AGE, SEX AND REPRODUCTIVE STATUS OF PACIFIC WALRUS HARVESTED IN THE BERING STRAIT REGION, 1994-1996

BY

JOEL GARLICH-MILLER

U.S. Fish and Wildlife Service
Marine Mammals Management
1011 East Tudor Road
Anchorage, Alaska 99503

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ABSTRACT

Between 1994 and 1996, a total of 3,423 harvested walrus were recorded during spring subsistence hunts in Alaska at the Native villages of Little Diomede, Gambell, Savoonga and Wales. The recorded harvest consisted of: 840 calves (25%), 33 yearlings (1%), 177 subadults (5%), 2,365 adults (69%), and 8 animals of unknown age class. The sex ratio of the harvest was 1.8 females:male. Frequency distributions of age estimates indicated sex-linked differences in age structure of the harvest; the mean age of sampled females was lower than the mean age of sampled males for each sample year ($P < 0.0001$). Examination of sampled female reproductive tracts indicated the mean age of first birth was approximately 7 years. Approximately 24% of the mature females had ovulated in the most recent reproductive cycle. On average, the proportion of mature females bearing a calf per annual cycle was 59%. Comparisons with previously reported data suggest that the present population may be below the carrying capacity of its environment.

INTRODUCTION

For thousands of years, walrus hunting has been an important component of the economy and culture of Native communities along the Bering and Chukchi Sea coasts (Ray 1975). Today, the Pacific walrus (*Odobenus rosmarus divergens*) remains a valuable resource to coastal Natives as a source of food and raw materials for traditional equipment and handicrafts. Each spring, as the pack ice recedes northward, hunters from coastal communities in the Bering Strait have access to herds of walrus as they migrate to their summer range. Harvest data indicate that approximately 80% of the annual reported walrus harvest in Alaska occurs in this region (Fay and Bowlby 1994).

With the passage of the Marine Mammal Protection Act (MMPA) in 1972, the U.S. Federal Government established, with certain exceptions, a moratorium on the taking (hunting, harassing, capturing or killing) of marine mammals in U.S. waters. Coastal Alaska Natives were granted an exemption to this moratorium permitting them to take marine mammals for subsistence purposes. The legislation of the MMPA allows for the subsistence harvest of walrus and other marine mammals to be carried out without regulation so long as populations are maintained within Optimum Sustainable Population (OSP) ranges (FWS 1994).

The U.S. Fish and Wildlife Service (FWS) is the agency responsible for managing Pacific walrus in the U.S. As part of their management strategy, the FWS conducts a Walrus Harvest Monitoring Project (WHMP). Each spring, harvest monitors stationed at the primary walrus hunting villages in the Bering Strait region collect information on the size and demography of the walrus harvest. A key component of the WHMP is the collection and analysis of biological samples. Tooth samples are collected for age determination and female reproductive organs are collected to assess reproductive status. These life history data contribute to an assessment of the impact of the harvest on the population, and of population status relative to its OSP range.

This report summarizes the results of field and laboratory investigations of the age-sex composition and reproductive status of walrus harvested in 1994, 1995 and 1996, from the four primary walrus hunting villages in Alaska: Inalik on Little Diomede Island (hereafter referred to as Diomede), Gambell and Savoonga on St. Lawrence Island, and Wales on the Seward Peninsula (Figure 1).

METHODS

Sample collection

Walrus harvest monitors stationed at each village met boats as they returned from walrus hunting trips to collect biological samples and harvest information (Seagars et al. 1995; Dickerson et al. 1996). Harvest monitors attempted to identify and record the gender and age class of every walrus retrieved during the monitoring period. The gender and age class of walrus were determined based upon body and tusk morphology (Fay 1982; Stephensen et al. 1994).

Hunters were asked to voluntarily provide 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 in labeled manila envelopes. Reproductive tracts were stored frozen, or in 10% buffered formalin. All samples were shipped to the FWS, Marine Mammals Management laboratory in Anchorage for analysis.

Age determination

When more than one tooth was provided, the best tooth was selected for analysis. Criteria for tooth selection included avoiding broken or partial teeth and selecting those teeth that would provide the best longitudinal section through the center core area. Unused teeth were archived as reference material.

A longitudinal thin section, 0.4-0.6 mm thick, was cut through the central core of each tooth using a lapidary saw, outfitted with water cooled, high concentration diamond wafering blades (Seagars et al. 1995). Tooth sections were stored in a mixture of 35% ethanol, 5% glycerine and 60% water. Each tooth section was examined under reflected light using a variable-power stereoscopic dissecting microscope. Ages were estimated by counting incremental growth layer groups (GLG) in the tooth cementum (Fay 1982; Garlich-Miller et al. 1993). One cemental GLG was assumed to represent one year of growth (Fay 1982). For each tooth section, cemental GLGs were counted three times in blind replicates. The final age estimate was the median value of the three readings. For each final age estimate, a precision index (PI) and the range between high and low replicate counts were calculated. The PI was the number of identical readings among the three replicate readings. Possible PI values were: 3 (final age estimate = the median value of 3 identical readings), 2 (final age estimate = the median value of 2 identical readings and 1 unique reading), and 1 (final age estimate = the median value of 3 unique readings). Precision index values were used to investigate sex-linked differences in the precision of the aging technique, and to examine the relationship between age and the precision of the estimate.

Reproductive tract analysis

All reproductive material stored frozen was thawed and fixed in 10% buffered formalin for a minimum of three weeks prior to examination. Reproductive status was investigated by macroscopic investigation of the reproductive organs. Following the laboratory methods of Fay and Stoker (1982), each reproductive tract was examined for evidence of sexual maturity, reproductive maturity, recent ovulation and fecundity. The presence of corpora lutea or corpora albicantia in the ovaries was the criteria for sexual maturity (the ability to ovulate). The gross morphology of uterine horns, and the presence or absence of placental scars or embryos in the uterus were used to assess reproductive maturity (the ability to produce a calf). An ovary with a newly formed corpus luteum was considered evidence of ovulation in the most recent reproductive cycle. Fecundity was assessed by examining the reproductive tracts for evidence of recent reproductive activity. The presence of an identifiable embryo or a nidation chamber in the uterus was the criterion for determining a new pregnancy. The presence of a newly formed corpus albicans in association with a greatly enlarged and thickened uterine horn, bearing an incompletely healed placental scar was considered evidence of recent parturition. Specimens lacking macroscopically visible evidence of pregnancy or recent parturition were described as quiescent. This category included all reproductively immature animals, as well as reproductively mature specimens with no evidence of pregnancy in the most recent reproductive cycle.

RESULTS

Age-sex composition of the sampled harvest

During the 1994 spring harvest, 984 walrus were recorded through the WHMP. The recorded harvest consisted of 672 females, 249 males, and 63 animals of unknown gender. For animals of known gender, the sex ratio was 2.7 females:male. One hundred and fifty five (15.8%) of the retrieved walrus were calves, 15 (1.5%) were yearlings, 50 (5.1%) were subadult animals, and 763 (77.6%) were adults. One retrieved walrus of unknown age-class was also recorded (Table 1).

In 1995, 1,205 walrus (females: n = 628, males: n = 458, unknown gender: n = 119) were recorded. The sex ratio of the harvest was approximately 1.4 females:male. The harvest consisted of 280 calves (23.3%), 12 yearling animals (1%), 37 subadults (3.1%), 875 adults (72.6%), and 1 animal of unknown age class.

A total of 1,234 harvested walrus were recorded in the spring of 1996. Of these, 705 were female, and 398 were male (sex ratio: 1.8 females:male). The gender of 131 animals was not recorded. The 1996 walrus harvest consisted of 405 calves (33%), 6 yearlings (0.5%), 90 subadults (7.3%), 727 adults (59.2%) , and 6 animals of unknown age class.

Between 1994 and 1996, a total of 3,423 walrus were recorded through the WHMP. The sex ratio of the total recorded harvest was 1.8 females:male (females: n = 2,005, males: n = 1,105, unknown gender: n = 313). The total recorded harvest over the three year period, consisted of: 840 calves (24.5%), 33 yearlings (1.0%), 177 subadults (5.2%), 2,365 adults (69.2%), and 8 animals of unknown age class.

Walrus hunters contributed teeth from 42% of all non-calf walrus of known gender (Table 2). Teeth were not collected from calf or yearling animals, for which age was estimated based on morphological characteristics (Fay 1982; Fay and Kelly 1989).

A total of 1,061 walrus teeth (females: n = 649, males n = 412) were processed for age determination. Female teeth were generally more difficult to interpret than male teeth. The difficulty associated with interpreting female teeth was reflected by lower precision in age estimates, and larger ranges of values among replicate readings for most year classes (Table 3). The mean PI (± 1 SE) for all female teeth (1.70 ± 0.03) was significantly lower than the mean PI for all male teeth (1.79 ± 0.03; t = -2.0, df = 1,059, $P < 0.05$). In general, PI values decreased, and the range of values among replicate readings increased with age. This trend was apparent for both sexes (Table 3).

The mean age of sampled walrus is presented as an index for examining inter-annual and sex-linked differences in the age structure of the sampled harvest (Table 4). There was a significant difference in the mean age of sampled male walrus among sample years (ANOVA: F = 13.6, df = 2, $P < 0.0001$). Pair-wise multiple comparisons (Student-Newman-Keuls Method) indicated that all between-year differences in the mean ages of sampled males were significant ($P < 0.05$). There was no significant difference in the mean ages of sampled female walrus among sample years (ANOVA: F = 1.97, df = 2, $P > 0.05$).

Frequency distributions of age estimates for sampled walrus indicated sex-linked differences in age structure of the harvest (Figures 2-3). The mean age of sampled females was consistently lower than the mean age of sampled males (1994: t = 3.16, 1995: t = 8.27, 1996: t = 7.34; for all years: $P < 0.0001$; Figure 2; Table 4). The mean age (± 1 SE) of all sampled females (15.5 ± 0.20) was significantly lower than the mean age of all sampled males (19.7 ± 0.31; t = 11.9, df = 1,059.0, $P < 0.0001$; Figure 3; Table 4).

Reproductive status of sampled females

During the 1994, 1995 and 1996 spring harvests, hunters contributed a total of 224 female walrus reproductive tracts for analysis (Table 2). One hundred and twenty nine of the tracts were complete (consisting of paired uterine horns and ovaries), while 95 tracts were missing one or more uterine horns or ovaries. Missing reproductive material often prevented a full assessment of reproductive status.

Sexual maturity - Macroscopic examination of the ovaries indicated that 223 of the 224 sampled females were sexually mature (having had at least one prior ovulation). These animals ranged in age from 5 to 44 years (Table 5). An assessment of sexual maturity could not be made for one 7-year old sample that was missing both ovaries.

Reproductive maturity - The uterine horns of one 7-year old, and four 8-year old females carried no evidence of past or present pregnancies (Table 5). These animals were considered reproductively immature (never pregnant). All other reproductive tracts, collected from female walrus ranging in age from 5 to 44 years, were reproductively mature (n = 200), or were missing sufficient material to assess reproductive maturity (n = 19). Nine females, ranging in age from 5 to 9 years, had recently given birth to their first calf. One 6-year old female was estimated to have given birth to her first calf the previous spring (estimated age of first pregnancy = 5 years). The mean age (± 1 SE) of first birth among these ten animals was 7.2 ± 0.47.

Ovulation rate - All ovaries were examined for evidence of recent ovulation (the presence of a corpus luteum). Of the 183 sexually mature reproductive tracts for which both ovaries were available, 44 (24%) had ovulated in the most recent reproductive cycle (Table 5).

Reproductive rates - The uterine horns of 200 reproductively mature female walrus were assessed for fecundity (Table 6). Three of the recently ovulated specimens carried macroscopically visible evidence of a new pregnancy. The uterine horns of 77 (39%) reproductively mature females lacked any macroscopic evidence of pregnancy or birth in the current reproductive cycle. It is important to note that these samples were collected at a time of the year normally associated with a phase of delayed implantation (Fay et al. 1984), and that unimplanted embryos are difficult to detect macroscopically (Fay 1982). The proportion of the annual sampled harvest of mature females bearing a calf ranged from 35% to 79%. On average, the proportion of mature females bearing a calf per annual cycle was 59%.

DISCUSSION

Sample biases

The data presented in this study were obtained from harvested specimens and therefore do not represent a random sample of the population. Biases associated with the harvest, which include hunter selection as well as the behavior and distribution of walrus, influence the age-sex structure of the harvest and preclude direct extrapolation of results to the entire population.

The influence of individual hunter selection biases on the composition of the harvest are difficult to quantify. Anecdotal information collected by harvest monitors indicate that some hunters exhibited a strong selection preference for females and calves (Dickerson et al. 1996). Hunter selection biases may differ between villages; Fay et al. (1986; 1989*a*) reported a strong selection for females with newborn calves by St. Lawrence Island hunters. This is consistent with the current study, where on average, 63% of the adult female walrus sampled at Gambell, and 79% of the adult females sampled at Savoonga had recently given birth to a calf. Hunters also appear to select for adult age classes of walrus, presumably for the valuable ivory tusks of mature animals (Fay and Stocker 1982; Fay et al. 1986; Dickerson et al. 1996). This is consistent with the results of the current study, in which juvenile age classes of walrus were poorly represented in the sampled harvest.

Environmental conditions can influence the distribution of walrus as well as the success and timing of subsistence hunting activities. Walrus are normally closely associated with pack ice for most of the year (Fay 1982). Variation in ice cover can affect the availability of walrus to subsistence hunters (Fedoseev 1990). For example, in 1995, walrus hunters at Diomede experienced one of their lowest spring walrus harvests on record. Diomede hunters attributed their poor success to a lack of pack ice. Meanwhile, hunters in Savoonga, benefiting from favorable wind and ice conditions, had their highest recorded harvest in a decade (Dickerson et al. 1996). Subsistence walrus hunting in the monitored communities is typically carried out in small, open boats, which can only be operated during favorable weather conditions (Dickerson et al. 1996). Hunting success appears to be dependant upon weather conditions suitable for boating, coinciding with the availability of walrus within the range of the hunting parties.

Walrus often show a tendency to segregate into relatively homogeneous groups of animals of similar age, sex, or reproductive status. Each spring, most adult female Pacific walrus and dependant calves migrate northward with the pack ice, from the Bering Sea to the Chukchi Sea, while many adult males move to haul out sites in Bristol Bay and at various locations along the western coastline of the Bering and Chukchi Seas (Fay 1982; Fedoseev 1990; FWS 1994). Volokhov (1991), reported that during a scientific cruise in the Bering Sea in the spring of 1991, most mature female walrus encountered in the vicinity of St. Lawrence Island were either pregnant or with a newborn calf, while relatively few of the females encountered in the Gulf of Anadyr were pregnant or with calf. The segregation of different sex or reproductive classes of walrus is likely to affect the structure of the harvest at various geographical locations. For example, the relatively high proportion of females bearing calves traditionally taken by St. Lawrence Island hunters (Fay and Stocker 1982; Fay et al. 1986; this study), may in part reflect the proximity of these communities to areas frequented by pregnant females. Furthermore, differences in the migratory patterns of various groups of walrus may interact with the intermittent timing of favorable hunting conditions to produce inter-annual variation in the composition of the harvest.

Precision of age estimates

For each tooth sample, age was estimated based on the median value of three blind replicate counts of cemental growth layers. This technique provided a measure of confidence for each final age estimate. Age estimates based upon three (PI = 3) or two (PI = 2) identical values were considered more reliable than age estimates based on a single (median) value among three unique readings (PI = 1) . In general, PI values decreased with age. While most animals 10 years of age or younger had PI values of 2 or 3, many of the age estimates associated with older animals were based upon the median value of 3 unique readings (PI = 1). Age estimates for any animal with a PI of 1 should be interpreted cautiously.

Although the average range of values among each set of replicate readings was only 2.13 for males and 2.32 for females, there was considerable individual variation. In general, the range of values among replicate readings increased with age. Selecting the median value of the three replicate readings as the final age estimate helped eliminate the influence of potential outliers among the replicate readings. For example, the largest range of values for any single age estimate was 12, however this sample, which had a final age estimate of 17 years, had a PI of 2, suggesting that the third reading may have been in error.

Errors associated with age estimates could potentially bias results for age-specific parameters such as the onset of sexual or reproductive maturity. However, these life history events usually occur within the first 10 years of life (Fay 1982; Fay et al. 1989*b*; Garlich-Miller 1994), when the confidence in age estimates is generally fairly high (Garlich-Miller et al. 1993).

Age-sex composition of the sampled harvest

The sampled walrus harvest was dominated by newborn calves and adult animals, while yearling and subadult animals were poorly represented. This is consistent with reported hunter selection biases favoring calves and adult animals (Fay and Stocker 1982; Fay et al. 1986; Dickerson et al. 1996). Over the range of sample years, the sex ratio of the harvest favored females, while the mean age of sampled males, was consistently older than for sampled females. It is unclear to what extent these differences can be attributed to sex-linked differences in sample selection biases, ageing errors, or survivorship. Field observations of the age-sex composition of walrus herds in the spring pack ice are required to quantify the relative proportions of various age and sex classes available to hunters (Fay and Kelly 1989).

Sexual and reproductive maturity

In the present collection, the poor representation of juvenile and adolescent age classes made interpretation of the onset of sexual and reproductive maturity difficult. All of the samples examined, ranging in age from 5 to 44 years, were sexually mature (had previously ovulated). Ovulation does not always result in pregnancy; five of the sexually mature animals examined had never produced a calf. The available data suggest that females give birth to their first calf sometime between the ages of 5 and 9 years. The mean age of first birth for 10 primiparous specimens was 7 years. The quality of estimates of mean age of sexual or reproductive maturity are dependant upon the availability of age specific reproductive data (DeMaster 1978). Increased sample sizes of young age classes are required to more accurately quantify the mean ages of sexual or reproductive maturity.

Reproductive rates

The walrus has the lowest reproductive rate of any pinniped species (Fay 1982). Reproductive events in one season are constrained by reproductive events from the previous season. A 3-4 month delay before implantation of the embryo, followed by approximately 11 months of active gestation, result in a supra-annual reproductive cycle. A pregnancy lasting through the next breeding season, means that the minimum interval between successful births is two years. Prolonged nursing by dependant calves, failure to ovulate or conceive, aborted pregnancies, reproductive senescence, and density dependent mechanisms may increase the inter-birth interval to three years or more (Fay 1982; Garlich-Miller 1994).

In the present study, the timing of sample collection (prior to implantation and development of the embryo) precluded a meaningful evaluation of pregnancy rates. Samples collected later in the reproductive cycle are necessary to quantify what proportion of the ovulated specimens had conceived. Birth rates were estimated based upon the proportion of the reproductively mature female harvest consisting of animals that carried a near term fetus or bore evidence of recent parturition. The proportion of near term and recently postpartum females in the sampled harvest (0.59) was higher than might be expected from a population where females producing a calf every two (0.50) or three (0.33) years. The higher than expected frequency of recent births suggest the influence of sample selection biases.

Comparisons with previous studies

Fay and Bowlby (1994), present information on the size and composition of the Pacific walrus harvest between 1931 and 1989. Their compiled information represents retrieved animals only, and was not corrected for an unknown number of animals that were struck and lost. During the 1930s, the combined harvest of Pacific walrus by the U.S. and Russia (formerly the Soviet Union) ranged from approximately 5,000 to 9,500 animals per year, and consisted of approximately equal numbers of males and females. In the 1940s and 1950s, the combined harvest ranged from approximately 4,500 to 6,500 animals per year. The sex ratio of the catch during this period is poorly known. During the 1960s the number of retrieved walrus dropped to approximately 2,000-4,000 animals per year, while the proportion of the harvest consisting of females shifted from approximately 50% to less than one third. The recorded annual harvest increased again in 1980s, ranging from approximately 4,000-8,500 animals per year. During the 1980s, the Russian component of the harvest (approximately 60% of the total harvest) favored males, while in the U.S. the subsistence harvests of Alaska Natives favored females.

Between 1990 and 1994, the combined harvest of Russia and U.S. ranged from approximately 2,000-5,000 animals (FWS 1995). Information on the sex ratio of the Russian component of the 1990-1994 harvests is unavailable, however, in the U.S., the 1990-1994 harvests were slightly skewed towards females. During the early 1990s, the Russian component of the harvest declined steadily from approximately 3,300 to less than 1,000 animals, while in the U.S., harvest levels remained fairly constant, averaging approximately 1,600 animals per year (FWS 1995). Since 1994, harvest monitoring programs in Russia have deteriorated, precluding meaningful estimates of the size and composition of recent Russian harvests (FWS 1995).

Prior to the introduction of firearms and significant levels of commercial exploitation, the Pacific walrus population was probably represented by least 200,000 animals (Fay 1957; 1982). Since that time, the size of the Pacific walrus population has fluctuated markedly in response to varying levels of human exploitation (Fay et al. 1989*b*; Fay and Bowlby 1994). The magnitude of harvest levels in the 1930s and 1940s appears to have been of sufficient scale to have reduced the population to approximately 50-70,000 animals by the mid 1950s (Fay 1982; Sease and Chapman 1988; Fay et al. 1989*b*; Fay and Bowlby 1994). Protective measures enacted by the U.S. and Russia may have helped the population recover; survey data suggests that the population increased rapidly to about 250,000 animals by the early 1980s (Sease and Chapman 1988; FWS 1994). By the late 1970s, Native hunters and scientists began noticing changes in the physiology, diet and distribution of walrus consistent with density dependant responses of a population that had exceeded the carrying capacity (K) of its environment (Fay et al. 1989*b*; Fay and Bowlby 1994). The current size and trend of the population is unknown. The most recent survey, conducted in 1990, produced a minimum population estimate of 201,039 walrus (Gilbert et al. 1992), however, differences in survey methodologies and variation in ice cover hence walrus distribution, preclude making direct comparisons with previous surveys, and describing anything other than gross trends in the population (FWS 1994).

Assuming that selection biases remain relatively constant over time, changes in the composition of the harvest may provide an index by which population trends can be monitored. Given the potential for the composition of the harvest to vary from year to year in response to environmental conditions and/or distribution patterns, changes occurring at the population level may only be apparent from data collected consistently over a long period of time.

Life history characteristics can vary between temporally or geographically isolated populations of a species in relation to population density or food availability (Sergeant 1973; Pianka 1978). In other pinnipeds, shifts in population density have been linked to changes in maturation and fertility rates. Between 1950 and 1971, the population of northwest Atlantic harp seals (*Phoca groenlandica*) declined by more than 50% as a result of intense commercial harvesting (Winters 1978). During this time, the mean age of sexual maturity dropped from 6.2 to 4.5 years while pregnancy rates increased from 87 to 94% (Bowen et al. 1981). These shift in life history characters were believed to have been mediated by differences in food availability along an r-K continuum (Innes et al. 1981; Stewart and Lavigne 1984).

In comparing data collected in the present study with previously reported values, several lines of evidence support the hypothesis that the Pacific walrus population is no longer constrained by limited food resources.

The average age of reproductive maturity is a sensitive index by which the status of a population can be measured (Laws 1956; Sergeant 1973). Fay et al. (1989*b*) reported that the mean age of first birth for female Pacific walrus in the Bering Strait region shifted from approximately eight years of age for animals sampled between 1952-1972, to approximately ten years of age for animals sampled between 1975-1985. The increase in the mean age of first birth was attributed to an increase in population size relative to K. In the present study, all sampled females nine years of age or older, had previously given birth. The average age of first birth for ten primiparous specimens was seven years. Although this estimate is based on relatively few observations, a decline in the mean age of first birth is consistent with the hypothesis that the population is no longer constrained by limited food resources.

The observed reproductive rates of harvested animals may provide an index by which changes in the productivity of the population can be monitored. Fay et al. (1982; 1989*b*), reported a decline in the proportion of adult females bearing calves in the annual subsistence walrus harvest in the Bering Strait region from approximately 60% in the 1950s, to approximately 40% by the early 1980s. The authors attributed this decline to an overall decrease in fecundity, brought about by a shift in population status relative to K. Through the 1980s, the proportion of recently postpartum females in the sampled spring harvest fluctuated markedly, but generally remained below the high levels observed in the 1950s and 1960s (Fay and Stoker 1980;1982; Fay et al. 1989*a*;1989*b*). Between 1992 and 1996, the average proportion of the sampled adult female catch consisting of recently postpartum specimens was 52% (Table 7). Although the apparent increase in fecundity is consistent with the hypothesis that the population is below K, the large variation observed between sample years and potential affects of unquantified sample biases must also be considered. Field observations of the proportion of females accompanied by calves may be necessary to quantify changes in productivity (Fay and Kelly 1989).

The mean ages of walrus sampled from the 1994-1996 spring harvests were compared to data collected from previous years (Figure 4). In general, males were within the range of values reported over the past two decades. At Diomede, the mean ages of harvested females observed in this study were comparable with previously reported values, however the mean ages of female walrus collected by the St. Lawrence Island villages (Gambell and Savoonga) appears to have dropped over the past few years. The shift towards younger age classes of females may also be correlated with the observed increase in productivity; Fay (1982) reported that for Pacific walrus, reproductive rates decline with age. It is unknown whether the apparent decline in age of female walrus taken near St. Lawrence Island is an artifact of sample biases, or represents a true change in the age structure of the herds available to hunters. This question warrants further investigation, because a shift in the age composition towards younger females may indicate that hunting pressure has removed older age classes of female walrus from the population (Fay et al. 1989*b*).

In summary, information on the present size and composition of the Pacific walrus population is lacking (FWS 1994; 1995), however shifts in life history parameters seem to indicate that the population may presently be at a lower level along the r-K continuum than it was in the 1970s and 1980s (Fay 1989*b*; this study). The size and structure of the Alaskan harvest is fairly well documented, however political instability has resulted in the deterioration of harvest monitoring programs in Russia (Vladimirov *cited in* FWS 1995), therefore the size and composition of the total harvest is poorly known. Without knowledge of the size and structure of the annual catch, the potential exists for unsustainable harvest levels to occur, particularly if the harvest is skewed towards adult females and calves. There is a clear need to obtain a current estimate of population size, and to develop international monitoring programs to accurately assess removal rates from the population to insure that sustainable harvest levels are maintained.

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LITERATURE CITED

Bowen, W.D., C.K. Capstick, and D.E. Sergeant. 1981. Temporal changes in the reproductive potential of female harp seals (*Pagophilus groenlandicus*). Can. J. Fish. Aquat. Sci. 38: 495-503.

DeMaster, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can. 35: 912-915.

Dickerson, L., D. Burn, J. Garlich-Miller, T. Fischbach, S. Rice, J. Bouchard, and B. Howard. 1996. 1995 Walrus harvest monitor project: annual summary. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. 26 p.

Fay, F.H. 1957. History and present status of the Pacific walrus population. Trans. N. Am. Wildl. Conf. 22: 431-443.

Fay, F.H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna No. 74. 279 p.

Fay, F.H., and C.E. Bowlby. 1994. The Harvest of Pacific walrus, 1931-1989. U.S. Fish and Wildlife Service, Marine Mammals Management, Technical report MMM 94-2. 43 p.

Fay, F.H. and B.P. Kelly. 1989. Development of a method for monitoring the productivity, survivorship, and recruitment of the Pacific walrus population. Final report 89-0012. Minerals Management Service, Anchorage, AK. 51 p.

Fay, F.H., S. Hills, and L.T. Quakenbush. 1989*a*. Determination of the age of walrus taken in the Alaskan subsistence catch, 1985-1987, together with an analysis of reproductive organs and stomach contents from the 1985 sample. Final report WR-0439-85. U.S. Fish and Wildlife Service, Anchorage, AK. 81 p.

Fay, F.H., B.P. Kelly, and J.L. Sease. 1989*b*. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. Marine Mammal Science 5(1): 1-16.

Fay, F.H., B.P. Kelly, and J.L. Sease. 1986. Determination of age of walrus taken in recent spring harvests in the Bering Strait region. Final report WR-0439-85. U.S. Fish and Wildlife Service, Anchorage, AK. 110 p.

Fay, F.H., G.C. Ray, and A.A. Kibal'chich. 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *In* Soviet-American cooperative research on marine mammals. *Edited by* F.H. Fay and G.A. Fedoseev. Vol. 1-Pinnipeds, NOAA Technical report No. 12: 89-99.

Fay, F.H., and S.W. Stoker. 1980. Analysis of reproductive organs and stomach contents from walruses taken in the Alaskan Native harvest, spring 1980. Final report 14-16-0007-81-5216. U.S. Fish and Wildlife Service, Anchorage, AK. 86 p.

Fay, F.H., and S.W. Stoker. 1982. Final report to the Eskimo Walrus Commission: reproductive success and feeding habits of walrus taken in the 1982 spring harvest, with comparisons from previous years. Final report, Eskimo Walrus Commission, Nome, AK. 91 p.

Fedoseev, G.A. 1990. The role of ice in changes of Pacific walrus distribution and numbers. Pages 25-37 *in* The ecology and management of walrus populations - report of an international workshop. *Edited by* F.H. Fay, B.P. Kelly, and B.A. Fay. Final report MMC contract T68108850. NTIS PB91-100479: 185-186.

FWS. 1994. Conservation plan for the Pacific walrus in Alaska. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. 79 p.

FWS. 1995. Stock assessment, Pacific walrus (*Odobenus rosmarus divergens*): Alaska stock. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. 10 p.

Garlich-Miller, J.L. 1994. Growth and reproduction of Atlantic walrus (*Odobenus rosmarus rosmarus*) in Foxe Basin, Northwest Territories, Canada. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba. 116 p.

Garlich-Miller, J.L., R.E.A. Stewart, B.E. Stewart, and E.A. Hiltz. 1993. Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walrus (*Odobenus rosmarus rosmarus*). Can. J. Zool. 71: 163-167.

Gilbert, J.R., G.A. Fedoseev, D. Seagars, E. Razlivalov, and A. LaChugin. 1992. Aerial census of Pacific walrus, 1990. U.S. Fish and Wildlife Service, Marine Mammals Management, Technical report MMM 92-1. 33 p.

Innes, S., R.E.A. Stewart, and D.M. Lavigne. 1981. Growth in northwest Atlantic harp seals *Phoca groenlandica*. J. Zool. Lond. 194: 11-24.

Laws, R.M. 1956. Growth and sexual maturity in aquatic mammals. Nature 179: 193-194.

Pianka, E.R. 1978. Evolutionary ecology (2nd Ed). Harper and Row, New York. 397 p.

Ray, D.J. 1975. The Eskimos of the Bering Strait, 1650-1898. Univ. Washington Press, Seattle, WA. 305 p.

Seagars, D.J., P. Hessing, C.E. Bowlby, L. Noonan, and D.M. Burn. 1995. Annual summary: Information collected during the 1993 spring walrus harvest in Alaska. U.S. Fish and Wildlife Service, Marine Mammals Management, Technical Report MMM 95-1. 31 p.

Sease, J.L., and D.G. Chapman. 1988. Pacific walrus - Odobenus rosmarus divergens *in* Selected marine mammals of Alaska: Species accounts with research and management recommendations. *Edited by* J.W. Lentfer. Marine Mammal Commission, Washington, D.C. NTIS PB88-178462: 17-38.

Sergeant, D.E. 1973. Environment and reproduction in seals. J. Reprod. Fert. 19: 555-561.

Stephensen, W.D., D. Cramer, and D. Burn. 1994. Review of the Marine Mammal Marking and Reporting Program, 1988-1992. U.S. Fish and Wildlife Service, Marine Mammals Management, Technical Report MMM 94-1. 49 p.

Stewart, R.E.A., and D.M. Lavigne. 1984. Energy transfer and female condition in nursing harp seals (*Phoca groenlandica*). Holarct. Ecol. 7: 182-194.

Volokhov, V.I. 1991. Spring distribution and reproductive status of female Pacific walruses. Magadan, TINRO. 5 p.

Winters, G.H. 1978. Production, mortality, and sustainable yield of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 35: 1249-1261.

Table 1. Summary of age class and sex of harvested walrus recorded by harvest monitors, 1994-1996.

Year	Age Class	Female	Male	Unknown	Total
1994	Calf	59	43	53	155
	Yearling	7	3	5	15
	Subadult	31	19	0	50
	Adult	575	184	4	763
	Unknown	0	0	1	1
	Subtotal	**672**	**249**	**63**	**984**
1995	Calf	95	76	109	280
	Yearling	2	5	5	12
	Subadult	11	22	4	37
	Adult	519	355	1	875
	Unknown	1	0	0	1
	Subtotal	**628**	**458**	**119**	**1,205**
1996	Calf	142	135	128	405
	Yearling	3	2	1	6
	Subadult	61	28	1	90
	Adult	497	230	0	727
	Unknown	2	3	1	6
	Subtotal	**705**	**398**	**131**	**1,234**
All Years	Calf	296	254	290	840
	Yearling	12	10	11	33
	Subadult	103	69	5	177
	Adult	1591	769	5	2365
	Unknown	3	3	2	8
	Total	**2,005**	**1,105**	**313**	**3,423**

Table 2. Summary of walrus tooth and female reproductive tract samples collected at monitored villages, 1994-1996. Does not include material collected from animals of unknown gender.

Year	Non-calf Walrus	Tooth Samples	Teeth Sampled (%)	Adult & Subadult Walrus	Repro Samples	Repros Sampled (%)
1994	809	317	39.2	606	78	12.9
1995	907	450	49.6	530	56	10.6
1996	816	294	36.0	558	90	16.1
Total	**2,532**	**1,061**	**41.9**	**1,694**	**224**	**13.2**

Table 3. Precision of age estimates for sampled walrus. Individual age estimates were based upon the median value of three blind replicate counts of cemental growth layers in a tooth.

Age Class	Males			Females		
	Sample Size	Mean PI[a]	Mean Range[b]	Sample Size	Mean PI	Mean Range
3	1	3.00	0.00	0	.	.
4	0	.	.	0	.	.
5	0	.	.	1	3.00	0.00
6	0	.	.	2	2.50	1.00
7	4	2.25	0.75	10	1.90	1.30
8	12	2.33	0.75	24	2.21	0.96
9	9	1.89	1.22	38	2.24	1.16
10	12	2.00	1.67	27	1.96	1.41
11	12	2.17	0.92	37	1.97	1.41
12	13	2.31	1.46	45	1.78	2.36
13	9	1.44	2.33	64	1.81	1.88
14	12	1.92	1.25	42	1.55	2.43
15	14	1.86	1.50	51	1.63	2.29
16	27	1.93	2.11	70	1.57	2.34
17	21	1.76	1.57	42	1.67	2.52
18	25	2.00	1.84	37	1.57	2.51
19	26	1.73	2.27	36	1.69	2.53
20	30	1.83	2.00	26	1.38	2.81
21	24	1.79	2.00	21	1.33	3.57
22	24	1.58	2.67	17	1.41	4.12
23	25	1.68	2.48	14	1.43	3.57
24	21	1.67	2.52	15	1.27	4.20
25	24	1.67	3.04	5	1.80	3.60
26	10	1.90	1.90	6	1.50	3.00
27	10	1.20	4.60	5	1.60	2.20
28	8	1.50	2.63	5	1.40	4.80
29	15	1.67	2.00	1	2.00	2.00
30	6	1.50	2.00	3	1.00	5.00
31	4	1.25	3.25	2	1.00	3.00
32	5	1.00	4.40	0	.	.
33	3	1.67	2.33	0	.	.
34	5	1.20	3.20	0	.	.
35	1	2.00	5.00	1	1.00	5.00
36	0	.	.	0	.	.
37	0	.	.	0	.	.
38	0	.	.	0	.	.
39	0	.	.	1	1.00	4.00
40	0	.	.	0	.	.
41	0	.	.	0	.	.
42	0	.	.	0	.	.
43	0	.	.	0	.	.
44	0	.	.	1	1.00	3.00
All	**412**	**1.79**	**2.13**	**649**	**1.70**	**2.32**

[a] PI = Precision Index (number of identical readings among three blind replicate counts).
[b] Range = Range of values among three blind replicate readings.

Table 4. Ages (years) of walrus sampled from monitored villages, 1994-1996. Ages were determined by counts of cemental growth layer groups. Summary statistics do not include calves, yearlings, or animals of unknown gender.

Year	Males				Females			
	Sample Size	Range	Mean	Standard Error	Sample Size	Range	Mean	Standard Error
1994	86	7-27	17.0	0.53	231	7-39	15.1	0.30
1995	217	7-34	19.8	0.42	233	7-31	15.5	0.33
1996	109	3-35	21.5	0.64	185	5-44	16.1	0.42
All Years	**412**	**3-35**	**19.7**	**0.31**	**649**	**5-44**	**15.5**	**0.20**

Table 5. Age specific reproductive characteristics of female walrus sampled from monitored villages, 1994-1996.

Age Class	Sample Size	Sexual Maturity			Reproductive Maturity			Ovulation			Fecundity			
		I	M	U	I	M	U	Y	N	U	NE[a]	RB	Q[a]	U
5	1	0	1	0	0	1	0	0	1	0	0	1	0	0
6	2	0	2	0	0	2	0	0	2	0	0	2	0	0
7	4	0	3	1	1	2	1	0	3	1	0	2	1	1
8	11	0	11	0	4	5	2	4	4	3	0	5	4	2
9	11	0	11	0	0	11	0	1	9	1	0	10	0	0
10	8	0	8	0	0	7	1	0	4	4	0	7	0	1
11	13	0	13	0	0	12	1	1	10	2	0	9	3	1
12	15	0	15	0	0	13	2	2	10	3	0	9	4	2
13	24	0	24	0	0	22	2	2	18	4	0	15	7	2
14	8	0	8	0	0	7	1	1	5	2	0	3	4	1
15	15	0	15	0	0	15	0	6	8	1	2	7	6	0
16	23	0	23	0	0	22	1	5	15	3	0	12	10	1
17	13	0	13	0	0	12	1	2	9	2	0	6	6	1
18	10	0	10	0	0	9	1	3	6	1	0	3	6	1
19	15	0	15	0	0	14	1	4	7	4	1	3	7	4
20	9	0	9	0	0	7	2	2	6	1	0	3	4	2
21	4	0	4	0	0	3	1	1	3	0	0	2	1	1
22	5	0	5	0	0	5	0	3	0	2	0	2	3	0
23	6	0	6	0	0	6	0	1	4	1	0	5	1	0
24	4	0	4	0	0	3	1	1	2	1	0	2	1	1
25	3	0	3	0	0	3	0	1	1	1	0	1	2	0
26	2	0	2	0	0	2	0	1	1	0	0	0	2	0
27	1	0	1	0	0	1	0	0	1	0	0	0	1	0
28	2	0	2	0	0	1	1	0	1	1	0	0	1	1
30	1	0	1	0	0	1	0	0	1	0	0	1	0	0
44	1	0	1	0	0	1	0	0	1	0	0	0	1	0
U	13	0	13	0	0	13	0	3	7	3	0	7	6	0
Total	**224**	**0**	**223**	**1**	**5**	**200**	**19**	**44**	**139**	**41**	**3**	**117**	**82**	**22**

I=Immature, M=Mature, U=Unknown (missing reproductive material), Y=Yes, N=No, NE=New embryo, RB=Recent birth/Term pregnancy, Q=Quiescent (No visible embryo, no evidence of recent parturition).
[a]Un-implanted embryo's could not be detected macroscopically.

Table 6. Fecundity of reproductively mature female walrus sampled from monitored villages, 1994-1996 (% sample size).

Year	Sample Size	New Embryo[a]		Term pregnancy or Recent birth		Quiescent[b]		Unknown[c]	
1994	68	2	(2.9)	24	(35.3)	41	(60.3)	1	(1.5)
1995	51	1	(1.9)	29	(56.9)	21	(41.2)	0	(0.0)
1996	81	0	(0.0)	64	(79.0)	15	(18.5)	2	(2.5)
All Years	**200**	**3**	**(1.5)**	**117**	**(58.5)**	**77**	**(38.5)**	**3**	**(1.5)**

[a] Note: un-implanted blastocysts could not be detected macroscopically.
[b] No visible embryo (see footnote [a]) , no evidence of recent birth.
[c] Missing reproductive material precluded determination of fecundity.

Table 7. Estimated births per adult female walrus sampled from monitored villages, 1992-1996.

Sample Year	Sample Size	Term Pregnanacy or Recent birth		Source
1992	76	36	(47 %)	FWS unpublished data
1993	45	15	(33 %)	Seagars et al. 1995
1994	68	24	(35 %)	This study
1995	51	29	(57 %)	This study
1996	81	64	(79 %)	This study
All Years	**321**	**168**	**(52 %)**	

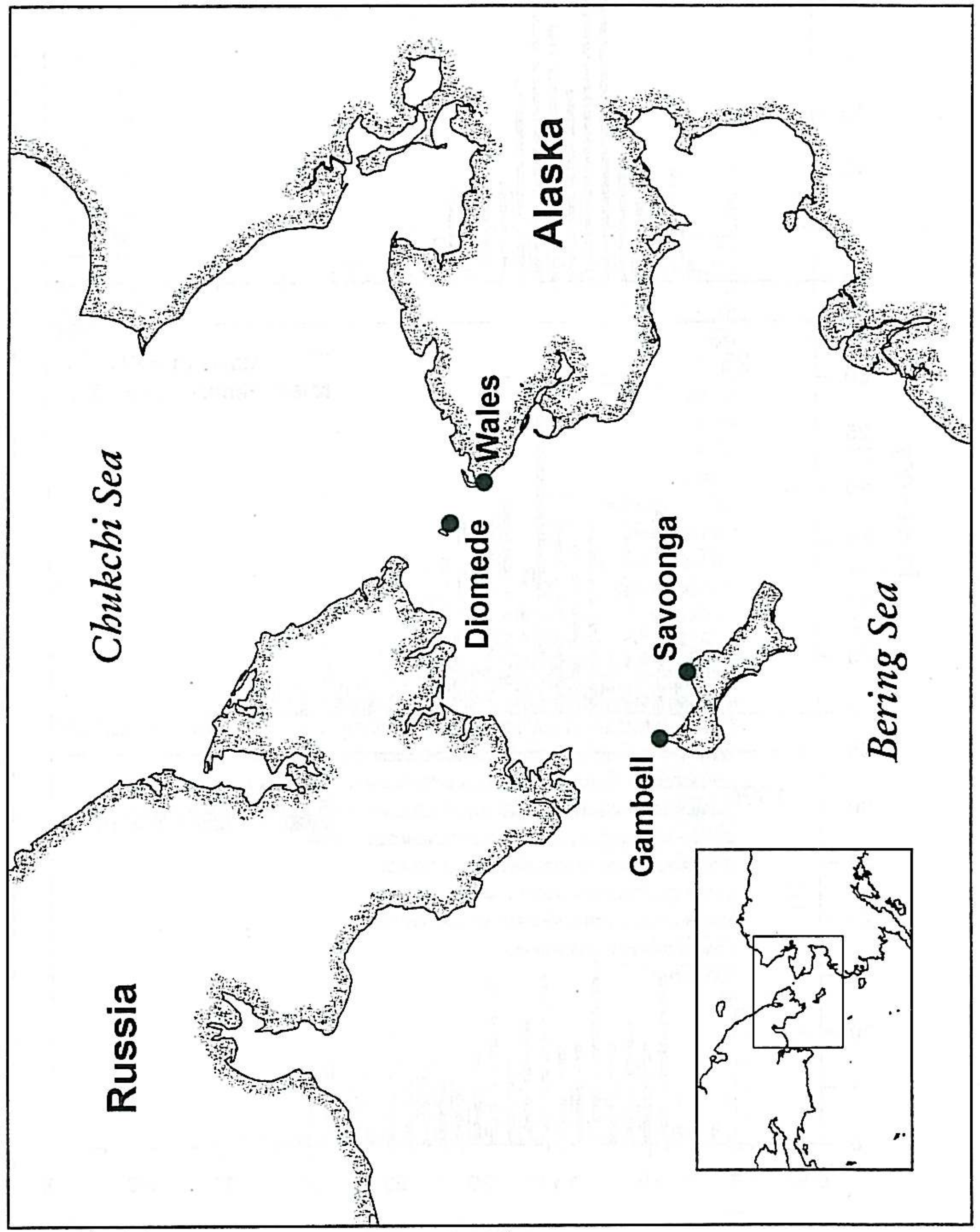

Figure 1. Location of Alaska villages where the Walrus Harvest Monitor Project was conducted, 1994-1996.

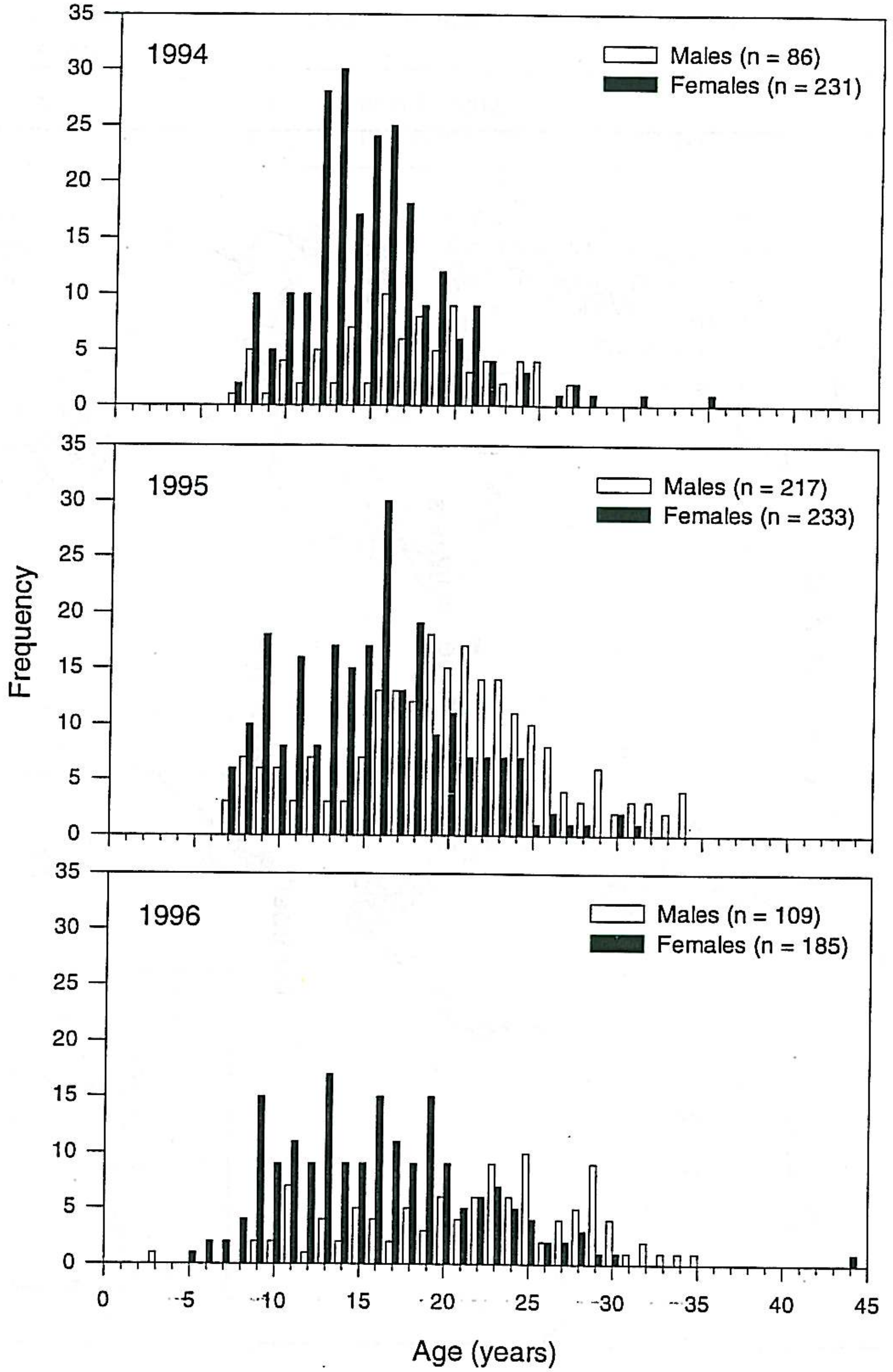

Figure 2. Age-sex composition of spring walrus harvests in the Bering Strait region of Alaska, 1994-1996. Does not include calf and yearling data, or animals of unknown gender.

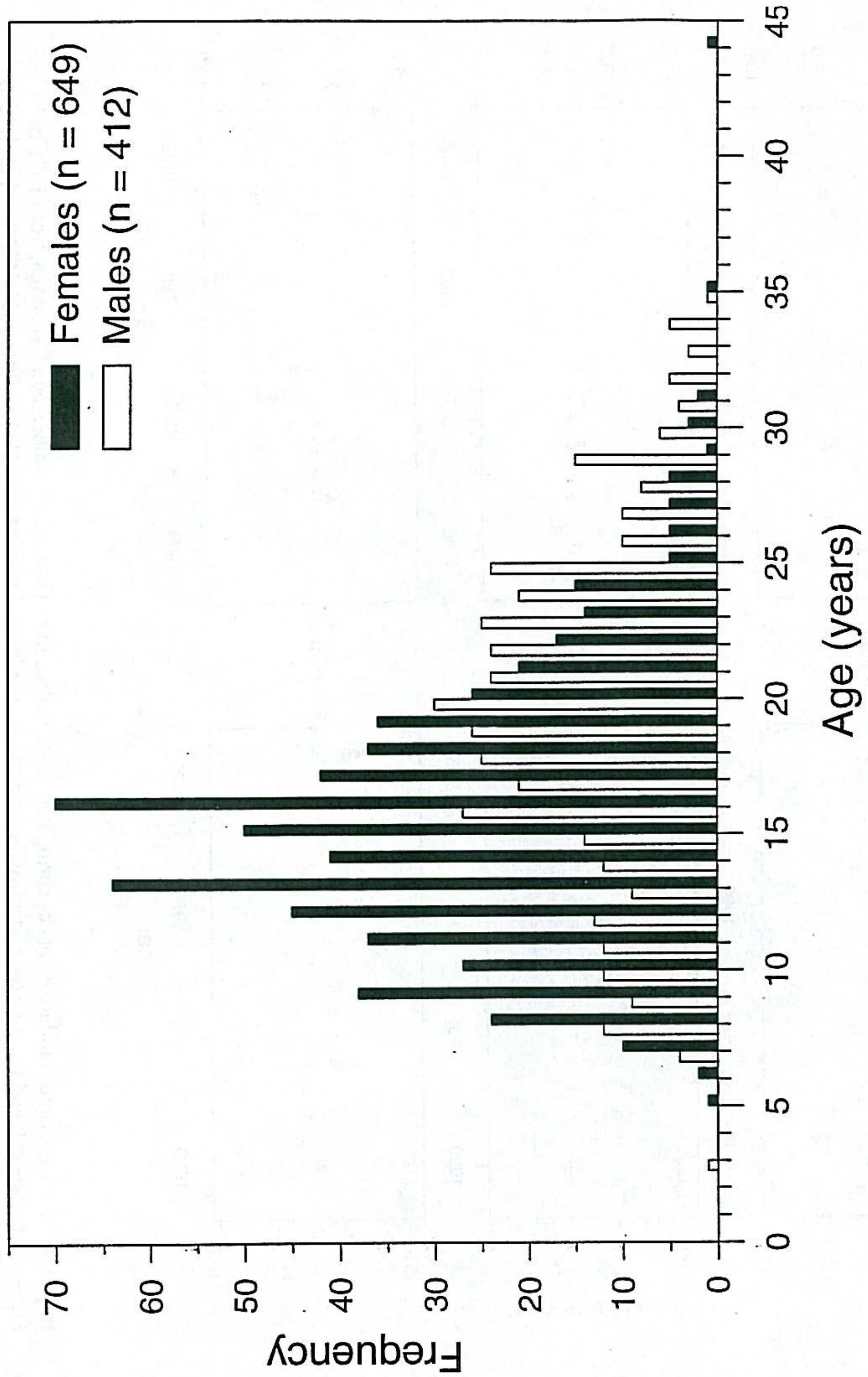

Figure 3. Age-sex composition of spring walrus harvests in the Bering Strait region of Alaska, 1994-1996. Does not include calf and yearling data, or animals of unknown gender.

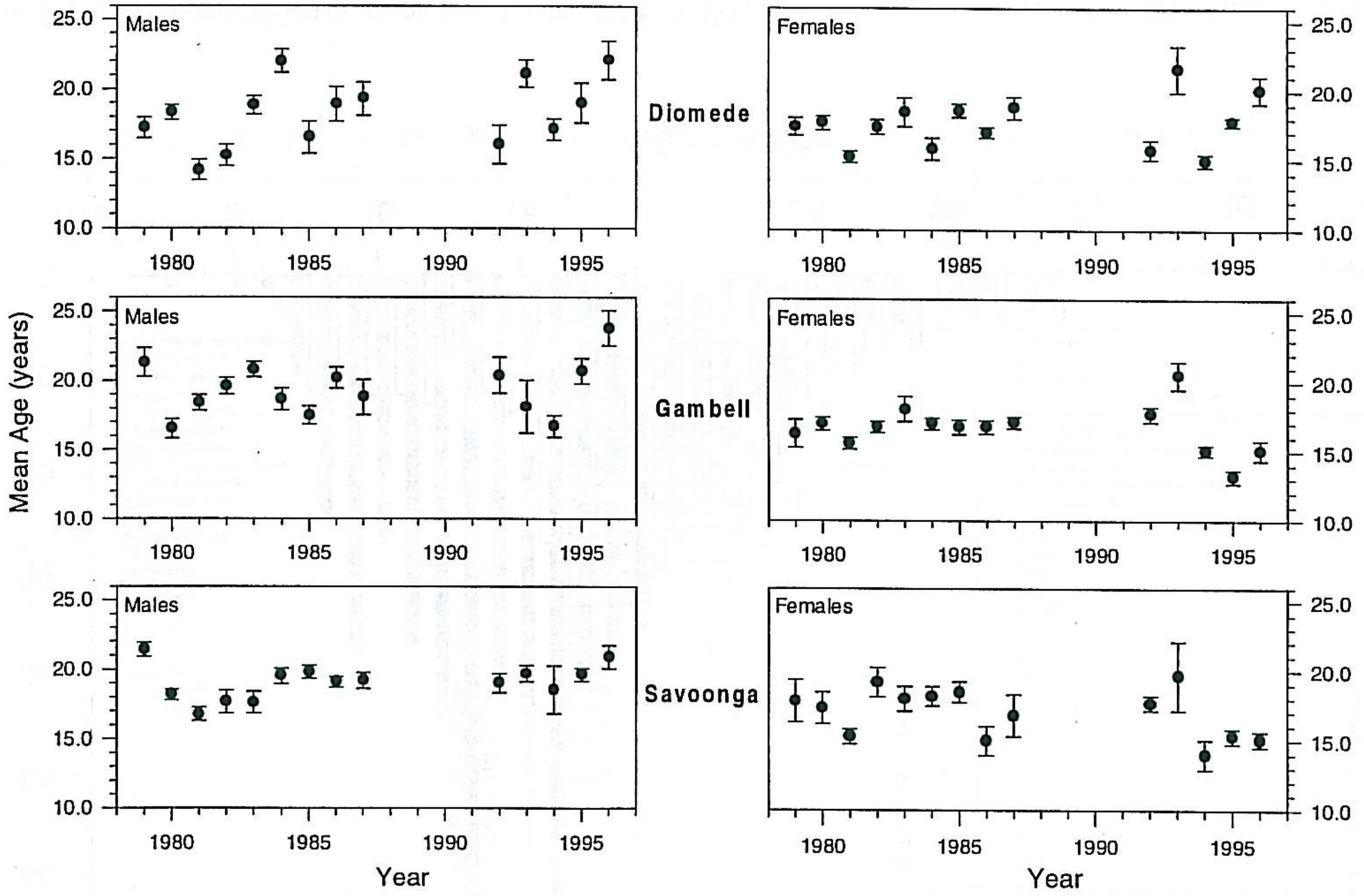

Figure 4. Mean ages and standard errors of spring harvested walrus from Diomede, Gambell and Savoonga, from 1979 to 1996. Does not include calf and yearling data, or animals of unknown gender. 1979-1984 (Fay et al. 1986); 1985-1987 (Fay et al. 1989); 1992 (Garlich-Miller unpublished data);1993 (Seagars et al. 1995).