Population Genetics of Hudson Bay Marine Mammals: Current Knowledge and Future Risks

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Abstract Hudson Bay has experienced, and is predicted to further undergo, significant environmental changes that may affect the distribution of marine mammals. These changes will affect gene flow among regions within the greater Hudson Bay ecosystem, as well as between Hudson Bay and the rest of the Arctic. Currently, there are few genetic studies that include marine mammals from Hudson Bay, even though this area is critical to understanding how Arctic species will adjust to climate changes. Within this region, some marine mammals may become extirpated or isolated (e.g., southern Hudson Bay polar bears), while other species may expand their ranges (e.g., killer whales, harbour seals) as a result of warmer temperatures. Researchers and the public should view the greater Hudson Bay ecosystem as an early warning system for the larger Arctic ecosystem.

For population geneticists, marine mammals pose a unique challenge because they show little differentiation over large spatial scales due to: large historical population sizes; high mobility; seasonal migration; and breeding patterns that promote gene flow. Genetic monitoring programs need to take these factors into account in order to be effective. If designed carefully, these programs can be used to track changes in marine mammal populations that result from climate change.

We survey current genetic data collected from marine mammals in Hudson Bay and suggest possible trajectories that may result from temporal shifts in ice thaw and decreasing overall ice cover. We also comment on sampling strategies that will allow for the effective monitoring of genetic changes.

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Introduction

Arctic mammals have evolved to survive long, harsh winters and to take advantage of brief, yet highly productive, summers. The close relationship between these species and environmental conditions suggests that climate change will lead to changes in the ecology, spatial and temporal distribution, and genetic structure of Arctic populations (Laidre et al. 2008; Post et al. 2009). These changes may result from adaptation to new conditions, or changing population sizes and increased isolation. Although there are a variety of ways that Arctic mammals may be affected by climate change, we are primarily concerned with population genetic structure (defined below) in this chapter. More specifically, this discussion is presented from the perspective of conservation and management, where the genetic delineation of populations, stocks, or management units[1] is of paramount importance. Therefore, this chapter summarizes the current level of knowledge regarding relevant patterns that have been observed, as well as proposed explanations for them. It will discuss the challenge of quantifying genetic variation in Arctic marine mammals and will suggest how studies should be designed to understand temporal and spatial genetic patterns. Finally, this chapter will consider how the distribution of neutral genetic variation (defined below) may change with a shifting environmental regime, in addition to highlighting areas where future research could be focused.

A Primer in Conservation Genetics and Population Genetics

Conservation is aimed at maintaining diversity at three levels: ecosystem, species, and genetic (McNeely et al. 1990). Within those levels, genetic diversity is fundamental to the conservation of biodiversity because the loss of this source of variability has been

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[1] In this chapter, we use the terms management unit, population, and stock in two ways: when referring to one particular species and when speaking more generally about Arctic mammals. The first use of these terms reflects the fact that several stakeholder groups are involved in the conservation and management of species in the greater Hudson Bay ecosystem. Since each of these groups uses different objectives and analyses to define biologically meaningful units, the terms used to describe these units will vary from species to species. For example, polar bears are defined according to management units that may include more than one genetic population because they correspond primarily to demographic boundaries, while beluga whales are managed as stocks that roughly coincide with both demographic and genetic population boundaries and bowhead whales are managed as a single population because numerous data support this as a meaningful biological unit. The second use of these terms will be a more general classification, where management units are considered jurisdictional, populations are genetic populations, and stocks are groupings that are affected by humans (e.g., harvested) and exist below the population level (i.e., meta-populations, groups with a learned behaviour like summering ground locations). An interesting discussion regarding the definition of stock can be found in Stewart (2008).

linked to lower fitness, especially when animals are confronted with environmental stressors (Coltman et al. 1999; Kristensen and Sørensen 2005; Woodworth et al. 2002). Thus, loss of genetic diversity may reduce the ability of individuals and populations to survive and adapt to changing conditions. Therefore, it is important to try to maintain natural levels of genetic diversity in all components of an ecosystem.

Throughout the following paragraphs we will discuss a number of conservation genetics and population genetics concepts that may, or may not, be familiar to the reader. It is important to note that conservation genetics is concerned with maintaining gene flow in some cases, while preventing gene flow in others. Why can't one objective fit all conservation dilemmas? To answer this, one must understand that conservation genetics is concerned with maintaining natural levels of gene flow among regions, based on the assumption that this rate of flow is adaptive in some way. Population genetic structure (or genetic structure) is a quantification of the genetic differences among groups (differentiation), which is a reflection of the amount of gene flow among groups, where low gene flow will usually lead to higher genetic structure. For example, when physical barriers fragment landscapes, fewer animals move among groups, which reduces gene flow. When these isolated groups are small, this will lead to a rapid increase in genetic structure. In some cases, barriers to gene flow allow populations to adapt to local conditions and these adaptations would be lost if new genes, or new gene combinations, were constantly being introduced in the population. In other cases, anthropogenic activities will create barriers to gene flow that isolate a portion of a population, leaving too few individuals or too little genetic diversity to adapt to new conditions. Therefore, recognizing that one strategy (e.g., increase gene flow) will not be effective in all situations, conservation genetics aims to maintain natural levels of diversity and structure in hopes that these will give species the best chances of survival in the long term.

Genetic diversity is difficult to conserve because: it is created through mutation; mutations are lost or maintained through selective processes; and important diversity can be lost by genetic drift. Genetic drift is the random loss of mutations, which tends to be more significant in smaller populations (Frankham et al. 1999). When a population experiences a dramatic reduction in population size and a corresponding reduction in genetic diversity, this is known as a bottleneck event. Therefore, population size is correlated with genetic diversity (Frankham 1996) and managers can maintain genetic diversity and gene flow by maintaining population sizes and landscape connectivity, which facilitates natural levels of movement of individuals among groups. In the context of the greater Hudson Bay ecosystem (GHBE), the loss of ice can result in two simultaneous threats for many species. First, habitat loss may lead to an overall reduction in population size and a parallel reduction in genetic diversity. Second, the landscape may become fragmented, which may create even smaller isolated populations where genetic drift will further erode genetic diversity.

Determining the natural levels of genetic diversity and existing genetic structure is critical to assessing potential impacts of climate changes on wild populations. To accomplish this, a number of genetic markers are used to detect and quantify genetic variation, each of which has different characteristics and strengths. In this chapter, we mention two broad classes of markers: those that are functional and those that are neutral. Functional markers are found in genes that are under selection, such as genes involved in disease resistance. Although the development of functional markers has increased in recent years and will become more important in the future, we primarily discuss neutral markers in this chapter. Neutral markers are not (theoretically) linked to genes under selection and thus should provide a better estimate of the relationships among individuals, groups, and populations. For an example of why this is the case, imagine two groups of animals that are only distantly related but are both living in a similar environment. Convergent evolution may cause the functional markers to be similar, but neutral markers would reveal that they are only distantly related.

Neutral markers can be further categorized as nuclear DNA (nDNA) or mitochondrial DNA (mtDNA). As the names imply, nDNA is present in the nucleus of cells, whereas mtDNA is found in the mitochondria. Both parents pass nDNA to their offspring. This allows researchers to identify close relationships (e.g., parent–offspring), as well as more distant relationships by comparing the patterns in nDNA within a group to the population as a whole. Only mothers pass mtDNA to their offspring (maternal inheritance), so this marker is valuable for tracing female contributions to gene flow. Similarly, but to a much lesser degree, Y-chromosome markers have been used to trace male contributions to gene flow. The discussions that follow in this chapter will be primarily based on the use of neutral genetic markers and the analyses that these markers lend themselves to: that of identifying temporal and spatial genetic changes.

An important first step in the process of monitoring, conserving, or managing is that of delineating biologically meaningful units and obtaining baseline data against which future changes can be detected (Amos and Balmford 2001; Haig 1998; Moritz 1994). In recent years, the number of population genetic studies of Arctic species has increased. Given the importance of this information, this chapter reports the current population genetic data for mammalian species that regularly occur in the GHBE. This includes 11 mammals that commonly occur in and on the waters of the GHBE: two terrestrial carnivores (Arctic fox (*Vulpes* [=*Alopex*] *lagopus*) and polar bear (*Ursus maritimus*)); five pinnipeds (walrus (*Odobenus rosmarus*), ringed seal (*Pusa* [=*Phoca*] *hispida*), harbour seal (*Phoca vitulina*), harp seal (*Pagophilus groenlandicus*), and bearded seal (*Erignathus barbatus*)); and four cetaceans (narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), killer whale (*Orcinus orca*) and bowhead whale (*Balaena mysticetus*)). Currently, harp seals and killer whales are being observed with greater frequency in the GHBE (Higdon and Ferguson this volume). Although their changing distribution and demography may provide compelling examples of changes already occurring in the GHBE, we will omit these species from our summary because little is currently known about their genetics in the region.

General Characteristics and Patterns

In studies of population genetic structure in Arctic marine mammals, investigators commonly observe a surprising lack of genetic differentiation over large distances (Brown Gladden et al. 1999; Davis et al. 2008; Paetkau et al. 1999).

This pattern, known as panmixia, is characterized by a high degree of genetic similarity (homogeneity) among locations, and is derived from a combination of processes that function over different time scales. Long-distance dispersal movements among regions and/or short-distance gene flow within continuous distributions contribute to the maintenance of genetic homogeneity over recent time scales. Over longer time scales, post-glacial range expansion and genetic storage (the retention of genetic diversity in long-lived life stages) can contribute to the maintenance of genetic homogeneity.

Numerous telemetry and mark-recapture studies, in addition to more recent genetic studies (Crompton et al. 2008; Petersen 2008), suggest a higher degree of breeding site fidelity than previously assumed in Arctic mammals. For example, although adult polar bears may travel many hundreds of kilometers in the interval between initial capture and recapture, they are often recaptured within 100 km of their original capture location (Taylor et al. 2001). Likewise, individual narwhal move between summer and winter locations with great fidelity (Heide-Jørgensen et al. 2003). Although site fidelity can lead to genetic structure at various levels, this form of differentiation is generally low in species found within the GHBE. The following paragraphs discuss the ways in which this apparent contradictory result can occur.

Evolutionary Legacy

Current patterns of genetic variation in a particular species are dictated by their evolutionary history, which has been shaped by successive cool and warm periods. The last interglacial period, which ended approximately 117,000 BP (years before present, Kukla et al. 2002), was warmer than current conditions and may have reduced the ranges of most ice-obligate species. The genetic signature of a population expansion in Arctic foxes dates roughly to the end of this interglacial period (Dalén et al. 2005). More recently, during the last glacial period (ca. 24,000–14,000 BP), the entire GHBE was covered by the Laurentide ice sheet (Dyke et al. 2002), which likely excluded all marine mammals. Subsequent range expansions into this area, coincident with population size increases, have likely contributed to the observed genetic homogeneity in the species that occur in the GHBE. The reduction in gene flow between populations within the GHBE and populations outside of the GHBE has occurred so recently in evolutionary time that divergence may be difficult to detect. This is consistent with other studies that show patterns of reduced genetic structure in taxa that have experienced a recent range expansion (Ibrahim et al. 1996; Ray et al. 2003).

More recently (ca. 8,200 BP), a short-duration cold anomaly, which is hypothesised to be linked to an influx of freshwater following the last outburst flood of glacial Lake Agassiz (Alley and Ágústsdóttir 2005), may have reduced populations of some cetaceans. It has been suggested that cetaceans were excluded from parts of the Canadian Arctic during this time, based on a lack of bowhead whale bones at archaeological sites from the same period (Dyke and England 2003; Dyke et al. 1996). This 8,000 BP event, and the Little Ice Age of recent times (1300s–1800s), may have reduced population sizes and caused genetic bottlenecks in some populations. Large-scale ice entrapments could also have occurred during times of rapid cooling and this may explain the lack of mitochondrial diversity in narwhal (Palsbøll et al. 1997).

Following these cold events, it is likely that populations expanded in size and re-colonized the GHBE. However, each cycle probably caused a bottleneck because population sizes were reduced and few lineages were able to re-colonize the GHBE. Based on sighting records, Higdon and Ferguson (2009) concluded that killer whales have been expanding their range into Hudson Bay since the 1950s. We would predict that this likely represents an invasion by relatively few lineages; and an ice-free Hudson Bay would initially contain a population of killer whales with low genetic diversity.

Anthropogenic Bottlenecks

Some Arctic mammals have been subject to intense hunting pressure, which may have had an impact on genetic diversity. From the 1600s to 1900s, bowhead whales were targeted extensively by European and Yankee whalers (Reeves and Cosens 2003; Reeves et al. 1983). These harvests reduced their numbers from hundreds of thousands of animals to only hundreds (Reeves et al. 1983). Although this drop in population size should coincide with a parallel loss of genetic diversity, this has not been detected in bowhead whales (Borge et al. 2007). This could be due to their longevity and mobility, which enabled existing genetic variation to be maintained despite bottleneck events.

In the face of harvest pressure, marine mammals in the GHBE have generally been able to maintain higher population numbers compared to species that occur in temperate and southern oceans. This is due, in part, to the difficulties of accessing and harvesting GHBE marine mammals over their entire range (e.g., Nares Strait walrus COSEWIC 2006). Local exceptions, like the commercial over-harvest of Eastern Hudson Bay beluga and Ungava Bay beluga, do occur where animals are accessible. However, these represent only portions of the species total range and the corresponding loss of diversity due to local extirpations may be minimal in the context of the entire species.

Life History

The life history characteristics of species also play an important role in the observed level of genetic structure. For example, Stirling and Thomas (2003) suggest several life history characteristics, including natal breeding site philopatry, population specific vocalizations, and mating strategy, are important determinates of population structure for seals. We highlight three characteristics that play an important role in determining the genetic patterns observed, or hypothesized, in the marine mammals that occur in the GHBE.

Dispersal and Mobility

Many theoretical models for the dispersal of genes across a landscape assume, or look for, a pattern of isolation-by-distance. In these models, breeding among individuals is limited by how far an individual can move and this creates a pattern where genetic differences are positively correlated with geographic distances. In other words, the closer individuals are in space, the more closely related to each other they tend to be (Epperson 1995; Wright 1943). As we will point out in the species summaries below, this pattern may be challenging to detect because all of the marine mammals within the GHBE have recorded annual movements that would allow them to disperse between any points in the GHBE over a relatively short time span. For example, although beluga summer concentration areas are discrete, most are closer to each other than the distance these whales travel between summering and wintering areas (COSEWIC 2004a). In beluga whales, and all other marine mammals discussed here, individuals can travel significant distances over the course of a season; and they could disperse their genes to any other part of their range over their reproductive life span. Therefore, the observation of genetic structure in any of these species suggests that movement ability is not influencing genetic structure and that gene dispersal among locations is a function of some other parameter, such as natal fidelity or social structure.

Annual variability in both the timing and patterns of ice formation has contributed to species having large areas of occurrence and/or long migration routes. However, these characteristics may also buffer populations from poor conditions that are short in temporal duration or local in spatial extent. In the event of a local extinction, animals with high mobility have a higher probably of re-colonizing, which lowers their overall vulnerability (Roberts and Hawkins 1999). On the negative side, if this mobility is associated with migration events, it may also expose a greater segment of the population to risks that occur along the migration route (Robinson et al. 2009). Whatever the benefits or costs associated with high mobility, researchers must account for it during their experimental designs, to ensure that they obtain samples from the times and places that are most likely to reveal genetic structure (e.g., breeding season and breeding grounds).

Mating Strategy

Post-glacial expansion into the GHBE has been limited to those animals adapted to seasonal ice cover. This has placed reproductive constraints on marine mammals in the GHBE and has shaped the evolution of their mating strategies. In ringed seals, the annual variability in location of suitable breeding habitat may prevent strict natal fidelity, thus promoting mating systems that would result in a predictably panmictic genetic structure (Coltman et al. 2007; Stirling 1983). In cetaceans, the use of the GHBE involves migration into and out of the region each year. Migration along traditional routes may provide an opportunity to maximize the number of potential mates and thus would lead to genetic homogeneity if mating occurred during migration. For the marine mammals that inhabit the GHBE, data suggest that mating occurs in the late winter or early spring. However, our ability to study mating systems is extremely limited during this period because the animals are under ice and usually far off shore. There are also few, if any, daylight hours to work with.

In some species, the seasonal concentration of animals at predictable wintering areas has likely influenced the evolution of mating strategies. For example, in these circumstances, males can compete for and defend harems of females. Walrus, harbour seals, and bearded seals are associated with areas that are ice free throughout the winter and are likely candidates for exhibiting strong population structure. Genetic structure based on mating strategy has been predicted for bearded seals based on vocalization patterns associated with breeding (Stirling and Thomas 2003), and genetic results seem to support this in areas outside of the GHBE (Davis et al. 2008). In contrast to this pattern, ringed seals are able to maintain breathing holes in ice and thus have a more dispersed distribution during the breeding season. Although the ringed seal mating system has not been described in detail, males likely defend territories that contain several females (Reeves 1998). This arrangement will facilitate gene flow to a much greater degree and would be predicted to result in a pattern of isolation-by-distance (Davis et al. 2008; Petersen 2008).

Longevity

Long life spans and overlapping generations increase effective population size by allowing multiple cohorts to simultaneously be part of the gene pool. Long lives provide a greater opportunity to increase lifetime dispersal distance and, potentially, the distance over which gene flow occurs. In long-lived species, large-scale movements can occur in the sub-adult life stage before an individual starts breeding, or in response to changes in environmental conditions. These types of movements may act to increase homogeneity of the population over time in the absence of breeding site fidelity. Again, this should be factored into the sampling design of temporal studies of Arctic marine mammals, because long life spans may create a time lag between the disruption in gene flow and the ability to detect it.

Long life spans and overlapping generations may maintain genetic variability in a temporally fluctuating environment, through the storage of genotypes by certain life stages (Ellner and Hairston 1994; Gaggiotti et al. 1997). If selection pressure varies over time and is focused on a single life stage (e.g., juveniles), then long-lived species will retain genetic diversity in the stage that is not selected against (e.g., adults). This “storage of genotypes” (Gaggiotti et al. 1997) or “storage effect”

(Chesson 1983) may account for the maintenance of genetic diversity in bowhead whales following whaling because all of the genetic information that survived the bottleneck event has been maintained. In marine mammals, pup/calf mortality rates are usually higher than all other age classes, while adult mortality is generally lower (e.g., ringed seals, Ferguson et al. 2005). If the environmental conditions in one time period do not favour the genotype of the adult, they may still be alive in a subsequent period when their genotype may be selected for.

An additional benefit to having a long life span is that fewer generations experience a bottleneck event and thus genetic diversity is buffered over an extended period of time (Kuo and Janzen 2004; Lippé et al. 2006). Extended longevity may make it more challenging to distinguish genetic groups for management purposes, but from an evolutionary perspective it is beneficial. Longer-lived species have likely experienced climate change towards a warmer Arctic in their recent evolutionary history and may have the variability to adapt to the changes.

Possible Future Genetic Changes

Although speculative, a number of factors may impact the population structure of marine mammals in the GHBE. In general, decreases in population size and range will act to increase population genetic structure, whereas increases in population size will have the opposite effect. The following paragraphs will summarize the expected genetic impacts due to changes expected in the Arctic. Although the rate of change has been the topic of much discussion, it is generally expected that sea ice extent and duration will continue to decrease in the GHBE region (Gough and Wolfe 2001; Parry et al. 2007).

To date, research that has examined sea ice trends has shown increased open water over the last several decades in Hudson Bay and Foxe Basin (Gough et al. 2004; Heide-Jørgensen and Laidre 2004). This reduction in sea ice will have obvious consequences for ice-adapted species, which are expected to lose habitat and presumably population size (Harwood 2001; Learmonth et al. 2006; Simmonds and Isaac 2007; Tynan and DeMaster 1997). For example, ringed seals are obligate ice breeders (Furgal et al. 1996; Reeves 1998; Smith and Stirling 1975), and reduced ice and snow have been correlated with lowered recruitment in this species (Ferguson et al. 2005). Likewise, spring rain is known to increase pup mortality in ringed seals (Stirling and Smith 2004). Over several years in the Baltic Sea, the absence of sea ice for most of the winter resulted in high pup mortality during the late 1980s (Härkönen et al. 1998). Therefore, a rapid trend towards less ice could result in a series of years with low recruitment and would be expected to translate into decreases in ringed seal populations. It is unlikely that this species would go extinct, but they may become extirpated from the southern portions of their range and isolated in other areas. For all species, reductions in population sizes due to reduced resources or available habitat will present challenges to maintaining gene flow and levels of diversity.

Conversely, loss of ice is expected to have a positive effect on some species. Increases in population size and a concordant reduction in genetic structure may also be observed in species that can respond to an increase in productivity resulting from a longer ice-free season. The current low density of harbour seals in Hudson Bay may be expected to increase because they are limited by the availability of ice-free areas during winter (COSEWIC 2007). In harbour seals, nothing is currently known regarding the rate of gene flow among locations; however, it is likely that the loss of sea ice would provide the opportunity for increased dispersal and thus gene flow among locations. Locally adapted populations may be lost through genetic swamping, which would lead to an overall reduction in functional adaptations (García-Ramos and Kirkpatrick 1997; Kawecki and Holt 2002).

Decreases in the duration and extent of ice cover may have major impacts on the species compositions of the GHBE. There are indications that some predators are increasing (e.g., killer whales, Higdon and Ferguson 2009, Higdon and Ferguson this volume), which could reduce other species or increase the costs of dispersal, leading to isolation of some areas. New competitors may also invade (e.g., harp seals, minke whales), and the resulting equilibrium that is established may not favour the existing species. These changes will affect each species and each web of species in a unique way. Changes in ice and food distribution may lead to changes in predator distribution, and could isolate or connect populations. The seasonal structure in southern and western Hudson Bay polar bears indicates the potential for changes in sea ice thaw to increase genetic differentiation over time (Crompton et al. 2008). In contrast, lineages that have been isolated in the eastern and western Arctic will be reconnected. For example, bowhead and beluga whale populations will be the first to reconnect if an ice-free route is established across the Canadian Arctic.

Changes in the ecosystem and climate will not only modify patterns of gene flow, they will also change selection pressures with unknown outcomes. Researchers should attempt to document these changes, while developing predictive models to help mitigate negative impacts. Berteaux et al. (2006) have pointed out that care must be exercised in developing these models, to maximize their utility. The following section highlights promising genetic analyses that can help develop models directly applicable to conservation and management.

Current and Future Directions for Research

Analytical Directions

Recent advances in molecular ecology have emphasized landscape genetics (Holderegger and Wagner 2006, 2008; Manel et al. 2003; Storfer et al. 2007) and spatial genetic approaches (Guillot et al. 2005, 2009; Jombart et al. 2008) as ways to use genetic variation to understand the complex interaction between individuals and their environment. Landscape genetics combines the fields of landscape ecology with population genetics and has made significant progress in recent years in examining and explaining patterns of gene flow over large scales. Several analyses have emerged that incorporate geographic information systems (GIS) technology to model gene flow in more complex ways than simple isolation-by-distance. These include using least-cost paths where habitat types are assigned values based on relative permeability to gene flow (Adriaensen et al. 2003; Coulon et al. 2004; Wang et al. 2008). For example, water may restrict gene flow in terrestrial species and would be given a high cost value. The correct cost structure is inferred when the correlation between genetic distance and cost is highest, which allows for important areas (i.e., corridors) to be identified. Similarly, resistance models incorporate both the cost of the length of the path and the width of the path (McRae and Beier 2007). While these developments are facilitating genetic studies in terrestrial populations, the dramatic seasonality experienced in the GHBE (i.e., from sea ice to open water) may prevent these approaches from being applied to some marine mammals, such as polar bears and cetaceans. At the very least, the applicability of these approaches will depend on sample designs that account for temporal changes in distribution. In this respect, the difference between seasonal and year round residents of the GHBE is a valuable distinction to make. We would suggest that landscape and other spatial genetic methods will be promising approaches to examine gene flow in resident species, where isolation-by-distance would likely be occurring. However, these approaches will be most successful if sampling designs take factors such as seasonal mixing into account. Two further items should be kept in mind when designing studies and analysing data; both relate to the apparent panmixia observed in many taxa.

First, the overall panmixia of GHBE populations likely reflects high mobility over an annual cycle, while observations of site fidelity indicate that some genetic discontinuities may exist during the mating season. This breeding structure may be masked if the assumption of geographic versus seasonal structuring is incorrectly applied. This requires careful consideration of when samples are collected and of which specific population genetic analyses are required. A recent review of spatial genetics stresses the need for geographic-based Bayesian structure analyses (Guillot et al. 2009). Bayesian methods are statistical analyses that cluster data based on theoretical assumptions (priors) rather than predefined grouping. In genetic analyses, the priors that are used to cluster individuals into groups are based on the genetic assumptions of populations (i.e., Hardy–Weinberg equilibrium and linkage disequilibrium), while newer analyses include continuous spatial data as a prior to inform clustering algorithms. This strategy is less applicable for studies of seasonal residents to the GHBE because pooling samples collected throughout the year for each location may mask the genetic structure present at the critical time when this structure would be defined: the breeding season. When samples are known to be sampled during the breeding season, and can be partitioned in the analyses as such, then traditional genetic structure estimates (e.g., F_{ST}) can be applied. If this is not the case, applying Bayesian genetic structure models such as STRUCTURE (Pritchard et al. 2000; Falush et al. 2005), that do not incorporate spatial data, are more appropriate than programs like Geneland (Guillot et al. 2005) or TESS (Chen et al. 2007), which will inaccurately weigh the sampling site into the model.

The second aspect to keep in mind corresponds to overall low genetic differentiation in GHBE marine mammals, even when structure is detected. Although panmixia is a useful null model and is a common genetic pattern among species in the GHBE, a panmictic population is not necessarily entirely homogeneous, nor would it be predicted to be homogeneous. Various aggregations can lead to significant and important genetic structure (Latch and Rhodes 2006). For example, aggregations of related individuals such as whale pods, or learned behaviour relating to the locations of feeding sites or nursery areas, can create genetic heterogeneity within a population. This structure is important for management and conservation, and it needs to be understood. Therefore, analyses that characterize heterogeneity below the population level and examine those patterns are promising directions to move in. By focusing on the connections among individuals or locations, researchers will be able to identify important areas that work to maintain overall connectivity in the system. One approach to identify and model connectivity is to represent individuals in the context of a network and apply graph theory to explore that network.

Graph theory is a mathematical framework used to represent and model interconnected observations; in this case, genetic data. Graph theory has been used extensively in computing and social sciences. It has gained ground in biological sciences in recent years (May 2006; Proulx et al. 2005; Whitehead 2008) and has been more recently applied to genetic data (Dyer and Nason 2004; Garroway et al. 2008; Petersen 2008). Essentially, a network is constructed wherein the nodes are individuals or locations, and the links that connect nodes can be weighted to represent the strength of the relationships among them. When connections between nodes are strong or numerous, we can infer a high degree of relatedness if the nodes represent individuals, or we can infer high connectivity if the nodes represent locations. The network that can be modeled: is not dependent on the existence of population level genetic structure; does not require that Hardy–Weinberg equilibrium assumptions be met; and can characterize relationships even within a panmictic population. When this genetic network is compared to geographic data, sites of high connectivity can be identified. In addition, statistical tests can be performed to assess the relative importance of these sites, by removing their associated nodes or links to determine if panmixia will be maintained. If the removal of one element from the network results in a significant change in the network structure, we can infer that the removed element is critical for the maintenance of gene flow in the system. Furthermore, we can infer that negative impacts (e.g., habitat modification) in that area would result in increased differentiation and subsequent isolation. A monitoring program, with comprehensive baseline data, would allow for these critical areas to be identified in a network context and for proactive management decisions to be made if those connections were being degraded. Adding data regarding the location of sensitive areas, such as shipping lanes or greatest changes in ice concentration, will further enhance our ability to proactively mitigate the damage to the network as a whole, as opposed to being forced into remediation efforts after detecting the problem.

Technical Directions

To be most effective and proactive, our first priority should be to remove the gaps in our collective knowledge, as identified in the species summaries below. Following this, a genetic monitoring strategy (that includes a comprehensive baseline dataset) needs to be devised so researchers can track genetic change over time and in relation to climatic variables. Finally, there is a need for a long-term commitment to sampling strategies.

By committing to sampling strategies, researchers will be able to improve, develop, and validate models such as those generated using graph theory. The specifics of these strategies will vary among species, and one broad strategy will not be appropriate, given the variation in species distributions and life history characteristics (i.e., a sampling plan for seals will not be appropriate for studies of killer whales). Furthermore, as with all work in the Arctic, sample designs will need to be logistically feasible. As a broad guide, researchers need to factor in seasonality, and samples should be collected as close to the season that ultimately defines the genetic structure of interest as possible. For example, for resident species where population level genetic structure is sought, the breeding season should be targeted. For seasonal visitors, genetic structure likely occurs below the population level and sampling should avoid migrating animals. However, in the absence of an overarching sample design, simple measures like collecting accurate data on time of year (exact date so that ice charts can be cross-referenced) and geographic location (precise GPS data) will significantly improve researchers' ability to examine temporal and spatial genetic patterns.

In addition, fine-scale approaches that examine patterns of relatedness, kinship, or sex-biased movements will only be possible with sampling design improvements that include increases in sample size. This will require researchers to incorporate non-invasive or minimally invasive (e.g., biopsy sampling) techniques to increase samples without negatively affecting the numbers or behaviours of these species.

The logistical challenges and financial costs of conducting research in the Arctic will require people to develop strong partnerships with northern communities. Sample-sharing collaborations with other researchers will also maximize the value, in terms of scientific insights, that each sample provides. Development of sampling designs and strategies that can be maintained over time, such as community-based monitoring programs like the International Polar Year – Global Warming and Marine Mammals project, will be key to monitoring changes in the GHBE.

Conclusions

It is important to understand how ecosystems will respond in the face of changing conditions. These changes will be simultaneously environmental and anthropogenic, and will likely be most pronounced in the GHBE. Researchers should view this ecosystem as the "canary-in-the-coalmine" with respect to early responses to climatic changes, ecosystem shifts, and anthropogenic disturbances, and should attempt to characterize and monitor it. This is critical, not just for the populations inhabiting the GHBE, but also to establish a framework to apply to other Arctic ecosystems.

For marine mammals, one way to monitor changes at a variety of scales is through the use of genetic data. These data can be applied to fine-scale issues of individual dispersal patterns or modified social structure, as well as to large-scale issues of connectivity or evolution. Because GHBE mammals have large population sizes, high individual mobility, and an evolutionary history of recent expansion, researchers will need to use genetic data and novel analytic approaches that are effective below the population level to monitor the coming changes. One critical consideration in monitoring in the GHBE is that baseline data will be required immediately so connections within a naturally panmictic population can be measured over time. This will put researchers in a position to build predictive models and suggest proactive measures for minimizing impacts related to the changing conditions in the GHBE.

Species Summaries

In the following species summaries, we have highlighted a number of population and life history characteristics that have likely resulted in the genetic patterns discussed in this chapter. These include: distribution and recognized units (i.e., management units, populations, or stocks) in the GHBE; life history parameters, such as life span and age of maturity; and details of the species' annual cycle and mating strategy. These summaries also include the current available information regarding genetic population structure. Because data are lacking for many species within the region, we have assumed some similarities to conspecifics in other regions where appropriate.

Arctic Fox (Vulpes [=Alopex] lagopus)

Arctic foxes are year round residents of the GHBE and extend their distribution onto the ice as they scavenge polar bear kills and prey on ringed seal pups (Audet et al. 2002). These winter food sources can comprise a major component of their diet, especially in years of low lemming (*Dicrostonyx* and *Lemmus* spp.) abundance (Roth 2002, 2003). Breeding occurs in March and April, coincident with the establishment of summer territories (Audet et al. 2002). These territories break down in the fall, when Arctic foxes redistribute themselves to take advantage of seasonally available resources such as carrion (Audet et al. 2002). Arctic foxes have an average longevity of 3–4 years and their maximum life span is 12–14 years (Audet et al. 2002).

Dalén et al. (2005) observed that a significant amount of genetic variation in Arctic foxes was portioned between inland and coastal ecotypes in Scandinavia. Subsequent research, using mitochondrial and nuclear markers, found that the greatest single predictor of genetic differentiation in this species was the presence of sea ice (Geffen et al. 2007). The frequency of sea ice, which provides a transport or corridor among islands, explained 40–60% of the genetic variation in Arctic foxes (Geffen et al. 2007) among locations. Both Dalén et al. (2005) and Geffen et al. (2007) were only able to include one GHBE location (Churchill, Manitoba) in their studies. Carmichael et al. (2007) obtained samples from the entire region and observed little differentiation within the GHBE and across their circumpolar distribution. This is not surprising, given the large population size observed, as well as their long-distance dispersal ability (>1,000 km Wrigley and Hatch 1976) and the presence of a land-based dispersal route that allows circumnavigation of the GHBE.

Arctic foxes face some threats that may impact their genetic structure in the future (Carmichael et al. 2007). Studies in Scandinavia have shown that competition with red foxes (*V. vulpes*) can reduce the range of Arctic foxes (Hersteinsson and Macdonald 1992). This competition throughout GHBE, and possible range reduction in the south, has the potential to isolate some regions. For example, the loss of range in the James Bay area could reduce gene flow between Quebec and Manitoba. Ice transport from northern areas could maintain gene flow in the near future, although a complete loss of ice could isolate Arctic foxes residing in northern Quebec and Labrador, given that permanently open water reduces gene flow (Geffen et al. 2007). Competition, reduction in dispersal opportunities and increased mortality due to disease or human interactions may collectively act to reduce gene flow in the future. Furthermore, although not yet reported, the potential for novel hybridization between Arctic foxes and red foxes through range expansion is possible and has been recently reported in other species (Garroway et al. 2010).

Polar Bear (Ursus maritimus)

Polar bears are year round residents of the GHBE, with southern Hudson Bay representing the farthest south that this species regularly occurs (DeMaster and Stirling 1981). Established based on data from capture-mark-recapture and satellite telemetry, as well political boundaries, four management units occur in this region: Foxe Basin, Davis Strait, western Hudson Bay, and southern Hudson Bay (IUCN/SSC Polar Bear Specialist Group 2005). These management units are estimated to include approximately 5,000 individuals in total (IUCN/SSC Polar Bear Specialist Group 2005, Peacock et al. this volume).

Breeding occurs in the spring, while polar bears are on the ice. Although male–male competition has been inferred from sexual dimorphism, little is known about mating strategies. Individual bears, particularly females, show site fidelity

(Mauritzen et al. 2001). There is no evidence of territoriality (Ramsay and Stirling 1986). The maximum life span is up to 40 years in captivity, but is likely 25–30 years in the wild (DeMaster and Stirling 1981). Polar bears mature a year earlier in the eastern Arctic than in the western Arctic; at 4 years in females (Stirling and Kiliaan 1980) and 6 years in males (DeMaster and Stirling 1981).

Polar bears show little overall genetic differentiation among regions (mean FST 0.04 (Paetkau et al. 1999): from Table 4), although significant differences have been detected at some scales (Crompton et al. 2008; Paetkau et al. 1999). Within the GHBE, there is evidence supporting three genetic units that roughly correspond to an eastern, western, and southern region (Crompton et al. 2008). Based on analysis of nDNA markers, Crompton et al. (2008) suggested the possibility that polar bears from James Bay form a genetically distinct group, albeit with gene flow with other management units.

Because polar bears are adapted to the marine environment, particularly to life on sea ice, they are sensitive to seasonal changes in ice extent and duration (Amstrup 2003; Stirling et al. 1999). In most of the GHBE, sea ice melts each summer (Etkin 1991; Wang et al. 1994), which forces bears ashore. In southern Hudson Bay, polar bears spend 4 or 5 months on shore waiting for ice to reform (Stirling et al. 2004), at which time they live primarily on stored fat reserves (DeMaster and Stirling 1981; Stirling et al. 2004). In recent years, there has been a significant trend towards earlier spring break-up in both western Hudson Bay (Stirling et al. 1999, 2004) and eastern and southern Hudson Bay (Gagnon and Gough 2005; Gough et al. 2004). Less time spent on the ice has been correlated with lower fat reserves, which can put bears at risk of starvation (Obbard et al. 2006; Stirling and Parkinson 2006, Peacock et al. this volume). Crompton et al. (2008) suggested that a continued trend towards earlier ice break-up could lead to decreased gene flow among Hudson Bay units and potential isolation of southern polar bears.

Walrus (Odobenus rosmarus)

Walrus are year round residents of GHBE, but their distribution is not uniform and three stocks have been recognised in the past: Foxe Basin; southern and eastern Hudson Bay; and northern Hudson Bay and Hudson Straight (Born et al. 1995). More recently, it has been suggested that these can be further subdivided (Stewart 2002, 2008). A population estimate for the GHBE is not available but there are likely less than 10,000 individuals there, most of which are in Foxe Basin as well as northern Hudson Bay and Hudson Straight (COSEWIC 2006).

Walrus are polygynous and breed during the winter (Fay 1985). Females exhibit delayed implantation and a long gestation period, such that pups are born the following spring between April and June (Fay 1985). Pups are weaned at 2 years of age and females first breed when they are 5–10 years old, while males are probably upwards of 15 years old before they breed (Fay 1985). Maximum longevity has been estimated to be 40 years (Nowak 1999).

To date, genetic studies have used nDNA and mtDNA markers to demonstrate significant genetic differences between Baffin Bay and Foxe Basin stocks of walrus (Buchanan et al. 1998; de March et al. 2002). This research was primarily aimed at testing if the Foxe Basin stock should be further subdivided, and it did not include samples from most of the GHBE. De March et al. (2002) did not find genetic evidence of differentiation between samples harvested from two communities in Foxe Basin (Igloolik and Hall Beach). This contrasted research using lead isotope signatures, which were significantly different in walrus harvested in the same two areas, suggesting the presence of two stocks (Outridge et al. 2003).

A decrease in ice cover has the potential to increase gene flow among areas. However, because walrus mating occurs near maximum ice cover (winter), almost complete ice loss would be needed, at which point changes in gene flow may not be the most significant concern. Female walrus are associated with ice to a greater degree than males (COSEWIC 2006), and thus may be impacted sooner by changes in ice cover and duration.

Ringed Seal (Pusa [=Phoca] hispida)

Ringed seals are common in the Canadian Arctic and have a circumpolar distribution (Reeves 1998). Within the GHBE, ringed seals are treated as a single stock. As ice forms, ringed seals start establishing territories that they will maintain during ice-covered months (Reeves 1998; Smith and Hammill 1981). Breathing holes are maintained during the winter, and lairs for resting and giving birth are dug out in snowdrifts that accumulate on the ice (Calvert and Stirling 1985; Furgal et al. 1996; Smith and Stirling 1975). Breeding occurs in late spring, after pups from the previous breeding season are weened (Reeves 1998; Smith and Hammill 1981). Ringed seals exhibit delayed implantation of approximately 3 months (Reeves 1998). Males and females mature at 5–7 years of age and can live for approximately 40 years (McLaren 1958).

No stocks have been identified in ringed seals, and genetic research has found little differentiation across the entire species range (Davis et al. 2008; Palo et al. 2001). Petersen (2008) observed geographic-related genetic differentiation between ringed seals harvested in Chesterfield Inlet, Nunavut and other locations, suggesting that gene flow can be reduced in some areas. The cause of this differentiation was not known, but may have to do with the physical characteristic of the Inlet. Over a larger scale, a pattern of isolation-by-distance has been detected in ringed seals from locations across the GHBE and eastern Canadian Arctic (Davis et al. 2008; Petersen 2008). In ringed seals, genetic structure exists but is most pronounced during the ice-covered season. When Petersen et al. (data on file) divided their data set of Hudson Bay ringed seals by sex and by season, they found less genetic structure during the open-water season, implying that seals from different areas are more mixed at this time. They also observed that both male and female seals are more structured during the ice-covered season, suggesting natal site fidelity in both sexes. Their results highlight the importance of sampling during the appropriate season when attempting to determine genetic patterns in Arctic marine mammals.

Ringed seals have been assessed as having a lower sensitivity to climate-related changes in habitat, because of large population sizes and extensive circumpolar distribution (Laidre et al. 2008). However, southern breeding populations may become extirpated due to reduced sea ice cover during the pupping season. In the Baltic Sea, Meirer et al. (2004) suggested that most suitable ringed seal breeding habitat would be lost with air temperature increases of 2–3°C. Similarly, ringed seals in southern Hudson Bay may be affected to a greater degree by climate changes than conspecifics in the high Arctic. These impacts will likely be detected first in Hudson Bay, because climate models predict that the rate of warming will be greatest in this region (Gough and Wolfe 2001) and observations from the last 30 years have supported this (Gough et al. 2004). Decreases in ice cover are likely to increase movement and thus gene flow. However, loss of breeding habitat and increased predation pressure from killer whales may act to fragment the range and increase genetic drift in isolated areas.

Harbour Seal (Phoca vitulina)

Harbour seals are year round residents in Hudson Bay and are primarily associated with the mouths of rivers where ice-free areas exist throughout the winter (COSEWIC 2007). This is because they lack claws that would enable them to maintain breathing holes in the ice, as ringed seals do. The full distribution of harbour seals in the GHBE is known only from anecdotal reports and includes the near shore environment within Hudson Bay and Hudson Strait, but not Foxe Basin (COSEWIC 2007). Harbour seals occurring in the GHBE are part of the stock that includes all eastern Canadian marine harbour seals and there are no estimates of numbers of animals within the Hudson Bay and Arctic regions (COSEWIC 2007).

Relatively little research has been conducted on harbour seals in the GHBE. However, in other parts of their range, harbour seals mature between 4 and 5 years of age and have a maximum life span of 36 years (Härkönen and Heide-Jørgensen 1990). Pupping season is thought to start in June in Hudson Bay (COSEWIC 2007). In the western Atlantic (New England to Baffin Island), there is a cline in peak pupping date that is negatively correlated with latitude (Bigg 1969). Harbour seals tend to show fidelity to haul-out sites, although tracking data indicate that they can move over hundreds of kilometres (COSEWIC 2007).

Harbour seals have received relatively little attention in Hudson Bay due to their rare occurrence, as well as their similarity with the ubiquitous ringed seal. Stanley et al. (1996) examined range-wide mtDNA variation and included samples from Churchill, Manitoba. They determined that these seals grouped with eastern Atlantic harbour seals, and hypothesized a post-glacial expansion that moved north from eastern North America and then east to Europe. Subsequent genetic research has been focused on Sable Island, Nova Scotia (Coltman et al. 1998) and freshwater forms in Quebec (COSEWIC 2007). These results, however, do not address the genetic structure of populations in the GHBE.

There is archaeological evidence that the numbers and range of harbour seals can increase in warm periods (Woollett et al. 2000), and it is suggested that current climate trends are increasing the number of harbour seals in the GHBE (Derocher et al. 2004; Stirling and Derocher 1993). Although this could support the prediction that gene flow may increase in the future, there are no data with which to evaluate or monitor this process.

Bearded Seal (Erignathus barbatus)

Bearded seals are year round residents in the GHBE and are harvested at low rates by Inuit in most communities (Cleator 1996; Priest and Usher 2004). There are currently no data regarding their numbers in the GHBE, although 190,000 individuals are estimated to inhabit all Canadian waters (Cleator 1996). No stock boundaries have been identified for management and harvests have declined over time (Cleator 1996). The greatest concentrations of bearded seals occur near polynyas and areas where regular leads form (Stirling 1997).

Bearded seals mature between 5 and 7 years of age and can live up to 25 years (Cleator 1996; Kovacs 2002). Breeding takes place after the pups are weaned, and males display using vocalizations (Cleator 1996). Juveniles disperse widely, but there are significant differences in vocalizations among locations, suggesting some degree of site fidelity (Cleator et al. 1989; Kovacs 2002; Stirling and Thomas 2003). Pups are born on the ice in the spring and quickly take to the water with their mother (Cleator 1996; Kovacs 2002).

Little genetic information is available regarding bearded seals in the GHBE. Davis et al. (2008) surveyed their global range and included samples from Arviat, Nunavut. They found significant population structure among locations, using nDNA markers. This conformed to expectations based on vocalization patterns (Stirling and Thomas 2003) and suggests that more research is needed to fully understand population structure and gene flow in this species.

Bearded seal numbers may increase in response to climate warming if it allows for greater winter access to benthic feeding areas. Because bearded seal pups can enter the water soon after birth, the loss of sea ice may not be a significant source of mortality during the pupping period. However, threats (e.g., from predators) that would accompany more open water are unknown. Increased population size could lead to increases in connectivity and gene flow among regions.

Narwhal (Monodon monoceros)

Narwhal are seasonal residents in the GHBE and are concentrated in northern regions. Animals migrate in through the Hudson Strait in the spring and concentrate in Repulse Bay and Lyon Inlet, Nunavut (Westdal and Richard this volume).

This northern Hudson Bay population (also stock) migrates out in the fall, to winter at the intersection of the Hudson and Davis Straits. This population is thought to contain less than 5,000 individuals, while the Baffin Bay population (made of multiple stocks) likely contains more than 50,000 animals (COSEWIC 2004b; DFO 2008). Narwhal are also observed in the Fury and Hecla Strait area of northern Foxe Basin.

Challenges in ageing narwhal have lead to uncertainty regarding its life span and maturity ages. However, estimates indicate that their average life span likely extends beyond 30 years (COSEWIC 2004b) and could be close to 100 years (Garde et al. 2007). Little is known regarding dispersal in this species. However, annual migration distances, recorded using satellite telemetry, show that animals could potentially migrate between any points in the species range with relative ease. Breeding occurs in the spring, although there may be a great degree of variability based on when newborn calves are observed (COSEWIC 2004b). Little is known about mating strategies or behaviours in this species.

Based on mtDNA marker frequencies, differentiation has been found among regions within eastern and western Greenland, but not between Canadian high Arctic and northern Greenland locations (Palsbøll et al. 1997). Using a combination of mtDNA and nDNA markers, de March et al. (2003) observed significant differentiation between samples from northern Hudson Bay (Repulse Bay) and locations in Baffin Bay. Narwhal show little genetic variability in the control region (a commonly used mtDNA marker), which suggests that they have experienced a significant bottleneck event and/or recent population expansion, possibly because of increased availability of habitat (expansion) following the last glacial maxima (bottleneck) (Palsbøll et al. 1997). The low mtDNA diversity in narwhal (17 haplotypes from 360 animals) is in striking contrast to beluga whales [over 75 haplotypes from 500 animals collected in GHBE (DFO 1993–2002)], the sister group to narwhal, which has many of the same life history traits.

Nuclear diversity in narwhal is similar to that observed in beluga whales. Buchanan et al. (1996) found a mean observed heterozygosity[2] of 0.65 over 13 nDNA markers (loci), while mean observed heterozygosity in narwhal was 0.79 over nine loci (DFO 1993–2002). Although not directly comparable, due to differences in loci used and sample sizes, it is likely that nuclear diversity is similar in the two species. Differentiation among locations has been observed to be low in narwhal (F_{ST} less than 0.024 de March et al. 2003), suggesting recent isolation, ongoing gene flow, or low marker resolution.

Changes in ice cover will likely have significant impacts on narwhal populations. Increases in ice cover have been observed in Baffin Bay and could lead to an increase in the frequency of entrapments, where groups of whales are unable to breath due to complete ice formation at the surface (Laidre and Heide-Jorgensen 2005). Conversely, decreases in ice could expose them to increased killer whale

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[2] Heterozygosity is a measure of genetic variability.

predation. Given the low level of differentiation among putative units, it is unlikely that climate changes will significantly modify genetic structure in this species although it may change the patterns of gene flow.

Beluga (Delphinapterus leucas)

Beluga whales are seasonal residents throughout the GHBE. Most individuals migrate into the region in the spring, from wintering grounds in the Hudson Strait and coast of Labrador, while a small number may be resident in James Bay (COSEWIC 2004a). Currently, the beluga whales in GHBE are divided into eastern Hudson Bay, western Hudson Bay, and Ungava Bay units (COSEWIC 2004a); with the possibility that the eastern Hudson Bay unit could be further divided to add a James Bay unit.[3] The most numerous stock in the GHBE is the western Hudson Bay stock, which may contain upwards of 57,000 animals concentrated in the Nelson, Churchill, and Seal River estuaries (Richard 2005).

Female beluga whales mature between 4 and 7 years, while males mature between 7 and 9 years (Stewart and Stewart 1989). Their average life span has been estimated to be 20–30 years (Stewart and Stewart 1989), although it should be noted that changes in the interpretation of toothaging assumptions may modify age estimates upwards (Stewart et al. 2006). Breeding occurs in the late winter and early spring, although this is variable among regions (COSEWIC 2004a; Stewart and Stewart 1989). Similar to other whales that occur in the GHBE, the distance covered during the annual beluga migration puts most portions of their range within dispersal distance.

Genetic data has suggested significant differentiation among some portions of the beluga whale range. Mitochondrial data suggest that they show matrilineal structure among summering areas, whereas nuclear data indicate that male-biased gene flow is having a homogenizing affect on genetic structure (Brown Gladden et al. 1999; de March and Postma 2003; Mancuso 1995). A large amount of genetic data has been produced for harvested beluga whales in the GHBE, although little has been published outside of federal government reports regarding harvests. The most recent examination of these data confirms the differentiation of eastern Hudson Bay and western Hudson Bay stocks (Turgeon et al. 2009). Ungava Bay and James Bay may also be distinct genetic units, but samples are currently not available to conduct these analyses.

Beluga whales are less adapted to ice than narwhal, and reductions in ice cover may not influence their genetic structure in the same way. One outcome may be the reconnection of Pacific and Atlantic sides of the Arctic Ocean, which could facilitate gene flow between these regions. Increases in the frequency of ice entrapments may have significant effects on population sizes in smaller stocks.

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[3] The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) considers these units to be populations while the Department of Fisheries and Oceans, Nunavut, and Quebec (Nunavik) considers them to be stocks.

Bowhead whale (Balaena mysticetus)

Bowhead whales are seasonal migrants into the GHBE. They are most regularly observed in Repulse Bay and further north in the Foxe Basin – Fury and Hecla Strait area. The latter area has been suggested to be a nursery ground, where females with calves are able to avoid killer whale predation on young (Cosens and Blouw 2003). Bowhead whales are considered to be part of a single stock, based on current genetic data (Postma et al. 2006) and telemetry evidence (COSEWIC 2009). There has been much debate and analysis of relatively few surveys, leading to the current population estimate of 6,000 whales or more (COSEWIC 2009).

Bowhead whales are extremely long-lived animals (over 100 years George et al. 1999), and they mature late in life (25 years). They breed in late winter and spring (COSEWIC 2009) and the calving interval is likely 3–5 years, based on western bowhead whale data (Rugh et al. 1992). Like all GHBE cetaceans, recorded annual movements put all portions of their eastern Arctic range within dispersal distance over the course of a relatively short period of time. Genetic information initially suggested the presence of two populations in the eastern Arctic: Hudson Bay and Baffin Bay (Maiers et al. 1999). However, with increased sampling and reanalysis, the data indicated a single population (Postma et al. 2006). Although bowhead whales were harvested intensively in the eighteenth to early twentieth centuries, there is no evidence that current genetic variation is lower than historical levels (Borge et al. 2007).

Given the longevity and mobility of this species, coupled with an increasing population size trend, it is unlikely that a genetic change in response to climate trends will be detectable within the GHBE. On a larger scale, it is highly likely that loss of ice cover will reconnect western and eastern Arctic populations of bowhead whales with unknown consequences.

Summary

The GHBE is predicted to experience environmental changes that will significantly affect the population size and distribution of marine mammals that occur there. Some marine mammals may become extirpated or isolated (e.g., southern Hudson Bay polar bears), while other species may expand their ranges (e.g., killer whales, harbour seals) as a result of warmer temperatures and reduced ice cover or duration. At the population level, these changes will modify patterns of gene flow and genetic structure. How will these changes affect the evolution of the species in the GHBE and, in turn, the ecosystem as a whole? Although this is difficult to predict, we can implement monitoring strategies that will allow for changes to be detected. In order to be effective, genetic monitoring programs need to take factors relating to mobility, seasonal migration, and breeding patterns into account. If designed carefully, these programs can also be used to mitigate negative impacts of climate changes on marine mammals. Given the southern latitudinal extent of the GHBE, major ecosystem changes will be observed there earlier that in other regions. This makes GHBE critical to understanding how Arctic species will adjust to climate changes, and researchers and the public should view this ecosystem as a bellwether for the larger Arctic ecosystem.

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