THE ATLANTIC WALRUS

Multidisciplinary insights into human-animal interactions

Edited by: Xénia Keighley, Morten Tange Olsen, Peter Jordan and Sean Desjardins



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CHAPTER

Molecular advances in archaeological and biological research on Atlantic walrus

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Introduction

Over the last 20 years, the application of molecular tools in biological and archaeological research has increased concurrently with technological advances (Star et al., 2018; Keighley et al., 2019a,b; Barrett et al., 2020). This has provided new possibilities for conducting genetic, stable isotope and fatty acid (FA) analyses on modern and historical samples to improve our understanding of Atlantic walrus biology and demography. The use of palaeontological, archaeological and historical remains, moreover, shows great promise for disentangling the impact of anthropogenic effects and environmental change on Atlantic walrus populations. Such analyses have the potential to provide insights on particular aspects of the behavioural ecology, demography and life-history of Atlantic walruses, including changes in the migratory routes, population size, dispersal rates, choice of haul-out sites, foraging/diet and mating behaviour, in response to particular environmental or climatic conditions, as well as past and present human activities such as hunting (Keighley et al., 2019a). From an archaeological and historical point of view, much can also be learned about the role of walruses to past human societies, and even historical ivory trading networks and their links to regional hunting grounds can be reconstructed through time using molecular data from bones and teeth (Star et al., 2018; Keighley et al., 2018, 2019a,b; Barrett et al., 2020). Gaining these past insights will play a crucial role in designing future conservation and management strategies for Atlantic walruses and ensuring sustainable futures for humans who still rely upon them.

In this chapter, we describe the different techniques and approaches used in genetic, stable isotope and FAs research and their suitability in providing information on population structure, population demography, life-history, diet or ecology of Atlantic walruses. It is important to consider whether samples are modern, historic or ancient when assessing which questions to ask and which methods to use. In this chapter, we define these three time categories as follows:

Modern: samples collected from living or recently deceased animals (usually associated with detailed information about the specimen: sex, age, size, precise location and date of sampling).

Historical (<300 years before present (BP)): specimens (bone, tooth, skin, etc.) collected from living animals and archives of museums or other research institutes (usually associated with detailed information about the specimen: sex, age, size, precise location and date of sampling).

Ancient (>300 years BP): bones and teeth from archaeological or palaeontological sites (often limited information available about the specimen, relies on chronometric or radiocarbon dating).

Population genetics

Nuclear and mitochondrial DNA

DNA resides within cells and constitutes the genetic code in all organisms from plants to animals. Walrus DNA, like that of all mammals, is located in two different organelles within the cell; the nucleus containing nuclear DNA (nuDNA) and mitochondria containing mitochondrial DNA (mtDNA) (Fig. 10.1). A copy of an individual's entire nuDNA or mtDNA is referred to as nuclear or mitochondrial genomes respectively. While both nuDNA and mtDNA consist of the same four building blocks (nucleotides, or bases), they differ in size and how they are inherited.

MOLECULAR TOOLS IN ARCHAEOLOGICAL AND BIOLOGICAL RESEARCH ON THE ATLANTIC WALRUS

Biologists and archaeologists are increasingly using genetic, isotopic and lipid analyses to uncover current and past walrus behaviour, life history, diet, migration, evolution and human interactions. For each method, and depending on whether studies are performed on live animals or archaeological material, a range of various target tissues are used (e.g. teeth and blubber).

▲ GENETIC RESEARCH

Both hard and soft tissues contain DNA. Soft tissue is normally the preferred source of DNA when available, while teeth and bone can be used to extract DNA from archaeological remains. DNA is found in two places within the animal cell. DNA from the nucleus is inherited from both parents while DNA from the mitochondria is almost entirely inherited from mother to offspring. Hence, while nuclear DNA reveals the genetic history of the entire population, mitochondrial DNA only reflects maternal history. Mitochondrial DNA however is typically more abundant and much simpler than nuclear DNA. This means it is easier to obtain for historic or ancient samples and more commonly included in current genetic research.

Tooth cementum:

- high abundance of mitochondrial DNA (high cell density),
- preferable material for DNA extraction with reduced DNA contamination and higher abundance,
- contains a similar mineral component to bone,
- thickest towards the root tip,
- formed in GLG (growth-layer groups) representing annual deposition.

ISOTOPIC RESEARCH

Animal tissue sample Cementum Cementum Cementum Construction Construct

Animal cell



Tooth **enamel** is composed primarily of a calcium phosphate mineral known as bioapatite and can preserve for millions of years. **Oxygen** in tooth enamel is derived from ingested waters and foods. **Lead** is ingested and substitutes for calcium.

Dentin has a similar structure to bone and contains 20%–25% organic material by weight, 90% of which is the protein Type I collagen and can preserve for up to 100,000 years. The **carbon** and **nitrogen** in the collagen are derived directly from the diet.

FIGURE 10.1

Description of the molecular tools and their application in archaeological and biological research on the Atlantic walrus (*Odobenus rosmarus rosmarus*). Illustration: Elena Kakoshina.

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FATTY ACIDS RESEARCH

Fatty acids are the most abundant type of lipid and most are incorporated into animal tissues directly from the diet, rather than being biosynthesized in vivo. Certain kinds of prey animals have characteristic fatty acid compositions that are passed on to consumers.

RESEARCH RESULTS:

○ □ △ − type of research

DEMOGRAPHIC HISTORY

Statistical analysis based on **variation in** genetic markers can identify periods of population expansion or bottleneck.

DIET 🔵 🗖

Stable **carbon** and **nitrogen** isotopes along with **fatty acid** composition can indicate prey type, trophic level, weaning age and other health parameters associated with pollution.

POPULATION STRUCTURE

These **isotopic measurements** can differentiate population subunits (e.g. stocks) and assess major shifts in distribution. **Only from genetics** showing the relatedness between certain groups or populations. Genetics also allows populations to be characterised, and the degree as well as direction of any connectivity to be determined.

LIFE HISTORY TRAITS

Sex composition can be determined using genetic and morphological analyses.

ECOLOGY AND LIFE HISTORY TRAITS

The kinds of environments in which an animal lived and the types of prey it consumed are reflected in **the fatty acid** and stable **carbon** and **nitrogen** isotopic compositions of its tissues. Isotopic and hormonal values can also be sequentially analysed to understand changes throughout an animal's lifetime.

MIGRATION AND MOBILITY 🔺 🗖

The location of an animal during the period of tissue formation can be determined using various isotopes such as **lead** and **oxygen** either as an average or as a cross-section through time. Additionally, genetics can offer insight into female or male biased movement resulting in reproductive success.

FIGURE 10.1

(Continued).

The nuclear genome is by far the largest, estimated to be approximately ~ 2400 million bases (megabases, Mb) in walruses (Foote et al., 2015) and is inherited from both parents. The mitochondrial genome (sometimes referred to as the mitogenome) is much smaller, only around 16,000–17,000 bases (base pairs, bp), with 37 genes (13 of which are protein coding) and inherited through the maternal line (Ballard and Whitlock, 2004). Hence, while nuclear DNA reveals the genetic history of the entire population, mitochondrial DNA only reflects maternal history (Ballard and Whitlock, 2004; Galtier et al., 2009). As such, different genetic patterns can be expected in species with sex-biased migration behaviour, as observed for many marine mammals including southern elephant seals (Mirounga leonina) and grey seals (Halichoerus grypus) (Hoelzel et al., 2001; Klimova et al., 2014). Another important difference between mtDNA and nuDNA is the number of copies of each genome within the cell. While mammals only have a single nucleus in each cell, the mitochondria can number in the thousands (Cole, 2016). The higher copy number of mitochondrial DNA makes it easier to extract sufficiently high DNA yields for downstream applications, even for highly degraded ancient samples (Foote et al., 2012). Additionally, the two sources of DNA differ in the extent of genetic recombination. Unlike the nuclear genome, mitogenomes rarely undergo genetic recombination, meaning that all genes are linked and hence inherited as one block (Galtier et al., 2009). The more conserved gene content and architecture of mitogenomes, their abundance in animal cells and our knowledge about specific regions with relatively slow and fast rates of evolution, has prompted widespread use of mtDNA (Galtier et al., 2009).

In the last 20 years, mtDNA has been the most frequently used marker for making population genetic inferences, and is the preferred marker for so-called genetic barcoding (Hebert et al., 2003). Here a gene, normally Cytochrome c oxidase subunit I, is used for conducting species or population identification in cases where mtDNA is diagnostic (DNA barcoding) (Hebert et al., 2003). However, using a single marker has many limitations as it only provides the evolutionary history of that particular region of the genome, rather than the organism or species being studied, and often cannot resolve detailed genetic patterns on shorter temporal scales (e.g. parentage assignment, individual identification or detailed demographic histories). The greater number of genetic markers available within the nuclear genome provides more information, thus increasing statistical power and genetic resolution. It is also worth noting that mtDNA is assumed to evolve neutrally (although see Galtier et al., 2009). While this is not a problem for most genetic analyses that assume neutrality (such as phylogeography and demographic history inference), it is of little use when investigating natural selection. Consequently, when focusing solely on mtDNA, potential genetic adaptations will go unnoticed (Keighley et al., 2019a). Such adaptations can reflect key differences between populations, which makes them important for informing conservation efforts (Fraser and Bernatchez, 2001; Saánchez-Molano et al., 2013), and understanding a species' or population's response to natural or anthropogenic pressures (Keighley et al., 2019a).

Historical and archaeological samples

DNA degrades over time due to both chemical and biological processes, which results in fragmentation as well as structural and base modifications (Pääbo et al., 2004). Although modern DNA may be more straightforward to analyse as it has not already degraded, postmortem historical or ancient biological material can still contain DNA, even after hundreds of thousands of years (Orlando et al., 2013). The extent of DNA degradation is influenced by factors of the biological material itself as well as the environmental conditions in which it is deposited. For example, while bone is the most common material recovered from walruses at archaeological sites, (Dyke et al., 1999; Gotfredsen et al., 2018) not all skeletal remains protect the DNA equally well. Differences in DNA preservation between different skeletal elements can be related in part to the density, porosity and structure of the bone. Denser, thicker walled and less-porous material is better at protecting DNA from degradation and microbial contamination (Bollongino et al., 2008; Parker et al., 2020; Keighley et al., 2021). Cementum from walrus teeth and tusks has been shown to have a higher percentage of target DNA in walruses from archaeological sites (Keighley et al., 2021). Generally, DNA is expected to degrade faster when exposed to warm and humid conditions, with climatic fluctuating, exposure to direct sunlight and strongly alkaline or acidic soils also negatively impacting on DNA preservation (Sosa et al., 2013; Nielsen-Marsh & Hedges, 2000; Bollongino et al., 2008; Pruvost et al., 2007; Allentoft et al., 2012; Kendall et al., 2017; Lindahl, 1993; Trueman and Tuross, 2002; Foote et al., 2012). Arctic and sub-Arctic environments tend to preserve DNA for longer periods of time, compared to temperate and tropical regions. Samples buried in cultural deposits, natural sediments or caves often exhibit better DNA preservation compared to samples that have been exposed at the surface for centuries or even millennia (Keighley et al., 2021).

To date, mitochondrial DNA has been the focus of the majority of non-human ancient DNA (aDNA) studies on archaeological samples (Foote et al., 2012), including walruses (Lindqvist et al., 2009, 2016; Star et al., 2018; Keighley et al., 2019b). This is largely due to the higher number of mitogenomes per cell compared to nuclear genomes that makes it easier to extract in sufficiently high DNA yield for downstream applications (Foote et al. 2012). However, recent advances in genetic methods have made it increasingly possible to also analyse nuclear DNA (nuDNA) from archaeological samples (see below).

Source of genetic information

As discussed above, DNA in mammals can be found in both the nucleus and mitochondria. Within each of these however, there are different analytical approaches that target particular regions or the entire genome. The choice of which approach depends on the study, that is, the question being asked and the information required to answer it (Table 10.1). Generally, due to the expected

Molecular marker	Genome	Application
mtRFLP	mtDNA	Population structure/migration
DNA sequences	Nuclear	Population structure/migration, demographic history
DNA sequences	mtDNA	Species identification/DNA barcode
Microsatellites	Nuclear	Individual identification, sex identification, kinship/parentage, population structure/migration, demographic history
SNPs	Nuclear	Individual identification, sex identification, kinship/parentage, population structure/migration, demographic history

Table 10.1 The different genetic markers used, where they are situated and the questions where they are applicable mentioned in the text.

mtDNA, Mitochondrial DNA; mtRFLP, mitochondrial restriction enzyme fragment length polymorphism; SNPs, single nucleotide polymorphisms.

genetic diversity (i.e. number of alleles of the different marker or polymorphism connected to the genetic marker) more alleles translates to more detailed information (the higher power) that can be gained from the marker, and more markers provide more information (Dussex et al., 2018).

To date, most genetic studies on walruses have relied on mtDNA restriction enzyme fragment length polymorphism (RFLP), single mtDNA gene sequencing and/or nuclear microsatellite markers (also known as short tandem repeats) (e.g. Andersen et al., 1998, 2009, 2014, 2017). Microsatellites are highly polymorphic, meaning they show large amounts of variation between individuals. This high variability led to a preference for microsatellites over other nuclear markers such as single nucleotide polymorphisms (SNPs). SNPs are mainly biallelic (two alleles) and around 100 SNPs are needed to obtain the same power as 10-20 microsatellites (Kalinowski 2002). However, with recent advances in molecular methods and sequencing technologies, it is increasingly easy and cost-efficient to sequence thousands or even hundreds of thousands of SNPs (Helyar et al., 2011). One of the most important developments for aDNA has been high-throughput DNA sequencing platforms (also referred to as next generation sequencing or NGS), which enable fast and cost-efficient sequencing of millions of short DNA sequence reads in parallel (Goodwin et al., 2016). With the cost of NGS steadily decreasing, it is now feasible to sequence a reduced part of the nuclear genome or even the whole genome for entire populations of nonmodel organisms, thus obtaining thousands of SNP markers for downstream analysis (Puckett, 2016). NGS technologies have furthermore advanced the field of ancient DNA where a tiny part of the extracted DNA may be of endogenous (i.e. target species) content. In these cases, the large sequence output using NGS allows the recovery of millions of target DNA sequences, even in highly degraded samples (Keighley et al., 2018). When endogenous DNA is present in very low amounts, NGS can be used in combination with DNA capture, a molecular method that allows for collection and upconcentration of species-specific target DNA before subsequently sequencing (e.g. Carpenter et al., 2013; Maricic et al., 2010).

Contemporary population structure and migration patterns

Assessment of population structure is one of the cornerstones of modern population genetic research. When a species shows population structure, it means that there has been very little migration (gene flow) between populations due to the occurrence of physical or reproductive barriers that has allowed populations to become increasingly differentiated from each other. When isolated from each other, populations will evolve in different directions because of the cumulative effects of mutation, selection and genetic drift (Mayr, 1942, 1963; Coyne and Orr, 2004). Population structure is not only evidence for a lack of migration, but more importantly, it can lead to the emergence of unique population-specific genetic variants that may be key for the survival of the specific populations (local adaptations), or for the long-term evolutionary potential of the species (Moritz, 1994; Crandall et al., 2000; Fraser and Bernatchez, 2001). For these reasons, the detection of population structure is one of the main criteria for the designation of conservation units (e.g. Moritz, 1994; Crandall et al., 2000; Fraser and Bernatchez, 2001) and several genetic software packages have been developed that allow for testing whether or not population structure exists (e.g. Excoffier and Heckel. 2006).

Multiple studies have analysed the genetic population structure in Atlantic walruses. The first comprehensive study was conducted by Andersen et al. (1998) and investigated population structure between West and East Atlantic walruses based on analysis of 11 nuclear microsatellite markers and RFLPs from the mtDNA. Analysis of the microsatellite markers revealed that Northwest Greenland, East Greenland and Svalbard-Franz Josef Land were separate populations, while the RFLP haplotypes suggested that Northwest Greenland was evolutionary distinct from the East Atlantic walruses. The study further indicated that very little gene flow occurred between West and East Atlantic walruses. After this pioneering study, several followed using the same overall methodology, but adding more populations from a broader geographical area (e.g. Andersen et al., 1998, 2009, 2014, 2017) and sometimes also including SNP markers (Shafer et al., 2014, 2015). Overall, these studies have so far recognised seven contemporary genetically different populations of Atlantic walrus (see Figures 4.2, 4.3 in Chapter 4, Stocks, Distribution and Abundance).

Differences in migration behaviour may exist between male and female walruses, and these patterns can be disentangled by analysing population structure using both nuclear and mitochondrial markers. For example, the study by Andersen and Born (2000) investigated genetic differentiation between walruses from Northwest Greenland (Thule) and off the coast of West Greenland (Attu-Sisimiut). Overall, they found evidence for population structure from both nuclear microsatellites and mtDNA RFLP markers. However, the structure was mainly driven by differences at the mtDNA level (different RFLP haplotypes) suggesting low levels of gene flow between females and high site fidelity (i.e. returning to the same site again and again). Such findings are supported by observed behavioural differences between males and females particularly in areas such as East Greenland, Svalbard-Franz Josef Land, Pechora Sea (Andersen et al., 2017) and are in line with that observed for other species of marine mammals, including southern elephant seals and grey seals (Hoelzel et al., 2001; Klimova et al., 2014). However, walruses sometimes also undertake long-distance migrations or straying behaviour. This is best illustrated by the finding of a single individual with a Pacific walrus mtDNA haplotype in the East Greenland population (Andersen et al., 1998, 2017).

Migration patterns can be analysed directly between populations, which is crucial for understanding potential source sink populations and important knowledge for conservation efforts. Andersen et al. (2009) estimated the strength and direction of historical and contemporary nuclear gene flow between Western Greenland and Hudson Strait subpopulations. The results suggested that walruses in Hudson Strait might be the source for West Greenland walruses, supporting an earlier suggested counter-clockwise movement of walruses in the area (Freuchen, 1921; Vibe, 1950). A more direct method to detect migration between populations is to identify the same individual in several populations using the genetic markers as a genetic tag or DNA profile (Table 10.1, 'Microsatellites', 'SNPs'). If the genetic tag or DNA profile is 'recaptured', it can be possible to estimate census population size through mark-recapture analysis (Kindberg et al., 2011 (e.g. brown bear); Sethi et al., 2016 (e.g. Pacific walrus)). Further, genetic tags can also be used for identifying parentage and kinship, but this has so far not been applied in any genetic studies on Atlantic walrus.

Population structure in historical and archaeological walrus populations

While analysis of contemporary samples allows us to investigate the current population structure and migration behaviour of walruses, it does not give conclusive insight into the overall stability of this structure over time. With the advances in aDNA methods, it is now possible to investigate whether substantial changes have occurred between modern, historical and archaeological walruses in terms of genetic diversity, migration and distribution, which may be associated to particular anthropogenic effects like hunting, or as a response to climatic and environmental shifts (Keighley et al., 2019a). Multiple genetic studies of walruses have focused on historical or archaeological samples. The first genetic study conducted on walrus bone remains aimed to clarify the number of walrus subspecies. At the time there were three recognised subspecies: Atlantic walrus (*Odobenus rosmarus rosmarus*), Pacific walrus (*Odobenus rosmarus divergens*) and Laptev walrus (Odobenus rosmarus divergens laptevi) (Lindqvist et al., 2009). The study extracted and analysed mtDNA sequences from presumed Laptev walrus remains collected from 1832–1936, along with samples from Atlantic and Pacific walruses. Lindqvist et al. (2009) showed that genetic sequences could be obtained from the historical walrus samples and that the presumed Laptev walruses clustered with samples from the North Pacific. This implied that the Laptev walrus was a part of the westernmost population of the Pacific walrus and not a separate subspecies.

Detailed information about population structure can also improve our understanding of past human-walrus interactions. For instance, McLeod et al. (2014) investigated the potential causes behind the disappearance of walruses inhabiting the Canadian Maritimes (waters of the eastern Canadian provinces of Quebec, New Brunswick, Nova Scotia and Prince Edward Island). This area was inhabited by >100,000 walruses in the 17th century, but none exist today (Naughton, 2012). Whether they were extirpated or changed behaviour, abandoning the region due to the heavy hunting pressure was however unknown. Comparing the mtDNA control region sequences from 37 'Maritime' walrus bones to those from 88 contemporary walruses from Baffin Island and Nunavik revealed that none of the haplotypes (n = 8) observed in the Maritime walruses were found in the modern walruses. When these genetic results were integrated with results on morphological differences between the contemporary and Maritime walruses, McLeod et al. (2014) concluded that the Maritime walrus represented a unique and possible evolutionary distinct walrus population that went extinct due to anthropogenic impact. Similarly, at Svalbard, walruses were already being hunted by Europeanss from the early 1600s and were exploited on a more industrial scale from around 1820 through to 1952. Comparing genetic sequences from remains collected at historical haul-out sites on Bjørnøya (dated to 1867) and Håøya (dated to 1852) to contemporary samples, Lindqvist et al. (2016) showed that some of the historical haplotypes were not observed in the contemporary walruses, although these clustered around modern haplotypes. Lindqvist et al. (2016) concluded that the intense hunting of Atlantic walruses at haul-out sites on Bjørnøva and Håøva probably resulted in behavioural changes, with a shift in distribution rather than local extinction.

The discovery of population structure within a species also allows for sourcing of archaeological artefacts to distinct populations, thereby offering clues into past hunting grounds and trade routes. For instance, according to historical sources, walrus hunting by the Norse during the Viking Age mainly took place around Disko Bay in West Greenland from at least the 13th century (Enghoff, 2003; Keller, 2010; Frei et al., 2015). However, walruses were also hunted in the eastern Atlantic, as far as the Barents Sea and Russia, as documented in historical records from the 9th century (Roesdahl, 2001; Bately and Englert, 2007). Star et al. (2018) analysed mitogenomes obtained from archaeological walrus remains (around 10th–17th centuries) traded with Western Europe and compared these to published modern and 19th-century samples from the Canadian Arctic, Greenland and the Barents Sea region (Andersen et al., 1998; Lindqvist et al., 2009, 2016;

Andersen et al., 2017). The authors found that out of the seven samples predating 1120 CE, all but one belonged to the eastern clade of Atlantic walruses, and could originate from various places in Greenland, but most likely from the northeastern Atlantic. These results suggested that early phases of the Norse ivory hunt targeted populations in the northeastern Atlantic, whereas the Norse walrus hunt in subsequent centuries increasingly targeted walruses in West Greenland and Canada, probably at a time when the eastern stocks were becoming increasingly depleted (Star et al., 2018). Norse walrus hunting and ivory trade have also been studied in Icelandic walruses by Keighley et al. (2019b) who analysed archaeological samples from a now-extinct Icelandic walrus population. The study found a unique lineage that disappeared shortly after Norse arrival in Iceland, implying that Norse walrus hunting and the international ivory trade played a significant role in this local extinction.

Life-history patterns

Life-history parameters such as age, sex, reproductive status and body condition have important consequences for a species' behaviour, survival and ecology. Such information is not easily obtained using molecular markers. However, sex determination from both soft and hard tissues is possible using genetic approaches that target sex chromosomes within the nuclear genome (Table 10.1). Information about sex is important in population genetic studies and archaeology making it possible to detect any past or present sex-biased dispersal and thus changes in migration or distribution patterns that may differ between male or female walruses. When studying hunted walruses, understanding the sex ratio of the catch offers clues into hunting practices and strategies (Keighley et al., 2019a). Genetic markers have been specifically developed for walruses that allow sex identification by targeting a region of 327 and 288 base pairs from the X and Y chromosome, respectively (Fischbach et al., 2008). Andersen et al. (2017) applied the method in a population genetic study on eastern Atlantic walruses. Andersen et al. (2017)'s finding confirmed observations that walruses along the east coast of Greenland and Svalbard-Franz Josef Land are sexually segregated, with male groups in the southern part and females with calves in the northern part of the distribution area (Wiig et al., 2007). Robertson et al. (2018) developed a simpler sex determination method for pinnipeds using a quantitative polymerase chain reaction assay. However, given the highly degraded state of DNA from historical and ancient samples, genetic markers used on such material need to target short regions (e.g. Foote et al., 2012) or use whole-genome sequencing approaches to compare the obtained sequences (including sex chromosome sequences) to a reference genome (Bro-Jørgensen et al., 2020).

Demographic history and population size change

Changes in genetic diversity reflect a species' evolutionary history, as well as its future evolutionary potential, which is paramount for a species' ability to adapt to

environmental change. Generally, large stable populations hold higher genetic diversity, and thus greater adaptive potential, compared to smaller ones (Frankham, 1996). Changes in demographic history of populations are directly linked to genetic diversity. Source populations are expected to show higher genetic diversity compared to newly established populations (Hewitt, 1999). Additionally, population expansion is expected to lead to an increase in genetic diversity, while a severe reduction in effective size (so-called effective population size not equal to the total population size) will lead to rapid loss of genetic variation, fixation of deleterious alleles and inbreeding depression (Frankham, 1996). Changes in population size may be linked to environmental or anthropogenic impacts (Andersen et al., 2009, 2017; Shafer et al., 2015; Keighley et al., 2019b). For instance, population expansion may occur in response to factors such as an increase in available habitat, improved environmental conditions, greater availability of prey items or reduced hunting pressure (Vilá-Cabrera et al., 2019). Conversely, deteriorations in local environmental conditions or increases in human hunting pressures can cause population decline, which in severe cases can create genetic bottlenecks that see the loss of large amounts of genetic diversity.

Currently several genealogy-based (coalescent-based) methods have been developed to estimate effective population size changes for individual populations, or multiple populations simultaneously to account for the effects of potential gene flow (e.g. Cornuet and Luikart, 1996; Piry et al., 1999; Gutenkunst et al., 2009; Excoffier and Foll, 2011; Bouckaert et al., 2019). In addition to the scale and nature of population size change, the timing can be estimated when the genetic mutation rate is known or can be estimated directly from the data. Such methods can be applied to a wide array of genetic markers like microsatellites, sequence data and SNPs and can infer the demographic history of a population based solely on contemporary samples, as well as historical and ancient samples (Drummond et al., 2003; Ramakrishnan et al., 2005). Here, the use of several unlinked genetic markers and/ or the use of temporal samples increase the statistical power and genetic resolution.

To date, all contemporary genetically identified populations of Atlantic walrus have been analysed using nuclear microsatellite markers, but no evidence for bottlenecks due to historical hunting pressure have been found (Andersen et al., 2009, 2017). The reasons for this are still unknown. One possibility is simply that populations responded to human hunting by changing migratory behaviour, fleeing to more-remote and less-accessible areas or that the actual reductions were too small to detect given the sample size and genetic markers used (Andersen et al., 2009). Alternatively, any hunting effect may have been hidden due to errors in technical assumption, for example, of mutation rate models (Peery et al., 2012), or in some cases detecting the signals of past demographic events require ancient DNA approaches. The latter is definitely true of extinct populations, such as the Icelandic (Keighley et al., 2019b) and Maritimes walrus (McLeod et al., 2014) that might have left little or no traces of contemporary genetic samples.

Effective population size change in Atlantic walruses has also been analysed across deeper time scales, using different analytical methods and markers. Shafer et al. (2015) analysed 4854 SNPs to reconstruct the demographic history of

walruses from the Canadian Arctic by comparing observed genetic variation in walruses with several modelled demographic scenarios. Overall, a model with divergence between northern and southern Canadian Arctic walruses followed by modest and asymmetric gene flow migration from the northern to the southern cluster showed the best fit to the data. A relatively recent bottleneck event was detected in the high Arctic, while an older bottleneck was indicated in the central Arctic. The older bottleneck and population size decrease was potentially caused by the Last Glacial Maximum and subsequently led to the recolonisation of the Northern Canada waters. Contrary to this result, Andersen et al. (2017) detected a constant effective female population size for Atlantic walruses in East Greenland, and an increase in Svalbard-Franz Josef Land and Pechora Sea walruses starting around 40–30 thousand years ago using mtDNA. These differences in demographic history for two Atlantic walrus stocks may be associated with sea ice distribution, which might have caused geographic variability in the availability of food and haul-out sites for walruses (Andersen et al., 2017).

Stable isotopes and fatty acids Diet and ecology

Stable isotopes

Stable carbon (δ^{13} C), nitrogen (δ^{15} N) and sulphur (δ^{34} S) isotopic compositions of animal tissues reflect the weighted average of the foods consumed during the period of tissue formation. For example, the isotopic composition of liver reflects the average diet over a period of days (Hobson and Clark, 1992; Tieszen et al., 1983), while the isotopic composition of bone collagen reflects the average diet over years or decades (Hedges et al., 2007). Stable isotopes have been used extensively to characterise the diet and ecology of many animal taxa, both extinct and extant. Stable isotope techniques have been especially valuable in characterizing the ecology of marine mammals (Newsome et al., 2010) because of the difficulties associated with observing these animals and the ethical issues surrounding conducting lethal sampling activities (e.g. for analysis of stomach contents) on sufficiently large numbers of individuals.

Stable carbon isotope compositions are generally conserved across trophic levels, and consumer tissue δ^{13} C values reflect the ultimate source of primary production. In polar seas, pelagic phytoplankton and sea-ice-associated algae have been observed to have δ^{13} C values that differ from one another by 5%–12% (France et al., 1998; McMahon et al., 2006; Søreide et al., 2006), allowing the contribution of production derived from sea ice algae in higher trophic levels to be quantified (Kohlbach et al., 2016; Søreide et al., 2013; Stasko et al., 2018). Animals that forage in benthic habits tend to have higher tissue δ^{13} C values than those that forage in pelagic habitats (McConnaughey and McRoy, 1979), a product of differences in discrimination against ¹³C during uptake and assimilation of

dissolved inorganic carbon by benthic versus pelagic algae driven by water turbidity (France, 1995). Because of these benthic—pelagic differences, it is also the case that animals foraging in inshore habitats have higher tissue δ^{13} C values than animals foraging offshore (Cherel and Hobson, 2007; Hobson, 1993; Hobson et al., 1994). The δ^{13} C value of CO₂ in the atmosphere and oceans has decreased significantly since the late-19th century due to the industrial and domestic combustion of isotopically light fossil fuels; the rate of this decline has increased over time (Eide et al., 2017; Quay et al., 1992). Accordingly, these changes must be accounted for when δ^{13} C time series are developed from animal tissues sampled across multiple years, or when comparisons are made between preindustrial and more recent samples (Hilton et al., 2006; Laws et al., 2002).

Stable nitrogen isotopic compositions (δ^{15} N) increase by 3.4% on average with each trophic level (Minagawa and Wada, 1984; Post, 2002). As with δ^{13} C, the δ^{15} N values at the base of the food web can also vary. Where N2-fixing cyanobacteria are dominant, the δ^{15} N values in consumers are relatively low in comparison to areas where phytoplankton predominate (Montoya, 2008). Areas characterised by strong upwelling and anoxic conditions (favouring denitrification) have particularly high δ^{15} N values throughout the food web (Voss et al., 2001). This variation at the base of the food web is reflected in the tissues of consumers at higher trophic levels, meaning that δ^{15} N cannot be used to compare the trophic position of a given taxon across space without accounting for variation at the base of the food web (Lorrain et al., 2015; Pethybridge et al., 2018). The δ^{15} N values at the base of the food web can vary significantly over time (on temporal scales of $10^2 - 10^6$ years), with variation in sediment core records being interpreted primarily in light of varying rates of denitrification and N₂ fixation (Altabet, 2006). There may be significant age-related variation in mammal tissue δ^{15} N caused by nursing. Nursing animals possess δ^{15} N values that are higher than those of the mother (Fogel et al., 1989), making strict interpretations of trophic position less straightforward. This nursing effect has been recorded in both soft tissues with rapid turnover rates and bone collagen for marine mammals (Gorlova et al., 2012; Habran et al., 2010; Newsome et al., 2006).

Relative to other endemic Arctic marine mammals, a relatively small number of light stable isotope compositions have been determined for Atlantic walrus tissues. The bulk of these data have been collected to contextualise other data, such as tissue Hg concentrations (Atwell et al., 1998; Rigét et al., 2007a; Rigét et al., 2007b) and persistent organic pollutants (Muir et al., 1995; Scotter et al., 2019). A few studies have measured the δ^{13} C and δ^{15} N values of various marine food web components and include measurements on walrus, although the sample sizes for walruses are always very small (Hobson et al., 2002; Hobson and Welch, 1992; Linnebjerg et al., 2016). When compared to other marine mammals or food web components, walruses occupy the lowest trophic position (on the basis of their δ^{15} N values) and these studies have concluded that walruses forage primarily on benthic invertebrates, consistent with what is known about their diets based on other lines of evidence (Fay, 1985; Fisher and Stewart, 1997). There are few published δ^{34} S measurements on Atlantic walrus tissues, but one recent study suggests that these may prove valuable in

discerning the importance of production derived from benthic microalgae versus pelagic phytoplankton (Szpak and Buckley, 2020).

As with modern walruses, there have been sparingly few isotopic measurements on archaeological specimens. These data have primarily been generated for the purpose of providing a baseline for reconstructing ancient human diet (Coltrain et al., 2004; Nelson et al., 2012; von Steinsdorff and Grupe, 2006). One exception is the study conducted by Jaouen et al. (2016) for archaeological marine mammals from Little Cornwallis Island dating to the Late Dorset period. Consistent with modern studies, these data demonstrate that walruses occupy the lowest trophic position relative to other endemic Arctic marine mammals, such as polar bear, ringed seal (Pusa hispida) and bearded seal (Erignathus barbatus). One interesting pattern that has emerged from the few studies that have compared walruses to other taxa is the lack of a distinction in δ^{13} C between walruses and other pinnipeds. Given that δ^{13} C values are frequently cited as a distinguisher between benthic and pelagic consumers, it is surprising that walruses possess comparable or even lower δ^{13} C values than ringed or bearded seals (Fig. 10.2). This may simply be a product of very tight benthic-pelagic coupling and low in situ benthic productivity in the regions that have been studied. Alternatively, because there is a modest increase in consumer δ^{13} C values with trophic level, the low trophic position of walruses relative to bearded seal and ringed seal may serve to obscure differences in δ^{13} C related to benthic-pelagic gradients.



FIGURE 10.2

Stable carbon and nitrogen isotopic compositions for ancient walruses compared to other marine mammals from (A) Little Cornwallis Island in the central Canadian Archipelago (Jaouen et al., 2016) and (B) Skraeling Island, eastern Ellesmere Island, Canada (Szpak Unpublished Data).

A key question that has emerged in relation to walrus diet is the extent to which walruses rely on higher trophic-level prey (pinnipeds and seabirds), a behaviour that has been recorded in both Atlantic and Pacific walruses (Fay, 1960; Fox et al., 2010; Lowry and Fay, 1984; Mallory et al., 2004). This behaviour is noteworthy because it may be linked to climate change, with the occasional or more permanent loss of sea ice habitats potentially increasing the extent to which walruses feed on seals and seabirds (Seymour et al., 2014). These dietary shifts should be easily detectable with stable isotope analyses, although detection of changing feeding strategies in more ancient walrus specimens would require that there had been a significant contribution of higher trophic-level prey over many years due to the slow turnover rate of bone collagen. In the most extensive isotopic study of walruses (Atlantic or Pacific), Clark et al. (2019) examined the δ^{13} C and δ^{15} N values of ancient and modern Pacific walruses over the last 4000 years in the Chukchi Sea. They did not find differences in mean isotopic compositions in periods where high or low sea ice productivity was indicated by dinocysts, although there was greater isotopic (and hence dietary) variation when sea ice extent was low. They also observed relatively low $\delta^{15}N$ values in contemporary walruses (especially males) relative to archaeological specimens. Given that these low $\delta^{15}N$ values were not observed in times of low sea ice extent in the past, they suggested that this is indicative of changes in the diet of walruses that may deviate from patterns of long-term stability for the last 4000 years.

Rather than focusing on walrus diet (and changes therein) as reflected in tissue stable isotope compositions, a more productive avenue of research might involve the utilisation of isotopic measurements of ancient walrus tissues to track changes at the base of the food web. Given that their diets are so consistently dominated by bivalves, walrus tissue isotopic compositions are more likely to reflect shifts in nutrient regimes and community composition of primary producers than changes in trophic position (see Newsome et al., 2007; Sherwood et al., 2014). A similar approach has been utilised with ringed seals in both Alaska (Szpak et al., 2018) and the central Canadian Arctic Archipelago (Szpak et al., 2019) to attempt to track changes in the productivity of sea ice algae in the Late Holocene. A common challenge of all such studies utilising archaeological materials is the uneven temporal distribution of sites within a region and the resulting 'floating sequences' that are produced, potentially leading to long periods of time that lack appropriate materials to sample. The best means by which to overcome this challenge is to focus on archaeological sequences where walruses were persistently abundant in archaeofaunal assemblages (Desjardins, 2013; Dyke et al., 2019) or to use palaeontological materials derived from natural strandings (Dyke et al., 1999) that are more likely to produce a more-or-less continuous time series.

Fatty acids

Analysis of the FAs found in the tissues of marine mammals has proven useful for better understanding their diets and food web structure (Budge et al., 2006; Dalsgaard et al., 2003; Iverson et al., 2004; Kelly and Scheibling, 2012). Relative

differences in diet composition among taxa, among geographic regions, or over time can be inferred in a qualitative sense using FA signatures (Beck et al., 2007; Falk-Petersen et al., 2004; Iverson et al., 1997). Quantitative FA signature analysis (QFASA) has been proposed as a method that provides more refined estimates of prey composition relative to stable isotope analysis (Iverson et al., 2004) because the isotopic compositions of particular types of prey are rarely unique enough from one another for their proportions in the diet to be accurately estimated, particularly for consumers that eat a large number of different prey (Phillips et al., 2014).

FAs, the primary class of lipids in animal tissues, are liberated from triacyglycerols in the process of digestion but are thereafter generally incorporated with minimal modification (relative to proteins and carbohydrates) into consumer tissues (Iverson et al., 2004). While primary producers can synthesise a wide range of FAs, animals have a very limited capacity to do so (Guschina and Harwood, 2009). Considering marine mammals such as walrus, many FAs are ubiquitous among their prey and are therefore not useful as diet tracers, but in some cases, FAs can trace the relative importance of specific prey items or classes of primary producers at the base of the food web. In practice, a quantitative interpretation of these data is far more complicated and requires both an extensive understanding of the FA composition of all potential prey and taxon-specific 'calibration coefficients' that account for lipid metabolism in the target consumer (Happel et al., 2016; Iverson et al., 2004; Nordstrom et al., 2008).

One example of a specific class of FA that can be traced to specific prey types are the nonmethylene-interrupted (NMI) C20 and C22 FA, which are synthesised by benthic invertebrates such as molluscs (Barnathan, 2009; Joseph, 1982; Zhukova, 1991). These FAs have been used to investigate the extent of dietary niche overlap between Pacific walruses and bearded seal in Alaska (Budge et al., 2007). Both species contained substantial quantities of NMI FA, but the proportions varied between the two taxa (Fig. 10.3). Such elevated levels of NMI FA in marine mammal blubber are rare, suggesting that walruses and bearded seal both consumed benthic invertebrates (or other prey that consumed these invertebrates) to a large extent, but differed in the specific types of prey consumed (Budge et al., 2007). Stable carbon and nitrogen isotope analyses of walruses and bearded seal have also confirmed distinct niches for these two species, with bearded seals consuming a larger quantity of epibenthic fish and hence feeding at a much higher trophic level than walrus (Fig. 10.3) (Finley and Evans, 1983). The lone FA study of Atlantic walruses confirmed NMI FAs in the dermis, inner and outer blubber (Skoglund et al., 2010) but at lower relative abundances than in the study of Pacific walruses from Alaska (Budge et al., 2007). These NMI FAs were also present in all of the potential benthic prey species that were sampled, precluding the possibility of more quantitative assessments of prey composition.

A particularly relevant series of lipid biomarkers (highly branched isoprenoids, HBIs) have been identified in diatoms and subsequently in higher trophic-level consumers such as pinnipeds (Brown et al., 2014; Brown et al., 2013), belugas



FIGURE 10.3

Proportions of nonmethylene-interrupted fatty acids in Pacific walruses and bearded seal from Little Diomede Island, Alaska, United States.

Data from Budge et al. (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. Marine Ecology Progress Series, 336:305–309. doi: 10.3354/meps336305.

(Brown et al., 2017) and polar bears (Brown et al., 2018). Several of these HBIs are produced by sea-ice-associated diatoms during the spring bloom, while others are produced by pelagic phytoplankton during the summer bloom (Belt, 2018; Belt and Müller, 2013). An index of these different HBIs has been developed to quantify the relative importance of sympagic and pelagic productivity in Arctic food webs (Brown et al., 2014). These techniques can be used to examine the relative importance of sympagic production that is delivered to the benthos (Oxtoby et al., 2017) and how this might change over time, particularly when combined with stable isotope measurements of these FAs. Such shifts may have significant impacts on walrus populations (Grebmeier et al., 2006).

Compound-specific stable isotope analysis (CSIA) provides an opportunity to examine the isotopic compositions of particular compounds (such as FAs and amino acids) that are isolated via gas chromatography-combustion-isotope ratio mass spectrometry (GC/C-IRMS). A major advantage of these techniques over bulk isotopic measurements is that they reduce equivocality (i.e. ambiguities arising from a single outcome arising from two or more possible scenarios that cannot be differentiated from each other) in the interpretation of the data. For example, δ^{13} C values of bulk consumer tissues may be influenced by either a change in the diet of a consumer, or a shift in the δ^{13} C value at the base of the food web. Individual FAs that are unique to particular kinds of producers have δ^{13} C values that more faithfully reflect the conditions at the base of the food web (Budge et al., 2008). These techniques have been applied to FA derived from Arctic pinnipeds, including Pacific walrus, to quantify the relative importance of

pelagic and sympagic production (Oxtoby et al., 2017; Wang et al., 2016). Essential amino acid δ^{15} N values reflect the δ^{15} N value at the base of the food web, while nonessential amino acid δ^{15} N values reflect the trophic position of the consumer (McClelland and Montoya, 2002; Popp et al., 2007). CSIA therefore provides an opportunity to discern shifts in trophic position from shifts in the δ^{15} N value at the base of the food web. This is a particularly prescient concern for studying ancient ecosystems since we might expect large-scale environmental changes to be accompanied by shifts in the diet of particular consumers.

The analysis of FA from archaeological vertebrate tissue samples remains largely unstudied. It is unclear whether the FAs preserved in ancient bones are comparable to those obtained from blubber biopsy samples, or if FAs trapped within the cortical bone microstructure vary significantly among different taxa. FAs have been isolated from bone samples that are thousands of years old (Kostyukevich et al., 2018) and their carbon isotopic compositions have been measured (Colonese et al., 2015; Colonese et al., 2017). Given the excellent organic preservation of archaeological vertebrate remains at high latitude sites where walruses may occur, the possibility exists that ancient FA composition and isotopic measurements of ancient FAs may be informative with respect to past environmental conditions.

Population structure and migration

Stable isotopes

While carbon and nitrogen isotope compositions of consumer tissues are influenced by the foods that they consume, a range of other isotope systems vary predictably across space, influenced by either the local climate (particularly precipitation regime) or underlying geology (Hobson, 1999). The oxygen (δ^{18} O) and hydrogen (δ^{2} H or δ D) isotopic compositions of meteoric waters vary widely across the globe, in accordance with factors such as temperature, latitude, altitude, distance from the coast and rainfall amount (Gat, 1996). The δ^{18} O values of ocean waters are relatively homogenous but surface waters do exhibit geographic variation at different latitudes (LeGrande and Schmidt, 2006) and coastal areas, particularly those influenced by large freshwater discharge, may have distinct δ^{18} O values relative to open ocean (Cooper et al., 2005). The oxygen isotope compositions of many consumer tissues are directly correlated to those of local waters, allowing δ^{18} O measurements, as well as the related δ^{2} H, to be used for the study of migrations among terrestrial taxa (Bowen et al., 2005).

Strontium and lead substitute for calcium in biological tissues including bones and teeth (Trueman and Tuross, 2002). The isotope ratios of strontium (⁸⁷Sr/⁸⁶Sr) and lead (e.g. ²⁰⁶Pb/²⁰⁷Pb, ²⁰⁸Pb/²⁰⁷Pb, ^{20x}Pb/²⁰⁴Pb) in consumer tissues reflect the underlying geology and are therefore sensitive tracers of locality (Aggarwal et al., 2008; Bentley, 2006). Sr isotope ratios of human enamel have been used extensively to study migration in ancient populations; however, Sr isotope ratios

of bones appear to be less suited as they are often significantly contaminated from the local burial environment (Hoppe et al., 2003) owing to the greater porosity and smaller size of the bioapatite mineral crystallites in bone (Trueman and Tuross, 2002).

Geographic (rather than dietary) isotope systems have been utilised infrequently to study marine mammal ecology and biogeography (relative to δ^{13} C and δ^{15} N), although a series of case studies involving modern and ancient walruses highlight the potential for future research in this area. For example, it has been shown that oxygen isotope compositions of marine mammal tissues can differentiate animals inhabiting different ocean basins, particularly across a large range of latitudes (Matthews et al., 2016). Walrus tissue δ^{18} O values are unlikely to be useful discriminators of stock structure in modern populations because the spatial scales over which oceanic δ^{18} O values vary is quite large (but see Vighi et al., 2016). Sequential analyses of incrementally growing tissues, such as dentine annuli, could provide insight into fine-scale seasonal movements, as has been demonstrated for sperm whales (Borrell et al., 2013). The possibility also exists that oxygen isotope compositions of walrus ivory could aid in eliminating potential source areas for historically traded objects. Positively identifying a particular source area with this technique is, however, unlikely due to the fact that geographically disparate areas may share similar δ^{18} O values in meteoric waters.

Although Sr isotope ratios have been successfully applied to understand the migrations of fish such as salmon (Brennan et al., 2015; Kennedy et al., 2000; Koch et al., 1992), the single study that has been performed on walruses from the Canadian Arctic revealed no meaningful spatial variation, with all of the walrus ⁸⁷Sr/⁸⁶Sr ratios falling around the global average for seawater (Davis et al., 1998). On the other hand, significant spatial variation has been found in the lead isotope ratios of modern walrus bulk tooth cementum from the Canadian Arctic and Greenland (Outridge et al., 2003; Outridge and Stewart, 1999). These studies revealed that walrus populations exploited by different communities in the Canadian Arctic tended to have distinct tissue lead isotope ratios (particularly ²⁰⁸Pb/²⁰⁴Pb and ²⁰⁸Pb/²⁰⁷Pb). Walrus tooth lead isotope ratios were related to those of the local geological lead sources; however, lead isotope ratios were more homogenous in the animals than the underlying bedrock. This difference in lead isotope ratios is a common phenomenon and reflects the ability of consumers to effectively average the bioavailable lead or strontium across space (Price et al., 2002). These data suggested that there is a greater number of discrete stocks of Atlantic walruses in the Canadian Arctic than has been previously supposed (Born et al., 1995).

One limitation of using bulk cementum is that multiple years of the animal's life are averaged. Two or more areas with disparate lead isotope ratios in the underlying geological formations may potentially be integrated, resulting in a signature that is unrepresentative of any specific period of the animal's life. These limitations can be mitigated by serial-sampling of the incrementally growing portions of the teeth (Stern et al., 1999), an approach that Stewart et al. (2006) applied to a subset of the individual walruses analysed by Outridge et al. (2003).

Individuals with 'local' bulk cementum lead isotope ratios had little variation in the incrementally sampled tissue, suggesting relatively little long-distance movement throughout their lives. Some walruses that had outlier lead isotope ratios (relative to other 'local' animals) appeared to be either immigrants (those that lived elsewhere and migrated to the area where they were harvested, settling long enough to acquire to local geological signature) or what the authors dubbed 'prodigal sons' (animals that may have been born locally, migrated elsewhere after weaning and reacquired the local signature as mature adults).

The results of the study by Outridge et al. (2003) demonstrated the potential for using lead isotope measurements of walrus ivory to determine its source region and trace the trade in various objects, similar to studies conducted with elephant ivory (van der Merwe et al., 1990; Vogel et al., 1990). This particular application has yet to be fully realised. Frei et al. (2015) conducted a pilot study with modern, historic and ancient walrus bone and ivory to explore the potential of utilising the approach of Outridge et al. (2003). Unlike bone, enamel is highly resistant to diagenesis, and Sr and Pb isotopic compositions are assumed to be relatively stable in the burial environment. Their results demonstrated that it should be feasible to differentiate walrus ivory that was obtained from Greenland, Iceland and the White Sea, opening up the possibility for testing specific hypotheses about the motivation for the Norse colonisation of Iceland and Greenland.

Future perspectives in genetics, stable isotopes and fatty acids research

Given the advances in NGS technologies, it is now possible to conduct genome scale analyses of nonmodel organisms by sequencing either reduced or full genomes of nuclear or mitochondrial DNA (Ellegren, 2014; da Fonseca et al., 2016; Goodwin et al., 2016). Currently, few studies on Atlantic walruses have applied NGS methods (Shafer et al., 2015; Star et al., 2018; Keighley et al., 2019b), but more are underway (e.g. Keighley et al., 2018). The genomic datasets will increase genetic resolution (e.g. Drummond et al., 2003; Foote et al., 2012), which in turn will pave the way for detailed information about walrus biology, demography and human interactions. New insights are likely to include better estimates of divergence timing, demographic event characterisation and the extent of local genetic adaptation within populations (Drummond et al., 2003; Keighley et al., 2019a). As genome-scale studies become increasingly affordable and feasible there is enormous potential to analyse the wealth of hitherto unstudied paleogenetic samples which are now stored in museums worldwide (Keighley et al., 2018). The sequencing of historic and ancient samples will provide novel information on past human-walrus interactions and provide insights into the nature, scale and duration of any impact of anthropogenic practices on Atlantic walruses past and present (Keighley et al., 2019a; Keighley et al., 2019b; Barrett et al., 2020).

Combining genetic and isotopic analyses of skeletal remains can provide highly complementary information. It is often difficult to assign biological sex to vertebrate remains, but molecular sexing techniques can allow for the investigation of sexual segregation in foraging habitats in the ancient past (Szpak et al., 2020; Bro-Jørgensen et al., 2020). In some cases, genetic and isotopic markers can be used in combination to assess the population structure of organisms, both modern (Clegg et al., 2003) and ancient (Eda et al., 2012; Hutchinson et al., 2015). This approach would likely be effective with Atlantic walruses given the genetic and isotopic differences that are known to exist within the range of this species today. Molecular techniques have the potential to identify the presence of populations that are now extinct (Nichols et al., 2007; Keighley et al., 2019b), and isotopic techniques can provide the opportunity to study the ecology of these populations (Moss et al., 2006; Szpak et al., 2012). Combining the two techniques, it will be possible to test hypothesis regarding the possible convergence of changes in feeding ecology and population structure over time, as well as comparing contemporary and archaeological samples of walruses to provide clues as to how climate or humans may have impacted walruses (Alter et al., 2012). Theoretically, this could be modelled and used to predict future consequences of climate change and human activities on walruses across their range.

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THE ATLANTIC WALRUS

Multidisciplinary insights into human-animal interactions

Xénia Keighley, Morten Tange Olsen, Peter Jordan and Sean Desjardins

A comprehensive assessment of more than 4000 years of interactions between humans and the Atlantic Walrus.

The Atlantic Walrus: Multidisciplinary insights into human-animal interactions addresses the key dimensions of long-term humanwalrus interactions across the Atlantic Arctic and subarctic regions, over the past millennia. This book brings together research from across the social and natural sciences to explore walrus biology, human culture, environmental conditions and their reciprocal effects. Together, 13 chapters of this book reconstruct the early evolution of walruses, walrus biology, the cultural significance and ecological impact of prehistoric and indigenous hunting practices, as well as the effects of commercial hunting and international trade. This book also examines historic and ongoing management strategies and, the importance of new research methodologies in revealing hitherto unknown details of the past, and concludes by discussing the future for Atlantic walruses in the face of climate change and increased human activities in the Arctic.

This volume is an ideal resource for those who are seeking to understand an iconic Arctic species and its long and complex relationship with humans. This includes individuals and researchers with a personal or professional connection to walruses or the Arctic, as well as marine biologists, zoologists, conservationists, paleontologists, archaeologists, anthropologists, historians, indigenous communities, natural resource managers and government agencies.

Key Features:

- Provides succinct overviews of the biology of the Atlantic walrus, as well as human cultures within the North Atlantic Arctic and the surrounding region by consolidating research which until now has been scattered across fields and academic publications
- Editorial team of inter-disciplinary researchers ensuring the breadth, depth and integration of material covered throughout the volume
- Thirteen chapters, each authored by leading international researchers and experts on the Atlantic walrus (*Odobenus rosmarus rosmarus*)
- Considers the inter-relatedness and complexity of species biology, ecological change, human culture, and anthropogenic pressures onto the Atlantic walrus, all while remaining accessible to readers from different disciplines or a more generalist audience
- Draws upon the latest methods in marine mammal and archaeological research
- Assesses historical management of the species, while also considering current and future conservation efforts in light of human activities and climate change
- Text supported by striking and insightful new maps and scientific illustrations, ideal for teaching and outreach

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