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POPULATION GENETICS STUDIES OF THE
WALRUS (*ODOBENUS ROSMARUS*): A
SUMMARY AND INTERPRETATION OF
RESULTS AND RESEARCH NEEDS

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ABSTRACT

A summary of population genetics data is presented for the walrus (*Odobenus rosmarus*). Current information on the ecology and behavior of the species is highlighted to aid in the interpretation of genetics results and to suggest future areas of research. Walruses are discontinuously distributed across the Arctic and are currently subdivided into six regional populations on the basis of historical distribution and morphology. Few population genetics studies have been conducted on the walrus. Only three of the six regional populations have been surveyed with biochemical or molecular techniques. Analysis of mitochondrial DNA (mtDNA) variation among walruses from the northern Pacific (Chukchi Sea) and western Atlantic (Greenland) regions revealed 13 haplotypes; 6 were found only in Pacific walruses while 7 were unique to the Atlantic subspecies. Estimates of sequence divergence between Atlantic and Pacific haplotypes were 1.0%–1.6%. No evidence of microgeographic structuring within the northern Pacific or western Atlantic regional populations was found on the basis of mtDNA haplotype frequency distributions or multilocus minisatellite band sharing. Minisatellite analysis of adult-juvenile and adult-adult pairs suggests that assemblages of walruses on individual ice floes

are made up at least in part by groups of related individuals from more than one generation. Furthermore, high mtDNA haplotype diversities and low minisatellite band-sharing values suggest that both the northern Pacific and western Atlantic walrus have retained a high degree of genetic variability.

Recent advances in molecular biology have greatly expanded the number of informative, heritable markers that may be used to characterize individuals, populations, and higher taxonomic groupings. Despite growing appreciation of the applications for these new techniques, and despite their increased use in basic and applied research on many marine mammal species, comparatively few genetics studies have been conducted on walrus (*Odobenus rosmarus*).

The general objectives of this report are to summarize aspects of walrus biology pertinent to the interpretation of empirical genetics data. Specifically, we synthesize background information on walrus ecology, which enables us to provide a series of working hypotheses pertaining to the extent of intra- and interpopulation genetic variation, and to outline further critical areas in which genetics data may provide valuable information. In addition, we wish to highlight results of the few empirical genetics studies that have relevance to systematics, issues of macro- and microgeographic population structuring, and conservation.

BACKGROUND

Odobenus rosmarus is the only extant species of walrus. This species is discontinuously distributed across the entire Arctic Basin and has been coarsely subdivided into six regional populations on the basis of historical distributions and morphology (AI, Hudson Bay–Davis Strait; AII, Eastern Greenland; AIII, Svalbard and Franz Josef Land; AIV, Kara Sea and Novaya Zemlya; PI, Laptev Sea; and PII, Bering and Chukchi Seas; Fig. 1; Fay 1982; Stewart *et al.* 1993; Fay *et al.* 1990¹). Walrus from the first four populations are considered Atlantic walrus (*O. rosmarus rosmarus*), and those from the Bering and Chukchi Seas are considered Pacific walrus (*O. r. divergens*). Walrus from the Laptev Sea have been included in either subspecies by different authors and therefore have been designated as a separate subspecies (*O. r. laptevi*) by Chapskii (1940; cited in Fay 1982) on the basis of morphology. Historically, a seventh regional population was recognized in the eastern Canadian maritime regions around the Gulf of St. Lawrence, Newfoundland, and Nova Scotia. However, walrus were absent from these areas more than 100 yr ago.¹ Dramatic reductions in population numbers in other areas and extirpation of many historical populations may have significantly affected genetic variability within and among populations across the species range.

Low fecundity and the species' polygamous mating regime suggest that

¹ Fay, F. H., B. P. Kelly and B. A. Fay. 1990. The ecology and management of walrus populations. Marine Mammal Commission Report, U.S. National Technical Information Service PB91-100479. 186 pp.

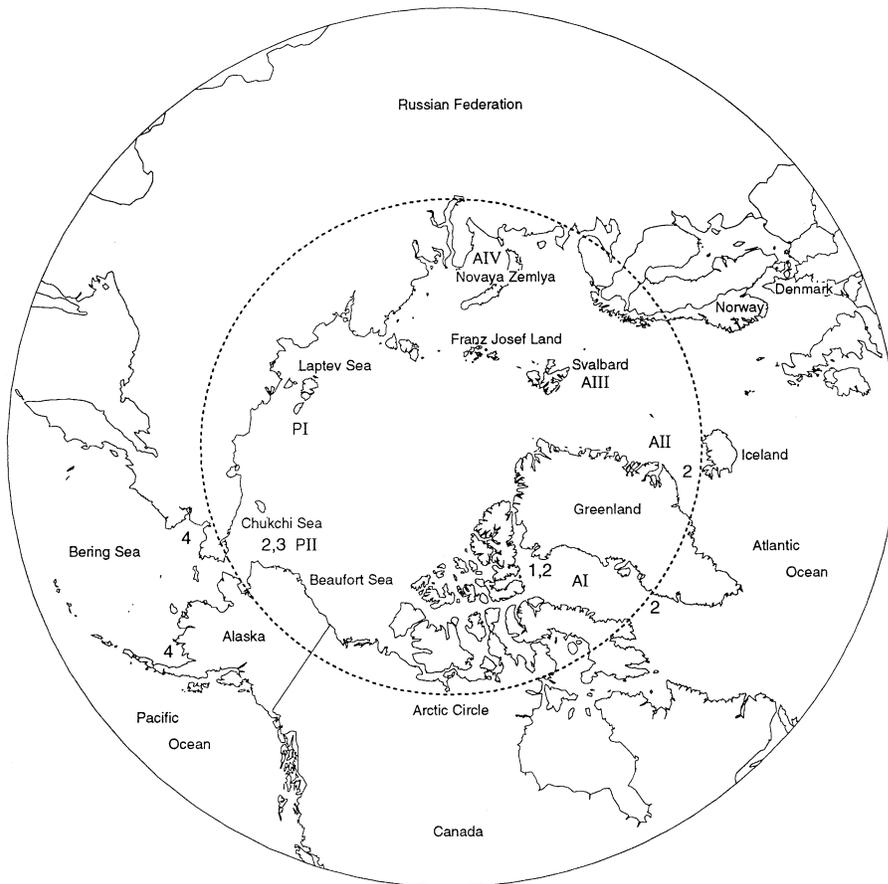


Figure 1. Range distribution of the walrus (*Odobenus rosmarus*) showing the locations of proposed population boundaries (AI, AII, AIII, AIV, PI, and PII; see text for descriptions) and sampling locales (Arabic numerals) of the population genetic studies detailed in Table 1.

populations may be susceptible to loss of genetic variation. Total population size does not necessarily reflect effective population breeding numbers. Walrus are long-lived (± 30 yr), and reproductive rates are relatively low. Age at first reproduction for females varies from 4 to 12 yr, and the gestation period may vary from 15 to 16 mo (Fay 1982). The maximum rate of production is one calf every two years. Most males become fertile at 9–10 yr of age. But because of an apparently highly polygamous breeding system, males are not likely to participate until physically mature, some 5–6 yr later (Fay 1982, Fay *et al.* 1984²).

² Fay, F. H., B. P. Kelly, P. H. Gehrlich, J. L. Sease and A. A. Hoover. 1984. Modern populations, migrations, demography, trophics, and historical status of Pacific walrus. Unpublished report RU-611. Environmental Assessment of the Alaska Continental Shelf.

Interpretation of spatial heterogeneity in genetic characteristics must be based on the movement ecology of the species. Walruses are usually found in relatively shallow-water areas over the continental shelves, where they feed on benthic invertebrates to depths of 107 m (Fay and Burns 1988). Walruses seem to prefer to haul out on ice to rest, molt, and bear young, although they also haul out on land (mainly small rocky islands or sand spits) when no ice is available (Fay 1982). Most populations migrate seasonally with the advance and retreat of sea ice. Although Pacific walruses may migrate more than 3,000 km per year (Fay 1957), Atlantic walruses travel somewhat less. The species' high vagility and highly concentrated nature of breeding activities suggests that little genetic structuring should exist over considerable geographic areas (*e.g.*, the Bering and Chukchi Seas in the northern Pacific).

PACIFIC WALRUS ECOLOGY

The distribution and abundance of the Pacific walruses has been affected greatly by human activities (Fay *et al.* 1989). By the mid-1800s, large herds of male walruses that summered in Bristol Bay and the Pribilof Islands were nearly extirpated by hunters. Herds of females and young on the sea ice to the north were probably not greatly affected (Fay 1957). From 1848 to 1880, whalers harvested increasing numbers of walruses coincident with worldwide declines in whale abundance. By 1880, the Pacific walrus population was reduced to about half its former size. Commercial walrus harvest continued at a reduced rate until about 1914, when the world market for walrus products collapsed (Fay *et al.* 1984, 1989). Continued harvest by natives and traders virtually extirpated the southern herds of summering males in the Bering Sea.

Poorly regulated Soviet harvests from 1931 to 1956 resulted in further depletion of walrus herds. Harvest records indicate that the Pacific population may have reached its lowest historical level in the mid 1950s (Fay 1982). Kleinenberg (1957) noted that of the 33 traditionally used coastal concentration areas on the Chukchi Peninsula, only three remained in use by 1954. Rigid harvest restrictions were enacted in both Russia and Alaska in the late 1950s and population numbers increased. The population in 1960 was estimated at 70,000–100,000 (Fay 1982). For Pacific walruses, nearly all the pre-nineteenth-century range is now occupied. The minimum population estimate for the Bering–Chukchi region, based on the most recent (1990) census, is 201,000.³

After breeding in the Bering Sea (December–March), female adults, young of the year, subadults of both sexes, and some adult males move north with the retreating sea ice (April–June) to summer in the northern Gulf of Anadyr and the Chukchi Sea (July–September). Most adult male Pacific walruses do not migrate northward but summer in the Bering Sea on traditional haul-outs

³ Gilbert, J. R., G. Fedoseev, D. Seagars, E. Ruzlivalov and A. Lachugin. 1992. Aerial census of Pacific walrus, 1990. U.S. Fish & Wildlife Service Administrative Report R7/MMM 92-1, 33 pp.

in Bristol Bay (Alaska) and on the Russian Chukchi and Koryak coasts (Fay 1982). Resightings of marked males at the same summer haul-out areas in different years suggest that males exhibit a high degree of site fidelity to specific summer areas (Taggart 1987). Little information is available about females' fidelity to summering areas.

The location of breeding concentration areas varies greatly from year to year due to climatic conditions and the southern extent of sea ice. Two main concentration areas have been observed for Pacific walruses during the breeding season; these areas coincide with the location of major polynyas southwest of Nunivak and St. Lawrence Islands (Fay 1982). Juxtaposition of these aggregations to one another varies greatly from year to year depending on the southern extent of winter sea ice. Little is known of the significance of spatially segregated breeding, foraging, or haul-out areas. Current management of the Chukchi-Bering Sea population is based upon the assumption that individuals in these two areas are part of one panmictic group.

ATLANTIC WALRUS ECOLOGY

Many hypotheses but few data exist on stock relationships of Atlantic walruses in the eastern Canadian Arctic and Western Greenland. Freuchen (1921) and Vibe (1950, 1956) proposed that walruses migrate seasonally in a counterclockwise manner. Walruses wintering in central Greenland move northward in May and June to join those that winter in northern Baffin Bay and Smith Sound. In October, walruses are believed to migrate south along eastern Baffin Island, crossing the Davis Strait to winter along the west Greenland coast. Vibe (1967) thought some individuals remained on the pack ice in the Davis Strait and occasionally joined walruses in southeastern Baffin Island. Dunbar (1956) suggested that the Hudson Bay, Hudson Strait, and southeast Baffin Island walruses were one population. Richard (1990)⁴ estimated the number of walruses to be 5,500 in Foxe Basin, 1,500–2,600 in northern Hudson Bay, and 1,000–2,000 in Hudson Strait. Movements of walruses in these areas are poorly known.

Walruses of northwest Greenland (Thule area) winter mainly at the edge of the Baffin Bay North Water. Individuals move northward into Smith Sound and Kane Basin in spring, and westward toward Ellesmere Island, Lancaster, and Jones Sound in summer.⁵ No reliable estimate of population size is available.

From observations and recent tagging studies, it appears that walruses found

⁴ Richard, P. 1990. The status of Hudson Bay-Foxe Basin walruses. Pages 3–5 in F. H. Fay, B. P. Kelly and B. A. Fay, eds. The ecology and management of walrus populations. Marine Mammal Commission Report, U.S. National Technical Information Service PB91-100479. 186 pp.

⁵ Born, E. W. 1990. Distribution and numbers of Atlantic walruses in Greenland. In F. H. Fay, B. P. Kelly, and B. A. Fay, eds. The ecology and management of walrus populations. Marine Mammal Commission Report, U.S. National Technical Information Service PB91-100479. 186 pp.

in the Barents, Kara, and White Seas, and in northeastern Greenland, Svalbard, Franz Josef Land, and Novaya Zemlya may be one stock.¹ Although this area is large, and although hunting has been prohibited for the last 30 yr, the number of walrus is estimated to be only roughly 2,000.

The most recent census of walrus in the Laptev Sea estimated the population to be 4,000–5,000 (Fedoseev 1983). These walrus winter in the two polynyas that form along the east coast of the Tiamyr Peninsula and among the New Siberian Islands.⁶ In summer the ice moves offshore over deep water, and the walrus haul out on land along the west shore of the Laptev Sea.

POPULATION GENETIC STRUCTURE

There are few data about levels of genetic variability or degree of population structuring in walrus (Table 1). Several early cytogenetic studies compared walrus to other pinnipeds (Fay *et al.* 1967; Arnason 1974, 1977). These studies have shown that the walrus karyotype is easily distinguished from those of all other pinnipeds by a large pair of submetacentric satellite chromosomes. G-banding studies by Arnason (1977) indicated that walrus chromosomes are basically homologous with those of the otariid karyotype, though somewhat modified in arrangement. Population genetic research has been limited to two published accounts (Simonsen *et al.* 1982, Cronin *et al.* 1994) and to two additional studies that are in progress.^{7,8}

Simonsen *et al.* (1982) examined 102 walrus from the Thule region of northwestern Greenland. Thirty-two loci were surveyed with protein allozyme electrophoresis. Three loci were found to be polymorphic, and direct-count heterozygosity was estimated to be 0.033. All samples were obtained from the same area over a two-year period (1977–1978). The authors reported no significant differences in allele frequency between years. No evidence for nonrandom mating (based on deviations from Hardy-Weinberg expected genotypic frequencies) was observed in either year's collection.

Cronin *et al.* (1994) surveyed 87 walrus from the Atlantic (30 from three locations in Greenland; Fig. 1) and the Pacific (57 from four locations in the Chukchi Sea) subspecies. The authors used restriction fragment analysis of PCR-amplified mtDNA to survey variation within three regions of the mtDNA molecule (ND-1, 1931 bp; ND-2, 2283 bp; and ND-3/4, 2213 bp). Twenty restriction enzymes were used for each of the three regions. A total of

⁶ Vishnevskaya, T. Iu., and V. A. Bychkov. 1990. The Laptev walrus. Pages 155–176 in F. H. Fay, B. P. Kelly, and B. A. Fay, eds. The ecology and management of walrus populations. Marine Mammal Commission Report, U.S. National Technical Information Service PB91-100479. 186 pp.

⁷ Scribner, K. T., Alaska Science Center, Biological Resources Division–U.S.G.S., 1011 E. Tudor Road, Anchorage, AK 99503; Steven R. Fain, USFWS Forensics Laboratory, 1490 East Main Street, Ashland, OR 97520; and Sue Hills, Institute of Marine Science, University of Alaska–Fairbanks, Fairbanks, AK 99775. Unpublished data.

⁸ Eric Born, Greenland Fisheries Institute, Tagensvej 135, 2200 Copenhagen, Denmark, and Úlfur Arnason, Genetics Department, University of Lund, Solvegaton 29, Lund S-22362, Sweden, personal communication, September 1994.

Table 1. Literature pertaining to genetic analyses of walrus (*Odobenus rosmarus*).

Study ^a	Reference	N	Genetic marker	Technique	Objectives	Levels of genetic variation	
						Within pop.	Between pop.
1	Simonsen <i>et al.</i> (1982)	102	Allozymes	SGE ^b	Genetic variation	Moderate	—
2	Cronin <i>et al.</i> (1994)	87	mtDNA	PCR-RFLP ^c	Systematics	Moderate	Moderate
3	Scribner <i>et al.</i> (unpubl.)	81	VNTR	Multilocus minisat. ^d	Breeding structure	Moderate	Low
4	Scribner <i>et al.</i> (unpubl.)	68	mtDNA	PCR-RFLP	Spatial variation	High	Low

^a See Figure 1 for locations of studies.

^b Starch-gel electrophoresis.

^c Restriction fragment analysis of PCR-amplified segments of the mitochondrial genome.

^d Jeffreys *et al.* (1985a, b) polycore minisatellite loci.

13 mtDNA haplotypes were resolved. Seven haplotypes were found solely in the Atlantic subspecies samples, and six haplotypes were found only in the Pacific subspecies samples. Estimates of sequence divergence between Atlantic and Pacific haplotypes were 1.0%–1.6%. Estimates of divergence among haplotypes within each region were considerably lower ($P = 0.04\%$ to 0.75%). Haplotype diversity was lowest in the Pacific walrus; 90% possessed the same mtDNA haplotype. Differences in haplotype frequency distributions among the three Atlantic locations suggested some degree of geographic structuring. The three Atlantic locales also differed in nucleotide and haplotype diversity, though results may be dependent on sample size ($n = 10$ per location).

Recently, Scribner *et al.*⁷ extended the work of Cronin *et al.* (1994) by examining additional Pacific walrus samples from the Bering Sea. These collections were made immediately after the breeding season from each of four locations: two in Russian waters (Anadyr Gulf and Koryak) and two along the U.S. coast (Nunivak Island and St. Lawrence Island). Two regions of the mitochondrial genome were surveyed with PCR-amplified mtDNA. Variations in the ND-2 region (surveyed with six restriction enzymes) reported by Cronin *et al.* (1994) and in the previously uninvestigated control region (surveyed with five restriction enzymes) were assayed. Restriction fragment analysis of the control region revealed nine distinct haplotypes that formed two distinct clades. Individuals possessing haplotypes within each major clade were present in each of the four populations and were equally represented in both Russian and U.S. samples (frequencies of haplotypes within clades A and B were 0.555 and 0.445 in Russian samples and 0.564 and 0.435 in U.S. samples; Scribner *et al.*⁷). No significant differences in haplotype frequency were observed among the four locations ($\chi^2 = 23.86$, 27 df, $P > 0.05$). With the ND-2 data alone, moderate (though nonsignificant) levels of haplotype frequency differences were observed between the 1991 Bering Sea and 1987 Chukchi Sea collections ($\chi^2 = 4.45$, 2 df, $P > 0.05$), possibly indicating that different portions of the population were surveyed during each year.

Higher estimates of haplotype diversity from that described by Cronin *et al.* (1994) reflect the high rate of nucleotide substitution in the control region. Sequence analysis based on 400 bp of the control region surveyed for two individuals from two separate sampling locations revealed 19 distinct nucleotide substitutions.

Scribner *et al.*⁷ used multilocus minisatellites (33.15, 33.6—Jeffreys *et al.* 1985*a, b*; and MS1) to investigate the extent of macro- and microgeographic structuring, interindividual relationships, and levels of genetic variability within locales. Samples included Atlantic walruses ($n = 15$) from Thule in western Greenland and Scoresby from eastern Greenland, and Pacific walruses from the four Bering Sea locales ($n = 66$).

For both Pacific and Atlantic walruses, Scribner *et al.*⁷ found that individuals within locales did not exhibit DNA multilocus minisatellite restriction fragment profiles that were significantly more similar to one another than to individuals from a different population (as assayed using the proportion of shared bands of homologous *size—i.e.*, band sharing; Lynch, 1990). For ex-

ample, for Atlantic walruses, band-sharing coefficients (S_i) within the Thule and Scoresby collections were estimated as 0.50 and 0.43, respectively, while interlocation similarities (S_{ij}) were estimated to be 0.41. For Pacific walruses, intralocation band-sharing coefficients were comparatively smaller (range 0.35–0.42). Intersample similarities between eastern and western Bering Sea locations were also comparatively lower (range 0.27–0.37) than was observed for Atlantic walruses. Lower band-sharing coefficients of Pacific walruses relative to Atlantic walruses could suggest larger effective population sizes over historical times, less population structuring, or regional differences in behavioral and movement ecology. No pairwise estimates of divergence among locations were significant within Pacific and Atlantic groups ($P > 0.05$ for all F' statistics), suggesting a lack of geographic structuring within each region.

Average band-sharing values among individuals within locales provide estimates of levels of genetic variation. This information may be used to make inferences of past population demography and social structure. Average band sharing among individuals collected from the same ice floe within a sampling locale were generally low (Scribner *et al.*⁷; $S_i = 0.35$ – 0.42), but several pairs of individuals in three of four of the Pacific sampling locales: Nunivak ($n = 4$), St. Lawrence Island ($n = 3$), and Anadyr ($n = 4$) exhibited band-sharing values of 0.59–0.67. These values far exceeded the averages obtained from their respective sampling locales, but fall within the range of known mother-fetus relationships (0.61–0.67⁷). These comparisons included both adult-juvenile and adult-adult pairs, suggesting that assemblages of walruses on individual ice floes comprise, at least in part, relational groups from more than one generation. The relatively low similarity levels within sampling locations suggest that Pacific and western Atlantic walruses have retained a high degree of genetic variability.

A series of walrus microsatellite loci have recently been cloned and characterized.⁷ Plans are under way for additional work using the hypervariable mtDNA control region and the newly described nuclear microsatellite markers to investigate the extent of microgeographic spatial structuring in Pacific walrus. An additional study of geographic variation in mtDNA haplotype frequencies for walruses from eastern Greenland, Svalbard, and Franz Josef Land is also being conducted.⁸

DISCUSSION

Direct measures of the degree of walrus population structuring have only recently begun (Stewart *et al.* 1993). The earliest stock identification appraisals were based on historical distribution patterns and morphology (Stewart *et al.* 1993), but because of complexities posed by accessibility, handling constraints, and the aquatic habits of walruses, direct methods such as mark-recapture and telemetry have severe limitations as the sole means of stock assessment.

The molecular studies to date suggest that on a macrogeographic scale (*e.g.*, Atlantic *vs.* Pacific), stocks of walruses are indeed genetically divergent. Pacific walruses from the Bering–Chukchi Seas and Atlantic walruses from Hudson

Bay–Davis Strait and Greenland are reciprocally monophyletic with regard to mtDNA haplotype. Relatively high levels of sequence divergence (1.0%–1.6%) further argue for a prolonged period of separation. On a microgeographic level, studies have focused only on the Hudson Bay–Davis Straits, Eastern Greenland, and Pacific Bering–Chukchi Sea populations. Analyses of mitochondrial and nuclear DNAs suggest little population structuring within each region. The large number of haplotypes (Cronin *et al.* 1994, Scribner *et al.*⁷) and low band-sharing values⁷ argue strongly for the retention of high levels of genetic variability and possibly for extensive gene flow. The paucity of comparable data for other regions of the species' range precludes further comparative analyses.

Genetics data must be interpreted in the context of the species' history of exploitation, reproductive biology and behavior, and movement ecology. Centuries of intensive harvest caused dramatic declines in worldwide population numbers and eliminated walrus from large portions of their historical range. If populations were severely reduced in numbers and distribution, subsequent population growth and recolonization of vacant habitat from remnant refugia should produce a diagnostic genetic "signature" on contemporary interpopulation genetic relationships and on levels of genetic variability within each population. Microgeographic comparisons within a region reveal little evidence for substantial levels of spatial variation, suggesting that extant populations may indeed have arisen from a common, remnant population. In contrast to expectations based on historical reductions in population size, walrus (at least those from the Bering–Chukchi Seas and Canadian–Greenland populations) appear to have retained high levels of genetic variation. Populations from Eurasian regions of the Arctic Basin have been harvested for a long time, and current population estimates are considerably lower than those for western Atlantic and Pacific populations (Stewart *et al.* 1993). Thus, walrus populations from the Barents, Kara, White, and Laptev Seas may have retained comparatively lower levels of genetic variation.

The effects of genetic drift (and accumulation of spatial variation in gene frequencies) due to a low effective breeding population may have been countered by the species' propensity for extensive movements. On the basis of sightings of marked individuals and from telemetry data, walrus movements have been recorded between eastern Greenland and the Svalbard Archipelago, and between Svalbard and Franz Josef Land (Stewart *et al.* 1993, Fay *et al.* 1990¹). Population expansion from remnant population refugia after the period of extensive harvest may have homogenized gene frequencies.

The range and seasonal distribution of walrus are intimately tied to movements of sea ice. Walrus generally follow the expansion and retreat of sea ice, which varies dramatically from year to year. The extent of southern movements of winter sea ice can markedly affect the position and potential composition of spring breeding aggregations. For example, during mild winters when contiguous ice sheets are confined to the northern Bering Sea, the entire North Pacific population may be admixed. Alternatively, during severe winters characterized by extensive southerly movements of sheet ice, breeding may

occur in areas associated with major eastern and western polynyas on the United States and Russian sides of the Bering Sea.

RESEARCH NEEDS

Determination of population structure must be considered one of the most pressing research needs. Relatively little is known about the extent of gene flow or the level of genetic variability across the range of the species. Research has concentrated on three of the six recognized stocks. Populations that have yet to be studied are those that warrant the greatest attention due to comparatively low population numbers and broad distributions.

Furthermore, little is known about breeding ecology. What is the reproductive success of individual males? Is there a genetic basis for localized breeding aggregations? Do annual differences in ice floe patterns affect the juxtaposition of local breeding aggregations and thus lead to episodic changes in population breeding structure? Do individuals migrate seasonally in extended familial groups, and are these groups philopatric to traditional breeding, foraging, summering, and haul-out areas? Preliminary data from multilocus minisatellites⁷ suggest that highly polymorphic genetic markers may indeed provide the necessary resolution to address questions about the behavioral ecology of the species.

Because of limited accessibility, sampling has been opportunistic and has not been done to assess directly these questions. We believe, however, that population genetics data will contribute substantially to our understanding of walrus ecology.

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