Biology of the Bearded Seal (*Erignathus barbatus*) in Alaska, 1961–2009

Final Report to:

National Marine Fisheries Service

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EXECUTIVE SUMMARY

The Alaska Department of Fish and Game (ADF&G) has been monitoring the health and status of bearded seals (*Erignathus barbatus*) in Alaska since 1962 by collecting information and samples from the Alaska Native subsistence harvest. This monitoring program 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 bearded seal abundance or population trend are lacking. Retrospective analyses of data provided by this monitoring program allow us to examine how parameters that affect population size 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 bearded 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 bearded seal numbers (availability) at any location. The majority of respondents from all villages reported that bearded 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 943 bearded seals collected between 1961 and 2009, we identified 213 different fish and invertebrate prey of which 113 were common. Using percent frequency of occurrence, bearded seals were 21.8 times more likely to consume fish in the 2000s than during the 1960s ($P < 0.01$) and 16.8 times more likely in the 1970s than during the 1960s ($P < 0.01$). The increase in general fish consumption over time was strongly correlated with changes in the consumption of sculpin ($r = 0.67$), suggesting changes in the consumption of sculpin were likely responsible for variations we observed among all fish. In the 2000s, bearded seals consumed a greater diversity of fish species ($D = 0.21$) than during the 1960s ($D = 0.35$) and 1970s ($D = 0.30$) based on Simpson's diversity index.

Bearded seals commonly consumed invertebrates in all decades; over 95% of stomachs with food included invertebrate prey. Changes in the consumption of invertebrate prey were largely explained by changes in crustacean consumption ($r = 0.67$), specifically decapods ($r = 0.55$). Bearded seals consumed fewer crustaceans during the 2000s than in the 1960s or 1970s ($P < 0.01$), which did not differ from each other ($P = 0.24$).

Contaminants—Liver ($n = 42$) and kidney ($n = 16$) tissues from bearded seals collected during 2003 and 2007 were analyzed for concentrations of potentially toxic elements such as arsenic, cadmium, mercury, and lead. Within Alaska, bearded seals had the second highest concentrations of cadmium and mercury of the four species of ice seals in our studies (only ribbon seals were higher); lead levels were very low in all ice seals analyzed. Blubber ($n = 33$)

and liver (n = 23) tissues were analyzed for persistent organochlorine compounds and compared to ringed, spotted, and ribbon seals in Alaska, bearded seals had the lowest levels of total HCH (hexachlorocyclohexane), DDT (dichlorodiphenyltrichloroethane), and PCB (polychlorinated biphenyls) and the second lowest levels of CHL (chlordanes) in our studies.

Disease—Antibodies for *Brucella* and phocine herpesvirus were detected in bearded seals at levels below or similar to those observed during 1978–1990. No antibodies of phocine or canine distemper, *Leptospira*, or *Toxoplasma* were detected. Screening for toxic algae detected domoic and saxitoxin at very low levels in three and four of 14 individual ringed seals, respectively.

Growth rates—We analyzed growth rate using length at age data for 289 bearded seals ≥1 years old. Seals were identified as being longer or shorter than expected, given their age, and were then classified by birth year. Bearded seals were significantly longer than expected in 1964, 1967, 1968, 1969, and 2007, and were shorter than expected in 1979, 1996, and 2004. In general, bearded seals were shorter in the 2000s than in the 1970s. Compared with the 1970s, bearded seals sampled in the 2000s were shorter in 8 of 10 age classes, although there were only statistically significant differences for older age classes, including ages 8, 9, and ≥10 years of age. Asymptotic length, calculated as the average length of seals >10 year of age, was 208.6 cm (95% CI ± 5.4) in the 2000s and 218.6 (95% CI ± 3.1) in the 1970s.

Body condition—Using the blubber thickness of 68 subadult and 172 adult bearded seals collected between 1975 and 2010, model results indicated that bearded seals had less blubber than expected in 1977, 1978, 1979, and 1991, although there were only statistically significant differences in 1978 and 1991. In contrast, blubber thickness was greater than average between 2004 and 2010, although there were only statistically significant differences in 2008 and 2010.

Age distributions—We analyzed age at harvest for 208 bearded seals harvested in the 1960s, 2,044 in the 1970s, and 527 in the 2000s. We found fewer pups in the 1960s than the 1970s or 2000s ($P < 0.01$). Overall, the mean age at harvest of bearded seals was greater in the 1960s ($\bar{x}$ = 6.8 years) and 2000s ($\bar{x}$ = 5.2 years) than in the 1970s ($\bar{x}$ = 4.4 years; $P < 0.01$). Differences in mean age by time period were largely due to variation in how many pups were harvested.

Sex ratios— Sex ratios of pups were generally near, or statistically indistinguishable from, unity. Sex ratios of adults were generally female biased, but more so in the Chukchi Sea than in the Bering Sea. Sex ratios of subadults varied by decade and region.

Age at maturity and pregnancy rate—Sexual maturity was determined for 367 female ringed seals; 96 harvested in the 1960s, 183 in the 1970s, and 88 in the 2000s. The average age of maturity was statistically indistinguishable by decade, averaging 4.01 years of age in the 1960s, 3.97 in the 1970s, and 3.90 since 2000. Average age at maturity for all years combined was 3.97 years of age (95% CL = 3.5 to 4.4). Female reproductive tracts were analyzed for percent pregnant at harvest. The 1960s was the lowest at 88.3%, followed by 91.2% in the 1970s and 93.9% in the 2000s.

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 bearded seals have been positively and negatively affected by past and current conditions. Currently, bearded seals grow to a shorter asymptotic length than they did in the 1970s; however, statistically significant differences were observed only in seals 8, 9, and ≥10 years of age. Most of a seal's growth occurs in the first two or three years after birth; as such, decreased length in these seals likely reflects poor foraging conditions in the 1990s or early 2000s. In contrast, metrics that reflect current environmental conditions had rates that were similar to or greater than what was observed earlier. For example, we found no evidence that age at maturation has changed over time. Blubber thickness and pregnancy rates are currently higher than was observed previously. In addition, there are similar proportions of pups in the harvest now as in the 1970s and twice as many as in the 1960s. The high number of pups in the harvest indicates that pups are surviving long enough to be harvested (*i.e*., pups survive to weaning). Hunter responses to questionnaires indicate that bearded seal numbers have not decreased. Sex ratios are currently equal and correspond to a period with high pregnancy rates and a high number of pups in the harvest. Levels of contaminants in bearded seals are lower than levels of other ice seal species harvested in Alaska 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 population size is not possible. Parameters that determine the status of the bearded seal population in the Bering, Chukchi, and Beaufort seas are currently neutral or more favorable than during the 1960s and 1970s.

INTRODUCTION

In Alaska, the bearded seal (*Erignathus barbatus*) 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 ringed seal (*Phoca hispida* or *Pusa hispida*), the spotted seal (*Phoca largha*) and the ribbon seal (*Histriophoca fasciata*). Bearded seals have a wide Arctic distribution that includes the Chukchi and Beaufort seas of Alaska, as well as Arctic Canada, Svalbard and Russia, but they are also found in the subarctic Bering Sea, the Sea of Okhotsk and the Sea of Japan (Burns 1981). Bearded seals are predominantly benthic feeders and require shallow water depths (generally <500 m), which limits their distribution. Bearded seals are capable of maintaining breathing holes in heavy ice but are more typically found in broken ice, where maintaining breathing holes is not required. Bearded seals give birth on top of the ice from March to May (Burns 1981) and pups are weaned after ~3 weeks (Gjertz *et al*. 2000). In spring (April–June), many bearded seals move north through the Bering Strait to spend the open-water season near sea ice in the Chukchi Sea, although recent telemetry studies have shown they rarely haul out even when ice is available for resting (Frost *et al*. 2008, Cameron *et al*. 2010). Many return to the Bering Sea in late fall to winter. Not all bearded seals leave the Bering Sea in summer and some, especially juveniles, are found in open water and up some rivers (Burns 1981). Bearded seals are not believed to haul out on land in the Bering-Chukchi region, although they are known to come ashore in other parts of their range (*e.g.*, Sea of Okhotsk, White and Laptev Sea; see Burns 1981).

Bearded seals are currently being considered for listing as Threatened under the Endangered Species Act, largely due to concerns regarding how changes in sea ice resulting from climatic warming may affect the species (50 CFR 223 Vol. 75, No. 237:77496–77515). 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.

Population estimates for bearded seals are difficult to obtain due to problems related to conducting surveys over large areas of ice-covered waters and the lack of information to correct for seals in the water during surveys. Currently, there are no reliable estimates of population abundance or trend.

The Alaska Department of Fish and Game (ADF&G) has been collecting information and samples from the Alaska Native subsistence harvest of all ice seal species including bearded seals for more than 40 years in order to monitor the health and status of the populations in the absence of reliable population estimates and trends. Retrospective analyses of data provided by this monitoring program allow us to examine how parameters that affect population size 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 bearded seals in Alaska (Fig. 1).

In this report we analyze bearded seal measurements and samples collected between 1961 and 2009 in order to evaluate how diet, growth rates, body condition, age distribution, productivity, and composition of the harvest have changed over time. The purpose of this report is to make unpublished data, collected by the State of Alaska, available for researchers, managers, subsistence hunters, and others with an interest in the status of bearded seals in Alaska.

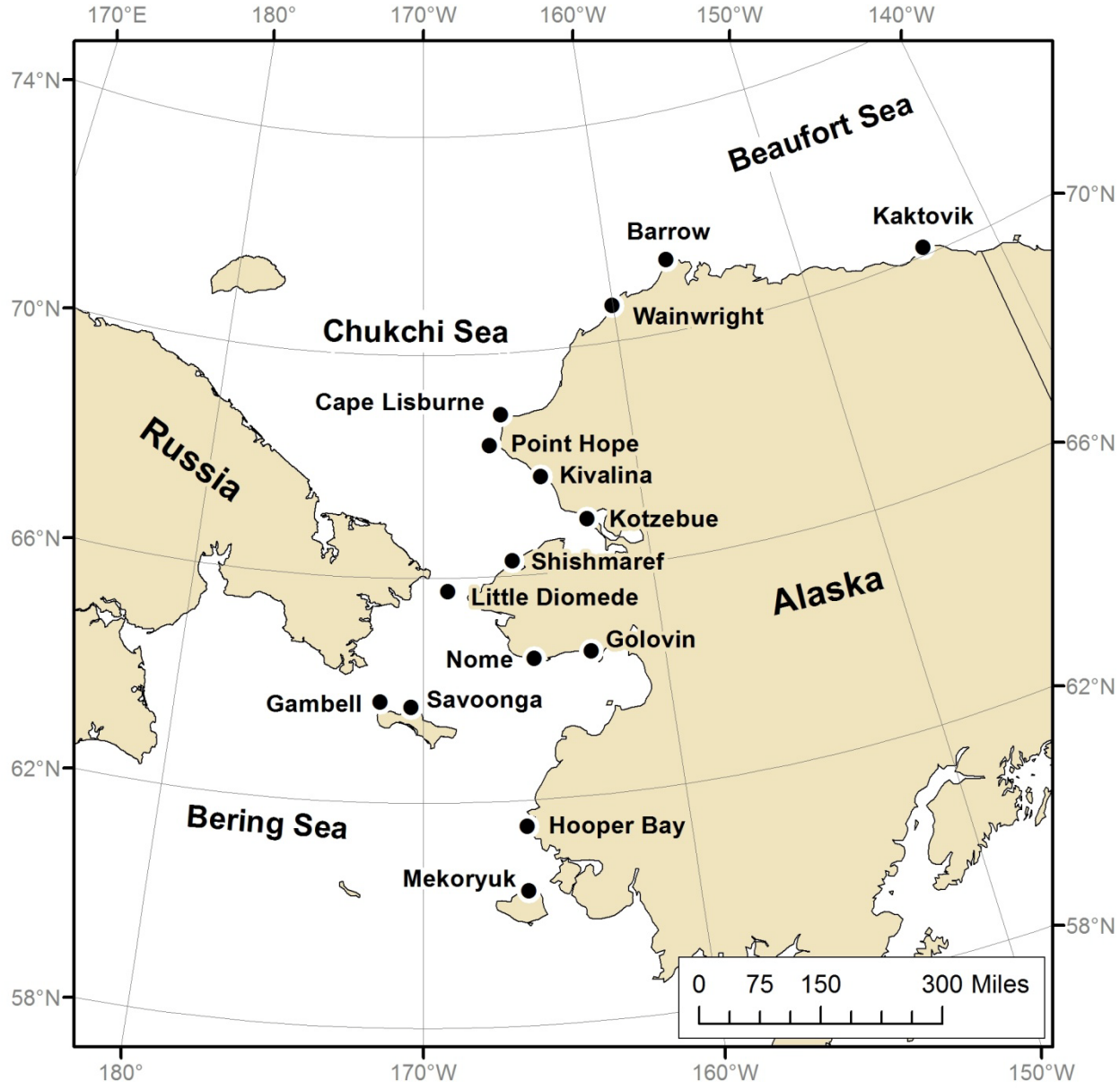

Figure 1. Collection locations.

METHODS

Sampling years

Bearded seals from the subsistence harvest were sampled between 1961 and 2009; however, sampling effort and opportunity were not consistent. The majority of bearded seals sampled were harvested during two time periods, 1960–1979 (1960s and 1970s) and 1998–2009 (2000s; Fig. 2). Bearded seals were also collected on scientific cruises in 1968, 1972, and 1976–1979 (n = 150); seals from cruises were included in our analyses when appropriate. Cruise data

were included in analyses of diet, age at maturation, and pregnancy rate. Cruise data were also included in the analysis of age distribution after preliminary statistical analyses indicated that the age distribution of cruise data did not differ from that of the subsistence harvest ($P = 0.28$). We were able to include data from 128 bearded 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 were able to acquire 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.

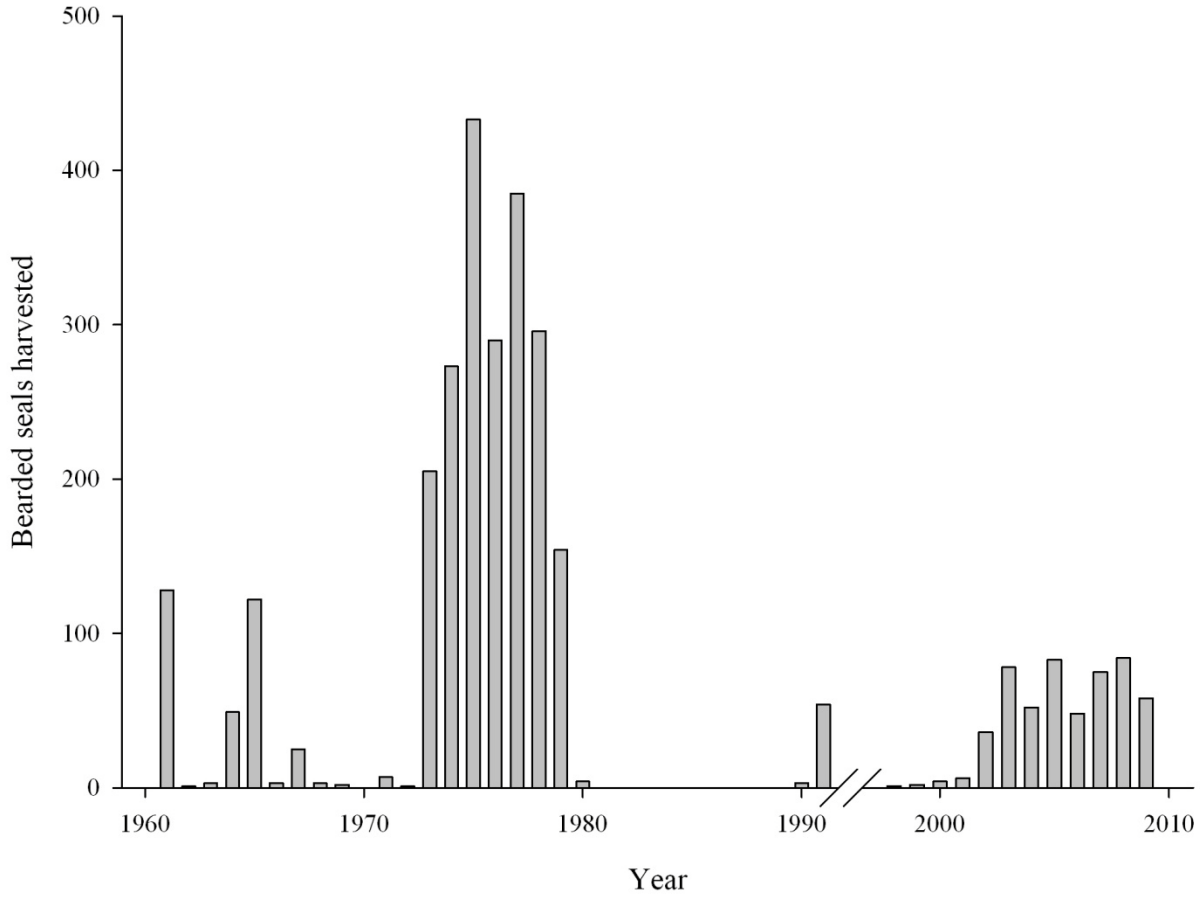

Figure 2. Number of bearded seals sampled in Alaska, by year, for which ages are known, 1961–2009. Sample sizes differed slightly for each analysis, as not all measurements or samples were collected for each seal. Although sample sizes differ by analysis, this figure illustrates the general distribution 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. In addition to hunter questionnaires we also attend Ice Seal Committee meetings where regional reports are presented and we collect Traditional Knowledge in relation to other projects where information about bearded seals is shared.

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 is defined as the straight line distance measured 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 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). Growth ridges on claws were found to be reliable for aging bearded seals for at least 8 years, after which time claw wear makes them reliable for a minimum age only (Burns 1969, 1981). 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 (McLaren 1958). 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 bearded seals from 1961–2009 to determine if the frequency of prey items has changed over time. Stomachs from bearded seals harvested by Alaskan Natives and during scientific cruises were collected, frozen, and shipped to ADF&G offices in Fairbanks. Stomachs 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 bearded seal diet, we first calculated the frequency of occurrence (FO) for each item of prey. 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 also 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 software (Version 9.2; PROC CORR, SAS Institute Inc., Cary, NC, USA) to examine correlations among annual FO values for all prey items across all decades and within each decade. 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 bearded seal diet had changed over time, we used logistic regression to calculate odds ratios (OR) and test for differences in the presence (0 = absent, 1 = present) of prey species in stomachs containing prey. Variables of interest included decade (1960s, 1970s, and 2000s), sex, region (Bering and Chukchi seas), season (spring-summer and fall-winter), and age class (pup: <1, subadult: 1–6, adult: ≥7). We used OR 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 with SAS software (PROC LOGISTIC) and the best model was selected using a backward elimination procedure that sequentially removed statistically non-significant variables (P >0.05) until only statistically significant variables remained.

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 category *i* (*e.g.*, fish), divided by the cumulative number of fish taxa identified in all bearded 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 are 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 bearded 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 with 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 bearded 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 total number of all individual prey items identified (total) or the total number of stomachs (occurrences).

For invertebrate prey, we only used occurrences of prey items 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—Bearded 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 that allowed the required sample quantity 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 tissue was 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, 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, 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*. (2000a, 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 (wet wt). 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 tissue 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 are reduced to 3 mL by evaporative solvent reduction. A 100 μL aliquot is removed and weighed to determine lipid weight. The remaining sample portion is 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 are 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 was 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 (ppb) and parts-per trillion (ppt) 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 bearded 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 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—When length-at-age data are available, growth rates are usually estimated with non-linear, asymptotic models, such as von Bertalanffy or Richards' curves (*e.g.*, McLaren 1993). We fit a variety of asymptotic models to length-at-age data for bearded seals, but were not satisfied with the levels of error we observed. Specifically, most models appeared to estimate asymptotic length well, but no models adequately described growth between one and five years of age as virtually all the residuals were positive for this range of ages. To compare the 1970s with the 2000s, we decided to compare age categories directly. Seals were classified into one of ten age categories: 1, 2, 3, 4, 5, 6, 7, 8, 9, and ≥10 years of age. By age 10, seals appeared to have reached asymptotic length, so all seals ten years of age or greater were grouped together. To allow for small sample sizes in some age categories, standard length was rank transformed. Such a non-parametric test has less power than the parametric alternative; hence, this test is conservative if data are normally distributed. The full model examined rank transformed standard length as a function of seal age (years), sex (male or female), decade (1970s or 2000s), the interaction of sex and age, and the interaction of age and decade. We then used Type III sums of squares to determine if variables were significant ($P < 0.05$) and sequentially dropped non-significant variables from the model. Statistical contrasts were then used to identify specific age categories that differed by decade.

We were also interested in determining if standard length was associated with particular cohorts of seals. We first calculated the average length for each year age. Then 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 age. We then looked for years or strings of years associated with seals that were long (or short), given their age at harvest.

In our analyses, we did not include seals less than one year of age. We also chose to include ages determined by claws. In the 1970s, some bearded seals were aged by counting claw annuli, which is accurate for seals younger than 8 years of age, after which some of the annuli are worn away (Burns 1981). Ageing seals by counting layers of cementum was expensive and reserved for older seals, where claw annuli were likely worn away. Few young seals were aged with teeth and few old seals were aged with claws; however, what overlap exists follows the overall pattern of growth closely (Fig. 3); note how young seals aged with teeth fall within the range of lengths for seals of similar claw-derived ages. Old seals aged with claws also fall within the range of lengths for seals of similar tooth-derived ages. Hence, pooling of claw- and tooth-derived ages appears appropriate.

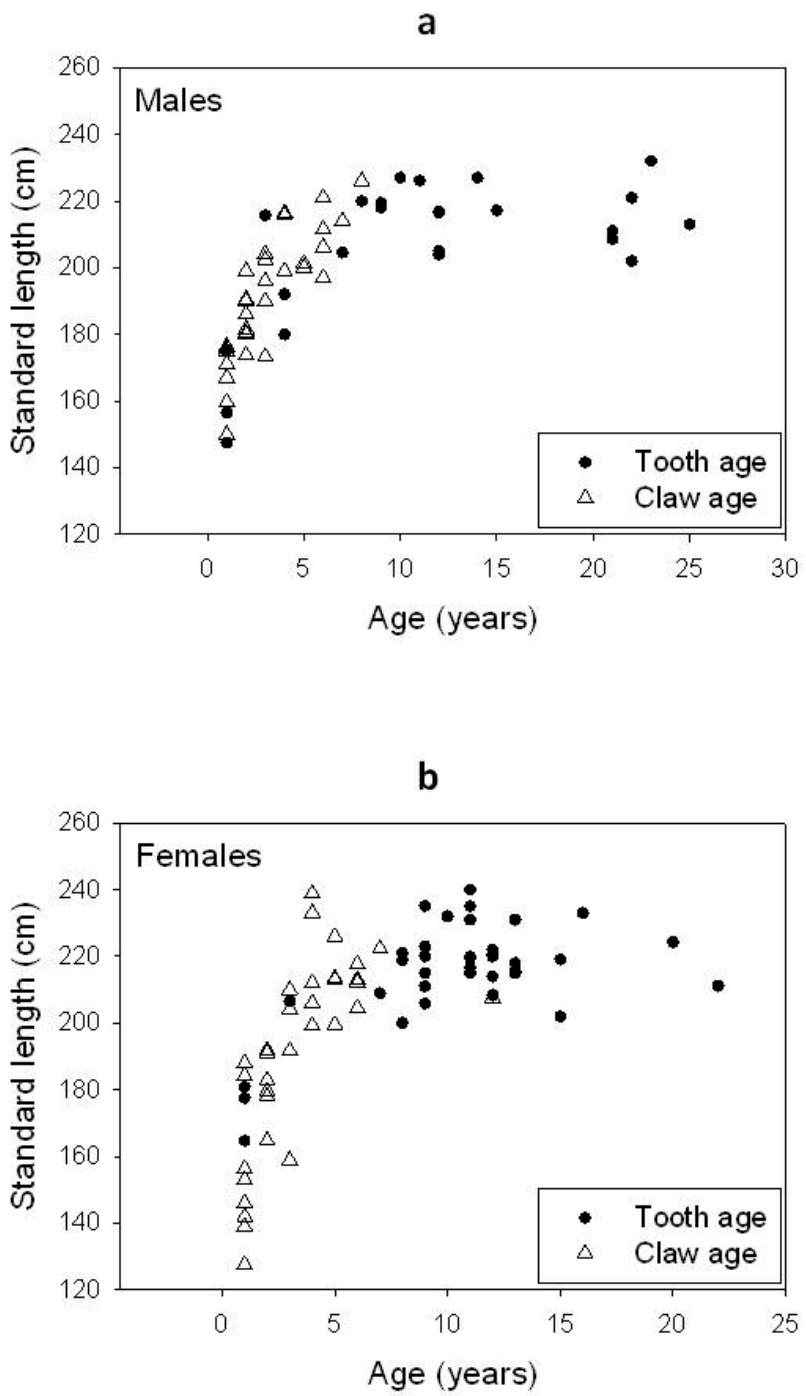

Figure 3. Comparison of standard lengths (cm) by age for seals aged via claws (triangles) or teeth (circles) for a) males and b) females.

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*, Arnould 1995, Gales and Renouf 1994). 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 and June as these months had samples in most years. Covariates were tested for significance using Type III sums of squares and non-significant parameters ($P > 0.05$) were dropped from the model, one-at-a-time. For seals $\geq$1 year of age, we examined the effect of month (May or June), age (years), age squared, sex (male or female), and the interaction between month and sex. Month was included because seals are expected to gain and lose mass seasonally (Ryg *et al*. 1990b). An examination of blubber thickness for all months (years pooled) indicated that blubber thickness may increase with age in a linear fashion. We speculate that the cost of molting and breeding are largely fixed costs. If these costs are fixed, we would expect bigger seals, mostly older seals, to lose less blubber during the breeding season. To account for possible curvilinear effects, age squared was included. We also included an age category where seals were either classified as subadults (1 to 4 years of age) or adults ($\geq$5 years of age). This approach is similar to that used for ringed seals, except that we used standard length instead of age when examining blubber thickness in ringed seals (Quakenbush *et al.* 2011). Here we use age instead of standard length as a covariate, because standard length was not measured on most bearded seals in the 1970s. 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 age, sex, or harvest month.

Population parameters

Age distribution—We characterized the age distribution of bearded seals harvested for subsistence in the 1960s, 1970s, and 2000s by plotting the proportions of seals in each age class. The seal harvest was sampled from 1962–1979 and 1998–2009; however, sampling effort and opportunity were not consistent (Fig. 2). Seals collected on research cruises in the 1970s (n = 150) were included in this analysis because the distribution of age classes from cruises and the subsistence harvest did not differ ($P = 0.28$) within the 1970s.

To compare age distributions over time, we categorized our sample into six groups and calculated chi-square statistics (Skalski *et al*. 2005). The age groups were <1 (Pup), 1–5, 6–10, 11–15, 16–20, and >20 years of age. For each age classification, we tested for differences in the proportion of seals harvested in the 1960s, 1970s, and 2000s using chi-squared statistics in SAS (PROC FREQ).

Mean age of harvest—We estimated mean age of bearded seals harvested during 1962–2009. To isolate the effect of including pups in our calculations, we estimated mean age both including and excluding pups. If hunters harvested bearded seals randomly with respect to age, differences in mean harvest ages may represent actual changes in the age structure of the bearded 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 used model selection and logistic regression to examine how sex ratios changed over time. Logistic regression is an appropriate framework for analysis as seals are either male (1) or female (0) and can be treated as having a binomial distribution. Variables included decade (1960s, 1970s, and 2000s), region (Bering and Chukchi seas), and a decade by region interaction. For each age class (pups: <1; subadults: 1–6; adults ≥7), the best model was selected using a backward elimination procedure. We only included data for which decade by region combinations had >20 samples. There were only three pups sampled in the Chukchi Sea during the 1960s, so this group was removed from the analysis. While logistic regression helps identify regional or temporal patterns in sex ratios, it does not directly examine how sex ratios differ from unity (*i.e.*, equal male:female ratio). To interpret how sex ratios compared to unity, we plotted the proportion of males and 95% confidence limits.

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 examined how age at maturity changed over time using a model selection framework with generalized linear models. We examined five models of age at maturity, differing in how age at maturity changed over time. For example, one model assumed that age at maturity was the same over time periods and another assume that age at maturity differed by each time period. Models were selected using Akaike Information Criterion (Burnham and Anderson 2002). AIC is equal to the -2 log likelihood of the model, plus 2 times the effective number of parameters. We first used AIC to determine if a logistic or a probit link function fit the data best. Traditionally, age at length models are fit with probit link functions (*e.g.*, Trippel and Harvey 1991), but a logistic link may fit the data best. Models were optimized within SAS using PROC GENMOD and PROC PROBIT.

RESULTS

Local knowledge

A total of 176 questionnaires were analyzed from five Bering and Chukchi sea villages. At all locations, the majority of respondents thought that bearded seal abundance had not changed over time (Table 1). The majority of respondents from all villages also reported that bearded seals were found in the same locations as in the past and that timing of hunting had not changed.

Although the majority of Point Hope and Hooper Bay hunters reported preferences for certain types of bearded seals their preferences were highly variable. In Point Hope, many of the preferences were for the best skins to cover whaling boat frames (umiaks). In general, Point Hope hunters preferred big seals for boat coverings; however, some thought female skins were better because they had fewer scars while others thought males were better because the female teats made thin areas in the skin. For food, some hunters at Hooper Bay preferred big seals because they have more meat and oil while others preferred small seals for more tender meat. The majority of hunters in Shishmaref and Diomede thought that all bearded seals are good food and did not target specific types. Others said that they catch what they see and that they cannot tell the difference.

In addition to our questionnaires we had the opportunity to talk to many hunters during sample collections, Ice Seal Committee co-management meetings, and during Traditional Knowledge interviews for walrus projects. During these activities we have heard of places where bearded seals haul out on land. These locations include islands in the southern and central Bering Sea, and in the Chukchi Sea. In the Bering Sea, bearded seals have been observed hauled out on a barrier island near Egegik in summer. Spotted seals were hauled out on one side of the island and bearded seals on the other. Bearded seals were reported to routinely haul out on the south side of Hagemeister Island while spotted seals would haul out on the north and west sides. In an isolated event, two bearded seals were reported on land near Rocky Point (northern tip of Hagemeister Island) in the 1970s. The barrier islands along the Chukchi coast, between Cape Lisburne and Wainwright, are reported to be a common bearded and spotted seal haulout area, especially near Icy Cape. Occasionally 50–100 bearded seals have been known to haul out near Cape Sabine. It is unclear how many of the bearded seals in these reports are adults, as most of the reports refer to either young bearded seals or just “bearded seals” without any age distinction. It is possible, however, that bearded seals in the Bering-Chukchi region haul out on land more often than what has been implied by the literature (Burns 1981).

Table 1. 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 and 1970s, stomachs from 841 bearded seals were examined and 645 (77%) contained prey items (Fig. 4); 248 were from the Bering Sea and 397 were from the Chukchi Sea. Samples from the Bering Sea came from nine villages (221) and three research cruises (27). Samples from the Chukchi Sea (397) were from six villages, but most were from Shishmaref (187). We also used data from 133 stomach samples collected as part of the Project Chariot investigation (1960–1961); 112 from Point Hope and 21 from Kivalina (Johnson *et al*. 1966). Stomachs were collected during the spring-summer (432) and fall (204) subsistence seal harvests. Between 1998 and 2009, stomachs from 378 bearded seals were examined and 298 (79%) contained prey items (Fig. 4); 155 were from five villages in the Bering Sea and 141 were from four villages in the Chukchi Sea, the most samples were contributed by Little Diomede (120) in the Bering Strait located between the two seas. These stomachs were collected during the spring-summer (209) and fall (61) subsistence seal harvests. No bearded seal stomachs with contents were collected in 1962–1965, 1968, 1972, or 1980–1997 (Fig. 4).

We identified 213 different prey taxa in 943 bearded seals sampled. The most common prey taxa identified (113) and their frequency of occurrence (%FO) in stomachs is given in Table 2. There was no significant difference in occurrence of prey in the diets of males and females; therefore, sexes were pooled for all diet analyses.

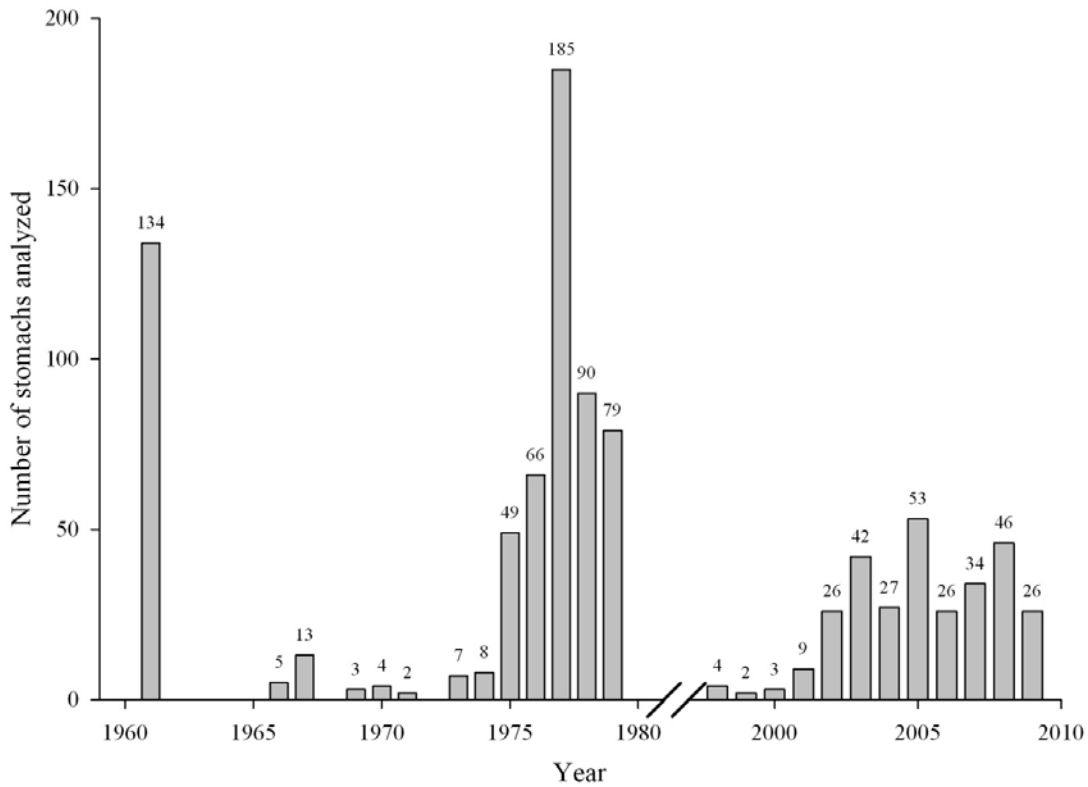

Figure 4. Number of stomachs from bearded seals harvested in Alaska, 1961–2009 that contained prey. No stomachs were analyzed in 1962–1965, 1968, 1972, or 1980–1997.

Fishes—Fish were consumed by bearded seals more frequently during the 2000s (88%) than the 1970s (77%) and more frequently during the 1970s than during the 1960s (30%; Table 2, Fig. 5); although the difference between the 2000s and 1970s was not statistically significant ($P = 0.42$). We were able to identify significant increases in occurrence for 12 fish taxa (*i.e.*, genera or species; Table 2). There was no evidence that fish consumption was different between the Bering and Chukchi seas during the 1960s ($P = 0.22$) and 2000s ($P = 0.75$). During the 1970s, however, fish consumption was higher in Chukchi Sea than the Bering Sea (Table 3). There were no significant differences between summer and winter consumption during any time period. Changes in general fish consumption over time were strongly correlated with changes in sculpin consumption ($r = 0.67$), suggesting changes in sculpin consumption were likely responsible for variations we observed among all fish.

In the 1960s, sculpin from the Family Cottidae were the most dominant taxa (19%). The occurrence of sculpin was higher in the Bering Sea (27%) than the Chukchi Sea (18%); but was equally common in summer and winter. In order of occurrence, sculpin were followed by cod (8%), flatfish (5%), and prickleback (2%). Of the cod, only Arctic (*Boreogadus saida*; 6%) and saffron cod (*Eleginus gracilis*; 3%) were detected (Table 2).

In the 1970s, in addition to sculpin (60%), cod (43%) and flatfish (33%) were dominant taxa. Sculpin were consumed more in the Chukchi Sea (66%) than the Bering Sea (51%). Saffron cod was the dominant species of cod (34%), followed by Arctic cod (11%). No species of flatfish was dominant, but overall flatfish occurred more frequently in the Chukchi Sea than the Bering Sea in all time periods (Table 3).

In the 2000s, sculpin (67%), cod (47%), and flatfish (53%) continued to be the dominant fish taxa although they were consumed more frequently than in the past. Arctic staghorn sculpin (*G. tricuspis*) was first detected in the 2000s and was consumed frequently (39%). *Enophrys* spp., detected at low levels in the 1960s and 1970s, was not detected in the 2000s (Table 3). Arctic and saffron cod were still the dominant species of cod in the 2000s, but walleye pollock (*Theragra chalcogramma*) was also detected (7%). For flatfish, longhead dab (*Limanda proboscidea*; 25%) and yellowfin sole (*Limanda aspera*; 18%) were dominant during the 2000s, but Alaska plaice (*Pleuronectes quadrituberculatus*) also occurred at 8%. For prickleback, the slender eelblenny (*Lumpenus fabricii*) occurred at 12% (Table 2). In addition to prickleback, several other secondary fish prey items were present during the 2000s, including Pacific sand lance (*Ammodytes hexapterus*; 15%) and snailfish (*Liparis* spp.; 13%). Additionally, snailfish and prickleback were consumed more often in the Bering Sea than in the Chukchi Sea (Table 3).

Based on Simpson's Diversity Index, bearded seals currently consume a greater diversity of fish species ($D = 0.21$) than during the 1970s ($D = 0.30$) and 1960s ($D = 0.35$). Beginning in the mid 1970s, and continuing through the 2000s, diets were regularly comprised of five or more fish taxa, whereas in the 1960s only three to five were consumed (Fig. 6). In the 1960s, the fish diet was dominated by sculpin (mostly the genus *Myoxocephalus*). In the 1970s, the diversity increased to include cod (mostly saffron cod), sculpin, and flatfish. In the 2000s, fish diversity increased further to include four species of fish with occurrences of >20%: Arctic cod, saffron cod, longhead dab, and two genera of sculpin (*Gymnocanthus* and *Myoxocephalus*; Table 2)

including Arctic staghorn sculpin (*G. tricuspis*). Three other species or genera occurred at 15% or more: Pacific sand lance, eelblenny (*Lumpenus* spp.), and yellowfin sole.

Although cod (>40%) and sculpin (>60%) were consumed frequently during the 1970s and 2000s, their RO to other fish prey decreased in response to an increase in diet diversity. The RO of cod in bearded seal diets increased from the 1960s (21%) to 1970s (29%) but decreased during the 2000s (21%; $P < 0.01$). Sculpin RO decreased from the 1960s (54%) and 1970s (40%) to the 2000s (30%; $P < 0.01$). Conversely, Pacific sand lance, snailfish, and pricklebacks were identified more frequently and more consistently in bearded seal diets during most years of the 2000s ($P < 0.01$), whereas their occurrence during earlier decades was less consistent (Fig. 6). The yearly RO of flatfish was also more consistent during the 2000s than in the 1960s and 1970s (Fig. 6), however differences were not significant ($P = 0.28$). In general, consumption of fish did not vary by seal age class, except for Arctic cod and sculpin. Adult and subadult seals were more likely to consume Arctic cod and sculpin than pups ($P < 0.01$).

Table 2. Percent frequency of occurrence (%FO$_i$) of prey identified from bearded seal stomachs collected in Alaska by decade, 1961–2009. Shaded rows are discussed in the text.

	Decade	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	155	490	298
All Fish *		29.68	77.35	87.92
Pacific herring (*Clupea pallasii*)		0.00	0.20	1.01
Smelt (*Osmerus mordax*)		0.00	0.20	2.01
Pacific sand lance (*Ammodytes hexapterus*) *		1.94	3.67	14.77
All Cod (Gadidae) *		7.74	43.06	46.64
Arctic cod (*Boreogadus saida*) *		6.45	10.61	31.21
Saffron cod (*Eleginus gracilis*) *		2.58	33.47	21.14
Walleye pollock (*Theragra chalcogramma*) *		0.00	1.43	7.05
All Eelpout		0.00	5.71	5.70
Lycodes spp.		0.00	4.90	5.70
All Sculpin (Cottidae) *		19.35	59.80	67.11
Enophrys spp.		0.65	5.31	0.00
Gymnocanthus spp. *		2.58	6.12	39.26
Arctic staghorn sculpin (*Gymnocanthus tricuspis*) *		0.00	0.00	38.93
Myoxocephalus spp. *		9.68	19.18	50.00
All Poacher (Agonidae)		0.00	1.43	4.03
All Snailfish (Liparidae) *		0.00	0.61	12.75
Liparis spp. *		0.00	0.61	11.07
All Pricklebacks (Stichaeidae) *		1.94	3.88	21.14
Blackline prickleback (*Acantholumpenus machayi*)		0.00	0.00	6.04
Eelblenny (*Lumpenus* spp.) *		0.65	2.65	18.79
Slender eelblenny (*Lumpenus fabricii*) *		0.00	1.63	12.42
All Flatfish (Pleuronectidae) *		5.16	33.06	52.01
Yellowfin sole (*Limanda aspera*) *		0.00	0.41	18.46
Longhead dab (*Limanda proboscidea*) *		0.00	1.02	24.83
Arctic flounder (*Pleuronectes glacialis*)		0.00	2.24	1.01
Alaska plaice (*Pleuronectes quadrituberculatus*) *		0.65	2.65	8.39
All Invertebrates *		98.06	98.16	96.31
Porifera *		9.03	4.08	16.44
Annelida *		1.94	22.86	19.46
Polychaeta *		1.94	22.86	19.13
Nereidae		0.00	2.04	1.01
All Mollusca *		52.90	53.06	51.68
Gastropoda		27.10	26.73	21.81
Trochidae		0.00	0.00	3.36
Velutina spp. *		6.45	2.24	1.68
Natica spp. *		1.29	4.49	1.68
Polinices spp. *		3.87	13.47	0.34
Buccinum spp. *		6.45	10.61	2.68
Bivalvia *		36.77	43.47	39.93
Musculus spp. *		0.00	9.18	1.34
Clinocardium spp. *		2.58	7.55	1.68
Serripes spp. *		5.81	20.82	2.01
Mactromeris spp. *		0.00	12.65	1.01
Siliqua spp. *		0.00	5.10	0.34
Tellina spp.		0.00	4.29	3.02
Macoma spp.		0.00	0.00	4.03
Mya spp.		0.00	0.41	1.34
Cephalopoda *		0.65	8.37	11.74
Octopus (Octopodia) *		0.65	8.37	6.71

All Crustacean *	97.42	97.96	90.60
All Mysidacea *	3.23	14.08	1.68
Mysidae *	1.94	13.27	1.68
Mysis spp. *	0.00	5.51	0.34
Neomysis spp. *	0.00	8.57	1.01
Neomysis rayii *	0.00	6.94	0.67
All Isopoda *	10.32	24.90	9.40
Saduria entomon *	10.32	22.65	2.01
All Amphipoda *	5.81	31.63	18.79
Ampeliscidae	2.58	3.47	2.01
Ampelisca spp.	2.58	3.27	0.34
Atylus spp.	0.00	2.65	0.34
Rhacotropis spp.	0.00	4.90	0.00
Melitidae	0.00	1.63	2.01
Gammaridae	2.58	2.24	4.36
Gammarus spp.	0.65	1.22	2.01
Anonyx spp. *	0.65	14.49	5.37
Anonyx nugax *	0.00	12.45	1.01
Acanthomysis spp. *	0.00	15.10	0.34
Acanthostepheia behringiensis	0.00	2.24	0.34
All Decapods *	97.42	97.14	86.24
All Shrimp*	91.61	93.67	75.17
Hippolytidae *	21.29	33.67	13.42
Spirontocaris spp.	0.65	4.49	2.01
Lebbeus spp. *	14.84	8.57	1.34
*Lebbeus groenlandicus**	14.84	7.55	0.67
Eualus spp. *	0.00	28.98	5.03
Eualus fabricii *	0.00	4.90	0.34
Eualus gaimardi *	0.00	26.33	3.02
Pandalidae *	16.77	21.43	15.44
Pandalus spp. *	11.61	21.43	13.42
Pandalus goniurus *	3.23	18.37	4.70
Crangonidae *	80.00	85.71	63.76
Crangon spp. *	23.23	47.96	38.93
Crangon dalli *	2.58	7.35	4.70
Crangon alaskensis *	3.23	40.00	23.49
Sclerocrangon spp. *	50.32	30.82	10.74
Argis spp. *	33.55	41.43	33.56
Argis lar *	6.45	35.92	25.50
Argis crassa	2.58	6.12	3.69
Sabinea spp.	0.00	2.45	0.67
All Crab *	77.42	77.55	64.09
Infraorder Anomura *	25.16	31.63	6.71
Paguridae *	18.06	29.18	5.37
Pagurus spp. *	18.06	26.53	1.01
Hapalogaster grebnitzkii *	4.52	2.86	0.34
Paralithodes spp.	0.65	2.24	0.00
Infraorder Brachyura *	67.74	73.27	49.33
Telmessus spp. *	4.52	25.51	13.09
Telmessus cheiragonus *	3.87	25.51	11.74
Majidae *	1.29	6.94	1.68
Hyas spp. *	21.94	31.84	21.81
Hyas coarctatus *	7.10	30.82	17.79
Chionoecetes spp. *	9.03	25.31	30.20
Chionoecetes opilio *	1.94	17.14	14.43

Echiuridae *	24.52	23.88	25.50
Priapulida	0.65	3.06	0.00
Bryozoa *	0.00	2.45	6.04
Echinodermata	0.65	2.24	3.69
Sea Urchin (Echinoidea)	0.65	1.84	2.68
Sea Cucumber (Holothuroidea)	0.65	1.63	2.01
Urochordata	1.94	4.29	6.04
Tunicate (Ascidiidae)	1.29	1.84	4.70

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

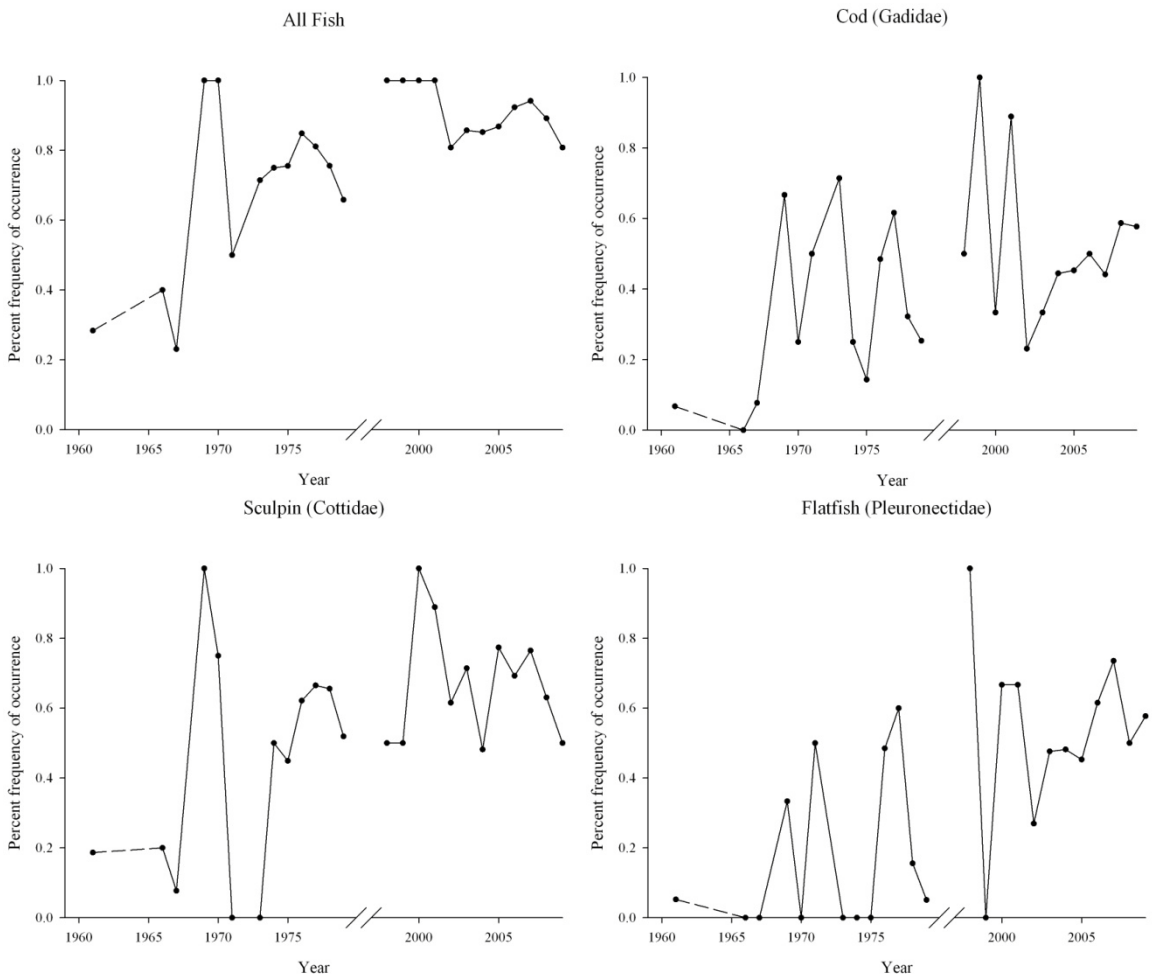

Figure 5. Yearly patterns in percent frequency of occurrence (%FO_i) of primary fish prey identified from stomachs of bearded seals harvested in Alaska, 1961–2009. No stomachs were analyzed in 1962–1965, 1968, 1972, or 1980–1997. Dashed line represents missing trend line between 1962 and 1965.

Table 3. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of fish prey identified from bearded seal stomachs collected in Alaska, 1961–2009. Shaded rows are discussed in the text.

		Region						Season					
		Bering			Chukchi			Spring-Summer			Fall-Winter		
	Decade	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	22	226	155	133	264	141	14	418	209	141	63	61
All Fish [ac]		40.91	65.33	86.45	27.82	86.59	89.36	28.57	77.03	86.60	29.79	77.78	95.08
Pacific herring (*Clupea pallasii*)		-	0.50	1.29	-	-	0.71	-	-	-	-	-	3.28
Smelt (*Osmerus mordax*)		-	0.50	0.65	-	-	3.55	-	-	0.96	-	-	6.56
Pacific sand lance (*Ammodytes hexapterus*)		-	1.51	10.97	2.26	3.83	19.15	-	3.11	15.79	2.13	-	13.11
All Cod (Gadidae) [ac]		13.64	21.61	45.16	6.77	58.24	48.23	-	44.74	45.93	8.51	31.75	47.54
Arctic cod (*Boreogadus saida*) [a]		9.09	9.05	36.13	6.02	8.43	25.53	-	9.81	32.06	7.09	15.87	26.23
Saffron cod (*Eleginus gracilis*) [abcd]		9.09	14.07	5.16	1.50	50.57	39.01	-	35.65	18.66	2.84	19.05	27.87
Walleye pollock (*Theragra chalcogramma*) [ab]		-	2.01	12.90	-	-	0.71	-	0.96	4.31	-	4.76	14.75
All Eelpout [ab]		-	5.03	9.68	-	3.45	1.42	-	3.35	5.26	-	22.22	8.20
Lycodes spp. [ab]		-	4.02	9.68	-	3.07	1.42	-	2.39	5.26	-	22.22	8.20
All Sculpin (Cottidae) [ac]		27.27	50.75	70.32	18.05	66.28	63.12	14.29	60.05	66.99	19.86	60.32	68.85
Enophrys spp. [a]		4.55	12.06	-	-	0.77	-	7.14	4.07	-	-	12.70	-
Gymnocanthus spp. [ab]		9.09	10.05	42.58	1.50	2.30	34.75	-	6.46	45.93	2.84	4.76	13.11
Arctic staghorn sculpin (*Gymnocanthus tricuspis*) [ab]		-	-	41.94	-	-	34.75	-	-	45.45	-	-	13.11
Myoxocephalus spp.		9.09	21.61	53.55	9.77	18.77	46.10	-	19.38	49.28	10.64	19.05	50.82
All Poacher (Agonidae)		-	2.01	3.23	-	0.77	4.26	-	1.44	4.78	-	1.59	3.28
All Snailfish (Liparidae) [a]		-	0.50	23.23	-	0.77	1.42	-	0.48	10.05	-	1.59	18.03
Liparis spp. [a]		-	0.50	20.00	-	0.77	1.42	-	0.48	9.09	-	1.59	14.75
All Pricklebacks (Stichaeidae) [a]		4.55	4.02	30.97	1.50	3.07	10.64	-	3.83	20.57	2.13	3.17	16.39
Blackline prickleback (*Acantholumpenus machayi*) [a]		-	-	10.32	-	-	1.42	-	-	5.26	-	-	6.56
Eelblenny (*Lumpenus* spp.) [a]		4.55	1.01	27.10	-	3.07	9.93	-	2.63	17.70	0.71	3.17	16.39
Slender eelblenny (*Lumpenus fabricii*)		-	-	18.06	-	3.07	6.38	-	1.91	11.00	-	-	14.75
All Flatfish (Pleuronectidae) [abc]		4.55	5.53	38.71	5.26	55.94	67.38	-	33.73	46.89	5.67	33.33	70.49
Yellowfin sole (*Limanda aspera*) [ab]		-	-	7.74	-	0.38	30.50	-	0.24	12.44	-	1.59	44.26
Longhead dab (*Limanda proboscidea*) [ac]		-	-	7.74	-	1.92	43.97	-	1.20	24.88	-	-	24.59
Arctic flounder (*Pleuronectes glacialis*)		-	-	1.94	-	4.21	-	-	1.91	-	-	4.76	4.92
Alaska plaice (*Pleuronectes quadrituberculatus*)		4.55	-	14.84	-	4.98	1.42	-	3.11	7.66	0.71	-	11.48

[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 decades: Interaction Decade×Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and decades: Interaction Decade×Season ($P < 0.05$).

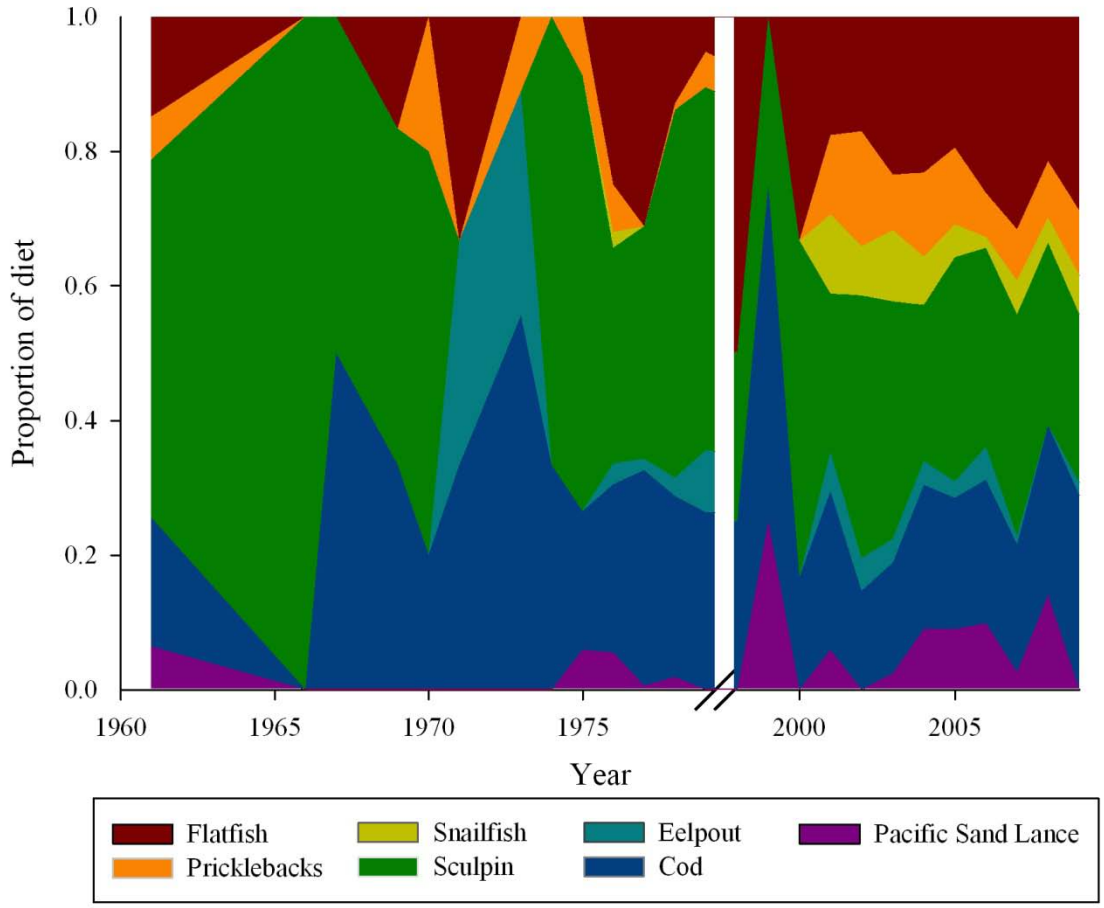

Figure 6. Yearly proportions (relative occurrence) of fish prey identified in the stomachs of bearded seals harvested in Alaska, 1961–2009. Numbers of stomachs containing fish that were analyzed each year are listed above bars. No stomachs were analyzed in 1962–1965, 1968, 1972, or 1980–1997.

Invertebrates—Invertebrate prey items were commonly consumed by bearded seals across all decades, in the Bering and Chukchi seas, and in all seasons (>95%; Tables 2, 4, 5, 6, and 7). We identified a total of 63 taxa with major representation from five phyla (Porifera, Annelida, Mollusca, Crustacea, and Echiurida), of which crustaceans and mollusks were most common. The occurrence of all invertebrates was strongly correlated with the occurrence of crustaceans (r = 0.67), specifically decapods (r = 0.55). Therefore, changes in invertebrate consumption over time were largely explained by changes in the consumption of crustaceans. Bearded seals consumed fewer crustaceans during the 2000s than in the 1960s or 1970s, which did not differ from each other (P = 0.24; Table 2, Fig. 7).

The majority of prey items came from four Orders of crustaceans: Mysidacea (2–14%), Isopoda (9–25%), Amphipoda (6–32%), and Decapoda (86–97%; Table 2). Decapods were the most dominant class and their occurrence was strongly correlated with the occurrence of shrimp (r = 0.67), and somewhat correlated with the occurrence of crab (r = 0.43). Bearded seals consumed fewer shrimp in the 2000s (75%) than during the 1960s (92%) and 1970s (94%; Table 2). During the 2000s, seals in the Chukchi Sea consumed more shrimp than seals in the Bering Sea, however, consumption was similar in both seas during the 1960s (P = 0.75) and 1970s (P = 0.85; Table 6). Summer versus winter consumption was variable with no difference between seasons in the 1960s (P = 0.71), higher summer consumption in the 1970s, and higher winter consumption in the 2000s (Table 6).

Shrimp from three families (Hippolytidae, Pandalidae, and Crangonidae) composed the primary invertebrate prey identified. Of these three families, Crangonidae was the most dominant and consumption ranged from 64–86% through all decades (Table 2). Within this family, three genera were dominant: *Crangon*, *Sclerocrangon*, and *Argis* and varied in their consumption by decade and season (Tables 2 and 6). Regionally, bearded seals in the Chukchi Sea consumed more crangonid shrimp than seals in the Bering Sea (Table 6).

Shrimp from the Family Hippolytidae were next in dominance ranging from 13 to 34% through time (Table 2). *Lebbeus* and *Eualus* were the most dominant genera and were consumed more frequently in the Bering Sea than in the Chukchi Sea, and more often in summer than winter (Table 6). Bearded seals consumed less *Lebbeus groenlandicus* during the 1970s and 2000s than the 1960s (Table 2). *Eualus gaimardi* was commonly consumed only in the 1970s. It was not identified in any bearded seal stomachs before 1974; however, it was consumed by 26% of seals in the 1970s and by only 3% in the 2000s (Table 2). Subadults (16%; P = 0.02) and pups (26%; P < 0.01) consumed more *Eualus gaimardi* than adults (11%); however, consumption did not vary between subadults and pups (P = 0.66).

Shrimp from the Family Pandalidae were consumed least, ranging from 15 to 21% through time (Table 2). *Pandalus* was the only genus consumed and occurrence did not change between the 1960s and 2000s (P = 0.45), but was higher during the 1970s (Table 2). *Pandalus* was also consumed more in the Bering Sea than in the Chukchi Sea (Table 6).

Crabs of two infraorders (Anomura, 7–32%, and Brachyura, 49–73%) were dominant decapods identified in bearded seal diets (Table 2). Changes in general crab consumption were

correlated with changes in Brachyura crabs (r = 0.82), and within Anomura, the occurrence of crabs from the Family Paguridae was strongly correlated with *Pagurus* spp. (r = 0.92). Consumption of *Pagurus* spp. increased from the 1960s to 1970s but decreased in the 2000s (Table 2). Three genera within Brachyura were dominant: *Telmessus*, *Hyas*, and *Chionoecetes* (including the commercial species *C. opilio*). More *Chionoecetes* spp. were consumed in the Bering Sea than in the Chukchi Sea (P <0.01). In the Bering Sea, consumption of crabs did not vary by decade (P = 0.60). In the Chukchi Sea, however, seals consumed similar frequencies of crabs during the 1960s and 1970s (P = 0.59) but consumed less in the 2000s (Table 7). Generally, bearded seals consumed more crabs during the summer than in the winter (Table 7). Adult (70%) and subadult (74%) bearded seals consumed more Brachyurans than pups (49%); however, consumption did not differ between adults and subadults (P = 0.26).

Of the remaining Orders of Crustacea (Mysidacea, Isopoda, and Amphipoda), all were consumed more in the 1970s than other decades (Table 2). Amphipoda was the most frequent ranging from 6 to 32%, and the genera *Anonyx* and *Acanthomysis* were the most dominant. The occurrence of all amphipods was strongly correlated with the occurrence of *Anonyx* spp. (r = 0.58) and *Acanthomysis* spp. (r = 0.53). Amphipods were uncommon in bearded seal diets until the mid-1970s and were identified in only twelve seals prior to 1975, after which they were identified in 61% of stomachs. In the 1970s, *Anonyx* was consumed more in the Bering Sea than Chukchi Sea, but the opposite was true for *Acanthomysis* (Table 5).

Isopods were represented by one species *Saduria entomon*, which had the highest consumption in the Chukchi Sea in the 1970s (Table 5). During the 1970s seals consumed more isopods in summer, however, during the 2000s the opposite was true (Table 5). Although bearded seals consumed few mysids, there was evidence that mysid occurrence increased from the 1960s to the 1970s, but decreased in the 2000s (Table 2). Seals consumed more mysids in the Chukchi Sea than in the Bering Sea (Table 5).

Mollusks were common prey found in >50% of stomachs examined throughout our investigation (Table 2) and included gastropods, bivalves, and cephalopods. Annual FO values for all mollusk taxa were correlated with gastropods (r = 0.55) and bivalves (r = 0.80), suggesting changes in gastropod and bivalve consumption were likely responsible for variations we observed among all mollusks.

Although overall gastropod consumption did not change over time (Table 2), bearded seals consumed more *Polinices* spp. during the 1970s, and less of *Polinices* spp., and *Buccinum* spp., during the 2000s (Table 4). Bearded seals consumed more gastropods in the summer than winter during all time periods (Table 4).

In general, bivalve consumption was lowest in the 1960s (37%), highest in the 1970s (44%), and somewhat lower in the 2000s (40%; Table 2). This pattern was similar to that in the Chukchi Sea, however in the Bering Sea bivalve consumption was highest in the 1960s, lowest in the 1970s (Table 4). The most frequently consumed bivalves in the 1970s were *Serripes* spp. (21%) and *Macromeris* spp. (13%). No dominant species were identified in the 1960s or 2000s (Table 2). More bivalves were consumed in summer than winter in the 1960s and 1970s, but consumption was similar between seasons in the 2000s (Table 4).

Cephalopod consumption was exclusively of octopus and increased through time, however, the 1970s and 2000s were not significantly different ($P = 0.34$; Table 4). Bearded seals consumed more octopus in the Bering Sea than the Chukchi Sea (Table 4). Adults (12%) consumed more octopus than subadults (5%; $P = 0.02$) and pups (5%; $P < 0.01$), however, consumption by subadults and pups did not differ from each other ($P = 0.68$).

The three remaining phyla, in order of occurrence, were Echiurida (24–26%), Annelida (2–23%), and Porifera (4–16%; Table 2). Consumption of echiurids did not change through time (Table 2), but were consumed more in the Chukchi Sea than in the Bering Sea, and more in summer than winter (Table 7). Consumption of annelids (polychaetes) was higher in the 2000s (19%) and 1970s (23%) than in the 1960s (2%; Table 2). Bearded seals consumed more polychaetes in the Bering Sea during the 1960s and 2000s than in the Chukchi Sea (Table 4). During the 1970s, however, consumption of polychaetes in the Bering Sea was lower than the Chukchi Sea. Seals also consumed more polychaetes during the summer than winter (Table 4). Sponges (Porifera) were consumed more frequently by bearded seals in the 2000s (16%) than in the 1960s (9%) and 1970s (4%; Table 2) and more in the Bering Sea than in the Chukchi Sea in all decades (Table 4).

Table 4. Regional and seasonal differences in frequency of occurrence (%FO_i) of invertebrate (non-crustaceans) prey identified from bearded seal stomachs collected in Alaska, 1961–2009. Shaded rows are discussed in the text.

		Region						Season					
		Bering			Chukchi			Spring-Summer			Fall-Winter		
	Decade	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	22	226	155	133	264	141	14	418	209	141	63	61
All Invertebrates [bd]		95.45	97.49	97.42	98.50	98.47	95.04	100.00	99.52	95.69	97.87	95.24	98.36
Porifera [a]		22.73	7.54	19.35	6.77	1.92	13.48	14.29	4.78	18.66	8.51	-	11.48
All Annelida [ac]		4.55	19.60	29.68	1.50	23.75	8.51	-	24.16	20.10	2.13	14.29	14.75
Polychaeta [abd]		4.55	19.60	29.03	1.50	23.75	8.51	-	24.16	20.10	2.13	14.29	13.11
Nereidae		-	1.51	1.94	-	2.68	-	-	2.15	0.96	-	1.59	-
All Mollusca [abcd]		68.18	40.70	58.06	50.38	60.54	43.97	85.71	56.22	53.59	49.65	38.10	44.26
Gastropoda [b]		31.82	22.61	26.45	26.32	27.20	15.60	42.86	28.23	24.88	25.53	19.05	6.56
Trochidae		-	-	5.16	-	-	1.42	-	-	3.35	-	-	1.64
Velutina spp.		4.55	4.52	0.65	6.77	0.77	2.84	7.14	2.63	1.91	6.38	-	-
Natica spp. [a]		-	2.51	0.65	1.50	4.60	1.42	-	4.55	2.39	1.42	4.76	-
Polinices spp. [a]		-	4.52	0.65	4.51	19.16	-	-	13.88	0.48	4.26	11.11	-
Buccinum spp. [a]		22.73	9.55	4.52	3.76	6.90	-	28.57	10.29	3.35	4.26	14.29	-
Bivalvia [abcd]		59.09	28.64	45.16	33.08	54.41	33.33	71.43	47.37	39.71	33.33	22.22	39.34
Musculus spp. [a]		-	10.55	0.65	-	7.66	2.13	-	8.85	0.96	-	12.70	3.28
Clinocardium spp. [ab]		13.64	2.01	0.65	0.75	11.88	2.84	21.43	8.85	1.91	0.71	-	1.64
Serripes spp. [bd]		40.91	16.08	3.23	-	23.37	0.71	42.86	23.44	2.39	2.13	4.76	1.64
Mactromeris spp. [a]		-	1.51	0.65	-	22.61	1.42	-	14.83	0.48	-	-	3.28
Siliqua spp. [a]		-	0.50	-	-	9.20	0.71	-	5.74	-	-	1.59	1.64
Tellina spp. [a]		-	0.50	1.29	-	7.66	4.96	-	5.02	1.44	-	-	9.84
Macoma spp.		-	-	2.58	-	-	5.67	-	-	2.39	-	-	9.84
Mya spp.		-	-	-	-	0.77	2.84	-	0.48	1.44	-	-	1.64
All Cephalopoda [a]		-	8.54	18.71	0.75	5.36	4.26	-	7.66	12.92	0.71	14.29	9.84
Octopus (Octopodia) [a]		-	8.54	10.32	0.75	5.36	2.84	-	7.66	9.09	0.71	14.29	-

[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 decades: Interaction Decade×Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and decades: Interaction Decade×Season ($P < 0.05$).

Table 5. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of invertebrate (Mysids and amphipods) prey identified from bearded seal stomachs collected in Alaska, 1961–2009. Shaded rows are discussed in text.

		Region						Season					
		Bering			Chukchi			Spring-Summer			Fall-Winter		
	Decade	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	22	226	155	133	264	141	14	418	209	141	63	61
All Crustacean		95.45	96.98	90.97	97.74	98.47	90.07	100.00	99.28	89.47	97.16	95.24	93.44
All Mysidacea [a]		-	10.55	0.65	3.76	16.09	2.84	-	14.59	1.44	3.55	12.70	1.64
Mysidae [a]		-	10.05	0.65	2.26	14.94	2.84	-	13.64	1.44	2.13	12.70	1.64
Mysis spp. [a]		-	2.51	0.65	-	8.43	-	-	5.98	0.48	-	3.17	-
Neomysis spp.		-	8.04	-	-	7.66	2.13	-	8.37	0.96	-	11.11	-
Neomysis rayii		-	7.54	-	-	6.13	1.42	-	6.70	0.48	-	9.52	-
All Isopoda [abcd]		-	6.53	9.03	12.03	40.61	8.51	-	27.27	6.70	11.35	12.70	21.31
Saduria entomon [abcd]		-	5.03	1.29	12.03	37.93	2.13	-	24.88	0.96	11.35	11.11	6.56
All Amphipoda [a]		4.55	31.66	25.16	6.02	29.50	12.06	-	33.49	15.79	6.38	23.81	21.31
Ampeliscidae [a]		-	5.03	3.23	3.01	0.38	0.71	-	3.35	1.44	2.84	4.76	1.64
Ampelisca spp. [a]		-	4.52	-	3.01	0.38	0.71	-	3.11	-	2.84	4.76	-
Atylus spp.		-	3.02	0.65	-	2.68	-	-	3.11	-	-	-	1.64
Rhacotropis spp. [a]		-	7.04	-	-	1.53	-	-	4.31	-	-	9.52	-
Melitidae [a]		-	2.51	3.87	-	0.77	-	-	1.91	1.91	-	-	1.64
Gammaridae [b]		-	1.01	6.45	3.01	2.30	2.13	-	1.67	2.39	2.84	6.35	4.92
Gammarus spp. [b]		-	0.50	3.23	0.75	1.92	0.71	-	0.72	0.48	0.71	4.76	1.64
Anonyx spp. [a]		4.55	22.61	6.45	-	7.28	4.26	-	15.07	5.26	0.71	12.70	4.92
Anonyx nugax [a]		-	18.59	0.65	-	6.90	1.42	-	12.92	0.48	-	11.11	1.64
Acanthomysis spp. [a]		-	7.54	0.65	-	20.31	-	-	16.51	0.48	-	7.94	-
Acanthostepheia behringiensis [a]		-	2.51	0.65	-	1.15	-	-	2.15	0.48	-	3.17	-

[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 decades: Interaction Decade×Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and decades: Interaction Decade×Season ($P < 0.05$).

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

		Region						Season					
		Bering			Chukchi			Spring-Summer			Fall-Winter		
	Decade	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	22	226	155	133	264	141	14	418	209	141	63	61
All Decapods [abd]		95.45	96.98	87.10	97.74	96.93	86.52	100.00	98.56	84.69	97.16	93.65	91.80
All Shrimp [abd]		90.91	94.47	69.68	91.73	94.25	82.27	92.86	95.93	70.81	91.49	84.13	86.89
Hippolytidae [ab]		-	46.23	18.71	24.81	21.84	7.80	-	35.65	12.44	23.40	23.81	11.48
Spirontocaris spp. [a]		-	7.54	3.23	0.75	1.53	0.71	-	4.78	1.44	0.71	3.17	3.28
Lebbeus spp.		-	13.57	1.94	17.29	4.21	0.71	-	8.13	0.48	16.31	11.11	1.64
Lebbeus groenlandicus		-	11.56	0.65	17.29	3.83	0.71	-	6.94	0.48	16.31	11.11	-
Eualus spp. [ab]		-	37.69	7.74	-	19.54	2.13	-	31.82	5.26	-	14.29	3.28
Eualus fabricii [a]		-	11.56	0.65	-	0.38	-	-	5.26	-	-	3.17	1.64
Eualus gaimardi [ab]		-	33.17	4.52	-	18.01	1.42	-	29.19	3.83	-	11.11	-
Pandalidae [a]		36.36	35.18	23.87	13.53	11.11	6.38	21.43	20.81	15.31	16.31	25.40	11.48
Pandalus spp. [a]		27.27	35.18	21.29	9.02	11.11	4.96	7.14	20.81	12.92	12.06	25.40	11.48
Pandalus goniurus [a]		4.55	28.14	6.45	3.01	10.73	2.84	-	19.38	3.83	3.55	12.70	6.56
Crangonidae [abd]		68.18	78.39	52.26	81.95	92.34	77.30	71.43	87.56	59.33	80.85	79.37	77.05
Crangon spp. [ab]		13.64	32.66	20.00	24.81	62.84	60.28	-	48.09	35.41	25.53	47.62	52.46
Crangon dalli [ac]		-	13.07	3.23	3.01	2.30	6.38	-	7.18	5.74	2.84	4.76	3.28
Crangon alaskensis [abc]		13.64	19.10	3.87	1.50	60.15	45.39	-	40.67	20.10	3.55	38.10	37.70
Sclerocrangon spp. [abc]		54.55	42.71	9.03	49.62	22.99	12.77	71.43	32.78	10.05	48.23	20.63	4.92
Argis spp. [abcd]		27.27	53.27	30.97	34.59	31.03	36.88	7.14	43.78	36.84	36.17	26.98	16.39
Argis lar [abc]		9.09	47.24	22.58	6.02	27.59	29.08	-	38.76	28.71	7.09	17.46	13.11
Argis crassa [ab]		13.64	14.57	5.16	0.75	0.38	2.13	-	5.74	0.96	2.84	9.52	8.20
Sabinea spp. [a]		-	-	-	-	2.68	1.42	-	1.44	0.48	-	9.52	1.64

[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 decades: Interaction Decade×Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and decades: Interaction Decade×Season ($P < 0.05$).

Table 7. Regional and seasonal differences in frequency of occurrence (%FO_i) of invertebrate (Crabs, Echiurids, Priapulids, Bryozoan, Echinoderms, and Urochordates) prey identified from bearded seal stomachs collected in Alaska, 1961–2009. Shaded rows are discussed in the text.

		Region						**Season**					
		Bering			**Chukchi**			**Spring-Summer**			**Fall-Winter**		
	Decade	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**	**1960s**	**1970s**	**2000s**
Prey (*i*)	***n***	22	226	155	133	264	141	14	418	209	141	63	61
All Crab [ab]		86.36	74.87	74.84	75.94	77.39	53.19	92.86	82.30	69.38	75.89	52.38	45.90
Infraorder Anomura		27.27	30.65	5.81	24.81	31.42	7.80	21.43	32.78	8.13	25.53	23.81	-
Paguridae		9.09	25.13	5.16	19.55	31.03	5.67	7.14	30.62	6.70	19.15	20.63	-
Pagurus spp.		9.09	23.12	0.65	19.55	27.59	1.42	7.14	27.75	1.44	19.15	19.05	-
Hapalogaster grebnitzkii [a]		18.18	7.04	-	2.26	-	0.71	14.29	2.39	-	3.55	4.76	-
Paralithodes spp. [a]		4.55	5.03	-	-	0.38	-	7.14	2.63	-	-	-	-
Infraorder Brachyura [ad]		77.27	69.35	57.42	66.17	73.95	41.13	78.57	77.99	54.55	66.67	49.21	29.51
Telmessus spp. [acbd]		4.55	5.03	3.23	4.51	44.06	24.11	-	28.71	11.00	4.96	6.35	11.48
Telmessus cheiragonus [ab]		4.55	5.03	1.94	3.76	44.06	22.70	-	28.71	10.53	4.26	6.35	6.56
Majidae		4.55	6.53	3.23	0.75	7.66	-	-	7.42	2.39	1.42	4.76	-
Hyas spp. [ab]		72.73	44.72	31.61	13.53	20.31	11.35	78.57	33.73	25.84	16.31	22.22	8.20
Hyas coarctatus [ab]		4.55	42.71	26.45	7.52	19.92	8.51	-	32.78	22.01	7.80	20.63	3.28
Chionoecetes spp. [a]		4.55	32.16	36.77	9.77	16.48	23.40	-	24.88	33.01	9.93	28.57	13.11
Chionoecetes opilio [a]		4.55	18.09	20.00	1.50	13.03	8.51	-	16.27	16.27	2.13	23.81	4.92
Echiuridae [abc]		13.64	6.03	21.29	26.32	37.93	30.50	-	25.84	27.27	26.95	14.29	21.31
Priapulida [a]		-	2.51	-	0.75	1.53	-	-	2.39	-	0.71	7.94	-
Bryozoa		-	3.02	5.81	-	2.30	6.38	-	2.87	6.70	-	-	1.64
Echinodermata		-	2.01	3.23	0.75	1.92	4.26	-	1.44	3.83	0.71	7.94	-
Sea Urchin (Echinoidea) [b]		-	2.01	1.94	0.75	1.53	3.55	-	1.44	2.39	0.71	4.76	-
Sea Cucumber (Holothuroidea)		-	2.01	1.94	0.75	1.15	2.13	-	1.44	1.91	0.71	3.17	-
Urochordata		-	7.54	5.81	2.26	1.92	6.38	-	5.02	6.22	2.13	-	6.56
Tunicate (Ascidiidae)		-	3.52	4.52	1.50	0.77	4.96	-	2.15	4.31	1.42	-	6.56

[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 decades: Interaction Decade×Region ($P < 0.05$).
[d] Significant difference in the occurrence of the prey item between seasons and decades: Interaction Decade×Season ($P < 0.05$).

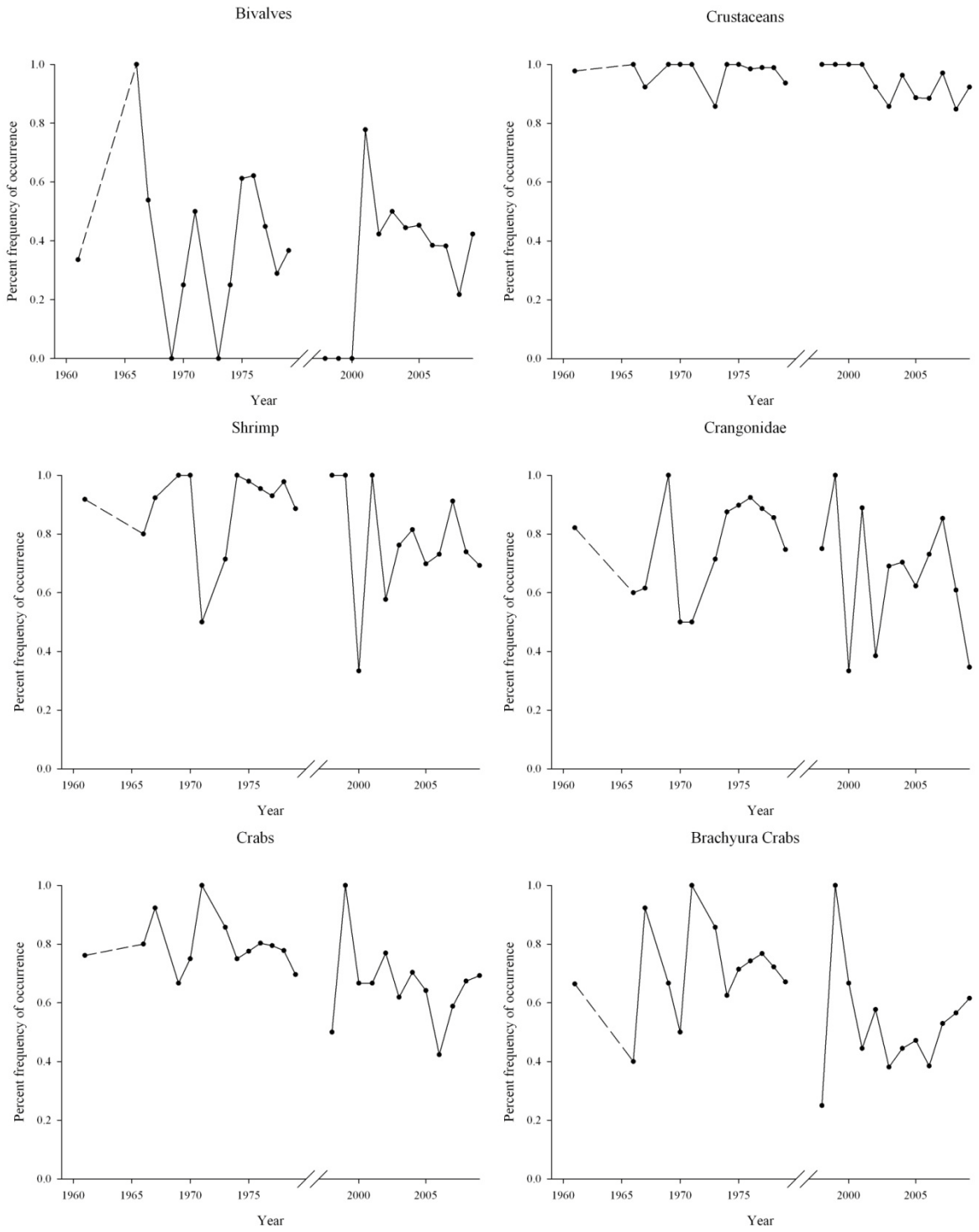

Figure 7. Yearly patterns in percent frequency of occurrence (%FO_i) of primary invertebrate prey identified from stomachs of bearded seals harvested in Alaska, 1961–2009. No stomachs were analyzed in 1962–1965, 1968, 1972, or 1980–1997. Dashed line represents missing trend line between 1962 and 1965.

Contaminants

Metals and other elements—Concentrations of 19 trace elements were quantified in liver (n = 42), kidney (n = 16), and muscle (n = 4) tissue of bearded seals. Some of the elements we tested are essential nutrients (*e.g*., Cu, Fe, and Mg) and others are potentially toxic at high levels (As, Cd, Hg, and Pb). Concentrations of selected trace elements in liver, kidney, and muscle are presented in Table 8. Some essential elements and those where information is not available to biologically evaluate concentrations are not included here.

In addition to total mercury (THg), we also analyzed the more toxic form, methyl mercury (MeHg), in liver tissue of 16 bearded seals (five females and 11 males) ranging in age from 1–23 years old ($\bar{x}$ = 11.25 µg/g wet wt, SD = 6.55). The mean age of females was younger (7.6 years) than for males (13.9). When MeHg was expressed as a percentage of THg the values ranged from 0.20–8.82% ($\bar{x}$ = 2.09%, SD = 2.02). Males and females had similar low mean values (1.56 and 2.29%, respectively). We also evaluated MeHg in kidney tissue of one male bearded seal in which age was not available. For this bearded seal, kidney contained a higher percentage of MeHg (11.3%) than liver (4.0%).

Organochlorines—Concentrations of organochlorines (OC) were summarized in the blubber (n = 37) and liver (n = 24) of bearded 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 (Table 9). The relationship among the compounds differed slightly between blubber and liver; ΣHCH < ΣDDT < ΣCHL < ΣPCB in blubber (Table 9). In liver tissue, ΣHCH remained the lowest and ΣPCB the highest, however ΣDDT was higher than ΣCHL (Table 9). Of the six compounds composing ΣDDT in blubber tissue, the most dominant compound detected was 4,4’ DDE (97.0%).

Of the 84 PCB congener and congener groups, three made up the more than half (53.4%) of the ΣPCBs in blubber. They were, in decreasing dominance, 153/132 (28.6%), 138/160 (16.3%), and 101/90 (8.5%; Table 10). Five compounds made up more than half (56.1%) of the ΣPCBs in liver (Table 11). In liver, congener 153/132 was also dominant and accounted for 13.3% of the ΣPCBs. The other dominant compounds, in decreasing order, were 101/90 (12.5%), 66 (12.0%), and 138/160 (10.3%).

Table 8. Geometric mean (Gmean), arithmetic mean (Amean), and range of concentrations (µg/g wet wt = ppm) of selected elements in liver (*n* = 42), kidney (*n* = 16), and muscle (*n* = 4) of bearded 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.

	As	**Cd**	**Cu**	**THg**	**Mg**	**Mn**	**Pb**	**Se**	**Zn**
Liver									
Gmean	0.38	2.55	**23.80**	**2.13**	181.93	**4.61**	0.04	4.07	**58.13**
Amean	0.44	6.19	**27.69**	**4.26**	182.80	**4.76**	0.05	4.99	**60.05**
Range	0.04–1.15	0.01–39.93	**6.20–70.74**	**0.13–28.31**	127.9–221.3	**2.62–7.72**	0.03–0.48	1.29–18.48	**30.83–115.19**
Kidney									
Gmean	**0.40**	**12.75**	5.58	0.49	141.70	1.28	nd	4.10	32.94
Amean	**0.45**	**21.99**	5.78	0.52	142.08	1.29	nd	4.24	34.56
Range	**0.15–0.83**	**0.83–79.39**	3.79–9.17	0.29–0.78	123.5–158.5	0.95–1.60	nd	2.42–7.00	19.02–52.96
Muscle									
Gmean	0.19	0.02	0.77	nd	**216.73**	0.09	0.09	0.75	30.46
Amean	0.20	0.03	0.77	nd	**218.70**	0.10	0.18	0.81	30.94
Range	0.13–0.32	0.01–0.07	0.70–0.90	nd	**173.1–244.4**	0.06–0.13	0.03–0.42	0.48–1.39	24.21–39.59

Table 9. Geometric mean (Gmean), arithmetic mean (Amean), and range (ng/g or ppb wet wt) of concentrations for total organochlorines by chemical category in blubber (*n* = 37) and liver (*n* = 24) from bearded seals harvested in Alaska, 2003–2007. Contaminants that were not detected during analysis are denoted by nd.

	Compound			
	∑ HCH	**∑ CHL**	**∑ DDT**	**∑ PCB**
Blubber				
Gmean	13.37	100.78	89.11	188.15
Amean	15.04	114.84	115.59	224.28
Range	(1.82–28.34)	(25.21–414.51)	(12.19–604.75)	(48.31–942.50)
Liver				
Gmean	2.57	6.70	8.89	29.21
Amean	1.60	5.26	5.79	20.71
Range	(nd–14.29)	(1.31–20.42)	(1.03–38.72)	(5.06–85.81)

Table 10. Geometric mean (Gmean), arithmetic mean (Amean), and range (ng/g or ppb wet wt) of concentrations of dominant PCB congeners in blubber (*n* = 37) from bearded seals harvested in Alaska, 2003–2007.

	Dominant PCB Congeners		
	153/132	**138/160**	**101/90**
Blubber			
Gmean	51.69	30.18	14.72
Amean	64.20	36.64	19.01
Range	11.71–300.51	7.06–159.93	nd–93.25
% of total	28.62	16.34	8.48

Table 11. Geometric mean (Gmean), arithmetic mean (Amean), and range (ng/g or ppb wet wt) of concentrations of dominant PCB congeners in liver (n = 24) from bearded seals harvested in Alaska, 2003–2007. Congeners that were not detected during analysis are denoted by nd.

	Dominant PCB Congeners			
	153/132	**101/90**	**66**	**138/160**
Liver				
Gmean	3.14	1.73	1.00	2.64
Amean	3.87	3.64	3.50	3.00
Range	nd–10.82	nd–23.56	nd–24.91	nd–7.56
% of total	13.26	12.47	11.99	10.27

Disease

We identified *Brucella* antibodies (*i.e.*, evidence of exposure but not infection) in 2.2% (1 of 46) and PhHV-1 antibodies in 38.2% (39 of 102) of bearded seal sera tested (Table 12). We found no antibodies for PhHV-2 in 23 individuals and no antibodies for CDV or PDV in 86 and 103 individuals, respectively. We found no antibodies to any of the six *Leptospira* species we tested for in 71 bearded seals. We did identify Toxoplasma in 3.6% (3 of 83) of bearded seals tested. Bearded seal tongue tissue was tested for the parasite *Trichinella* but none were found (*n* = 85).

Stomach or intestinal contents of 14 bearded seals (12 harvested in 2007 and two in 2009) were tested for toxic algae (domoic acid and saxitoxin). Three seals had levels of domoic acid above the detection limit of 4 ng/ml and four had levels of saxitoxin above the same detection limit. Domoic acid concentrations ranged from 9.0 to 47.8 ng/ml and saxitoxin ranged from 4.2 to 14.8 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 of the bearded seals contained both toxins. The bearded seals tested were harvested in Point Hope, Shishmaref, Diomede, Gambell, Savoonga, and Hooper Bay. The bearded seal with the highest level of domoic acid was from Hooper Bay and the one with the highest level of saxitoxin was from Point Hope; the southernmost and northernmost locations sampled, respectively. To further investigate the seals that tested positive using stomach and intestinal samples, we also tested liver, kidney or muscle but no algal toxins were detected in those tissues.

Table 12. Serum antibody prevalence for 12 disease agents in bearded seals harvested near Point Hope, Kotzebue, Little Diomede, and Shishmaref, Alaska, 1998, 2002–2010.

	Antibody prevalence No. positive/No. tested (%)
Disease Agent	
Brucella spp.	1/46 (2.2)
Canine distemper virus	0/86 (0)
Phocine distemper virus	0/103 (0)
Phocine herpesvirus-1	39/102 (38.2)
Phocine herpesvirus-2	0/23 (0)
Leptospira bratislava	0/71 (0)
Leptospira canicola	0/71 (0)
Leptospira grippotyphosa	0/71 (0)
Leptospira hardjo	0/71 (0)
Leptospira icterrohemorrhagiae	0/71 (0)
Leptospira pomona	0/71 (0)
Toxoplasma spp.	3/83 (3.6)

Morphometrics

Growth rate—There were 289 seals of known age and length; 1 in 1969, 124 in the 1970s, 1 in 1980, and 163 in the 2000s. Both the seal sampled in 1969 and the seal sampled in 1980 were pooled with the seals sampled in the "1970s."

The best fitting model included age (P <0.01), decade (P = 0.02), and the interaction of age and decade (P <0.01). The model did not include sex (P = 0.39) or the interaction of sex and decade (P = 0.64). Statistical contrasts revealed that seal lengths were only significantly different (α = 0.05) between the 1970s and 2000s for some age classes. Specifically, seals in the 1970s were longer at ages 8 (P = 0.01), 9 (P <0.01), and $\geq$10 (P <0.01) than seals in the 2000s (Fig. 8). Seals in the 2000s were longer at age 5 (P = 0.04) than seals in the 1970s; however, average lengths were shorter in the 2000s in 8 of 10 age classes. Asymptotic length, estimated as the average length of seals in the $\geq$10 year of age category, was shorter in the 2000s ($\bar{x}$ = 208.6, 95% CI $\pm$ 5.4) than in the 1970s ($\bar{x}$ = 218.6, 95% CI $\pm$ 3.1).

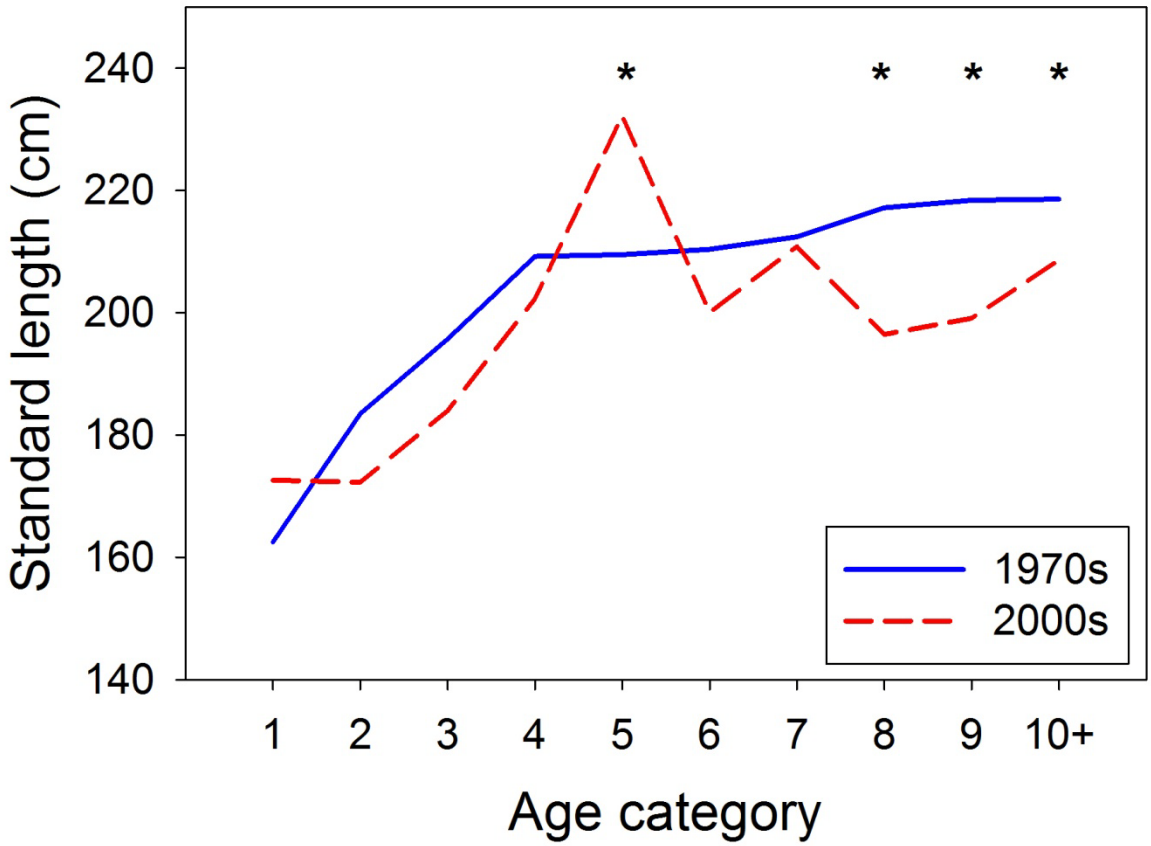

Figure 8. Average length of seals (cm) for different age categories. Asterisks are above age categories with statistically significant differences (P <0.05) in length by decade.

Interestingly, the variance in standard length was greater in the 2000s than in the 1970s (Table 13). In general, the standard deviation in length measurements was twice as large in the 2000s than in the 1970s. The high variance could be due to measurement error, as professional biologists measured many of the seals in the 1970s and hunters measure most seals now. Professional biologists still measure all seals at Point Hope; hence, we can compare Point Hope to other locations to see how variability in standard length might compare. However, some of the largest and smallest seals were measured at Point Hope (Fig. 9) and we conclude that measurement error is not a likely explanation.

When we examined the residual length of seals while controlling for age, we found seven birth years that were characterized by lengths statistically different than the mean length (Fig. 10). Five years were characterized by having seals that were longer than expected, given their age, including 1964, 1967, 1968, 1969, and 2007. Three years were characterized by having seals that were shorter than expected, given their age, including 1979, 1996, and 2004.

Table 13. Mean standard lengths (cm), sample sizes (*n*), and standard deviations (*SD*) for bearded seals sampled in the 1970s and 2000s. The "ratio" is the ratio of standard deviations of the 2000s divided by the standard deviations of the 1970s. In general, standard length of seals is twice as variable in the 2000s than in the 1970s.

Age	**1970s**			**2000s**			**Ratio**
	mean	***n***	***SD***	**mean**	***n***	***SD***	
1	162.5	21	16.6	172.6	35	26.8	1.6
2	183.5	14	8.7	172.3	11	25.6	2.9
3	195.7	11	16.8	184.0	7	39.6	2.4
4	209.2	10	18.0	202.3	12	23.4	1.3
5	209.5	7	9.8	232.2	3	21.2	2.2
6	210.4	8	7.6	200.0	13	14.6	1.9
7	212.4	4	7.6	210.8	12	15.4	2.0
8	217.2	5	10.0	196.5	7	25.7	2.6
9	218.4	8	8.7	199.1	8	17.2	2.0
$\geq$10	218.6	38	9.7	208.6	55	20.4	2.1

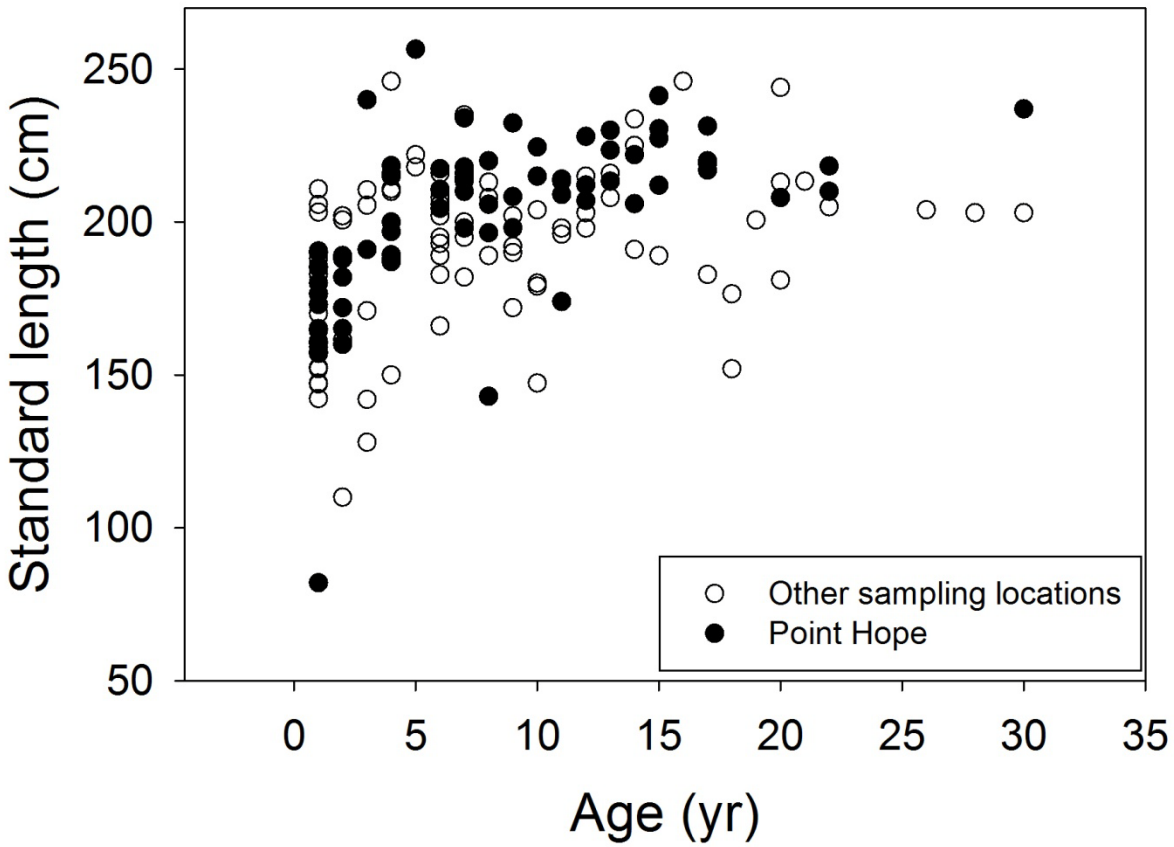

Figure 9. Standard length for seals harvested in the 2000s at Point Hope (filled circles) and other locations (open circles).

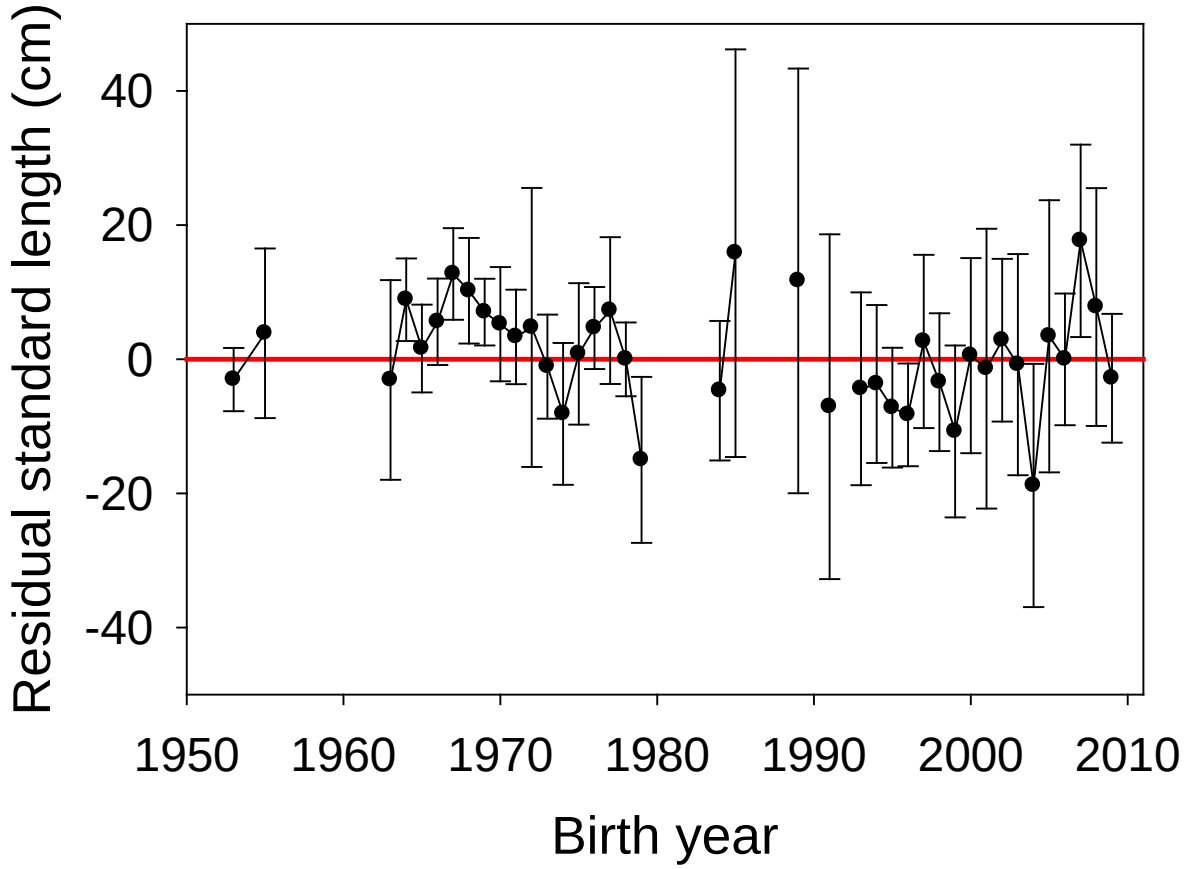

Figure 10. Residual growth (cm) of bearded seals by birth year. Residual is calculated as the observed length minus the average length for each year age. Birth age is calculated as the sample year minus the year age. Error bars are 1.96 standard deviations and approximate 95% confidence limits.

Body condition— As expected, average blubber thickness varied seasonally (Fig.11). Maximum blubber thickness was observed in March and April; however, there were no samples from December, January, or February, when blubber is expected to be thickest. The months we compared (May and June) correspond to the time when blubber thickness is declining at the highest rate (Fig.11). Sternal blubber thickness was compared in 240 bearded seals, 68 were classified as subadults and 172 as adults (Table 14).

For bearded seals, only month was a significant predictor of blubber thickness (P <0.01). Age (P = 0.37), age squared (P = 0.16), sex (P = 0.84), and the interaction of month and sex (P = 0.45) were dropped from the model. Neither was age class (<5 or >5 years of age) a significant predictor (P = 0.13). Average blubber thickness declined from 5.3 cm (SD = 1.43) in May to 4.6 cm (SD = 1.00) in June. Blubber thickness was less than average in 1977, 1978, 1979, and 1991, although there were only statistically significant differences in 1978 and 1991. In contrast, blubber thickness was greater than average between 2004 and 2010, although there were only statistically significant differences in 2008 and 2010 (Fig. 12).

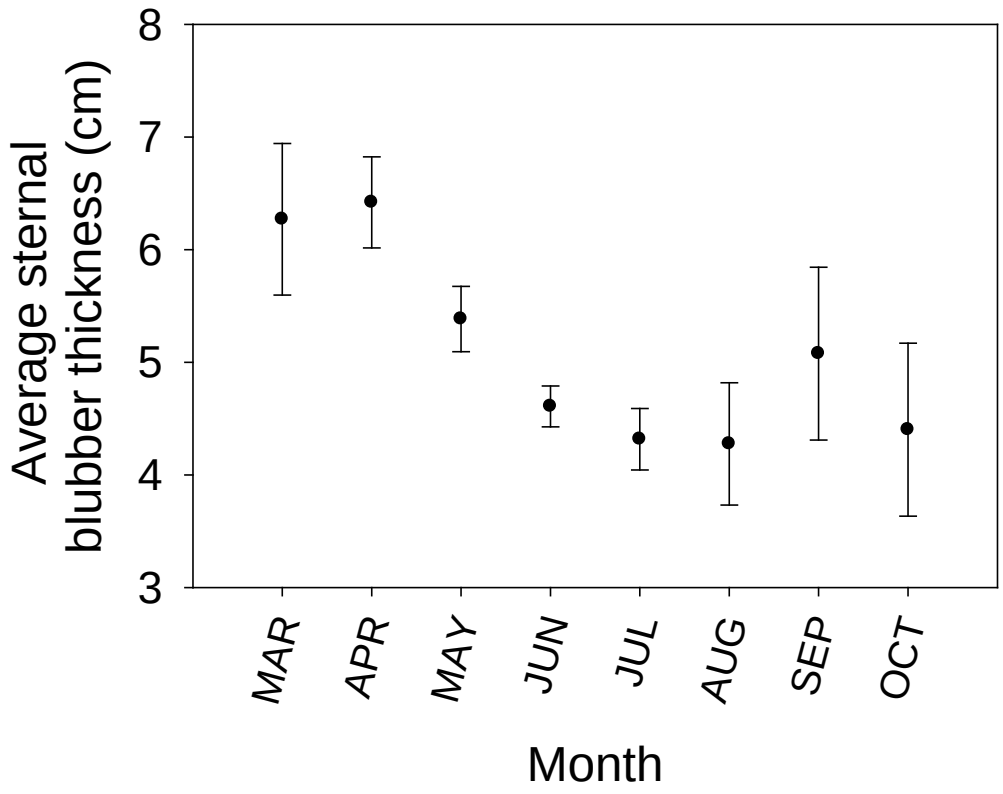

Figure 11. Seasonal variability in mean sternal blubber thickness of bearded seals, all years and sexes combined. Error bars represent 95% confidence limits. Analyses by year only compared May and June, as these are the only months where seals were sampled in most years.

Table 14. Sample sizes of bearded seals harvested in May and June, which had data on sex, age, and sternal blubber thickness.

Year	Subadults	Adults	Total
1975	4	8	**12**
1977	12	10	**22**
1978	16	52	**68**
1979	5	8	**13**
1991	1	29	**30**
2004	7	6	**13**
2005	6	13	**19**
2006	--	14	**14**
2007	5	7	**12**
2008	6	11	**17**
2010	6	14	**20**
Total	**68**	**172**	**240**

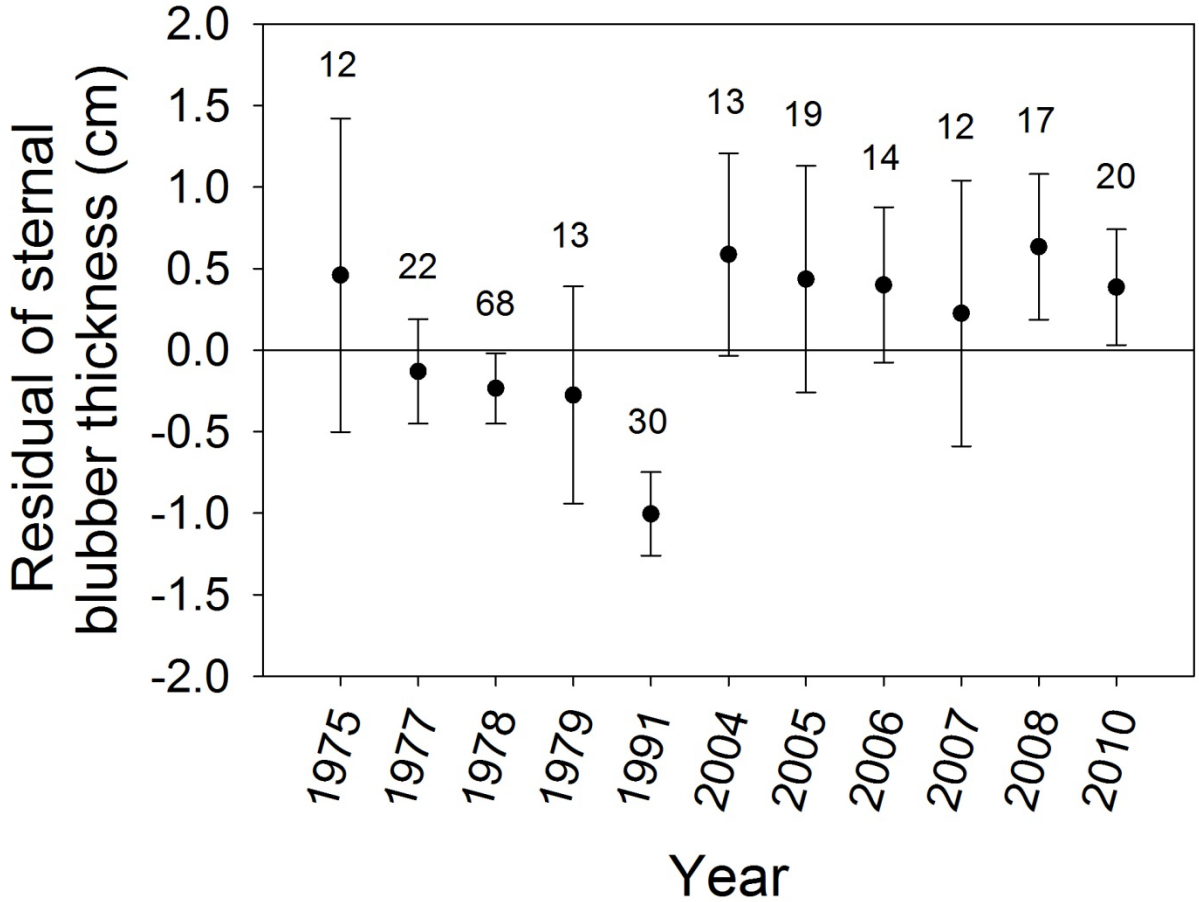

Figure 12. Residual of sternal blubber thickness by time period for subadult and adult bearded seals. Error bars are 95% confidence limits; statistically significant differences have error bars that do not overlap a residual of zero. Sample sizes are presented above error bars. Time periods with negative residuals had seals with less sternal blubber than expected, given the month of harvest. Time periods with positive residuals had seals with more sternal blubber than expected, given the month of harvest.

Population parameters

Age distribution—We examined age-at-harvest for 208 bearded seals harvested in the 1960s, 2,044 in the 1970s, and 527 in the 2000s. Annually, the proportion of pups in the harvest ranged from 0 in 1967 (n = 25) to 64% in 2003 (n = 78). When grouped into decades, we found fewer seals <1 year of age (pups) in the 1960s versus the 1970s or 2000s (P <0.01; Fig. 13). Because age classes are proportional, a smaller proportion of pups in the 1960s should result in higher proportions in other age classes. While there was a higher proportion of seals in the 6–10 and 11–15 year age classes, there were no seals in the >20 year age class from the 1960s (Fig. 14). Given the proportion of seals >20 years of age that were harvested in the 1970s (0.8%) and

2000s (2.7%), and given the total number of seals harvested in the 1960s (n = 208), we would expect to find between one and six seals >20 years of age in the 1960s.

Mean age at harvest—Overall, the mean age within the harvest declined from 6.8 years (95% CL = 5.8–8.1) in the 1960s, to 4.4 years (95% CL = 4.2–4.7; P <0.01) in the 1970s, and then increased to 5.2 years (95% CL = 4.7–5.8; P = 0.03) in the 2000s. The older mean age in the 1960s was largely due to fewer pups in the harvest during that time period. Excluding pups from the calculation of mean age resulted in a mean ages that were more similar. Mean ages without pups, declined from 8.3 (95% CL = 7.4–9.3) in the 1960s to 7.1 (95% CL = 6.9–7.5) in the 1970s, but increased to 8.1 (95% CL = 7.4–8.8) in the 2000s. Mean age in the 1960s and 2000s were not significantly different (P = 0.68).

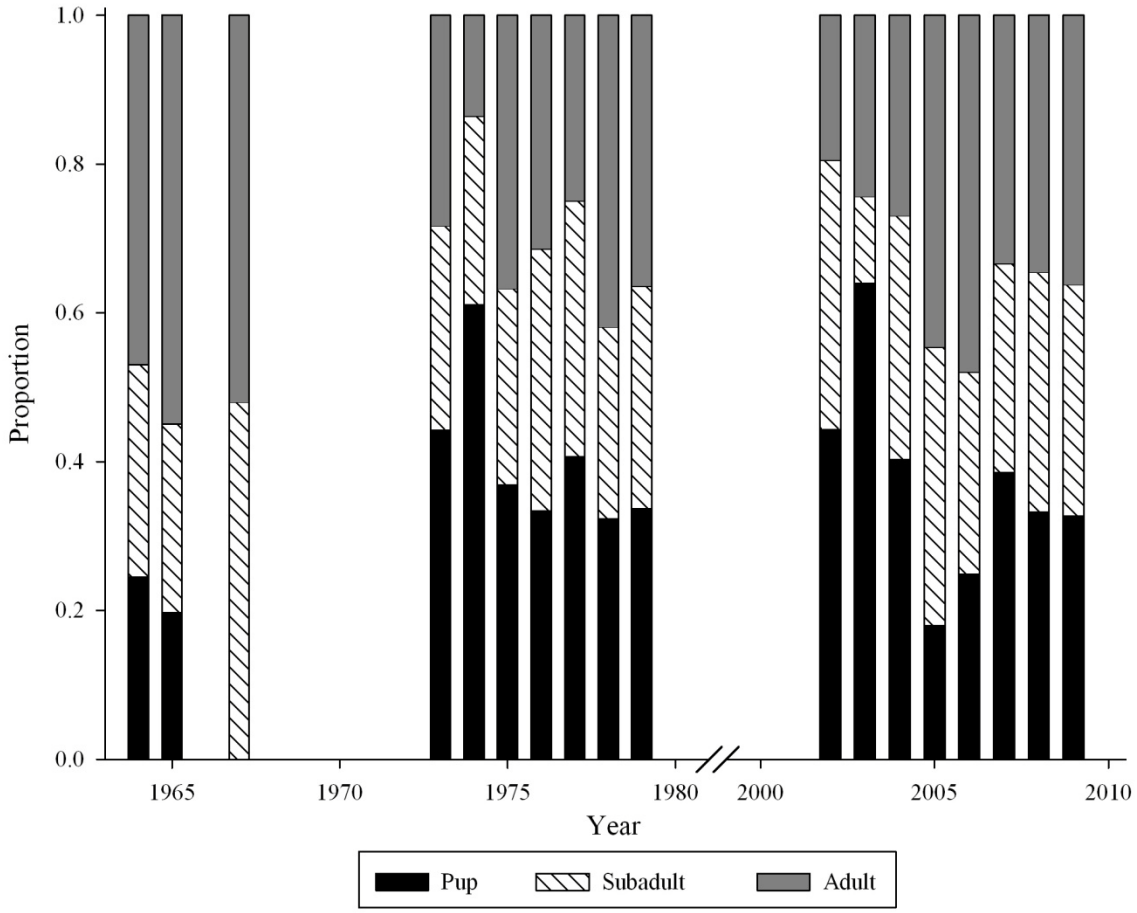

Figure 13. Proportion of bearded seals by age category (pup: <1 year; subadult: 1–6 years; adult: ≥7 years) that were harvested in Alaska, 1964–2009. Only years with >10 seals harvested are presented.

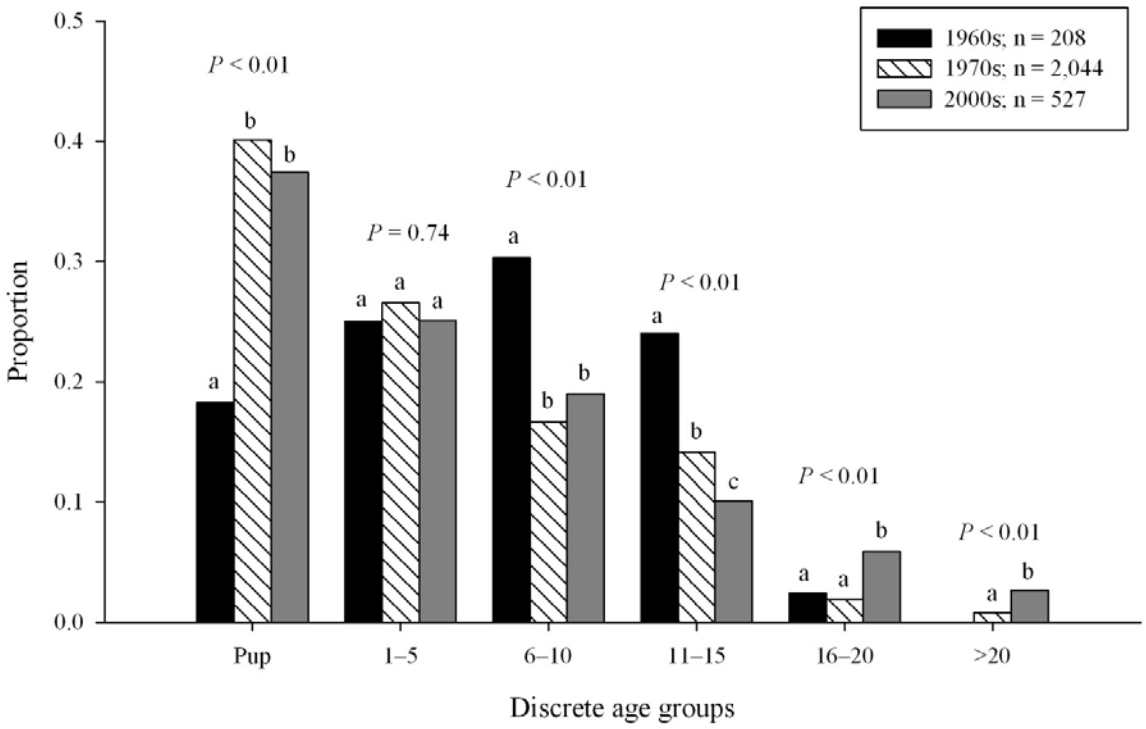

Figure 14. Proportions of bearded seals harvested during three decades in Alaska, 1962–2009, for six different age categories.

Sex ratios—For pups, sex ratios were either near, or statistically indistinguishable from, unity (Fig. 16). Sex ratios did not vary by decade (P = 0.61) or between regions (P = 0.14). We did not include 1960s pups in the Chukchi Sea because the sample size was insufficient (n = 3).

For subadults, sex ratios varied by decade and region (P <0.01). In the Bering Sea, sex ratios were near unity in the 1960s (48% male) and the 1970s (55%), but shifted to male biased in the 2000s (72%; P <0.01; Fig. 15a). In the Chukchi Sea, sex ratios of subadults were near unity in the 1970s (42%) and 2000s (44%), but heavily skewed towards females in the 1960s (13%; P <0.01).

For adults, sex ratios varied by region (P <0.01) but not by decade (P = 0.40). Sex ratios were skewed towards females in both regions, but on average the level of skew was greater in the Chukchi Sea (29%) than in the Bering Sea (43%). In the Bering Sea sex ratios were indistinguishable from unity in the 1960s and 2000s (Fig. 15).

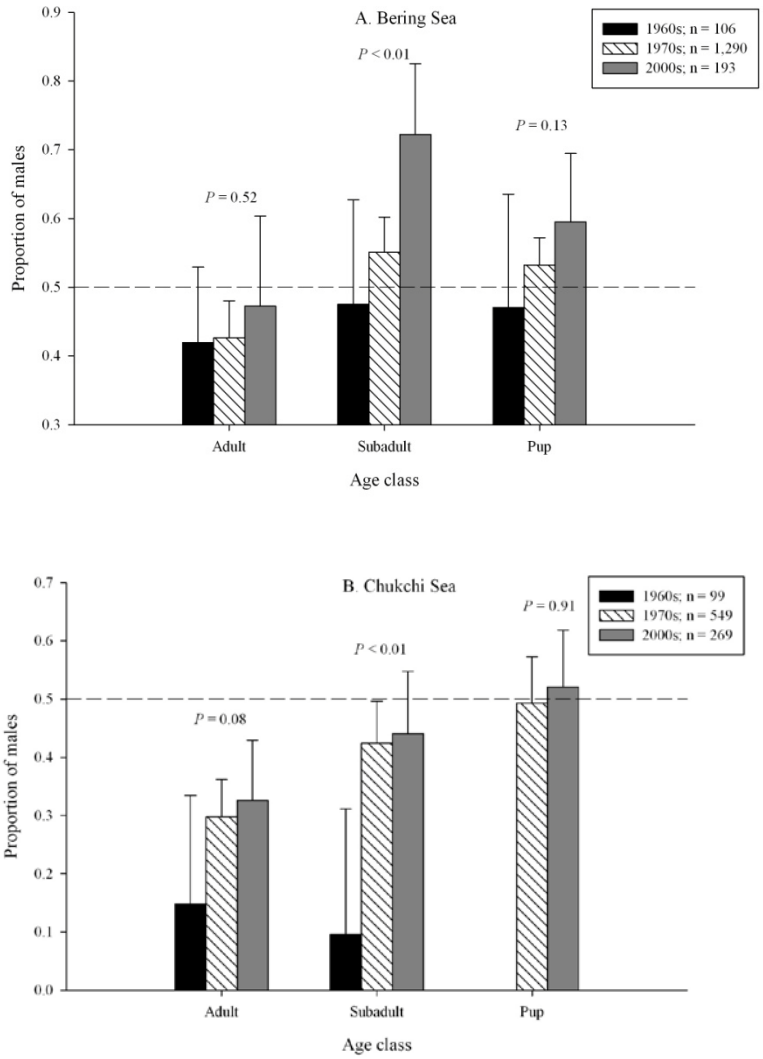

Figure 15. Proportions of male adult (≥7 years), subadult (1–6 years), and pup (<1 year) bearded seals harvested in the a) Bering and b) Chukchi seas during three decades in Alaska, 1960–2009. Error bars depict 95% confidence intervals. Sex ratios are significantly different from unity (P ≤ 0.05) when error bars do not overlap the dashed line which represents equal male:female ratios. P-values correspond to differences among decades within each age class by region group. We only included data for which decade by age class by region combinations had ≥20 seals (e.g., 1960s pups in the Chukchi Sea were not included, n = 3).

Age at maturity and pregnancy rate—Sexual maturity status was determined for 96 female bearded seals in the 1960s, 183 in the 1970s, and 88 in the 2000s. The accuracy of estimating age at maturity is largely dependent upon how many seals are sampled within age classes of intermediate maturity status (DeMaster 1978), these are age classes where the proportion of mature seals are greater than zero, but less than one. For bearded seals in our sample, the intermediate age classes are those between two to five years of age (Fig. 16). Our sample of seals within intermediate age classes was 22 in the 1960s, 39 in the 1970s, and 19 in the 2000s.

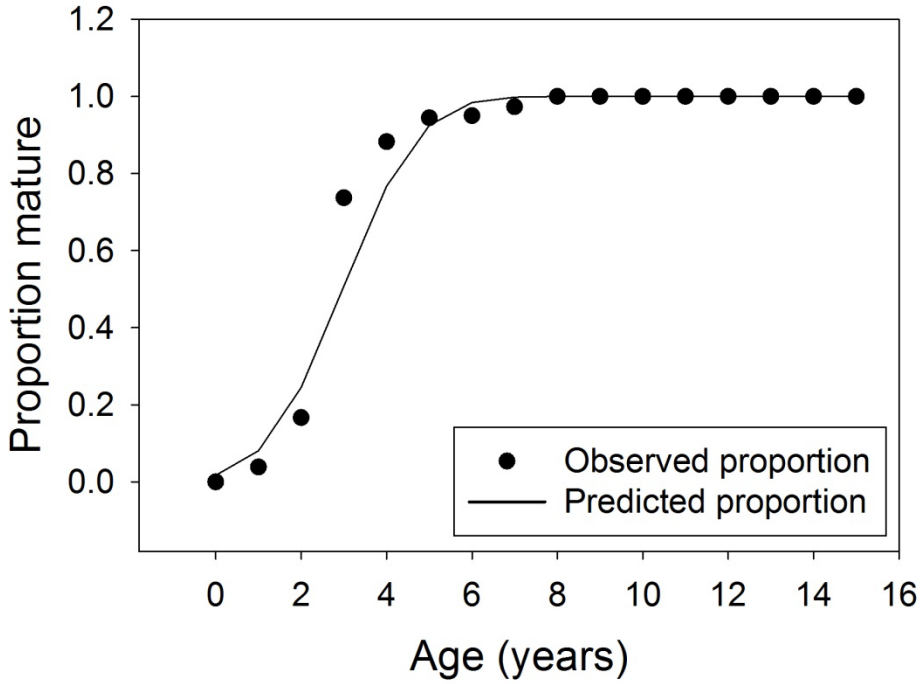

Figure 16. Observed proportion of mature female bearded seals (dots) and the predictions from the best fitting probit model (line). This model assumes there is no variation in age of female maturity by decade, so all decades are pooled. The average age of maturity is predicted to be 3.6 years of age.

A probit link function fit the data better than a logistic link function (Δ AIC = 6.0) and was used for all models. The best approximating model indicated that age at maturity was similar for all time periods (Table 15). Three models were within 2 AIC units of the best approximating model (Δ AIC ranged from 0.3 to 1.53). These models indicated that some time periods might differ in when females reached maturity. However, there was not enough structure in the data to support all time periods being different (Δ AIC = 2.26) and, most important for management, there was little evidence that the 2000s differed from prior decades (Δ AIC = 1.53). Average age of maturity was 4.01 years in the 1960s, 3.97 years in the 1970s, and 3.90 years since 2000. Hence, we conclude that there is little evidence that the age of maturity has changed over time. Average age at maturity for all years combined was 3.97 years of age (95% CL = 3.5–4.4; Fig. 16). Note that we used the presence of ovulation to define maturity; thus, the average age of maturity (3.97 years) is likely younger than the average age of first pregnancy.

Table 16. Models for the average age of maturity for bearded seals in the 1960s, 1970s, and 2000s. All models assume a probit link function and a binomial error distribution.

Model	LogL	#Parameters	AIC	Δ AIC
All decades similar (constant)	-113.82	1	229.65	0.00
60s=2000s, 70s differ	-112.97	2	229.94	0.30
70s=2000s, 60s differ	-113.47	2	230.93	1.29
60s=70s, 2000s differ	-113.59	2	231.17	1.53
All decades differ	-112.95	3	231.91	2.26

1960s. Of the 227 reproductive tracts analyzed for sexual maturity from the 1960s, 64 were immature, 38 had ovulated once, 111 had ovulated more than once, and 14 were mature but the number of ovulations was unknown. Ages were available for 38 of 64 immature females and females that had never ovulated were <1–5 years old. Females ovulating for the first time were 4–15 years old (ages available for 23 of 38), and females that had ovulated more than once were 5–17 years old (ages available for 60 of 111). Although females of unknown age could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 163 sexually mature females, 144 (88.3%; 95% CL = 83–93%) were pregnant in the year in which they were harvested.

1970s. Of the 316 reproductive tracts analyzed from the 1970s, 123 were immature, 25 had ovulated once, 161 had ovulated more than once, and seven were mature but the number of ovulations was unknown. Females that had never ovulated were <1–8 years old (ages available for 121 of 123). Females ovulating for the first time were 2–11 years old (ages available for 23 of 25) and females that had ovulated more than once were 4–22 years old (ages available for 143 of 161). Although females of unknown age could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 193 mature females, 176 (91.2%; 95% CL = 87–95%) were pregnant when harvested.

2000s. Of the 109 reproductive tracts analyzed from the 2000s, 43 were immature, nine had ovulated once, 54 had ovulated more than once, and three were mature but the number of ovulations was unknown. Females that had never ovulated were <1–3 years old (ages available for 41 of 43). Females ovulating for the first time were 4–10 years old (ages available for 7 of 9) and females that had ovulated more than once were 4–21 years old (ages available for 45 of 54). Although females of unknown age could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 66 mature females, 62 (93.9%; 95% CL = 88–99%) were pregnant when harvested.

DISCUSSION

Local knowledge

The majority of hunters thought that bearded seals were as abundant as ever. Even though the ice forms later and leaves earlier, they also reported that bearded seals are found in the same areas and they hunt them in the same months as in the past (Table 1). Although we do not think that hunters can detect small changes in abundance, they should be able to detect large changes; currently bearded seals are commonly harvested in all villages. While there is much variability in responses, we would expect a consensus to converge if the abundance of bearded seals or the timing of hunting changed greatly.

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. The majority of hunters from Point Hope wanted big seals for boat covers, but some wanted big males and others wanted big females. In Hooper Bay, some wanted big seals for the quantity of meat and oil and others wanted small seals to satisfy preferences for taste and tenderness. In contrast, the majority of hunters from other locations did not target specific types of bearded seals.

To assess if hunters from Point Hope and Hooper Bay were harvesting older seals, we calculated the average age of seals in the harvest for Point Hope and Hooper Bay, and then compared this to other villages. We focused on age, as older seals should be larger seals. Most of our metrics simply rely on having a sample of seals of known age, across a variety of ages. As such, bias in the distribution of seal size is not important. For example, a harvest that is skewed towards larger, older seals does not bias the average age of maturation, the pregnancy rate of mature seals, or growth rate, as all these analyses account for age. However, age distributions might be biased if only old seals are harvested. The average age of harvest (including pups) was 2.8 years in Hooper Bay, 7.4 in Point Hope, and 5.3 for all other village combined. Hence, at Hooper Bay, hunters may prefer large seals, but those preferences are not biasing the sample towards older seals. We suspect that hunters at Hooper Bay prefer older, larger seals, but are willing to harvest any seal. However, hunters at Point Hope may harvest older seals. Most of the difference in average age is due to hunters harvesting fewer pups at Point Hope; if we exclude pups from the sample, the average age of harvest at Point Hope is 8.4 years versus 7.9 years for other villages. As mentioned above, we do not expect such bias to affect most of the parameters we estimated and Point Hope is only one of more than eight villages sampled. However, the age distribution of seals taken at Point Hope is likely biased towards subadults and adults.

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 bearded seals shifted between the 1961–1979 time period and the 2000s (1998–2009). In general, seals still eat the same prey (*i.e.*, shrimp, crabs, mollusks, and fish), but the proportion of fish in the diet significantly increased. Specifically, the frequency of occurrence of fish increased from 41% to 86% in the Being Sea and from 28% to 89% in the Chukchi Sea (Table 3). In the 2000s, bearded seals consumed fish more frequently than was identified in previous studies in the Bering and Chukchi seas (Antonelis *et al*. 1994, Kosygin 1971, Lowry *et al*. 1980, Pikharev 1941); however, current fish consumption rates are similar to those reported for bearded seals in the Canadian High Arctic (Finley and Evans 1983) and the Svalbard area (Hjelset *et al*. 1999). In contrast, the frequency of occurrence of invertebrates in general did not change much in the Bering Sea (95–97%) or the Chukchi Sea (99–95%) during the same time periods (Table 4); however, specific invertebrate prey taxa did vary among decades, regions, and seasons (Tables 2 and 4–7).

Bearded seals are also consuming a greater diversity of fish than they did in the 1960s, when sculpin (19%) were the primary fish prey (Table 2). Bearded seals consumed an increasing diversity of fish in the 1970s and 2000s. In the 2000s, the most common fish consumed were still sculpin (67%), specifically *Gymnocanthus* spp. (39%) and *Myoxocephalus* spp. (50%); however, other common fish included flatfish (52%), specifically longhead dab (25%), Arctic cod (31%), saffron cod (21%), prickleback (21%), and Pacific sand lance (15%).

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*., Bluhm and Gradinger 2008, Grebmeier *et al*. 2006*b*, Moore *et al*. 2003, Mueter and Litzow 2008). As such, we would expect to see more pelagic fishes (such as cod) and less benthic prey (such as, sculpins, mollusks, or decapods) in the diet of bearded seals. Although the occurrence of cod has increased, so have benthic sculpin and flatfish, and patterns are not clear for benthic invertebrates. For example, while the occurrence of bivalves in the Bering Sea decreased in 1970s, it actually increased in the 2000s; whereas bivalves in the Chukchi Sea increased in the 1970s before decreasing in the 2000s (Table 4). If benthic prey is becoming less common, perhaps the magnitude of change is not yet great enough to override seal preference or great enough to be detected by occurrence statistics.

Inferences into how dietary changes affect bearded seals must be made with caution. We observed changes in the occurrence of prey, but we do not know what quantity of prey is necessary to meet caloric requirements. Bearded seals are generally considered benthic specialists, consuming prey items in different quantities and habitats than spotted seals (pelagic specialists) and ringed seals (generalists). As such, bearded seals may be more vulnerable to changes in prey populations, especially if benthic prey communities decline as has been predicted (Bluhm and Gradinger 2008, Mueter and Litzow 2008). However, our study suggests that bearded seals in the Bering and Chukchi seas consume a diverse assemblage of invertebrates (63 taxa) and fish (20 taxa) in both benthic and pelagic zones. This may indicate bearded seals consume prey opportunistically, utilizing a wide variety of organisms that are regionally and seasonally abundant.

The lowest frequency of occurrence of all cod during the 1970s was in 1975 (Fig. 5). No other prey taxa, fish or invertebrate, had similar declines in 1975. This is interesting, as we observed a similar pattern for ringed seals in 1975 (Quakenbush *et al*. 2011). For ringed seals, the drop in cod consumption corresponded with reduced growth rates of seals born between 1974 and 1976; in 1976 few pups were harvested, presumably due to low birth rates or pup survival, and those that were harvested had below average blubber thickness (Quakenbush *et al*. 2011). However, for bearded seals, 1975 and 1976 were associated with average growth rates (Fig. 10) and an average proportion of pups in the harvest (Fig. 13). Unfortunately, there were not enough samples to examine blubber thickness of bearded seal pups in 1975. However, the event that occurred around 1975 that affected ringed seals did not affect bearded seals in a similar manner.

Although bearded seal diets have changed significantly through time, they have apparently adjusted successfully. It is unlikely that the current diet is unfavorable, as growth rates, body condition, and pregnancy rates are all average or above average.

Our analyses have also 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. We could also monitor whether prey taxa vulnerable to ocean acidification are occurring less often in the diet.

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. Little is known about what the normal ranges are for marine mammals. Cd and Hg are commonly present at high concentrations in liver and kidney tissue of marine mammals. Cd can be toxic at elevated levels; however, in the kidney and liver of marine mammals it tends to be bound to metallothionein, which makes it less bioavailable and therefore less toxic (Goyer 1991, Groten *et al.* 1990). Marine mammals are 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).

Bearded seals had the highest concentration of total Hg and the second highest concentration of Cd of the four species of ice seals in our studies (Table 17; Quakenbush and Citta 2009). Spotted seals had the lowest concentration of both elements and ribbon seals had the highest concentration of Cd. Pb levels were barely above detection limits in any ice seal species (Table 17). Our concentrations of Cd in liver were lower than for bearded seals sampled near Barrow, AK (Dehn *et al*. 2005), but higher than three bearded seals sampled near Nome, AK (Mackey *et al*. 1996). No data from Canada or other regions were available for comparison of Cd.

Table 17. 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	35	42	17	9
Cd	Mean	1.62	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	1.32	**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)

Although bearded seals had the highest concentrations of total Hg (THg) compared to other species in our studies (Quakenbush and Citta 2009), they had the lowest percentages of the toxic form MeHg (Table 18). Values for 16 bearded seals between the ages of 1–23 ranged from 0.04–0.19 µg/g wet wt representing 0.2–8.8% (Table 18). Our concentrations of total Hg in liver were much lower than those of bearded seals in Canada (Smith and Armstrong 1975, Smith and Armstrong 1978) but similar to other studies in Alaska (Mackey *et al*. 1996, Dehn *et al*. 2005).

Table 18. Geometric mean concentration and ranges (µg/g or ppm wet wt) for total and methyl mercury in liver from ice seals harvested in Alaska 2003–2007. The highest concentration for each form is in bold.

Mercury		**Species**		
		Ringed	**Bearded**	**Spotted**
THg	*n*	35	42	17
	Mean	1.32	**2.13**	0.88
	Range	(0.14–12.88)	**(0.13–28.31)**	(0.03–5.61)
MeHg	*n*	4	16	2
	Mean	0.18	0.07	**0.43**
	Range	(0.12–0.27)	(0.04–0.19)	**(0.28–0.68)**
	% mean	7.62%	1.48%	**25.9%**
	% range	(2.9–14.3%)	(0.20–8.8%)	**(14.5–46.4%)**

Organochlorines—Compared to other ice seals species in our studies, bearded seals had the lowest geometric mean concentrations of ΣHCH levels (13.4 ng/g lipid wt), ΣDDT (89.1 ng/g lipid wt), and ΣPCB (118.1 ng/g lipid wt), and the second lowest of ΣCHL (100.8 ng/g lipid wt) in blubber tissue (Table 19).

Few contaminant studies are available for bearded seals; however our ΣHCH, ΣCHL, ΣDDT, and ΣPCB concentrations for bearded seals were much lower than those for ringed seals in Canada, Norway (Weis and Muir 1997), and Russia (Nakata *et al*. 1997). Direct comparisons can also be confounded by the analysis of different OC congeners and concentrations may depend both on sex and age, so differences in mean concentrations may have more to do with the sex or age ratio of the seals sampled than the location or time period.

Other contaminants— Polybrominated diphenyl ethers (PBDEs) have been analyzed in the blubber of bearded 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). Of the Alaska ice seal species, bearded seals had the lowest (3.4 ng/g) mean level of total PBDEs followed by ringed seals (5.9 ng/g wet wt), then spotted seals (12.4 ng/g wet wt); ribbon seals had the highest level (16.5 ng/g wet wt); 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 bearded seals (Quakenbush and Citta 2008a). 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*a*). When compared to other Alaskan ice seals, bearded seals had the lowest concentrations of PFOS, PFNA, PFDA, and PFUnDA (Quakenbush and Citta 2008*a*). PFOS has been identified as the predominant PFC in wildlife. There are no comparable studies of bearded seals in other regions, however studies of ringed seals Canada (Martin *et al.* 2004) and Greenland (Bossi *et al.* 2005) generally find levels of PFOS 4–21 times higher than what we observed in bearded seals (Quakenbush and Citta 2008*a*). 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 19. 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	37	17	9
∑ HCH	Mean	51.8	13.4	**104.8**	93.9
	SD	1.65	1.75	**1.56**	1.64
	Range	(17–150)	(2–28)	**(35–313)**	(53–228)
∑ CHL	Mean	96.5	100.8	193.6	**338.6**
	SD	2.12	1.65	1.96	**2.10**
	Range	(24–342)	(25–415)	(38–580)	**(199–1979)**
∑ DDT	Mean	129.3	89.1	199.5	**456.5**
	SD	1.85	2.06	2.19	**2.06**
	Range	(39–628)	(12–605)	(30–695)	**(168–1382)**
∑ PCB	Mean	278.7	188.2	404.1	**552.0**
	SD	1.71	1.80	1.97	**1.94**
	Range	(92–908)	(48–943)	(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 bearded seals in this study (2.2%, 1 of 46) than we did in ringed seals (8.3%, 4 of 48; Quakenbush *et al*. 2011), spotted seals (16.2%, 6 of 37; Quakenbush *et al*. 2009) and ribbon seals (14.3%, 2 of 14; Quakenbush and Citta 2008*b*). 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 bearded, ringed, spotted, and ribbon seals, or polar bears do on sea ice and this may explain the higher prevalence in them.

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 38.2% (39 of 102) for PhHV-1 antibodies in bearded seals and no antibodies for PhHV-2 (0 of 23) were much lower than 61% (11 of 18) and 17% (3 of 18), respectively reported by Zarnke *et al*. (1997). Our sample size was much larger (102 vs. 18) for PhHV-1, which may explain the different results, although the sample sizes for PhHV-2 (23 vs. 18) were similar. Our studies of ringed (Quakenbush et al. 2011), spotted (Quakenbush *et al*. 2009) and ribbon seals (Quakenbush and Citta 2008*b*) also found lower prevalence of PhHV-1 and -2 than Zarnke *et al*. (1997; Table 20).

Table 20. Comparison of serum antibody prevalences (%) for Phocine herpesvirus-1 (PhHV-1) and PhHV-2 in bearded, ringed, spotted, and ribbon seals. Our samples were collected during 2003–2007, Zarnke et al. 1997 samples were collected during 1978–1992.

	PhHV-1		**PhHV-2**	
Species	**Our studies**	**Zarnke et al. 1997**	**Our studies**	**Zarnke et al. 1997**
Bearded[1]	39/102 (38.2)	11/18 (61)	0/23 (0)	3/18 (17)
Ringed[2]	14/84 (16.7)	2/4 (50)	0/5 (0)	2/4 (50)
Spotted[3]	12/36 (33.3)	23/32 (72)	0/16 (0)	5/32 (16)
Ribbon[4]	0/11 (0)	7/24 (29)	0/11 (0)	7/24 (29)

[1]This study; [2]Quakenbush *et al*. 2011; [3]Quakenbush *et al*. 2009; [4]Quakenbush and Citta2008*b*

More disease screening is necessary to verify the prevalence of PhHV-1 and -2. There may also be variability in results from different labs and changes in the tests used between studies. 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 = 103) or CDV (n = 86) in bearded seals (Table 12). We also did not find PDV or CDV antibodies in spotted seals (n = 37, n = 22 respectively) or ringed seals (n = 82, n = 82) from the Bering and Chukchi seas (Quakenbush *et al*. 2009). However, both PDV and CDV have the potential to cause high mortality in 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). 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).

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. 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). 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).

CDV epizootics are believed to be caused by seals coming into contact with terrestrial carinvores, which serve as reservoirs for CDV. 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).

Fortunately, exposure to PVD and CDV does not guarantee an epizootic event. For example, some phocids are largely immune to PVD. Only one harp seal has shown clinical disease attributed to PDV (Daoust *et al.* 1993) and there are no cases of clinical disease in bearded seals. Transmission rates are also affected by seal behavior. Bearded seals are not considered social and rarely haul out in numbers during any time of year, thus they are not as likely to be susceptible to an epizootic. However, continued monitoring of PVD and CDV is warranted.

In addition, there were no detections of *Trichinella* (n = 85) or *Leptospira* (n = 71), and a lower prevalence of exposure to Toxoplasma (3.6%) in bearded seals than was found in ringed seals (5.0%; Quakenbush et al. 2011.)

Morphometrics

Growth rate—Asymptotic length, the length of seals ≥10 years of age was longer (218.6 cm, 95% CI ± 3.1) in the 1970s than in the 2000s (208.6 cm, 95% CI ± 5.4). Seals in the 1970s were also significantly longer at ages 8 and 9 than seals in the 2000s (Fig. 8). In the 2000s, seals were only longer at age 1 and age 5, and only significantly so at age 5. While it might be tempting to conclude that currently conditions are unfavorable for growth, seals were only consistently (*i.e.*, significantly) shorter for the older age classes. Perhaps conditions were unfavorable eight or more years ago. In support of this idea, the length of seals, given their age, was consistently shorter than expected between 1990 and 2000 (for all years except 1997; Fig. 10). Since 2000, five of nine years resulted in seals longer than expected, given their age. The only year that stands out as being particularly unfavorable was 2004. Blubber thickness is currently average or better (Fig. 12) while the skinniest seals we observed were harvested in 1991. Hence, we suspect that a shorter asymptotic length was due to unfavorable conditions sometime before 2000. Unfortunately, we have little or no data from the 1980s or 1990s and we cannot discern when conditions were poor or for how long.

Our asymptotic length for the 1970s is shorter ($\bar{x}$ = 218.6, *SE* = 1.6) than what is reported by McLaren (1993; $\bar{x}$ = 223.0, *SE* = 2.5) for the Bering and Chukchi seas, using data from Burns and Frost (1983). There are two reasons for this difference. First, the datasets are not identical. McLaren used 117 seals within the same dataset from the 1970s, and we used 124. Second, our methods for estimating asymptotic length differed. We estimated asymptotic length by averaging all seals ≥10 years of age; however, McLaren fit a von Bertalanffy curve to data from all ages. Without many older seals, asymptotic length is difficult to estimate accurately with growth curves and we suspect McLaren's estimate is biased high. Interestingly, Burns and Frost (1983) report that average length of seals ≥9 years of age is 219.7 cm (*n* = 37), only 1.7 cm longer than what we found.

The high variance in length measurements for the 2000s is puzzling, as outliers (*i.e.*, short or long seals) are not of the same cohort. For example, the three large seals that were sampled in the 2000s at age 5 (Fig. 8) were all sampled in different years, had different birth years, and were found at different locations. High variance is not likely due to measurement error, as seals measured by biologists had similar levels of variability as those measured by hunters. Food quality or favorable environmental conditions may simply be more spatially variable today. This would lead to more variability in seal lengths without a discernable annual pattern.

Blubber thickness—Sternal blubber thickness has changed little between the 1970s and the 2000s. In general, seals harvested in the late 1970s had less blubber than expected and seals harvested since 2004 have had more blubber than expected (Fig. 12). Seals sampled since 2004 had an average of 0.5 cm more blubber than expected. The only year characterized by particularly skinny seals was 1991, when seals had an average of 1 cm less sternal blubber than expected.

We do not know if these changes are biologically significant. For example, we do not know if seals with 1 cm less sternal blubber have lower survival or fecundity. However, we can

conclude that seals harvested since 2004 do not appear to be doing less well than seals harvested between 1977 and 1979 or in 1991 (Fig. 12).

Population parameters

Age distribution and mean age of harvest—With the exception of the 1960s, the proportion of pups in the harvest has remained fairly constant (Figs. 13 and 14), and averaged approximately 40%. In contrast, the proportion of pups in the harvest in the 1960s was less than 20%. In addition, no seals >20 years of age were harvested in the 1960s. We hesitate to conclude that the 1960s were unfavorable for bearded seals. Sample sizes were generally low in the 1960s and fewer pups in the harvest might be due to sampling biases. The lack of seals >20 might be due to chance, as we would only expect 1–6 seals in this age class, given the proportion of seals within this age class harvested in the 1970s and 2000s. However, we are confident in concluding that age distributions observed in the 2000s are similar to those in the 1970s. Both decades have similar proportions of pups in the harvest, indicating that pups are being born and are surviving to be harvested.

Mean age was younger in the 1970s and 2000s than the 1960s, largely reflecting an increase in the number of pups harvested in the 1970s and 2000s. After excluding pups, mean age of seals were more similar averaging 8.3 years in the 1960s, 7.1 years in the 1970s, and 8.1 years in the 2000s.

Sex ratios—In general, the sex ratio of pups was either near, or statistically indistinguishable from, unity (Fig. 15). Interestingly, the sex ratio of adults was skewed towards females in both the Chukchi and Bering seas, although more strongly so in the Chukchi Sea. For subadults, sex ratios were inconsistent. Female bias in the sex ratio of bearded seals has been observed in a number of studies (*e.g.*, Johnson *et al.* 1966, Smith 1981). If the harvest is a representative sample of the population, female bias could result from males having lower survival rates than females (Burns and Frost 1979). However, the harvest may not be representative of the population. Johnson *et al.* (1966) noted that adult females, especially pregnant females, float better than adult males when shot. Hence, the harvest may be biased towards females because the retrieval rate of males is lower. Smith (1981) suggested that sexual segregation or seasonally increased vulnerability may explain why more females might be harvested.

However, the patterns we observed are better explained by changes in survival than differential recovery rates or sexual segregation. For adults and subadults, sex ratios differed by region and decade. It seems unlikely that the retrieval rate of females (*i.e.*, how hunters retrieve harvested seals) would vary between regions or within a region over time. Likewise, it seems unlikely that sexual segregation or seasonal increases in the vulnerability of females could explain changes in sex ratios over time or within regions. While these might be confounding factors, we think it most likely that changing patterns of survival explain regional shifts in sex ratios over time. Unfortunately, this question cannot be answered with the data at hand. Studies that focus on animal movement and survival are required to conclusively determine why sex ratios of bearded seals are generally female biased.

Age at maturity and pregnancy rate—We did not detect statistically significant differences in the average age of maturation over time. The average age of maturity declined from 4.01 years in the 1960s to 3.97 in the 1970s, and was 3.9 years for seals sampled since 2000. Pregnancy rates are also relatively static; pregnancy rates were 88.3% in the 1960s, 91.2% in the 1970s, and 93.9% in the 2000s. Hence, there is not information to suggest reproduction is declining.

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. Currently, bearded seals grow to a shorter asymptotic length than they did in the 1970s; however, statistically significant differences were observed only in seals 8, 9, and ≥10 years of age. Most of a seal's growth occurs in the first two or three years after birth; as such, decreased length in these seals likely reflects poor foraging conditions in the 1990s or early 2000s. In contrast, metrics that reflect current environmental conditions had rates that were similar to or greater than what was observed earlier. For example, we found no evidence that age at maturation for females has changed over time. Blubber thickness and pregnancy rates are currently higher than previously observed. In addition, there are similar proportions of pups in the harvest now as in the 1970s and twice as many as in the 1960s. The high number of pups in the harvest indicates that pups are surviving long enough to be harvested (*i.e.*, pups survive to weaning). Hunter responses to questionnaires indicate that bearded seal numbers have not decreased. Current sex ratios are near unity and correspond to a period with high pregnancy rates and a high number of pups in the harvest. Levels of contaminants in bearded seals are lower than levels of other ice seal species harvested in Alaska and the prevalence of diseases has remained stable.

An important consideration is how powerful our methods are to detect change. We have fewer samples available for bearded seals than we had for ringed seals (Quakenbush *et al*. 2011), concluding that "not much has changed" may be an artifact of low statistical power. While we found little evidence that the 2000s were better or worse than the 1970s on average, we did detect years that were associated with positive or negative population parameters. For example, the growth of bearded seals born between 1964 and 1972 was clearly above average and statistically significant in 4 of 9 years (Fig. 10). We can also detect changes in growth from the 2000s; for example, 2004 was clearly an unfavorable year, while 2007 was clearly a favorable year (Fig. 10). We can also detect statistically significant changes in blubber thickness for both the 1970s and 2000s (Fig. 12) and changes in diet over time (*e.g.*, Table 2). Hence, while collecting more seals would help strengthen our inferences, we conclude that our sample sizes are not too small to detect changes in the parameters we measured.

A more important 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. With these data, we can rule out some potential sources of population decline. For example, we know that the reproduction of bearded seals is currently robust. Pregnancy rates are high, pups are surviving to be harvested, and pups compose a large proportion of the harvest. Hence, bearded seals are reproducing as well as or better than they have since the 1960s. Blubber thickness of adults is currently similar to or higher than what was observed in the 1970s. Hence, it is likely that they are finding enough food (even though diet has shifted). As such, population declines due to poor reproduction, pup survival, or starvation are unlikely. 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 bearded seals has not changed over time, large changes in abundance are unlikely. At a coarse scale, we can conclude that bearded 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 bearded 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. Bearded seals were petitioned to be listed under the Endangered Species Act primarily due to concerns that changing ice conditions may threaten population persistence because sea ice suitable for pup maturation and molting would not be located near benthic feeding areas or that ocean acidification will alter prey communities (Cameron *et al.* 2010). Although sea ice is declining now and we have documented a shift in diet to more fish, we have yet to observe declines in seal health, growth, or reproduction. We think it reasonable to assume that changing ice conditions will affect the status of bearded seals; however, predicting the magnitude and timing of those effects is speculative at best. Given that there are no estimates of abundance or trend, this monitoring program is the best tool available for assessing the status of bearded seals.

The monitoring program, however, does have limitations. While changes in survival or reproduction will likely be detectable in age ratios and growth rates, we will not know how these changes directly relate to abundance. We also do not know how sensitive our indices are; subtle changes in survival or reproduction may not be detectable, yet may considerably affect population growth. As such, changes in growth, reproduction, and age distributions may not be detected until a number of years after changes occur. As such, efforts should continue to determine how to quantify the abundance of bearded seals.

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 bearded seal abundance or population trend are lacking. This monitoring program is capable of detecting

changes in population parameters that are of concern for bearded seals. The proposed listing of bearded seals is based upon concerns that climate will no longer provide ice that is sufficient for pup maturation or molting near benthic feeding areas and that ocean acidification will lead to changes in prey communities that may not support bearded seals (Cameron *et al.* 2010). Hence, warming is predicted to affect pup survival, growth rates, body condition, and/or diet, all of which are parameters we monitor within our program. Until abundance can be quantified, this monitoring program will provide the best information available for assessing the status of bearded 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.

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