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Reconstruction of marine mammals' historical distribution and abundance: setting a baseline to understand the past, inform the present and plan the future

Sophie Monsarrat

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THÈSE

Pour obtenir le grade de
Docteur

Délivré par l'UNIVERSITE DE MONTPELLIER

Préparée au sein de l'école doctorale SIBAGHE
Et de l'unité de recherche CEFE, CNRS UMR 5175

**Spécialité : Ecologie, Evolution, Ressources Génétiques,
Paléontologie**

Présentée par **Sophie MONSARRAT**

**Reconstruction de la distribution et de l'abondance
historiques des mammifères marins :
Etablir un niveau de référence pour comprendre le
passé, renseigner le présent et planifier l'avenir**

Soutenance le Jeudi 07 Mai devant le jury composé de

Mme Ana RODRIGUES, Chargée de recherche, CEFE-CNRS, Montpellier	Co-Directrice de Thèse
Mr Francesco BONADONNA, Directeur de recherche, CEFE-CNRS, Montpellier	Co-Directeur de Thèse
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UNIVERSITE DE MONTPELLIER

THESE

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Ecole doctorale : Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosiences,
Environnement (SIBAGHE)

Par

Sophie MONSARRAT

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**Reconstruction of marine mammal's historical distribution and abundance:
Setting a baseline to understand the past, inform the present and plan the future**

Co-Directrice: Dr. Ana RODRIGUES (CEFE-CNRS, Montpellier)

Co-Directeur: Dr. Francesco BONADONNA (CEFE-CNRS, Montpellier)

Soutenance: Jeudi 7 Mai 2015

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Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, 34090 Montpellier, France

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« Au moindre coup de Trafalgar, C'est l'amitié qui prenait l'quart

C'est elle qui leur montrait le nord, Leur montrait le nord.

Et quand ils étaient en détresse, Qu'leur bras lançaient des S.O.S.,

On aurait dit les sémaphores, Les copains d'abord. »

George Brassens

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TITRE :

Reconstruction de la distribution et de l'abondance historiques des mammifères marins :
Etablir un niveau de référence pour comprendre le passé, renseigner le présent et planifier
l'avenir

Mots-clés :

Abondance, Baleine franche de l'Atlantique Nord, Distribution, Etat de référence, *Eubalaena glacialis*, Mammifères marins, Modèles de distribution d'espèces.

RESUME COURT :

La mise en place d'objectifs de conservation adéquats repose sur la définition d'états de référence appropriés pour la distribution et l'abondance des espèces. Cependant, l'étendue des impacts cumulés de l'homme sur les écosystèmes est aujourd'hui largement sous-estimée. Dans ce projet, je m'intéresse aux opportunités qu'offre l'utilisation de données historiques combinées à différentes méthodes analytiques pour définir ces états de référence ainsi qu'aux défis posés par ce type d'approche. Des données de présence ont été recueillies pour sept espèces de cétacés et trois espèces de pinnipèdes à partir de sources archéologiques, historiques et industrielles, révélant des réductions dans la distribution et l'abondance des espèces depuis la préhistoire à nos jours. Des modèles de distribution d'espèces ont été développés pour cinq espèces de cétacés, combinant des données de chasse baleinière du 19ème siècle à des variables environnementales afin d'estimer la distribution historique des espèces avant qu'elles n'aient été chassées. J'ai obtenu pour la baleine franche de l'Atlantique Nord (*Eubalena glacialis*) une estimation détaillée de sa distribution et de son abondance avant qu'elle ne soit exploitée, en extrapolant des connaissances sur la distribution et l'abondance d'une espèce congénérique, la baleine franche du Pacifique Nord (*E. japonica*). Ces résultats suggèrent que la baleine franche de l'Atlantique Nord occupe une portion réduite de sa distribution historique, et que son abondance actuelle ne représente qu'une infime portion (<5%) de son abondance passée. Plus généralement, ces résultats soulignent l'importance de considérer des données historiques pour comprendre le niveau d'impact par l'homme sur les espèces, évaluer leur niveau de déplétion et renseigner leur potentiel de rétablissement dans l'avenir.

Laboratoire d'accueil :

Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, 34293 Montpellier 5

TITLE:

Reconstruction of marine mammal's historical distribution and abundance: setting a baseline to understand the past, inform the present and plan the future

Keywords:

Abundance, Baseline, *Eubalaena glacialis*, Distribution, Marine mammals, North Atlantic right whale, Species distribution models

BRIEF ABSTRACT:

Relevant baselines on the historical distribution and abundance of species are needed to support appropriate conservation targets for depleted species, but the full scale of cumulative human impacts on ecosystems is highly underestimated. In this project, I investigated the challenges and opportunities of combining historical data with analytical methods to improve these historical baselines. Occurrence data from archaeological, historical and industrial sources were reviewed for seven cetacean and three pinniped species, revealing range contractions and population depletions from prehistorical times to today. For five whale species, I used species distribution modelling to combine 19th Century whaling records with environmental data, to estimate pre-whaling distributions. For the highly depleted North Atlantic right whale, (*Eubalaena glacialis*), I obtained a detailed estimate of pre-whaling distribution and abundance by inferring from the historical distribution and abundance of its congeneric North Pacific right whale (*E. japonica*). These results suggest that the North Atlantic right whale occupies a small fraction of its historical range and that its current population represents <5% of its historical abundance, with implications for the management, monitoring and conservation targets of this species. More generally, these results emphasize the utility of considering historical data to understand the extent to which species have been impacted by humans, assess their current level of depletion, and inform the options available for their future recovery.

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TABLE OF CONTENTS

I. INTRODUCTION.....	19
SHIFTING BASELINES AND THE RISE OF “HISTORICAL ECOLOGY”	19
<i>The shifting baseline syndrome</i>	19
<i>Implications for conservation</i>	20
<i>Applied historical ecology</i>	21
MARINE HISTORICAL ECOLOGY AND THE OVEREXPLOITATION OF MARINE RESOURCES	22
<i>Marine historical ecology</i>	22
<i>Consequences of the overexploitation of marine resources</i>	23
OPPORTUNITIES FOR SETTING APPROPRIATE POPULATION BASELINES	24
<i>Historical occurrence data</i>	25
<i>Methodological opportunities for setting baselines from historical data</i>	28
FOCUS ON MARINE MAMMALS	29
<i>A brief history of marine mammal exploitation</i>	29
<i>Marine mammals as an interesting case study</i>	33
OBJECTIVES	34
STRUCTURE	35
II. USING SPECIES’ HISTORICAL OCCURRENCE DATA TO INVESTIGATE RANGE CONTRACTIONS: A REVIEW FOR TEN MARINE MAMMAL SPECIES AND POSSIBLE APPLICATIONS.....	39
ABSTRACT	39
INTRODUCTION	40
STRATEGY FOR REVIEWING HISTORICAL DATA.....	42
SPECIES REVIEWS	44
<i>Walrus (Odobenus rosmarus)</i>	44
<i>Caribbean monk seal (Monachus tropicalis)</i>	47
<i>Mediterranean monk seal (Monachus monachus)</i>	47
<i>Bowhead whale (Balaena mysticetus)</i>	48
<i>North Atlantic right whale (Eubaleana glacialis)</i>	49
<i>North Pacific right whale (Eubalaena japonica)</i>	50
<i>Southern right whale (Eubalaena australis)</i>	51
<i>Gray whale (Eschrichtius robustus)</i>	54
<i>Humpback whale (Megaptera noveaengliae)</i>	57
<i>Sperm whale (Physeter macrocephalus)</i>	57
CHALLENGES AND OPPORTUNITIES IN HISTORICAL OCCURRENCE DATA.....	58
<i>Archaeological remains</i>	58
<i>Historical accounts</i>	59

<i>Industry statistics</i>	60
APPLICATIONS OF SPECIES’ HISTORICAL OCCURRENCE DATA	61
<i>Improving understanding of the ecology of depleted species</i>	61
<i>Mapping the historical envelope of species’ occurrence</i>	62
<i>Mapping the sequence of historical depletion of a species</i>	64
<i>Modeling a species’ historical distribution based on its environmental preferences</i>	65
DISCUSSION AND CONCLUSION	69
III. COMBINING HISTORICAL DATA AND SPECIES DISTRIBUTION MODELS TO FILL INFORMATION GAPS FOR SPECIES WITH VARIOUS LEVELS OF DEPLETION	75
ABSTRACT	75
INTRODUCTION	77
<i>Three species, three histories of exploitation</i>	78
<i>Challenges and Opportunities</i>	88
MATERIAL AND METHODS.....	89
<i>Nineteenth century whaling data</i>	89
<i>Environmental data</i>	90
<i>Species distribution models</i>	92
RESULTS AND DISCUSSION	94
<i>Limitations and caveats</i>	94
<i>Humpback whale (Megaptera novaeangliae)</i>	96
<i>Bowhead whale (Balaena mysticetus)</i>	100
<i>Gray whale (Eschrichtius robustus)</i>	103
<i>Interest of the modeling approach</i>	107
CONCLUSION	110
APPENDIX	111
<i>Appendix S1. Model selection, performance and validation</i>	111
<i>Appendix S2. Fitted functions of the species-environment relationships produced by the BRT</i>	111
IV. HISTORICAL SUMMER DISTRIBUTION OF THE ENDANGERED NORTH ATLANTIC RIGHT WHALE (EUBALAENA GLACIALIS): A HYPOTHESIS BASED ON ENVIRONMENTAL PREFERENCES OF A CONGENERIC SPECIES117	
ABSTRACT	117
INTRODUCTION	118
MATERIAL AND METHODS.....	119
<i>Historical records of North Pacific right whales</i>	119
<i>Environmental data</i>	120
<i>Species distribution modeling</i>	120
<i>Historical records of North Atlantic right whales</i>	121

RESULTS.....	122
<i>Historical records of North Pacific right whales</i>	122
<i>Species distribution model</i>	122
<i>Model predictions</i>	122
<i>Historical records of North Atlantic right whales</i>	123
DISCUSSION.....	126
<i>Assumptions and caveats</i>	126
<i>Comparison between the model predictions and species records in the North Atlantic</i>	128
CONCLUSIONS.....	130
APPENDICES	133
<i>Appendix S1: Historical records of North Pacific right whales</i>	133
<i>Appendix S2: Environmental data</i>	134
<i>Appendix S3: Fitted functions</i>	135
<i>Appendix S4: Complementary Analyses</i>	137
<i>Appendix S5: Historical distribution records of the North Atlantic Right Whale</i>	140
<i>Appendix S6: Extended discussion</i>	149
V. HOW MANY RIGHT WHALES WERE THERE IN THE NORTH ATLANTIC BEFORE COMMERCIAL WHALING? AN ESTIMATE BASED ON NORTH PACIFIC WHALING RECORDS.....	159
ABSTRACT	159
INTRODUCTION	160
METHODS AND RESULTS	163
<i>Data on the distribution of catches of North Pacific right whales</i>	163
<i>Environmental predictors</i>	164
<i>Abundance modeling in the North Pacific</i>	165
<i>Model validation</i>	167
<i>Estimates of total population size in the North Pacific</i>	168
<i>Estimates of total population size in the North Atlantic</i>	169
DISCUSSION.....	171
<i>Uncertainties and assumptions</i>	171
<i>Agreement between predictions, the historical record and genetic analyses</i>	173
<i>Implications for the present and future of the North Atlantic right whale</i>	175
CONCLUSION	176
APPENDICES	177
VI. DISCUSSION.....	181
RECONSTRUCTING THE PAST: FROM DESCRIPTION TO PREDICTION	182
<i>Interpretation of historical anecdotes</i>	182
<i>Estimates of historical catches</i>	184

<i>Maps of historical occurrence</i>	185
<i>Envelopes of historical occurrence</i>	189
<i>Predictive models of historical distribution</i>	190
<i>Predictive models of historical abundance</i>	197
LESSONS LEARNED FROM THE ANALYSIS OF HISTORICAL DATA	198
<i>Understanding species' habitat preferences and how they have been affected by humans</i>	198
<i>Understanding past distributions and anthropogenic range contractions</i>	198
<i>Understanding past abundances and human-caused population depletions</i>	200
BIODIVERSITY CONSERVATION IN A CHANGING WORLD	201
<i>How to define the historical baseline?</i>	201
<i>Is the historical baseline an achievable/desirable target for conservation?</i>	203
REFERENCES	209

LIST OF FIGURES

FIGURE I-1. ILLUSTRATION OF THE SHIFTING BASELINE SYNDROME AND THE CHANGE IN LIVING MEMORY FROM OLD TO YOUNG FISHERMEN IN THE GULF OF CALIFORNIA.	19
FIGURE I-2. SCHEMATIC REPRESENTATION OF ECOLOGICAL DATA AVAILABILITY AND POSSIBLE SOURCES, OVER THE LAST 10,000 YEARS.	25
FIGURE I-3. TWO PAGES FROM AN AMERICAN WHALING LOGBOOK, FROM THE SHIP <i>ABIGAIL</i> OF NEW BEDFORD, BENJAMIN CLARK, MASTER.	28
FIGURE I-4. SITE OF BANGU-DAE, CARVED PLATES (A, B, C, D, E) OF THE MAIN WALL (ULSAN, SOUTH KOREA; 6,000-1,000 YEARS BP).	30
FIGURE I-5. POSSIBLE WHALING SCENES (DETAILS FROM BANGU-DAE PETROGLYPHS, ULSAN, SOUTH KOREA; 6,000-1,000 YEARS BP).	30
FIGURE I-6. OLAUS MAGNUS' WALRUS, 1555, <i>HISTORIA DE GENTIBUS SEPTENTRIONALIBUS</i>	31
FIGURE I-7. TOTAL NUMBER OF WHALES KILLED IN INDUSTRIAL WHALING, 1900-99.	32
FIGURE II-1. CURRENT RANGE AND HISTORICAL OCCURRENCE DATA COLLECTED FOR THE WALRUS (<i>ODOBENUS ROSMARUS</i>).	45
FIGURE II-2. CURRENT RANGE AND HISTORICAL OCCURRENCE DATA FOR TWO SPECIES OF MONK SEAL: THE CARIBBEAN MONK SEAL (<i>MONACHUS TROPICALIS</i> , IN GREEN) AND THE MEDITERRANEAN MONK SEAL (<i>MONACHUS MONACHUS</i> , IN ORANGE).	48
FIGURE II-3. CURRENT RANGE AND 19TH CENTURY WHALING RECORDS FOR THE BOWHEAD WHALE (<i>BALAENA MYSTICETUS</i>).	49
FIGURE II-4. CURRENT SUMMER RANGE AND HISTORICAL OCCURRENCE DATA COLLECTED FOR THE NORTH ATLANTIC RIGHT WHALE (<i>BALAENA MYSTICETUS</i>).	50
FIGURE II-5. CURRENT RANGE AND 19TH CENTURY WHALING RECORDS FOR THE NORTH PACIFIC RIGHT WHALE (<i>EUBALAENA JAPONICA</i>).	51
FIGURE II-6. CURRENT RANGE AND HISTORICAL DATA COLLECTED FOR THE SOUTHERN RIGHT WHALE (<i>EUBALAENA AUSTRALIS</i>).	52
FIGURE II-7. CURRENT RANGE AND HISTORICAL DATA COLLECTED FOR THE GRAY WHALE (<i>ESCHRICHTIUS ROBUSTUS</i>).	55
FIGURE II-8. 19TH CENTURY WHALING RECORDS FOR THE HUMPBACK WHALE (<i>MEGAPTERA NOVAEANGLIAE</i>).	57
FIGURE II-9. 19TH CENTURY WHALING RECORDS FOR THE SPERM WHALE (<i>PHYSETER MACROCEPHALUS</i>).	58
FIGURE II-10. HISTORICAL ENVELOPE OF OCCURRENCE FOR THE NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>).	63
FIGURE II-11. HISTORICAL ENVELOPE OF OCCURRENCE FOR THE CARIBBEAN MONK SEAL (<i>MONACHUS TROPICALIS</i>).	64
FIGURE II-12. SEQUENCE OF DEPLETION OF THE BREEDING DISTRIBUTION OF THE MEDITERRANEAN MONK SEAL (<i>MONACHUS MONACHUS</i>) OVER THE LAST CENTURY.	65
FIGURE II-13. DIAGRAM SHOWING THE STEPS IN STATISTICAL SPECIES DISTRIBUTION MODELING AND PREDICTIVE MAPPING.	68
FIGURE III-1. HISTORICAL WHALING DATA AND MODEL PREDICTIONS FOR THE GLOBAL WINTER DISTRIBUTION OF THE HUMPBACK WHALE.	98
FIGURE III-2. HISTORICAL WHALING DATA AND MODEL PREDICTIONS FOR THE SUMMER DISTRIBUTION OF BOWHEAD WHALE.	102
FIGURE III-3. HISTORICAL WHALING DATA AND MODEL PREDICTIONS FOR THE SUMMER DISTRIBUTION OF GRAY WHALE.	105
FIGURE III-4. FITTED FUNCTIONS SHOWING THE SPECIES-ENVIRONMENT RELATIONSHIPS PRODUCED BY THE BRT.	112
FIGURE IV-1. HISTORICAL DATA AND MODEL PREDICTIONS IN THE NORTH PACIFIC.	124
FIGURE IV-2. MODEL PREDICTIONS AND HISTORICAL DATA IN THE NORTH ATLANTIC.	125

FIGURE IV-3. FITTED FUNCTIONS SHOWING THE SPECIES-ENVIRONMENT RELATIONSHIPS PRODUCED BY THE BRT.....	136
FIGURE IV-4. ENVIRONMENTAL SUITABILITY FOR RIGHT WHALES IN SUMMER PREDICTED BY THE GAM.	139
FIGURE IV-5. HISTORICAL (PRE-1950) RECORDS OF NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>) IN THE SUMMER MONTHS (JUNE TO SEPTEMBER).....	147
FIGURE IV-6. RECENT (POST-1950) RECORDS OF NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>) IN THE SUMMER MONTHS (JUNE TO SEPTEMBER), OUTSIDE ITS MAIN KNOWN SUMMER GROUNDS.	148
FIGURE IV-7. HISTORICAL (PRE-1950) AND RECENT (POST 1950) RECORDS OF NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>) IN THE SUMMER MONTHS, ACCORDING TO DATE.	151
FIGURE V-1. HISTORICAL CATCHES OF NORTH PACIFIC RIGHT WHALES, AND MODEL PREDICTIONS OF ABUNDANCE IN THE NORTH PACIFIC.	167
FIGURE V-2. MODEL PREDICTIONS OF RIGHT WHALE ABUNDANCE IN THE NORTH ATLANTIC AND ABSOLUTE STANDARD ERROR OF THE PREDICTION.	170
FIGURE V-3. SMOOTH FUNCTIONS FOR THE FOUR SELECTED PREDICTORS.	177

LIST OF TABLES & BOXES

TABLE II-1. MARINE MAMMAL SPECIES REVIEWED IN THIS CHAPTER, WITH THEIR CURRENT IUCN RED LIST STATUS, AND A SHORT SUMMARY ON THE HISTORY OF THEIR EXPLOITATION.	43
TABLE II-2. NUMBER OF HISTORICAL RECORDS COLLECTED FOR THE TEN SPECIES CONSIDERED, AND NUMBER OF REFERENCES FROM WHICH THEY WERE EXTRACTED.	44
TABLE II-3. HISTORICAL RECORDS COLLECTED FOR THE WALRUS (<i>ODOBENUS ROSMARUS</i>).	46
TABLE II-4. HISTORICAL RECORDS COLLECTED FOR THE SOUTHERN RIGHT WHALE (<i>EUBALAENA AUSTRALIS</i>).	52
TABLE II-5. HISTORICAL RECORDS OF THE GRAY WHALE (<i>ESCHRICHTIUS ROBUSTUS</i>) IN THE NORTH ATLANTIC.	56
TABLE III-1. TABLE OF IDENTIFIED CURRENT WINTER GROUNDS FOR THE HUMPBACK WHALE.	79
TABLE III-2. NUMBER OF PRESENCES (DAYS WHEN THE SPECIES WAS SEEN OR CAUGHT) AND ABSENCES (DAYS WHEN THE SPECIES WAS NOT SEEN NOR CAUGHT) IN THE HISTORICAL WHALING DATASET.	90
TABLE III-3. ENVIRONMENTAL PREDICTORS USED IN THE SPECIES DISTRIBUTION MODELS.	91
TABLE III-4. SELECTED VARIABLES, PERFORMANCE AND VALIDATION PARAMETERS OF THE SPECIES DISTRIBUTION MODELS.	111
TABLE IV-1. ENVIRONMENTAL PREDICTORS USED IN THE SPECIES DISTRIBUTION MODELS.	135
TABLE IV-2. HISTORICAL (PRE 1950) RECORDS OF NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>) IN THE SUMMER MONTHS (JUNE TO SEPTEMBER).	140
TABLE IV-3. RECENT (POST 1950) RECORDS OF NORTH ATLANTIC RIGHT WHALE (<i>EUBALAENA GLACIALIS</i>) IN THE SUMMER MONTHS (JUNE TO SEPTEMBER).	145
TABLE IV-4. COMPARISON BETWEEN THE MODEL PREDICTIONS AND SPECIES RECORDS IN THE NORTH ATLANTIC.	152
TABLE V-1. ENVIRONMENTAL PREDICTORS USED IN THE ANALYSIS.	164
TABLE V-2. ESTIMATES OF THE TOTAL PRE-EXPLOITATION POPULATION OF NORTH ATLANTIC RIGHT WHALES.	171
TABLE V-3. COMPARISON OF THE EXPLICATIVE AND PREDICTIVE PERFORMANCE OF NEGATIVE BINOMIAL AND POISSON GAMS.	177
BOX III-1. SUMMARY OF THE HISTORY OF EXPLOITATION AND CURRENT CONSERVATION STATUS OF THE THREE WHALE SPECIES CONSIDERED.	87
BOX III-2. SUMMARY OF THE MODELS PREDICTIONS AND RELEVANCE OF THE MODELING APPROACH FOR THE THREE WHALE SPECIES CONSIDERED.	109
BOX VI-1. ABOUT THE NORTH ATLANTIC RIGHT WHALE: HISTORICAL ANECDOTES.	182
BOX VI-2. ABOUT THE NORTH ATLANTIC RIGHT WHALE: ESTIMATES OF HISTORICAL CATCHES.	184
BOX VI-3. ABOUT THE NORTH ATLANTIC RIGHT WHALE: MAPS OF HISTORICAL RECORDS.	187
BOX VI-4. ABOUT THE NORTH ATLANTIC RIGHT WHALE: ENVELOPE OF HISTORICAL OCCURRENCE.	189
BOX VI-5. ABOUT THE NORTH ATLANTIC RIGHT WHALE: PREDICTION OF HABITAT SUITABILITY.	196
BOX VI-6. ABOUT THE NORTH ATLANTIC RIGHT WHALE: PREDICTION OF HISTORICAL ABUNDANCE.	197
BOX VI-7. ABOUT THE NORTH ATLANTIC RIGHT WHALE: HISTORICAL KNOWLEDGE OF THE SPECIES' ECOLOGY.	198
BOX VI-8. ABOUT THE NORTH ATLANTIC RIGHT WHALE: UNDERSTANDING PAST DISTRIBUTION.	199
BOX VI-9. ABOUT THE NORTH ATLANTIC RIGHT WHALE: UNDERSTANDING PAST ABUNDANCE.	200
BOX VI-10. ABOUT THE NORTH ATLANTIC RIGHT WHALE: CONSERVATION IN A CHANGING WORLD.	206

CHAPTER I

INTRODUCTION

I. Introduction

Shifting baselines and the rise of “Historical ecology”

The shifting baseline syndrome

In their diaries, early travellers from the 16th to the 19th century described the Gulf of California as a place in which whales were ‘innumerable,’ turtles were ‘covering the sea’, large fish were so abundant that they could be taken by hand and pearl oyster reefs were large and widespread (Sáenz-Arroyo et al., 2006). These animals are still present in the Gulf of California today, but their numbers are far from being in accordance with such descriptions of richness and abundance. But it is not only animal abundances that are changing: human perceptions of those abundances are changing too. In a recent study, Sáenz-Arroyo and colleagues (2006) found that although

today’s fishermen in this area are aware that fisheries have had a detrimental effect on marine animal populations, their perception of how the ecosystem looked in the past is rapidly shifting. Indeed, they found that over only three generations, the memory of which species have been depleted from the area has been partially lost, with few young fishers aware that large species used to be common (Figure I-1). Their study illustrates how the reference of what is considered as the ‘natural’ state of an ecosystem can shift rapidly over consecutive human generations.



Figure I-1. Illustration of the shifting baseline syndrome and the change in living memory from old to young fishermen in the Gulf of California.

(From Lotze and McClenachan 2013, based on Saenz-Arroyo et al. 2005. By Anne Randall, Pier Thiret and Juan Jesus Lucero 2005. cobi.org.mx)

If species ultimately disappear from an area, they can be forgotten altogether, and quickly: Turvey and colleagues (2010) found over 70% of young fishermen (<40 years-old) interviewed in the middle-lower Yangtze basin (China) had never even heard of the Yangtze paddlefish (*Psephurus gladius*) or of the Yangtze river dolphin (*Lipotes vexillifer*), compared to <5% of their old peers (> 70 years-old). These two large species were still regularly seen and/or caught in the mid-20th century, but are now possibly extinct.

It is only recently that the practical implications of such collective amnesia – what Daniel Pauly called “the shifting baseline syndrome” (Pauly, 1995) – have started to be realised (e.g. Evans et al., 1982 in Kahn et al., 2009; Kahn & Friedman, 1995; Pauly, 1995). Indeed, Pauly noted such shifts taking place among fisheries scientists, possibly because each generation accepts as a baseline the abundance and species composition that occurred at the beginning of their career. The resulting “gradual accommodation of the creeping disappearance of resource species” leads to an underestimate of past changes and progressively less ambitious management strategies and recovery targets (Pauly, 1995)

A number of recent studies have attempted to quantify the “shifting baseline syndrome”, for example by correlating the results of extensive interviews of local communities with records of effective loss of biodiversity (Sáenz-Arroyo et al., 2005; Ainsworth et al., 2008; Papworth et al., 2009; Turvey et al., 2010). Papworth and colleagues (Papworth et al., 2009) distinguish two types of shifting baselines: 1) general amnesia (“individuals setting their perceptions from their own experience, and failing to pass their experience on to future generations”) and 2) personal amnesia (“individuals updating their own perception of normality; so that even those who experienced different previous conditions believe that current conditions are the same as past conditions”). Ultimately, the “syndrome” is a socio-psychological phenomenon, and its direct study is beyond the scope of this work. Here, I will focus on the biological changes underlying it, and their consequences in terms of our shifting expectations for the conservation and management of biodiversity. I focus on the species level, and therefore will use the term “baseline” to define the reference condition to which to compare the current status of populations in terms of distribution or abundance.

Implications for conservation

Conservation science is particularly vulnerable to the shifting baseline syndrome because of its reliance on recent trends, over years or generations (Frankham & Brook, 2004). Indeed, studies of population decline are often made over a short period of time: Bonebrake et al. (2010) found that only 15% of 265 “long-term” studies of animal population declines used data older than 100 years. Many of the datasets used in biodiversity assessments use temporal records that are less than 50

years (Willis et al., 2005), as do most quantitative biodiversity indicators (Butchart et al., 2010). Yet, human impacts on ecosystems have started millennia ago (Steadman, 2006; Estes et al., 2007; Roberts, 2007; Dulvy et al., 2009).

The absence of older baselines results in an underestimate of losses, particularly those that occurred before scientific surveys existed. This in turn affects management decisions, leading to an underestimation of the potential for recovery of species and unambitious conservation targets, which attempt to simply stop current declines rather than aiming for the richer state that occurred in the past. As Balmford (1999) put it, this “endlessly downgrading our conservation expectations may leave us fighting for remnant scraps of biodiversity, which, even if protected from direct human impacts, may be ecologically or evolutionarily moribund. We may do far better to keep our expectations relatively ambitious.”

Applied historical ecology

The recognition that conservationists and resource managers need appropriate ecological baselines led to a growing integration of tools and knowledge from Historical Sciences with Conservation Biology. The term “historical ecology” dates back to the 1950s (Nicholls, 1956), but the concept developed more recently, with the identification of a need to consider a “base datum” to understand and manage ecosystems (Swetnam et al., 1999). Rick and Lockwood (2013) defined this new discipline as “the use of historic and prehistoric data (e.g., paleobiological, archeological, historical) to understand ancient and modern ecosystems, often with the goal of providing context for contemporary conservation”. Historical Ecology aims is to understand human-environment interactions in the past and in the present (Szabó & Hédl, 2011) and to understand natural variation before and after human arrival (Dietl & Flessa, 2011). It is by definition multidisciplinary (Bonebrake et al., 2010), its aim of contributing to the management of species being encapsulated by the term “applied historical ecology”.

Even though tools and data from the palaeobiology, archaeology and history have many applications to determining the historical state of ecosystems and to inform conservation decisions, they are still quite rare in conservation journals (Lyman, 1996, 2006; Dietl & Flessa, 2011), and conservationists are thus not aware of the existence of such data. Furthermore, zooarchaeologists, not realizing the potential that their data have for biodiversity conservation efforts (Willis et al., 2005), often do not identify fossils to the species level. When they do, they often use as reference to their identifications the species currently found in the area. This may lead to a vicious cycle where species are not known by ecologists to have previously been found in an area, and not identified in archaeological records because they are not listed by ecologists. Better communication between archaeologists, historians

and ecologists is still needed to promote multi-disciplinary approaches, essential to integrating an historical perspective in our understanding of population declines (Bonebrake et al., 2010) and to raise awareness of the great potential historical ecology holds in conservation.

Marine historical ecology and the overexploitation of marine resources

“It is often thought that the impact of human activity on sea life is a modern phenomenon, a product of the last half century of pollution and industrial-scale fishing. [...]In many places the oceans were transformed long before scientists first began writing papers on marine ecology, or people of today’s generation first dipped their toes in the sea”.

Callum Roberts, *“The Unnatural History of the Sea”* (2007)

Marine historical ecology

The oceans represent 99 percent of the habitable space for life on earth, and provide many nations with a large proportion of their dietary intake in protein. As such, humans have always turned to the oceans for exploiting its resources (Erlandson et al., 2008). Perhaps because the condition of ocean ecosystems is difficultly observable to human, the seas have long been perceived as inexhaustible sources of food, unspoiled by human activities. This is illustrated by this quote from Thomas Huxley’s opening speech at the London fisheries exhibition, in 1883: *“I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea fisheries, are inexhaustible; that is to say, that nothing we do seriously affects the number of the fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless.”*

Huxley seriously underestimated human’s ability to exploit ocean resources, as evidenced by the later collapse of these fisheries (Roughgarden & Smith, 1996; Jackson et al., 2001). He also underestimated the impact humans had already caused to some of those fisheries at the time of his speech. For example, a recent archaeological study revealed how the origin of the cod consumed in London between the 9th and the 16th Centuries progressively shifted from local sources in the southern North Sea, to the northeast Atlantic, to the Baltic, to Newfoundland (Orton et al., 2014), likely indicative of a progressive depletion in each of these regions. Present day scientists often also underestimate the impact of centuries, or even millennia, of exploitation on marine populations (Jackson, 1997). In the absence of long-term historical perspective, observations fail to address declines predating modern ecological studies.

Marine historical ecology developed in response to this concern, starting in the late 1990's with the gathering of ecologists, historians, archaeologists and paleontologists to discuss "long-term ecological records of marine environments, populations and communities". This resulted in a foundational paper for the discipline in 2001 in *Science*: "Historical overfishing and the recent collapse of coastal ecosystems" (Jackson et al., 2001). At about the same time, the History of Marine Animal Populations (HMAP) project was founded under the Census of Marine Life program, to assess and explain the history of diversity, distribution, and abundance of marine life, in a collaborative effort by some 100 researchers around the globe, from various disciplines (Holm, 2002; Holm et al., 2010).

From these efforts emerged a number of studies from the archaeology (Rick & Erlandson, 2008a), history (Shaffer et al., 1998; Holm, 2002; Tingley & Beissinger, 2009; Schwerdtner Mnez et al., 2014) and marine ecology disciplines (Lotze & Worm, 2009; Lotze et al., 2010). These studies used a variety of tools to estimate the historical population size (genetic analyses, Roman & Palumbi, 2003; Alter et al., 2007; sum of historical catches, Scarff, 2001; Reeves & Smith, 2002; Smith & Reeves, 2010; population modeling, Rosenberg et al., 2005) and reconstruct the historical distribution of species (mapping historical occurrence, Kittinger et al., 2013; comparing site occupancy over time, Tingley & Beissinger, 2009; modeling species distribution; Newbold, 2010).

Additionally, huge amount of data were collected and made freely available. For instance, the HMAP database (www.hull.ac.uk/hmap/, University of Hull, 2012) contains ca. 350,000 records of historical marine resource occurrence, of which ca. 80% are available through OBIS (Ocean Biogeographic Information System, Grassle, 2000) (Holm et al., 2010).

Consequences of the overexploitation of marine resources

Studies in marine historical ecology revealed that overexploitation preceded any other anthropogenic disturbance to marine ecosystems and represents the most important alteration in the oceans over the past millennium. Jackson and colleagues classified the history of marine resources exploitation into three stages: 1) aboriginal use, the subsistence exploitation of near-shore, coastal ecosystems by human cultures with relatively simple technologies; 2) colonial use, the systematic exploitation and depletion of coastal and shelf seas by foreign mercantile powers incorporating distant resources into a developing market economy; and 3) global use, a more intense and geographically pervasive exploitation of coastal, shelf, and oceanic fisheries integrated into global patterns of resource consumption, with more frequent exhaustion and substitution of fisheries (Jackson et al., 2001). The timing of major impacts is often associated with European colonization and exploitation (Jackson et al., 2001), but aboriginal harvesting also had deleterious

impacts on marine life (e.g. Simenstad et al., 1978; Porcasi et al., 2000; Jones et al., 2002). The combined magnitude of loss in terms of biomass and abundance of large animals is enormous. Furthermore, at the ecosystem level, overfishing induces changes in the food web and community structure, and the extinction of entire trophic levels increase the vulnerability of ecosystem to disturbance (Jackson et al., 2001). The decline of large whales has for instance likely altered the structure and function of ocean ecosystems (Roman et al., 2014).

At least 20 human-caused extinctions of marine species have taken place since ca. 1500 AD, including four species of marine mammals that got extirpated by overexploitation: Steller's sea cow *Hydrodamalis gigas* (last seen in 1768; Anderson, 1995), the sea mink *Neovison macrodon* (last seen in 1860; Carlton et al., 1999), the Japanese sea lion *Zalophus japonicas* (not seen since the 1950's; Carlton et al., 1999) and the Caribbean monk seal *Monachus tropicalis* (last seen in 1952; McClenachan & Cooper, 2008) (Dulvy et al., 2009). To these four species can be added the Yangtze River dolphin or baiji (*Lipotes vexillifer*), likely to have become extinct due to by-catch in local fisheries in the late 20th century (Turvey et al., 2007).

Overexploitation has also been responsible for the extirpation of many species across part of their range (Dulvy et al., 2003) or their reduction in abundance to such extent that they can no longer fulfil their role in the ecosystem (Lotze et al., 2006). In this PhD, I focused mainly on these cases of local extirpation (leading to range contractions) and population depletion (reduction in abundance) caused by overexploitation.

Opportunities for setting appropriate population baselines

Conventional ecological data, even from "long-term" studies rarely go deeper than the last 20-50 years (Bonebrake et al., 2010) and are thus inappropriate to measuring ancient human impacts on natural ecosystems (Figure I-2). A different approach to gathering data than what ecologists are used to is required, using tools and data from a variety of disciplines to integrate data from archaeological, historical and industrial sources. Even though this comes at a cost – the loss of rigor that can be obtained when using single ecological sampling protocols and techniques – it allows a substantial expansion of the temporal extent surveyed (Sáenz-Arroyo et al., 2006; Lotze & Worm, 2009; Rick & Lockwood, 2013) (Figure I-2).

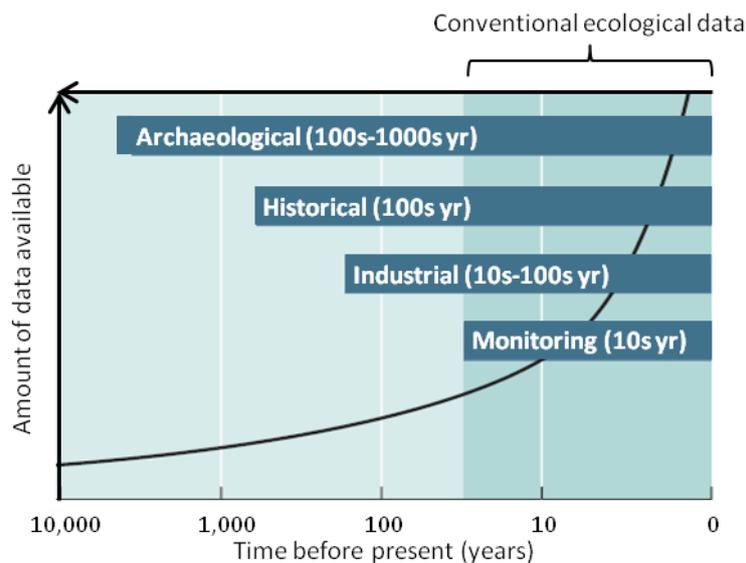


Figure I-2. Schematic representation of ecological data availability and possible sources, over the last 10,000 years.

Conventional ecological data only cover the last 20-50 years but the timeline of information can be expanded using data from different disciplines. (Adapted from Lotze & McClenachan, 2013)

Historical occurrence data

We define historical occurrence data as any information that provides evidence for the past presence or absence of a species, in a particular place and time, including anecdotal and observational data (Tingley & Beissinger, 2009). In this project, “historical” refers to a broad period from the beginning of the Holocene period (ca. 10,000 BP) to the early 20th century. Even though human utilization of marine ecosystems started even before that in some regions (Estes et al., 2007; Roberts, 2007; Rick & Erlandson, 2008b). I chose to focus on the Holocene period to reduce the confounding effect of major climate change associated with the end of the last ice age. Three types of historical occurrence data can be retrieved across this time period:

1) Archaeological records

Animal remains (e.g., shells, bones and teeth) can be found in in archaeological contexts, such as those associated with former human settlements. Archaeological remains can reflect the presence of species in coastal areas, the use people made of them (subsistence, ritual, architectural, ornaments...) and the timeline of their utilization (Rick & Erlandson, 2008b). They may also reveal information on the size, age and relative abundance of the animals used. The species can be identified from comparisons with reference collections or through genetic analyses. Information on the period at which remains were deposited can be obtained from other information in the same context (e.g. dated coins) or through radiocarbon dating, though the uncertainty around this dating is often very high. Somewhat counterintuitively, though, the larger a marine species is, the less likely it

is that it will be found in the archaeological record. Indeed, small species of fish and molluscs were typically brought inland for processing, their bones and shells then accumulating in large quantities in layered garbage piles (or middens), sometimes over several hundreds or thousands of years. In contrast, for large species such as whales, seals and tuna, processing was typically done on the beach, with the abandoned bones then dispersed and broken by the action of the waves (Smith & Kinahan, 1984). Their relative rarity in the archaeological record has contributed to an underestimate of ancient exploitation of marine mammals.

2) Historical accounts

Many studies considering historical records to document species decline use museum data or specimens, available in Natural History Collections (NHC) (Shaffer et al., 1998; Graham et al., 2004). With the development of Geographic Information System (GIS), databases and the internet, enormous amounts of biodiversity information have been made available through online biodiversity facilities. Five to ten percent of all natural history collections are included in online catalogues, of which 20-40% are integrated in centralized databases that allow queries over all participating institutions simultaneously (see Graham et al., 2004 for a review). The interest of these collections for current conservation concerns has been recognized, and a number of ecological studies now integrate them to inform conservation purposes (Shaffer et al., 1998; Graham et al., 2004; Tingley & Beissinger, 2009; Newbold, 2010, 2010; Ward, 2012).

Much less standardised is historical occurrence data derived from written accounts earlier than 1800 AD. These include reports by early naturalists or travellers, written information on catches and trade, legal documents regulating the exploitation of wildlife resources, and anecdotal references to species that can be found in old documents kept in libraries and archives.

Unfortunately, these types of historical data are often overlooked because they are scarce, scattered and difficult to localize and access. Written historical sources can also be difficult to interpret, being often written in dead or old languages (e.g. Latin, Greek, old English), and sometimes associated to social, economic and legal phenomena that are difficult to understand without good knowledge of the historical context. Such anecdotal information is also difficult to reconcile with other data types, as they are not standardized to the same format. This makes it difficult to integrate them in ecological and conservation biology studies. Collaborations with historians to locate, interpret and turn these data into relevant information for ecological studies is thus advisable (Szabó & Hédli, 2011). Retrieving and using these data is important in a conservation context, as they can provide valuable insights into species' former distribution, abundance, behavior, habitat, and uses humans

made of them, all of which are particularly useful to understanding past changes and reconstructing historical baselines for depleted species.

3) Industry statistics

When considering the marine environment, the earliest forms of standardized historical written sources come from industrial catch statistics, such as records of arrivals to ports and logbooks kept on-board fishing and whaling vessels. These sources are generally associated to industrial operations and the monitoring of commercial fisheries, being particularly informative of trends over the second half of the twentieth century (Myers & Worm, 2003). For marine mammals, whose commercial exploitation lasted centuries, valuable information can be found going back to the 1500s, but information quantity and quality improves considerably with time. For example, 17th century records of Basque whaling ships arriving to major French commercial ports occasionally include information on number of whales taken, oil obtained, and general area where whaling took place (Du Pasquier 2000); 18th century Dutch ship owners and investors keep detailed records of total whales caught and total oil production per ship, and the general whaling area (De Jong, 1983); and 19th century American whaling ships kept detailed logbooks of each trip, including the coordinates, species and date of each whale caught (Figure I-3, Maury, 1852).

Fortunately, substantial numbers of these American logbooks have been preserved in public and private collections (Sherman, 1986) and these have received considerable attention. The first large-scale collections of data from these logbooks was performed by Matthew Fontaine Maury of the US Navy in the 1850's (Maury, 1852) and then by Charles Haskins Townsend and his assistant Arthur C. Watson in the 1920's in New York (Townsend, 1935). Recently, the Census of Marine Life (CoML) World Whaling History project digitized Maury and Townsend's original data sheets and extracted data from additional logbooks (Smith et al., 2012). The three combined datasets represent roughly 10% of the American whaling voyages between 1780 and 1920, providing tremendous amount of spatially-explicit information on the daily occurrences of whales sighting and catches for six species of whales (the sperm whale (*Physeter macrocephalus*), the bowhead whale (*Balaena mysticetus*), the humpback whale (*Megaptera novaeangliae*), the gray whale (*Eschrichtius robustus*), the southern right whale (*Eubalaena australis*), the North Atlantic right whale (*Eubalaena glacialis*), and the North Pacific right whale (*Eubalaena japonica*)), as well as information on the days were none of these 6 species were observed.

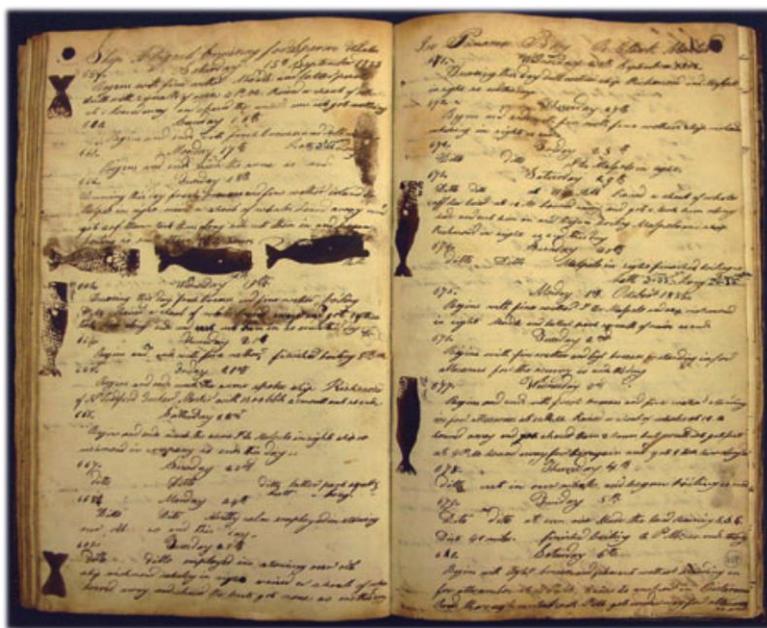


Figure I-3. Two pages from an American whaling logbook, from the ship *Abigail* of New Bedford, Benjamin Clark, master.

The logbook was written in a voyage from November 1831 to June 1835 to the North and South Atlantic and South Pacific Oceans. (From Holm et al., 2010, courtesy of New Bedford Whaling Museum)

Methodological opportunities for setting baselines from historical data

An obstacle to integrating historical occurrence data in conservation biology remains their increasing scarcity as we go back in time and the differences in spatial and temporal resolution and extent when compared to modern ecological data. However, by extending the timeline considered, they can help to establish more appropriate baselines, to document historical changes and to inform desirable future conditions (Rick & Lockwood, 2013). This makes it worthwhile to collect these data and find ways to include them in contemporary analyses. In this PhD, a literature-based review of historical occurrence records was performed for several species of marine mammals, to identify the challenges and opportunities that these type of data offer for reconstructing historical baselines.

Lotze and Worm (2009) and Lotze and McClenachan (2013) provide a view of the different possible approaches to combine or compare data to reconstruct the past. These include: temporal comparisons (contrasting two periods for the same region), time-series analyses (of abundance or distribution, to indicate trends and fluctuations over time), hindcasting (to backcalculate population abundance using population models calibrated with present abundance, historical catch data and life-history traits), and “space-for-time” comparisons (i.e. the use of surveys from unexploited regions to provide insights into the former status of species in exploited regions where other conditions are similar (e.g. Sandin et al., 2008)).

In this PhD, I investigate a set of analytical methods to reconstruct the historical distribution and abundance of species from spatially-explicit historical occurrence data. This includes mapping the historical occurrences of the species, mapping the historical envelope of occurrence, and relating

environmental conditions with historical records to predict its distribution using species distribution modeling (SDM). Each approach will be further developed and discussed in the next chapters.

Focus on marine mammals

Though the broad questions addressed in this PhD are relevant to all wildlife species, I will consider them through the lens of marine mammals. There are approximately 125 marine mammal species worldwide, categorized in several groups: cetaceans (whales, dolphins and porpoises), sirenians (dugongs and manatees) and carnivores (pinnipeds, sea otters and polar bears). My main focus in the core of this PhD is on cetaceans, though the case of three species of pinnipeds (the Walrus *Odobenus rosmarus*, the Caribbean monk seal *Monachus tropicalis* and the Mediterranean monk seal *Monachus monachus*) are addressed in Chapter 2.

A brief history of marine mammal exploitation

Easily accessible coastal species of marine mammals were particularly vulnerable to human exploitation and have been for millennia the target of aboriginal subsistence for the meat, oil, bones and fur they provide. Pinnipeds, that need to come to land for reproduction, were targeted particularly early (e.g. Giles-Pacheco et al., 2008). But some whale species coming close to shore for part of their life-cycles were also accessible. It is not clear when exactly whaling has started, but one of the earliest testimony of what appears to be active hunting is the representation of whaling scenes in petroglyphs dated from 6,000-1,000 years Before Present (BP) in Bangu-dae, Ulsan, South Korea (Lee & Robineau, 2004) (Figure I-4). These carvings represent cetaceans (identified as Balaenidae, Balaenopteridae and sperm whales) apparently hunted from boats with nets, harpoons and floats (Figure I-5). This suggests that the Neolithic populations living along the coast of Korea were actively hunting whales, and with relatively simple technologies.



Figure I-4. Site of Bangu-dae, carved plates (A, B, C, D, E) of the main wall (Ulsan, South Korea; 6,000-1,000 years BP).

Scale: 1m (adapted from Lee & Robineau, 2004).



Figure I-5. Possible whaling scenes (details from Bangu-dae petroglyphs, Ulsan, South Korea; 6,000-1,000 years BP).

1. boat, cetacean harpooned and a possible float. 2. Boat with a crew of five men, sort of float? and a large whale seen from above. 3. U shaped net and profile of a large whale blowing. Scale: 20cm. (adapted from Lee & Robineau, 2004)

Commercial hunting for marine mammals started in the middle ages in the North Atlantic. The first commercial sealing operation we have records of targeted walrus in the North Atlantic. The species had a high economic value then: its tusks were traded all over Europe and its hides were used to make ropes for boats. In a report to King Alfred of Wessex around 890 AD, the Scandinavian traveller Ohthere reports catching 60 walrus in the Norwegian coast. Olaus Magnus, a Swedish Catholic churchman and scholar (1490-1557) represented a walrus hunting scene in his "*Historia de gentibus septentrionalibus*" ("*History of the northern people*"), basing his description on a 13th century accounts of walrus hunting in the northern European Ocean (Magnus, 1555) (Figure I-6).

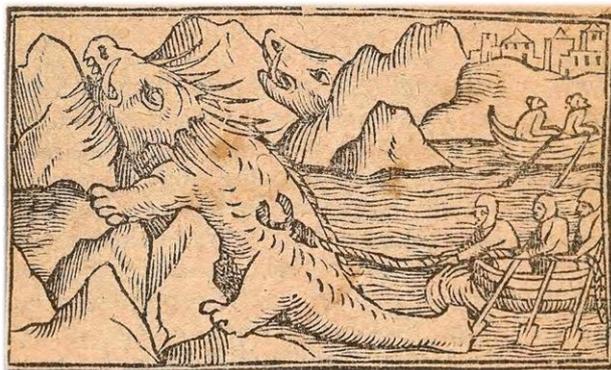


Figure I-6. Olaus Magnus' Walrus, 1555, *Historia de Gentibus Septentrionalibus*

<http://biodiversitylibrary.org/page/41862934>

Large scale exploitation of seals, sea lions and fur seals for their meat, oil and the fur of some species started in Newfoundland in the 16th century. In the early 18th century, it grew as a massive global industry that lasted almost two centuries, targeting in particular pinniped colonies in the South Seas (Busch, 1985). The scale of commercial sealing has declined considerably since the 1960's, though it is still conducted today, at a much smaller scale, by five nations: Canada, Greenland, Namibia, Norway and Russia.

The North Atlantic right whale was the first whale species to be commercially exploited by the Basques in the French and Spanish Basque country in the 11th century (Aguilar, 1986). The species was a relatively easy target, as it came close to shore to breed in the winter, swam slowly and floated when dead (and so it could be dragged to shore once killed). Other species, such as the gray whale *Eschrichtius robustus* and the sperm whale *Physeter macrocephalus* may have been secondary targets of this commercial operation. This early whaling was conducted from shore with boats pursuing the animal once spotted, using harpoons attached to lines to catch the whale. As right whales the coasts of the Bay of Biscay, the Basques moved to the other side of the North Atlantic, in Newfoundland and Labrador, in the 16th century. There, Basque whalers started to hunt the bowhead whale *Balaena mysticetus* which yielded even more oil than right whales (Ross, 1979; McLeod et al., 2008). This exploitation lasted half a century before overhunting led to the disappearance of whaling activities in this area around 1630. In 1610, the English Muscovy Company, based on Basque expertise, discovered bowhead grounds around Spitsbergen, where several European nations fought for dominion of the whaling shore stations in Spitsbergen and Jan Mayen (De Jong, 1983). As whalers developed new methods to process whales in the sea - using furnaces to try out whale blubber on board - they were released from the obligation to return on land often, paving the way to the pelagic whaling industry.

In the American colonies of New England, 17th century coastal whalers also caught right whales and possibly gray whales. In 1712, a boat that was blown offshore Nantucket managed to secure a sperm whale, highly valuable for the quality of its oil. This event marked the beginning of a pelagic whaling industry that would over the course of the following two centuries expand to all the world's oceans (except Antarctica), targeting mostly sperm, right, bowhead, gray and humpback whales. Whales had great value at that time in the economy of North America, with oil used for lighting, as industrial lubricant and for producing soap and the baleens used to make umbrellas and women corsets. As populations progressively became depleted, whalers went further afield to keep up with the demand for oil and baleens. The sequence of exploitation developed from the coast of New England, the Gulf of Mexico, the Caribbean Sea, the Azores the Cape Verde Islands, the west coast of Africa and Brazil and into the Indian Ocean and the Pacific. Multiple-year voyages allowed whalers to reach every corner of the globe, and the whaling industry to continue to prosper as whalers constantly switched from depleted to new whaling grounds where whales had not yet been slaughtered (Smith et al., 2012).

In the 1860s, steam-powered whale catchers and the exploding harpoon gun were developed by the Norwegian, allowing for the first time the exploitation of the large and fast rorquals. This modern whaling era started off the Norwegian coasts before expanding to all the world's oceans. The Antarctic, so far unexploited, became the main whaling grounds in the 1900's. Over the next decades, and with increasing efficiency thanks to improving technologies, the whaling industry extirpated the remaining whale populations one by one, bringing many species to the brink of commercial extinction. With an estimate of minimum 2.9 millions whales killed in a century, the modern whaling period is considered as the largest cull of any animal in human history in terms of total biomass (Rocha et al., 2014) (Figure I-7).

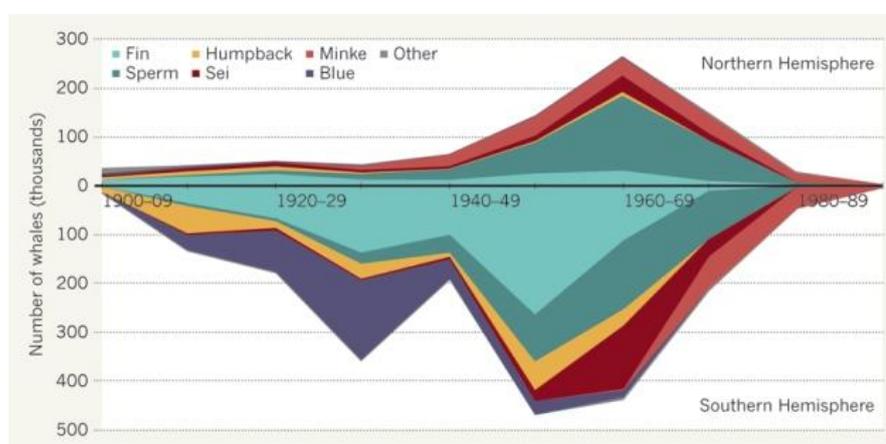


Figure I-7. Total number of whales killed in industrial whaling, 1900-99.
(Source: Cressey, 2015 ; Adapted from Rocha et al., 2014)

The International Whaling Commission (IWC) was established in 1949 to regulate whaling quotas to allow the long-term sustainability of the whaling industry. However, the IWC has been unable to regulate whaling and avoid overexploitation, the member nations failing to come to a consensus on the status of whale stocks. It was only in 1982, when the commercial extinction of most stocks was undeniable, that the IWC members agreed to suspend all commercial whaling activities, with a moratorium that took effect in 1986. This ban on commercial whaling is still effective today, apart from exceptions authorized by the IWC under special scientific permits (but see Clapham et al., 2003) and for aboriginal subsistence whaling (Reeves, 2002).

Marine mammals as an interesting case study

Several characteristics make marine mammals an interesting case study to learn about the consequences of the shifting baseline syndrome on our perception of the status of species, and the resulting decisions for the conservation of these species.

The serial depletion of whales started in the middle ages in Europe and persisted until the late 20th century. The cumulative impact of almost a millennia of exploitation had dramatic consequences for whale populations, leading several species to the brink of extinction. Despite the ban on commercial whaling since the 1980's, several species or populations remain very depleted and at high risk of extinction, such as the Endangered North Pacific right whale *Eubalaena japonica* (Reilly et al., 2008e), North Atlantic right whale *Eubaleana glacialis* (Reilly et al., 2012) and the blue whale *Balaenoptera musculus* (Reilly et al., 2008). Others have recovered to levels where they are no longer considered at risk of extinction, such as the southern right whale *Eubalaena australis* (Reilly et al., 2008c) and the humpback whale *Megaptera novaeangliae* (Reilly et al., 2008b), even if they are still far from having recovered to pre-exploitation levels.

Appropriate management decisions for these species, notably by the IWC, rely on the assessment of population status, which is based on a comparison with historical population level and distribution. But given the long history of exploitation of marine mammals, it is challenging to set an appropriate historical baseline for these species. The shifting baseline syndrome is likely to affect our perception of the initial state of their populations, resulting in an underestimation of the overall level of past human impacts. Studying the challenges and opportunities in using historical data to reconstruct these baselines is thus an important step towards informing the conservation of these species. This approach is notably facilitated by the possibility to build on existing interdisciplinary efforts that have already gathered historical occurrence data for marine mammals (e.g. Smith et al., 2012).

In our long history of interaction, the relationship between marine mammals and humans has varied from a fascinated respect (e.g. monk seals in antiquity myths; Johnson & Lavigne, 1999b, an irrational

fear (e.g. whales in medieval times; Szabo, 2005, 2008), and pragmatic exploitation (e.g. medieval Basque whaling; Aguilar, 1986), with high variation across cultures and epochs. In the past half-century, the public attitude towards marine mammals has evolved, with a growing interest for the welfare and the conservation of these animals, to the current state where marine mammals are much more often considered as emblematic and charismatic species, in need of protection, than as consumptive resources (especially true in nonwhaling countries; Hamazaki & Tanno, 2001). Marine mammals are therefore a particularly interesting group to serve as a flagship species for communicating about the shifting baseline syndrome to both academic and public audiences. I hope that this project might stimulate an interest in gathering knowledge on the history of exploitation, the causes of depletion, and the recovery trends for other taxa and ecosystems where species have also been historically depleted.

Studying marine mammals is thus interesting in its own to inform current conservation and management decisions for these species that have been heavily depleted by whaling. The work presented in this PhD is partly intended to inform management for these particular species. But in a larger perspective, lessons can be learned from this case study to address more fundamental questions about the conservation of depleted species in a shifting baseline context.

Objectives

There are two main objectives to this project:

- 1) To improve understanding of the historical distribution and abundance of marine mammals in order to contribute to their conservation.

More specifically, I review and synthesize information on the historical distribution of a set of selected species (walrus *Odobenus rosmarus*, Caribbean monk seal *Monachus tropicalis*, Mediterranean monk seal *Monachus monachus*, bowhead whale *Balaena mysticetus*, North Atlantic right whale *Eubalaena glacialis*, North Pacific right whale *Eubalaena japonica*, southern right whale *Eubalaena australis*, gray whale *Eschrichtius robustus*, humpback whale *Megaptera novaeangliae* and sperm whale *Physeter macrocephalus*). I also develop approaches for combining historical data with environmental data to fill gaps in knowledge and apply it to a set of species (the humpback, bowhead and gray whales). Finally, I propose a hypothesis for the past distribution and abundance of one particularly depleted species, the North Atlantic right whale, using the best available data to reconstruct a pre-exploitation baseline and inform this species' conservation.

- 2) To extract lessons about the challenges and opportunities of using historical data to set appropriate historical baselines and inform conservation, that are applicable to marine mammals and to other taxa and systems.

Structure

The chapters follow a logic of increasing level of complexity in data analysis. In **Chapter 2**, I present the results of a literature-based review of historical data for ten marine mammal species. I use these results to illustrate the diversity of data types available, their limitations, and how they can be used to improve our understanding of species' ecology and historical distribution. In **Chapter 3**, I combine 19th century American whaling records with environmental data to model the species-environment relationships for three depleted whale species (the humpback whale *Megaptera novaeangliae*, the bowhead whale *Balaena mysticetus* and the gray whale *Eschrichtius robustus*), in order to fill gaps in their historical distribution record. I discuss implications for the management of the three considered species, and the interest of using such modeling approach, according to the level of depletion of the species, and the knowledge we have of their pre-exploitation distribution. **Chapters 4 and 5** focus on the case of the North Atlantic right whale (*Eubalaena glacialis*), which came close to extinction after centuries of overexploitation and is one of the world's most threatened whale species. Setting an appropriate baseline for this species is made difficult by the scarcity of records over its very long whaling history. I take advantage of the well-documented pre-exploitation distribution of a congeneric species, the North Pacific right whale (*E. japonica*), and use species distribution modelling to generate a spatially-explicit statistical prediction of the environmental suitability (chapter 4) and of the carrying capacity (chapter 5) of the North Atlantic for right whales, as an attempt to reconstitute the pre-whaling baseline for *E. glacialis*. In **Chapter 6**, I discuss the overall approach undertaken in this PhD, by discussing the possible ways of reconstructing the past based on historical data, from descriptive to predictive approaches, emphasizing the lessons learned from the analyses of historical data for the ecology, range contraction and depletion of species. I conclude with a discussion on the definition and use of historical baselines to inform biodiversity conservation in a changing world.

CHAPTER II

USING SPECIES' HISTORICAL OCCURRENCE DATA TO INVESTIGATE RANGE CONTRACTIONS: A REVIEW FOR TEN MARINE MAMMAL SPECIES AND POSSIBLE APPLICATIONS

II. Using species' historical occurrence data to investigate range contractions: a review for ten marine mammal species and possible applications

Abstract

Assessing the decline of a species in space is necessary based on a comparison between its current and past distribution, which requires setting a historical baseline to which to refer. In this context, historical occurrence data are useful to bring context and reconstruct the pre-exploitation range of a species. Archaeological data, historical anecdotes and industry statistics can be used in this purpose. Yet, because such data are scarce, scattered and often difficult to identify and access, the task may prove difficult, and is seldom undertaken. Here, I present the results of a compilation of historical occurrence data for a set of marine mammal species which have been depleted following a long history of human exploitation. Data were collected from the ecological, archaeological, zooarchaeological, and historical literatures and spatially-explicit records of past occurrence were mapped to be compared with the current range of the species. I discuss the challenges and opportunities inherent to each type of data and detail possible applications, to illustrate how gradually more complex utilization is possible, depending on the amount of information contained in the data. This review highlights the interest of historical occurrence data to reveal evidences of range contractions, and to challenge our perception of the ecology of these species. Despite the difficulty in collecting scattered historical data from a variety of sources, and the errors and biases inherent to this type of data, I argue that there is an important need to pursue this reviewing effort, especially for species with a long history of exploitation, in order to add historical context into current conservation concerns.

Introduction

Historical records of species' past occurrence represent an opportunity to contribute to a better understanding of biodiversity trends over long period of times (Shaffer et al., 1998; Graham et al., 2004; Tingley & Beissinger, 2009; Kittinger et al., 2013). Species historical occurrence data can come from a variety of sources, including archaeological remains (Kirch, 2005), natural history collections (Shaffer et al., 1998) and catch statistics (e.g. Smith et al., 2012). Less attention has been given to historical anecdotes (in this case defined as written accounts of a species past occurrence and/or abundance provided by an observer, independently of any scientific or commercial purpose), though they can prove as useful to understand and overcome the shifting baseline syndrome (Pauly, 1995).

Marine mammals have been the target of human exploitation for millennia, leading to the depletion of many populations before formal collection of scientific data began. Even today, there are species whose distribution is still poorly known (e.g. such as some deep-diving beaked whales, that even today are only known through stranded specimens; MacLeod et al., 2006), but knowledge on species' distributions is even worse when we go back in time. To properly assess marine mammals' declines, the consideration of historical records is thus crucial.

The main difficulty for researchers to obtain historical records of species' occurrence is the accessibility of source material, as discussed in Reeves et al (2007). To be useful, a document must meet several conditions. First, it has to have been written by someone in the past, which is likely the main filter, as most events were never recorded in written format, particularly for the oldest ones. Then, it needs to have survived through time in a readable format. There are many reasons why this second condition may not be met, including loss, damage or illegibility of the document, which is why the available historical sources represent only a fraction of the written material that has been originally recorded. Finally, these sources have to be accessible to researchers, meaning that they need to be identified, located and obtained. Even accessible sources are sometimes difficult to find and obtaining them requires a great deal of personal, technical and financial resources. For some sources that are originally produced for a different purpose than recording species' occurrence (e.g. personal journals, navigator logbooks...), finding those that are likely to be relevant for a particular species is particularly challenging. A language issue also arises for nontranslated foreign references. In my case, I was able to access (myself or with help of MORSE collaborators) references in French, English, Spanish, Portuguese and Italian, but other references remained out of reach (e.g. references written in Greek, Latin, German, and all the Asian languages). Sometimes, I had to rely on second-hand interpretations of texts written in foreign languages, as the original source was no accessible to

me (e.g. Lindquist' interpretation of Icelandic, Danish and Swedish sources from 1000 AD to 1792; Lindquist, 2000).

If the above conditions are met and the desired reference is identified and located, there is still a challenge for accessing its content. Interlibrary loans are adapted in some cases where one would like to obtain a particularly promising reference, but are time consuming and not free of cost. Thanks to increasing technology, digitization of books now represents an incredible opportunity to gain access to thousands of references at a limited cost. Indexation enables the search for a particular reference from a search engine, while character recognition makes it possible to search for particular words within the text, reducing the time needed to process a reference. For instance, one can search online for the word "walrus" in a 1885 book, written by the explorer A.E. Nordenskiöld on his voyage in the Arctic, and identify in which pages the species is mentioned, among the book's 330 pages (digitized book made available by The Internet Archive/Million Book Project; www.ulib.org, www.archive.org/details/universallibrary). This achievement facilitates a lot the search for historical written accounts. However, there will always be inaccessible or untraceable references, precluding any hope of making an exhaustive review of historical sources.

As part of the MORSE project, historical occurrence data have been collected by members of the project and myself, for several species of marine mammals throughout the globe. This review focused on historical records of species' past occurrence outside their current ranges, over the past 10,000 years. We focused on a subset of species for which we had reasons to believe a contraction in their distribution may have taken place due to a known or suspected history of past exploitation by Humans and for which records of occurrence were likely to be accessible to us (e.g. groups difficult to identify to the species level, like dolphins, were excluded). Species that approach human-occupied coastlines during at least part of their life cycle (e.g. seals, coastal whales) were particularly promising, as these are most likely to have a long history of anthropogenic impact and to appear in archaeological records. The well-documented industrial whaling period enabled us to consider some large species of whales as particularly promising (sperm whale *Physeter macrocephalus*, the three species of right whales *Eubalaena sp.*, bowhead whale *Balaena mysticetus*, humpback whale *Megaptera novaeangliae*, gray whale *Eschrichtius robustus*). The sheer number of possible data sources as well as their dispersed nature rendered it impossible to do a fully comprehensive review for every considered species within the timeframe of this PhD. However, some interesting results have nonetheless emerged on the challenges and opportunities of collecting historical data, which I present and discuss in this chapter.

First, I aim to illustrate the diversity of data types available for understanding species' historical distributions, and the challenges to obtaining and compiling those data. I'll present results from a

reviewing effort for a set of ten marine mammal species, mapping those records that have explicit locations. Then, I'll emphasize how compilations of historical distribution data can be used to improve understanding of species' original ecology and distribution, and of the impacts of human activities, using examples extracted from this set of ten species.

Strategy for reviewing historical data

In order to improve our efficiency in finding historical records of occurrence in the literature, we settled on a strategy for reviewing them. First, we looked for existing reviews or compilations of historical/pre-historical data for a particular species. This entailed searching specifically for references on the species in question, through scientific papers and academic reports. Then, we searched for records associated with particular areas, focusing on areas outside the species' current EOO either at the edge of the range or in areas which represent "gaps" in the current distribution. Indeed, if range contractions did occur for these species, such areas are the most likely regions for those contractions to have taken place. Finally, records of historical occurrence encountered opportunistically during the review process (e.g., records for walrus found when reviewing the history of bowhead whaling) were also included in the dataset. I entered the records into a database capturing information on the species, the location, the time, record details and the reference in which it was found.

We focused on records within the past 10,000 years (beginning of the Holocene period) to reduce the confounding effects of climate change during the last ice age and so to focus primarily on the impact of human exploitation on marine mammal's range shift. We looked for historical and pre-historical records of species occurrence from three types of sources: 1) archaeological and zooarchaeological remains (from 10,000 years before present to today); 2) historical anecdotes, particularly from marine travel records (over the last few hundred years); and 3) statistics from the whaling and sealing industries (from the late 18th to the early 20th century).

While the combined effort of members of the MORSE project enabled the collection of historical records for more than twenty species, I chose to present the results for a selection of species, for which we have collected more than 30 records of past occurrence, which concerns ten marine mammal species, in six families. I list these species in Table II-1, providing a short summary on the history of their exploitation and current IUCN Red List status.

Table II-1. Marine mammal species reviewed in this chapter, with their current IUCN Red List status, and a short summary on the history of their exploitation.

Red List status: DD=Data Deficient; LC=Least Concern; VU=Vulnerable; EN=Endangered; CR=Critically Endangered; EX=Extinct.

Species	Family	Summary of the history of exploitation	Red List Status
Walrus <i>Odobenus rosmarus</i>	Odobenidae	Exploited by indigenous people in the Arctic for millennia. Populations were severely depleted by commercial hunting from the 18 th to the mid-20 th centuries. Walrus' hunting for subsistence by natives of the Arctic continues today.	DD
Mediterranean monk seal <i>Monachus monachus</i>	Phocidae	Has suffered from a long story of interaction with humans throughout the Mediterranean basin including subsistence hunting, commercial harvest and persecution. Once inhabiting open sandy beaches, now restricted to cave habitat in a very small portion of its historical range. It is the most endangered pinniped species in the world and one of the most endangered mammals.	CR
Caribbean monk seal <i>Monachus tropicalis</i>	Phocidae	Reported in Columbus 1494 trip to the Caribbean, it was intensively exploited afterwards for its skin and oil. Has not been seen since 1952, and is therefore considered extinct.	EX
Bowhead whale <i>Balaena mysticetus</i>	Balaenidae	Subsistence exploitation ongoing for millennia and still happening today. Commercial hunting in the North Atlantic started in the 16 th century and continued until the early 1900s. In the North Pacific, commercial exploitation occurred from the mid-1840s to the early 20 th century. The Okhotsk sea and Spitsbergen stocks remain severely depleted.	LC
Southern right whale <i>Eubalaena australis</i>	Balaenidae	Extensively hunted from the early 17 th to the 19 th centuries by American and European whalers, and then by other nationalities during the modern whaling era. The species seems to have partially recovered and the population trend is increasing.	LC
North Atlantic right whale <i>Eubalaena glacialis</i>	Balaenidae	Commercially exploited for over a thousand years, first by the Basques and then by other European nations and by Americans as one of the most desired targets of the 17 th -19 th century whaling industry. Became close to biological extinction and now survives as a small population off the eastern coast of North America.	EN
North Pacific right whale <i>Eubalaena japonica</i>	Balaenidae	The bulk of commercial exploitation happened in the mid-19 th century, as American pelagic whalers nearly extirpated it in the 1840s. Populations remain severely depleted; the eastern population in particular is in danger of extinction, with only a few tens individuals remaining in the Bering Sea.	EN
Gray whale <i>Eschrichtius robustus</i>	Eschrichtiidae	In the North Pacific, was commercially exploited from the mid 19 th to early 20 th century. It seems to have recovered in the eastern part of its range, while the western subpopulation remains severely depleted. Was extirpated from the North Atlantic (with last records in the early 1700s) for undefined reasons, though human exploitation is suspected to be at least partially responsible for it.	LC
Humpback whale <i>Megaptera novaeangliae</i>	Balaenopteridae	Were a secondary seasonal target of American shore-based and ship-based open-boat whalers in the late 18th century and much of the 19th century, and a target of the modern whaling industry until the mid 20 th century. The species seems to have recovered throughout its range, except for the Arabian Sea, western North Pacific and Oceania subpopulations.	LC
Sperm whale <i>Physeter macrocephalus</i>	Physeteridae	Sperm whaling was a major global industry that lasted from the early 18 th to the mid-20 th centuries, inducing a global decline in sperm whale populations. There is still considerable uncertainty on whether the species is recovering from depletion since the end of modern whaling, but encouraging observations are made for some populations that appear relatively healthy (e.g. in the North Atlantic).	VU

The number of records collected for each species and the number of references from which they were extracted are summarized in Table II-2. Records were mapped in Google Earth (v. 7.1.1.2041). Maps showing the historical occurrence data and the species' extent of occurrence were then produced in ArcGis 10.0. Maps for the walrus, the southern right whale and the gray whale are associated to a table containing details on the historical records collected.

Table II-2. Number of historical records collected for the ten species considered, and number of references from which they were extracted.

WWH: World Whaling History dataset; BP: Before Present

Species	Dataset	Nb of records (nb of references)
Walrus <i>Odobenus rosmarus</i>	This review	32 (11)
Mediterranean monk seal <i>Monachus monachus</i>	This review	124 (31)
Caribbean monk seal <i>Monachus tropicalis</i>	Adam & Garcia, 2003	118 (1)
Bowhead whale <i>Balaena mysticetus</i>	WWH	819
North Atlantic right whale <i>Eubalaena glacialis</i>	This review	175 (40)
North Pacific right whale <i>Eubalaena japonica</i>	WWH	6,414
Southern right whale <i>Eubalaena australis</i>	This review WWH	34 (12) 8,070
Gray whale <i>Eschrichtius robustus</i>	This review WWH	14 (7) 340
Humpback whale <i>Megaptera novaeangliae</i>	WWH	1,453
Sperm whale <i>Physeter macrocephalus</i>	WWH	14,597

Species reviews

Below is a presentation of the results, species per species, with a short description of the collected data. Extended discussion on the implications for each species is not provided here, as it is further developed later in the manuscript, in the literature or in forthcoming scientific papers.

Walrus (*Odobenus rosmarus*)

We found 32 historical occurrence records for the walrus from 3,930 years BP to 1880 AD, including 21 outside the current extent of occurrence of the species (Table II-3), mostly found through opportunistic sampling of historical sources. There is a bias towards records in the North Atlantic, with literature from northern Europe and America being more accessible than one from Asia.

The current range of the species is illustrated by its extent of occurrence (EOO), as provided by the IUCN Red List for Threatened Species. The EOO, as mapped by the IUCN Red List, is a visual representation of a species' distribution, determined by using known occurrences of the species, knowledge of its habitat preferences, remaining suitable habitat, environmental limits, and other

expert knowledge of the species and its range. It gives a broad idea of the current distribution of each species, but tends to overestimate species' ranges (including areas where the species may not be present) (Rondinini et al., 2006).

Many historical records were found south of the species' current range that cannot be attributed to vagrancy, as testified by descriptions of "abundant" group of walrus in "herds" or "banks". Many records are associated with active exploitation of the species and sometimes refer to "previous abundance" or "rarity", suggesting depletion of the populations.

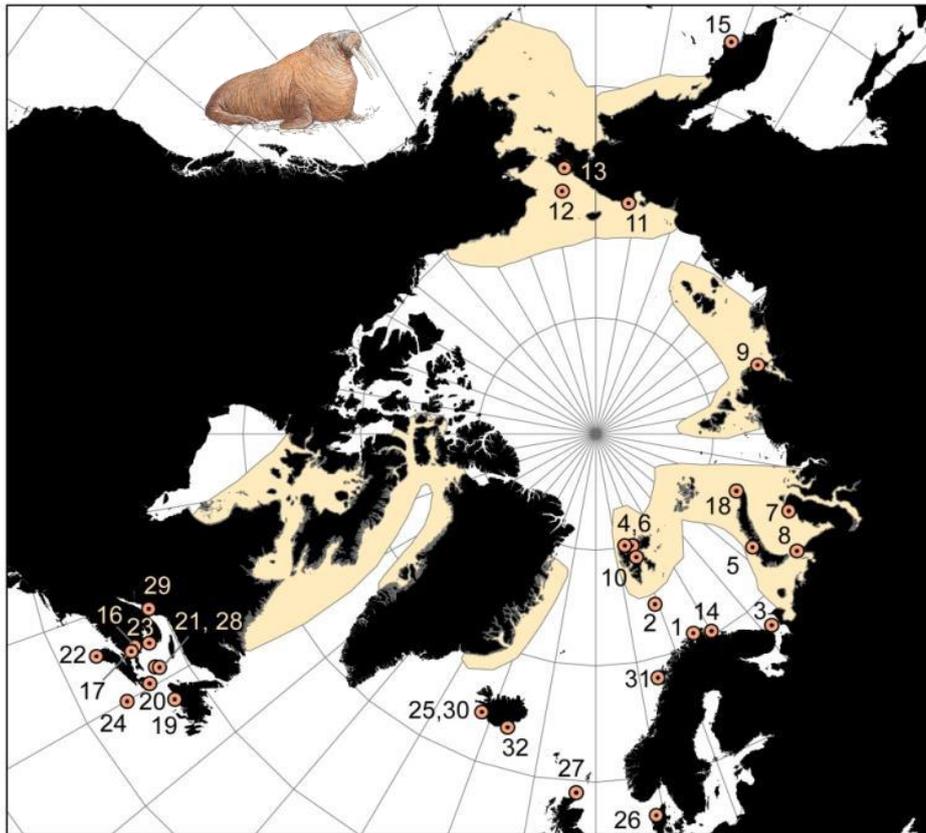


Figure II-1. Current range and historical occurrence data collected for the Walrus (*Odobenus rosmarus*).

The light orange polygons represent the species' extent of occurrence (EOO) provided by the IUCN Red List for Threatened Species. Orange dots correspond to historical records, obtained by reviewing the literature for historical occurrences of walrus. Numbers on the map refer to the Map Id column in Table II-3. Map is in North Pole Azimuthal Equidistant projection, centered on the North Pole and the Greenwich meridian.

Table II-3. Historical records collected for the walrus (*Odobenus rosmarus*).

Map ID	Details	References
1	Walrus caught in Finmark (c. 1698)	(Lilienskiold 1968 in Lindquist, 1994)
2	Bear Island: from very abundant (1606) to gone (by 1880)	(Nordenskild, 1881, p.117)
3	Mouth of the White Sea: walrus still captured yearly (c. 1876)	(Nordenskild, 1881, p.41)
4	Hinloopen St, Spitzbergen: from abundant (1861) to gone (1872-3)	(Nordenskild, 1881, p.122)
5	Novaya Zemlya: Ongoing hunting grounds but becoming scarce (c. 1880)	(Nordenskild, 1881, p.12)
6	Muffin island, walrus banks (c 1880)	(Nordenskild, 1881, p.118)
7	Coast of Yalmal, walrus bank (c 1880)	(Nordenskild, 1881, p.118)
8	Walrus killed at Vaygats Island, 1556	(Nordenskild, 1881, p.124)
9	Herds of walrus North of Preobraschenie Island (1878)	(Nordenskild, 1881, p.353)
10	Hunting in Spitzbergen: started in the late 1700s; declined by 1860-1870	(Nordenskild, 1881, p.224)
11	Past Cape Chelagskoj, one walrus seen (1878) evidence of indigenous hunting	(Nordenskild, 1881, p.329)
12	Walrus North of the Behring's straits, rare in 1878 but abundant in 1778	(Nordenskild, 1881, p.336)
13	East of Kolyutschin Bay, the native Chukches hunted walrus (1878)	(Nordenskild, 1881, p.464)
14	Northern Scandinavia: walrus hunting (Ohthere's travel, c 890 AD)	(Nordenskild, 1881, p.40-41)
15	East coast of Kamschatka: walrus bank discovered in 1648	(Nordenskild, 1881, p.18)
16	Walrus remains in a Micmac Indian refuse heap, Richibucto, New Brunswick (undated)	(Manville & Favour, 1960, p.499)
17	Walrus at Shippegan Island (1761)	(Manville & Favour, 1960, p.499)
18	Two hundred walrus at the Orange Islands, N Novaya Zemlya (1594)	(Allen, 1880, p.38)
19	Very abundant and heavily hunted in the isle of Ramea in 1534-1591	(Allen, 1880, p.66)
20	30-40 in the Bird Islands, off Cape Breton (ca. 1590)	(Allen, 1880, p.66)
21	Abundant and heavily exploited in the Magdalen Islands (1755), only bones by 1880	(Allen, 1880, p.67)
22	Past abundance (testified by bones) near Cape Sable (ca. 1867)	(Allen, 1880, p.68)
23	Previously abundant (many bones) at Bay Chaleur (1869)	(Allen, 1880, p.68)
24	Present in the 17th-18th centuries, maybe later, at Sable Island	(Allen, 1880, p.68)
25	Walrus bones Settlement Period (ca. 870-930) in downtown Reykjavik	(Amorosi et al., 1997)
26	Subfossil jaw and canine, Salling peninsula, Denmark (ca. 3930 BP)	(Møhl, 1974)
27	Walrus in the Orkneys (ca. 1500)	(Boece, 1821, p.li)
28	Several walrus in Brion island (25 June 1534)	(Cartier et al., 1865, p.35)
29	Walrus in the St Lawrence River (1535)	(Stephens, 1890, p.74)
30	Walrus bones, Iceland (Alþingisreitur, Reykjavik), between 871-1226 and 1226-1500 AD	(Buckley et al., 2014)
31	Many walrus at Lofoten and Vesteralen (1591)	(Lindquist, 1994, p.206-207)
32	Oreafi district, Iceland: a walrus came ashore and people ate from it (1606)	(Lindquist, 1994)

Caribbean monk seal (*Monachus tropicalis*)

Historical occurrence data for the Caribbean monk seal were extracted from a review by Adam and Garcia (2003) where localities of the species past occurrence were derived from historical, archaeological, paleontological and place names data. The full table including details on each record and references was not reproduced here, but it can be found in this review (Adam & Garcia, 2003, p.311:317). The data indicate that this species inhabited isolated islands and reefs throughout the Greater and Lesser Antilles, in the southern Caribbean Sea along the northern coast of central and South America, in the Gulf of Mexico and as far north as the coast Georgia in southeastern America (Figure II-2).

Mediterranean monk seal (*Monachus monachus*)

An extensive review has been performed for the Mediterranean monk seal as part of an internship by Christel Vidaller, supervised by Ana Rodrigues and myself, which aimed at mapping the historical breeding distribution of the species. A paper is being written based on this review (Vidaller et al., *In Prep*), which includes detailed information about the reviewing methods, the criteria for identifying monk seal reproduction areas, the complete list of records and associated references, and a discussion of the results. The location of historical records indicates that the species used to breed throughout the Mediterranean basin, in the eastern Black Sea, in the coasts of Senegal, Mauritania and Western Sahara, and in the Cape Verde, Canary and Madeira archipelago (Figure II-2). Gaps around the Lybian and Egyptian coasts are mostly attributed to the inability to find historical sources rather than to the species' absence in these areas.

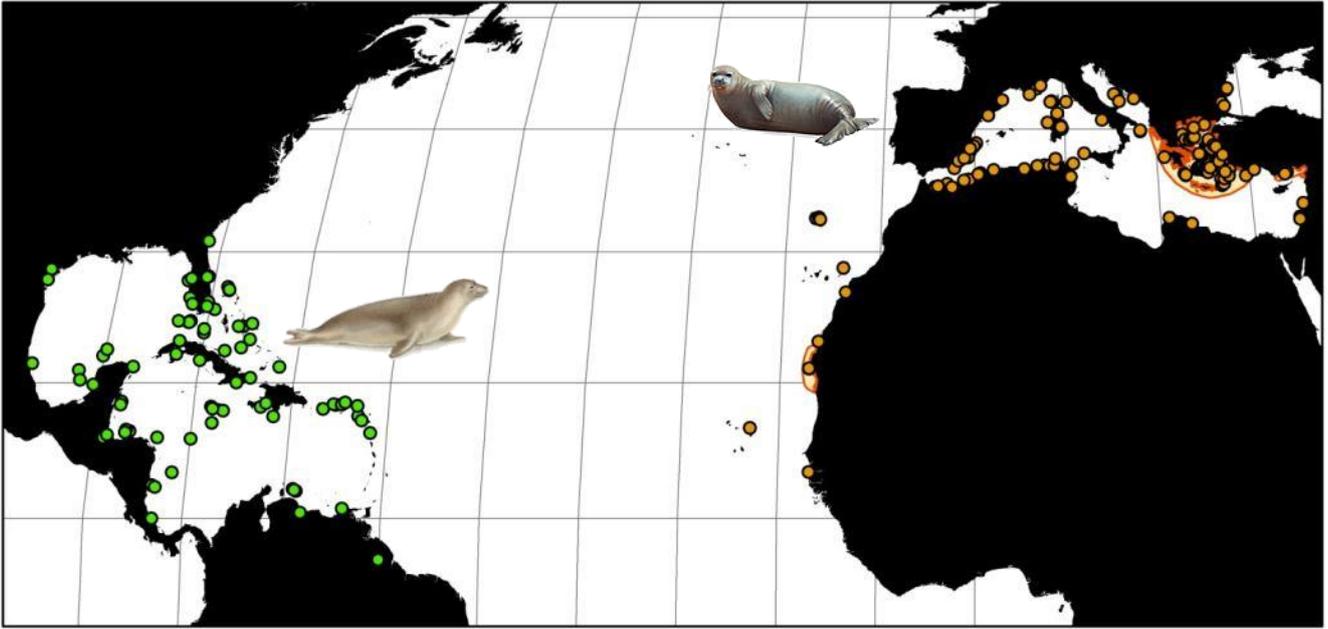


Figure II-2. Current range and historical occurrence data for two species of monk seal: the Caribbean monk seal (*Monachus tropicalis*, in green) and the Mediterranean monk seal (*Monachus monachus*, in orange). Green dots are historical occurrences of the Caribbean monk seal, mapped after the review by Adam and Garcia (2003). Orange dots correspond to historical records of historical and current breeding colonies for the Mediterranean monk seal, obtained by reviewing the literature (Vidaller et al., *In Prep*). The orange polygons represent the extent of occurrence (EOO) for the Mediterranean monk seal, provided by the IUCN Red List for Threatened Species. Map is in Eckert IV projection (centered on Greenwich meridian).

Bowhead whale (*Balaena mysticetus*)

The historical data presented for this species deserve a particular attention, as the vast majority of historical records presented in this chapter come from a similar source. These data were retrieved from a database built as part of a project focusing on the 19th century American offshore whaling period. This decade long project, named the World Whaling History project, began in 2001 as part of the History of Marine Animal Populations (HMAP) project, which is in turn part of the Census of Marine Life (CoML). The World Whaling History database was compiled from information on whale catches and sightings, extracted from a representative subset of logbooks of known American offshore whaling voyages for the period 1780-1920. A single trip usually lasted multiple years and could span multiple oceans: the Arctic, the Atlantic, the Pacific and the Indian Ocean. The whalers focused specifically on seven species of whales, which are thus the most represented in the database: the sperm whale (*Physeter macrocephalus*), the three species of right whale (*Eubalaena* sp.), the bowhead whale (*Balaena mysticetus*), the humpback whale (*Megaptera novaeangliae*) and the gray whale (*Eschrichtius robustus*) (Smith et al., 2012). Records were extracted and compiled by Lt. Commander Matthew Fontaine Maury in the 1840s, by Charles Haskins Townsend and his assistant Arthur C. Watson in the 1920s, and by the Census of Marine Life (CoML) World Whaling

History project between 2001 and 2010, as described in Smith et al. (2012). In the Maury and CoML datasets, each daily record includes date (year, month and day), vessel location (latitude and longitude), information on species presence (days where at least one individual was seen or caught) and absence (days when the species was neither sighted nor caught). Townsend's data differ from the two other sources in that they only report presences, i.e., records of locations and dates for whale catches. Access to this database was provided by Tim D. Smith and Randall R. Reeves.

Historical occurrence data for the bowhead whale extracted from a sample of these American whaling logbooks provide information both on the species presence (days when the species was sighted or caught; in red) and absence (days when this species was neither seen nor caught, in blue) (Figure II-3). Encounters with the species took place mostly in summer between 1845 and 1891 in the northern Okhotsk Sea, northern Bering Sea and Chuckchi Sea. Historical whaling records are well included within the current extent of occurrence of the species.

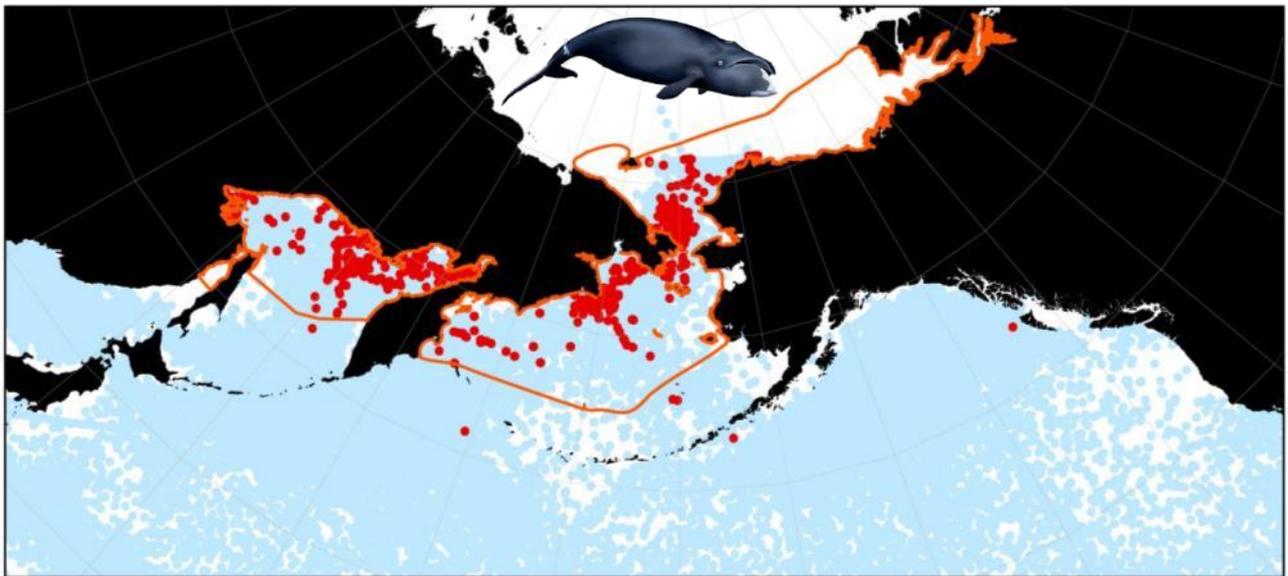


Figure II-3. Current range and 19th century whaling records for the Bowhead whale (*Balaena mysticetus*). The orange line represent the species' extent of occurrence (EOO) provided by the IUCN Red List for Threatened Species. Orange dots correspond to the species presence (days where bowhead whales were seen or caught) and blue dots to absence records (days where no bowhead whales were reported in the examined logbooks), obtained from a sample of 19th century American whaling logbooks. Map is in Bonne projection (standard parallel: 30°N , central meridian: 170°W).

North Atlantic right whale (*Eubaleana glacialis*)

Historical occurrence data of the North Atlantic right whale correspond to records of the species in summer (June to September), generally associated with whaling activities and spanning a period of nearly 400 years (Figure II-4). The EOO provided by the IUCN Red List includes areas where the species is suspected to be locally extinct or occur only as a vagrant (e.g. northeast Atlantic). This

representation was not very useful to discuss range contraction for the species, and in this case, I refined the EOO by identifying the species' current summer range using information from the literature and current sightings (NOAA-NEFSC, 2013).

Extensive information on these data and discussion on the implications for the species can be found in Chapter 4 (see in particular Appendix S5).

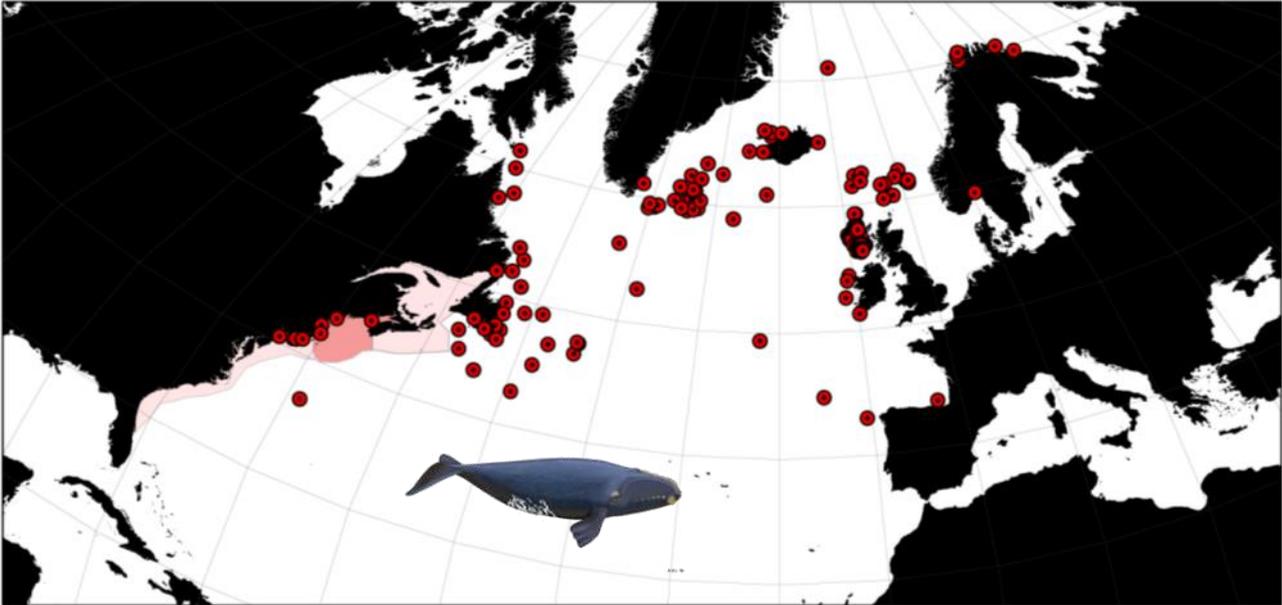


Figure II-4. Current summer range and historical occurrence data collected for the North Atlantic right whale (*Balaena mysticetus*).

The area shaded in red corresponds to the main feeding grounds for the current population (Bay of Fundy; Browns Bank; Great South Channel; Massachusetts Bay; Gulf of Maine; Jeffreys Ledge; Georges Bank; Grand Manan Bank) concentrating 98.6% of June to September recorded sightings (sum of number of individuals in NOAA 2013). The coastal areas southwards to Florida and northwards to the Scotian Shelf and Gulf of Saint Lawrence have 1.3% of the sightings together. All data are presented on a $1^{\circ} \times 1^{\circ}$ grid in Bonne projection (standard parallel: 30°N , central meridian: 20°W).

North Pacific right whale (*Eubalaena japonica*)

Sightings and catches of North Pacific right whales in the WWH dataset occurred between 1822 and 1904, with the bulk of exploitation in the 1840's. Whaling records indicate that NPRW were historically concentrated in the summer in five main areas: the Gulf of Alaska, the southeastern Bering Sea, east of Kamchatka and the Kuriles, the Sea of Okhotsk and the Sea of Japan (Figure II-5). Records in the Gulf of Alaska, southeast of Kamchatka and in the Sea of Japan are not included in the current EOO of the species, indicating that the species used to occupy a much broader range than it does today.

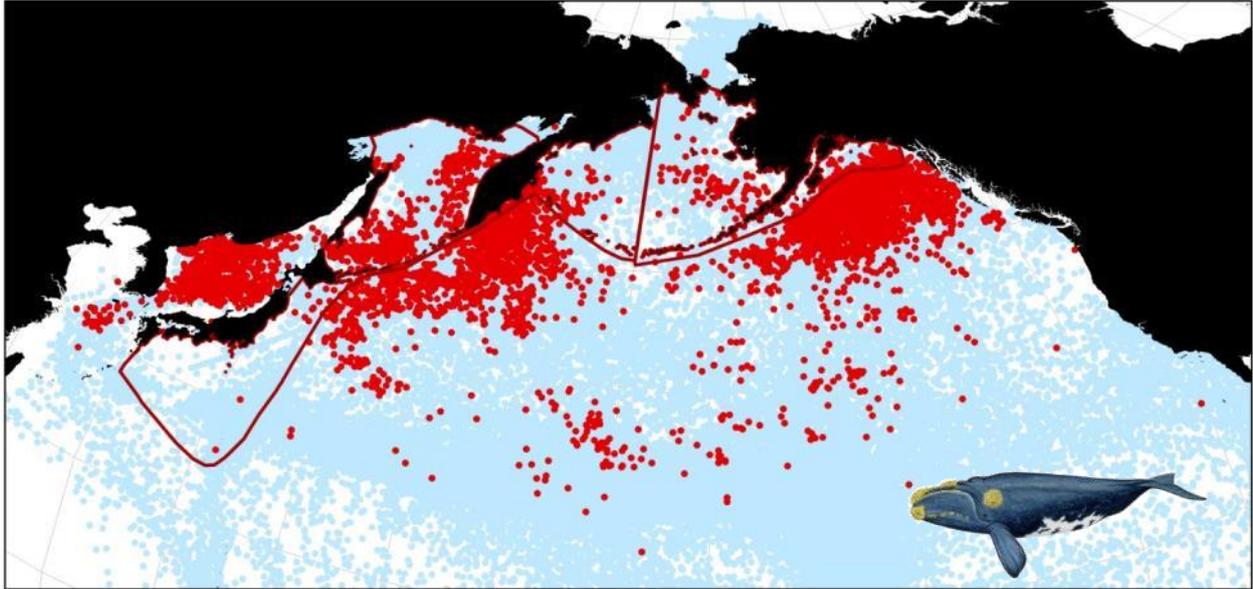


Figure II-5. Current range and 19th century whaling records for the North Pacific right whale (*Eubalaena japonica*).

The red line represent the species' extent of occurrence (EOO) provided by the IUCN Red List for Threatened Species. Red dots correspond to the species presence (days where right whales were seen or caught) and blue dots to absence records (days where no right whales were reported in the examined logbooks), obtained from a sample of 19th century American whaling logbooks. Map is in Bonne projection (standard parallel: 30°N; central meridian: 170°W).

Southern right whale (*Eubalaena australis*)

For this species, I compiled 19th century American whaling data (species presence recorded from 1792 to 1912) with historical occurrence records (Figure II-6). Records labeled 1-14 correspond to summer records while records numbered 15-34 are winter records of identified or suspected calving grounds, often associated with bay whaling (Table II-4). Some of these records are located further north than the current EOO of the species, suggesting a possible range contraction.

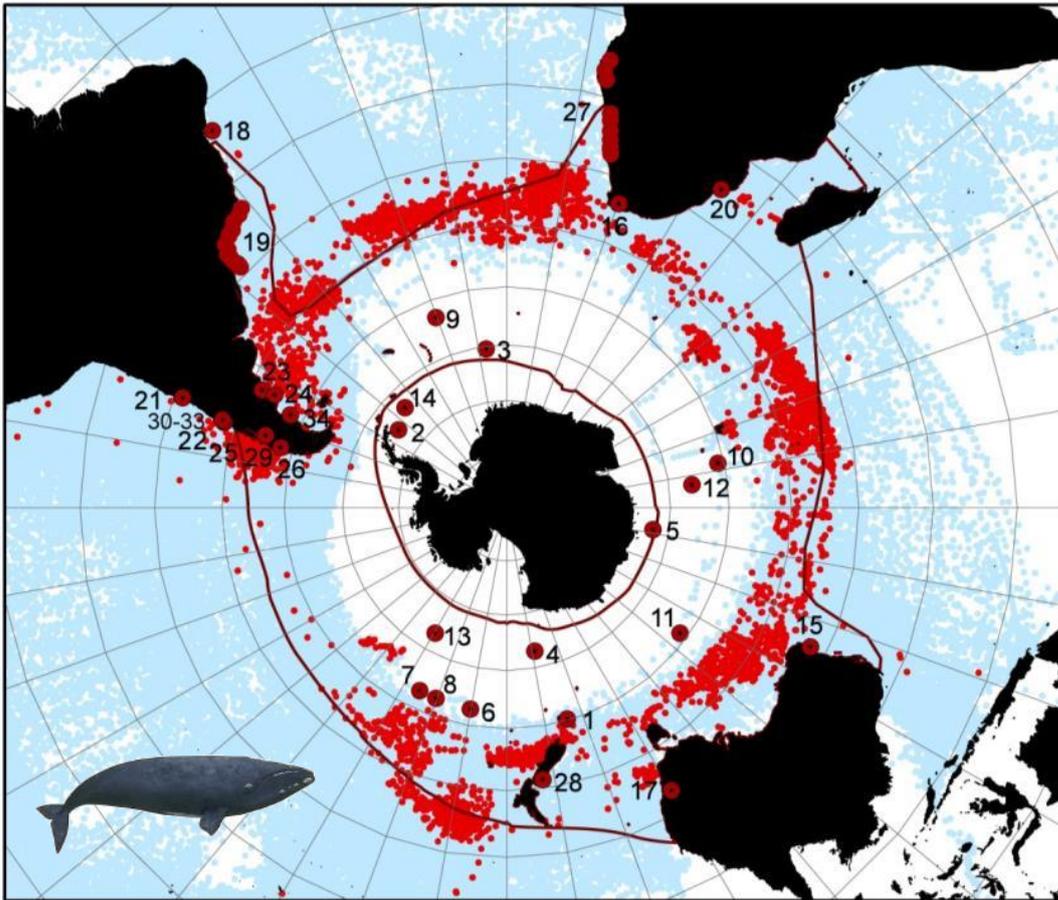


Figure II-6. Current range and historical data collected for the southern right whale (*Eubalaena australis*). The red line represent the species' extent of occurrence (EOO) provided by the IUCN Red List for Threatened Species. Red dots correspond to the species presence (days where right whales were seen or caught) and blue dots to absence records (days where no right whales were reported in the examined logbooks), obtained from a sample of 19th century American whaling logbooks (Smith et al., 2012). Historical records of the species occurrence were also collected from the literature and mapped as black dots with a red circle. Numbers on the map refer to the Map ID column in Table II-4. Map is projected in UPS South, centered on the South Pole.

Table II-4. Historical records collected for the southern right whale (*Eubalaena australis*).

Map ID	Details	References
1	Whales [right and sperm] in Laurie Harbour, New Zealand (Nov 1840)	(Ross, 1847, p.140)
2	Abundant whales in the Antarctic coast/South Shetlands (1842)	(Ross, 1847, p.327, 332)
3	S of Bouvet island, right whales, fin whales in deep water sea ice (December 1822)	(Morrell, 1832, p.59)
4	Abundant whales [mainly right; also sperm and humpbacks], south of New Zealand, Dec 1840	(Ross, 1847)
5	Right whale near Antarctica 16 Feb	(Charcot & Joubin, 1913, p.10)
6	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
7	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
8	Sightings data collected by Japanese research vessels during the years	(Ohsumi & Kasamatsu, 1986)

Map ID	Details	References
	1965/66-1981/82	
9	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
10	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
11	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
12	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
13	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
14	Sightings data collected by Japanese research vessels during the years 1965/66-1981/82	(Ohsumi & Kasamatsu, 1986)
15	Hunting in breeding bays, Vasse and Burbury, Australia (1856)	(Whitecar, 1860)
16	Breeding in the Cape of Good Hope, (ca. 1843)	(Hamilton, 1843)
17	Shore-based whaling in Frenchman's bay, Australia (1857)	(Whitecar, 1860)
18	Brazilian bay whaling: area baleeira do Reconcavo Baiano -17th to 19th century	(Ellis, 1969)
19	Brazilian bay whaling - 17th to 19th century	(Ellis, 1969)
20	Whaling in Delagoa Bay (Maputo Bay), Mozambique - 17th-19th century	(Banks & et al., 2011)
21	Great numbers of right whales in Coquimbo harbour (ca. 1800)	(Delano, 1817, p.299)
22	Plenty of right-whales in Santa Maria (ca. 1800)	(Delano, 1817, p.316)
23	St Antonio Harbour, right whales cows and calves from September to December	(Morrell, 1832, p.41)
24	Golfo Nuevo, several cow right-whales of large size and perfectly tame (25 Sept 1822)	(Morrell, 1832, p.41)
25	St Maria Island, Right whales in the calving season (1823)	(Morrell, 1832, p.105)
26	Right whales in the calving season, Peninsula de Taytao	(Morrell, 1832, p.157)
27	African bay whaling - 19th century	(Morrell, 1832, p.319; Lacroix, 1997)
28	Calving bays and migration around New Zealand	(Lacroix, 1997)
29	Cow and calf, Guaitecas Island Chile, 3 April 1838	(Margain & Pasquier, 2006, p.136)
30	Isla Santa Maria (Arauco) – bay frequented by whales, with several whaling boats in May 1838	(Margain & Pasquier, 2006, p.143)
31	Isla Quiriquina (Talcauano) – bay frequented by whales (from the 25 May 1838)	(Margain & Pasquier, 2006, p.150)
32	Baia de San Vicente (Talcauano) – bay frequented by whales & whalers end of May - June 1838	(Margain & Pasquier, 2006, p.150)
33	Calving area in Coquimbo, Chile, sometime pre 1866	(Eschricht et al., 1866, p.10)
34	Golfo S Jorge suitable for whaling in the calving season	(Morrell, 1832, p.43)

Gray whale (*Eschrichtius robustus*)

Gray whale presence records in the North Pacific correspond to sightings and catches by American whalers between 1845 and 1885. They indicate that the species used to be found in the coasts of Baja California, in northern Bering and Chukchi seas and in northern Okhotsk Sea. These records are well within the current EOO of the species.

The species was already extirpated from the North Atlantic at the time when American pelagic whalers started their industry. The species presence in this ocean is only attested by subfossil remains in Europe and the eastern coast of the United States (Table II-5) and a few literature accounts that were too imprecise to map: In the western North Atlantic, Dudley wrote a letter about whales off the coasts of New England and described a “scrag whale” whose back is “scragged with half Dozen Knobs or Knuckles”, “nearest the right whale in Figure and for Quantity of Oil; his Bone is white, but won’t split” (Dudley, 1725). This description fits the gray whale characteristics and testifies of the species’ presence along the coast of New England at that time. The gray whale was also found in Iceland, according to 12th to 18th century texts referring to “Sandaeta”, “Sandlaegja”, “Hrannlaegja” (respectively translated as sand-eater, sand-lier, and reef-lier, in accordance with the species’ behavior; Lindquist, 2000) and drawings representing the species (Gudmundsson, 1640). Gudmundsson’s 17th century description of the species corresponds well to both the morphology and behavior of the species: *“Sandlaegja. Well edible. It has white baleen plates which project from the upper jaw, instead of teeth, as in other balleen whales [...]. It is very tenacious of life and is able to lie on sand as a seal [does] for a whole day. But in sand it never fails. - Sandlaegja, reaches 30 ells, has baleen and is well edible”*.

In 1611, Thomas Edge was commissioned to exploit whales in Spitsbergen for the Muscovy Company. In a previously prepared list (of Basque origin) indicating the species of economic interest they could find was the Otta Sotta, which corresponds to the gray whale: *“The fourth sort of Whale is called Otta Sotta, and is of the same colour of the Trumpa [sperm whale], having finnes [i.e, baleen] in his mouth all white, but not above half a yard long, being ticker than the Trumpa but not so long: he yeelds the best Oyle, but not above 30 hogsheads”* (Mead & Mitchell, 1984).

The species was also part of the list of the whales known at Nantucket prior to 1670, as the “Scragg whale” (Macy, 1835).

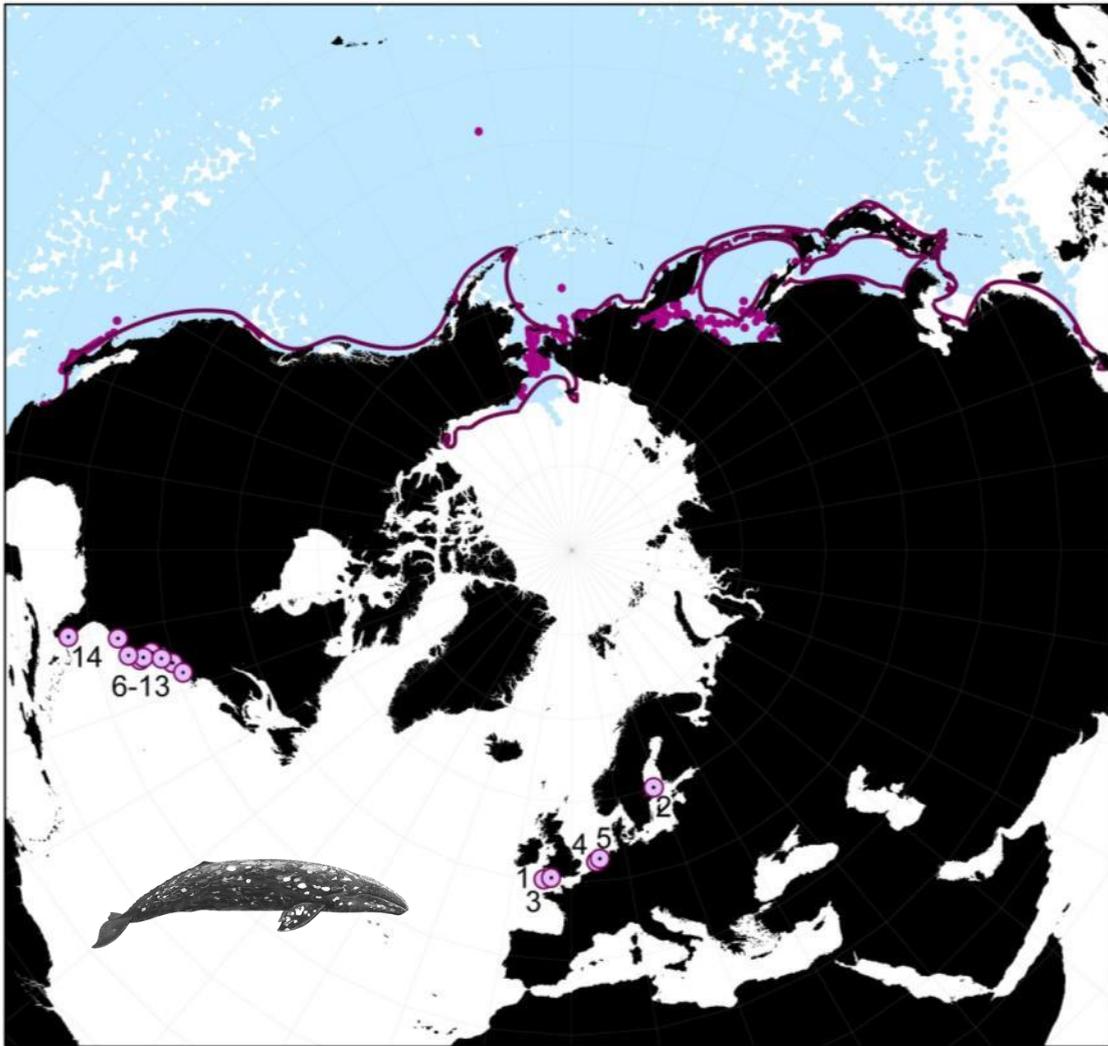


Figure II-7. Current range and historical data collected for the gray whale (*Eschrichtius robustus*). The purple line represent the species' extent of occurrence (EOO) provided by the IUCN Red List for Threatened Species. Pink dots in the North Atlantic correspond to the historical records of occurrence for the species collected in the literature. Numbers on the map refer to the Map ID column in Table II-4. Map is in North Pole Lambert Azimuthal Equal Area projection (central meridian: Greenwich).

Table II-5. Historical records of the gray whale (*Eschrichtius robustus*) in the North Atlantic.

Map ID	Record details	References
1	Partial skeleton of a single individual, excavated in 1829 at Pentuan, Cornwall, England; 1,329 ± 195 yrs BP	(Flower, 1872; Bryant, 1995)
2	Remains found on the coast of the Gulf of Botnia at Gräsö, Roslagen, Sweden; 4,395 ± 155 yrs BP	(Lilljeborg, 1861; Bryant, 1995)
3	Remains found in 1861 and 1865 at Babbacombe Bay, England, dated by Bryant 1995; 340 ± 260 yrs BP	(Gray, 1864, 1866; Bryant, 1995)
4	Two museum specimens described by van Deirse and Jung at Ijmuiden on the North Sea coast of the Netherlands: one collected in 1879, dated 8,330 ± 85 yrs BP by Bryant 1995 and the other one found in 1916, dated 1,400 yrs BP by van Deirse and Jung 1937;	(van Deirse & Junge, 1937; Mead & Mitchell, 1984; Bryant, 1995)
5	Partial skeleton found at Wieringermeer-polder, Netherlands, in 1935, first described by van Deirse and Jung in 1937 and dated by Bryant, 1995; 4,195 ± 45 yrs BP	(van Deirse & Junge, 1937; Mead & Mitchell, 1984; Bryant, 1995)
6	Jaw bone collected in Toms River, New Jersey, USA; 455 ± 90 yrs BP	(Mead & Mitchell, 1984)
7	Partial skeleton of a large adult found in 1959 at Myrtle Beach, South Carolina, USA; 865 ± 165 yrs BP	(Mead & Mitchell, 1984)
8	Partial skull of a juvenile found near the mouth of Chesapeake Bay, Virginia, USA in 1969; 10,140 ± 125 yrs BP	(Mead & Mitchell, 1984)
9	Left mandibule of a juvenile found near Nags Head, North Carolina, USA in the 1970's; 865 ± 50 yrs BP	(Mead & Mitchell, 1984)
10	Two specimens: a fragment of a right squamosal of a young gray whale found on the beach at Corolla, North Carolina, USA in 1976, dated 2415 ± 90 yrs BP; and an adult cranium found in 1977, undated;	(Mead & Mitchell, 1984)
11	Left mandibule of a juvenile found on the beach at Southampton, Long Island, New York, USA in 1977; 275 ± 35 yrs BP	(Mead & Mitchell, 1984)
12	A fragment of the squamosal of an adult found on the beach at Rehobeth, Delaware, USA in 1978;	(Mead & Mitchell, 1984)
13	Cranium of a juvenile found on the beach at Cape Lookout, North Carolina, USA, in 1979;	(Mead & Mitchell, 1984)
14	Cranium found on Jupiter Island, Florida; 1,190 ± 245 yrs BP	(Mead & Mitchell, 1984)

Humpback whale (*Megaptera novaeangliae*)

Humpback whales were a secondary target of American pelagic whalers, hunted throughout their range, in winter on their calving grounds in tropical and subtropical waters (e.g. Baja California, coast of northwest South America, coast of Angola, Cape Verde, Lesser Antilles), in summer in their feeding grounds (e.g. northwest North Pacific, Bering sea), and along the species' migration routes (e.g. mid North Atlantic, Gulf of Alaska, southern coasts of Chile and Argentina) (Figure II-8). Hunting for humpbacks occurred during almost the entire commercial whaling period, with encounters reported from 1792 to 1902.

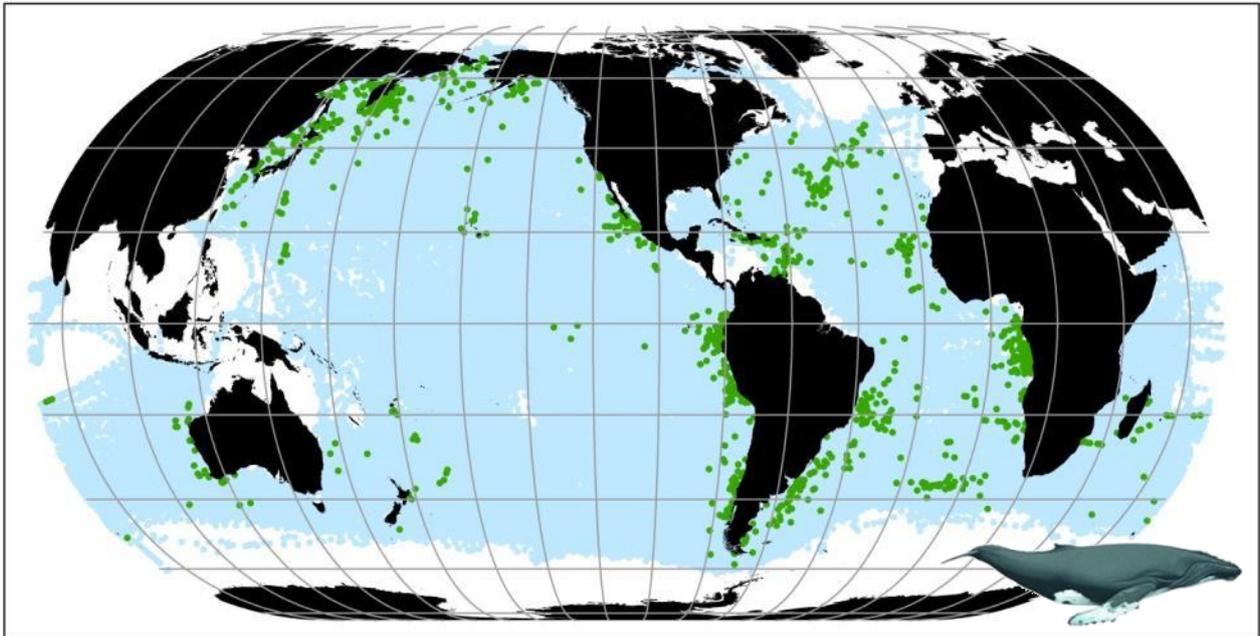


Figure II-8. 19th century whaling records for the humpback whale (*Megaptera novaeangliae*).

Green dots correspond to the species presence (days where humpback whales were seen or caught) and blue dots to absence records (days where no humpback whales were reported in the examined logbooks), obtained from a sample of 19th century American whaling logbooks (Smith et al., 2012). Map is in Eckert IV projection (standard parallel: 0°N; central meridian: 110°W).

Sperm whale (*Physeter macrocephalus*)

Sperm whales were the main target of the American pelagic whaling industry. Whaling data show that this species was hunted throughout its range (Figure II-9), in bands along the equator in the Pacific, between 20°N-40°N in the North Hemisphere, along South America, Western Australia, Oceania and eastern Africa. Hunting occurred year-round, during the entire period of commercial whaling (encounters reported from 1776 to 1921).

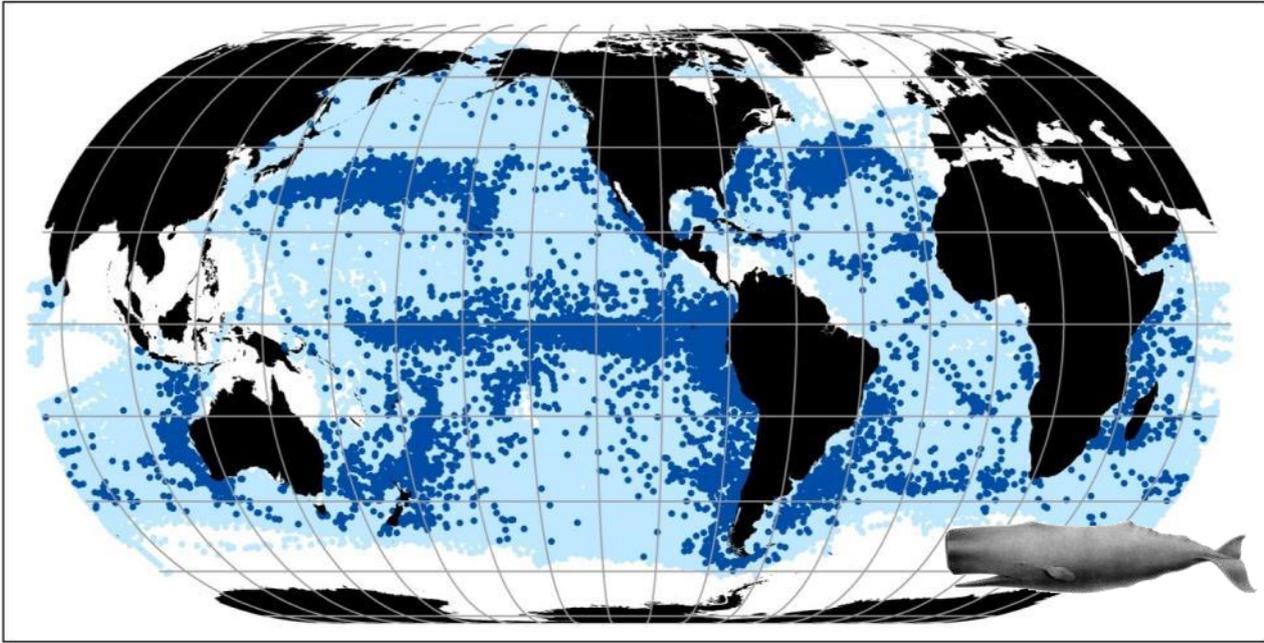


Figure II-9. 19th century whaling records for the sperm whale (*Physeter macrocephalus*).

Blue dots correspond to the species presence (days where sperm whales were seen or caught) and blue dots to absence records (days where no sperm whales were reported in the examined logbooks), obtained from a sample of 19th century American whaling logbooks (Smith et al., 2012). Map is in Eckert IV projection (standard parallel: 0°N; central meridian: 110°W).

Challenges and opportunities in historical occurrence data

Archaeological remains

Remains of whales in archaeological sites are scarce. This is notably due to the “invisible whale” phenomena, where whale remains are often absent from settlements because the size of most whale bones limits their transport beyond the beach where the whale was stranded or killed (Smith & Kinahan, 1984). The meat and blubber were directly processed on the beach, leaving little or no organic evidence to document the use of whale resources.

When archaeological remains are found, they are not always identified to the species level, as a result of technical difficulties regarding the identification of morphological and physical characteristics, or of a lack of interest from the archaeologist relative to its area of interest. In this case, genetic analyses or collagen fingerprinting identification (Buckley et al., 2014) may be adapted, but have an additional cost.

Bone remains and specimens may have been moved, such that their location is not necessarily representative of the place where the species used to live. When the study considers a large spatial scale, localized displacements have little consequences, but large-scale trade of resources from

marine mammals (e.g. Walrus ivory trade in the Atlantic; Pierce, 2009) can bring substantial uncertainty to the interpretation of zooarchaeological remains and museum specimens.

However, despite these limitations, archaeological records represent a unique opportunity to extend the timeline studied beyond the recent past, and offer a viewpoint on the condition of the ecosystem long before written accounts started to exist.

Historical accounts

The quality and quantity of historical anecdotes decline as we go backward in time. There is a bias towards recent historical records, as old written references are more likely to have disappeared or to be inaccessible. Identification of the species is plagued by taxonomic uncertainty, with marine mammal classification becoming fuzzier as we go back in times (Romero, 2012a) and descriptions being sometimes imprecise (e.g. no distinction between pinniped species, often referred to as “seals”). Background information is often useful to discriminate between species: a behavioral description, the time of the year when the species was reported, the use that human had of it, etc. can be as many clues of the species identity and should not be overlooked.

Geographic position can be imprecise as well, with references to very broad areas (e.g. “off the coast of Iceland”), and imprecise coordinates (as methods for accurately measuring longitude at sea have only been available since the late-18th Century).

Historical accounts are also biased taxonomically, spatially and temporally. Species that are coastal for at least part of their life cycle are more likely to come into contact with human, and thus to be present in historical references. Historical sampling is also spatially biased towards coastal areas, developed countries and less remote regions (Newbold, 2010).

Nonetheless, these limitations should not prevent researchers and practitioners to use this type of historical data, as they provide much valuable information on the past state of species and ecosystems that would go unnoticed otherwise.

For example, below is an historical account from a 330-page book describing the voyage the Swedish ship *Vega* to the Northeast Passage (the sea route between Europe and Asia through the Arctic Ocean), under the leadership of Adolf Erik Nordenskiöld, a Finnish arctic explorer. This quote illustrates the great amount of information that historical anecdotes can provide:

“During Stephen Bennet’s third voyage to Bear Island in 1606, 700 to 800 walruses were killed there in six hours, and in 1608 nearly 1,000 in seven hours. [...] A Norwegian skipper was still able during a wintering in 1842-1825 to kill 677 walruses. But when Tobiesen wintered here in 1865-66 he killed only a single walrus, and on the two occasions of my landing there I did not see one. Formerly the

hunters almost every year, during late autumn when the drift-ice had disappeared found “walrus on land”, i.e. herds of several hundred walruses which had crept up on some low, even, sandy beach, to pass days and weeks there in an almost motionless state. During this period of rest most of them appear to be sunk in deep sleep, yet not all, for- according to the concurrent statements of all the walrus-hunters with whom I have conversed on this subject – they keep a watch to warn their comrades when danger is near. If necessary precautions are observed, i.e. if the hunters approach the beach where the animals are assembled when the wind blows from the land, and kill with the lance those that lie nearest the water, the rest are slaughtered without difficulty, being prevented by the carcasses of their dead comrades from reaching the sea. Now such an opportunity for the hunter happens exceedingly seldom; there are famous headlands on which in former times the walrus was found by hundreds, in whose neighborhood now not a single one is to be seen. ”

Adolf Erik Nordenskiöld, *The Voyage of the Vega Round Asia and Europe. Vol. I., 1881*

This short extract contains valuable information about the historical occurrence of the species in Bear Island (outside walrus' current extent of occurrence), its abundances (well above 1,000), about the timeline of its depletion (from 677 in “a wintering in 1842-1825” to apparently extirpated by the late 1860's), about its behavior (“in an almost motionless state”, “most of them appear to be sunk in deep sleep”, “keep a catch to warn their comrades”), its habitat (“low, even, sandy beach”), and the method of hunting (“the hunters [...] kill with the lance those that lie nearest the water, the rest are slaughtered without difficulty, being prevented by the carcasses of their dead comrades from reaching the sea”). It is unlikely that conservation biologists and managers interested in the conservation of the walrus ever come across such record by chance, which is a shame given the amount of information included in it that can inform current concerns for the conservation of the species. The aim of applied historical ecology is thus to make such information available to practitioners.

Industry statistics

The dataset extracted from American whaling logbooks is by far the one that provides the best information on the occurrence of species, with global coverage and spatially-explicit data on both species' presence and absence, at a daily resolution. It requires a huge amount of effort to be collected, as only an estimated 10% of the total logbooks were digitized by the 10-year long World Whaling History project. This dataset is not without limitations, some of which are further developed in Chapter 4. Notably, it focuses on a limited set of species exploited by American whalers, and is only informative of the situation in the 19th century. Earlier human impacts (e.g. gray whales and right whales in the North Atlantic) are thus not covered by this dataset.

Applications of species' historical occurrence data

Improving understanding of the ecology of depleted species

In his chapter on the walrus in the *Encyclopedia of Marine Mammals*, Kastelein describes the species' ecology in these terms: "The walrus is found in the Arctic, where its distribution is limited by the availability of shallow water foraging grounds and thickness of ice" (Kastelein, 2009). And indeed, it is a well-accepted fact that walrus are associated with sea ice for most of their lives (Fay, 1982; Moore & Huntington, 2008). Hence, the presence of a single walrus in the Orkneys in March 2013, way further south than the species' range, raised much attention and was interpreted as the wandering of a lost individual. When reviewing the presence of the species in this area, one might find that its presence was mentioned in Scotland in the 19th century (Boece, 1821; Southwell, 1881). However, this is not sufficient evidence that the species was regularly found in this area, where the habitat is very different from the ice-covered regions currently used by the species. Only a larger-scale perspective on the species former distribution may bring further context to the possibility that it may have once inhabited terrestrial habitat further south of its current distribution.

Here, we present records of the species occurrence outside of its current range and spanning several millennia, including in Iceland, Scotland, the Netherlands, the Gulf of St Lawrence and the eastern coast of Canada south of 50°N. In the North Pacific, a single record was found, referring to a walrus bank discovered in 1648 along the eastern coast of Kamchatka, south of its current distribution. Many of these records are not associated with vagrancy, as testified by the use of words describing abundance of the species ("abundant", "herds", "banks") or references to hunting traditions.

The accumulation of historical records south of the current distribution of the species raises interesting questions: Did the walrus once inhabit these ice-free areas? Did we lose memory of its presence here? Would the walrus be able to recolonize this habitat now that the threat of hunting is gone?

Historical records seem to support the hypothesis that historical populations of walrus were able to live in these areas. In 2010, an « extra-limital » walrus found in the Faroe islands originated from the Svalbard population and returned back to it, suggesting not a lost individual but one exploring (Born et al., 2014).

Potential effect of climate change (e.g. colder climate, little ice age period) could explain to some extent a range shift for this species, but the historical data span a broad period of time and reconstruction of past extent of the ice sheet during the Holocene don't support the idea that ice was covering areas this far south in the North Atlantic (Dyke & Prest, 1987).

Moreover, observations of walrus in Norway have been increasing (despite general climatic warming), consistent with a recolonization of an ancient range (Gjertz et al., 1993).

References to the heavy exploitation and depletion of hunting grounds support the hypothesis of a range contraction due to overexploitation of the populations. Two processes might explain the depletion of the southernmost populations: On one hand, walruses inhabiting ice free areas may have been more exposed and more impacted by human exploitation than those inhabiting the ice sheet. On the other hand, walruses may have found shelter from human pressure by moving north and using only the most remote areas of their distribution. If the walrus exhibit some level of philopatry (Sonsthagen et al., 2012), the loss of lineages associated with ice-free areas could have resulted in the loss of this behavior in the population. Genetic and morphological data indicate that the walruses of the Gulf of St Lawrence were a distinct group. Range contraction in this area may thus be associated with loss of diversity (and possibly of a phenotype more adapted to southern latitudes) (McLeod et al., 2014). In the end, this review of historical data brings context to our knowledge of the ecology of the species and questions current concerns about the resilience of walrus populations to climate change (Moore & Huntington, 2008).

Mapping the historical envelope of species' occurrence

The simplest spatial representation of the historical distribution of a species is an envelope which encompasses all the known occurrences of the species.

Here, I present two examples of such historical envelopes of occurrence, for the summer range of the North Atlantic right whale (which was already heavily depleted by the 19th century and for which we have little information on its historical range), and for the Caribbean monk seal (which got extinct by the mid-20th century). For both species, I draw an envelope around the historical occurrence data mapped in Figure II-2 and Figure II-4, using a smoothed convex hull polygon (with a detail level of 5% for a closer fit of the data) (Figure II-10, Figure II-11). For the North Atlantic right whale, I also considered information on the current distribution of the species, by including the southeastern coast of the US in the envelope.

The resulting envelopes of occurrence give simplistic views of the historical range of the species, but are nonetheless informative of the level of depletion when compared to the current range of the species (overall extirpation for the Caribbean monk seal, restriction to the eastern coast of North America for the North Atlantic right whale in summer). This gives an idea of regions from which the species has become extinct. If multiple species are considered within the same area, it is useful to quantify and map the level of human impact. Mapping the extinct part of species' ranges is useful for understanding the composition of past communities in these regions, and is a useful context to

zoarchaeologists who try to identify specimens from a pool of candidate species, which is needed to counteract the shifting baseline syndrome.

This approach is very sensitive to any cases of vagrancy, which will artificially exaggerate the historical range of the species, and a great care must be taken to identify reliable records justifying an inclusion in the range: for example the accumulation of records (even imprecise) from the same area, and reliable descriptions of a former population. While every known sighting are supposed to be included in this envelope, every part of the envelope was not necessarily used by the species, as a result of habitat unsuitability, environmental limits, interaction with other species, etc. The IUCN Red List extent of occurrence (EOO) is likely to better take these factors into account, and in that sense is a more elaborate version of the envelope of occurrence proposed here. Nonetheless, in the absence of better information on the historical distribution of a species (e.g. species depleted early in time with little information on their pre-exploitation distribution, or extinct species), this envelope can be relevant as a first step towards a better understanding of its historical status. It can be used to assess the species' decline in terms of range contraction. It also adds some contexts for recent cases of vagrancy in areas outside of the species current range, to know whether the area is possibly within the historical range of the species or not.

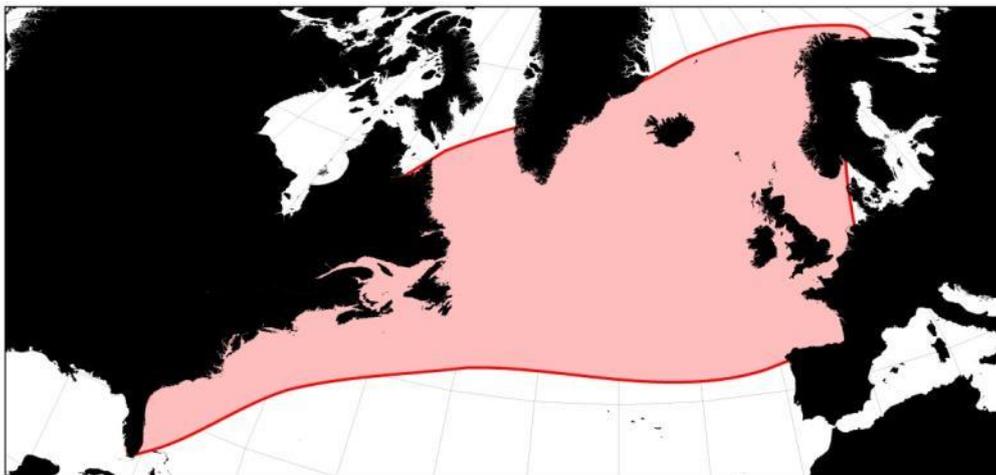


Figure II-10. Historical envelope of occurrence for the North Atlantic right whale (*Eubalaena glacialis*).

The envelope encompasses historical occurrence data and the current range of the species, as mapped in Figure II-4.

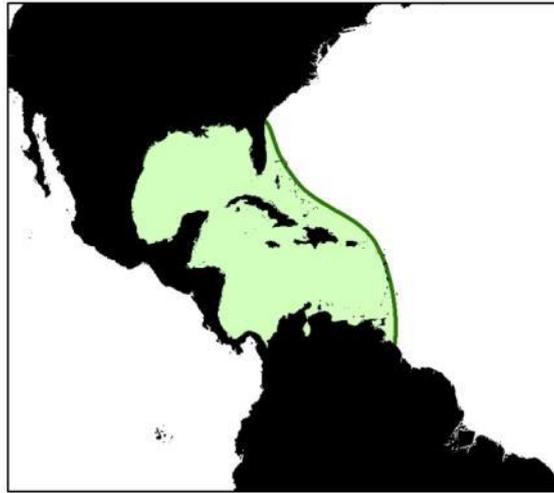


Figure II-11. Historical envelope of occurrence for the Caribbean monk seal (*Monachus tropicalis*).

The envelope encompasses all historical occurrence data, as mapped in Figure II-2.

Mapping the sequence of historical depletion of a species

If the spatial and temporal coverage of the collected data is informative enough, one can map the sequence of depletion of a species over time. This in turn informs the rate of range contraction in response to human impacts and enables to identify areas where the species was recently extirpated.

As an illustration, I present here preliminary results from Vidaller et al. (*In Prep*) based on information on the geographical locations of breeding records of the Mediterranean monk seal through time, in all areas from where it was historically recorded. We divided the study area into 55 regions, for which we summarized all breeding records collected (Figure II-2) in order to obtain an overview of the historical timeline of breeding and (if appropriate) of extirpation for 5 time periods: pre 1900, 1901-1950, 1951-1980, 1981-2000, and 2001-Today. For each period, we classified the species according to its status (breeding, possibly breeding, extirpated or possibly extirpated) in the region. Regions were mapped in ArcGIS 10.0 and 5 maps were created. Each map corresponds to a time period, where regions are coded according to the species' status (Figure II-12). From this representation, it is clear that extirpation of the monk seal occurred at different time throughout its range, at a particularly high level between the 1980's and 2000. Further interpretation of these maps and an extended discussion on the implications for the monk seal will be the subject of a different paper (Vidaller et al., *In prep*).

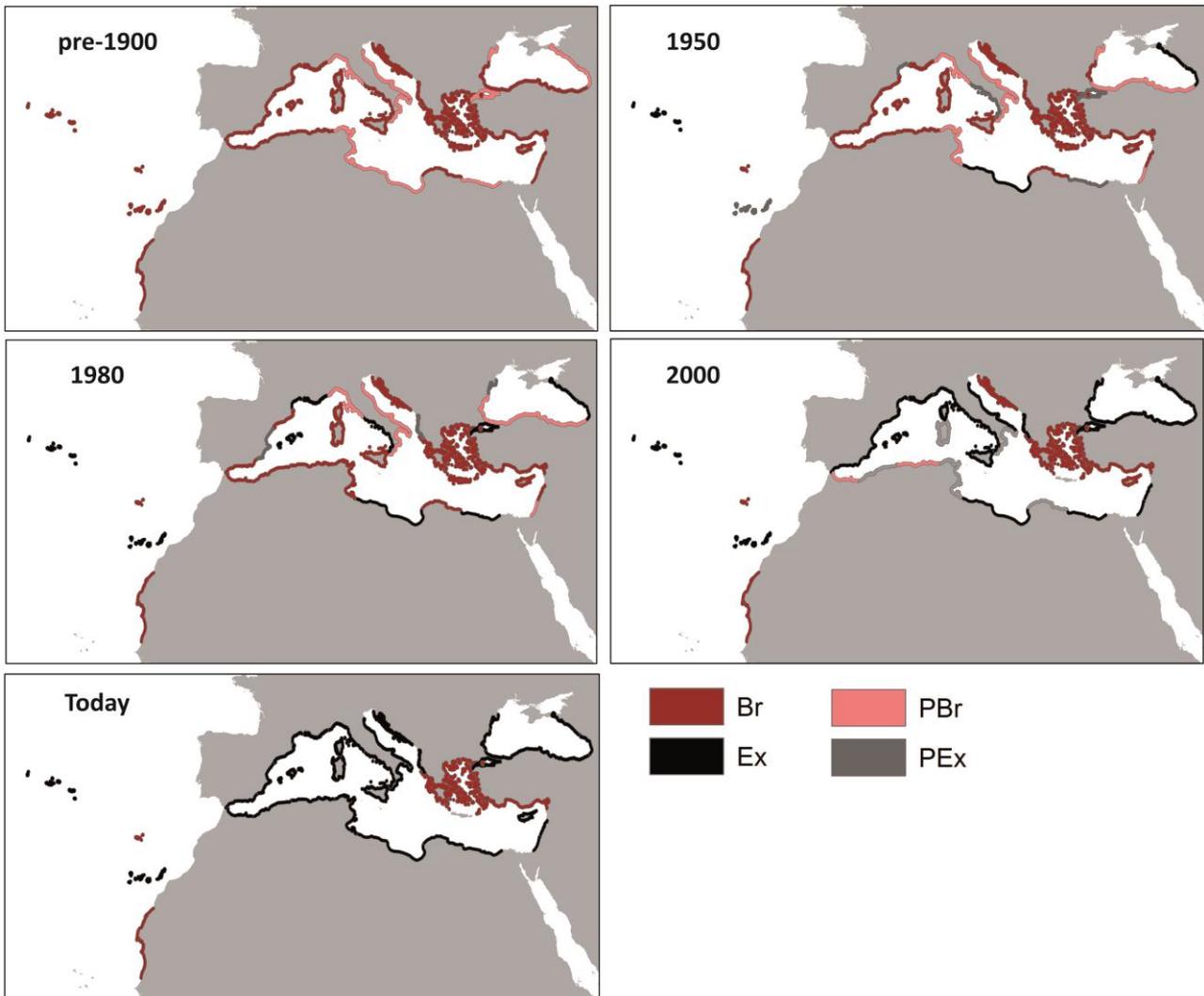


Figure II-12. Sequence of depletion of the breeding distribution of the Mediterranean monk seal (*Monachus monachus*) over the last century.

Regions of interest are represented as a buffer zone of 20km off the shore line, color coded according to the species' status. Br: Breeding, PBr: Possibly breeding, Ex: Extirpated, PEx; Possibly extirpated.

Modeling a species' historical distribution based on its environmental preferences

If the quality and quantity of historical occurrence data collected allows it, one can consider using species distribution models to propose hypotheses for the historical distribution of species.

Species distribution models relate field observations (presence, presence-absence or abundance) to environmental predictors through a statistically or theoretically derived response, to model the correlation between a species presence and its habitat and to produce a geographic description of the potential distribution of the species (Guisan & Zimmermann, 2000). The conceptual framework of SDMs relate to the concept of species niche, defined by Hutchinson as the combination of environmental characteristics in which a population can survive and reproduce (that can be represented in the n -dimensional space as a hypervolume; Hutchinson, 1957). Hutchinson

distinguished the fundamental niche (“the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions”; Pearman et al., 2008) from the realized niche (“the portion of the fundamental niche in which a species has positive population growth rates, given the constraining effects of biological interactions, such as competition”; Pearman et al., 2008). Most studies identify the outcome of SDMs as the realized niche of the species (Austin, 2002; Guisan & Thuiller, 2005), as they are based on occurrence data that are already constrained by biological interactions. When this realized niche is mapped into the geographical space, it represents the potential distribution of the species, or habitat suitability (Araújo & Guisan, 2006; Soberón, 2007). The application of the niche concept in static SDMs involves strong assumptions on the quasi-equilibrium of the species with its environment (Guisan & Zimmermann, 2000; Austin, 2002) and the conservatism of niche over space and time (in an extrapolative context) (Pearman et al., 2008).

The environmental factors that affect species’ distributions can be distinguished between proximal (causal, e.g. food resources) and distal (proxy, e.g. temperature, altitude) components, based on whether they have a direct or indirect action on the species occurrence (Austin, 2002). Distal variables are often more accessible and easier to compute in SDMs, but decrease the applicability of the model to other temporal or spatial conditions. However, as it is very difficult to provide GIS coverage for proximal variables, their use in SDMs is impractical (Austin, 2002).

The following elements are required for building species distribution models (Figure II-13; Austin, 2002; Franklin, 2009):

- A conceptual model of the environmental factors controlling species distribution, in order to select the appropriate environmental variables to include in the model and define the appropriate scale at which to perform the analysis.

The environmental predictors should be optimally chosen to reflect the limiting factors controlling species’ eco-physiology and the resources they use, as well as the disturbances affecting the environmental system (Guisan & Thuiller, 2005).

- Spatially-explicit data on species occurrence (presence/absence or abundance of the species), either collected by random or stratified field sampling, or through opportunistic observations (e.g. Graham et al., 2004).
- Maps of environmental variables supposed to control species distribution, in the form of digital spatial maps, generally derived from remote sensing or from spatial models of environmental processes.
- A statistical model linking species occurrence to the environmental predictors (see Guisan & Zimmermann, 2000 for a review of modeling approaches). The model can be statistical,

descriptive, logical or rule-based (Burgman et al., 2005). Only statistical SDMs have been developed in this study.

- Data and criteria to evaluate the model and validate the predictions, using either an independent validation dataset or by performing internal cross-validation between a calibration and a validation dataset, representing subsamples of the overall dataset available.

SDMs are particularly useful in a predictive framework, to fill spatial and temporal gaps in knowledge of the species distribution. They can thus have direct applications for reconstructing the historical distribution or abundance of depleted species from fragmentary historical occurrence data.

The minimum number of occurrence data needed to perform this analysis is subject to debate, but studies have emphasized the possibility to build species distribution models from very few (10-20) occurrences (Pearson et al., 2006; Papeş & Gaubert, 2007). Limitations of habitat models based on historical records include: errors and biases in the historical records (taxonomic, temporal, spatial and environmental) (Graham et al., 2007; Loiselle et al., 2007; Hortal et al., 2008; Lobo et al., 2010; Newbold, 2010), difficulty to choose the rationale for defining pseudo-absences when using presence-only data (Lobo et al., 2010), potential effect of climate change (Zurell et al., 2009) and niche conservatism over space and time (Wiens & Graham, 2005; Hirzel & Le Lay, 2008). Despite these limitations, SDMs are the main predictive tool in ecology (Dawson et al., 2011), and in a shifting baseline context, they represent a great opportunity to fill temporal and spatial gaps in our knowledge of the historical distribution of a species (Raxworthy et al., 2003; Newbold, 2010).

Within the species presented in this chapter, the best candidates for being used in habitat models are the whale species for which data on the 19th century American whaling period were collected. The dataset associated with this phase of whaling is remarkably rich in its temporal and spatial coverage of the species distribution. Moreover, the fact that it contains both species' presences and absences is an advantage for building models with a good statistical power (Brotons et al., 2004). Promising presence-only datasets were also collected in this effort, and could be used in a habitat modeling approach. The Mediterranean monk seal, for example, is a species with high conservation concerns for which the data presented here represent, to our knowledge, the most comprehensive collection of historical locations of the breeding distribution. It is an interesting case study to develop presence-only habitat models to predict the historical distribution of colonies, prior to extirpation, with interesting implications for the management of this species.

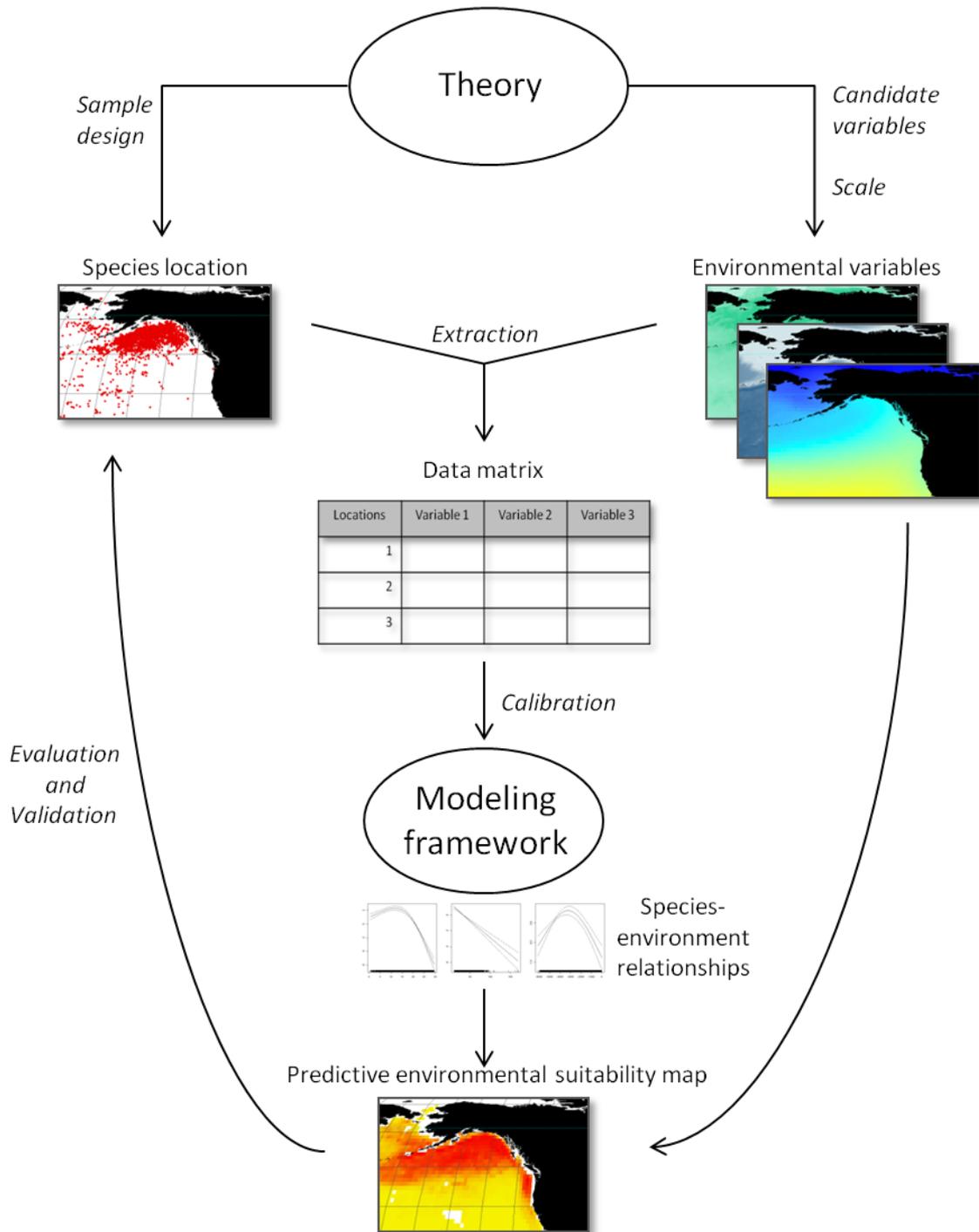


Figure II-13. Diagram showing the steps in statistical species distribution modeling and predictive mapping. Biological and ecological theory frames the problem and identifies the characteristics of the species and environmental data required. Species occurrence data are linked with maps of environmental predictors to extract the value of environmental variables at each location of the species. A statistical model is calibrated that describes the relationship between species occurrence and environmental data. The species-environment response functions are applied to environmental maps to produce a map of predicted environmental suitability. (Adapted from Franklin, 2009).

Discussion and Conclusion

As species declines can only be assessed through a comparison with an historical baseline, historical data are essential to inform a species' status. Evaluating the level of range contraction thus requires historical occurrence data that can inform us on where the species used to be extant and how it got depleted from these areas. For many species, we only have a general idea of what used to be their distribution, based on scattered data from regional case studies, expert knowledge or gray literature. Adam and Garcia's review of the Caribbean monk seal (Adam & Garcia, 2003) past distribution is a good example of a review that brings together comprehensive information on the historical occurrence of a species, though in this case it will not benefit the species' management, as it is already extinct. But such studies are unfortunately rare, leaving practitioners and conservationists with a tedious task if they want to gather information on the history of a particular species. Putting together all the information at a basin-wide scale is thus useful in its own to contextualize the history of exploitation of a species and inform its conservation. Records that are associated to human exploitation are also informative of the use that human had of this species, and eventually of the circumstances of its extirpation. The environmental distribution of historical occurrence data might also inform the ecology of the species, by challenging our beliefs on what is its "natural" habitat, with interesting perspectives for the study of future impacts of global changes. Besides purely descriptive approaches, other applications can be made of these historical occurrence data, including using them to map a species' historical envelope of occurrence, its sequence of depletion, or building habitat models to predict its historical distribution based on its environmental preferences.

The collection of historical records presented in this chapter is very incomplete. However, it represents to our knowledge the most comprehensive collection of historical data for several species of marine mammals and is therefore a useful contribution to a reviewing process that should to be pursued. It highlights important range contractions for some species (e.g. for the Mediterranean monk seal, North Pacific right whale, North Atlantic right whale, gray whale), informs on the original distribution of an extinct species (the Caribbean monk seal), raises questions about the ecology of a species (the walrus), etc. Next steps for this set of species would be to complete the review of historical occurrence data using a multidisciplinary approach, focusing on areas where the sampling for historical resources was too low. Resulting datasets need to be consolidated and flaws in the data identified. Once these steps completed, more advanced analyses could be performed. In particular, using habitat models to predict the historical distribution of these species is a promising perspective, which I develop in the next chapters. First, I use habitat models to fill distributional gaps in the distribution of species with various levels of depletions (Chapter 3), then I provide hypotheses for the distribution of a depleted species based on environmental preferences of a congeneric species

(chapter 4), and finally, I estimate the distribution of abundance and the overall pre-exploitation population size of a depleted species, based on the number of catches (chapter 5).

Overall, I recommend researchers and practitioners who are interested in the conservation of a depleted species to take historical occurrence data into account to better understand the historical distribution of the species. Analytical approaches can be considered, but always acknowledging for the limits inherent to each type of data. Care must be taken to identify the spatial, temporal and taxonomic errors and biases associated to these data, as they have strong consequences for the analyses that can be performed. A multidisciplinary approach combining knowledge and tools of the ecology, history and archaeology disciplines is recommended to overcome some difficulties related to the acquisition and processing of the data.

CHAPTER III

COMBINING HISTORICAL DATA AND SPECIES DISTRIBUTION

MODELS TO FILL INFORMATION GAPS FOR SPECIES WITH

VARIOUS LEVELS OF DEPLETION

III. Combining historical data and species distribution models to fill information gaps for species with various levels of depletion

Abstract

Exploitation of ocean resources has led to various levels of depletion for marine species, ranging from reduction in abundance to species extinctions. Currently protected but having been exploited for millennia, and with little information on their pre-exploitation distribution, marine mammals are an interesting case study to investigate our ability to respond to conservation challenges for species with various spatial levels of depletion. Since the end of whaling, some species of whales have substantially recovered throughout most of their range (e.g. the humpback whale *Megaptera novaeangliae*), while others remain heavily depleted in large subsets of their distribution (e.g. the bowhead whale *Balaena mysticetus*, for which the originally most abundant Spitsbergen population currently hosts just a few tens individuals). There are also extreme cases of populations extirpated from an entire ocean basin, the species being otherwise severely depleted in part of its residual distribution (e.g. the gray whale *Eschrichtius robustus*, extinct in the North Atlantic and Critically Endangered in the western part of its North Pacific range). Estimating the historical distribution of these species is key for guiding current management effort and informing potential conservation options for the future. Historical whaling data can be informative of the species past occurrence but are often not representative of the full historical range of the species. However, provided that there is enough information contained in these historical data, distributional gaps can be filled using species distribution models, which can provide predictions of suitable habitat based on the species environmental preferences. The aim of this chapter is to present an innovative use of historical whaling data to inform the conservation of species with various levels of depletion, through the use of recent habitat modeling methods. In practice, I combined historical data of 19th century American whaling catches with a set of environmental variables to build species distribution models for three species with different history of exploitation and facing incremental levels of depletion: the humpback, the bowhead and the gray whales. For each species, model predictions were geographically extrapolated to provide values of habitat suitability at a global scale and compared with our knowledge of the current range of the species. I discuss implications for the management of the three considered species, highlighting promising areas for monitoring and providing hypotheses on the location of yet unidentified stocks. More generally, I emphasize that models' predictions are

more informative for species that are depleted in part of their range and for which we have at least an approximate knowledge of where they used to be found. The absence of qualitative information on the occurrence of species in areas where they are depleted today prevents any validation of the model, limiting our faith in the spatial prediction. In contrast, for species that have spatially recovered throughout their range, validation of the prediction is possible, but the benefit of the approach is limited, since there are no spatial gaps to be filled.

Introduction

Successive decades of exploitation have resulted in the depletion of many marine mammal species, and of cetaceans in particular. Despite the ban on commercial whaling by the International Whaling Commission (IWC) in 1986, many populations of whales remain depleted (Magera et al., 2013). Conservation status and management measures for these species can be informed by a better knowledge of their historical distribution, which sheds light on the impact of past hunting on whale populations and on their potential for recovery in space. Information on the spatial distribution of these species' populations is key to their management, as illustrated by the unit chosen by the IWC, which is based on spatially defined "stocks". This use of a spatial unit of management asks for a thorough understanding of the spatial distribution of these populations, which has been the subject of much research in recent decades. However, information on the current range occupied by these species does not give the full picture of their potential for recovery, especially for populations that have been depleted through range contractions early in history and for which we have little data on their past occurrence. In other words, by overlooking the pre-exploitation distribution of these species, we limit our options for their management today and in the future. According to the level of depletion of species, the potential value of historical data for understanding their historical distribution is likely to vary.

In a previous chapter, I presented how historical occurrence data can be used to highlight the impacts of human exploitation on marine mammal distribution. Here, I present how more advanced analyses, namely habitat models based on the environmental preferences of species, can bring further information on their pre-exploitation distribution and can in turn inform management measures.

In this chapter, I will focus on three case studies: the humpback whale (*Megaptera novaengliae*), the bowhead whale (*Balaena mysticetus*) and the gray whale (*Eschrichtius robustus*). These three species have been vulnerable to human exploitation for subsistence since prehistory, being coastal for at least part of their life cycle and slow swimmers (Reeves & Smith, 2006). They were later exploited to near depletion in commercial operations that extended through their entire ranges, with some populations driven to near or complete extirpation. After decades of protection, the populations of these species remain depleted at different levels, from some thought to have recovered to pre-exploitation levels, to others that show no sign of recovery since the end of industrial whaling and are threatened of extinction. Our level of knowledge of their historical distribution is also varying, from a virtual loss of memory regarding the historical distribution of gray whales in the North

Atlantic, to a rather comprehensive view of the distribution of the humpback whale, today and in the past.

Three species, three histories of exploitation

Humpback whale (Megaptera novaeangliae)

The humpback whale is one of the best known whale species. It is cosmopolitan and migrates between low-latitude coastal breeding grounds and high latitude feeding grounds (Clapham, 2009), with the exception of one resident subpopulation in the Arabian Sea, where whales remain in tropical waters year-round (Mikhalev, 1997). Humpbacks feed in summer, on euphausiids and small schooling fish, engulfing their prey with their large mouth, and spend the winter in tropical and subtropical waters, in calving bays close to shore, islands or reefs (Clapham, 2009). The locations of current known breeding grounds were reviewed, listed in Table III-1 and mapped in Figure III-1.B. In the North Pacific, the migration occurs broadly from four breeding grounds in Japan/Philippines, Hawaii, Mexico and Central America to feeding areas in the Bering Sea, western Gulf of Alaska and western North Pacific. In the North Atlantic, humpback whale feeding grounds are located in the northeastern coast of North America, Greenland, Iceland and Norway. North Atlantic humpback whales breed in the West Indies in winter (Whitehead & Moore, 1982), but some individuals are known to use an alternative breeding ground in Cape Verde (Wenzel et al., 2009) where the species was historically caught (Smith & Reeves, 2003). Based on sightings of feeding individuals that were never identified in known breeding grounds, the existence of a third breeding ground in the North Atlantic has been proposed, but its locality remains unknown (International Whaling Commission, 2002). In the southern hemisphere, the International Whaling Commission recognizes seven breeding stocks, labeled A to G (Figure III-1, Table III-1), from which individuals migrate to summer feeding grounds in circumpolar waters around the Antarctic (Calambokidis et al., 2001; Clapham, 2009; Fleming & Jackson, 2011).

Table III-1. Table of identified current winter grounds for the humpback whale.

The Map ID column refers to the names indicated in Figure III-1.B.

Map ID	Details	Reference
A	IWC breeding stock A	(International Whaling Commission, 2011a)
B1	IWC breeding stock B1: from Guinea to 18°S	(International Whaling Commission, 2012)
B2	IWC breeding stock B2: from 18°S to west South Africa. (Most likely representing a migration corridor or a feeding ground)	(International Whaling Commission, 2012)
C	IWC breeding stock C: Mozambique, Madagascar and the islands of the Mozambique channel	(International Whaling Commission, 2011a)
D	IWC breeding stock D: northwestern Australia	(International Whaling Commission, 2011a)
E1	IWC breeding stock E1: northeastern Australia	(International Whaling Commission, 2011a)
E2	IWC breeding stock E2: New Caledonia	(International Whaling Commission, 2011a)
E3	IWC breeding stock E3: Tonga	(International Whaling Commission, 2011a)
F	IWC breeding stock F: Cook Islands and French Polynesia	(International Whaling Commission, 2011a)
X	IWC breeding stock X: Gulf of Oman and Arabian Sea coasts of Oman	(International Whaling Commission, 2011a; Minton et al., 2011)
HI	Hawaii	(Calambokidis et al., 2008)
MX	Mainland Mexico	(Calambokidis et al., 2008)
Phil	Philippines	(Acebes et al., 2007)
Okin	Okinawa (Ryukyu Islands)	(Calambokidis et al., 2008)
Ogas	Ogasawara (Bonin Islands)	(Calambokidis et al., 2008)
Rev	Revillagigedos Islands	(Calambokidis et al., 2008)
Baja	Baja California	(Calambokidis et al., 2008)
CAm	Sightings from Guatemala to Panama	(Rasmussen et al., 2012)
CV	Cape Verde currently supports a small population of humpback whales in summer. It was also an important 19th century whaling ground.	(Reeves et al., 2002a; Wenzel et al., 2009)
WI	Whaling for humpback whales occurred in the Lesser Antilles in the 19th century. Today, the West Indies are the major breeding/calving grounds for humpback whales in the North Atlantic, with a small aboriginal hunt remaining in Bequia (0-6 animals/year)	(Reeves et al., 2001; Fleming & Jackson, 2011)

The cosmopolitan distribution of humpbacks and their coastal behavior made them an easy target for human exploitation from prehistoric times (e.g. by native tribes in northwestern America, Huelsbeck, 1988; by the Inuit and Yupik in the Bering-Chuckchi Sea area, Whitridge, 1999) to the present day. In the past four centuries, humpbacks have greatly suffered from the cumulative impact of multiple whaling operations throughout the world. Their cosmopolitan distribution makes it difficult to exhaustively list all the whaling operations that have targeted humpbacks in a systematic or opportunistic manner. In the North Atlantic however, successive operations have been thoroughly documented, identifying not less than 27 fisheries and subfisheries that have targeted humpbacks as a main or secondary target (Reeves & Smith, 2002; Smith & Reeves, 2010). These have been regrouped in three categories, differentiated by the level of mechanization of the whaling technique (i.e. sail power vessels and hand-thrown non-explosive harpoons vs engine-powered vessels and gun-launched, explosive harpoons) and by whether the operations were land-based (shore) or pelagic (offshore whaling):

1) *Nonmechanized shore whaling*. It occurred off Greenland, Canada, northeastern United States, Bermuda, West Indies and the Cape Verde Islands, beginning in the 17th century with a peak in the 19th before declining to very low levels in the 20th century. It accounts for nearly 30% of the estimated total catches of humpbacks in the North Atlantic. Today, only one of these fisheries remains, in St Vincent and the Grenadines (West Indies).

2) *Nonmechanized offshore whaling*. It includes the American (“Yankee”) whaling industry targeting humpbacks in a number of breeding areas including the West Indies and Cape Verde (in a worldwide operation that spread throughout the world’s oceans in the late 18th century and much of the 19th century, targeting primarily sperm, right and bowhead whales, the humpbacks being only a secondary target, Smith et al., 2012). A Canadian offshore fishery has also been implemented along the southern shore of the Gulf of St Lawrence throughout most of the 19th century. Overall, nonmechanised offshore whaling is estimated to be responsible for nearly 35% of the total landing of humpbacks in the North Atlantic.

3) *Mechanized whaling*. It began with the development of modern whaling techniques in Norway in the late 19th century and continued throughout most of the 20th century. Humpbacks were among the principal target species of this industry that spanned all the world’s oceans, and in the North Atlantic ranged from Spitsbergen in the north to Grenada, southeastern Caribbean Sea, in the south (Reeves & Smith, 2002; Smith & Reeves, 2010). An estimated one third of the humpbacks landed in the North Atlantic were the result of mechanized whaling.

These three types of fisheries were not limited to the North Atlantic, and exploitation of humpback whales occurred extensively in the North Pacific and the southern hemisphere too, in particular during the American ship-based coastal whaling in the late 18th and the 19th centuries, and during the modern whaling era from the late 19th to the 20th century. In the southern hemisphere alone, more than 200,000 humpbacks were caught by modern whaling (Findlay, 2001).

Whaling for humpbacks was prohibited by the International Whaling Commission in 1955 in the North Atlantic, 1963 in the Southern Hemisphere and 1966 in the North Pacific, but illegal Soviet whaling occurred in the Southern Hemisphere until the early 1970's. Today, small subsistence hunting is conducted under restriction of the IWC in St Vincent and the Grenadines, Lesser Antilles, and in a few other unregulated locations (Reeves, 2002).

Despite considerable depletion by commercial whaling, humpback whale populations have recovered at various levels throughout the species range. This recovery is low in some areas (e.g. in the Cape Verde breeding ground which used to be an important whaling ground and now hosts only a few tens individuals), but overall, the species' range was apparently not significantly reduced by human exploitation, explaining why we qualify this species as having a low level of depletion. The species is qualified as Least Concerned by the IUCN Red List (Reilly et al., 2008b), on the criteria that its range is not restricted, that its global population totals more than 60,000 individuals and that it has recovered beyond the threshold (50% of the 1940 level) that would qualify the species as Vulnerable. Some populations however still face a risk of extinction. The Arabian Sea and Oceanic populations, for example, are both very small and isolated, and listed as Endangered.

*Bowhead whale (*Balaena mysticetus*)*

The bowhead whale (*Balaena mysticetus*) lives in Arctic and sub-Arctic waters, and is closely associated with the ice cap, undertaking seasonal migrations as the ice sheet expands southward in winter and retreats northward in summer (Moore & Reeves, 1993; Rugh & Shelden, 2009). The bowhead feeds on zooplankton, mainly copepods and euphausiids (Lowry, 1993; Lowry et al., 2004), skimming for its prey at the surface or feeding in the water column. In spring and summer, it is associated with areas whose features promote high concentration of zooplankton (Laidre et al., 2007; Citta John et al., 2014).

The International Whaling Commission recognizes five stocks for this species: 1) the Bering-Chukchi-Beaufort Seas stock (also called the "Bering Sea" or "Western Arctic" stock), where individuals winter in the western and central Bering Sea and then migrate to feeding grounds in the eastern Beaufort Sea via the Chukchi Sea; 2) the Okhotsk Sea stock, ranging from Russia to Kamchatka Peninsula, north of ca. 54°N; 3) the Hudson Bay-Foxe Basin stock, with populations found in the northwestern part of

Hudson Bay, southeastern part of Foxe Basin and in Hudson Strait ; 4) the Davis Strait-Baffin Bay stock, where the species aggregates in Baffin Bay in summer and migrates south to the southern Labrador Sea in winter, with historical evidences suggesting that the species was present in the Strait of Belle Isle and the Gulf of St Lawrence, further south than its current distribution, in the 16th-17th centuries (Cumbaa, 1986; McLeod et al., 2008); 5) the Svalbard-Barents Sea stock (“Spitsbergen” stock), ranging from the waters east of Greenland to the northwest of the central Eurasian Arctic, and limited in the south by the northern coast of Iceland and the coasts of North Cape in northern Norway.

Bowheads are slow swimmers, float after death and come close to shore, making them an easy target for hunters. The species has been exploited for at least the last 2.000 years for subsistence by indigenous whalers at various time periods and locations throughout the species range, from Okhotsk Sea to the Aleutians and Alaska and from eastern Canada to northern Europe, but there is no evidence that the mortality associated with such whaling has threatened any bowhead population (Stoker & Krupnik, 1993). In the commercial whaling period that started in the mid-16th century, bowheads were hunted for their oil and baleen bones, and less so for their meat, which was usually cast adrift by the whalers. Oil tried out from the whales’ blubber was used as fuel for oil lamps, in the manufacture of soap, paint and varnish, in the processing of fabrics and as lubricant in the industry.

The first commercial exploitation of bowheads started by 1540 in the northwestern North Atlantic, along the southern coast of Labrador and Strait of Belle Isle (Ross, 1993; McLeod et al., 2008). It was initiated by Basques whalers, who already had a long experience of North Atlantic right whaling in European coasts. This industry lasted for about half a century, during which whalers exploited bowheads from shore-based whaling stations. After 1590, overhunting lead to the gradual diminution of whaling in this area, and by 1630, there was no more whaling industry in the Strait of Belle Isle.

The Spitsbergen stock was discovered and first exploited by the English Muscovy Company in 1610, based on Basque expertise (Muscovy Company, 1905). Bowheads were hunted from shore-based stations in Spitsbergen and Jan Mayen. Other whaling European nations joined the hunt, but the Dutch soon dominated the industry. Dutch, British and Danish companies controlled the industry for the next twenty years, until they lost their influence and the hunt for bowhead was opened to all nations. Numerous shore-based stations then developed in Spitsbergen, but by 1670, they had closed down following the disappearance of bowheads near the coasts. Whalers had by then developed methods that allowed them to expand into pelagic whaling, whereby the whales were flensed on board and the blubber brought back ashore for boiling. Released from the constraint of processing whales ashore, whalers expended their activity to the open sea, looking for bowheads

along the ice edge off eastern Greenland. To keep up with the Dutch supremacy, the Basques introduced a new method to process the blubber at sea, with on-board furnaces (De Jong, 1983). By the end of the 17th century, catches had become uncertain in the Greenland Sea, and whalers turned to new whaling grounds in Davis Strait and Baffin Bay, west of Greenland. Whaling activities in this region included both pelagic hunting by European vessels and local shore-based whaling stations in western Greenland operated by the Danes. The Dutch dominated the 18th century Davis Strait whaling and the British the 19th, with the participation at various times of whaling vessels from Germany, Denmark, France, Spain and the United States. Starting in 1860, American whalers from New England exploited the bowhead stock off the northern coast of Hudson Bay for half a century, though at a much smaller scale than that of the Spitsbergen and Davis Strait fisheries, with less than 1,000 whales captured in Hudson Bay out of the ca. 120,000 bowheads estimated to have been caught in the North Atlantic over the previous two and a half century of whaling (Ross, 1979, 1993; De Jong, 1983; Sanger, 2005).

Commercial bowhead whaling in the North Pacific developed later than in the North Atlantic, starting in the mid-1840's when American whalers discovered the yet unexploited populations of Okhotsk and Bering Seas (Bockstoce & Burns, 1993). The fishery endured for seven decades, largely dominated by American (Yankee) whalers from New England and Long Island. Whalers left their home ports in the autumn, going round Cape Horn to reach the Arctic in the summer, where they could chase bowheads in ice-free waters of the Bering, Chuckchi and Beaufort Seas, harvesting occasionally the Okhotsk Sea population in the meantime. The intensity of exploitation quickly reduced the population of bowheads in the Arctic, and the whalers completely turned to the Okhotsk Sea stock in the mid-1850, decimating the population in just three years. Returning to the Arctic in 1858, they continued the exploitation of bowhead for the next half-century, compensating the low encounter rate due to depletion of the stocks with increased technology enabling them to access the most remote northern feeding grounds, and with the settlement of shore whaling stations for the exploitation of bowheads migrating along the shore in spring (Bockstoce & Burns, 1993).

In the 1910's, the scarcity of bowhead whales and the substitution of whale oil and baleen by other products reduced the economic value of bowhead exploitation, putting an end to their commercial whaling. The last individual taken at sea was caught in 1921. The species has been officially protected since the inception of the International Whaling Commission in 1946, with only limited aboriginal subsistence whaling permitted from the Bering-Chuckchi-Beaufort Seas stock. Despite substantial recovery, notably from the Bering-Chuckchi-Beaufort Seas stock and to a lesser extent from the Hudson Bay-Foxe Basin and Baffin Bay-Davis Strait stocks, the current population size of bowhead is only a fraction of its pre-exploitation level (Woodby & Botkin, 1993), and it remains heavily depleted

in part of its range, in particular in The Okhotsk Sea and Svalbard-Barents Sea subpopulations. These subpopulations remain very small, and are respectively classified as Endangered and Critically Endangered by the IUCN Red List of Threatened Species (Goldsworthy & Gales, 2008).

Gray whale (Eschrichtius robustus)

Gray whales are currently only found in the North Pacific. The eastern population has the longest known migration of any mammals, traveling between feeding areas in the Bering, Chukchi and Beaufort Seas, to winter breeding grounds on the west coast of Baja California (Mexico), with some individuals summering and feeding along the North American coast from Vancouver Island to central California (Moore & Ljungblad, 1984; Jones & Swartz, 2009). The western population has known feeding grounds off northeastern Sakhalin Island and is seen in summer off Kamchatka and the northern coast of Okhotsk Sea. Locations of winter breeding grounds are suspected to be along the coast of southern China, but remain unknown (Weller et al., 2002). Using a variety of foraging techniques, it has a generalist diet, primarily composed of benthic amphipods and pelagic zooplankton (Nerini, 1984).

The gray whale used to be found in the North Atlantic, as revealed by subfossil remains from Europe, Iceland and North America and several literature accounts (see Chapter 2). Lindquist (2000) advanced the hypothesis that the North Atlantic gray whale was hunted by coastal inhabitants in three regions: around the North Sea and the English Channel from prehistoric times to High Middle Ages; in Iceland by Icelandic peasant fishermen from 900AD to ca. 1730; in New England by European settlers, and possibly by native Indians from the mid 17th to ca. 1730. The Basques may have also hunted the gray whale occasionally in the latter half of the 16th century and in the early 17th century, though the locations remain imprecise. The species has apparently been extirpated from the North Atlantic in the early 17th century, possibly as a consequence of human hunting. A very surprising sighting of a gray whale in the Mediterranean Sea in 2010 raised hypotheses about a possible passage between northern Pacific and northern Atlantic, possibly as a result of the opening of the northern passage with global warming and the melting of the ice cap (Scheinin et al., 2011).

The slow swimming, coastal behavior of gray whales and the meat, oil, bones and baleens they provide made gray whales attractive for human exploitation since prehistoric times. In the eastern North Pacific, native Indians groups from the Aleutian Islands to Washington state actively hunted gray whales using poisoned-lance whaling and harpoon whaling with line and floats (O'Leary, 1984). In northeast Asia, aboriginal whaling was traced back as early as the first centuries AD in several locations from the Chukotka peninsula, Kamchatka and the northern sea of Okhotsk with a variety of techniques including harpoon whaling from skin boats with line and floats, and bay whaling on young

whales and calves with harpoon, poisoned-lance and nets (Krupnik, 1984). In most areas, aboriginal whaling almost disappeared following contact with American whalers in the second half of the 19th century, except in the Chukotka peninsula, where it was very active up to the 1960s. Today, the International Whaling Commission allows limited subsistence whaling on the eastern whale subpopulation for the nutritive and cultural needs of the native populations of the Chukotka Peninsula, with a quota set at 620 whales for five years, with a maximum of 140 whales per year (Reeves, 2002). The impact of early aboriginal whaling on the populations of gray whale remains unclear, especially in the absence of reliable quantitative information (O'Leary, 1984), but if abundance of whales has possibly been reduced in some way, the species' range has probably remained broadly the same.

Shore whaling was practiced from the mid-1850s to the early 1900s from 17 shore-based stations located all along the coast of California and Baja California, and operated by Portuguese immigrants from the Azores and Cape Verde. This activity took place from December to April when whales cruised up and down the coast in their migration between their southern calving bays and northern feeding grounds (Scammon, 1874; Starks, 1923; Sayers, 1984). Reeves and Smith (2010) estimated a total removal of 3,150 gray whales in the period 1854-1899 by California shore whaling.

In parallel, ship-based whaling developed, as American whalers from Long Island and New England found their way in the Pacific, sequentially discovering stocks of sperm, right and bowhead whales while exploring the northernmost grounds. Though not the whaler's primary target, gray whales were hunted both in winter on their breeding grounds along the coasts of California and Baja California ("lagoon whaling"), on their migration routes along the western coast of North America ("coastal" or "alongshore" whaling) and in their summer feeding grounds in Okhotsk Sea and the Arctic Ocean (Henderson, 1984; Reeves et al., 2010). This commercial activity began in 1846, with a bonanza period from 1854 to 1865 before its decline by the mid 1870's in the south and the mid 1880's in the Arctic (Henderson, 1984). Estimates of total removal of gray whales from this ship-based whaling industry, including struck but lost whales and non-American vessels' catches, range between 6,124 and 8,021 (Reeves et al., 2010), making it a particularly deleterious operation for gray whale populations.

The next whaling operation targeting gray whales in the North Pacific was the modern commercial pelagic whaling in the 20th century, different from the previous operations in that it is "conducted by one or more vessels that catch the whales and process them on board, or deliver the carcass to a floating processing plant", with "techniques and implements centered on the use of explosives and engines, involving deck-mounted cannons, explosive grenades, direct fastening to the whale, and diesel, gas or steam-powered boats and ships" (Mitchell & Reeves, 1980). Four main whaling nations

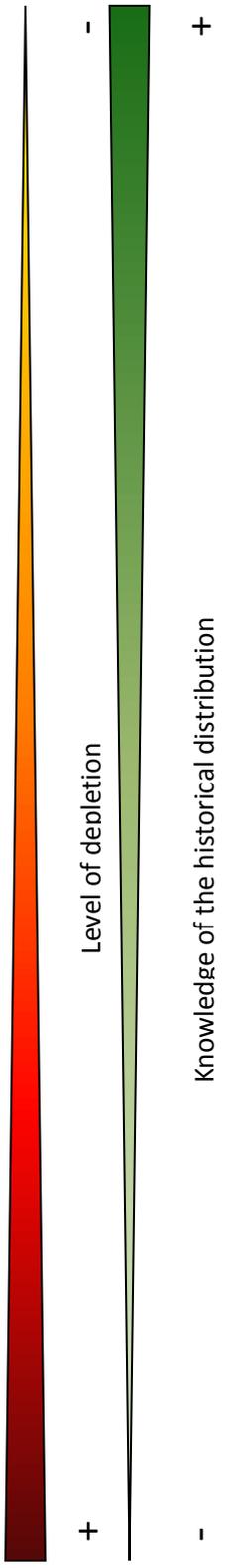
were involved in this operation: The United States, Japan, Norway and the Soviet Union. The western population in particular was greatly impacted by modern commercial whaling off Korea and Japan. By the early 1930's, it has likely been depleted to commercial extinction (Weller et al., 2002).

The International Whaling Commission banned commercial whaling for gray whales in 1946. From this date, the only gray whales caught were for aboriginal subsistence whaling in the Bering and Chukchi seas (ongoing) and catches under special scientific permits (about 320 individuals in the 1960's), as well as 138 whales caught during the illegal soviet whaling period in the 1960's. The western population now survives at a highly depleted state, being close to extinction and listed as Critically Endangered by the IUCN Red List. The eastern population in contrast is thought to have recovered at near carrying-capacity and is considered not threatened (but see Alter et al., 2007). Overall, the level of depletion of this species is very high, considering its total extirpation from the North Atlantic basin, and the occupation of only a reduced portion of its historical range in the western North Pacific, while our knowledge of its historical distribution in the North Atlantic is quasi-inexistent.

Box III-1. Summary of the history of exploitation and current conservation status of the three whale species considered.

On the right are the gradients of depletion (extent to which the species still occupies its original range or not) and of our knowledge of its historical distribution. The level of depletion is different from the IUCN Red List status, which describes the species' risk of extinction based on a set of criteria including population size and trends, geographic range, etc. LC: Least Concern, EN: Endangered, CR: Critically Endangered, EX: Extinct.

<p>Humpback whale <i>Megaptera novaengliae</i></p> 	<p>In addition to being exploited by natives throughout their range since antiquity, humpback whales have been a secondary seasonal target of American shore-based and ship-based open-boat whalers the late 18th century and much of the 19th century. They were also a target of the modern whaling industry until the mid-20th century and the IWC ban for commercial whaling. These successive centuries of exploitation have led humpbacks to a severe decline, with a global population of only a few thousand animals in the 1960s. The species has strongly recovered since, with an estimated world population of over 60,000 animals. However, concern remains for some small populations that don't show signs of recovery (Arabian Sea, western North Pacific and Oceania populations).</p> <p>References: (Mitchell & Reeves, 1983); (Clapham, 2009); (Reeves & Smith, 2002); (Reeves & Smith, 2006); (Reilly et al., 2008b)</p>	<p>IUCN Red List Status</p> <p>LC</p> <p>Subpopulations :</p> <p>Oceania EN</p> <p>Arabian Sea EN</p>
<p>Bowhead whale <i>Balaena mysticetus</i></p> 	<p>The Basques first hunted the bowhead whale in the North Atlantic in the 16th-17th century around Newfoundland and Labrador, later joined by other European nations around Svalbard, Davis Strait and Baffin Bay from the 1720s to the early 1900s.</p> <p>In the North Pacific, the Bering Sea bowhead population started to be sought in 1848, just a decade before the whalers turned to the Okhotsk Sea population around 1855. Bowheads were then pursued to the least accessible corners of the Arctic until the market collapsed in the early 20th century. All populations were severely depleted by that time and while significant recovery has been noted for some stocks, the Svalbard-Barents and Okhotsk Sea stocks show no evidence of recovery.</p> <p>References: (Burns et al., 1993); (Goldsworthy & Gales, 2008)</p>	<p>IUCN Red List Status</p> <p>LC</p> <p>Subpopulations :</p> <p>Bering-Chukchi-Beaufort Sea LC</p> <p>Okhotsk Sea EN</p> <p>Svalbard-Barents Sea CR</p>
<p>Gray whale <i>Eschrichtius robustus</i></p> 	<p>The gray whale was once found in the North Atlantic, as revealed by the recent finding of subfossil remains in Europe, supported by historical accounts of living gray whales from Iceland and New England. This population was extinct by the early 1700s, possibly as a result of human exploitation, though the exact causes of its extirpation remain unclear.</p> <p>In the North Pacific, gray whales have been hunted by natives on both the eastern and the western side. The succession of shore whaling in California from the mid 1850s to the early 1900s, pelagic whaling in the 19th century and modern commercial whaling in the 20th century resulted in the severe depletion of both the western and eastern Pacific stock. Since the end of commercial whaling, only the eastern North Pacific subpopulation has shown signs of recovery, while the western stock remains at only a small fraction of its past population level.</p> <p>References: (Jones et al., 1984); (Bryant, 1995); (Reilly et al., 2008c)</p>	<p>IUCN Red List Status</p> <p>LC</p> <p>Subpopulations :</p> <p>Western Pacific CR</p> <p>North Atlantic EX</p>



Challenges and Opportunities

Knowledge of these species' historical distribution is uneven and fragmented. As we go back in time, records of occurrence are both less abundant and less precise, as a result of whale taxonomy becoming progressively fuzzier (Cuvier, 1836), spatial localization becoming less accurate (e.g., longitude only began to be accurately recorded in ships at the end of the 18th Century), and written testimonies getting lost throughout history. Hence, the challenge is even greater for species that have been depleted early. For example, information on the distribution of the extinct population of gray whales in the North Atlantic is virtually inexistent, with only some literature accounts and a few fossil remains as witnesses of its past occurrence. The distribution of the Spitsbergen population of bowhead whale, already depleted by the late 17th century, suffers from the same uncertainty, as historical records covering the main period of its exploitation are very scarce (De Jong, 1983). The World Whaling History dataset provides a coverage of the presence and absence of these three species of whales in the whaling grounds and voyage routes used by American open-boat pelagic whalers, in the late 18th and 19th century. It represents an exceptional spatial and temporal coverage of the species distribution at this period (for a more detailed description of this dataset, see Chapter 2 and Smith et al., 2012). Just looking at the spatial distribution of sightings and catches provides vast amount of information about the distribution of gray, bowhead and humpback whales before they got depleted by commercial exploitation. However, spatial gaps remain, as some populations were already depleted by the 18th century and 19th century American whalers naturally missed these previously exhausted grounds (e.g. in the North Atlantic). As a result, despite its very high quality, this dataset only covers part of the original range of these species.

Correlative species distribution models (SDMs) represents a unique opportunity to bridge the gap in our knowledge of the distribution of species with heterogeneous history of exploitation. SDMs can be generated from relatively simple distributional data combined with readily available environmental information to produce a geographic description of the potential distribution of a species (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009a). Given their wide applicability, they have been described as the main predictive tool in ecology (Dawson et al., 2011; Bellard et al., 2012). SDMs can be extrapolated across space (e.g., for predicting the potential distributions of invasive species; Peterson & Vieglais, 2001; Ficetola et al., 2007) and across time (e.g., for predicting range shifts under future climate scenarios; Araújo et al., 2005; Thuiller et al., 2005; Garcia et al., 2012), sometimes on the basis of historical exploitation data (Torres et al., 2013).

Here, I will predict the potential global distribution of gray, bowhead and humpback whales from SDMs combining 18th-19th century whaling records with a set of environmental predictors. I will investigate the inputs of the models' predictions for our knowledge of these species' historical

distribution and I will build on these three case studies to investigate how species distribution models can be informative for species suffering various levels of depletion.

Material and Methods

Nineteenth century whaling data

I used historical whaling data extracted from a sample of logbooks of American whaling voyages (corresponding to the open-boat nonmechanized pelagic whaling operation), from the late 18th century to the end of the 19th century. The data were collected by Lt. Commander Matthew Fontaine Maury in the 1840s, Charles Haskins and his assistant Arthur C. Watson Townsend in the 1920s and the Census of Marine Life project between 2001 and 2010, as described in Smith et al. (2012). Each day's data included year, month and day, vessel location (latitude and longitude) and a separate record for each species of whale encountered, with number of whales struck and numbers processed on board (if any) as well as information on the days when none was reported (more information on this dataset in Appendix S1 of chapter 4). Data were gridded on a 1°x1° grid in which cells containing at least one positive occurrence were defined as 'presence' and the others as 'absence'. Cells with fewer than three observations were discarded to reduce the number of false absences (see Appendix S4 in chapter 4).

For humpback whale, I focused on data from December to March in the North hemisphere and June to September in the South hemisphere, between 40° and 40°S, to characterize its environmental preferences in winter, when it is on its calving and breeding grounds (Table III-2; Figure 1-A). Indeed, Humpbacks were mainly observed by American whalers in tropical waters in winter and spring, in their breeding grounds (Smith et al., 2012). The whalers rarely ventured south of 50°S and rarely visited the northeastern North Atlantic (Smith et al., 2012), and humpback whales' summer feeding grounds are thus underrepresented in the WWH dataset.

For bowhead and gray whales, I subsampled the dataset to consider the summer period (June to September), north of 45°N, when the individuals are on their feeding grounds (Table III-2; Figure III-2.A and Figure III-3.B). The habitat modeling of gray whales preferences in their calving bays would require a different, finer-scale, approach. As for bowheads, they were mainly accessible in their icy environment during spring and summer (Smith et al., 2012).

Table III-2. Number of presences (days when the species was seen or caught) and absences (days when the species was not seen nor caught) in the historical whaling dataset.

Species	Season	Period with sightings	Presence	Absence	Prevalence
Humpback whale	Winter	1792-1902	221	5825	3.7%
Bowhead whale	Summer	1845-1891	95	873	9.8%
Gray whale	Summer	1857-1885	50	918	5.2%

Environmental data

I considered environmental variables that are expected to explain well the preferences of gray whales and bowhead whales on their feeding areas. I considered both oceanographic and topographic variables, known to be correlated to the presence of whales : sea surface temperature SST, mixed layer depth MLD, depth DEPTH, distance to land LANDDIST and slope SLOPE (Hamazaki, 2002; Kaschner et al., 2006; Forney et al., 2012; Mannocci et al., 2013). Bowhead and gray whales are both zooplankton feeders: in their summer grounds, bowheads feed mainly on copepods and euphausiids (Lowry et al., 2004; Pomerleau et al., 2011), while gray whales main prey in their northern feeding grounds are benthic amphipods (Nerini, 1984). Primary productivity is known to be correlated with zooplankton biomass (Norberg & DeAngelis, 1997) and would have been an interesting variable to include in the model. However, satellite-derived primary productivity estimates in the Arctic were unsatisfying regarding the spatial coverage of areas of interest (partial coverage of the areas north of 70°N).

I chose the appropriate environmental datasets according to several criteria: those with a global coverage, across the largest period of time possible (in order to reduce the effect of inter-annual variability and leave only the long-term seasonal signal in the data), and which had fine spatial resolution (at least 1 degree resolution) (Table III-3).

MLD and SST were both extracted from NODS_WOA94 long-term monthly mean climatology provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their web site at <http://www.esrl.noaa.gov/psd/>. MLD was computed from climatological monthly mean profiles of potential temperature and potential density based on a density change from the ocean surface of 0.125 (sigma units) (Monterey & Levitus, 1997). NODS_WOA94 SST field calculation is described in Levitus & Boyer (1994). Although not contemporaneous with the whaling data used in the analyses, these two datasets provided a long-term climatology (averaged across the period 1900-1992), which I assume to be representative of the environmental conditions in the 20th century, with the benefit of

mitigating the effect of climate change by retaining only the strong seasonal signals in the data (Gregr, 2011).

Although humpback whales do not feed in their breeding grounds, they are nonetheless expected to respond to some of the same variables mentioned above, and others may be useful surrogates for relevant variables that cannot be directly measured. For consistence, I performed the model selection for the humpback whale with the same set of environmental predictors as for the other species.

SST and MLD were averaged over the summer months (June to September in the North hemisphere and December to March in the South hemisphere) for modeling the bowhead and gray whales' distribution (SST_{summer} MLD_{summer}). In contrast, I averaged SST and MLD over the winter period for the humpback whale model (SST_{winter} and MLD_{winter}).

Depth was derived from the NOAA-NGDC ETOPO1 Global Relief Model (Amante & Eakins, 2009), a 1 arc-minute global relief model of Earth's surface that integrates land topography and ocean bathymetry. The slope was then calculated from the depth with the slope function of the 'SDMTools' package (VanDerWal et al., 2014) in R 3.0.2. Distance to land at a 0.5°x0.5° resolution was retrieved from the AquaMaps dataset (Kaschner et al., 2008).

Environmental data were gridded at a 1° x 1° resolution, using the 'raster' package (Hijmans, 2014) in R 3.0.2 (R Development Core Team, 2013).

Table III-3. Environmental predictors used in the species distribution models.

The summer season corresponds to the averaged conditions from June to September in the North hemisphere and from December to March in the South hemisphere (and inversely for the winter season).

Variable	Season	Acronym	Period Averaged	Derived from	Reference
Sea Surface Temperature (°C)	Winter	SST_{winter}	1900-1992	NODC WOA94	Levitus & Boyer, 1994
	Summer	SST_{summer}			
Mixed Layer Depth (m)	Winter	MLD_{winter}	1900-1992	NODC WOA94	Monterey & Levitus, 1997
	Summer	MLD_{summer}			
Depth (m)	-	DEPTH	-	NOAA-NGDC ETOPO1	Amante & Eakins, 2009
Distance to Land (km)	-	LANDDIST	-	AquaMaps	Kaschner et al., 2008
Slope	-	SLOPE	-	derivative of DEPTH	-

Species distribution models

I generated Boosted Regression Trees (BRTs) to model the relationship between the species presence-absence data and the associated environmental predictors. BRTs are based on classification trees, avoiding assumptions regarding variable distributions and optimizing model predictions through iterative bootstrapping. They are able to fit complex nonlinear relationships between predictors and the response variable (Elith et al., 2008), and have been shown to perform among the best when evaluating presence-absence classification rates (Elith et al., 2006). Number of trees for each model were optimized using the 'dismo' (Hijmans et al., 2013) packages in R. Models were built with an interaction depth of 2 and shrinkage of 0.01 using a Bernoulli distribution. Variable selection was performed by removing predictors that contributed to less than 5% to the model.

Predictions of environmental suitability from the BRT were projected onto a 1°x1° grid, by assigning a probability value to each cell based on its environmental values and the models' fitted functions. The variable contribution to the model was given by its relative influence in percentage, measured by the number of time it was selected for tree splitting (Elith et al., 2008). To avoid extrapolating the predictions outside the range of the environmental conditions encountered in the dataset used to build the model, I only calculated the predicted suitability in cells for which the environmental values were contained in the 99% quantile interval represented by the original dataset.

The quality of predictions for the BRT was assessed through an internal 5-fold cross validation in which the relationship between occurrence data and the environmental variables was modeled using a training dataset (a random selection of 75% of the whaling data) and the quality of predictions was then assessed using a validation dataset (the remainder 25% of the whaling data), as advised by Fielding & Bell (1997). I repeated this calibration-validation procedure 5 times, and averaged the resulting measures of model performance. During the model validation process, a confusion matrix is generated, which records the number of true positive, false positive, false negative and true negative cases predicted by the model. Sensitivity and specificity are then derived respectively as the proportion of observed presences/absences that are accurately predicted as such. The threshold used to transform the predicted environmental suitability into a binary presence/absence response was defined by the value that maximizes the sum of specificity and sensitivity (Jiménez-Valverde & Lobo, 2007). The True Skill Statistics (TSS), calculated as (specificity + sensitivity – 1) and introduced by Allouche et al. in 2006, is a simple and intuitive measure to assess the performance of species distribution models. TSS ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random. An alternative method to assess model accuracy is the Receiver Operating Characteristic (ROC) curve (Fielding & Bell, 1997), which is obtained by plotting sensitivity against the corresponding proportion of false positives (equal to 1 –

specificity) for a range of threshold probabilities. From this curve, one can calculate the Area Under the ROC curve (AUC), which is a threshold-independent measure to assess the discrimination capacity of a model, or in other words, its ability to correctly distinguish between occupied and unoccupied sites (Pearce & Ferrier, 2000). Values of AUC from 0.5 to 0.7 depict a model with poor discrimination ability, whereas values above 0.9 indicate very good discrimination ability. Model validation was performed using the 'PresenceAbsence' package (Freeman & Moisen, 2008) in R 3.0.2. I used ArcGIS 10.0 to create the maps of predicted distribution. I applied a min-max stretch to the predicted environmental suitability, the minimum value being the threshold defining the species potential presence envelope. Fitted functions, providing information on the effect of each predictor on the response variable are given in Appendix S of this chapter.

Information about the current distribution of the three species was collected and mapped to be compared with the model's prediction of habitat suitability. The bowhead and gray whales current distributions were retrieved from the IUCN Red List website, which provides maps of the extent of occurrence (EOO) of all marine mammal species (IUCN, 2011). These EOO correspond to a general polygon including all the known areas of presence of the species, excluding cases of vagrancy. Because this approach doesn't discriminate well areas where the species may not be present, the species' ranges tend to be overestimated. It also considers the distribution of the species throughout the year, meaning that calving/breeding areas and migratory routes for the bowhead and gray whales are also represented in the EOO. Despite these limitations, EOO were mapped to bring context in the discussion and for comparison with the model predictions. The humpback whale being cosmopolitan, the EOO provided by the IUCN Red List for this species, is not informative for this analysis. The literature was reviewed to assemble our current knowledge of the winter distribution of the species, as a basis for identifying and mapping the current known breeding grounds for humpback whales at a global scale. Given the broad interest of scientists and managers for humpback whales, a large number of studies have been published that investigate their distribution. I considered recent reports reviewing the species status at a large spatial scale, which represent the most comprehensive collection of information on our current knowledge of the species (Calambokidis et al., 2008; Fleming & Jackson, 2011; International Whaling Commission, 2011b).

Results and discussion

Limitations and caveats

This modeling exercise is not without limitations, and potential caveats in the data and the models need to be discussed before the results can be interpreted¹.

First, despite the high quality of the whaling data in terms of spatial coverage and the amount of presence/absence records they contain, the dataset contains a number of biases which could affect the habitat model. A number of false absences might be included: visited cells where whales were present but not recorded. False absences are more expected in regions with low sampling effort, and effort is spatially very biased in the whaling dataset. However, sampling effort in this case was highly driven by presence, as whalers actively searched for and then spent most of their time in areas known to be good whaling grounds (e.g. for sperm whales, across the western Pacific at 30°N; for bowhead whales, north of 60°N in the North Pacific; for right whales, ca. 40° and 60°N in the North Pacific). Regions of low effort are therefore likely to reflect true absences outside of whaling grounds, especially for the bowhead whale, as one of the main target of the industry, for which whalers were willing to make huge efforts to find them. Gray and humpback whales were generally taken in a more opportunistic way and, in some grounds where whalers were focused on other species, it is more likely that the dataset includes false absences for these two species.

In addition, low effort may also correspond to areas where whaling conditions were less favorable, for example for geographic (e.g., regions further from whaling ports), climatic (e.g., areas of harsher winds and heavier sea states) or political reasons (e.g., zones of high conflict or outright exclusion). Furthermore, the data extracted by Maury and CoML likely included days when some whalers were not maintaining watch for whales or when sightings were not being recorded because of operational factors (e.g., when whales were being processed on board, or when the vessel was in transit between whaling grounds). Another possible source of false absences is a temporal bias in the spatial records. Indeed, although I have treated all data as corresponding to a uniform summer/winter season, there was variation across months in the distribution of both whales and whalers and whales could have been missed in some areas if the whalers were not visiting these areas at the right season.

¹ *Note: Most of the limitations mentioned in this paragraph are common to chapter 4, which is based on a similar modeling approach. I refer the reader to the discussion section and appendices of the 4th chapter for additional discussion on these issues.*

In contrast, false presences can also appear, resulting from location errors (e.g., incorrect coordinates) or identification errors (wrong species). I tried to reduce the number of false absences by considering only cells with at least three days of effort (hence reducing the chance of misidentifying a cell as an absence because of low sampling effort). The occurrence of false presences is probably limited by the ability of whalers to correctly identify the three species of whales considered. However, the fact that the bowhead whale was initially confounded with the closely related right whale *Eubalaena japonica* in logbooks, may have brought confusion in the identification of the two species in the overlapping part of their ranges.

I selected data corresponding to a particular season, assuming that the resulting dataset would correspond to a particular behavior (i.e. feeding in summer for the bowhead and the gray whales, breeding in winter for the humpback whale). However, all individuals from a population are not necessarily engaged in the same behavior at the same time, even within a particular season, and the selected data might capture migrating individuals, or, in the case of humpback whales, non-breeding individuals that are not aggregated in the usual calving grounds for the species. As these behaviors could not be differentiated in the whaling data, model predictions should rather be considered as informative of the environmental suitability for the species in summer/winter in general, including for marginal habitat where the species might not be strictly engaged in feeding/breeding.

The modeling approach relies on the geographic extrapolation of the relationship found between whale presence and their environment in an area, making the assumption that whales react in the same manner to their environment in geographically distinct areas. To limit the uncertainty associated with predictions made under new scenarios (Zurell et al., 2009), I limited the predictions to the environmental envelope sampled by whalers in the whaling dataset, ensuring that environmental conditions in areas where we predict high environmental suitability are represented in the dataset used to calibrate the model. However, other differences between areas might exist (e.g. interactions between environmental conditions, prey availability, species competition...), that I was unable to account for.

In addition to geographical extrapolation, the predictions were also extrapolated in time, with whaling data from the 18th-19th century associated with environmental conditions of the 20th century. Climatic variations, both long-term (e.g., warming since the end of the Little Ice Age; Mann et al., 2008) and short term (e.g., El Niño Southern Oscillation, Nicholls, 2008 ; Pacific Decadal Oscillation, Mantua & Hare, 2002) might be responsible for shifts in the species distribution, in ways I was unable to account for. A strong assumption is being made, that the use of a long-term climatology (MLD and SST averages over the period 1900-1992) mitigates these effects by keeping only the long-term, persistent seasonal signal in the data (Gregn, 2011).

For comparison purposes, I used the same environmental variables to build the species distribution models for the three species. However, to be applicable in a management context, such approach would benefit from a more dedicated review of the species environmental preferences, in order to select the most appropriate predictors for each species.

With these limitations in mind, I discuss the results from the species distribution models for the three species, emphasizing agreement and discrepancies between the predictions and our knowledge of the species distributions.

Humpback whale (*Megaptera novaeangliae*)

In winter, American whalers concentrated their efforts around the main whaling grounds for the most desirable species (e.g. for sperm whales around 0°N in the Pacific, for southern right whales around 40°S in the South Atlantic) and along the corridors between whaling grounds and the main ports (Figure III-1.A). Humpback whales were hunted throughout the vast majority of their known winter calving grounds, with exceptions in some areas where the whalers did not go (e.g. northeastern coast of Australia, Arabian Sea, Philippines). As humpbacks were only a secondary target of American open-boat whalers at a time when they were chasing several other whale species throughout the world's oceans, the prevalence of humpback in the whaling datasets is very low (3.7% of presences), which may reduce the model predictive performance (Barbet-Massin et al., 2012). Nonetheless, these absence data are useful to discriminate the non-suitable habitat for humpback in winter (e.g. pelagic habitat in the mid-ocean, cold waters).

Thirteen areas have been identified as current breeding/calving grounds for humpback whales (Figure III-1B, Table III-1). Seven of them are in the southern hemisphere, labeled A to G according to the IWC nomenclature (International Whaling Commission, 2011b), with some of them subdivided according to different history of exploitation and population genetics (e.g. stocks B1 and B2 on the west coast of Africa; International Whaling Commission, 2012). In the north hemisphere, three main breeding areas are currently identified in the North Pacific (the Hawaiian Islands, the eastern North Pacific and the western North Pacific; Acebes et al., 2007; Calambokidis et al., 2008; Rasmussen et al., 2012), and two in the North Atlantic (Wenzel et al., 2009; Fleming & Jackson, 2011). In addition, a resident population of humpbacks was identified in the Arabian Sea (breeding stock X; International Whaling Commission, 2011b; Minton et al., 2011).

The response functions provided by the BRT relating humpback whale occurrences and the selected environmental variables indicate a preference in winter for coastal, relatively warm (15°C-25°C) waters with a low depth of the mixed layer (Figure III-4.A in Appendix S2). The model predicts as suitable the known winter grounds for the species, but also a much larger area including most coastal

areas of mid tropical and tropical waters throughout the globe. There are two not mutually exclusive hypotheses to explain this pattern: 1) The model may be overestimating the breeding distribution of the species, as a result of the presence of occurrence data from non-breeding individuals in the whaling dataset, or because of missing environmental covariates to discriminate the conditions that make a suitable breeding ground . The coasts of southern South America or the coasts of eastern and western Australia, for example, are known migratory routes (International Whaling Commission, 2011a), suggesting that the model captures migratory habitat. 2) The known current breeding grounds may not represent all the historical and potential current grounds for the species. For example, repeated sightings in areas outside the main breeding grounds (e.g. in the Galapagos, Castro & Merlen, 2009, in the Gulf of Mexico, Jefferson & Schiro, 1997, off the coast of US mid-Atlantic states, Barco et al., 2002) raise a doubt on the existence of other grounds suitable for the species in winter.

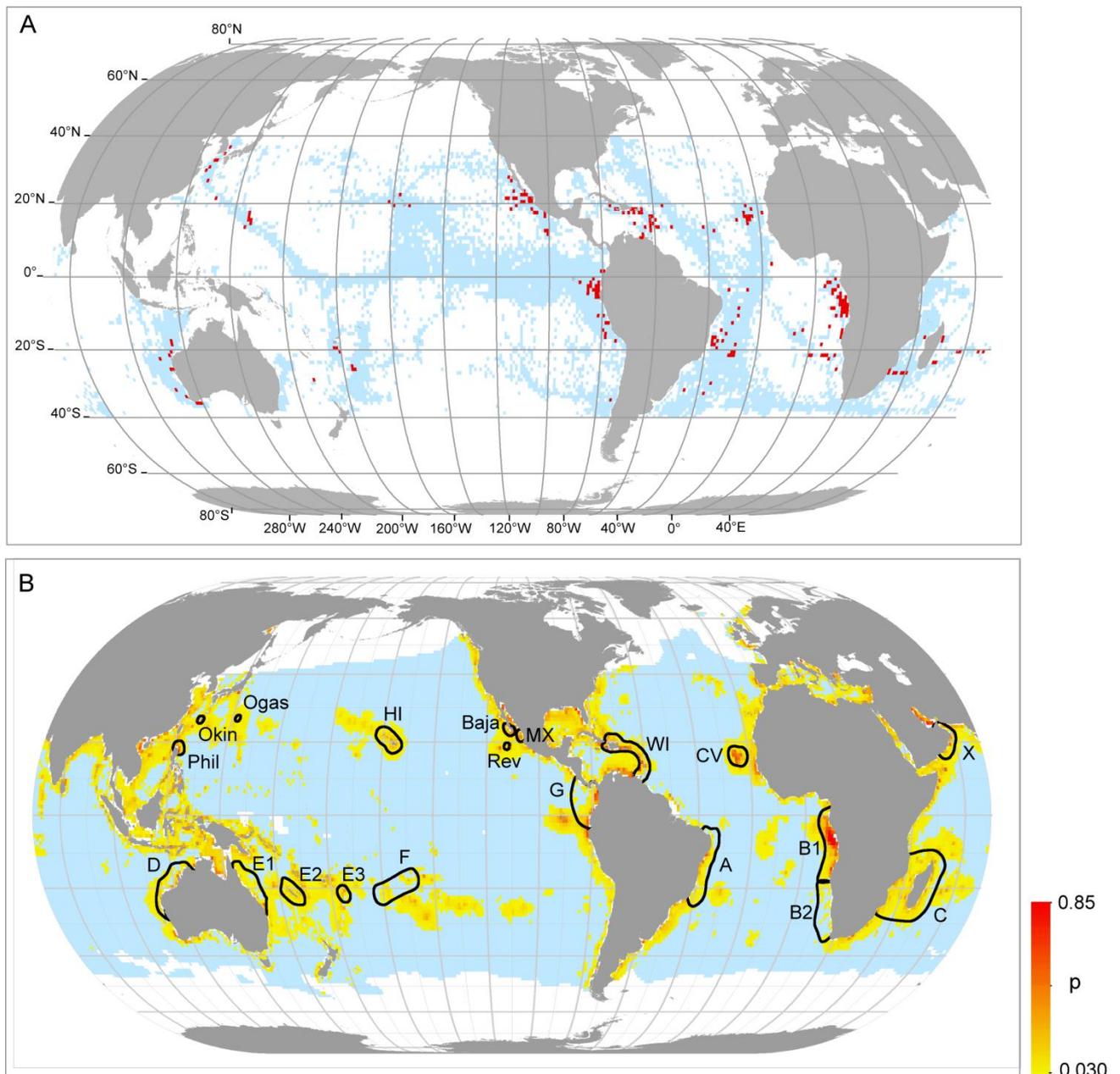


Figure III-1. Historical whaling data and model predictions for the global winter distribution of the humpback whale.

A) Historical distribution of humpback whales in winter (December to March in the North Hemisphere, June to September in the South Hemisphere), based on whaling records from the late 18th and 19th century, between 40°S and 40°N. Data include both presence (in red, where humpback whales were seen or caught) and absence records (blue, cells visited by whalers but where no humpback whales were reported in the examined logbooks); white cells were visited less than three times and were not included in the dataset used to train the model. B) Predicted environmental suitability from a species distribution model fitted to the historical records. Shades of red indicate progressively higher suitability as predicted by the BRT models (above the $p=0.030$ threshold); blue cells correspond to areas where the species is predicted as absent; white cells are areas for which no reliable predictions can be made. Black contours indicate current known breeding grounds for the species in winter (see text for details).

The model prediction for this species provides limited information, for two main reasons. 1) the global distribution of whaling data makes the model predictions very broad, which is coherent with our knowledge of the cosmopolitan distribution of the species but which is little informative for the management of the species at the stock level. A more spatially restricted analysis considering a particular stock of this species would certainly be more useful for management purposes at a medium or local scale. 2) The fact that the species is occupying most of its former range and has a well-known current distribution leaves little room for a model based on historical data to bring new information. Species distribution models built with current data would also be interesting to investigate the potentially suitable areas for the species today.

Nonetheless, some interesting information can be extracted from this modeling approach. First, it confirms what is known about the species preference in terms of habitat and its capacity to live in a wide variety of regions throughout the world. Then, it adds context to some hypotheses that were proposed for additional unknown breeding grounds for the species. An example of that is the hypothesis raised by Smith & Pike (2009), of a third breeding ground in the North Atlantic, in addition to the two well-known Cape Verde and West Indies grounds. This idea was based on early 20th century catches of females bearing nearly full-term fetuses off Finnmark, Norway (Ingerbrigtsen, 1929), suggesting the existence of an additional breeding grounds in the North Atlantic, given the difficulty for these whales to cover the very long distance to the closest known breeding grounds of Cape Verde (ca. 7 000 km). In addition, acoustic recordings of singing humpbacks in winter off the British Isles (Charif et al., 2001) and in the southern Norwegian sea (International Whaling Commission, 2002) bring further evidences of a wintering activity north of 50°N. Our model does not contradict this hypothesis, as suitable wintering habitat is predicted north of the current known breeding grounds, around the Canary Islands and the Azores, along the coast of Portugal and in the Mediterranean and Celtic seas. The model prediction also suggests that there is no suitable winter habitat for humpbacks in the central North Atlantic. In this particular case, the model prediction could prove useful, as there is yet little information to support Smith and Pike's hypothesis and to guide monitoring in the wide North Atlantic region. However, to bring further depth to the debate, this would deserve a North Atlantic-centered prediction, based on the relationship between breeding individuals and their environment in winter.

Other potential suitable regions are highlighted by the model prediction, and while I cannot rule out the possibility of the model inability to accurately predict the species winter habitat, some areas may deserve further investigation: In the Mediterranean Sea, occurrences of humpback whales are rare, but have increased recently. Only two sightings have been reported until 1989, but occurrence have apparently increased in recent times, with 9 new occurrences between 1990 and 2004 (Frantzis et

al., 2004). The emptiness of the Mediterranean basin in terms of cetacean species is puzzling, and while this remains speculative, the hypothesis that millennia of human activities may have led to the depletion of whale species in the Mediterranean basin is worth giving attention. Humpbacks could have effectively used the Mediterranean waters as wintering grounds before being depleted by human exploitation. In this case, the reappearance of individuals in the Mediterranean could be the result of a recolonization event, now that hunting pressure on the species has disappeared, rather than vagrancy. Humpback whales show a strong maternally directed fidelity for breeding sites (e.g. in the West Indies breeding grounds, Clapham & Mayo, 1987; Palsbøll et al., 1995) and it is possible that recolonization historical breeding grounds takes time because of the extinction by whaling exploitation of maternal lineages that showed fidelity to a particular site.

Two populations of humpbacks are endangered today, in the Arabian Sea and Oceania. In the Arabian Sea, which hosts a resident population of humpback whales, the model predicts highly suitable winter habitat in the Gulf of Oman and the Persian Gulf, suggesting that monitoring in this area would be interesting to increase our knowledge of the distribution of this endangered population. In Oceania, the model predictions suggest that the current winter grounds for the species are only a subset of the potential areas that the species could use in winter.

Bowhead whale (*Balaena mysticetus*)

In their summer journeys to the North Pacific, American open-boat whalers encountered bowhead whales at high latitudes, in the Northern Bering Sea, the Chukchi Sea and the Sea of Okhotsk (Figure III-2.A), in agreement our knowledge of the concentration of whales in these areas in summer (Bockstoce & Burns, 1993).

The selected BRT model explains 53.4% of the deviance and has good predictive power, with an AUC value of 0.93 and a TSS value of 0.74 (Table III-4 of Appendix S1). Fitted functions for the selected variables indicate that the species presence is mainly associated with shallow and cold waters (Figure III-4.B of Appendix S2). While the distribution of bowhead whales is generally driven by the boundaries of the ice cap (Moore & Reeves, 1993), I was unable to retrieve this variable for the 19th century. While this may be affecting the model prediction in the northernmost latitudes, the consideration of sea surface temperature in the model is likely to mitigate this limitation, as SST should be strongly correlated with the proximity of ice in high latitudes.

In the North Pacific, the model predicts the current summer feeding grounds in the eastern Beaufort Sea and to some extent the migration corridor through the Chukchi and northern Bering Sea. Predictions of suitable summer habitat in the eastern Bering Sea are not supported by current or historical summer occurrences of the species. This could be due to model limitations, but also raises

the possibility that this area is part of the potential distribution of the species in summer but is unused, due to environmental constraints or competition with right whales that are also feeding in the south eastern Bering Sea in summer (Shelden et al., 2005). In the Okhotsk Sea, the model is well supported by the southern boundary of the species' extent of occurrence, and by historical catches of this species that occurred in the northern Okhotsk Sea (Bockstoce & Burns, 1993).

When extrapolated to the North Atlantic, the model predicts suitable areas that are well within the IUCN extent of occurrence proposed for this species (Baffin Bay, Davis Strait, Hudson Bay, Svalbard and Barents Seas). This suggests the relevance of the modeling approach, confirming what is known of the species historical distribution based on historical catches of the species before it got depleted in these areas (Ross, 1993). However, there are some discrepancies between the model prediction and the extent of occurrence of the species, which need further discussion.

In general, the prediction tends to predict suitable summer habitat further south than expected from the extent of occurrence of the species (e.g. in the coasts of Labrador, Gulf of St Lawrence, northeastern coast of the US, Baltic Sea), which is even more dubious as the EOO also encompasses the distribution of the species in winter, when individuals are on their southern breeding grounds. Several non-mutually exclusive hypotheses, including model limitations due to missing covariates, climatic variations, etc. can be proposed to explain this result, but in some area, whaling history can shed light on this apparent inconsistency. The predictions along the coast of Canada and the Gulf of St Lawrence are reminiscent of historical records of Basque shore whalers hunting this species in the Strait of Belle-Isle and the Gulf of St Lawrence in the 16th and 17th centuries (Cumbaa, 1986; McLeod et al., 2008). The fact that bowhead whaling in this area likely occurred in winter rather than summer could suggest the model inability to discriminate unsuitable summer feeding grounds in lower latitudes. However, records from the late 18th century suggests that whales, probably bowheads, could still be caught in the ice-fields along the coast of Labrador as late as July (Reeves & Mitchell, 1986a), suggesting that the model predictions in this area are not irrelevant. Moreover, just as suggested for the prediction in the northeast Bering Sea, the possible competition with right whales on these summer feeding grounds might explain the absence of bowheads in these areas, even if they were potentially suitable for the species, and misidentifications between both species, especially in the early commercial whaling period might bring confusion in the interpretation of whaling records.

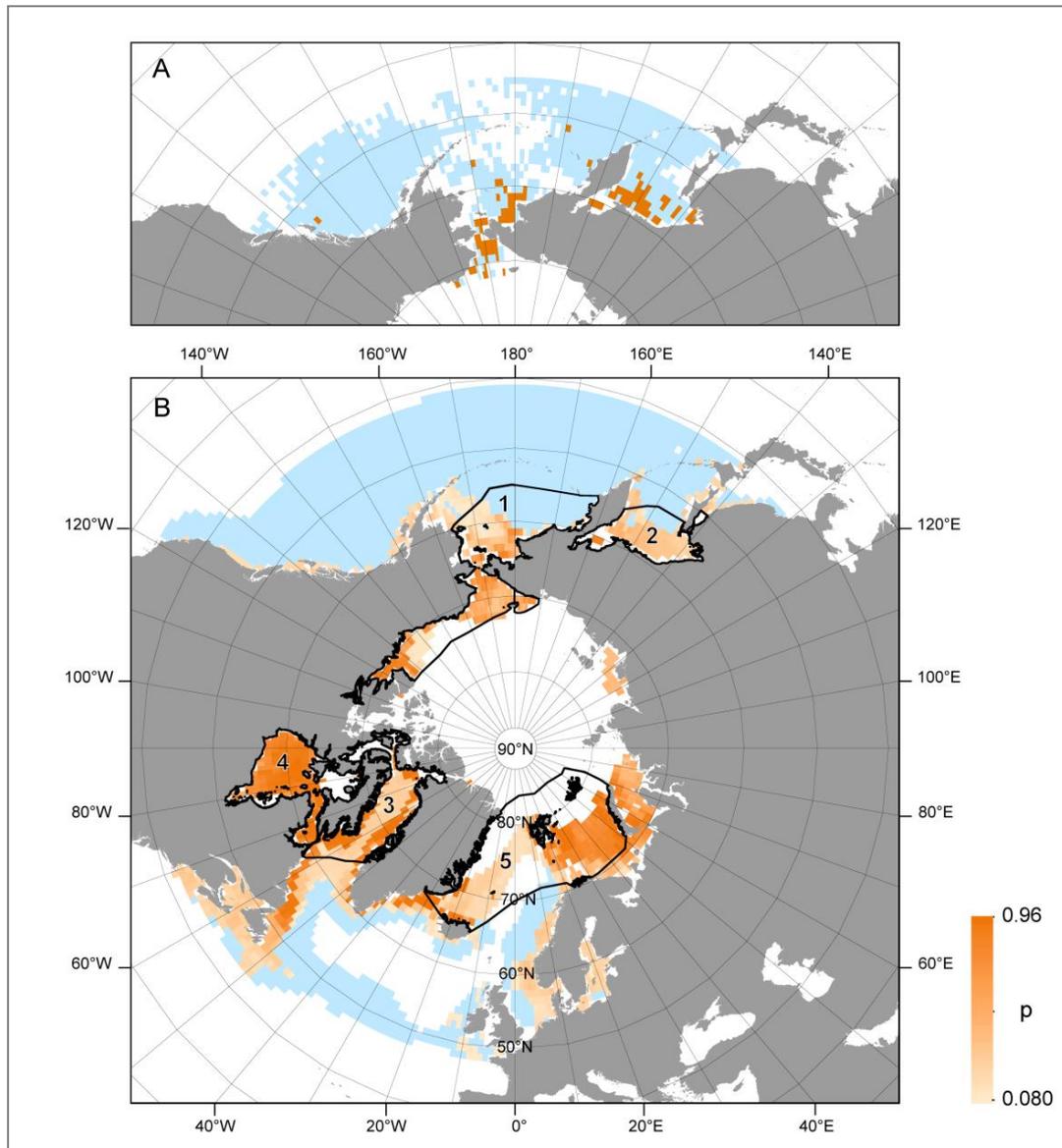


Figure III-2. Historical whaling data and model predictions for the summer distribution of bowhead whale.

A) Historical distribution of bowhead whales in summer (June to September), based on whaling records from the late 18th and 19th century, north of 45°N. Data include both presence (in orange, where bowhead whales were seen or caught) and absence records (blue, cells visited by whalers but where no bowheads were reported in the examined logbooks); white cells were visited less than three times and were not included in the dataset used to train the model. B) Predicted environmental suitability from a species distribution model fitted to the historical records. Shades of orange indicate progressively higher suitability as predicted by the BRT models (above the $p=0.080$ threshold); blue cells correspond to areas where the species is predicted as absent; white cells are areas for which no reliable predictions can be made. The IUCN Red List extent of occurrence, represented with a black contour line, shows the location of the 5 stocks recognized by the International Whaling Commission: 1. Bering-Chuckchi-Beaufort Sea; 2. Okhotsk sea; 3. Davis Strait-Baffin Bay; 4. Hudson Bay-Foxe Basin; 5. Svalbard-Barents Sea.

Hudson Bay is predicted as highly suitable for the species in summer. And while this is not contradicted by the species' extent of occurrence, current sightings and historical catches in the Hudson Bay-Foxe Basin are actually restricted to northwestern Hudson bay (Moore & Reeves, 1993; Reeves & Cosens, 2003), and there are no historical or recent evidences of the species being present in the south of the Bay in summer (Reeves et al., 1983). Here, the model exaggeration could be explained by the shallowness of Hudson Bay (mean depth = 125m) which drives the prediction towards high suitability, as the DEPTH variable contributes to more than 50% to the model prediction (Table III-4). This artifact is not necessarily representative of the true suitability of Hudson Bay, as the conditions in this area are mainly conditioned by wind and current-driven mechanisms that could not be included in the model (Prinsenber, 1986).

The predictions between Greenland and Spitsbergen, north of Iceland are well supported by the IUCN EOO for the species and by whaling catches in this area (Ross, 1993). The prediction extends further east, with suitable habitat predicted in the Kara Sea and Laptev Sea. While these areas are usually not considered as part of the bowhead range, evidences of the species presence, at least occasional (Moore & Reeves, 1993), suggests the existence of "either an eastern stock of bowheads in the Barents and Kara Seas or a part of the Spitsbergen stock which spent at least part of some years in these waters" (Reeves, 1980). The model predictions brings further support to this hypothesis, indicating that the habitat in this area is suitable for the species in summer, at least in regard to the environmental variables considered. Considering that the Spitsbergen stock of bowheads is listed as Critically Endangered by the IUCN Red List, this suggests that more attention should be given to the Kara Sea, which may represent suitable habitat for the species, and turn out as a key area for management and monitoring of this stock.

Overall, the model predictions are well supported by current and historical records of the species occurrence and, though possible model limitations should be kept in mind, raise the hypothesis that bowheads' suitable habitat extends further south along the coast of Canada and northeastern US and further east in the waters off northern Russia. In terms of management, the model predictions raise interesting hypothesis that could inform future monitoring for depleted populations in the North Atlantic.

Gray whale (*Eschrichtius robustus*)

The whaling data indicate that gray whales in the North Pacific aggregated in summer in the northern Okhotsk and Bering seas and southern Chukchi Sea, with no gray whale sighted south of 50°N, despite extensive sampling effort throughout the study area (Figure III-3.A).

Fitted functions provided by the BRT indicate a correlation between gray whale presence in summer and shallow, cold and coastal waters, with a mixed layer depth < 15m (Figure III-4.C in Appendix S2). Predictions in the North Pacific are consistent with our knowledge of the species current summer distribution, with identified feeding grounds in the northern Bering and southern Chuckchi seas for the eastern population (Braham, 1984) and off northeastern Sakhalin Island for the western population (Weller et al., 2002). The whaling data and the model prediction suggest areas of high suitability in the northern Okhotsk Sea, which is little supported by the current distribution of the species' in summer (Weller et al., 2002). Nineteenth century European and American whalers captured a large number of gray whales in these waters from the 1840s to perhaps the beginning of the 20th century (Henderson, 1984), suggesting that this area was an important historical feeding ground, which got heavily depleted by whaling. Predictions of suitable habitat in mid-latitude coastal areas are coherent with the fact that eastern gray whales occasionally feed along the North American Pacific coast during the summer (Braham, 1984; Nerini, 1984; Calambokidis et al., 2002).

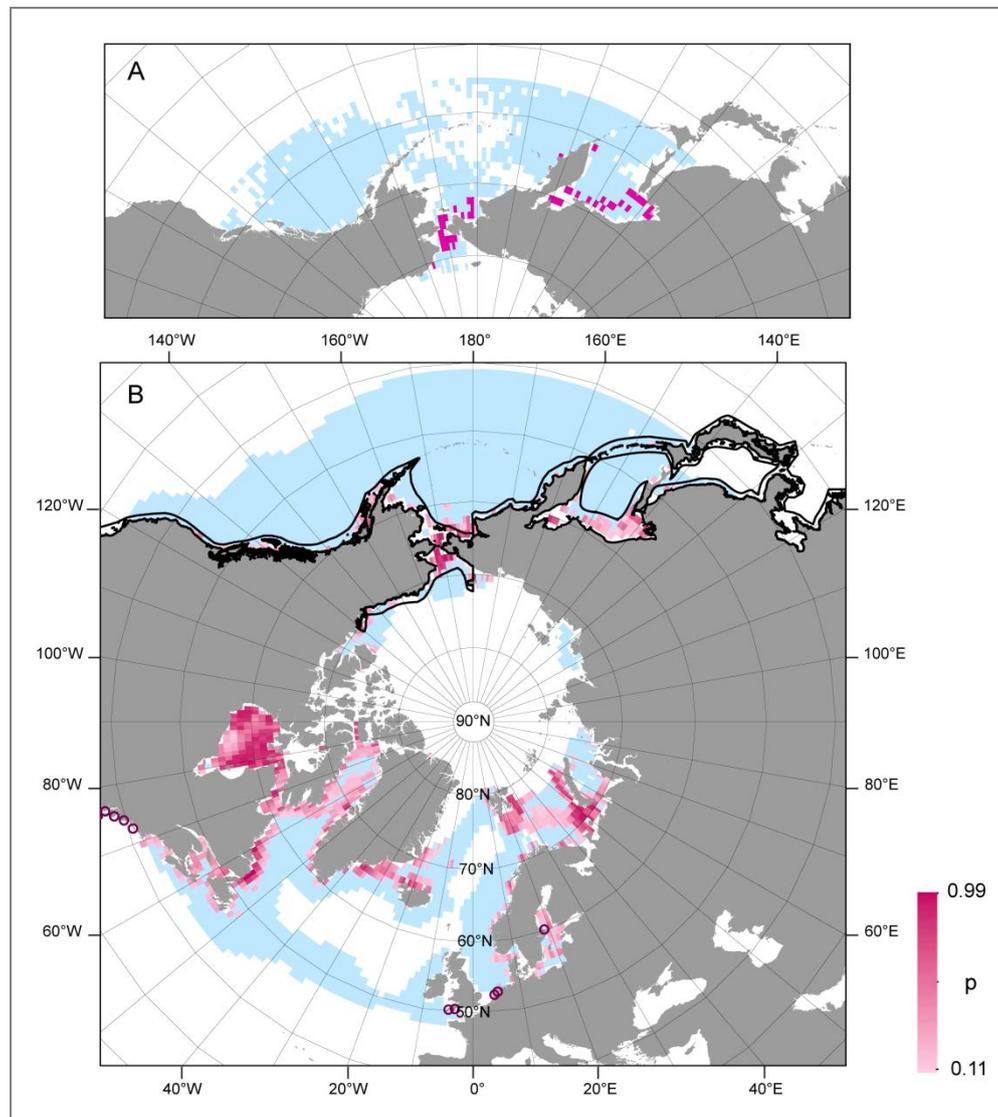


Figure III-3. Historical whaling data and model predictions for the summer distribution of gray whale.

A) Historical distribution of gray whales in summer (June to September), based on whaling records from the late 18th and 19th century, north of 45°N. Data include both presence (in pink, where gray whales were seen or caught) and absence records (blue, cells visited by whalers but where no gray were reported in the examined logbooks); white cells were visited less than three times and were not included in the dataset used to train the model. B) Predicted environmental suitability from a species distribution model fitted to the historical records. Shades of pink indicate progressively higher suitability as predicted by the BRT models (above the $p=0.11$ threshold); blue cells correspond to areas where the species is predicted as absent; white cells are areas for which no reliable predictions can be made. Purple dots in the North Atlantic represent historical records of the gray whale, as presented in the chapter 2. The IUCN Red List extent of occurrence is represented with a black contour line.

In the North Atlantic, the model's prediction provides a first hypothesis for the suitable habitat for the species in summer, which cannot currently be validated by historical occurrences for this species given their scarcity. Interestingly, this prediction is visually extremely similar to the results of a habitat model for the months of July to September based on observational data available from sightings along the eastern Pacific coast of North America and two environmental variables, bathymetry and sea surface temperature (unpublished; result maps available in National Institute of

Invasive Species Science, 2015). The predicted summer distribution of gray whales encompasses the location of only one subfossil remain in Europe, found on the coast of the Gulf of Botnia at Gräsö, Sweden. Other records for this species are located around 50°N in the eastern side and below 40°N on the western side of the North Atlantic, suggesting that they are more likely to correspond to the winter period, when whales migrate to their breeding grounds. Fossils are most likely to be found in these areas where the species would have come very close to shore, rather than in its summer distribution when gray whales have a slightly more pelagic behavior, even if they stay quite coastal throughout the year. Northernmost locations (Davis Strait, Hudson Bay, Greenland, north of Norway, Spitsbergen) are also the place where we are less likely to find fossils because of reduced sampling effort in these areas with a low density of people. Literature accounts of the presence of gray whales in Iceland (Lindquist, 2000b) and New England (Dudley's scrag whale) support the model prediction (Mead & Mitchell, 1984). Lindquist (2000) provides hypotheses for the distribution of North Atlantic gray whales, with a western population breeding along the coasts of North Carolina and Florida, an eastern population breeding between southern Portugal and Northwest Africa, both of them converging to summer feeding grounds around Iceland. The model suggests that gray whales may have used feeding grounds further north than Iceland, in Hudson Bay, Greenland, Spitsbergen and the Kara Sea. It is possible that the model is not capturing all the conditions constraining gray whales distribution in the northernmost latitudes. However, given known affinity of gray whales for arctic waters in the North Pacific, there is no reason to believe that the North Atlantic population would have avoided this habitat. Lindquist (2000) mentions a personal comment by Dr Krupnik in 1996 claiming that he had never come upon any reference to the presence of gray whales in the Barent and Kara Seas (Lindquist, 2000b). In the light of new information presented here about the potential suitable habitat for this species in the North Atlantic, additional effort could be spent to look for archaeological evidence of the species' presence in these northernmost latitudes.

In addition, it would be interesting to model the winter distribution of gray whales, to test the hypothesis that this species was accessible to hunters from coasts on both sides of the Atlantic. Information on the environmental conditions encountered by gray whales on their Californian calving grounds would be the most suited for building this model. However, these correspond to only two calving lagoons, and the locations of breeding grounds for the western Pacific population remain unknown, limiting the geographical and environmental coverage of the data used to calibrate the model.

The singular event of a gray whale sighting in the Atlantic in 2010 raised the possibility of the existence of a passage between the northern Pacific and the northern Atlantic (Scheinin et al., 2011). Further analyses of the potential for dispersal of the species between the Pacific and the North

Atlantic, based on ancient DNA analyses, radiocarbon dating and predictive habitat modeling, suggest that an expansion of the species beyond its currently realized range is possible (Alter et al., 2015). If this reveals true and an event of recolonization of the North Atlantic through the Arctic Ocean is made possible, such modeling exercise would prove extremely useful to identify potential suitable grounds and understand the potential for recovery of this species in its former North Atlantic range.

Interest of the modeling approach

As the shifting baseline phenomenon is limiting our perception of the human impacts on species' distribution and the options we have for their recovery in the future, habitat models are an interesting tool to inform and challenge our perception of the distribution that the species used to have before human exploitation. The applications of this approach for management purposes, as highlighted in this chapter, range from guiding future research in the history of exploitation of the species (e.g. for the extinct population of gray whale in the North Atlantic), identifying suitable that the species could recolonize (mostly for the bowhead whale today or for the gray whale too if individuals from the North Pacific manage to reach the North Atlantic through the northern passage; Scheinin et al., 2011), or informing current management monitoring for depleted populations (e.g. for the Spitsbergen population of bowhead whale).

However, the interest of its habitat modeling approach varies according to the level of depletion of species, and the knowledge we have of their pre-exploitation distribution.

The prediction tends to be more informative for species that got depleted in a substantial part of their original range before the commercial exploitation period in the 18th-19th century, as spatial extrapolation of the prediction can fill the distributional gaps in areas where the species is depleted. This situation is illustrated by the bowhead and gray whales, which were severely exploited in the North Atlantic before the 18th century, and remain severely depleted today, with the gray whale having even been extirpated from the North Atlantic. For these species, the model's prediction brings valuable hypotheses for their pre-exploitation distribution. In contrast, the recovery of the humpback whale throughout its range makes it a poorer candidate for this modeling approach, as the current and historical distributions are comparable. Nonetheless, even for this species, the model's prediction provides interesting hypotheses for the location of unknown breeding grounds in the North Atlantic (Smith & Pike, 2009).

The level of knowledge that we have of these species' historical distribution determines also the interest of using habitat models to reconstruct their pre-exploitation distribution. Indeed, while predictions for the humpback whale can be easily validated - or invalidated – by our knowledge of

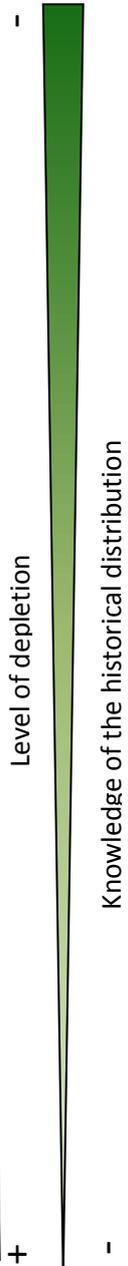
the species current and historical distribution, the validity of the model's prediction for the gray whale cannot be told, as there is virtually no historical occurrence data to support the predicted distribution. In between, the general knowledge that we have of the bowhead's history of exploitation is useful to validate the model prediction in areas where it was hunted.

As a result, the interest of the modeling approach for these three species varies according to a trade-off between their level of depletion and the knowledge we have of their historical and current distribution, as emphasized in Box III-2.

This discussion is based on just three species, which differ in other ways than their level of threat (e.g. range size, abundance, migration behavior, diet) and the lessons learned from this exercise in terms of management implications should not be generalized to other cases without many precautions. Each of these three species would deserve a more thorough effort to review their environmental preferences in order select the most appropriate covariates and provide a more comprehensive description of their potential suitable habitat, and a dedicated search for historical records of occurrence to validate the model predictions. For the gray whale, which was extirpated from the North Atlantic before formal scientific records were collected, the task of finding more evidences of its historical distribution will reveal very difficult. For the bowhead in contrast, a thorough review of historical accounts of occurrence of the species, in particular those associated with its exploitation, would be worth performing to validate the model prediction.

Box III-2. Summary of the models predictions and relevance of the modeling approach for the three whale species considered.

	Summary of findings	Relevance of the modeling approach
<p>Humpback whale <i>Megaptera novaeangliae</i></p> 	<p>The model predicts suitable winter habitat off most coastal waters between 40°N and 40°S, describing all the potential distribution of the species in winter rather than just its breeding/calving grounds.</p>	<p>LOW</p> <p>The low level of depletion of the species and the fact that we have good knowledge of its historical distribution gives limited value to a modeling approach based on historical whaling data.</p> <p>However, some insights were provided about the location of a hypothetical breeding ground in the North Atlantic, suggested by Smith & Pike (2009).</p>
<p>Bowhead whale <i>Balaena mysticetus</i></p> 	<p>The model prediction extends further than what is known of the current distribution of the species, especially in the North Atlantic, where suitable habitat for the species is predicted further south along the coasts of Canada and northern US and further east, in the Kara and Laptev Seas.</p>	<p>HIGH (North Atlantic)</p> <p>The model prediction highlights our possibly biased perception of the historical distribution of the species, and provides insights for current management and monitoring of the depleted populations.</p>
<p>Gray whale <i>Eschrichtius robustus</i></p> 	<p>The predicted habitat in the North Pacific is supported by the current distribution of the species. In the North Atlantic, the model provides the first reconstruction of the species summer distribution before it got extinct: the suitable habitat is located in a coastal band along the shore of northern US and Canada, Greenland, Iceland, the Baltic Sea, Norway, Spitsbergen and Kara Sea.</p>	<p>MEDIUM (North Atlantic)</p> <p>Given the level of depletion of the species, and the possibility of a recolonization of the North Atlantic through the northern passage, there is a strong interest of using habitat modeling predict suitable habitat for the species.</p> <p>However, predictions cannot be validated with historical occurrence data of the species, which are virtually inexistent.</p>



Conclusion

The spatial distribution of whaling records is informative by itself to investigate the historical distribution of depleted species (Smith et al., 2012). But using these historical data in a habitat modeling context adds another level of information, by extrapolating the prediction of suitable habitat in areas that were not sampled by the whalers and/or where the species is not present today. However, the interest of this approach varies according to the level of depletion of the species considered and to our knowledge of its historical distribution.

On one hand, the interest of using a modeling approach to “fill the gaps” in the distribution is higher for depleted species, for which extrapolation is necessary, than for species that are supposedly extant throughout their historical range. On the other hand, a minimum level of knowledge of the species historical range is necessary to validate the model’s prediction, at least qualitatively, to ensure that the prediction is relevant.

In response to this trade-off between level of depletion and level of knowledge, I argue that this habitat modeling approach is most relevant for species that were depleted in part of their range, and for which we have at least qualitative information of where it used to be found, in order to validate the model’s prediction.

In order to make the best of habitat modeling approaches to inform the management of depleted species, an effort should be made to collect historical occurrence data and information on the historical exploitation of species to be able to validate the models’ predictions.

In the next chapters, I present such an analysis for a species that meets the two conditions of high spatial depletion and availability of information regarding its history of exploitation: the North Atlantic right whale *Eubalaena glacialis*.

Appendix

Appendix S1. Model selection, performance and validation

Table III-4. Selected variables, performance and validation parameters of the species distribution models.

Area Under the Receiver Operating Characteristic Curve; TSS = True Skill Statistics; Threshold = value used to transform the predicted probability of presence into a binary presence/absence response (defined as the value which accurately predicts as “presence” 95% of the presences contained in the training dataset)

Species	Variables (% contribution)	Number of trees	Deviance explained	AUC	TSS	Threshold
Humpback whale	LANDDIST (33.8) MLD _{winter} (27.7) SLOPE (16.5) SST _{winter} (13.3) DEPTH (8.7)	1950	33.1%	0.81	0.48	0.030
Bowhead whale	DEPTH (54.9) SST _{summer} (25.7) MLD _{summer} (13.3) SLOPE (6.1)	550	53.4%	0.93	0.78	0.080
Gray whale	DEPTH (29.7) MLD _{summer} (27.9) SST _{summer} (23.6) LANDDIST (12.0) SLOPE (6.8)	950	69.5%	0.96	0.86	0.11

Appendix S2. Fitted functions of the species-environment relationships produced by the BRT

Fitted functions, although not perfect representations of species-environment relationships, show the effect of each predictor on the response variable and provide valuable information on the characteristics of the habitat preferred by species. The relative influence of each variable, indicated as a percentage in Figure III-4, is measured by the number of times this variable is selected for tree splitting (Elith et al., 2008). The distribution of data across the variable gradient indicated on the x-axis, in deciles, gives an indication of our confidence in the shape of the response curve along the environmental gradient. This information is particularly important to assess the quality of predictions in the context of model extrapolation across ocean basins.

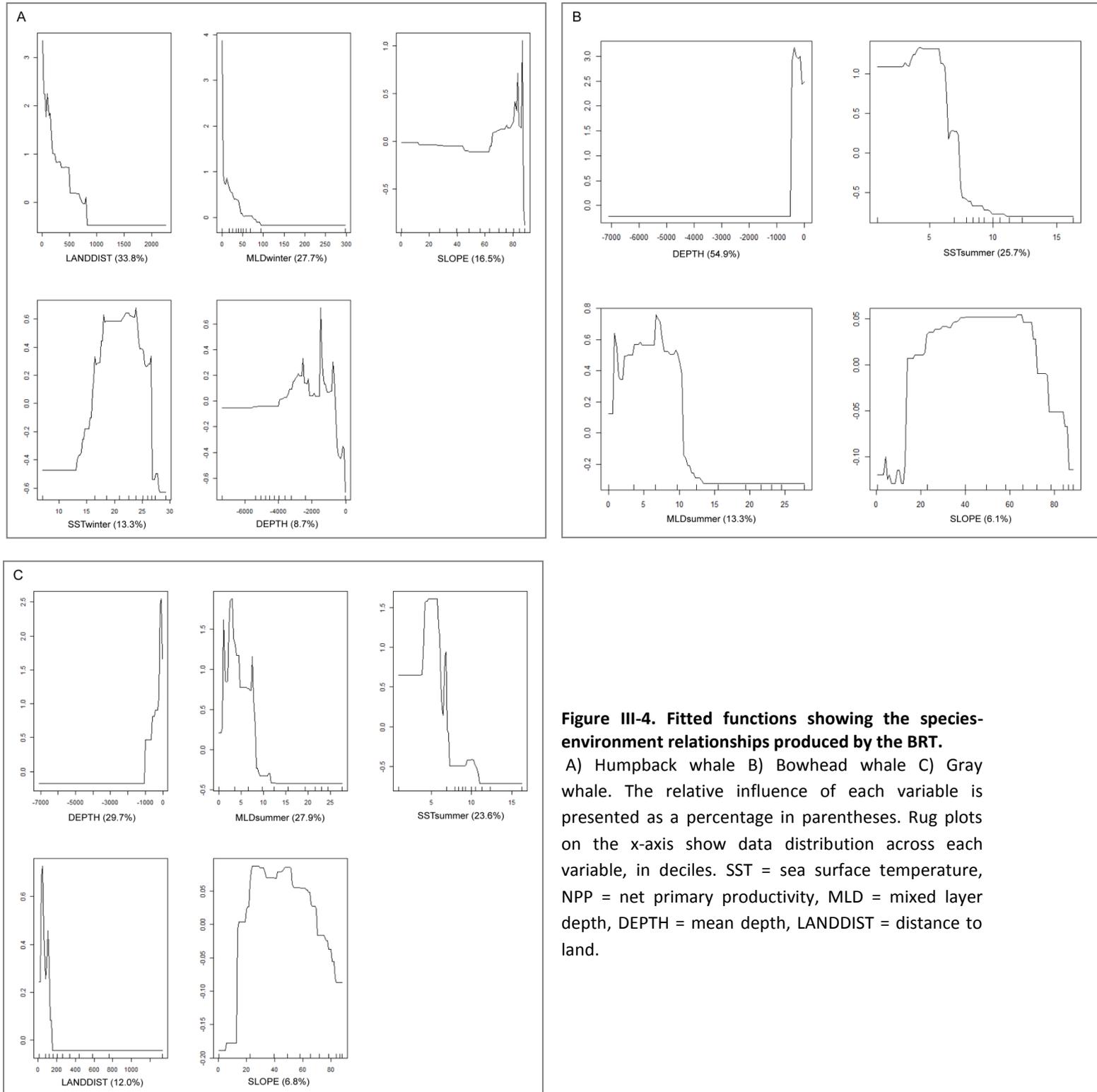


Figure III-4. Fitted functions showing the species-environment relationships produced by the BRT.

A) Humpback whale B) Bowhead whale C) Gray whale. The relative influence of each variable is presented as a percentage in parentheses. Rug plots on the x-axis show data distribution across each variable, in deciles. SST = sea surface temperature, NPP = net primary productivity, MLD = mixed layer depth, DEPTH = mean depth, LANDDIST = distance to land.

CHAPTER IV

**HISTORICAL SUMMER DISTRIBUTION OF THE ENDANGERED
NORTH ATLANTIC RIGHT WHALE (*EUBALAENA GLACIALIS*): A
HYPOTHESIS BASED ON ENVIRONMENTAL PREFERENCES OF
A CONGENERIC SPECIES**

IV. Historical summer distribution of the endangered North Atlantic right whale (*Eubalaena glacialis*): a hypothesis based on environmental preferences of a congeneric species

Adapted from:

Sophie Monsarrat, M. Grazia Pennino, Tim D. Smith, Randall R. Reeves, Christine N. Meynard, David M. Kaplan, Ana S.L. Rodrigues. (2015) Historical summer distribution of the endangered North Atlantic right whale (*Eubalaena glacialis*): a hypothesis based on environmental preferences of a congeneric species. *Diversity and Distributions*. DOI: 10.1111/ddi.12314

Abstract

The North Atlantic right whale (*Eubalaena glacialis*) is one of the world's most threatened whale species. It was previously widespread in the North Atlantic, but after centuries of hunting only survives as a small population (c. 500 individuals) off eastern North America. Because its exploitation began before formal records started, information about its historical distribution is fragmentary. We aim to obtain a plausible reconstitution of the historical distribution of North Atlantic right whales (*Eubalaena glacialis*) in their summer feeding grounds. We linked historical records of North Pacific right whales (*E. japonica*; obtained from 19th century American whaling voyage logbooks) with oceanographic data to generate a species distribution model. Assuming that the two species have similar environmental preferences, the model was projected into the North Atlantic to generate probabilities of presence for North Atlantic right whales. The reliability of these predictions was assessed by comparing the model results with historical and recent records in the North Atlantic. Our model predicts that the North Atlantic right whale's summer range have occupied a wide continuous band from the eastern coast of North America to the North Cape in Norway, mostly offshore. This is well supported by historical and recent records, although not by the current main summer grounds in the Bay of Fundy, Gulf of Maine, and Scotian Shelf. These results highlight possibilities for additional research both on the history of exploitation and on the current summer distribution of this species. In particular, better survey coverage of historical whaling grounds could help inform conservation efforts for this endangered species. More generally, this study illustrates the challenges and opportunities in using historical data to understand the original distribution of highly depleted species.

Introduction

The North Atlantic right whale (NARW, *Eubalaena glacialis*) is a migratory species that feeds during the summer at high latitudes, and migrates in the winter to calve in more temperate coastal waters (Kenney et al., 2001). It is thought to have occurred previously as at least two populations (eastern and western Atlantic), although genetic analyses suggest they were not genetically differentiated (Rosenbaum et al., 2000b). Its commercial exploitation spanned over a thousand years, first by the Basques (Aguilar, 1986), then by the Dutch, English, Americans and other nationalities, as one of the most desirable targets of the 17th - 19th centuries whaling industry (Reeves et al., 2007). By 1750 NARWs were considered commercially extinct (Allen, 1908), but as the few remaining individuals continued to be opportunistically taken by whalers, the species became close to biological extinction before it was given full legal protection in 1935 (Reeves et al., 2007). Today, it is classified as Endangered by the International Union for Conservation of Nature's Red List of Threatened Species (Reilly et al., 2012). There are currently around 500 right whales in the western North Atlantic (Pettis, 2013). In the eastern Atlantic, they are considered functionally extinct, with only a few records in the past 50 years (Reilly et al., 2012).

Understanding the historical pre-whaling distribution of NARWs can shed light not only on the impact of past hunting, but also on the potential for recovery now that the main historical threat has been eliminated. However, given the ancient history of exploitation, data on this species' historical distribution are very fragmented, with ancient observations plagued by taxonomic and spatial uncertainty. As we go back in time, it becomes more difficult to identify records to species, as a combination of less detail and fuzzier whale taxonomy (Romero, 2012b). Older records also often have little geographic precision, particularly those corresponding to summer occurrences. Indeed, whereas right whale exploitation in the winter mainly targeted females and calves in calving bays or along their coastal migration routes, summer whaling was not necessarily coastal. With methods for accurately measuring longitude at sea only available from the late-18th Century, earlier offshore records are scarce. Even today, a bias remains towards coastal occurrences, with the bulk of monitoring effort on the eastern North American coast (Winn et al., 1986; Pettis, 2013; Whitt et al., 2013).

As seen in the previous chapter, correlative Species Distribution Models (SDMs) are a useful tool to compensate for the limited knowledge we have of the historical distribution of a species (Chapter 3). In a conservation context, they can help identify priority areas for additional sampling of rare species (e.g. Engler et al., 2004; Guisan et al., 2006), or support conservation planning efforts (Rondinini et al., 2006). SDMs have even been used specifically to guide management decisions affecting

threatened whale populations (e.g. Keller et al., 2012; Mannocci et al., 2013; Bombosch et al., 2014; Gowan & Ortega-Ortiz, 2014), sometimes on the basis of historical exploitation data (Torres et al., 2013). SDMs have been extrapolated across species (e.g., to identify areas likely to harbor still undescribed species; Raxworthy et al., 2003). The North Pacific right whale (NPRW, *Eubalaena japonica*), was also nearly driven to extinction by whaling, but the history of its exploitation is quite different. Despite some ancient whaling (Omura, 1986; Huelsbeck, 1988; Lee & Robineau, 2004), the bulk of its exploitation occurred in relatively recent times, mainly in the mid-19th century (Josephson et al., 2008). Whaling took place across the entire summer range, as American pelagic whalers explored the entire North Pacific. This particular episode of the history of whaling is well documented in the logbooks of American whaling ships (Smith et al., 2012), which thus provide a unique snapshot of the summer distribution of this species prior to its severe depletion.

These two species of right whales have a similar feeding behavior, being both slow cruisers and specialist copepods filter feeders (Kenney, 2002), sharing the same body morphology in adaptation to this particular diet (Woodward et al., 2006). In fact, for lack of evidence of significant differences, they were long considered a single species (Rice, 1998), and only recently distinguished through genetic analyses (Rosenbaum et al., 2000a; Sasaki et al., 2005). Phylogenetically related species often share the same ecological traits that affect how their distributions relate to environmental conditions (Wiens et al., 2010). Historical occurrence data for the NARW are too deficient to generate a basin-wide SDM. But if these two species share similar environmental preferences, data from the well-documented historical summer distribution of the NPRW can inform the little-known historical feeding grounds of the North Atlantic species.

Here, we predict the potential summer distribution of NARWs from a SDM incorporating environmental data and whaling records of NPRWs, assuming that the two species select the same type of environments. We then investigate how informative such predictions are by discussing whether they are supported by historical records in the North Atlantic.

Material and Methods

Historical records of North Pacific right whales

Distribution records of NPRWs were obtained from 19th and early 20th century logbooks kept aboard American offshore whaling ships (Maury, 1852; Townsend, 1935; Smith et al., 2012). Logbooks provide information on the date, location and species of whales seen or caught, as well as information on the days when none were reported. We examined records of NPRW presence and

absence in summer (June to September) north of 20°N, obtained from a sample of these logbooks (Smith et al., 2012). The dataset included c. 46,000 point records, including c. 4,400 presences, between 1819 and 1904 (91% of presence records from 1840 to 1850). Point records were gridded at a 1° x 1° resolution, excluding grid cells with fewer than three observations to minimize the effect of false absences (Appendix S4). We tallied the number of observations of right whales and the number of observations where no right whales were reported. The sampling effort was 2176 grid cells, of which 611 were presences. See Appendix S1 for details.

Environmental data

During the summer months, right whales are actively engaged in feeding, and their distribution is believed to be mostly driven by the distribution of their prey, mainly copepods (Nemoto, 1970; Murison & Gaskin, 1989; Mayo & Marx, 1990). No dataset is currently available on the distribution of copepods at a global scale, but other oceanographic and topographic variables correlated to their distribution can be used (Rutherford et al., 1999; Friedlaender et al., 2006; Gregr & Coyle, 2009).

We considered three climate variables – Sea Surface Temperature SST (Norberg & DeAngelis, 1997; Rutherford et al., 1999; Gregr & Coyle, 2009), Mixed Layer Depth MLD (Baumgartner & Mate, 2003) and Net Primary Productivity NPP (Norberg & DeAngelis, 1997) – and three bathymetric variables – depth DEPTH, slope SLOPE and distance to land LANDDIST (Hamazaki, 2002; Kaschner et al., 2006; Gregr, 2011; Torres et al., 2013). They were selected for being known to be correlated with the presence of right whales and/or copepods in summer (see Appendix S2). SST, MLD and NPP were averaged over the summer months (June to September) to capture the environmental conditions encountered during the main feeding period of NPRWs (Clapham et al., 2004a). A long-term climatology was obtained by averaging SST and MLD over almost the entire 20th century (1900-1992) and for NPP, which relies on more recent satellite data, over the period 1998-2007. Environmental data were aggregated at a 1°x1° resolution, using the ‘raster’ package (Hijmans, 2014) in R 3.0.2 (R Development Core Team, 2013) to match the occurrence data.

Species distribution modeling

We used Boosted Regression Trees (BRT, Elith et al., 2008) to combine environmental data with NPRW historical records to generate predictions of the environmental suitability for right whales in the North Atlantic. We performed a formal training of BRT models using the ‘caret’ package in R (Kuhn, 2008). The ‘train’ function uses resampling to evaluate the effect of model tuning parameters on performance, and chooses the "optimal" model across different parameters. The caret package showed an important increase in accuracy from interaction depth 1 to 2, but small benefit above 2, and we opted for keeping the models simpler and easier to interpret. The model was built with the

following parameters: 5650 trees, interaction depth of 2 and shrinkage of 0.01, using a Bernoulli distribution. Fitted functions and relative influence of each variable, measured by the number of times this variable is selected for tree splitting (Elith et al., 2008), are presented in Appendix S3. Predictions of environmental suitability from the BRT were mapped on a 1°x1° grid in the North Pacific and the North Atlantic, by assigning a probability value to each cell based on its environmental values and the model's fitted functions. Before predicting into new areas, we eliminated cells with environmental values outside the range used to calibrate the models. The envelope of predicted presence was defined by applying a threshold which maximizes the sum of sensitivity and specificity (defined respectively as the proportion of accurately predicted absences/presences) (Jiménez-Valverde & Lobo, 2007). Statistics on classification rates were then calculated to check on the predictive ability of the model within the calibration area by performing a 5-fold cross validation with a training and test dataset (a random selection of respectively 75% and 25% of the whaling data). The area under the receiver operator curve (AUC) (Pearce & Ferrier, 2000) and the True Skill Statistics (TSS) (Allouche et al., 2006) were used to evaluate the model in this context (Appendix S3).

I refer the reader to the Method section in Chapter 3 for more details on the calibration and validation process for the BRT, which are similar in both analyses.

To test the extent to which the modeling assumptions affect the results, we also generated a SDM using a Generalized Additive Models (GAMs; Hastie & Tibshirani, 1986). Results are similar to those of the BRT model (see Appendix S4), and are not further discussed.

Historical records of North Atlantic right whales

We reviewed the literature for confirmed or likely records of NARWs up to 1950, known or strongly suspected to have occurred between June and September. We concentrated on secondary sources reviewing the history of whaling by the main people known to have exploited right whales in the North Atlantic (Spanish and French Basques, Norse, Americans, English and Dutch), complemented by selected primary sources. We focused on records for which there was high confidence in species identification and high spatial precision (close or within 1°), but we have also included records with some taxonomic ambiguity (in particular, risk of confusion with bowhead whales *Balaena mysticetus*) as well as some records for which location was less precise. For further context, we also mapped recent records (post-1950) outside the main areas where the species is currently found. Data were entered into a database capturing each record's location, time, spatial/taxonomic uncertainty and sources.

The resulting dataset is not of sufficient quality for a quantitative validation of the model's predictions in the North Atlantic. It was therefore used in a qualitative validation, contextualized by broader information on the history of whaling across the North Atlantic.

Results

Historical records of North Pacific right whales

Records of NPRW presence or absence were widely distributed across space, with a bias in sampling effort towards exploited whaling grounds and corridors connecting whaling grounds and main ports (e.g. Hawaii) (Figure IV-1.A). As shown by previous authors (Maury, 1852; Clapham et al., 2004a; Gregr, 2011; Smith et al., 2012) whaling records indicate that NPRW were historically concentrated in the summer in five main areas: the Gulf of Alaska, the southeastern Bering sea, east of Kamchatka and the Kuriles, the Sea of Okhotsk and the Sea of Japan (Figure IV-1.B).

Species distribution model

The BRT fitted the data very well, explaining 67.2% of the deviance. An AUC value of 0.93 illustrates its good discrimination ability, *i.e.*, the ability to correctly distinguish between occupied and unoccupied sites. The True Skill Statistics value (TSS) of 0.74 indicates a good agreement between the predicted and observed values. The BRT prediction was mostly driven by SST, NPP and MLD (respectively 43.1%, 23.4% and 13.5% of relative influence). The fitted functions indicated that the suitable feeding habitat for the NPRW was characterized by a surface temperature comprised between 5°C and 15°C, net primary productivity above 500 mg C/m²/day and mixed layer depth <20m (Figure IV-3). DEPTH and LANDDIST contributed respectively to 10.9% and 9.0% of the model. SLOPE contributed to less than 5% to the model and was removed from the analysis.

Model predictions

In the North Pacific (Figure IV-1.C), the model predicts high environmental suitability in a wide band across the northern extent of the basin, including all the whaling grounds but extending somewhat into a few other areas such as coastal Oregon and Washington States (USA) and the Yellow Sea.

In the North Atlantic, high environmental suitability is predicted in a wide continuous band extending from the eastern coast of North America (north of Virginia) to northern Norway (Figure IV-2.B). A few small pockets of high suitability were predicted around the Iberian Peninsula and in the northern Mediterranean Sea.

The species' potential presence envelope was defined in both basins to encompass cells with a predicted environmental suitability superior to a threshold $p=0.32$ (Figure IV-2.C). Areas in the North Atlantic for which no predictions could be made (*i.e.*, with environmental conditions that were not adequately sampled by whaling records in the North Pacific; Appendix S3) include a patch east of Greenland as well as most of the Arctic regions, the Baltic Sea, and the southern North Sea.

Historical records of North Atlantic right whales

We found a total of 145 pre-1950 records, generally related to whaling activities, and spanning a period of nearly 400 years (Table IV-2; Figure IV-2.C, Figure IV-5). These included 19 records for which species identity was not certain and 33 for which the location was only approximate. We also recorded and mapped 30 recent records (post-1950) outside the main current summer grounds (Table IV-3; Figure IV-2.C, Figure IV-6). Both historical and recent records cover a wide area across the North Atlantic.

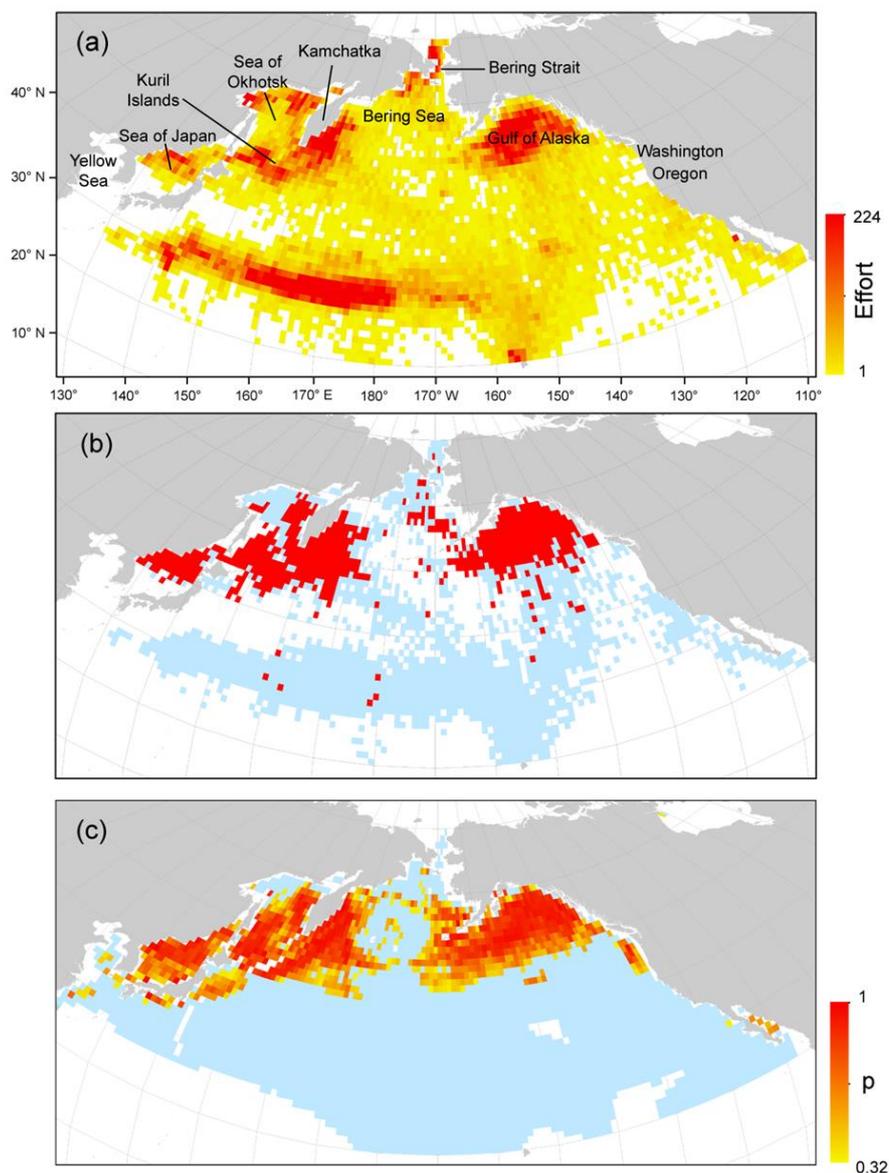


Figure IV-1. Historical data and model predictions in the North Pacific.

A) Sampling effort (measured as number of days when whalers were present in each cell according to 19th Century American whaling records) and geographic locations mentioned in the text. Effort was concentrated in the main whaling grounds for: sperm whales, around 30° N; bowhead whales near the Bering Strait; and North Pacific right whales in the Gulf of Alaska, east of Kamchatka, in the Sea of Okhotsk and in the Sea of Japan. B) Historical distribution of North Pacific right whales in the summer months (June to September), based on the whaling records. Data include both presence (red, where right whales were seen or caught) and absence records (blue, cells visited by whalers, but where no right whales were reported in the examined logbooks); white cells were not visited. C) Predicted environmental suitability from a species distribution model fitted to the historical records. Shades of red indicate progressively higher suitability as predicted by the BRT models (above the $p=0.32$ threshold); blue cells correspond to areas where the species is predicted as absent; white cells are areas for which no reliable predictions can be made. All data are presented on a $1^\circ \times 1^\circ$ grid in Bonne projection (standard parallel: 30°N; central meridian: 170°W).

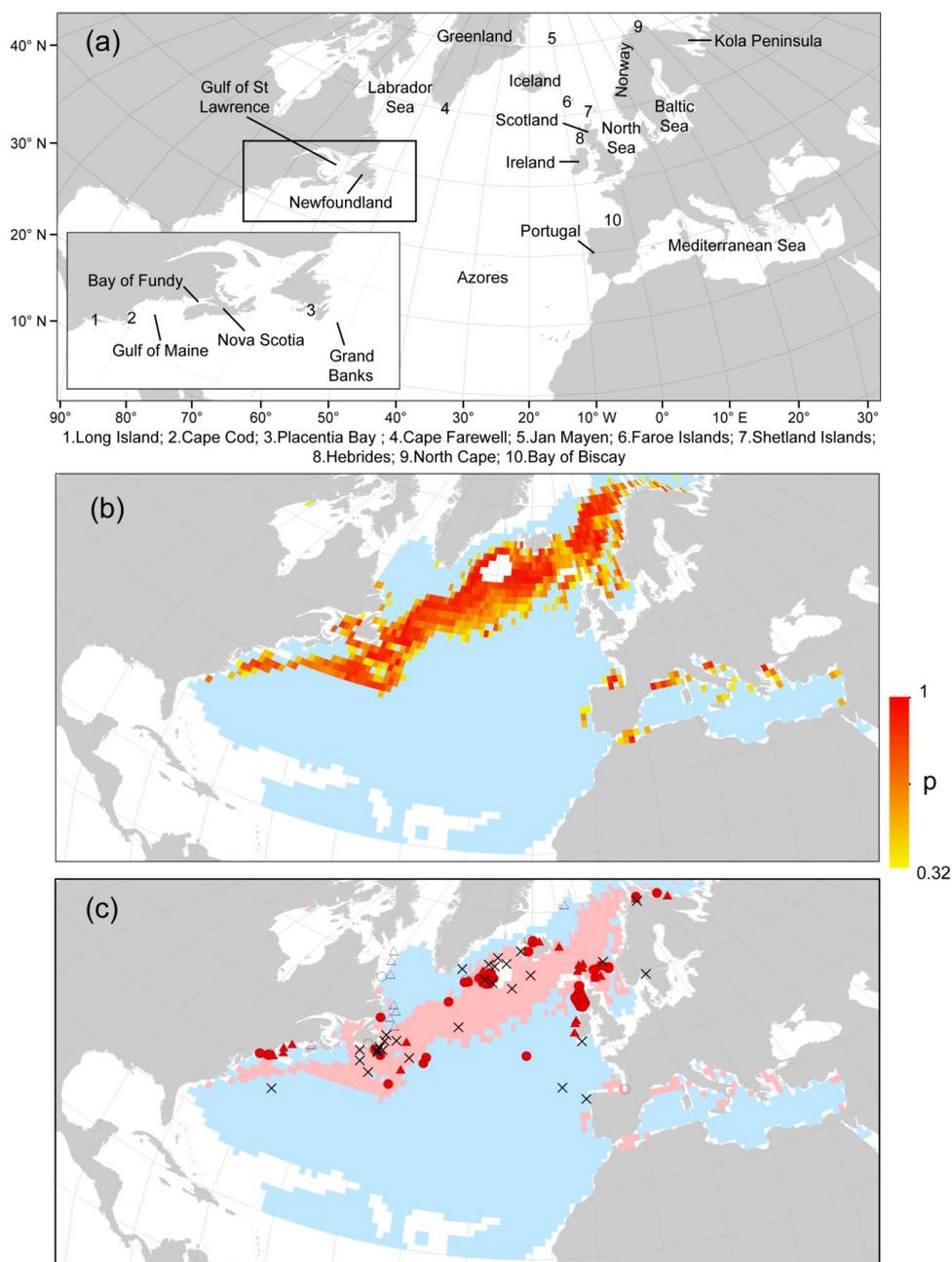


Figure IV-2. Model predictions and historical data in the North Atlantic.

A) Map of the North Atlantic indicating place names mentioned in the text. B) Predicted historical distribution of the North Atlantic right whale in the summer months (June to September) based on a species distribution model (BRT) fitted to whaling records for the North Pacific right whale and extrapolated geographically into the Atlantic. Shades of red indicate progressively higher environmental suitability as predicted by the model (above the $p=0.32$ threshold); blue cells correspond to areas where the species is predicted as absent; white cells are areas for which no reliable predictions can be made. C) Historical records, obtained by reviewing the literature for confirmed or likely records from June to September. The area shaded in pink corresponds to the envelope of predicted presence as mapped in B (presented to facilitate comparisons with B). Symbols correspond to: 142 historical (pre-1950) records from 1583 to 1935, distinguishing those for which there is higher (red symbols) or lower (open symbols) confidence in the species' identity and those for which there is higher (circles) or lower (triangles) precision in location. In addition, the map includes 26 recent (post-1950) records outside the main summer grounds (black crosses). See figures and tables in Appendix S5 for details on each record. All data are presented on a $1^\circ \times 1^\circ$ grid in Bonne projection (standard parallel: 30°N , central meridian: 20°W).

Discussion

We found good – but not perfect – agreement between the model’s predictions (Figure IV-2.B) and the spatial extent of the historical records of the NARW (Figure IV-2.C). Both suggest that this species’ historical feeding grounds extended across the North Atlantic, in a wide band from eastern North America to northern Norway, over the Grand Banks of Newfoundland, south and east of Greenland’s Cape Farewell, south of Iceland, north of the British Isles and in the Norwegian Sea. This distribution pattern was mainly driven by cold temperatures, high productivity and low mixed layer depth.

Before discussing in more detail the extent to which the historical records support the model’s predictions, we discuss key assumptions and caveats of our study that must be taken into consideration (also see Appendix S6).

Assumptions and caveats

Species distribution models represent the realized distribution of a species at a given time and place (Peterson et al., 2011), not differentiating among the factors limiting species distribution (such as prey availability, presence of competitors, or dispersal limitations). This calls for caution when interpreting the results of models transferred across species and across temporal or geographical scenarios (Randin et al., 2006; Sinclair et al., 2010).

The model we have generated is only informative of the historical distribution of the NARW if this species’ environmental requirements are similar to those of the NPRW. Given this strong assumption, the model’s predictions must be interpreted as a hypothesis for – rather than as a reconstruction of – the historical distribution of the NARW. As previously discussed, the species’ similarities in ecology and morphology justify that we explore this hypothesis. The main drivers of our prediction (SST, NPP and MLD) are consistent with those found in previous studies on the distribution of right whales (Baumgartner & Mate, 2003; Gregr, 2011; Torres et al., 2013), reinforcing our assumption that right whales’ distributions are generally driven by the same mechanisms.

The North Pacific whaling records are an exceptional dataset for developing a SDM. They can nonetheless include a number of false absences and false presences, as a result of biases (in sampling effort across space and time) and errors (in location and in species’ identifications). We attempted to reduce these by analyzing only cells with a reasonable sampling effort, and by reducing sources of confusion with bowheads (Appendix S1). Nonetheless, we were unable to correct for the poor representation of shallow-depth data in the NPRW records (given that they correspond to offshore

whaling operations), and its potential effects on the model's discriminative power in shallow-depth areas.

Our analysis is based on a geographic extrapolation from one ocean basin (the North Pacific) to another one (the North Atlantic). To reduce potential errors resulting from this extrapolation, we restricted predictions to the environmental envelope sampled by whalers in the Pacific Ocean. This ensures that areas where we predict high environmental suitability are represented in the dataset used to calibrate the model, reducing one of the main sources of uncertainty under predictions of new scenarios (Zurell et al., 2009). We were however unable to control for other potential differences between basins (e.g., in prey availability, in the interactions between oceanographic conditions) which might limit the transferability of the statistical correlation found in one ocean basin into the other one (Randin et al., 2006). Process-based models combining behavioral and environmental factors could lead to a better understanding of the underlying processes driving right whales distribution (Palacios et al., 2013) but would require extensive physiological and behavioral information that are difficult to gather for these rare species.

By fitting the model using occurrence data mainly from the mid-19th century (1840-1850) and environmental data from the 20th century (MLD and SST 1900-1992; NPP 1998-2007), we necessarily assumed that the environmental spatial structure of the data has remained unchanged. Climatic variation, both longer-term directional changes (e.g., warming since the end of the Little Ice Age; Mann et al., 2008) and shorter-term cycles (e.g., El Niño Southern Oscillation, Nicholls, 2008 ; Pacific Decadal Oscillation, Mantua & Hare, 2002), is known to affect the distribution of marine species (e.g., Evans & Bjørge, 2013), and may therefore affect the results of our analyses. However, the use of occurrence data collected throughout the 19th century and of environmental data obtained by averaging long-term climatologies is likely to mitigate these effects, by retaining the strong, persistent, seasonal signals in the data (Gregn, 2011). Furthermore, in a previous study facing a similar challenge, Gregn (2011) found that a review of climatic reconstructions did not reveal major differences in the North Pacific climate between the mid-19th and the 20th centuries.

The NARW historical records we compiled constitute the most comprehensive dataset currently available on the historical summer occurrence of this species. Yet, they are strongly biased spatially (towards coastal areas, where whales were more accessible) and temporally (towards a recent period when records became more detailed, despite the species being rarer). They are also plagued by geographic imprecision (location is only approximate for 23% of records) and by taxonomic uncertainty (for 13% of records). These limitations preclude the use of these data in a quantitative validation of the model's predictions. Instead, we discuss qualitatively, region-by-region, the extent

to which the historical (Table IV-2) and recent (Table IV-3) records either support or contradict the model's predictions (Figure IV-2.C, Figure IV-5, Figure IV-6), keeping in mind the strengths and limitations of both the data and the model.

We place this discussion within the broader background of the history of whaling in each region, which provides additional records at the regional scale (too imprecise to map) and insights on whaling effort that contextualize the records in each region. Moving from west to east across the Atlantic (see Figure IV-2 for the locations mentioned in the text), we discuss in particular the few instances where the model and records disagree.

Comparison between the model predictions and species records in the North Atlantic

The model predicts an area of suitable habitat for NARWs off the eastern coast of the United States south of Cape Cod, supported by a few historical records from coastal whaling operations, as well as by recent records (NOAA-NEFSC, 2013).

North of Cape Cod, the model predicts suitable areas over the continental slope, but absence in the shelf areas (Gulf of Maine, Nova Scotia; no predictions for the Bay of Fundy). The records show little evidence of historical presence of right whales in summer along this coast (Reeves et al., 1999, 2002b), and therefore present no major contradiction to the model predictions. However, both the model predictions and the historical records disagree with today's known distribution of NARWs, as this shelf area appears to be the main region where right whales currently concentrate in the summer (NOAA-NEFSC, 2013; Wikgren et al., 2014). This discrepancy likely results from the model's poor capacity to discriminate habitat in shallow waters (having been calibrated mainly with deep waters data; Figure IV-1). But the scarcity of historical records also raises the possibility that this region might not have been as important historically this species, at least in relative terms, as it is today.

The model predicts a broad suitable area over and around the Grand Banks of Newfoundland, well supported by 18th century American whaling records (e.g., specifically referring to right whaling "east of the Grand Banks"; Reeves & Mitchell, 1986, and an earlier map of an 'abandoned' right whale ground in this general area ; Clark 1880).

Historical and recent records also support the predictions of suitable habitat around the coast of Newfoundland and into the Gulf of Saint Lawrence. This region was well-known to 16th and 17th centuries Basque whalers (Ciriquiain-Gaiztarro, 1961; Du Pasquier, 2000), but studies of the history of Basque whaling have focused on the northern Gulf of Saint Lawrence and Strait of Belle Isle (Barkham, 1974), with recent genetic studies indicating that bowheads were the focus (McLeod et

al., 2008). But a 1538 report explicitly mentions whaling in southeast Newfoundland (Haie, 1889), suggesting Basques exploited a wider area. Furthermore, historical references to separate summer and early winter whaling seasons suggest that both right whales and bowheads were targeted (but see McLeod et al. 2008).

A few historical records off northern Labrador are not supported by the model's predictions. However, species identity is uncertain for these records, which may plausibly correspond to bowheads, as this falls within the historical summer distribution of this species (Reeves et al., 1983). These records are therefore not a main challenge to the model's predictions.

A large area of high suitability is predicted south and southeast of Greenland, and south of Iceland. This includes the area known as the Cape Farewell Ground, where the historical presence of right whales is well supported by 19th century American whaling records (Reeves & Mitchell, 1986a; Reeves et al., 2007). Basque whalers might have also caught right whales in this region during the 17th-18th centuries (Du Pasquier, 2000). Furthermore, it is one of the few regions outside the eastern North American coast where NARWs have been recorded recently (Brown et al., 2007; Mellinger et al., 2011).

Predictions of presence off the southern coast of Iceland are supported by historical records, including by additional whaling records too imprecise to map ("about 50 miles to the west of that island", "to the south-east of Iceland"; Collett, 1909; Du Pasquier, 2000). Several historical records off northwestern Iceland seem to contradict the model's predicted absence (Lindquist, 1994; Edvardsson & Rafnsson, 2006) but are in fact located within coastal cells where the model makes no predictions.

The Faroe Islands are well within the model's predicted area of historical presence, whereas the Shetlands are at the edge. Historical records indicate that right whales were taken off both archipelagos (Jonsgård, 1977).

Model predictions are contradicted by a concentration of historical records off the Hebrides and Ireland, a region predicted as unsuitable. This may again reflect the model's limited predictive capacity in shallow depth regions. However, these records correspond to a specific whaling period, whose well-documented details (Haldane, 1905, 1907; Collett, 1909; Thompson, 1918) suggest an exceptional rather than regular presence of NARWs. Indeed, despite ongoing whaling effort (for fin and sei whales, *Balaenoptera physalus* and *B. borealis*) no right whales were reported off the British Isles between 1889 and 1904. In contrast, 63 were captured between 1905 and 1914, with "several hundred" seen in 1908 (Collett, 1909). This is reminiscent of concentrations occasionally observed in other pelagic fisheries, associated with exceptional oceanic conditions (e.g., exceptional catches of

yellowfin tuna off the Seychelles in 2004–2005; Fonteneau et al., 2008). If an oceanic anomaly is the explanation for these records, they would in any case be impossible to predict with a model based on a long-term averaged climatology.

The model predicts suitable habitat in the Norwegian Sea and around the North Cape. This is supported by a few coastal whaling records, reflecting a 17th-18th century right whaling ground (see Smith et al., 2006 for a review). Du Pasquier (2000) collected >200 records of Basque whaling trips to “Norway” that we could not map but which could have plausibly corresponded to whaling in this area. There are also two recent records for this region.

Outside the main band of predicted suitability, the model predicts a few patches of suitable habitat around the Iberian Peninsula and in the northern Mediterranean Sea. Of these, only in the Gulf of Biscay we found an historical summer record, but in an area where whaling historically took place in the winter (Aguilar, 1986; Azpiazu, 2000; Barkham, 2000a). These areas are known to have high concentrations of zooplankton that support feeding populations of whales (e.g. of fin whales *Balaenoptera physalus* in the northwestern Mediterranean Sea; Notarbartolo-Di-Sciara et al., 2003), but given the lack of support for the predicted presence of NARWs we cannot rule out the possibility that the model overestimates the historical distribution of the foraging grounds for this species.

Conversely, there are a few records outside the area predicted by the model. A historical record off Jan Mayen (of low species certainty) and a recent record in the Baltic (where the model makes no predictions) are not major challenges to the model. But a historical record north of the Azores and two recent records to the northwest of the Iberian Peninsula contradict the model’s predicted absence. These are reminiscent of a few isolated records in the central North Pacific (between 20°-40°N, also outside the area predicted by the model; Figure IV-1.A), where their rarity despite high whaling effort (for sperm whales) suggests that they correspond to migrating individuals rather than regular feeding grounds.

Conclusions

The generally high agreement between the model predictions and the historical records suggests that the model based on NPRW whaling data is informative of the historical summer distribution of NARWs. If so, this distribution extended across the North Atlantic in a wide continuous band from eastern North America to northern Norway, including substantial areas of offshore habitat outside known records.

Nonetheless, there are discrepancies between the model's predictions and the historical data that point to potential limitations. In particular, failure to predict both the current summer grounds off North America and the historical whaling grounds off the British Isles suggest lack of predictive power in shallow-depth, shelf regions. Additionally, predictions in areas for which we have no evidence that they were historical NARW foraging grounds (e.g., in the Mediterranean) suggest further limitations in the model. The model's predictions should therefore be mainly seen as a hypothesis for the summer offshore distribution of the NARW.

Our results pave the way for additional avenues of research and monitoring with potential implications for the conservation of the endangered NARW. Indeed, the model predictions raise hypotheses that should be further explored in two ways. Firstly, exploration of the surviving historical record in the light of these results can help to clarify the history of the exploitation of this species. In particular, the model's results suggest that more attention is warranted to whaling records in and around Newfoundland, and in offshore grounds around the Grand Banks, south of Greenland/Iceland, and in the Norwegian Sea. A better understanding of pre-whaling distribution can inform future conservation perspectives for this species, even if these areas are currently unoccupied. Secondly, the model highlights regions potentially used by today's populations. Indeed, nearly all recent records outside the main known summer grounds fall within the area predicted as suitable by the model, suggesting that these records correspond to purposeful visits to suitable feeding areas rather than vagrancy or extra limit straying. With many individuals not accounted for every year in the intensive surveys at the main grounds (Hamilton et al., 2007), identification of other regularly used areas is key to guiding strategic conservation efforts. Passive acoustic methods such as those used by Mellinger et al. (2011) may be a cost-effective option for sampling such areas.

More broadly, our analysis illustrates the challenges and opportunities of combining historical and environmental data to improve understanding of the original distribution of highly depleted species. Because the quality of the historical record generally declines strongly as we go back in time, relatively recent population declines are much better documented than century- or millennia-old declines, which are often underestimated or even forgotten (Pauly, 1995). Nonetheless, the spatial heterogeneity of historical human impacts creates opportunities for using information from the more recently impacted, better-known regions to fill gaps in knowledge elsewhere, using species distribution models to extrapolate between the two. The challenges are particularly significant for species that have suffered ancient impacts across their entire range. For some of these, extrapolation from ecologically-similar phylogenetically-related species can be used to generate hypothesis that add depth to the fragmentary historical record. As understanding of the ecological and evolutionary

processes that drive species' spatial distribution improves, the informative value of these extrapolations across space and taxa will increase, making historical data even more useful.

Appendices

Appendix S1 Historical records of North Pacific right whales

Appendix S2 Environmental data

Appendix S3 Species Distribution Models

Appendix S4 Complementary analyses

Appendix S5 Historical records of North Atlantic Right Whale

Appendix S6 Extended discussion

Appendices

Appendix S1: Historical records of North Pacific right whales

We analyzed records of North Pacific right whale (NPRW) species presence (seen or caught) and absence from daily data obtained from a sample of logbooks kept aboard 19th and early 20th century American whaling voyages. For the purposes of the present analysis, we selected whaling voyages which occurred in the North Pacific Ocean (north of 10°N latitude and longitude between 100°E and 100°W). Most voyages entering the North Pacific did so early in a calendar year and remained there throughout that year, or occasionally for two and rarely three years. To account for this operational pattern, we divided the voyage data according to calendar year to define data segments that we referred to as voyage-years.

We defined temporally continuous segments of the data for each voyage within the North Pacific, and further divided each of those segments in which logbook entries were available on a near daily and continuous basis. Subsegments were formed when the vessels were in port or otherwise not whaling, or when there were temporal or spatial gaps in the reported data. Extended temporal gaps occurred for two reasons. First, the keeper of the logbook may not have made entries for a time period or pages may have been removed or otherwise lost from the logbook itself. Second, the data extractor may have failed to include some observations that were recorded in the logbook, either in error (e.g. pages stuck together) or by intention in certain circumstances. The latter occurred occasionally in Maury's data, for example when vessels entered bays or other enclosed areas for extended periods of whaling. We have identified this pattern in the North Pacific (e.g., Sea of Okhotsk, Anadyrskiy Gulf). Not recording data in such circumstances was likely part of the data collection protocol used by Maury's data extractors because his interest appears to have been primarily in open water rather than coastal oceanic patterns. Extended spatial gaps were frequently associated with temporal gaps, but also occurred from time to time as a result of errors in logbook recording (e.g. transposition of digits), errors in data extraction (e.g. transposition of digits or failing to adjust hemisphere designation as the vessel crossed the International Date Line or the Equator). We examined maps of voyage tracklines and corrected obvious errors by comparing to original logbooks where available (see Smith et al., 2012). However, some unexplained spatial gaps without a temporal gap remained, and we defined subsegments to reflect those situations. This voyage segmenting procedure occasionally left subsegments with only one logbook entry, and the data for such subsegments were omitted.

The sightings and catches were usually identified (or reliably identifiable from the context) to species, and those that were not were omitted. Maury's data were being extracted from logbooks at a time

when right and bowhead whales were not always distinguished in the North Pacific. We noticed that Maury's data included no observations of bowhead whales in areas where both species are known to have occurred (Townsend, 1935; Bockstoce et al., 2010), and discarded Maury's data in those regions (north of 54°N in the Okhotsk Sea and north of 56°N in the Okhotsk Sea).

The American whaling data included information on the distribution of another species of right whale: the southern right whale (*Eubalaena australis*), present across the Southern Ocean. We did not include those data in construction of the species distribution model for two reasons. First, only part of the distribution of this species is covered by the whaling data. Indeed, although coverage is quite complete up to about latitude 60°S, it is practically absent further south, maybe because rough seas rendered whale processing too difficult (e.g., as Lacroix, 1997 mentions for the Falklands). Accordingly, other historical sources mention right whales at higher latitudes, and up to the Antarctic shelf (Morrell, 1832; Ross, 1847; Charcot & Joubin, 1913; Ohsumi & Kasamatsu, 1986). Second, bowhead whales (*Balaena mysticetus*) are present at high latitudes in the northern but not in the southern hemisphere. This species may compete directly with right whales for food, as it also feeds on copepods (Lowry et al., 2004), and its presence may thus affect the distribution of the North Pacific and North Atlantic species, but not of the Southern right whale. We therefore considered that a species distribution model obtained solely from data on the North Pacific right whale was more relevant to make predictions on the distribution of the North Atlantic species than a model including both the North Pacific and the southern right whales. Accordingly, we found in exploratory analyses that including whaling data from the Southern Hemisphere did not improve the models' predictive power.

Appendix S2: Environmental data

Sea surface temperature (SST) has a strong correlation with the distribution and abundance of zooplankton (Norberg & DeAngelis, 1997; Rutherford et al., 1999; Gregr & Coyle, 2009) and has been found to be a good predictor of right whale distribution in previous analyses (Murison and Gaskin 1989; Gregr 2011). Previous authors found that Mixed Layer Depth (MLD) is strongly correlated ($r=0.865$, $p<0.0001$) with the diving depth of North Atlantic right whales (NARW; Baumgartner & Mate, 2003).

Net primary productivity (NPP) was included given that is known to be positively correlated with zooplankton biomass (Norberg & DeAngelis, 1997). We retrieved 1080x2160 global grids of NPP, calculated as a function of chlorophyll, available light, and photosynthetic efficiency using the Vertically Generalized Production Model (VGPM) algorithm (Behrenfeld & Falkowski, 1997) for the entire SeaWiFS 1998-2007 chlorophyll record, on the Ocean Productivity web site

(<http://www.science.oregonstate.edu/ocean.productivity/index.php>). We then averaged NPP over the summer months (June to September) to compute the seasonal climatology.

Ocean bathymetric features have frequently been used as predictors of right whale distribution (Hamazaki, 2002; Kaschner et al., 2006; Gregr, 2011; Torres et al., 2013). We integrated depth (DEPTH), slope (SLOPE) and distance to land (LANDDIST) in the model.

Table IV-1. Environmental predictors used in the species distribution models.

Variable	Acronym	Derived from	Period Averaged	Reference
Net Primary Productivity (mg C/m²/day)	NPP	Ocean Productivity web site	1998-2007	Behrenfeld & Falkowski, 1997
Sea Surface Temperature (°C)	SST	NODC WOA94	1900-1992	Levitus & Boyer, 1994
Mixed Layer Depth (m)	MLD	NODC WOA94	1900-1992	Monterey & Levitus, 1997
Depth (m)	DEPTH	NOAA-NGDC ETOPO1	-	Amante & Eakins, 2009
Distance to Land (km)	LANDDIST	AquaMaps	-	Kaschner et al., 2008
Slope	SLOPE	Depth	-	-

Appendix S3: Fitted functions

While the purpose of this study is not to provide a quantitative description of the feeding habitat of NPRW (see an in-depth discussion of this topic in Gregr & Coyle, 2009 and Gregr, 2011), we discuss the species-environment relationships for the NPRW in summer, as a basis for understanding the underlying processes driving the predicted distribution of right whales in our model.

Relative importance and fitted functions for the predictors used in the BRT are comparable to previous studies on the ecology or distribution of right whales in summer. The importance of sea surface temperature and the selection of areas with low sea surface temperature (5°C-15°C) are consistent with previous studies of right whale distribution, both in the North Pacific and in the Southern Oceans (Gregr, 2011; Torres et al., 2013). Our results indicate that the model is also strongly driven by NPP, with the presence of right whales being correlated to a primary productivity superior to 500 mg C/m²/day. Accordingly, even if not directly comparable, chlorophyll a concentration also appears as an important predictor of right whale distribution in previous studies (Torres et al., 2013). The scarcity of occurrence data associated with high values of productivity call for caution when interpreting the shape of the response curve above 1000 mg C/m²/day. The importance of MLD in our models and the finding that NPRW presences are associated with low MLD is coherent with a previous study on NARW foraging ecology, which identified a correlation between the depth of the mixed layer (MLD) and the diving depth of feeding right whales (Baumgartner &

Mate, 2003). Depth has a non-negligible influence in our model. The North Pacific whaling dataset however is biased towards offshore waters, as can be seen from the distribution of data along the depth gradient (Figure IV-3) and the extrapolation of the model in shallow areas should be considered with care. The bulk of North Pacific right whale presences was associated with habitat distant from 0 to 800 km away of the coastline, though some presences occurred further offshore (< 1200 km away from the coast).

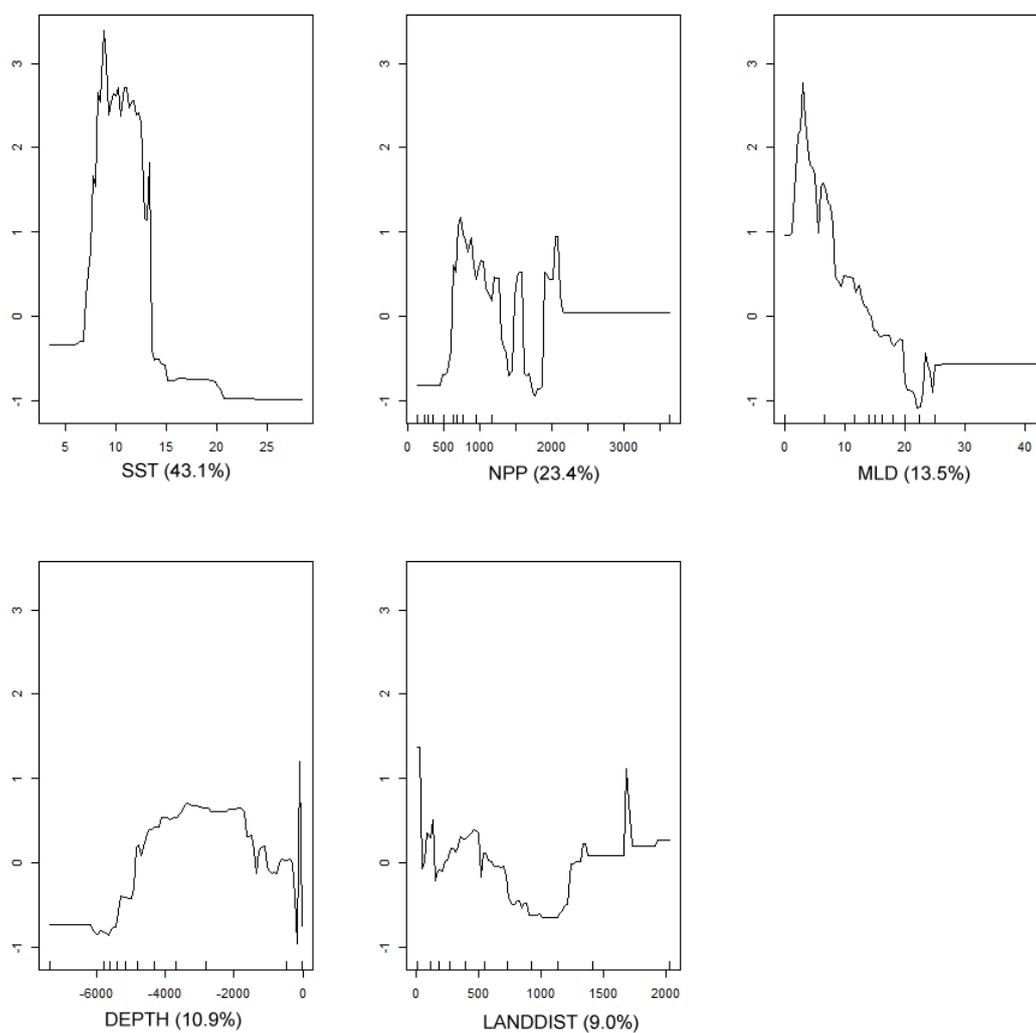


Figure IV-3. Fitted functions showing the species-environment relationships produced by the BRT.

The relative influence of each variable is presented as a percentage in parentheses. Rug plots on the x-axis show data distribution across each variable, in deciles. SST = sea surface temperature, NPP = net primary productivity, MLD = mixed layer depth, DEPTH = mean depth, LANDDIST = distance to land.

Appendix S4: Complementary Analyses

Sensitivity to the inclusion of records with low sampling effort

The sampling effort was not uniform across the entire North Pacific (Figure IV-1.A). American whalers directed their effort towards areas where the density of whales (not only right whales, but also sperm, bowhead, gray, and humpback whales) was expected to be relatively high. Corridors of navigation between ports and the main whaling grounds were also oversampled compared to other areas in the North Pacific. Although these differences in effort give us information on the real distribution of whales (as in fisheries today, 19th century whalers had prior knowledge of which areas whales were more easily found, and targeted these preferentially; Townsend, 1935), they can induce flaws in the structure of the model as not all absences are equally informative (e.g., an absence in a cell visited only once is more likely to be a false absence, where the species was actually present but not detected, than a cell visited multiple times). An analysis was conducted to assess the differences in predicted environmental suitability for models built with the overall dataset, or with cells that were visited at least two or three times by a whaling ship. The results show very minor differences in the predicted distribution of right whales. The similarity between the different predictions was always greater than 85% in the North Atlantic and greater than 90% in the North Pacific when making pairwise similarity comparison between the different prediction maps. However, the models' explanatory and predictive power increased when selecting only the cells with more than two days of effort in the dataset used to build the model, indicating that the strategy of discarding cells with very low effort was justified.

Sensitivity to the exclusion of medium-latitude data

The whaling dataset contains a large patch of records around 30°N, characterized by an intense survey effort (for sperm whales) coupled with a virtual absence of NPRW sightings. In a previous modelling analysis, Gregr (2011) chose to include only data north of 40°N, which cover the vast majority of the presence records for the NPRW. To test the leverage that medium-latitude data have in the model, we built a BRT on North Pacific whaling data north of 40°N (" $>40^{\circ}\text{N}$ model") and compared its predictions with those of the main model (" $>20^{\circ}\text{N}$ model") presented in this analysis.

We found that these medium-latitude data had a significant effect on the model's predictions in the North Atlantic. Indeed, although predictions in high latitudes remained unchanged, the $>40^{\circ}\text{N}$ model predicted a wider area of suitable habitat in mid-latitudes regions (e.g. a patch on the coast of California, a band from the gulf of Biscay and Portugal to the Azores). Given that there is no support for these predictions (from either historical or recent data), this suggests that the $>40^{\circ}\text{N}$ model is less capable of discriminating habitat preferences in mid-latitudes latitudes, having apparently a higher

likelihood of commission errors (false positives). These errors should be avoided in a conservation context, where potentially suitable areas need to be identified to guide strategic conservation efforts (Loiselle et al., 2003; Rondinini et al., 2006).

The inclusion of data from the North Pacific between 20°N and 40°N seems therefore to provide valuable information to the model - leading to a better discrimination of areas of low suitability – justifying their inclusion in the analysis.

Sensitivity to modelling assumptions (BRT vs GAM)

To assess whether our results are sensitive to the type of statistical model used, we performed a second analysis on the same dataset using a Generalized Additive Models (GAM; Hastie & Tibshirani, 1986). GAMs are often used for their ability to deal with non-linear and non-monotonic relationships between the response variable and the explanatory variables (Hastie & Tibshirani, 1986; Wood, 2006). This type of model has been shown to perform well for modelling species distribution (Guisan et al., 2002) and particularly in the case of species with complex distribution patterns, i.e. where occurrences do not respond to environmental variables according to a predefined 'shape' (Segurado & Araujo, 2004). Variable selection was performed on a forward-stepwise selection based on optimizing Akaike Information Criterion (AIC), Un-Biased Risk Estimator (UBRE), and deviance explained. The method used to assess the quality of predictions was the same as for the BRT (see Appendix S3). Over dispersion in the residuals was assessed by calculating the value of the dispersion parameter ϕ described by Zuur et al. (2009). A value of $\phi=1.12$ indicated no over dispersion in the residuals.

The selected GAM included the six environmental predictors (SST, NPP, MLD, DEPTH, SLOPE and LANDDIST) and two additional interactions (SST*MLD, SST*DEPTH). As the BRT, the GAM was mainly driven by SST, NPP and MLD, with a preference for cold and productive waters with a mixed layer depth inferior to 20m. The performance of the GAM was very satisfactory (deviance explained = 51.3, AUC=0.92, TSS=0.71), though lower than the BRT (deviance explained= 67.2%, AUC= 0.93, TSS=0.74), which justified our decision to base the discussion on the results of the BRT.

There was a very high agreement between the predictions of the GAM and BRT models both in the North Pacific and North Atlantic (Figure IV-1.C, Figure IV-2.B, Figure IV-4), indicating that the areas predicted as being suitable summer habitats are not dependant of the type of modelling technique used.

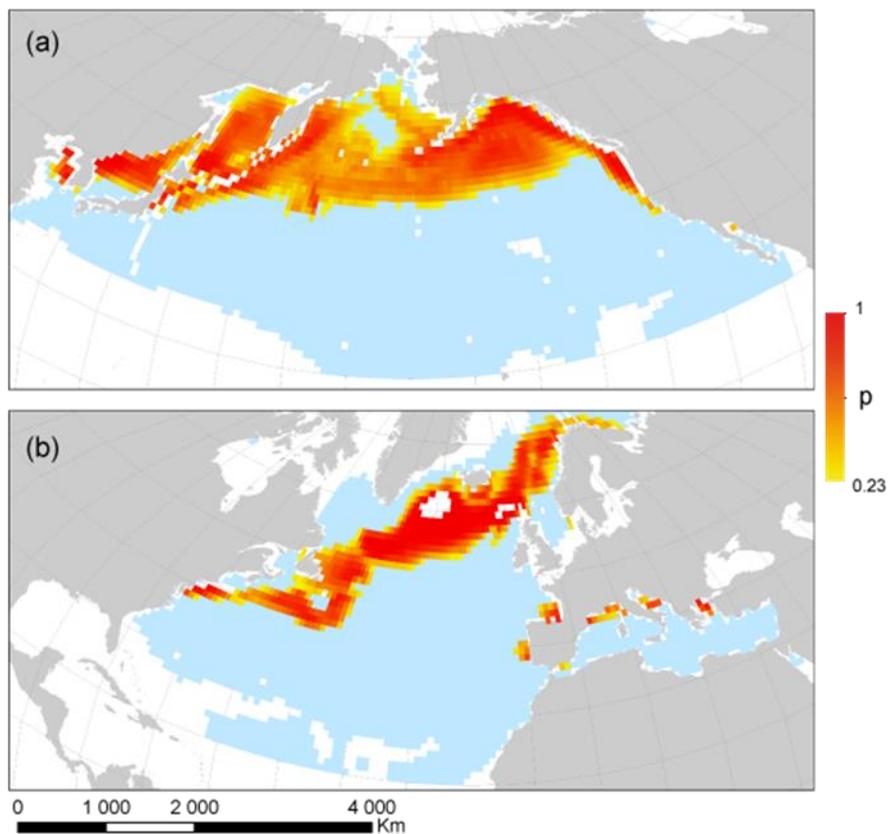


Figure IV-4. Environmental suitability for right whales in summer predicted by the GAM.

(A) In the North Pacific and (B) in the North Atlantic. Shades of red indicate progressively higher suitability as predicted by the model (above the $p=0.32$ threshold); blue colour corresponds to areas where the species is predicted as absent. White colour indicates areas outside the environmental envelope, where no prediction was made. All data are presented on a $1^{\circ} \times 1^{\circ}$ grid in the Bonne projection.

Appendix S5: Historical distribution records of the North Atlantic Right Whale

Table IV-2. Historical (pre 1950) records of North Atlantic right whale (*Eubalaena glacialis*) in the summer months (June to September).

"Map ID" corresponds to the number on Figure IV-5. ● : species reliable, location reliable; ▲ : species reliable, location uncertain; ○ : species uncertain, location reliable; △ : species uncertain, location uncertain.

Map ID	Date	Record details	References
Eastern United States, Bay of Fundy, Nova Scotia			
1 ●	July 1699	"12-13" whales	Reeves & Mitchell, 1986a (Table 1)
2 △	August 1733	"A whale was taken in the Bay of Fundy by a Captain Hussey, and brought into Boston in August." According to Reeves et al. (1999), this was "probably a right whale"	page 169 in Starbuck, 1878 (also mentioned in Reeves et al., 1999)
3 ▲	ca. 1 September 1838	"A Right Whale, about 40 feet long, was found dead off Newburyport, Mass., about September 1st, and towed ashore at Salisbury Point. It was estimated that it would make about forty barrels of oil (Newburyport Herald). This is unusually early in the fall for this species to appear on our coasts."	Allen, 1916 (p. 135)
4 ●	31 July 1839	"40 ft, 40 bbls"	Reeves & Mitchell, 1986a (Table 1)
5 ○	1 June 1841	"Whale seen in Gardiners Bay"	Reeves & Mitchell, 1986a (Table 1)
6 ●	28 July 1841	2 killed	Reeves & Mitchell, 1986a (Table 1)
7 ▲	ca. 1 June 1860	1, found floating	Reeves & Mitchell, 1986a (Table 1)
8 ○	18 June 1866	1 seen	Reeves & Mitchell, 1986a (Table 1)
9 ●	June 1872	2 killed	Reeves & Mitchell, 1986a (Table 1)
10 ▲	ca. 1 June 1888	"Right Whale encountered off Cape Cod about the first of June, 1888, whose calf was first harpooned and killed, while the cow, refusing to leave her offspring, circled around and around until she succumbed after nine bomb-lances had been shot at her (Nantucket Journal, vol. 10, no. 36, June 7, 1888)."	Allen, 1916 (p. 131); also Reeves et al., 1999
11 ●	August 1896	1 struck and lost	Reeves & Mitchell, 1986a (Table 1)
12 ●	22 July 1913	"A large whale chased by several boats"	Reeves & Mitchell, 1986a (Table 1)
13 ●	9 August 1918	One taken, one struck and lost. "Young whale 'exceptionally fat' expected to produce 25-30 bbls. Only 30 gals of oil recovered, none sold". "Last whale landed by the Long Island shore whalers."	Reeves & Mitchell, 1986a (Table 1)
14 ▲	Summer 1919	"A right whale came ashore dead in Sheepscot Bay in summer 1919"	Reeves et al., 1999 (p. 7, citing Norton, 1930)
15 ●	late June 1926	"60 ft. female and 25 ft. calf sighted", "not chased"	Reeves & Mitchell, 1986a (Table 1)
Grand Banks, Newfoundland and Gulf of Saint Lawrence			
16 ○	Summer 1583	A report of Gilbert's 1583 trip to Newfoundland includes in the list of the commodities of the country "abundance of whales, for which also is a very great trade in the bays of Placentia and the Grand Bay, where is made train oils of the whale". The trip was in the summer but it is not clear if he saw the "train oils" being made.	Haie, 1889
17 ●	11 August 1760	"killed a right Whale & she sunk". "ca. 12-14 leagues [36-42 nmi] E of the Great Bank". Original source: whaler logbook (<i>Enterprise</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)
18 ▲	30-31 August 1754	30 August "saw a Noble Right Whale close" but escaped; 31 August "chased 3 but could not strike". Original source: whaler logbook (<i>Phebe</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)
19 ●	13 Sept 1765	"saw two & chased, secured one". Original source: whaler logbook (<i>Diamond</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)
20 ●	5 August 1763	"saw one and chased but could not strike". Original source: whaler logbook (<i>Dolphin</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)
21 ▲	7 August 1763	"saw a Right Whale and chased but could not strike". Original source: whaler logbook (<i>Dolphin</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)
22 ▲	23 July 1754	23 July 1754, "saw several right whales", one struck and lost. Position corresponds to 19 July. Had seen "Icy Islands" on the 20 July. Original source: whaler logbook (<i>Phebe</i> , USA; main activity Sperm whaling).	Reeves & Mitchell, 1986a (Table 1)

Map ID	Date	Record details	References
23 ○	1850	"The last Right Whale killed in New-foundland was taken near Gaultois, on the south coast, in 1850." The author uses the term "right whale" to refer to bowheads too. No season is given, so presumed summer.	Millais, 1907
24 ●	"mid-August 1937"	"A right whale killed in Placentia Bay in mid-August 1937 was the first of its kind taken at the Rose-au-Rue whaling station during more than 19 years of operation" Photos included.	Mitchell et al., 1986
25 ●	Sept 1937	"capture" "1,130cm female"; "The files of the Division of Mammals, USNM, have a photograph of a 37 ft (1,130) female right whale that was taken by the catcher boat Morelos 14 miles southeast of Cape Race, Newfoundland"	Mead, 1986 (Appendix 2)
26 ●	Ca. 1595-1610	Genetic analyses of bones found in a marine excavation associated with a sunken galeon in Red Bay (Basque whaling). A single bone of right whale found (among many of bowheads).	McLeod et al., 2008
Labrador Sea			
27 △	15 August 1587	From the record of John Davis' third voyage: "The 17 we met a ship at sea, and as farre as we could judge it was a Biskaine: we thought she went a fishing for whales; for in 52 degrees or thereabout we saw very many." The 15 of August they left the coast of Newfoundland/Labrador at about 52 degrees latitude (about the entrance to Belle Isle) and headed eastwards, so presumed that whales were seen east of Belle Isle. "	Janes, 1906
28 ○	10 July 1806	1 killed, young, 20 ft (est.). "Possibly a right whale (Eubalaena)?"	Reeves et al., 1983 (Table 1)
29 △	25-28 July 1768	Context: On the 27 May they say "some whales run" among thick ice (Bowheads?) but then no more whales were reported until the 25 of July. After that, whales frequently reported until the 20 August, between ca. 60° and 51°N off the coast of Labrador (Right Whales?), including: 25 July "Saw a Rite Whale bound to Nward, gave her chase 6 hours Could Not Strike Her" (24 July: 60.06°N); 26 July "Sar Rite Whales Very Plenty Could Not Strike them."; 28 July "Saw Whales plenty" at 60°N (29 July - 61°48'N, "Within 20 Leagues of Land"). Original source: whaler logbook (Reliance, USA; main activity right [bowhead?] whaling).	Reeves & Mitchell, 1986a (Table 1)
30 △	9 August 1768	Context: On the 27 May they say "some whales run" among thick ice (Bowheads?) but then no more whales were reported until the 25 of July. After that, whales frequently reported until the 20 August, between ca. 60° and 51°N off the coast of Labrador (Right Whales?), including: 9 August "Saw a Rite Whale gave her Chase Could Nots Strike her", "Saw Rite Whales [bowheads?] Plenty" (latitude 10 August 58°N). Original source: whaler logbook (Reliance, USA; main activity right [bowhead?] whaling).	Reeves & Mitchell, 1986a (Table 1)
31 △	12-13 August 1768	Context: On the 27 May they say "some whales run" among thick ice (Bowheads?) but then no more whales were reported until the 25 of July. After that, whales frequently reported until the 20 August, between ca. 60° and 51°N off the coast of Labrador (Right Whales?) including: 12 August "Lots Whalle"; spoke Capt Goodspeede who "told Us WHales Was plenty on the Coste" (53°18N); 13 August "Saw Whales [balaenids?] Struck one Lost her Lost one Iron", "Saw whales gave them Chase Could Not Strike". Original source: whaler logbook (Reliance, USA; main activity right [bowhead?] whaling).	Reeves & Mitchell, 1986a (Table 1)
32 △	14 August 1768	Context: On the 27 May they say "some whales run" among thick ice (Bowheads?) but then no more whales were reported until the 25 of July. After that, whales frequently reported until the 20 August, between ca. 60° and 51°N off the coast of Labrador (Right Whales?) including: 14 August "Saw whales plenty" (54°06N). . Original source: whaler logbook (Reliance, USA; main activity right [bowhead?] whaling).	Reeves & Mitchell, 1986a (Table 1)
33 △	19-21 August 1768	Context: On the 27 May they say "some whales run" among thick ice (Bowheads?) but then no more whales were reported until the 25 of July. After that, whales frequently reported until the 20 August, between ca. 60° and 51°N off the coast of Labrador (Right Whales?) including: 19 August "Saw whales" (51°05N); 20 August "Kild one Whale [...] sunken" (51°16N); 21 August "Cutting the head", "Wents to trying"; 22 August "Rafts of blubber"; 23 August "Stowed away our oyl". Original source: whaler logbook (Reliance, USA; main activity right [bowhead?] whaling).	Reeves & Mitchell, 1986a (Table 1)
34 △	1887	"They [right whales, Eubalaena] are taken during the summer months off the southern end of Greenland and to a limited extent in the lower part of Davis Strait, near Resolution Island". Clark distinguished right whales from bowheads (whose distribution is described separately) but given the high latitude of this record it is nonetheless assumed to be taxonomically uncertain.	Clark, 1887 (p. 15)
Southeast Greenland and the Cape Farewell grounds			
35 ●	June 1858	"found these whales [the proper Black whale] first on 11 June at 60°30'N, 35° W", "coming from the Eastwards, where they must have been some time in April & May" and then followed them "bound west a little southerly true course down off Cape Farewell". Two were taken at 61°30'N, 34-36° W in June. Source: letter from Captain C. Chapel (Violet), to Cpt. William Jackson (16 Oct 1859).	Reeves & Mitchell, 1986a (p. 225)
36 ▲	1866	"Right whale ground": Lat 60.00 N to 62.00N; Long. 33.00W to 35.00W. Original source: a note in the abstract of the schooner <i>Petrel</i> (USA)	Reeves & Mitchell, 1986a (p. 226)
37 ●	5 July 1868	1 saved, 1 struck and lost; cow and calf killed 5 July [1868]; cow sunk, calf produced 26bbbls. Original source: whaler logbook (<i>Ansel Gibbs</i> , USA)	Schevill & Moore, 1983 (Table 1 and Fig 1); Reeves & Mitchell, 1986a

Map ID	Date	Record details	References
38 ●	5 June 1872	Some seen. Original source: whaler logbook (<i>Ansel Gibbs</i> , USA)	Reeves et al., 2007 (Table 2.2)
39 ●	10 June 1872	1 killed. Original source: whaler logbook (<i>Ansel Gibbs</i> , USA)	Reeves et al., 2007 (Table 2.2)
40 ●	12 June 1872	Some seen. Original source: whaler logbook (<i>Ansel Gibbs</i> , USA)	Reeves et al., 2007 (Table 2.2)
41 ●	25-28 June 1866	Day 1: 2 seen; day 2: two seen; day 3: 1 killed and sank; day 4: 1 killed (coordinates taken on the 25th June). Original source: whaler logbook (<i>Pacific</i> , USA).	Reeves et al., 2007 (Table 2.2)
42 ●	4 July 1866	1 killed and sank. Original source: whaler logbook (<i>Pacific</i> , USA).	Reeves et al., 2007 (Table 2.2)
43 ●	9 July 1866	1 seen. Original source: whaler logbook (<i>Pacific</i> , USA).	Reeves et al., 2007 (Table 2.2)
44 ●	17 June 1877	Right whale cow & calf; calf killed and tried (estimated 20 bbls), cow struck and lost (estimated 100 bbl). Original source: ship logbook (<i>Daniel Webster</i> , New Bedford). Likely correspond to the 2 individuals recorded by Schevill & Moore for June 1878.	Schevill & Moore, 1983; Reeves & Mitchell, 1986a (Table 2); Reeves et al., 2007 (p. 39)
45 ●	27 July 1878	Some seen. Original source: whaler logbook (Adeline Gibbs, USA).	Reeves et al., 2007 (Table 2.2)
46 ●	11 June 1878	Encountered Right whales 11 June 1878, one captured. "Although only one whale was captured, Ferguson believed the vessel was 'into the middle of quite a school of whales, for they could be heard spouting in different directions all around us any time during the night". Original source: whaler logbook (Abbie, Bradford).	Reeves & Mitchell, 1986a
47 ○	13-15 June 1878	Whales seen by the Schooner <i>Astoria</i> (1878), reported in the abstract of the <i>A.J. Ross</i> .	Reeves & Mitchell, 1986a (p. 226)
48 ○	July 30-Aug 3 1878	Whales seen. Original source: whaler logbook (<i>Astoria</i> , USA).	Reeves & Mitchell, 1986a
49 ○	4-8 Aug 1878	Whales seen, by the Schooner <i>Astoria</i> (1878). Reeves & Michell (1986) assume they are right whales.	Reeves & Mitchell, 1986a
50 ▲	July-August 1886	"sailed 24 June for 'Hudson bay' [...]. By 17 July, however, the <i>Palmetto</i> was at 61°14'N, 36°12'W, i.e. on the Cape Farewell Ground. Right whales were first sighted 20 July, and by 9 August the crew had taken their fifth whale alongside". 15+ whales (5 saved, 2 struck and 8+ sighted). Original source: whaler logbook (<i>Palmetto</i> , USA).	Schevill & Moore, 1983 (Table 1); Reeves & Mitchell, 1986a (p. 227)
51 ●	23 June 1891	1 right whale seen. Original source: whaler logbook (<i>Petrel</i> , USA).	Reeves et al., 2007 (Table 2.2)
52 ●	13 July 1891	1 seen. Original source: whaler logbook (<i>Petrel</i> , USA).	Reeves et al., 2007 (Table 2.2)
53 ●	23-25 July 1891	Day 1: 3 seen, 1 killed (sank); day 2: 2 seen; day three: 1 killed. Original source: whaler logbook (<i>Petrel</i> , USA).	Reeves et al., 2007 (Table 2.2)
54 ●	22 July 1891	1 killed. Original source: whaler logbook (<i>Petrel</i> , but reporting catches by the <i>Mermeid</i>)	Reeves et al., 2007 (Table 2.2)
Iceland			
55 ●	1610 – 1650	"Archaeological excavations at Strákatangi strongly suggest that the site is a foreign whaling station from the 17th century, with many similarities with whaling stations from the 17th century in the North Atlantic region, especially Red Bay in Labrador. It is impossible to say from the archaeological material which nationality occupied the station but local tales suggest that the whalers at Strákatanga were Basques that came from the Basque regions in North Spain and South France. [...] These remains suggest that foreign whalers built stations on land and used them during the whaling season. The artifacts give us a relative date for the occupation of the site, which indicate a occupation in the period 1610 – 1650. No animal bones were recovered during the excavation and sieving of cultural deposits with a 5 mm sieve did neither produce animal nor fish bones." (in Edvardsson & Rafnsson 2006). However, Magnús Rafnsson personal comm (email 18/11/2013): "A couple of skulls were found around the ruins and DNA research said they were from right whales."	Edvardsson & Rafnsson, 2006
56 ●	1613	The first whaling ship arrived in Strandir in 1613, causing fear among the inhabitants who were not used to seeing ocean-going vessels. The local pastor arrived on the scene and pointed the Spaniards to a suitable harbor in Steingrímsfjörður, near his abode, all with the consent of the sheriff, Ari Magnússon. The Basques caught 17 whales.	Edvardsson & Rafnsson, 2006 (citing Jón Guðmundsson)
57 ●	1614-1615	1614: According to Jón Guðmundsson, four ships were whaling in Reykjarfjörður close to where he lived. 1615: That same summer Jón tells of sixteen ships by Strandir, most of which sailed east to Russia but four ships spent the summer whaling from Reykjarfjörður in Strandir.	Edvardsson & Rafnsson, 2006 (citing Jón Guðmundsson)

Map ID	Date	Record details	References
58 ○	1752	"J. Eiriksson (1768: 253f) mentions French "sléttbakur" whaling in Ísafjarðardjup in 1752; furthermore: 'it is also probable that his whale fish breeds inside the fiords of Ísafjarðarsysla and Barðastandasysla, and ... raises there its young during the summer, in ... May, June and July, and leaves them late in the month of August, when then some of these abandoned ones occasionally fall prey to the inhabitants.' Eiriksson could be referring to the, mainly, humpback calf whaling in Arnarfjörður."	Lindquist, 1994 (p. 201; citing J. Eiriksson 1768)
59 ●	between 1770-1780	"even American vessels, as late as between 1770 and 1780, occasionally caught Nordkapers in Brede Fiord and Faxe Bay, in Iceland."	Eschricht & Reinhardt, 1866 (citing Pontoppidan 1785)
60 ▲	1802	"Another good slettboku-hvlalur (i.e. black right whale) came ashore at Naust near Hofson"	Lindquist, 1994 (p. 849)
61 ▲	April to August, ca. 1873	"Iceland Grounds. Right Whales. April to August Lat 63 to 67 Long 11 to 16 W." Souce: cryptic anotation in an anonymous compilation of American whaling abstracts, not dated but in the same page with memoranda concerning cruises in 1867 and in 1872-73.	Reeves & Mitchell, 1986a
Norwegian and Barents Seas			
62 ▲	2-25 July 1667	Hamburg vessel left the Svalbard (Spitzbergen) bowhead whaling ground during midsummer to hunt right whales off northern Norway between 2-25 July, in "bay whaling" centred in Lophavet, the Loppa Sea. Of the Finnmark coast in July, this ship encountered "many" right whales, as well as Dutch, French, Flemish and German whaleships (about 20 of which used the Loppa Sea as a roadstead). Original source: journal kept by Christian Bullen (coxswain aboard an unidentified Hamburg whaleship).	Smith et al., 2006 and Reeves & Smith, 2006 (citing Barthelmeß, 2003)
63 ●	pre 1884	Bones identified as the N Atlantic Right Whale, presumed to corresponded to Dutch whaling in the previous centuries.	Guldberg, 1884
64 ●	pre 1884	Bones identified as the N Atlantic Right Whale + old try pots (in an area called the Dutchman Hill), presumed to correspond to Dutch whaling in the previous centuries.	Guldberg, 1884
65 ▲	1935	"A Biscayan whale was last observed at the coasts of the Kola Peninsula in summer 1935; it was found dead in the surface of the sea and towed to Murmansk (local newspapers erroneously described it as "Greenland whale")"	Tomilin, 1967 (p. 55)
Faroes and Shetlands			
66 ▲	summer 1892	"One specimen captured off the Faroe Islands"; by Norwegian whalers.	Collett, 1909
67 ▲	7 July 1898	Collet (1909) refers to "One specimen taken near the Faroe Islands (a female accompanied by a young one)"; by Norwegian whalers, in the summer. Possibly the same 2 individuals in the IWC database taken on the 7th July 189 by Norwegian whalers (station/factory: Strømnæs, Faroe).	Collett, 1909; IWC, 2013
68 ▲	summer 1903	Collet (1909) refers to "One specimen taken off the Faroe Islands"; by Norwegian whalers. Possibly the same individual mentioned in t IWC database as taken in the Faroe Islands by Norway (station/factory: Lopra. A/S Suderø) in 1903.	Collett, 1909; IWC, 2013
69 ▲	summer 1907	"Two specimens were also taken off the Faroe Islands"; by Norwegian whalers.	Collett, 1909
70 ▲	14 August 1671	"In our home-voyage to Hamburg I saw an example of this enmity of a North-caper whale and a sword-fish, near to Hitland ; they fought and struck at one another so vehemently that the water flew about like dust, sometimes one, sometimes the other was uppermost". Original source: Friderich Martens' report of a 1671 whaling voyage.	White, 1855 (p. 115)
71 ▲	1903 (presumably summer)	"The only other specimen I have heard of was got in 1903 by a Faroe whaler 50 miles off Shetland"	Haldane, 1907 (p. 13)
72 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
73 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
74 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
75 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
76 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
77 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
78 ●	Summer 1905-1914	One of 66 points mapped by Thompson (1918); whales taken off the Hebrides and off the Shetlands between 1908 and 1914, in the summer (June to August)	Thompson, 1918 (Fig. 1)
British Isles (Hebrides, Ireland)			

Map ID	Date	Record details	References
79 ▲	Summer 1905	"One was wounded off St. Kilda, but escaped"	Collett, 1909
80 ▲	Summer 1906	"six killed, and more seen [...] off the Hebrides, between the 13th June and the 4th August", by Norwegian whalers.	Collett, 1909
81 to 139 ●	Summer 1905-1914	59 points mapped by Thompson (1918) as whales taken off the Hebrides between 1908 and 1914 (of 66: 3 in May; 43 in June; 19 in July; 1 in August). In 1908 "the schools this year consisted of several hundred", and "the plankton-bearing currents probably flowed nearer land than in 1907, for the whales might be met with quite in the shallow water between islands and rocks. Their stay this year was of only three week's duration" (Collett 1909). Taken by Norwegian whalers (coastal whaling from bases in the Hebrides).	Collett, 1909; Thompson, 1918 (Fig. 1); Reid et al., 2003; IWC 2013
140 ▲	8-13 June 1908	"Five specimens [...] captured off Inishkea, Ireland, between June 8th and June 13th (among them one female and a young one)"; "They were all separate, and no schools were observed" (Collett 1909). By the Arranmore Whaling Company, on the island of S. Inishkea; under Norwegian management (Lillie 1910). The same record (5 individuals, in "Ireland N", by the UK, station/factory: Iniskea Is, Arranmore Whal. Co) is in the IWC database (2013).	Collett, 1909; Lillie, 1910; IWC, 2013
141 ▲	"first fortnight of June" 1909	Five taken by the Arranmore Whaling Company (shore whaling, Norwegian management); "within a radius of 70 miles north, south and west of Innishkea" (Lillie 1919). The same record (5 individuals, in "Ireland N", by the UK, station/factory: Iniskea Is, Arranmore Whal. Co) is in the IWC database (2013).	Lillie, 1910; IWC, 2013
142 ▲	summer 1910	9 taken: five by the Arranmore Whaling Company (S. Inishkea island), four by the Blacksod Whaling company (Mullet peninsula St Mayo); shore whaling, companies run by Norwegians (Lillie 1910). Likely to include the 4+4 individuals, in "Ireland N", taken by the UK (4 by station/factory Iniskea Is, Arranmore WhCo and 4 by station/factory Ardely Pt, Belmullet. BlacksodWhC) in the IWC database (2013).	Lillie, 1910; IWC, 2013
Mid-Atlantic			
143 ●	2 July 1876	"boats where lowered, without success, for 'a Right Whale' at 49°25'N 22°22'W, squarely on the Commodore Morris Ground". Original source: "a journal kept by the captain's wife (whaler <i>Ohio</i> , USA).	Reeves & Mitchell, 1986a (p. 231)
Jan Mayen			
144 △	1618	"whales both Greenland and right, were very plentiful round Jan Mayen when [King] James granted the fishing to Hull [i.e., 1618]". However, Lubbock provides no support to this statement (no references, no further information).	Lubbock, 1978 (p. 71)
Spain			
145 ○	25 July 1850	"It was at one time supposed that the <i>Balaena biscayensis</i> had become quite extinct; but this is certainly not the case. Whales are seen on the Cantabrian coast at intervals of about ten years. [...] On the 25th of July 1850, early in the morning, a whale appeared off Guetaria. Boats quickly pursued it; but the harpooner missed his aim, and the whale went off, heading N.W." The record is clearly described as Righ Whale, but assumed of low certainty given the unusual season.	Markham & Flower, 1881 (p. 975)

Table IV-3. Recent (post 1950) records of North Atlantic right whale (*Eubalaena glacialis*) in the summer months (June to September).

“Map ID” corresponds to the number on Figure IV-6. ● : species reliable, location reliable; ▲ : species reliable, location uncertain; ○ : species uncertain, location reliable.

Map ID	Date	Region	Record details	References
1 ●	September 1951	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 46); in Mitchell et al. 1986 (citing Sergeant 1966): "taken 'in error' from a Newfoundland shore station in 1951"	Mitchell et al., 1986; NOAA NEFSC, 2013
2 ○	July 1959	Grand Banks, Newfoundland and Gulf of Saint Lawrence	"An animal 'probably from this species' was seen in Dildo Arm, Trinity Bay, in July 1959"	Mitchell et al., 1986 (citing Sergeant 1966)
3 ●	18 June 1964	British Isles (Hebrides, Ireland)	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 4269)	Jacobsen et al., 2004 (Table 1; citing Maul & Sergeant, 1977); NOAA NEFSC, 2013
4 ○	8 June 1974	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Probable; ID: 464)	NOAA NEFSC, 2013
5 ▲	September 1977	Off Spain	Sighting offshore N Spain. From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 612)	NOAA NEFSC, 2013; Jacobsen et al., 2004 (Table 1; citing Aguilar 1981)
6 ●	10-21 July 1978	Grand Banks, Newfoundland and Gulf of Saint Lawrence	"Reported frequent feeding activity". Also in the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 638)	Lien et al., 1989; NOAA NEFSC, 2013
7 ●	2 August 1979	Southeast Greenland and the Cape Farewell grounds	Observation of 'in all probability two bowhead whales' by Norwegian whalers, but given the historical absence of bowheads from the W coast of Greenland, particularly in the summer, Reeves & Mitchell (1986b) consider it likely to correspond to right whales.	Reeves & Mitchell, 1986a (citing Jonsgard 1981)
8 ●	25 August 1979	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 801)	Lien et al., 1989; NOAA NEFSC, 2013
9 ●	31 August 1981	Grand Banks, Newfoundland and Gulf of Saint Lawrence	Female alone, matched to an individual seen off the US coast. Bonavista Bay; Newman's Cove.	Knowlton et al., 1992; Mitchell et al., 1986, citing Beamish 1981.
10 ●	26-28 July 1984	Grand Banks, Newfoundland and Gulf of Saint Lawrence	"was entrapped in a codtrap and resisted all attempts by humans to come near it. [...] Eventually the animal towed the codtrap and all its supporting grapnels out to sea". From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 2140)	Lien et al., 1989; NOAA NEFSC, 2013
11 ●	4 July 1987	Mid-Atlantic	From the the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 4268).	NOAA NEFSC, 2013
12 ●	5 July 1989	Southeast Greenland and the Cape Farewell grounds	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 4269). Matched to an individual seen 15 June 1989 in the Nova Scotial Shelf.	Knowlton et al., 1992; NOAA NEFSC, 2013
13 ●	5 August 1989	Mid-Atlantic	Mother + Calf. From the NOAA "Interactive North Atlantic Right Whale Sightings Map"; (reliability = Definite; ID: 5531). Both matched to individuals also seen off the US coast.	Knowlton et al., 1992; NOAA NEFSC, 2013
14 ●	6 September 1990	Grand Banks, Newfoundland and Gulf of Saint Lawrence	Female alone, matched to an individual seen off the US coast.	Knowlton et al., 1992
15 ●	21 July 1995	Southeast Greenland and the Cape Farewell grounds	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 9421). Also mentioned by Hamilton et al. 2007 (individual Eg # 1412, also seen in the Gulf of Maine as well as in 2003 west of Iceland)	NOAA NEFSC, 2013; Hamilton et al., 2007

Map ID	Date	Region	Record details	References
16 ○	18 August 1999	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Unknown; ID: 17738)	NOAA NEFSC, 2013
17 ●	17 September to 22 October 1999	Norwegian and Barents Seas	Observed from 17 September to 22 October. Sightings were confined to a rather small area in a sound between the mainland and a small island, Skorpa. It was matched to a Right Whale individual previously seen off Cape Cod, Massachusetts (41°54'N, 68°30'W) on 23 May, 1999. Also: from the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 18227).	Jacobsen et al., 2004; NOAA NEFSC, 2013
18 ○	28 July 2000	Faroes and Shetlands	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Probable; ID: 19607).	NOAA NEFSC, 2013
19 ○	August-Sept 2001	Norwegian and Barents Seas	"From August to September 2001 there was a right whale observation claimed to have been made in Oslo fjord, Southern Norway. The whale was observed at short distance, 50-100m, moving northwards east of Tofteholmene (59° 31'N, 10° 34'E). The next day the presumed same animal was seen in the same area moving southwards. The observation was made by a fisherman with 6 yr experience onboard a whale catcher in the Antarctic and he insisted that this was a right whale. However, the incident was not photo documented"	Jacobsen et al., 2004
20 ●	22-23 June 2003	Iceland	From the NOAA "Interactive North Atlantic Right Whale Sightings Map": 2 sightings in consecutive days of a group of 2 individuals, coordinates are the first day (reliability = Definite; ID: 26004 and 26005). Also mentioned by Hamilton et al. 2007 (individual Eg # 1412, also seen in the Gulf of Maine as well as in 1995 in the Farewell Grounds)	NOAA NEFSC, 2013; Hamilton et al., 2007
21 ●	14 July 2003	Southeast Greenland and the Cape Farewell grounds	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (reliability = Definite; ID: 26078).	NOAA NEFSC, 2013
22 ●	31 July 2005	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 29280).	NOAA NEFSC, 2013
23 ●	28 September 2006	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Definite; ID: 31979).	NOAA NEFSC, 2013
24 ○	4 July 2007	Mid-Atlantic	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Unknown; ID: 33604).	NOAA NEFSC, 2013
25 ●	August to Nov 2007	Southeast Greenland and the Cape Farewell grounds	Sound recordings from passive acoustic moorings - August to November 2007 (63 calls on 22 days, mainly in August and September)	Mellinger et al., 2011
26 ●	August to Nov 2007	Southeast Greenland and the Cape Farewell grounds	Sound recordings from passive acoustic moorings - August to November 2007 (931 calls on 22 days, nearly all in August)	Mellinger et al., 2011
27 ●	July to Dec 2007 + 8 July 2008	Southeast Greenland and the Cape Farewell grounds	Sound recordings from passive acoustic moorings - July to December 2007 (979 calls on 21 days; nearly all in July and August); Calls were also detected the next season on 8 July 2008	Mellinger et al., 2011
28 ●	Sept 2007	Southeast Greenland and the Cape Farewell grounds	Sound recordings from passive acoustic moorings - September 2007 (42 calls on 3 days)	Mellinger et al., 2011
29 ●	August 2007	Southeast Greenland and the Cape Farewell grounds	Sound recordings from passive acoustic moorings - August 2007 (1 call on 1 day)	Mellinger et al., 2011
30 ●	9 September 2010	Grand Banks, Newfoundland and Gulf of Saint Lawrence	From the NOAA "Interactive North Atlantic Right Whale Sightings Map" (Reliability: Unknown; ID: 40576).	NOAA NEFSC, 2013

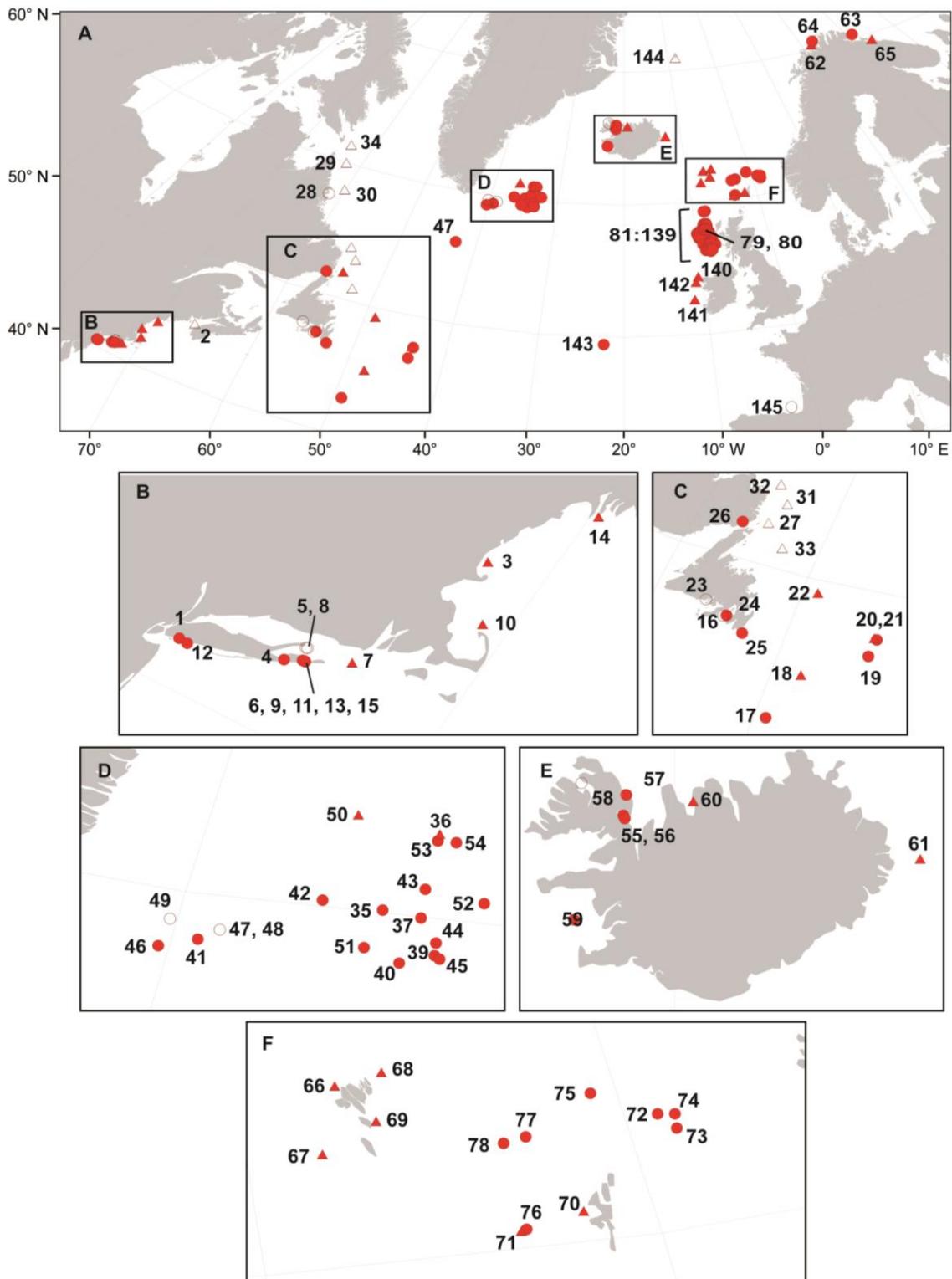


Figure IV-5. Historical (pre-1950) records of North Atlantic right whale (*Eubalaena glacialis*) in the summer months (June to September).

A) in the North Atlantic; B) Eastern United States; C) Grand Banks and Newfoundland; D) Southeast Greenland and the Cape Farewell Ground; E) Iceland; F) Faroes and Shetlands, distinguishing those for which there is higher (red symbols) or lower (open symbols) confidence in the species' identity and those for which there is higher (circles) or lower (triangles) precision in location. All data are presented on a $1^\circ \times 1^\circ$ grid in Bonne projection (standard parallel: 30°N , central meridian: 20°W). See Table IV-2 for a list of records.

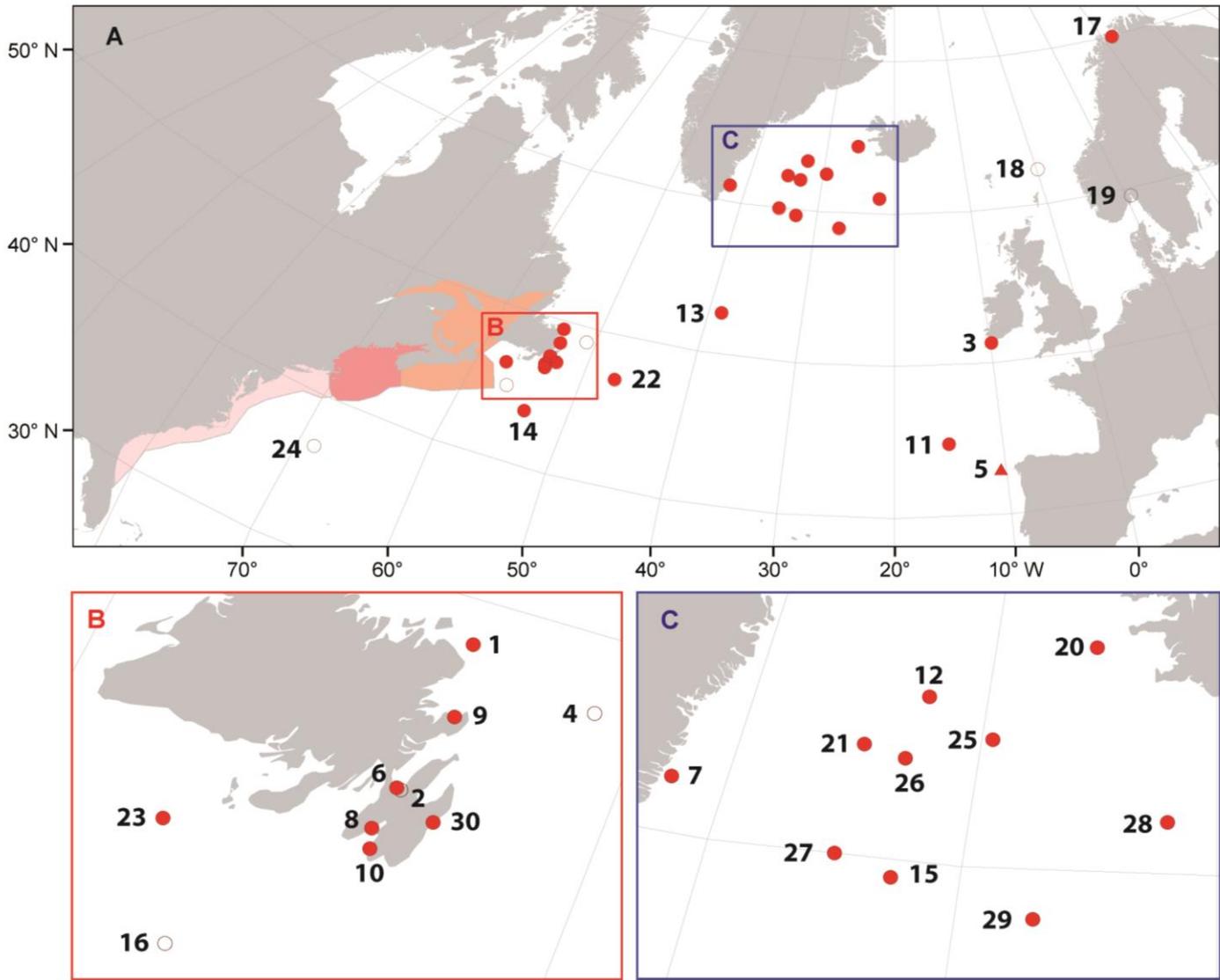


Figure IV-6. Recent (post-1950) records of North Atlantic right whale (*Eubalaena glacialis*) in the summer months (June to September), outside its main known summer grounds.

A) In the North Atlantic; B) Newfoundland; C) Southeast Greenland and Western Iceland, distinguishing those for which there is higher (red symbols) or lower (open symbols) confidence in the species' identity and those for which there is higher (circles) or lower (triangles) precision in location. The area shaded in red corresponds to the main feeding grounds for the current population (Bay of Fundy; Browns Bank; Great South Channel; Massachusetts Bay; Gulf of Maine; Jeffreys Ledge ; Georges Bank; Grand Manan Bank) concentrating 98.6% of June to September recorded sightings (sum of number of individuals in NOAA 2013). The coastal area southwards to Florida (in pink) has 0.4% of the sightings, while the Scotian Shelf and Gulf of Saint Lawrence to the north (in orange) have 0.9% of the sightings. All data are presented on a 1°x1° grid in Bonne projection (standard parallel: 30°N, central meridian: 20°W). See Table IV-3 for a list of records.

Appendix S6: Extended discussion

North Pacific whaling records and model predictions

North Pacific whaling records are impressive in their spatial coverage and sample sizes, far exceeding even today's standards of cetacean sightings surveys (Kaschner et al., 2012). Furthermore, as a result of whalers' search for new grounds, these records are likely to cover very well the geographic summer range of the species, including both areas where it was present and wide areas where it was not. It is therefore not surprising that the statistical models obtained from these data perform extremely well in predicting the occurrence of NPRWs. Nonetheless, these data and the models built from them have some intrinsic limitations that can lead to mismatches between the empirical observations and the model predictions.

This modelling exercise assumes that the whaling records come from a set of individuals with similar environmental preferences. However, in a previous study, Gregr (2011) found that separate environmental correlate models for right whales in the eastern and western North Pacific fitted the data better than a common model. This may reflect differences between separate populations, or differences in the spatial biases in the eastern and western data.

Although these data are impressive in their coverage, they are likely to include a number of false absences: visited cells where whales were present but were not recorded due to low sampling effort or temporal bias in the spatial records. For example, the United States coast north of San Francisco was visited by whalers in the late summer (August and September; see monthly maps in figures 10-13 of Smith et al., 2012 and video in Schmidt, 2012). If right whales were present along the US coast earlier in the summer, they would have been missed by these whalers.

There was also temporal variation across years. During the main period of NPRW exploitation, whalers moved broadly from east to west, exploiting new areas as whaling grounds were successively exhausted (Schmidt, 2012). If whales moved between these areas, the population using a given ground might have been depleted by whaling elsewhere before whalers reached and discovered that ground.

The whaling data may also include a number of false presences. In high latitudes there is a particularly high risk of confusion with bowhead whales, and although we have attempted to reduce this source of error (see Appendix S1), some incorrect assignments might remain, biasing the predicted distribution of right whales.

In summary, the species distribution model fit well the whaling data for the NPRW, but its spatial prediction may be affected by model limitations (a failure to capture all nuances of the

environmental conditions favoured by right whales), by data limitations (false absences, false presences, temporal and spatial biases), and by a combination of both.

Historical records in the North Atlantic

Historical records of NARWs in the summer are extremely biased temporally: two from the 16th Century; 8 from the 17th; 14 from the 18th; 40 from 19th; and 81 from the 20th Century. They mainly correspond to recent observations despite the fact that the species became progressively scarcer (Reeves et al., 2007) and was already considered commercially extinct by the 1750s (Allen, 1908). The historical records we collected therefore represent the final observations and captures of a nearly extinct species, unlikely to be perfectly representative of the species' original range. Indeed, given that the history of its exploitation has a strong spatial pattern, with particular whaling grounds successively exploited and exhausted (Reeves et al., 2007), this temporal bias comes inevitably associated with a strong spatial bias. In addition, there is more pervasive spatial bias towards coastal regions, where whales were more accessible and where records can be more easily mapped (i.e. more likely to be associated with a landmark). Indeed, offshore whaling records with accurate location information are very scarce: the most consistent and reliable source of offshore historical records is 19th century American whaling logbooks (Smith et al., 2012), but by 1800 NARWs were rare (Reeves et al., 2007).

Even though we concentrated on records for which there was a reasonable degree of geographic certainty, for 33 of the historical records (and one of the recent), only an approximate location is known that could not be mapped with reasonable certainty to a 1° cell. These include, for example, general locations referring to a landmark (e.g. "off the Faroes"), records at sea where only general coordinates were given (e.g. a "right whale ground" between 60-62°N and 33-35°W), records where precise coordinates existed but for a different date (e.g. whaler was at 49.19°N - 48.50°W on the 19 July 1754, and saw whales on the 23 July), and records where there was a precise latitude but only approximate longitude (e.g. 47°63'N "just E of the Grand Bank"; examples from Collet 1909 and Reeves & Mitchell, 1986; and see Table IV-2). Others correspond to precise coastal locations, but refer to dead whales that could have drifted from elsewhere (e.g. "a right whale came ashore dead in Sheepscot Bay in summer 1919"; Reeves et al., 1999).

Also, despite our effort to focus on records with a high level of taxonomic certainty, for 19 of our records (and six of the recent) the species is suspected but not confirmed as right whale. In particular, some of these could plausibly correspond to bowhead whales (e.g. whales seen and taken by the American whaler *Reliance* off the coast of Labrador between the 25 July and the 21 August

1768; Reeves & Mitchell, 1986) given that the two species were often not clearly differentiated in such early records.

Potential effects of climate variation

Most of the data on the distribution of the NPRW used to calibrate the models comes from a very narrow temporal window mainly in the mid-19th century (91% of presence records from 1840 to 1850). The environmental data, on the other hand, correspond to 20th century conditions (MLD and SST 1900-1992; NPP 1998-2007). The historical and recent records for NARW, in turn, span 400 years (1699 to 2010). Oceanic bathymetry variables are constant within the time scale of our analyses, but other environmental variables are not. In addition to the point of discussion provided in the discussion section in the main text, we present a map of NARW historical records color coded according to the date they correspond to (Figure IV-7). Our dataset of NARW records does not show a general tendency for a polewards shift over time (Figure IV-7), as could perhaps have been expected from a general temperature warming over this period (Mann et al., 2008), but the effects of climate change on the distribution of whales might in any case be more complex than that because of non-linear effects of climate on sea conditions (e.g. Moffa-Sánchez et al. 2014). Exploring these effects is beyond the scope of this paper.

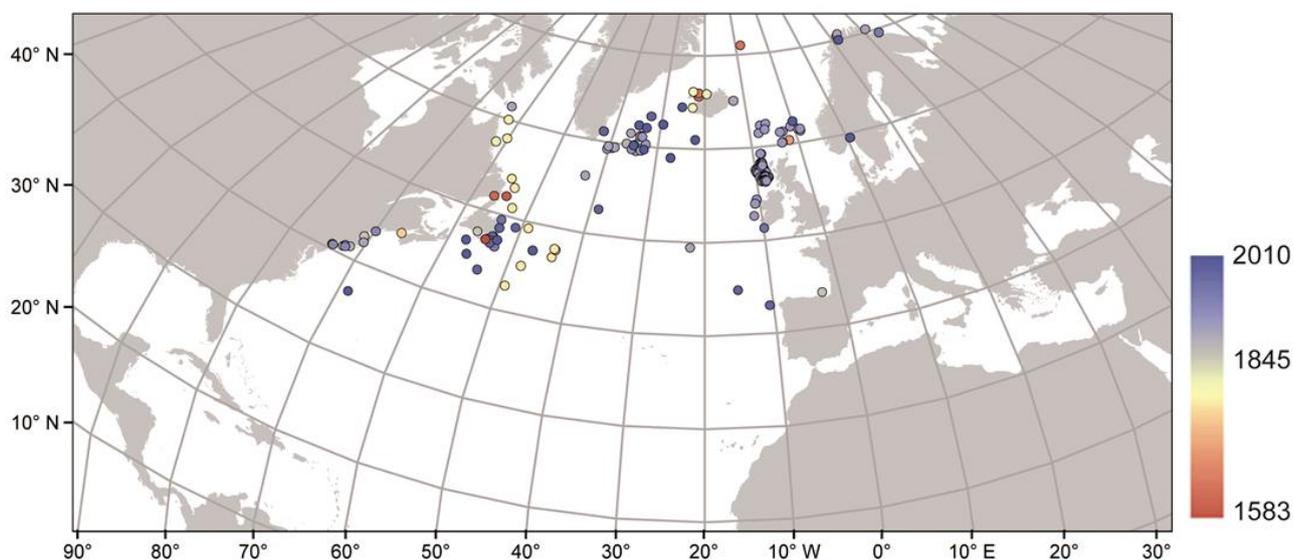


Figure IV-7. Historical (pre-1950) and recent (post 1950) records of North Atlantic right whale (*Eubalaena glacialis*) in the summer months, according to date.

Only recent records outside the main current summer grounds are presented. Records are color coded in relation to 1845, the peak of right whale exploitation in the North Pacific. The map is presented on a Bonne projection (standard parallel: 30°N, central meridian: 20°W).

Table IV-4. Comparison between the model predictions and species records in the North Atlantic

Region-by-region overview of the levels of agreement between the model's predictions for the summer distribution of the North Atlantic right whale and locations of known summer records for this species.

Region	Model prediction	Historical data	Recent data	Agreement	Discussion
USA coast from Delaware to Cape Cod	Coastal presence	A few coastal whaling records	A few coastal observations	Good	A few historical and recent records confirm the model's prediction of right whale presence in the summer, even if the relative rarity of these records (compared to much higher numbers of spring and winter records, both historical and recent) shows that the species is rare in this season.
Gulf of Maine, Bay of Fundy, Scotian Shelf	Absence near the coast (no predictions for the Bay of Fundy), presence in an offshore band	The few records do not suggest a regular summer presence in the coastal areas	The bulk of today's summer observations are this coastal area.	Poor	The model's predictions of absence in the coastal area are not contradicted by the historical data (that provides no evidence of a regular summer presence). However, they are strongly contradicted by recent data, as this is the species' most important current summer ground. May reflect the model's lack of predictive ability in shallow-depth regions.
Over and around the Grand Banks of Newfoundland	Presence	Well supported by whaling records	A few observations	Very good	The model's prediction of presence is well supported by a few precise historical records as well as by a 1880 map of an abandoned whaling ground.
Coastal Newfoundland and Gulf of St. Lawrence	Presence	Well supported by whaling records	A few observations around coastal Newfoundland, an increasing number of records in the Gulf of St Lawrence	Very good	The model's prediction of presence is supported by historical as well as recent records. The region was well known to 16 th and 17 th centuries Basque whalers, with historical records referring to two whaling seasons, the summer one potentially corresponding to right whales as predicted by the model.

Northern coast of Labrador	Absence	A few whaling records, but of uncertain species (potentially bowheads)	No observations	Medium	The few historical records are not a major challenge to the model's prediction of absence given that they may all plausibly correspond to bowhead whales.
Southeast Greenland and Cape Farewell Ground	Presence	A concentration of whaling records	Severall recent records	Very good	A relative concentration of historical combined with several recent records support very well the model's prediction for presence.
Iceland	Presence on the southern coast, absence on the northern coast	Historical records on both the southern and the northwestern coasts	One recent record just west of Iceland	Good	Predicted presence on the southern coast well supported by historical data. Absence on the north-eastern coast seems contradicted by historical records, but they are within coastal cells where the model makes no predictions.
Faroes and Shetlands	Presence around the Faroes; Shetlands at the edge of predicted area	Historical records in both archipelagos	One unconfirmed observation just north of the Shetlands	Good	Historical records mostly in cells of predicted presence, or at the edge of those.
British Isles (Hebrides, Ireland)	Absence	An exceptional concentration of historical catches	One observation south of Ireland	Bad	The model's prediction of absence is strongly contradicted by a concentration of historical whaling records and by a recent record. This may reflect the model's lack of predictive ability in shallow-depth regions, and/or its inability to predict temporally exceptional oceanic conditions.
Norwegian and	Presence	A few precise coastal	Two observations	Very good	The model's prediction of presence is well supported for the

Barents Seas (including the North Cape and Kola Peninsula)		whaling records in the North Cape, known as a coastal whaling ground). Possible region of destination for Basque pelagic whaling trips.			coastal North Cape region, which was also the location of a well-known historical whaling ground. The predicted presence in offshore areas in the Norwegian Sea is compatible with many records of Basque pelagic whaling trips to “Norway”. Also, it is worth nothing that the Dutch name of the species is Noordkaper.
Jan Mayen	Absence	A single historical record, but not a particularly reliable one	No observations	Medium	The single record is not a major challenge to the model’s prediction of absence. Indeed, it comes from a single sentence in a secondary source (Lubbock 1978 claimed “whales both Greenland and right, were very plentiful round Jan Mayen [in 1618]”) where it was provided unsupported. Jan Mayen was a base for Dutch bowhead whaling, and we found no other references to the presence of right whales in there.
Baltic Sea	No prediction	No historical records	A single recent record	No model prediction	The Baltic Sea is outside the area where the model makes predictions.
Iberian Peninsula (Bay of Biscay, Portugal) and Mediterranean Sea	Presence in five small coastal patches: in the Bay of Biscay, off central Portugal and in the northern Mediterranean	A single historical summer coastal record in the Bay of Biscay	No observations	Poor	An historical summer record brings some support to the model’s prediction of a suitable coastal patch in the Bay of Biscay (but the area was known as a winter whaling ground, so this record is considered exceptional rather than representative). An archaeological record in Portugal is of unknown season. No support to the predictions of summer presence in the Mediterranean (the few records for this region are in the winter).

Offshore central North Atlantic	Absence	One offshore record northeast of the Azores	Two offshore records (> 100 km to the NW of the Iberian Peninsula)	Medium	These records are in offshore areas where the model predicts absence. They are however not seen as a major challenge to the model's predictions given that similarly isolated records are also found in the central North Pacific outside the area predicted by the model, corresponding to rare presences in a region where there are many more records of whale absence. In that sense, the scarcity of records in the central North Atlantic is supported by the model's prediction of absence in this area.
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CHAPTER V

**HOW MANY RIGHT WHALES WERE THERE IN THE NORTH
ATLANTIC BEFORE COMMERCIAL WHALING? AN ESTIMATE
BASED ON NORTH PACIFIC WHALING RECORDS**

V. How many right whales were there in the North Atlantic before commercial whaling? An estimate based on North Pacific whaling records

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Abstract

The North Atlantic right whale (NARW, *Eubalaena glacialis*) is one of the world's most threatened whale species. Previously widespread, it came close to extinction after centuries of overexploitation, and currently persists as a population of only ca. 500 individuals in the western North Atlantic. Setting appropriate conservation targets for this species requires an understanding of its historical population size, as a baseline for measuring level of depletion and progress towards recovery. However, this is made difficult by the scarcity of records over its very long whaling history. Here, we propose a new estimate of the pre-exploitation population size of NARW based on a calculation of the carrying capacity of the North Atlantic for right whales. To obtain this estimate, we took advantage of a spatially explicit dataset on historical catches of North Pacific right whales (NPRW, *Eubalaena japonica*) to model the relationship between right whale density and the environment. Assuming that these two congeneric species select the same type of environmental conditions, we projected this model into the North Atlantic, to obtain a spatially explicit prediction for the summer distribution of relative abundance for the NARW. By scaling this with estimates of the pre-whaling NPRW population, we obtained high and low estimates of between 9,091 and 21,328 individuals for the overall abundance of NARW prior to exploitation. These results support previous estimates based on the historical record indicating that the NARW is still very far from recovery, but they are difficult to reconcile with recent genetic analyses. Our results also predict that there were two main areas of high summer density in the North Atlantic: north of the Grand Banks of Newfoundland and in the Norwegian Sea. We recommend these as priorities for future summer survey effort, with potential relevance to the conservation of this endangered species.

Introduction

Species conservation often involves setting population targets for the desirable overall number of individuals to be conserved, as baselines for measuring level of depletion, and as benchmarks for assessing progress towards recovery (Sanderson, 2006). Historical baselines are often considered for these purposes (Sanderson, 2006; McClenachan et al., 2012), but they are subject to human perceptions of what constitutes the “natural” state of populations prior to human impacts. This can be strongly biased for species that have been impacted over a long period of time (the “shifting baseline syndrome”; Pauly, 1995; Jackson, 2001; Kittinger et al., 2013).

Whales have been exploited for centuries as key economic resources across the world (Reeves & Smith, 2006), leading to reductions in population abundance (Woodby & Botkin, 1993; Roman & Palumbi, 2003), range contractions (Bockstoce & Botkin, 1983; Reeves et al., 2007) and even extirpations across entire oceans (Mead & Mitchell, 1984). The North Atlantic right whale (NARW, *Eubalaena glacialis*) was the first whale species exploited at an industrial scale, in what Reeves et al. (2007) described as “one of the most extensive, prolonged, and thorough campaigns of wildlife exploitation in all of human history”. The history of its exploitation extended for nearly a millennium, resulting in its near-extinction. Today, it persists as a small population of c. 500 individuals in the western North Atlantic, being listed as Endangered by the International Union for Conservation of Nature’s Red List of Threatened Species (Reilly et al., 2012).

Given the long history of its exploitation, there is considerable uncertainty regarding the original population size for the NARW. Several attempts have nonetheless been made to estimate it, focusing on the better-recorded western population. Aguilar (1986) estimated that from 1530 to 1610 Basque whalers took 25,000 to 40,000 whales from the coasts of Newfoundland and Labrador, including unknown proportions of right and bowhead whales (*Balaena mysticetus*). From the osteological identification of whale bones at a 16th Century Basque whaling station, Cumbaa (1986) concluded that roughly equivalent numbers of the two species were taken, leading Gaskin (1991) to estimate total catches of 12,000 to 15,000 right whales. Consistent with this, the population size in the northwestern North Atlantic was assumed to correspond to about 10,000 individuals, a figure adopted as a baseline for discussions of carrying capacity and extent of recovery (Reeves et al. 2007). However, the 50/50 ratio of bowheads to right whales in Basque catches was subsequently invalidated by DNA analyses, which revealed a single right whale among many bowheads (Rastogi et al., 2004a; McLeod et al., 2008). This led McLeod et al. (2008) to conclude that bowheads were the

principal target of Basque whalers in this region, and to question whether the impact of Basque whaling on right whales was actually substantial.

Further south, along the eastern coast of today's United States, a coastal right whaling industry focused on the winter calving grounds and spring northwards migration (Reeves & Mitchell, 1986c; Reeves et al., 1999, 2007), reaching its peak in the early 1700s (Reeves et al., 2007). Eighteenth century American pelagic whalers also captured right whales near the Grand Banks of Newfoundland (Reeves & Mitchell, 1986a). Building from a review of records of captures and of exports of baleen from American colonies, Reeves et al. (2007; see also Reeves et al. 1999) estimated that a minimum of 5,500 animals were killed between 1634 and 1951 (mainly pre-1750), consistent with a total population of "at least a few thousand whales present in the mid-1600s" in the western North Atlantic.

In the eastern North Atlantic, cows and calves in their wintering grounds were the main target of Basque whalers in the Gulf of Biscay, from the 11th to the 17th century (Aguilar, 1986; Azpiazu, 2000; Barkham, 2000b; Du Pasquier, 2000). Aguilar (1986) estimated that fewer than one hundred were taken per year. Right whales may have also been a target of Medieval coastal whaling further north in the English Channel (Musset, 1964) and further south off Portugal (Brito, 2011; Teixeira et al., 2014). 17th century Basque whalers captured right whales in the summer months off Iceland (Edvardsson & Rafnsson, 2006) and Norway (Du Pasquier, 2000). A right whaling ground off the North Cape in northern Norway was exploited by 17th-18th century Danish, Norwegian, Dutch and Basque whalers (Smith et al., 2006). Arctic whalers focusing on bowheads (mainly Dutch, but also British, German and Basque) may have occasionally taken right whales (De Jong, 1983; Reeves et al., 2007).

Even though the species was already very scarce by the mid-1800s, a few hundred were subsequently taken throughout the North Atlantic before they became legally protected in 1935 (Reeves et al., 2007). Today's population concentrates in the western North Atlantic, with only a few records in the eastern North Atlantic in the past 50 years (Reilly et al., 2012).

Besides what can be learned from whaling records, information on past populations can be obtained from genetic analyses. Today's NARW population has levels of genetic variation that are significantly lower than those of the southern right whale, *E. australis*, consistent with the fact that the latter, although also strongly affected by whaling, has survived in substantially larger numbers (Waldick et al., 2002). However, bottleneck analyses of living NARWs (Waldick et al., 2002) as well as of late-19th and early-20th centuries specimens suggest no substantial loss of genetic diversity in the past two

centuries (Rosenbaum et al., 2000a). More puzzlingly, the analysis of a 16th century bone from Labrador suggests genetic characteristics have not changed substantially since then (Rastogi et al., 2004a; Frasier et al., 2007; McLeod et al., 2010). This was an unexpected result, as NARWs are believed to have been depleted as a result of whaling over the past four centuries. Waldick et al. (2002) proposed that today's low genetic variation may have resulted from a slow but continual erosion of alleles over eight centuries of whaling, but to reconcile this with the genetic analyses would imply that the most important declines took place before the 16th century, not apparently compatible with the history of whaling in the western North Atlantic.

Here we attempt to inform discussions on the original population of the NARW by approaching the subject from a very different perspective: we estimate the ecological carrying capacity of the North Atlantic for right whales, based on whaling records for a congeneric species, the North Pacific right whale (NPRW, *E. japonica*). These two species of right whales are phylogenetically close (Rosenbaum et al., 2000a; Sasaki et al., 2005) and as specialist copepod filter feeders they have similar morphology (Woodward et al., 2006) and feeding behavior (Kenney, 2002). Another copepod specialist, the bowhead whale (Lowry et al., 2004), potentially affected the northern limit of both right whale species' ranges. Assuming that the similarities translate into comparable environmental preferences, the pre-whaling population of the North Pacific right whale, and the distribution of its abundance across space, can be used to estimate the right whale carrying capacity of the North Atlantic.

Like the NARW, the NPRW was extensively depleted, but its decline is more recent and better documented than that of the NARW. Indeed, the bulk of its exploitation was undertaken by 19th century American offshore whalers, whose exploits were recorded in their ship logbooks. A recent project (Smith et al., 2012), building from and expanding on previous efforts (Maury, 1852; Townsend, 1935), compiled data from a representative sample of these logbooks, mapping the locations of right whale catches across the entire North Pacific. With the bulk of NPRW whaling having taken place in a single decade (1840 to 1849; Josephson et al., 2008), catch records for this period provide extraordinarily detailed insights on the overall population size and distribution.

Here we combine information on historical catches of North Pacific right whales with environmental data to create a spatially explicit prediction of the relative abundance of right whales, from which we derive an estimate of the pre-whaling population size of North Atlantic right whales.

Methods and Results

The first step in our analysis consisted on compiling counts of right whales catches in the North Pacific from a set of 19th century American whaling logbooks. We then calibrated a statistical model describing variations of abundance over environmental gradients. This model was used to predict relative abundances in the North Atlantic, within the envelope of predicted presence obtained in a previous analysis (Chapter 4). Because these predictions relate to catches over a 10-year window in the North Pacific during which right whales were almost completely extirpated, we calibrated the predicted relative abundance with the total number of catches in the North Pacific, to obtain an estimate of the total abundance in the North Atlantic, which we consider as representative of the carrying capacity of the North Atlantic for right whales.

Data on the distribution of catches of North Pacific right whales

Spanning the world's oceans, often in multi-year trips to target mainly right and sperm whales (Reeves & Smith, 2006), 19th century American whalers successively exploited one North Pacific ground after the other. This resulted in a sequence of discovery-exploitation-depletion of local 'grounds' in a very short period of time (Josephson et al., 2008; Smith et al., 2012). Logbooks from these voyages contained information on the date, location and number of right whales struck as well as the days when no encounters or catches of right whale were reported. We obtained historical catch records of right whales in the North Pacific from a sample of these logbooks, extracted and compiled by Maury in the 1840s and by the Census of Marine Life (CoML) World Whaling History project in recent years (Appendix S1 in Chapter 4; Smith et al., 2012).

We considered as "catches" all the whales struck, rather than just those secured and processed on board, as a better approximation of the total mortality (given that struck whales often subsequently died from their wounds; Scarff, 2001). We focused on summer records (June to September), believed to be the main feeding period of North Pacific right whales (Clapham et al., 2004b), because the North Pacific was well explored by American whalers in this season (Smith et al. 2012), and hence summer catches should give a fairly reliable overview of the spatial distribution of the NPRW population. We focused on catches during the 1840-1849 period because this corresponds to the bulk of NPRW exploitation (80% of the catches; Scarff, 2001), and this period is short enough in relation to the life cycle of right whales (NARW's reach sexual maturity at about nine years; Kraus et al., 2001) to allow us to assume that recruitment during this period had little effect on overall catches.

We mapped on a 1°x1° grid the number of catches per cell, noting as zero those where whalers were present but no right whales were caught. We considered only cells north of 20°N, with a sampling effort of at least three days (in order to reduce the risk of false absences – visited cells where whales were present but not recorded), within the envelope of predicted presence of right whales in summer (Chapter 4). The bulk of catches was located primarily in the Gulf of Alaska, east of Kamchatka and along the Kuril Islands, and less importantly in the Sea of Japan and Sea of Okhotsk (Figure V-1.A).

We considered for analytical purposes that this map approximates the density of NPRWs across the Pacific pre-whaling. We did not correct for sampling effort (number of visits per cell) because fishing effort is often driven by abundance, with fishermen focusing on those areas known to be suitable to the target species (“preferential sampling”; Diggle et al., 2010). We also assumed that whales did not change their distribution substantially during the analyzed period (e.g., by moving away from the exploited areas, or because of environmental variation), which we believe is a reasonable assumption given the short duration of the period.

Environmental predictors

We selected as predictors environmental variables known to be correlated with the distribution of right whales and/or their main prey in summer. They consisted of three climatic variables (averaged over June to September) – Sea Surface Temperature, SST (Norberg & DeAngelis, 1997; Rutherford et al., 1999; Gregr & Coyle, 2009), Mixed Layer Depth, MLD (Baumgartner & Mate, 2003) and Net Primary Productivity, NPP (Norberg & DeAngelis, 1997) – and three bathymetric features – depth, DEPTH, slope, SLOPE and distance to land, LANDDIST (Hamazaki, 2002; Kaschner et al., 2006; Gregr, 2011; Torres et al., 2013). Environmental datasets were selected such that they cover both the North Pacific and the North Atlantic basins, across the largest period of time possible, and with a spatial resolution of at least 1 degree of latitude/longitude (Table V-1).

Table V-1. Environmental predictors used in the analysis.

Acronym	Variable	Derived from	Period averaged	Reference
SST	Sea Surface Temperature (°C)	NODC WOA94	1900-1992	Levitus & Boyer, 1994
MLD	Mixed Layer Depth (m)	NODC WOA94	1900-1992	Monterey & Levitus, 1997
DEPTH	Depth (m)	NOAA-NGDC ETOPO1	-	Amante & Eakins, 2009
LANDDIST	Distance to Land (km)	AquaMaps	-	Kaschner et al., 2008

Abundance modeling in the North Pacific

We predicted the relative abundance of NPRWs by modeling the relationships between catch statistics for the period 1840-1849 and the associated environmental conditions. Species abundance is generally modeled with a Poisson distribution, which is appropriate to the nonnegative, discrete nature of count data (Cameron et al., 1998). However, this distribution relies on some assumptions that may be invalidated by overdispersion caused by the high proportion of zeros in the count data (i.e., 'zero-inflation') often found in field surveys for rare species (Welsh et al., 1996). This in turn affects the computation of the model, potentially resulting in erroneous conclusions about the explanatory power of the predictors included in the model and incorrect predictions (Welsh et al., 1996; Ridout et al., 1998; Tu, 2006). To address this problem, zero-inflated count data can be modeled by a two-step mixture-model: first modeling a binary presence/absence response with a logistic regression; then modeling the count data (e.g. with a Poisson regression) to obtain predictions of abundance, conditional on the species presence (Welsh et al., 1996; Barry & Welsh, 2002). Modeling presence and abundance separately allows the selection of different environmental and geographical covariates, acknowledging that spatial patterns of occurrence and of abundance can be driven by different factors (Ridout et al., 1998). By modeling the count data with a distribution not truncated at zero, mixture-models implicitly allow the prediction of unoccupied suitable sites, acknowledging the existence of stochastic processes driving the abundance of species (Potts & Elith, 2006).

The subset of whaling data on which we focused included a high proportion of zeros (>85%), reflecting the wide coverage of whaling effort in the North Pacific both inside and outside the right whale whaling grounds (e.g. covering sperm whale grounds across 30°N and bowhead grounds north of 60°N; Smith et al. 2012). To model right whale abundance from these zero-inflated count data, we have drawn from the mixture-model approach by separately modeling NPRW presence and abundance. The envelope of predicted presence in the summer months was obtained from a previous study (Chapter 4) that used Boosted Regression Trees (BRT, Elith et al., 2008) to combine environmental data with NPRW presence/absence records to generate predictions of the probability of occurrence. By applying a threshold to this probability of occurrence (Jiménez-Valverde & Lobo, 2007) we obtained the predicted distribution range of the species. 638 cells were included in this envelope, of which 304 contained at least one record of NPRW, for a total of 1030 catches. We then modeled the count data within this envelope using a Generalized Additive Model (GAM; Hastie & Tibshirani, 1986).

GAMs are regression-like models that use smoothing splines to relate the response and the explanatory variables, allowing non-linear relationships (Hastie & Tibshirani, 1986). These are often used to model the relationships between species and their environment (Guisan et al., 2002) and provide great flexibility in modeling complex ecological relationships with no predefined shape (Barry & Welsh, 2002). Standard Poisson often fails to fit overdispersed data, commonly associated with ecological counting datasets (Barry & Welsh, 2002). Negative Binomial regression has shown good ability to deal with extra-Poisson variation (Lawless, 1987; Ver Hoef & Boveng, 2007). We tested residual overdispersion for both Poisson and Negative Binomial distributions, by comparing the value of the dispersion parameter described by Zuur et al. (2009). The predictive power of the Poisson model was slightly higher but only the Negative Binomial accounted efficiently for overdispersion in the residuals (Table V-3 of Supplementary Information) so we have fitted our model with this distribution. We allowed for four degrees of freedom for each spline to avoid overfitting and selected the default thin plate regression splines as the smoothing function (Wood, 2003). GAM was implemented using the *mgcv* package (Wood, 2011) in R (R Development Core Team, 2013) where the dispersion parameter θ of the Negative Binomial is determined internally in model fitting.

We selected the variables and interaction terms to include in the GAM through a stepwise forward approach, based on optimizing the Akaike Information Criterion (AIC) and deviance explained. This resulted in the selection of four out of the six environmental variables in Table V-1 (SST, MLD, DEPTH and LANDDIST), plus one interaction (SST*DEPTH) as predictors of NPRW abundance.

Predictions of the spatial distribution of the relative abundance of right whales from this GAM were projected into a $1^\circ \times 1^\circ$ grid in the envelope of predicted presence, by assigning a number of individuals to each cell based on local environmental values and the model's fitted functions (Fig. 1B). The absolute values of standard error estimates were also calculated for each predicted cell and mapped, as measures of the uncertainty in the spatial predictions of the model. The selected GAM explained 31.9% of the deviance with an R-squared of 0.30. Smooth functions for each of the selected covariates are provided in Figure V-3 of Supplementary Information. They indicate that the abundance of NPRW in the summer is associated with low sea surface temperature (less than 10°C), at a distance from the coast comprised between ca. 200 and 600 kilometers. NPRW density is negatively correlated with the mean depth and the depth of the mixed layer.

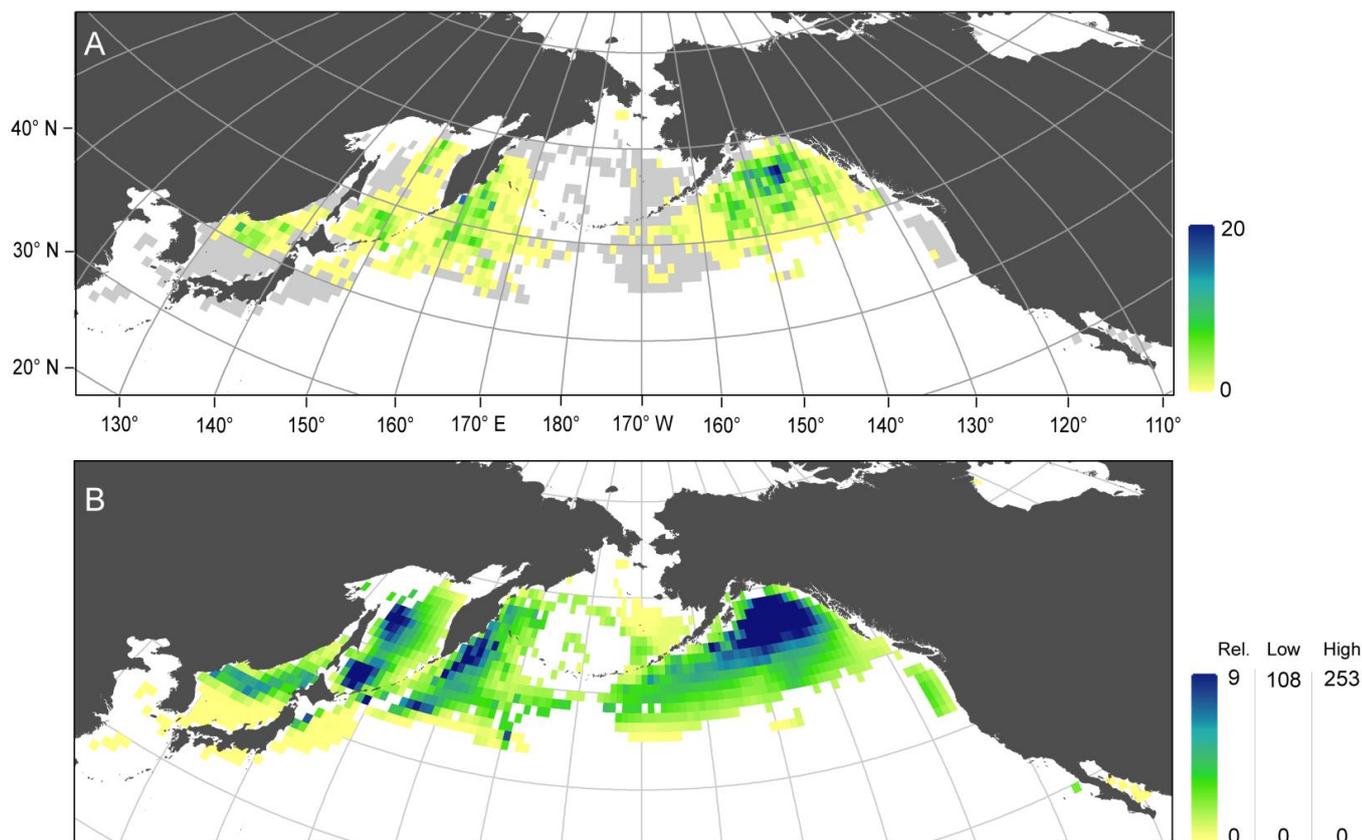


Figure V-1. Historical catches of North Pacific right whales, and model predictions of abundance in the North Pacific.

A) Data used to calibrate the species distribution model. The number of right whales caught in the summer months (June to September) are represented, based on 1840-1849 American whaling records. Grey areas represent cells within the envelope of predicted presence of NARW (Chapter 4), which had no data from the subset of data used to model abundance. B) Predicted abundance from a GAM fitted to the historical catch data, within the envelope of predicted presence; white cells are outside of this envelope. Values correspond to relative abundances (Rel., based on the sample of whaling data analysed) as well as low and high bounds of absolute abundance per cell (after calibration with total mortality data across the North Pacific). All data are presented on a $1^\circ \times 1^\circ$ grid in Bonne projection (standard parallel: 30°N ; central meridian: 170°W).

Model validation

Two approaches were used to assess the predictive accuracy of the selected model: we first compared the predicted and observed values per cell using the full dataset, then performed a 50-fold cross validation using a random half of the dataset to build the model and the remaining data to test the prediction (Fielding & Bell, 1997).

For both of these approaches, three statistics were calculated: Pearson's correlation coefficient r , Root Mean Square Error RMSE and the average error AVE_{error} . Pearson's correlation coefficient, r , measures the linear dependence between predicted and observed values. It can vary from -1 to 1,

with 1 representing a perfect positive correlation between the two datasets. RMSE represents the standard error of the differences between predicted values and observed values and AVE_{error} the mean error between observed and predicted values. The closer these two statistics are to zero, the better the prediction (see Potts & Elith, 2006 for further explanation on these different statistics).

We obtained reasonably high values for the Pearson correlation coefficient ($r=0.56$ in the validation with the original dataset; $r=0.46$ in the 50-fold cross validation with half of the dataset), and low values of RMSE and AVE_{error} (RMSE= 2.25 and $AVE_{\text{error}}=0.033$ in the validation with the original dataset; RMSE= 2.55 and $AVE_{\text{error}}=-0.014$ in the cross validation with half of the dataset), indicating a good performance of the model in the North Pacific.

Estimates of total population size in the North Pacific

We assume, conservatively, that the total NPRW mortality between 1840 and 1849 is equivalent to the total pre-whaling population size. To account for the uncertainties that may affect this estimate, we considered a low bound based on the most pessimistic values for a number of parameters, and a high bound based on the most optimistic values.

We considered three sources of uncertainty (Table V-2). First, in the calculation of the total catches of right whales in the North Pacific, Best (1987) obtained two estimates for the 1840-1849 period: a lower estimate (of 10,976 individuals) based on oil and whalebone yields imported into the United States, corrected by estimated proportions of different species of whale; and a higher estimate (11,306 individuals) based on catches per voyage stratified by voyage type. Second, total catches account for just a fraction of total mortality, given that a non-negligible number of individuals are killed but not processed, including those that escape after being harpooned but die later from the injuries and those that sink or otherwise not secured after being killed. Scarff (2001; his Table 1) reviewed the literature for struck-but-lost factors for pelagic right whaling, as well as proposing new values based on his own calculations. We retained the lowest and the highest values among these (respectively, 1.2 and 2.43 whales killed for each processed). Third, although right whaling in the North Pacific was mainly by American whalers, there was a non-negligible contribution by other whaling nations. Based on a preliminary review of historical sources, Scarff (2001) concluded that “non-American registered ships may have constituted as much as 15-20% of the whaleships on the northern right whale grounds”. We used 10% and 20% as low and high bounds. From these parameters, we reached a low estimate of 14,635 and a high estimate of 34,342 right whales killed in the North Pacific between 1840 and 1849 (Table V-2).

Estimates of total population size in the North Atlantic

Summing (across all cells where the species was predicted as present) the predicted values of counts of right whales in the North Pacific results in a total of 1227 individuals. This represents just a fraction of the number of catches made during the overall whaling effort (Smith et al. 2012). Hence, the ratio between the estimate of overall mortality and 1227 quantifies the relationship between the total population size and the relative abundance as predicted by the model. We obtained a ratio of 11.93 for the low bound and of 27.99 for the high bound (Table V-2). Multiplying the values of predicted (by the GAM) relative abundance per cell by these ratios produces a map of predicted absolute abundance per cell (Figure V-1.B).

Extrapolating the GAM's predictions into the North Atlantic (within the envelope of predicted presence), we obtained a prediction of the distribution of relative abundances of right whales in this basin, based on the assumption that they have environmental preferences similar to right whales in the North Pacific. The NARW is predicted to have occurred at high abundance in two main regions: east of the Grand Banks of Newfoundland and in the Norwegian Sea (Figure V-2.A). These two areas are characterized by shallow and cold waters, with a relatively low depth of the mixed layer and a distance to the coast of between 200 and 600 kilometers. The map of absolute standard error around the estimates indicates high certainty of the model in these areas (absolute standard errors < 2.0), while model predictions at the edge of the presence envelope are less reliable (e.g. in the Mediterranean, off the eastern United States coast; absolute standard errors > 4.0).

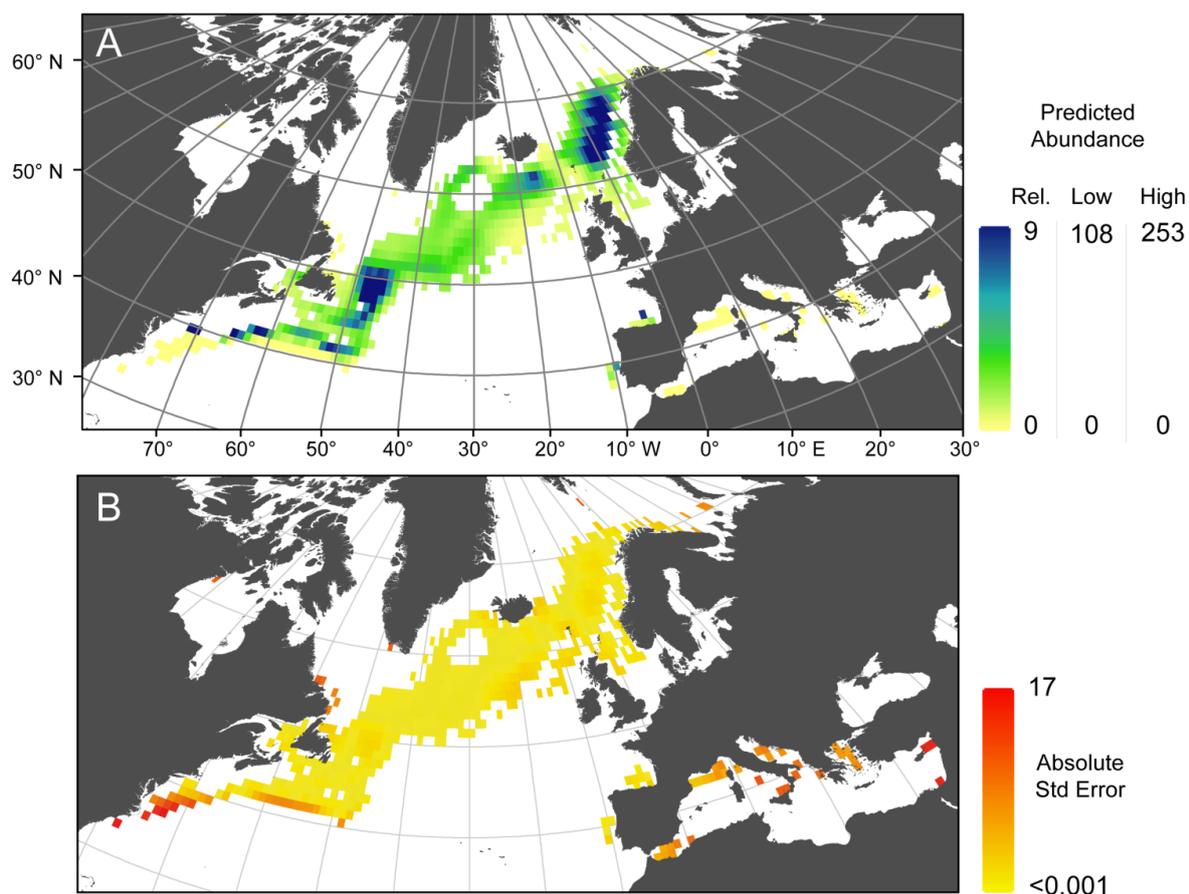


Figure V-2. Model predictions of right whale abundance in the North Atlantic and absolute standard error of the prediction.

A) Predicted abundance from a GAM fitted to historical catches records for the North Pacific right whale and extrapolated to the North Atlantic within the envelope of predicted presence; white cells are outside this envelope. Values correspond to relative abundances (Rel., based on the sample of whaling data analysed) as well as low and high bounds of absolute abundance per cell (after calibration with total mortality data across the North Pacific). B) Absolute values of standard error for the model estimates. Higher values represent higher uncertainty in the model prediction of abundance. All data are presented on a 1°x1° grid in Bonne projection (standard parallel: 30°N; central meridian: 30°W).

The sum of the predicted relative abundance values across the North Atlantic was 762. By multiplying this by the ratios (11.93 and 27.99) defined above, we estimate that the total carrying capacity of the North Atlantic for right whales is, or was, between 9,091 and 21,328 individuals (Table V-2), including 3,913–9,181 in the western North Atlantic (west of 30°W) and 5,178–12,147 in the eastern North Atlantic.

Table V-2. Estimates of the total pre-exploitation population of North Atlantic right whales.

The calculation uses the relationship between the estimated total mortality in the 1840-1849 period and the predicted relative abundance for the North Pacific (NP) to estimate total population sizes for the North Atlantic (NA) based on the predicted relative abundance in the latter. Two scenarios are presented (low bound and high bound) based on either the lower or the higher values in the literature for the relevant parameters. 1Estimate of overall numbers of right whales taken in the North Pacific in the 1840-1849 period, from Best (1987). The low estimate based on oil production statistics, and the high to records of catches per voyage. 2Correction factors for the number of whales killed by whalers that were lost (hence not accounted for in the total catches), corresponding to the lowest and the highest values among those reviewed or proposed by Scarff (2001). 3Contribution of non-American whaling to the total mortality. The low bound ignores non-American whaling, the high bound follows Scarff's (2001) assumption of 10% non-American participation. 4Estimated total mortality in the North Pacific in the 1840-1849 period, obtained by multiplying the total catches in the North Pacific by the struck-but-lost factors and (in the case of the higher bound) assuming 10% non-American whaling. 5Ratio between the total mortality and the sum of the predicted abundance across the North Pacific as predicted by the GAM model (1227). 6Predicted carrying capacity of the North Atlantic to right whales, obtained by multiplying the ratio (the previous column) by the sum of the predicted abundance across the North Atlantic (762). Values between parenthesis correspond to the predictions to the west and to the east of 30°W.

	Total catches in the NP ¹	Struck-but-lost factors ²	Non-American whaling ³	Total mortality in the NP ⁴	Ratio mortality/overall predicted NP abundance ⁵	Predicted carrying capacity in the NA (West/East) ⁶
Low bound	10,976	1.2:1	10%	14,635	11.93	9,091 (3,913/5,178)
High bound	11,306	2.43:1	20%	34,342	27.99	21,328 (9,181/12,147)

Discussion

We provide a new estimate for the basin-wide pre-whaling population of the North Atlantic right whale (Table V-2), as well as a prediction of its spatial distribution of abundance (Figure V-2). Given that these results are based on a set of strong assumptions and multiple sources of uncertainties that are worth putting in context and discussing. Below we discuss the strengths and limitations of these results, the extent to which they are supported or contradicted by the historical record and genetic analyses, and their implications for the conservation of the North Atlantic right whale.

Uncertainties and assumptions

The history of whaling in the North Pacific is reasonably well documented. However, considerable uncertainty remains about the overall mortality of right whales inflicted by mid-1800s whalers

(resulting from uncertainty in total catches, in rates of animals struck and lost, and in the contribution of non-American whaling; Best, 1987; Scarff, 2001), which propagates into uncertainty around our estimates of the carrying capacity of the North Atlantic.

Given these considerations, the estimates of the total population size for the NARW are likely to be conservative (i.e., underestimates) for three reasons. First, they assume that the NPRW population was at full carrying capacity in the mid-1800s, which may be somewhat incorrect, given that native people from both coasts of the Pacific exploited right whales to some extent (e.g. Japanese whalers, Omura, 1986; indigenous people of north-western North America, Huelsbeck, 1988). Second, although the NPRW was highly depleted in 1840-1849 (Josephson et al., 2008), sufficient individuals survived to support catches of >2,000 individuals in the subsequent decade (Scarff, 2001), and so the overall population size was larger than the total mortality in this decade. Third, the abundance model was only applied in the North Atlantic within the envelope of environmental conditions found in the North Pacific (Chapter 4), which might exclude areas where the NARW was occasionally present.

The extrapolation from the North Pacific to the North Atlantic relies on two strong assumptions (see Chapter 4 for a detailed discussion). First, we assumed that the original distribution and abundance of the two right whale species were driven by similar environmental conditions. This is something which we cannot demonstrate, but the perceived similarities in the ecology, morphology and phylogeny of these two species (Nemoto, 1970; Rosenbaum et al., 2000a; Woodward et al., 2006) justify the interest in building from this assumption. Furthermore, in a previous study we found that predictions for the distribution of the NARW based on correlations between the historical distribution of the NPRW and environmental predictors were generally well supported by historical and recent distribution data in the North Atlantic (Chapter 4), suggesting that this approach is informative.

Second, we assumed that right whale abundances respond similarly to environmental conditions in the two ocean basins. We only made predictions within the envelope of predicted presence of NARW, where the values of predictor variables are within the range of environmental conditions encountered in the calibration dataset, which reduces the level of uncertainty associated with the extrapolation from the North Pacific to the North Atlantic. Nonetheless, there may be differences in the way species' abundances respond to oceanic processes under similar environmental conditions that we did not account for (e.g., if the abundances of their main prey species respond differently to similar environmental conditions; if the overall carrying capacity of the two ocean basins is affected differently by other factors such as availability of calving areas).

In the absence of sufficiently fine-scaled, spatially explicit climatologies for the mid-19th Century, there is a time lag between the whaling data (1840 to 1849) and two of the environmental predictors used to construct the models (SST and MLD, averaged over 1900-1992). The use of a long-term climatology is likely to mitigate the effects of climatic variation on the quality of the model's predictions (Gregr, 2011). On the other hand, we are assuming that spatial structure (i.e. the fact that some regions support higher abundances than others) is the same through time. Our approach would not be affected by uniform changes in environmental conditions across the study area. However, climate change may nonetheless affect the predicted distribution of abundance in the North Atlantic in ways we could not account for, for example through fundamental changes in the ways our predictors related to each other in mid-19th century with respect to current conditions.

Agreement between predictions, the historical record and genetic analyses

Our results suggest that the North Atlantic once harbored a total population of ten to twenty thousand right whales. This estimate is compatible with the surviving historical record, under the reasonable assumption that the latter is very incomplete (Reeves et al., 2007) and hence total catches are likely to have been considerably greater than is shown in that record.

Overall, the fact that today's population of c. 500 (Pettis, 2013) is a small fraction of the predicted carrying capacity agrees well with the knowledge that the NARW was previously much more widespread than it currently is, and hence much of its historical distribution across the North Atlantic appears to be currently unoccupied (Chapter 4).

The GAM results for the spatial distribution of abundance (Figure V-2) predict two main concentrations in the summer months: east of the Grand Banks of Newfoundland, and in the Norwegian Sea. There is some evidence of whaling in these areas (that would have only be accessible to whalers after the 17th century development of methods for whale processing in the high seas; Reeves & Smith, 2006). Logbooks of a few 18th century American whalers report catches east of the Grand Banks (Reeves & Mitchell, 1986a) and Clark (1880) mapped an (already exhausted by then) right whaling ground in this general location. In a review of Basque offshore whaling trips, from records of arrivals to major French whaling ports, (2000) found evidence of more than two hundred 17th century voyages working "in Norvège". This plausibly may refer to the Norwegian sea, rather than (as generally assumed) the North Cape (Smith et al., 2006) or the Arctic seas further north (where bowhead whales would have been the target).

Having said that, the migratory behavior of right whales means that the areas predicted by our model as peaks of summer abundance are not necessarily where most whaling took place. Indeed,

on both sides of the North Atlantic there were well-developed coastal whaling operations in the winter calving grounds and along the migration routes that might have substantially affected the populations, particularly because of their focus on adult females and calves (Aguilar, 1986; Fujiwara & Caswell, 2001). Even though Aguilar (1986) estimated that only “some dozens, possibly reaching one hundred” whales would have been taken annually by Basque whalers in the Gulf of Biscay, the cumulative impact over nearly eight centuries (11th-17th) might have been considerable. Coastal whaling in Europe may also have been more widespread than only in the Gulf of Biscay, given evidence of medieval whaling in the English Channel (Musset, 1964) and in Portugal (Brito, 2011; Teixeira et al., 2014), potentially affecting a large expanse of the NARW’s original eastern calving grounds. On the American coast, a (mainly) coastal right whaling industry from Georgia to Massachusetts lasted from the 17th to the early 20th century peaking in the early 1700s (Reeves & Mitchell, 1986a; 1988; Reeves et al., 1999, 2007). Based on records for this fishery, Reeves et al. (2007) estimated that there were “at least a few thousand whales present in the mid-1600s” in the western North Atlantic, compatible with our prediction for a western population of about four to nine thousand individuals (Table V-2).

Much more challenging is to reconcile our estimates – and the historical record (Reeves et al., 2007) – with the results of recent genetic analyses that found no evidence of a major loss of genetic diversity in the past four centuries (Rastogi et al., 2004a; Frasier et al., 2007; McLeod et al., 2010). Even though based on a single bone, these results are contrary to the expectation that the low current genetic diversity of the NARW (Waldick et al., 2002) might be the result of a substantial population decline after the 16th century, as a result of whaling by the Basques, Americans and (perhaps more opportunistically) other European whaling nations (Reeves et al., 2007). The latest genetic results raise three hypotheses. First, relatively low levels of genetic variability may be a result of natural events that preceded impacts by humans (Waldick et al., 2002). Second, low genetic diversity may be a result of slow but continual erosion of alleles over centuries (Waldick et al., 2002), but mostly before, rather than after, the 16th century. For the eastern population, this could be explained if European coastal whaling (mainly but not only by the Basques) had a stronger early impact than currently assumed, but this would still leave a relatively large population with breeding grounds on the American coast, for which there is no evidence of significant pre-16th century exploitation. And third, contrary to our results and to the current interpretation of the historical record (Reeves et al., 2007), the original NARW population might have been relatively small, and so the impact of whaling might not have been as important as currently assumed (Frasier et al., 2007; McLeod et al., 2010). Future genetic analyses, particularly of old material from middens, artefacts etc., will be key to disentangling among these hypotheses.

Implications for the present and future of the North Atlantic right whale

If our estimate for the carrying capacity of the North Atlantic is within the right magnitude, the current basin-wide population of North Atlantic right whales is very far from full recovery, at less than 6% for the total population size, and less than 13% for the western population. With the original main cause of decline (whaling) halted since 1935, when the species became legally protected (Reeves et al., 2007), the population should now be on a firm ascending trajectory, as observed in some other whale populations (Magera et al., 2013). This has not been the case for the North Atlantic right whale, as the species remains at risk of extinction (Greene & Pershing, 2004; Reilly et al., 2012), with an apparent high mortality rate (Moore et al., 2007). The main current threats include entanglement in fishing gears and collision with ships (Knowlton & Kraus, 2001; Johnson et al., 2007; Knowlton & Brown, 2007), possibly about to be exacerbated by climate change (Greene & Pershing, 2004; Kenney, 2007).

If our assumption that the environmental preferences of North Atlantic right whales are similar to those of their North Pacific congeners is correct, then we predict that the main suitable summer habitats for this species should be found near the Grand Banks of Newfoundland and in the Norwegian Sea. This agrees well with previous analyses modeling the abundance of calanoid copepods (*Calanus finmarchicus*), the primary food of NARWs (Baumgartner et al., 2007), which predicted high summer concentrations over these two areas (Speirs et al., 2006). The main (known) current summer grounds of the NARWs are found further south in the Gulf of Maine, Bay of Fundy, and Scotian Shelf (NOAA-NEFSC, 2013), but our model makes no predictions for these areas (a result of the fact that the NPRW catch data used to calibrate the model comes mainly from data from deep offshore waters) even if we predict some cells of relatively high abundance further offshore (Figure V-2.A). Data from ongoing monitoring based on individual photo-identification indicates that a substantial number of individuals are not accounted for every year in the known grounds, raising the possibility that other important summer grounds exist (e.g. Cape Farewell, Gulf of St Lawrence; Hamilton et al., 2007). Our results raise specific hypotheses for the location of these grounds, and hence priority areas for future surveys. The area east of the Grand Banks is particularly promising, given its closer proximity to the breeding grounds off Florida and Georgia. If these areas are found to be regularly occupied by NARWs, they will correspond to hitherto unacknowledged priority areas for the conservation of this species.

Conclusion

The history of the exploitation of the North Atlantic right whale is still being written, as new analyses question previously established assumptions about its original population size and of catches through whaling (Rastogi et al., 2004a; Frasier et al., 2007; McLeod et al., 2008, 2010). To inform this discussion, we present a new estimate of the pre-whaling population size based on calculations of the North Atlantic carrying capacity. This new approach bypasses the difficulties inherent to reconstructing an historical baseline after centuries of poorly-documented overexploitation (Reeves et al., 2007), but comes with important (unverified) assumptions.

Our predictions support previous estimates based on the historical record that there were thousands of right whales in the North Atlantic, and that this species is still very far from recovery. We have also generated a prediction of the spatial distribution of the summer abundance across the North Atlantic, with immediate applications to guiding future surveys, and potential implications for the conservation of this species. Our results are generally compatible with the historical record, but more difficult to reconcile with recent results of genetic studies suggesting that the pre-whaling population may not have declined as much as previously believed over the past four centuries.

Future work is still needed to clarify how many right whales there were in the North Atlantic, a question with implications for understanding the extent of human impacts on this species, and informing our vision for the options available for its future.

Appendices

Table V-3. Comparison of the explicative and predictive performance of negative binomial and poisson GAMs.

θ is the dispersion parameter for the negative binomial. r = Pearson correlation coefficient; RMSE = Root Mean Square Error; AVE_{error} = Average error; ϕ = residuals dispersion parameters, as described by Zuur et al. (2009)

	Negative Binomial ($\theta=0.91$)	Poisson
R^2	0.30	0.37
Dev. Expl. (%)	31.9	37.8
Validation with the original data	$r = 0.56$; RMSE=2.25 ; $AVE_{error}=0.033$	$r = 0.63$; RMSE=2.11 ; $AVE_{error}<1e^{-10}$
50-fold Cross validation with $\frac{1}{2}$ of the data	$r = 0.46$; RMSE=2.55 ; $AVE_{error}= -0.014$	$r = 0.52$; RMSE= 3.41 ; $AVE_{error}= -0.12$
Residuals overdispersion	NO ($\phi = 1.13$)	YES ($\phi = 2.92$)

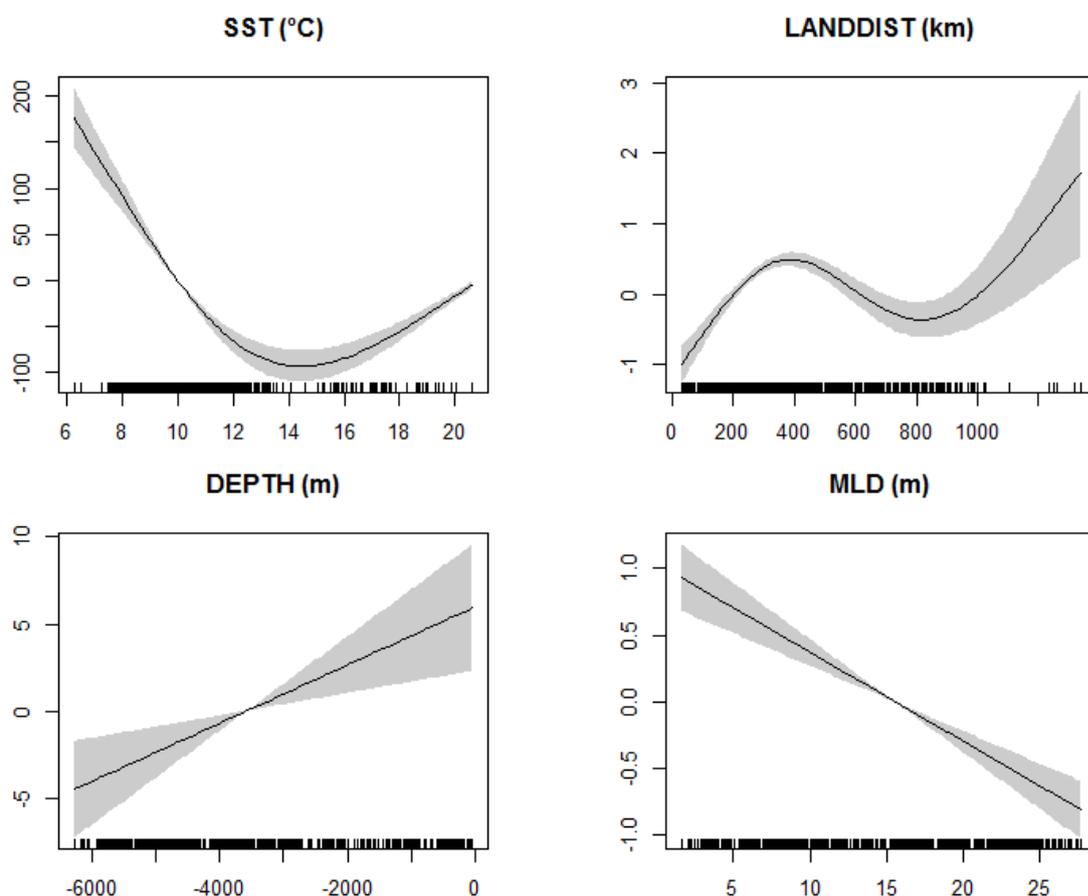


Figure V-3. Smooth functions for the four selected predictors.

Solid lines represent the smooth functions and grey intervals are one standard-error above and below the estimate. The rug plot at the bottom of corresponds to the distribution of the response variable along the environmental gradient. The y-axis represents the effect of each covariate, with zero meaning no effect. SST=sea surface temperature; LANDDIST = distance to land; DEPTH = mean depth; MLD= mixed layer depth.

CHAPTER VI

DISCUSSION

VI. Discussion

The work presented in the previous chapters emphasized the lessons learned from using historical occurrence and abundance data for estimating the historical distribution and population size of marine mammal species, using data containing increasing levels of information and methods of increasing complexity. In this chapter, I will build from these analyses to discuss the different application of historical data, from descriptive to predictive approaches, and emphasize the lessons learned for our understanding of changes in species' ecology, distribution and abundance. I will then conclude with a broader discussion of the concept of shifting baseline and the challenges related to the conservation of biodiversity in a changing world.

Much of the focus of this PhD project was on the North Atlantic right whale (NARW, *Eubalaena glacialis*). This species meets all the criteria that make it an interesting case study to discuss the challenges and opportunities raised by the use of historical data to inform conservation in a shifting baseline context. It came close to extinction after centuries of overexploitation and is one of the world's most threatened whale species. Setting appropriate conservation targets for this species requires an understanding of its historical distribution and abundance, as a baseline for quantifying its decline and measuring progress towards recovery, which is made difficult by the scarcity of records over its very long whaling history. A thorough review of historical occurrence data for this species was performed, and advanced statistical methods for estimating its pre-exploitation distribution and population size were developed, with implications for its management and conservation. Throughout this chapter, I'll use the case of the NARW as a guiding thread, to illustrate each section with concrete examples related to this species.

Reconstructing the past: from description to prediction

In reviewing historical occurrence records for marine mammals, we collected data that varied in the level of information they provide as well as in their spatial and temporal resolution. The approaches to analyze these data vary accordingly, from a mere descriptive interpretation of historical anecdotes to the combination of spatially-explicit data with statistical models to predict the distribution or abundance of species. Here, I come back on these different possible approaches, following a logic of increasing level of complexity. The focus is on marine mammal species, but the concepts discussed are applicable to other biological systems.

Interpretation of historical anecdotes

Historical anecdotes are a source of information that is often overlooked (Pauly, 1995). However, they provide useful background information that can bring context and a better understanding of species' historical status.

The simplest form of anecdotal information is a record of occurrence of a species in a broad geographic area. If the species is currently absent from this area, this anecdotal information becomes informative, suggesting that the species might have been extirpated from it. Accumulation of such anecdotes in space and in time will strengthen the interpretation, even if just in a qualitative way. This can be illustrated by the case of the gray whale (*Eschrichtius robustus*), for which a handful of historical accounts of its presence in the North Atlantic testify of its previous occurrence in this basin, even if they tell us little about where exactly it occurred, its abundance, and timeframe of its disappearance (Chapter 2).

Historical anecdotes can be informative even when taxonomically imprecise. For example, a 1st century record of whales off Cadiz refers simply to "*ballaenae*" (Pliny the Elder, 1855), but the ecological information provided ("winter solstice", "at periodical seasons they retire and conceal

Box VI-1. About the North Atlantic right whale: Historical anecdotes

Historical anecdotes for the NARW demonstrate its presence in several areas where it was extant before being extirpated by over-exploitation. For example, written documents regulating whaling operation from the 11th to the 17th century support the evidence for Basque whaling in the Bay of Biscay, an operation for which the North Atlantic right whale was the major target. The right whale is also described as one of the species inhabiting the Iceland seas, in an ancient Norwegian educational text, the "King's Mirror" (Larson, 1917) (see also Gudmundsson's 17th century description; Gudmundsson, 1640).

However, if the accumulation of historical anecdotes is informative of the presence of right whales in some parts of the North Atlantic, these evidences remain too coarse in their spatial and temporal resolution to be used for estimating the historical distribution of the species.

themselves in some calm capacious bay, in which they take a delight in bringing forth”, killer whales attacking “the females which have just brought forth, and, indeed, while they are still pregnant”) narrows it down to three possible coastal whales species (North Atlantic right, gray and humpback whales), none of which currently reproduces in the area.

Historical anecdotes can sometimes provide information on the use that human had of species, shedding light on the history of their exploitation and causes of their decline. Records referring to exploitation, manufacturing, trade and legislation can be particularly informative to reconstruct the history of exploitation of a species in a particular area (e.g. Aguilar, 1986; Brito & Sousa, 2011).

Some anecdotes can provide details of historical abundance, providing an idea of the order of magnitude of the population that can be compared with current population sizes. For example, William Dampier, an English buccaneer, sea captain and scientific observer from the 17th century, described in his travel logs the numbers of seals in the Juan Fernández archipelago (Chile) in the following terms: *“Seals swarm as thick about this island as though they had no other place to live in, for there is not a bay nor rock that one can get ashore on but is full of them. [...] Here are always thousands—I might say millions of them, either sitting on the bays, or going and coming in the sea round the island, which is covered with them”* (Dampier, 1697). This species was subsequently so heavily hunted it was thought extinct, until a small population was found in the mid twentieth century. Today, the population is increasing and estimated at around 12,000 individuals (Aurioles & Trillmich, 2008), still substantially below its apparent 17th century level.

Finally, anecdotes can also be used to qualitatively validate patterns of distribution and abundance obtained from statistical models, in areas where there are seldom validation data (e.g. see chapter 3 for an example of qualitative validation of predicted patterns of distribution, based on general knowledge of the history of exploitation of whales).

Historical anecdotes can therefore be highly valuable, though they are difficult to reconcile in quantitative or statistical analyses, as a result of a coarse spatial, temporal and taxonomic resolution, and lack of precision (e.g. too vague abundance estimates). A certain level of interpretation is required, especially for the earliest records, which can be informed by combining interdisciplinary knowledge of historians, philologists and marine ecologists.

Estimates of historical catches

The magnitude of historical catches can sometimes be estimated for species that have been exploited as part of an industry or for commercial purposes. In the case of marine mammals, such information is often available in catch statistics records from the whaling or sealing industries.

For example, records of the sealing bonanza for New Zealand fur seal (*Arctocephalus forsteri*) in the early 19th century give such information: conservative estimates of the total kills for the period 1804-1809 count at least 250,000 New Zealand fur seal taken in the Antipodes islands only (Richards, 1994). This figure can be compared with the current abundance of New Zealand fur seal in the Antipodes, which has been estimated in the 1990's at about 2,000 individuals (Taylor, 1992). More generally, around two million sealskins are estimated to have been marketed from the New Zealand region in less than a decade, which is ten times the current population level of New Zealand fur seal (Goldsworthy & Gales, 2008). These values only provide a qualitative estimate of the order of magnitude of the pre-exploitation population size of New Zealand fur seal, but the comparison with current populations is a first indicator of the level of depletion caused by human exploitation.

Whaling logbooks can provide information on the number of whales killed, or more indirectly on the quantity of oil produced, which can in turn be used to estimate the overall number of individuals extirpated from a particular area. Such estimates have been made for several species of whales, including humpback whales in the North Atlantic (Smith & Reeves, 2003, 2010), bowhead whales (Bockstoce & Botkin, 1983), the North Atlantic right whale (Reeves et al., 2007), the North Pacific right whale (Scarff, 2001), and the Sperm whale (Bannister et al., 1983; Best, 1983). These estimates have often been used as a basis to provide hypotheses for the pre-exploitation population size of these species. Catch statistics data can sometimes be reasonably precise in quantity but not always in their spatial location. Examples include the statistics of records of bowhead whale catches reaching Dutch ports (De Jong, 1983) that were only classified by general region ("West Greenland"/"East Greenland").

Box VI-2. About the North Atlantic right whale: Estimates of historical catches

There is a considerable difficulty in estimating the overall number of NARW caught, given the long history of its exploitation. Statistics catches exist for Basque whaling in the northeast Atlantic (Du Pasquier, 2000) or from American oil export statistics from the northwest Atlantic (Reeves & Mitchell, 1986a). Several attempts have been made to estimate the total catches for the species, focusing on the better known western population (Aguilar, 1986; Gaskin, 1991; McLeod et al., 2008). Its pre-exploitation population size was also estimated, based on its history of exploitation (Reeves et al., 2007) or genetic analyses (Rosenbaum et al., 2000a; Waldick et al., 2002; Rastogi et al., 2004b; Frasier et al., 2007; McLeod et al., 2010).

Historical anecdotes and catch statistics can become more informative as information on species occurrence or abundance becomes spatially-explicit. The consideration of scale is important here, as the definition of “spatially-explicit” may vary with the spatial resolution wanted in the study. If the study aims at reconstructing the distribution of species at a very fine spatial scale (e.g. in a particular bay, an estuary), then records of occurrence at a larger scale (e.g. off the coast of a city or an island) will not be informative. In this study, I considered a large spatial scale, looking at global patterns of distribution and abundance, which allowed the inclusion of records at an intermediate spatial resolution. I differentiated between data that can be represented in global maps as a point (e.g. a city, a small island, a specific site in the coast) vs. those that were too vague to be mapped (e.g. records attributed to a region or a country). In the rest of this section, I focus on historical data that contain spatially-explicit information on species occurrence/abundance and present how they can be used in increasingly complex analyses to estimate the historical distribution and abundance of species.

Maps of historical occurrence

As presented in chapter 2, visualizing historical occurrence data on a map is informative in itself as it gives a general overview of the spatial distribution of historical occurrences of a species, to be compared with our knowledge of its current distribution. In particular, it can help identify particular sites where the species used to be extant, which can be re-sampled today to assess changes in occupancy (Tingley & Beissinger, 2009). An accumulation of historical occurrence records outside the species' range may lead to a reconsideration of the original borders of this range (e.g. Matthews & Heath, 2008). Additional details in records on the species' behavior can be useful to understand the context in which the occurrence was recorded, and associate it to a particular biological activity (breeding, foraging...), or to identify the type of interaction with humans (subsistence use, commercial exploitation, trade...).

However, historical occurrence data might contain errors, gaps and biases that affect our interpretation of these records. Ward (2012) listed the shortcomings of natural history collection data as being “1) geographically biased towards more easily accessed locations; 2) taxonomically incomplete, giving undue weight to some taxa, 3) temporally biased, and 4) *ad hoc* in collecting effort”. This statement applies to most of the historical data collected in this study. Below, I discuss the spatial, temporal and taxonomical errors as well as the gaps and biases likely found in historical occurrence data.

Errors

Spatial errors may result from bad accuracy of spatial measurements, or vague description of location, as the coordinates associated to such descriptions will necessarily be imprecise. There is also an uncertainty associated to zooarchaeological records, as they may have been displaced from their original location, for example as a result of commercial or cultural trade. For example, walrus or narwhal tusks found in an archaeological site are not necessarily representative of the species' presence in this site, as ivory has been traded for centuries and tusks may have been moved over long distances (Laufer & Pelliot, 1913; Pierce, 2009). In general, historical data are poorly adapted to very fine-scale studies, with spatial uncertainty typically increasing when we go back in time. Statistical methods accounting for spatial uncertainty have been developed to overcome this problem (Wieczorek et al., 2004; Guo et al., 2008), but it is strongly advised to carefully check the historical dataset for possible outliers and to correct spatial errors when possible.

Temporal imprecision in historical sources arise when the exact date at which a record was collected is not indicated. Inference is sometimes necessary, for example by using the date at which the source was written as a proxy for the year at which a sighting was made. Information on the season can help to distinguish at which stage in its life cycle the individual was (e.g. breeding vs. foraging period), particularly important for migratory species, but this information is not always provided. There is great variability in the temporal uncertainty associated with different sources of historical data. For example, whaling logbooks provide information on the exact day at which an individual was sighted, while radiocarbon dating of zooarchaeological remains provides estimates with confidence intervals up to several centuries. This variability makes it challenging to reconcile historical records in a standardized format.

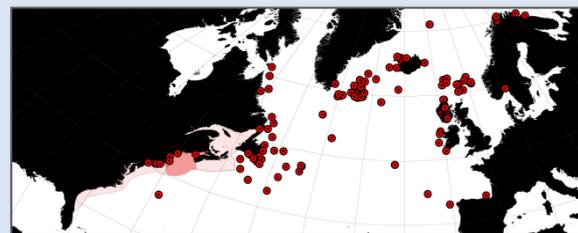
Errors in taxonomy can result from the misidentification of specimens (either of a live individual by the observer referred to in a historical record, or of archaeological bone remains), or from subsequent errors in the historical record, for example in the translation or interpretation of the original source. Misidentifications can be suspected if there are obvious outliers that exist in different geographical or environmental space than the rest of the records of a given species (although apparent outliers may also be the most interesting evidence of past changes). They can then be checked by a careful consideration of the information associated to the record (e.g. description of the species behavior, anatomy...). Museum specimens present the advantage of being accessible for re-examination to check the species identification (Newbold, 2010), and in the case of archaeological records, DNA analyses can be performed to complement anatomical identification (Newman et al., 2002).

Gaps and biases

Historical data are biased spatially, temporally, taxonomically and environmentally (Graham et al., 2004; Newbold, 2010). First, there is generally a bias in historical sources towards areas of high human concentration and those that are more accessible to humans (e.g. cities, roads, rivers, coasts) (Newbold, 2010 and references therein). In the case of marine mammals, most of the interactions with humans occurred near the coastline, and hence this is where most records come from, with the exception of some exceptional historical whaling datasets that cover the world's oceans (Townsend, 1935; Smith et al., 2012). This spatial bias might in turn result in an environmental bias, if the sampled areas do not completely capture the range of environmental conditions inhabited by the

Box VI-3. About the North Atlantic right whale: Maps of historical records

175 occurrence records have been collected for the North Atlantic right whale in summer, outside of its current grounds. Their distribution indicates that the species used to occur in summer throughout the North Atlantic, in a band from the northeast coast of the USA to northern Norway.



Historical occurrence data and current range of the NARW in summer

(Adapted from figures in chapter 4)

This dataset is to our knowledge the most comprehensive collection of NARW historical records in summer. Nonetheless, these data are spatially biased towards coastal areas and temporally biased towards the most recent years. There is also a substantial level of uncertainty in localization and identification of the species for several of these records, which we indicated in the corresponding maps and tables (Chapter 4). These limitations reduce the possibilities of using these data in quantitative analyses. Yet, they are extremely valuable to give qualitative information and to validate statistic predictions on the past distribution of NARW.

species, something to be kept in mind when performing environmental-based analyses (e.g. habitat modeling).

Language barriers can also cause an artificial spatial sampling bias, if it causes data from particularly regions to become inaccessible to the reviewer and hence absent from databases. For historical records in particular, such language barriers may also result in temporal biases, with older records using old languages and dialects becoming progressively less accessible to the non-specialist.

Recent historical records are likely to be more represented in the dataset than older ones, as the availability of historical sources becomes more fragmentary when we go back in time.

Finally, historical sources are taxonomically biased towards species for which human had an interest, for subsistence use, commercial or recreational purposes (Newbold, 2010), and towards those that are more identifiable.

Overall, some recommendations can be made to increase the representativeness and reliability of historical datasets, especially if they are to be used in more complicated, predictive analyses, as discussed in the rest of this section:

- To detect biases, occurrence records can be plotted in geographical, temporal and environmental space to identify regions, periods or environmental contexts that may have been poorly sampled;
- The reviewing effort for historical sources should focus on the geographical and environmental space that are currently underrepresented, to reduce gaps and biases in the data;
- A multi-disciplinary approach is advised, as knowledge and tools from the disciplines of ecology, archaeology, history and philology can be combined to access a larger range of historical sources and have complementary answers to the challenges raised for each type of historical sources;
- Data should be standardized to a similar spatial and temporal resolution, to be able to combine them in a coherent dataset for further statistical analyses;
- Once the data are corrected for errors and standardized, they can then be integrated into online biodiversity information databases (reviewed in Graham et al., 2004) to be made available to the scientific community.

Envelopes of historical occurrence

With all their gaps and biases, historical occurrence data do not accurately reflect the full historical and/or current distribution of species. Hence, sites with occurrence records are almost certainly just a subset of the sites where the species actually occurred. Further analyses are needed to predict species' presence in sites that were not sampled.

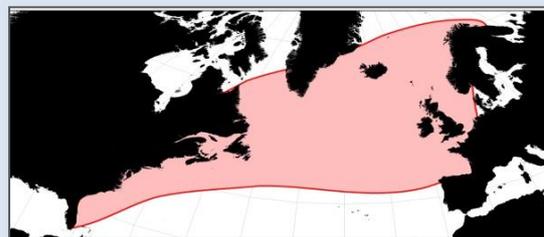
Mapping the envelope that contains all the known historical records, using boundary delineating methods (or hull methods) (Burgman & Fox, 2003), can provide an estimate of a species' historical extent of occurrence. If records span a large period of time, the sequence of range contraction for a species can be deduced by mapping the envelope of occurrence at different time periods (e.g. McClenachan & Cooper, 2008).

Because boundary delineating methods are constructed around extreme points in space, they are very sensitive to errors and biases in locations (Burgman & Fox, 2003). The spatial location of each historical record must thus be considered with care. Cases of vagrancy might appear in the historical records, while not being informative of the species historical distribution, and artificially enlarge the envelope. Just as today's newspapers relate unusual cases of vagrancy as remarkable events (e.g. the visit of a walrus in Orkney, Scotland, in March 2013; BBC, 2012), historical sources may present a bias towards exceptional events, which sometimes are the focus of entire references (e.g. as illustrated by a 19th century book describing a right whale taken in Tarento, Italy, as the first capture of a true whale in the Mediterranean; Gasco, 1878). For this reason, it is preferable to have an accumulation of evidence of a species' presence in a given area (e.g. repeated occurrences of individuals in the same area, mentions of vast concentrations, reference to organized hunting activity) before considering

Box VI-4. About the North Atlantic right whale: Envelope of historical occurrence

Drawing the envelope that contains all the occurrence records collected for the NARW in summer (in this case, both historical data and current sightings) gives a first approximation of the predicted historical extent of occurrence of the species in that season. Comparing this envelope with the current summer range of the species is a first step towards estimating its spatial depletion. However, the method is very sensitive to any outliers, and given the uncertainty and biases in the historical data, such prediction is probably an overestimation of the species actual historical distribution with limited application to inform the management of the species.

In this case where historical data are full of gaps and biases, the analysis would benefit from information on the environmental preferences of right whales, in order to refine the prediction.



Envelope of historical occurrence for the NARW in summer

(Original figure in page 63)

that particular area as part of the species' historical range. Context information on how a particular record was produced can also be informative of its likelihood to be an outlier or not (e.g., a single record in a seldom visited region is more meaningful than a single record in a highly sampled region).

Extents of occurrence obtained by the minimum convex polygon method provide an estimate of the range of the species, but often overestimate the species actual distribution (Burgman & Fox, 2003) and are not informative of what portions of the distribution contain suitable habitat that the species actually use (Elith & Leathwick, 2009b). Moreover, interpolation methods are based on spatial information alone, and cannot be used to extrapolate the distribution in time or space to similar environments outside of the region with records. This limitation is particularly problematic to estimate the distribution of depleted species, as historical occurrence data present many gaps.

Predictive models of historical distribution

Species Distribution Models (SDMs) combine occurrence data with environmental variables to quantify species–environment relationships, and can be used to predict the geographic distribution of probability of presence of a species (Guisan & Thuiller, 2005). A variety of statistical methods have been proposed to model species' distribution with presence only or with presence-absence datasets (Guisan & Thuiller, 2005; Elith et al., 2006). The later perform generally better, as absence data enhance model calibration (Brotons et al., 2004). This PhD project does not pretend to provide a comparison of the ability of these different methods to model species distribution based on historical data. However, it can be noted that the two methods considered in this project, Generalized Additive Models (GAMs; Hastie & Tibshirani, 1986) and Boosted Regression Trees (BRTs; Elith et al., 2008), have proved to be efficient in predicting species distribution based on historical presence-absence data, as shown by the high explicative and predictive power of the models (see Chapters 3 and 4). This can be in part explained by the quality of the calibration dataset used, which is exceptional in coverage (both spatially and temporally) and in the information it contains on both presences and absences of species. The ability of these two methods to cope with errors and biases in the calibration data make them promising tools for modeling species' distributions based on historical occurrence data (Graham et al., 2007; Naimi et al., 2011). For presence-only data, methods that have been recommended by previous authors (not tested here) include machine learning methods such as Maxent (Phillips et al., 2006) and GARP (Stockwell and Noble, 1992), which have been shown to provide very accurate models of species' distributions (Elith et al., 2006). The development of such methods with some of the datasets presented in chapter 2 (e.g. Mediterranean monk seal dataset of historical breeding colonies) would be interesting, though many challenges remain to combine historical data with different spatial and temporal resolution and biases.

Built with historical occurrence data, SDMs provide an opportunity to improve our understanding and interpretation of the past distribution of species (Graham et al., 2004; Newbold, 2010). For depleted species, current occurrence records are not necessarily representative of the full environmental space that the species is able to occupy and are thus potentially insufficient as a basis for reconstructing the entire past range. In this case, there is a high interest in calibrating the model with historical occurrence data in addition to current data, as it can add information on the environmental preferences of the species.

The interest of species distribution models for reconstructing the historical ranges of species is that predictions can be generalized to other contexts along three axes: space (i.e. predicting in sites that were not part of the calibration dataset), time (i.e. predicting for another time period than in the calibration dataset) and the environment (i.e. predicting outside the environmental space sampled in the calibration dataset). Generalization within the calibration range is referred as “interpolation” while generalization beyond the calibration range is “extrapolation”. Extrapolation in the environmental space is hazardous and should be avoided, but extrapolation in space and time can prove useful to fill gaps in the historical distribution of depleted species, providing predictions in areas or time periods for which there are no occurrence data available (Hirzel & Le Lay, 2008, but see Torres et al., 2015). An innovative approach developed in this study was the extrapolation of predictions across taxa: under the assumption that they share the same environmental preferences, species-environment relationships derived from the distribution of a better-known species can be used to predict the pre-depletion distribution of poorly known species (chapter 4). When possible, information on the historical occurrence of the latter should then be used to validate the prediction, and hence test the assumptions of transferability of the model.

SDMs produce surfaces of probability of presence. In some cases, it is useful to convert these into binary presence/absence surface to map the predicted envelope of presence of the species. This requires applying a threshold on the predicted values of probability of presence, above which the species is predicted as present. The choice for the value of this threshold has consequences on the rate of omission and commission errors (respectively, the number of false negatives and of false positives), and on the model predictive performance (Liu et al., 2005). Each type of errors has different consequences in terms of management (Rondinini et al., 2006). It has been shown for example that reserve networks proposed by models minimizing omission errors (false negatives), provided a better match with priority areas identified by specialists (Loiselle et al., 2003), overestimating species’ occurrence thus misleading conservation decisions. However, the opposite can be true, as classifying a site of true presence as an absence can be costly in terms of conservation (Jiménez-Valverde & Lobo, 2007). The choice of the threshold should ultimately depend on the user’s

intention for the model and the risks s/he is willing to tolerate in using it for conservation planning (Wilson et al., 2005; Rondinini et al., 2006; Jiménez-Valverde & Lobo, 2007). However, a binary representation loses the information on some characteristics of the environment that make an area more suitable for the species than others, which in turn affects our understanding of the actual distribution of the species. Mapping both information – envelope of predicted presence and probability of presence within this envelope – is probably the best compromise to make the best of the model's prediction.

Limits of SDMs built with historical occurrence data

There is a substantial body of literature discussing the limits of SDMs in general, in terms of the underlining ecological assumptions, calibration data and statistical methods used (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Austin, 2007; Dormann, 2007a; Elith & Leathwick, 2009c).

More particularly, considering the ecological assumption on which SDMs are based, studies have focused on the use of bioclimatic niche to describe the distribution of species (Pearson & Dawson, 2003), the assumption of equilibrium of the species with its environment (Zurell et al., 2009), niche conservatism in space and time (Pearman et al., 2008; Peterson, 2011) and model transferability in space (Randin et al., 2006).

Discussion on the calibration data include the effect of sample size (Stockwell & Peterson, 2002; Hernandez et al., 2006; Wisz et al., 2008), errors in taxonomy (Lozier et al., 2009), errors and biases in space (Graham et al., 2007; Naimi et al., 2011; Syfert et al., 2013), impact of survey design (Reese et al., 2005), choice of pseudo-absences (Chefaoui & Lobo, 2008; Lobo et al., 2010; Lobo & Tognelli, 2011; Barbet-Massin et al., 2012) and spatial autocorrelation (Segurado et al., 2006; Dormann, 2007b; Record et al., 2013).

Finally, many studies have evaluated the benefits and drawbacks of different statistical methods to model species-environment relationships based on presence-absence or presence-only data (Guisan & Zimmermann, 2000; Guisan et al., 2002; Elith et al., 2006), and according to model complexity (Merow et al., 2014).

I refer the reader to the articles mentioned above for a thorough discussion on these topics. Here, I will develop some of the limits that are particularly relevant in the context of SDMs built with historical occurrence data to estimate the historical distribution of species.

The discussion around the consequences of using biased calibration data is particularly relevant in the context of models built with historical occurrence data, as these are produced by an *ad-hoc* sampling which incorporates many geographical, temporal and environmental biases, as discussed

above. While a spatial bias may not substantially reduce model accuracy if it does not result in an environmental bias (Kadmon et al., 2004), the contrary will induce a bias of the prediction towards environments that have received more sampling (Araújo & Guisan, 2006). If the calibration dataset cannot be corrected for the uncertainty and environmental biases it contains, the effect on model predictions must be kept in mind to avoid over-interpreting the predictions (e.g., bias against shallow areas in the predictions for the North Atlantic right whale, see Box VI-5).

Small location errors in the calibration dataset are likely to reduce the model performance, though accurate predictions of species distribution are still possible, with boosted regression trees model performing particularly well in this case (Graham et al., 2007). Spatial autocorrelation in the environmental predictors can reduce the effect of positional uncertainty, even though it cannot totally compensate for it (Naimi et al., 2011). To identify outliers in space or the environment, a sensitivity analysis can be ran to test the robustness of the model to the exclusion of a particular point data. The discussion of the model predictions can then be performed with this information in mind.

Combining data resulting from very different sampling approaches and that are very different in resolution or biases is a challenge. Reside and al. (2011) argued that the incorporation of low-resolution historical species location data in species distribution models reduced the model performance and tended to overpredict the species range in comparison to models that use only more precise recent (post-1990) data. This limitation must be kept in mind when building species distribution models with historical data. In particular, there is a risk in predicting a wider potential range for the species that may misdirect conservation actions (Loiselle et al., 2003). However, the reduction in model performance may be a necessary evil to allow the incorporation of historical data that are sometimes the only source of information available for the historical distribution of a depleted species.

In using SDMs to understand the past distribution of species, we assume that ecological niches are conserved sufficiently over the time periods analyzed that they can serve as a basis for predicting the potential distribution of species. However, studies have emphasized the capacity of some organisms to rapidly adapt to changing environments, suggesting that rapid evolutionary processes can occur in a short period of time (Whitney & Gabler, 2008). But this mostly concerns species with short generation times and large population sizes (Hoffmann & Sgrò, 2011). A study testing niche conservatism in mammals by assessing the ability of projected range to predict occurrences of species in another time period found evidence for widespread niche conservatism in the 23 mammal species studied (Martínez-Meyer et al., 2004). More generally, previous analyses suggest that ecological niche characteristics are highly conserved over moderate time spans (up to thousands of

years) (Peterson, 2011). These findings are encouraging for the ability of species distribution models to be extrapolated in space and time in order to estimate species' historical distribution, especially over intermediate time scales of a few centuries. However, the niche conservatism assumption should be better tested using independent validation in different time periods, and care must be taken not to over-interpret predictions.

An important ecological assumption in all species distribution modeling is that the species' distribution can be described by bioclimatic factors only. This does not directly take into account other processes affecting species distribution, such as dispersal, biotic interactions or demographic processes. However, at a large spatial scale, the influence of bioclimatic factors is believed to be dominant over biotic interactions (Pearson & Dawson, 2003). In the case of models built with historical occurrence data, the spatial resolution of the analysis is likely to be coarse already, as a result of uncertainty and biases in the calibration data. Besides, information on the historical structure of the community may not be available to take biotic interactions into account. To model historical data, the use of a bioclimatic niche is thus relevant, in the absence of more detailed information on the other aspects of the species niche.

Climate change causes shifts in species ranges (Parmesan & Yohe, 2003; Root et al., 2003), and is a possible confounding effects when studying potential human-caused range contractions. Disentangling the two processes in the historical record is not straightforward. Here, the decision to focus on the Holocene period, which starts at the end of the last ice age 10,000 years ago, overcomes the impact of the major climate change phenomena that occurred at this period. Global warming has accelerated dramatically in the last 100 years, and especially after the mid-1970's (IPCC (WG I & II), 2001). The consideration of historical data prior to the 20th century is thus likely to reduce the effect of recent global warming on the collected dataset. However, other sources of climatic variability remain, including some at the century scale (e.g. little ice age c. AD 1650-1850; Matthews & Briffa, 2005) or at the decade scale (e.g. El Niño Southern Oscillation, Pacific Decadal Oscillation, North Atlantic Oscillation; Wanner et al., 2008). To differentiate between anthropogenic and climatic effects on species' range contractions, the conditions in which each historical record was recorded are worth considering, as background information on the climatic context in which it was collected. For example, in a study on the extirpation of New Zealand fur seal *Arctocephalus forsteri*, Smith (2005) investigated the cause of the species' spatial depletion, highlighting changes in seal distribution during each phases of human exploitation. He concludes that human overexploitation, and not climate change, has been responsible for the species' depletion.

The effect of climate change can in principle be explicitly integrated in a species distribution model based on historical data, by associating each record with the environmental conditions in the location

and time the record refers to. However, this requires spatially-explicit reconstructions of past environmental conditions (e.g. temperature, primary productivity, sea level), which are not always available. The lack of bioclimatic variables contemporary to the calibration data induces a time-lag between the calibration data and the environmental covariates used to construct the model. In this case, climate change may affect the model's prediction in a way that is difficult to account for. The best should be done to retrieve contemporaneous climatic data, but in their absence, the use of a long-term climatology should be favored to mitigate the effects of climatic variation on the quality of the model's predictions (Gregr, 2011).

Box VI-5. About the North Atlantic right whale: Prediction of habitat suitability

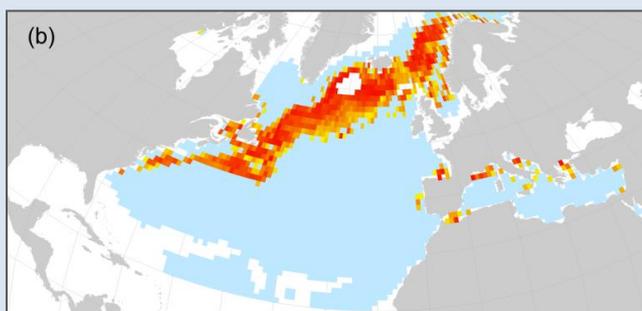
While historical occurrence/abundance data for the NARW suffer from a lot of uncertainty and gaps, the history of exploitation of a congeneric species, the North Pacific right whale (NPRW) was well recorded in 19th century American whaling logbooks. We used species distribution modeling as an opportunity to fill gaps in knowledge of the pre-whaling distribution and abundance of the NARW.

We modeled the relationship between NPRW occurrences and their environment. Assuming that the two species shared the same environmental preferences, we projected the model into the North Atlantic to predict the spatial variation in environmental suitability for the NARW.

We used Boosted Regression Trees and Generalized Additive Models, which have been shown to be among the best performing methods to model presence-absence data.

To define the envelope of predicted presence, we applied a threshold on the predicted probability of presence. We choose the threshold that maximized the sum of specificity and sensitivity, advised by Jiménez-Valvedez & Lobo (2007) as the one which minimized false negative errors, arguing that omission errors would be detrimental for informing the management of this species.

We predict that the NARW's summer range occupied a relatively narrow (width $\sim 10^\circ$ in latitude), mostly offshore, band from the eastern coast of North America to the North Cape in Norway.



Predicted habitat suitability for the NARW

(Original figure in page 125)

The prediction has been extrapolated in geographic space (from the North Pacific to the North Atlantic) and across taxa (from the NPRW to the NARW) but not in environmental space (as we restricted the prediction to the environmental envelope sampled in the calibration dataset). This model is based on the strong assumption that the two species of right whales share the same environmental preferences. Demonstrated niche conservatism between sister species (Peterson et al., 1999), coherence with historical records of NARW and similar response to environmental predictors between our analysis and previous studies seem to support this assumption.

We attempted to reduce the impacts of errors and biases in the calibration dataset by analyzing only cells with a reasonable sampling effort, and by reducing sources of confusion with bowheads in the northernmost latitudes. However, the environmental bias in the calibration data towards offshore habitats induced lower discriminative ability of the model in coastal, shallow-depth areas. In the absence of sufficiently fine-scaled, spatially-explicit climatologies for the 19th century, we had to assume that the use of a long-term climatology mitigated the effect of climate variations.

Despite these limitations, the prediction is generally well supported by historical and current occurrence data, which raises our confidence in the relevance of such modeling approach to estimate the historical distribution of depleted species.

Predictive models of historical abundance

Similar species distribution modeling approaches can be used to model the relationship between a species environment and its abundance, in order to provide spatially-explicit predictions of relative abundance. Spatially-explicit historical catch statistics are a valuable data source to be used in such analysis (e.g. see Rosenberg et al., 2005, Chapter 5 of this study). As presence and abundance can be influenced by different environmental factors (Nielsen et al., 2005), two-stage modeling is a powerful tool to describe abundance, first modeling the occurrence of the species then its abundance where it is predicted as present (Welsh et al., 1996).

However, historical count data are difficult to obtain, with historical sources often only providing occurrence data. Environmental suitability predictions derived from presence/absence modeling are sometimes used as a surrogate to predicting the abundance of species (Pearce & Ferrier, 2000; VanDerWal et al., 2009), under the assumption that relative abundance and probability of presence are correlated (VanDerWal et al., 2009, but see Nielsen et al., 2005), but the relationship between these probabilities needs to be further tested to validate this approach.

Box VI-6. About the North Atlantic right whale: Prediction of historical abundance

- **Prediction of density distribution**

We modeled the relationships between 1840-1849 catch statistics for the North Pacific right whale and the associated environmental conditions, and extrapolated the model in the North Atlantic to predict the density distribution of the NARW before whaling within its predicted envelope of occurrence.

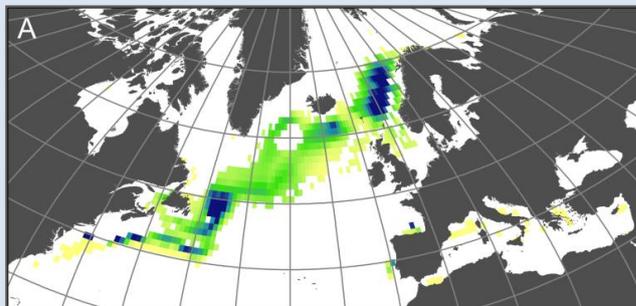
We predict that there were two main areas of high summer density in the North Atlantic: north of the Grand Banks of Newfoundland and in the Norwegian Sea.

Limitations due to biases and errors in the calibration dataset are similar to those encountered for the distribution modeling approach.

- **Estimate of the pre-exploitation population size**

By scaling the predicted density distribution in the North Atlantic with estimates of the pre-whaling NPRW population, we estimated that the total carrying capacity of the North Atlantic for right whales is, or was, **between 9,091 and 21,328 individuals**, including 3,913–9,181 in the western North Atlantic (west of 30°W) and 5,178–12,147 in the eastern North Atlantic.

There is uncertainty around these estimates resulting from the assumptions that the NPRW population was at full carrying capacity in the mid-1800s and that the sum of total catches in the North Pacific for the period 1840-1849 is comparable to the total population size of NPRW. If these two assumptions prove wrong, our estimate of the total pre-exploitation population size of NARW is probably conservative.



*Predicted distribution of relative abundance for the NARW
(Original figure in page 170)*

Lessons learned from the analysis of historical data

Understanding species' habitat preferences and how they have been affected by humans

If a species was depleted in part of its range, current occurrences may not be representative of the full environmental space that the species is able to occupy. In this case, historical occurrence data can broaden our perception of the environmental preferences of this species. Historical anecdotes describing the habitat previously occupied can be informative. Descriptions of walrus colonies laying on the sand and not on ice in Bear Island (Nordenskiöld, 1881) or of Mediterranean monk seals reproducing on beaches and not in caves (as it is the case today) (Johnson & Lavigne, 1999b) challenges our perception of the habitat preferences of species, suggesting that these have been modified by human disturbance or exploitation. Relating spatially-explicit historical occurrence data with the associated environmental conditions can help define the niche of the species before it got depleted. If the species' niche can be characterized at different time periods, niche overlap measures (e.g. Colwell & Futuyama, 1971; Hurlbert, 1978; Broennimann et al., 2012) can be used to characterize the changes in species niche before and after it has been affected by human (Hirzel & Le Lay, 2008).

In a conservation perspective, this information can prove very useful to understand the ability of species to recolonize a habitat and enhance predictions of species response under future climate change.

Box VI-7. About the North Atlantic right whale: Historical knowledge of the species' ecology

If the current distribution of North Atlantic right whales suggests a preference of the species for coastal habitats, historical records of occurrence and historical anecdotes suggest that the species used to occupy offshore habitats (see Chapter 4). Its current distribution is probably not representative of the habitat that the species can potentially occupy. While we cannot rule out the possibility that depletion of this species in most of its range may have counter-selected individuals that favored pelagic habitats, there is still a possibility that the species is still adapted to this habitat and recolonize it one day.

Understanding past distributions and anthropogenic range contractions

Mapping the historical distribution of species based on one or more of the different approaches presented above (mapping sites of historical occurrence, drawing the historical envelope of occurrence, modeling the species-environment relationship using species distribution modeling) can have several applications to the management of depleted species.

First, it can be used to quantify range contractions. Besides a visual comparison between current and historical range, envelope-based analyses can be performed to quantify the overlap between current

and historical extent of occurrence (Sadahiro & Umemura, 2001; Fortin et al., 2005). This may be adapted to compare current and past envelope of occurrence obtained from models built respectively with current and historical occurrence data.

Second, it can inform monitoring efforts, highlighting areas that could potentially be used by the current population or colonized in the future, in order to guide strategic conservation efforts. In a world with limited resources allocated to conservation, it is important to prioritize our actions and direct survey effort towards the most promising areas. SDMs predictions are particularly valuable in this case as they can identify areas with high probability of presence.

The predictions provided by the analyses of historical occurrence data are only a representation of the potential distribution of the species if it had not been depleted, which is potentially different from the range that the species would occupy if it was given the possibility to recover, as a result of changes in the environment over time (see discussion below). However, in the absence of better information on the species potential distribution, the historical range is also informative of areas where the species used to be extant and puts emphasis on areas that are worth considering for an in-depth analysis to estimate their potential for the future recovery of the species.

Finally, historical range maps can be used to inform the conservation status of species. Indeed, a decline in the species' extent of occurrence (within the past 10 years or three generations; whichever is longer) is among the criteria used by the IUCN Red List to categorize extinction risk under Criteria B (IUCN SSC, 2001).

**Box VI-8. About the North Atlantic right whale:
Understanding past distribution**

The comparison between the distribution of historical occurrences and the current distribution of the species is a first attempt to assess range contraction. The envelope containing both these historical data and the current grounds for the species gives a broad idea of its historical extent of occurrence in summer. It emphasizes a range contraction from a previous basin-wide distribution extending from the eastern coast of North America to Norway, to the current distribution mainly restricted off the eastern coast of North America.

From these data, it is however not clear how the population was structured or where were the main grounds for the species, limiting their use for the management of the remaining population.

The use of SDMs in this case is relevant to refine the distribution pattern, providing hypotheses for the location of the main historical grounds and inform decisions for the management of the species. In particular, the prediction can guide monitoring effort to identify potential areas used by today's population.

This work focused on a species-centered approach, but analyses at the community level could also be interesting, investigating the changes in species richness over time (McCorquodale et al., 2007; Grixti et al., 2009), to identify areas of high human footprint.

Understanding past abundances and human-caused population depletions

Estimates of previous abundance can be compared with current population levels to inform how species have been depleted. In a management context, this can help assessing the current conservation status of species (Jeppsson et al., 2010), as population trend is among the criteria used by the IUCN Red List to categorize the risk of extinction of species. However, this only applies to recent cases of depletion, as the criteria concerning reduction in population size only considers the last 10 years or 3 generations (IUCN SSC, 2001). In the case of currently exploited populations, it can also be used as an indicator to set realistic goals for management that are not just based on recent abundance trends (Rosenberg et al., 2005).

Spatially-explicit information on past abundance can help us understand which areas were in fact the best for species, guiding management efforts for their recovery (rather than simply focusing on current range that may well be marginal to its original habitat).

The interest of estimating populations' past abundance to settle appropriate management objectives can be illustrated by the rules decided by the International Whaling Commission (IWC) to manage whale populations. In its attempt to regulate quotas of baleen whales catches in 1974, the International Whaling Commission advocated a New Management Procedure (NMP) (International Whaling Commission, 1976) in which the current population size of whales would have to be compared to its original one to set harvesting quotas and classify the species into management categories (Allen, 1981). After the IWC placed a moratorium on commercial whaling in 1986, the Revised Management Procedure (RMP) was created, along with a method to determine the maximum quotas allowed if commercial whaling was to be resumed (International Whaling Commission, 2011c; Cooke et al., 2012). The commission also stated that "catches should not be allowed on stocks below 54% of the estimated number the environment can

Box VI-9. About the North Atlantic right whale: Understanding past abundance

Estimates of pre-exploitation abundance are needed to set targets for the management of NARW, but there is considerable uncertainty regarding the original population size.

Our estimate of a pre-whaling population of ten to twenty thousand individuals strongly suggests that the current population is extremely depleted (less than 6% of the total historical population size), but also show the realms of possibility for future recovery.

Our spatially-explicit prediction of abundance raises hypotheses for the location of historical grounds for the species, hence informing future monitoring surveys to identify areas currently occupied by the extant population, with potential implications for the conservation of the species.

support, known as the ‘carrying capacity’, or the estimated unexploited population size”, specifying that this objective should be given the “greatest priority” (IWC, 2014). Thus, assessment of baleen whales population's status requires agreement upon a reference level, for comparison with the present population level.

Biodiversity conservation in a changing world

How to define the historical baseline?

Assessing a species’ decline involves looking at the past for a reference point, a baseline, to be compared with the current status of this species. While the need for this baseline is widely accepted, its definition, notably concerning the appropriate timescale to be considered, is unclear. Choosing the appropriate reference point to which to compare the current situation is not straightforward, and arbitrary decisions have to be made as to which historical baseline should be used to assess such changes. Current conservation approaches generally consider changes in relation to a relatively recent date (e.g., the Living Planet Index uses 1970 as the reference year for measuring population trends; WWF et al., 2014), and/or within a few years or generations (e.g., the IUCN Red List uses 10 years or three generations, whichever is longer, as the scale over which to consider population declines; IUCN SSC, 2001 see also Frankham & Brook, 2004). Throughout this study, I highlighted the fact that this short time-scale is not always appropriate for assessing changes in species distributions and abundances, and advised for the consideration of a longer time scale.

Natural changes in species’ ranges and abundance have occurred since the beginning of life, as the result of processes occurring at various time scales: from geological processes such as glacial and interglacial periods and catastrophic events, at the scale of millions of years; to ecological processes at the scale of years or decades, conditioned by short-term demographic and dispersion processes. In-between, evolutionary processes also impact species distribution through the emergence and extinction of species and evolutionary adaptations (e.g. changes in species’ niche). One could argue that the purpose of conservation is to mitigate the impacts of humans on biodiversity, and not to counteract natural processes, even if they induce similar patterns of change. From a management perspective, we might thus want to define the historical baseline for species as their status before it was impacted by human. But deciding how far back into the past to go is not straightforward, because the further back we go the more difficult it is to distinguishing between natural and human-caused of change.

Overexploitation is among the earliest effects on wildlife populations (Burney & Flannery, 2005), having started centuries or even millennia ago (e.g. compared to climate change for example, which

is relatively recent in comparison). Thus, in the case of species that have had a long history of human exploitation, the appropriate historical baseline to assess declines in distribution in abundance could be considered as their pre-exploitation status. However, I have here focused on the last 10,000 years (with most of the data analyzed much more recent than that) in order to reduce the effects of natural climatic variation, associated with the end of the last glacial period, on species' abundances and distributions, even though for some species and regions human impacts started earlier than that (Burney & Flannery, 2005).

The definition of "pre-exploitation" itself suffers from a shifting perception. Species' commercial or industrial exploitation are often perceived as the main causes of human impact. This may be true for many species, as these intensive operations are likely to have caused major range contractions and population depletions. But this definition is not adapted for species that have been depleted earlier, as a cumulative effect of smaller-scale levels of exploitation. Particularly for species that are easily accessible to human and whose exploitation does not require advanced technologies, the impact of early hunting, including for subsistence, may have been underestimated. In the case of whales for example, the commercial whaling period in the 19th and 20th centuries is often considered as the first most impacting period of exploitation, which is true for many species (e.g. blue whales, beaked whales). But it is a simplification for others that were already heavily exploited as soon as the Middle Ages and strongly depleted before industrial or scientific records started (e.g. the North Atlantic right whale, the gray whale in the North Atlantic). For the latter, setting the baseline as the status of the populations in the 19th century would seriously underestimate the level of human impact and reduce perspectives for their recovery.

The assessment of human impact thus suffers from a shifting perception, in part explained by the lack of information we have of early stages of exploitation. Because early impacts leave little trace in the historical records, very early states are difficult to estimate. This case of collective amnesia can lead to a vicious circle where the historical baseline is defined as the status of species before industrial exploitation for a lack of earlier data, and earlier data are disregarded as not useful for estimating the historical baseline.

Overall, the choice for an historical baseline is relative, and there is no general answer for the appropriate period that should be considered as the reference state of a system. Efforts should be made systematically on a case-by-case basis to consider the history of interaction with humans, as a first step towards identifying the moment at which human activities started to have an impact on the system considered. Only through a better understanding of the history of human exploitation of natural resources will we be able to estimate the level of human impact on species and ecosystems in general.

Is the historical baseline an achievable/desirable target for conservation?

Assuming an historical baseline of abundance and/or distribution for a given species is well understood, important questions remain concerning its usefulness in a conservation context, and in particular its relevance as a target for conservation actions. In a globally changing and progressively human-dominated planet, it is pertinent to ask how much space is there for the recovery of depleted species.

Species distributions and abundances are the product of interactions between the species traits with biotic (i.e. interactions with other species within the community) and abiotic (i.e. climatic and physical conditions met in the environment) factors. Humans have profoundly affected all three of these aspects, with direct and indirect effects on the current as well as potential distribution of species.

The local extirpation of entire populations may have resulted in the loss of particular physiological and/or behavioral adaptations, for example the killing of individuals adapted to warmer waters, or those that preferred open habitats, or of lineages with breeding philopatry. If so, recolonization of the historical range by the remaining individuals may take a long time, even after human impacts ceases. The loss of a particular adaptation to an environment is also likely to prevent recolonization of a particular habitat for which the remaining individuals would not be totally adapted. For example, the remaining individuals of an exploited population might be those that were able to seek refuges in remote places, and the “open-habitat” adaptation might have been lost with the removal of the most approachable individuals. To identify potential sites that a species could recolonize, it is important to keep in mind that the remaining population may not necessarily have retained the ability to live in all of its former range.

Species’ distributions are also shaped by abiotic factors, themselves impacted by anthropogenic activities. It is expected that recent human-induced climate change (affecting temperature, rainfall, extreme events, CO₂ concentration and ocean dynamics) may cause range shifts, both in marine and terrestrial systems (Walther et al., 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Bellard et al., 2012). The potential distribution of depleted species can thus be different from their former realized distribution, as a result of shifts in the spatial extent of their bioclimatic envelope.

The physical environment encountered by species has also changed. Both on land and in the seas, the landscape is now strongly urbanized, and the space for species to recover is more and more reduced, as result of direct competition with human for space and increasing risks of mortality. For example, the Mediterranean monk seal that previously had colonies in open beaches along the French Mediterranean coast are unlikely to be able to recolonize such habitat, which is now a hotspot for tourism and recreational activities (Johnson & Lavigne, 1999a). In the marine

environment, increases in shipping, oil and gas exploration and fishing are likely to increase the risks related to pollution, noise disturbance, collision with ships, bycatch and entangling in nets (Alter et al., 2010). . The human response to mitigate climate change also has many indirect effects. For example, the development of infrastructure to produce sustainable energies (e.g. wind farms) has consequences on biodiversity, both in marine (Madsen et al., 2006) or terrestrial (Kuvlesky et al., 2007) systems, through direct mortality or impacts on species' behavior (Leung & Yang, 2012). These are a brake to recovery, as they may lower the growth rate of populations.

The community of other species with which a given species previously interacted is likely to be very different from what it would find today if it was to recolonize its former range. Human activities have modified the community structure of ecosystems (through overexploitation, introduction of invasive species, etc.) such that the guild of predators, preys, competitors and parasites have been modified. Example of such alteration in the marine environment includes the reduction in mean trophic levels of marine species caused by the gradual depletion by fisheries of species at higher trophic levels ("Fishing down marine food web"; Pauly et al., 1998). Depletion of taxa can in turn impact the structure of the food web through chain reactions. Industrial whaling is for example suspected to have induced an indirect collapse in population of seals, sea lions and sea otters in the North Pacific as the result of a shift in killer whales predation from baleen whales to smaller marine mammals (Springer et al., 2003, 2008). If so, whaling may have had important impacts on the whole marine ecosystem in this area, including the reduction of kelp forests by sea urchins (whose numbers have increased following the depletion of their main predator, sea otters), and modifications in physiology, demography and behavior of myriads of associated species (Estes et al., 2009). Humans themselves can be strong competitors for resources and represent a direct obstacles for the recovery of predator species, either because the availability of their prey is reduced by human exploitation or through persecution of such predator species viewed as undesirable by fishers or hunters (e.g. competition between marine mammals and fisheries; Kaschner & Pauly, 2005). The full scope of consequences of human impacts on ecosystems is difficult to apprehend and requires extensive amount of studies on the changes in ecosystem structures. But it should be kept in mind, as it can cause changes in the carrying capacity of the environment for a particular species (through changes in prey or competitor occurrence and abundance), in the predation risks and in the risk of contracting diseases (through changes in parasites or pathogens communities). A good knowledge of the species' ecological requirements and of the ecosystem structure (both historical and current) is thus important to clarifying the potential for an area to be recolonized.

For all of these reasons, the environment that a species encountered before being extirpated from an area is not necessarily the same as the one it would encounter today if it was to recolonize it. It is

difficult to predict how such changes affect the potential for recolonization of an area from which a species was extirpated, bringing uncertainty as to whether it is still suitable for the species. The expectation that species can recover to their level prior to human impact is thus probably naïve. Aiming for this level of recovery is perhaps desirable to set ambitious conservation targets but effectively attaining the pre-exploitation baseline is most likely unachievable, except in very particular cases where none of the factors mentioned above are limiting.

Historical baselines are nonetheless useful as a comparison point to assess the level of depletion of species, inform monitoring and infer the potential for its recovery. Measures of the level of depletion are lacking in current efforts to estimate species conservation status. For example, the conservation status according to the IUCN Red List of Threatened Species is about extinction risk, which has great importance in conservation, but misses this concept of depletion compared to an initial population level/range. Indeed, the IUCN Red List criteria only consider a short period of time (3 generations) to assess the decline of a species (IUCN SSC, 2001). Measures of human impact based just on extinction risk (e.g. Red List Index; Butchart et al., 2006) or recent declines (e.g. Living Planet Index, WWF et al., 2014) give therefore a biased perception of the overall level of impact on species, contributing to the shifting baseline syndrome. These indicators should therefore be complemented by efforts to keep track and quantify the absolute levels of depletion of species, to provide society with a clearer vision of the past state of ecosystems and human impact on them. I believe that revealing the potential diversity of ecosystems and abundance of species can encourage efforts for mitigating current threats, so that species are given the chance and the space to recover. Finally, efforts for understanding the history of human impacts on biodiversity should be motivated by the need to remember our actions and avoid doing the same mistakes in the future. As the philosopher George Santanaya summarized it, “those who cannot remember the past are condemned to repeat it” (Santanaya, 1905).

Box VI-10. About the North Atlantic right whale: Conservation in a changing world

Which baseline?

In the light of our knowledge of the history of exploitation of the species, and according to the definition of the historical baseline provided above, I propose that the historical baseline for the NARW is defined as its status before the Basques started its exploitation in the 11th century. Given current knowledge, this seems to have marked the beginning of substantial human impact on NARW populations, though I cannot rule out the possibility that forgotten whaling activities impacted the distribution and/or abundance of the species even earlier. I therefore assume that my reconstructed distribution and abundance for this species correspond to such a baseline.

How much human impact?

The comparison between my reconstituted baseline of distribution and abundance with current range and population size indicate that the species is heavily depleted both in space and in numbers. Current range off the eastern coast of North America is a small fraction of the predicted past distribution, which extended from northeastern America to northern Norway. The current population is a mere 2.5 to 5% of the estimated past population.

Is this baseline an achievable target?

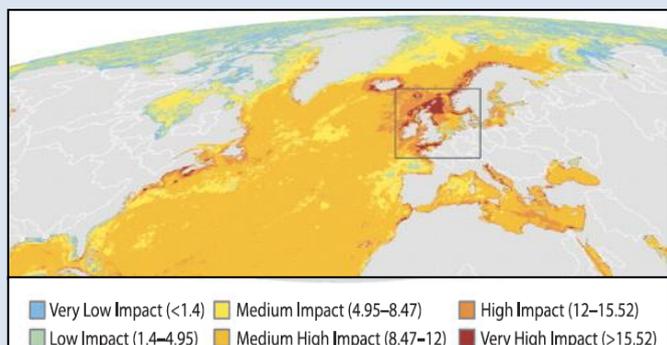
These baselines show an enormous potential for the recovery of this species. However, a number of limitations mean that they are probably unrealistic conservation targets for such recovery. The predicted pattern of probability of presence is only a representation of the distribution of suitable habitat for the NARW if it had not been depleted, which is not necessarily identical to the areas it could recolonize today.

The species currently occupies a restricted portion of its historical distribution. Though highly speculative, there is a possibility that the remaining individuals have lost the ability to recolonize their former habitat, as a result of losses in genetic lineages or particular adaptations. This could explain the current lack of recovery in the Eastern North Atlantic, though cases of vagrancy in the northeast Atlantic are encouraging for the recolonization of the historical range.

The species biotic and abiotic habitat has also been strongly impacted by human activities. Human influence has altered abundance and composition of trophic level in the food web (Lotze & Milewski, 2004), with unknown implications for the recovery of baleen whales. The depletion of the bowhead whale, a direct competitor of NARW for food, may have potentially opened new areas of low competition in the northern part of the NARW range, which could benefit its future recovery.

Current threats for the species include collision with ships (Knowlton & Kraus, 2001; Knowlton & Brown, 2007), entanglements (Johnson et al., 2007) and ship noise-induced stress (Rolland et al., 2012). NARW will also potentially be threatened by future offshore infrastructure, such as wind turbines (Whitt et al., 2013), though current efforts to mitigate this threat are undertaken (Petruny et al., 2014).

The map of cumulative impacts provided by Halpern et al. (2008) (see map below) highlight the high level of human impact on marine ecosystem throughout the North Atlantic, and raises questions about the ability for NARW to recover in this urbanized ocean. In addition, questions can be raised about the available space for NARW in their former breeding grounds in the Bay of Biscay, a now highly inhabited and touristic coast. Finally, the effect of climate change on the demography of NARW may make the North Atlantic right whale even more vulnerable than predicted (Greene & Pershing, 2004).



Map of cumulative human impact in the North Atlantic basin

(Adapted from Halpern et al., 2008)

The eventual recovery of the NARW at its historical level is unlikely to happen in a human-dominated planet where competition with human for resources is so important, and where direct and indirect impacts of human activities are limiting the growth rate of the current population. Nonetheless, even if the historical target is not to be reached, efforts to mitigate these threats should be done to give the necessary space for the species to increase in number, recolonize its former range, and eventually return to a state where it is no longer threatened of extinction.

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Reconstruction de la distribution et de l'abondance historiques des mammifères marins : Etablir un niveau de référence pour comprendre le passé, renseigner le présent et planifier l'avenir

La mise en place d'objectifs de conservation adéquats repose sur la définition d'états de référence appropriés pour la distribution et l'abondance des espèces. Cependant, l'étendue des impacts cumulés de l'homme sur les écosystèmes est aujourd'hui largement sous-estimée. Dans ce projet, je m'intéresse aux opportunités qu'offre l'utilisation de données historiques combinées à différentes méthodes analytiques pour définir ces états de référence ainsi qu'aux défis posés par ce type d'approche. Des données de présence ont été recueillies pour sept espèces de cétacés et trois espèces de pinnipèdes à partir de sources archéologiques, historiques et industrielles, révélant des réductions dans la distribution et l'abondance des espèces depuis la préhistoire à nos jours. Des modèles de distribution d'espèces ont été développés pour cinq espèces de cétacés, combinant des données de chasse baleinière du 19^{ème} siècle à des variables environnementales afin d'estimer la distribution historique des espèces avant qu'elles n'aient été chassées. J'ai obtenu pour la baleine franche de l'Atlantique Nord (*Eubalena glacialis*) une estimation détaillée de sa distribution et de son abondance avant qu'elle ne soit exploitée, en extrapolant des connaissances sur la distribution et l'abondance d'une espèce congénérique, la baleine franche du Pacifique Nord (*E. japonica*). Ces résultats suggèrent que la baleine franche de l'Atlantique Nord occupe une portion réduite de sa distribution historique, et que son abondance actuelle ne représente qu'une infime portion (<5%) de son abondance passée. Plus généralement, ces résultats soulignent l'importance de considérer des données historiques pour comprendre le niveau d'impact par l'homme sur les espèces, évaluer leur niveau de déplétion et renseigner leur potentiel de rétablissement dans l'avenir.

Mots-clés : Abondance, Baleine franche de l'Atlantique Nord, Distribution, Etat de référence, *Eubalaena glacialis*, Mammifères marins, Modèles de distribution d'espèces.

Reconstruction of marine mammal's historical distribution and abundance: setting a baseline to understand the past, inform the present and plan the future

Relevant baselines on the historical distribution and abundance of species are needed to support appropriate conservation targets for depleted species, but the full scale of cumulative human impacts on ecosystems is highly underestimated. In this project, I investigated the challenges and opportunities of combining historical data with analytical methods to improve these historical baselines. Occurrence data from archaeological, historical and industrial sources were reviewed for seven cetacean and three pinniped species, revealing range contractions and population depletions from prehistorical times to today. For five whale species, I used species distribution modelling to combine 19th Century whaling records with environmental data, to estimate pre-whaling distributions. For the highly depleted North Atlantic right whale, (*Eubalaena glacialis*), I obtained a detailed estimate of pre-whaling distribution and abundance by inferring from the historical distribution and abundance of its congeneric North Pacific right whale (*E. japonica*). These results suggest that the North Atlantic right whale occupies a small fraction of its historical range and that its current population represents <5% of its historical abundance, with implications for the management, monitoring and conservation targets of this species. More generally, these results emphasize the utility of considering historical data to understand the extent to which species have been impacted by humans, assess their current level of depletion, and inform the options available for their future recovery.

Keywords: Abundance, Baseline, *Eubalaena glacialis*, Distribution, Marine mammals, North Atlantic right whale, Species distribution models