

Bowhead Whales, and Not Right Whales, Were the Primary Target of 16th- to 17th-Century Basque Whalers in the Western North Atlantic

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ABSTRACT. During the 16th and 17th centuries, Basque whalers travelled annually to the Strait of Belle Isle and Gulf of St. Lawrence to hunt whales. The hunting that occurred during this period is of primary significance for the North Atlantic right whale, *Eubalaena glacialis* (Müller, 1776), because it has been interpreted as the largest human-induced reduction of the western North Atlantic population, with ~12 250–21 000 whales killed. It has been frequently reported that the Basques targeted two species in this region: the North Atlantic right whale and the bowhead whale, *Balaena mysticetus* L., 1758. To evaluate this hypothesis and the relative impact of this period of whaling on both species, we collected samples from 364 whale bones during a comprehensive search of Basque whaling ports from the 16th to the 17th century in the Strait of Belle Isle and Gulf of St. Lawrence. Bones were found and sampled at 10 of the 20 sites investigated. DNA was extracted from a subset (n = 218) of these samples. Analysis of the mitochondrial cytochrome *b* region identified five whale species. The identification of only a single right whale bone and 203 bowhead whale bones from at least 72 individuals indicates that the bowhead whale was likely the principal target of the hunt. These results imply that this whaling had a much greater impact (in terms of numbers of whales removed) on the bowhead whale population than on the western North Atlantic right whale population.

Key words: *Balaena mysticetus*, *Eubalaena glacialis*, whaling, Basque, Little Ice Age, historical population size, DNA, bone, cytochrome *b*

RÉSUMÉ. Aux XVI^e et XVII^e siècles, les baleiniers basques se rendaient tous les ans au détroit de Belle Isle et au golfe du Saint-Laurent pour faire la chasse aux baleines. La chasse qui s'est effectuée pendant cette période revêt une grande importance pour la baleine franche ou baleine noire de l'Atlantique Nord, *Eubalaena glacialis* (Müller, 1776), car cette activité serait interprétée comme la plus grande réduction de la population de baleines franches de l'Atlantique Nord causée par l'être humain, au rythme d'environ 12 250 à 21 000 baleines tuées. On a souvent signalé que les Basques visaient deux espèces dans cette région, soit la baleine franche de l'Atlantique Nord et la baleine boréale, *Balaena mysticetus* L., 1758. Pour évaluer cette hypothèse et l'incidence relative de cette période de pêche aux baleines sur ces deux espèces, nous avons recueilli des échantillons provenant de 364 ossements de baleines dans le cadre d'une recherche approfondie de ports basques de chasse à la baleine remontant aux XVI^e et XVII^e siècles dans le détroit de Belle Isle et le golfe du Saint-Laurent. Des ossements ont été trouvés et échantillonnés à 10 des 20 sites ayant fait l'objet de notre recherche. De l'ADN a été extrait d'un sous-ensemble (n = 218) de ces échantillons. L'analyse mitochondriale cytochrome *b* de la région a permis d'identifier cinq espèces de baleines. L'identification d'un seul os de baleine franche et de 203 os de baleines boréales provenant d'au moins 72 individus laisse croire que la baleine boréale était probablement la cible principale des chasseurs. Ces résultats impliquent que la chasse à la baleine a eu des incidences beaucoup plus grandes (en termes de nombres de baleines éliminées) sur la population de baleines boréales que sur la population de baleines franches de l'ouest de l'Atlantique Nord.

Mots clés : *Balaena mysticetus*, *Eubalaena glacialis*, chasse à la baleine, Basque, petit âge glaciaire, taille de la population historique, ADN, ossement, cytochrome *b*

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INTRODUCTION

Historical tissue samples can be useful for assessing the population biology and past demography of threatened and endangered species. For many species, historical specimens are often not available for direct comparisons of genetic characteristics that existed prior to anthropogenic impacts with those of modern populations (Bouzat, 2001) and instead geographically distinct populations or sister species are used as surrogates (e.g., Palo et al., 2003). However, this reasoning by analogy can be inappropriate if the groups compared have differing demographic and phylogenetic histories. Analyses of historical specimens can provide information on historical levels of genetic diversity (e.g., Bouzat et al., 1998; Hadly et al., 1998; Groombridge et al., 2000; Matocq and Villablanca, 2001; Larson et al., 2002; Paxinos et al., 2002; Nyström et al., 2006); responses to climate change (e.g., Orlando et al., 2002; Barnosky et al., 2003; Hadly et al., 2003; Shapiro et al., 2004; Chan et al., 2005); systematics (Goldstein and Desalle, 2003; Krause et al., 2006; Poulakakis et al., 2006); rates of evolution (e.g., Lambert et al., 2002); bottleneck events (e.g., Hadly et al., 2003); and historical population dynamics (e.g., Leonard et al., 2000; Pertoldi et al., 2001; Barnes et al., 2002; Orlando et al., 2002; Shapiro et al., 2004). Many of these analyses have potential application in conservation genetics for species management, the evaluation of species recovery, and even the projection and prediction of biological responses to future environmental changes.

Whaling over the past five centuries represents one of the earliest and most detrimental human impacts on the marine ecosystem (Reeves and Smith, 2006). The industry was significant for its international distribution and participation and the “commercial extinction” of most large whale species. Not only did whale oil light the streets of Europe and America, fuel economies, and lubricate factories, but the industry left most large whale species endangered (Clapham et al., 1999) and may have affected food webs across hemispheres (e.g., Springer et al., 2003; but see Wade et al., 2007). Although the means to assess how whaling may have impacted large whale species are limited, it has been demonstrated that DNA can be successfully extracted from historical whale bones (Tebbutt et al., 2000; Rastogi et al., 2004; Morin et al., 2006; Borge et al., 2007), teeth (Pichler et al., 2001; Morin et al., 2006) and baleen specimens (Rosenbaum et al., 1997; Eastop and McEwing, 2004). This represents an important step towards using historical specimens to evaluate pre-exploitation levels of genetic diversity, population sizes, and catch composition.

The North Atlantic right whale (*Eubalaena glacialis*) and the bowhead whale (*Balaena mysticetus*) are two baleen whale species that have exhibited relatively limited recovery despite more than 70 years of international protection. The North Atlantic right whale is currently recognized as “endangered” (IUCN, 2006). Although it was once a trans-Atlantic species, the only viable population

that remains is found primarily in the western North Atlantic (but see Knowlton et al., 1992; Martin and Walker, 1997; Reeves, 2001; Jacobsen et al., 2004) with 300–350 individuals remaining (IWC, 2001; Kraus et al., 2001, 2005). In addition to having a very small population size, this species has low genetic diversity (Schaeff et al., 1991, 1997; Malik et al., 2000; Waldick et al., 2002) and a low reproductive rate (Knowlton et al., 1994; Kraus et al., 2001), two factors that have been assumed to be a result of population reductions caused by whaling. The bowhead whale has ~ 9000–14400 individuals remaining worldwide (Zeh et al., 1993; Moshenko et al., 2003; George et al., 2004), which are found within five designated stocks (Bering/Chukchi/Beaufort Sea, Okhotsk Sea, Hudson Bay/Foxe Basin, Davis Strait/Baffin Bay, and Spitsbergen (Moore and Reeves, 1993; but see Heide-Jørgensen et al., 2006). However, ~8100–13500 (90–94%) of these whales are found in the Bering/Chukchi/Beaufort Sea (George et al., 2004), and the status of recovery for the remaining four bowhead stocks has not been thoroughly evaluated. The Okhotsk Sea and Davis Strait/Baffin Bay stocks are currently recognized as “endangered,” the Hudson Bay/Foxe Basin as “vulnerable,” and the Spitsbergen stock as “critically endangered” (IUCN, 2006).

Sixteenth-century Basque whaling in the Strait of Belle Isle and Gulf of St. Lawrence represents the first directed commercial hunt of whales in the western North Atlantic. From approximately 1530 to 1630, Basque whalers travelled annually from the Bay of Biscay to the Strait of Belle Isle, a narrow strait located between Newfoundland and Labrador, Canada, to hunt whales, primarily for their oil (Barkham, 1977, 1978, 1984; Aguilar, 1986; Huxley [Barkham], 1987; Barkham, 1991). It has been suggested that 25000–40000 whales were killed during this time (Aguilar, 1986), encompassing both right and bowhead whales, and that each species comprised approximately half of the catch (Cumbaa, 1986). On the basis of this information, it was suggested that ~12250–21000 whales were removed from the historical population of right whales (Cumbaa, 1986; Gaskin, 1991). This is in comparison to subsequent whaling activities between 1634 and 1951 in the western North Atlantic, which are estimated to have taken at least 5500 right whales (and possibly double this number) (Reeves et al., 2007). Thus Basque whaling in the 16th and 17th centuries could represent the largest human-induced population reduction in the history of the western North Atlantic population of right whales (Gaskin, 1991) and possibly the species.

However, data from whale bones found at Red Bay, Labrador, a primary 16th-century whaling port, revealed a predominance of bowhead whales, a finding that brought into question the assumption that right whales were a principal target in this region (Rastogi et al., 2004). In contrast to Cumbaa’s (1986) osteological analyses of 17 whale humeri from the 16th century, which suggested that right whales accounted for half of the Basque catch, Rastogi et al.’s (2004) genetic species identification using

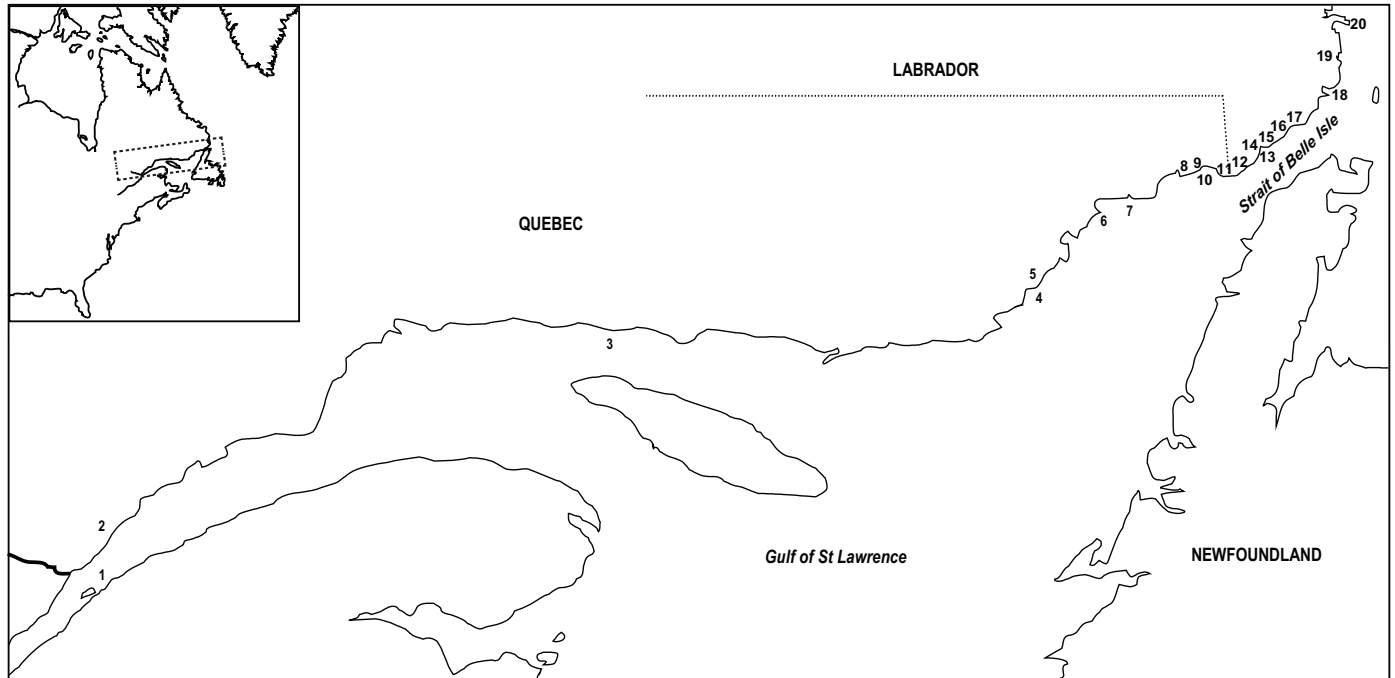


FIG. 1. Sixteenth-century Basque sites investigated in this study. Numbers 1–20 correspond to the sites indicated in Table 1.

sequence analysis of the mitochondrial cytochrome *b* gene (including the same specimens assessed by Cumbaa, 1986) indicated that only one humerus was from a right whale, and 20 were from bowheads (5% right, 95% bowhead). While these results suggested that the right whale represented a small proportion of the 16th-century catch in this region, and thus that bowheads may have been taken on a larger scale than has been recognized, the sample set was small and came from a single whaling site.

To evaluate which whale species were hunted by the Basques in the western North Atlantic and the relative involvement of each species, we have continued the analyses of Rastogi et al. (2004) with a larger sample set from a wider geographical distribution. This study expands the regional coverage to the major expanse of known Basque sites in southern Labrador and eastern Quebec, both in eastern Canada. We collected 364 samples from bones found at 10 of these sites for molecular species identification, including those analyzed previously by Cumbaa (1986) and Rastogi et al. (2004). This survey encompasses the majority of identified Basque whaling sites on the western North Atlantic seaboard, all of which are located on the north shore of the Strait of Belle Isle and Gulf of St. Lawrence and in the St. Lawrence River.

METHODS

Site Identification and Sample Collection

To identify 16th- to 17th-century Basque sites to include in this study and to locate terrestrial bone deposits within these sites, we consulted the available historical

and archaeological literature (Table 1), archaeologists and historians (e.g., S.H. and M. Barkham; L. Turgeon; P. Drouin; W. Fitzhugh), and local townspeople. Extensive historical records suggest that all primary Basque whaling stations in northeastern North America during most of the 16th century were concentrated on the south coast of Labrador facing the Strait of Belle Isle, and that it was not until after about 1580 that Basques whaled west of Rivière St. Paul, Quebec, and thus west of the Strait of Belle Isle and into the Gulf of St. Lawrence (Fig. 1; Barkham, 1978). This expansion, however, occurred after the peak of Basque whaling in the region.

We investigated twenty 16th- to 17th-century coastal Basque sites located in Quebec and Labrador, Canada, for the presence of whale bones (Fig. 1, Table 1). This investigation involved walking along the coastline of each site and searching the soil surface (i.e., no excavation) for whale bones. Shores were searched from the water's edge to at least 10 m inland from the storm tide line. Samples were collected from identified bone specimens. In addition, samples were collected from underwater bone deposits in the harbour of Red Bay, Labrador, and from the collections of the Parc de l'aventure basque en Amérique (Trois-Pistoles, QC), the Whiteley Museum (Rivière St. Paul, QC), the Centre de Conservation du Québec (Quebec, QC) and the Red Bay National Historic Site of Parks Canada (Red Bay, NL).

A small area of each bone specimen was cleaned with a biological decontamination agent (Decon®) and 0.25–0.5-inch holes were drilled. Shavings from the outside of the bone were discarded to minimize microbial and other soil-associated contamination, and with a clean drill bit, 0.5–4 g of bone shavings were collected from the inner

TABLE 1. Sites investigated in Quebec and Labrador, relevant references, number of samples collected and analyzed from each site, and minimum number of individuals represented from each site (MI). Samples collected from terrestrial and marine samples are designated as 'T' and 'M' respectively.

Contemporary Placename	Occupation	Reference	Collected			Analyzed			MI
			T	M	Total	T	M	Total	
1. Île aux Basques, QC	~1580–1650	Lalande, 1991; Auger et al., 1992, 1993; Fitzgerald et al., 1997; Turgeon, 1998	10	0	10	10	0	10	3
2. L'Anse à la Cave/Bon Désir, QC	early 1600s	Lalande, 1989a, b, 1990; Turgeon, 1998	0	0	0	0	0	0	
3. Île Nue (Mingan Islands), QC	late 1500s–early 1600s	Barkham, 1978, 1984; Drouin, 1988;	0	0	0	0	0	0	
4. Petit Mécatina, QC	late 1500s–early 1700s	S. Barkham, pers. comm. 2000; Fitzhugh, 2001; Fitzhugh and Gallon, 2002; Fitzhugh and Sharp, 2003; Fitzhugh et al. 2004, 2006	4	1	5	3	1	4	2
5. Havre Boulet, QC	late 1500s–early 1600s	Fitzhugh and Gallon, 2002	0	0	0	0	0	0	
6. Ile du Vieux Fort, QC	~1536–1632	Local reference	0	0	0	0	0	0	
7. Île du Bonne Espérance, QC	~1536–1632	Huxley [Barkham], 1987; Local reference	4	0	4	4	0	4	4
8. Five Leagues Harbour, QC	~1536–1632	Huxley [Barkham], 1987; Niellon, 1986; Niellon and McGain, 1987	5	0	5	5	0	5	2
9. Middle Bay, QC	~1536–1632	Barkham, 1977, 1980; Niellon, 1986; Niellon and McGain, 1987	10	0	10	10	0	10	5
10. Bradore Bay, QC	~1536–1632	S. Barkham, pers. comm. 2003	0	0	0	0	0	0	
11. Blanc Sablon, QC	~1536–1632	Barkham, 1977, 1978	0	0	0	0	0	0	
12. Schooner Cove, NL	~1536–1632	Barkham, 1977, 1978, 1980	0	0	0	0	0	0	
13. Capstan Island, NL	~1536–1632	Barkham, 1978	2	0	2	2	0	2	1
14. West St. Modeste, NL	~1536–1632	Barkham, 1978, 1984	1	0	1	1	0	1	1
15. East St. Modest/ Lily and Nelly Islands, NL	~1536–1632	Barkham, 1977, 1978, 1980	0	0	0	0	0	0	
16. Carrol Cove, NL	~1536–1632	Barkham, 1977, 1978, 1980	0	0	0	0	0	0	
17. Red Bay, NL ¹	~1536–1632	Barkham, 1977, 1978, 1980, 1984	55	172	227	42	99	141	42
18. Chateau Bay/Henley Harbour, NL	~1536–1632	Barkham, 1977, 1980, 1984; Azkarate et al., 1992	70	0	70	22	0	22	12
19. Pleasure Harbour, NL	~1536–1632	Barkham, 1980	30	0	30	19	0	19	8
20. Cape Charles, NL	~1536–1632	Huxley [Barkham], 1987; Azkarate et al., 1992; Stopp, 1997	0	0	0	0	0	0	

¹ Includes Red Bay, Kelpy Cove, Steamer Cove, and Little Capstan Cove, NL.

core of each bone in a sterile weigh boat. Between each use, drill bits were soaked and cleaned with Decon® and then rinsed thoroughly with double-distilled water (ddH₂O). While terrestrial bones yielded dry shavings, those from marine specimens were often wet and therefore required drying at 25–30°C for 12 to 24 hours immediately after sampling. All samples were then stored in plastic vials and placed in long-term storage at -20°C upon return to the laboratory.

Historical DNA Handling

All sample handling prior to polymerase chain reaction (PCR) amplification was performed in a laboratory where genetic analyses with extant cetaceans have never been conducted. Therefore, all bone samples, reagents, and tools were physically isolated from any extant or PCR-amplified whale DNA. Care was taken to minimize and monitor contamination by regularly cleaning and decontaminating the workspace and all tools and appliances with a 30% bleach solution or Decon® or both. Null samples (or “negatives”) were included in each step of the DNA analysis (DNA extraction, amplification, PCR purification, and sequencing). These are tubes that are treated exactly as the regular samples are treated, but without the addition of DNA.

DNA Extraction

DNA was extracted from 150–300 mg of bone shavings as per Rastogi et al. (2004) using a modified version of the QIAamp® protocol for isolation for genomic DNA from compact bone (Qiagen, Mississauga, ON).

Species Identification

A 478 base pair (bp) region of the mitochondrial cytochrome *b* gene of each sample was amplified using the oligonucleotide primers CBMYSTF1 (5'-CACATGG-ACTTCAACCATG-3') and CBMYSTR (5'-CCTCAGATTTCATTCGACTA-3'), which amplify a region of the gene corresponding to positions 14197 to 14675 of the bowhead whale (Arnason et al., 2004; accession AJ554051). Polymerase chain reaction (PCR) cycling conditions consisted of an initial five-minute denaturation step at 94°C; 50 cycles of 94°C for 30 seconds, 60°C for one minute, and 72°C for one minute; and a final extension step at 65°C for 45 minutes. PCR cocktail conditions were as follows within a 50 µl reaction: 5 µl DNA extract, 1X PCR buffer (20 mM Tris-HCl pH 8.4, 50 mM KCl) (Invitrogen, Burlington, ON), 2 mM MgCl₂ (Invitrogen, Burlington, ON), 0.2 mM each dNTP (Amersham Biosciences,

Piscataway, NJ), 0.3 µg/µl BSA (Sigma, Oakville, ON), 0.1 U/µl *Taq* polymerase (Invitrogen, Burlington, ON), and 0.3 µM of each primer.

To determine product quantity and quality, amplified mitochondrial DNA was electrophoresed within a 1.5% agarose gel stained with ethidium bromide and then visualized under UV light. The product was then purified for sequencing using the QIAquick® PCR purification kit (Qiagen, Mississauga, ON) and sequenced in both directions with primers CBMYSTF1 and CBMYSTR using a MegaBACE™ DYEnamic™ ET dye terminator kit (GE Healthcare, Piscataway, NJ). Sequenced PCR product was then electrophoresed and visualized using a MegaBACE™ 1000 (GE Healthcare, Piscataway, NJ) and analyzed with MegaBACE™ Sequence Analyzer 3.0 software.

Sequences were first aligned and edited by eye and then aligned using Clustal X (Thompson et al., 1997). Distinct mitochondrial haplotypes were designated if the sequences were observed in at least two samples. Sequences observed only within a single sample were re-amplified and sequenced in both directions for confirmation. Likelihood ratio tests (implemented in MODELTEST version 3.7 [Posada and Crandall, 1998]) were used to determine the best-fit model of molecular evolution for the data set. Phylogenetic relationships between sequences were then determined in TREE-PUZZLE version 5.2 (Strimmer and von Haesler, 1996; Schmidt et al., 2002), using quartet puzzling maximum likelihood and 10 000 puzzling steps. The Tamura-Nei model of molecular evolution (Tamura and Nei, 1993) with gamma-distributed rate variation across nucleotide sites (Yang, 1993, 1994) was used (as indicated by MODELTEST). One representative cytochrome *b* sequence from each baleen whale species available in Genbank was included in the analyses, along with a sequence from the killer whale (*Orcinus orca*) as an outgroup sample. Representative whale species included in the phylogenetic analyses (Fig. 2), Genbank accession numbers, and original citations are included in Table 2.

The species of each bone specimen was identified by determining the known whale species each sample grouped with and confirming that primary branching patterns had more than 80% nodal support. Mean and pairwise haplotype distances were calculated in Mega 3.1 (Kumar et al., 2004) using a Tamura-Nei model of nucleotide substitution (Tamura and Nei, 1993) and gamma-distributed rate variation across sites (Yang, 1993, 1994). Nucleotide diversity (π) (Nei, 1987) and haplotype diversity (h) (Nei, 1987) were calculated using DnaSP (Rozas et al., 2003).

Minimum Number of Individuals

To identify the minimum number of individual whales within the sample set, the haplotype, sampling site, and bone type of the bone specimens were cross referenced. Samples were identified as coming from different individuals if they had different cytochrome *b* haplotypes or were from different sampling sites. Samples with a shared

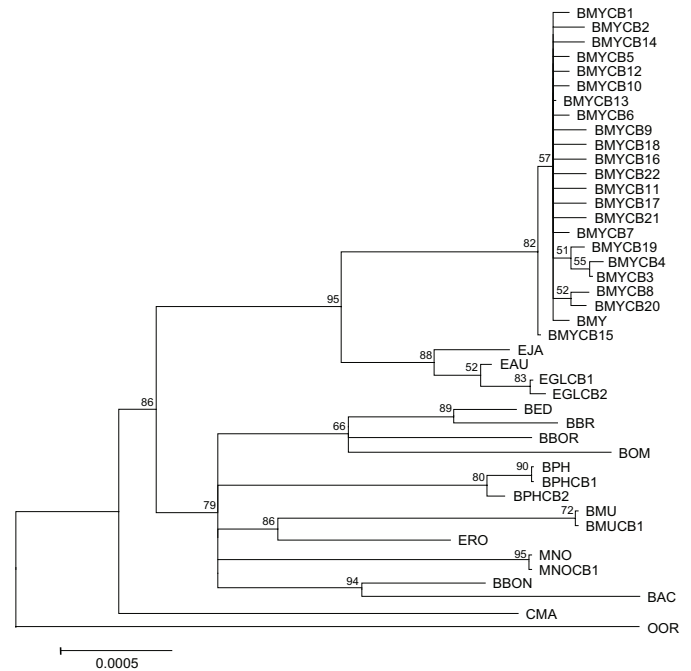


FIG. 2. Quartet maximum likelihood phylogenetic tree of cytochrome *b* sequences from 16th-century bone samples analyzed in this study, representative baleen whale sequences, and a killer whale (*O. orca*) outgroup sequence obtained from genbank. Numerical values on the branches indicate the percentage of 10 000 quartet puzzling steps supporting this branching pattern.

haplotype and site location, yet from a bone type existing only singly in a skeleton (e.g., right humerus, cervical 1–7 vertebrae), were also identified as different individuals.

RESULTS

Between 1999 and 2005, whale bones were sampled at 10 of the 20 Basque sites investigated in Quebec and Labrador, Canada (Table 1). Bones were not found at the remaining ten sites. A total of 364 bone specimens were sampled. These included 85 bones found underwater during the 1978–85 marine excavation of the *San Juan* in Red Bay, Labrador (Barkham, 1984; Tuck, 1985; Grenier, 1985), sampled from the collection of the Red Bay National Historic Site of Parks Canada; 87 bones sampled from the harbour of Red Bay during the 2004 Parks Canada marine refurbishment of the sunken galleon site; 191 bones found in terrestrial deposits at various sites, including samples from the collections of the Whiteley Museum (Rivière St. Paul, QC), the Centre de conservation du Québec (Québec, QC), and the Parc de l'aventure basque en Amérique (Trois-Pistoles, QC); and one bone sampled during the Gateways/Smithsonian Institution marine investigation of Petit Mécatina, Quebec, now in the collection of the Centre de conservation du Québec (Québec, QC) (Table 1). Three sites with relatively large concentrations of whale bones were Red Bay, Chateau Bay/Henley Harbour, and Pleasure Harbour. At these sites, bones that can be found only singly within an individual, such as skulls and the fused cervical

TABLE 2. Species abbreviation, scientific and common names, accession number, and source reference for representative whale cytochrome *b* sequences of species included in the phylogenetic tree (Fig. 2).

Abbreviation	Species	Accession Number	Reference
BAC	<i>Balaenoptera acutorostrata</i> (minke whale)	AJ554054	Arnason et al., 2004
BBOR	<i>Balaenoptera borealis</i> (sei whale)	AP006470	Sasaki et al., 2005
BBON	<i>Balaenoptera bonaerensis</i> (Antarctic minke whale)	AP006466	Sasaki et al., 2005
BBR	<i>Balaenoptera brydei</i> (Bryde's whale)	AP006469	Sasaki et al., 2005
BED	<i>Balaenoptera edeni</i> (pygmy Bryde's whale)	AB201258	Sasaki et al., 2006
BMU	<i>Balaenoptera musculus</i> (blue whale)	X72204	Arnason and Gullberg, 1993
BMY	<i>Balaena mysticetus</i> (bowhead whale)	AJ554051	Arnason et al., 2004
BOM	<i>Balaenoptera omurai</i> (Omura's whale)	AB201257	Sasaki et al., 2006
BPH	<i>Balaenoptera physalus</i> (fin whale)	X61145	Arnason et al., 1991
CMA	<i>Caperea marginata</i> (pygmy right whale)	X75586	Arnason and Gullberg, 1994
EAU	<i>Eubalaena australis</i> (southern right whale)	AP006473	Sasaki et al., 2005
EGL	<i>Eubalaena glacialis</i> (North Atlantic right whale)	AY398662	Rychel et al., 2004
EJA	<i>Eubalaena japonica</i> (North Pacific right whale)	AP006474	Sasaki et al., 2005
ERO	<i>Eschrichtius robustus</i> (gray whale)	X75585	Arnason and Gullberg, 1994
MNO	<i>Megaptera novaeangliae</i> (humpback whale)	AP006467	Sasaki et al., 2005
OOR	<i>Orcinus orca</i> (killer whale)	AF084060	Leduc et al., 1999

vertebrae (1–7), were preferentially sampled, while at other sites all available bone specimens were sampled.

To identify the species of origin of the specimens, DNA was extracted and cytochrome *b* sequences were amplified from a subset of the bone samples ($n = 218$). This subset encompasses all samples from sites where fewer than 20 samples were found, and 182 samples from three sites of historical importance: 141 from Red Bay, 22 from Chateau Bay, and 19 from Pleasure Harbour. At these three sites, samples with a greater likelihood of representing a single individual were preferentially extracted. Cytochrome *b* sequences were also obtained from six contemporary right whale and bowhead “control” specimens (2 *E. glacialis*, 4 *B. mysticetus*).

The phylogenetic tree using maximum likelihood inference of phylogeny identified five species within the sequences from 218 bones: bowhead whale ($n = 203$), right whale ($n = 1$), humpback whale (*Megaptera novaeangliae*) ($n = 6$), fin whale (*Balaenoptera physalus*) ($n = 7$), and blue whale (*B. musculus*) ($n = 1$) (Fig. 2, Table 3). To estimate the minimum number of individuals represented within the sample set, we cross-referenced the sampling location, species, haplotype, and bone types of the samples collected. We determined that the sample subset ($n = 218$) consists of a minimum of 80 individuals, encompassing one right whale, one blue whale, and at least three fin whales, three humpback whales, and 72 bowhead whales, with no perceivable pattern of distribution of species across sites. The minimum number of individuals identified at each site is indicated in Table 1.

Among the 224 samples sequenced (including bones and control samples), 28 haplotypes were identified, encompassing 458 bp spanning positions (14 197–14 655) of the bowhead whale (Table 3; Genbank accession numbers EU303313–EU303340). Four haplotypes were identical to the sequences of several species included from Genbank (BMU = BMYCB7, BPH = BPHCB1, MNO = MNOCB1, BMU = BMUCB1) (Fig. 2). Twenty-two of the 28 haplotypes were identified as bowhead whale in the

phylogenetic tree (Fig. 2). These haplotypes encompass 20 variable sites, all of which are transitions (Table 3). Of these 22 haplotypes, two had relatively high frequencies (BMYCB7, $n = 102$, and BMYCB13, $n = 41$), while the remaining 20 were present in only 1–16 specimens each (Table 3). Three haplotypes (EGLCB2, BMYCB19, BMYCB22) were found only in the “control” contemporary right and bowhead whale samples and not within any historical specimens.

To determine the amount of sequence variation present within the bowhead cytochrome *b* haplotypes, we calculated mean within-species distance (0.006, SE 0.002) and compared this to the mean sequence distance for all baleen whale haplotypes ($n = 15$, calculated using one haplotype from each species included in the phylogenetic tree) (0.038, SE 0.010). Nucleotide polymorphism (P), nucleotide diversity (π), and haplotype diversity (h) for the bowhead sequences were 0.039, 0.003 (SE 0.00018), and 0.697 (SE 0.029) respectively. Note that this calculation of haplotype diversity is likely downward biased, as multiple bones may be from a single individual.

DISCUSSION

Genetic analyses of Rastogi et al. (2004) suggested that instead of large numbers of both right and bowhead whales being hunted by the Basques in the epicenter of their Strait of Belle Isle and Gulf of St. Lawrence whale fishery during the 16th and 17th centuries (Red Bay, Labrador), the bowhead whale was the primary species hunted. This finding was significant because it was the first observation to call into question previous suggestions that this period of whaling was responsible for removing large numbers of right whales (approximately half [Cumbaa, 1986] of an estimated 25 000–40 000 kills between approximately 1530 and 1610 [Aguilar, 1986]) from the supposed historical population of right whales in this region. However, this work was based upon a relatively small sample set ($n = 21$) from a single whaling

port. To further investigate the whale species comprising the 16th- and 17th-century Basque catch in the western North Atlantic we identified the species of origin of a much larger number of bone specimens remaining in marine and terrestrial deposits from the majority of identified Basque sites along the coasts of Quebec and Labrador, Canada. In concordance with the results of Rastogi et al. (2004), mitochondrial cytochrome *b* analysis revealed that the majority of the bone specimens collected are from bowhead whales, suggesting that this species was the principal target species of the hunt. The finding of only a single right whale bone suggests that this hunt had a minimal impact on the species (in terms of numbers of whales killed) and does not support the suggestion that the Basques killed 12 000–15 000 right whales in this region (Gaskin, 1991), a removal which has been thought to have been a primary cause of the decline of the species in the western North Atlantic. The presence of fin, blue, and humpback whales within the sample set may be a result of the occasional hunt of rorqual species or natural whale stranding events, or both. However, despite the variety of species identified, this whaling clearly had a much larger impact on the 16th-century North Atlantic population of bowhead whales than has previously been recognized.

The bowhead whale population(s) currently found in the eastern Arctic (Baffin Bay/Davis Strait) have a distribution ranging from ~60° N to 85° N (Moore and Reeves, 1993; Fig. 1), and thus it is surprising to find 16th- to 17th-century bowhead whale specimens as far south as 50° N (Petit Mécatina, QC) and 48° N (Île aux Basques, QC). The presence of bowhead whales at these sites that were occupied during the late 16th-century (Table 1) provides proof of very recent occupation of the area by this species. Because whaling operations were shore-based (that is, whales were observed from shore and then hunted from several small boats or *chalupas*) (Reeves and Smith, 2006), the whale bones identified are representative of the whales found in the area. However, it remains to be determined whether the presence of the bowhead whale in this area is a result of a wider distribution of a historically larger population prior to whaling, or a reflection of the climatic cooling induced by the Little Ice Age (Lamb, 1995), which may have excluded bowheads from more northerly extensions of their range, or both. Although stranded bowheads have been found twice in recent times around Newfoundland (Ledwell et al., 2007), the most recent “physical” indication of bowhead whales occupying this more southerly region near the mouth of the St. Lawrence River date to the age of the Champlain Sea (10 000–13 000 years ago) (e.g., Cameron, 1951; Harington, 1977). However, species identification has not been genetically confirmed. If the change in distribution of bowheads was due to climatic phenomena, it is also reasonable to question how this may also have affected the distribution of the right whale in the western North Atlantic.

Despite what is known about the climatic affects of the Little Ice Age, it is difficult to evaluate exactly how the

distributions and migratory patterns of these species may have been affected. The Little Ice Age, which lasted from ~1400 to ~1850, was characterized by colder conditions that caused glacial advancement, decreased sea surface temperatures, increased sea ice, and by an expanded Arctic front (Lamb, 1995). During this time, climatic cooling led to colder summer temperatures (Schledermann, 1976; Kreutz et al., 1997), increased storminess, and an increased thermal gradient between approximately 50° and 65° N (Lamb, 1995). These conditions may have led to a more southerly distribution of the bowhead whale as a result of an expanded Arctic front (Schledermann, 1976; De Jong, 1983; Moore and Reeves, 1993). In fact, 16th-century Thule people abandoned areas of northern Greenland and the central/northern Canadian Arctic, likely as a result of reduced access to marine mammals (Schledermann, 1976; McGhee, 1969/70; Stoker and Krupnik, 1993; Henshaw, 2003). Increased sea ice and colder summer conditions may have resulted in a temporally shifted whale migration, perhaps with longer annual occupancy of more southerly areas of its historic distribution.

Such conditions may have also resulted in a more southerly distribution of the right whale. The Strait of Belle Isle has often been cited as a historical right whale habitat area that has never been re-occupied (e.g., Greene et al., 2003; Greene and Pershing, 2004). But, given the results of our analysis, it appears that the region was not frequented by this species during the period in question. In general, the distributional ecology of both species is very complex and likely influenced by a variety of factors, including (but not limited to) sea surface temperature, ice thickness and concentration, regional/seasonal/annual variability, food availability, and oceanographic processes (such as areas of upwelling) (Moore and Reeves, 1993; Moore et al., 2000). However, it is likely that climatic changes of the Little Ice Age affected both the distribution and the migratory patterns of these species both temporally and spatially.

Characteristics of the timing of the 16th-century Basque hunt in the Strait of Belle Isle revealed by historical research appeared to support the original hypothesis that both right whales and bowhead whales were targeted. In the 1540s, the Basques arrived in the region for the “coming of the whales” (*la venida de las ballenas*) or “summer whaling season” in June/July, following which they returned to Europe. However, in the 1550s, after discovering a second influx of whales in September/October, they began staying later for the “return of the whales” (*el retorno de las ballenas*) or “winter whaling season” (Huxley [Barkham], 1987; M. Barkham, pers. comm. 2005). It has frequently been suggested, partly on the basis of the present-day migratory timing and distribution of these two species, that the whales hunted during the summer were a different species from those hunted during the winter (e.g., Eschricht and Reinhardt, 1866; Reeves et al., 1983; Cumbaa, 1986; Reeves and Mitchell, 1986; Woodby and Botkin, 1993). Under this hypothesis, the right whale,

TABLE 3. Variable sites for the haplotypes obtained in this study (Genbank accession EU303313–EU303340) and their frequencies. The reference sequence (AF554051) matches BMYCB7. Dots indicate sequence similarity to the reference sequence. Numbers in parentheses indicate the number of haplotypes that were additionally found in control samples.

Seq Position	39	40	42	45	46	48	49	51	55	57	60	63	66	69	78	79	84	87	93	96	102	111	117	
AF554051	T	A	T	T	G	C	G	C	A	C	C	C	C	C	T	A	T	A	A	C	T	T	T	
BMYCB 1	C
BMYCB 2	C
BMYCB 3	A	C
BMYCB 4	A	C
BMYCB 5	C
BMYCB 6	G
BMYCB 7
BMYCB 8
BMYCB 9
BMYCB 10
BMYCB 11
BMYCB 12
BMYCB 13
BMYCB 14	C
BMYCB 15
BMYCB 16
BMYCB 17
BMYCB 18
BMYCB 19	C
BMYCB 20	C
BMYCB 21	G
BMYCB 22
EGLCB 1	T	.	.	.	T	T	C	.	.	
EGLCB 2	T	.	.	.	T	T	.	.	.	
BPHCB 1	C	G	C	C	.	.	.	A	G	.	T	G	.	C	C	C	C	
BPHCB 2	C	G	C	C	.	.	.	A	G	.	T	G	.	C	C	C	C	
MNOCB 1	.	.	C	C	.	.	A	A	.	T	T	A	C	C	.	
BMUCB 1	C	.	C	C	.	T	.	A	.	T	T	.	T	.	C	.	C	.	.	.	C	C	C	
Seq Position	120	121	123	126	127	165	174	179	196	198	204	207	210	219	222	225	227	232	234	237	240	243	244	
AF554051	C	C	G	T	A	C	T	C	A	T	C	C	T	A	C	C	T	A	C	C	A	T	T	
BMYCB 1
BMYCB 2	.	.	.	C
BMYCB 3
BMYCB 4
BMYCB 5
BMYCB 6
BMYCB 7
BMYCB 8
BMYCB 9
BMYCB 10
BMYCB 11
BMYCB 12
BMYCB 13
BMYCB 14	T
BMYCB 15
BMYCB 16
BMYCB 17
BMYCB 18
BMYCB 19
BMYCB 20
BMYCB 21
BMYCB 22
EGLCB 1	T	.	A	.	.	.	C	.	.	C	T	
EGLCB 2	T	.	A	.	.	.	C	.	.	C	T	
BPHCB 1	.	T	A	.	.	.	C	.	G	C	.	.	C	G	T	.	C	.	T	.	.	C	.	
BPHCB 2	.	.	A	.	.	.	C	.	G	C	.	.	C	G	T	.	C	.	T	.	.	C	.	
MNOCB 1	.	T	A	.	.	.	C	.	G	C	T	T	C	.	T	.	.	C	.	
BMUCB 1	.	T	A	.	G	T	C	T	G	C	T	T	C	.	.	T	C	G	T	T	G	C	T	

TABLE 3 *continued*:

Seq Position	249	255	258	261	264	276	286	288	294	297	300	301	303	312	319	322	324	326	327	329	342	345	348
AF554051	T	T	A	C	C	C	G	T	A	A	T	G	C	T	C	G	C	T	T	A	C	T	G
BMYCB 1
BMYCB 2
BMYCB 3
BMYCB 4	A
BMYCB 5
BMYCB 6
BMYCB 7
BMYCB 8	A
BMYCB 9	A
BMYCB 10	G
BMYCB 11	C
BMYCB 12
BMYCB 13
BMYCB 14
BMYCB 15
BMYCB 16
BMYCB 17
BMYCB 18	A
BMYCB 19	A
BMYCB 20	A
BMYCB 21
BMYCB 22	C
EGLCB 1	.	C	.	.	.	T	.	C	.	.	C	.	.	C	T	.	.	.	C	.	.	.	A
EGLCB 2	.	C	.	.	.	T	.	C	.	.	C	.	.	C	T	.	.	.	C	.	.	.	A
BPHCB 1	.	.	G	T	T	A	.	.	.	C	T	.	.	.	C	G	T	.	A
BPHCB 2	.	.	G	T	T	.	.	C	.	A	.	.	.	C	T	.	.	.	C	G	T	.	A
MNOCB 1	.	.	G	A	.	.	.	C	T	.	.	.	C	G	.	C	A
BMUCB 1	.	C	C	G	.	A	.	T	C	.	.	T	.	.	G	T	.	A

Seq Position	351	354	366	367	369	378	381	387	390	393	396	397	399	420	426	432	435	441	444	447	455	457	Freq
AF554051	A	C	A	G	C	T	A	G	C	T	C	T	A	T	C	C	C	C	T	C	C	A	
BMYCB 1	C	G	16 (2)
BMYCB 2	C	G	4
BMYCB 3	C	G	13
BMYCB 4	C	G	1
BMYCB 5	C	1
BMYCB 6	C	1
BMYCB 7	102
BMYCB 8	3
BMYCB 9	1
BMYCB 10	C	8
BMYCB 11	1
BMYCB 12	.	.	.	A	C	1
BMYCB 13	C	41
BMYCB 14	C	G	1
BMYCB 15	A	.	.	.	C	2
BMYCB 16	T	2
BMYCB 17	T	2
BMYCB 18	1
BMYCB 19	C	G	(1)
BMYCB 20	C	G	1
BMYCB 21	1
BMYCB 22	(1)
EGLCB 1	G	C	G	C	T	1(1)
EGLCB 2	G	C	G	C	T	(1)
BPHCB 1	T	T	.	.	T	C	.	A	.	C	.	C	G	C	.	T	A	T	C	.	.	.	6
BPHCB 2	T	T	.	.	T	C	.	A	.	C	.	C	G	C	.	T	A	.	C	.	.	.	1
MNOCB 1	T	T	.	.	T	.	.	A	.	C	.	C	.	C	C	T	.	.	6
BMUCB 1	T	T	G	A	.	C	.	C	G	C	C	.	.	.	1

Total 218 (6)

which is found in its most northerly expanse of its range in the summer, might correspond to the Basques' "summer coastal whaling season" (*la costera del verano*) while the

bowhead whale, which is most southerly in the winter, might be that of their "winter coastal whaling season" (*la costera del invierno*) (Aguilar, 1986; Cumbaa, 1986).

However, to date there are no direct data or Basque records to support this.

On the basis of the results presented here, which show no evidence of a right whale–targeted hunt, we suggest that the two distinct summer and winter whaling seasons of the Basques may have represented particular sex or age classes of bowheads with differing migration patterns. Bowhead whales are known to migrate and segregate at particular times of the year by distinct “classes” often based on age and sex (e.g., Brown, 1868; Southwell, 1898; Cabbage and Calambokidis, 1987; Finley, 1990; Moore and Reeves, 1993). Sometimes distinct behavioural traits (such as those of “rocknose” whales: Southwell, 1898; Finley, 1990), migratory patterns, and habitat choices (such as open water vs. ice edge) are associated with particular groups of whales (e.g., Southwell, 1898; Reeves et al., 1983; Finley, 1990; Würsig and Clark, 1993; Cosens and Blouw, 2003). These characteristics were so evident to whalers in earlier centuries that bowheads were described as being composed of distinct “tribes” (Scoresby, 1820; Southwell, 1898). Potentially, the groups of whales migrating to the Strait of Belle Isle that were hunted by the Basques were distinct classes with differing migratory patterns. Thus, the catch may have represented (like most whaling) a non-random removal of particular groups within the historical population. Again, it is not known how the climatic effects of the Little Ice Age may have affected the timing of migration and distribution of either species.

It has been suggested that bones remaining from the whales hunted during the summer whaling season (a seasonal hunt that had largely been abandoned by the mid 1570s) might be found at greater soil depths than those of whales hunted in the years that followed (during the winter whaling season). Under this proposition, if the whale hunted during the summer season was a different species than the whale hunted during the winter season, bones remaining from this species might be found at greater archaeological depths and would not be found when sampling at the soil surface. However, at the one place where strata were extensively searched (Red Bay), there is no evidence of any existing strata relating to species. Our sample set encompasses 85 whale bones from the 104 m² marine excavation of the sunken galleon (Grenier et al., 2007), an excavation spanning from pre-Basque to post-Basque deposits, and only a single right whale bone has been identified. This specimen was recovered from post-1565 deposits. Further research on possible strata is recommended.

The identification of such a large number of 16th- to 17th-century bowhead specimens represents a rare opportunity to investigate historical genetic diversity and the effects of whaling activities on genetic diversity in such a long-lived species. Our calculated values of within-species (0.0006) and between-species (0.038) distances are in concordance with expected levels of genetic divergence of the cytochrome *b* gene in mammalian species (e.g., Johns and Avise, 1998). However, although this is one of the most widely sequenced genes in vertebrates,

there is a lack of information (for any mammalian species) on measures of variation within species such as nucleotide polymorphism, nucleotide diversity, and haplotype diversity. To further evaluate temporal variation in genetic diversity and to make inferences on historical population sizes, we have now analyzed the mitochondrial control region and a number of nuclear microsatellite loci (B. McLeod, unpubl. data).

CONCLUSION

The results presented here provide strong evidence that the bowhead whale was the principal target of 16th- to 17th-century Basque whaling in the western North Atlantic. Thus the impact of this whaling on the bowhead whale population in the Arctic waters adjacent to the northwest Atlantic was much greater than previously recognized, with the majority of an estimated 25 000–40 000 whales killed being bowhead whales. Although this is a crude estimate of the whales killed during this ~80 year period, it is roughly equivalent to (if not greater than) the number of whales killed from the Davis Strait population in the centuries of pelagic whaling that followed (1719–1915; $n = \sim 28\ 000$) (Ross, 1993). Clearly, the pre-exploitation population size of the Hudson Bay/Davis Strait population(s) of this species was much larger than has been estimated previously.

Conversely, our results suggest that the right whale did not comprise 50% of an estimated 25 000–40 000 Basque kills between 1530 and 1610 (Aguilar, 1986), and instead represented a very small proportion of the whales hunted. Therefore, the pre-exploitation population size of this species was much smaller than has been previously estimated (10 000–15 000) (Gaskin, 1991; NMFS, 1991), and likely was similar to the population size of the mid-1600s of at least a few thousand whales in the western North Atlantic (Reeves et al., 2007). This altered view of the history of the North Atlantic right whale is important because these estimates of pre-exploitation population size and number of whales killed are frequently used to evaluate recovery (e.g., Greene et al., 2003).

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