A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas

Crawford, Justin A.[a], Quakenbush, Lori T.[a], and Citta, John J.[a]

(a) Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska, 99701, USA

Corresponding author: Justin A. Crawford; 907-459-7328; Justin.Crawford@alaska.gov

Abstract

Reductions in summer sea ice in the Chukchi and Beaufort seas are expected to affect what has been an ice-adapted marine food web in the Pacific Arctic. To determine whether recent decreases in sea ice have affected ice-associated marine predators (i.e., ringed, *Pusa hispida*, and bearded seals, *Erignathus barbatus*) in the Bering and Chukchi seas we compared diet, body condition, growth, productivity, and the proportion of pups harvested (an index of weaning success) for seals of each species harvested by 11 Alaskan villages during two periods; a historical (1975–1984) and a recent period (2003–2012). We also examined how changes in indices of seal health may be correlated with the reduction of sea ice characteristic of the recent period. For ringed seals ≥1 year of age, the % frequency of occurrence (%FO) of Arctic cod (*Boreogadus saida*), walleye pollock (*Gadus chalcogramma*), rainbow smelt (*Osmerus mordax*), and Pacific herring (*Clupea pallasi*) increased from the historic to the recent period, while the %FO of invertebrates decreased for both pups and seals ≥1 year of age. For bearded seals ≥1 year of age, the %FO of Arctic cod, pricklebacks, and flatfish increased during the recent period, while the %FO of saffron cod (*Eleginus gracilis*) decreased for pups. Although invertebrates did not change overall for either age class, decreases occurred in 10 of 24 specific prey categories, for bearded seals ≥1 year of age; only echiurids increased. The %FO of gastropods and bivalves increased for pups while isopods and one species of shrimp and crab decreased in occurrence.

During the recent period ringed seals grew faster, had thicker blubber, had no change in pregnancy rate, matured 2 years earlier, and a larger proportion of pups was harvested than during the historical period. Correlations with spring ice concentration showed that the growth and blubber thickness of seals ≥1 year of age, blubber thickness of pups, and the proportion of pups in the harvest all declined for ringed seals when ice concentrations were higher in the historic period. However, only the correlations between high ice concentrations and growth of ringed seals ≥1 year of age and the proportion of ringed seal pups in the harvest were statistically significant. Although adult bearded seal growth was slower during the recent period, it was similar to the average over the entire time series, and blubber thickness increased. Pup growth and blubber thickness did not change between periods. There was no change in pregnancy rate, but females matured 1.6 years earlier, and a larger proportion of pups were harvested. Correlations with spring ice concentration showed that the growth of seals ≥1 year of age, the growth of pups, blubber thickness of pups, and proportion of pups in the harvest also declined for bearded seals when sea ice concentrations were higher. However, no relationships between bearded seals and sea ice were statistically significant. Overall, our results suggest that ringed seals in the Alaskan Bering and Chukchi seas have adjusted to changes in diet, are growing faster and possibly weaning more pups in the recent compared to the historic period. These patterns are less evident for bearded seals. Although the ringed and bearded seals we examined have not exhibited the declines in body condition, growth, or reproduction observed in other populations, continued monitoring and comparison among seal populations is vital to understanding the effects of changing environmental conditions in the Pacific Arctic region.

Key words: ice-associated pinnipeds; body condition; productivity; weaning success; Arctic cod; sea ice; climate change; Bering Sea; Chukchi Sea; Alaska.

1 Introduction

Ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals are ice-associated seals that have a circumpolar distribution (Allen, 1880; Chapskii, 1938; McLaren, 1958a; Burns, 1967; Burns, 1970; Smith, 1973). In Alaska, these seals range throughout the Bering, Chukchi, and Beaufort seas (Burns, 1970). Although movements in winter months are restricted by sea ice, these seals move widely in spring, summer, and fall (Crawford et al., 2012; Harwood et al., 2012a). Both species tend to inhabit areas that are seasonally ice covered; however, some seals, especially juveniles, are found in open water in summer and fall (Burns et al., 1980; Harwood and Stirling, 1992). Ringed seals feed mostly in the water column on pelagic and semi-demersal fish and invertebrates (Dunbar, 1941; McLaren, 1958a; Fedoseev, 1965; Johnson et al., 1966; Lowry et al., 1980b). Bearded seals feed on a wide variety of benthic invertebrates and fish (Chapskii, 1938; Dunbar, 1941; Burns, 1967; Lowry et al., 1980a; Smith, 1981; Antonelis et al., 1994).

There is concern that recent changes in sea ice and water temperatures may alter the diversity, distribution, or abundance of demersal and pelagic fish and invertebrates (Hunt et al., 2002; Mueter and Litzow, 2008; Wassmann, 2011). Arctic sea ice has undergone major reductions in recent decades with record decreases in summer ice extent, multiyear ice, and ice thickness (Comiso, 2012; Laxon et al., 2013), leading to a longer ice-free season and warmer waters (Stroeve et al., 2014). In Alaskan waters, decreases in sea ice have been greatest in the Chukchi and Beaufort seas, which had previously retained some ice in shelf waters throughout the year. In recent years, sea ice typically retreats north of the Beaufort and Chukchi shelf breaks in summer (July–September). Conversely, the Bering Sea, has consistently had an ice-free season in the summer (Mahoney et al., 2011), and the maximum extent of sea ice in winter

(December–April) has not declined (Moore and Laidre, 2006; Wendler et al., 2013). However, the duration of the ice-free season is expected to increase (Douglas, 2010).

Forecasts for continued declines in sea ice (Holland et al., 2006; Wang and Overland, 2009), reductions in snow cover (Hezel et al., 2012), and changes in the distribution and availability of fish and invertebrates (Bluhm and Gradinger, 2008; Cooper et al., 2009; Wassmann, 2011) are expected to negatively affect diet, body condition, productivity, and pup survival of ice-associated seals (Grebmeier et al., 2006a; Moore and Huntington, 2008; Cameron et al., 2010; Kelly et al., 2010; Kovacs et al., 2011), especially for ringed and bearded seals, both of which were listed as threatened under the Endangered Species Act in 2012 due to concern over these anticipated threats (U.S. Federal Register, 2012a; U.S. Federal Register, 2012b). The bearded seal listing, however, was vacated by a court decision on 25 July 2014 (Case No. 4:13-cv-00018-RRB Document 78, U.S. District Court for the District of Alaska); currently the Beringia distinct population segment in Alaska is not listed.

Our objective is to determine if ringed and bearded seal diets (i.e., stomach contents) or parameters influenced by diet (i.e., blubber thickness, growth, age at maturity, pregnancy rate, and proportion of pups in the harvest) have changed over time and if these changes covary with changes in sea ice. To do this, we compare data collected from seals harvested by 11 villages bordering the Alaskan Bering and Chukchi seas during a historical period (1975–1984) and a recent period (2003–2012). The historical period predates the time of rapid sea ice retreat in the Pacific Arctic that began in the early 1990s (Serreze et al., 1995; Maslanik et al., 1996). The recent period includes rapid decreases in summer ice volume and extent (Stroeve et al., 2007; Cavalieri and Parkinson, 2012). To better understand how sea ice relates to seal health and productivity, we also directly compare seal body condition, growth, and the proportion of pups in the harvest with spring sea ice extent within the two time periods.

2 Methods

2.1 Collection and handling of specimens

The Alaska Department of Fish and Game (ADF&G) has been monitoring the health and status of ringed and bearded seals in Alaska since 1960 by collecting information and samples from the Alaska Native subsistence harvest. In this manuscript, we consider data collected from 1975 to 1984 by ADF&G (J. J. Burns, K. J. Frost, and L. F. Lowry), funded by the Department of Commerce, Outer Continental Shelf Environmental Assessment Program (OCSEAP) and data collected from 2003 to 2012, funded by National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service. Retrospective data analyses from this long-term monitoring program allow us to examine how parameters that affect population size and status may vary over time and how current and past parameters compare relative to changes in environmental conditions. Although we expect the parameters we examined to relate to population size, the results of these analyses do not allow us to draw any conclusions about changes in actual seal abundances.

Ringed and bearded seals from subsistence harvests of 11 villages along the Bering and Chukchi Sea coasts of Alaska (Fig. 1) were sampled each year; however, sampling effort and opportunity was not consistent. For each analysis, sample size differed slightly because not all measurements or samples were collected for each seal. We pooled samples from the Bering and Chukchi seas for all analyses except diet and the proportion of pups harvested (see Section 2.4.2). Our analysis of diet relied on examining stomach contents which reflect recent diet

(Murie and Lavigne, 1986). Because prey taxa and, therefore, stomach contents may be location specific, we restricted our comparisons of diet to specific locations (see below). Pooling is appropriate for other analyses, however, because satellite telemetry studies indicate that ringed seals travel widely throughout the Bering, Chukchi, and Beaufort seas, and are not restricted to localized areas, at least not during the open-water season (Crawford et al., 2012; Harwood et al., 2012a). Satellite telemetry studies of bearded seals tagged in Kotzebue, Alaska, USA, indicate they also travel widely throughout the Bering, Chukchi, and Beaufort seas, especially during the open-water season (Cameron et al., 2006; Frost et al., 2008; Cameron and Boveng, 2009; Boveng et al., 2012). Therefore, our analyses of blubber thickness, growth, age at maturity, and pregnancy rate are influenced by conditions seals encounter throughout their range and are not solely representative of their harvest location in the way that stomach contents are. We compared two ten-year periods for which we had sufficient sample sizes, a historical (1975–1984) period that predated the time of rapid reductions in sea ice and a recent period (2003–2012) that included the time of reduced sea ice.

Figure 1. Villages in the Bering and Chukchi seas where harvested ringed and bearded seals were analyzed for blubber thickness, growth, age at maturity, and pregnancy rate (1960–2013). Diet analyses were restricted to stomach contents from seals harvested in Shishmaref and Little Diomede. Age distribution analyses were restricted to the proportion of pups harvested in Shishmaref, Little Diomede, Gambell, and Hooper Bay.

For each seal, information collected included location, date harvested, date sampled, species, sex, standard length, and blubber thickness. We measured standard length along a straight line from nose to tip of tail with seals on their backs (American Society of Mammalogists, 1967) and blubber thickness through a small incision to the sternum, midway between the front flippers (McLaren, 1958a). Samples collected for both periods included a tooth, the female reproductive tract, and the whole stomach. During the historical period, an upper canine and a claw from the foreflipper were collected for aging, stomachs were injected with 10% buffered formalin, and female reproductive tracts were preserved in formalin. During the recent period, a lower canine was collected for age and stomachs and reproductive tracts were frozen in the field and shipped to ADF&G laboratory in Fairbanks, Alaska, USA for processing. During the historical period, age of ringed seals was determined by counting annuli in the dentine layers within decalcified longitudinal sections of canine teeth. Age of bearded seals was determined by counting annuli in the cementum layer (Hewer, 1960; Mansfield and Fisher, 1960; Burns, 1969; Stewart et al., 1996). Many ringed and bearded seals were also aged by counting annuli on the claws (McLaren, 1958a; Burns, 1969; Burns and Frost, 1983). Ages determined with claws are known to be biased low for seals older than 8 years of age, because claws wear over time (McLaren, 1958a; Burns, 1981). When both claws and teeth were available, we relied on tooth ages. During a previous study, however, we analyzed growth with and without claw ages and established that ages determined by teeth and claws were comparable (Fig. 3 in Quakenbush et al., 2011a; Fig. 9 inQuakenbush et al., 2011b). During the recent period, teeth were decalcified, sectioned longitudinally, mounted on slides, stained with Giemsa blood stain (Ricca Chemical Company, Arlington, TX, USA), and cementum annuli were counted by Matson’s Laboratory, Milltown, MT, USA, using a compound microscope at 10–160X.

2.2 Stomach content analysis

In the ADF&G laboratory, stomach contents were gently rinsed with freshwater over a 1.0 mm sieve and prey items were sorted and weighed to the nearest 0.1 g during both periods. For both periods, fish and invertebrate prey items were identified to the lowest taxonomic level. Sculpins (F. Cottidae) were identified using preopercular bones and otoliths during the historical period and using otoliths only during the recent period. It is not clear how this difference in methods affects the identification of sculpins to genus and species, therefore we only considered sculpins at the family level for our analyses. Otoliths from flatfish (F. Pleuronectidae), snailfish (F. Liparidae), and pricklebacks (F. Stichaeidae) are small and because stomachs were injected with 10% buffered formalin during the historical period, small otoliths may have degraded, possibly making them more difficult to identify to genus or species; therefore we only considered these fish taxa at the family level for our analyses.

Previous studies in Alaskan waters found differences in the stomach contents of ringed (Lowry et al., 1980b) and bearded (Lowry et al., 1980a) seals by location. Therefore, we limited our comparison of historical and recent diets of ringed and bearded seals to two harvest locations; one in the Chukchi Sea (Shishmaref) and another in Bering Strait (Little Diomede, referred to as Diomede) (Fig. 1). Prey availability also differs by season, especially for fish species that migrate; therefore we further limited our comparison to seals harvested from May through July (i.e., during the months of ice melt). These locations had sample sizes large enough to analyze differences between periods (ringed seals ≥1 year of age at both locations and pups at

Shishmaref only; bearded seals ≥1 year of age at Diomede and pups at Shishmaref). Digestion times in pinnipeds are relatively short; soft parts are typically identifiable within 6 hours (Sheffield et al., 2001) of ingestion and hard parts within 24 hours (Murie and Lavigne, 1986). As such, stomach contents likely represent the recent diet of prey items consumed near the sampling location.

We quantified diet as the percent frequency of occurrence (%FO) for each prey taxon, *i*, that was present in ≥20% of seal stomachs within either period. Percent FO_i was calculated as the number of stomachs that contained prey taxon *i* divided by the number of stomachs with contents (i.e., we did not include empty stomachs in the calculation) X 100. Because $\%FO_i$ is a proportion, it mediates the effect of large differences in sample sizes between collection periods (Sinclair et al., 2008). To determine statistical significance, we used logistic regression to test for differences in the presence (0 = absent, 1 = present) of prey taxa in stomachs containing prey. Models were fit using SAS software (Version 9.3; PROC LOGISTIC, SAS Institute Inc., Cary, NC, USA) and the best model was selected using a backward elimination procedure that sequentially eliminated statistically non-significant variables ($p > 0.05$) until only statistically significant variables remained ($p \leq 0.05$). We initially explored how diet may vary by sex and age class (ringed seals: pups <1 year of age, subadults 1–4 years of age, or adult ≥5 years of age; bearded seals: pups <1 year of age, subadults 1–6 years of age, or adult ≥7 years of age). We found no differences by sex ($p > 0.05$); however, ringed and bearded seal pups consumed many prey items at different frequencies than subadults and adults (seals ≥1 year of age; age class variable: $p \leq 0.05$), which were often similar ($p > 0.05$). Therefore, we pooled sexes and analyzed diets of pups and seals ≥1 year of age separately, combining subadults and adults.

2.3 Morphometrics

2.3.1 Body condition

We used sternal blubber thickness as an index for body condition. Ancillary data (e.g., axillary girth with standard length and body mass) necessary for calculating other indices of body condition (e.g., Parsons, 1977; Ryg et al., 1990a; Gales and Renouf, 1994; Arnould, 1995) were not collected consistently. We focused on seals harvested in May, June, and July by eight villages, because these months had samples in most years. Blubber thickness in seals may vary due to characteristics of the sample that are independent of a period. For example, blubber thickness in seals is known to vary by length (Ryg et al., 1990a), age, and/or month as seals lose mass during molt (McLaren, 1958a; Burns and Frost, 1983; Smith, 1987; Ryg et al., 1990b). If sampling is not completely random, we may mistakenly attribute changes in blubber thickness to a period if the sample of seal ages or the months in which they are sampled is consistently different between periods. Hence, we used a linear modelling framework to examine differences by period while controlling for differences in seal age class, length, and month. Specifically, for seals ≥1 year of age, we examined the effect of period (historical: 1975–1984 and recent: 2003–2012), month (May, June, or July), age class (subadult or adult), standard length (cm), standard length squared, and the interaction between age class and standard length. Covariates were tested for significance using Type III sums of squares and dropped from the model, one-at-a-time, if significance was $p > 0.05$. Similar methods were used for pups (<1 year of age). For pups, we examined how sternal blubber thickness varied by period (historical: 1975–1984 and current: 2003–2012) while controlling for month (May, June, or July) and standard length (cm). For pups, we assumed that length was a proxy for age in months; by controlling for standard length we account for variation in blubber thickness that is due to age and sampling date during a rapid growth period. Models were fit using SAS software (PROC GLM).

2.3.2 Analysis of growth

We examined residuals of growth (i.e., length given age) by period to determine if seals are on average longer or shorter during the recent period (2003–2012) compared to the historical period (1975–1984). Seals were harvested by 11 villages; pups were analyzed separately from seals ≥1 year of age. We used SAS software (PROC GLM) to calculate residuals of growth and compare growth between periods. Growth within the first year of age is essentially linear; therefore we fit a linear model to length at age in months, assuming all seals were born on 1 April.

Growth after the first year of age was clearly non-linear. To calculate residual growth of seals ≥1 year of age, we calculated the mean length at each age in years and then subtracted the mean length from the length of each seal within the same age class. We pooled seals ≥15 years of age, because there were few seals older than 15 and seals have generally reached their asymptotic length by that age (McLaren, 1958a; McLaren, 1958b; Burns, 1981; Quakenbush et al., 2011a; Quakenbush et al., 2011b).

We then linked the residual growth of each seal with its year of birth. Linking residual growth with birth year assumes the length of a seal is more dependent upon events that occur earlier in life rather than later in life. For example, we are assuming that a year with poor foraging conditions or a shortened nursing period will have lasting effects on individuals and will affect pups and one-year-olds more than eight- or nine-year-olds. This is reasonable because ringed (McLaren, 1958a; Frost and Lowry, 1981) and bearded (McLaren, 1958b; Andersen et al.,

1999) seals attain approximately 50% of their body length within approximately the first three years of life. Finally, for each birth year, we plotted the residual growth and looked for years or strings of years associated with seals that were long (or short), given their age at harvest.

2.4 Population parameters

2.4.1 Female age at maturity and pregnancy rate

We compared the age at maturity and pregnancy rates of female seals by period for seals harvested by 10 villages. We first examined female reproductive tracts 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, 1958a; Johnson et al., 1966; Smith, 1973). Evaluations were made by J. Burns during the historical period and by L. Quakenbush during the recent period. Seals that had never ovulated were classified as immature; seals that had ovulated at least once were classified as mature. We defined age at sexual maturity as the age at which the first ovulation occurred (McLaren, 1958a; Tikhomirov, 1966; Smith, 1973). Due to the delay between conception and implantation in pinnipeds (Harrison and Kooyman, 1968) pregnancy cannot be determined by the presence of a fetus between May and September. The presence of a corpora lutea indicates that the female ovulated and is likely to be pregnant, but whether or not the egg was fertilized cannot be confirmed visually during these months. Therefore, we considered all females with a corpora lutea that were harvested during May–September to be pregnant. Even though this method inflates the actual pregnancy rate, we have no reason to think the inflation would differ between periods; therefore, comparisons between periods are valid.

We then estimated the average age of maturity as the age at which 50% of females were mature. Each female seal of known age was classified as mature or immature (as described above) and average age of maturity for each period (historical: 1975–1984 and recent: 2003–2012) was estimated with a probit regression. A probit regression is a generalized linear model with a probit link function and a binomial error distribution (e.g., Trippel and Harvey, 1991), where seal age is the independent variable and maturity status is the dependent variable.   Like logistic regression, probit regression is designed to analyze data limited to two outcomes (i.e., binomial) and these two methods yield very similar parameter estimates. One advantage to fitting this model with a probit regression using SAS software (PROC PROBIT) is that the model directly estimates the average of the independent variable (i.e., age), with standard errors and confidence limits, that 50% of females were mature. A logistic regression typically only estimates the means and confidence limits of the dependent variable (i.e., proportion mature). The accuracy of estimating age at maturity is largely dependent upon how many seals are sampled within age classes that have some immature and some mature individuals (i.e., where the proportion of mature seals is greater than zero, but less than one (e.g., DeMaster, 1978). Within our sample, this was generally observed at 3–7 years of age for both ringed and bearded seals. After fitting a linear model for each period to estimate age at maturity, we assessed model fit using a log-likelihood chi-square test. Estimates of the average age at maturity for each period were statistically compared using the ratio test of Robertson *et al.* (2007) at the level of $p = 0.05$.

We defined pregnancy rate as the proportion of mature females that were pregnant. We estimated average pregnancy rates and evaluated differences between periods (historical: 1975–1984 and recent: 2003–2012) using a logistic regression model and SAS software (PROC

LOGISTIC). The logistic regression model analyzed how the probability that a mature seal was pregnant (1), versus not pregnant (0), differed by period.

2.4.2 Age distribution

If harvested seals are an unbiased sample of the population, the age distribution of the harvest should approximate that of the population. Therefore, we could expect that the proportion of pups (<1 year of age) harvested would be representative of their presence in the population and if pups were not being successfully weaned their presence in the harvest would decrease. We evaluated differences in the proportion of pups harvested during each period (historical: 1975–1984 and current: 2003–2012), for villages that sampled ≥50 seals during each period (four villages for ringed seals and three for bearded seals), using SAS software (PROC FREQ).

2.5 Sea ice comparison

We examined how sea ice concentration changed between periods within the Bering, Chukchi, and Beaufort seas to provide context for our examination of seal diet and indices of seal health. We used data from the Scenarios Network for Alaska and Arctic Planning, University of Alaska, Fairbanks, in the form of a Historical Sea Ice Atlas (http://seaiceatlas.snap.uaf.edu/, Scenarios Network for Alaska and Arctic Planning, 2014). These data are a compilation of data from many sources, integrated into a single gridded product with ¼ x ¼ degree spatial resolution. Satellite-derived sea ice data are only available since 1979, four years into the historical period (1975–1984). Sea ice data from 1975–1978 are interpolated from scanned ice charts and observations from the National Snow and Ice Data Center and the

U.S. Navy-National Oceanic and Atmospheric Administration Joint Ice Center Climatology. Data since 1979 were obtained from satellites, either from Scanning Multichannel Microwave Radiometer or Special Sensor Microwave/Imager sea ice concentration data available through the National Snow and Ice Data Center (http://nsidc.org/). We acquired sea ice data from monthly midpoints in May, representing the beginning of the annual sea ice retreat, and September, traditionally the month of minimum sea ice extent, for each year during the historical (1975–1984) and recent (2003–2012) periods. We then used the Spatial Analyst Tool in ArcMap 10.2 (ESRI Inc., Redlands, CA, USA, 2013) to calculate the mean sea ice concentration during each period for May and September. To determine whether the location of the sea ice edge changed between historic and recent periods for May and September we mapped the southern edge of the sea ice, which we defined as ≥10% ice concentration (Lowry et al., 2000), in each month for each period using the calculated monthly mean sea ice concentrations (Overland and Pease, 1982; Rigor et al., 2002; Rigor and Wallace, 2004; Ogi et al., 2008).

We also examined how changes in indices of seal health may be correlated with changes in sea ice. As an indicator of how much sea ice is present within a sampling year, we used the area with ≥50% sea ice concentration during May within the Bering Sea. Ice data was acquired from the Historical Sea Ice Atlas. Area covered by ≥50% concentration was calculated using the Spatial Analyst Tool in ArcMap 10.2. We then used linear regression to test for a correlation between the area with ≥50% sea ice concentration and the residuals from the final models of our analyses of body condition (blubber thickness) and growth (length), for ringed and bearded seal pups and seals ≥1 year of age. We also tested for a correlation between the area with ≥50% sea ice concentration and the proportion of ringed and bearded seal pups harvested. Models were fit using SAS software (PROC GLM). We considered correlations statistically significant at the level of $\alpha = 0.05$.

3 Results

3.1 Diet from stomach contents

Fish were commonly identified in the stomachs of ringed seal pups and seals ≥1 year of age during both periods (>67%, Tables 1 and 2). At Diomede, sample size was sufficient for only seals ≥1 year of age to be analyzed. There was no evidence that the overall percent frequency of occurrence (%FO) of fish differed between the periods for ringed seals ≥1 year of age from Shishmaref. However, the %FO of fish for pups from Shishmaref and seals ≥1 year of age from Diomede was higher during the recent period. Cod (F. Gadidae) were the most common fish prey taxa identified in stomachs of ringed seals of both age groups (Tables 1 and 2). There was a significant increase in %FO of Arctic cod for seals ≥1 year of age, from both Shishmaref and Diomede, during the recent period. However, the %FO of Arctic cod for pups from Shishmaref and the %FO of saffron cod (*Eleginus gracilis*) for both age groups remained relatively consistent between periods. Walleye pollock (*Gadus chalcogramma*) did not occur in seals ≥1 year of age from Diomede during the historical period but occurred at 35%FO during the recent period (Table 2). Similarly, rainbow smelt (*Osmerus mordax*) and Pacific herring (*Clupea pallasi*) rarely occurred in ringed seals near Shishmaref during the historical period; however, the %FO of rainbow smelt (for both age groups) and Pacific herring (for ≥1 year of age) increased during the recent period (Table 1).

Table 1. Percent frequency of occurrence (%FO$_i$) of prey identified in stomach contents of ringed seal pups and seals ≥1 year of age collected in Shishmaref, Alaska, during a historical (1975–1984) and recent (2003–2012) period. Prey items listed were consumed by ≥20% of at least one age group during one or both periods. Arrows indicate the trend in %FO between periods for each prey taxon and age group.

		Pups			**≥1 year of age**		
	Period	**Historical**	**Recent**		**Historical**	**Recent**	
Prey (*i*)	***n***	86	69		292	53	
All Fish		67.4	89.9*	↑	84.9	92.5	
All Cod (Gadidae)		61.6	72.5		71.2	77.4	
Arctic cod (*Boreogadus saida*)		24.4	36.2		21.9	49.1*	↑
Saffron cod (*Eleginus gracilis*)		58.1	58.0		64.4	73.6	
Rainbow smelt (*Osmerus mordax*)		0.0	31.9*	↑	1.4	47.2*	↑
Pacific herring (*Clupea pallasi*)		-	-		6.8	24.5*	↑
All Invertebrates		88.4	53.6*	↓	94.9	67.9*	↓
All Mysids		50.0	13.0*	↓	56.8	5.7*	↓
Neomysis rayii		37.2	13.0*	↓	50.0	3.8*	↓
All Amphipods		48.8	11.6*	↓	46.2	22.6*	↓
Gammarus sp.		33.7	0.0*	↓	27.1	11.3*	↓
Gammarus wilkitzkii		29.1	0.0*	↓	26.7	0.0*	↓
All Shrimp		73.3	26.1*	↓	88.0	60.4*	↓
Eualus gaimardii		23.3	0.0*	↓	34.9	0.0*	↓
Pandalus goniurus		33.7	1.4*	↓	41.4	1.9*	↓

Crangonidae	44.2	11.6*	↓	60.3	34.0*	↓
Crangon alaskensis	41.9	2.9*	↓	51.4	15.1*	↓
All Echiurids (Echiuridae)	-	-		21.9	9.4*	↓

* Significant difference in the occurrence of the prey item between periods within age group ($p < 0.05$).

Invertebrate prey items were commonly identified in the stomachs of ringed seals at both locations and during both periods (>54%, Tables 1 and 2). At Shishmaref, except for echiurids in pups, the %FO of all invertebrate taxa (including mysids, amphipods, and shrimp) decreased between periods (Table 1). In particular, the shrimp *Eualus gaimardii* and *Pandalus goniurus* occurred at 35% and 41%FO, respectively, for seals ≥1 year of age, during the historical period but at only <2%FO during the recent period (Table 1). At Diomede, the decrease in overall occurrence of invertebrates was not significant, although there were significant decreases in two species of shrimp (*Eualus gaimardii* and *Pandalus goniurus*) and amphipods overall, including the amphipods *Anonyx nugax* and *Themisto libellula* (Table 2). In particular, amphipods *Anonyx nugax* and *Themisto libellula* occurred at 50% and 32%FO, respectively, for seals ≥1 year of age during the historical period but were not detected during the recent period. Similarly, the shrimp *Eualus gaimardii* occurred at 64% for seals ≥1 year of age during the historical period but only at 18%FO during the recent period (Table 2).

Table 2. Percent frequency of occurrence (%FO_i) of prey identified in stomach contents of ringed seal seals ≥1 year of age collected in Diomede, Alaska, during a historical (1975–1984) and recent (2003–2012) period. Prey items listed were consumed by ≥20% of seals during one or both periods. Arrows indicate the trend in %FO between periods for each prey taxon.

		≥1 year of age		
	Period	**Historical**	**Recent**	
Prey (*i*)	***n***	22	17	
All Fish		68.2	94.1*	↑
All Cod (Gadidae)		40.9	94.1*	↑
Arctic cod (*Boreogadus saida*)		31.8	94.1*	↑
Walleye pollock (*Gadus chalcogramma*)		0.0	35.3*	↑
All Sculpins (Cottidae)		18.2	29.4	
All Invertebrates		90.9	76.5	
All Amphipods		77.3	17.6*	↓
Ampeliscidae		40.9	11.8*	↓
Anonyx nugax		50.0	0.0*	↓
Themisto libellula		31.8	0.0*	↓
All Shrimp		81.8	64.7	
Eualus gaimardii		63.6	17.6*	↓
Pandalus goniurus		40.9	17.6*	↓

* Significant difference in the occurrence of the prey item between periods within age group ($p < 0.05$).

Cod, sculpins, and flatfish were the fish taxa most commonly identified in the stomachs of bearded seals of both age groups. Sample sizes were sufficient for only pups in Shishmaref and only seals ≥1 year of age in Diomede to be analyzed. There was no evidence that the overall %FO of all fish or all sculpins differed between the periods for either age class or location (Table 3). The %FO of Arctic cod, pricklebacks, and flatfish increased for seals ≥1 year of age at Diomede, while saffron cod decreased for pups at Shishmaref. At Diomede, snailfish, pricklebacks, and flatfish did not occur in bearded seals ≥1 year of age during the historical period at all, however, during the recent period these fish taxa occurred at ≥20%FO (Table 3).

Table 3. Percent frequency of occurrence (%FO_i) of prey identified in stomach contents of bearded seal pups collected in Shishmaref, Alaska, and seals ≥1 year of age collected in Diomede, Alaska, during a historical (1975–1984) and recent (2003–2012) period. Prey items listed were consumed by ≥20% of at least one age group during one or both periods; <20% is indicated by a dash. Arrows indicate the trend in %FO between periods for each prey taxon and age group.

		Pups		**≥1 year of age**	
		Shishmaref		**Diomede**	
	Period	**Historical**	**Recent**	**Historical**	**Recent**
Prey (*i*)	***n***	42	31	18	40
All Fish		81.0	83.9	83.3	87.5
All Cod (Gadidae)		71.4	32.3* ↓	27.8	50.0
Arctic cod (*Boreogadus saida*)		-	-	22.2	50.0* ↑
Saffron cod (*Eleginus gracilis*)		71.4	19.4* ↓	-	-
All Sculpins (Cottoidea)		61.9	64.5	77.8	82.5
All Snailfish (Liparidae)		-	-	0.0	20.0
All Pricklebacks (Stichaeidae)		-	-	0.0	30.0* ↑
Slender eelblenny (*Lumpenus fabricii*)		-	-	0.0	20.0
All Flatfish (Pleuronectidae)		64.3	71.0	0.0	45.0* ↑
All Invertebrates		100.0	100.0	100.0	97.5
All Gastropods		9.5	35.5* ↑	38.9	37.5
Buccinum sp.		-	-	38.9	12.5* ↓
All Bivalves		11.9	45.2* ↑	50.0	57.5

Musculus sp.	-	-		33.3	0.0*	↓
Serripes sp.	-	-		33.3	2.5*	↓
All Cephalopods	-	-		44.4	20.0*	↓
Octopodidae	-	-		22.2	15.0	
Saduria entomon (Isopod)	57.1	6.5*	↓	-	-	
All Amphipods	-	-		38.9	10.0*	↓
Anonyx sp.	-	-		27.8	0.0*	↓
All Shrimp	95.2	93.5		83.3	65.0	
Eualus gaimardii	-	-		38.9	2.5*	↓
Pandalus sp.	-	-		61.1	17.5*	↓
Crangonidae	92.9	83.9		66.7	50.0	
Crangon alaskensis	81.0	48.4*	↓	-	-	
Sclerocrangon boreas	-	-		38.9	10.0*	↓
Argis lar	23.8	22.6		27.8	25.0	
All Crabs	54.8	54.8		83.3	82.5	
Pagurus sp.	23.8	0.0*	↓	38.9	0.0*	↓
Telmessus cheiragonus	28.6	16.1		-	-	
Hyas coarctatus	-	-		61.1	47.5	
Chionoecetes sp.	-	-		61.1	57.5	
Echiuridae	26.2	38.7		5.6	30.0*	↑
Polychaetes	-	-		27.8	37.5	

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* Significant difference in the occurrence of the prey item between periods within age group ($p <$ 0.05).

Invertebrates occurred at greater frequency in the diet of bearded seals (>98%) than fish (>81%) during both periods. Although the overall %FO of invertebrates did not differ between periods for either age group, the occurrence of 10 of 24 taxa declined for seals ≥1 year of age; only the occurrence of echiurid worms (F. Echiuridae) increased (Table 3). For bearded seal pups, the occurrence of all gastropods and all bivalves increased while an isopod, a shrimp, and a crab species decreased (Table 3). Changes in the occurrence of mollusks between periods, however, were different for each age group. For seals ≥1 year of age, the gastropod *Buccinum* sp., the bivalves *Musculus* sp. and *Serripes* sp., and all cephalopods occurred at lower %FO during the recent period (Table 3). Shrimp were a major invertebrate prey taxa identified in bearded seal stomachs of both age groups, locations, and periods (>65%) and although the overall %FO of all shrimp did not differ between periods for either age group or location, *Crangon alaskensis*, decreased for pups at Shishmaref. For seals ≥1 year of age, *Eualus gaimardii*, *Pandalus* sp., and *Sclerocrangon boreas* all occurred at a lower %FO during the recent period (Table 3). The overall %FO of crab did not differ between periods for either age group or location, however, *Pagurus* sp. was not identified in any bearded seal stomachs during the recent period and its %FO decreased (Table 3). The occurrence of the isopod *Saduria entomon* declined from 57 to 7%FO in pups. Amphipods had a lower %FO during the recent period in seals ≥1 year of age. Notably, the amphipod *Anonyx* sp. was not identified in any bearded seal stomachs during the recent period. The %FO of echiurid worms increased for seals ≥1 year of age during the recent period.

3.2 Morphometrics

3.2.1 Body condition

We compared sternal blubber thickness in 358 ringed seals ≥1 year of age and 126 pups. For ringed seals ≥1 year of age, month and period were significant predictors of blubber thickness ($p < 0.01$). Standard length, standard length squared, the interaction of standard length and age class, age class, and sex were all dropped from the model ($p > 0.05$). Average blubber thickness was lower in all months during the historical period (Fig. 2). Ringed seals ≥1 year of age had blubber that was 0.4 cm thinner during the historical period ($\bar{x}$ = 3.3 cm, 95% CL = 3.1–3.4 cm) than during the recent one ($\bar{x}$ = 3.7 cm, 95% CL = 3.4–4.0 cm; $p < 0.01$), after controlling for month (Fig. 2).

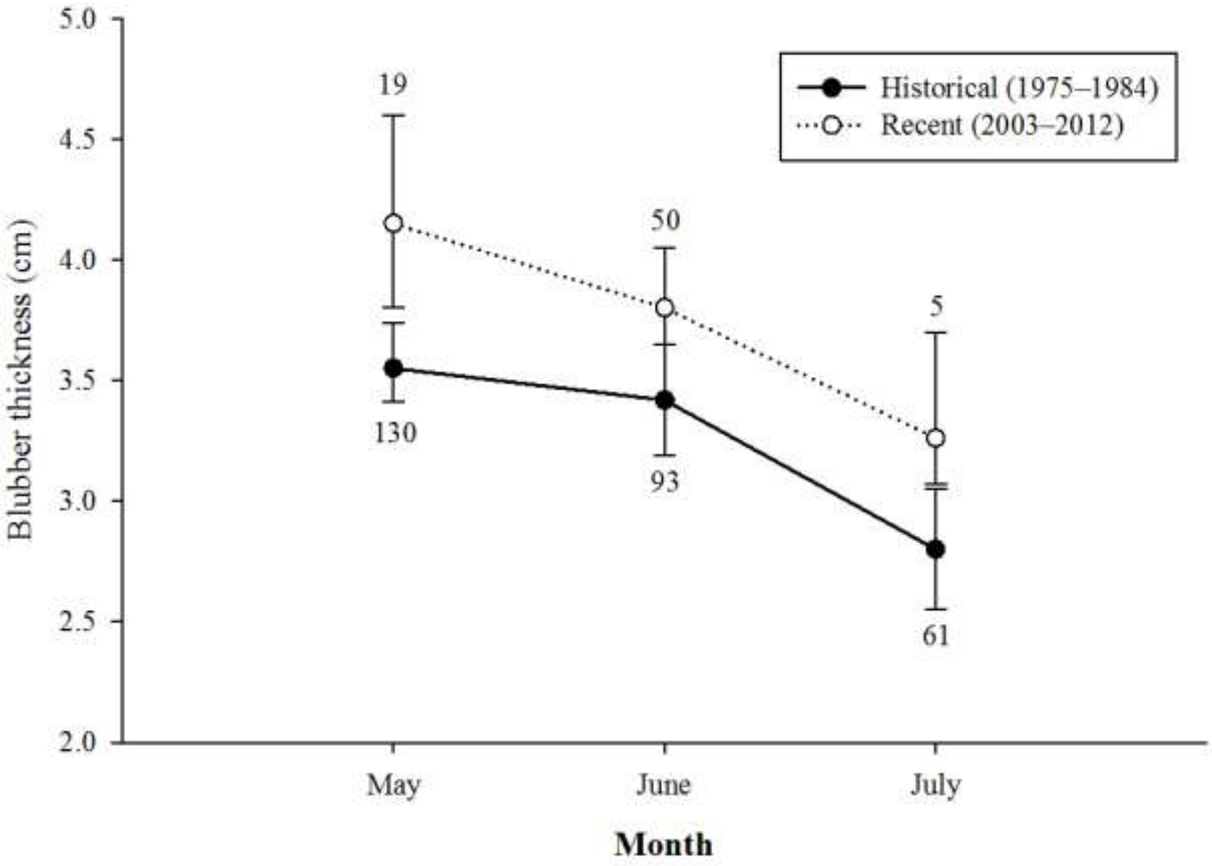

Figure 2. Average blubber thickness of ringed seals ≥1 year of age by month, measured over the sternum, during the historical (1975–1984) and recent (2003–2012) periods. Error bars represent

95% confidence intervals. Seasonal (spring-summer) mass loss is normal in ringed seals due in part to breeding and molting activities (Ryg et al., 1990b).

For ringed seal pups, both month and length were significant predictors of blubber thickness ($p < 0.01$). Average blubber thickness declined from 2.7 cm ($SE = 0.28$) in May to 1.9 cm ($SE = 0.80$) in July. Longer pups had thicker blubber, such that for every 10 cm increase in length, the blubber was 0.44 cm thicker ($SE = 0.10$). Blubber thickness did not differ between periods (historical: $\bar{x} = 2.4$ cm, 95% CL = 2.2–2.6 cm; recent: $\bar{x} = 2.2$ cm, 95% CL = 1.8–2.6 cm; $p = 0.65$), after controlling for month and length.

We compared sternal blubber thickness in 336 bearded seals ≥1 year of age and 120 pups. Month, length, and period were significant predictors of blubber thickness for bearded seals ≥1 year of age ($p < 0.01$). Average blubber thickness declined from 5.6 cm ($SE = 0.21$) in May to 4.4 cm in July ($SE = 0.63$) (Fig. 3). Longer seals had thicker blubber, such that for every 10 cm increase in length, the blubber was 0.08 cm thicker ($SE = 0.03$). After accounting for month and length, overall, bearded seals ≥1 year of age had on average 0.4 cm thinner blubber during the historical period ($\bar{x} = 4.7$ cm, 95% CL = 4.5–4.9 cm) than the recent one ($\bar{x} = 5.1$ cm, 95% CL = 4.9–5.3 cm; $p < 0.01$). While seals had thinner blubber during the historical period in June and July, they had thicker blubber in May (Fig. 3).

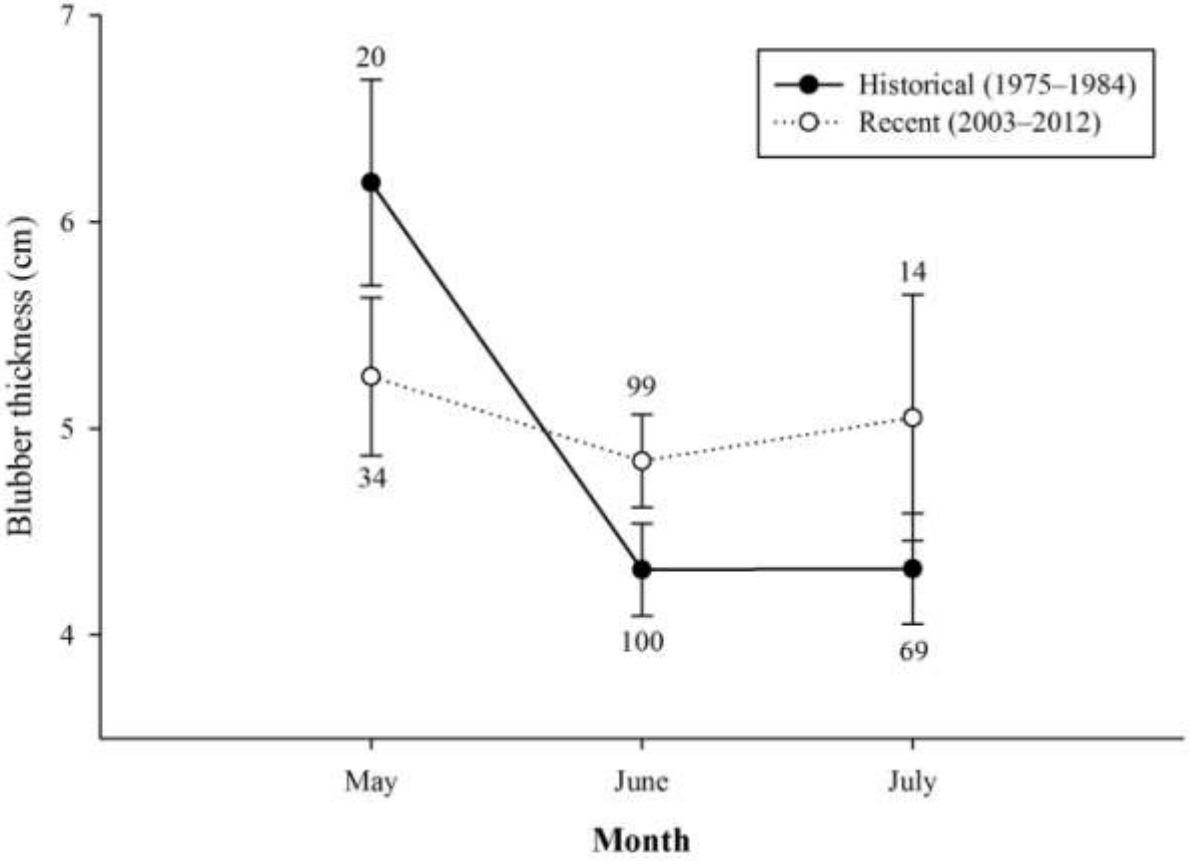

Figure 3. Average blubber thickness of bearded seals ≥1 year of age by month, measured over the sternum, during the historical (1975–1984) and recent (2003–2012) periods. Error bars represent 95% confidence intervals.

For bearded seal pups, month ($p < 0.01$) was a significant predictor of blubber thickness, but not length or period ($p > 0.05$). Average blubber thickness declined from 4.7 cm ($SE = 0.35$) in May to 3.2 cm ($SE = 0.28$) in July. Blubber thickness did not differ between periods (historical: $\bar{x} = 4.2$ cm, 95% CL = 3.9–4.5 cm; recent: $\bar{x} = 4.2$ cm, 95% CL = 3.8–4.6 cm; $p = 0.92$), after controlling for month.

3.2.2 Analysis of growth rates

Our analyses of standard length included 1,610 ringed seals ≥1 year of age and 587 pups. The birth year of seals ≥1 year of age ranged from 1951 to 2011 (Fig. 4) and the birth year of pups ranged from 1975 to 2012 (Fig. 5).

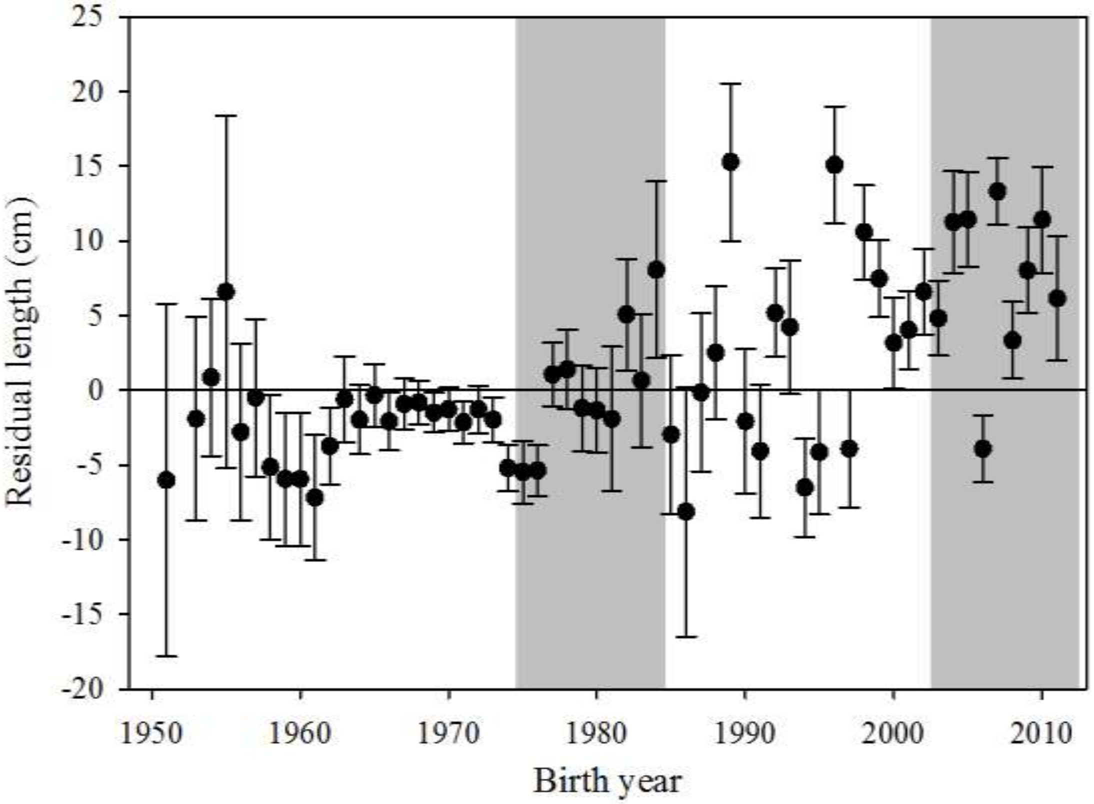

Figure 4. Residual growth of 1,610 ringed seals ≥1 year of age when harvested, plotted by birth year. Negative residuals indicate that seals were shorter than average, for their age. Error bars represent standard errors. Years shaded in gray represent the historical (1975–1984) and recent (2003–2012) periods.

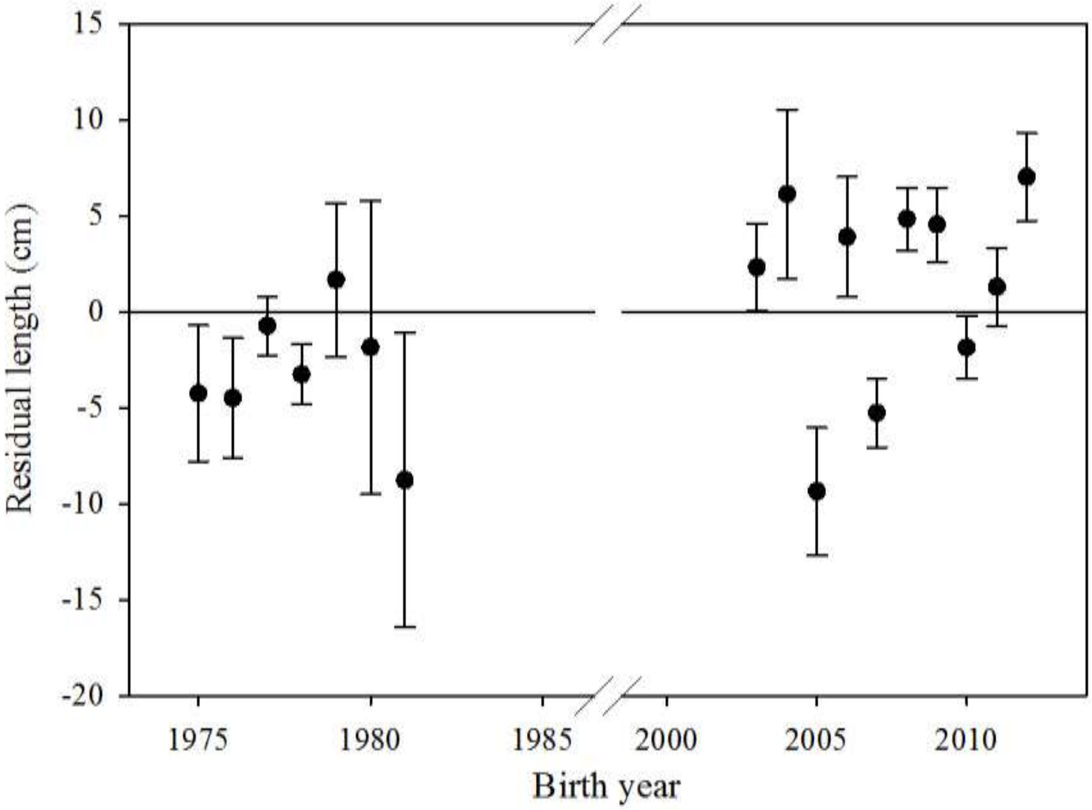

Figure 5. Residual growth of 587 ringed seal pups plotted by birth year. Negative residuals indicate that seals were shorter than average, given the month of harvest. Error bars represent standard errors.

For ringed seals ≥1 year of age, averaged residuals ranged from -8.1 cm in 1986 to 15.2 cm in 1989; both of which occurred between our periods of comparison (Fig. 4). In general, ringed seals born after 1998 tended to be larger (i.e., have positive residuals) than seals born before 1982. Specifically, ringed seals ≥1 year of age were 7.9 cm longer during the recent period ($\bar{x}$ = 115.9 cm, 95% CL = 114.5–117.3 cm; $p < 0.01$) than during the historical period ($\bar{x}$ = 108.0 cm, 95% CL = 107.0–108.9 cm) after controlling for the age of the seal. Compared to the overall time-series, the average residual growth of seals ≥1 year of age and born during the historical period was less (-1.2 cm, 95% CL = -3.7–1.2 cm) than for seals ≥1 year of age and born during the recent period (+7.3 cm, 95% CL = 3.1–11.5 cm; $p < 0.01$) (Fig. 4).

The averaged residuals for ringed seal pups ranged from -9.4 cm in 2005 to 7.0 in 2012 (Fig. 5). Six of 7 (86%) sample years had negative residuals between 1975 and 1984; whereas, 3 of 10 (30%) sample years had negative residuals between 2003 and 2012. Specifically, ringed seal pups were 8.0 cm shorter during the historical period ($\bar{x}$ = 82.7 cm, 95% CL = 79.5–85.8 cm) than during the recent one ($\bar{x}$ = 90.7 cm, 95% CL = 88.2–93.2 cm; $p < 0.01$), after controlling for the month the pup was harvested.

Our analyses of standard length included 422 bearded seals ≥1 year of age and 255 pups. The birth year of the seals ≥1 year of age ranged from 1955 to 2011 (Fig. 6) and the birth year of pups ranged from 1975 to 2012 (Fig. 7).

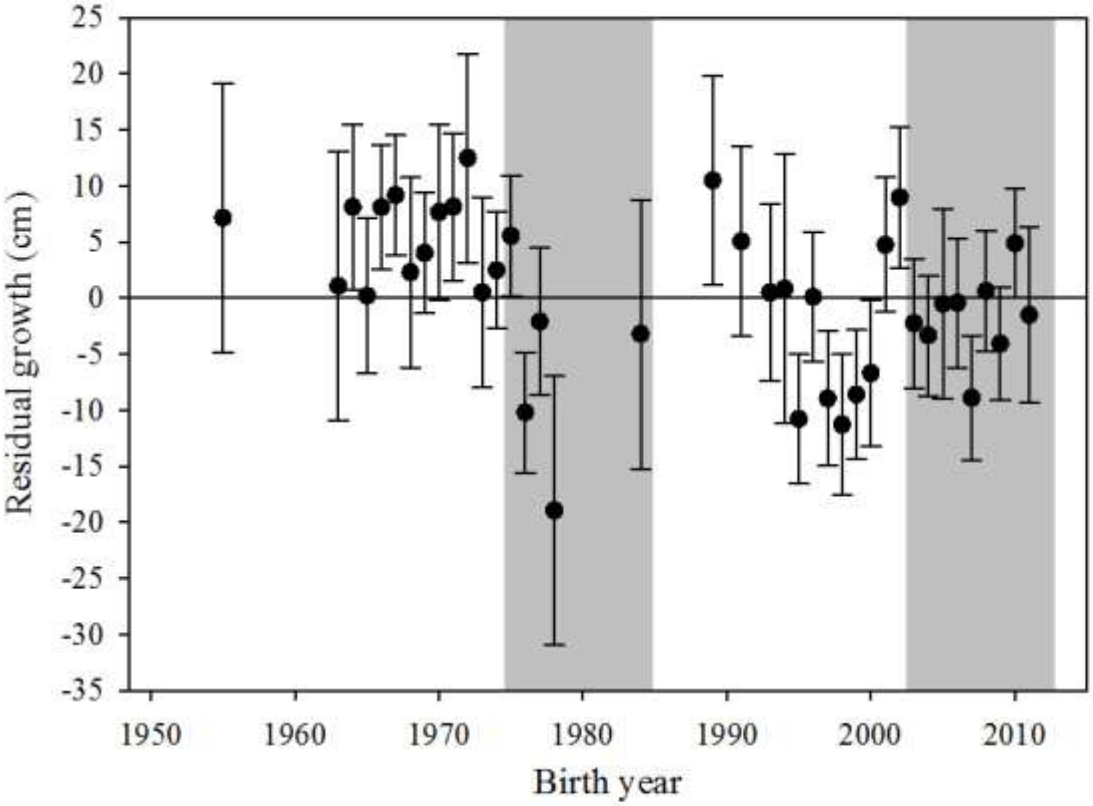

Figure 6. Residual growth of 422 bearded seals ≥1 year of age when harvested, plotted by birth year. Negative residuals indicate that seals were shorter than average, for their age. Error bars represent standard errors. Years shaded in gray represent the historical (1975–1984) and recent (2003–2012) periods.

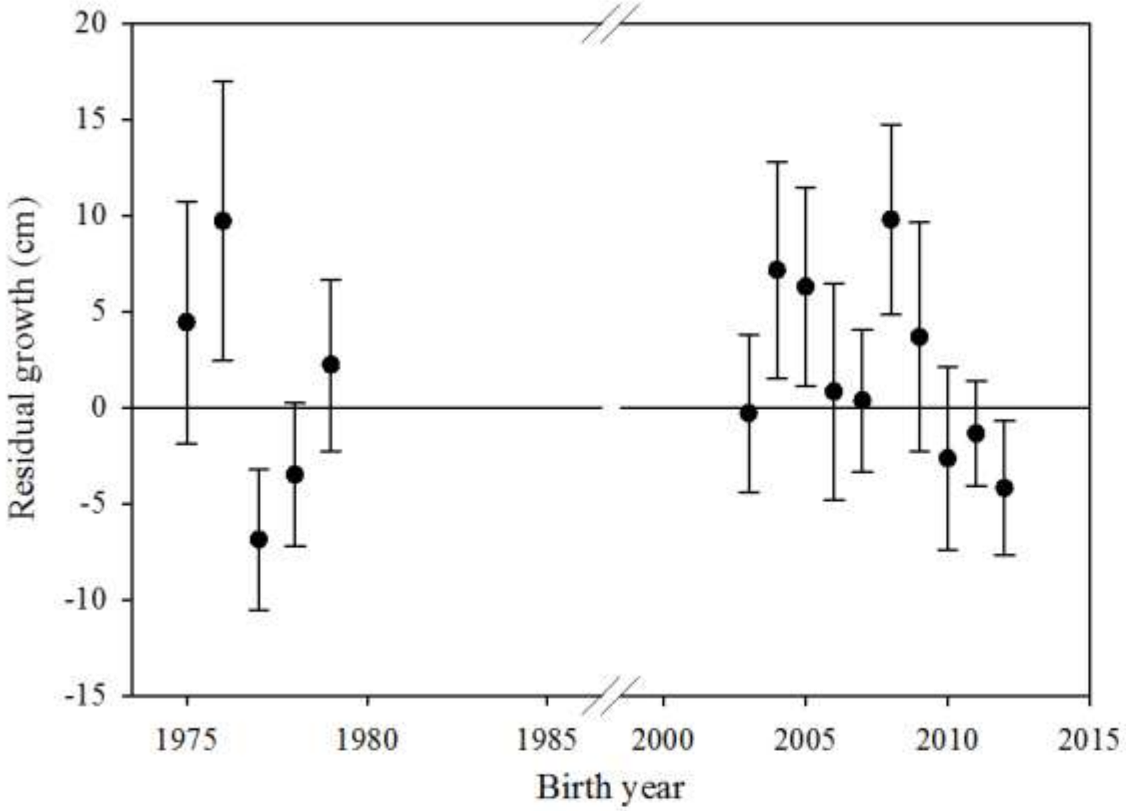

Figure 7. Residual growth of 255 bearded seal pups plotted by birth year. Negative residuals indicate that seals were shorter than average, given the month of harvest. Error bars represent standard errors.

For bearded seals ≥1 year of age, averaged residuals ranged from -19.0 cm in 1978 to 12.5 cm in 1972 (Fig. 6). In general, bearded seals born after the mid-1990s tended to be smaller (i.e., have negative residuals) than seals born in the 1960s and early 1970s. Specific to our periods of interest, bearded seals ≥1 year of age were 6.2 cm longer during the historical period ($\bar{x}$ = 202.4 cm, 95% CL = 198.9–205.8 cm) than the recent period ($\bar{x}$ = 196.2 cm, 95% CL = 193.2–199.2 cm; $p < 0.01$), after controlling for age. Compared to the overall time-series, however, the average residual growth of seals ≥1 year of age and born during the historical period was less (-6.3 cm, 95% CL = -10.9–-1.7 cm) than for seals ≥1 year of age and born during the recent period (+0.4 cm, 95% CL = -4.2–5.0 cm), but this difference was not significant (p = 0.07) (Fig. 6).

The averaged residuals for bearded seal pups ranged from -6.9 cm in 1977 to 9.8 in 2008 (Fig. 7). Two of 5 (40%) sample years had negative residuals between 1975 and 1984; and 4 of 10 (40%) sample years had negative residuals between 2003 and 2012, including the 3 most recent years (2010–2012). There was no evidence that the length of bearded seal pups differed between periods (historical: $\bar{x}$ = 145.3 cm, 95% CL = 139.6–150.9 cm; recent: $\bar{x}$ = 148.0 cm, 95% CL = 143.2–152.8 cm; p = 0.34), after controlling for the month the pup was harvested.

3.3 Population parameters

3.3.1 Female age at maturity and pregnancy rate

Of 757 female ringed seals analyzed for age at maturity, 223 from the historical period and 46 from the recent period were of ages where some seals were mature and some were immature (i.e., ages where the proportion of mature seals was greater than zero, but less than one). Probit regression models of the average age of maturity adequately fit the data for both periods ($p > 0.1$). Average age of maturity was ~2 years older during the historical period (6.0 years, 95% CL = 4.8–7.6) than the recent period (3.9 years, 95% CL = 3.1–5.0; $p < 0.05$).

During the historical period, reproductive tracts were collected from 559 female ringed seals; 257 (46.0%) were immature and 302 (54.0%) were mature (Table 4). Of the 302 mature females, 257 (85.1%, 95% CL = 80.6–88.7%) were pregnant when harvested. During the recent period, 198 reproductive tracts were collected; 130 (65.6%) were immature and 68 (34.3%) were mature. Of the 68 mature females, 53 (77.9%, 95% CL = 66.7–86.2%) were pregnant when harvested. There was no evidence that pregnancy rates differed between periods (p = 0.09).

Table 4. Reproductive information for ringed and bearded seals collected during a historical (1975–1984) and recent (2003–2012) period. Ovulation and pregnancy rates are based on the number of mature seals. Pregnancy rates were not significantly different ($p > 0.05$) between periods for either species.

	Mature (%)	**1 Ovulation (%)**	**>1 Ovulation (%)**	**Unknown no. of ovulations**	**Pregnant (%)**
Ringed seals					
Historical (*n*=559)	302 (54.0)	71 (23.5)	227 (75.2)	4	257 (85.1)
Recent (*n*=198)	68 (34.3)	23 (33.8)	29 (42.6)	16	53 (77.9)
Bearded seals					
Historical (*n*=303)	186 (61.4)	24 (12.9)	158 (84.9)	4	174 (93.5)
Recent (*n*=176)	111 (63.1)	16 (14.4)	89 (80.2)	6	107 (96.4)

Of 479 female bearded seals analyzed for age at maturity, 178 from the historical period and 71 from the recent period were of ages where some seals were mature and some were immature (i.e., ages where the proportion of mature seals was greater than zero, but less than one). Probit regression models of the average age of maturity adequately fit the data for both periods ($p > 0.1$). Average age of maturity was ~1.6 years older during the historical period (4.2 years, 95% CL = 3.3–5.4) than the recent period (2.6 years, 95% CL = 2.0–3.2; $p < 0.05$).

During the historical period, reproductive tracts were collected from 303 female bearded seals; 117 (38.6%) were immature and 186 (61.4%) were mature (Table 4). Of the 186 mature females, 174 (93.5%, 95% CL = 89.1–96.3%) were pregnant when harvested. During the recent period, 176 reproductive tracts were collected; 65 (36.9%) were immature and 111 (63.1%) were mature. Of the 111 mature females, 107 (96.4%, 95% CL = 91.1–98.6%) were pregnant when harvested. There was no evidence that pregnancy rates were different between periods (p = 0.48).

3.3.2 Age distribution

We analyzed age-at-harvest for 2,003 ringed seals in the historical period and 1,056 in the recent period. Villages where ≥50 ringed seals were sampled during both periods included Diomede, Gambell, Shishmaref, and Hooper Bay. A smaller proportion of pups were identified in the historical period ($\bar{x}$ = 14.8%, 95% CL = 13.3–16.4%) than the recent period ($\bar{x}$ = 51.1%, 95% CL = 48.1–54.2%; $p < 0.01$) (Table 5). During the historical period, seals were only sampled near these villages in five of the 10 years (1975–1979). None of those five years had larger pup proportions than the study average (27.4% pups), whereas, during the recent period, all 10 years (100%) had a larger proportion of pups than the study average (Fig. 8). This pattern was consistent within villages; each village harvested at least 25.7% (range: 25.7–55.4%) more pups during the recent than historical period (Table 5). Pup proportions were smallest in 1976 (5.9%, n = 524) during the Bering Sea regime shift (Ebbesmeyer et al., 1990; Miller et al., 1994) and largest in 2007 (72.0%, n = 82) and 2006 (63.8%, n = 47) (Fig. 8).

Table 5. The proportion of ringed and bearded seal pups harvested during the historical (1975–1984) and recent (2003–2012) periods. Villages listed harvested a minimum of 50 seals during each period. Pooled values include only data from the villages listed.

	Historical		**Recent**	
	Total seals harvested	**% Pups**	**Total seals harvested**	**% Pups**
Ringed				
Diomede	135	1.5*	181	56.9*
Gambell	79	41.8*	123	67.5*
Shishmaref	1,007	22.1*	616	49.5*
Hooper Bay	782	5.1*	136	36.0*
Pooled	2,003	14.9*	1,056	51.1*
Bearded				
Diomede	65	20.0*	140	37.9*
Gambell	160	41.9*	82	58.5*
Shishmaref	428	20.3*	264	54.9*
Pooled	653	25.6*	486	50.6*

* Significant difference in the proportion of pups harvested between periods ($p < 0.05$).

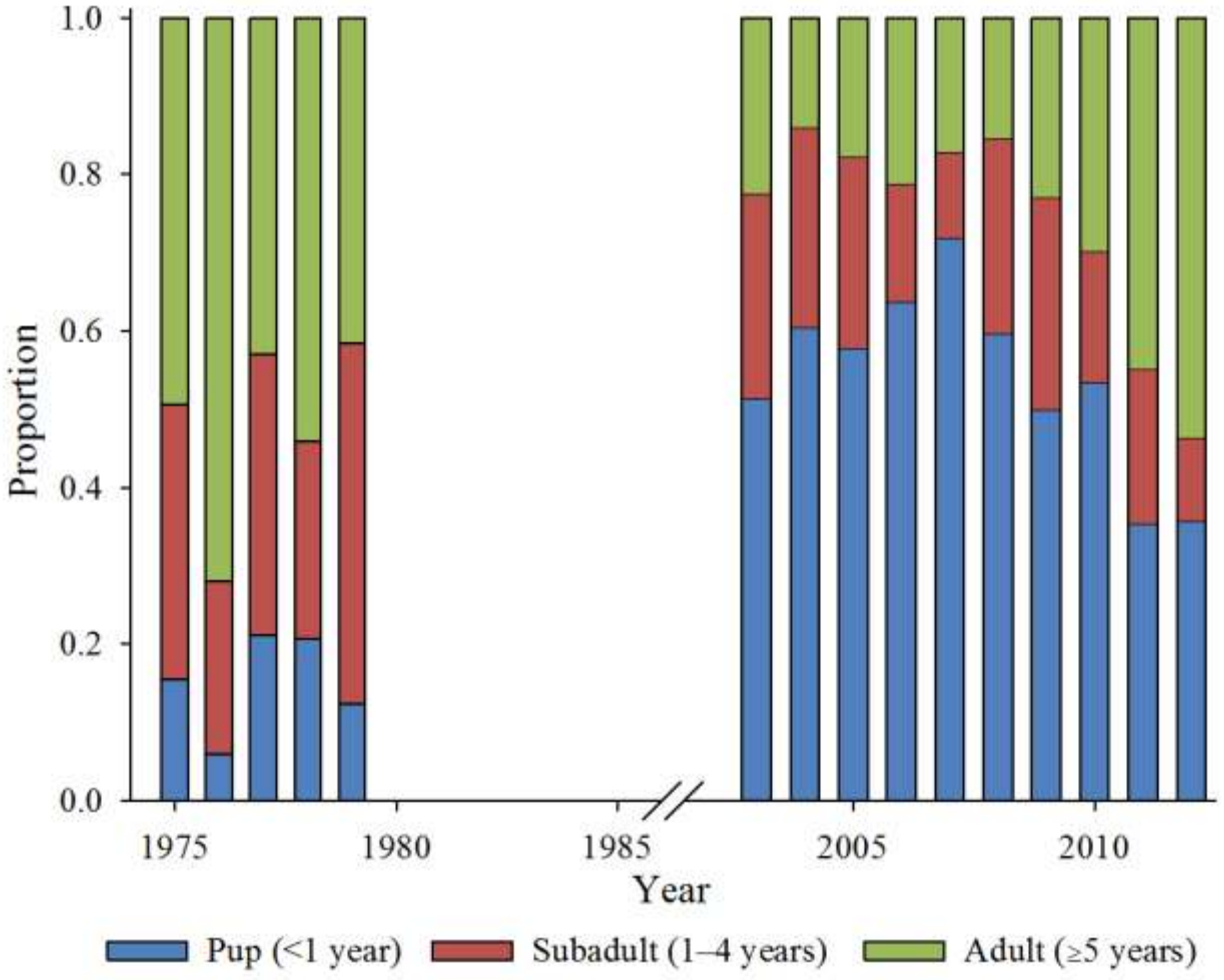

Figure 8. Proportion of ringed seals by age class harvested near Diomede, Gambell, Shishmaref, and Hooper Bay, Alaska, during the historical (1975–1984) and recent (2003–2012) periods. During the historical period, no seals were sampled from these villages from 1980 to 1984.

We analyzed age-at-harvest for 653 bearded seals harvested in the historical period and 486 in the recent period. Villages where ≥50 bearded seals were sampled during both periods included Diomede, Gambell, and Shishmaref. A smaller proportion of pups were identified in the historical period ($\bar{x}$ = 25.6%, 95% CL = 22.2–28.9%) than the recent period ($\bar{x}$ = 50.6%, 95%

CL = 46.3–55.1%; p = 0.01) (Table 5). During the historical period, seals were only sampled near these villages in five of the 10 years (1975–1979) and only 1979 (41.4%) had larger pup proportions than the study average (36.4% pups) whereas, during the recent period, 8 of 10 years (80%) had a larger proportion of pups than the study average (Fig. 9). This pattern was consistent within villages; each village harvested at least 16.7% (range: 16.7–34.6%) more pups during the recent than historical period (Table 5). Pup proportions were smallest in 1975 (15.9%, n = 145) and largest in 2010 (69.6%, n = 23) and 2011 (68.0%, n = 75) (Fig. 9).

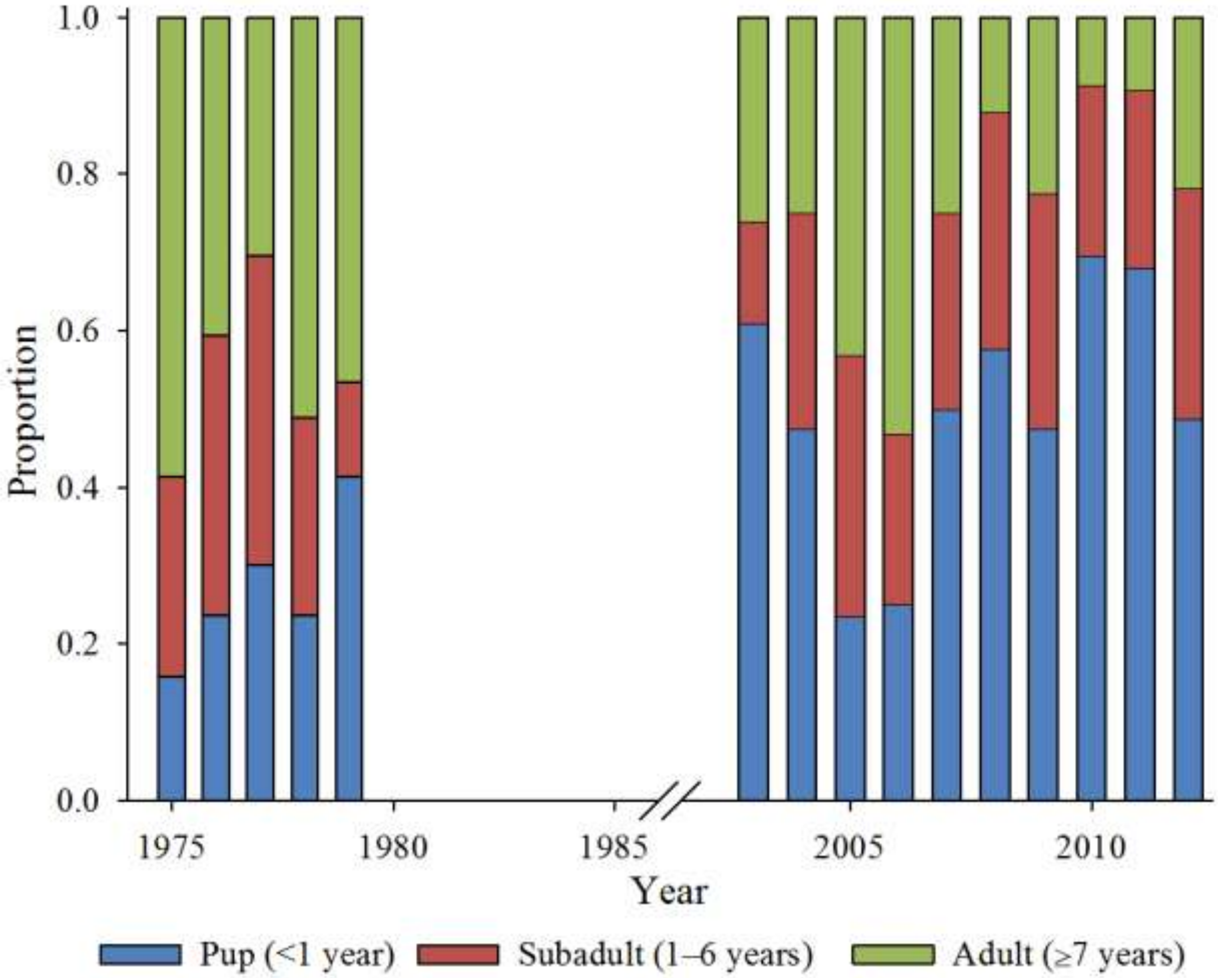

Figure 9. Proportion of bearded seals by age class harvested near Diomede, Gambell, and Shishmaref, Alaska, during the historical (1975–1984) and recent (2003–2012) periods. During the historical period, no seals were sampled from these villages from 1980 to 1984.

3.4 Sea ice comparison

The southern edge of sea ice, defined as ≥10% ice concentration (Lowry et al., 2000), shifted north during the recent period for both May and September. During spring, the mean May ice edge was 30–250 km farther north in the Bering Sea (Fig. 10). However, the extent of the sea ice in May was highly variable by year with extensive overlap between the two periods. During summer, the mean September ice edge was 475–650 km farther north, having shifted from the central Chukchi Sea into the Beaufort Sea (Fig. 10). Although the ranges of mean monthly ice edge estimates for each period still overlap in September, the overlap is minimal. The northern-most ice edge of the historical period only overlaps the southern-most ice edge of the recent period in the eastern Beaufort Sea.

For ringed seals, two of five indices of seal health were negatively correlated with the area of ≥50% sea ice concentration within the Bering Sea in May. The growth of ringed seals ≥1 year of age (Pearson's r = -0.23, $p < 0.01$, Fig. 11) and the proportion of ringed seal pups in the harvest (Pearson's r = -0.47, $p < 0.05$, Fig. 12) both decreased when the area of sea ice increased. Although the blubber thickness of seals ≥1 year of age (Pearson's r = -0.07, $p = 0.49$) and pups (Pearson's r = -0.23, $p = 0.13$) were both negatively correlated with sea ice area, indicating blubber thickness was thinner when there was more sea ice, these correlations were not statistically significant. The growth of pups (Pearson's r = 0.02, $p = 0.78$), however, increased slightly when the area of sea ice increased.

For bearded seals, there were no statistically significant correlations between area with ≥50% sea ice concentration within the Bering Sea in May and indices of seal health; although, four of five correlations were negative. Specifically, as the area of sea ice increased the growth of bearded seals ≥1 year of age (Pearson's r = -0.02, *p* = 0.89), the growth of pups (Pearson's r = -0.05, *p* = 0.59), blubber thickness of pups (Pearson's r = -0.08, *p* = 0.55), and proportion of bearded seal pups in the harvest (Pearson's r = -0.04, *p* = 0.88) decreased slightly, while blubber thickness of seals ≥1 year of age (Pearson's r = 0.10, *p* = 0.26) increased slightly.

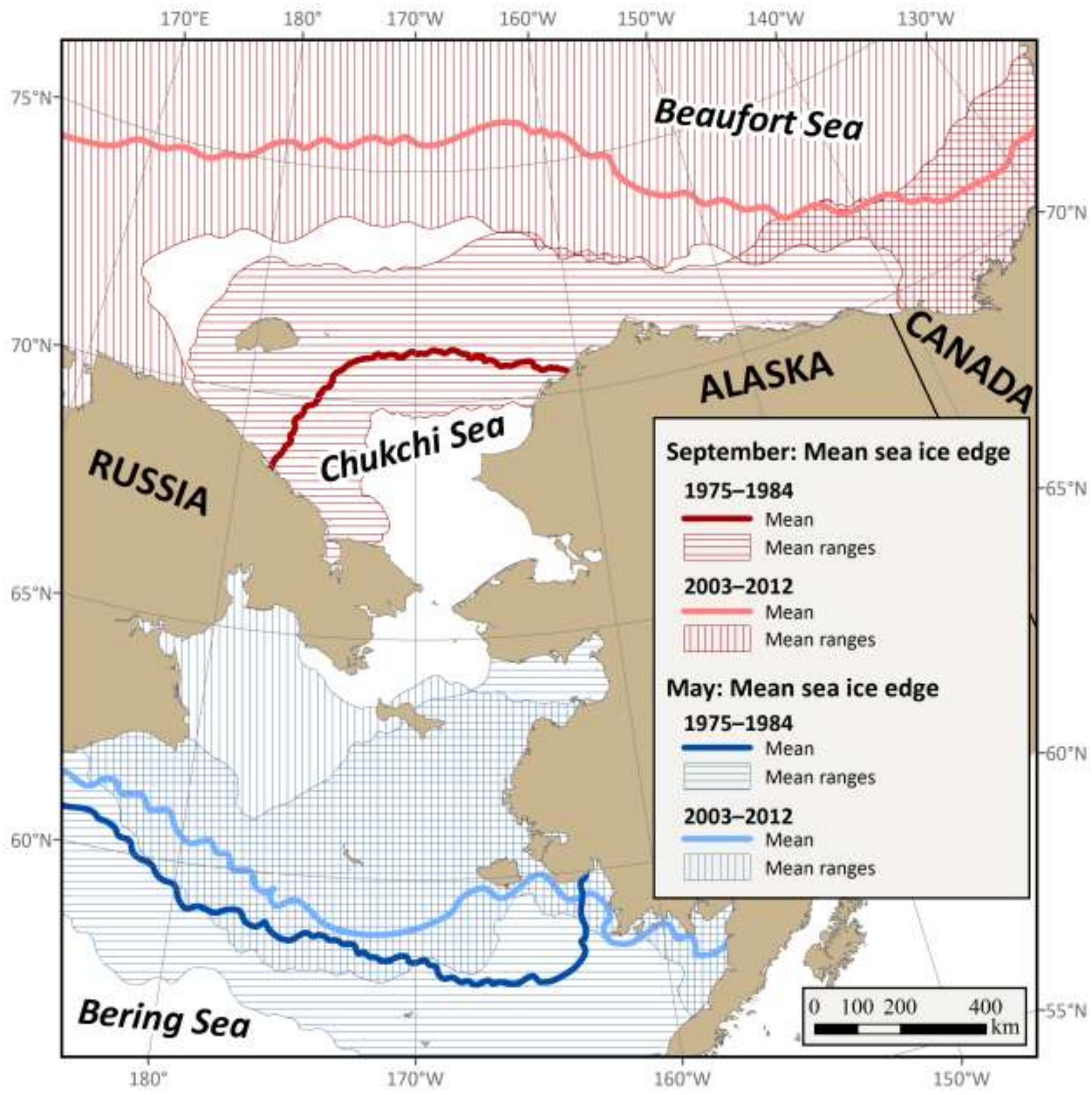

Figure 10. Mean monthly sea ice edges (10% concentration) for May and September during the historical (1975–1984) and recent (2003–2012) periods. Mean ranges represent the range in monthly means for each period (i.e., the southern-most and northern-most monthly mean during each period). Overlap of monthly ranges between periods is represented by both vertical and horizontal thatching.

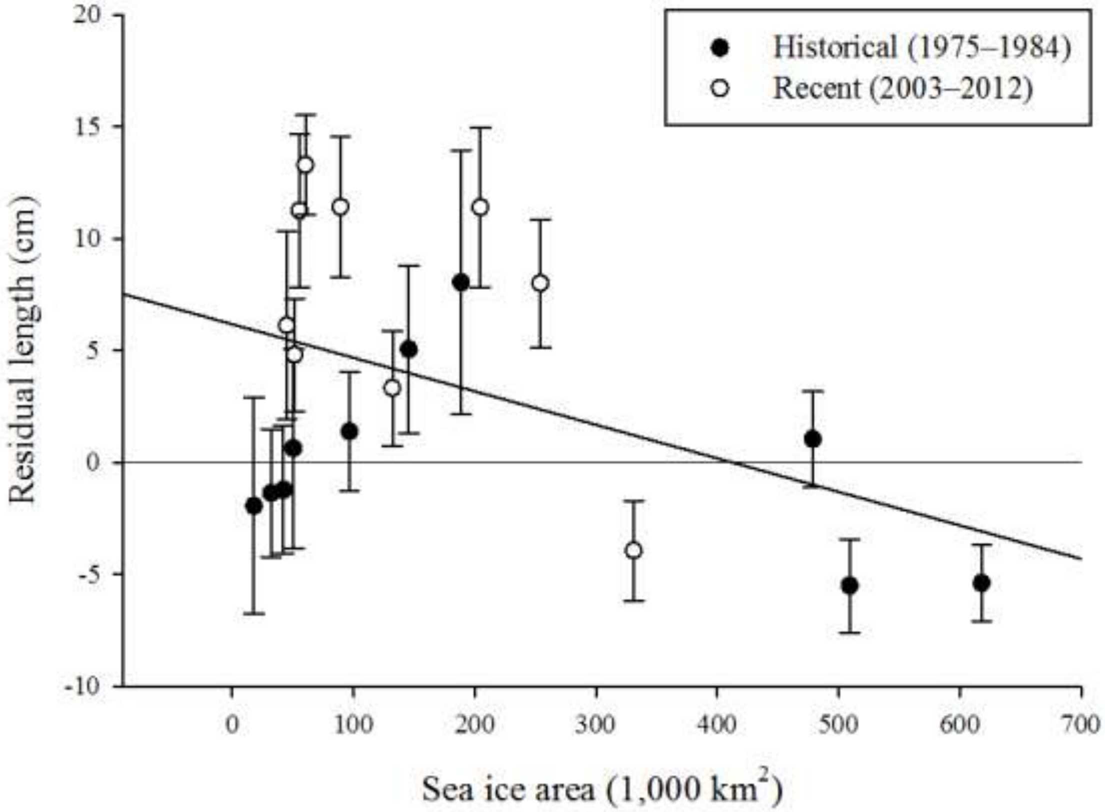

Figure 11. Correlation between the area with ≥50% sea ice concentration in the Bering Sea for May and residual growth of 353 ringed seals ≥1 year of age born during the historical (1975–1984) and recent (2003–2012) periods (Pearson's r = -0.23, $p < 0.01$).

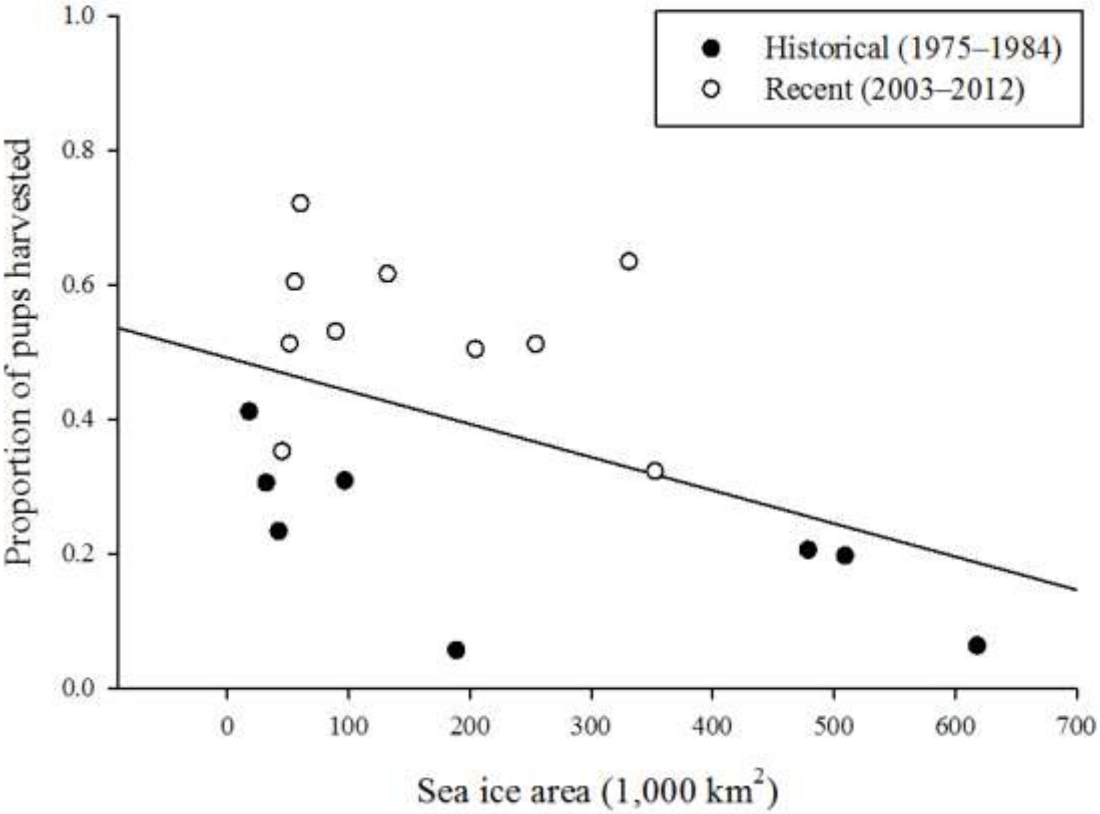

Figure 12. Correlation between the area with ≥50% sea ice concentration in the Bering Sea for May and the proportion of ringed seal pups harvested during the historical (1975–1984) and recent (2003–2012) periods (Pearson's r = -0.47, $p < 0.05$).

4 Discussion

4.1 Limits to inference

There are substantial limitations regarding how we describe seal diet. We know that an examination of stomach contents only reflects recent diet. In general, stomach content analysis represents diet over the prior 6–24 hours (Murie and Lavigne, 1986). Stomach content analysis also tends to underestimate soft prey that are digested quickly and overestimate prey with chitinous structures (e.g., cephalopod beaks and crustaceans) and fish otoliths that withstand digestion (Rae, 1973; Hyslop, 1980; Tollit et al., 2010). There were also changes to the methods between periods that warrant discussion. In the historical period, stomachs were injected with 10% buffered formalin to preserve contents prior to sorting and identification, while during the recent period stomachs were preserved by freezing. Otoliths stored in formalin for long periods (>150 days) can begin to deteriorate (McMahon and Tash, 1979), possibly making them more difficult to identify and, therefore, could cause lower %FOs during the historical period. This may be especially important for small otoliths from herring, smelt, snailfish, pricklebacks, sculpins, and flatfish. For invertebrates, preserving the contents in formalin is not known to alter the chitinous parts used for identification differently than freezing (Lincoln and Sheals, 1979).

Despite differences in methods, there is no reason to expect differences in how prey was digested between periods or that large changes in the frequency of occurrence of prey items, such as observing more fish in the diet of ringed seals, would not reflect changes in what seals consume. With that said, diet is a reflection of availability and preference, thus consumption of preferred prey may be disproportionate with its availability. In effect, dietary preference may mask changes in the abundance of prey items. As such, inferences into how diet relates to the availability or abundance of prey must be made with caution and linking changes in diet to climate change will require careful interpretation.

There are also limits to how our metrics of body condition, growth, and reproduction relate to population trend or abundance. While poor body condition or growth is indicative of nutritional stress and reduced reproduction eventually leads to reduced abundance, there is no easily definable relationship between these indices and population trend or abundance. In fact, if these indices are density dependent, we may document increasing body condition, growth, or reproductive rate when population abundance is low (Fowler, 1981; Svensson et al., 2011).

However, most population stressors, such as low food availability or heavy ice, are expected to cause declines in the survival of pups (detectable as a decline in the proportion of pups harvested), depressed growth rates, less blubber, an increase in age at maturity, a decline in pregnancy rate, or a combination thereof. As such, while we may be able to construct a scenario where multiple metrics of population status are increasing while the population is declining, such a scenario is not likely.

The interpretation of the proportion of pups in the harvest as an index of weaning success deserves special mention. Although finding pups in the harvest indicates that pups survived the weaning period to be harvested, the proportion of pups in the harvest may vary due to factors unrelated to how many pups are present in the population. A larger proportion of pups in the harvest could occur because there are fewer adult and subadults. If pups become easier to hunt or if hunters change their preferences, the number of pups harvested changes independent of the number present in the population. Although we do not know for certain that hunter behavior has been consistent, we have no evidence to suggest that hunter preference has changed over time and hunter survey data indicate that although hunters may prefer seals of certain sexes, ages, or sizes, they typically harvest seals as they are available (Quakenbush et al., 2011a; Quakenbush et al., 2011b). Regardless of what biases may be present in the proportion of pups in the harvest, the index has value because it will detect large shifts in pup survival. Pups must survive weaning to be harvested and shifts in the proportion of pups are worthy of investigation.

4.2 Ringed seals

4.2.1 Diet of ringed seals

As seasonally ice-covered oceans warm, pelagic organisms are generally expected to increase in abundance, while benthic organisms are expected to decline (Grebmeier et al., 2006b;

Coyle et al., 2007; Bluhm and Gradinger, 2008; Matsuno et al., 2011; Grebmeier, 2012; Cooper et al., 2013). Water masses also have specific fish assemblages (e.g., Barber et al., 1997; Norcross et al., 2010; Eisner et al., 2013). For example, Arctic cod are almost exclusively found in colder waters (e.g., Wyllie-Echeverria and Wooster, 1998; Norcross et al., 2010) while saffron cod are more likely to be found in warmer coastal waters (Mecklenburg et al., 2002; Norcross et al., 2010). As such, we expect that Arctic cod might be displaced by species associated with relatively warmer-water, such as saffron cod, rainbow smelt, Pacific sand lance, or capelin (Grebmeier et al., 2006b; Mueter and Litzow, 2008; Mueter et al., 2009).

The %FO of Arctic cod, however, increased for ringed seals ≥1 year of age from both Shishmaref and Diomede while the %FO of saffron cod remained consistent between periods. Juvenile Arctic cod (<60 mm) often associate with sea ice in surface waters (Eisner et al., 2013) and move into deeper water as they grow and larger (age 1+) fish are demersal (Frost and Lowry, 1981; Rand and Logerwell, 2011). Arctic cod are typically the most common demersal fish found in the central and northern Chukchi Sea (e.g., Frost and Lowry, 1983; Barber et al., 1997; Mueter et al., 2013; Norcross et al., 2013) and a recent comparison between the surveys of Barber et al. (1997) and data collected during 2012–2013 found no obvious trends in the abundance or distribution of Chukchi fishes (Mueter et al., 2013). However, data are limited for where we collected seal stomachs in the Bering Strait region (i.e., Diomede and Shishmaref). Eisner et al. (2013) found few Arctic or saffron cod near Diomede in mid-water trawls, however, we expect that ringed seals will forage on larger Arctic cod near the seafloor and saffron cod might be consumed near-shore. Norcross et al. (2010) found no Arctic and few saffron cod in bottom trawls near Diomede, but these trawls targeted juvenile and larval fish, not adults. To our knowledge, no trawls have been conducted near Shishmaref. Regardless, ringed seals harvested near Diomede and Shishmaref have access to both Arctic and saffron cod and we suspect it may be premature to assume that, in the future, marine mammals will no longer have access to Arctic cod as sea ice recedes (Cheung et al., 2008).

Both ringed seal pups and seals ≥1 year of age consumed a larger proportion of rainbow smelt near Shishmaref during the recent period. Rainbow smelt were absent from the diet of pups and almost absent from the diet of older seals (1.4%) during the historical period. Smelt are anadromous and travel up coastal rivers to spawn in summer, their range includes the Bering, Chukchi, and Beaufort seas (e.g., Thedinga et al., 2013). Although their distribution while at sea is largely unknown, they are generally considered to be a coastal species. Also during the recent period, ringed seals ≥1 year of age consumed a larger proportion of Pacific herring near Shishmaref and walleye pollock near Diomede. Pacific herring are generally pelagic and are distributed in nearshore waters of the Bering, Chukchi, and Beaufort seas, spawning in late spring in coastal waters (Wespestad and Barton, 1979). Walleye pollock are subarctic, semidemersal fishes that occupy a variety of habitats within the relatively warm waters (1 to 10°C) of the Bering Sea (Hunt et al., 2002; Mueter and Litzow, 2008; Bacheler et al., 2010). Abundance trends of Pacific herring and walleye pollock are cyclic in the eastern Bering Sea (Livingston, 1993; Hunt et al., 2002) but abundances may be increasing farther north in higher salinity water masses of the Chukchi Sea (Eisner et al., 2013) and warming nearshore waters, especially during spawning, making them available to ringed seals during the recent period.

The change in diet we observed does not represent a simple transition from cold water to warm water species. Perhaps this is to be expected. Warming of the southern Bering Sea shelf allowed the northward expansion of warm water species (e.g., Wyllie-Echeverria and Wooster, 1998; Mueter and Litzow, 2008; Spencer, 2008) and many assumed this trend would continue northwards. The northern limit of temperate Bering Sea fishes is governed by the ‘cold pool’, a mass of water <2° C, which forms under winter sea ice (Wyllie-Echeverria and Wooster, 1998; Mueter and Litzow, 2008). While the cold pool shifts northwards in warmer years (e.g., Wyllie-Echeverria and Wooster, 1998), winter sea ice continues to form in the northern Bering Sea and, even in warm years, the cold pool exists south of St. Lawrence Island. Based upon these observations, Stabeno et al. (2012) concluded that while the ecosystem in the northern Bering Sea will change, the change is not likely to be a simple northward shift of temperate fish taxa.

We observed an increase in the %FO of both fish associated with cold water (e.g., Arctic cod) and those associated with warmer and/or nearshore waters (e.g., rainbow smelt and Pacific herring). Perhaps this is because nearshore waters are warming more quickly than offshore and/or deeper waters. Interestingly, the occurrence of many species of pelagic invertebrates in ringed seal stomachs declined between periods (Tables 1 and 2). This pattern may indicate that the pelagic invertebrates ringed seals consumed are less common recently. Alternatively, pelagic fish may simply be more available and therefore consumed by more seals than invertebrate prey.

4.2.2 Growth, body condition, and reproductive rates of ringed seals

Regardless of the reason why ringed seal diet has shifted to include more fish and fewer invertebrates, ringed seals have apparently benefitted. Ringed seals (seals ≥1 year of age and pups) grew faster and were longer, given their age, during the recent period. Growth was more variable for ringed seals born after 1980, especially for seals ≥1 year of age (Fig. 4). Because inconsistencies in measurements could be responsible for the larger variability in recent years, we compared the measurement error of seals sampled by biologists in one community, Point

Hope, Alaska, against that of seals sampled by trained hunters and samplers from all other communities and found no differences in variability. It is also unlikely that mean growth rates would be consistently higher due to sampling error.

We found that heavy ice years negatively affect ringed seals, a result that largely agrees with studies from western Canada (Stirling et al., 1977; Smith, 1987; Stirling, 2002; Harwood et al., 2012b). In east Amundsen Gulf and west Prince Albert Sound, Canada, poorer body condition of adults and subadults was correlated with later spring break-up of shorefast ice (Harwood et al., 2012b). However, this relationship was only statistically significant for subadults. In the most extreme years, when break-up was latest, fewer adult females ovulated (Harwood et al., 2000; Harwood et al., 2012b). In the eastern Beaufort Sea, late break-up was also correlated with a smaller proportion of pups in the harvest (Harwood et al., 2012b). We did not specifically analyze ovulation rates as a function of sea ice, however, in our study, pregnancy rates did not change between periods and low ice concentration was correlated with a higher proportion of pups in the harvest (Fig. 12). We found that blubber thickness of ringed seals ≥ 1 year of age increased between the historical (higher ice concentration) and recent (lower ice concentration) periods (Fig. 2) and that ringed seals ≥ 1 year of age grew longer in years with low ice concentration (Fig. 11). The main difference between our findings and those from western Canada is that Harwood et al. (2012b) has documented a long-term decline in the body condition of ringed seals in the eastern Beaufort Sea, whereas we found the body condition of ringed seals increased in the Bering and Chukchi seas.

Studies of ringed seals in Hudson Bay, Canada, also found that in colder years with higher ice concentrations seals have lower pregnancy rates and fewer pups occur in the population (Holst et al., 1999; Ferguson et al., 2005; Stirling, 2005). In Hudson Bay, the 1990s were characterized by high ice concentrations while the 2000s were characterized by less ice. Ringed seals in Hudson Bay grew faster during the 2000s than in the 1990s and age of maturation decreased from 5.4 to 3.8 years of age (Chambellant et al., 2012). We observed a similar relationship with sea ice; the age of maturation declined from 4.2 to 2.6 years between the historical period with more sea ice and the recent period with less sea ice.

Cold years and heavy ice likely result in lower growth and productivity of seals for a variety of reasons. During cold years, sea ice retreats late in spring and forms early in fall, shortening the open water season. This is expected to result in less primary productivity, fewer zooplankton, and poorer feeding conditions for both fish and seals (Stirling et al., 1977). Seals may also have difficulty maintain breathing holes in thicker sea ice (Stirling et al., 1977). A longer ice-covered season may also expose pups to polar bear predation longer (Stirling et al., 1977; Stirling et al., 1982; Smith, 1987; Harwood et al., 2012b). Low growth rates in 1975 and 1976 (Figs. 4 and 5) likely correspond with cold years prior to the regime shift that occurred in the Bering Sea around 1977 (Stirling et al., 1977; Smith, 1987; Ebbesmeyer et al., 1990; Miller et al., 1994). Recently, however, sea ice conditions have been characterized by earlier sea ice retreat and later sea ice formation, especially since the mid-1990s (Comiso et al., 2008). Years with relatively less ice may favor higher primary production (Grebmeier et al., 2006a) and therefore larger abundances of pelagic prey, as well as make maintenance of breathing holes easier.

Although cold years and heavy ice result in reduced growth and body condition of ringed seals, current concerns about ringed seals relative to climate change are focused on the possibility there might not be enough ice to use as a platform for breeding, pupping, and molting, or that snow cover will be inadequate for the construction and maintenance of birth lairs (Kelly et al., 2010; U.S. Federal Register, 2012a). While years with high ice concentrations result in decreased growth, body condition, and the proportion of pups in the harvest (e.g., This study; Ferguson et al., 2005; Stirling, 2005; Chambellant et al., 2012; Harwood et al., 2012b), not having enough snow cover or sea ice is expected to primarily lower pup recruitment (Ferguson et al., 2005). In Hudson Bay, ringed seal recruitment was lower than average in the 1970s, higher in the 1980s, and lower again in the 1990s. Prior to the 1990s, low recruitment was associated with years of high ice concentrations and later ice break-up; however, in the 1990s, low recruitment was associated with low snowfall (Ferguson et al., 2005). During the recent period, we observed an above average proportion of pups in the harvest (Table 5). Presumably, the proportion of pups in the harvest will decline when/if snow or sea ice becomes insufficient. Interestingly, while the residual growth of ringed seals increased as the area of sea ice decreased (Fig. 11), the trend begins to reverse as the area of sea ice approaches zero. In Figure 11, note how the three left-most values of growth, associated with a small area of sea ice in the Bering Sea, are associated with growth that is well below average. While there is not enough data to draw any conclusions, this suggests there might be an optimal amount of spring ice for ice seals. This makes sense as we expect too much ice to have negative effects on the population, yet the ringed seals clearly use sea ice for resting, pupping, and molting. Chambellant et al. (2012) observed similar quadratic patterns between the proportion of pups in the harvest and snow depth, and between body condition and break-up date (See Fig. 6 in Chambellant et al., 2012), suggesting that having a break-up date that is too early or too late may be unfavorable. Likewise, having too little or too much snow may also be unfavorable (See Fig. 6 in Chambellant et al., 2012).

The relationship between ringed seals and polar bears (*Ursus maritimus*), which predominantly prey on ringed seals (Stirling and Archibald, 1977), also deserves mention. Body condition and recruitment of polar bears in the southeastern Beaufort Sea declined in the mid-1970s in conjunction with heavy ice conditions and a major decline in number and productivity of ringed and bearded seals (Stirling et al., 1977). Recent declines in body condition and productivity of polar bears in this same area are perhaps due to the recent declines in productivity of ringed seals in the Canadian Beaufort Sea (Harwood et al., 2012b) and/or major changes in sea ice (Stirling et al., 2008). In contrast, body condition and recruitment of polar bears in the Chukchi Sea have not declined (Rode et al., 2014), which is consistent with our results that body condition and productivity for ringed seals have not declined in the Bering and Chukchi seas. In the same region, bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort (BCB) stock have also shown improving body condition over time. Interestingly, body condition of BCB bowhead whales appears to increase as spring ice concentration in the Canadian Beaufort Sea decreases (George et al., *this issue*).

4.3 Bearded seals

4.3.1 Diet of bearded seals

In general, dietary shifts were smaller for bearded seals than for ringed seals and did not show consistent patterns. Fish and invertebrates, overall, were found at similar frequencies over time for both pups and seals ≥1 year of age. During the recent period, saffron cod occurred at a lower %FO for bearded seal pups near Shishmaref and Arctic cod occurred at a higher %FO for seals ≥1 year of age near Diomede (Table 3). Arctic cod generally were not detected in the stomachs of bearded seal pups, suggesting that pups either feed differently or in different locations than adults. Because adult saffron cod generally occur in warmer, often inshore waters (Mecklenburg et al., 2002), than Arctic cod, the difference between age classes may be due to sampling pups from an inshore area (Shishmaref) and seals ≥1 year of age from an island area, closer to deeper cooler water (Diomede). However, Arctic cod were detected in ringed seals near Shishmaref (Table 1). While the occurrence of fish in bearded seal stomachs may be an indicator of environmental change, it might not substantially impact seal condition. In the late 1970s, fish comprised only 7–11% of stomach volume near Shishmaref, suggesting fish are not a large component of bearded seal diet (Lowry et al., 1980a).

Bearded seals ≥1 year of age also consumed a number of species in the recent period that were rare or absent in the historical period (i.e., snailfish; pricklebacks, including slender eelblenny; and flatfish). Data from bottom trawls were limited near Shishmaref and Diomede and were highly variable and difficult to interpret relative to changes we identified in bearded seal diet (Barber et al., 1997; Norcross et al., 2010; Mueter et al., 2013). We do not think that increases in the detection of some fish in the recent period are a result of changes in our ability to identify otoliths to a lower taxonomic level because many of these fish species were also identified during the historical period (e.g., flatfish for pups at Shishmaref). Rather, changes in diet likely reflect changes in prey abundance.

The diet of bearded seal pups and seals ≥1 year of age showed different trends with respect to specific invertebrates (Table 3). Opposing trends could occur because prey communities are changing differently near Shishmaref, where pups were sampled, and near Diomede, where seals ≥1 year of age are sampled. Alternatively, differences in how pups feed could account for opposing trends. For bearded seals ≥1 year of age, the %FO of 10 invertebrate prey groups (including benthic invertebrates) declined from the historical to the recent period;

only echiurids increased. However, for pups, the %FO of three invertebrate prey groups decreased and two increased between periods. For bearded seals ≥1 year of age, mollusks, including the gastropod *Buccinum* sp., the bivalves *Musculus* sp. and *Serripes* sp., and cephalopods occurred at lower %FO during the recent period, however, for pups, the general categories of gastropods and bivalves occurred at a higher %FO. Benthic sampling conducted in the Chukchi Sea during the 2000s suggests that some gastropods may be declining (Feder et al., 2005; Bluhm et al., 2009). While bivalves overall do not show signs of decline (Grebmeier et al., 2006a; Feder et al., 2007; Grebmeier, 2012), the mollusks we found in bearded seal diet (*Buccinum, Musculus, Serripes*) were not common taxa identified in the southeastern Chukchi Sea.

In colder waters where sea ice lasts longer, zooplankton consume fewer phytoplankton during the spring bloom, leading to a more direct transfer of organic carbon to the benthos (Bluhm and Gradinger, 2008). This leads to a tight coupling between the pelagic primary production and deposition to the benthos (i.e., “pelagic-benthic” coupling), which supports a rich benthic food web in the northern Bering and Chukchi seas (e.g., Grebmeier et al., 2006a). As a result of ocean warming and earlier ice retreat, the northern Bering and Chukchi seas are expected to shift from benthic-dominated systems to a more pelagic system (Grebmeier et al., 2006a; Bluhm and Gradinger, 2008), as occurs on the southern Bering Sea shelf. With respect to bearded seals, as well as walruses, such a shift has been predicted (Grebmeier et al., 2006a; Kovacs et al., 2011) to result in a diet containing less benthic and more pelagic prey.

However, we did not observe a consistent shift in bearded seal diets from benthic to pelagic prey. This might be because the predicted environmental change has yet to occur or is of a different nature than predicted. The breakdown of strong pelagic-benthic coupling and a shift towards a more pelagic system is based upon the assumption that we know how primary production is linked to benthic productivity. This may be incorrect; recently, Arrigo et al. (2012) found massive phytoplankton blooms, extending >100 km under the sea ice in the Chukchi Sea (Arrigo et al., 2012). These phytoplankton blooms were 10 fold greater than previously thought to exist. Light transmission, necessary for the bloom, was enhanced by the recent increase in thinner first-year ice and by a high incidence of melt ponds (Frey et al., 2011). Blooms of the magnitude observed by Arrigo et al. (2012) would likely overwhelm the pelagic system and enhance benthic production (Lowry et al., 2014). As such, the prediction that northern Bering and Chukchi seas will shift from favoring benthic organisms to favoring pelagic organisms as the oceans warm may be too simplistic.

4.3.2 Growth, body condition, and reproductive rates of bearded seals

Bearded seals do not appear to be responding to environmental change in the same manner as ringed seals. While growth of bearded seals ≥1 year of age was slower during the recent period it was similar to the long-term average of the entire time series and the residual growth of seals born within our periods did not differ ($p = 0.07$). Bearded seals ≥1 year of age had thicker blubber recently. The growth of bearded seal pups did not change between the historical and recent periods; however there are relatively few sample years in the historical period (Fig. 7). Blubber thickness in bearded seal pups did not change between periods. Pregnancy rates did not differ between periods for bearded seals; however, the age at maturity for bearded seals decreased by 1.6 years, from 4.2 to 2.6 years of age, and is considerably younger than for bearded seals in eastern Canadian Arctic (6 years old, McLaren, 1958b), near Svalbard, Norway (5 years old, Andersen et al., 1999), and seals in the Sea of Okhotsk and western Bering Sea (5 years old, Tikhomirov, 1966). However, the age of maturity (5 years) observed by Tikhomirov (1966) was for seals collected from 1959 to 1962 and is similar to the age of maturity we saw in the historical period (4.2 years). The young age at maturity we observed during the recent period in the eastern Bering and Chukchi seas suggests that conditions are not currently limiting and female bearded seals are in a positive nutritional state.

We also found a larger proportion of bearded seal pups in the subsistence harvest during the recent period. Previous studies of the age distribution of harvested bearded seals (Burns and Frost, 1979) determined the proportion of pups harvested was significantly higher at more southerly villages on the Bering and Chukchi sea coasts. However, we did not see such a pattern (Table 5). Although bearded seal pups are born and nurse on top of the broken pack ice (Burns, 1967), can swim soon after birth (Krylov et al., 1964), and nurse for only 12–18 days before weaning (Burns, 1967), the disappearance of sea ice prior to weaning was predicted to decrease the survival of bearded seal pups (U.S. Federal Register, 2012b). However, we found no evidence to indicate that bearded seal pups are not surviving weaning. Again, while this index is not expected to be sensitive enough to detect small changes in pup survival, there are clearly no large declines in how pups survive to be harvested.

4.4 Conclusions

Ringed and bearded seals in Alaska do not appear to be negatively affected by current environmental conditions, possibly because sea ice and snow coverage are still adequate, there may be a lag time from when changes in ice and snow conditions affect population health and seal abundances, or seals may be more resilient than predicted. Because ringed seals forage primarily upon pelagic and semi-demersal species of fish and invertebrates, a warming ocean is expected to provide more prey (Hunt et al., 2002; Mueter and Litzow, 2008; Wassmann, 2011). As foraging generalists, changes in prey availability are less likely to be detrimental for ringed seals and changes observed to date have not caused declines in the indices of seal health we studied. Likewise, polar bears in the Chukchi Sea (Rode et al., 2014) and bowhead whales in the BCB stock (George et al., *this issue*) have increasing or stable reproductive rates and body conditions. This contrasts with declines of ringed seal body condition and reproduction in the eastern Beaufort Sea (e.g., Harwood et al., 2012b) and Hudson Bay (e.g., Chambellant et al., 2012), where polar bears also exhibit declining body condition and/or reproduction (Stirling et al., 1982; Cherry et al., 2009; Regehr et al., 2010; Rode et al., 2010). While indices of bearded seal health did not improve as consistently as with ringed seals in the recent period, there is little evidence to suggest that the population is currently declining in the Bering or Chukchi seas.

Warming waters and an earlier sea ice melt was predicted to allow the expansion of sub-Arctic fishes into the Arctic and an earlier ice melt was predicted to delay the phytoplankton bloom and favor pelagic prey over benthic prey (Grebmeier et al., 2006b; Coyle et al., 2007; Bluhm and Gradinger, 2008; Matsuno et al., 2011; Grebmeier, 2012; Cooper et al., 2013). However, recent studies (Arrigo et al., 2012; Stabeno et al., 2012; Lowry et al., 2014) underscore that while the Arctic food web may be simple with regards to those at lower latitudes, it is still too complex to precisely predict how marine organisms will respond to a changing environment, especially for predators that eat numerous species, such as ice seals.

As upper trophic level marine predators, ice seals are potential indicators of change in the Arctic marine ecosystem where sampling is difficult and expensive (Harwood et al., *this issue*). Examining both ringed and bearded seals allows us to gain insight into the state of both pelagic and benthic systems. Although ringed and bearded seals have not exhibited the declines in body condition, growth, or reproduction observed in other populations, the Arctic is undergoing a period of rapid change. As such, continued biosampling of the subsistence harvest is important for detecting shifts in the population status of ringed and bearded seals and for understanding the mechanisms that link changes in sea ice and/or prey communities to those populations.

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