

TRENDS IN AGE STRUCTURE AND PRODUCTIVITY OF PACIFIC WALRUSES HARVESTED IN THE BERING STRAIT REGION OF ALASKA, 1952–2002

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ABSTRACT

Pacific walruses (*Odobenus rosmarus divergens*) are harvested by subsistence hunters in Alaska as they migrate north through the Bering Strait in the spring. Harvest records and biological specimens have been collected from the Bering Strait communities of Little Diomedea, Gambell, and Savoonga since the 1950s. Harvest levels in the Bering Strait region peaked in the late 1980s and declined thereafter; however, there was considerable variation in the size and composition of the harvests among communities and over time. The relationships among characteristics of the community harvests and the presence of temporal trends were investigated using generalized linear models. The proportion of females in the catch increased over time in all three communities, while the proportion pregnant among harvested females declined over the range of sample years. The ages of harvested walruses increased over time in all three communities through the 1980s, after which trends in age stabilized or began to decline. The age of first reproduction was significantly older for females sampled in 1975–1985 than for females sampled between 1952 and 1962 or 1992 and 1998. Factors thought to have influenced the size and composition of the catch over the past 50 yr include hunter preferences, harvest management regimes, environmental conditions, and changes in the population itself.

Key words: Pacific walrus, *Odobenus rosmarus divergens*, harvest, age structure, productivity.

The Pacific walrus (*Odobenus rosmarus divergens*) ranges across the shallow continental shelf waters of the Bering and Chukchi seas between the United States and Russia. Although the cultural and economic importance of walruses to subsistence hunters in Alaska and Chukotka is well recognized (Brooks 1953, Ray 1975), the status of the Pacific walrus population is poorly known.

Walruses have an intrinsically low rate of reproduction and, therefore, are limited in their capacity to respond to exploitation (Fay 1982). In the late 19th century, American whalers intensively harvested walruses in the northern Bering and southern Chukchi seas. Between 1869 and 1879, catches averaged more than 10,000 per year (Bockstoce and Botkin 1982), with many more animals struck and lost (Fay and Bowlby 1994). The population was substantially depleted by the end of the century (Fay *et al.* 1989b) and the industry collapsed in the early 1900s (Bockstoce and Botkin 1982). Since 1930, the combined walrus harvests of the United States and Russia have ranged from 2,300 to 9,500 animals per year (Fig. 1). Notable harvest peaks occurred during 1930–1960 (4,500–9,500 per year) and in the 1980s (5,000–9,000 per year). These harvest levels were thought to be of sufficient scale to result in subsequent population declines (Fay *et al.* 1989b, 1997; Fay and Bowlby 1994). Commercial hunting continued in Russia until 1991 under a quota system of up to 3,000 animals per year (Garlich-Miller and Pungowiyi 1999).

Since 1992, the harvest of Pacific walruses has been limited to the subsistence catch of coastal communities in Alaska and Chukotka. Harvest levels through the 1990s ranged from approximately 2,400 to 4,700 animals per year (Fig. 1).

The size of the Pacific walrus population has never been known with any degree of precision. Fay *et al.* (1997) reviewed the results of aerial surveys conducted between 1960 and 1985 and concluded that the population had increased from 50,000 to 100,000 animals in the late 1950s to more than 250,000 animals by 1985. The authors attributed this population growth to hunting restrictions enacted in both the United States and Russia in the early 1960s that greatly reduced the size of the harvest and provided protection to females and calves. Based on evidence of changes in walrus distributions, condition indices, and life-history parameters, Fay *et al.* (1989b, 1997) postulated that the Pacific walrus population was approaching, or had already exceeded, the carrying capacity of its environment by the early 1980s. Noting a significant increase in United States and Russian harvest levels in the 1980s, there was concern that the combination of density-dependent regulatory mechanisms and high harvest levels could result in a precipitous population decline (Fay *et al.* 1989b, 1997). Information concerning population size and trend after 1985 is less certain. An aerial survey flown in 1990 produced a population estimate of 201,039 animals; however, large confidence intervals associated with this estimate preclude conclusions concerning population trend (Gilbert *et al.* 1992, Hills and Gilbert 1994). Efforts to survey the Pacific walrus population were suspended after 1990 due to unresolved problems with survey methods that produced population estimates with unacceptably large confidence intervals (Gilbert 1999). The current status and trend of the population are unknown.

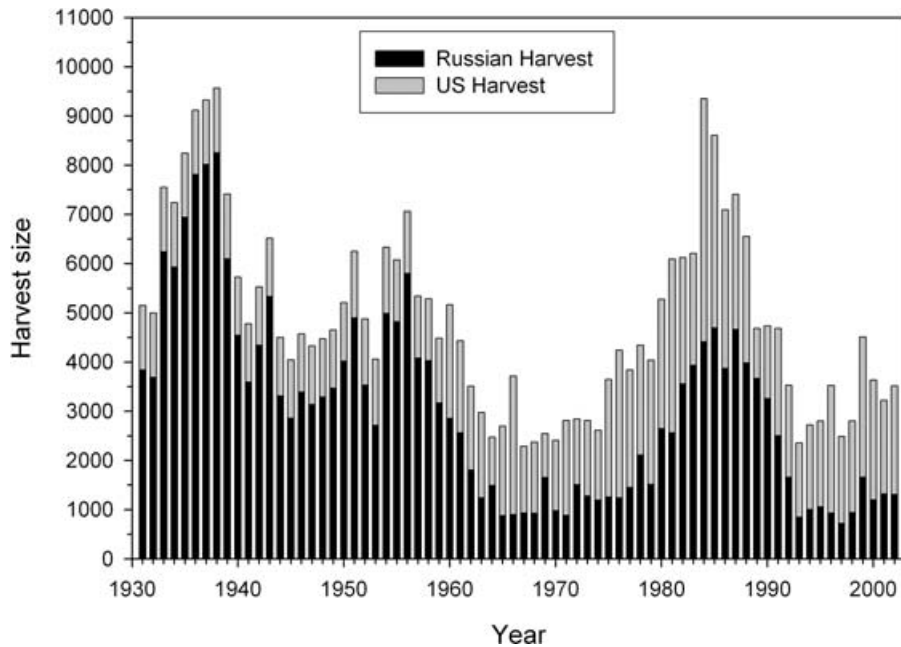


Figure 1. Annual harvest levels of Pacific walrus in the United States and Russia, 1931–2002. Harvest data for 1931–1989 compiled by Fay and Bowlby (1994). Harvest data for 1990–2002 from the U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503.

Harvest records and biological samples have been collected from walrus harvested in the Bering Strait region of Alaska since the early 1950s. The communities of Little Diomed (Diomed) on Little Diomed Island, and Gambell and Savoonga on St. Lawrence Island (Fig. 2) have the longest and best-kept harvest records. Fay and Bowlby (1994) estimated that these three communities account for approximately 80% of the annual walrus harvest in Alaska.

The objectives of this study were to standardize and report harvest statistics and life-history information collected in association with subsistence walrus harvests in the Bering Strait region of Alaska over the past 50 yr, and to investigate whether changes in the age structure, sex ratio, and productivity of harvested walrus had occurred. Factors thought to have influenced the size and composition of the catch over this time frame are also examined.

METHODS

Data Collection and Sample Analysis

Harvest data and biological samples were collected in association with spring (April–May and sometimes June) walrus harvests at Diomed, Gambell, and Savoonga between 1952 and 2002. Data sets for our analyses were compiled from a variety of published and unpublished sources (Appendices 1–3).

There was no official walrus harvest monitoring program in Alaska in the 1950s; however, Brooks (1954) and Fay (1955) opportunistically collected biological



Figure 2. Bering Strait region, showing locations of walrus hunting communities where harvest data and biological samples were collected.

specimens from walrus harvested in the Bering Strait region. In 1960, the Alaska Department of Fish Game initiated a walrus harvest monitoring program (WHMP) at Diomedé, Gambell, and Savoonga. The program was transferred to the U.S. Fish and Wildlife Service (USFWS) in 1980, and has been jointly administered by the USFWS and the Eskimo Walrus Commission since 1992.

WHMP monitors typically arrived in the communities in early April, prior to the onset of walrus hunting, and remained in the communities until all sea-ice, and associated walrus, had retreated beyond the range of hunters. The monitors met boats as they returned from walrus hunting trips to collect biological samples and harvest information. An attempt was made to identify and record the gender and age class of all walrus retrieved during the monitoring period. Gender and age class were determined based upon body and tusk morphology (Fay 1982, Stephensen *et al.* 1994). Walrus hunters also provided samples of teeth (usually the two lower canines) and female reproductive tracts (uterus and ovaries) from harvested walrus. Teeth were cleaned of blood and connective tissue and stored dry. Reproductive tracts were stored frozen, or in 10% buffered formalin.

Teeth were processed for age determination using methods described by Fay *et al.* (1989a) and Garlich-Miller (1997). Age was estimated by counting incremental growth layer groups (GLGs) in the cementum of a lower canine tooth (Fay *et al.* 1986, Garlich-Miller *et al.* 1993). Each cemental GLG was assumed to represent 1 yr of growth (Mansfield 1958, Fay 1982).

The reproductive status of sampled female walrus was determined by macroscopic examination of the reproductive organs following the methods of Fay and Stoker (1982a, b) and Garlich-Miller (1997). An ovary with a newly formed *corpus luteum* was considered evidence of a “new pregnancy.” Specimens bearing evidence of

recent births or term pregnancies (enlarged uterine horns, large incompletely healed placental scars, degenerating *corpora lutea*) were combined into a single reproductive class referred to as "term pregnancy." All females bearing evidence of a new pregnancy or a term pregnancy in the most recent reproductive cycle were considered "fecund." Sexually mature females lacking evidence of reproductive activity in the most recent reproductive cycle (no new or term pregnancy) were referred to as "quiescent."

Data Modeling and Analysis

Generalized linear models (Agresti 2002) were used to evaluate the presence of temporal trends and location (community) effects. Models were primarily constructed for descriptive, rather than predictive, purposes. The year in which data were collected was treated as a quantitative, rather than categorical, variable in all models. Animal gender and age were also considered as potential explanatory variables in some models. Model parameters were estimated using SAS PROC GENMOD (SAS 1999). Each analysis began by fitting a model containing terms for all explanatory variables and their interactions, termed the full model. The full model was compared with candidate-reduced models using the small-sample version of Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). The most parsimonious model providing reasonable fit was selected. The suitability of all models was further assessed by contrasting a plot of the model with a plot of the data being modeled.

Sex Ratio of Harvest

The sex ratio of harvested walruses, measured as the proportion of females in the adult harvest, was modeled using a logit link and a binomial error distribution (Agresti 2002), with location and year as explanatory variables (a logistic model). The full model contained an intercept and a coefficient of year for each community.

From 1960 to 1972, a regulation was in effect restricting hunters to five adult female walruses per year (Burns 1965, Sease and Chapman 1988, FWS 1994). There were no restrictions on the number of males that could be harvested. In order to examine the effect of this regulation on the harvest, we compared the number of females and males harvested in each village during years when the regulation was (1960–1971) and was not (1979–1992) in effect using a Mann-Whitney test (Zar 1984).

Age-at-Harvest

Age-at-harvest data were modeled with an identity link and a gamma error distribution to account for skewness in the data. Community, gender, and year were evaluated as explanatory variables, and a quadratic term for year was included to capture non-linearity through time. The full model had an intercept, a coefficient for year, and a coefficient for year-squared for each of the six combinations of location and gender. Including the scale parameter of the gamma distribution, the full model had 19 parameters.

Productivity

Two models were constructed to evaluate trends in productivity, measured as the proportion of fecund animals in the sampled female harvest. The first model contained

community and year as explanatory variables; the full model contained an intercept and a coefficient of year for each community. The second model was used to evaluate the relationship between fecundity (proportion fecund) and the age of harvested animals; age was the only explanatory variable. This age-fecundity model was fit to a subset of data, collected from 1992 to 1998, for which age and reproductive status were both known, under the assumption that year had little influence on fecundity over this narrow range of sample dates. Both models used a logit link and a binomial error structure.

Reproductive Maturity

Differences in the age of first reproduction for females sampled in the 1990s and those presented by Fay *et al.* (1989*b*) for walruses sampled during two earlier time periods (1952–1972 and 1975–1985) were examined using Kruskal-Wallis one-way ANOVA on ranks for non-normal data (Zar 1984). Dunn's multiple comparison method (Daniel 1990) was used to isolate groups that differed by testing for differences of rank means.

RESULTS

Between 1960 and 2002, 52,407 walruses were recorded during spring walrus harvests at Diomedé, Gambell, and Savoonga. The size and composition of the harvest varied between communities and over time (Appendix 1; Fig. 3).

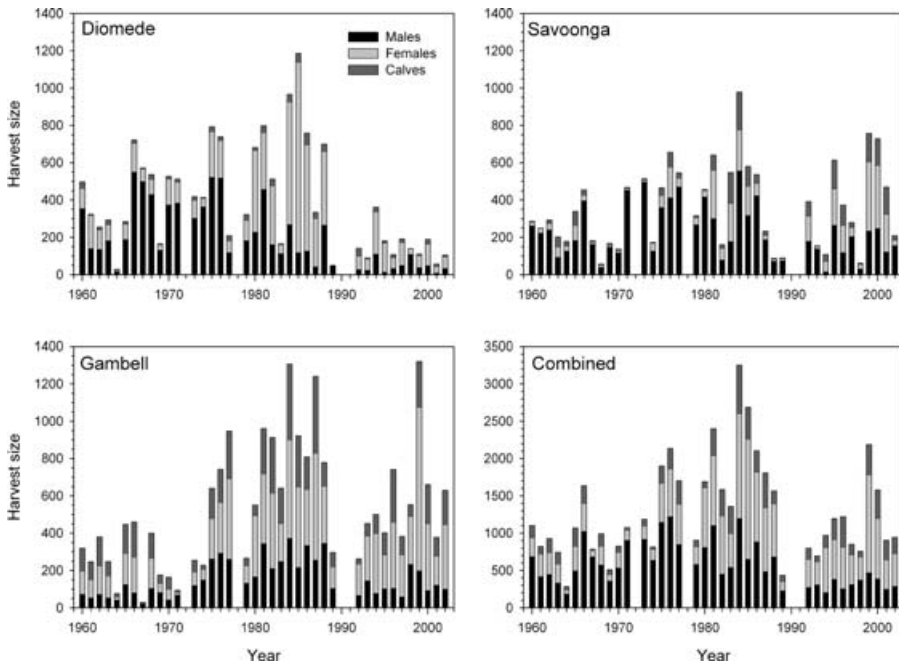


Figure 3. Harvest levels of Pacific walruses at Diomedé, Gambell, and Savoonga, 1960–2002. Data are not available for 1972, 1978, 1990, and 1991.

Table 1. Statistics summarizing candidate models of the proportion of an annual spring walrus harvest comprised of females; L denotes location-specific parameters and C denotes a single common parameter. Data are from Diomedé, Gambell, and Savoonga harvests from 1960 to 2002. Model 1 was selected as the preferred model and is plotted in Figure 4.

Model	Intercept	Year coefficient	No. of parameters	Log(L)	AIC _c	Delta	Akaike weight
1	L	L	6	-25754.96	51521.92	0.00	1.000
2	L	C	4	-26024.92	52057.84	535.91	0.000
3	C	L	4	-26027.97	52063.94	542.02	0.000
4	C	C	2	-27562.72	55129.43	3607.51	0.000

Sex Ratio of Harvest

The proportion of females in the adult harvest differed among communities and through time. The full model was selected as the preferred model (Table 1, model 1). The proportion of the harvest comprised of females increased through time in all three communities (Fig. 4).

The 1960–1972 regulation limiting the take of female walruses to five per hunter per year (Burns 1965, Sease and Chapman 1988, FWS 1994) appears to have been effective. All three villages harvested proportionally fewer females during the period the regulation was in effect ($P < 0.025$, Fig. 3). In Diomedé and Savoonga, the size of the total harvest was not significantly different between periods ($P > 0.20$), but in Gambell, the total harvest was significantly lower during the quota period than after it ended ($P < 0.001$).

Age-at-Harvest

Age estimates were available for a sample of individuals in most years between 1952 and 2002 (Appendix 2). A model having an intercept and a year coefficient for each of the six combinations of community and gender, as well as a single coefficient for the quadratic-year component, was selected as the preferred model (Table 2, model 1). The ages of harvested walruses increased over time in all three communities through the 1980s, after which trends in age stabilized or began to decline (Fig. 5).

Productivity

Data on the reproductive status of female walruses sampled at Diomedé, Gambell, and Savoonga between 1952 and 2002 are presented in Appendix 3. The relative proportion of newly pregnant, term pregnant, and quiescent animals was significantly different between villages ($\chi^2 = 76.2$, $df = 4$, $P < 0.0001$).

Only data from Diomedé and Gambell were considered in the analysis of the proportion of females that were fecund, because too few data were available from Savoonga in the early years for a meaningful trend analysis. Three candidate models described data approximately equally (Table 3). Because we were primarily interested in trends through time, we selected the model with two intercepts, one for each community, and a common year parameter as the final model (Table 3, model 2). The proportion of fecund animals among sampled females declined over time in both Diomedé and Gambell (Fig. 6).

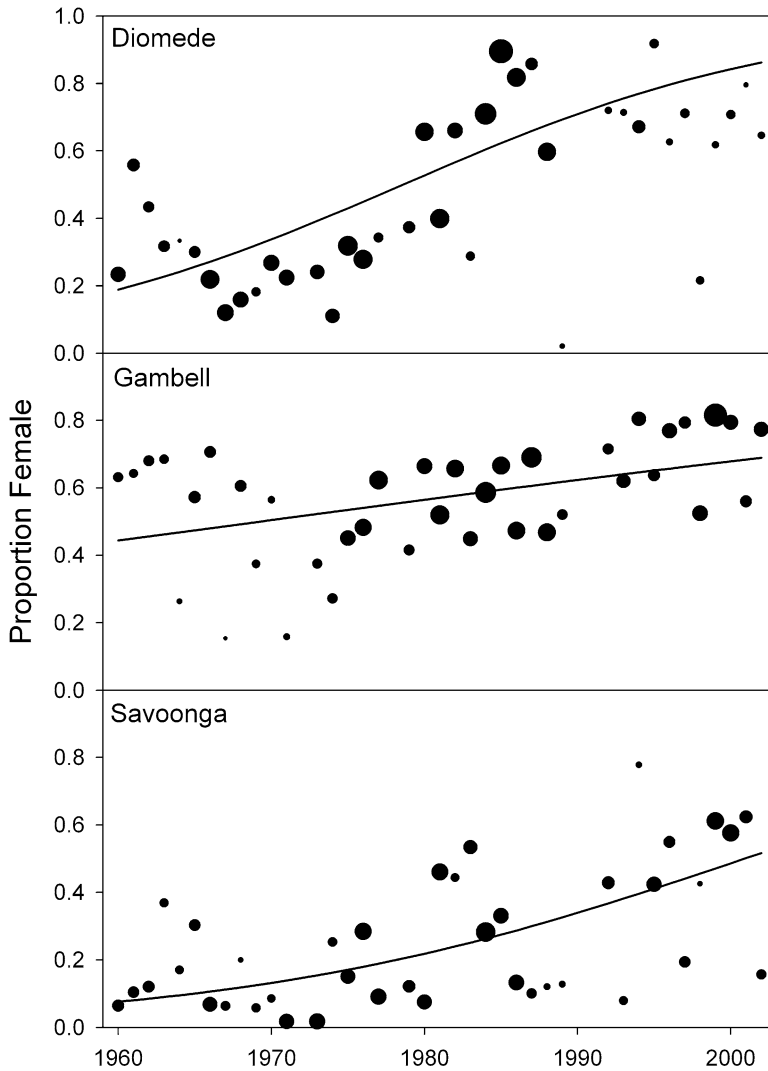


Figure 4. Trends in the sex ratio of walrus harvested at Diomedede, Gambell, and Savoonga, 1960–2002. Symbols represent the proportion of females in the adult harvest and their areas are proportional to sample sizes.

Because the mean age of harvested females also increased over time (Fig. 5), the relationship between fecundity and age was investigated for 874 animals of known age sampled from 1992 to 1998, under the assumption that year of harvest had little influence on fecundity over this relatively narrow range of years. The age parameter was significantly less than zero ($\chi^2 = 30.46$, $df = 1$, $P < 0.001$), indicating that the proportion fecund was inversely related to age through most of the 1990s (Fig. 7).

Table 2. Statistics summarizing candidate models of the age of walrus harvested in annual spring hunts; L denotes location-specific parameters, G denotes gender-specific parameters, and C denotes a single common parameter. Data are from Diomedea, Gambell, and Savoonga harvests from 1952 to 2002. Model 1 was selected as the preferred model and is plotted in Figure 5.

Model	Intercept	Year parameter	Year ² parameter	No. of parameters	Log(L)	AIC _c	Delta	Akaike weight
1	L*G	L*G	C	14	-40826.15	81680.32	0.00	0.422
2	L*G	L*G	G	15	-40825.25	81680.53	0.21	0.379
3	L*G	L*G	L*G	19	-40822.32	81682.69	2.37	0.129
4	L*G	L*G	L	16	-40825.93	81683.90	3.58	0.070
5	L*G	L	C	11	-40841.76	81705.55	25.23	0.000
6	L*G	G	C	10	-40863.21	81746.43	66.11	0.000
7	G	L*G	C	10	-40867.96	81755.94	75.62	0.000
8	L*G	C	C	9	-40869.45	81756.91	76.59	0.000
9	L	L*G	C	11	-40893.24	81808.50	128.18	0.000
10	L*G	L*G	-	13	-40991.30	82008.64	328.31	0.000
11	C	L*G	C	8	-41011.77	82039.56	359.24	0.000
12	L*G	-	C	8	-41181.47	82378.96	698.64	0.000

Reproductive Maturity

The age of first reproduction was determined for 48 sexually mature female walrus sampled between 1992 and 1998 and compared with results presented by Fay *et al.* (1997) for females sampled from the same region during two earlier time periods 1952–1972 ($n = 61$) and 1975–1985 ($n = 48$) (Fig. 6). A Kruskal-Wallis one-way ANOVA on ranks indicated that the difference in the median ages of first reproduction among the three time periods was significant ($H = 23.8$, $df = 2$, $P < 0.0001$). Pairwise multiple comparisons (Dunn's method) indicated a significant difference between 1975–1985 samples *vs.* 1990–1998 samples (Dif = 38.43, $Q = 4.43$, $P < 0.05$) and 1975–1985 *vs.* 1952–1972 samples (Dif = 37.43, $Q = 4.07$, $P < 0.05$). Differences between 1952–1972 and 1992–1998 data sets were not significant (Dif = 1.01, $Q = 0.116$, $P > 0.05$). Female walrus sampled during 1952–1972 and 1992–1998 reached reproductive maturity at younger ages than those sampled during 1975–1985 (Fig. 6).

DISCUSSION

There was considerable variation in the size and composition of the spring walrus harvests among the three communities and over time. Factors thought to have influenced the size and composition of the harvest over the past 50 yr include hunter preferences, harvest management regimes, environmental conditions, and changes in population status.

Hunter Preferences

Walrus tusks increase in size with age (Fay 1982) and hunters tend to select for the valuable ivory of mature animals (Fay and Stoker 1982*a, b*; Fay *et al.* 1986). A

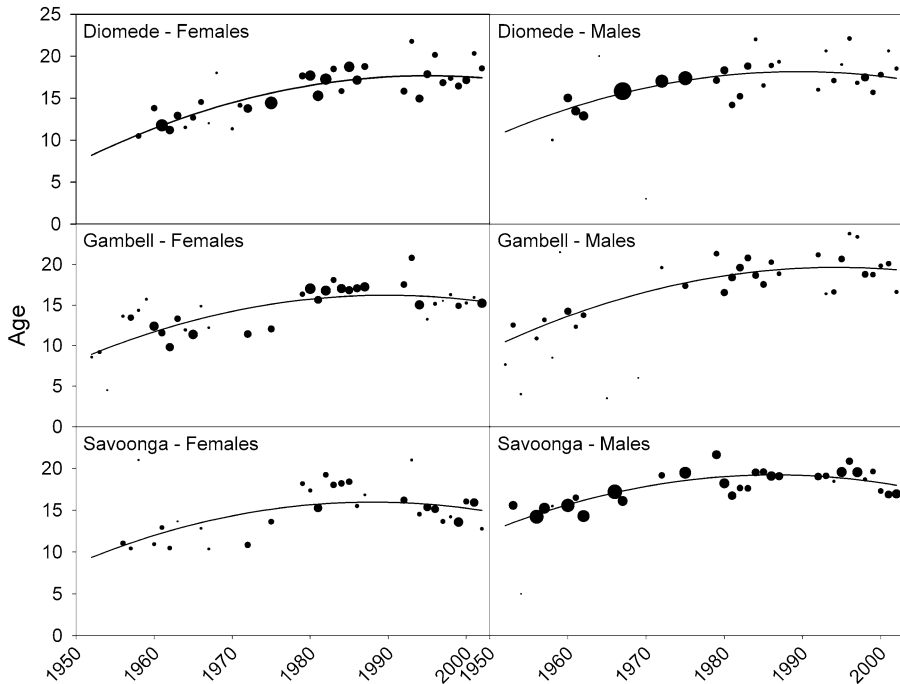


Figure 5. Trends in the ages of walrus harvested at Diomedé, Gambell, and Savoonga: 1952–2002. Symbols represent median ages and their areas are proportional to sample sizes.

preference for mature animals was apparent in the age-at-harvest data; there were relatively few juvenile animals (1–6-yr-old) represented in the sampled harvest.

St. Lawrence Island hunters are also reported to prefer female walrus with newborn calves (Burns 1965; Fay and Stoker 1982*a, b*; Fay *et al.* 1986; Dickerson *et al.* 1996). The selection preference for cow–calf pairs was evident in the reproductive samples collected from St. Lawrence Island hunters. The proportion of near-term and recently postpartum females in the sampled harvests of Gambell (0.57) and Savoonga (0.73) were higher than expected from a population where females normally produce a calf once every 2 (0.50) or 3 (0.33) yr (Fay 1982). The tendency for walrus

Table 3. Statistics summarizing candidate models of the proportion of harvested females that were fecund; L denotes location-specific parameters and C denotes a single common parameter. Data are from Diomedé and Gambell harvests from 1952 to 2002. Model 2 was selected as the preferred model and is plotted in Figure 6.

Model	Intercept	Year coefficient	No. of parameters	Log(L)	AIC _c	Delta	Akaike weight
1	L	L	4	−990.63	1989.28	0.00	0.334
2	L	C	3	−991.70	1989.41	0.13	0.316
3	C	L	3	−991.73	1989.45	0.18	0.306
4	C	C	2	−994.58	1993.16	3.89	0.048

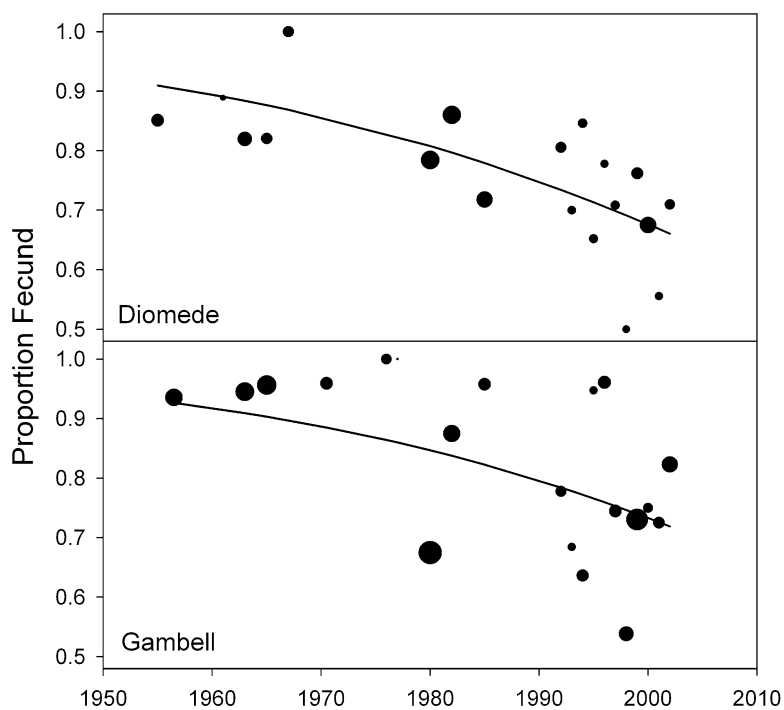


Figure 6. Trends in the proportion of fecund animals among sampled female walrus at Diomedes and Gambell: 1952–2002. Symbol areas are proportional to sample sizes.

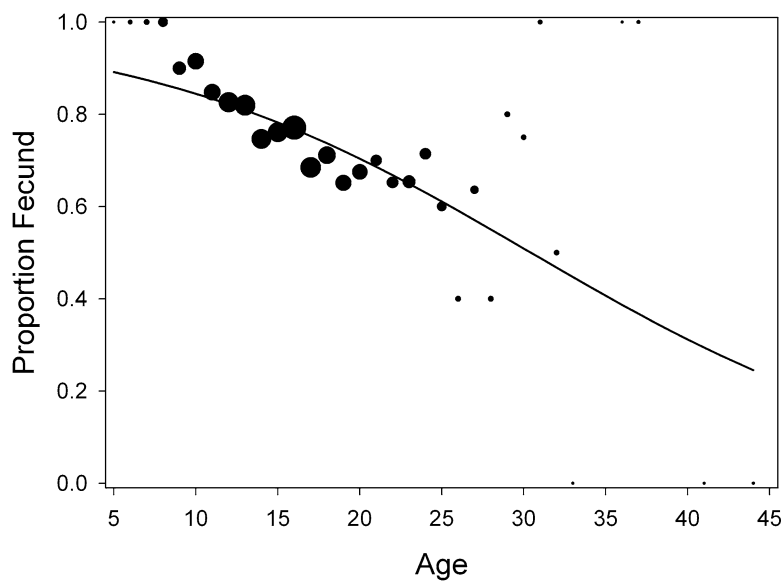


Figure 7. Proportion of fecund animals among sampled female walrus by age. Symbol areas are proportional to sample sizes.

to segregate into different sex or reproductive classes during migration (Fay 1982, Fedoseev 1990) may also have contributed to differences in the composition of the harvests between villages. For example, the relatively high proportion of females bearing calves traditionally taken by St. Lawrence Island hunters may in part reflect the proximity of these communities to spring migratory routes for pregnant females (Fay 1955, Burns 1965).

Anecdotal reports from WHMP monitors over the past 40 yr suggest that hunter selection bias in the Bering Strait region have remained relatively constant through time (*e.g.*, Burns 1965, Dickerson *et al.* 1996, Snyder 2001).

Harvest Management Regimes

Changes in management regimes are also thought to have influenced the size and composition of the catch over time. Management restrictions on the female harvest (1960–1972) apparently were effective in significantly reducing the number of females in the Bering Strait harvest. Harvest patterns in the three communities suggest that they responded to the quota system differently. For example, in Diomedes and Savoonga, it appears that hunters could substitute males for females without significantly altering their overall harvest levels. In Gambell, however, hunters apparently were not able to substitute males for females and their overall harvest during the quota period was significantly reduced. Females are generally more available during the spring migration past the community of Gambell (Fay 1955, Burn 1965) and once a hunter harvested five females he may have been reluctant to continue to hunt in order to avoid violating the quota.

Environmental Factors

Environmental conditions are known to influence the distribution of walruses (Fay 1982, Fedoseev 1990), and are also thought to influence the timing and success of subsistence hunting activities (Dickerson *et al.* 1996). Hunting success in any given year is dependent upon suitable weather and ice conditions for operating small boats coinciding with the availability of walrus herds within range of the communities (Garlich-Miller 1997). We suspect that variable spring hunting conditions may have contributed to large inter-annual and intra-village differences in hunting success (Fig. 3). For example, in 1998, heavy pack ice prevented Savoonga hunters from launching their boats for most of the spring hunting season and the community only managed to harvest 67 walruses (Snyder 1998). The following year, favorable weather and ice conditions prevailed, permitting Savoonga hunters to retrieve 759 walruses, the largest spring walrus harvest in more than a decade (Snyder 1999). Hunters also report that walruses often segregate into relatively homogeneous groups of similar age, sex, or reproductive status during the spring migration (Garlich-Miller 1997). Differences in the migratory patterns of various segments of the population may have interacted with the intermittent timing of favorable hunting conditions to produce inter-annual variation in the composition of the harvest (Appendix 1).

Regional climate trends might also have influenced hunting success over time. For example, it has been suggested that the declining harvest levels at Diomedes through the 1990s may have been influenced by shorter hunting seasons resulting from a rapid retreat of sea ice in the spring (Garlich-Miller 1997, Sheffield 2002).

Changes in Population Status

Although these harvest data do not directly represent the population as a whole due to hunter preferences, regulatory restrictions, and other factors, they may provide some insight into general population trends for a species for which few population estimates are available. Changes in the age structure and productivity of walrus sampled from Diomedé, Gambell, and Savoonga over the past 50 yr are consistent with putative changes in population size and productivity over this time frame (Fay and Kelly 1989; Fay *et al.* 1989b, 1997). During the 1960s and 1970s, the Pacific walrus population is thought to have increased greatly in size after several decades of intensive commercial exploitation (Fay *et al.* 1989b, 1997). Despite harvest restrictions on female walrus, harvest levels in the Bering Strait region increased steadily over this time frame, suggesting that walrus were generally more available to hunters in later years. We also found that the ages of harvested animals increased in all three communities through the 1950s, 1960s, and 1970s. If hunter bias toward older animals with larger tusks was constant through time, as we think it was, then older animals apparently were not as available in earlier years. Although information on population size after 1990 is lacking, Fay *et al.* (1989b, 1997) and Fay and Bowlby (1994) speculated that the combined subsistence and commercial harvests of the United States and Russia during the 1980s were of sufficient scale to impact population size (Fig. 1). Although declining harvest levels and shifts in the age composition of harvested animals in the Bering Strait region after 1980 are consistent with this hypothesis, large annual variations in hunting success and the effects of unquantified sampling biases must also be considered. Abundance estimates will ultimately be required to quantify recent trends in population size.

Fay (1982) and Fay *et al.* (1989b) reported a decline in the proportion of adult females bearing calves in the annual subsistence harvest in the Bering Strait region from approximately 60% in the 1950s, to approximately 40% by the early 1980s. Information regarding the age–sex composition of free-ranging walrus herds was also collected in association with a series of research cruises in the 1980s in the pack ice of the Chukchi Sea by Fay and Kelly (1989). These investigators found that the ratios of calves, yearlings, 2- and 3-yr-old animals to adult females were lower than expected from a stable or growing population. We found that reproductive rates in subsistence-harvested animals remained relatively low through the 1990s. While this is consistent with a hypothesis of continued density-dependent suppression of reproductive rates, we also found an inverse correlation between fecundity and age, indicating that reproductive senescence of older females may also have contributed to the decline in reproductive rates of sampled females. Selection for older aged animals with the largest tusks could potentially bias the sample towards animals with lower reproductive rates. If age-related senescence were a significant contributing factor, we would expect to see an increase in productivity should the ages of sampled females decline. Additional field observations of the proportion of females accompanied by calves may help quantify changes in productivity at the population level (Fay and Kelly 1989).

Life-history characteristics can vary within a species in response to temporal or geographic differences in population density or food availability (Laws 1956, Pianka 1978). Shifts in the age at first reproduction as a response to density-dependent factors has been demonstrated for some populations of seals and whales (*e.g.*, Sergeant 1973, Fowler 1981). Fay *et al.* (1989b) reported that the age of first birth for female Pacific walrus in the Bering Strait region shifted from approximately 8 yr of

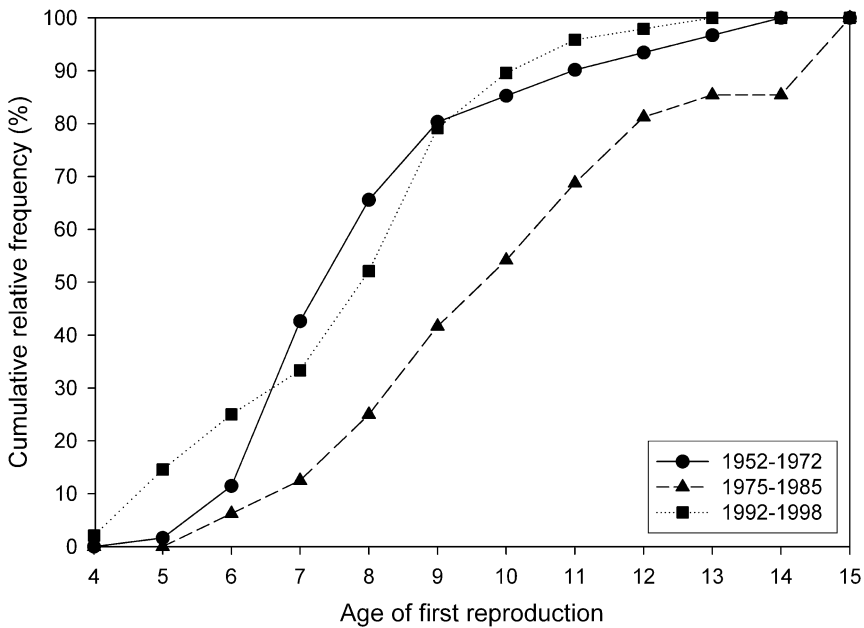


Figure 8. Cumulative relative frequency of ages at first birth for female walrus in the 1952–1972, 1975–1985, and 1992–1998 periods. Data from 1952–1972 and 1975–1985 periods from Fay *et al.* (1989b).

age for animals sampled in 1952–1972, to approximately 10 yr of age for animals sampled in 1975–1985 (Fig. 8). This shift in age at maturation was interpreted as a density-dependant response of a population approaching the carrying capacity of its environment (Fay *et al.* 1989b, 1997). We found that the median age of reproduction for females sampled from the same region in the 1990s was 8 yr. Although a decline in the age of first reproduction in the 1990s is consistent with a hypothesis of reduced density-dependent pressures, there are no recent data concerning the trend in abundance of the Pacific walrus population or the status of its prey base to verify this hypothesis. Whether density-dependent changes in life-history parameters might have been mediated by changes in walrus abundance, or by changes in the carrying capacity of the environment, is unknown.

Management Recommendations

The Pacific walrus population is a shared resource of the United States and Russia and is of critical importance to the subsistence lifestyle of coastal natives of Alaska and Chukotka. While recent harvest levels in the United States and Russia are lower than historical highs, the lack of information on population size or trend precludes an assessment of sustainable removal rates. Projected changes in the climate and marine ecosystems of the Arctic (Tynan and DeMaster 1997, Overland and Stabeno 2004) further underscore the need for population studies from which sound management decisions can be made.

Recent innovations in remote-sensing techniques (Burn *et al.* 2006) and satellite telemetry technology (Jay *et al.* 2006) have potential to overcome many of the

sampling limitations encountered in previous efforts to survey the Pacific walrus population (see Gilbert 1999 for a review) and will hopefully lead to a more reliable population estimate in the near future. In addition to an estimate of population size, estimates of survivorship and recruitment will also be necessary to evaluate population status and trend. This information could be gathered using the methods of Fay and Kelly (1989) to characterize the age–sex composition of free-ranging walrus herds. Close coordination between the United States and Russia on walrus research and harvest management is also necessary to ensure that walrus remain a sustainable resource for generations to come.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Supplementary Appendix 1

Supplementary Appendix 2

Supplementary Appendix 3