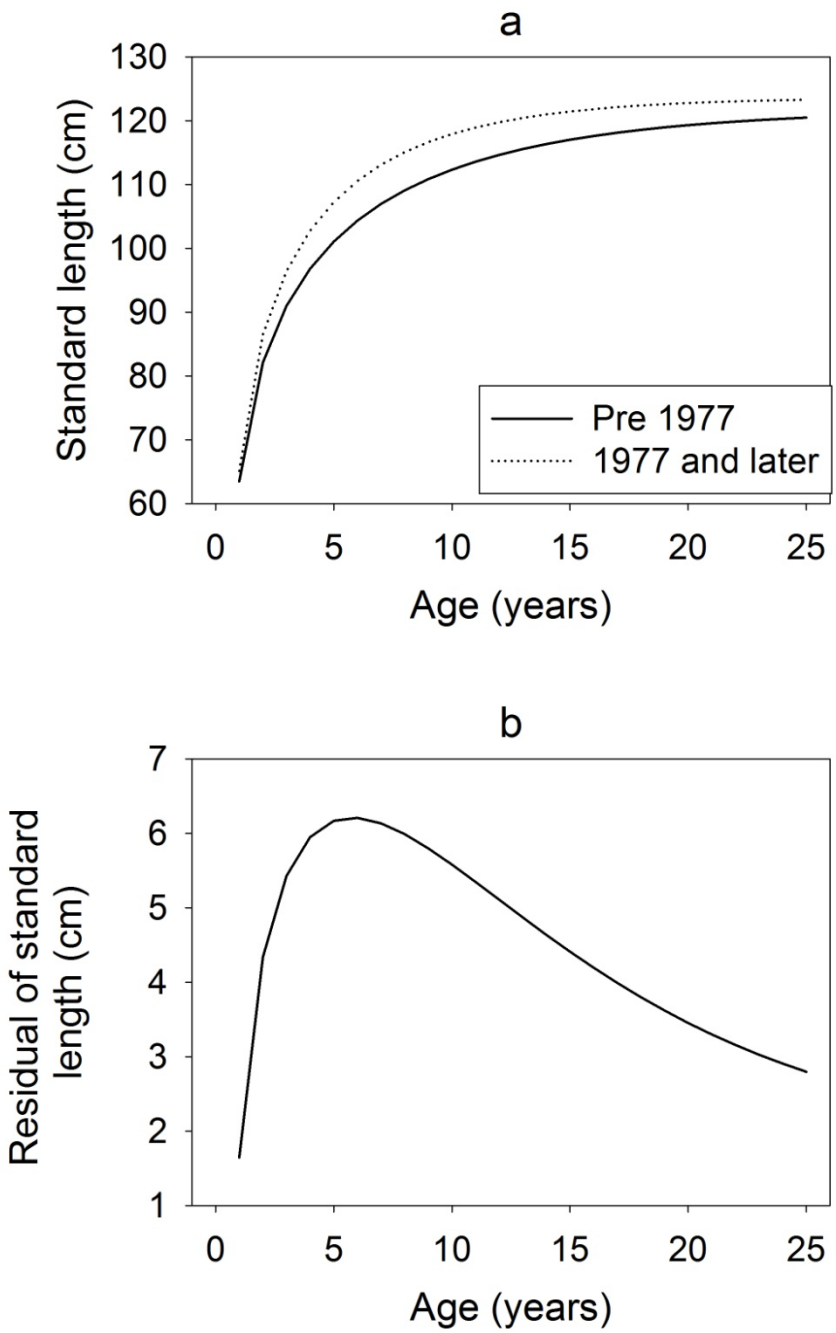

Figure 11. (a) Growth curves for ringed seals born prior to 1977 (solid line) and ringed seals born in 1977 and later (dotted line). (b) Average difference in standard length (cm) between the two time periods.

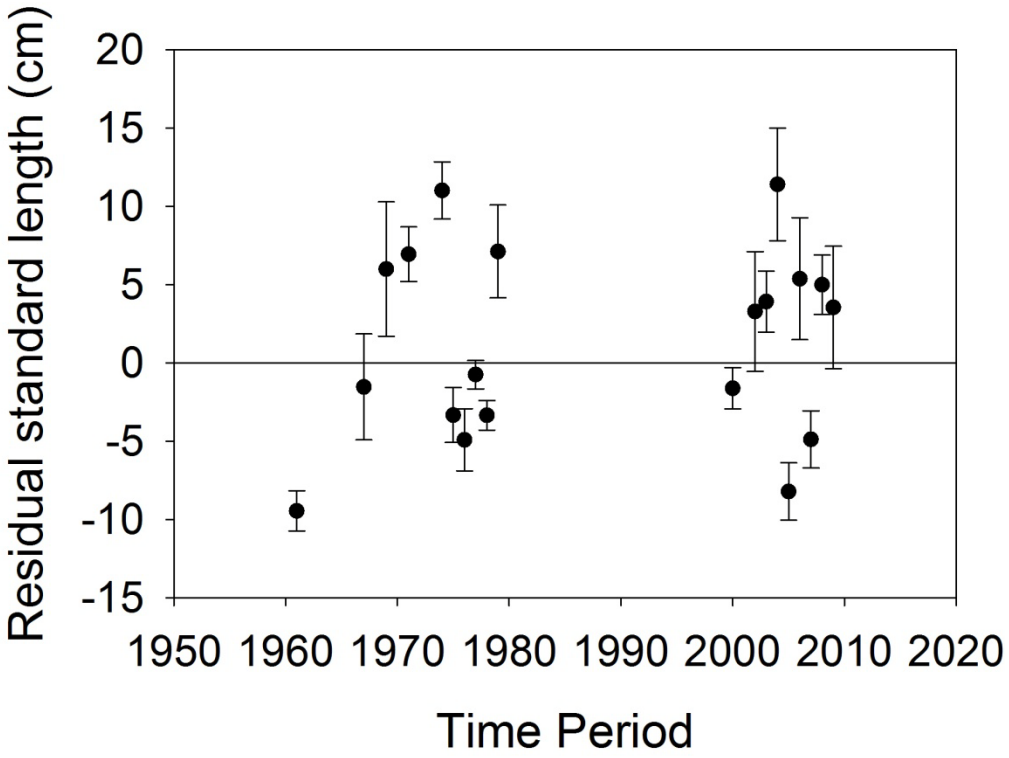

Figure 12. Residual growth of ringed seal pups by birth year. Negative residuals indicate that seals are shorter than average, given the month of harvest.

In general, years associated with shorter than average pups also had shorter than average seals ≥1 year of age. As with seals ≥1 year of age, pups born in 1961 were short given their age. Seals ≥1 year of age also had less growth if they were born between 1974 and 1976; averaging 3.8 cm shorter than expected if they were born in 1974, 3.4 cm in 1975, and 3.6 in 1976. Pups followed the same pattern for 1975 (3.3 cm shorter than expected) and 1976 (4.9 cm shorter than expected), but not for 1974 (11.0 cm longer than expected). The largest discrepancy between pups and older seals occurred in 2005 and 2007; in these years pups were short given the date of harvest, 8.2 cm shorter than expected in 2005 and 4.9 cm shorter than expected in 2007 (Fig. 12). However, seals >1 year of age had the highest growth rates we observed; 19.3 cm longer than expected in 2005 and 15.9 cm longer than expected in 2007 (Fig. 10).

Body condition—Average blubber thickness of subadult and adult ringed seals varied seasonally (Fig. 13). Maximum blubber thickness occurs in January or February and declines until July. The months we compared (May, June, and July) correspond to the time when blubber thickness is declining at the highest rate. Sternal blubber thickness was compared in 147 pups, 215 subadults (1–4 years of age), 189 adults (>5 years of age; Table 13).

For subadult and adult ringed seals, month and length were significant predictors of blubber thickness ($P < 0.05$). Standard length squared ($P = 0.57$), the interaction of standard length and age class ($P = 0.56$), age class ($P = 0.45$), and sex ($P = 0.19$) were dropped from the model. Average blubber thickness declined from 3.5 cm ($SD = 0.87$) in May to 2.7 cm ($SD =$

0.88) in July. Longer seals generally had thicker blubber (Fig. 14). The residuals of this model indicated that adult and subadult ringed seals had thinner blubber than expected in 1971 and thicker blubber than expected in 1978. Since 2002, blubber thickness has been average (Fig. 15).

For pups, both month ($P < 0.01$) and length ($P < 0.01$) were significant predictors of blubber thickness. Average blubber thickness declined from 2.8 cm ($SD = 0.99$) in May to 1.8 cm ($SD = 0.77$) in July (Fig. 16). Longer seal pups generally had thicker blubber (Fig. 17). The residuals of this model indicated that pups had less blubber than expected in 1971 and 1976 (Fig. 18). Since 2002, blubber thickness has been average (Fig. 18).

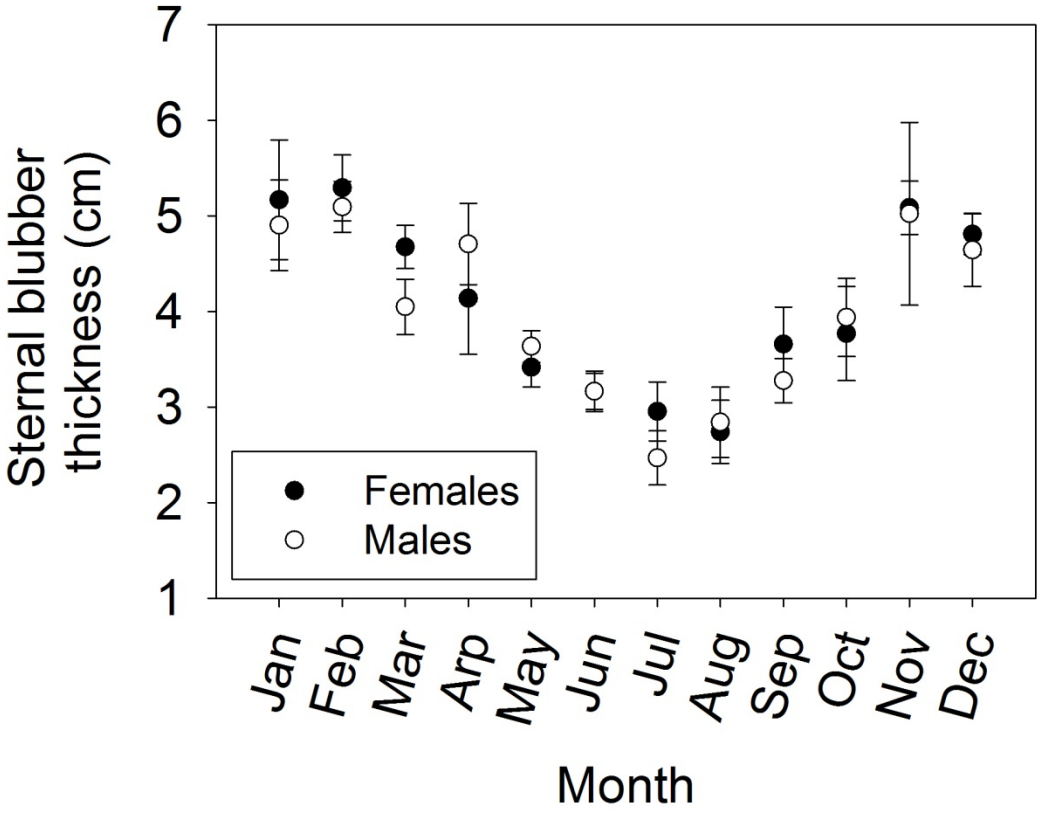

Figure 13. Seasonal variability in mean sternal blubber thickness of subadult and adult ringed seals, all years combined. Error bars represent 95% confidence limits.

Table 13. Sample sizes by year of ringed seals harvested in May, June, or July, which have data on sex, age, standard length, and sternal blubber thickness.

Period	Pups	Subadults	Adults
1971	19	46	18
1974	13	32	3
1975	8	49	29
1976	8	8	27
1977	32	23	29
1978	38	29	32
1979	6	7	21
1984	-	11	19
2002-2010	23	10	11
Total	**147**	**215**	**189**

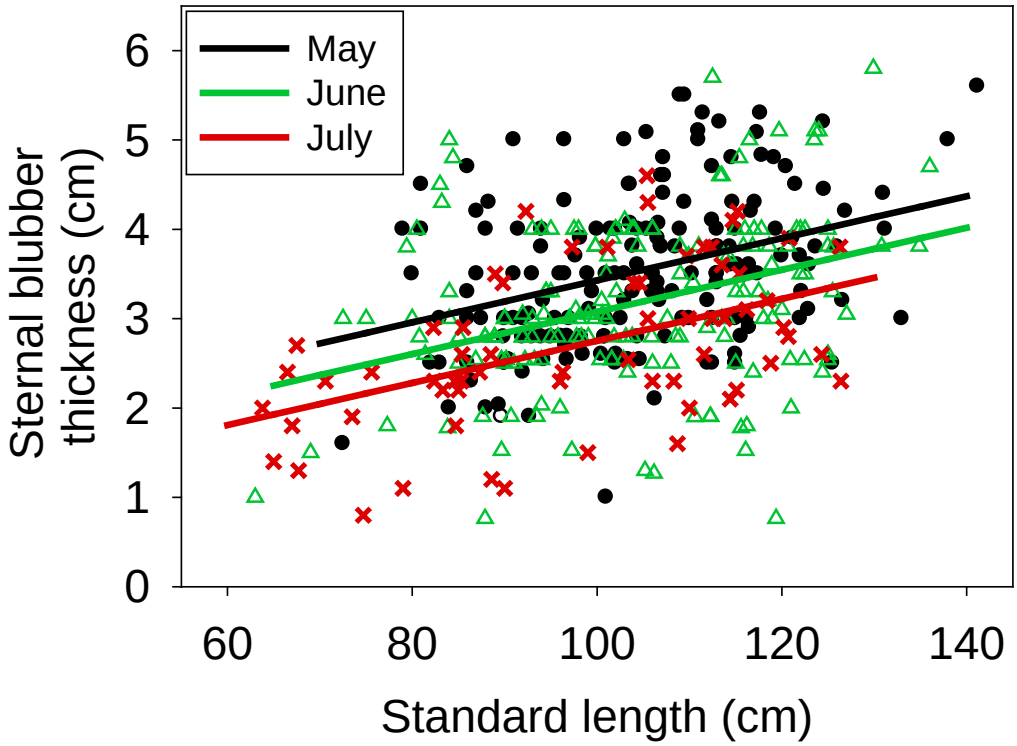

Figure 14. Relationship between standard length and sternal blubber thickness from the fitted model for subadult and adult ringed seals. Residuals of this model were used to identify years when seals had sternal blubber that was thicker or thinner than expected given their length and month of harvest.

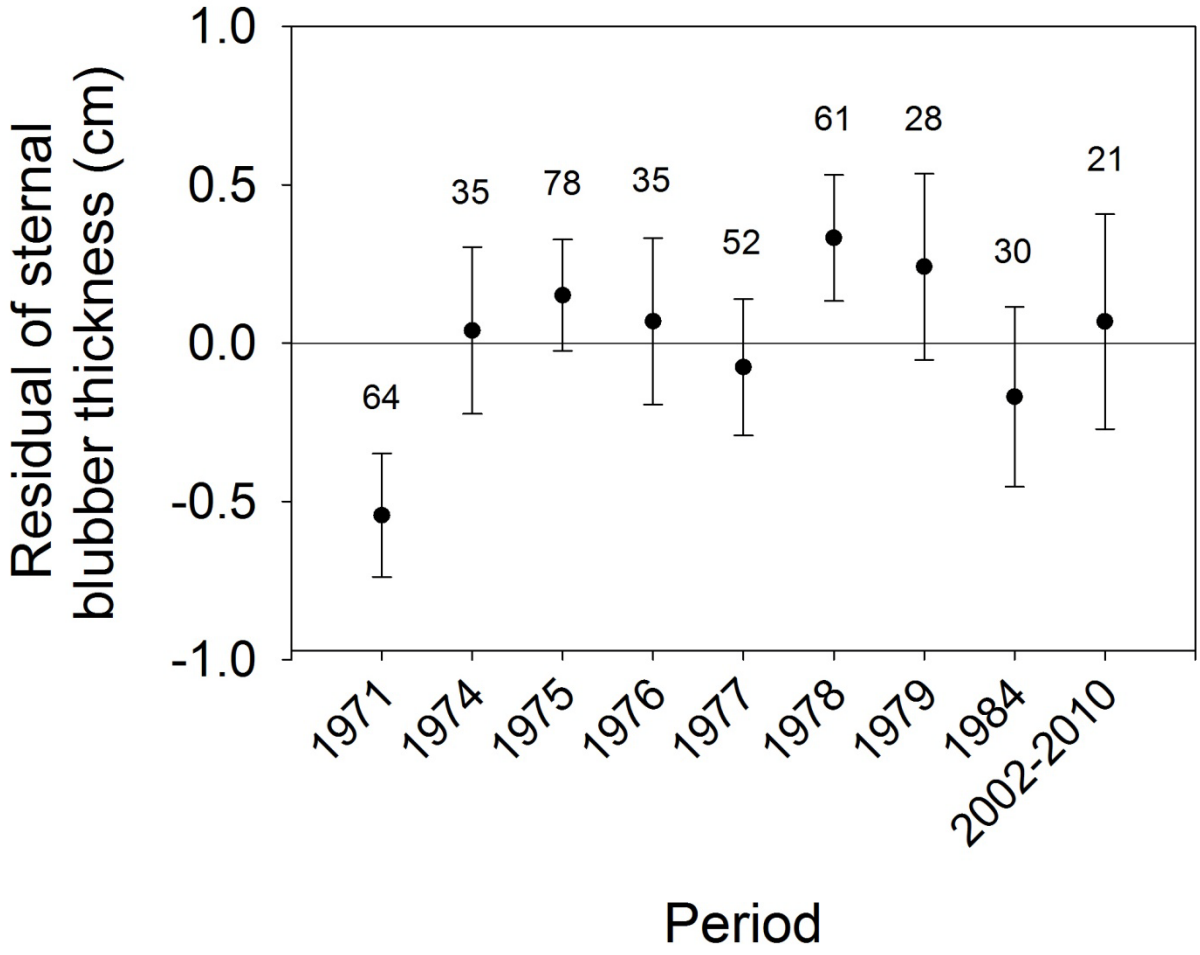

Figure 15. Residuals of sternal blubber thickness by time period for subadult and adult seals. Error bars are 95% confidence limits; statistically significant differences have error bars that do not overlap a residual of zero. Sample sizes are presented above error bars. Time periods with negative residuals had seals with less sternal blubber than expected, given their length and month of harvest. Time periods with positive residuals had seals with more sternal blubber than expected, given their length and month of harvest.

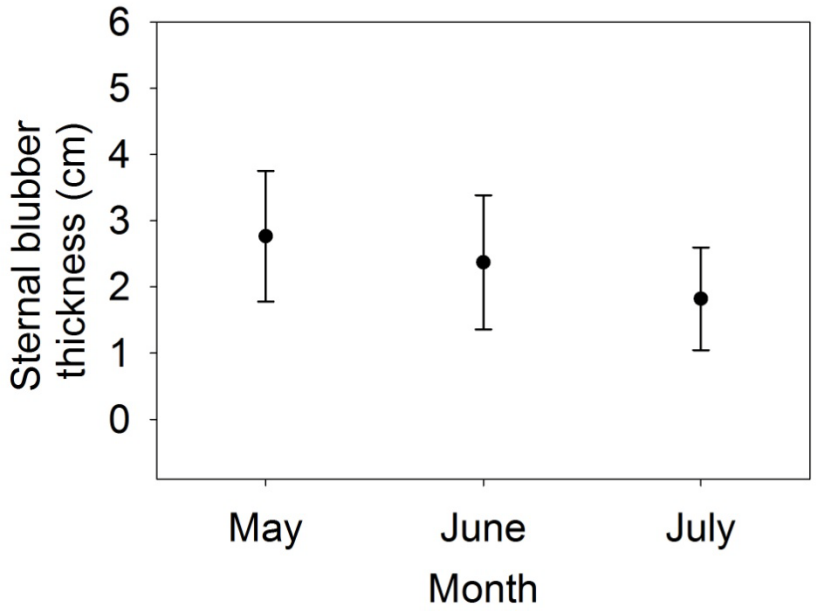

Figure 16. Average sternal blubber thickness by month for ringed seal pups. Error bars are 1 SD.

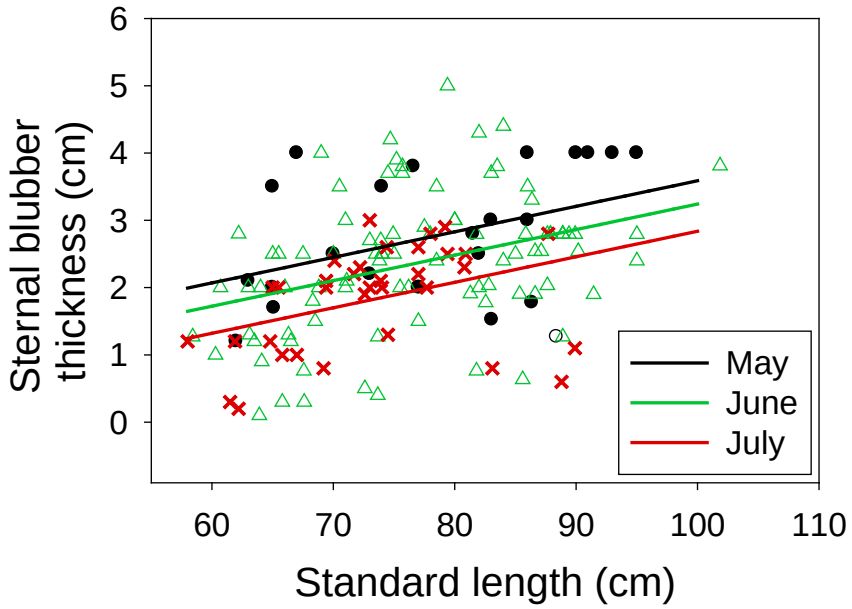

Figure 17. Relationship between standard length and sternal blubber thickness from the fitted model. Residuals of this model were used to identify years when seal pups had sternal blubber that was thicker or thinner than expected given their length and month of harvest.

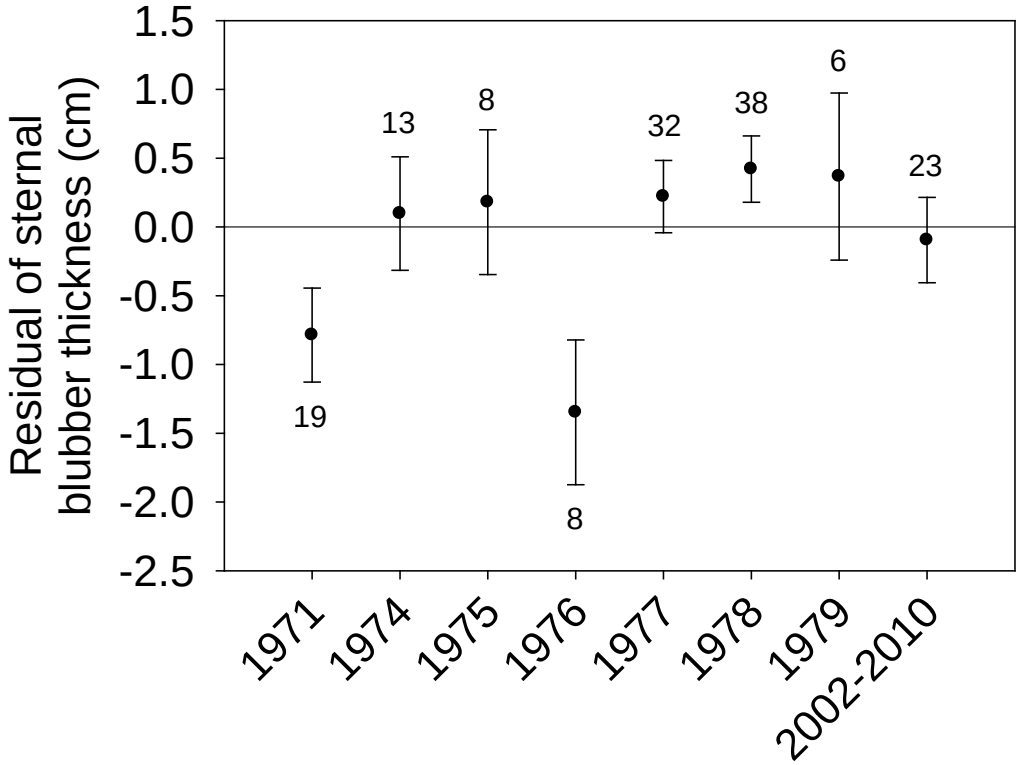

Figure 18. Residuals of sternal blubber thickness by time period for ringed seal pups. Error bars are 95% confidence limits; statistically significant differences have error bars that do not overlap a residual of zero. Sample sizes are presented above error bars. Time periods with negative residuals had seals with less sternal blubber than expected, given their length and month of harvest. Time periods with positive residuals had seals with more sternal blubber than expected, given their length and month of harvest.

Population parameters

Age distributions—We analyzed age-at-harvest for 528 ringed seals harvested in the 1960s, 4,694 in the 1970s, and 727 in the 2000s. During the 1970s, seven years had lower pup proportions than the study average ($\bar{x}$ = 26%; Fig. 19). Pup proportions were lowest in 1972 (12.5%; n = 106) and during the Bering Sea regime shift (Miller *et al.* 1994) in 1976 (6.4%; n = 676). A greater proportion of pups were identified in the 2000s (56%) than in the 1960s (14%; P <0.01) and 1970s (23%; P <0.01).

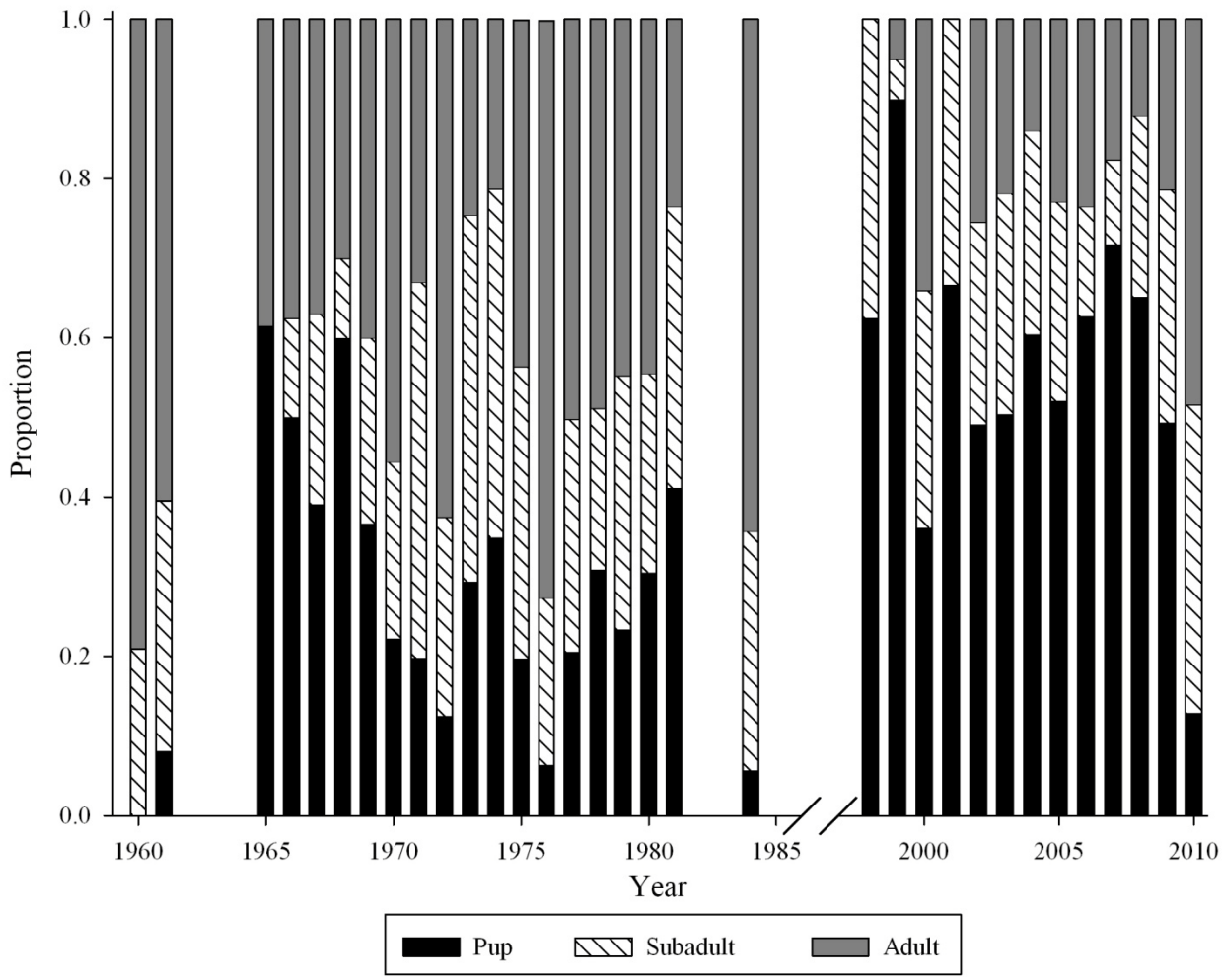

Figure 19. Proportion of ringed seals by age category (pup: <1 yr; subadult: 1–4 yr; adult: ≥5 yr) that were harvested in Alaska, 1960–2010.

Mean age at harvest—Overall, the mean age within the harvest declined from 7.4 years (95% CL = 6.8–8.1) in the 1960s, to 4.6 years (95% CL = 4.5–4.8) in the 1970s, and then declined further to 3.4 years (95% CL = 3.1–3.7) in the 2000s. Excluding pups from the calculation of mean age resulted in a mean ages of 8.5 (95% CL = 7.9–9.1) in the 1960s, 6.0 (95% CL = 5.8–6.1) in the 1970s, and 6.8 (95% CL = 6.3–7.4) in the 2000s. Differences among all decades with and without pups were significant (P <0.01).

Sex ratios— Sex ratios were generally male biased (Figs. 20 and 21). The proportion of males in the harvest varied significantly by decade, region, and season (P <0.01 for all parameters). For adults and subadults in the Bering Sea, sex ratios were somewhat female biased in the 1960s (36% male) but shifted to male biased in the 1970s (56%) and 2000s (69%; Fig. 20). In the Chukchi Sea, sex ratios were more heavily skewed toward males in the 1960s (73%) than in the 1970s (57%) and 2000s (61%).

For pups in the Bering Sea, sex ratios were near unity in the 1960s (48% male) and 1970s (48%), and male biased in the 2000s (61%; Fig. 21). Pups in the Chukchi Sea showed the same pattern as those in the Bering Sea, increasing from 45% males in the 1960s, to 54% in the 1970s, and 58% in the 2000s.

Seasonal effects were stronger for adults and subadults than for pups. On average, the harvest of adults and subadults was 10% more male biased during the winter. However, the effect was not uniform in that the proportion of males in the winter ranged from 36 (*i.e.*, a female bias) to 80%. On average, the harvest of pups was 5% more male biased during winter. As with adults and subadults, the seasonal effects were not uniform in that the proportion of males pups in the winter ranged from 36 (*i.e.*, a female bias) to 64%.

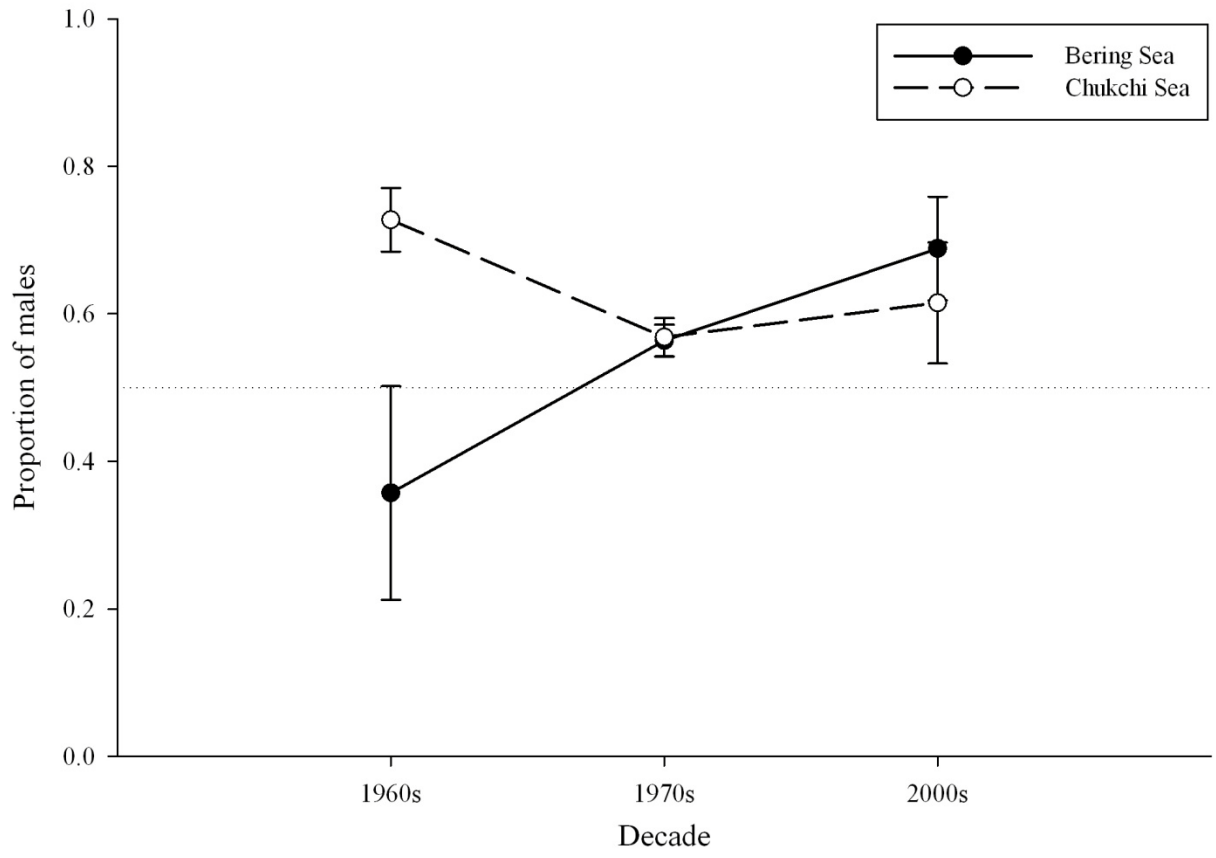

Figure 20. Proportions of adult (≥5 years) and subadult (1–4 years) male ringed seals, harvested in the Bering and Chukchi seas during three decades in Alaska, 1960–2010. Error bars depict 95% confidence intervals. Dotted line depicts equal male:female sex ratio.

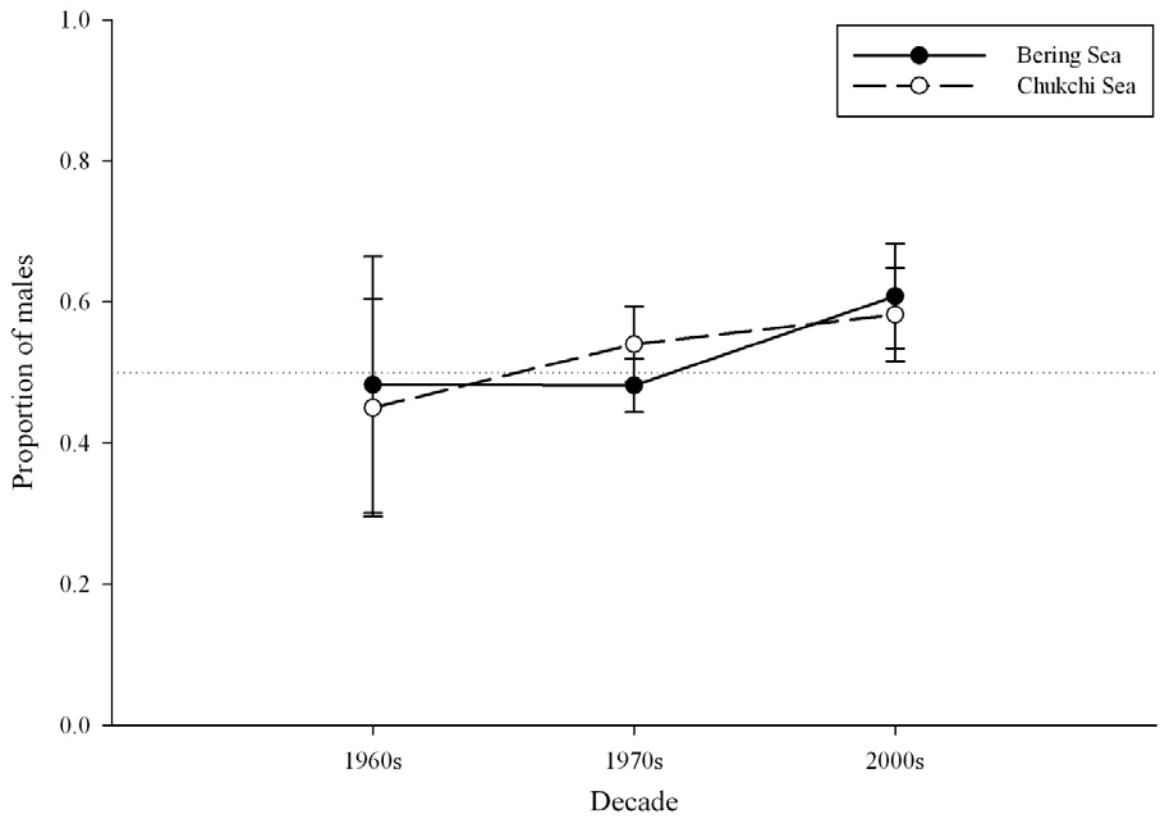

Figure 21. Proportions of pup (<1 year) male ringed seals harvested in the Bering and Chukchi seas during three decades in Alaska, 1960–2010. Error bars depict 95% confidence intervals. Dotted line depicts equal male:female sex ratio.

Age at maturity and pregnancy rate—Maturity status was determined for 690 ringed seals; 47 harvested between 1965 and 1975, 84 in 1976, 196 in 1977, 162 in 1978, 81 between 1979 and 1984, and 120 between 1999 and 2010 (Table 1). Probit regression adequately fit the data for all time periods (P >0.1). Average age of maturity was 5.3 years of age between 1965 and 1975, then increased to 6.4 in 1976, and 6.5 in 1977 (P <0.05; Fig. 22). In 1978, the average age of maturity significantly decreased by 1.5 years (P <0.05) to 5.0 years of age. Age at maturity was again higher from 1979–1984 (5.9 years). However, there were few intermediate age seals in this time period and variance could not be estimated as all seals <6 years of age were immature and all seals ≥6 were mature. Since 1999, the average age of maturity was the lowest observed (3.2 yrs), significantly lower than all other years (P <0.05 for all comparisons).

1960s. For the 1960s, data from both ADF&G and Project Chariot were available for calculation of pregnancy rates. Of the 41 reproductive tracts analyzed for sexual maturity from ADF&G data, nine (21.9%) were immature, 12 had ovulated once, 17 had ovulated more than once, and three were mature, however the number of ovulations was unknown. Of 32 sexually mature females, 32 (100%) were pregnant in the year they were harvested. Of the 696 reproductive tracts analyzed for sexual maturity from the Project Chariot data, 383 (55.0%) were immature,

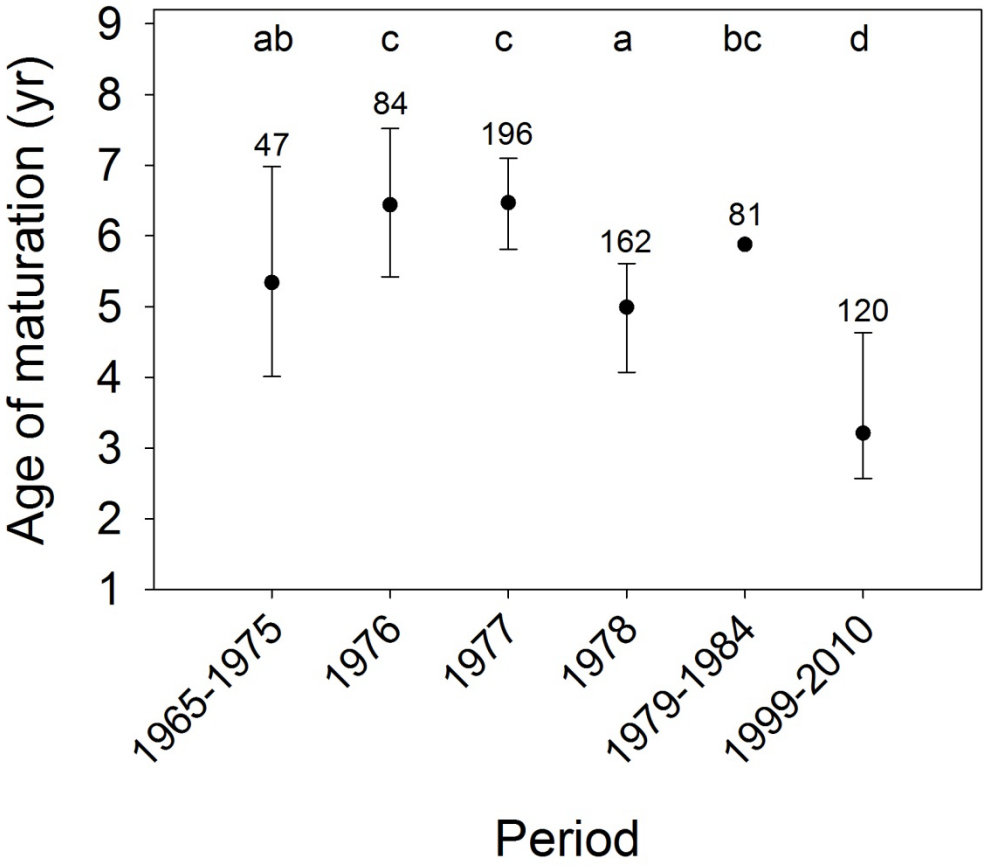

Figure 22. Mean age at maturity and 95% confidence limits for ringed seals sampled within each time period. Numbers above error bars represent sample sizes. Shared letters above time periods indicate periods that are not statistically significant at P >0.05. For example, "bc" is significantly different from periods with an "a" or "d" but similar to periods with a "b" or "c." Statistical contrasts show that seals sampled since 1999 have a younger age of maturation than seals sampled in all other time periods. Error bars are not shown for 1979–1984 as there was no overlap in years between mature and immature seals and, therefore, no error. Specifically, all seals <6 years of age were immature and all seals ≥6 years of age were mature.

but no data on the number of ovulations were available. Of 313 sexually mature females, 240 (76.7%) were pregnant in the year they were harvested. When the two datasets were combined, 272 of 354 (76.8%; 95% CL = 72–81%) mature females were pregnant when harvested.

1970s. Of the 527 reproductive tracts analyzed from the 1970s, 251 (47.6%) were immature, 68 had ovulated once, 204 had ovulated more than once, and four were mature but the number of ovulations was unknown. Of 276 mature females, 246 (89.1%; 95% CL = 85–93%) were pregnant when harvested.

1980s. Of the 47 reproductive tracts analyzed from the 1980s, 26 (55.3%) were immature, three had ovulated once, and 18 had ovulated more than once. Of 21 mature females, 16 (76.2%; 95% CL = 58–94%) were pregnant when harvested.

2000s. Of the 163 reproductive tracts analyzed from the 2000s, 119 (73%) were immature, 22 had ovulated once, 12 had ovulated more than once, and 10 were mature but the number of ovulations was unknown. Of 44 mature females, 35 (79.5%; 95% CL = 67–92%) were pregnant when harvested.

DISCUSSION

Local knowledge

We recognize that there is bias in hunter collected samples. Hunter questionnaires allow us to understand the bias so that we can evaluate whether changes in our results can be interpreted as changes in the population or if they are a result of changes in hunter behavior. Some hunters have preferences for certain types of seals, but those preferences are varied and include big, small, male, female, old, and young. Many hunters do not know what type of seal they are pursuing until after they retrieve it, and other hunters pursue any seal they observe. Only adult males in the spring are consistently avoided. Adult males in breeding condition can sometimes be identified by their black faces. Although the harvest was composed of a larger proportion of adult males than females, the proportion of males in the sample was 10% higher in the winter than in the spring.

Hooper Bay was the only location of our sample of five villages where more than half of the hunters who responded thought ringed seals numbers have declined. We hesitate to interpret the population as declining at Hooper Bay, as 47% of respondents thought the population was stable or increasing. Even though the ice forms later and leaves earlier, the majority of respondents from all villages report that ringed seals are found in the same areas and they hunt them in the same months as in the past.

Diet

Frequency of occurrence in stomach contents is an imperfect measure of ecological change. First, frequency of occurrence is a binomial variable; which does not include the volume of prey but simply records if a prey item occurred. As such, using occurrence can mask changes in prey volume until a prey item completely disappears from the diet. Second, dietary preference may ameliorate changes in prey abundance. If a preferred prey item decreases in availability, seals may still preferentially seek and consume that prey item, thus frequency of occurrence may not reflect the availability of prey in the environment. While these factors must be considered, changes in seal diet are still likely to reflect broad ecological changes. As long as dietary preferences of seals are static over time, changes in the frequency of occurrence of common prey items can be interpreted as changes in prey availability.

We found that the diet of ringed seals shifted between the 1961–1984 time period and the 2000s (*i.e*., 1998–2009). In general, seals still eat the same prey (*i.e.*, cod, amphipods, and shrimp). However, the proportion of fish in the diet has increased between the 1960s and 1970s, and the 2000s, while the proportion of invertebrates decreased. Specifically, the frequency of occurrence of fish increased from 75 to 91% in the Being Sea and from 84 to 95% in the Chukchi Sea (Table 4).

Ringed seals are also consuming a greater diversity of fish than they did in the 1960s and 1970s. For example, diet was dominated by Arctic cod (42%), saffron cod (37%), and sculpin (13%) in the 1960s and 1970s. In the 2000s, the most common fish species consumed by ringed seals were Arctic cod (61%), saffron cod (46%), smelt (27%), sculpin (15%), and walleye pollock (15%).

In contrast to fish, the frequency of occurrence of invertebrates decreased from 85 to 71% in the Bering Sea and from 90 to 60% in the Chukchi Sea during the same time periods (Table 3). We identified 103 invertebrate taxa and 30 of these significantly declined between time periods (Table 3). Prey items predominantly came from three Orders of the Class Crustacea: Mysidacea, Amphipoda, and Decapoda. Decapods were the most dominant class accounting for 66% in the early time period and 44% recently. Changes in the occurrences of crustaceans over time were correlated with changes in shrimp consumption (r = 0.60) and changes in general invertebrate consumption over time were strongly correlated with changes in crustaceans (r = 0.96).

Some authors have speculated that a longer open water period (*i.e.*, fewer months with sea ice) will cause the Bering and Chukchi seas to shift from predominantly benthic systems to pelagic ones and some studies have detected declines in benthic biomass within the northern Bering Sea (*e.g*., Moore *et al*. 2003, Grebmeier *et al*. 2006*b*, Mueter and Litzow 2008). As such, we would expect to see more pelagic fishes (such as cod) and less benthic prey (such as, sculpin or molluscs) in the diet of ringed seals. Although the occurrence of cod has increased, patterns are not as clear for benthic species. For example, while the occurrence of sculpin decreased in the Chukchi Sea, it actually increased in the Bering Sea. If benthic prey is becoming less common, perhaps the magnitude of change is not yet great enough to override seal preference or be detected by occurrence statistics.

Inferences into how dietary changes affect ringed seals must be made with caution. We observed changes in the occurrence of prey, not the quantity of prey consumed and we do not know what quantity of prey items is necessary to meet caloric requirements. Ringed seals have a more general diet that includes both pelagic and benthic species than spotted seals (pelagic specialists) and bearded seals (benthic specialists). As such, ringed seals may be less vulnerable to changes in prey populations. Interestingly, the lowest frequency of occurrence of all cod, especially Arctic cod, occurred in 1975 (Fig. 4). Seals born in 1975 and 1976 had low growth rates (Figs. 10 and 12); few pups were harvested in 1976 (Fig. 19), and those that were had poor body condition (Fig. 18). By 1977, growth rates and body condition rebounded. Hence, environmental conditions quickly improved or seals quickly adjusted to new conditions. Currently, it is unlikely that their diet is unfavorable; high growth rates, an early age at

maturation, high pregnancy rates, and good body condition all indicate ringed seals are finding sufficient prey to meet their caloric requirements, whatever those might be.

Our analyses have shown that even using frequency of occurrence our methods were robust enough to see differences by time, region, age, and season. In future analyses, we may be able to include number and size of fish eaten and combine ringed, bearded, and spotted seal diet data to better describe ecological changes in the pelagic and benthic systems.

Contaminants

Metals and other elements—Metals and other elements occur naturally in the marine environment and levels can vary widely in Alaska depending upon regional geology. The normal range of variation for metals is poorly understood in marine mammals and high concentrations of metals may not be toxic. For example, Cd and Hg are commonly present at high concentrations in liver and kidney tissue of marine mammals. While Cd can be toxic at elevated levels, in marine mammal kidney and liver it tends to bind with metallothionein, which makes it less bioavailable and therefore less toxic (Groten *et al.* 1990, Goyer 1991). Marine mammals are also known for their ability to use Se to detoxify Hg and elevated Hg levels are usually accompanied by elevated Se levels (Koeman *et al.* 1975). Most studies indicate that element concentrations generally increase with age (see review in Northern Contaminants Program 2003), yet few studies have sufficient samples to analyze for the affects of age. Alternatively, the concentrations of some elements may decline with age and some relationships may be non-linear (Dehn *et al.* 2005).

Ringed seals had the second lowest concentration of Cd, and Hg of the four species of ice seals in our studies (Table 14) with spotted seals having the lowest and ribbon seals having the highest. Pb levels were barely above detection limits in any species (Table 14). Our concentrations of total Hg in liver were lower than that of ringed seals in Canada (Dehn *et al*. 2005, Riget *et al*. 2005,), Greenland, and Russia, but similar to seals in Norway (Riget *et al*. 2005). Our Cd concentrations were lower than all the above countries including Norway (Dehn *et al*. 2005, Riget *et al*. 2005).

Table 14. Geometric mean concentration, geometric standard deviations (*SD*), and ranges (µg/g or ppm wet wt) for potential metals of concern in liver from ice seals harvested in Alaska 2003–2007. The highest concentration for each metal is in bold.

Metal		**Species**			
		Ringed	**Bearded**	**Spotted**	**Ribbon**
	n	32	42	17	9
Cd	Mean	1.59	2.55	0.38	**3.64**
	SD	2.86	6.19	3.98	**3.65**
	Range	(0.17–20.80)	(0.01–39.93)	(0.02–6.40)	**(0.42–15.21)**
Hg	Mean	1.21	**2.13**	0.88	2.10
	SD	3.20	**4.26**	4.16	4.10
	Range	(0.14–12.88)	**(0.13–28.31)**	(0.03–5.61)	(0.41–18.06)
Pb	Mean	0.04	0.04	0.04	0.04
	SD	1.57	0.05	1.67	1.68
	Range	(0.03–0.12)	(0.03–0.48)	(0.03–0.22)	(0.03–0.13)

Organochlorines—Compared to other ice seals species in our studies, ringed seals had the lowest geometric mean concentrations of ΣCHL (96.5 ng/g lipid wt), and the second lowest of ΣHCH levels (51.8 ng/g lipid wt), ΣDDT (129.3 ng/g lipid wt), and ΣPCB (278.7 ng/g lipid wt) in blubber tissue (Quakenbush and Citta 2008a, Quakenbush *et al*. 2009; Table 15).

Our ΣHCH, ΣCHL, ΣDDT, and ΣPCB concentrations were much lower than ringed seals in Canada, Norway (Weis and Muir 1997), and Russia (Nakata *et al*. 1997). However, direct comparisons can be confounded by the analysis of different OC congeners. Concentrations may also depend both on sex or age, so differences in mean concentrations may have more to do with the sex ratio or age of the seals sampled than with the location or time period.

Other contaminants— Polybrominated diphenyl ethers (PBDEs) have been analyzed in the blubber of ringed seals (Quakenbush 2007). PBDEs are chemicals widely used as flame retardant additives in carpets and upholstery, and in plastics used in electrical appliances, televisions, and computers. It is thought that PBDEs enter the food chain by being released slowly into the air through the life of the products that contain them (Strandberg *et al.* 2001). Although little is known about the toxicology of PBDEs, PBDEs and their congeners are structurally similar to PCBs and thyroid hormones. Lab studies indicate that PBDEs may disrupt thyroid function and neurodevelopment (Darnerud 2003, Viberg *et al*. 2004). Ribbon seals had the highest mean level of total PBDEs (16.5 ng/g wet wt) followed by spotted seals (12.4 ng/g wet wt) and ringed seals (5.9 ng/g wet wt); bearded seals had the lowest (3.4 ng/g wet wt) of the Alaska ice seal species, but all had lower levels compared to seals from other regions of the Arctic (Quakenbush 2007).

Perfluorinated contaminants (PFCs) have been analyzed in the liver of ringed seals (Quakenbush and Citta 2008b). PFCs affect cellular function and intercellular communication; however, the concentrations at which PFCs become toxic to seals are unknown. PFCs are not lipophilic like OCs, instead they are lipophobic, and the way they are acquired and how they bioaccumulate are not known. Perfluorooctane sulfonate (PFOS), perfluorononanoic acid (PFNA), perfluorodecanoic acid (PFDA), and perfluoroundecanoic acid (PFUnDA) were detected in most samples (Quakenbush and Citta 2008*b*). When compared to other Alaskan ice seals, ringed seals had the highest concentrations of PFOS, PFNA, PFDA, and the second highest concentration of PFUnDA (Quakenbush and Citta 2008*b*). PFOS has been identified as the predominant PFC in wildlife. Studies of ringed seals in Canada (Martin *et al.* 2004) and Greenland (Bossi *et al.* 2005) generally find levels of PFOS twice as high as what was observed in ringed seals (Quakenbush and Citta 2008*b*). However, our mean levels of PFNA were higher. Because little is known about the transport mechanism, the way the different compounds are acquired, and how they affect seals we have no explanation for why concentrations are different in Alaskan ice seals or whether they are harmful.

Table 15. Geometric mean concentration, geometric standard deviations (*SD*), and ranges (ng/g or ppb wet wt) for total organochlorines in blubber from ice seals harvested in Alaska 2003–2006. The highest concentration for each compound is in bold.

Compound		**Species**			
		Ringed	**Bearded**	**Spotted**	**Ribbon**
	n	32	33	17	9
∑ HCH	Mean	51.8	14.5	**104.8**	93.9
	SD	1.65	1.55	**1.56**	1.64
	Range	(17–150)	(3–28)	**(35–313)**	(53–228)
∑ CHL	Mean	96.5	104.2	193.6	**338.6**
	SD	2.12	1.60	1.96	**2.10**
	Range	(24–342)	(51–415)	(38–580)	**(199–1979)**
∑ DDT	Mean	129.3	91.2	199.5	**456.5**
	SD	1.85	1.95	2.19	**2.06**
	Range	(39–628)	(26–605)	(30–695)	**(168–1382)**
∑ PCB	Mean	278.7	193.0	404.1	**552.0**
	SD	1.71	1.76	1.97	**1.94**
	Range	(92–908)	(69–943)	(99–1256)	**(231–1467)**

Disease

Brucella—In general, low prevelence of *Brucella* antibodies have been found in Arctic seal species. We identified a lower prevalence of *Brucella* antibodies in ringed seals in this study (6.4%, 3 of 47) than we did in spotted seals (16.2%, 6 of 37; Quakenbush *et al*. 2009) and ribbon seals (14.3%, 2 of 14; Quakenbush and Citta 2008*a*). Nielsen *et al.* (1996) identified *Brucella* antibodies in 4.0% (10 of 248) of ringed seals in the Canadian Arctic and Tryland *et al.* (2001) identified *Brucella* antibodies in 5.4% (16 of 297) of polar bears near Svalbard. In contrast, Zarnke *et al.* (2006) found a high incidence, 46.0% (46 of 100), of *Brucella* antibodies in harbor seals from the Gulf of Alaska, similar to incidence rates, 49.0% (147 of 300), observed in harbor seals from Scotland (Foster *et al.* 2002). Harbor seals experience closer contact with one another on their terrestrial haulouts than ringed seals, or polar bears do on sea ice and this may explain the higher prevalence in them. Spotted seals are closely related to harbor seals and use terrestrial haulouts in summer, which may bring them in closer contact with one another than occurs with other ice seal species, although, they did not show a higher exposure.

Neither mortality, nor reproductive disorders were noted in any of the studies cited above and it is believed that Brucellosis is not a significant source of reproductive failure in seals. However, Foster *et al.* (2002) notes there is little or no data on abortion rates, so Brucellosis may be more important than what is currently assumed.

PhHV-1 and -2—Our findings of 16.7% (14 of 84) for PhHV-1 antibodies and no antibodies for PhHV-2 (0%, 0 of 5) in ringed seals were much lower than 50% (2 of 4) for each reported by Zarnke *et al*. (1997). Our sample size was much larger (84 vs. 4) for PhHV-1, which may explain the different results, although the sample sizes for PhHV-2 (5 vs. 4) were similar. Our previous study of spotted seals also reported a lower prevalence of PhHV-1 (33.3%, 12 of 36; Quakenbush *et al*. 2009) than that found by Zarnke *et al.* (1997) who identified antibodies in 72% (23 of 32) and antibodies of PhHV-2 in 16% (5 of 32) of spotted seals sampled near southeastern Kamchatka and in the Bering and Chukchi seas.

Our findings for ribbon seals also contrasted with Zarnke *et al*. (1997) in that we found no antibodies of either PhHV-1 or 2 (Quakenbush and Citta 2008*a*), whereas he found antibodies for both in 29.2% (7 of 24) of ribbon seals sampled in the Bering Sea. More disease screening is necessary to verify the prevalence of PhHV-1 and -2 in ringed seals. PhHV-1 was first identified in 1984, when it caused the deaths of 11 harbor seal pups in the Netherlands (Osterhaus *et al.*1985). Symptoms include fever, vomiting, and diarrhea (Visser *et al.* 1991). Colegrove *et al.* (2005) sampled live stranded harbor seals in California and found that 3–6% of live strandings were primarily or secondarily attributable to PhHV-1, although in some years PhHV-1 was responsible for 10–20% of strandings. PhHV-2 has been detected in harbor seals from the North Atlantic (Harder *et al.* 1996) and the North Sea (Lebich *et al.* 1994).

PDV and CDV— We found no antibodies for PDV (n = 82) or CDV (n = 82) in ringed seals (this study). We also did not find PDV or CDV antibodies in spotted seals (n = 37, n = 22), respectively from the Bering and Chukchi seas (Quakenbush *et al*. 2009).

It is thought that PDV is circulating within Arctic species (*e.g.*, Barrett *et al.* 1995, Duignan *et al.* 1997, Härkönen *et al.* 2006) and that harp seals (*Phoca groenlandica*) may be the

major reservoir for PDV in the Arctic (Barrett *et al.* 1995, Duignan *et al.* 1997). Harp seals have a high prevalence of PDV antibodies (83%; 130 of 157; Duignan *et al.* 1997) and exhibit attributes conducive for maintaining a virus, such as a large population size and dense aggregations. In contrast to our findings, Duignan *et al.* (1997) found that ringed seals had a high prevalence rate (41%; 106 of 259), which is surprising given their dispersed population structure. The prevalence of antibodies was highest where ringed seal and harp seals overlap in range, supporting the idea that harp seals might serve as a reservoir. Harp seals are also believed to be the source of the 1998 PDV outbreak in the northern Europe (Heide-Jørgensen *et al.* 1992, Härkönen *et al.* 2006). Migrating harp seals have been observed in the North Atlantic and they are believed to have transferred PDV to grey seals (*Halichoerus grypus*), which are largely immune (Heide-Jørgensen *et al.* 1992, Barrett *et al.* 1995, Härkönen *et al.* 2006). PDV has been documented as persisting within grey seal populations (Barrett *et al.* 1995, Hammond *et al.* 2005) and both the 1988 and 2002 outbreaks of PDV in harbor seals have been traced to a single haulout on the island of Anholt, Denmark. This haulout is notable in that both grey and harbor seals haul out together and mix (Härkönen *et al.* 2006).

An outbreak of CDV killed thousands of Baikal seals (*Phoca sibirica*) in 1988 (Grachev *et al.*1989, Mamaev *et al.* 1995) and over 10,000 Caspian seals (*Phoca caspica*) in 2000 (Kennedy *et al.* 2000). Both epizootics are believed to have been caused by seals coming into contact with terrestrial carnivores that were disease vectors. Given that ringed seals in Alaska rarely haul out on land, they are less likely to contact terrestrial carnivores. CDV is the dominant morbillivirus in polar bears making polar bears a potential vector for ringed seals hauled out on pack ice. Follmann *et al.* (1996) found morbillivirus antibodies in 35% (68 of 191) of polar bears from Alaska and Russia; these antibodies were later identified as antibodies for CDV (Garner *et al.* 2000).

Zarnke *et al.* (2006) found a 1% (2 of 160) prevalence rate of PDV antibodies in harbor seals within the Gulf of Alaska. Recently, antibodies to PDV were detected in 40% (30 of 77) of sea otters in the eastern Aleutian Islands, Alaska Peninsula, and Kodiak Archipelago (Goldstein *et al*. 2009). However, exposure does not guarantee an epizootic. Although PDV results in high mortality rates in harbor seals (an outbreak of PDV in northern Europe killed over 23,000 harbor seals in 1998 and 30,000 in 2002; Härkönen *et al.* 2006), other phocids are largely immune to PDV. For example, grey seals are much less susceptible to PDV (Barrett *et al.* 1995, Härkönen *et al.* 2006) than harbor seals, only one harp seal has shown clinical disease attributed to PDV (Daoust *et al.* 1993), and there are no cases of clinical disease in ringed seals. Transmission rates are also affected by seal behavior, which changes seasonally. Ringed seals, however, are not very social and do not haul out in numbers during any time of year, thus they are not as likely to be susceptible to an epizootic as spotted seals, which may haul out together on gravel shoals or islands in summer.

Morphometrics

Growth rate—Examination of growth rates indicated significant variability in the length of ringed seals over time. Seals varied from 6.2 cm shorter than expected to 19.3 cm longer than expected, depending upon the year in which they were born (Fig. 10). In general, seals $\geq$1 year of age have been growing larger since 1977. Most of the difference is in the rate of growth, not

asymptotic length. In other words, while seals are growing longer, the main difference between growth curves is that seals are currently growing faster and attaining asymptotic length more quickly (Fig. 11). Given their age at harvest, seals ≥1 year of age have grown from 2.4 to 19.3 cm longer than expected since 2000.

As with seals ≥1 year of age, there are no indications that the growth of pups in recent years is reduced in comparison with past years (Fig. 12). Between 2000 and 2009, six of nine breeding seasons had pups that were larger than expected, based upon their harvest date. However, we must be cautious when interpreting pup growth, as changes in parturition date may confound measurements of length. For example, pups born in 2005 and 2007 were short given the date of harvest; 8.2 cm shorter than expected in 2005 and 4.9 cm shorter than expected in 2007. However, seals >1 year of age had the highest growth rates we observed; 19.3 cm longer than expected in 2005 and 15.9 cm longer than expected in 2007. Furthermore, the proportion of pups in the harvest was over 50% in both 2005 and 2007, indicating that many pups were born and survived to be harvested (Fig. 19). Perhaps parturition date was delayed in 2005 and 2007, leading to pups that were shorter at harvest. Likewise, years with longer than average pups may have earlier parturition dates.

However, some years characterized by poor growth of seals >1 year of age were also characterized by poor growth of pups. For example, the lowest growth rates we observed was for seals born in 1961, this was true for both pups and seals ≥1 year of age (compare Figs. 10 and 12). All the seals sampled in 1961 were from Point Hope, in the Chukchi Sea. As such, all the data from pups came from Point Hope and we have no information on pup growth for the Bering Sea. However, none of the seals >1 year of age that were born in 1961 were sampled at Point Hope; hence, it is likely that 1961 was a poor year for ringed seals throughout the Bering and Chukchi seas. Other years included seals sampled in both the Bering and Chukchi seas and differences by region were undetectable.

Seals grow rapidly for the first two or three years of age (Fig. 11) and we expect unfavorable conditions to affect pups and yearlings more than older seals. Hence, years with unfavorable conditions may affect seals born in prior years, but to a lesser extent than seals born in the current year. As an example, consider 1974 to 1976, a string of three years with shorter than expected growth (Fig. 10). Seals ≥1 year of age averaged 3.8 cm shorter than expected if they were born in 1974, 3.4 cm in 1975, and 3.6 in 1976. During this same time, pups were 11.0 cm longer than expected in 1974, 3.3 cm shorter than expected 1975, and 4.9 cm shorter than expected in 1976 (Fig. 12). The proportion of pups in the harvest also decreased from 35% in 1974, to 20% in 1975, and then to 6% in 1976, the second lowest proportion of pup ever observed in the harvest (Fig. 19). Hence, it is likely that low growth rates observed in seals born between 1974 and 1976 was mostly due to an environmental perturbation that started in 1975 and peaked in 1976.

It is unclear what environmental effects may lead to poor growth. Low growth rates in 1975 and 1976 may correspond with the regime shift thought to occur in the Bering Sea in 1977 (Miller *et al*. 1994). The frequency of occurrence of fish in the mid 1970s was low relative to other time periods, especially for Arctic cod (Fig. 4). Stirling (2002) noted years of poor ringed seal recruitment were associated with heavy ice conditions. During cold years, sea ice retreats

late in spring and arrives early in fall, shortening the open water season and lowering primary productivity. Hence, years with heavy ice may affect the availability of prey for ringed seals.

Growth was more variable for seals ≥1 year of age sampled after 1980 (Fig. 10). Some of the variability may be due to sampling error, as biologists worked more directly with fewer native seal hunters in the 1960s and 1970s. However, it is unlikely that mean growth rates would be consistently higher due to sampling error.

We cannot adequately address the possibility that ringed seals consist of multiple, distinct morphological types. A number of authors have noted that ringed seals breeding in landfast ice are larger and mature more slowly than seals breeding in drifting pack ice (*e.g.*, Finley *et al*. 1983, Fedoseev 2000). However, the seals in our sample are mostly harvested during open water periods, when distinct morphological types, if present, would be mixed. If the sample were clearly delineated into distinct morphological types, we would expect to see posterior distributions that were bimodal in our Bayesian analysis. However, the posterior distributions of growth parameters were unimodal, indicating that there was only one population of seals. Hence, if different morphological types are present, they are either rare or, perhaps there is substantial overlap in the growth parameters of the different morphological types.

Body condition—In general, growth rates and body condition are expected to be correlated. Good conditions likely lead to longer, fatter seals. As such, using regression to control for length could mask changes in foraging conditions that affect both growth and blubber thickness simultaneously. For older seals, such simultaneous changes are not likely. Most growth occurs within the first few years of life, so short-term changes in prey availability (and blubber thickness) cannot be perfectly correlated with growth.

For pups, we assumed that controlling for length removes variability in blubber thickness due to parturition date. This implicitly assumes longer pups were born earlier in the season and that nutritional stress leads to skinnier pups. If pups that are nutritionally stressed grow more slowly, but maintain constant blubber thickness, controlling for length may mask changes in blubber thickness by time period.

However, after controlling for length, residual blubber thickness was not constant through time. Hence, it is reasonable to assume that length and blubber thickness are decoupled enough to identify years where foraging conditions were particularly good or bad.

Sternal blubber thickness was less than expected in 1971 for both pups and seals ≥1 year of age. However, the perturbation associated with 1976 only affected pups. Interestingly, pups were extremely skinny in 1976 (Fig. 18), but adults had average blubber thickness (Fig. 15). As described elsewhere in this report, few pups were harvested that year, indicating that recruitment rates were low. The growth rate of seals born in 1976 was also lower than expected. However, it appears that whatever happened in 1976 primarily affected pups, not adults.

Comparisons with other studies are limited as most researchers examined other indices of body condition. Holst and Stirling (2002) examined blubber thickness in two populations of ringed seals in Baffin Bay, between May and July. Blubber thickness for pups was 4.4 (*SD* =

1.1) in Grise Fiord and 2.4 (*SD* = 1.5) in Qaanaaq. Our mean, all years combined, declined from 3.5 cm (*SD* = 0.87) in May to 2.7 cm (*SD* = 0.88) in July (Fig. 18). For seals >1 year of age, the average blubber thickness ranged from 3.7 to 4.4 in Baffin Bay (Holst and Stirling 2002). In our study, average blubber thickness declined from 3.5 cm (*SD* = 0.87) in May to 2.7 cm (*SD* = 0.88) in July (Fig. 13).

Population parameters

Age distribution—In general, the demographic characteristics of ringed seals in the Bering and Chukchi seas have changed over the last four decades. The proportion of pups in the harvest of ringed seals was significantly greater during the 2000s (56%) than the 1960s (14%) and 1970s (23%; $P < 0.01$) and was also greater than would be expected (30%) based on previous observations of ringed seals throughout the Arctic (McLaren 1958, Fedoseev 1965, Smith 1973, Smith 1987, Holst *et al.* 1999, Holst and Stirling 2002, Stirling 2005). Because age ratios are proportional, a higher proportion of pups in the sample may indicate that adult survival decreased or that reproduction increased. Based upon other information, however, it is most likely that reproduction has increased. For example, growth rate, age of maturation, pregnancy rate, and blubber thickness are average or better than expected, and hunter responses to questionnaires indicate that ringed seal numbers have not decreased. The high proportion of pups in the harvest also indicates that pups survive long enough to be harvested (*i.e.*, pups survive to weaning).

Likewise, a low proportion of pups in the harvest may indicate years when reproduction or pup survival was low. For example, few pups were harvested in 1961, 1976, and 1984 (Fig. 19). We also observed low growth rates for seals born in 1961 and 1976 (Figs. 10 and 12; no comparable data for 1984). Blubber thickness of pups (Fig. 18) and average age of maturation was also older in 1976 (Fig. 22; no comparable data for 1961 or 1984). As such, it appears that the proportion of pups in the harvest is a useful indicator of environmental conditions. However, we cannot determine if declines in harvested pups are due to pup production or survival. Studies suggest low pup production is related to heavy ice conditions (*e.g.*, Harwood *et al*. 2000, Stirling 2005) or ecosystem productivity (Holst and Stirling 2002). Pup survival may be related to snow depth (Ferguson *et al.* 2005) or rain on snow events, which increase predation pressure (Hammill and Smith 1991).

Mean age of harvest—The mean age of seals in the harvest declined with time, largely reflecting the increasing proportion of pups. Mean age at harvest is currently lower in our study than what is observed elsewhere. Currently, including pups, mean age for males is 5.0 years and mean age for females is 4.5 years. Holst *et al*. (1999) examined mean ages of ringed seals in Hudson Bay between 1991 and 1992. In spring, the mean age was 13.9 and 14.9 years for males and females, respectively. In fall, the mean age declined to 9.1 and 8.7 years for males and females, respectively, presumably because more pups were available for harvest. At Svalbard, Lydersen and Gjertz (1987) found males and females had mean ages of 14.3 and 14.9 years, respectively, and thought younger age classes, including pups, were underrepresented in their sample because harvest occurred during breeding and pupping. They suspected that territorial males were forcing younger seals farther into marginal ice habitat, where they were harder to

hunt. Also, pups were largely unavailable because they were in lairs and that females with pups are were more wary.

Sex ratios—The sex ratio of the harvest was generally male biased for subadults and adult ringed seals. This was not expected, as sex ratios are more commonly near unity (*e.g.*, Holst *et al*. 1999, Holst and Stirling 2002), or have a female bias (*e.g.*, Lydersen and Gjertz 1987). Most studies suggest the cost of maintaining territories reduces survival of adult males, thereby creating a female bias in sex ratio. Because sex ratio was calculated from harvested individuals, perhaps hunter bias accounts for a bias in males. However, we think this unlikely. Adult males and females had similar asymptotic lengths in our study. As such, hunters cannot target males by targeting large seals. The only time hunters can reliably distinguish males is during the spring, when males have darkened faces, but are likely avoided due to their "gasoline" smell. We did, in fact, see a decrease in the number of males harvested in spring. As such, it is likely that females have lower survival rates than males. We doubt this is of concern, as most other parameters we quantified are currently positive (*e.g.*, high growth rates, high proportion of pups, high pregnancy rates) or neutral (*e.g.*, average blubber thickness).

We also found male bias in the number of pups harvested, albeit much smaller than that for subadults and adults. The male bias only existed in the 2000s, as the harvest in the 1960s was female biased and the harvest in the 1970s was near unity.

Age at maturity and pregnancy rate—The average age of maturity varied significantly in time. The average age of maturity was highest in 1976 and 1977, 6.4 and 6.5 years of age, respectively (Fig. 22). In 1978, the average age of maturity significantly decreased to 5.0 years of age. Since 1999, the average age of maturity has been the lowest observed (3.2 years).

We expect the average age of maturity to increase when environmental conditions are unfavorable or limiting and decrease when environmental conditions are favorable or not limiting. In effect, we expect healthy seals with unlimited resources to grow faster and larger, and to mature younger. As such, 1976 and 1977 were likely unfavorable years. This generally agrees with other analyses that indicate seals born in 1976 had lower growth rates and less sternal blubber. Although adults had average blubber thickness in 1976, individuals did not begin breeding until they were a year older on average. Since 1999, environmental conditions have been favorable and seals are breeding at a young age.

Female reproductive tracts were analyzed for percent pregnant at harvest. The decades with the lowest percentage was the 1960s (76.8%) and the 1980s (76.2%). The 1970s had the highest percentage at 89.1% and the 2000s were next highest at 79.5%. We have yet to examine annual patterns in pregnancy rate. However, pregnancy rate is currently similar to or higher than what was observed in past years.

Conclusions

Our analyses show that ringed seals have been positively and negatively affected by past and current conditions. Currently, ringed seals are growing faster, have average blubber thickness, are maturing at the youngest age to date (indicating females are in a positive nutritional state allowing them to grow faster and become mature at an earlier age), and have the

second highest pregnancy rate to date. These factors indicate that environmental conditions are currently as favorable (or better) than they were in the 1960s or 1970s. We have little data from the 1980s and 1990s, and cannot comment on those decades. In addition, there are more pups in the harvest now. Because age ratios are proportional, a higher proportion of pups in the sample may indicate that adult survival decreased or that reproduction increased. Based upon other information, however, it is most likely that reproduction has increased. For example, growth rate, age of maturation, pregnancy rate, and blubber thickness are average or better than expected, and hunter responses to questionnaires indicate that ringed seal numbers have not decreased. The high proportion of pups in the harvest also indicates that pups survive long enough to be harvested (*i.e.*, pups survive to weaning). Sex ratios are currently male biased; however, this is probably not a concern as it corresponds to a period with high pregnancy rates and increasing numbers of pups. Levels of contaminants in ringed seals harvested in Alaska are lower than levels reported in Canada, Europe, and Russia, and the prevalence of diseases has remained stable.

A major consideration is how these indices relate to abundance. Most of the indices we quantified relate to the physiology of individuals (*e.g.*, body length or blubber thickness). While we can conclude that individuals are in good health, determining how individual health relates to population growth or abundance is more difficult. For example, individuals may exhibit high growth rates, early maturation, and high body condition in a low density population if demographics are density dependent. Clearly, inferences must be made with caution.

In some situations, however, responsible population-level inferences can be made. The physiology of individuals in our sample is representative of the population and we have decades of data for comparison. For example, we know that the reproduction of ringed seals is currently robust. Pregnancy rates are high, pups are surviving to be harvested, and pups compose a large proportion of the harvest. Hence, ringed seals are reproducing as well as or better than they have since the 1960s. Blubber thickness is currently similar to what was observed in the 1970s, but ringed seals are growing faster and maturing younger. Hence, it is likely that they are finding enough food. Using these physiologically based data, the likelihood that the population is declining due to poor reproduction, pup survival, or starvation is very low. However, detecting changes in survival that affect all age classes in a similar fashion will be problematic. For example, if predation or overharvest decreases the abundance of all age classes equally, the proportion of individuals in each age class will remain the same over time and a population decline would go undetected. Because hunter questionnaires generally indicate that the availability of ringed seals has not changed over time, it is unlikely that large changes in abundance have occurred. At a coarse scale, we can certainly conclude that ringed seals are still harvested annually throughout the Bering and Chukchi seas. Smaller, more gradual changes in abundance will be difficult to detect with questionnaires.

We have also provided baseline information for ringed seals and shown how indices vary over time. While we are primarily interested in current conditions, understanding past conditions allows us to put current conditions in context and make comparisons. Ringed seals were petitioned to be listed under the Endangered Species Act due to concerns that changing ice conditions may threaten population persistence. Although sea ice is declining now, the most significant declines in ringed seal physiological parameters to date occurred around 1961 and

1976. We do not know what caused the perturbation in 1961, but the perturbation in 1976 may have been related to a regime shift in the Bering Sea, believed to occur in 1977. Following this shift, demersal and benthic fishes decreased, while the production of zooplankton and pelagic fish increased (See review in Benson and Trites 2002). Most of the information on the 1977 regime shift comes from commercial fisheries data in the southern and central Bering Sea, which only partially overlaps the range of ringed seals in Alaska. While the regime shift is poorly understood in the northern Bering and Chukchi seas, we found evidence of physiological stress in ringed seals in 1976. Depressed physiological parameters rebounded in 1978, suggesting that conditions either improved or ringed seals quickly adapted.

We think it reasonable to assume that changing ice conditions will affect the status of ringed seals; however, predicting the direction and magnitude of those effects is speculative at best. A longer open water season is predicted to favor pelagic fish species over benthic species (*e.g.*, Grebmeier *et al*. 2006*a*, 2006b). Stirling (2002) found reduced productivity of ringed seals in heavy ice years, and speculated this was due to a shorter open water season and reduced primary productivity. As such, ringed seal productivity might be increasing as the open water season increases. However, Kelly *et al*. (2010) speculate that these benefits, if they exist, will eventually be outweighed by increased costs of pup predation and thermoregulation. Hence, in the short-term, reduced sea ice may have positive effects. If sea ice habitat changes too much, seals may be negatively affected in the long-term, but it is unclear when this will happen.

Given that there are no estimates of ringed seal abundance or trend, a critical question is whether or not this monitoring program could detect demographic changes that are the basis for listing ringed seals under the Endangered Species Act. Kelly *et al*. (2010) predict that climate warming will lead to less spring snow cover, reducing the availability of subnivean habitat ringed seals use for pupping lairs. Specifically, pups without lairs will be exposed to high mortality due to freezing and predation. Such changes will likely be detectable within the current monitoring program. If pups have non-lethal thermoregulation costs, we will likely see changes in the blubber thickness of pups and declining growth rates of seals. While we cannot directly document survival, we can identify changes in the proportion of pups in the harvest. For example, 1976 was clearly characterized by very few pups in the harvest and seals born in 1976 grew less than expected.

However the monitoring program does have limitations. While changes in pup survival will likely be detectable in age ratios and growth rates, we will not know how these changes directly relate to abundance. As such, efforts should continue to determine how to quantify the abundance of ringed seals. We also do not know how sensitive our indices are; subtle changes in survival or reproduction may be non-detectable, yet significantly affect population growth. As such, changes in growth, reproduction, and age distributions may not be detected until a number of years after changes occur. Because there are currently large numbers of ringed seals, this is probably not a serious limitation.

Recommendations

The importance of this monitoring program is difficult to overstate, and it is especially important because agencies have yet to overcome the logistical constraints necessary to estimate

seal abundance in remote, ice covered waters. As such, reliable estimates of ringed seal abundance or population trend are lacking. This monitoring program is capable of detecting changes in population parameters that affect abundance. While we cannot directly assess how abundance is changing, we should be able to detect changes predicted to occur with warming climate (*e.g.*, thermoregulatory stress and mortality of pups). Until abundance can be quantified, this monitoring program will provide the best information available for assessing the status of ringed seals in Alaskan waters. If abundance is eventually quantified, the data collected by this monitoring program will also provide valuable insights of the mechanisms driving changes in abundance. As such, we recommend this harvest-based monitoring program be continued.

ACKNOWLEDGMENTS

This study would not be possible without the willingness of the hunters to contribute samples from their harvest, the support of their communities, local governments, and Tribal Councils. Participating communities include Barrow, Wainwright, Point Hope, Kotzebue, Shishmaref, Diomede, Gambell, Savoonga, and Hooper Bay. We appreciate the support from the North Slope Borough and the Association of Village Council Presidents. John Burns, Kathy Frost, Lloyd Lowry, and others were instrumental in the development of this project and its great value comes from their early efforts to collect and process samples, as well as archive the data. We thank Gay Sheffield, Letty Hughes, Anna Bryan, and Mark Nelson for assistance in field collection and sample processing; Juan Leon Guerrero, Heidi Isernhagen, Louise Foster, and Andrew Brenner assisted with processing samples in the lab, entering and error checking historic and recent data. Funding for collections from Little Diomede Island during 2000–2005 was provided by the National Science Foundation (OPP Grant No. 9910319). The majority of funding for sample collection and analysis since 2002 was provided by the National Marine Fisheries Service with partial funding in 2005 from the North Pacific Research Board. Otoliths and cephalopod beaks were identified by William Walker at the National Marine Mammal Laboratory. Invertebrates were identified by Chris Stark at the Institute of Marine Science, University of Alaska, Fairbanks. Marine Mammal samples were collected under NMFS Permit Nos. 358-1585, 358-1787. Copies of original data from Project Chariot were provided by Gary Shugart of the Slater Museum of Natural History at the University of Puget Sound and we thank Juan Leon Guerrero for assistance with entering it. We thank Jill Seymour at the University of Alaska for testing for *Trichinella*, and Elizabeth Frame at Northwest Fisheries Science Center for testing for toxic algae.

LITERATURE CITED

AMERICAN SOCIETY OF MAMMALOGISTS. 1967. Standard measurements of seals. Journal of Mammalogy 48:459–462.

ARNOULD, J. P. Y. 1995. Indices of body condition and body composition in female Antarctic fur seals (*Actocephalus gazelle*). Marine Mammal Science 11:301–313.

BARRETT, T., M. BILIXENKRONE-MØLLER, G. DI GUARDO, M. DOMINGO, P. DUIGNAN, A. HALL, L. MAMAEV, A. D. M. E. OSTERHAUS. 1995. Morbilliviruses in aquatic mammals: report on round table discussion. Veterinary Microbiology 44:261–265.

BECKER, P. R., S. A. WISE, B. J. KOSTER, AND R. ZEISLER. 1991. Alaska Marine Mammal Tissue Archival Project: revised collection protocol. U.S. Dept. Commerce, National Institute of Standards and Technology Laboratory, Gaithersburg, MD. 33 pp.

BENGTSON, B. J., L. M. HIRUKI-RARING, M. A. SIMPKINS, AND P. L. BOVENG. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999–2000. Polar Biology 28:833–845.

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

BLUHM, B. A., AND R. GRADINGER. 2008. Regional variability in food availability for arctic marine mammals. Ecological Applications 18(2) Supplement, S77–S96.

BOSSI, R., F. F. RIGET, AND R. DIETZ. 2005. Temporal and spatial trend of perfluorinated compounds in ringed seal (*Phoca hispida*) from Greenland. Environmental Science and Technology 39:7416–7422.

BURNS, J. J. 1969. Marine Mammal Report. Alaska Department of Fish and Game, Pittman-Robertson Project Report. Volume X, W-17-1. 25 pp.

BURNS, J. J., L. H. SHAPIRO, AND F. H. FAY. 1981. Relationship of marine mammal distribution, densities, and activities to sea ice conditions. Outer Continental Shelf Environmental Assessment Program, Final Report 11:489–670.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference, 2nd edition. Springer, New York, NY.

COLEGROVE, K. M., D. J. GREIG, AND F. M. D. GULLAND. 2005. Causes of live strandings of northern elephant seals (*Mirounga angustirostris*) and Pacific harbor seals (*Phoca vitulina*) along the central California coast, 1992–2001. Aquatic Mammals 31:1–10.

CONGDON, P. 2003. Applied Bayesian modeling. John Wiley and Sons, Ltd. West Sussex, UK.

COMISO, J. C. 2006. Arctic warming signals from satellite observations. Weather 61(3):70–76.

DAOUST, P-Y., D. M. HAINES, J. THORSEN, P. J. DUIGNAN, AND J. R. GERACI. 1993. Phocine distemper in a harp seal (*Phoca groenlandica*) from the Gulf of St. Lawrence, Canada. Journal of Wildlife Diseases 29:114–117.

DARNERUD, P.O. 2003. Toxic effects of brominated flame retardants in man and in wildlife. Environment International 29: 841–853.

DEHN, L-A., G. G. SHEFFIELD, E. H. FOLLMANN, L. K. DUFFY, D. L. THOMAS, G. R. BRATTON, R. J. TAYLOR, AND T. M. O'HARA. 2005. Trace elements in tissues of phocid seals harvested in the Alaskan and Canadian Arctic: influence of age and feeding ecology. Canadian Journal of Zoology 83:726–746.

DEHN, L-A., E. H. FOLLMANN, D. L. THOMAS, G. G. SHEFFIELD, C. ROSA, L. K. DUFFY, AND T. M. O'HARA. 2006. Trophic relationships in an Arctic food web and implications for trace metal transfer. Science of the Total Environment 362:103–123.

DEMASTER, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. Journal of the Fisheries Research Board of Canada. 35:912–915.

DUIGNAN, P. J., O. NIELSEN, C. HOUSE, K. M. KOVACS, N. DUFFY, G. EARLY, S. SADOVE, D. J. ST. AUBIN, B. K. RIMA, AND J. R. GERACI. 1997. Epizootiology of morbillivirus infection in harp, hooded, and ringed seals from the Canadian arctic and western Atlantic. Journal of Wildlife Diseases 33:7–19.

EBBESMEYER, C. C., D. R. CAYAN, D. R. MCLAIN, F. H. NICHOLS, D.H. PETERSON, AND K. T. REDMOND. 1991. 1976 step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984. Pages 129–141 *in* J. L. Bentancourt and A. V. Tyler, eds.

Proceedings of the Seventh Annual Pacific Climate Workshop, April 1990, California Department of Water Resources Interagency Ecological Studies Program Technical Report No. 26.

FEDOSEEV, G. A. 1965. Age and sex composition of the kill of the ringed seal (*Phoca hispida ochotensis* Pall.) as an index of the age structure of the population. Fisheries Research Board of Canada Translation Series No. 799 (1966).

FEDOSEEV, G. A. 2000. Population biology of ice-associated forms of seals and their role in the northern Pacific ecosystems. Center for Russian Environmental Policy, Russian Marine Mammal Council, Moscow. 271 pp.

FERGUSON, S. H., I. STIRLING, AND P MCLOUGHLIN. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. Marine Mammal Science 21:121–135.

FINLEY, K. J., G. W. MILLER, R. A. DAVIS, AND W. R. KOSKI. 1983. A distinctive population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic 36:162–173.

FOSTER, G., A. P. MACMILLAN, J. GODFROID, F. HOWIE, H. M. ROSS, A. CLOECKAERT, R. J. REID, S. BREW, I. A. P. PATTERSON. 2002. A review of *Brucella* sp. infection of sea mammals with particular emphasis on isolates from Scotland. Veterinary Microbiology 90: 563–580.

FOLLMANN, E. H., G. W. GARNER, J. F. EVERMANN, AND A. J. MCKEIRNAN. 1996. Serological evidence of morbillivirus infection in polar bears (*Ursus maritimus*) form Alaska and Russia. Veterinary Record 138:615–618.

FROST, K. J., AND L. F. LOWRY. 1981. Ringed, Baikal and Caspian seals—*Phoca hispida*, *Phoca sibirica*, and *Phoca caspica*. Pages 29–53 *in:* S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Vol. 2 Seals. Academic Press, New York.

FROST, K. J., L. F. LOWRY, J. R. GILBERT, AND J. J. BURNS. 1988. Ringed seal monitoring: relationships of distribution and abundance to habitat attributes and industrial activities. Final Report Contract No. 84-ABC-00210 to USDI, Minerals Management Service, Anchorage, AK. 66 p + Appendices.

GALES, R., AND D. RENOUF. 1994. Assessment of body condition of harp seals. Polar Biology 14:381–387.

GARLICH-MILLER, J. L., L. T. QUAKENBUSH, AND J. F. BROMAGHIN. 2006. Trends in age structure and productivity of Pacific walruses harvested in the Bering Strait region of Alaska, 1952–2002. Marine Mammal Science 22: 880–896.

GARNER, G. W, J. F. EVERMANN, J. T. SALIKI, E. H. FOLLMANN, A. J. MCKEIRNAN. 2000. Morbillivirus ecology in polar bears (*Ursus maritimus*). Polar Biology 23:474–478.

GELMAN, A., J. B. CARLIN, H. S. STERN, AND D. B. RUBIN. 2004. Bayesian data Analysis, 2nd ed. Chapman and Hall/CRC, Boca Raton, FL.

GOLDSTEIN, T., J. A. K. MAZET, V. GILL, A. M. DOROFF, K. A. BUREK, AND J. A. HAMMOND. 2009. Phocine distemper virus in northern sea otters in the Pacific Ocean, Alaska, USA. Emerging Infectious Diseases 15(6):925–927.

GOYER, R. A. 1991. Toxic effects of metals. Pages 634–638 *in* M. O. Amdur, J. Doull, and C. D. Klassen, eds. The Basic Science of Poisons. Pergammon Press, NY.

GRACHEV, M. A., V. P. KUMAREV, L. V. MAMAEV, V. L. ZORIN, L. V. BARANOVA, N. N. DENIKINA, S. I. BELIKOV, E. A. PETROV, V. S. KOLESNIK, R. S. KOLESNIK, V. M. DOROFEEV, A. M. BEIM, V. N. KUDELIN, F. G. NAGIEVA, AND V. N. SIDOROV. 1998. Distemper virus in Baikal seals. Nature 338:209.

GREBMEIER, J. M., J. E. OVERLAND, S. E. MOORE, E. B. FARLEY, E. C. CARMACK, L. W. COOPER, K. E. FREY, J. H. HELLE, F. A. MC LAUGHLIN, AND S. L. MCNUTT. 2006*a*. A major ecosystem shift in the northern Bering Sea. Science 311:1461–1463.

GREBMEIER, J. M., L. W. COOPER, H. M. FEDER, AND B. I SIRENKO. 2006*b*. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. Progress in Oceanography 71:331–361.

GROTEN, J. P., E. J. SINKELDAM, J. B. LUTEN, AND P.J. VAN BLADEREN. 1990. Comparison of the toxicity of inorganic and liver-incorporated cadmium: A 4-wk feeding study in rats. Chemical Toxicology 28(6):435–441.

HAMMILL, M. O., T. G. SMITH. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. Marine Mammal Science 7:123–135.

HAMMOND, J. A., P. P. POMEROY, A. J. HALL, AND V. J. SMITH. 2005. Identification and real-time PCR quantification of phocine distempervirus from two colonies of Scottish grey seals in 2002. Journal of General Virology 86:2563–2567.

HARDER, T. C., M. HARDER, H. W. VOS, K. KULONEN, S. KENNEDY-STOSKOPF, B. LIESS, M. J. G. APPEL AND A. D. M. E. OSTERHAUS. 1996. Characterization of phocid herpesviruses type-1 and type-2 as putative α- and γ-herpesviruses of North American and European pinnipeds. Journal of General Virology 77:27–35.

HARDY, M. H., E. ROFF, T. G. SMITH, AND M. RYG. 1991. Facial skin glands of ringed and grey seals, and their possible function as odoriferous organs. Canadian Journal of Zoology 69:189–200.

HÄRKÖNEN, T., R. DIETZ, P. REIJNDERS, J. TEILMANN, K. HARDING, A. HALL, S. BRASSEUR, U. SIEBERT, S. J. GOODMAN, P. D. JEPSON, T. DAU RASMUSSEN, P. THOMPSON. 2006. The 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Diseases of Aquatic Organisms 68:115–130.

HARRISON, R. J., AND G. L. KOOYMAN. 1968. General physiology of the pinnipedia. Pages 211–296 *in:* R. J. Harrison *et al*., eds. The Behavior and Physiology of Pinnipeds. Appleton-Century-Crofts, New York, NY.

HARWOOD, L. A., T. G. SMITH, AND H. MELLING. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in Western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53(4):422–431.

HEIDE-JØRGENSEN M.-P., T. HÄRKÖNEN, R. DIETZ, AND P. M. THOMPSON. 1992. Retrospective of the 1988 European seal epizootic. Diseases of Aquatic Organisms 13:37–62.

HEWER, H. R. 1960. Age determination of seals. Nature 187:959–960.

HOLST, M. and I. STIRLING. 2002. A comparison of ringed seal (*Phoca hispida*) biology on the east and west sides of the North Water Polynya, Baffin Bay. Aquatic Mammals 28**:** 221–230.

HOLST, M., I. STIRLING and W. CALVERT. 1999. Age structure and reproductive rates of ringed seals (*Phoca hispida*) on the northwestern coast of Hudson Bay in 1991 and 1992. Marine Mammal Science 15:1357–1364.

JOHNSON, M. L., C. H. FISCUS, B. T. OSTENSON, AND M. L. BARBOUR. 1966. Marine mammals. Pages 877–924 *in:* N.J. Wilimovsky and J. N. Wolfe, eds. Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Commission, Oak Ridge, TN.

KELLY, B. P., J. L. BENGTSON, P. L. BOVENG, M. F. CAMERON, S. P. DAHLE, J. K. JANSEN, E. A. LOGERWELL, J. E. OVERLAND, C. L. SABINE, G. T. WARING, AND J. M. WILDER. 2010.

Status review of the ringed seal (*Phoca hispida*). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-212. 250 pp.

KENNEDY, S. 1998. Morbillivirus infections in aquatic mammals. Journal of Comparative Physiology 119:201–225.

KENNEDY, S., T. KUIKEN, P. D. JEPSON, R. DEAVILLE, M. FORSYTH, T. BARRETT, M. W. G. VAN DE BILDT, A. D. M. E., OSTERHAUS, T. EYBATOV, C. DUCK, A. KYDYRMANOV, I. MITROFANOV, AND S. WILSON. 2000. Mass die-off of Caspian seals caused by canine distemper virus. Emerging Infectious Diseases 6:637–645.

KOEMAN, J. H., W. S. M. VAN DE VEN, J. J. M. DE GOEIJ, P.S. TJIOE, AND J.L. VAN HAAFTEN. 1975. Mercury and selenium in marine mammals and birds. Science of the Total Environment 3:279–287.

LEBICH, M., T. C. HARDER, H. R. FREY, I. K. G. VISSER, A. D. M. E. OSTERHAUS, AND B. LIESS. 1994. Comparative immunological characterization of type-specific and conserved B cell epitopes of pinniped, felid and canid herpesviruses. Archives of Virology 136:335–347.

LYDERSEN, C., AND I. GJERTZ. 1987. Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. Canadian Journal of Zoology 65:1021–1027.

MACMILLAN, A. 1992. Conventional serological tests. Pages 153–197 *in:* K. Nielsen and J. R. Duncan (eds.), Animal brucellosis. CRC Press, Boca Raton, FL.

MARTIN, J.W., SMITHWICK, M.M., BRAUNE, B.M., HOEKSTRA, P.F., MUIR, D.C.G., AND MABURY, S., 2004. Identification of long-chain perfluorinated acids in biota from the Canadian Arctic. Environmental Science and Technology 38:373–380.

MAMAEV, L. V., N. N. DENIKINA, S. I. BELIKOV, V. E. VOLCHKOV, I. K. G. VISSER, M. FLEMING, C. KAI, T. C. HARDER, B. LIESS, A. D. M. E. OSTERHAUS, T. BARRETT. 1995. Characterization of morbilliviruses isolated from Lake Baikal seals (*Phoca sibirica*). Veterinary Microbiology 44:251–259.

MANSFIELD, A. W., AND H. F. FISHER. 1960. Age determination in the harbour seal, *Phoca vitulina* L. Nature 186: 92.

MCLAREN, I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Fisheries Research Board of Canada Bulletin No. 118. 97 pp.

MCLAREN, I. A. 1993. Growth in pinnipeds. Biological Review 68:1–79.

METHOD 1630. EPA-821-R-01-020. 2001. Methyl mercury in water by distillation, aqueous ethlyation, purge and trap, and CVAFS. U.S. Environmental Protection Agency, Office of Water, Office of Science and Technology, Washington, D.C.

MILLER, A. J., D. R. CAYAN, T. P. BARNETT, N. E. GRAHAM and J. M. OBERHUBER. 1994. The 1976–77 climate shift of the Pacific Ocean. Oceanography 7:21–26.

MILLER, W. G., L. G. ADAMS, T. A. FICHT, N. F. CHEVILLE, J. B. PAYEUR, D. R. HARLEY, C. HOUSE, AND S. H. RIDGWAY. 1999. Brucella-induced abortions and infections in bottlenose dolphins (*Tursiops truncatus*). Journal of Zoo and Wildlife Medicine 30:100–110.

MOORE, S. E., J. M. GREBMEIER, AND J. R. DAVIES. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81:734–742.

MOULTON, F. D., W. J. RICHARDSON, T. L. MCDONALD, R. E. ELLIOTT, AND M. T. WILLIAMS. 2002. Factors influencing local abundance and haulout behavior of ringed seals (*Phoca hispida*) on landfast ice of the Alaskan Beaufort Sea. Canadian Journal of Zoology 80:1900–1917.

MUETER, F. J. and M. A. LITZOW. 2008. Sea ice retreat alters the biogeography of the Bering Sea Continental Shelf. Ecological Applications 18:309–320.

NAKATA, H., S. TANABE, R. TATSUKAWA, Y. KOYAMA, N. MIYAZAKI, S. BELIKOV, AND A. BOLTUNOV. 1998. Persistent organochlorine contaminants in ringed seals (*Phoca hispida*) from the Kara Sea, Russian Arctic. Environmental Toxicology and Chemistry, Vol. 17(9):1745–1755.

NIEBAUER, H. J. 1980. Sea ice and temperature fluctuations in the eastern Bering Sea and the relationship to meteorological fluctuations. Journal of Geophysical Research 85:7505–7515.

NIEBAUER, H. J. 1983. Multiyear sea ice variability in the eastern Bering Sea: An update. Journal of Geophysical Research 88:2733–2742.

NIEBAUER, H. J. 1988. Effects of El Niño-Southern Oscillation and North Pacific weather patterns on interannual variability in the subarctic Bering Sea. Journal of Geophysical Research 93:5051–5068.

NEILSEN, O., K. NIELSEN, AND R. E. A. STEWART. 1996. Serologic evidence of *Brucella* spp. exposure in Atlantic walruses (*Odobenus rosmarus rosmarus*) and ringed seals (*Phoca hispida*) of Arctic Canada. Arctic (49)4:383–386.

NORTHERN CONTAMINANTS PROGRAM. 2003. Canadian Arctic contaminants assessment report II: Contaminant levels, trends, and effects in the biological environment. Minister of Public Works and Government Service Canada, Ottawa, Canada.

OSTERHAUS, A. D. M. E., H. YANG, H. E. M. SPIJKERS, J. GROEN, J. S. TEPPEMA, AND G. VAN STEENIS. 1985. The isolation and partial characterization of a highly pathogenic herpesvirus from the harbor seal (*Phoca vitulina*). Archives of Virology 86:239–251.

PARSONS, J. L. 1977. Metabolic studies on ringed seals (*Phoca hispida*). MS thesis, University of Guelph, Guelph, Canada.

QUAKENBUSH, L. T. 2007. Polybrominated diphenyl ether compounds in ringed, bearded, spotted, and ribbon seals from the Alaskan Bering Sea. Baseline/Marine Pollution Bulletin 54:226–246.

QUAKENBUSH, L. T., AND J. J. CITTA. 2008*a*. Biology of the ribbon seal in Alaska. Unpublished report to NMFS. 45 pp.

QUAKENBUSH, L. T., AND J. J. CITTA. 2008*b*. Perfluorinated contaminants in ringed, bearded, spotted, and ribbon seals from the Alaskan Bering and Chukchi seas. Marine Pollution Bulletin 56:1802–1814.

QUAKENBUSH, L. T., J. J. CITTA, AND J. A. CRAWFORD. 2009. Biology of the spotted seal. Unpublished report to NMFS. 66 pp.

RAFTERY, A. E., AND S. M. LEWIS. 1995. The number of iterations, convergence diagnostics and generic Metropolis algorithms. In Practical Markov Chain Monte Carlo (W.R. Gilks, D.J. Spiegelhalter and S. Richardson, eds.). London, U.K.: Chapman and Hall.

RAMSEY, F. L., AND D. W. SCHAFER. 2002. The statistical sleuth: A course in methods of data analysis. Second edition. Duxbury, Pacific Grove, CA, USA.

RIGET, F., D. MUIR, M. KWAN, T. SAVINOVA, M. NYMAN, V. WOSHNER, AND T. O'HARA. 2005. Circumpolar pattern of mercury and cadmium in ringed seals. Science of the Total Environment 351–352:312–322.

RIGOR, I. G., AND J. M. WALLACE. 2004. Variations in the age of Arctic sea-ice and summer sea-ice extent. Geophysical Research Letters, Vol. 31, L09401, doi:10.1029/2004GL019492.

ROBERTSON, J. L., R. M. RUSSELL, H. K. PREISLER, AND N. E. SAVIN. 2007. Bioassays with arthropods, 2nd Edition. CRC Press. 224 pp.

RYG, M., C. LYDERSEN, N. H. MAKUSSEN, T. G. SMITH, AND N. A. ORISLAND. 1990a. Estimating the blubber content of phocid seals. Canadian Journal of Fisheries and Aquatic Sciences 47:1223–1227.

RYG, M., T. G. SMITH, AND N. A. ORISLAND. 1990b. Seasonal changes in body mass and body composition of ringed seals (*Phoca hispida*) on Svalbard. Canadian Journal of Zoology 68:470–475.

RYG, M., Y. SOLBERG, C. LYDERSEN, AND T. G. SMITH. 1992. The scent of rutting male ringed seals (*Phoca hispida*). Journal of Zoology, London 226:681–689.

SALIKI, J. T., AND T. W. LEHENBAUER. 2001. Monoclonal antibody-based competitive enzyme-linked immunosorbent assay for detection of morbillivirus antibody in marine mammal sera. Journal of Clinical Microbiology 39:1877–1881.

SAS Institute Inc. 2004. SAS/STAT 9.1 User's Guide. Cary, NC, USA.

SCHNUTE, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences 38:1128–1140.

SERREZE, M. C., M. M. HOLLAND, AND J. STROEVE. 2007. Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533–1536.

SIMPSON, E. H. 1949. Measurement of diversity. Nature (London) 163:688.

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

SKALSKI, J. R., K. E. RYDING, AND J. J. MILLSPAUGH. 2005. Wildlife demography: Analysis of sex, age, and count data. Elsevier Academic Press. San Diego, California, USA. 656 pp.

SMITH, T. G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Fisheries Research Board of Canada Bulletin No. 181. 55 pp.

SMITH, T. G. 1987. The ringed seal, *Phoca hispida*, of the Canadian Western Arctic. Canadian Bulletin of Fisheries and Aquatic Sciences 216: 81pp.

SPIEGELHALTER, D. J., N. G. BEST, B. P. CARLIN , AND A. VAN DER LINDE. 2002. Bayesian measures of model complexity and fit (with discussion). Journal of the Royal Statistical Society, Series B. 64:583–640.

SPIEGELHALTER, D., A. THOMAS, N. BEST, AND D. LUNN. 2003. WinBUGS user manual, version 1.4. Available online at: http://www.mrc-bsu.cam.ac.uk/bugs/ winbugs/manual14.pdf.

STEWART, R. E. A., B. E. STEWART, I. STIRLING, E. STREET. 1996. Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). Marine Mammal Science 12:383–401.

STIRLING, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. Arctic 55(Supplement): 59–76.

STIRLING, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991–2000. Polar Biology 28:381–387.

STRANDBERG, B., N. G. DODDER, I. BASU, AND R.A. HITES. 2001. Concentrations and spatial variations of polybrominated diphenyl ethers and other organohalogen compounds in Great Lakes air. Environmental Science and Technology 46:745–755.

STROEVE, J., M. SERREZE, S. DROBOT, S. GEARHEARD, M. M. HOLLAND, J. MASLANIK, W. MEIER, AND T. SCAMBOS. 2008. Arctic sea ice extent plummets in 2007. Eos Transactions, American Geophysical Union 89:13–14.

TIKHOMIROV, E. A. 1966. On the reproduction of the seals belonging to the family Phocinae in the North Pacific. Zoological Journal 45:275–281. FRBC Translation No. 1889.

TRENBERTH, K. E. 1990. Recent observed interdecadal climate changes in the Northern Hemisphere. American Meteorological Society 71(1):988–993.

TRIPPEL, E. A. AND H. H. HARVEY. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences 48:1446–1459.

TRYLAND, M., A. E. DEROCHER, Ø. WIIG, AND J. GODFROID. 2001. *Brucella* sp. antibodies in polar bears from Svalbard and the Barents Sea. Journal of Wildlife Diseases 37:523–531.

VIBERG, H., FREDRIKSSON, A., AND ERIKSSON, P. 2004. Investigations of strain and/or gender differences in developmental neurotoxic effects of polybrominated diphenyl ethers in mice. Toxicological Sciences 81:344–353.

VISSER, I. K. G., J. S. TEPPEMA, AND A. D. M. E. OSTERHAUS. 1991. Virus infections of seals and other pinnipeds. Reviews in Medical Microbiology 2:105–114.

WEIS, I. M., AND D.C. G. MUIR. 1997. Geographical variation of persistent organochlorine concentrations in blubber of ringed seal (*Phoca hispida*) from the Canadian Arctic: univariate and multivariate approaches. Environmental Pollution 96(3):321–333.

Wheeler, M. W., R. M. PARK, AND J. A. BAILER. 2006. Comparing median lethal concentration values using confidence interval overlap or ratio tests. Environmental Toxicology and Chemistry 25:1441–1444.

WILIMOVSKY, N. J., AND J. N. WOLFE, EDITORS. 1966. Environment of the Cape Thompson region, Alaska. United States Atomic Energy Commission. Washington, D.C., USA. 1250 pp.

WOSHNER, V.M., O'HARA, T.M., BRATTON, G.R., SUYDAM, R.S. AND BEASLEY, V.R. 2001*a*. Concentrations and interactions of selected essential and non-essential elements in bowhead and beluga whales of Arctic Alaska. Journal of Wildlife Diseases 37:693–710.

WOSHNER, V.M., O'HARA, T.M., BRATTON, G.R. AND BEASLEY, V.R. 2001b. Concentrations and interactions of selected essential and non-essential elements in ringed seals and polar bears of Arctic Alaska. Journal of Wildlife Diseases 37:711–721.

ZARNKE, R. L., T. C. HARDER, H. W. VOS, J. M. VER HOEF, AND A.D.M.E. OSTERHAUS. 1997. Serologic survey for phocid herpesvirus-1 and -2 in marine mammals from Alaska and Russia. Journal of Wildlife Diseases 33:459–465.

ZARNKE, R. L., J. T. SALIKI, A. P. MACMILLAN, S. D. BREW, C. E. DAWSON, J. M. VER HOEF, K. J. FROST, AND R. J. SMALL. 2006. Serologic survey for *Brucella* spp., phocid herpesvirus-1, phocid herpesvirus-2, and phocine distemper virus in harbor seals from Alaska, 1976–1999. Journal of Wildlife Diseases 42:290–300.