# Chapter 6

# Molecular Genetic Studies of Population Structure and Movement Patterns in a Migratory Species: The Beluga Whale, *Delphinapterus leucas*, in the Western Nearctic

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## INTRODUCTION

Advances in the fields of molecular biology, evolutionary biology, and population genetics over the past few decades have enabled us to examine variation within species at the molecular level and to interpret the nature of this variation in terms of the evolution and ecology of species and the behavior of individuals within species. By describing patterns of polymorphism at genetic loci, coupled with an understanding of how these loci vary (modes and rates of evolution) and are passed from one generation to the next (modes of inheritance), it is possible to do the following: (1) reconstruct the evolutionary histories of taxa; (2) learn about patterns of dispersal and gene flow which can be of particular relevance to defining units of species management; and (3) assign paternity and determine kinship and thus gain insights into breeding behavior and social organization (Maynard Smith, 1989; Avise, 1994; Mortiz, 1994).

In recent years, molecular genetic techniques have found wide application in the study of marine mammals, a diverse group of organisms that share a common habitat, which traditionally has made their investigation both difficult and expensive (Amos et al., 1993; Baker et al., 1994; Hoelzel, 1993). In this chapter we present findings of a long-term study of the evolutionary history and population structure of beluga whales, *Delphinapterus leucas*, using mitochondrial DNA (mtDNA) and take this opportunity to highlight the utility of this marker in biogeographic and demographic studies of natural populations.

The evolution, distribution, and ecology of the beluga whale has been greatly influenced by the dynamic nature of both the polar ice and seasonal pack. This association with ice, however, presents many challenges to the study of the evolutionary and behavioral ecology of this highly social and wide-ranging marine mammal. Apart from seasonal occurrences near shore, beluga whales remain mostly inaccessible to human observation throughout much of the year. Despite these restrictions, centuries of observation by aboriginal hunters, and in recent years by biologists, have provided us with a basic picture of the major annual events in the life of this species. Over much of its range, the beluga whale migrates hundreds, or even thousands, of kilometers each year between wintering grounds in polynyas or the southern margins of the pack ice and summering grounds in ice-free coastal and adjacent offshore waters of the arctic and subarctic (Kleinenberg et al., 1964; Frost and Lowry, 1990; Richard et al., 1990). They tend to follow established migration routes and occupy geographically distinct traditional summering areas, often in large numbers, where they molt, feed, and rear their young before moving south once more with the advancing ice (Seaman et al., 1982; Caron and Smith, 1990; St. Aubin et al., 1990; Smith et al., 1992, 1994). Because of their predictable occurrence along the coast, either in nearshore leads in spring ice or in coastal waters following ice breakup in summer, beluga whales have long been an important subsistence resource for many coastal residents (McGhee, 1974; Lowry et al., 1989; Heide-Jörgensen, 1994; Savelle, 1995). Their reliance on coastal waters, however, may expose beluga whales to other human-related pres-

sures, including disturbance, pollution and habitat loss (O'Corry-Crowe and Lowry, 1997). This vulnerability, coupled with the fact that some populations have not recovered from past commercial harvest (Reeves and Mitchell, 1987, 1989), highlights the need for a greater understanding of the ecology and population structure of this species and of the impact of human-related mortality on their distribution and productivity. Management units need to be identified and levels of dispersal among these units need to be estimated.

Much of what we know about the distribution and abundance of beluga whales in Alaska and northwest Canada is from sightings made from shore or shore-fast ice (Frost et al., 1983; Burns and Seaman, 1986). More recently, our knowledge has been improved by aerial surveys conducted primarily in the coastal zone during the open water season (e.g., Frost et al., 1993; Lowry et al., 1996; but see Harwood et al., 1996). Inference about population structure and movement patterns is based in large part on compilations of such sighting data. Based primarily on the nonuniform distribution of beluga whales along the coast in the open water season, five separate management stocks of beluga whales have been proposed for waters off Alaska and northwest Canada (Seaman et al., 1988; Frost and Lowry, 1990): a small, geographically isolated stock in Cook Inlet, and four stocks that represent geographically distinct summering concentrations in Bristol Bay, the eastern Bering Sea (primarily Norton Sound), the eastern Chukchi Sea, and the eastern Beaufort Sea (Figure 6.1). The general movement patterns of, and interrelationships among these provisional stocks have been inferred from the timing

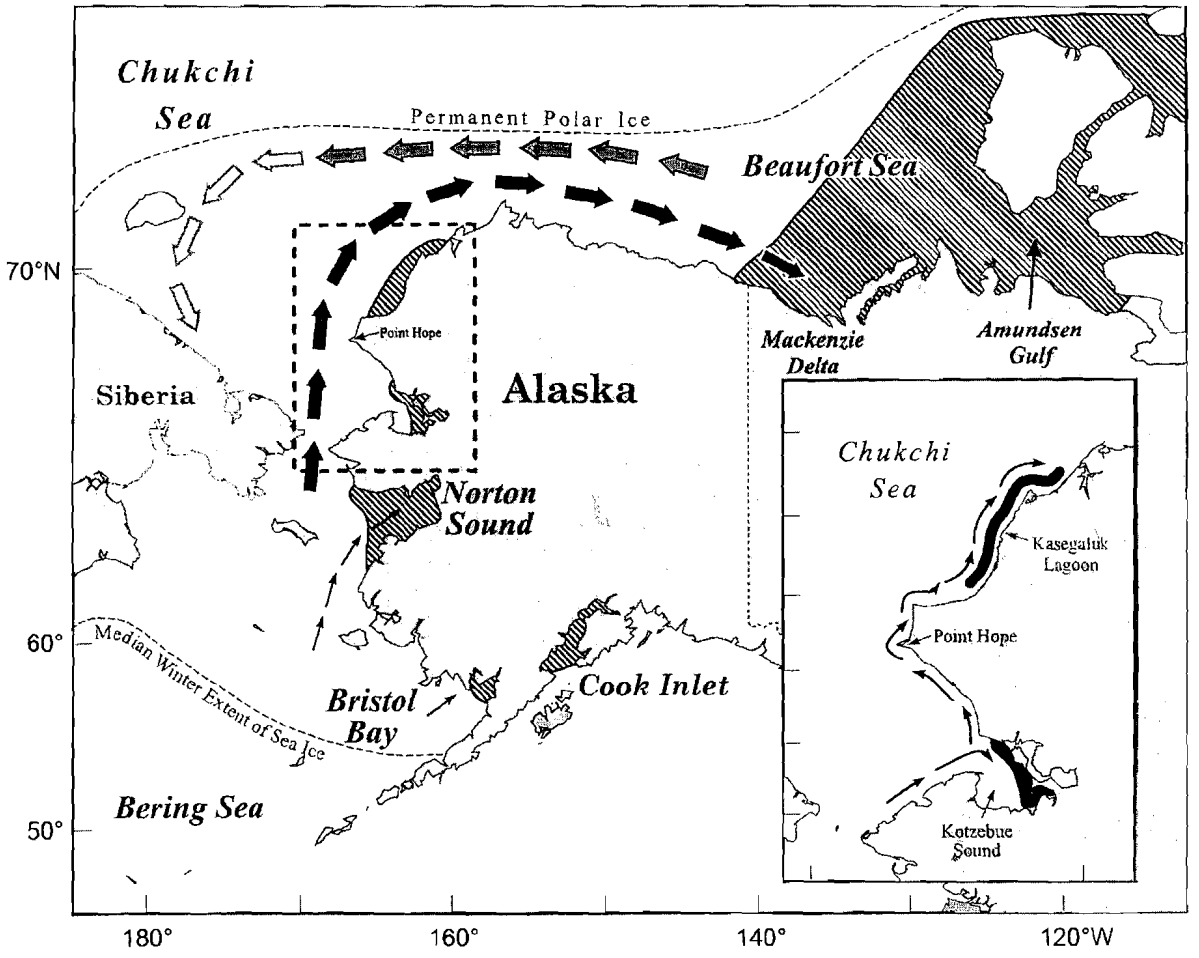


Figure 6.1. The major summering areas (hatched pattern) of beluga whales in Alaska and northwest Canada. From north to south: (1) eastern Beaufort Sea; (2) eastern Chukchi Sea (Kasegaluk Lagoon and Kotzebue Sound; (3) eastern Bering Sea (Norton Sound and the Yukon River delta); (4) Bristol Bay; and (5) Cook Inlet. Black arrows represent spring migration routes, gray arrows represent known autumn routes, and clear arrows represent hypothesized autumn routes. The insert is a more detailed representation of the major concentrations areas (black) and hypothesized movement patterns (→) of beluga whales in the eastern Chukchi Sea (highlighted by the dashed box) during the open water season.

of whale sightings at different locations along the coast. Whales that migrate northward through leads in the ice in spring past Point Hope have been hypothesized to belong to the same stock of whales that enters the shallow coastal waters of the eastern Beaufort Sea and Amundsen Gulf in July (Figure 6.1; Burns and Seaman, 1986; Frost and Lowry, 1990). Similarly, sequential sightings of beluga whales, from south to north, along Alaska's Chukchi Sea coast in summer, along with estimates of abundance at various locations, have led investigators to conclude that the whales which enter Kotzebue Sound in the first half of June continue migrating northward along the coast and eventually arrive at Kasegaluk Lagoon by late June–early July (Frost et al., 1983; Burns and Seaman, 1986; Frost and Lowry, 1990; Figure 6.1).

Such approaches to stock identification, however, have limitations due to incomplete knowledge of year-round distribution, movement patterns, and breeding behavior. No obvious geographic barriers separate the four proposed stocks in Bristol Bay, and the eastern Bering, Chukchi, and Beaufort Seas. In fact, all may share a common wintering ground in the pack ice of the central Bering Sea (Burns and Seaman, 1986; Frost and Lowry, 1990). As breeding apparently coincides with the period of maximum ice extent or spring retreat (Braham, 1984; Burns and Seaman, 1988; Brodie, 1989; Heide-Jörgensen and Teilmann, 1994), interbreeding, as well as individual exchange, among geographic summer concentrations may occur on the common wintering ground or during spring migration. Furthermore, considering the vast distances over which beluga whales can range (Martin et al., 1993; Richard et al., 1997), there may be other opportunities for dispersal among summer concentrations.

With the development of techniques to examine variation within gene products or the DNA itself, it is now possible to address these and some other previously intractable questions. We have used a number of molecular genetic markers, including mtDNA and microsatellite DNA, combined with other kinds of evidence, to study the population structure and behavioral ecology of beluga whales in Alaska and northwest Canada. Much of our research has focused on examining nucleotide sequence variation within mtDNA (O'Corry-Crowe et al., 1997). This extranuclear genome possesses a number of properties, including a maternal mode of inheritance and rapid rate of evolution relative to nuclear coding regions that make it a marker of choice in this type of investigation (Hutchison et al., 1974; Brown et al., 1979; Brown, 1983; Avise, 1986; Moritz et al., 1987). These properties also facilitate the reconstruction or evolutionary relationships among mtDNA haplotypes, which can be compared with their present day geographic distribution to assess the relative importance of historical versus current processes governing population genetic structure (Avise et al., 1987). In this chapter we review recent mtDNA findings on the population structure and evolutionary history of beluga whales in the western Nearctic. We take this opportunity to highlight recent advances in the analysis of mtDNA variation at the intraspecific level. Additional, previously unpublished data is presented to augment earlier data sets and further discuss stock boundaries and migration patterns. Findings of a detailed study on patterns of mtDNA variation within the eastern Chukchi Sea are presented, and we use inferences from this data to underscore the limitations of relying on sighting data alone to reveal movement patterns and define stock boundaries.

**Table 6.1.** Locations From Which Beluga Whales Were Sampled

| Location | No. of sampling sites | Sample size | Haplotype diversity ($H$) | Nucleotide diversity % |
|---|---|---|---|---|
| Cook Inlet | 6 | 38 | 0.514 | 0.23 |
| Bristol Bay | 8 | 24 | 0.163 | 0.12 |
| Norton Sound | 6 | 66 | 0.492 | 0.19 |
| Kotzebue Sound | 6 | 20 | 0.726 | 0.38 |
| Kasegaluk Lagoon | 2 | 156 | 0.730 | 0.58 |
| Eastern Beaufort Sea | 9 | 123 | 0.735 | 0.38 |
| *Mackenzie Delta and Amundsen Gulf* | 7 | 86 | 0.726 | 0.37 |
| *Point Hope* | 2 | 37 | 0.769 | 0.42 |
| All locations | 37 | 427 | 0.844 | 0.51 |

## MATERIALS AND METHODS

Beluga whale tissue samples, primarily skin, have been collected from 37 separate geographic locations, representing six areas of summer concentration and one spring migration route, in the waters adjoining Alaska and northwest Canada over a 20-year period from 1977 to 1997 (Figure 6.1; Table 6.1). Specimens sampled were either from individuals taken during aboriginal hunts or from beachcast or biopsied animals. Many of the samples collected by native hunters were obtained through the Alaska Beluga Whale Committee. Sample preservation and DNA extraction followed standard protocols, and the hypervariable region of the mitochondrial genome was amplified and the sequence determined as described in O'Corry-Crowe et al. (1997). Both strands were sequenced and analyzed on an ABI 373A or 377 Automated Sequencer, and the data was edited and aligned with the SeqEd™ multiple sequence editor program (ABI, 1992).

The amount and nature of DNA polymorphism within the control region were assessed by estimating both haplotypic (Nei and Tajima, 1981) and nucleotide (Nei, 1987) diversity. Traditional phylogeny reconstruction methods such as maximum parsimony (character-based) and neighbor-joining (distance-based) are of limited value and are often inappropriate in analyzing intraspecific mtDNA data sets. This is because mtDNA data at this taxonomic level often possesses extensive homoplasy (parallel mutations and reversals), low numbers of informative sites, and/or few differences among sequences. Classical phylogenetic inference would result in multiple alternative phylogenies making it difficult to estimate the true phylogeny. Thus, phylogenetic relationships among nucleotide sequences within the beluga whale were inferred from a minimum spanning network of the unique haplotypes (Excoffier et al., 1992; Excoffier and Smouse, 1994; Bandelt et al., 1995). With the aid of the MINSPNET (Minimum Spanning Network) (Excoffier and Smouse, 1994) and NTSYS-pc (Numerical Taxonomy and Multivariate Analysis System) (Rohlf, 1990) computer programs, haplotypes were connected by a series of mutational events to all other haplotypes through a set of equally parsimonious pathways. Intermediate consensus haplotypes were reconstructed to obtain most parsimonious connections among haplotypes. In these networks, haplotypes serve both as nodes and branch tips, and all character conflicts are included in the form of reticulations. Optimal trees were chosen from the set of alternative minimum spanning trees (MSTs) by incorporating information on haplotype frequency and geographic location (Excoffier et al., 1992; Crandall and Templeton, 1993; Excoffier and Smouse, 1994).

Two main approaches were used to measure the degree of genetic differentiation among geographic strata. The first was based on a traditional analysis of haplotype frequencies. Wright's fixation index of population subdivision $F_{ST}$ was estimated by an analysis of the distribution of haplotypes among areas according to Excoffier et al.'s (1992) analysis of molecular variance (AMOVA) method using the ARLEQUIN version 1.1 program (Schneider et al., 1997) where the significance of the test statistic is determined by multiple permutation of the original data. The second approach incorporates information on genetic differences among haplotypes as well as their frequencies into the same *anova* format. The model we used for estimating the evolutionary distances between pairs of sequences was that of Tamura and Nei (1993). Pairwise distances were calculated using the MEGA version 1.0 computer program (Kumar et al., 1993). For a more detailed description of the analytical methods see O'Corry-Crowe et al. (1997).

## RESULTS

In the original study, 29 unique mtDNA haplotypes were found among 324 individual whales sampled from what were considered the five major summering areas (Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chukchi Sea, and eastern Beaufort Sea) and one migration route (animals collected off Point Hope during the northward migration in the spring). Overall haplotype diversity was high (0.844) relative to values for individual locations (0.163–0.736) suggesting significant differences in haplotypic composition among areas. Nucleotide diversity varied widely among areas (0.15%–0.57%), and no evidence was found for selection acting on the 410 base pair segment of the mitochondrial genome analyzed (O'Corry-Crowe et al., 1997). Samples from an additional 103 whales, primarily from the Chukchi and Beaufort Seas, have been analyzed in an effort to clarify relationships among groupings of whales along the coast in summer or migrating through leads in the seasonal ice in spring. The pattern of genetic diversity found within and among sampling areas in this larger sample set was similar to our initial findings (Table 6.1).

## Phylogeography

Two new haplotypes, nos. 33 and 34, were described in the recent analysis. Phylogenetic relationships among all unique haplotypes were inferred from a minimum spanning network. The overall frequency of and relationships among the 31 unique sequences recorded in Alaskan and northwest Canadian waters are represented on the network in Figure 6.2. This network is characterized by a number of starlike phylogenies with several rarer haplotypes linked to a phyletically more abundant central haplotypes. Optimal trees were chosen from this network using information on haplotype frequency and geographic distribution. Haplotype diversity among the major summer concentration areas is presented in Figure 6.3 as a series of one most probable minimum spanning tree where highlighted circles represent the presence of a given haplotype in a particular area. Haplotype 5 was the most commonly recorded haplotype and was present in all six summering areas (i.e., treating Kotzebue Sound and Kasegaluk Lagoon separately). A number of less abundant haplotypes (e.g., 1, 2, 4, and 9) were found in two or three subpopulations while the majority were rare and typically encountered in only one subpopulation. The haplotypes from particular areas tend to occupy specific portions of the optimal tree. This representation of haplotype frequency and interrelationships by area suggests that geographic differentiation is a combination of evolutionary radiation and frequency changes due to drift and gene flow.

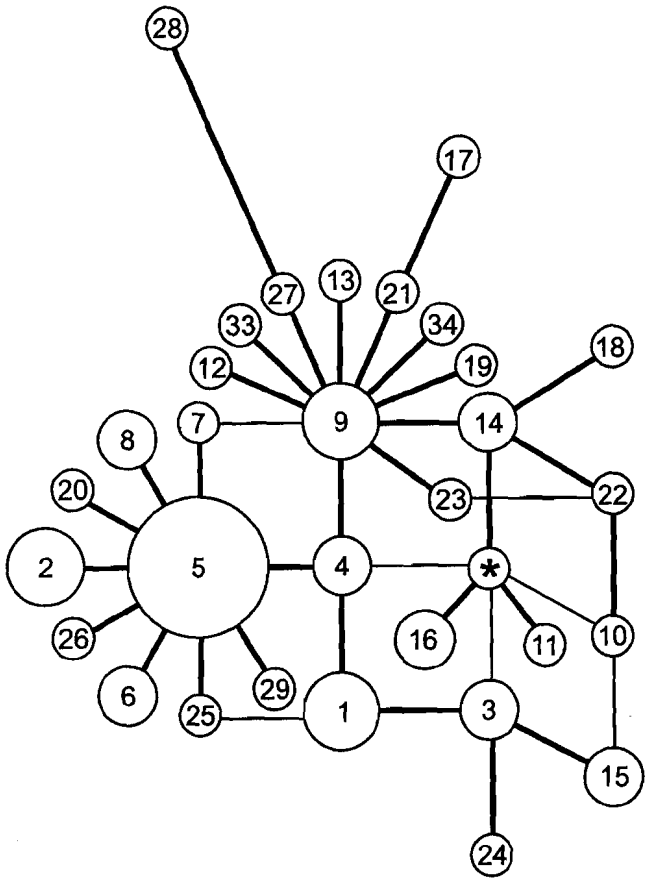


Figure 6.2. Minimum spanning network of the 31 unique mtDNA haplotypes. The reconstructed consensus haplotype is denoted by an asterisk. Each link represents a unique mutational event, except in the case of the link between haplotypes 27 and 28 which represents two mutations. Haplotype sizes reflect their abundance in the total sample. Haplotypes are numbered as referred to in the text. A single most parsimonious tree is indicated by the bold lines. (Note that haplotypes nos. 30, 31, and 32 have been documented from the Sea of Okhotsk in Russia and are not presented here.)

## Geographic Subdivision

In the earlier analyses, both the frequency-based $F_{ST}$ and distance-based $\Phi_{ST}$ statistics revealed a high degree of genetic subdivision among the five provisional stocks (O'Corry-Crowe et al., 1997). We also found that whales caught in the spring off Point Hope were indistinguishable from whales that summer in the eastern Beaufort Sea. In this case, however, the former sample was significantly differentiated from the geographically closer summer concentrations in the eastern Chukchi and Bering Seas, respectively. The molecular genetic analysis therefore agreed with our knowledge of movement and seasonal distribution patterns in that animals which migrate past Point Hope in spring are part of the same stock that occur in the eastern Beaufort Sea in summer (Figure 6.1). Therefore, samples from both locations were combined in future analyses of the eastern Beaufort Sea stock.

Analysis of the larger data set (n = 427) confirmed our earlier findings of significant genetic subdivision among summering grounds and not between the spring migration route (i.e., Point Hope) and the Beaufort Sea (Table 6.2). By contrast, the expanded analysis found structure within the eastern Chukchi Sea with Kotzebue Sound significantly differentiated from Kasegaluk Lagoon ($F_{ST} = 0.244$, $P < 0.001$; $\Phi_{ST} = 0.167$, $P < 0.001$, see insert in Figure 6.1). The majority of Kotzebue samples (15/20) were from a single year, 1996, raising the possibility that the significant result may be an artifact of sampling bias. Further analysis revealed, however, that the animals sampled in Kotzebue Sound in June 1996 were significantly differen-

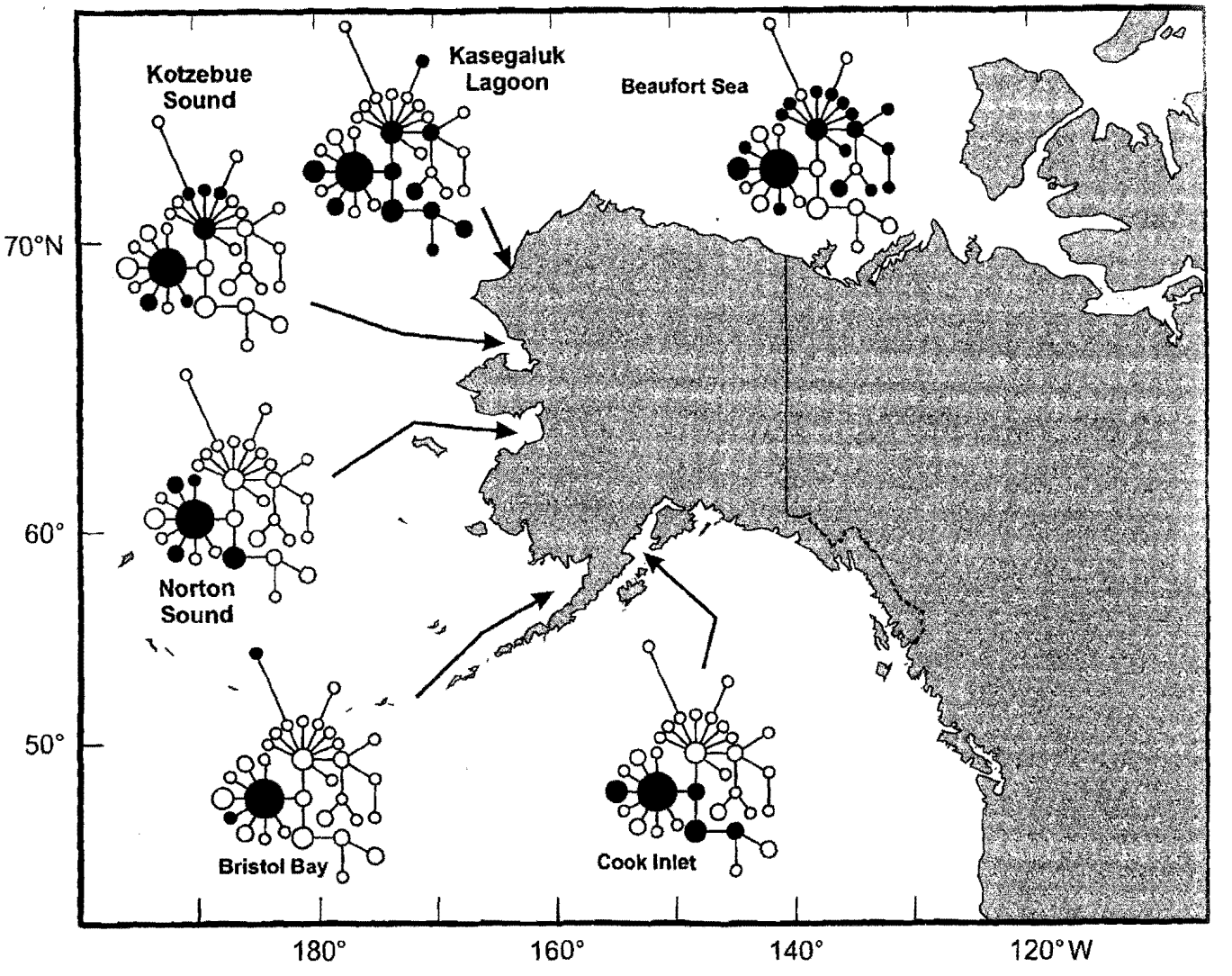


Figure 6.3. Haplotype diversity among the summering groups of beluga whales in Alaska and northwest Canada represented on an optimum minimum spanning tree. Solid circles indicate the set of haplotypes in the tree that were found in each group. Haplotype size reflects overall frequency, not frequency within each area.

tiated from whales sampled along the Chukchi Sea coast at Kasegaluk Lagoon (n = 37) 2–3 weeks later ($F_{ST} = 0.182$, $P < 0.001$; $\Phi_{ST} = 0.174$, $P < 0.01$). The increased sample size from Point Hope enabled us to compare sets of samples collected 20 years apart. We were unable to differentiate among samples collected at this location in the spring of 1977 (n = 15) and 1997 (n = 13) ($F_{ST} = 0.016$, $P = 0.248$; $\Phi_{ST} = -0.004$, $P = 0.441$).

## DISCUSSION

### Phylogeography and the Origins of Populations

Insights into the historical and contemporary processes governing intraspecific population structure can be gained from a comparison of the phylogenetic relationships among mtDNA haplotypes and the geographic distribution of these lineages. We believe that parsimony networks are often the most appropriate method for reconstructing intraspecific mtDNA phylogenies, and can be particularly useful in such phylogeographic (analyses, Avise et al., 1987) analyses at this taxonomic level. This approach to phylogenetic inference, unlike more traditional methods, accommodates the possibility that for the geological time scales involved (thousands instead of millions of years), most of the ancestral as well as descendent haplotypes may still be extant. These networks are also probably the most successful method at accommodating, and presenting in an easily interpretable manner, the polychotomous nature of evolution

Table 6.2. $\Phi_{ST}$ (A) and $F_{ST}$ (B) Estimates (below Diagonal) and Significance (P) Values From 1000 Permutations (above Diagonal) Among the Six Major Summering Areas and the Spring Migration Route

| A | I | II | III | IV | V | VI | *VII* | *VIII* |
|---|---|---|---|---|---|---|---|---|
| I Cook Inlet | — | .00001 | .00001 | .00001 | .00001 | .00001 | *.00001* | *.00001* |
| II Bristol Bay | 0.584 | — | .1189 | .0140 | .00001 | .00001 | *.00001* | *.00001* |
| III Norton Sound | 0.514 | 0.019 | — | .00001 | .00001 | .00001 | *.00001* | *.00001* |
| IV Kotzebue Sound | 0.430 | 0.147 | 0.158 | — | .00001 | .00001 | *.00001* | *.00001* |
| V Kasegaluk Lagoon | 0.210 | 0.200 | 0.203 | 0.167 | — | .00001 | *.00001* | *.00001* |
| VI Eastern Beaufort Sea[a] | 0.430 | 0.430 | 0.443 | 0.178 | 0.291 | — | | |
| *VII Point Hope* | *0.419* | *0.433* | *0.453* | *0.142* | *0.241* | | — | *.8272* |
| *VIII Mackenzie–Amundsen* | *0.455* | *0.459* | *0.473* | *0.192* | *0.296* | | *−0.012* | |
| **B** | | | | | | | | |
| I Cook Inlet | — | .00001 | .00001 | .00001 | .00001 | .00001 | *.00001* | *.00001* |
| II Bristol Bay | 0.617 | — | 0.140 | .00001 | .00001 | .00001 | *.00001* | *.00001* |
| III Norton Sound | 0.431 | 0.067 | — | 0.170 | .00001 | .00001 | *.00001* | *.00001* |
| IV Kotzebue Sound | 0.378 | 0.192 | 0.074 | — | .00001 | .00001 | *.00001* | *.00001* |
| V Kasegaluk Lagoon | 0.273 | 0.430 | 0.341 | 0.244 | — | .00001 | *.00001* | *.00001* |
| VI Eastern Beaufort Sea | 0.344 | 0.396 | 0.312 | 0.124 | 0.211 | — | | |
| *VII Point Hope* | *0.348* | *0.447* | *0.334* | *0.119* | *0.187* | | — | *.9141* |
| *VIII Mackenzie–Amundsen* | *0.355* | *0.409* | *0.320* | *0.123* | *0.219* | | *−0.012* | |

[a]Eastern Beaufort Sea is Point Hope and Mackenzie–Amundsen combined.

where mutation within a lineage or haplotype may give rise to several new lineages, all of which may coexist for some time. Analyses based on coalescent theory make it possible to identify ancestral haplotypes in these intraspecific phylogenies (Crandall and Templeton, 1993). Older haplotypes tend to have higher frequencies, occur in the interior of phylogenies, and possess greater numbers of mutational connections (Donnelly and Tavaré, 1986; Crandall and Templeton, 1993). Furthermore, in subdivided populations ancestral haplotypes are predicted to have the widest distribution among subpopulations (Takahata, 1988), while empirical studies suggest that a rapid radiation of a species from an ancestral population into several discrete populations will result in a pattern of common, widespread haplotypes connecting to several other population-specific haplotypes in a starlike phylogeny (Lavery et al., 1996).

The phylogeography of mtDNA haplotypes in the beluga whale, when viewed in conjunction with the chronology of postglacial events (ice shelf retreat, isostatic rebound, and sea level change), enables us to reconstruct the recent evolutionary history of this species. The starlike phylogenies, coupled with the low level of sequence divergence (i.e., nucleotide diversity) observed in beluga whales compared to other cetacean species (e.g., Baker et al., 1993; Dizon et al., 1994; Rosel et al., 1994), are consistent with a relatively recent radiation of beluga whale into the western Nearctic following the retreat of the Pleistocene ice sheets. The high frequency, widespread distribution, and central position of haplotype 5 in the beluga whale phylogeny (Figures 6.2 and 6.3) suggests that this haplotype was present in the ancestral population and was subsequently distributed among all colonizing summer concentrations once the ice retreated. Since then, population-specific haplotypes have evolved, or through limited gene flow and drift have become restricted to individual populations (e.g., haplotype 26 in Bristol Bay, haplotypes 7 and 8 in the eastern Bering Sea, haplotype 29 in Kotzebue Sound, and haplotypes 20 and 25 in the Beaufort Sea). The predominant localization of the star phylogeny centered on haplotype 9 within the Beaufort Sea may reflect a population expansion that occurred in this region following the opening of the Bearing land bridge 11,000 years ago (Figures 6.2 and 6.3; Denton and Hughes, 1981; Elias et al., 1996). Significantly perhaps, the two haplotypes discovered in the most recent analysis were part of this assemblage and were also from the Beaufort Sea subpopulation (Figures 6.2 and 6.3). A number of other independent studies have been conducted on mtDNA variation in beluga whales throughout Canada and Greenland and have

made similar inferences about the postglacial biogeography of this species (Brennin et al., 1997; Brown Gladden et al., 1997). A detailed analysis of all available data on molecular genetic variation in conjunction with a review of glacial history would be revealing.

### Geographic Subdivision

Analysis of sequence variation within the mitochondrial genome revealed substantial levels of genetic subdivision among summer concentrations of beluga whales in the western Nearctic that are comparable with some of the highest values found in cetaceans to date (Rosel, 1992; Archer, 1996; Palsbøll et al., 1997). Cook Inlet is the most genetically distinct of all geographic subpopulations with respect to mtDNA, an indication perhaps that the Alaska Peninsula is an effective barrier to genetic exchange or that drift in this small population offsets any homogenizing effects of gene flow. Although no obvious geographical barriers exist between the remaining summer concentrations, all were found to be genetically differentiated from each other. The discrepancy between the frequency-based and distance-based analyses regarding the relationship between Norton Sound and Bristol Bay (Table 6.2) raises an important question over the choice of the correct statistic in the analysis of geographic subdivision. With the advent of DNA sequencing, information on evolutionary distances among haplotypes can be incorporated into an analysis of genetic subdivision and thus help differentiate among natural groupings that have diverged long enough ago that there is some phylogeographic signal (Excoffier et al., 1992; Hudson et al., 1992). In the case of mtDNA, this is typically in the order of several thousand years. In situations where there is little or no phylogeographic structure and each haplotype does not differ by much from all other haplotypes, as in the Norton Sound-Bristol Bay comparison, average interhaplotypic differences within populations may not differ significantly from average differences between populations, even if there are significant differences in haplotypic frequency, and therefore limited dispersal, between populations. Under these circumstances the choice of a distance-based analysis may act to conceal rather than resolve population structure.

Although it is difficult to prove a null hypothesis (Avise, 1994; Dizon et al., 1995; Taylor and Dizon, 1996), the failure to discriminate between the Point Hope and eastern Beaufort Sea samples supports earlier speculations that whales which migrate past Point Hope in spring are part of the same stock that occur along the eastern Beaufort Sea coastline in summer (Fraker, 1980; Moore et al., 1993). Similarly, the lack of differentiation among sample sets collected 20 years apart at Point Hope suggests that the genetic composition of subpopulations remains stable at least over a period of a few generations.

### Maternally Directed Philopatry

In light of the limited significance of geographic barriers and the long-distance dispersal capabilities of beluga whales, the mtDNA population structure indicates strong philopatry to discrete summering areas. Such site fidelity is particularly impressive considering the possibility that some subpopulations may overwinter in a common area. Maternally directed philopatry to seasonal habitats, as opposed to physical barriers to movement, has been identified as a major influence on population genetic structure in a number of other highly migratory species, including marine turtles (Meylan et al., 1990; Bowen et al., 1992), shore birds (Wenink et al., 1993), and great whales (Baker et al., 1994; Palsbøll et al., 1995; Larsen et al., 1996). There are probably selective advantages in returning to a familiar habitat with predictable food resources, climate, and oceanographic conditions. The prolonged period of association between beluga whale mothers and offspring, estimated at two to three years (Smith et al., 1994), probably aids in the cultural transmission of migratory destinations and facilitates the development of matrilineal population structure. Geographic subdivision at the mtDNA locus, however, does not necessarily mean that geographic populations are genetically isolated because male-biased dispersal and gene flow may limit or eliminate population structure at nuclear loci (Karl et al., 1992; Palumbi and Baker, 1994; Avise, 1995). Nevertheless, from an ecological perspective, mtDNA can provide important information on how to define biologically relevant management units. Because recruitment is dependent on female reproductive success, limited female dispersal results in demographically independent populations, irrespective of whether there is extensive male dispersal or gene flow (Moritz, 1994; Avise, 1995). One prediction of this matrilineal population structure is that colonization of depleted populations will be slow due to limited recruitment from outside females. This has been recorded in green turtles, *Chelonia mydas* (Bowen et al., 1992), and is consistent with the failure of some beluga whale summer concentrations to recover following near extirpa-

tion more than a century ago (Reeves and Mitchell, 1987, 1989).

### Limitations of Traditional Methods of Population Inference

The results from our initial study (O'Corry-Crowe et al., 1997) in many ways confirmed much of what was inferred about large-scale population structure of beluga whales in Alaska and northwest Canada from the timing and distribution of sightings (Frost and Lowry, 1990). More detailed genetic analysis on a finer geographic scale, however, has highlighted the limitations of relying on these methods to determine population ranges and movement patterns. The significant genetic differentiation found between Kotzebue Sound and Kasegaluk Lagoon requires a reevaluation of the original hypothesis of a northward movement of beluga whales along the Chukchi Sea coast in summer from Kotzebue Sound around the Lisburne Peninsula to Kasegaluk Lagoon (insert, Figure 6.1). A review of all the ecological evidence taken as supporting this hypothesis reveals a number of events that could just as easily be taken as supporting the alternative hypothesis of geographic subdivision. For example, sighting and harvest information revealed that the number of belugas utilizing Kotzebue Sound in summer decreased dramatically in 1984 and, apart from 1 or 2 years, has remained low through 1995 (Frost et al., 1983; Seaman et al., 1988; Lowry et al., 1989; Frost and Lowry, 1990; K. Frost, 1996, pers. comm.). By contrast, the number of beluga whales using the Kasegaluk Lagoon region in the summer appears to have remained constant over the past two decades, if not longer (Frost et al., 1983, 1993; Seaman et al., 1988; Frost and Lowry, 1990; Lowry et al., 1996). The reasons for the dramatic decline in Kotzebue Sound are not entirely clear. A number of factors have been suggested including changes in the distribution of killer whales, *Orcinus orca*, a principal natural predator of beluga whales, in the Sound (Frost and Lowry, 1990), and mortality associated with an ice-entrapment that occurred in the winter of 1984–1985 on the Chukchi Peninsula in Russia some 500 km southwest of Kotzebue Sound in which an estimated 1000 whales were hunted or perished (see Ivashin and Shevlyagin, 1987). The decline has also been attributed to displacement of whales due to increased motorboat traffic in this region, such that today the eastern Chukchi belugas bypass Kotzebue Sound altogether and head directly to Kasegaluk Lagoon (Lowry et al., 1989; Frost and Lowry, 1990). In 1996 large numbers of beluga whales (reported as several hundred, W. Goodwin, 1997, pers. comm.) were once again seen in Kotzebue Sound from early to mid-June. Aerial surveys revealed that by late June the whales had left the Sound and that more than 1000 were at Kasegaluk Lagoon (Lowry et al., 1996). Thus, from sighting information it appeared that, as before, the eastern Chukchi Sea stock had visited Kotzebue Sound before moving to the northeast Chukchi Sea coast. Finally, although the general sequence of sightings along the coast holds in most years, large numbers of beluga whales have occasionally been sighted almost simultaneously at Kotzebue and Kasegaluk. In early July 1978 for example, approximately 1000 belugas were seen in Kotzebue Sound during the same week that over 1000 whales were recorded near Kasegulak Lagoon (Frost et al., 1983). Such events have been taken as evidence that the eastern Chukchi Sea stock does not always travel as one large group (Frost and Lowry, 1990). Although one cannot exclude the possibility that in some years the same whales may visit both areas, these events may indeed be further evidence that Kotzebue and Kasegaluk whales are indeed separate groupings.

### Factors Influencing Beluga Whale Distribution and Movements in Summer

Further comparisons between these two groups of beluga whales that occur in the eastern Chukchi Sea in summer may add to our understanding of the factors than influence movement patterns in this species. Despite the various reasons proffered to explain the dramatic decline in the mid-1980s, the number of whales entering Kotzebue Sound each summer appears to vary naturally from year to year (Frost et al., 1983). This may reflect a greater variation in the timing and pattern of annual ice breakup in these sheltered waters than along the more exposed coastline of the northeast Chukchi Sea. It may also indicate that whales are not as dependent on nearshore habitat in Kotzebue Sound in summer as are whales at Kasegaluk Lagoon. At a number of locations throughout the Canadian arctic it has been demonstrated that beluga whales enter estuarine waters in summer to molt by actively rubbing on the substrate nearshore (Finley, 1982; Smith et al., 1994). Frost and Lowry (1990) and Frost et al. (1993) speculated that beluga whales congregate at nearshore gravel beds adjacent to Kasegaluk Lagoon also to molt. Conversely, it appears that whales enter Kotzebue Sound primarily to

feed and possibly to rear their young (Seaman et al., 1982; Frost et al., 1983). Thus, the predictable annual return of beluga whales to one coastal location compared to the more erratic occurrence at the other, may reflect a dependence on a stationary resource (gravel beds) versus a mobile, sometimes ephemeral resource (food), the availability of which could be strongly linked to the prevailing ice conditions. These inferences along with the recent genetic findings suggest that although beluga whales tend to be philopatric to natal subpopulation and summering area, movement patterns are somewhat flexible and relate to changes in prey distribution, prevailing ice conditions, and access to molting sites.

## CONCLUSIONS

The beluga whale is a medium-sized toothed whale that is highly adapted to life in the sea ice. It is capable of traveling great distances, of surviving in rigorous environments, and its gregarious nature suggests it is capable of forming complex societies. The secretive nature of beluga whales and the almost complete absence of natural markings that might aid in the reidentification of individuals adds to the difficulty of studying their behavior and ecology in the wild. The development of molecular genetic techniques has enabled us to address many of these previously intractable questions. Mitochondrial DNA studies, in particular, have helped us in unraveling the historical record of individual populations and has provided vital information of relevance to management priorities concerned with demographic connectedness among geographically distinct groupings.

Much of our current understanding of beluga whale distribution and movement patterns has come from years of observations made from land or from shore-based hunting operations and aerial surveys. This has resulted in a tendency to characterize the beluga whale as primarily a coastal species during the open water season. However, beluga whales actually spend a very small proportion of their time in the coastal zone. Recent genetic studies reveal that some subpopulations spend even less time in this habitat than previously thought. If we are to acquire a more complete understanding of the ecology and movements of this species, we need to extend the area of study farther offshore. Limited aerial surveys of the northeast Chukchi Sea have indeed located beluga offshore in the loose pack (Burns and Seaman, 1986; Frost et al., 1993) while extensive surveys in the Beaufort Sea have documented large numbers of whales offshore both in open water and at the ice front (Moore et al., 1993; Burns and Seaman, 1986; Harwood et al., 1996). Aerial surveys, however, are restricted in range and duration and limited ultimately by expense. The behavior and ecology of beluga whales offshore may be studied by more remote methods such as satellite-linked telemetry where the movements and dive profiles of beluga whales can be continuously recorded over several months (Martin et al., 1993; Richard et al., 1997).

The evolution and ecology of the beluga whale is strongly linked to this species' association with sea ice (Kleinenberg et al., 1969; Sergeant and Brodie, 1969) yet the basis for this association is not fully understood (Burns and Seaman, 1988; Frost and Lowry, 1990). Beluga movement patterns, and therefore the distribution of markers that reflect these movements, such as mtDNA, are influenced by the timing and pattern of ice breakup in spring and subsequent formation in late summer or fall. To clarify the relationship between sea ice and movements of beluga whales, current research is concentrating on investigating the relationship between spatial and temporal changes in patterns of genetic variation and year-to-year variation in ice conditions.

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# Molecular and Cell Biology of Marine Mammals

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