Preliminary Report

Biology of the Spotted Seal (*Phoca largha*) in Alaska from 1962 to 2008

Report to:

National Marine Fisheries Service

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INTRODUCTION

In Alaska, the spotted seal (*Phoca largha*) is one of four species of seals that are dependent on sea ice during some portion of the year; the other three species include the bearded seal (*Erignathus barbatus*), the ringed seal (*Pusa hispida*), and the ribbon seal (*Histriophoca fasciata*). Spotted seals range from the Yellow Sea of China and Korea, northward to the Sea of Japan, the Sea of Okhotsk, along all outer margins of the Bering Sea, throughout the Chukchi Sea, and eastward in the Beaufort Sea, at least as far as Herschel Island, Canada (summarized in Quakenbush 1988). In the Bering Sea, when ice is present, spotted seals are found along the pack ice edge where the ice is loosely packed (Fay 1974) and the water is less than 200 m deep, which often corresponds with the southern margin of the continental shelf (Braham et al. 1984). This area can vary in width depending upon winds and currents, and satellite-linked tagging studies conducted in 1991–1994 showed that spotted seals used an area of up to 300 km from the ice edge during November–April (Lowry et al. 1998, 2000). Spotted seals give birth, rear their pups, and molt on ice floes, but they are the least ice adapted and the least ice dependent species in that they prefer loose pack ice and they will readily haul out on land, which they do frequently in summer (e.g., Frost et al. 1993, Lowry et al. 1998). Pupping in the Bering Sea occurs in March and April and pups are weaned after three to four weeks (Burns 1986). The distribution of spotted seals shifts northward and toward the coasts as sea ice recedes in May and June and many spotted seals enter bays and rivers and haul out on sand bars and barrier islands (Burns 1986).

The status of the spotted seal is currently under review due to concerns regarding how changes in sea ice resulting from climatic warming may affect the species (50 CFR 223 and 224, March 28, 2008). Sea ice is changing in thickness, persistence, and distribution (Rigor and Wallace 2004, Comiso 2006, Serreze *et al.* 2007). 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.* 2006), which suggests changes in the ecosystem may be occurring as well.

Population estimates for spotted seals are difficult to obtain due to problems related to conducting surveys over large areas of ice-covered waters far from shore. The most recent estimate is from the Bering Sea in the 1970s when the spotted seal population was estimated from ship surveys during the breeding season. The average distance between breeding pairs was determined, and by assuming an even distribution throughout the area estimated to be available breeding habitat, a population estimate of 200,000 to 250,000 was calculated (Burns 1973, Burns and Harbo 1977). There are no current estimates of abundance.

Even though population estimates are not available, Russian commercial harvests and native subsistence harvests have never exceeded a sustainable level (Burns 1973). The Russians began a commercial harvest in 1961 and removed ~2,500 spotted seals annually until 1968. Between 1969 and 1985 the harvest was ~4,000 annually and between 1986 and 1990 it decreased to 1,600 per year (Fedoseev 2000). The commercial harvest combined with the subsistence harvest in Russia and Alaska was estimated to be <7,000 per year (Burns 1973).

The Alaska Department of Fish and Game (ADF&G) has been collecting information and samples from the Alaska Native subsistence harvest of spotted seals for over 40 years, relying on the cooperation of coastal 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, and included the islands in the Bering Sea (Fig. 1), an area that covers virtually the entire range of spotted seals along the Alaska coast.

In this report we analyze results from spotted seal measurements and samples collected between 1963 and 2008 in order to evaluate how diet, growth rates, body condition, age distribution, and productivity have changed over time. The purpose of this report is to make unpublished data, collected by the State of Alaska, available for researchers, managers, and others interested in spotted seals.

METHODS

Sampling years

Spotted seals from the subsistence harvest were sampled between 1963 and 2008; however, sampling effort and opportunity were not consistent. The majority of spotted seals sampled were harvested during two time periods, 1963–1979 and 1998–2008 (Fig. 2). Spotted seals were also collected on scientific cruises in 1971–1972, 1976–1979, 1981, 1984–1985, and 1991. We were not able to find ages for many specimens collected during cruises in the 1980s and 1991 and no samples were collected from subsistence harvests in the 1980s or early 1990s thus, there are no data from these years included in our analyses. Therefore for most of our analyses we grouped samples into two distinct time periods 1963–1979 (1960s and 1970s) and 1998–2008 (the 2000s). Data from the scientific cruises were included in our analyses of diet and pregnancy rates but not in age at harvest or survival.

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 numbers and behavior, or may be due to changes in harvest methods. 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. Only the villages with eight or more respondents were summarized.

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 either frozen in the field or preserved in formalin and then 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 persist 9–15 years (Burns 1969). 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 spotted seals from 1966–2008 to determine if the frequency of prey items has changed over time. Stomachs from spotted seals harvested by Alaskan Natives and during scientific cruises were collected, frozen, and shipped to ADF&G offices in Fairbanks. Stomach were thawed in the laboratory and the contents were rinsed with freshwater through two sieves with mesh sizes of 1.0 mm and 0.5 mm and prey items were indentified to the lowest taxonomic level and weighed to the nearest 0.1 g.

To provide an overall description of spotted seal diet, we first calculated the frequency of occurrence (FO) for each item of prey. FO_i is the percentage of stomachs that contained one or more individuals of the prey species *i* out of the number of stomachs with digested material. 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 since 1998 were grouped using the same categories used prior to 1998. We used Pearson Correlation Coefficients in SAS (Proc CORR) to examine correlations among annual FO values for all prey items. 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 spotted seal diet had changed over time, we used logistic regression (Ramsey and Schafer 2002) 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 time period (1966–1981 and 1998–2008), sex, region (Bering and Chukchi seas), season (summer and winter), and age class (pup: <1, subadult: 1–4, adult: >5). We used OR to asses the strength of an association between an explanatory variable and the presence of a prey item. For example, 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 (i.e., in the 2000s, a prey item was 'X' times more likely to be consumed by a spotted seal than in the 1960s and 1970s). Models were fit using SAS (Version 9.1; PROC LOGISTIC, SAS Institute Inc., Cary, NC, USA) and the best model was selected using a backward elimination procedure. This procedure starts with a model that contains all variables and then sequentially eliminates all non-significant variables until only significant variables remain. We considered variables statistically significant at the level of α=0.10. We chose a more "liberal" alpha level than α=0.05 because we wanted the opportunity to investigate patterns that might be biologically interesting, but not strong enough to be detected at α=0.05.

While FO evaluates how often a specific prey item occurred in all stomachs examined, it does not account for occurrence relative to other prey items found. Therefore, in order to evaluate the occurrence of each fish taxa relative to the occurrence of all fish taxa, we determined the relative occurrence (RO) of each fish taxa among the occurrences of all fish taxa found in spotted seal stomachs each year. RO_i is the ratio of the number of stomachs with fish taxa $_i$ to the total number of fish taxa present in all spotted seal stomachs each year. For example, in 1966, five stomachs contained fish. Herring, cod, and greenling were each found in only one stomach, and sculpin were found in all five stomachs, resulting in eight fish occurrences of four fish taxa. Using the RO metric, herring, cod, and greenling 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, herring, cod, and greenling each occurred in 1 of 5 (20%) stomachs and sculpin occurred in 5 of 5 (100%) stomachs. The RO of fish prey allows us to assess the diversity of fish taxa consumed by spotted seals and does not treat each prey item in isolation. For each fish taxa we evaluated differences in RO ratios by time period (1960s and 1970s: 1966–1981 and 2000s: 1998–2008) using chi-squared statistics in SAS (Version 9.1; PROC FREQ, SAS Institute Inc., Cary, NC, USA).

Contaminants

Tissue preparation—Spotted seal samples collected in 2003–2006 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 contaminants were quantified by TDI – Brooks International, Inc., B&B Laboratories, Inc., College Station, TX. Individual seals were analyzed for contaminants 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.

Metals and other elements—Only liver tissue was analyzed for trace metals. Liver 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 10th 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 10th 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.

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 is used for analyte confirmation. A data acquisition system continuously acquired and stored all data for quantitation. This method is capable of producing data at parts-per billion and parts-per trillion concentrations. The surrogate spiking solution includes 4,4'-dibromooctaflurobiphenyl (DBOFB), 2,2',4,5',6 pentachlorobiphenyl (PCB 103), and 2,2',3,3',4,5,5'6 octachlorobiphenyl (PCB 198). Surrogate solution (100 µL) is added to all samples and quality control samples prior to extraction. Surrogate compounds are resolved from, but elute in close proximity to, the analytes of interest. The recovery of PCB 103 is used to correct analyte concentrations. Spikes, duplicates, and blanks were analyzed for quality control with each batch of 20 samples or less.

Disease

We tested serum from the blood of spotted seals collected near Little Diomede Island, Shishmaref, and Kotzebue, between 1998 and 2008, for four diseases known to affect phocids; *Brucella abortus*, 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 *et al.*1989). 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.

Morphometrics

Growth rate— Because growth is nearly linear in pups but becomes more curvilinear as seals age (e.g., McLaren 1993), we examined the growth rates of seals using two separate analyses. For seals greater than one year of age we used curvilinear models and for seals less than one year of age we used linear models.

For seals greater than one year of age, we investigated the change in growth rates over time by fitting von Bertalanffy growth curves (e.g., Schnute 1981, McLaren 1993) to age-at-length data. The model is:

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

Where

L_x is the standard length of harvested individuals,

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

L_x and x are vectors of empirical data, from harvested seals; L_{inf}, a, and b are estimated parameters. McLaren (1993) recommends setting x_0 to a constant, rather than estimating x_0 from the Bertalanffy growth curve. We follow McLaren's (1993) recommendation for spotted seals sampled in the Bering Sea and use -0.55 years for x_0.

We estimated L_{inf}, a, and b within a Bayesian framework using Gibbs sampling (Congdon 2003, Gelman et al. 2004) in WinBugs (Speigelhalter et al. 2003). Bayesian methods use simulations to describe the probability distribution of a parameter, such as L_{inf}, given the data (Gelman et al. 2004). Each simulation is commonly referred to as a 'chain'. We ran four chains, 40,000 iterations each, to confirm that all chains converged on the same solution. We discarded the first 10,000 iterations (i.e., the 'burn-in') to remove the effect of initial values on the posterior distribution. To confirm that our model was converging on a stable solution, we examined Gelman-Rubin plots (Gelman and Rubin 1992) and the iterative histories for each parameter in each chain.

Rather than statistically comparing estimates of L_{inf}, a and b, we treated different models of seal growth as hypotheses. Models were selected using Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). DIC is equal to the -2 log likelihood of the model, calculated with the posterior means of the model parameters, plus 2 times the effective number of parameters. DIC are used for model selection in a similar fashion as Akaike Information Criterion (Burnham and Anderson 2002); models greater than 4 DIC units from the best approximating model are considered to have little statistical support.

We were primarily interested in determining if spotted seal growth changed between time periods. However, relatively few old seals (>20 years of age) were collected in any time period, and we were forced to estimate L_{inf} for the data pooled across all time periods. We first determined if L_{inf} varied by seal gender when all time periods were pooled. After estimating L_{inf} for the pooled data, we then treated L_{inf} as a constant and estimated a and b, when comparing models of spotted seal growth. We compared seven models (Table 1); five models combined time periods in different ways. For example, one model assumed growth rates were the same during all time periods and another assumed growth rates differed in all time periods. Two additional models examined gender specific growth rates. One assumed that growth varied only by gender and not time period. One included growth rates that varied by time period and gender, but for the 1960s and 1970s only, as there was not enough data to estimate gender effects for data collected in the 2000s.

For seals less than one year of age, we assumed the parturition date of all seals was the same (1 April). We do not know exactly when seals were born and had to assign a parturition date to account for how we expect seals to grow quickly within their first year. The actual day we assigned is unimportant. However, seals born earlier in the year may appear longer given their assumed date and seals born later in the year may appear shorter. If parturition date varies within time periods, this will result in observed growth rates being more variable. We assumed that standard lengths was normally distributed within each month and used ANOVA to compare different time periods within each month when samples were available. Sampling across all periods only occurred within May and June; hence we first examined the growth of seals as a function of gender and time period for May and then repeated the test for June. A linear model would provide a comparison that integrated seasonal effects more efficiently. However, samples were generally not well distributed across months and we did not think that intercepts and slopes from linear models were biologically meaningful.

Body condition—We used sternal blubber thickness as an index for body condition because we did not have enough ancillary data (e.g., standard length or axillary girth) to calculate indices of body condition that are known to be more correlated with the true blubber content of a seal (*e.g.*, Ryg *et al.* 1990*a*, Arnould 1995, Gales and Renouf 1994, Parsons 1977). To allow for small sample sizes, we rank transformed sternal blubber thickness and then used ANOVA to test for differences by gender (male vs. female), time period (1960s, 1970s, and 2000s), and month. Month was included to account for seasonal fluctuations in blubber thickness; seals are expected to gain and lose mass seasonally (Ryg *et al.* 1990*b*) and it is important to control for season when comparing separate time periods. We used Type III sums of squares to determine if variables were significant and then sequentially dropped non-significant variables from the model.

Population parameters

Age and sex distributions—We characterized the age and sex distribution of spotted 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 1963–1985 and 1998–2008 (Fig. 2); however, sampling effort and opportunity were not consistent. Seals collected on research cruises in the 1970s (n=397) were not included in the analysis of age and sex distributions because pups were disproportionally targeted by researchers (i.e., 81% of all seals sampled and aged from cruises were pups). We acknowledge that we must make inferences cautiously from harvest data because hunter preferences may affect how the age distribution of the harvest is biased relative to the true age distribution of the population. However, because hunters cannot distinguish the age of mature seals by sight, and because hunters do not usually forego opportunities to harvest spotted seals, the sample of adult seals should be effectively random.

To compare age distributions over time and to identify where age distributions deviated, we categorized our sample into six groups and calculated chi-square statistics (Skalski et al. 2005). The age groups were 0–1, 2–5, 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 (Version 9.1; PROC FREQ, SAS Institute Inc., Cary, NC, USA).

We evaluated differences in sex ratios by decade for all seals harvested, and among age classes using chi-squared statistics in SAS. Thresholds for seal age classes were 0–1 (juvenile), 2–3 (subadults), and >4 (adults) years of age. We also examined age specific sex ratios for spotted seals at least 10 years of age. Seal hunters do not target a specific gender of spotted seals, therefore the sex of each harvested seal should not be subject to hunter bias and a change in the sex ratio of spotted seals over time may represent a change in the population structure.

Survivorship schedule—Annual variation in recruitment was estimated for spotted seals harvested in the 1960s, 1970s, and 2000s. Recruitment was defined as the survival of fetuses to the age of harvest and included all potential mortality risks including abortion, predation, and competition. We calculated birth years for aged seals harvested during 1963–1980 and 1998–2003 and created a pooled survivorship curve (Ferguson et al. 2005). Seals collected on research cruises in the 1970s (n=397) were not included in this analysis because the collection was biased toward pups. Survivorship was predicted by fitting the birth year (age) frequency to a smooth function $y=ae^{bx}$, where y is the number of spotted seals predicted to be in the sample, x is the year of birth, e is the base of the natural logarithm, and a and b are constants. The log-survivorship curve represents the predicted number of seals born in a year that survived to be harvested. We estimated the constants in the curvilinear function using SAS and Proc NLIN (SAS Institute 2004). Deviations between the actual and predicted number of survivors (residuals) for each year were used to identify years that had better or worse than expected recruitment. Log-survivorship curves were based on the assumptions that pregnancy rates, neonate survival, and juvenile recruitment varied while conception rates remained constant (Ferguson et al. 2005).

We estimated survivorship for seals in the Bering and Chukchi seas during two time periods, 1963–1980 and 1998–2003. A cut-off year was established for each dataset to improve the fit of the log-survivorship curve and limit the analysis mainly to years in which harvest was occurring. For example, harvested seals may have been born long before the sampling began in 1963. As recommended by Ferguson et al. (2005), we started our analysis with the most recent year, prior to harvest sampling, with fewer than fours seal births (1956 and 1991, respectively). As recommended by Ferguson et al. (2005), we also excluded the most recent year (1980 and 2003, respectively) from consideration as a larger proportion of young-of-the-year seals (50–65% of the annual harvest) were represented in the harvest of all years, possibly due to greater susceptibility.

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 can not 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; models differed 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 (SAS Institute 2004).

RESULTS

Local knowledge

A total of 90 questionnaires were analyzed from five Bering and Chukchi sea villages. Responses did not indicate decreases in spotted seal population abundance at any location (Table 2). The majority of respondents from all villages reported that spotted seals were found in the same locations as in the past. The timing of hunting had not changed for spotted seals in any village. Hooper Bay hunters tried for small, young spotted seals because they are tender and taste better, but the majority of hunters in the other villages did not try for specific types of spotted seals (Quakenbush and Sheffield 2007).

Diet

In the 2000s, stomachs from 436 spotted seals were examined and 291 (67%) contained prey items (Fig. 3). Of the stomachs examined during the 2000s that contained prey items, 85 were from four villages in the Bering Sea and 206 were from three villages in the Chukchi Sea, the most samples were contributed by Shishmaref (204). The number of specimens from other villages ranged from one in Kotzebue to 48 from Diomede. These stomachs were collected during the spring-summer (70) and fall (221) subsistence seal harvests.

In the 1960s and 1970s, stomachs from 236 spotted seals were examined and 175 (74%) contained prey items. Of the stomachs examined in the 1960s and 1970s that contained prey items, 134 were from the Bering Sea and 41 were from the Chukchi Sea. Samples from the Bering Sea came from seven villages (94) and four research cruises (40). All samples from the Chukchi Sea (41) were from three villages, and again most were from Shishmaref (38). The number of specimens from other villages ranged from one in Diomede and Golovin Bay to 30 from Savoonga. These stomachs were collected during the spring-summer (106) and fall (69) subsistence seal harvests.

No spotted seal stomachs with contents were collected in 1968, 1973, 1974, and 1999. A list of the prey taxa identified and their frequency of occurrence (FO) in stomachs is given in Table 3. The frequency of all prey items consumed by males and females did not differ; therefore, occurrence data for both sexes were pooled for all diet analyses. The final logistic model and general changes in diet over time for each prey item considered are shown in Tables 4 and 5.

Fishes—Fishes were commonly identified in spotted seal stomachs across all sample periods (Table 3). In the 2000s, however, fish consumption was higher (>95%, p<0.0001; Table 4) compared to the 1960s and 1970s (Fig. 4). For example, after accounting for variation in the occurrence of prey items due to season and age of the seal, a spotted seal stomach was 20.82 times more likely to contain fish in the 2000s than during the 1960s and 1970s. Throughout this study, fish consumption was higher in winter than summer (p=0.0003). In the 2000s, four species of fish, Pacific herring (*Clupea pallasi*), smelt (*Osmerus mordax*), arctic cod (*Boreogadus saida*), and saffron cod (*Eleginus glacialis*) occurred at frequencies >30% (Table 3), whereas the most commonly identified fish in the 1960s and 1970s was saffron cod (23.43%).

Pacific herring occurred in >40% of all spotted seals harvested in the Chukchi Sea, which was greater than samples from the Bering Sea (p<0.0001; Table 6). During the 2000s, spotted seals consumed Pacific herring more frequently than in the 1960s and 1970s (p=0.0116). Smelt were also consumed 3.52 times more frequently in the 2000s than in the 1960s and 1970s (p=0.0030; Fig. 4), after accounting for regional and seasonal differences. During the 1960s and 1970s smelt were consumed by <10% of spotted seals harvested in both the Bering and Chukchi seas (5.97% and 0.00%, respectively; Table 6). During the 2000s, however, consumption of smelt shifted completely to the Chukchi Sea (40.29%; Time*Region, p=0.0200). Conversely, a regional shift in consumption of Pacific sand lance (*Ammodytes hexapterus*) away from the Chukchi Sea also occurred (Time*Region, p=0.0264). During the 1960s and 1970s, seals harvested in the Chukchi Sea consumed 3.43 times more Pacific sand lance than seals in the Bering Sea; during the 2000s, however, the consumption of Pacific sand lance has not varied regionally (Table 6).

Fish from the Family Gadidae are important prey species for spotted seals and were found in 38.29% of stomachs examined in the 1960s and 1970s and in 62.20% of the stomachs examined during the 2000s. This increase in cod consumption between time periods was significant (p=0.0346) across all regions and seasons; however, the frequency of cod increased steadily after 1975 (Fig. 4). Generally, more cod were consumed in the Bering Sea than in the Chukchi Sea (p=0.0015). In the 2000s, spotted seals were 8.77 times more likely to consume arctic cod than during the 1960s and 1970s (p<0.0001). Arctic cod were consumed more frequently by spotted seals in the Bering Sea than in the Chukchi Sea (p<0.0001) for all time periods studied; there was also evidence that the consumption of arctic cod in the 2000s has increased more substantially for winter harvested seals than seals harvested in the summer (Time*Season, p=0.0442; Table 6). Spotted seal consumption of saffron cod also increased in the 2000s (Table 6; p=0.0276). Regional and seasonal differences in the occurrence of saffron cod in spotted seal stomachs were also identified; seals consumed more saffron cod in the Chukchi Sea than in the Bering Sea (p=0.0015) and more during winter than summer (p=0.0096; Table 6). Occurrence of walleye pollock (*Theragra chalcogramma*) in spotted seal stomachs was higher in the Bering Sea than in the Chukchi Sea (p=0.0004) and higher in winter than summer (p=0.0210); however, there was no change in the consumption of walleye pollock over time (Time: p=0.1969).

Flatfish of the Family Pleuronectidae were uncommon in spotted seal diets until the 2000s and were identified in only three seals in 1976 and two in 1978 (Fig. 4). In the 2000s, consumption of flatfish was higher (p=0.0015); spotted seals harvested in the 2000s were 5.09 times more likely to consume flatfish than seals harvested in the 1960s and 1970s. Although flatfish were uncommon in spotted seal diets before the 2000s, most were found in stomachs from the Chukchi Sea. In the 2000s, flatfish were more likely to be found in stomachs from the Bering Sea (Time*Region, p=0.0262; Table 6). Although the overall consumption of eelblenny (*Lumpenus* spp.) over time has not changed p=0.2411); spotted seals harvested in the Bering Sea were 10.00 time more likely to consume eelblenny in the 2000s than during the 1960s and 1970s (p=0.0346).

While the occurrence of most fishes in spotted seal stomachs was higher in the 2000s compared to the 1960s and 1970s, the occurrence of sculpins (Cottidae; p=0.0002) and greenling (*Hexagrammos* spp.; p=0.0085) was lower. Seals harvested during the 2000s were 0.54 times less likely to consume sculpins than seals from the 1960s and 1970s (Table 6). The decrease in sculpin occurrence was, however, not consistent for all Cottidae identified; sculpins in the genus *Gymnocanthus* were more frequently consumed by seals during the 2000s than during the 1960s and 1970s (Table 3; p=0.0012). During the 2000s, greenling were not found in the stomachs.

Consumption of fish by seal age class was not consistent between time periods. During the 1960s and 1970s, older seals consumed fish more frequently than younger seals. Adult seals were 16.00 times more likely to have eaten any taxa of fish than subadults (p=0.0089) and 72.00 times more likely to have eaten fish than pups (p=0.0004). Similarly, subadults were 4.50 times more likely to consume fish than pups (p=0.0369). During the 2000s, consumption of fish did not differ among age classes (p=0.7363). Across all time periods, the consumption of Pacific herring also varied by age class as it was 2.78 times more likely to be eaten by adults than pups (p=0.0018) and 2.18 times more likely to be eaten by subadults than pups (p=0.0191). There was no evidence that Pacific herring consumption differed between adults and subadults (p=0.4310). The consumption of cod by age class has also been inconsistent between time periods (Time*Age, p=0.0221). The consumption of cod by adult seals did not vary significantly between time periods (p=0.2770), only increasing from 51.02% to 55.42%. Pups and subadults, however, consumed greater frequencies of cod in the 2000s than during the 1960s and 1970s, increasing from 10.00% to 60.52% for pups (p=0.0058) and 40.38% to 62.50% for subadults (p=0.0031). Consumption of flatfish also varied by age class; adult spotted seals were 4.14 times more likely to have eaten a flatfish than pups (p=0.0090). There was no evidence that flatfish consumption differed between adults and subadults (p=0.1999) or pups and subadults (p=0.1946).

In the 2000s, spotted seals consumed a greater diversity of fish species than during the 1960s and 1970s based on relative occurrence (RO); recent diets were regularly comprised of five or more fish taxa (Fig. 5). Sculpin, however have not been part of that diversity in recent years even though they accounted for ~50% of the fish consumed by spotted seals during the late 1960s and mid 1970s. The RO of sculpin in spotted seal diets decreased from the 1960s and 1970s (15.93%) to the 2000s (3.27%; p<0.0001). Conversely, the RO of smelt was greater during the 2000s (18.40%) than the earlier time period (4.40%; p<0.0001). There was also minimal evidence of an increase in the RO of flatfish in the 2000s (p=0.0664). Furthermore, cod, Pacific herring, smelt, Pacific sand lance, and flatfish have been identified in seal diets every year in the 2000s, whereas their occurrence during the 1960s and 1970s was less consistent (Fig. 5).

Invertebrates—Invertebrate prey have been consumed less frequently in seals harvested in the 2000s compared to those harvested in the 1960s and 1970s (p=0.0032); changes in the consumption of invertebrates were, however, less consistent than changes identified in fish. Consumption of all invertebrates did not vary by seal age class (p-values ranged from 0.2098 to 0.9996). Of all invertebrate prey, only mollusks and crabs were consumed more frequently during the 2000s (Table 3 and 5). Spotted seals were 5.22 times more likely to consume mollusks in the 2000s than during the 1960s and 1970s (p=0.0047). Furthermore, mollusks were not consistently identified in spotted seal stomachs until the mid 1970s (Fig. 6). Mollusks were also 3.16 times more likely to be consumed by seals in summer than winter (p=0.0088). There was minimal evidence of an increase in the occurrence of crab in the 2000s when all regions and seasons were considered (p=0.0949). During the summer, however, spotted seals consumed 5.20 times more crab in the 2000s than during the 1960s and 1970s (p=0.0476). The consumption of octopus (Octopodia) did not change over time (p=0.9671).

Although spotted seals consumed fewer invertebrates in the 2000s, the occurrence of invertebrates was strongly correlated with the occurrence of crustaceans (r=0.9515) and the final logistic regression model for invertebrates was identical to that of crustaceans (Table 5). Therefore, changes in spotted seal diets over time are almost entirely explained by changes in crustacean consumption. We found fewer crustaceans in seal stomachs sampled during the 2000s than in the 1960s or 1970s (p=0.0014; Table 3); however, the change in FO was not equal across regions (Time*Region: p=0.0059) or seasons (Time*Season: p<0.0001). In the Bering Sea, the occurrence of crustaceans was similar (~45%) during the two time periods (p=0.0539). Within the Chukchi Sea, however, seals consumed fewer crustaceans in the 2000s compared to the 1960s and 1970s (p=0.0002; Table 7); therefore shifting the dominant region that crustaceans were found in spotted seal diets from the Chukchi Sea to the Bering Sea. A seasonal shift in the consumption of crustaceans has also occurred during the 2000s (Table 7) with fewer eaten in summer (p=0.0002) and more eaten in winter (p=0.0295) than in the 1960s and 1970s. Seals harvested in the winter during the 2000s consumed 2.26 times more crustaceans than in the 1960s and 1970s. During the 1960s and 1970s, crustaceans were consumed more frequently during the summer than the winter (p<0.0001). In the 2000s, however, the consumption of crustaceans has not varied seasonally (p=0.8371).

The overall consumption of mysids was significantly (p=0.0035; Table 3) lower in the 2000s, and only one spotted seal stomach contained them. Pooling both time periods, mysids were identified as prey more frequently in summer than winter (p=0.0268; Table 7). Although spotted seals consumed few isopods, there was evidence that isopod occurrence was lower in the 2000s (p=0.0138) with the greatest reduction occurring in the Chukchi Sea (p=0.0132) and some evidence of a reduction in the Bering Sea (p=0.0590).

In general, the consumption of amphipods also was lower during the recent time period (p=0.0475; Table 3); changes were not, however, consistent between regions or seasons (Table 7). While spotted seals in the Chukchi Sea now consume fewer amphipods than in the 1960s and

1970s (*p*=0.0121), seals in the Bering Sea consume more than in the past (*p*=0.0390). Generally, amphipods were two times more likely to be consumed in the summer than winter (*p*=0.0094), but seasonal changes in the proportion of amphipods were also observed (Time*Season: *p*=0.0470). During the 1960s and 1970s, seals harvested in the summer were 5.45 times more likely to have eaten amphipods than seals harvested in winter (*p*=0.0078). During the 2000s, however, there was no evidence that seasonal differences in consumption remain (*p*=0.7092) as FO for each season differed by only ~3.4%. Changes in amphipod occurrence were primarily driven by declines in *Gammarus* spp. (*p*=0.0019) and *Parathemisto* spp. (*p*=0.0033). Seals harvested in the Chukchi Sea consumed significantly less *Gammarus* spp. in the 2000s than during the 1960s and 1970s (Table 7; *p*=0.0019). This decline was likely responsible for the inclusion of the interaction term Time*Region (*p*=0.0155) in the final model for *Gammarus* spp. During the 2000s, the overall frequency of *Parathemisto* spp. decreased from frequencies observed in the 1960s and 1970s (*p*=0.0033; Table 7).

Although decapods remained common prey items throughout our investigation, they occurred less frequently in the 2000s than during the 1960s and 1970s (Table 3). Annual FO values for all decapod taxa were strongly correlated with shrimp (*r*=0.9526), suggesting changes in shrimp consumption were likely responsible for variations we observed among all decapods. Shrimp (Caridae) were the primary invertebrate prey item identified throughout our study; however, their occurrence was lower in the 2000s (20.27%) than during the 1960s and 1970s (36.57%) (Table 3; *p*=0.0057). There was strong evidence that the seasonal consumption of shrimp shifted between the early and recent time period (Time*Season: *p*<0.0001) to a lower occurrence in summer (*p*<0.0001) and a higher occurrence in winter (*p*=0.0057). Furthermore, during the 1960s and 1970s a seal was 22.88 times more likely to consume shrimp during the summer than winter (*p*<0.0001); during the 2000s, however, there was no evidence that consumption varied seasonally (Table 7; *p*=0.3744). More specifically, the occurrence of shrimp from the genera *Eualus* (*p*=0.0013) and *Pandalus* (*p*=0.0066) declined from frequencies detected in the 1960s and 1970s (Table 3). In fact, during the 2000s no shrimp from the genera *Lebbeus* and *Eualus* have been identified in spotted seal stomachs.

Shrimp from the Family Crangonidae were common in spotted seals diets (Table 3); however, their overall FO decreased in the 2000s (*p*=0.0329). The overall reduction in occurrence, however, has not been consistent between seasons (Time*Season: *p*=0.0008). Spotted seals harvested in the summer consumed fewer Crangonidae shrimp during the 2000s (Table 7; *p*=0.0030) while seals harvested in winter consumed more (*p*=0.0329). During the 1960s and 1970s consumption of Crangonidae was 13.56 times more likely during the summer than winter (*p*=0.0005). In the 2000s, however, the summer consumption of Crangonidae decreased significantly (Table 7; *p*=0.0151); resulting in similar occurrences of Crangonidae in summer and winter diets of spotted seals during the recent time period (*p*=0.5375).

The Pearson correlation analysis of prey item occurrence did not identify any positive or negative correlations in occurrence of prey items from differing taxa that would suggest that the availability or abundance of prey items might be linked (i.e., covary). There was only support for correlations within taxonomic groups. Consumption of crustaceans and shrimp (*r*=0.7722) and decapods and shrimp (*r*=0.9526), all of which decreased since the early time period, were correlated. Similarly, the occurrence of Gadidae was correlated with arctic cod (*r*=0.5770) and saffron cod (*r*=0.6619). These correlations suggest that changes in shrimp consumption were likely responsible for variations we observed among all decapods and crustaceans, while occurrences of arctic and saffron cod were responsible for variations in the Family Gadidae.

Years where fish occurred at high proportions in the diet of spotted seals coincided with years where crustaceans (including shrimp) occurred at low frequencies (Fig. 7). The inverse is also true; during the 1960s and 1970s, in years in which seals consumed less fish than the mean FO for that time period (1967, 1975, and 1978) they consumed more crustaceans (including shrimp) than were observed over that entire time period. These trends, however, were only somewhat negatively correlated (fish and crustaceans: *r*=-0.3562; fish and shrimp: *r*=-0.3920). Years in which spotted seals consumed few sculpin coincided with years in which they consumed high frequencies of all fish (Fig. 4; *r*=0.0946).

Contaminants

Metals and other elements—Concentrations of 19 trace elements were quantified in liver tissue of 17 spotted seals (four females and 13 males) and kidney tissue was also analyzed for six of those 17 seals (five males and one female). Five elements were below detection limits in both liver and kidney of all spotted seals tested (Ba, Be, Cr, Mo, and Ni) and Pb was below detection limits in all but one spotted seal; a 22-yr-old male. Some of the elements we tested are essential nutrients (Cu, Fe, Mg) and others are potentially toxic at high levels (As, Cd, Hg, Pb). Concentrations of selected trace elements in liver and kidney 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), a more toxic form called methyl mercury (MeHg) was analyzed in liver tissue of two male spotted seals; one pup-of-the-year and one 22 year old. When MeHg was expressed as a percentage of THg the younger spotted seal had 46.35% and the older one had 14.49% MeHg.

Organochlorines—Organochlorines (OC) were quantified and summarized in the blubber (*n*=17) and liver (*n*=15) of spotted seals sampled during 2003–2006. We examined four compounds of hexachlorocyclohexane (HCH; Alpha-HCH, Beta-HCH, Delta-HCH, Gamma-HCH), seven compounds of chlordane (CHL; Heptachlor, Heptachlor-Epoxide, Oxychlordane, Alpha-Chlordane, Gamma-Chlordane, Trans-Nonachlor, Cis-Nonachlor), six compounds of dichlorodiphenyltrichloroethane (DDT;2,4'-DDD, 4,4'-DDD, 2.4'-DDE, 4,4'-DDE, 2,4'-DDT, 4,4'-DDT), and 82 congener and congener groups of polychlorinated biphenyls (PCB) in both blubber and liver tissues.

In general, OC concentrations in blubber tissue were at least one order of magnitude higher than in liver (Table 9 and 10). The relationship among the compounds differed slightly between blubber and liver with ΣHCH < ΣCHL < ΣDDT < ΣPCB in blubber (Table 9). In liver tissue, ΣHCH remained the lowest and ΣPCB the highest, however ΣDDT was higher than ΣCHL (Table 10).

Of the six compounds composing ΣDDT in blubber tissue, the most dominant compound detected was 4,4’ DDE (89.0% in females, 92% in males). The geometric mean sum of DDTs (ΣDDT = Σ2,4’- and 4,4’- DDD and DDE and DDT) was 199.5 ng/g wet wt and was lower in females (148.76 ng/g wet wt) than males (218.41 ng/g wet wt) (Table 9).

Of the 82 PCB congener and congener groups, three made up the more than half (54.8%) of the ΣPCBs in blubber (Table 11). They were, in decreasing dominance, 153/132 (25.2%), 101/90 (15.6%), and 138/160 (14.0%). Four compounds made up more than half (51.6%) of the ΣPCBs in liver (Table 11). In liver, congener 153/132 was also dominant and accounted for 17.6% of the ΣPCBs. The other dominant compounds, in decreasing order, were 138/160 (14.0%), 187 (12.6%), and 101/90 (7.4%).

Disease

We identified *Brucella* antibodies in 16.2% (6 of 37) and PhHV-1 antibodies in 33.3% (12 of 36) of spotted seal sera tested. We found no antibodies for PhHV-2 in the serum of 16 individuals and no antibodies for CDV or PDV in 22 and 37 individuals, respectively.

Morphometrics

Growth rate— For seals greater than one year of age, our analysis of standard length included 311 seals of known length and age (Fig. 8). Of these seals, 62 were harvested in the 1960s, 163 in the 1970s, and 86 in the 2000s. With time periods pooled, asymptotic length (L_{inf}) was not clearly gender specific. A model that specified L_{inf} varied by gender was 1.1 DIC units greater than one that specified L_{inf} was the same for males and females. Visual inspection of the growth rate data also did not indicate L_{inf} varied by gender. We assumed that L_{inf} was the same for males and females; the estimate of L_{inf} was 160.1 cm (SD=2.9).

The model with the most support (Δ DIC = 0) indicated that the growth rates of spotted seals in the 2000s were similar to rates observed in the 1960s, but were lower in the 1970s (Tables 1 and 12, Fig. 9a). The difference in standard length between seals in the 1970s and other time periods is highest at birth and decreases as seals age (Fig. 9b). Seals born in the 1970s were predicted to be approximately 9.1 cm shorter at one year of age, 7.2 cm shorter at 2 years of age, and 5.8 cm shorter at 3 years of age. By 20–25 years of age, seals in the 1970s were of similar length as seals from other time periods (Fig. 9b). All models within 4 DIC units of the best approximating model also indicated that seals grew more slowly in the 1970s.

The inclusion of seals aged by claws did not affect our analysis or our results. Few spotted seals were aged by counting claw ridges in the 1960s (7 of 62) and none of the samples aged by claws were outliers. Half of all seals from the 1970s were aged by claws (82 of 163); however, removing claw ages had little affect on predictions of seal length by time period (Fig. 9a). When not including claw ages in the analysis, the average length of seals in most age classes was shorter (Fig. 9b).

For seals less than one year of age, our analysis included 80 seals sampled in the 1960s, 49 in the 1970s, and eight sampled in the 2000s. We detected no differences in growth rates by gender for either May (*p*=0.99) or June (*p*=0.21) and dropped gender from the model. For the month of May, the average length of seals sampled in the 2000s ($\bar{x}$=97.5; *SE*=2.90) was significantly longer than that for the 1960s ($\bar{x}$=89.3; *SE*=1.18; p<0.01) and in the 1970s ($\bar{x}$=96.8; *SE*=1.71; *p*=0.01). However, we suspect this difference might be an artifact due to a small sample size in the 2000s (n=8). For the month of June, there were no significant differences by time period (*p*=0.42) and a plot of standard length by month for each period (Fig. 10) shows no consistent differences in growth by time period.

Body condition—Neither gender (*p*=0.30) nor time period (*p*=0.87) were supported as significant sources of variation in sternal blubber thickness. Sternal blubber thickness varied significantly by month (p<0.001) and average thickness ranged from 2.6 cm (SE=0.13) in June to 6.5 cm (SD=0.75) in December (Fig. 11).

Population parameters

Age and sex distribution—We analyzed age-at-harvest for 290 spotted seals harvested in the 1960s, 1,124 in the 1970s, and 528 in the 2000s. Age distribution in each time period was similar (i.e., the proportion of seals harvested in each age group decreased with increasing age; Fig. 12); however proportions varied among decades. Seals aged 0–1 were >50% of the total harvest in all decades; in the 1960s and 2000s their proportion was larger than in the 1970s (p<0.0001). Conversely, seals aged 2–5 were harvested in greater proportions during the 1970s and 2000s than in the 1960s (*p*=0.0009). Similarly, seals aged 6–10 were also harvested in greater proportions in the 1970s than the 1960s or 2000s (p<0.0001). Individuals 16–20 years of age were <5% of the total harvest during any decade; in the 1970s their contribution was significantly smaller than in the 1960s or 2000s (p<0.0001).

To characterize sex ratios, we used the age-at-harvest and sex of 1,731 spotted seals (n=287 in 1960s, n=1,053 in 1970s, and n=391 in 2000s). The sex ratio of harvested individuals was 1:1 in the 1960s but became significantly male biased in the 1970s and 2000s (Fig. 13; *p*=0.0009). Juveniles and subadult sex ratios were also male biased, but they did not vary among decades (juvenile: *p*=0.2889; subadult: *p*=0.3439). The proportion of adults harvested, however, varied significantly among decades (p<0.0001) as harvests in the 1970s and 2000s were male biased (63% and 68%, respectively) and harvests in the 1960s were female biased (69%). After 9 years of age, sex ratios approached 1:1 but we lacked the sample size to statistically compare older adults to those <9 years of age (Fig. 14).

Survivorship schedule—A survivorship schedule was estimated for 1,413 spotted seals harvested from 1963–1979 (Fig. 15). The survivorship curve suggested that the success of seal recruitment was higher than expected from 1964 to 1974, and lower than expected from 1977–1979. Recruitment was generally twice that predicted in 1967, 1973, and 1974. Because seals less than 5 years of age comprised 81% of the harvest in the 1960s and 1970s (Fig. 15), and harvest data were collected for 17 consecutive years, we are reasonably confident that our model was able to detect variations in recruitment during this time period.

We estimated a survivorship schedule for 201 spotted seals harvested from 1998–2002 (Fig. 16). Annual recruitment of seals born from 1998–2002 was highly variable and may have been due to our limited sample size of aged seals from the 2000s. The survivorship curve suggested recruitment of spotted seals was poor during the 1980s; however, our limited sample size may have also limited our ability to detect recruitment patterns prior to 1998.

Age at maturity and pregnancy rate—Sexual maturity status was determined for 123 female spotted seals in the 1960s, 140 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 spotted seals in our sample, the intermediate age classes are those between three to six years of age. Our sample of seals within intermediate age classes was 10 in the 1960s, 44 in the 1970s, and 24 in the 2000s.

A probit link function fit the data marginally better than a logistic link function (Δ AIC = 1.1) and was used for all models. The best approximating model indicated that age at maturity was different for each time period (Table 13). However, two models were within 2 AIC units of the best approximating model and they had identical AIC values. One model indicated that age at maturity in the 1960s was equal to that in the 1970s and the other indicated that age at maturity in the 1960s was equal to that in the 2000s. Statistical contrasts indicated that the 1960s were indistinguishable from either the 1970s (p=0.45) or the 2000s (p=0.45). However, the age at maturity was significantly older in the 1970s than the 2000s (p=0.05). Average age at maturity was estimated to be 3.7 years of age in the 1960s, 4.1 years of age in the 1970s, and 3.36 years of age in the 2000s (Fig. 17).

1960s. Of the 123 reproductive tracts analyzed for sexual maturity from the 1960s, 85 were immature, seven had ovulated once, 23 had ovulated more than once, and eight were mature but the number of ovulations was unknown. Females that had never ovulated were <1–5 years old (Table 14). Females ovulating for the first time were 3–7 years old and females that had ovulated more than once were 5–35 years old. An additional seven reproductive tracts were available from mature females that were not aged. Although these could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 45 sexually mature females, 36 (80.0%; 95% CL=68% to 92%) were pregnant in the year they were harvested.

1970s. Of the 140 reproductive tracts analyzed from the 1970s, 71 were immature, nine had ovulated once, 59 had ovulated more than once, and one was mature but the number of ovulations was unknown. Females that had never ovulated were <1–6 years old (Table 15). Females ovulating for the first time were 3–6 years old and females that had ovulated more than once were 4–35 years old. An additional six reproductive tracts were available from mature females that were not aged. Although these could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 75 mature females, 67 (89.3%; 95% CL=82% to 96%) were pregnant when harvested.

2000s. Of the 88 reproductive tracts analyzed from the 2000s, 62 were immature, seven had ovulated once, 17 had ovulated more than once, and two were mature but the number of ovulations was unknown. Females that had never ovulated were <1–4 years old (Table 16). Females ovulating for the first time were 2–5 years old and females that had ovulated more than once were 3–24 years old. An additional nine reproductive tracts were available from mature females that were not aged. Although these could not be used to determine age of maturity they were useful for calculating the percent pregnant. Of 31 mature females, 20 (64.5%; 95% CL=47% to 82%) were pregnant when harvested.

DISCUSSION

Potential bias of harvest data

Any analysis of biological parameters based on harvest data must address potential biases due to non-random sampling. We expect that bias due to hunter selectivity is low. Our questionnaire indicated that few hunters avoided harvesting spotted seals or attempted to selectively harvest any particular segment of the population. Pups molt from their natal lanugo to adult pelage by the time they are three months old, thus age can only be distinguished visually by size. There are no differences in pelage by sex, and after age two it would be difficult to visually distinguish spotted seals by age. Hence, we do not think the distribution of age classes or sex bias of the harvest was due to hunter bias.

Potential bias of age data

Ageing techniques have changed in the last 40 years and this might be another source of bias. Counting annual ridges on claws to estimate age was common in the 1960s and 1970s. Because annual ridges may wear off with age, old seals may appear younger than what they actually are, thereby biasing age distributions towards younger seals in the 1960s. Burns (1969) states that spotted seals in the Bering Sea retain annual ridges for 9–15 years, indicating that the bias may only be for seals greater than nine years of age. The inclusion of seals aged by claws did not affect our analysis or our results. Growth rates were slower in the 1970s, with or without inclusion of seals aged by claws (Fig. 9a).

Stomach contents

Although components of the spotted seal diet have changed over the last half century, schooling fish, such as gadids and herring, have remained principal prey items. In our study, during the 1960s and 1970s, fish occurred in 81.71% of spotted seal stomachs; 79.10% in stomachs from the Bering Sea and 90.24% in stomachs from the Chukchi Sea. The frequencies of occurrence of fish that we observed in the Bering Sea (79.10%) during this time period were lower than that found for the Gulf of Anadyr in the late 1960s (90%, Gol'tsev 1971) and the Bering Sea in the late 1970s (95%; Bukhtiyarov et al. 1984). The frequency of occurrence of fish we observed during the 2000s, however, were greater (98.97%) than those observed by Gol'tsev (1971) and Bukhtiyarov et al. (1984).

Fish consumed most frequently by spotted seals were not consistent between time periods or among regions. During the 1960s and 1970s, the most common fish taxa found in our study were gadids (38.29%), specifically saffron cod (23.43%); Pacific herring (17.71%) and sculpin (16.57%). Spotted seal diets from the Gulf of Anadyr in the late 1960s varied somewhat from our study, however, arctic cod (20%), Pacific sand lance (11%), and sculpin (11%) occurred most frequently (Gol'tsev 1971). During the late 1970s, fish consumed by spotted seals varied regionally across the Bering Sea (Bukhtiyarov et al. 1984). Spotted seals from the central Bering Sea consumed walleye pollock (80%) and eelpout (80%) most commonly. Capelin (86%) and walleye pollock (43%) occurred with the highest frequency in the southeastern Bering Sea, and arctic cod (92%), saffron cod (42%), capelin (42%), and sculpin (42%) occurred with the highest frequency in the northern Bering Sea. In our study, beginning in the late 1970s (Fig. 4) and during the 2000s (37.46%) arctic cod occurred at frequencies similar to those in the Gulf of Anadyr (Gol'tsev 1971), but remained less than those in the northern Bering Sea (Bukhtiyarov et al. 1984). Walleye pollock (6.29%), Pacific sand lance (7.43%), capelin (9.71%), and especially eelpout (0.57%) were less common in our study during the same time period.

In our study, occurrences of most fish taxa were greater in the 2000s than the 1960s and 1970s. During the 2000s, the most common fish species consumed by spotted seals were saffron cod (39.18%), arctic cod (37.46%), Pacific herring (35.40%), and smelt (30.93%), all of which were consumed more frequently than in the 1960s and 1970s. In the 2000s, consumption of Pacific herring was also more common than was in Anadyr Gulf in the late 1960s (2%, Gol'tsev 1971) and Bering Sea in the late 1970s (0–25%, Bukhtiyarov et al. 1984). Furthermore, smelt did not occur in the diets of seals analyzed by Gol'tsev (1971) and Bukhtiyarov et al. (1984). Sculpin, which occurred in >10% of spotted seal diets in all three studies from the 1960s and 1970s, were consumed less commonly in the 2000s (5.50%).

In our study, invertebrates were consumed considerably less frequently than fish and their occurrences decreased from the 1960s and 1970s (36.57%) to the 2000s (20.27%). Although spotted seals consumed less shrimp recently, they were the most common invertebrate prey item during both time periods. Shrimp, however, were consumed less commonly by spotted seals in the Gulf of Anadyr in the late 1960s (24%, Gol'tsev 1971) and in the northern Bering Sea in the late 1970s (<1%, Bukhtiyarov et al. 1984) than in our study. Spotted seals in the Gulf of Anadyr, however, consumed considerably more octopus (36%, Gol'tsev 1971) than seals in our study, during both the 1960s and 1970s (1.14%) and 2000s (0.34%), and seals in the northern Bering Sea (3%, Bukhtiyarov et al. 1984).

Differences in the consumption of prey items among these studies was like due to regional and seasonal differences in principal forage fish and invertebrate distribution and abundance. All studies analyzed stomach contents; therefore difference observed should not be related to study design. Changes in climate and in nutrient availability in the pelagic zone may be responsible for the increased consumption of pelagic fish. Similarly, changes in climate that affect nutrient availability in the benthic zone may be altering the distribution and abundances of benthic prey items, such as sculpins and invertebrates, therefore limiting their availability to spotted seals.

One of the more interesting patterns we observed was how spotted seals switch between consuming forage fish and crustaceans (Fig. 7). If spotted seals prefer to consume forage fish, then the 1970s were characterized by years with low availability of forage fish and seals supplemented their diet with crustaceans. Interestingly, the lowest FO of forage fish occurred in the late 1970s, when recruitment was failing, growth rates were slower, and age of maturation was older. Since 1998, seals have had a consistently high FO of forage fish in their stomachs.

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 marine mammal kidney and liver 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). We did not have enough samples to examine bioaccumulation by age or gender, hence inferences are tentative.

There are few studies of trace elements in spotted seals therefore comparing element concentrations among locations is difficult for spotted seals. Dehn *et al.* (2005, 2006) reported Ag, Cd, Cu, THg, MeHg, Se, and Zn in liver and kidney tissue from seals harvested near Diomede and Shishmaref in the Bering Sea. Moses et al. (2009) reported As, Ag, Ca, Cd, Cu, Fe, THg, MeHg, Mg, Mn, Mo, Pb, and Zn in blubber, liver, kidney, and muscle from spotted seals harvested near Kotzebue. Using arithmetic means in μg/g ww for comparison (Table 8), we found higher levels of Cd and Hg in both liver and kidney than what was observed by Dehn et al. and similar levels to those found by Moses et al. Our Cd level in liver was 0.93 (SD 1.65, range 0.02–6.40) compared to Dehn et al. 0.39 (SD 0.48, range 0.09–2.18) and Moses et al. 0.48 (SD 0.16, range 0.35–0.67). Our Cd level in kidney was 4.90 (SD 6.29, range 1.17–17.53) compared to Dehn et al. 2.58 (SD 1.56, range 0.79–7.76) and Moses et al. 3.49 (SD 0.54, range 2.83–4.04). Our Hg level in liver was 1.72 (SD 1.73, range 0.03–5.61) compared to Dehn et al. 0.68 (SD 0.68, range 0.10–2.62) and Moses et al. 1.99 (SD 1.17, range 0.61–3.14). Our Hg level in kidney was 0.38 (SD 0.34, range 0.21–1.13) compared to Dehn et al. 0.31 (SD 0.21, range 0.08–0.90) and Moses et al. 0.44 (SD 0.13, range 0.16–3.14). Becker et al. (1997) reported on one spotted seal collected in Nome in which both Cd and Hg levels were below detection limits. For Pb, Moses et al. reported low levels similar to ours; Dehn et al did not analyze Pb.

We do not think that the higher levels we observed are a cause for concern. First, Dehn et al. (2005, 2006) sampled near Diomede and Shishmaref, which is within our sampling area. Second, the lowest levels of Cd and Hg we observed were lower than, or comparable to, what Dehn et al. observed. We suggest that there is a high degree of variability in Cd and Hg levels between seals and suspect that we sampled a few older seals with higher concentrations. Our samples were mostly from males (13 of 17), the oldest of which was 22 yrs.

When comparing concentrations of Cd and Hg in the liver tissues of seals harvested in the Bering and Chukchi seas, we find that spotted seals have the lowest concentrations of all ice seals (Table 17). This is unexpected because ribbon seals have the highest concentrations of these elements and spotted and ribbon seals are thought to share a similar distribution in the Bering Sea and have similar piscivorous diets (Frost and Lowry 1980, Bukhtiyarov *et al.*1984). Mean Pb levels were very low and similar among species (Table 17).

Our mean Hg (1.72 µg/g ww SD 1.73) and Cd (0.93 µg/g ww SD 1.65) levels in liver were lower than those reported by Riget *et al.* (2005) for ringed seals from Barrow, Alaska (Hg = 3.52 µg/g ww, SD 5.07; Cd = 5.72, SD 3.21), Canada (Hg mean range 9.4–31.9, SD 15.0–58.9; Cd mean range 2.73–12.5, SD 2.96–9.18), and Greenland (Hg mean range 1.40–6.22, SD 2.50–5.54; Cd mean range 8.48–13.0; SD 7.29–13.1). Our mean Hg level was higher than Svalbard (0.97, SD 0.65) but lower than the White Sea (2.25, SD 2.14). Our mean Cd levels were lower than Svalbard (3.90, SD 3.59) and the White Sea (2.56, SD 3.02) (Riget *et al.* 2005).

Elemental or total Hg (denoted as THg) is comprised of a toxic form of Hg called methyl mercury (MeHg). Although spotted seals in Alaska had low concentrations of THg, they also had the highest mean percentage of MeHg (geometric mean 25.92%, SD 22.53%, range 14.49–46.35%) relative to ringed seals (geometric mean 7.62%, SD 5.5%, range 2.94–14.32%) and bearded seals (geometric mean 1.82%, SD 2.2%, range 0.2–8.8%) (Quakenbush and Sheffield 2007). Moses et al. (2009) reported 22.9% MeHg in spotted seals ranging in age from 3 to 6 yrs. The individual with the highest concentration of MeHg in our study was a spotted seal pup 46.3%). Because, the total concentration of Hg was low (0.52 µg/g ww), even though the percentage of MeHg was high the actual amount was also low. This result is unexpected because spotted seals are piscivorous and would be expected to have higher mercury levels than ringed or bearded seals that have a more mixed diet.

Organochlorines—Compared to other ice seals in Alaska (Quakenbush and Sheffield 2007), ribbon seals had the highest geometric mean concentrations of ΣCHL (357.8 ng/g lipid wt), ΣDDT (446.6 ng/g lipid wt), and ΣPCB (547.8 ng/g lipid wt) in blubber tissue (Table 18). However, spotted seals had the higher ΣHCH levels (103.0 ng/g lipid wt) than ribbon seals (93.9 ng/g lipid wt).

We found no studies of organochlorine concentrations in spotted seals for comparison, however, the levels are generally lower than for ringed seals in Canada (*e.g*., Muir et al. 1999). In addition to problems caused by inter-species comparisons, studies often examine different OC congeners, making direct comparisons impossible. Also, concentrations may depend both on gender and age, so differences in mean concentrations may have more to do with the sex ratio of the seals sampled than the location or time period.

Other contaminants— Polybrominated diphenyl ethers (PBDEs) have been analyzed in the blubber of spotted 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 polychlorinated biphenyls (PCBs) and thyroid hormones. Lab studies indicate that PBDEs may disrupt thyroid function and neurodevelopment (Darnerud 2003, Viberg et al. 2004). Ribbon seals had the highest mean level of total PBDEs (16.5 ng/g wet wt) followed by spotted seals (12.4 ng/g wet wt); bearded seals had the lowest (3.4 ng/g) of the Alaska ice seal species, but all had lower levels compared to seals from other regions of the Arctic (Quakenbush 2007).

Perfluorinated contaminants (PFCs) have been analyzed in the liver of spotted 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 2008a). When compared to other Alaskan ice seals, spotted seals had the second highest concentrations of PFOS, PFDA, and PFUnDA and the third highest concentration of PFNA. PFOS has been identified as the predominant PFC in wildlife. Studies of ringed seals in Canada (Martin *et al.* 2004) and Greenland (Bossi *et al.* 2005) generally find levels of PFOS twice as large as what was observed in spotted seals (Quakenbush and Citta 2008a). However, they found larger mean levels of PFNA, PFDA and PFUnDA. 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.

Disease

Brucella—In general, low levels of *Brucella* have been found in Arctic species. We identified *Brucella* antibodies in 16.2% (6 of 37) of spotted seals in this study and 14.3% (2 of 14) of ribbon seals previously (Quakenbush and Citta 2008b). 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 high incidence, 46.0% (46/100), of *Brucella* antibodies in harbor seals from the Gulf of Alaska, similar to incidence rates, 49.0% (147/300), observed in harbor seals from Scotland (Foster *et al.* 2002). Harbor seals experience closer contact with one another on their terrestrial haulouts than ribbon seals, ringed seals, or polar bears do on sea ice and this may explain the higher prevalence in them. Spotted seals are closely related to harbor seals and use terrestrial haul outs in summer, which may bring them in closer contact with one another than occurs with other ice seal species, however, they did not show a higher exposure.

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

PhHV-1 and -2—Our findings of 33.3% (12 of 36) for PhHV-1 antibodies and no antibodies for PhHV-2 in spotted seals tested are lower than those found by Zarnke *et al.* (1997) who identified antibodies of PhHV-1 in 72% (23 of 32) and antibodies of PhHV-2 in 16% (5 of 32) of spotted seals sampled near southeastern Kamchatka and in the Bering and Chukchi seas.

Our findings for ribbons seals also contrasted with Zarnke et al. (1997) in that we found no antibodies of either PhHV-1 or 2 (Quakenbush and Citta 2008b), whereas he found antibodies for both in 29.2% (7 of 24) of ribbon seals sampled in the Bering Sea. More disease screening is necessary to verify the prevalence of PhHV-1 and -2. 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 = 37) or CDV (n = 22) in spotted seals from the Bering and Chukchi seas. It is thought that PDV is circulating within Arctic species (*e.g.*, Barrett *et al.* 1995, Duignan *et al.* 1997, Härkönen *et al.* 2006) and that harp seals (*Phoca groenlandica*) may be the major reservoir for PDV in the Arctic (Barrett *et al.* 1995, Duignan *et al.* 1997). Harp seals have a high prevalence of PDV antibodies (83%; 130 of 157) (Duignan *et al.* 1997) and exhibit attributes conducive for maintaining a virus, such as a large population size and dense aggregations. Duignan *et al.* (1997) also found that ringed seals had a high prevalence rate (41%; 106 of 259), which is surprising given their dispersed population structure. The prevalence of antibodies was highest where ringed seal and harp seals overlap in range, supporting the idea that harp seals might serve as a reservoir. Harp seals are also believed to be the source of the 1998 PDV outbreak in the northern Europe (Heide-Jørgensen *et al.* 1992, Härkönen *et al.* 2006). Migrating harp seals have been observed in the North Atlantic and they are believed to have transferred PDV into grey seals (*Halichoerus grypus*), which are largely immune (Barrett *et al.* 1995, Härkönen *et al.* 2006, Heide-Jørgensen *et al.* 1992). PDV has been documented as persisting within grey seal populations (Barrett *et al.* 1995, Hammond *et al.* 2005) and both the 1988 and 2002 outbreaks of PDV in harbor seals have been traced to a single haulout in Denmark (Anholt). This haulout is notable in that both grey and harbor seals haulout together and mix (Härkönen *et al.* 2006).

An outbreak of CDV killed thousands of Baikal seals (*Phoca sibirica*) in 1988 (Grachev *et al.*1989, Mamaev *et al.* 1995) and over 10,000 Caspian seals (*Phoca caspica*) in 2000 (Kennedy *et al.* 2000). Both epidemics are believed to have been caused by seals coming into contact with terrestrial carnivores that were disease vectors. Given that spotted seals haul out on land in summer, they may be more likely to contact terrestrial carnivores than other ice seals. CDV is the dominant morbillivirus in polar bears making polar bears a potential vector for spotted seals hauled out on pack ice as well. 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).

Spotted seal distribution overlaps that of both ringed and harbor seals. We have detected PDV antibodies in ringed seals (ADF&G unpublished data) and Zarnke *et al.* (2006) found a 1% (2 of 160) prevalence rate of PDV antibodies in harbor seals within the Gulf of Alaska. Recently, antibodies to PDV were detected in 40% (30 of 77) of sea otters in the eastern Aleutian Islands, Alaska Peninsula, and Kodiak Archipelago (Goldstein et al. 2009). However, exposure does not guarantee an epizootic. Although PDV results in high mortality rates in harbor seals (an outbreak of PDV in northern Europe killed over 23,000 harbor seals in 1998 and 30,000 in 2002; Härkönen *et al.* 2006), other phocids are largely immune to PDV. For example, grey seals are much less susceptible to PDV (Barrett *et al.* 1995, Härkönen *et al.* 2006) than harbor seals, only one harp seal has shown clinical disease attributed to PDV (Daoust *et al.* 1993), and there are no cases of clinical disease in ringed seals. Transmission rates are also affected by seal behavior, which changes seasonally. Spotted seals haul out together on gravel shoals and islands in summer. This is likely when they would be most susceptible to an epidemic. We doubt an epizootic could form during the winter and spring, when spotted seals are more dispersed.

Trends in population parameters

Sex ratios—Sex ratios were generally male biased (Figs. 13 and 14). However, the patterns were not consistent through time or by age class. Although a trend for an increasing proportion of males over time is apparent when all age classes are pooled, this trend is not present for all age classes. If sex ratio truly represents the sex ratio of the population, then changes in sex ratios may represent changes in survival rates. However, patterns may also be indicative of non-random harvest. For example, spring conditions in some years may allow females to stay with pups on the sea ice longer and thus males may travel to the coast sooner than females making them more available for harvest.

Survivorship curves and age distributions—The log-survival curves must be interpreted with caution. If the model of exponential growth does not fit the data well, then identifying years associated with above or below average recruitment is impossible. An assumption of the model is that residuals are random. If recruitment fails for a prolonged period, this might affect the fit of the model and bias the estimate of average recruitment.

As such, we think it best to use the survivorship curves to identify broad patterns rather to focus on individual years or the absolute amount that recruitment deviates from the curve. For example, we are confident that recruitment into the population was lower than expected in the late 1970s (Fig. 15). However, we cannot determine exactly how poor recruitment was. Poor recruitment since 1976 likely "pulls down" the log-survival curve. In other words, we are forcing the curve to fit the string of poor recruitment years in the late 1970s and this decreases the slope of the curve. In turn, the years prior to the late 1970s appear to better than they likely were (i.e., larger positive residuals) and the late 1970s do not appear as bad as they likely were (i.e., smaller negative residuals). Regardless, it appears that recruitment began to falter around 1975 or 1976 and persisted until 1979 when data collection stopped.

Likewise, recruitment may have faltered during the most recent years of data collection for which we have aged seals, 2001 and 2002 (Fig. 16). Including more recent data will verify or refute this pattern.[1]

These patterns are supported by the analyses of age distributions. We found fewer seals 0–1 years of age in the 1970s versus the 1960s or 2000s. Seals in this age class compose between 50–65% of the population. Hence, small changes in the proportion of young seals will

[1] We are currently waiting for more recent tooth ages to come back from Mattson's Lab. Preliminary data analyses indicate that 2001 and 2002 may have been poor recruitment years, but that recruitment has since rebounded. We do not think that 2001 and 2002 represent a trend towards poor recruitment.

affect the proportions in other age classes. As such, larger proportions of seals aged 2–5 years and 6–10 years were observed in the 1970s (i.e., to make up for a dearth of 0–1 year old seals).

There were no clear patterns in age distributions beyond 10 years of age. As such, there is no evidence to indicate that survival of older age classes has changed over time.

Body condition (blubber thickness)—We detected no differences in body condition by time period or gender. Perhaps blubber thickness is not sensitive enough to index true body condition (e.g., Gales and Renouf 1994) or perhaps seals are able to maintain body condition by forgoing breeding. Resorption of fetuses or non-implantation of the blastocyst after delayed implantation might be other mechanisms by which females can adjust to food availability and maintain body condition.

Age at maturity and pregnancy rate – As with most of the indices we examined, age at maturity indicated that environmental conditions might be less favorable for seals in the 1970s than the 1960s or the 2000s. Average age at maturity was significantly older in the 1970s (4.1 yrs.) than the 1960s (3.7 yrs.) or 2000s (3.4 yrs.; Fig. 17). However, pregnancy rate indicated environmental conditions might be currently less favorable for spotted seals than in the 1970s. Pregnancy rates were approximately 80% in the 1960s, 89.3% in the 1970s, and 64.5% in the 2000s. The lowest pregnancy rate was observed in the 2000s when our sample size was also the smallest. To illustrate how sensitive proportions are to sample sizes, we use Thompson's (2002; page 38) equation for estimating sample sizes for proportions. To estimate a rate of 64.5% to within 10% with 95% confidence would require approximately 160 samples. To estimate a rate of 64.5% to within 20% with 95% confidence would require approximately 40 samples. In the 2000s, we only have 31 mature females. Clearly, more sampling is necessary to verify that pregnancy rates have declined.

Summary

Most of our indices of seal health indicate that conditions were less favorable for spotted seals in the 1970s. Spotted seals grew at a slower rate and matured more slowly in the 1970s compared to the 1960s or since 1998. The age distribution was also skewed away from individuals 0–1 years of age in the 1970s, indicating that recruitment may have faltered. This agrees with the results from the log-survivorship models, which indicate that recruitment, defined as reproduction and survival to harvest, may have decreased in the 1970s. However, our analyses of body condition, growth rates of pups, and sex ratios were inconclusive. Although pregnancy rate could not be estimated precisely, there is some evidence to indicate that pregnancy rates may have declined recently. A larger sample size is required to verify this pattern.

We do not know if ice conditions, required for pupping and molting, were poor in the 1970s; however, we observed changes in diet during this time. The frequency of occurrence of fish in the diet of spotted seals was highly variable in the late 1960s and 1970s. It is believed that fish are the primary prey of spotted seals and, assuming that spotted seals prefer to consume fish when it is available, changes in the frequency of fish occurrence in the diet will reflect fish availability in the environment. It is possible that the 1970s were characterized by a high level of variability in forage fish availability. If food availability were limited, this could manifest as slower growth rates of adults and delayed maturity.

We detected no differences in the growth rates of pups by decade. However, when food is available, we would not expect pups to grow slowly. If seals largely forgo breeding when forage conditions are poor, this would explain why pups did not grow more slowly in the 1970s. Curiously, we also detected no differences in body condition in the 1970s. Perhaps blubber thickness is not sensitive enough to index true body condition or perhaps seals are able to maintain body condition by forgoing breeding.

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Table 1. Models for spotted seal growth.

Model	**Effective parameters**	**DIC**	**Δ DIC**
1960s=2000s, 1970s	5.0	2449.5	0
All time periods differ	6.8	2453.4	3.9
Gender*period	12.1	2455.3	5.8
1960s=1970s, 2000s	4.9	2457.8	8.3
Common growth rate	3.0	2461.0	11.5
Gender	4.9	2461.4	11.9
1960s, 1970s=2000s	4.7	2464.3	14.8

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

		Location				
Species	**Question**	**Point Hope** n = 16	**Diomede** n =19	**Shishmaref** n = 14	**Gambell** n =13	**Hooper Bay** n = 28
Ringed	Have numbers remained the same?	31	33	43	54	15
	Have numbers decreased?	31	44	36	31	27
	Have numbers increased?	13	0	7	15	0
	Are seals found in the same areas?	73	88	85	83	37
	Does the hunt occur at the same time?	71	89	71	85	87
	Do you try for certain types of this seal?	86	44	36	85	57
	What is the hunting season?	Jan–Aug	Sept–Jun	Jun; Sept–Nov	Aug–Mar; Jun	Sept–May
Bearded	Have numbers remained the same?	56	47	64	62	19
	Have numbers decreased?	19	11	7	8	33
	Have numbers increased?	13	5	21	23	10
	Are seals found in the same areas?	100	78	92	83	47
	Does the hunt occur at the same time?	100	100	71	100	90
	Do you try for certain types of this seal?	56	29	50	23	57
	What is the hunting season?	May–Jun	Apr–Jun; Oct–Dec	May–Jun	Sept–Jun	Aug–Jun
Spotted	Have numbers remained the same?	56	53	36	38	26
	Have numbers decreased?	13	26	36	38	22
	Have numbers increased?	0	5	21	15	35
	Are seals found in the same areas?	100	94	85	83	53
	Does the hunt occur at the same time?	94	100	100	100	94
	Do you try for certain types of this seal?	44	29	31	46	68
	What is the hunting season?	May–Aug	Sept–Nov	Jun; Sept–Nov	Aug–Dec	Year round
Ribbon	Have numbers remained the same?	15	42	40	54	13
	Have numbers decreased?	23	17	0	15	28
	Have numbers increased?	0	17	0	15	6
	Are seals found in the same areas?	55	82	43	83	36
	Does the hunt occur at the same time?	89	92	80	60	77
	Do you try for certain types of this seal?	0	20	33	44	58
	What is the hunting season?	May–Jun	May–Jun	May–Jun; Oct–Nov	May–Jun	Year round

Table 3. Percent frequency of occurrence (%FO_i) of prey identified from spotted seal stomachs collected in Alaska, 1966–2008.

Collection period	**1966-1981**	**1998-2008**
Sample size (# stomachs analyzed)	**175**	**291**
Prey (*i*)	**%FO_i**	**%FO_i**
All Fish *	81.71	98.97
Pacific herring (*Clupea pallasi*) *	17.71	35.40
Capelin (*Mallotus villosus*)	9.71	13.40
Smelt (*Osmerus mordax*) *	4.57	30.93
Eelpout (*Lycodes* spp.)	0.57	0.69
Greenling (*Hexagrammos* spp.) *	5.71	0.00
Pacific sand lance (*Ammodytes hexapterus*)	7.43	8.25
All Cod (Gadidae) *	38.29	62.20
Arctic cod (*Boreogadus saida*) *	10.86	37.46
Saffron cod (*Eleginus glacialis*) *	23.43	39.18
Walleye pollock (*Theragra chalcogramma*)	6.29	5.15
All Sculpin (Cottidae) *	16.57	5.50
Antlered sculpin (*Enophrys* spp.)	0.57	0.69
Sculpin (*Gymnocanthus* spp.) *	0.57	3.78
Brightbelly sculpin (*Microcottus sellaris*)	0.57	0.00
Sculpin (*Myoxocephalus* spp.)	9.71	4.81
All Pricklebacks (Stichaeidae)	1.14	1.03
Eelblenny (*Lumpenus* spp.)	0.57	2.06
All Flatfish (Pleuronectidae) *	2.86	10.65
Snailfish (*Liparis* spp.)	1.14	0.00
ALL Invertebrates *	48.57	34.71
All Mollusca *	2.86	7.56
Gastropod and Bivalve Mollusca	1.14	4.47
Octopus (Octopodia)	1.14	0.34
All Crustacean *	46.86	31.96
All Mysida *	11.43	0.34
Mysis spp.	2.86	0.00
Neomysis spp. *	9.14	0.00
Isopoda (*Saduria* spp.) *	2.86	1.72
All Amphipoda *	16.00	13.06
Scud amphipods (Gammaridae)	1.71	2.41
Gammarus spp. *	4.00	1.72
Ampelisca spp.	2.29	0.34
Anonyx spp.	2.86	0.00
Parathemisto spp. *	8.00	4.81
Euphausiacea (*Thysanoessa* spp.)	2.29	0.34
ALL Decapods *	37.71	22.68
All Shrimp (Caridea) *	36.57	20.27
Lebbeus spp.	3.43	0.00
Eualus spp. *	9.14	0.00
Pandalus spp. *	8.00	2.06
All Crangonidae shrimp *	21.14	13.06
Crangon spp. *	11.43	9.28
Sclerocrangon spp.	3.43	0.00
Argis spp. *	3.43	0.34
All Crab *	2.75	2.86
Pagurus spp.	1.14	0.00
Hyas spp.	1.71	0.00
Urochordata	0.57	0.00

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

Table 4. Final logistic regression models for frequency of occurrence of fish prey that were identified in spotted seal stomachs collected in Alaska, 1966–2008.

Prey (*i*)	**Final Model [ab]**	***P*-value [c]**	**Odds-Ratio [d]**	**Δ over time [e]**
All Fish	Year + Season + Age	<0.0001	1.122	▲
Pacific Herring (*Clupea pallasi*)	Time + Season + Region + Age	0.0220	13.650	▲
Capelin (*Mallotus villosus*)	Year[b] + Season + Region[b] + Year*Region[b]	0.0643	1.172	▲
Smelt (*Osmerus mordax*)	Time + Season + Region + Year*Region	0.0390	19.489	▲
Eelpout (*Lycodes* spp.)	-	-	-	
Greenling (*Hexagrammos* spp.)	Year	0.0059	0.915	▼
Pacific sand lance (*Ammodytes hexapterus*)	Region + Year*Region	-	-	
All Cod (Gadidae)	Year + Region + Year*Region	0.0346	1.055	▲
Arctic cod (*Boreogadus saida*)	Time + Region + Age[b]	<0.0001	11.424	▲
Saffron cod (*Eleginus glacialis*)	Year + Season + Region + Region*Season	0.0043	1.109	▲
Pollock (*Theragra chalcogramma*)	-	-	-	
All Sculpin (Cottidae)	Year + Region + Season[b] + Year*Season[b]	0.0192	0.961	▼
Antlered sculpin (*Enophrys* spp.)	-	-	-	
Sculpin (*Gymnocanthus* spp.)	Year + Season + Region	0.0009	1.133	▲
Brightbelly sculpin (*Microcottus sellaris*)	-	-	-	
Sculpin (*Myoxocephalus* spp.)	Year + Season + Region[b] + Year*Season	0.0418	0.961	▼
All Pricklebacks (Stichaeidae)	-	-	-	
Eelblenny (*Lumpenus* spp.)	-	-	-	
All Flatfish (Pleuronectidae)	Year + Age	1.047	0.0200	▲
Snailfish (*Liparis* spp.)	-	-	-	

[a]Time – Class variable for time period: Old (1960s and 1970s), Recent (since 1998)
Year – Yearly time trend
Region – Class variable for region: Bering Sea and Chukchi Sea
Season – Class variable for season: Summer (May – September) and Winter (October – April)
Age – Class variable for age class: Pup (<1), Subadult (1-3), Adult (>4)
[b]Variables not statistically significant but may be biologically important ($p<0.10$)
[c]P-value for year or time period variable included in final model
[d]Odds-Ratio for year or time period variable included in final model
[e]Δ over time – Yearly or time period changes in prey occurrence: Increasing (▲), decreasing (▼)

Table 5. Final logistic regression models for frequency of occurrence of invertebrate prey that were identified in spotted seal stomachs collected in Alaska, 1966–2008.

Prey (*i*)	**Final Model [ab]**	***P*-value [c]**	**Odds-Ratio [d]**	**Δ over time [e]**
All Invertebrates	Time + Season + Time*Season + Region + Time*Region	0.0032	0.557	▼
All Mollusca	Time + Season	0.0047	5.219	▲
Gastropod and Bivalve Mollusca	Time[b]	0.0575	7.285	▲
Octopus (Octopodia)	-	-	-	
All Crustacean	Time + Season + Time*Season + Region + Time*Region	0.0014	0.527	▼
All Mysida	Time + Season	0.0035	0.046	▼
Mysis spp.	-	-	-	
Neomysis spp.	Time	0.0013	0.036	▼
Isopoda (*Saduria* spp.)	Time + Region + Time*Region	0.0138	0.578	▼
All Amphipoda	Time + Season + Time*Season + Region + Time*Region	0.0475	0.783	▼
Scud amphipods (Gammaridae)	-	-	-	
Gammarus spp.	Time + Region + Time*Region	0.0019	0.230	▼
Ampelisca spp.	Time[b]	0.0835	0.143	▼
Anonyx spp.	-	-	-	
Parathemisto spp.	Time + Region + Time*Region	0.0033	0.566	▼
Euphausiacea (*Thysanoessa* spp.)	-	-	-	
ALL Decapods	Time + Season + Time*Season	0.0170	0.501	▼
All Shrimp (Caridea)	Time + Season + Time*Season	0.0057	0.669	▼
Lebbeus spp.	-	-	-	
Eualus spp.	Time	0.0013	0.036	▼
Pandalus spp.	Time	0.0066	0.255	▼
All Crangonidae shrimp	Time + Season + Time*Season	0.0329	0.777	▼
Crangon spp.	Time + Region	0.0127	0.396	▼
Sclerocrangon spp.	-	-	-	
Argis spp.	Time	0.0483	0.114	▼
All Crab	Time[b]+ Season + Time*Season	0.0949	2.112	▲
Pagurus spp.	-	-	-	
Hyas spp.	-	-	-	
Urochordata	-	-	-	

[a]Time – Class variable for time period: Old (1960s and 1970s), Recent (2000s)
Region – Class variable for region: Bering Sea and Chukchi Sea
Season – Class variable for season: Summer (May – September) and Winter (October – April)
Age – Class variable for age class: Pup (<1), Subadult (1-3), Adult (>4)
[b]Variables not statistically significant but may be biologically important (p<0.10)
[c]P-value for Time variable included in final model
[d]Odds-Ratio for time variable included in final model
[e]Δ over time – Changes in prey occurrence over time: Increasing (▲), decreasing (▼)

Table 6. Regional and seasonal differences in frequency of occurrence (%FO_i) of fish prey identified from spotted seal stomachs collected in Alaska, 1966–2008.

	Region				Season			
	Bering		Chukchi		Summer		Winter	
Collection period	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**
Sample size (# stomachs analyzed)	134	85	41	206	106	66	62	221
Prey (*i*)	**%FO_i**	**%FO_i**	**%FO_i**	**%FO_i**	**%FO_i**	**%FO_i**	**%FO_i**	**%FO_i**
All Fish [b]	79.10	98.82	90.24	99.03	70.75	98.48	100.00	99.10
Pacific Herring (*Clupea pallasi*) [ab]	9.70	3.53	43.90	48.54	13.21	27.27	25.81	38.01
Capelin (*Mallotus villosus*) [b]	12.69	22.35	0.00	9.71	4.72	6.06	19.35	15.84
Smelt (*Osmerus mordax*) [abc]	5.97	8.24	0.00	40.29	0.94	19.70	11.29	33.94
Eelpout (*Lycodes* spp.)	0.75	2.35	0.00	0.00	0.94	1.52	0.00	0.45
Greenling (*Hexagrammos* spp.)	7.46	0.00	0.00	0.00	6.60	0.00	3.23	0.00
Pacific sand lance (*Ammodytes hexapterus*) [a]	5.22	10.59	14.63	7.28	9.43	7.58	4.84	8.60
All Cod (Gadidae) [ac]	39.55	75.29	34.15	56.80	35.85	63.64	41.94	61.99
Arctic cod (*Boreogadus saida*) [ab]	13.43	52.94	2.44	31.07	14.15	40.91	3.23	36.20
Saffron cod (*Eleginus glacialis*) [ab]	20.90	30.59	31.71	42.72	20.75	27.27	29.03	43.44
Pollock (*Theragra chalcogramma*) [ab]	8.21	16.47	0.00	0.49	2.83	6.06	12.90	4.98
All Sculpin (Cottidae) [a]	20.15	11.76	4.88	2.91	16.04	10.61	17.74	4.07
Antlered sculpin (*Enophrys* spp.)	0.75	2.35	0.00	0.00	0.94	3.03	0.00	0.00
Sculpin (*Gymnocanthus* spp.) [ab]	0.75	11.76	0.00	0.49	0.94	12.12	0.00	1.36
Brightbelly sculpin (*Microcottus sellaris*)	0.75	0.00	0.00	0.00	0.94	0.00	0.00	0.00
Sculpin (*Myoxocephalus* spp.) [bd]	11.19	9.41	4.88	2.91	8.49	10.61	11.29	3.17
All Pricklebacks (Stichaeidae)	1.49	3.53	0.00	0.00	1.89	1.52	0.00	0.90
Eelblenny (*Lumpenus* spp.)	0.75	7.06	0.00	0.00	0.94	3.03	0.00	1.81
All Flatfish (Pleuronectidae)	1.49	15.29	7.32	8.74	4.72	13.64	0.00	9.95
Snailfish (*Liparis* spp.)	0.00	0.00	4.88	0.00	1.89	0.00	0.00	0.00

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

Table 7. Regional and seasonal differences in frequency of occurrence (%FO$_i$) of invertebrate prey identified from spotted seal stomachs collected in Alaska, 1966–2008.

	Region				Season			
	Bering		Chukchi		Summer		Winter	
Collection period	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**	**1966-1981**	**1998-2008**
Sample size (# stomachs analyzed)	134	85	41	206	106	66	62	221
Prey (*i*)	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**	**%FO$_i$**
All Invertebrates [abcd]	44.78	48.24	60.98	29.13	66.04	37.88	17.74	33.03
All Mollusca [b]	2.24	9.41	4.88	6.80	2.83	15.15	1.61	4.98
Gastropod & Bivalve Mollusca	0.00	4.71	4.88	4.37	0.00	7.58	1.61	3.17
Octopus (Octopodia)	1.49	1.18	0.00	0.00	1.89	0.00	0.00	0.45
All Crustacean [abcd]	43.28	47.06	58.54	25.73	64.15	34.85	16.13	30.32
All Mysida [b]	8.96	1.18	19.51	0.00	16.04	0.00	3.23	0.45
Mysis spp.	2.24	0.00	4.88	0.00	4.72	0.00	0.00	0.00
Neomysis spp.	6.72	0.00	17.07	0.00	12.26	0.00	3.23	0.00
Isopoda (*Saduria* spp.) [ac]	1.49	4.71	7.32	0.49	3.77	4.55	1.61	0.90
All Amphipoda [abcd]	12.69	20.00	26.83	10.19	21.70	15.15	4.84	11.76
Scud amphipods (Gammaridae)	0.75	2.35	4.88	2.43	2.83	4.55	0.00	1.81
Gammarus spp. [ac]	0.75	2.35	14.63	1.46	4.72	3.03	1.61	1.36
Ampelisca spp.	2.24	1.18	2.44	0.00	3.77	1.52	0.00	0.00
Anonyx spp.	2.99	0.00	2.44	0.00	4.72	0.00	0.00	0.00
Parathemisto spp. [ac]	5.97	10.59	14.63	2.43	9.43	0.00	4.84	5.88
Euphausiacea (*Thysanoessa* spp.)	2.99	0.00	0.00	0.49	3.77	0.00	0.00	0.00
ALL Decapods [bd]	34.33	27.06	48.78	20.87	53.77	24.24	8.06	22.17
All Shrimp (Caridea) [bd]	32.84	20.00	48.78	20.39	53.77	16.67	4.84	21.72
Lebbeus spp.	4.48	0.00	0.00	0.00	5.66	0.00	0.00	0.00
Eualus spp.	9.70	0.00	7.32	0.00	14.15	0.00	0.00	0.00
Pandalus spp.	6.72	4.71	12.20	0.97	11.32	1.52	1.61	2.26
All Crangonidae shrimp [bd]	17.91	10.59	31.71	14.08	31.13	10.61	3.23	14.03
Crangon spp. [a]	5.97	4.71	29.27	11.17	16.04	7.58	3.23	9.95
Sclerocrangon spp.	3.73	0.00	2.44	0.00	4.72	0.00	0.00	0.00
Argis spp.	2.99	1.18	4.88	0.00	4.72	0.00	0.00	0.45
All Crab [bd]	2.99	9.41	2.44	0.00	1.89	9.09	3.23	0.90
Pagurus spp.	1.49	0.00	0.00	0.00	0.94	0.00	1.61	0.00
Hyas spp.	1.49	0.00	2.44	0.00	0.94	0.00	1.61	0.00
Urochordata	0.00	0.00	2.44	0.00	0.94	0.00	0.00	0.00

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

Table 8. Geometric mean (Gmean), arithmetic mean (Amean) and range of concentrations (µg/g ww = ppm) of selected elements in liver (n=17) and kidney (n=6) of spotted seals harvested in Alaska, 2003–2006.

	As	**Cd**	**Cu**	**THg**	**Mg**	**Mn**	**Pb**	**Se**	**Zn**
Liver									
Gmean	0.37	0.38	8.79	0.88	210.80	4.01	0.04	2.04	45.70
Amean	0.43	0.93	10.54	1.72	211.45	4.34	0.05	2.29	46.97
Range	0.28-1.67	0.02-6.40	0.99-22.47	0.03-5.61	186.3-242.2	0.68-6.17	0.03-0.22	0.82-4.74	25.81-66.12
Kidney									
Gmean	0.20	3.02	5.10	0.38	146.66	0.90	nd	2.79	32.06
Amean	0.20	4.90	5.29	0.45	147.05	0.90	nd	2.86	33.76
Range	0.16-0.30	1.17-17.53	3.03-6.75	0.21-1.13	129.9-163.5	0.74-1.04	nd	1.78-3.62	25.97-60.76

Table 9. Geometric mean and range (ng/g or ppb wet wt) of concentrations for total organochlorines in blubber from 17 spotted seals harvested in Alaska, 2003–2006.

	Compound			
	∑ HCH	**∑ CHL**	**∑ DDT**	**∑ PCB**
Gmean	104.8	193.6	199.5	404.1
Range	(59–313)	(199–1979)	(30–695)	(99–1256)

Table 10. Geometric mean and range (ng/g or ppb wet wt) of concentrations for total organochlorines in liver from 15 spotted seals harvested in Alaska, 2003–2006.

	Compound			
	∑ HCH	**∑ CHL**	**∑ DDT**	**∑ PCB**
Gmean	1.8	5.6	4.6	16.0
Range	(0–10)	(2–67)	(1–99)	(4–174)

Table 11. Geometric mean and range (µg/g or ppm wet wt) of concentrations of dominant PCB congeners in blubber (n=17) and liver (n=15) from spotted seals harvested in Alaska, 2003–2006.

	Dominant PCB Congeners			
	153/132	**101/90**	**138/160**	**187**
Blubber				
Gmean	90.91	61.56	53.10	10.58
Range	19.91-365.30	9.75-268.96	13.16-173.39	3.27-46.32
Liver				
Gmean	2.25	0.74	1.65	0.96
Range	0.46-41.92	0.07-12.81	0.60-36.92	0.05-38.46

Table 12. Growth rate parameters from the best approximating model of spotted seal growth.

Growth rate parameter	**Posterior means (95% credibility intervals)**	
	1970s	**1960s and 2000s**
a	-0.1867 (-0.2371 - -0.1413)	-0.1870 (-0.2597 - -0.1242)
b	0.1870 (0.2410 - 0.3811)	0.2456 (0.1755 - 0.3330)
***Linf* (constant)**	160.1	160.1

Table 13. Models for the average age of maturity for spotted seals in the 1960s, 1970s, and 2000s. All models assume a probit link function and a binomial error distribution.

Model	**LogL**	**#Para**	**AIC**	**Δ AIC**
All periods differ	-46.94	3	87.88	0
1960s=1970s, 2000 differ	-46.95	2	89.9	2.02
1960s=2000s, 1970s differ	-46.95	2	89.9	2.02
1970s=2000s, 1960s differ	-48.53	2	93.06	5.18
constant	-48.56	1	95.12	7.24

Table 14. Reproductive status (ovulation by age) of female spotted seals harvested in Alaska during 1964–1969.

Age	Not yet ovulated		First ovulation		More than one ovulation		Total in age class
	No.	%	No.	%	No.	%	
Pup	66	100	0	0	0	0	66
1	9	100	0	0	0	0	9
2	5	100	0	0	0	0	5
3	1	50	1	50	0	0	2
4	1	33	3	67	0	0	4
5	1	33	1	33	1	33	3
6	0	0	0	0	0	0	0
7	0	0	2	100	0	0	2
7+	0	0	0	0	29	100	29
Total	**83**		**7**		**30**		**120**

Table 15. Reproductive status (ovulation by age) of female spotted seals harvested in Alaska during 1970–1979.

	Not yet ovulated		First ovulation		More than one ovulation		
Age	**No.**	**%**	**No.**	**%**	**No.**	**%**	**Total in age class**
Pup	20	100	0	0	0	0	20
1	15	100	0	0	0	0	15
2	19	100	0	0	0	0	19
3	10	83	2	17	0	0	12
4	3	37.5	4	50	1	12.5	8
5	3	25	2	17	7	58	12
6	1	9	1	9	9	82	11
7	0	0	0	0	10	100	10
7+	0	0	0	0	32	100	32
Total	**71**		**9**		**59**		**139**

Table 16. Reproductive status (ovulation by age) of female spotted seals harvested in Alaska during 1998–2008.

Age	Not yet ovulated No.	Not yet ovulated %	First ovulation No.	First ovulation %	More than one ovulation No.	More than one ovulation %	Total in age class
Pup	32	100	0	0	0	0	32
1	15	100	0	0	0	0	15
2	6	75	2	25	0	0	8
3	6	75	1	12.5	1	12.5	8
4	3	37.5	3	37.5	2	25	8
5	0	0	1	25	2	75	3
6	0	0	0	0	3	100	3
6+	0	0	0	0	8	100	8
Total	**62**		**7**		**16**		**85**

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	32	38	17	9
Cd	Mean	1.59	2.28	0.38	**3.64**
	SD	2.86	7.12	3.98	**3.65**
	Range	(0.17-20.80)	(0.01-39.93)	(0.02-6.40)	**(0.42-15.21)**
Hg	Mean	1.21	1.91	0.88	**2.10**
	SD	3.20	3.69	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	1.71	1.67	1.68
	Range	(0.03-0.12)	(0.03-0.48)	(0.03-0.22)	(0.03-0.13)

Table 18. 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 metal is in bold.

Compound		**Species**			
		Ringed	**Bearded**	**Spotted**	**Ribbon**
	n	32	33	17	9
∑ HCH	Mean	51.8	14.4	**104.8**	93.9
	SD	1.65	1.55	**1.56**	1.64
	Range	(17-150)	(3-28)	**(35-313)**	(53-228)
∑ CHL	Mean	96.5	104.2	193.6	**338.6**
	SD	2.12	1.60	1.96	**2.10**
	Range	(24-342)	(51-415)	(38-580)	**(199-1979)**
∑ DDT	Mean	129.3	91.2	199.5	**456.5**
	SD	1.85	1.95	2.19	**2.06**
	Range	(39-628)	(26-605)	(30-695)	**(168-1382)**
∑ PCB	Mean	278.7	193.0	404.1	**552.0**
	SD	1.71	1.76	1.97	**1.94**
	Range	(92-908)	(69-943)	(99-1256)	**(231-1467)**

Figure 1. Collection locations.

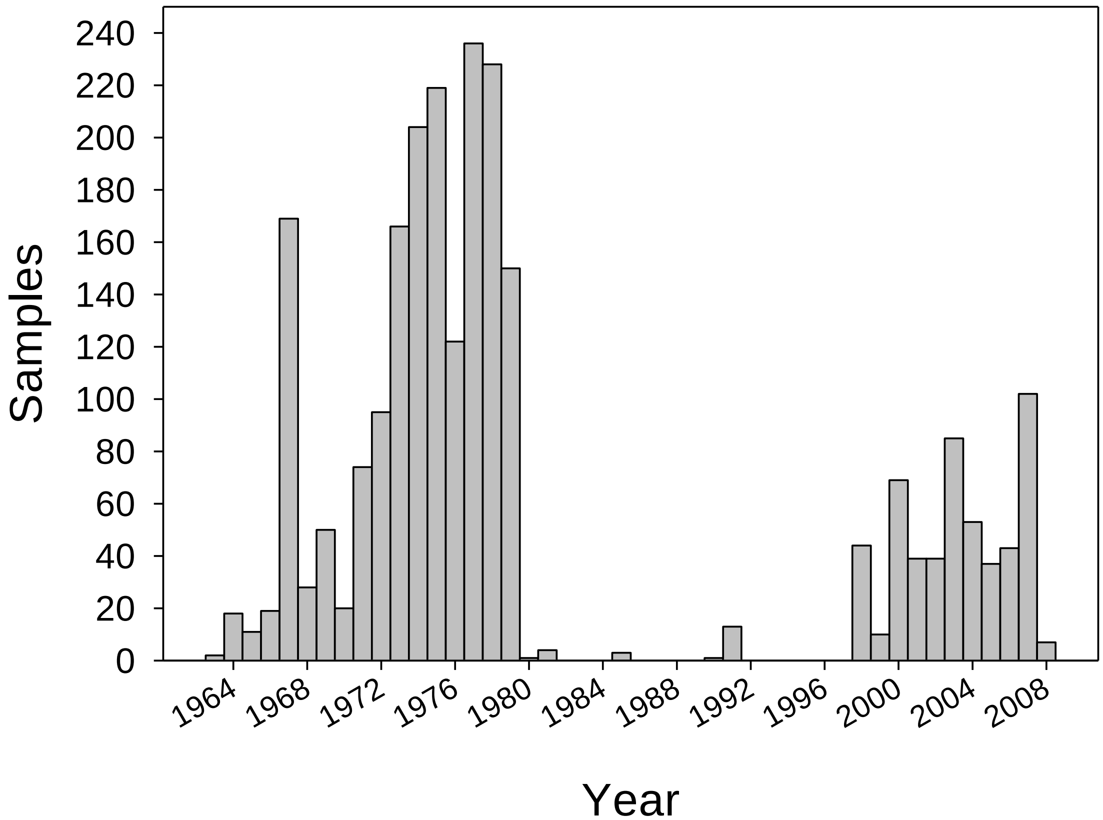


Figure 2. Number of spotted seals sampled in Alaska, by year, for which ages are known. The sample size of seals differed slightly for each analysis, as not all measurements or samples were collected for each seal. Although sample sizes differ by analysis, this figure illustrates the distribution of samples by year.

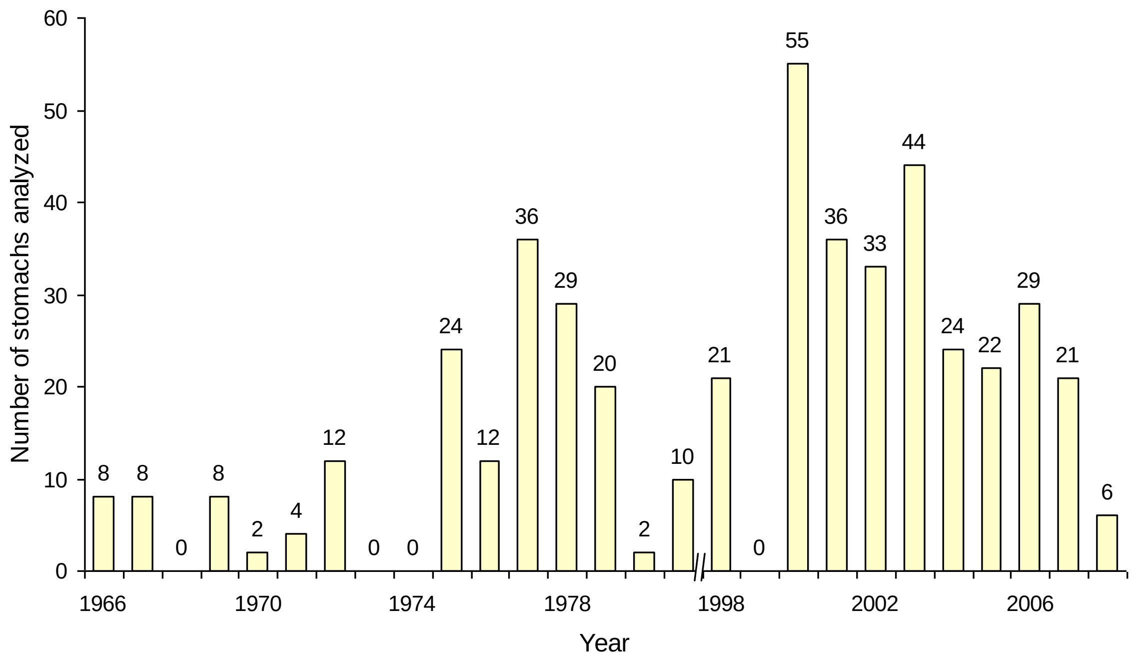


Figure 3. Number of spotted seal stomachs that contained prey items. Spotted seals were harvested in Alaska, 1966–2008. No stomachs were analyzed in 1968, 1973, 1974, 1982–1997, and 1999.

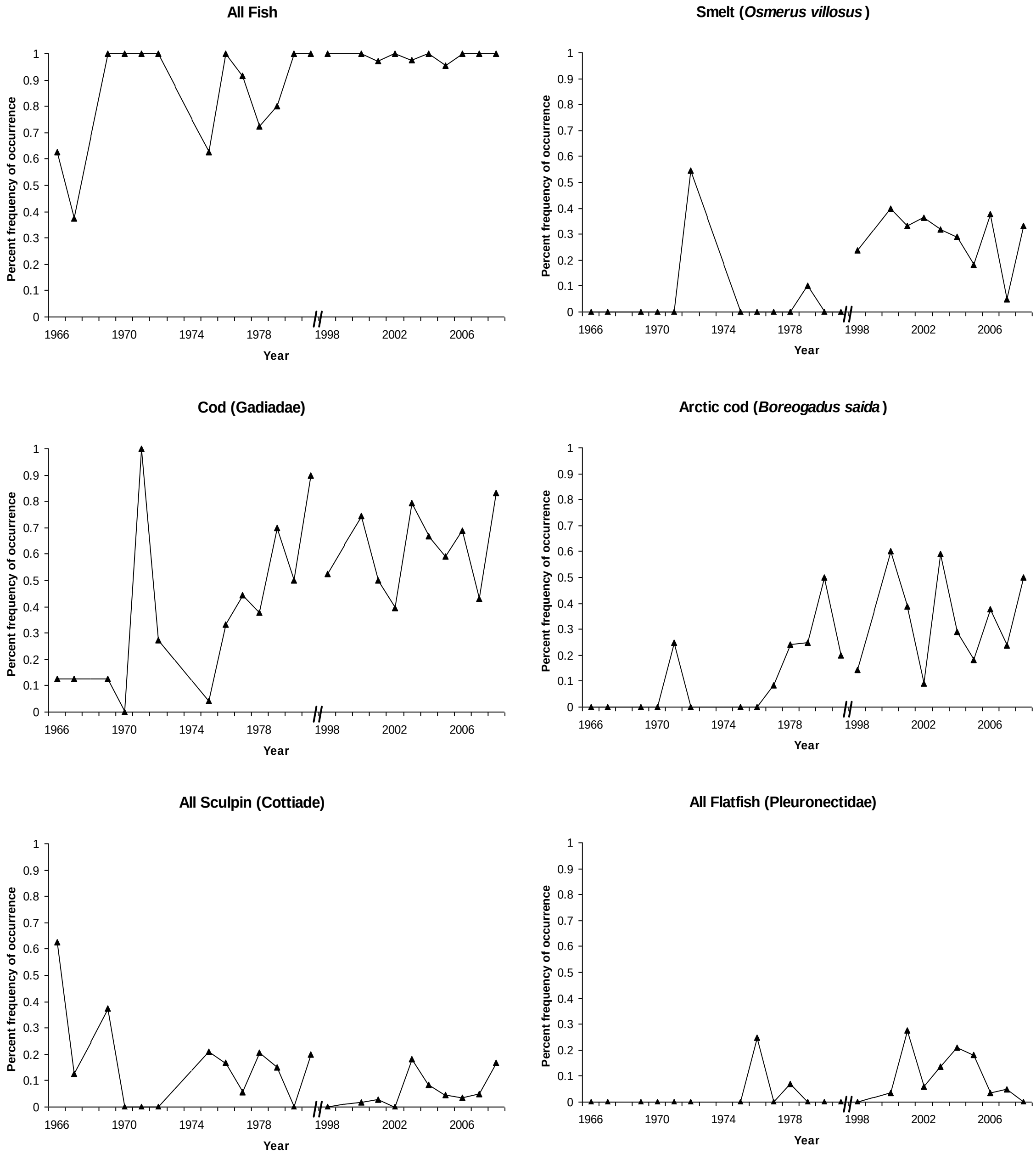


Figure 4. Yearly patterns in percent frequency of occurrence (%FO_i) of primary fish prey identified from stomachs of spotted seals harvested in Alaska, 1966–2008. No stomachs were analyzed in 1968, 1973, 1974, 1982–1997, and 1999.

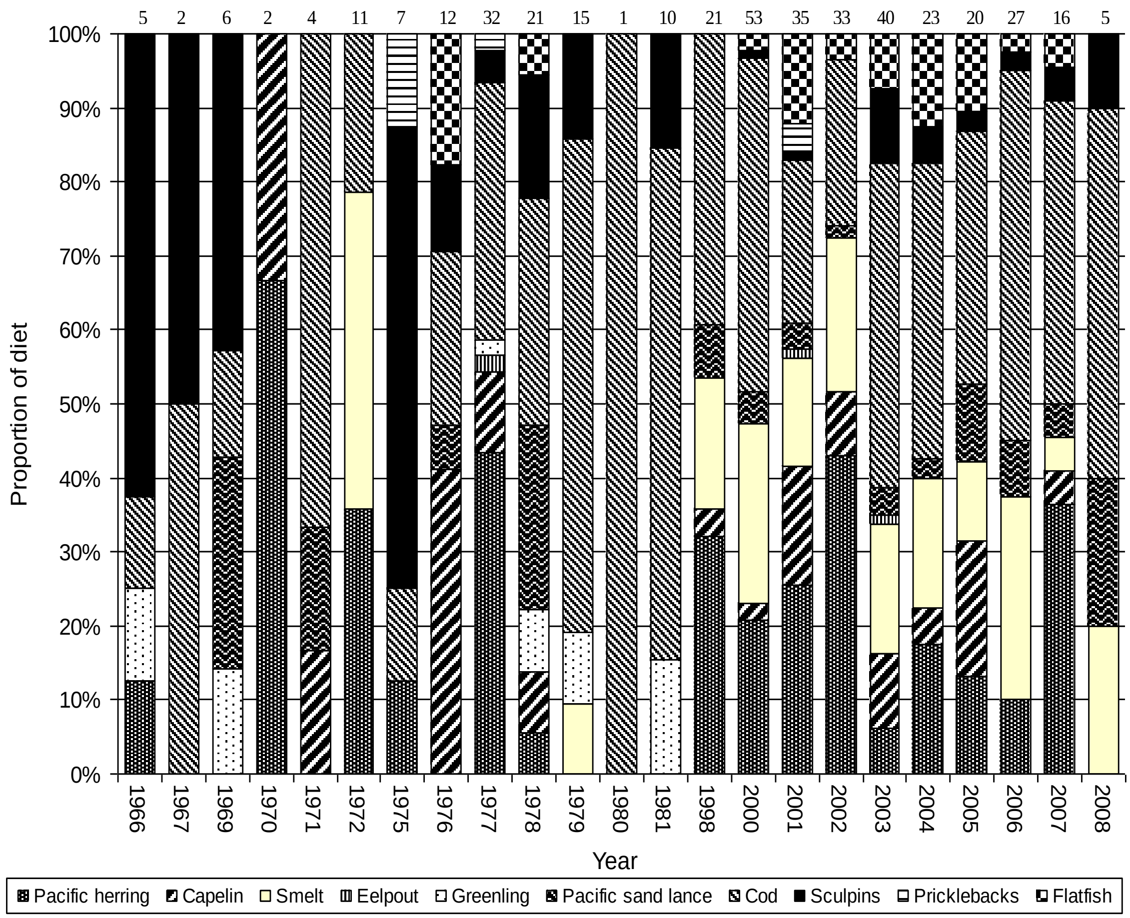


Figure 5. Yearly proportions of fish prey identified in the stomachs of spotted seals harvested in Alaska, 1966–2008. Numbers of stomachs containing fish that were analyzed each year are listed above bars. No stomachs were analyzed in 1968, 1973, 1974, 1982–1997, and 1999.

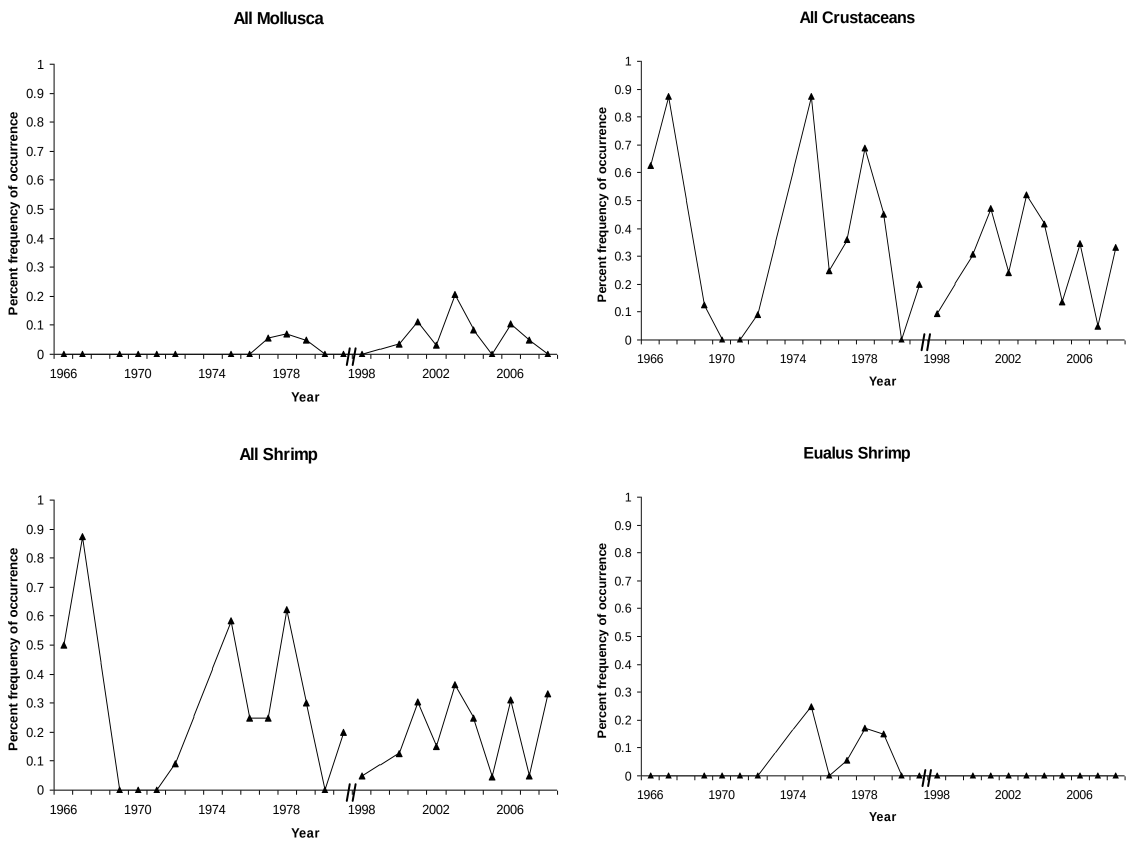
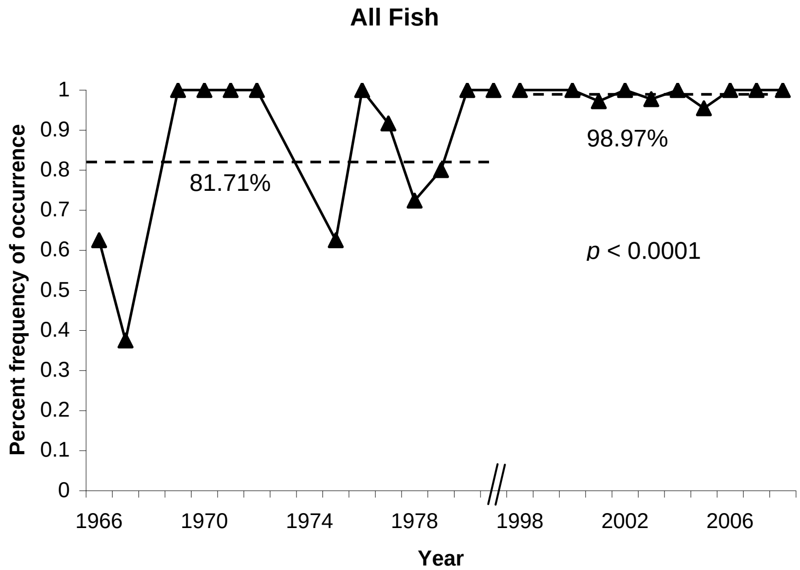


Figure 6. Yearly patterns in percent frequency of occurrence (%FO_i) of primary invertebrate prey identified from stomachs of spotted seal harvested in Alaska, 1966–2008. No stomachs were analyzed in 1968, 1973, 1974, 1982–1997, and 1999.



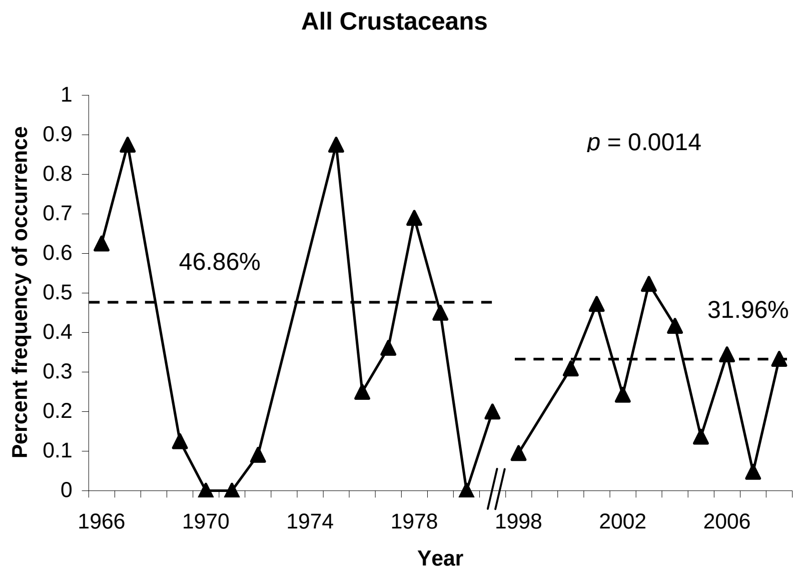


Figure 7. Yearly patterns in percent frequency of occurrence (%FO_i) for all fish and all crustacean prey in stomachs of spotted seals harvested in Alaska, 1966–2008. No stomachs were analyzed in 1968, 1973, 1974, 1982–1997, and 1999. Dashed lines are the mean %FO_i for two time periods, 1966–1981 and 1998–2008. *P*-values are reported from the final logistic model for each prey item.

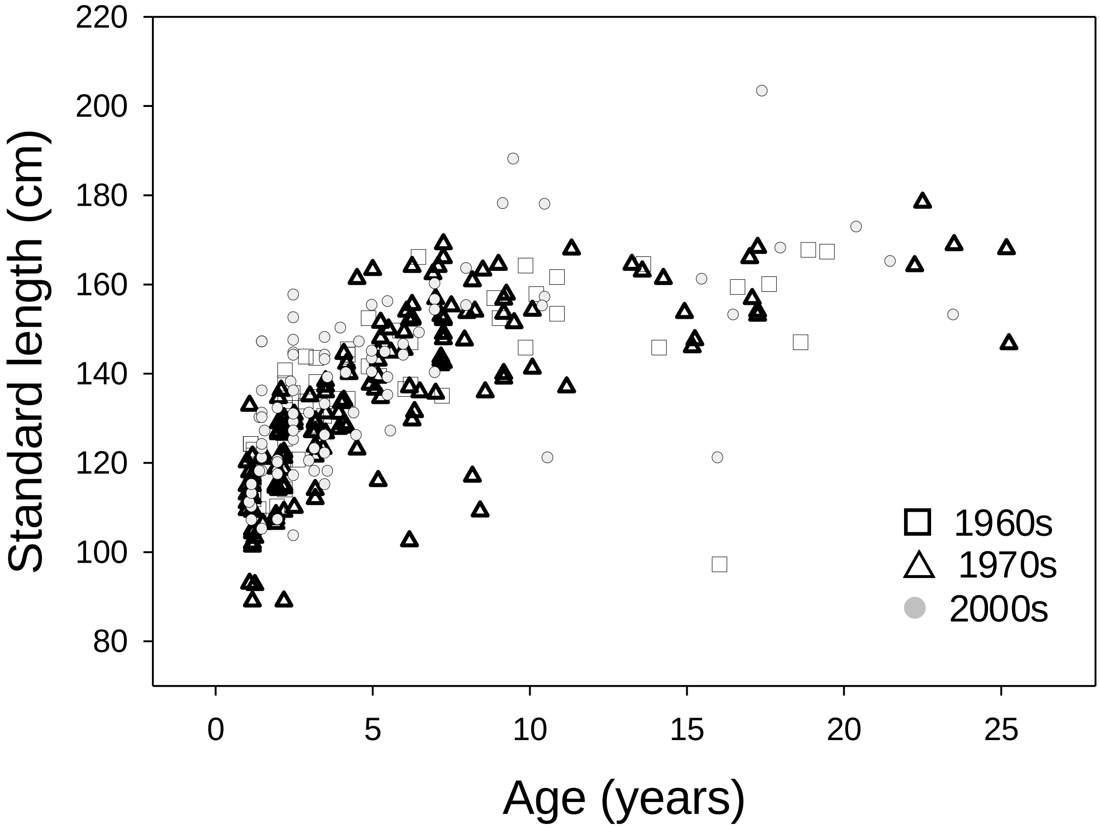
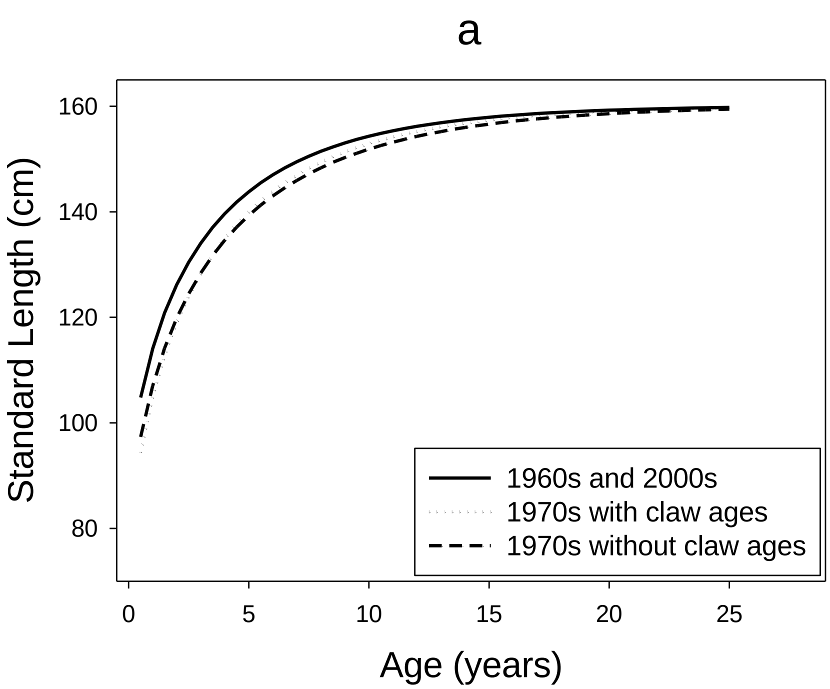


Figure 8. Plot of length-at-age for three time periods.



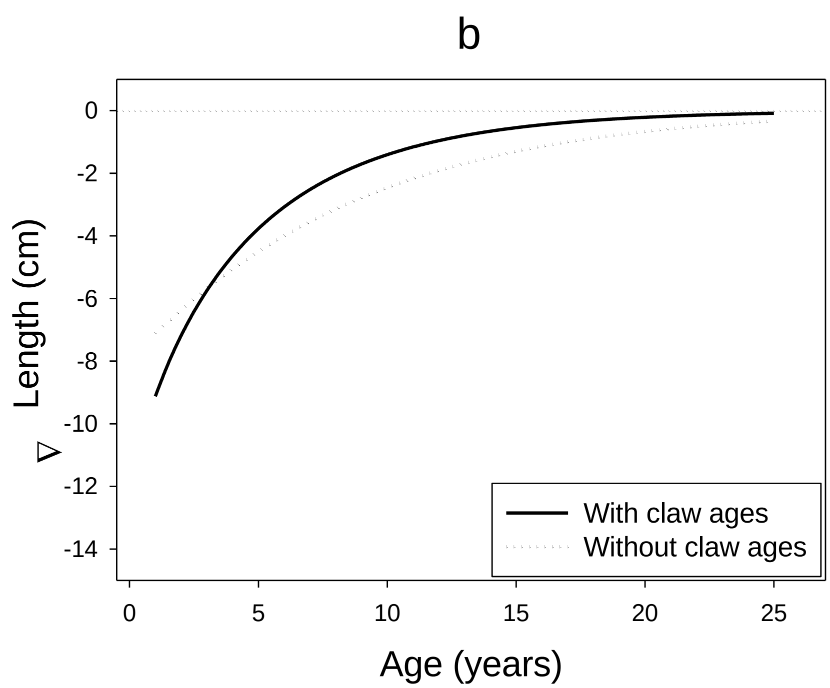


Figure 9. a) Mean predictions of length-at-age from the best approximating model of spotted seal growth; b) Plot of the average difference in length between seals in the 1970s and the 1960s or 2000s.

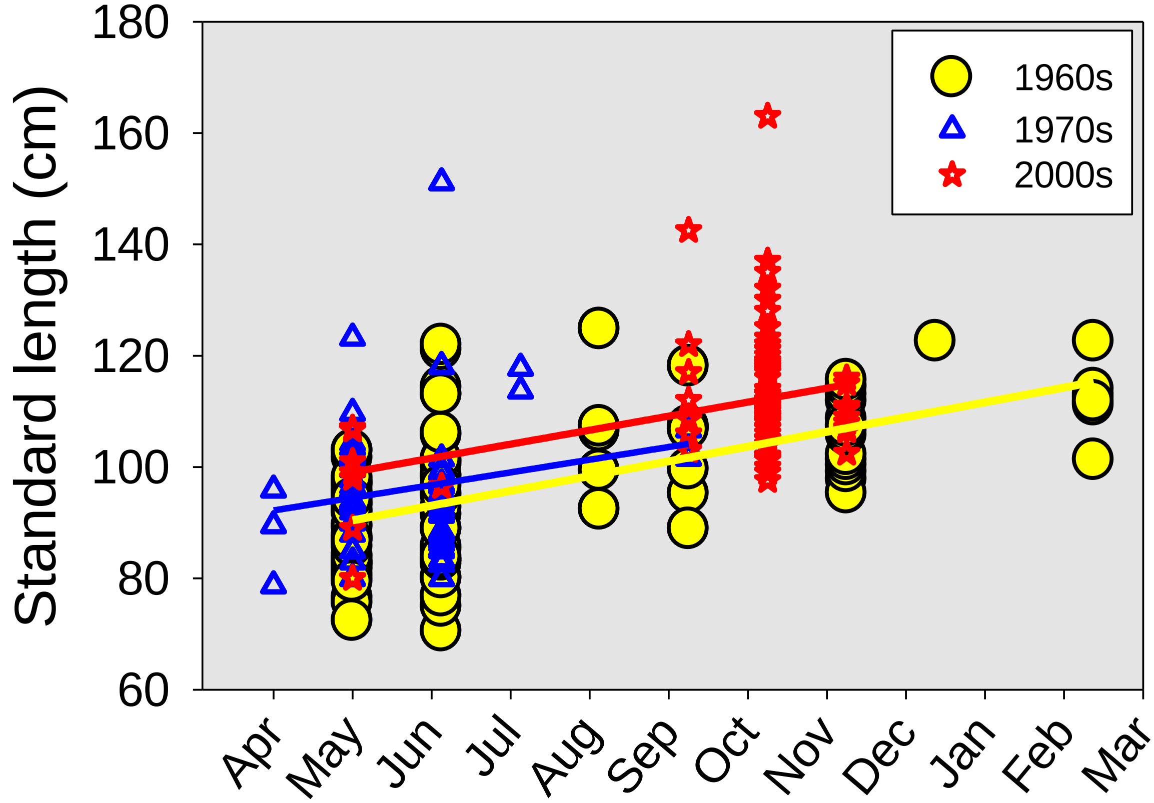


Figure 10. Standard length (cm) by month of spotted seal pups harvested in Alaska over three time periods.

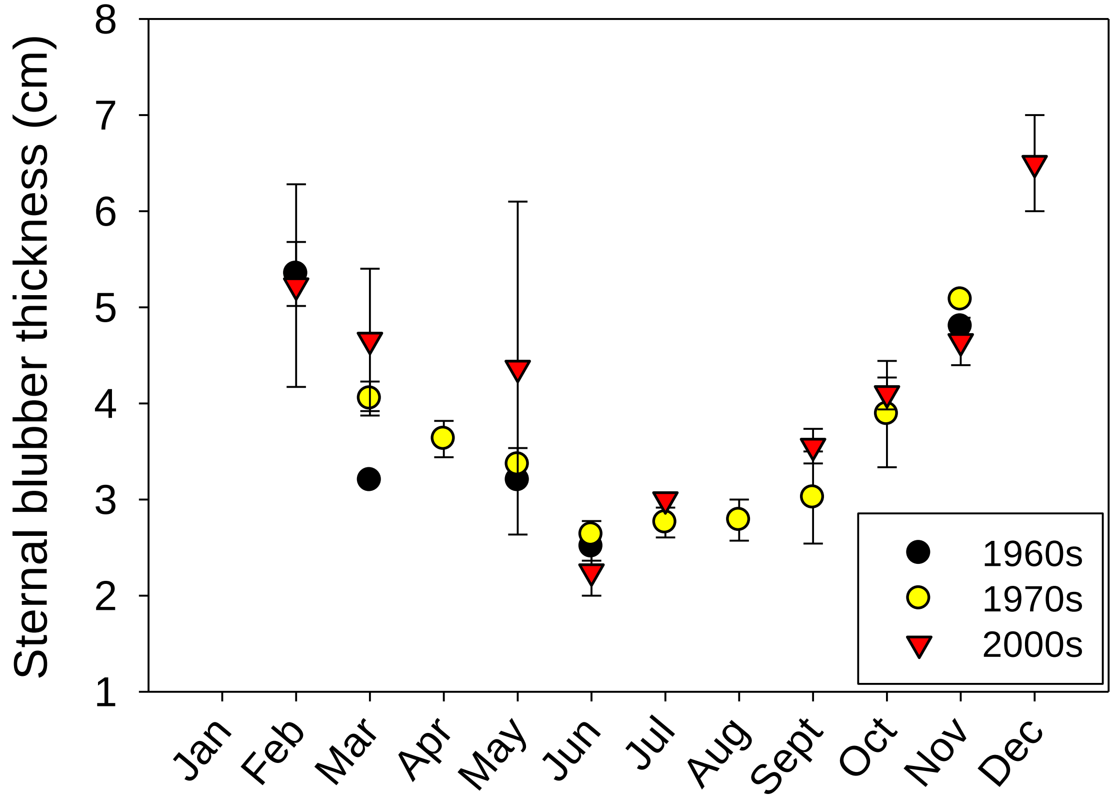


Figure 11. Mean sternal blubber thickness by month of sampling for seals three years of age or greater. Error bars represent one standard deviation.

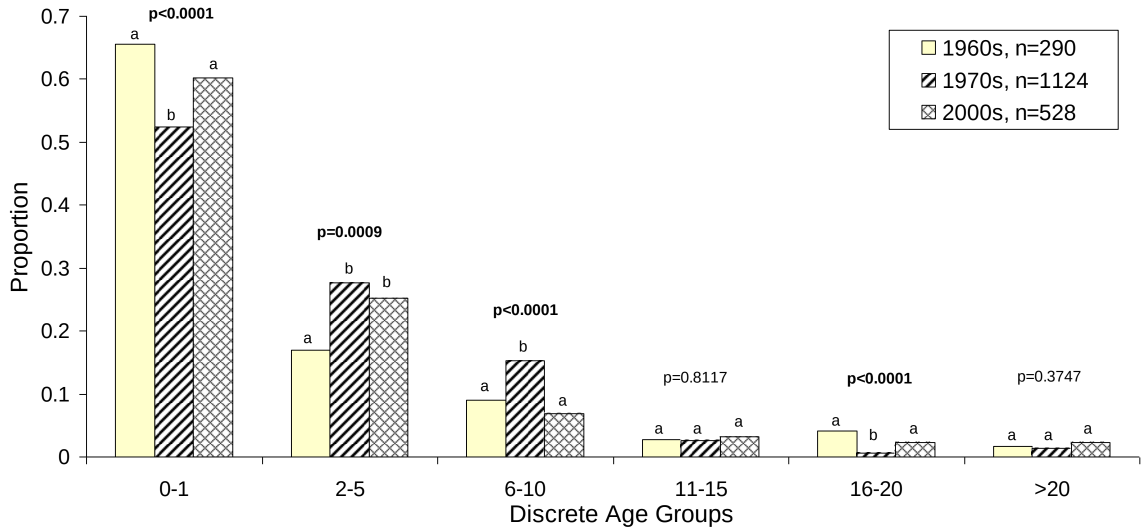


Figure 12. Proportions of spotted seals harvested within six different age categories and three time periods in Alaska, 1963–2008.

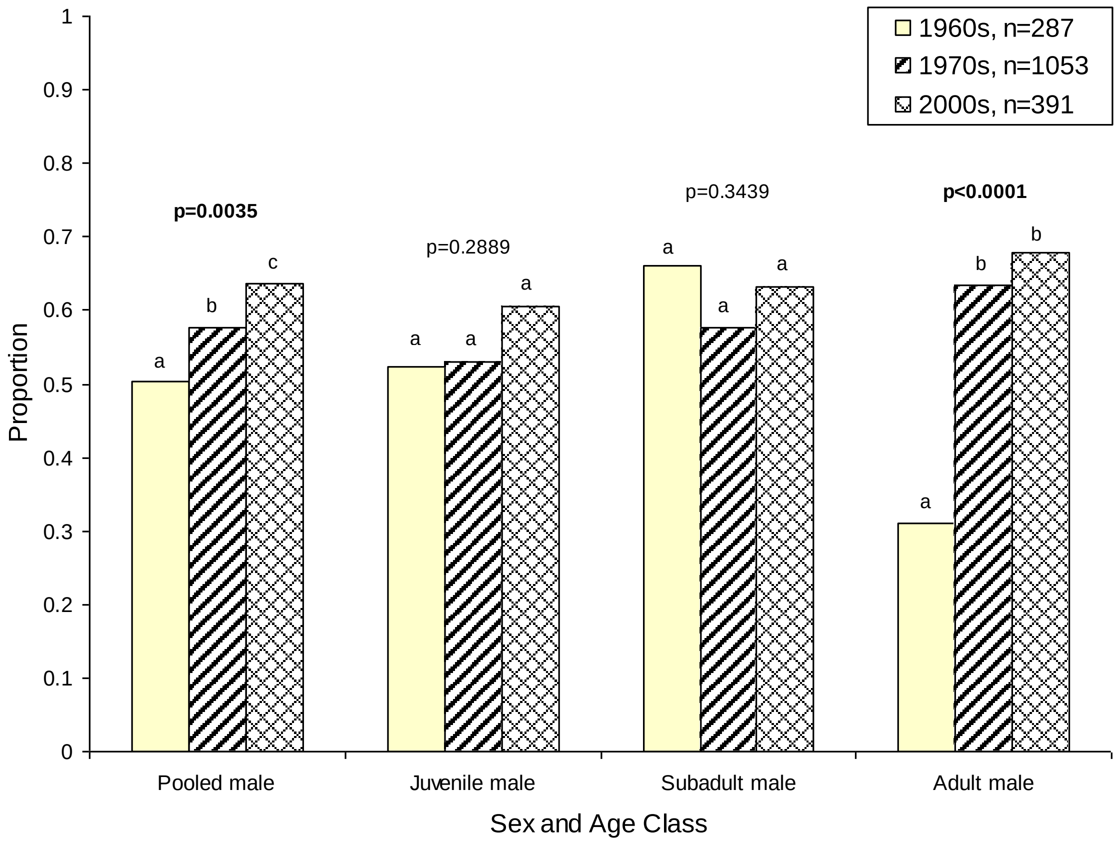


Figure 13. Proportions of male spotted seals, pooled and by age class, harvested by decade in Alaska, 1963–2008. Sample sizes represent both male and female spotted seals harvested during each decade.

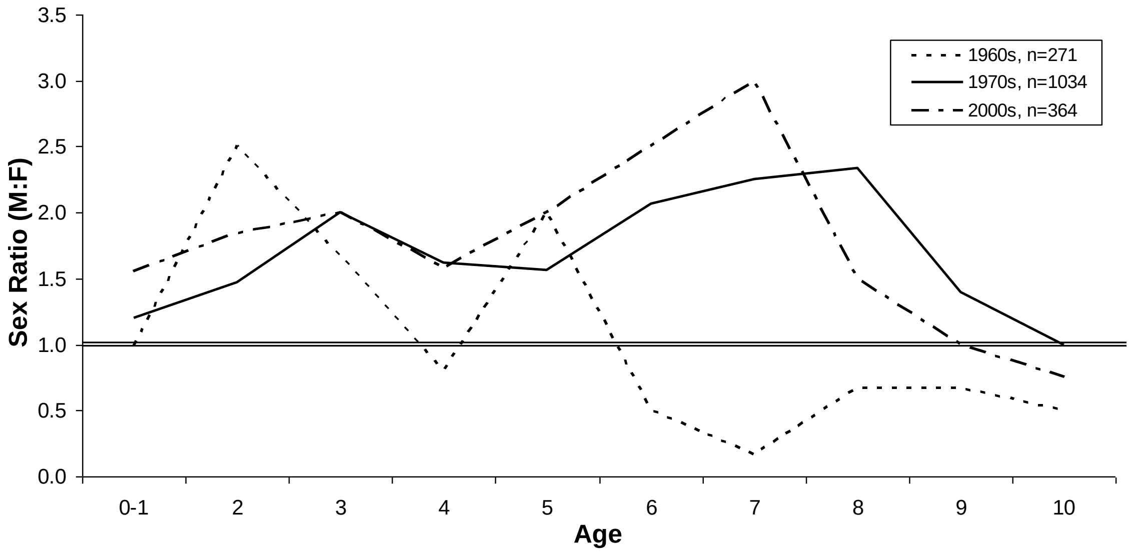


Figure 14. Sex ratios of spotted seals, age 0–10 years old, harvested within three decades in Alaska, 1963–2008. Sample sizes represent both male and female spotted seals harvested during each decade.

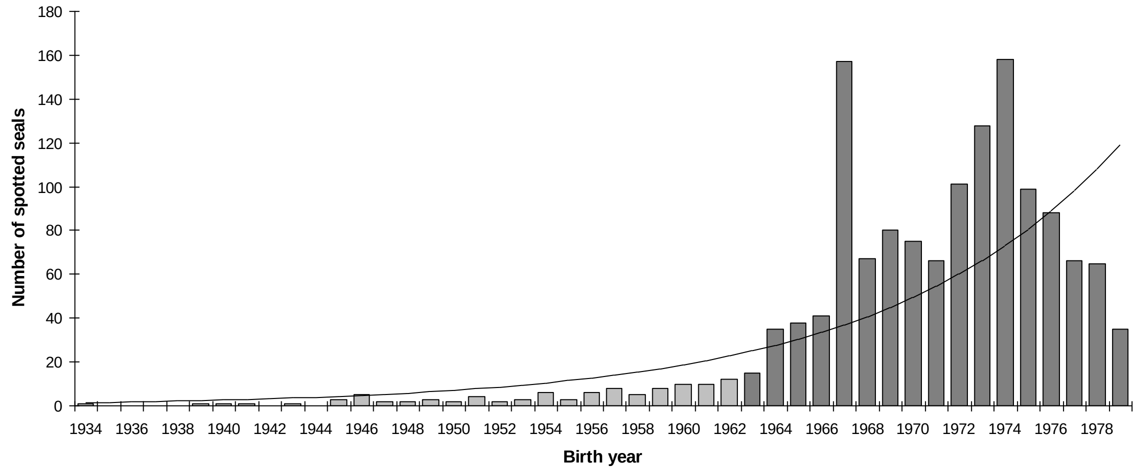


Figure 15. Survivorship schedule for 1,413 spotted seals harvested in Alaska, 1934–1979. The function $y = ae^{bx}$ predicted survivorship, where y is the number of spotted seals predicted to be in the sample, x is year of birth, e is the base of the natural logarithm, and a and b are fitted constants (a=1.05E-82, b=0.0978). Harvests for 1963–1979 were used for estimating the survivorship curve and are shade in dark grey.

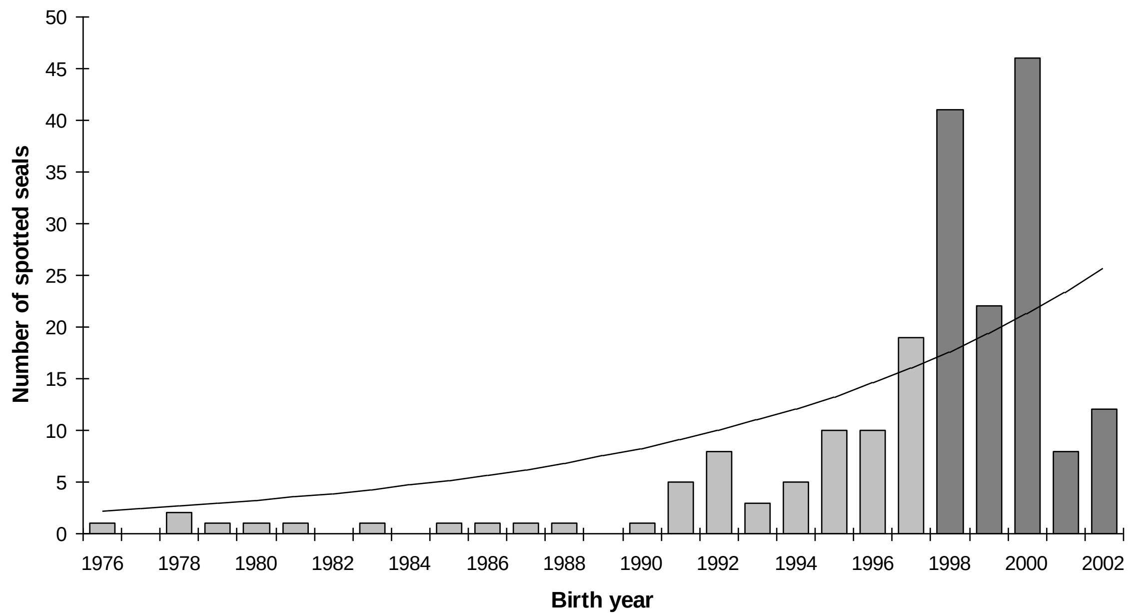


Figure 16. Survivorship schedule for 201 spotted seals harvested in Alaska, 1976–2003. The function $y = ae^{bx}$ predicted survivorship, where y is the number of spotted seals predicted to be in the sample, x is year of birth, e is the base of the natural logarithm, and a and b are fitted constants (a= 1.76E-81, b=0.0945). Harvests for 1998–2002 were used for estimating the survivorship curve and are shade in dark grey.

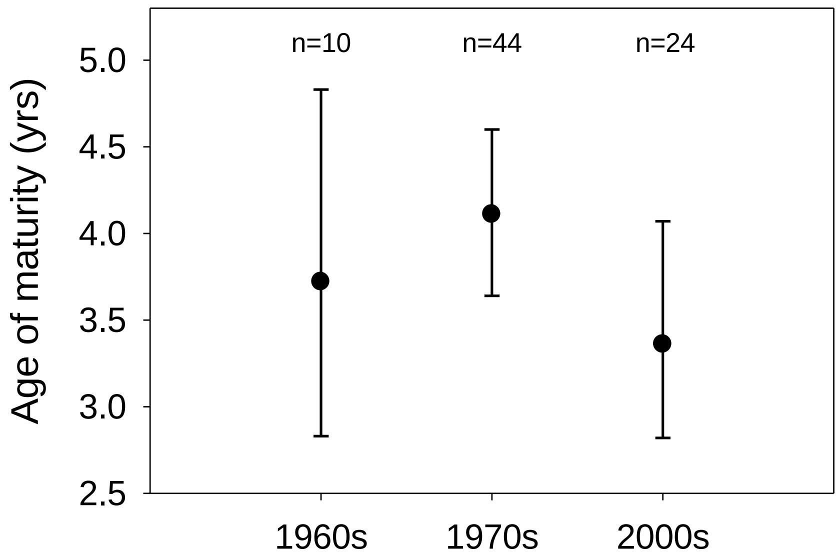


Figure 17. Mean age at maturity and 95% confidence limits for spotted seals from the best approximating model. Statistical contrasts indicated that the 1960s were indistinguishable from either the 1970s (p=0.45) or the 2000s (p=0.45). However, the age at maturity was significantly older in the 1970s than the 2000s (p=0.05). Samples sizes are only for seals between three and six years of age; these are the age classes where the proportion of seals mature is > 0 and < 1.