EFFECTS OF SEISMIC OPERATIONS ON BOWHEAD WHALE BEHAVIOUR: IMPLICATIONS FOR DISTRIBUTION AND ABUNDANCE ASSESSMENTS

by

Frances Charlotte Robertson

M.Res. University of Aberdeen, 2004

B.Sc. (Hons), University of Aberdeen, 2003

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

July 2014

© Frances Charlotte Robertson 2014

Abstract

Assessments of distribution and abundance are a common means of gauging impacts of anthropogenic activities on wildlife. However, the influence of behavioural responses on estimated numbers and distributions of animals is rarely considered within this context. I used behavioural data collected in the Beaufort Sea from 1980-2000 to investigate the effects of seismic operations on the distribution and abundance of bowhead whales (*Balaena mysticetus*). Bowhead whales are known to vary their dive and surface-respiration behaviour when exposed to seismic survey operations, although it is unknown whether these changes in behaviour differ by season, reproductive status and activity (feeding, socializing and travelling). Overall, I found that changes in behaviour of whales exposed to seismic operations were context dependent (i.e., they were contingent on the whale's circumstance and activity). I then investigated the effects of these behaviour changes on the sightability of whales to aerial observers conducting line-transect surveys. I calculated and compared sightability correction factors specific to whales exposed and not exposed to seismic operations and found that whales in all circumstances were less available for detection when exposed to seismic sounds. In particular, non-calves were the least available to observers during autumn when exposed to seismic activities, regardless of activity state. I used line-transect distance sampling and spatial modeling methods to generate corrected density estimates for bowhead whales in an area of the southern Alaskan Beaufort Sea ensonified by seismic operations between late August and early October 2008 to investigate the extent to which density analyses were affected by changes in whale availability. The resultant density surface models revealed a wide-spread nearshore distribution of whales within the ensonified area with some spatial segregation related to activity state. Density estimates that accounted for variations in whale behaviour due to seismic operations were also 25–64 % higher than previous estimates. Collectively, these findings suggest that seismic activities may not have displaced bowhead whales as previously thought, but altered their dive behaviours instead ,making them less visible for counting. My research demonstrates the importance of accounting for behavioural reactions when assessing impacts of seismic operations on distributions and abundances of whales

Preface

I performed all data analysis presented in this thesis. I also designed and conducted the field of view experiment described in Chapter 3. I prepared and wrote Chapters 2, 3, and 4 as manuscripts which benefited from comments and edits by co-authors W. R. Koski (Chapters 2, 3 & 4), T. A. Thomas (Chapters 2 & 3), W. J. Richardson (Chapter 2), B. Würsig (Chapter 2), J. Brandon (Chapter 3) and A.W. Trites (Chapters 2, 3 & 4).

A version of Chapter 2 has been published as: Frances C. Robertson, Koski, W. R., Thomas, T. A., Richardson, W. J., Würsig, B., and Trites, A. W. (2013) Seismic operations have variable effects on dive-cycle behaviour of bowhead whales in the Beaufort Sea. Endang Species Res. 21: 143-160.

All research and data analysis were performed on archival data collected from 1980 to 2000 and in 2008. Permission to use these data was provided by the United States Bureau of Ocean Energy Management and by Shell Alaska. The behaviour and sightings databases were made available to me by LGL Ltd.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

ADFG	Alaska Department of Fish and Game
AIC	Akaike Information Critera
a.s.l.	Above sea level
a(x)	Probability that a whale is at the surface and available for detection by aerial observers, at least once as the survey platform passes overhead.
BCB	Bering-Chukchi-Beaufort
BOS	Behavioural Observation Session
CDS	Conventional Distance Sampling
CI	Confidence Interval
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CV	Coefficient of Variation
DASAR	Directional Autonomous Seafloor Acoustic Recorders
easting	Geographic Cartesian coordinate for longitude in meters (m), where coordinates have been projected in NAD83/Alaska Albers
ESA	Endangered Species Act
GAM	Generalized Additive Model
g(0)	The probability that an object that is on the line or point is detected
$g_a(0)$	The probability that an object is available to be detected
GCV	Generalized Cross Validation
GEBCO	General Bathymetric Chart of the Oceans
GIS	Geographic Information System
GPS	Global Positioning System
IWC	International Whaling Commission
LME	Linear Mixed Effects
MCDS	Multi Covariate Distance Sampling
MMPA	Marine Mammal Protection Act
NSERC	National Science and Engineering Research Council
s()	Smooth function of explanatory variables included in Generalized Additive Models
se	Standard error
SRD	Surface Respiration Dive
STOL	Short Take Off and Landing

REML	Restricted Maximum Likelihood
UAV	Unmanned Aerial Vehicle
VIF	Variance Inflation Factor

Acknowledgements

First and foremost I would like to thank Andrew Trites and Bill Koski for giving me the opportunity to pursue my PhD. I have had the privilege of learning how to be a scientist from two very fine examples. There would not have been a PhD without Bill. His insights into the issues and deep understanding of bowhead whales and industry provided a constant source of guidance. I have learnt how to conduct aerial surveys from the best that there is and I have learnt how to look at every aspect of the bigger picture. Thank you for being a fantastic (unofficial) supervisor. As a supervisor, Andrew has shown great patience in me and has had continued faith in my abilities—even when my own faith wavered. Andrew has been instrumental in teaching me how to write and communicate science—skills that will be invaluable to me throughout my career.

I thank my committee members John Ford and Steve Martel for their guidance over the course of my degree, particularly for their comments and suggestions that kept my thesis on track.

NSERC and LGL Ltd provided the majority of my funding that allowed me the opportunity to pursue my PhD studies. Additional assistance provided by the Faculty of Graduate Studies, Department of Zoology, the Dean Fisher Memorial Scholarship, the American Cetacean Society and Society of Marine Mammalogy allowed me to share my research and attend international conferences.

My research would not have been possible without the years of effort from many observers, biologists and pilots that resulted in the rich archival bowhead behaviour database that was available to me. Access to this database was provided by Charles Monnett at the Bureau of Ocean Energy Management and Michael Macrander at Shell Alaska Ventures. I am also indebted to Michael Macrander for providing permission to use Shell's 2008 aerial survey sightings and effort data.

I am appreciative for the opportunities that I have had to work with many individuals from LGL Ltd over the course of my degree—and am grateful for numerous discussions that I have had with Craig Reiser, Darren Ireland, Meike Holst, John Brandon and Tannis Thomas that have helped broaden my understanding of issues related to marine mammal mitigation in Alaska. I particularly appreciated the many useful insights that Tannis gave me into the bowhead behaviour data and survey protocol. There are also many other observers and pilots that I have had the opportunity to work with over my aerial survey seasons in Alaska, all of whom have helped make me a better observer. Suzie Hanlan has been a faithful friend, keeping me grounded throughout, from my very first aerial season till the last. I feel privileged to have worked with Renee Hobson, as well as Minnie Nashookpuk and Roy Oktolik all of whom were so willing to teach me about their culture and the importance of the bowhead whale.

There are a number of individuals that have been influential to my thesis and my personal progression as a scientist. I am indebted to John Brandon for his statistical guidance and R-coding abilities, as well as his insights into navigating between academia and industry. Uko Gorter took my crude diagrams and created the superior figure of a bowhead surface-dive cycle that I used throughout my thesis. Mari Smultea has been wonderfully encouraging and inspiring, as well as extending me the opportunity to learn how cetacean behaviour data are collected from aerial platforms. Also I am exceedingly lucky for the considerable insights and expertise of Bernd Würsig and John Richardson as I navigated my way through the analysis, write-up and publication of Chapter 2. Jonathan Stern has had a significant influence on the way that I now think about marine systems and I am grateful for his mentorship over these years, and hopefully for many years to come. Additional thanks are also extended to Alison Gill, without whose encouragement I would never have ventured offshore as a marine mammal observer—an experience which ultimately led to this PhD.

Over the course of my degree I have had the pleasure of working with students and researchers in the Marine Mammal Research Unit, as well as many other individuals at the Fisheries Centre. I am especially grateful for the firm friendships that I have formed with Tiphaine Jeanniard du Dot, Susana Cardenas, Brian Battaile, Rowenna Gryba, Erin Rechsteiner, Anna Hall and Ruth Joy. These individuals, along with David Miller, Chad Nordstrom and John Brandon have also provided valuable help with R-coding. For Chapter 4, I received GIS help from Matthew Forester, Erin Rechsteiner, Chad Nordstrom and James Stott. I extend my thanks to Aaron Greenberg, Jeff Laake, David Borchers, David Miller and Rowenna Gryba for their helpful comments and guidance in the calculation of the availability correction factors in Chapter 3 and density surface modelling in Chapter 4.

Parts of my thesis were written from the beautiful setting of the 'whale cabin' on the west side of San Juan Island. Thank you Sharon and Paul for letting me stay at your delightfully inspiring cabin during some winter weeks of 2011, 2012 and 2013, where the first drafts of my thesis took form.

My family have provided unwavering love and support throughout my degree. I would like to thank my parents for instilling in me the independence and determination to pursue my studies as well as giving me the freedom to follow a path in a field that they knew would be challenging—a path that has also seen me move half-way around the world. I am also so very lucky to have had the support of my two younger sisters, Gabriel and Jessie. I would not have been able to finish my degree without the financial support provided by my parents and grandparents over the last few years. My grandmother, Gwen, has taught me that there will always be `bumps in the road` but that we can always get over them. She has also listened faithfully to my progress updates over the years—to the extent where she once awoke from a night dreaming of equations!

And finally, thank you Daniel for making this last year so enjoyable and above all for continuing to teach me how art and science are so beautifully intertwined.

To Maxine, my constant source of strength and inspiration.

Chapter 1: General Introduction

The distribution of animals within their environment has been described as one of the cornerstones of ecology (e.g., Andrewartha & Birch 1984, Tregenza 1995). Animal distribution is influenced and often limited by a combination of demographic, evolutionary, ecological, physiological, and anthropogenic-related factors. Animals are closely adapted to their habitat, and can be considered a part of it (Elton 1950, Bourlière 1954).

Animal behaviour influences how animals distribute themselves within the habitat they occupy, and behaviour can vary due to specific life-history activities (e.g. foraging and reproduction), or in response to variations in individual physiological capabilities (Morris 2003). Animal behaviour is also influenced by the introduction of disturbance stimuli such as human activities (Beale 2007). But behavioural responses are complex and highly contextual, depending on factors such as quality of the habitat occupied, distance to and quality of other suitable habitats, risk of predation, density of competitors in different sites, and the investment that the individual has made at a site (Gill et al. 2001, Bejder et al. 2009). The perceived effects of disturbance must therefore be factored into the decisions made by animals because of their influence on how an animal utilizes and is distributed within its habitat (Bejder et al. 2009).

The degree of 'predation risk' also influences how individuals distribute themselves. Disturbance may have a similar effect on how an animal locates and exploits available resources, and has traditionally been considered within the same theoretical framework as predation risk (Sutherland 1996, Frid & Dill 2002). Disturbance is often assessed by determining either the distance from the source of disturbance at which individuals begin to move away, or the time that elapses before they return to their normal behaviours after being disturbed (Sutherland 1996). However, accurately assessing disturbance requires a good understanding of how animals respond behaviourally to disturbance (Gill & Sutherland 2000).

The influences of human activities in the terrestrial and marine environments are broad, and animal responses to human activities are wide ranging—depending on the type of activity and the sensitivity of the individual animal. Animals may be able to adapt in order to take advantage of opportunities introduced by the human activity (e.g. a foraging or habitat-related opportunity; Laist & Reynolds 2005). However, in many cases human activities are considered to have negative effects on animal populations, ranging from short-term responses such as habitat displacement and changes in behavioural patterns, to long-term impacts with possible population level consequences. Human activities deemed to have a negative effect on animal populations are considered a disturbance. In the marine environment human activities that emit sound are examples of activities that potentially disturb animals.

Animals exhibit a range of responses when exposed to stimuli from human sources including physiological, psychological and behavioural responses. Animal behaviour has traditionally been the main focus of studies investigating the effects of disturbance on animal populations, and is an important discipline for understanding how animals respond to human disturbance (Gill & Sutherland 2000, Gill et al. 2001, Beale & Monaghan 2004b). It is particularly important to understand how individuals and populations respond to disturbances both in the short-term (to mitigate and limit the immediate effects of a disturbance), as well as in the long-term (Gill & Sutherland 2000, Gill et al. 2001, Beale & Monaghan 2004b).

An animal's behavioural response to anthropogenic disturbances is contextual in the sense that there are a variety of factors that influence the decisions made by animals (to ensure the overall viability of a population; Bejder et al. 2006). The results of these decisions may be reflected in the animal's distribution with respect to the disturbance, and may have significant consequences for subsequent management and conservation strategies. Long-term habitat loss through avoidance may have population-wide consequences, while short-term impairment of foraging opportunities may affect an individual for a limited time period, without population level impacts. Therefore, understanding the impacts of human disturbances and mitigating short-term effects and long-term impacts on exposed populations can be better achieved by taking a behavioural approach that accounts for differential responses (Beale 2007).

In the marine environment, marine mammal populations are faced with increasing levels of human activity. In many parts of the world dedicated marine mammal monitoring and mitigation procedures are required to minimize the effects of such activities. Key components of these protocols are the assessment of the distribution and abundance of animals near these activities. However, these assessments rarely consider the behavioural responses of animals to human activities.

Behavioural responses of marine mammals to human activities vary and often affect their detectability by observers in the field. Changes in behaviour may result in a reduced detection rate by observers, which may in turn influence analyses of relative abundance and distribution, a clear understanding of which are critical to management and conservation strategies. This issue of variable detectability of animals in the field has implications for mitigating human activities, and highlights the need to consider key aspects of behaviour and other life history characteristics of a population.

Distribution and abundance assessments are mostly dependent on the ability to detect animals, either through visual or acoustic detection. Visual detection of marine mammals commonly takes place from ship-based or aerial platforms and is dependent on how visible the animal is to the observer. Cetaceans are only visible to observers when at the surface. The longer a cetacean spends at the surface and the shorter the periods it spends below the surface, the higher the probability of it being visually detected. Differences in surfacing and diving behaviour as a function of reproductive status, animal activity, and habitat influence how visible an animal is to an observer and therefore the probability of detection. Therefore it is important to understand the contexts within which animals make their behavioural choices in response to the physical and biological processes in their environment (Beale 2007, Bejder et al. 2009), and the subsequent behavioural variation must be accounted for within animal abundance estimates. Estimates of distribution and abundance are key elements of impact assessment models that are designed to quantify the effects of anthropogenic activities on animal populations. Incorporating a theoretical framework, based on individual decision making, into impact assessment models allows for the behavioural outcomes of a disturbance to be understood (Gill & Sutherland 2000, Gill et al. 2001, Frid & Dill 2002, Bejder et al. 2009). In turn, this understanding can refine the predictive ability of species-distribution assessments with respect to disturbance impacts on wildlife populations.

Currently, assessments of distribution and abundance of marine mammals relative to industry operations are often limited through their inability to incorporate animals' fine-scale behavioural responses into the assessments. These assessments are essential components to the reasonable management and effective conservation for wildlife populations, particularly in regions where there are increasing levels of competition for natural resources with high cultural, economic and environmental values.

Research Objectives

Industrial activities such as seismic operations overlap with the distribution of bowhead whales in the Alaskan Beaufort Sea in late summer and autumn. This has led to concerns that industrial activities are impacting the distribution and behaviour of whales, as well as the subsistence hunt. The main research goal of my thesis was thus to assess factors that influenced the dive and surface-respiration behaviours of bowhead whales in the presence and absence of seismic operations. I also sought to determine whether behavioural variation influenced analyses of bowhead whale density in the Beaufort Sea.

The overall objective of my research was to understand the behavioural response mechanisms of bowhead whales to seismic operations, and to determine how these may affect subsequent analyses of distribution and relative abundance of bowhead whales during their autumn migration through the southern Beaufort Sea. I used a combination of bowhead behavioural data spanning approximately 20 years and sightings data from industry monitoring surveys conducted August-October 2008 to address the following hypotheses:

1. Exposure to seismic operations causes bowhead whales to change their dive and surface-respiration behaviours.
2. The availability of bowhead whales for visual detection during aerial surveys changes when whales are exposed to seismic operations.

3. Variable availability of bowhead whales due to seismic operations biases density analyses.

Research Question Justification, Study Area and Species

A wide range of human activities can affect the behaviour and life history of cetaceans. Human activities may lethally impact cetaceans through hunting, bycatch associated with harvests of other species, collisions, and stranding as a direct result of attempted avoidance of human activities. While other activities, such as those that produce sound, (e.g. seismic survey operations) may cause changes in cetaceans' normal behaviour, including changes to surface-dive, swim and acoustic patterns, and possible displacement and avoidance. Such effects may be non-lethal, but may still have significant conservation consequences. For example, disturbance may activate a stress response in cetaceans (Richardson et al. 1995b) that involves a combination of the animal's nervous, hormonal and behavioural response systems. Although there are few studies (Rolland et al. 2012) providing direct evidence of noise–induced stress in cetaceans, anthropogenic noise may contribute in a cumulative manner to stress experienced by cetaceans (e.g., Richardson et al. 1995b).

In the marine environment, anthropogenic sound has contributed to measured increases in ambient sound levels, particularly low-frequency sound (Richardson et al. 1995b, Southall et al. 2007). Cetaceans are considered especially susceptible to acoustic-related disturbances because they rely on acoustic signals to detect conspecifics, prey, predators, and obtain information on their surrounding environment (Richardson et al. 1995b, Southall et al. 2007). Potential noise-induced effects on cetaceans include auditory masking; which may range from temporary to permanent auditory threshold shifts; and changes in behaviour patterns.

There is increased interest in understanding how cetaceans respond to anthropogenic sounds, and what impacts these responses may have at a population level. Behavioural studies are often the only way to measure and quantify an animal's response to disturbance stimuli due to limitations associated with costs, logistics and time (Bejder et al. 2006, 2009, Beale 2007). As a result, animal behaviour has been the main focus of disturbance studies (Vos et al. 1985, Gill et al. 2001, Beale & Monaghan 2004b). In the marine environment, the behavioural reactions of whales may range from subtle changes in surface and dive patterns to overt avoidance behaviour (Richardson et al. 1995b). Exposure to anthropogenic sound often results in animals changing their general activities. However, disturbance effects are expected to be context specific, depending on species, activities, the received level of sound, and the associated water depth (Richardson et al. 1995b). Studies of behavioural responses generally aim to characterize cause and effect relationships associated with short-term responses, and can usually only make inferences about the possible long-term biological significance of short-term responses (Bejder et al. 2009).

In the Arctic, the global demand for energy and better technologies is resulting in an increased interest in the region's apparently abundant energy resources. This is evident in the southern Beaufort Sea off the coasts of Alaska and Canada. As a consequence, there are growing concerns over the impact of oil and gas-related activities on the region's environment, particularly Arctic marine mammals. The cultures of the Arctic's people are closely interlinked with the region's ecosystems, and the bowhead whale is of particular cultural significance to the Alaskan Iñupiat (Koski et al. 2005).

The bowhead whale (*Balaena mysticetus*) has a circumpolar distribution in the northern hemisphere. Four populations of bowhead whale are recognized by the International Whaling Commission (IWC) for management purposes, of which the Bering-Chukchi-Beaufort (BCB) population is the largest. Due to heavy commercial exploitation in the mid- to late 19th Century the bowhead whale is listed as endangered under the US Endangered Species Act and as a species 'of special concern' in Canada (COSEWIC 2005). However the population has shown remarkable recovery and is now estimated to number 16,892 (95% CI 15,704-18,928) (Givens et al. 2013) despite a subsistence harvest of 8-55 whales per year since 1974 (Brandon & Wade 2007, Suydam & George 2012)[1].

Most members of the Bering-Chukchi-Beaufort population of bowhead whales undergo an annual migration between their wintering grounds in the Bering Sea and their summer feeding grounds in the eastern Beaufort Sea and Amundsen Gulf. The autumn migration coincides with the time that the water is ice free and most easily accessible to offshore industrial activity in the Beaufort Sea (Angliss & Outlaw 2006). Concerns regarding the impacts of industrial activities on this population have resulted in the collection of extensive behavioural and distributional data. These data are from both long-term annual government research programs and industry-related monitoring and research programs and provide a rich archival dataset from which to assess both the behavioural responses of bowhead whales to industrial activities, such as seismic surveys, and subsequent effects of behaviour on the detectability of whales to visual observers conducting monitoring surveys for assessments of abundance and distribution relative to industrial operations. Such detailed data do not exist for other cetacean species—making this population the ideal study species for this study.

Bowhead whale behavioural studies to investigate the response of whales to human activities, particularly those associated with seismic exploration for oil and gas, were first initiated in the 1980s (Richardson et al. 1985, 1986). These studies presented evidence for localized displacement, changes in dive and surface-respiration variables over larger distances (Richardson et al. 1986) and avoidance of nearshore seismic operations by more than 20 km in migrating bowhead whales (Richardson et al. 1999,

[1] The IWC catch limits for the Bering-Chukchi-Beaufort Sea stock of bowhead whales for the period 2008-2012 are for a total of 280 bowhead whales to be landed, with no more than 67 whales struck in any year (and up to 15 unused strikes may be carried over each year).

Manly et al. 2007). The most recent studies have reported only localized avoidance of seismic operations, especially by animals engaged in feeding activities (Miller et al. 2005, Koski et al. 2009).

The behavioural responses of bowhead whales to seismic operations appear to be context specific. Although migrating whales have been observed to avoid seismic operations at distances of 20–30 km in the Alaskan Beaufort Sea (Richardson et al. 1999, Manly et al. 2007), whales on summer feeding grounds appear much more tolerant, only exhibiting strong avoidance responses in cases where active seismic vessels have approached bowhead whales within 3-7 km, where received levels of airgun sounds were 152–178 dB re 1μPa-rms (Richardson et al. 1986, Miller et al. 2005). Avoidance behaviour around active seismic operations in the Alaskan Beaufort Sea during the 1996, 1997 and 1998 seasons suggested that most migrating bowhead whales were avoiding an area out to 30 km of operating airguns, where broadband received noise levels were reported to be approximately ≥120–130 dB re 1 μPa-rms (Richardson et al. 1999). These avoidance responses indicated that near-shore seismic operations could cause offshore displacement of bowhead whales during their autumn migration under certain conditions. However, other variables may also have contributed to these observed differences in bowhead whale distribution that could not be investigated within the region and season when the 1996–1998 study was conducted (Richardson et al. 1999).

In contrast, bowhead whales appear tolerant of seismic operations while engaged in feeding or socializing activities (Miller & Davis 2002, Koski et al. 2009). During 2007 and 2008, feeding bowhead whales in the Alaskan Beaufort Sea appeared to tolerate seismic sounds until received levels approached ~160 dB ref 1μPa-rms, and some feeding whales appeared to tolerate higher levels of ~170–180 dB ref 1μPa-rms (Koski et al. 2009). However, observations of bowhead whales in close proximity to seismic operations suggest that they vary their dive and surface-respiration patterns while remaining in the area to feed; and those subtle effects on behaviour may extend to substantial distances even on the feeding grounds (Richardson et al. 1986). Comparisons of bowhead whale behaviour recorded in the presence and absence of seismic operations have shown a decrease in the mean durations of surfacings and dives and in the number of blows per surfacing while whales were in the presence of seismic operations (Richardson & Malme 1993). Studies to date suggest that when exposed to seismic survey sounds, bowhead whales engaged in feeding exhibit less avoidance behaviour than do animals engaged in active travel, suggesting that the behavioural responses exhibited by bowhead whales depend upon their activity state.

Variations in surface-respiration-dive cycles are key indicators of whale activity states, but they may also be related to age-class, water-depth, ice cover and exposure to seismic survey operations. For example, subadult whales have a lower median blow interval than adults and mothers, shorter dive durations during travelling, and marginally shorter surface durations during feeding than adults and mothers (Thomas et al. 2002b). These characteristics are related to shallower water depths, where younger whales occur in higher numbers than farther offshore in deeper waters (Koski & Miller 2009). Seasonal differences in surface-respiration-dive cycles are apparent in mothers and calves, which is probably attributable to calf size and differences in maternal care of younger versus older calves.

Differences in reproductive status, whale activity and habitat may affect the average time a whale is present at the sea surface and therefore these variations are hypothesized to influence 'whale availability' for observer detection. Visual sighting surveys are commonly used to determine the relative abundance and distribution of bowhead whales in the Beaufort Sea, and factors that influence the 'availability' of bowhead whales that can be seen by surveyors are likely to directly affect subsequent assessments of relative abundance and distribution. As a consequence, estimates of abundance near seismic survey operations may be biased and distribution estimates in a survey area near such operations may not be accurate if behavioural changes are not accounted for. These fine-scale behavioural responses should therefore be considered in such assessments, particularly as they may affect decisions regarding mitigation protocols in regions where there are increasing levels of competition for natural resources with high cultural, economic and environmental values.

Thesis Outline

My thesis is organized into five chapters. **Chapter 1** provides a general introduction outlining the background to my study, my research questions and the main motivations behind my study. In **Chapter 2**, I investigate the effects of exposure to seismic operations on bowhead whale dive and surface-respiration behaviour using a linear mixed model approach. This chapter has been published in Endangered Species Research (Robertson et al. 2013). In **Chapter 3**, I incorporate the results from Chapter 2 into equations to estimate the availability bias for bowhead whales. I have calculated the availability bias correction factors for both presumably undisturbed bowhead whales and whales exposed to seismic operations in order to assess the extent to which bowhead numbers may be under- or over-estimated in a survey area. In **Chapter 4**, I test the effects of incorporating the availability correction factors calculated in Chapter 3 in density analyses of raw survey sighting data. I performed density analyses following Distance methodology by using the two-step Density Surface Modeling approach within Distance. And finally in **Chapter 5**, I summarize my findings and present my concluding remarks. I also discuss possible caveats in my research and make recommendations for future research focus and model refinement.

Chapter 2: Seismic operations have variable effects on dive-cycle behaviour of bowhead whales in the Beaufort Sea

Summary

Surfacing, respiration and diving (SRD) behaviour of bowhead whales is known to change upon exposure to seismic operations. However, it is unknown whether these changes differ naturally by season, reproductive status (calves, mothers, and non-calves), and whale activity (traveling, foraging or socializing). Such SRD behavioural responses to seismic operations might influence detectability of whales during aerial surveys. I addressed these questions by applying non-parametric univariate tests and Linear Mixed Models to behavioural data collected by aerial observation of bowheads in the Beaufort Sea from 1980 to 2000. Durations of surfacings were found to decrease upon exposure to seismic operations, especially for traveling or socializing non-calf whales. The mixed models also indicated that dive durations were affected by presence of seismic operations, but that the effects depended on other variables such as season and whale activity. Overall, my results suggest that changes in behaviour exhibited by bowhead whales exposed to seismic operations are context dependent (i.e., responses to seismic operations depend on both the circumstance and activity of the whale). Level of perceived threat may also be important based on similarities with behavioural changes observed in other air-breathing aquatic foragers facing dangers. I conclude that seismic-induced changes in bowhead SRD behaviours may affect availability of bowhead whales for visual detection in some circumstances. This in turn means that estimates of abundance and distribution of bowhead whales near seismic surveys should be context-sensitive and incorporate correction factors that account for sound exposure, season, reproductive status, and whale activity

Introduction

Arctic marine systems are experiencing rapid changes in ice coverage and anthropogenic activities. Northern wildlife populations, such as the bowhead whale, may have to contend with growing levels of human activity if human exploitation of natural resources increases and if longer ice-free periods allow new shipping routes to open through Arctic waters (Reeves et al. 2012). Indigenous people inhabiting this region will also have to continue to adapt to these changes while trying to maintain traditional cultural values and activities. Growing levels of human activity have raised concerns about their potential impacts on the environment and Iñupiat subsistence whaling. Many of these concerns relate to increases in anthropogenic sound in the marine environment, particularly low-frequency sounds (Richardson et al. 1995b, Southall et al. 2007, Moore et al. 2012).

The coastal Arctic waters of northern Alaska and northwestern Canada are typically partly or totally free of ice in summer and early autumn (July to October). During that period, bowhead whales of the Bering-Chukchi-Beaufort (BCB) population forage and migrate west—and offshore industrial operators undertake many of their oil and gas exploration activities. During summer, BCB bowhead whales predominantly feed in the Canadian Beaufort Sea and Amundsen Gulf (Würsig et al. 1985, Moore & Reeves 1993) though whales occasionally congregate off northern Alaska to feed if prey are abundant (Landino et al. 1994). From late August, bowhead whales begin their westward migration, pausing to feed during the early stages of migration through the Alaskan Beaufort Sea when prey are sufficiently dense (Moore et al. 1989, 2010, Richardson & Thomson eds. 2002). Activities of bowhead whales during summer and autumn are likely influenced by whether local prey abundance is sufficient for efficient foraging.

Behavioural studies of bowhead responses to human activities associated with the oil and gas industry were initiated in the early 1980s (Richardson et al. 1985, 1986, Ljungblad et al. 1988), and showed that some bowhead whales exhibit localized displacement (1.3–7.2 km) when exposed to industrial sounds. However, subtle changes in surfacing and diving behaviour were detectable over larger distances, possibly (at times) as much as 70 km (Richardson & Malme 1993). Surfacing and diving behaviour has been quantified by measuring how long a whale is visible at or near the surface, the number of times it exhales during a surfacing event, the intervals between successive blows (blow intervals), and the dive duration (Würsig et al. 1984). Brief and shallow submergences between respirations are generally not considered to be dives or interruptions of a surfacing, while the regular series of surfacings and dives are referred to as surface-respiration-dive (SRD) behaviours and are commonly used as indicators of disturbance (Richardson et al. 1986, Ljungblad et al. 1988).

Bowhead whales sometimes change their SRD behaviour in the presence of seismic operations, and show a statistically-significant tendency to have shorter surfacings, shorter dives, and reduced numbers of blows per surfacing in the presence of sound pulses from seismic operations—though results are variable (Richardson et al. 1986, 1995a, Ljungblad et al. 1988). However, it is not known how the SRD behaviour of bowhead whales is affected by the interaction between naturally-varying factors and exposure to seismic and other industry operations. Naturally-varying factors include region, whale activity, water depth, reproductive status, and time of year—and are known to influence the SRD behaviours of undisturbed bowheads (Würsig et al. 1984, Dorsey et al. 1989, Richardson et al. 1995a).

More recent studies have found that bowhead whales avoid seismic survey vessels during migration, but not while feeding (Richardson et al. 1999, Miller et al. 2005, Koski et al. 2009). They have also shown different reactions to similar sound levels that suggests context dependent responses—feeding and socializing whales appear more tolerant of potential sources of disturbance than migrating whales

(Koski et al. 2009). Behavioural responses of bowhead whales to human activities could also be similarly context-dependent (Beale & Monaghan 2004a, Ellison et al. 2012). Thus factors such as activity state, season and surrounding environment need to be considered when assessing behavioural responses of bowhead whales—particularly when behavioural responses are linked to management decisions.

Changes in SRD behaviour that result in whales spending less (or more) time at the surface may bias assessments of distribution and abundance of whales relative to industrial operations. These assessments are integral to current management requirements in Alaskan waters because they provide information on numbers of whales that may have been impacted by industrial operations. These assessments use sighting data collected by aerial observers who are only able to record animals at the surface. However, the assessments do not consider how behavioural responses of animals to human activities affect the observers' ability to detect whales. Altered detectability resulting from changes in SRD behaviour could lead to under- or over-estimates of the numbers of whales exposed to seismic sounds, and to incorrect conclusions about their distribution relative to seismic operations if changes in SRD behaviour are large. A clear understanding of how acoustic stimuli affect the distribution of whales is needed to address concerns about the possible impacts that industrial activities may have on bowhead whales and Iñupiat subsistence whaling.

The objectives of this chapter were to determine how sounds from seismic survey operations affect bowhead SRD behaviour, and in particular how reproductive status, season and whale activity influence those variables. Such information is needed to characterize the varying detectability of bowhead whales during aerial surveys and to assess the extent to which seismic operations affect detectability and alter bowhead distribution in Arctic waters.

Methods

Data sources and collection

Bowhead behaviour data were collected in the southern Beaufort Sea in summer and autumn during five studies conducted from 1980 to 2000 (Fig. 2.1, see Richardson & Thomson eds. 2002). These data were collected either during periods when whales had not been recently exposed to potential sources of disturbance (i.e., presumably undisturbed) or during periods when whales were exposed or recently exposed to industrial seismic operations or experimental sources of seismic sounds (potentially disturbed). Consistent with previous related studies, recent exposure to seismic activities was defined as exposure within the previous 30 min (Richardson et al. 1985, 1986, Würsig et al. 1985, Dorsey et al. 1989, Richardson & Thomson eds. 2002). Bowhead behaviour data were collected from fixed-wing aircraft circling at an altitude ≥457 m (1500 ft) in a manner that ensured whales were not detectably disturbed by the observation aircraft (Richardson et al. 1985, 1987, Würsig et al. 1985, Richardson & Thomson eds. 2002) — see also Patenaude et al. (2002).

The standardized procedures for systematically studying and comparing bowhead whale behaviour were described by Würsig et al. (1985) and Richardson et al. (1985). In summary, a behavioural observation session was initiated after a group of whales was detected; focal groups were observed from the circling aircraft for up to 3.5 hours. Bowheads with distinctive markings/scars allowed re-identification of individual whales from one surfacing to the next (either in real time with the aid of binoculars or from later examination of video) and also enabled dive durations to be measured. Fluorescein dye markers were dropped to reference approximate locations of whales during dives. Data concerning a whale's SRD behaviours, other general activities, reproductive status, and environmental variables such as ice presence were recorded in real time onto voice recorders and video cameras. SRD behaviours, summarized in Figure 2.2, were defined as follows: dives were defined as sounding dives when the whale submerged out of sight; surfacings were defined as the period when a whale was at the surface or visible just below the surface (Dorsey et al. 1989). For non-calf whales, shallow submergences

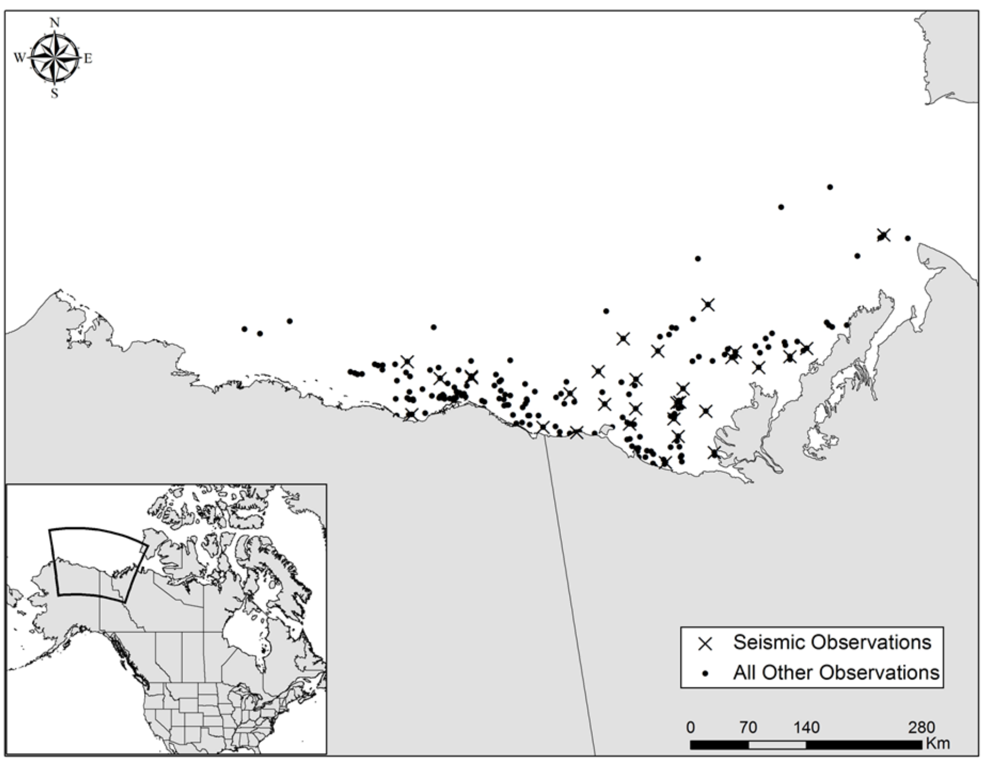

Figure 2.1 Locations where behavioural observations of bowhead whales were acquired in 1980–2000 while presumably undisturbed by seismic sounds (•) and while in the presence of seismic sound (×).

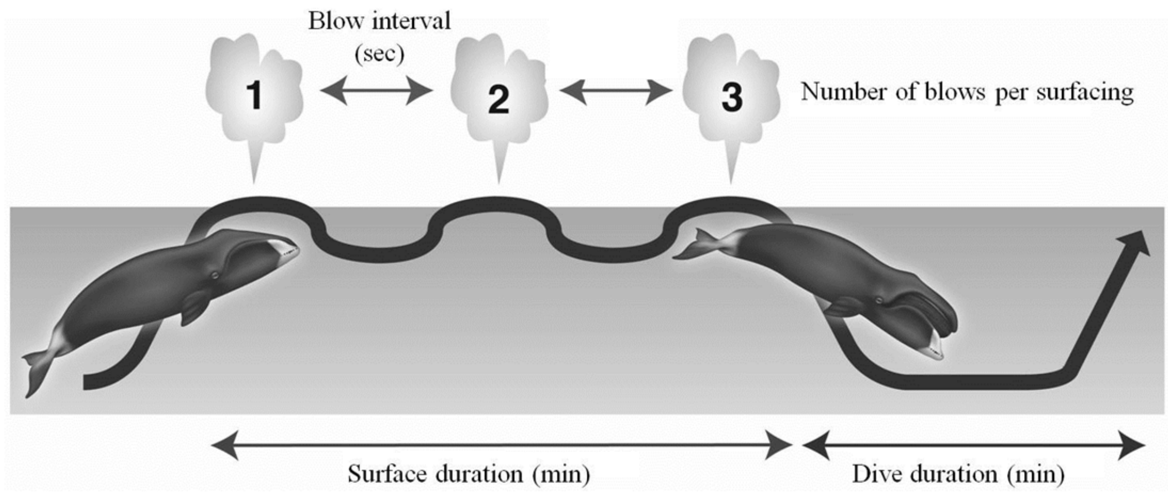

Figure 2.2 Depiction of the key surface-respiration-dive behaviours recorded from bowhead whales during aerial based behavioural observation sessions.

of < 60 sec, occurring between breaths, were defined as serial dives, and were not counted as dives or as interruptions of a surfacing (Dorsey et al. 1989). Studies conducted in the early 1980s often did not provide information about the sizes of the whales observed, so data from all non-calf whales (adults without calves and subadults) were combined to investigate effects of seismic operations on bowhead whale behaviour.

During the 1980-1984 bowhead behaviour-disturbance study (Richardson et al. 1985, 1986), there were 21 occasions of opportunistic observations when whales were exposed to detectable seismic pulses. The distance of the seismic sources from whales ranged from 6 to 99 km, and received sound-pulse levels near the whales were determined via sonobuoys, hydrophones or propagation equations (Richardson et al. 1986). During this period, four different seismic vessels and six sound source types were used. These included sleeve exploders, open bottom gas guns, single air-guns and airgun arrays. Pulses received from these source types had similar spectral and temporal characteristics (Greene Jr. & Richardson 1988). Behavioural studies of bowhead whales near a drilling rig in 1986 also allowed for opportunistic observations of bowhead whales exposed to seismic pulses (Koski & Johnson 1987), and these data were also included in this chapter. The variety of different exposure conditions in which behaviour data were collected meant there was often only approximate information on received levels of seismic sound, and that precluded incorporating specific data on sound exposure into my analysis.

Table 2.1 Total number of SRD behaviour observations available for the Bering-Chukchi-Beaufort bowhead whales while presumably undisturbed and while in the presence of seismic sounds**.**

	Surface time	Dive time	No. of blows per surfacing	Median blow interval
Seismic	586	162	487	836
Undisturbed	1314	538	1126	2584

Observations during experimental exposures to airgun sounds provide an important contribution to investigate the impact of seismic operations on bowhead whale behaviour. Systematic behavioural observations (as summarized above) of bowhead whales during six experimental exposures were available. During 1980–1984, five such tests were performed using a single 40 in^3 Bolt air gun (source level ~222 dB re 1 μPa-m_{p-p}) deployed 2–5 km from the focal group of whales (Richardson et al. 1986). The pulse characteristics and measured (via sonobuoys) received levels of the airgun sounds, at least 118–123dB re 1 μPa-m_{p-p} near the whales, were similar to those > 20 km from full scale seismic vessels. Coordination with an operating geophysical vessel also allowed for one experiment with a full-scale airgun array. The vessel was directed to pass 1.5 km to the side of six feeding bowhead whales under observation from an aircraft (Richardson et al. 1986). These experiments allowed behavioural observations of whales to be collected before, during and, where possible, after the whales had been exposed to seismic pulses, and were early examples of controlled exposure experiments.

From the SRD observations on focal whales during the aforementioned studies, I created an individual record of each surfacing and dive, and an individual record for the number of blows and median blow interval for each individual surfacing. Sample sizes are shown in Table 2.1.

Data analysis

Whales were presumed to be undisturbed when no industrial sounds (e.g., vessel activity, drilling, dredging, seismic sounds and aircraft < 457 m a.s.l) were detected via sonobuoys deployed during observation sessions or, in the absence of sonobuoy data, no such activities were present within distances where sounds from these activities were normally detectable underwater. In contrast, whales were considered potentially disturbed by seismic when seismic pulses were detected via sonobuoys (Richardson et al. 1985), or when seismic vessels were confirmed to have been operating within distances where they could potentially be heard by whales. On occasion, other anthropogenic activities, most often vessel-related, were also present when seismic sounds were detected. This is expected because seismic operations often include support vessels, e.g., to assist with maintenance of streamers. These occasions were included in the exposed-to-seismic dataset. The preliminary analysis showed that the SRD (surface-respiration-dive) variables of whales in the presence of seismic alone did not differ from SRD variables observed while whales were in the presence of seismic plus other anthropogenic activities. With one exception, the latter data were subsequently included in the exposed-to-seismic category. The one instance excluded (1 August 1984) involved an extreme behavioural flight response; it was unclear whether the whale in question reacted to the seismic sounds, the observation aircraft or both (Richardson et al. 1986).

A post-hoc power analysis via statistical program g*Power 3 (Faul et al. 2007) determined that a minimum sample size of 45 observations per treatment was required to minimize the likelihood of type II errors and detect an actual effect from exposure to seismic sounds at the $p \leq 0.05$ level. Due to the small sample sizes available, I set a minimum sample size of 15 observations per treatment to maximize the data available in analyses of the effects of seismic operations on whale SRD behaviour. However, this only allowed a 40 % chance of detecting an effect from exposure to seismic, and gave a higher chance of type II errors.

Blow rate and proportion of time at the surface were calculated for each completely-documented SRD cycle (Fig. 2.2). Blow rate, defined as the number of breaths per minute, is a function of the number of blows per complete surfacing and dive cycle, i.e., dive time plus the subsequent surface time. Blow rate was calculated following the methods of Würsig et al.(1984) and Dorsey et al. (1989). Proportion of time spent at the surface for each SRD cycle was defined as the time at the surface divided by the total duration of the surfacing-dive cycle (dive time plus subsequent surface time). This proportion is important in estimating the fraction of time that whales are potentially sightable during aerial surveys (Davis et al. 1982, Dorsey et al. 1989).

Summary statistics were computed for all SRD behaviours within each category of reproductive-status, season and whale activity (Table 2.2). Confidence intervals (95 %) for the mean were computed using a bootstrap technique where each group was re-sampled 10,000 times (R-package boot, v. 1.3.1, Canty & Ripley 2011).

Table 2.2 Whale status, group activity and season categories used to assess the effects of seismic sound on bowhead whale SRD behaviour. Whale status, group activity and season categories used to assess the effects of seismic sound on bowhead whale SRD behaviour. The effect of seismic operations on non-calf whales were further investigated by season and whale activity state. Foraging was separated into two depth categories because previous studies identified water depth as important in explaining differences in SRD behaviours (e.g., Richardson et al. 1986, Koski & Johnson 1987).

Exposure state	Group	Category	
Seismic OR Presumably undisturbed	Whale status	Non-calf (all whales excluding mothers and calves)	
		Mother	
		Calf	
	Season	Summer	< 25 August
		Autumn	≥25 August
	Whale activity	Travel	
		Feed-shallow	≤ 20m water depth
		Feed-deep	> 20m water depth
		Social	

Distributions for each of the dive-cycle behaviours were highly skewed. As a result, non-parametric Mann-Whitney U-tests were used to determine whether SRD variables in the presence of seismic differed significantly from those when whales were presumably undisturbed. A correction for multiple hypothesis testing was applied using the False Discovery Rate (FDR) approach, following Storey (2002), so as to avoid inflation in the Type I error rate. This correction was implemented using the q-value package in R (Storey 2002). When the corrected p-values did not indicate a significant effect of seismic, post-hoc power tests were used to investigate the likelihood of Type II errors. Kruskal-Wallis non-parametric tests were used to test for significant differences in each SRD behaviour among reproductive status or activity categories. These tests were carried out separately for presumably undisturbed and seismic conditions. Where significant differences within groups were detected, post-hoc tests using the Bonferroni corrections were used to determine which categories of whales differed in SRD behaviour. However, the results of these non-parametric tests may be overstated because they did not allow for multiple observations from the same whale. Therefore, stated significance levels were considered nominal and little emphasis was given to differences whose nominal significance levels were $q > 0.01$. Despite this, the results of simple univariate tests provided a useful starting point for interpreting how seismic operations and context affected each SRD variable.

Statistical modeling

Linear Mixed Effects (LME) models were used to characterize the dependence of each bowhead SRD variable on environmental and whale-related variables. As a first step, I examined the SRD data using exploratory data analysis tools within the statistical analysis program R to identify key issues that may affect the overall fit of each model**.** All observations from calves were removed from the data because their SRD cycles were significantly different from those of other whales (Richardson & Thomson eds. 2002). This left the observations collected from non-calf whales and mothers. Outliers were identified with Cleveland dot plots and pair plots in combination with Pearson's correlation coefficients. Variance-Inflation-Factor (VIF) values were used to identify the presence of collinearity between explanatory variables. Only water depth and distance from shore were possibly collinear (VIF = 0.6); depth was retained in the analysis and distance from shore was dropped to avoid multicollinearity and minimize model performance issues (Zuur et al. 2010). I excluded SRD records in which values of one or more explanatory variables were unknown.

Ten variables were hypothesized to be potential predictors of SRD cycle parameters (Table 2.3). The number of whales within 1 km of the focal animal (N.1KM) was log transformed to obtain an even spread of values. All other explanatory variables were factorial and were divided into levels (Table 2.3). Whale identification (id) numbers were assigned when the data were coded, with a new id number being assigned when it was uncertain whether a whale had been seen earlier in the observation session. In this analysis, whales with different id numbers were treated as unique, though some had presumably been seen before.

Before analysis, SRD variables were transformed to reduce skewness in their distributions. Dive duration, median blow interval, and number of blows per surfacing were log-transformed; while surface duration was square-root transformed. Transformed data for each SRD variable were individually modeled as a function of environmental and whale related variables, including a variable describing the presence of seismic operations, using LME models. Only two-way interaction terms where the effect of seismic may have been dependent on another variable were included in the model. This allowed me to investigate whether (a) presence of seismic had a significant effect on each behaviour, and (b) if the effect of seismic depended on other environmental or whale related variables. Variation resulting from multiple observations of individual whales (when recognized) was included as a random effect in each model.

LME models were fitted using the nlme package, v. 3.1-101 (Pinheiro et al. 2011), for R using Restricted Maximum Likelihood (REML) estimation. Model selection followed a backward stepwise methodology, as recommended by Diggle et al. (2002) and Zuur et al. (2009), using a combination of likelihood-ratio tests and AIC. The selected models were validated through graphical examination of the normalized residuals and assessed for the presence of homogeneity as well as the presence of spatial and temporal correlation. When the presence of temporal autocorrelation was identified in a model, an autoregressive (AR-1) correlation structure was included (Zuur et al. 2009).

The effects of explanatory variables and interaction terms were deemed significant if the 95 % Confidence Intervals of the parameter estimates did not overlap zero (Johnson 1999). The goodness of fit for each model was assessed through the calculation of the R^2 coefficients (Vonesh et al. 1996, Kramer 2005, Liu et al. 2008). R^2 statistics based on the likelihood ratio R^2_{LR}, were calculated using functions available from package lmmfit, v.1.0 for R (Maj 2011).

A retrospective sensitivity analysis was performed to investigate the robustness of each optimal model. Each model was fit to successively smaller cohorts of behaviour data, where every model in turn had one year of data removed. R^2 statistics based on likelihood ratio R^2_{LR}, were calculated and model results compared graphically to assist interpretation of model robustness and identify evidence of retrospective bias in each behaviour model.

Table 2.3 Environmental and bowhead whale related variables included in the Linear Mixed Effects Models.

Explanatory variable	Scale	Number of blows	Median blow interval	Surface time	Dive time
Environmental variables					
Season	autumn (≥ 25 August)†	X	X	X	X
	summer (< 25 August)	X	X	X	X
Water depth	< 10 m†	X	X	X	X
	10–19 m	X	X	X	X
	20–49 m	X	X	X	X
	50-–199m	X	X	X	X
	> 200m	X	X	X	X
Ice % > 5%	≤ 5% ice†	X	X	X	X
	> 5% ice	X	X	X	X
Seismic sound	Presumably undisturbed†	X	X	X	X
	seismic present	X	X	X	X
Whale variables					
Group activity state	feeding (all types of feeding) †	X	X	X	X
	travel	X	X	X	X
	social	X	X	X	X
Motion	no motion/milling†	X	X	X	-
	slow	X	X	X	-
	moderate	X	X	X	-
	fast	X	X	X	-
	changing	X	X	-	-
Whale status	non-calf (excluding mothers & calves) †	X	X	X	X
	mother (adult whales with a calf)	X	X	X	X
Group size	1 whale†	X	X	X	X
	2–3 whales	X	X	X	X
	≥ 4 whales	X	X	X	X
Number of whales in 1km	Log(N.1KM)	X	X	X	X
Aerial behaviour	no aerial behaviour observed†	-	X	X	-
	aerial behaviour observed	-	X	X	-

† Delineates the category of each variable against which all other categories within that variable were compared.

– Indicates that this variable was not included in the model

Results

The four measurable variables that make up the SRD cycle of a bowhead whale (number of blows per surfacing; median blow interval; surface duration; and dive duration) varied with reproductive states, activities and seasons. They also revealed behavioural changes associated with the presence of seismic operations (Tables 2.4, 2.5, & 2.6).

In general, mothers had the longest mean SRD cycle (13.0 min total surface plus dive time in presumably undisturbed conditions) and calves had the shortest (4.7 min), while non-calves (i.e., all adult and subadult whales excluding mothers and calves) fell in between (9.6 min). However SRD cycle times varied with season and activity state. Most notably, SRD cycles were shortest for socializing whales and for those feeding in shallow waters and were longest for travelling whales (lasting an average of 13.3 min).

SRD behaviours also varied in the presence of seismic operations. In some circumstances, presence of seismic operations was associated with whales exhibiting mean surface durations shorter, to a nominally-significant extent, than those without seismic. This is best understood by a closer examination of the individual effects of seismic sound on each dive-cycle behaviour.

Number of blows per surfacing

The average numbers of blows per surfacing was lower in the presence of seismic operations, but the difference was nominally significant only among non-calf whales (for which the mean was 24 % lower with seismic, Table 2.4). This effect was consistent between seasons, although average number of blows was lower in summer than in autumn (Fig. 2.3, Table 2.5). The apparent effects of seismic operations were most notable for travelling non-calf whales (Fig. 2.3, Table 2.6). Overall, average number of blows per surfacing varied between seasons and among activity states in both the presence and absence of seismic operations.

When the various factors hypothesized to be related to SRD behaviour were considered simultaneously, the number of blows per surfacing was significantly related to 5 variables and two interaction terms (Table 2.7). However, this best fitting LME model could only explain 13 % of the observed variation in the number of blows. The number of blows per surfacing was related to interactions of seismic with activity state (Fig. 2.4) and the number of whales within 1 km. The LME further suggests that number of blows per surfacing was related to season, water depth, ice coverage, and whale motion (Table 2.7).

Table 2.4 Summary statistics for each surface-dive behaviour type of bowhead whales by whale-status group for both undisturbed and seismic categories. Corrected nominally significant differences at the q ≤ 0.01 level between seismic and undisturbed are highlighted in bold. Corrections have been based on the False Discovery Rate (FDR) method for multiple hypothesis testing. The differences between whale statuses are shown by the p-value.

Surface-Dive Behaviours	Non-calf			Mother			Calf			Differences between Reproductive states
	n	$\bar{x}$	*se*	*n*	$\bar{x}$	*se*	*n*	$\bar{x}$	*se*	*p-value*
Number of Blows										
Presumably undisturbed	911	**5.22**	0.11	67	6.21	0.43	148	3.94	0.31	**< 0.001**
Seismic	417	**3.96**	0.15	26	5.62	0.83	44	3.36	0.40	0.06
Median Blow Interval (sec)										
Presumably undisturbed	2252	13.55	0.15	147	17.32	0.44	185	13.48	0.55	**< 0.001**
Seismic	744	14.25	0.26	43	17.55	1.09	49	16.06	1.39	**< 0.001**
Surface Time (sec)										
Presumably undisturbed	1070	**73.9**	1.7	80	121.7	7.6	164	55.8	5.1	**< 0.001**
Seismic	504	**61.1**	2.1	29	96.4	15.6	53	55.4	9.1	**0.003**
Dive Time (sec)										
Presumably undisturbed	333	504.7	23.6	67	656.8	46.7	138	225.0	25.0	**< 0.001**
Seismic	106	528.7	49.4	18	740.5	125.7	38	229.3	43.3	**< 0.001**
Proportion of time at surface										
Presumably undisturbed	292	0.175	0.008	60	0.198	0.017	129	0.255	0.017	**< 0.001**
Seismic	96	0.171	0.015	16	0.144	0.031	36	0.221	0.039	0.718
Blow Rate (per sec)										
Presumably undisturbed	256	0.013	0.001	52	0.011	0.001	121	0.035	0.004	**< 0.001**
Seismic	76	0.014	0.001	15	0.010	0.002	32	0.028	0.003	**< 0.001**

Blow intervals

Presence of seismic operations had no observable effect on median blow intervals of bowhead whales categorized by season or by whale reproductive status (Tables 2.4 & 2.5). However, median blow intervals of non-calf bowheads categorized by whale activity showed some nominally significant differences (Fig. 2.3, Table 2.6). In the presence of seismic operations, median blow intervals of whales foraging in shallow waters differed significantly from those of both travelling and socializing whales (Mann-Whitney U-tests; travel, $p = 0.035$; social, $p < 0.001$).

The LME model for median blow interval showed it to be a function of 7 variables and four interaction terms (Table 2.8). However, this best fitting LME model could only explain 14 % of the observed variation in median blow intervals of bowhead whales. Median blow interval was related to interactions of seismic with season, water depth, whale activity, and aerial behaviour (Fig. 2.4, Table 2.8). After allowance for the numerous interaction effects, median blow interval also appeared to depend on presence of seismic and several other variables (Table 2.8).

Table 2.5 Summary statistics for each surface-dive behaviour variable for non-calf bowhead whales by season for both undisturbed and seismic categories. Corrected nominally significant differences at the q ≤ 0.01 level between seismic and undisturbed groups are highlighted in bold, while the differences between seasons are shown by the p-value.

Surface-Dive Behaviours	Summer			Autumn			Difference between Seasons
	n	$\bar{x}$	*se*	*n*	$\bar{x}$	*se*	*p-value*
Number of Blows							
Presumably undisturbed	370	**4.39**	0.16	541	**5.79**	0.15	**< 0.001**
Seismic	234	**3.55**	0.17	183	**4.50**	0.26	**0.046**
Median Blow Interval (sec)							
Presumably undisturbed	851	13.60	0.29	1401	13.52	0.16	0.155
Seismic	378	14.06	0.35	366	14.45	0.37	0.348
Surface Time (sec)							
Presumably undisturbed	414	**66.6**	2.3	656	**78.5**	2.3	**< 0.001**
Seismic	281	**56.4**	2.3	223	**67.0**	3.6	0.067
Dive Time (sec)							
Presumably undisturbed	84	394.2	38.7	249	542.0	28.3	**< 0.001**
Seismic	71	371.0	38.2	35	848.6	110.5	**0.002**
Proportion of Time at Surface							
Presumably undisturbed	75	0.169	0.013	217	0.177	0.010	0.918
Seismic	67	0.191	0.019	29	0.124	0.019	0.096
Blow Rate (per sec)							
Presumably undisturbed	70	0.014	0.001	186	0.012	0.001	0.066
Seismic	55	0.015	0.001	21	0.011	0.002	0.193

Surface durations

In the presence of seismic operations, the average surface duration for non-calf whales was lower, by a nominally significant amount, as compared with presumably-undisturbed bowheads (Table 2.4, Fig. 2.3). This was evident in both summer and autumn, and for both travelling and socializing non-calf whales (Tables 2.5 & 2.6, Fig. 2.3). Travelling whales exhibited a mean surfacing duration that was 41 % lower in the presence of seismic sounds (Fig. 2.3). Also, mean surface durations depended on reproductive status: both with and without seismic operations, calves had short surface times and mothers had long surface times relative to other bowhead whales (Table 2.4, Fig. 2.3).

Surface duration was a function of 7 variables and two interaction terms (Table 2.9), and this best fitting LME model explained 24 % of the variation in the observed surface durations (Table 2.9). Surface duration was related to interactions of seismic with whale activity (Fig. 2.4) and the number of whales within 1 km. After allowance for interaction effects, surface duration also appeared to depend on season, whale motion, reproductive status, ice cover, and water depth (Table 2.9).

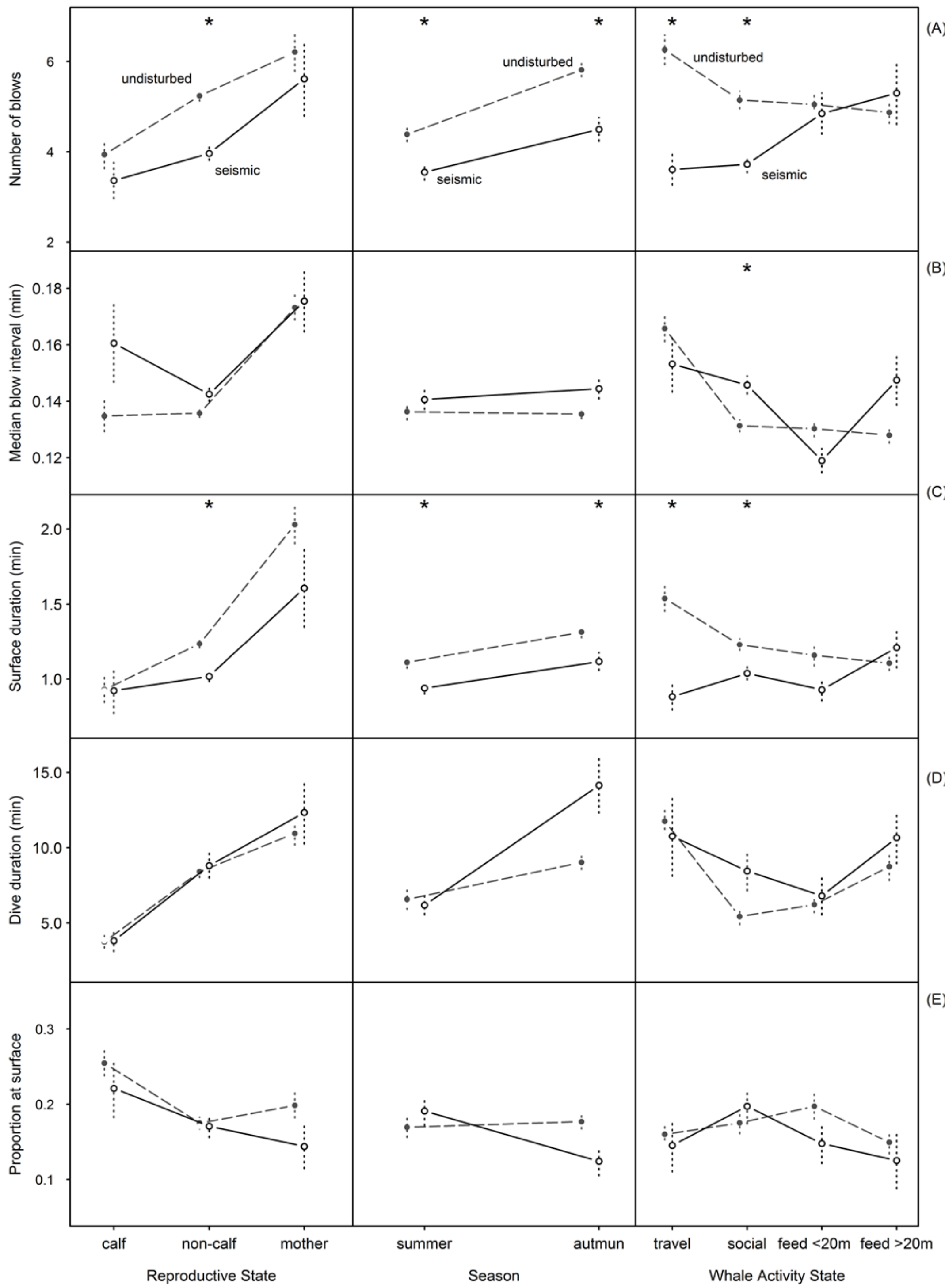

Figure 2.3 Mean SRD behaviours of bowhead whales by season, activity and reproductive state while in the presence (○) or absence (●) of seismic sounds. SRD behaviours (± 95 % CI) include (A) number of blows per surfacing, (B) median blow interval, (C) time on the surface, (D) duration of the dive, and (E) the proportion of time spent on the surface during a dive cycle. Significant differences in behaviour between seismic and presumably-undisturbed conditions are denoted with an asterisk (q < 0.01, corrected Wilcoxon-rank based test).

Table 2.6 Summary statistics for each surface-dive behaviour for non-calf bowhead whales by activity state for both undisturbed and seismic categories. Corrected nominally significant differences between seismic and undisturbed are highlighted in bold ($q \leq 0.01$). The differences between activity states are shown by the p-value.

Surface-Dive Behaviours	**Travel**			**Social**			**Feed Shallow**			**Feed Deep**			**Differences between activity states**
	n	*x*	*se*	*n*	*x*	*se*	*n*	*x*	*se*	*n*	*x*	*se*	*p-value*
Number of Blows													
Presumably undisturbed	110	**6.15**	0.33	299	**5.15**	0.20	205	5.05	0.22	194	4.87	0.24	**0.003**
Seismic	66	**3.61**	0.34	268	**3.72**	0.19	39	4.85	0.46	30	5.30	0.70	**0.007**
Median Blow Interval (s)													
Presumably undisturbed	206	16.59	0.48	765	**13.10**	0.22	503	12.99	0.29	549	12.79	0.27	< **0.001**
Seismic	63	15.32	1.00	469	**14.57**	0.32	99	11.89	0.43	88	14.75	0.89	< **0.001**
Surface Time (min)													
Presumably undisturbed	120	**1.51**	0.08	369	**1.23**	0.04	258	1.16	0.07	213	1.11	0.05	< **0.001**
Seismic	79	**0.88**	0.09	326	**1.04**	0.04	46	0.93	0.08	38	1.21	0.14	0.1
Dive Time (min)													
Presumably undisturbed	77	11.76	0.93	66	5.44	0.55	97	6.22	0.54	47	8.74	0.92	< **0.001**
Seismic	18	10.76	2.66	44	8.45	1.32	21	6.81	1.26	20	10.66	1.72	0.476
Proportion of time at surface													
Presumably undisturbed	70	0.16	0.015	58	0.18	0.014	91	0.20	0.017	42	0.15	0.015	0.263
Seismic	14	0.15	0.035	42	0.20	0.023	20	0.15	0.026	17	0.13	0.038	0.051
Blow Rate (per sec)													
Presumably undisturbed	61	0.627	0.001	55	0.829	0.001	74	0.803	0.001	39	0.702	0.001	**0.005**
Seismic	8	0.838	0.003	33	0.872	0.002	17	0.666	0.001	15	0.695	0.002	0.388

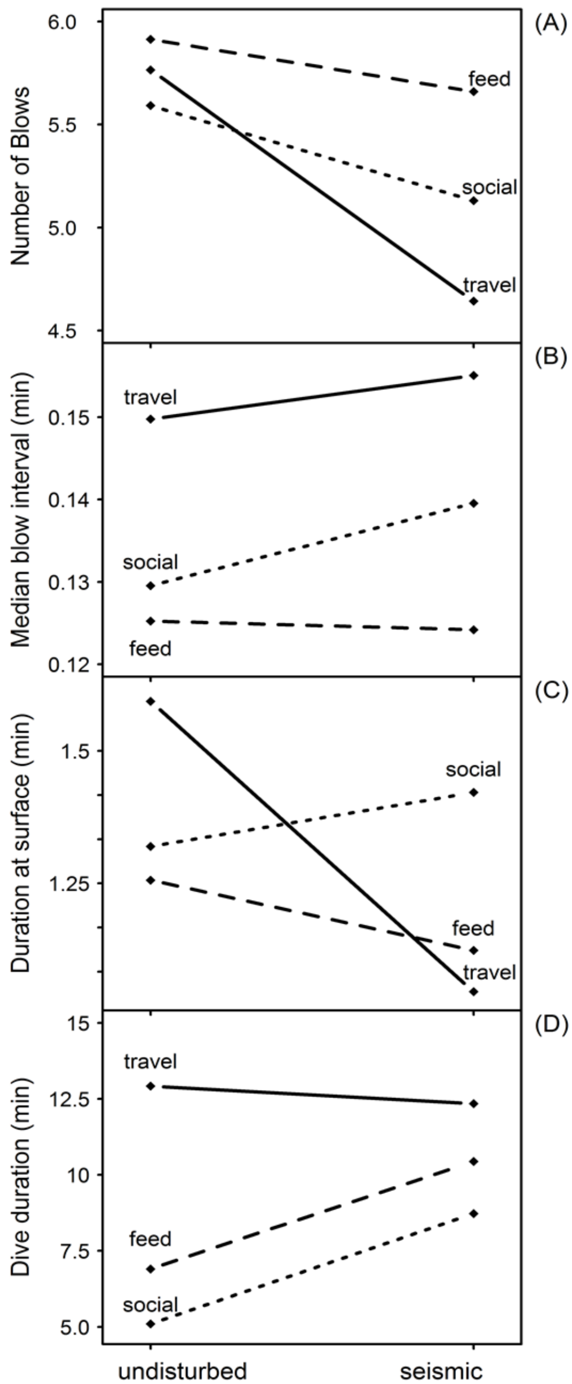

Figure 2.4 The interaction between LME model factors activity state and sound exposure (presumably undisturbed vs. seismic) for each SRD behaviour of bowhead whales: median number of blows per surfacing (A), median time between breaths (B), time on the surface (C) and dive duration (D).

Dive durations

Exposure to seismic operations had no significant effect on the average dive duration of mothers, non-calves, or calves (Table 2.4). Similarly there was no apparent association between the presence of seismic and the average dive times of non-calf whales observed in different seasons or engaged in different activities (Tables 2.5 & 2.6). Mean dive times of non-calf whales were longer in the autumn than during the summer regardless of the presence of seismic operations (Mann Whitney U-tests: presumably undisturbed, $p < 0.001$; seismic, $p = 0.002$).

The best fitting LME model showed dive duration was a function of 6 variables and three interaction terms (Table 2.10), and explained 39 % of the variation in the observed dive durations. Dive duration depended on the interactions of seismic with season, number of whales within 1 km, and whale activity (Fig. 2.4). The LME model identified effects of seismic on dive duration that were not evident from the univariate comparisons. After allowance for interaction effects it was evident that dive duration also depended on water depth, ice percentage, reproductive status, and group size (Table 2.10).

Blow rate and the proportion of time at the surface

Blow rate is a function of number of blows per surfacing, surface duration, and dive duration, each of which (at times) appeared to be affected by presence of seismic operations (see above). Blow rates apparently differed with whale reproductive status and whale activity (Tables 2.4 & 2.6). However, presence of seismic operations did not significantly affect the average blow rates of bowhead whales for any category of reproductive status, season, or whale activity (Tables 2.4, 2.5 & 2.6).

Similarly the presence of seismic operations had no apparent effect on the proportion of time that mothers, non-calves, or calves spent at the surface (Fig. 2.3, Table 2.4). Though not significantly different, it should be noted that the proportion of time that non-calf whales spent at the surface during autumn was 17.7 % in presumably undisturbed conditions, but only 12.4 % with seismic operations (Table 2.5). Further investigation of the effects of seismic operations on blow rates and the proportion of time that bowheads spent at the surface (with allowance for other variables) was limited by available sample sizes.

Table 2.7 Linear mixed effects models of the mean number of blows per surfacing for bowhead whales. A log transformation was used to normalize the dependent variable. Nominally significant relationships are highlighted in bold. The final model produced an R^2 coefficient based on likelihood ratio of 0.135.

Parameter		β	p-value	95 % CI
Intercept		**1.74**	**0.000**	**1.45, 2.02**
Season	autumn†			
	summer	**-0.22**	**0.001**	**-0.35, -0.10**
Depth	< 10 m†			
	10–19 m	-0.11	0.325	-0.34, 0.11
	20–49 m	-0.06	0.572	-0.28, 0.16
	50–199 m	0.10	0.461	-0.17, 0.36
	> 200 m	**0.37**	**0.016**	**0.07, 0.67**
Ice %	≤ 5%†			
	> 5%	**0.27**	**0.000**	**0.12, 0.41**
Seismic	undisturbed†			
	present	**0.60**	**0.005**	**0.18, 1.02**
Log(whales in 1km)		-0.03	0.511	-0.14, 0.07
Activity	forage†			
	travel	0.07	0.423	-0.10, 0.24
	social	0.07	0.332	-0.07, 0.22
Motion	none†			
	fast	**-0.35**	**0.006**	**-0.60, -0.10**
	moderate	-0.15	0.066	-0.30, 0.01
	slow	-0.04	0.606	-0.18, 0.11
	changing	**0.26**	**0.002**	**0.10, 0.42**
Seismic × forage†				
	seismic x travel	**-0.42**	**0.016**	**-0.76, -0.08**
	seismic x social	-0.28	0.057	-0.56, 0.01
Seismic × log(whales in 1km)		**-0.30**	**0.010**	**-0.53, -0.07**

† Delineates the category of each variable against which all other categories within that variable were compared

Table 2.8 Linear mixed effects models of the median blow interval for bowhead whales. A log transformation was used to normalize the dependent variable. Significant relationships are highlighted in bold. The final model produced an R^2 coefficient based on likelihood ratio of 0.137.

Parameter		β	p-value	95 % CI
Intercept		**4.63**	**0.00**	**4.56, 4.69**
Season	autumn†			
	summer	**0.05**	**0.018**	**0.01, 0.09**
Depth	**< 10 m†**			
	10–19 m	**0.10**	**0.004**	**0.03, 0.17**
	20–49 m	**0.12**	**0.000**	**0.06, 0.19**
	50–199 m	**0.11**	**0.012**	**0.03, 0.19**
	> 200 m	**0.14**	**0.022**	**0.02, 0.26**
Seismic	undisturbed†			
	present	**0.37**	**0.000**	**0.20, 0.54**
Whale status	non-calf†			
	mother	**0.19**	**0.000**	**0.11, 0.27**
Activity	forage†			
	travel	**0.19**	**0.000**	**0.15, 0.24**
	social	0.01	0.512	-0.03, 0.05
Group size	1–2†			
	2–3	**0.09**	**0.000**	**0.06, 0.13**
	> 4	0.01	0.883	-0.07, 0.08
Aerial	none†			
	present	**0.08**	**0.009**	**0.02, 0.15**
Seismic × autumn†				
	seismic × summer	**-0.19**	**0.000**	**-0.27, -0.11**
Seismic × < 10 m†				
	seismic × 10–19 m	**-0.32**	**0.000**	**-0.49, -0.15**
	seismic × 20–49 m	**-0.31**	**0.000**	**-0.47, -0.14**
	seismic × 50–199 m	-0.06	0.541	-0.25, 0.13
	seismic × > 200 m	**-0.25**	**0.018**	**-0.46, -0.04**
Seismic × forage†				
	seismic × travel	**-0.15**	**0.013**	**-0.26, -0.03**
	seismic × social	0.02	0.573	-0.06, 0.10
Seismic × no aerial†				
	seismic x aerial	**0.32**	**0.006**	**0.09, 0.54**

† Delineates the category of each variable against which all other categories within that variable were compared

Table 2.9 Linear mixed effects models of the mean surface duration for bowhead whales**.** A square-root transformation was used to normalize the dependent variable. Significant relationships are highlighted in bold. The final model produced an R^2 coefficient based on likelihood ratio of 0.239.

Parameter		β	p-value	95 % CI
Intercept		**9.67**	**0.000**	**8.63, 10.71**
Season	autumn†			
	summer	**-0.55**	**0.018**	**-1.01, -0.10**
Depth	< 10 m†			
	10–19 m	-0.05	0.904	-0.82, 0.73
	20–49 m	0.16	0.681	-0.60, 0.92
	50–199 m	**1.10**	**0.023**	**0.16, 2.05**
	> 200 m	**2.31**	**0.000**	**1.15, 3.47**
Ice %	≤5%†			
	> 5%	**0.94**	**0.002**	**0.34, 1.55**
Seismic	undisturbed†			
	present	**1.67**	**0.031**	**0.15, 3.20**
Whale Status	non-calf†			
	mother	**1.50**	**0.004**	**0.49, 2.50**
Activity	forage†			
	travel	**0.69**	**0.034**	**0.05, 1.32**
	social	0.29	0.276	-0.23, 0.81
Motion	none†			
	fast	**-2.79**	**0.000**	**-3.79, -1.81**
	moderate	**-2.10**	**0.000**	**-2.64, -1.56**
	slow	**-1.19**	**0.000**	**-1.66, -0.72**
Log(whales in 1km)		-0.15	0.449	-0.55, 0.25
Seismic × forage†				
	seismic × social	-0.19	0.715	-1.22, 0.83
	seismic × travel	**-2.35**	**0.000**	**-3.59, -1.10**
Seismic × log(whales in 1km)		**-0.88**	**0.032**	**-1.68, -0.08**

† Delineates the category of each variable against which all other categories within that variable were compared

Table 2.10 Linear mixed effects models of the mean dive duration for bowhead whales. A log transformation was used to normalize the dependent variable. Significant relationships are highlighted in bold. The final model produced an R^2 coefficient based on likelihood ratio of 0.386.

Parameter		β	p-value	95 % CI
Intercept		**6.03**	**0.000**	**5.57, 6.49**
Season	autumn†			
	summer	-0.07	0.669	-0.37, 0.24
Depth	< 10 m†			
	10–19 m	0.06	0.795	-0.38, 0.50
	20–49 m	0.38	0.072	-0.03, 0.80
	50–199 m	0.34	0.172	-0.15, 0.84
	> 200 m	**0.63**	**0.022**	**0.09, 1.18**
Ice %	≤ 5%†			
	> 5%	**0.30**	**0.034**	**0.02, 0.58**
Seismic	undisturbed†			
	present	**1.08**	**0.002**	**0.41, 1.75**
Whale Status	non-calf†			
	mother	**0.50**	**0.007**	**0.14, 0.86**
Group Size	1–2†			
	2–3	**-0.25**	**0.011**	**-0.44, -0.06**
	> 4	-0.53	0.192	-1.33, 0.27
Activity	forage†			
	travel	-0.02	0.908	-0.35, 0.32
	social	-0.34	0.052	-0.68, 0.00
Log(whales in 1km)		**-0.24**	**0.014**	**-0.44, -0.05**
Seismic × autumn†				
	seismic x summer	**-0.54**	**0.037**	**-1.04, -0.03**
Seismic × forage†				
	seismic × social	**0.77**	**0.016**	**0.15, 1.40**
	seismic × travel	**-0.83**	**0.019**	**-1.52, -0.14**
Seismic × log(whales in 1km)		**-0.50**	**0.011**	**-0.88, -0.12**

† Delineates the category of each variable against which all other categories within that variable were compared

Caveats and Sensitivity analysis

Despite some uncertainty about the effects of some explanatory variables on bowhead SRD behaviour, the overall results of the retrospective sensitivity analysis confirmed that presence of seismic operations did affect bowhead SRD behaviours—and sensitivity analyses (see below) suggested that the selected final models were reasonably robust. Furthermore, the results indicate that effects of exposure to seismic operations sometimes varied according to whale reproductive status, season, and whale activity.

The sensitivity analysis confirmed the importance of a number of explanatory variables in the model for each of the four SRD variables despite the sequential removal of data (Appendix A1-A4). Most notably, the apparent effect of seismic as a predictor of SRD behaviour remained evident for each SRD behaviour, either on its own or when interacting with other variables. For example, presence of seismic was identified as important in all models for dive duration that included data from three or more years (Appendix A4). Other important effects corroborated by the sensitivity analysis included those of season and movement speed as explanatory variables for number of blows per surfacing and duration of surfacing, while water depth had a nominally significant effect (Appendix A1 & A3). However, the apparent effect of depth on dive duration varied greatly with removal of data and depth was included as a nominally significant factor in only 5 of 9 models for dive duration.

Small and unequal sample sizes, a result of compiling behaviour data from multiple studies, may also have contributed to the observed differences among LME models. This was evident from the sensitivity analysis for surface duration (Appendix A3) where the sequential removal of data and refitting of models led to an increasing apparent significance of season, which in turn reflected the sample sizes available from summer and autumn. All behaviour data collected after 1985 were from autumn, resulting in a seasonal unbalance in the data.

In summary, the presence of seismic operations generally resulted in shorter surfacings. This was particularly apparent for non-calf whales engaged in travel and socializing. My mixed model analysis also established that the presence of seismic affected the dive times of bowhead whales, but that the effect depended on season, whale activity state, and numbers of whales near-by.

Discussion

Exposure to seismic operations resulted in subtle changes to bowhead whale surfacing, respiration and dive behaviours. The observed behavioural responses corresponded with the skittish behaviours reported by subsistence whalers (Jolles ed. 1995) as well as anti-predation behaviours observed in other air-breathing aquatic foragers (Dunphy-Daly et al. 2010, Wirsing et al. 2011). The effects of such industrial operations on bowhead behaviours have implications for the detectability of bowhead whales during aerial surveys, thereby influencing the ability to adequately assess the effects of industry on bowhead whale distribution. Allowance for these effects on detectability will lead to improvements in the management of industrial operations in the Alaskan Arctic.

Effects of seismic operations on bowhead whale behaviour

LME models proved to be a more powerful tool than the univariate and stepwise multiple regression analyses used in earlier studies to assess the effects of seismic operations on bowhead SRD behaviour in the Beaufort Sea. The LME models confirmed that seismic operations significantly affected bowhead SRD behaviour and showed that the degree of behavioural change depended on factors such as season, activity states, and the number of whales within 1 km of the affected whale. Although some of the earliest studies detected subtle differences in dive-cycle behaviours in the presence vs. absence of seismic sounds (e.g., Richardson et al. 1986, 1995b, Ljungblad et al. 1988), they did not attempt to allow for the confounding effects of other key variables or to account for repeated observations of individual whales.

Pooling data from multiple studies enabled me to investigate the seasonal effects of seismic operations and other factors on bowhead behaviours. The results suggest that non-calf whales had stronger reactions to seismic operations in autumn than in summer. Similarly, seismic operations had a greater effect on SRD behaviour while non-calf whales were travelling than while whales were engaged in feeding or socializing activities (as indicated by some significant interactions between seismic and whale activity in the behaviour models).

During the westward autumn migration through the Alaskan Beaufort Sea, the primary activity is travelling, although bowheads intersperse periods of travelling with feeding (Ljungblad et al. 1986, Richardson & Thomson eds. 2002, Koski et al. 2009). Tagging studies have confirmed that residence times of most bowhead whales in the Alaskan Beaufort Sea during the autumn are less than a few days (Quakenbush et al. 2010, ADFG 2012), indicating that feeding in that area and season is likely opportunistic. My findings suggest that travelling whales exposed to seismic operations spent the least time at the surface, and had markedly reduced numbers of exhalations per surfacing. They also indicate that behaviour of non-calf whales was more notably affected by seismic operations during autumn migration than during summer when feeding and socializing are key activities. However, my results should be interpreted with caution due to the inadequate sample sizes for travelling non-calf whales during the summer, which prevented me from comparing the behaviour of travelling whales exposed to seismic operations in summer and autumn.

My results lend support to the hypothesis that feeding and socializing whales are more tolerant of seismic operations than are travelling whales. Feeding bowhead whales exposed to seismic operations may vary their SRD behaviours (Richardson et al. 1986), but often stayed near seismic activities (Richardson et al. 1986, Miller et al. 2005, Koski et al. 2009). This was in sharp contrast to migrating whales that appeared to avoid seismic operations by distances of 20–30 km (Richardson et al. 1999, Manly et al. 2007). Gray whales *Eschrichtius robust* (Gailey et al. 2007, Yazvenko et al. 2007) and sperm whales *Physeter macrocephalus* (Madsen et al. 2002, Miller et al. 2009) have also been observed foraging near seismic operations, but there is less information for those species about their relative response to seismic during foraging vs. migration. My findings further suggest that travelling bowhead whales may not avoid ensonified areas to quite the extent reported in previous aerial-studies (e.g., Richardson et al. 1986, Manly et al. 2007). Earlier studies may have slightly overestimated the degree of avoidance because they did not recognize or allow for the fact that bowheads exposed to seismic operations may be less available for detection at the surface due to changes in SRD behaviour.

Cetaceans commonly alter their SRD behaviours in response to human activities. Navy sonar, aircraft, ship traffic, ice breaking, and marine construction have all led to observable behavioural changes in cetaceans (Richardson et al. 1995b, Southall et al. 2007). For example, low frequency sounds led to longer dives in humpback whales *Megaptera novaeangliae* (Frankel & Clark 1998), while harbor porpoises *Phocoena phocoena* varied their surfacing patterns by moving away or increasing dive times in response to imaging sonar systems (Hastie 2012). Gray whales sometimes avoid airgun operations (e.g. Malme et al. 1984), and also change their movement patterns and dive durations as exposure to seismic sound increases (Gailey et al. 2007). However, cetaceans may also show little if any behavioural response to a human activity in some circumstances, such as reported for humpback whales exposed to blasting (Todd et al. 1996), or sperm whales exposed to distant explosions (Madsen & Møhl 2000). The variation in behavioural responses of cetaceans to human activities suggests that responses are context dependent and vary with the circumstances and activity of the animals as well as the level of perceived threat (Richardson et al. 1995b, Ellison et al. 2012).

The behavioural responses of bowhead whales to seismic sounds are similar to anti-predator or anti-threat responses observed in other air-breathing aquatic foragers (Frid et al. 2007, Dunphy-Daly et al. 2010, Wirsing et al. 2011). The behavioural changes exhibited by bowhead whales in the presence of human activities are sometimes subtle and can result in the whales apparently becoming more secretive. Similar behavioural reactions have been recognized by Iñupiat subsistence whalers. Whaling captains report that bowheads are easily startled by sudden noises, resulting in the whale surfacing less and moving further out to sea (Jolles ed. 1995). Gray whales have also been observed to adopt a distinctive low-profile breathing technique, known as snorkeling, when faced with the threat of predation from killer whales *Orcinus orca* (Reeves et al. 2006, Ford & Reeves 2008). These behaviours presumably reduce whale susceptibility to potential subsurface predators such as the killer whale that pose a threat to diving animals at the surface by restricting fleeing movement laterally or downwards (Heithaus & Frid 2003). Numbers of bowhead whale calls have also been reported to be lower when exposed to seismic sounds

(Greene Jr. et al. 1999, Blackwell et al. 2013). Reduced calling behaviour is hypothesized to be related to secretiveness, particularly as silent whales are likely harder for killer whales to detect. However, lower rates of call detection in the presence of seismic sounds are presumably also partly related to documented avoidance reactions (i.e., the presence of fewer whales in the area of active seismic).

Implications for management

Aerial surveys are often used to estimate distributions and densities of animals near industrial activities, such as a seismic operation. However, a whale is only available for visual detection when it is at or very near the surface. Any changes in behaviour that result in whales spending less time at the surface during a typical SRD cycle, or being less conspicuous when at the surface, reduce an observer's ability to sight them. Not accounting for these behavioural changes will result in underestimates of numbers of animals present.

Results from this chapter will be incorporated into calculations of availability correction factors that account for the reduced probability of detecting an animal at the surface (Buckland et al. 2001). These correction factors will be particularly useful when incorporated into the analysis of sightings data collected during aerial monitoring of seismic survey activities during the autumn migration of bowhead whales. Understanding and quantifying the effects of seismic operations on bowhead SRD behaviours will result in more accurate density assessments from sightings surveys, and better estimates of the numbers of whales that were likely exposed to a seismic operation. It should also help provide more accurate estimates of the probability of avoidance around seismic operations.

Study limitations

These analyses expanded on previous studies of seismic effects on SRD behaviour by attempting to account for repeated observations of individual whales and for the various factors and interactions of factors that influence SRD variables. Similar mixed model analyses have been successfully applied in behavioural response studies of humpback whales (Dunlop et al. 2013). However, these improved analyses of the effects of seismic on bowhead whale SRD behaviour remain subject to some limitations.

A key caveat to my analyses centers on the issue of statistical independence. Mann-Whitney U-tests and Kruskal Wallis tests assume independent samples. Individual whales were often observed more than once during a Behavioural Observation Session (BOS), leading to repeated measures of SRD behaviours from some individual whales. I partly addressed this by acknowledging that calculated significance levels were nominal, and by giving little emphasis to differences whose nominal significance levels had $q > 0.01$. I also applied mixed effects models to these data, with individually-identified whales (when recognized) treated as a random factor. However, it was often impossible to know whether a whale observed for one or more surfacings was involved in a previously-observed surfacing. I treated the observations in such cases as coming from separate whales. Thus, the results of these mixed-effects models may overstate statistical significance to some extent. Future analyses of such data could consider using the behavioural observation session (rather than the assumed individual whale) as the random effect, which would ensure that the assumption of independence is robust. This approach would further help address any synchronicity in the behaviours of whales observed in close proximity during a single BOS. However, these analyses were outside the scope of this chapter.

Most of the behavioural observations near seismic operations were collected in an opportunistic fashion with little control over where and when observations of whales exposed to seismic operations occurred, and with only approximate information on the highly variable seismic sound levels to which the animals were exposed (Richardson et al. 1986, Koski & Johnson 1987). As a result, data were not collected under all of the desired situations, such as for travelling whales in summer. Also it was not possible to include received sound level as a probable explanatory variable in the statistical tests, and that presumably reduced their statistical power. The variety of conditions (including the range of sound exposure levels) over which observations were collected probably led to increased variability in SRD behaviours, and some of this variation was detected in the sensitivity analysis.

To maximize the data available for analysis, I chose to categorize variables such as water depth and group size (rather than treating them as continuous or nearly so). This may have led to a loss of statistical power. However, depth category was selected as a significant variable in the LME models for all four SRD variables, and there was an apparent progression in beta coefficients with increasing depth for 3 of 4 SRD variables—number of blows per surfacing, surface duration, and dive duration (Tables 2.5a, 2.5c & 2.5d). This indicates the importance of depth in explaining the variation in each SRD behaviour. My application of LME models allowed me to address some of the variability in the data. Although the selected models explained < 40 % of the variation in the data, the results provided insights into the effect of seismic sound that have not been previously achievable.

Variability in the presence of ice and the distribution and availability of prey affect the distribution of whales and thus the sites of behavioural observations. Such variability resulted in my having small and unequal sample sizes under different conditions. I was also unable to quantify or include some factors in the models, such as prey abundance, which is likely an important determinant of distribution, activity state, and effects of seismic operations on the whales. Failure to include these variables may have contributed to the limited predictive capacity of the models. Behavioural data collected in the presence of seismic operations were also limited. All systematic aerial observations of bowhead behaviour in the presence of seismic operations were in the early to mid 1980s (e.g., Richardson et al. 1986, Koski & Johnson 1987). It was not possible to collect such data during more recent studies of bowheads near seismic operations. The number of observations of dive-duration (and thus proportion of time at surface) in the presence of seismic operations was particularly small. That limited my investigations of the effects of season and whale activities on those parameters to non-calf whales only, and precluded multivariate (LME) analysis of the key "proportion of time at the surface" variable. But more importantly, the small samples and frequent lack of specific sound exposure information meant that I was unable to incorporate distance to the sound source or received level of sound into my analyses. Thus I was restricted to a relatively simple analysis based on the presence or absence of seismic sounds.

The limited available data show that the presence of seismic operations led in some circumstances to changes in the SRD behaviour of bowhead whales. They also show that responses to seismic operations varied with season and some activity states of the whales. Although the biological consequences are unknown, subtle changes to SRD behaviours are likely to affect the detectability of bowhead whales by aerial observers. Quantitative data on SRD behaviour in relation to context (including presence/absence of seismic sound) can improve understanding of the effects of seismic operations on bowhead distribution and subsistence activities in the Beaufort Sea. Similar principles likely apply to vessel-based surveys, and to other seasons, species and regions—although my data are specific to aerial observations of bowhead whales in the Beaufort Sea in summer and autumn.

Chapter 3: Correction factors account for the availability bias of bowhead whales exposed to seismic operations in the Beaufort Sea

Summary

The accuracy of estimates of cetacean density from line-transect survey data depends in large part on how visible the target species is to the observer. Behavioural data (i.e., surface and dive times) from government- and industry-funded aerial observation programs (1980–2000) were used to calculate availability correction factors needed to estimate the number of bowhead whales from aerial survey sighting data. Correction factors were calculated for bowheads exposed and not exposed to seismic operations. Non-calves were found to be less likely to be available for detection than other whales while travelling, and their availability further declined in the presence of seismic operations. Non-calves were also less available to observers during autumn when exposed to seismic operations than when not exposed, regardless of activity (travelling or otherwise). Such differences in detectability appear to reflect behavioural responses to seismic sound that alters the surfacing and diving patterns of bowhead whales. Localised abundance estimated from aerial surveys may be as much as 64% higher in areas ensonified by seismic operations if correction factors are applied to account for differences in availability associated with the presence of seismic operations, compared to abundance estimates derived from analyses that only account for changes in availability of undisturbed whales. These results provide the first empirical estimates of availability bias for bowhead whales exposed to seismic operations and highlight the implications of not correcting availability biases related to seismic sound in density analyses in the vicinity of seismic operations.

Introduction

Aerial surveys are a common means to assess the abundance of animals that range over wide areas (e.g. Laake et al. 1997, Hain et al. 1999, Huber et al. 2001, Evans et al. 2003, Forcada et al. 2004, Pollock et al. 2006, Edwards et al. 2007, Southwell et al. 2007, Richard et al. 2010). Such surveys typically use systematic line-transect methods and consist of one or more observers recording the numbers, locations and distances from the transect line of detected animals. These data are then analysed using methods such as Distance sampling (Thomas et al. 2010) to estimate the density of individuals that were present within the surveyed area. However, the accuracy of these estimates depends on the reliability with which the animals can be detected (Caughley 1974, Marsh & Sinclair 1989, Steinhorst & Samuel 1989).

Distance sampling methodology incorporates a detection function $g(x)$ for modeling the effect of the perpendicular distance (x) from the transect line on the probability of detection. The quantity $g(0)$ is central to the concept of distance sampling (Buckland et al. 2001), and denotes the probability of detecting an object given that it is on or near the transect line. Conventional line-transect methodology assumes that all animals on or near the transect line are detected (i.e. $g(0) = 1$; Buckland et al. 2001). Hence, a source of negative bias in density estimates can occur when animals along the transect line either cannot be seen or are missed by observers (i.e. when $g(0) < 1$).

The probability of failing to detect an animal is composed of two components ― perception bias (animals that are potentially visible to observers but not seen) and availability bias (animals that are not available to observers because they are submerged or concealed) (Samuel & Pollock 1981, Marsh & Sinclair 1989, Laake & Borchers 2004). These probabilities may be functions of animal behaviour, survey platform specifications, and environmental factors (e.g. sea state and ice cover) (Caughley 1974). It is therefore necessary to estimate and correct for any biases associated with perception and availability to obtain unbiased density estimates (Marsh & Sinclair 1989).

Differences in availability make it particularly difficult to obtain unbiased estimates of cetacean abundance from aerial survey observations. Individual or groups of cetaceans are generally considered available when they are at or near the surface of the water, and considered unavailable to be seen when submerged below the surface (Laake & Borchers 2004). Availability bias for a species of cetacean may be estimated as a function of the proportion of time that individuals would be expected to spend at the surface, and the duration of time that the animal, even if submerged, would be within the range of detectability of the observer (described as the time-in-view). The expected proportion of time at the surface can be calculated from surface-respiration-dive (SRD) behaviour data (Hain et al. 1999). The time that an animal may be in view can in turn be determined by survey speed, altitude and the field of view (Fig. 3.1) from the survey platform (Caughley 1974, Hain et al. 1999, Laake & Borchers 2004). Consideration of these variables allows correction factors for availability bias to be estimated and incorporated into density estimates.

In the Beaufort Sea, aerial surveys are commonly used to study the distribution of the Bering-Chukchi-Beaufort seas population of the bowhead whale. Line-transect sightings data from industry-sponsored aerial surveys have also been used to monitor for effects of offshore industrial activities and estimate localised densities. These density estimates have been used to provide management with estimates of the number of animals exposed to different received levels of seismic sound (Brandon et al. 2011). In the Beaufort Sea, offshore industrial activities occur primarily during the late summer and autumn when the waters are often ice-free and most easily accessible. Hence, industry-sponsored aerial surveys have also occurred during that time.

The westward migration of this bowhead population also takes place during the late summer and autumn (Moore & Reeves 1993). The migration occurs in pulses (e.g. Blackwell et al. 2007), segregated both temporally and spatially by age class, and bowhead distribution is influenced by sea-ice conditions and water depth (Ljungblad et al. 1986, Moore et al. 2000, Treacy et al. 2006, Koski & Miller 2009). While the predominant activity of bowhead whales at that time of year is travel, they sometimes pause to feed along the migration corridor at places and times where prey is abundant (Koski et al. 2009). Activity state, age class, ice conditions and water depth influence the SRD behaviour of bowhead whales (Würsig et al. 1984, Dorsey et al. 1989, Richardson et al. 1995a, Chapter 2), and potentially the proportion of time that they spend at the surface.

The durations of surfacings and dives of bowhead whales are also influenced by sounds produced by industrial operations such as seismic exploration (Richardson et al. 1986, Ljungblad et al. 1988, Chapter 2). The availability bias for bowhead whales was first assessed by Davis et al. (1982), who recognised the need to account for bowhead whales missed due to variations in their surface and dive behaviour. Davis et al. (1982) calculated the correction factors for availability bias following the method derived by McLaren (1961). More recently, Thomas et al. (2002a) expanded their work and calculated availability bias correction factors for presumably undisturbed bowhead whales engaged in different activities. Availability bias correction factors have not yet been derived for bowhead whales or other cetacean species exposed to seismic or other industrial operations.

Disturbance and other factors are known to influence SRD behaviour, but it is not known whether they also affect availability and the density estimates of bowhead whales calculated from line-transect surveys. While changes in the surfacing and diving variables noted above would be expected, they do not necessarily correspond with changes in availability. For example, if surfacings and dives are both reduced or increased by ~25 % then the availability of the whales to be detected by observers would be approximately the same. The objective of this chapter was therefore to assess whether the availability of bowhead whales to aerial observers differs in the presence and absence of seismic operations in the Beaufort Sea. Availability correction factors for bowhead whales in different reproductive states that were engaged in different activities during summer and autumn while in the presence and absence of seismic operations were estimated. I also assessed the extent to which seismic sounds could result in over- or under-estimates of the local abundance of whales if this potential source of bias is not accounted for.

Methods

Data sources and collection

Bowhead behaviour data were obtained from five studies conducted from 1980 to 2000 in the southern Beaufort Sea during summers and autumns. For a summary of these studies, see Koski and

Johnson (1987), Richardson et al. (1986) and Richardson and Thomson (2002). All behavioural observations were made using the same standardised procedures as Würsig et al. (1985) and Richardson et al. (1985). In brief, the data were collected from fixed-wing aerial observation platforms in a manner that ensured whales were not appreciably disturbed by the observation aircraft (Richardson et al. 1985, 1987, Würsig et al. 1985, Patenaude et al. 2002, Richardson & Thomson 2002). The observations included whales that had not been recently exposed to seismic operations or other types of human activity (presumably undisturbed behaviour), as well as whales that were exposed to industrial or experimental sources of seismic sounds (potentially disturbed behaviour) (Richardson et al. 1985;1986, Würsig et al. 1985, Dorsey et al. 1989, Richardson & Thomson 2002). The data included surface and dive durations. A dive as recognized here is based on the definition of a sounding dive by Würsig et al. (1984). A sounding dive is when a whale was submerged below the surface and out of sight for ≥ 60 seconds in duration.

Table 3.1 Categories for which bowhead whale availability bias correction factors [*a(x)*] were calculated and the corresponding sample sizes of surface and dive data available. Only dives ≥ 60s were included for analysis. Correction factors by season and by activity state were calculated for non-calf whales only. Non-calf whales included all whales without a dependent calf, and mothers were adult whales with a dependent calf.

Category	**Seismic**		**Undisturbed**		**Total**	
	surface	*dive*	*surface*	*dive*	*surface*	*dive*
Reproductive status						
Non-calf	504	106	1070	333	1574	439
Mother	29	18	80	67	109	85
Season						
Summer (<25 August)	281	71	414	84	695	155
Autumn (≥25 August)	223	35	656	249	879	284
Whale activity						
Travel	79	18	120	77	199	95
Feed-shallow (≤20m depth)	46	21	258	97	304	118
Feed-deep (> 20m depth)	38	20	213	47	251	67
Social	326	44	369	66	695	110

Mean surface and dive durations were calculated for disturbed and presumably undisturbed whales in different reproductive states (non-calf whales, including adult and subadult whales, and mothers with a dependent calf), engaged in different activities (travelling, socialising and feeding), and during summer and autumn; the available sample sizes for surface and dive data are summarized in Table 3.1. Note that all whales classified as undisturbed were presumed to be so, based on knowing that no seismic activities or other industrial activities were occurring in the region and the observation aircraft was > 457 m altitude. Data on surface and dive duration are key components in the calculation of availability bias correction factors [*a(x)*] for bowhead whales, where *a(x)* is defined as the probability that a whale is at the surface and available for detection by aerial observers.

Assessing the field of view from a Twin Otter

The field of view for a de Havilland Twin Otter aircraft was determined during September and October 2012. Twin Otter aircraft are one of the main platforms utilised for government- and industry-sponsored surveys for bowhead whales and other marine mammals in the Beaufort Sea. Visibility is often reduced within a certain lateral distance of the transect line and also forward and aft for these aircraft (Thomas et al. 2002a); therefore, complete detection on or near the transect line cannot be assumed even if all whales present were at the surface and available to be seen. For this reason bowheads will only be available for detection within a certain viewing area. This area is referred to as the field of view.

The field of view can be described as a pie-slice. It is a function of the forward and aft angles-of-view (θ_f and θ_a, respectively), and a perpendicular distance representing the maximum visible range (X) from the transect line (Fig. 3.1). The survey platform, altitude and the eye sight of the observer can affect the parameters of the field of view.

The experiment to estimate the time-in-view for the de Havilland Twin Otter aircraft consisted of flying the aeroplane along parallel tracks past a static object (in this case a small structure) at pre-selected discrete distances, increasing from 160 m to 1,600 m from the object. Each experiment was performed at a standard survey speed of 220 km/h (averaging 62.3 m/s) and an altitude of 305 m above surface level. A single observer (FCR) was used to collect the data in this experiment. For each parallel track the discrete distance was randomly selected and only known to the pilots, ensuring that the observer was not cued into a particular search pattern. The observer was asked to maintain their “normal” search pattern (i.e. to avoid actively searching for the object) and record three time measures: (1) the time at which the object first came into view ahead of the plane (t_1), (2) the time when the object was perpendicular to the plane (t_2) and (3) the time when the object left the observer’s view to the rear of the aircraft (t_3). Two time measures were calculated from these data: (1) time forward: $t_f = t_2 - t_1$ and (2) time aft: $t_a = t_3 - t_2$.

I fitted separate linear models to the forward time-in-view and aft time-in-view data as a function of perpendicular distance (x), assuming normal sampling error on recorded times.

$$t_i = \alpha_i + \beta_i x \qquad 3.1$$

where i denotes either forward or aft ($i = a$ or f) of the line perpendicular to the transect line, and α and β are the model coefficients. The model coefficient β_i was then incorporated into a trigonometric model to estimate θ_f and θ_a — the forward and aft angles of view.

$$\theta_i = arctan(\beta_i \cdot speed) \qquad 3.2$$

The dimensions of the field of view allowed forward and aft view times to be evaluated at each perpendicular distance (x) from 0–2000 m. A maximum perpendicular distance of 2000 m (X) was selected because bowhead sighting data are often truncated at a perpendicular distance of ~2000 m from the transect line (Fig. 3.1).

$$t_i(x) = \frac{\alpha_i + x \cdot tan(\theta_i)}{speed} \qquad 3.3$$

This allowed the lateral distances (y) at each perpendicular distance to be determined, where the lateral distance was the swath of sea surface within the observer's field of view in which a whale would have to be at the surface to be detected (Fig. 3.1).

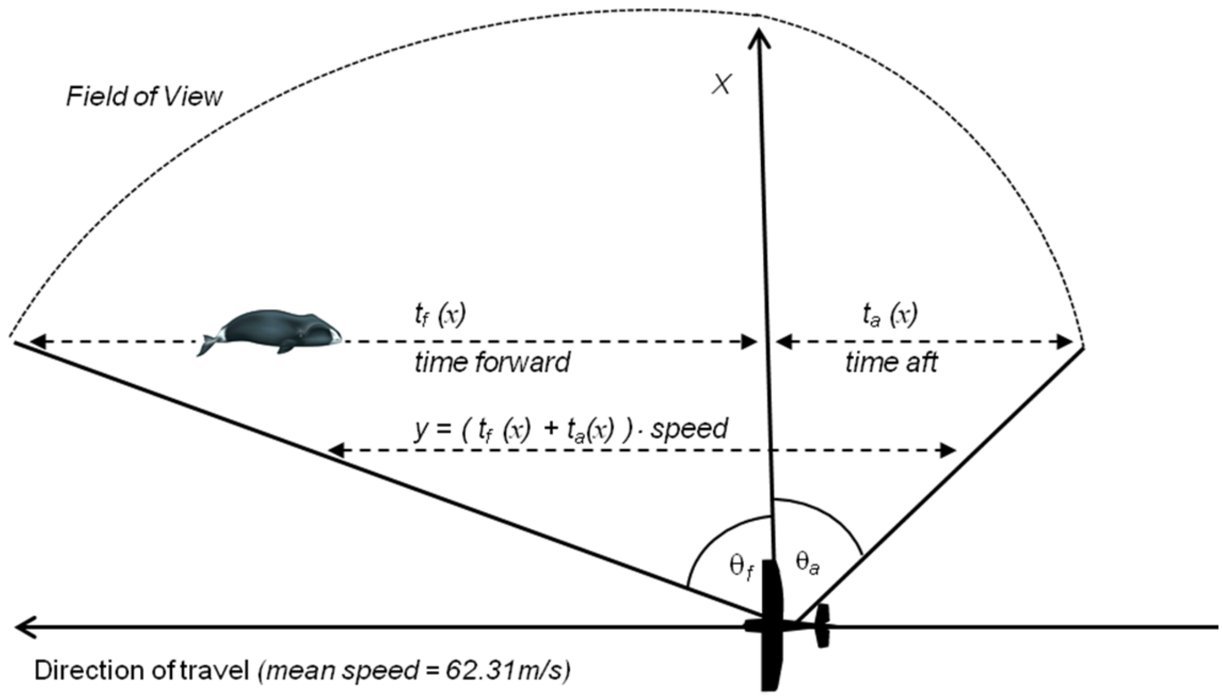

Figure 3.1 A depiction of the field of view of an observer from a de Havilland Twin Otter. The maximum visible range is denoted X. Observers generally scan an area from θ_f to 90 + θ_a, which gives a maximum angle of view. The field of view aft is smaller than might be expected because search effort is generally focused forward of the plane and perpendicular to it. The total time-in-view (time forward plus time aft) is a function of the perpendicular distance (*x*), survey speed and altitude. The lateral distance (*y*) is the swath of the sea surface that is within the observer's field of view.

Correction factors for availability bias

I calculated correction factors for availability bias [*a(x)*] for bowhead whales in the presence and absence of seismic operations—and for whales of different reproductive states and for non-calf whales during summer and autumn and while engaged in different activities. Calves were excluded from the analysis because they had different dive profiles and were in close association with an adult whale (the mother). Observers often detect calves after their attention has been drawn to the mother. Correction factors for availability bias were thus calculated for whales in the presence and absence of seismic operations to determine whether the presence of seismic affected the probability of a bowhead whale being available to be seen during an aerial survey.

Availability bias correction factors were calculated following the method outlined by Laake et al. (1997) to describe the availability of harbour porpoise (*Phocoena phocoena*) during an aerial survey study in the coastal waters of Washington State. Their model assumes that animal availability is an alternating Poisson process of being available (time at the surface; rate parameter λ) or unavailable (the length of the dive; μ), and that both parameters are independent random variables) (Laake & Borchers 2004). Therefore the probability that an animal will be at the surface and available at perpendicular distance x is

$$P(x) = \frac{\lambda}{\lambda+\mu} + \frac{\mu\left[1-e^{\{-\lambda t(x)\}}\right]}{\lambda+\mu} \quad 3.4$$

where the average length of a surfacing event is $s = 1/\lambda$, the average duration of a dive is $d = 1/\mu$, and the sum of these is the average length of the surface-dive cycle (Laake & Borchers 2004). This equation can then be re-written (Laake et al. 1997) as

$$a(x) = \frac{s}{s+d} + \frac{d\left[1-e^{\left\{{-t(x)}/{d}\right\}}\right]}{s+d} \quad 3.5$$

where $t(x)$ was the average time in view ($\bar{t}$) over 0-2000 m (estimated using Eqn. 3.3). Correction factors were calculated for the different categories (e.g. reproductive status, activity state, season and exposure to seismic operations) based on their SRD data (Table 3.1). The Laake et al. (1997) method for estimating the probability that a whale would be at the surface and available for detection is suitable for animals that are considered to be intermittently available (e.g. a marine mammal). Intermittent availability is defined as occurring when an animal is available for more than an instant and its availability can change when it is within the field of view (Laake & Borchers 2004).

I investigated the effect of not applying the correct availability correction factor to bowhead whale sighting data collected in the presence of seismic operations by calculating the percentage change between the presumably undisturbed localised abundance estimates and those when seismic operations are present, derived from the application of the appropriate correction factors. The percentage change was calculated as

$$\%\ change = \frac{(N_s - N_{ns})}{N_{ns}} \times 100 \quad 3.6$$

Where N_{ns} is the estimated abundance of whales obtained when applying the availability correction factor for presumably undisturbed whales and N_s is considered the true abundance estimate for whales in the presence of seismic operations when the appropriate availability correction factor for disturbed whales is applied. I used the same approach to assess the difference between applying correction factors derived from the use of t estimated by Thomas et al. (2002a) and correction factors derived from t estimated in this study. However, Thomas et al. (2002a) assumed that the field of view was a constant rectangular swath of water running parallel to the trackline with a lateral distance of 1.25 km, and only considered time forward (t_f). Correction factors were therefore also calculated using only t_f for a lateral distance (y) of ~1.25 km and the difference between abundance estimates derived from the application of these correction factors was assessed using the same method as laid out in Eqn. 3.6.

Variance calculations

I estimated variances specific to each estimated correction factor *a(x)* using the multivariate delta method. From the multivariate delta method the variance is

$$V = \left(\nabla P(X)\right)\Big|_{X=\gamma}^{T} \Sigma\left(\nabla P(X)\right)\Big|_{X=\gamma} \qquad 3.7$$

$$\left(\nabla P(X)\right) = \begin{bmatrix} -\dfrac{d\left(1-e^{\left(-t/d\right)}\right)}{(d+s)^2} - \dfrac{s}{(d+s)^2} + \dfrac{1}{d+s} \\ -\dfrac{d\left(1-e^{\left(-t/d\right)}\right)}{(d+s^2)} - \dfrac{s}{(d+s)^2} + \dfrac{1-e(-t/d)}{d+s} - \dfrac{e(-t/d)t}{d(d+s)} \\ \dfrac{e(-t/d)}{d+s} \end{bmatrix} \qquad 3.8$$

In Eqns 3.7 and 3.8, ($\nabla P(X)$) is the column vector of the partial derivatives (Eqn 3.8) of *a(x)* given by Eqn 3.5 and $\left(\nabla P(X)\right)|_{X=\gamma}$ is the same as ($\nabla P(X)$) except that the values *s, d,* and *t* (the elements of the vector *X* in Eqns 3.7 and 3.8) are replaced by their estimated mean values $\bar{s}$, $\bar{d}$, and $\bar{t}$ (the elements of the vector γ that appears in the subscripts of Eqn 3.7). Also in Eqn 3.7, T denotes the transpose of the vector, and Σ is a three diagonal matrix with the variances $V(\bar{s})$, $V(\bar{d})$, and $V(\bar{t})$ on its diagonal.

Results

The field of view for a Twin Otter

The experiment to determine the field of view for a Twin Otter was conducted opportunistically 18 times over a two-month period with the same observer (FCR) on each occasion. Line-transect surveys were conducted at a mean survey speed of 62.31 m/s. Linear models fitted to the forward and aft time-in-view data provided the coefficients used to estimate the fore and aft angles (θ) that determined the boundaries of the area searched by the observer (Fig. 3.2). The coefficients estimated for the forward time-in-view data were 31.41 (*se*=7.17) for α and 0.02 (*se*=0.007) for β, while the coefficients for the aft time-in-view data were 6.37 (*se*=1.42) for α and 0.01 (*se*=0.001) for β. This resulted in a search sector that spanned 37.6º forward and 31.2º aft of perpendicular for the de Havilland Twin Otter survey aircraft used in this experiment (Fig.3.1). Considering a maximum perpendicular detection distance of X=2000 m the average time ($\bar{t}$) that a whale could be within the field of view at an average survey speed of 62.31 m/s and 305 m survey altitude was 31.33 s (*se*=4.16). Equivalently the lateral distance of the swath of water in view to an observer given $\bar{t}$ was 1.95 km.

The effect of seismic sound exposure on availability bias of bowhead whales

The presence of seismic sound resulted in a lower probability of bowhead whales being available for visual detection within the observer's field of view (Table 3.2). For a presumably undisturbed non-calf whale, the overall probability of it being available for detection was $a(x)$ = 0.180; however this dropped to $a(x)$ = 0.155 in the presence of seismic sound. The probability of a whale with a dependent calf being at the surface and available for detection was higher than that for the average non-calf in presumably undisturbed conditions. However in the presence of seismic operations, both non-calves and those with dependent calves had a similar availability (Table 3.2). Both non-calf and mother whales displayed a lower probability of being available for visual detection in the presence of seismic operations. Not correcting for this availability bias (using the appropriate correction factors for whales potentially disturbed by seismic operations) would have resulted in an underestimation of the estimated number of whales by 16 % for non-calves and 34 % for mothers.

The presence of seismic operations had little effect on the availability of non-calves in the summer (Table 3.2). However, Table 3.2 shows that non-calf bowhead whales exposed to seismic operations were the least available for visual detection in the autumn. This means that the density analyses of non-calf whales exposed to seismic operations in the autumn would be underestimated by 64 % if the effects of seismic sound on whale behaviour were not accounted for.

There was a similar effect of seismic operations on non-calves that were travelling, socialising and feeding. The probability of being available for detection declined for all behaviours in the presence of seismic operations (Table 3.2). When whales were presumably not disturbed, travelling whales had the lowest probability of being available for detection ($a(x)$ = 0.152). Their probability of being available for detection dropped further when seismic operations were present to $a(x)$ = 0.120 (Table 3.2). This means that density analyses derived from aerial observations of travelling whales in the presence of seismic operations would be underestimated by 27 % if appropriate correction factors were not applied.

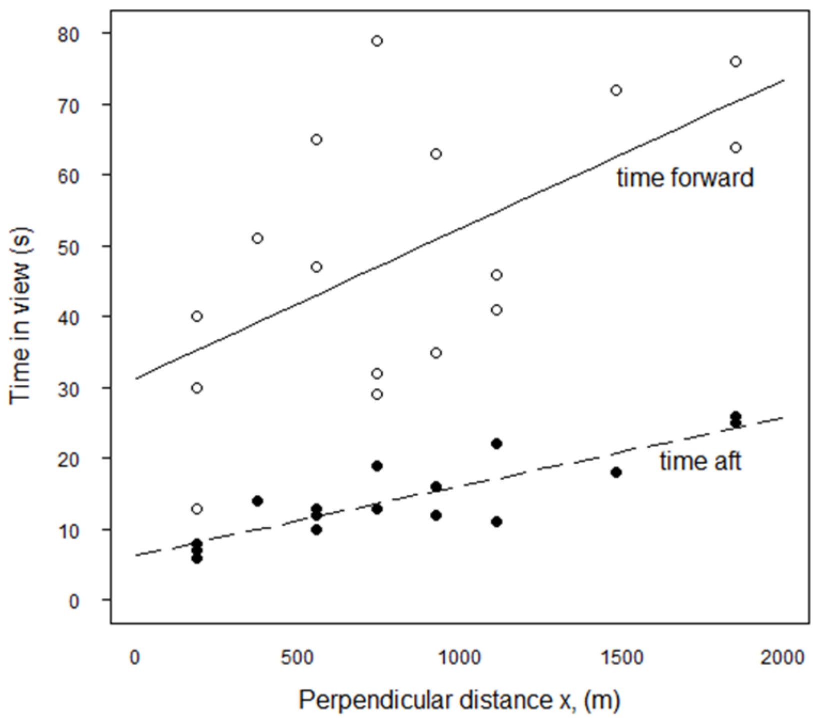

Figure 3.2 Linear models fitted to the forward and aft time-in-view data collected during the 18 sampling occasions. The resulting α and β coefficients were incorporated into the trigonometric model used to estimate the field of view that observers scan while surveying (Eqn. 3.1-3.3).

Undisturbed socialising whales exhibited the greatest probability of being available for detection, but their availability declined in the presence of seismic operations by 59 % so that their abundance would be underestimated if the appropriate *a(x)* were not used. Seismic sound also resulted in a lower probability of feeding whales being available for detection—although the effect was less than that for travelling or socialising whales. Density analyses of feeding whales exposed to seismic sounds would underestimate abundance by 21 % for whales feeding in shallow waters and 13 % for whales feeding in deep waters if appropriate correction factors were not used (Table 3.2). Overall, estimates of abundance for bowhead whales observed in areas ensonified by seismic operations may be underestimated by as much as 64 % if correction factors were not applied to account for behavioural changes.

Table 3.2 Availability bias correction factors, *a(x)*, for presumably undisturbed bowhead whales and those exposed to seismic operations, from Eqn. (5). Bowhead behaviour data were collected from the southern Beaufort Sea; mean surface ($\bar{s}$) and dive durations ($\bar{d}$) and mean time-in-view (31.33 s) are recorded in seconds. Only sounding dives (≥ 60 s) were included in the dive category as per Würsig et al. (1985, 1989). The standard error (*se*) was derived from the square root of the variance, which was calculated based on the multivariate delta method, (Eqns. 3.6-3.8). The percentage by which abundance estimates would be underestimated by if the incorrect correction factor were applied is also given.

Category	***Seismic***				***Undisturbed***				*% change in abundance estimates*
	$\bar{s}$	$\bar{d}$	*a(x)*	*se*	$\bar{s}$	$\bar{d}$	*a(x)*	*se*	
Reproductive Status									
non-calf	61.1	528.7	0.155	0.15	73.9	504.7	0.180	0.16	16
mother	96.4	740.5	0.152	0.13	121.7	656.8	0.203	0.12	34
Season									
summer	56.4	371.0	0.202	0.17	66.6	394.2	0.210	0.18	4
autumn	67.0	848.6	0.107	0.01	78.5	542.0	0.176	0.15	64
Whale Activity									
travel	53.0	645.9	0.120	0.13	90.4	705.3	0.152	0.11	27
social	55.8	408.5	0.163	0.17	69.5	373.3	0.259	0.20	59
feed shallow	72.6	639.8	0.185	0.15	66.3	524.6	0.225	0.20	21
feed deep	62.3	507.1	0.145	0.11	73.8	326.2	0.164	0.12	13

This chapter also highlights the importance of incorporating survey specific field of view estimates into the calculation of availability correction factors. The time-in-view estimated for this study (31.33 s) resulted in correction factors that would lead to density estimates between 6 and 12 % lower than those density estimates derived from correction factors calculated with the time-in-view estimate produced by Thomas et al. (2002a) (21.6 s, Table 3.3). The time-in-view estimate produced by Thomas et al. (2002a) is currently used in the availability correction factors that are applied to aerial survey sighting data (e.g., Brandon et al. 2011), but this estimate of time-in-view assumes the lateral field of view is constant. Under the same assumptions *t* calculated in this chapter was comparable and the difference in estimates was negligible (Table 3.4). However, the results of the experiment to determine the field of view for a Twin Otter suggested that *t* increases with perpendicular distance and is not constant. This implies that estimates of bowhead whale density derived from aerial surveys in areas ensonified by seismic operations should account for survey specific variables (such as survey platform, survey speed, observer search patterns and altitude) as well as whale behavioural changes.

Table 3.3 A comparison of the availability bias correction factors, *a(x)*, for presumably undisturbed bowhead whales and those exposed to seismic operations derived from a time-in-view (t) of 21.6 s for a lateral distance of 1.25 km as reported by Thomas et al. (2002a), and a $\bar{t}$ of 31.33 s calculated using the methods proposed by this study, equating to a lateral distance of 1.95 km.

Category	Seismic			Undisturbed		
	a(x)		*% change in abundance estimates*	*a(x)*		*% change in abundance estimates*
	t = 21.6	t = 31.3		t = 21.6	t = 31.3	
Reproductive Status						
non-calf	0.139	0.155	-10	0.165	0.180	-9
mother	0.141	0.152	-7	0.184	0.203	-10
Season						
summer	0.181	0.202	-10	0.190	0.210	-9
autumn	0.096	0.107	-10	0.161	0.176	-8
Whale Activity						
travel	0.106	0.120	-11	0.142	0.152	-6
social	0.146	0.163	-10	0.237	0.259	-9
feed shallow	0.165	0.185	-11	0.204	0.225	-9
feed deep	0.132	0.145	-9	0.148	0.164	-10

Table 3.4 A comparison of the availability bias correction factors, *a(x)*, for presumably undisturbed bowhead whales and those exposed to seismic operations derived from a time-in-view (t) of 21.6 s for a lateral distance of 1.25 km as reported by Thomas et al. (2002a), and a t of 20.1 s calculated using only t_f for a lateral distance of 1.25 km.

Category	Seismic			Undisturbed		
	a(x)		*% change in abundance estimates*	*a(x)*		*% change in abundance estimates*
	t = 21.6	t = 20.1		t = 21.6	t = 20.1	
Reproductive Status						
non-calf	0.139	0.137	2	0.165	0.162	2
mother	0.141	0.139	1	0.184	0.182	1
Season						
summer	0.181	0.178	2	0.190	0.187	2
autumn	0.096	0.095	2	0.161	0.159	2
Whale Activity						
travel	0.106	0.104	2	0.142	0.141	1
social	0.146	0.144	2	0.237	0.233	2
feed shallow	0.165	0.162	2	0.204	0.201	2
feed deep	0.132	0.130	2	0.148	0.146	2

Discussion

This is the first study to investigate and quantify availability bias for bowhead whales exposed to seismic sounds. It shows that the probability that a bowhead whale will be available for visual detection is lower when whales are exposed to seismic operations, resulting in the possibility that numbers of whales previously estimated to have been in seismic survey areas exposed to various sound levels from seismic operations have been underestimated, and that estimates of avoidance to seismic operations have been overestimated. In the presence of seismic operations, the probability of detecting a bowhead whale within the field of view of an observer is lowest in the autumn when whales are migrating west through areas of the Beaufort Sea where there are (at some places and times) offshore industrial activities, including seismic surveys. In general, the presence of seismic operations leads to a lower probability of bowhead whales being available for visual detection. It is possible that a similar potential bias may exist for other whale species exposed to seismic operations.

The availability correction factors calculated in the earlier studies were for bowhead whales that were presumed to be undisturbed (e.g. Davis et al. 1982, Thomas et al. 2002a) and were specific to the aerial survey protocols of those individual studies. The field of view, and therefore the time-in-view (*t*) for observers to detect an animal at the surface, on or near the transect-line, is specific to the survey platform and is a function of platform specifications, survey speed, altitude and the individual observers (Caughley 1974). Therefore *t* may vary between surveys, especially if different observers, survey platforms, survey speeds, altitudes and strip widths or scanning patterns are used; availability correction factors derived for one survey may lead to inaccurate results if used in the analysis of data collected from a different platform under differing conditions (Pollock & Kendall 1987, Marsh & Sinclair 1989).

Earlier studies conducted in the Beaufort Sea estimated the time-in-view (*t*) to be between 18 s (Davis et al. 1982) and 21.6 s (Thomas et al. 2002a). These estimates are shorter than the 31.3 s I calculated for a Twin Otter aircraft (with bubble windows) flying at an altitude of 305 m at a standard survey speed of 220 km/h. In this case, the lateral swath of water within the field of view was assumed to increase with perpendicular distance, while Thomas et al. (2002a) assumed that the lateral distance of observable water parallel to the trackline was constant (1.25 km) and visible for a constant time (21.6 s). Thomas et al. (2002a) also considered *t* to only be forward of the perpendicular (defined as t_f in Fig. 3.1). Applying such assumptions (i.e., forward (*tf*) and a lateral distance of ~1.25 km) to my study yields a time-in-view of 20.1 s and a perpendicular distance of 930 m. These estimates are comparable to those proposed by Thomas et al. (2002a), and highlight the importance of how the field of view for an aerial survey is defined. The survey data I had used to model *t* suggested the field of view was not constant across increasing perpendicular distances, and resulted in a larger mean field of view when taken into account. It is thus important to consider survey specific data and observer search patterns when calculating *t* to obtain accurate density estimates of whale numbers within survey areas.

The proportion of time that the whale spends at the surface during a typical SRD cycle and the time-in-view (*t*) of a location on the water are the key components needed to assess the availability of a whale for visual detection. Variations in SRD behaviour affect the overall proportion of time that whales spend at the surface, such that a whale that spends a higher proportion of its time submerged, and so is unavailable for detection, will decrease the probability of detection. Activity state, season, reproductive status and exposure to seismic operations all influence the availability of a whale for visual detection.

Subtle variations in SRD behaviour of bowhead whales exposed to seismic operations have been identified in early behavioural response studies (e.g. Richardson et al. 1985, 1986, Koski & Johnson 1987, Ljungblad et al. 1988). During the autumn when whales are migrating west through the central Beaufort Sea and have been exposed to seismic operations there, travelling is the primary activity, interspersed with occasional feeding bouts (Richardson & Thomson 2002, Koski et al. 2009). It is during this time and for travelling whales that my analysis of pooled behavioural data (from studies conducted during 1980 to 2000) in Chapter 2 found non-calf bowhead whales to be most responsive to seismic sounds. My results based on the same behavioural data are consistent with this finding and suggest that non-calf bowhead whales are the least available for visual detection while travelling and in the autumn when exposed to seismic operations. Variation in the availability of a whale for visual detection may result in underestimates of the number of whales exposed to various levels of seismic operations in the Beaufort Sea, especially in autumn and for travelling bowhead whales.

The surface and dive behaviours of bowhead whales vary with activity state. Differences in behaviours among activity states are also reflected in a whales' availability for visual detection. Thomas et al. (2002a) determined that travelling whales had the lowest probability of detection while whales engaged in social activities had the highest probability of detection. My study corroborates this finding for presumably undisturbed bowhead whales. However, the probability of being available for detection declines by more than a third when socialising whales are exposed to seismic operations—a level that is below that of whales feeding in shallow waters in the presence of seismic operations.

A large seasonal effect of seismic on the availability of bowhead whales was also determined. Most notably, seismic operations had little effect on the availability bias during summer when feeding is the predominant activity (Würsig et al. 1985). However, during autumn, seismic operations had a notable effect on the availability of whales when travelling becomes increasingly more common as the whales begin their westward migration. Previous analyses of availability bias focussed on presumably undisturbed bowhead whales and, therefore, are not applicable in analyses of sighting data collected in the presence of seismic and possibly other industrial operations.

During autumn, non-calves exposed to seismic sounds have a low probability of being detected, followed by presumably undisturbed non-calves that are travelling. This is consistent with the finding that whales observed in the autumn or engaged in travel are more sensitive to seismic operations than are whales engaged in feeding (Chapter 2). Undisturbed bowhead whales in the eastern and central Beaufort Sea spend the majority of the late summer and early autumn feeding, but also spend approximately one-third of their time travelling (Würsig et al. 2002). During years of particularly low prey density, the time whales spend travelling increases as whales continue their westward migration rather than stopping to feed (Würsig et al. 2002).

Bowhead whales react to seismic sounds by subtly changing their SRD behaviour (Richardson et al. 1985, 1986, Koski & Johnson 1987, Ljungblad et al. 1988), which affects the proportion of time that they spend at the surface. These changes are reflected in the probability of the whales being available for detection during an aerial survey. Aerial surveys are commonly part of environmental monitoring programs for oil and gas exploration in the US Beaufort Sea and elsewhere. These surveys monitor marine mammal presence and distribution relative to the industry's operations. However analyses of bowhead sighting data from these surveys have accounted for availability bias by incorporating correction factors estimated for undisturbed animals. Therefore, they likely underestimate the numbers of whales potentially exposed to seismic sounds and overestimate avoidance of seismic operations.

The presence or absence of industrial operations and the activity states of the whales seen during surveys will dictate which $a(x)$ estimate (presented in this chapter) should be incorporated into density analyses. For example, should a survey yield adequate sighting data where the majority of whales were observed feeding in an area with active seismic operations, then it is appropriate to select the correction factor for potentially disturbed feeding whales. Alternatively, analyses of surveys without information on activity states would be stratified by season with the appropriate correction factor selected depending on whether or not seismic operations were present. Selection and use of the appropriate correction factors during analysis will lead to improved estimates of the number of whales exposed to different received levels of seismic sound, as required by regulators.

There are a number of limitations to the approach I used to calculate the availability correction factors for bowhead whales exposed to seismic operations. The highly visible nature of the sighting object used in this experiment meant that the field of view estimates likely represent the maximum potential detectability, and therefore the maximum time-in-view. The linear model approach used to estimate time forward and time aft was likely limited by the sampling design of the time-in-view experiment. The use of time recorded when the sighting object was perpendicular to the plane in both the calculation for time-forward, $t_f = t_2 - t_1$ and time aft: $t_a = t_3 - t_2$ will have led to correlated errors. Future analysis of data collected under such a sampling design should consider the use of a joint-regression where the errors of t_1 and t_3 are independent but the errors of t_2 is the same for each calculation of t_f and t_a.

The time-in-view experiment also did not allow an investigation of the influence of environmental variables (e.g. sea state, sea ice coverage and glare) on the boundaries of the search area. During high sea states, for instance, observers will reduce their search area because more time is taken to decide whether a potential sighting is, or is not, a marine mammal. Observer scanning behaviour and individual variation are also known to influence the duration of detectability and the time-in-view was based on measurements from a single observer. Thus the earlier-used values for t may be more realistic values than the one we calculated. Future studies could use a mixed-effects modeling framework to account for variation due to observer scanning behaviour, and also might produce better estimates of variance around the correction factors. Despite the limitations associated with this experiment it was a first experimental attempt to determine a survey specific time-in-view estimate for the Twin Otter aircraft commonly used for bowhead surveys in the Alaskan Beaufort and has built on previous methods that have only estimated time-in-view based on aircraft speed (e.g. Davis et al. 1982) or simple trigonometry (e.g. Forcada et al. 2004).

Overall availability will also be influenced by whale group size. Groups of two or more whales tend to be more detectable to observers. Surface active groups of North Atlantic right whales have been found to have the highest availability with a mean of 93 %, while the availability of individual right whales ranged from 40-60 % (Hain et al. 1999). Bowhead whales engaged in surface skim feeding or socialising activities are often observed in groups of two or more whales (Würsig et al. 1985, 1989). Such group activities by socialising bowhead whales and by whales feeding in shallow waters tend to increase disturbance of the surface waters, leading to higher probabilities of detection.

Environmental, observer and whale related variables inevitably influence both the time-in-view as well as the overall availability of a bowhead whale for visual detection by an aerial observer. Because I was unable to account for the effects of many of these variables, these correction factors should be considered to be better than past values, but not optimal values for bowhead whales within each of the categories examined. Future measurements of the time-in-view in marine areas and subsequent estimates of bowhead whale availability should investigate and incorporate the effects of environmental, observer and whale related variables so that more accurate measures of detectability can be determined for a wider range of conditions. Despite these caveats, the correction factors calculated in this study can be considered the best available for bowhead whales in the Beaufort Sea, both in presumably undisturbed conditions and for areas with seismic operations.

Understanding how the behaviour, distribution and habitat use of bowhead whales is affected by industrial operations is needed to evaluate the potential effects of oil and gas exploration and development activities on individual whales and their populations. These analyses have shown that seismic operations generally resulted in whales being less available for visual detection by aerial observers. Although these methods are specific to aerial observations of bowhead whales in the Beaufort Sea during summer and autumn, the same principles apply to aerial surveys and vessel-based surveys for other seasons, species and regions. Future studies investigating the effects of anthropogenic sounds on cetacean distribution, local abundance, and behaviour should calculate availability correction factors specific to the species of interest at the time and in the circumstances of exposure. This is necessary to avoid under- or over-estimating the number of individuals exposed to potential sources of disturbance and to avoid over- or underestimating the degree of avoidance around those activities. This will require situation-specific data on surfacing and dive behaviour of the cetaceans. Such data can be obtained by visual methods (such as here) or by tagging and/or telemetry methods. With such data, appropriate correction factors can be incorporated into analyses of sighting data for cetaceans to better estimate the numbers of animals that may have been exposed to disturbances, such as seismic operations, and in turn, how exposure may influence cetacean distribution and habitat use.

Chapter 4: Variable detectability affects density and distribution assessments of bowhead whales during seismic survey operations in the southern Beaufort Sea, Alaska.

Summary

Aerial surveys are a common means to assess the densities of animals that range over wide areas, such as bowhead whales. In the Alaskan Arctic, aerial surveys to estimate numbers of whales present are typically part of the environmental monitoring programs on the effects of oil and gas exploration activities. However, numbers of whales present during surveys may be over- or under-estimated if seismic operations affect the behaviour, and hence how visible a whale is to aerial observers. The objective of this chapter was two-fold—first to generate corrected density predictions of bowhead whales in the southern Beaufort Sea; and second to determine the extent to which seismic operations alter availability and affect the predicted densities of bowhead. I analyzed sightings of bowhead whales recorded during industry monitoring surveys of seismic operations conducted in the southern Beaufort Sea from late August to early October 2008. I fit the data with density surface models (corrected for availability bias) and predicted densities for non-calf whales, as well as for feeding and travelling whales. To determine the sensitivity of density predictions to variable availability of bowhead whales related to the presence of seismic operations, I compared predicted densities corrected for differences in behaviour associated with the presence or absence of seismic operations. The predictive models indicated that bowhead whales occurred in the shallower, nearshore waters—with few if any whales present in the deeper slope waters. They showed feeding whales were concentrated towards Camden Bay, while travelling whales occurred in lower densities from Prudhoe Bay into Harrison Bay. Density estimates that accounted for variations in whale behaviour due to seismic operations were 25–64 % higher than previous estimates. This suggests that seismic activities may not have displaced bowhead whales as previously thought, but altered their dive behaviours instead and made them less visible for counting. As a consequence, previous estimates of numbers of whales exposed to moderate sounds related to seismic operations appear to have been underestimated.

Introduction

The overlap between human activities and marine mammals in the Arctic is substantial (Moore et al. 2012, Reeves et al. 2014). As a result, Arctic marine environments are subject to increasing levels of anthropogenic sound (Moore et al. 2012, Reeves et al. 2012, 2014), including sounds related to seismic survey operations. Seismic surveys are commonly used to map geological features of the seabed and are used extensively by the oil and gas industry to identify sources of oil and gas. Seismic operations typically employ an array of air guns which release high pressure bolts of air at regular intervals, which travel through the water column to penetrate the seabed and substrate below (Caldwell & Dragoset 2000). Air-guns produce intense sounds with source levels ranging from ~ 222 to 264 dB re 1μPa-m_{p-p} (Richardson et al. 1995b). Typical high-energy arrays emit most of their energy at low frequencies of <500 Hz (Potter et al. 2007), but higher frequencies also contribute to the emitted energy (Goold & Coates 2006). As a result, there is overlap with the calling and hearing frequencies of low frequency specialists such as the bowhead whale (Clark & Johnson 1984, Würsig & Clark 1993).

The effects of seismic operations on bowhead whales have been studied in the US and Canadian Arctic since the early 1980s (e.g. Fraker et al. 1985, Richardson et al. 1985, 1986, 1987, Ljungblad et al. 1988, Greene Jr. et al. 1999, Blackwell et al. 2010, 2013). Bowhead whales have been observed in the presence of seismic operations in both their summer feeding areas in the Canadian Beaufort Sea (Richardson et al. 1986, Miller et al. 2005, Harwood et al. 2008, 2010), as well as along parts of their westward autumn migration in the Alaskan Beaufort (Ljungblad et al. 1988, Blackwell et al. 2013, Quakenbush et al. 2013b) and the Chukchi Seas (Moore & Clarke 1993, Quakenbush et al. 2010). The concerns surrounding the possible impacts of anthropogenic sound have resulted in the development of regulations to limit the exposure of marine mammals to strong sounds associated with specific activities such as seismic operations (Moore et al. 2012).

In Alaska, the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA) provide regulations for managing and protecting marine mammals. The MMPA requires that activities that might harm, incidentally harass a marine mammal, or interrupt any Arctic subsistence activity be planned to minimize potential impacts. Permits for such activities are issued with the understanding that, at most, only a small, predetermined number of animals will be subject to possible harassment, and that the activity will have negligible population level impacts and can be mitigated in a manner to minimize any harm, harassment or availability of marine mammals to hunters (MMPA 1972, Moore et al. 2012). A key requirement involves the development of marine mammal monitoring and mitigation plans, where mitigation measures are intended to minimize harm to marine mammals while monitoring is required to determine what effects there might be over a larger area than mitigation can reasonably be implemented

(Moore et al. 2012). Monitoring includes the collection of data to estimate how many animals might have been exposed to or may have diverted from the activity.

Seismic operations commonly employ marine mammal observers on ships for mitigation, but in the Arctic aerial surveys have also been utilized for monitoring and mitigation purposes because they are an effective means of obtaining information about numbers and distributions of marine mammals over large areas in short periods of time. Aerial surveys are the only practical method to assess the presence and density of wide ranging animals, like the bowhead whale (Harwood et al. 2008, 2009, Funk et al. 2010, Bisson et al. 2013). They are used in Canada to determine density and presence of feeding aggregations so that restrictions on the areas where activities can be conducted may be implemented (Harwood et al. 2008, 2009). In the US, wide areas around seismic operations are monitored using aerial surveys to assess distributions and estimate numbers of whales present in areas with different estimated sound levels. These estimates are sometimes required by US regulators as a condition of permits to conduct activities (MMPA 1972, Moore et al. 2012). Such information on whale distribution relative to industrial activities is also useful to assess possible impacts of industrial activities on local Iñupiat whaling success.

Subtle behavioural reactions of whales to seismic operations could affect how visible whales are to observers. Not accounting and correcting for such behavioural variations could result in over- or under-estimates of the number of animals that were present (Hain et al. 1999, Chapters 2 & 3).

Bowhead whales have been found to vary their behaviour when exposed to seismic sounds, resulting in subtle changes related to the whales' surfacing, respiration and dive behaviour (Richardson et al. 1986, Ljungblad et al. 1988, Richardson & Malme 1993, Chapter 2). A reanalysis of bowhead behaviour data collected from 1980–2000 determined that bowhead whales respire fewer times and have significantly shorter surfacing times when in the presence of seismic operations (Chapter 2). Variations in surface and dive behaviour in turn influence how visible a whale is to aerial observers because observers can only detect, and therefore count, whales that are at the surface of the water (Hain et al. 1999, Thomas et al. 2002a, Chapter 3). However, it is possible to account for whales that are submerged below the surface and not seen on surveys by calculating the probability that a whale will be at the surface and available for visual detection under different circumstances (Laake et al. 1997, Hain et al. 1999).

I used correction factors from Chapter 3 to account for the likelihood of whales being seen less frequently when exposed to seismic operations, and applied these correction factors to aerial survey data collected in the southern Beaufort Sea in 2008. The objective of this chapter was therefore to 1) predict corrected densities of bowhead whales in the southern Alaskan Beaufort Sea in an area ensonified by seismic operations, and to 2) determine the extent to which predicted densities of bowhead whale change due to variations in availability associated with seismic operations. Distance sampling methods provided a means to succinctly address my objectives by allowing the sighting data and changes in behaviour of whales while in the presence of seismic operations to be combined within the same modelling framework.

Methods

Collection of effort and sighting data

Bowhead whale sighting data were collected during systematic line-transect aerial surveys in the southern Alaskan Beaufort Sea during the late summer and autumn of 2008. The surveys were designed to monitor the area in and near seismic survey operations conducted by Shell Offshore Inc. (Funk et al. 2010). Surveys consisted of randomly placed transect lines running perpendicular to the coast in a north-south direction. The length and density of the transects varied to reflect the monitoring requirements dictated by the different seismic operations being monitored in the area but overall resulted in good coverage of the study area (Fig. 4.1, Funk et al. 2010).

Surveys were conducted from a specially modified DHC-300 Twin Otter fixed wing airplane. Modifications included a STOL (Short Take Off and Landing) kit to allow for slow survey speeds, bubble windows to enhance the viewing field available to observers, and an inverter which supplied 110 V AC power to run the survey equipment (Funk et al. 2010). All surveys were conducted at 305 m above sea level and at standard survey speeds of ~222 km/h. Flight durations were determined by fuel capacity, weather conditions and pilot daily flight hour limits.

Surveys were conducted using standardized procedures. Survey teams consisted of two pilots and up to five trained observers. Two primary observers and up to two secondary observers sat at bubble windows on either side of the plane, continuously scanning the water for marine mammals within approximately 2 km of the transect line (Funk et al. 2010), while a data recorder entered sighting and effort-related data into a GPS-linked laptop computer. The observers rotated positions between primary, secondary and data recorder positions approximately every two to three transects in order to maintain alertness. Observers recorded environmental data (Beaufort wind force scale, ice cover percentage and type, amount of glare in the viewing area and an overall measure of sightability) that could influence sightability at two-minute time intervals and at the end of each transect (Funk et al. 2010).

When a bowhead whale was sighted, observers recorded the time when the sighting was perpendicular to the aircraft heading, the group size, sighting cue, age-class, activity, heading, swim speed and an inclinometer angle. The inclinometer angle and time were used to calculate the precise location of each sighting. The GPS position of the aircraft at the time of the sighting was obtained from the GPS log file and the angle reading allowed the perpendicular distance of the whale from the trackline to be calculated and the whale location to be determined (Funk et al. 2010). Primary and secondary observers were independent (i.e. secondary observers did not announce their sightings), and the sighting data of secondary observers were coded to reflect the observers` position. Observers recorded sighting and effort data onto digital recorders and transcribed data into an Excel spreadsheet after each survey. The spreadsheet was verified to ensure that all data were entered correctly.

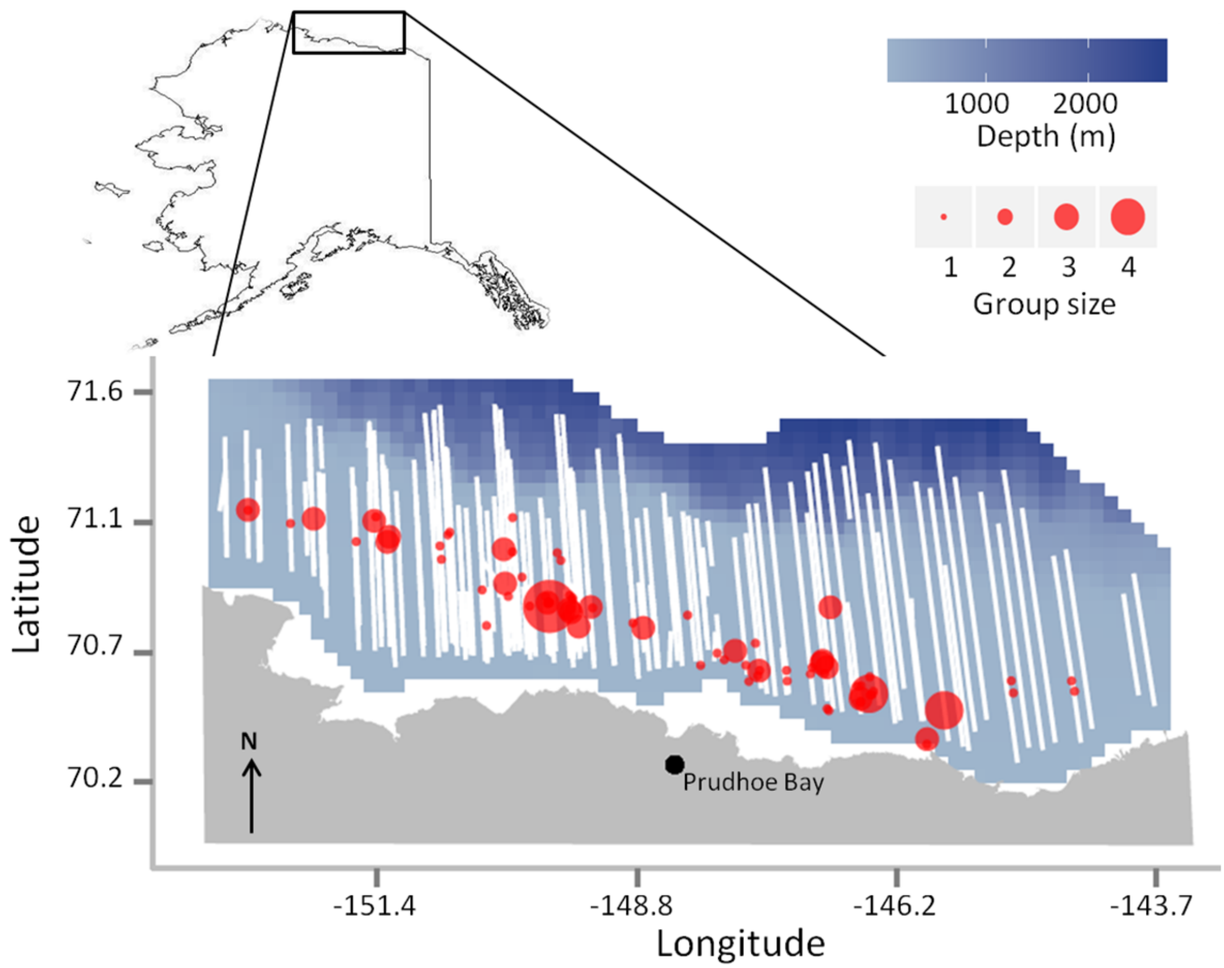

Figure 4.1 Aerial surveys conducted over the southern Alaskan Beaufort Sea 25 August to 10 October 2008. The usable transect lines are depicted by the white lines while sightings of non-calf bowhead whales are shown by the red circles. The size of the circle corresponds with the recorded group sizes of 1 to 4 whales. Depth within the study area is also shown on a gradient scale (0-2500 m); the majority of the study area is on the continental shelf—shown in lighter blue while the continental slope is shown by the darker blue.

Data analysis

Survey data collected from 25 August onward were selected for analysis because it is when the majority of the Bering-Chukchi-Beaufort population of bowhead whales migrate west through the southern Beaufort Sea. Only data considered as 'on transect' were selected. This included sighting and effort data collected while the aircraft was level and flying pre-determined north-south transect lines at the standard survey speed and altitude (Funk et al. 2010). To minimize the impact of poor sighting conditions (e.g. high sea states, glare and low-lying cloud), the sighting and effort data were filtered so that only data that met the following criteria were retained for analysis. Useable sighting conditions included those where the Beaufort wind force was four or less, glare covered 30 % or less of the viewing area and the overall sightability was subjectively described as excellent to moderately impaired by observers (Table 4.1, Funk et al. 2010). Filtering the data to meet these strict criteria reduced the impact of poor sighting conditions on subsequent analyses of the data.

I used a 3-step process to predict bowhead whale density within the study area following a distance sampling methodology (Buckland et al. 2001, Thomas et al. 2010, Miller et al. 2013a). The first step involved fitting a detection function to the bowhead whale sighting data. The detection function model was then expanded into a spatial model that investigated the importance of a set of spatial and temporal covariates in relation to bowhead sightings. Finally, the results of the spatial model were used to predict a 2-D density surface for bowhead whales across the study area.

Table 4.1 Sighting and environmental covariates considered for the detection function model and for the DSM model fitted to the 2008 bowhead whale sighting data. Ice % was not included in either model due to all sightings occurring in open water conditions with no ice present**.**

Model	covariate	scale
Detection function	Beaufort wind force	BF scale 0-7
	Sightability	Excellent – moderately impaired
	Half month	25-31 Aug, 1-15 Sep, 16-30 Sep, 1-10 Oct
	Perpendicular Distance	meters
	Group size	
Density surface model		
	Water depth	Meters, log transformed
	Distance from shore	Meters, square root transformed
	Half month	25-31 Aug, 1-15 Sep, 16-30 Sep, 1-10 Oct
	Latitude	Meters – easting*
	Longitude	Meters - easting

*Geographic Cartesian coordinate for longitude in meters (m), where coordinates have been projected in NAD83/Alaska Albers projection.

Step 1: Detection function modeling

Distance sampling models were fit to sighting data collected by both primary and secondary observers, to estimate the detection function $g(x)$ of detected bowhead whales at distance x from the transect line. Standard distance sampling methods assume that all animals at the surface are observed on the transect center line. However, animals are harder to detect with increasing distance from that center line (Buckland et al. 2001, Thomas et al. 2010). A fitted detection function allows the proportion of animals missed by the survey for this reason to be estimated.

I considered both conventional (CDS) and multiple covariate (MCDS) distance sampling models for the detection function model. Conventional models incorporate heterogeneity and are considered pooling robust when many factors may affect detectability (Marques & Buckland 2004, Thomas et al. 2010)—while multiple covariate models account for heterogeneity by allowing covariates to be included into the detection function model (Marques & Buckland 2004). Covariates considered likely to influence the detectability of bowhead whales included group size, Beaufort wind force, and overall sightability. Ice percentage and glare are also assumed to influence detectability (Givens et al. 2010), but were not considered because all whale sightings in 2008 occurred in ice-free conditions and glare was considered in our overall sightability. Prior to model fitting, I examined the covariate data using methods recommended by Zuur et al. (2010). I investigated outliers with Cleveland dotplots, and identified collinearity between covariates with Pearson's correlation coefficients and variance inflation factor (VIF) values (Zuur et al. 2010). I found sightability and Beaufort wind force were collinear (Pearson's correlation coefficient = 0.7). I therefore retained Beaufort wind force and dropped sightability from further consideration to avoid issues with multicollinearity and to minimize model performance issues (Zuur et al. 2010). Variables considered to affect detectability included Beaufort wind speed, group size and half-month time period.

Detection function models were fit to sighting data collected by primary and secondary observers that were coded as On-transect using the R Package 'Distance' v 0.7.3 (Miller 2013, R Core Team 2013). A total of 93 sightings of 131 whales were available to fit the model. The use of primary and secondary observer sightings allowed me to maximise the sighting data available to me as >40 sightings are recommended for fitting a detection function in distance (Buckland et al. 2001). These sightings included both non-calf bowhead whales (classified as all subadult and adult whales without a dependent calf) and bowhead cows with a dependent calf. Two candidate detection function models were considered—the half-normal key function (eqn. 4.1), and the hazard rate key function (eqn.4.2),

$$g(x) = exp^{\left(-x^2/2\sigma^2\right)} \qquad 4.1$$

$$g(x) = 1 - exp^{\left[-(x/\sigma)^{-\beta}\right]} \qquad 4.2$$

where x is the perpendicular distance from the transect line and σ is the scale parameter, whereas the hazard rate key function contains an additional parameter (β) which defines the shape of the detection function (eqn. 4.2) (Buckland et al. 2001).

Aerial survey sighting data often require some left truncation in the absence of a window that allows the transect line to be observed directly. Investigation of several possible left truncation distances determined that the fitted detection function model for my sighting data remained robust with no left truncation. However, a right-truncation (based on where the detection probability fell below 10 %; Buckland et al. 2001) was required and resulted in my excluding all sightings further than 2000 m from the transect line. Akaike Information Criterion (AIC, Burnham & Anderson 2002), and visual inspection of the detection function histograms were used to assess model fit (Buckland et al. 2001, Thomas et al. 2010). AIC scores were computed over all candidate models, and the model with the smallest AIC score and realistic detection function was selected as the best model. This model was incorporated into the subsequent spatial model.

Step 2: Density surface modeling

The presence of potentially detectable air-gun activity in areas coinciding with regions where an aerial survey was flown on a given day was determined from 38 Directional Autonomous Seafloor Acoustic Recorders (DASARs), distributed in 6 separate groups across the study area for the duration of the 2008 survey season (Blackwell et al. 2013, Fig. B1). All but two surveys flown from 25 August to 11 October were conducted where air-gun activity was detected by the DASARS and assumed to be audible to nearby bowhead whales. Therefore, only those surveys where air-gun activity was assumed to be detectable to whales were retained for analysis, because one of the excluded surveys occurred on the 11 October, models were only fit to data collected until the 10 October. Some of the surveys included, however, may have had relatively low levels of seismic sounds that originated from outside of the study area or from arrays within the study area that were operating at reduced power. Transect lines were divided into segments of length l_j (based on combined two-minute time periods) used by observers to record environmental effort data during each survey (Funk et al. 2010). This resulted in 730 segments averaging a length of 14.26 km, and ranging from 7.03 km to 21.64 km. Bowhead whales were detected in 45 (6.16 %) segments, although neither abiotic nor biotic conditions varied appreciably within any given segment (Hedley & Buckland 2004, Miller et al. 2013a). Using only sightings recorded by a primary observer within 2000 m of the transect line when air-gun activity was presumably audible to the whales resulted in 65 sightings of 92 whales being available for spatial analysis. Of these sightings, only 6 were of mother-calf pairs. Given that the behaviour of cows with dependent calves differs from that of other whales, I chose to avoid the potentially confounding issues related to influence of a dependent calf and only fit the models to the remaining 59 sightings of 80 non-calf whales (Fig. 4.1).

Whale sighting data were also categorized by activity state. Whales were classified as feeding or travelling based on a combination of data recorded at the time of the sighting. These included behaviour, orientation and swim speed. Whales recorded as swimming at medium to fast speed with a westerly orientation were classified as travelling, while whales observed with easterly orientations, moving slowly or not at all, with mouths open when they surfaced, or with mud streaming from their mouth or their body were classified as feeding (Würsig et al. 1985, 1989, Koski et al. 2009).

Spatial and temporal covariate data assumed to influence the location of the whales were summarized for each segment (Table 4.1). Covariate data associated with each segment included depth, distance to shore, half month, latitude and longitude. The average water depth for each segment midpoint was calculated using bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO 2003), while distance to shore, latitude and longitude for each segment midpoint were determined using ArcMAP 9.3 (ESRI 2008). The survey season was divided into four time periods: 25–31 August, 1–15 September, 16–30 September and 1–10 October.

Prior to model fitting, covariate data were subjected to the same exploratory analysis as detailed in the modelling of the detection function in Step 1. Water depth and distance from shore were collinear (Pearson's correlation coefficient = 0.9) and latitude also presented evidence of collinearty with both distance from shore and depth. Therefore, both latitude and distance from shore were dropped from further consideration in the model to avoid multicollinearity. Three final variables were considered for inclusion in the model: water depth (log-transformed to improve the spread of the data), longitude (standardized to easting, in meters) and half-month time period. Ice % was not considered for inclusion in the model because no ice was present on the majority of surveys in 2008 and no bowhead whale observations were recorded in the presence of ice.

I fit the spatial model using the 2-step count method proposed by Hedley and Buckland (2004) using the R package 'dsm' v2.0.1 (Miller et al. 2013b). This approach is also referred to as density surface modelling (Miller et al. 2013a). The number of whales per segment n_j, of contiguous transect was modeled within a Generalized Additive Model (GAM) framework as a function of spatial and temporal covariates, z_{ik}, where z_{ik} is the value of the kth covariate in the i^{th} segment (Hastie & Tibshirani 1990, Wood 2006, Givens 2009) with the structure (Eqn. 4.3),

$$E(n_i) = \hat{p}_i A_i exp[\beta_0 + \sum_k f_k(z_{ik}) + z_{ik}] \qquad 4.3$$

where f_k are smooth functions of the covariates and β_0 is the intercept term (Miller et al. 2013a). Segment area A_i multiplied by the probability detection function, $\widehat{p_i}$ modelled in step 1, gives the effective area for segment *i* (Thomas et al. 2010, Miller et al. 2013a), and is included in the model as an offset term.

A Tweedie distribution, in which variance is proportional to some power of the mean was used to account for the zero-inflated count data (Jørgensen 1987, Shono 2008, Williams et al. 2011, Miller et al. 2013a). The Tweedie distribution is a flexible and straight forward method of modelling count data when there are a high proportion of zeros in the data (Miller et al. 2013a).

Smoothness selection was by REML (Restricted Maximum Likelihood). The objective function optimized by REML has more pronounced optima than methods such as Generalized Cross Validation/AIC, so models tend to be estimated more accurately (Wood 2006, 2011). I fit the model in a forward step-wise manner and the decision whether to retain a term or drop it from further consideration was based on examining the approximate p-values of each term, the AIC score (where possible), and the randomized quantile residual plots. AIC scores could only be compared when candidate models were fit with a combination of the same fixed effects. Once the smooth functions of the continuous covariates were selected, the value of the Tweedie parameter (θ) was assessed using quantile residual diagnostic plots generated from the qres function in the 'statmod' package in R (Dunn & Smyth 1996, Smyth et al. 2013). Visual inspection of residual plots for different values of θ is thought to be adequate as overall results are usually not very sensitive to θ (Williams et al. 2011). Finally, temporal and spatial residual autocorrelation were investigated using variograms and bubble plots.

Step 3: Density prediction and variance estimation

Correction factors for availability bias (Marsh & Sinclair 1989, Laake & Borchers 2004) were incorporated into the selected density surface model, fit to only the non-calf sighting data, by dividing the predicted density of each grid cell by the correction factor. The correction factor for the availability bias [*a(x)*] of non-calf bowhead whales exposed to seismic operations in the autumn was chosen because only surveys conducted during the autumn during which bowhead whales would have been exposed to air-gun activity were considered in the density surface model DSM. The correction factor values were from Chapter 3 (Table 4.2), and were calculated from Eqn 4.4,

$$a(x) = \frac{s}{s+d} + \frac{d\left[1-e^{\left\{-t(x)/d\right\}}\right]}{s+d} \qquad 4.4$$

where *s* is the mean surface time and *d* is the mean dive time of a bowhead whale, and *t(x)* is the average time that a patch of sea surface is in the view field of the observer (Chapter 3). A prediction grid divided into 5 km^2 grid cells was created in Quantumn GIS 1.8.0 (QGIS 2004) to encompass the study area and

Table 4.2 Availability bias correction factors for foraging and travelling non-calf bowhead whales and all non-calf whales in the autumn for both undisturbed whales and those exposed to seismic. Correction factors were calculated in Chapter 3, though here a correction factor that combines all foraging whales regardless of depth has been calculated.

Category	Undisturbed *a(x)*	Seismic *a(x)*
Autumn	0.18	0.11
Foraging	0.20	0.16
Travelling	0.15	0.12

values for each explanatory variable retained in the final model were generated for the midpoint of each grid cell. The availability bias-corrected model was used to predict the number of whales in each 5 km^2 grid cell of the study area resulting in a 2-D density surface of whales. Variance estimation followed the variance propagation method detailed in Williams et al. (2011) and was incorporated into the R-package 'dsm' (Miller et al. 2013a, 2013b). This method incorporated the uncertainty in the estimation of the detection function into the variance of the spatial model (Williams et al. 2011, Miller et al. 2013a) and is considered computationally efficient and comparable to bootstrap equivalents (Miller et al. 2013a).

Following the same prediction procedures detailed in Part 3, the effects of variable availability related to the presence of seismic operations was assessed by comparing prediction grids generated from the use of availability correction factors based on the behaviour of presumably undisturbed non-calf whales in the autumn to predictions corrected for the variable behaviour of non-calf whales exposed to seismic operations in autumn (Table 4.2, Chapters 2 & 3).

The density surface modelling and prediction steps were repeated for feeding non-calf whales and travelling non-calf whales and predicted densities with their associated variance were estimated. The effects of variable availability related to presumed exposure of whales to seismic operations was assessed by again comparing the predicted densities corrected for variable behaviour of presumably undisturbed non-calf whales to those predicted densities that were corrected for the variable behaviour of whales in the presence of seismic operations.

Results

Density Surface models revealed that bowhead whales were distributed nearshore in an area where seismic survey operations occurred in the southern Beaufort Sea in autumn 2008 (Fig. 4.3 & 4.4). They also showed some spatial segregation of the whales by activity state (i.e., whether travelling or feeding, Fig. 4.7). Correcting for variable detectability associated with the presence of seismic operations resulted in density predictions ranging from 25-64% higher than predictions which only corrected for the variable detectability of whales that were not exposed to sounds from any type of industrial activity (Fig. 4.4, Table 4.10 & 4.11).

Detection function

A pooling robust conventional distance sampling model with a half-normal key function and no adjustment terms was selected as the best model through AIC and visual inspection of the detection curves (Table 4.3, Fig. 4.2). None of Beaufort wind force, group size, or half-month in multiple covariate distance sampling models improved the fit of the detection function (Table 4.3).

Density surface model predictions of densities of non-calf bowhead whales

Two candidate models were considered after forward stepwise selection. Model 1 had a lower AIC (Table 4.4) and was selected as the better model. Smoothed functions of depth (log transformed) and longitude (easting), and the factor half-month time period were all important in explaining the numbers of bowhead whales in each segment (Table 4.5, Fig. 4.3 & Appendix C1). The model suggested that the whales had an apparent preference for shallower depths instead of deeper slope waters. Higher numbers of non-calf whales were predicted for late August and early September with numbers decreasing through late September and into October. Examination of model residuals revealed no serious issues with temporal or spatial correlation.

Table 4.3 Summary of detection function models fitted to the 2008 bowhead whale sighting data. The models are sorted from best to worst, as classified by AIC and AIC differences, Δ_i.

Model	AIC	Δ_i
half-normal	1368.21	0.00
half-normal + Beaufort + ½ month	1368.53	0.32
hazard rate + Beaufort	1368.77	0.56
hazard rate	1368.91	0.70
half-normal + Beaufort	1369.36	1.15
half-normal + ½ month	1369.79	1.58
hazard rate + group size + Beaufort	1369.82	1.61
half-normal + group size	1370.17	1.96
hazard rate + Beaufort + ½ month	1370.37	2.16
half-normal + group size + ½ month + Beaufort	1370.51	2.30
hazard rate + group size + ½ month + Beaufort	1371.11	2.90
half-normal + group size + Beaufort	1371.32	3.11
half-normal + group size + ½ month	1371.69	3.48
hazard rate + ½ month	1371.93	3.72
hazard rate + group size + ½ month	1372.43	4.22

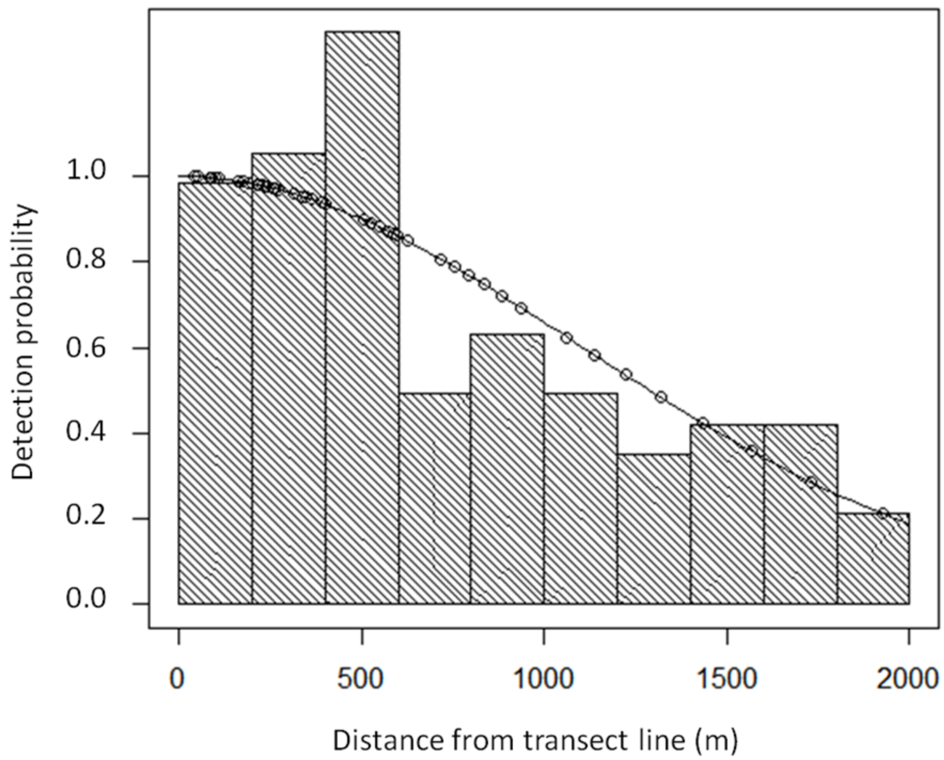

Figure 4.2 The fitted detection function for the selected best distance sampling model for sightings of bowhead whales collected during aerial surveys in the southern Alaskan Beaufort Sea in 2008. The best selected model was a pooling robust conventional distance sampling (CDS) model with a half-normal key function and no adjustment terms.

Predicted densities of non-calf bowhead whales

The predicted densities indicate that non-calf whales were concentrated in the central southeast portion of the study area toward Camden Bay, but were present in much lower densities in the southwest region of the study area (from Prudhoe Bay into Harrison Bay), with the exception of a small area of higher densities on the extreme western edge of the study area (Fig. 4.4, panel B). The estimates of relative abundance, their associated variances and the mean and maximum whale density per 5 km^2 grid cell are summarized by half-month time period in Table 4.6. The highest densities of whales were predicted for late August with densities decreasing through September and into October when the lowest densities of whales were predicted (Fig. 4.4, panel B). Whales appeared to be concentrated in the nearshore waters with little or zero densities predicted in the deeper slope waters (Fig. 4.4, panel B).

Table 4.4 Candidate models for predicting densities of non-calf bowhead whales in the southern Alaskan Beaufort Sea late August to early October 2008**.**

Candidate models	**AIC**	**θ**
1) N~ s(log(depth)) + factor(half.month) + s(easting)	1012.56	1.2
2) N~s(log(depth)) + s(easting) * factor(half.month)	1020.59	1.2

Table 4.5 Density surface model results for the general density of non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Significant relationships are in bold. 730 segments of useable effort and 59 sightings of 80 bowhead whales were available for the model.

Parametric Coefficients	Estimate	se	p-value
Intercept	**-19.538**	**1.322**	**< 0.0001**
Half month (August 25-31)			
September 1-15	-0.394	0.262	0.132
September 16-30	**-0.972**	**0.253**	**0.0001**
October 1-10	**-1.798**	**0.422**	**<0.0001**
Approx. Significance of smooth terms	edf	Ref. df	p-value
s(log(depth))	**2.631**	**3.168**	**< 0.0001**
s(easting)	**4.021**	**5.098**	**< 0.0001**
N		730	
R-squared (adjusted)		0.04	
REML Score		279.20	
Deviance explained		25.4%	

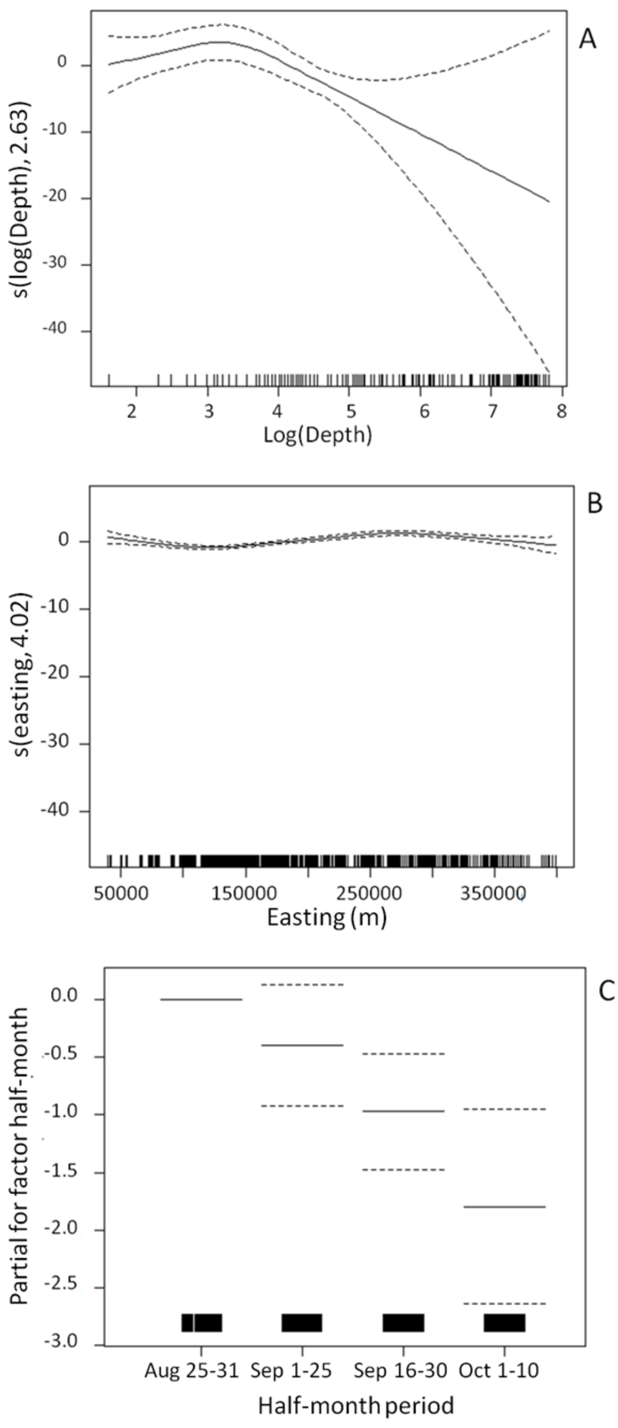

Figure 4.3 Significant smoothed functions for the variables depth, on a log-transformed scale, on 2.63 degrees of freedom (plot A) and longitude, on a standardized easting scale, on 4.02 degrees of freedom (plot B). These plots indicate that higher numbers of non-calf bowhead whales in the autumn of 2008 occurred in depths of around 25-55 m and that slightly more whales were towards the east of the study area. Plot C for the factorial covariate half-month time period shows a clear decrease in the numbers of whales as the season progressed from 25 August to 10 October 2008. The locations of data points are shown along the x-axis by the tick marks and the dotted lines represent the variance as two *se* above and below the fitted smooth functions (Plots A & B) and estimates (Plot C).

Table 4.6 Predicted relative abundance, associated standard errors and CVs, and mean and maximum densities of non-calf bowhead whales exposed to air-gun pulses within the survey area for each half month time period for 2008.

Time Period	*estimate*	*se*	*CV*	*95%CI*	*mean density/5km^2*	*max density/5km^2*
August 25-31	1663	413	0.25	1030-2685	1.0	9.4
September 1-15	1121	223	0.20	762-1648	0.7	6.0
September 16-30	629	99	0.16	463-854	0.4	3.5
October 1-10	275	112	0.41	128-595	0.2	1.6

Table 4.7 Density surface model results for feeding non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Significant relationships are in bold. 730 segments of useable effort and 30 sightings of 41 non-calf whales were available for the model.

Parametric Coefficients	**Estimate**	**se**	**p-value**
Intercept	**-25.131**	**2.289**	**< 0.0001**
Approx. Significance of smooth terms	edf	Ref. df	p-value
s(log(depth))	**2.437**	**2.857**	**< 0.0001**
s(easting)	**4.286**	**5.258**	**< 0.0001**
R-squared (adjusted)		0.06	
REML Score		134.89	
Deviance explained		45%	

Predicted densities for feeding non-calf bowhead whales

For feeding whales, the best model included only the smooth functions of depth (log transformed) and longitude (easting) (Table 4.7, Fig 4.5 & Appendix C2). Densities of feeding non-calf whales were predicted to occur in the study area after correcting for variable availability of feeding non-calf whales in the presence of seismic operations ($a(x)$ = 0.16). The 2-D density surface indicates that the whales were predominantly feeding in the southeastern part of the study area with the exception of a small region at the far western edge of the study area (Fig. 4.7, plot B). There were few if any feeding whales in the central and southwestern portions of the study area (Fig.4.7, plot B). The maximum predicted density within the survey area was 4.1 whales/5 km^2 grid cell, while the mean density predicted across the study area was 0.2 whales/5 km^2 grid cell (Fig. 4.7, plot B). A total of 366 feeding non-calf whales (se = 47, CV = 0.13, 95% CI = 285–469) was estimated (Table 4.8) for the survey area shown in Fig. 4.7.

A **B**

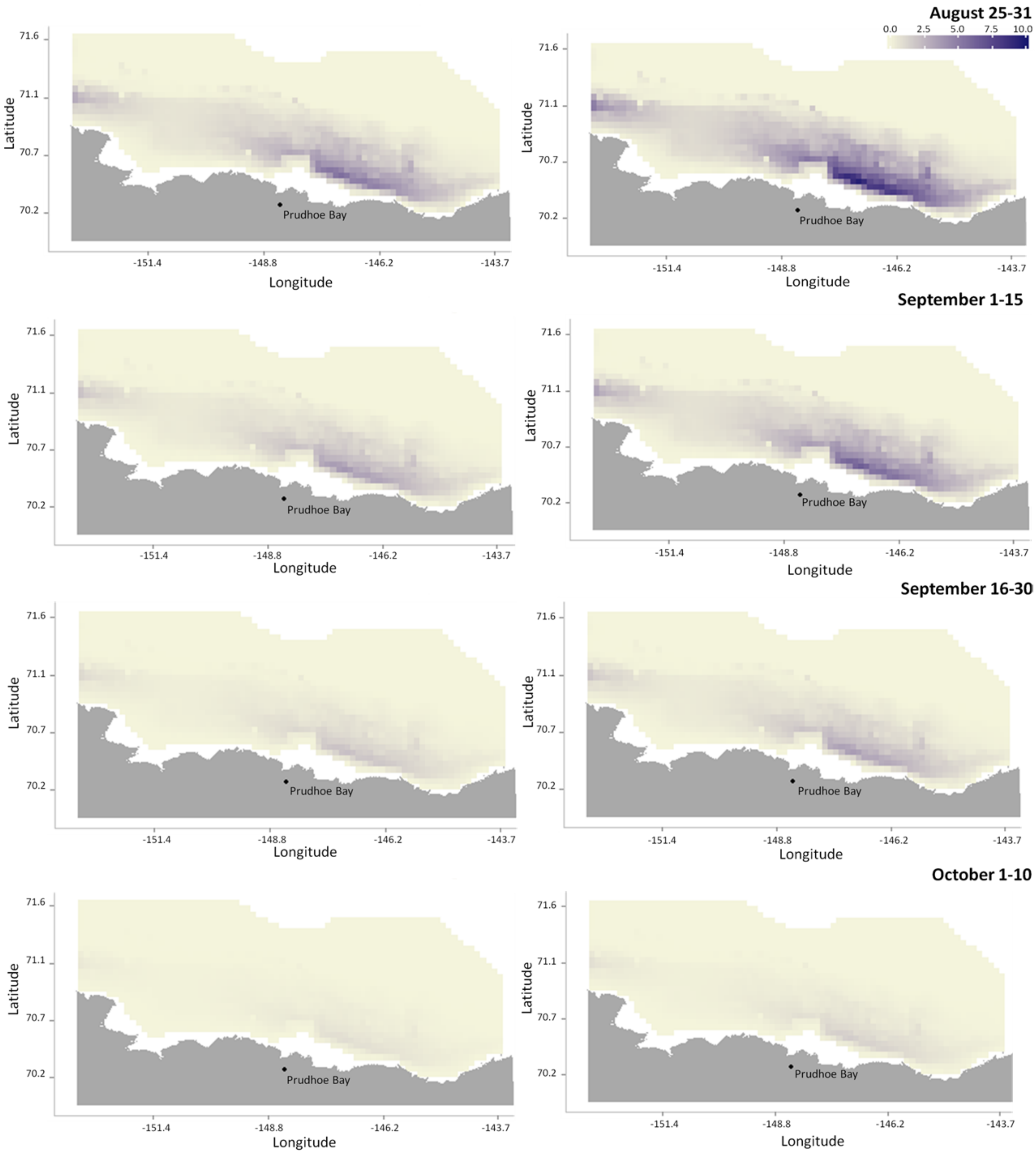

Figure 4.4 Predicted densities for non-calf bowhead whales in the southern Alaskan Beaufort Sea, 25 August to 10 October 2008. Plots in Panel A have been corrected for availability bias for undisturbed bowhead whales while density plots in Panel B have been corrected for the availability bias of non-calf whales exposed to seismic survey operations. All plots in this figure have been produced on the same scale as that shown at the top of Panel B.

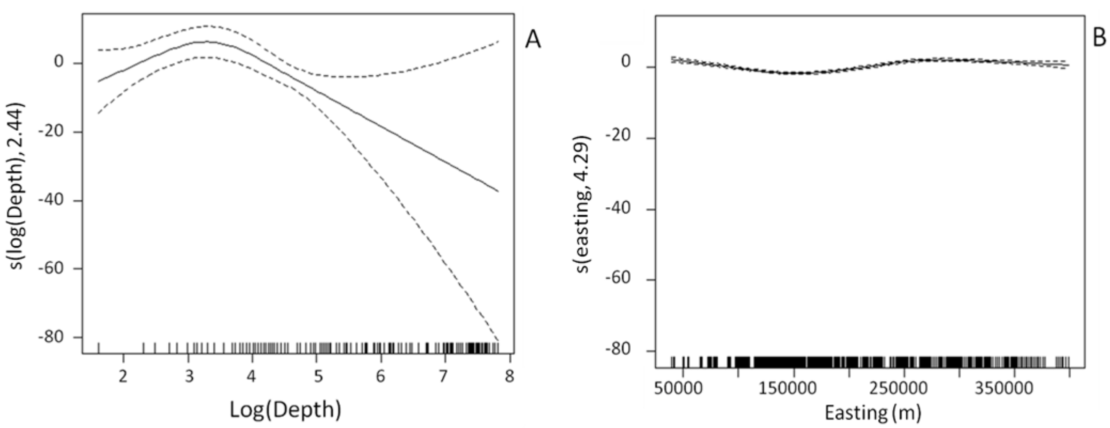

Figure 4.5 Significant smoothed functions for depth on a log transformed scale, on 2.44 degrees of freedom (plot A), and longitude (plot B), on a standardized easting scale, on 4.29 degrees of freedom for foraging non-calf bowhead whales in the Southern Beaufort Sea, 25 August – 11 October 2008. The plots predict that numbers of feeding whales are highest at depths of 25-55 m, and that numbers of whales are lower for the central west region of the study area. The locations of data points are shown along the x-axis by the tick marks and the dotted lines represent the variance as two *se* above and below the fitted smooth functions (Plots A & B).

Predicted densities for travelling non-calf bowhead whales

For travelling non-calf whales, the best model included smooth functions depth (log transformed) and longitude (easting)—and also the factorial covariate half-month (Table 4.9, Fig 4.6 & Appendix C3). Densities of travelling non-calf whales were predicted in the study area for each half-month period, except 1–15 September. Densities of travelling non-calf whales were predicted in the study area after correcting for variable availability of travelling non-calf whales in the presence of seismic operations (*a(x)* = 0.12) (Fig. 4.7, plot D). Estimates of relative abundance, their associated variances and the mean and maximum whale density per 5 km^2 grid cell by half-month period (Table 4.8) varied from those for feeding non-calf whales. Travelling whales were predicted to have occurred in the central southwest region of the study area from Prudhoe Bay into Harrison Bay, while feeding whales were predicted to have occurred east of there. When averaged across the season the predicted densities of travelling whales were similar to those for feeding whales, but much lower densities were predicted for later in the season in late September and early October (Table 4.8). The maximum density predicted for travelling non-calf whales was 2.0 travelling whales/5 km^2 grid cell, while the mean density across the study area ranged from 0.4 travelling whales/5 km^2 grid cell in late August to 0.1 travelling whales/5 km^2 grid cell in early October (Fig. 4.7, plot D). These results, combined with those for feeding whales, suggest that non-calf whales did not feed in the central southwest region of the study area in 2008, but rather travelled through the area.

Table 4.8 Predicted relative abundance, associated standard errors and CVs, and mean and maximum densities of feeding and travelling non-calf bowhead whales exposed to air-gun pulses within the survey area. Predictions for feeding whales are for the period 25 August-10 October 2008, while predictions for travelling whales were generated for each half month time period. Whale presence was not predicted for the time September 1-15 as no travelling whales were recorded during this period in the study area in 2008.

	estimate	*se*	*CV*	*95%CI*	*mean density/5km²*	*max density/5km²*
Feeding whales	366	47	0.13	285-469	0.2	4.1
Travelling whales						
August 25-31	542	128	0.23	360-873	0.4	2.0
September 1-15	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
September 16-30	248	48	0.19	171-361	0.2	0.9
October 1-10	129	47	0.36	65-256	0.1	0.5

Table 4.9 Density surface model results for travelling non-calf bowhead whales in the southern Alaskan Beaufort Sea, late August to early October 2008. Data from the period 1-15 September were excluded from the model as no whales were sighted during this time. Significant relationships are in bold. 561 segments of useable effort and 29 sightings of 39 non-calf whales were available for the model.

Parametric Coefficients	**Estimate**	**se**	**p-value**
Intercept	**-18.595**	**0.427**	**< 0.0001**
Half month (August 25-31)			
September 1-15	*NA*	*NA*	*NA*
September 16-30	**-0.815**	**0.244**	**0.0009**
October 1-11	**-1.472**	**0.367**	**< 0.0001**
Approx. Significance of smooth terms	edf	Ref. df	p-value
s(log(depth))	**2.204**	**2.831**	**0.001**
s(easting)	**2.572**	**3.280**	**< 0.0001**
R-squared (adjusted)		0.02	
REML Score		149.74	
Deviance explained		22.5	

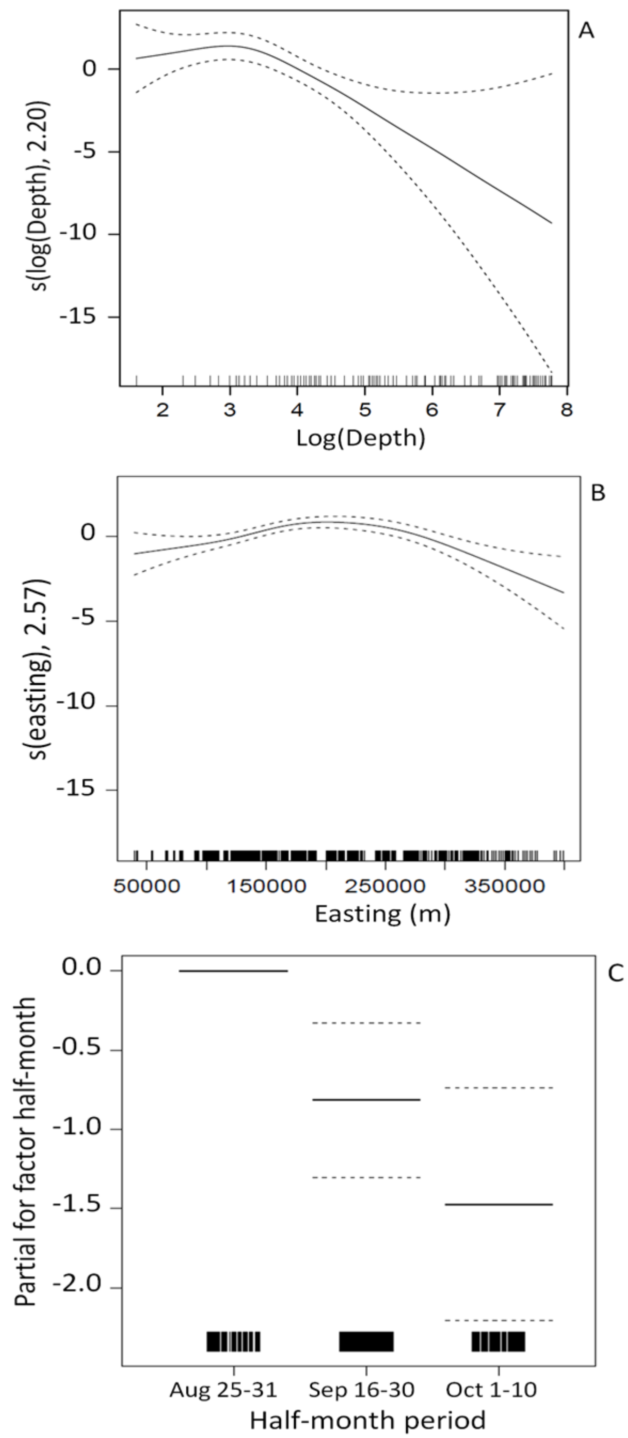

Figure 4.6 Significant smoothed functions for the variables depth, on a log-transformed scale, on 2.20 degrees of freedom (plot A) and longitude on a standardized easting scale, on 2.57 degrees of freedom (plot B) for travelling non-calf whales. These plots indicate that higher numbers of bowhead whales occurred in depths of around 30-50 m and in the central area of the study area. Plot C for the factorial covariate half-month time period shows a decrease in the numbers of whales as the season progressed from late August into early October in 2008. The locations of data points are shown along the x-axis by the tick marks and the dotted lines represent the variance as two *se* above and below the fitted smooth functions (Plots A & B) and estimates (Plot C).

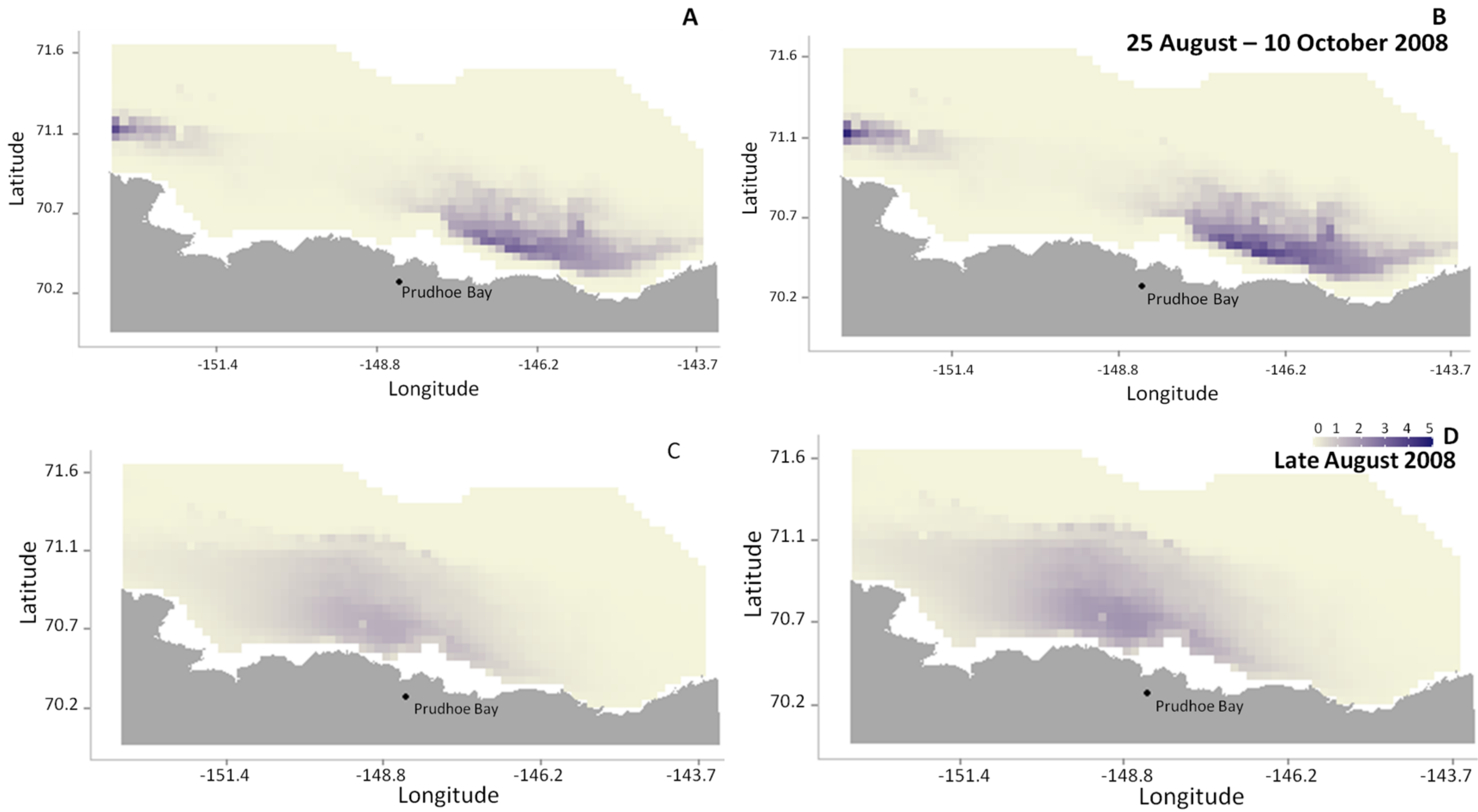

Figure 4.7 Predicted densities of feeding non-calf bowhead whales across the study area during the period 25 August – 10 October 2008; and for travelling non-calf whales in the study area in late August 2008. Variable behaviour for undisturbed feeding non-calf whales and undisturbed travelling whales have been accounted for in plot A and C, while changes in behaviour for feeding non-calf whales exposed to seismic operations have been accounted for in plot B, and changes in behaviour for travelling non-calf whales exposed to seismic operations have been accounted for in plot D.

Table 4.10 Predicted relative abundance, associated standard errors and CVs of non-calf bowhead whales for each half month period in an area of the southern Alaskan Beaufort Sea ensonified by seismic operations in 2008. Predictions on the left have not been corrected for variable behaviour due to the presence of seismic operations while predictions on the right have been corrected for the variable behaviour of whales exposed to seismic operations.

Non Calves	a(x) = undisturbed whales				a(x) = potentially disturbed				% change
	estimate	*se*	*CV*	*95% CI*	*estimate*	*se*	*CV*	*95% CI*	
August 25-31	1016	250	0.25	631-1636	1663	413	0.25	1030-2685	
September 1-15	685	135	0.20	468-1003	1121	223	0.20	762-1648	
September 16-30	384	59	0.15	285-519	629	99	0.16	463-854	
October 1-10	168	69	0.41	78-363	275	112	0.41	128-595	
Total	2253				3688				64

Comparison of densities with corrections for disturbed and non-disturbed whales

Not accounting for changes in surface and dive behaviours that occur in the presence of seismic survey operations results in the densities and abundance estimates of numbers of whales in the study area being lower and the general distribution of whales being more restricted to inshore waters (Table 4.10 and Fig. 4.4). The predicted densities that account for changes in behaviour due to exposure to seismic indicate that non-calf whales were more widely distributed across the southern region of the study area with higher densities occurring to the southeast, towards Camden Bay. Similar results were seen for feeding whales (Table 4.11, Fig.4.7, plots A & B) and for travelling whales (Table 4.11, Fig.4.7, plots C & D).

In summary, the models predicted a nearshore distribution of bowhead whales in the southern Alaskan Beaufort Sea in autumn 2008, regardless of ongoing seismic survey activities. Bowhead whales occurred in higher densities in the Camden Bay area, which was close to the main seismic survey, during the September and early October periods, and at lower densities from Prudhoe Bay into Harrison Bay―a region in which travelling whales were predicted to occur. Density predictions were found to be influenced by variations in whale behaviour associated with the presence of seismic operations.

Table 4.11 Predicted relative abundance, associated standard errors and CVs of feeding and travelling non-calf whales in an area of the southern Alaskan Beaufort Sea ensonified by seismic operations in 2008. Predictions on the left have not been corrected for variable behaviour due to the presence of seismic operations while predictions on the right have been corrected for the variable behaviour of whales exposed to seismic operations.

Non Calves	a(x) = undisturbed whales				a(x) = potentially disturbed				% change
	estimate	*se*	*CV*	*95% CI*	*estimate*	*se*	*CV*	*95% CI*	
Feeding whales	293	37	0.12	229-374	366	47	0.13	285-469	25
Travelling whales									
August 25-31	448	102	0.23	289-696	542	128	0.23	360-873	
September 1-15	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	
September 16-30	198	38	0.19	137-287	248	48	0.19	171-361	
October 1-10	103	37	0.36	52-204	129	47	0.36	65-256	
Total travelling	749				937				27

Discussion

This chapter highlights the influence of whale behaviour on density assessments of bowhead whales in the vicinity of seismic operations and suggests that the numbers of whales potentially exposed to different levels of seismic sound have been underestimated in previous analyses. Applying availability correction factors to account for changes in behaviour while in the presence of seismic operations resulted in higher estimated densities.

My analysis further suggests that whales were widely distributed and not displaced within the area presumed to be ensonified in 2008—contrary to the large scale avoidance previously believed to have occurred for bowhead whales exposed to seismic sounds during the fall migration period (Richardson et al. 1999). My results are not inconsistent with smaller scale displacement observed by earlier studies in the Alaskan Beaufort Sea in autumn (Ljungblad et al. 1988) and Canadian Beaufort Sea in summer (Richardson et al. 1987, Miller et al. 2005) because the scale of my analysis (5 km^2) did not allow me to evaluate small scale movements such as those described in the latter studies. Accounting for variable behaviour would improve accuracy of localized abundance estimates for whales potentially influenced by seismic operations.

In accounting for the changes in behaviour of whales in the presence of seismic operations, I found that bowhead whales presumably exposed to seismic operations during autumn 2008 were distributed in the nearshore southern Beaufort Sea. My corrected density predictions revealed both temporal and spatial patterns comparable to some previous findings including those that indicate the preference of bowhead whales for shallow shelf waters in light ice years (Moore 2000, Moore et al. 2000, Treacy et al. 2006). Higher densities of whales were predicted to occur in the southeast of the study region and lower densities occurred in the southwest, an area that has previously been noted for its low density (Givens 2009).

Predicted distribution and density of bowhead whales exposed to seismic operations

Bowhead whales exposed to seismic operations in the southern Alaskan Beaufort Sea during autumn 2008 displayed temporal and spatial patterns in their predicted distributions. Higher densities of whales were predicted during the earlier part of the study season, in late August, with predicted densities declining as the season progressed. This temporal pattern is contrary to what was previously illustrated by Miller et al. (2002), who examined distribution and abundance of bowhead whales by depth and geographic area based on aerial survey data collected from 1979 to 2000. Miller et al. (2002) found higher densities of whales in late September and early October than in late August or early September. They also found that abundance was consistently lower in the western portion of their study area (Camden Bay) than areas of the southern Beaufort Sea further to the east towards the US-Canadian border. Acoustic studies of the bowhead migration have revealed pulsed patterns in calling rates with clustering in space and time during the westward migration (e.g. Blackwell et al. 2007) that are also consistent with patterns of whale occurrence described by local whalers (Koski et al. 2005). The half-month time scale of my analyses does not provide the fine-scale temporal detail required to detect the pulsed nature of the migration, though this might be possible should the analyses be performed at finer time scales.

The annual autumn migration of bowhead whales in the western Arctic exhibits clear spatial patterns. Sea ice conditions, water depth, potential prey items and age-group all play important roles in dictating where whales are distributed along their migration corridor in the southern Alaskan Beaufort Sea (Ljungblad et al. 1986, Moore et al. 2000, Koski et al. 2005, Treacy et al. 2006, Koski & Miller 2009). My models highlighted similar spatial patterns with higher predicted densities of whales in the shallow near-shore continental shelf waters of the southern Alaskan Beaufort Sea.

Bowhead whales have shown a preference for nearshore shallow-water habitat during low-ice years (Moore et al. 2000, Moore & Laidre 2006, Treacy et al. 2006). My models supported this finding by predicting higher densities of whales in nearshore shallow shelf waters from August to October in 2008—a year in which the second lowest sea-ice extent occurred since records began in 1979 (Scott 2009). The apparent preference for these nearshore waters in 2008 occurred despite the presence of seismic operations suggesting that there was no major shift offshore in the whales' migration corridor. The bowhead whales were likely influenced by the presence and accessibility of opportunistic food resources in the nearshore waters. Koski and Miller (2009) noted that the more extensive use of nearshore waters in low ice years likely reflected the increased accessibility to food resources, and Koski et al.(2008, 2009) and I in Chapter 2, suggested that feeding whales appeared more tolerant of seismic sounds compared to travelling whales. In 2008, some feeding whales observed within the study area appeared to tolerate received levels of seismic sounds up to ~180 dB re 1μPa (rms) (Koski et al. 2009) and showed no evidence of avoidance in areas where seismic sounds were <150 dB. My analysis shows that certain parts of the southern Alaskan Beaufort Sea were more important than others to feeding bowhead whales in 2008 despite the presence of air-gun activity.

The models predicted concentrations of feeding non-calf whales in the Camden Bay area, toward the southeastern region of the study area, as well as an isolated patch on the far western edge of the study area. The eastern Alaskan Beaufort Sea appears to provide important feeding opportunities to whales in years when oceanographic conditions that cause zooplankton to concentrate in nearshore waters off the Yukon coast extend west into Alaska (Thomson et al. 1986, Moore et al. 2000, Richardson & Thomson 2002). It is likely that these conditions also occurred in the southern Alaskan Beaufort Sea in 2008. There were numerous observations of feeding whales from both the aerial surveys and vessels associated with a seismic survey operating in the area in 2008 (Koski et al. 2009) and the results of my models also indicated that the area was used by feeding whales in 2008. Similarly feeding whales were observed in the same region during 2007, also while in the presence of seismic operations (Koski et al. 2008, 2009).

The importance of the western Camden Bay area appears to vary from one year to the next. Recent tagging studies of mostly sub-adult whales, which are the most likely segment of the population to use nearshore habitats (Koski & Miller 2009) suggest that they are not spending significant amounts of time in the Camden Bay area during the autumn, with most of their time in the area spent travelling through it (Quakenbush et al. 2013b), although, two of 13 tagged whales were within the study area for 5 and 6 days. The overall low use of Camden Bay has also been confirmed by recent analysis of movement patterns and core range use of 54 whales tagged from 2006 to 2012 (Citta et al. in press). However, it is apparent from both the observations of feeding whales and from the results of my models that Camden Bay did provide at least some opportunistic feeding opportunities that were exploited by some migrating whales in 2008 despite the presence of seismic operations. There is increasing evidence to suggest that foraging whales will tolerate seismic operations and other human activities (Richardson et al. 1986, Koski et al. 2009, Chapter 2). Other species of foraging whales have also been observed near seismic operations, including gray whales (Gailey et al. 2007, Johnson et al. 2007, Yazvenko et al. 2007) and sperm whales (Madsen et al. 2002, Miller et al. 2009). My results lend further evidence of the apparent tolerance of feeding bowhead whales to seismic operations.

In contrast to feeding whales, the density surface models predicted that whales in the central southwestern region of the study area, from Prudhoe Bay toward Harrison Bay were primarily travelling. This was also the region where I had predicted much lower densities of whales and where previous studies have reported surprisingly low densities of bowhead whales (e.g. Givens 2009). The area of low density predicted by my overall model corresponded clearly with where travelling whales were predicted to have been in 2008. This suggests that the whales were not lingering to feed in the central southwestern region of the study area in 2008. Tagged whales have also been recorded traversing through areas with active industry operations, taking approximately a week to travel through the southern Beaufort Sea (Quakenbush et al. 2013b). From 2006–2012, 83.3 % of tagged whales spent an average of two days in the Prudhoe Bay area. Because it would take whales approximately two days to travel through that area if they did not stop to feed, Quakenbush et al. (2013b) suggested that whales were primarily migrating through this area rather than feeding there.

The propensity for whales to move through an area rather than linger will also influence the numbers of whales detected on surveys. While my results do not indicate any shifts toward deeper offshore shelf and slope waters, there is some evidence to suggest that bowhead whales increase their swim speeds when exposed to seismic sounds (Richardson et al. 1985, 1986, Ljungblad et al. 1988)—and that faster swim speeds results in significantly shorter surface durations and fewer respirations per surfacing event (Chapter 2). While shorter surface durations influence detectability, whales that increase their swim speed will spend shorter periods of time in the survey area—a factor that is also likely to affect detection rates.

Effects of variable availability on bowhead whale density estimates

Variations in bowhead surface and dive behaviours result in underestimates of densities of whales in areas presumably ensonified by seismic survey operations if the appropriate availability correction factors are not used. This chapter demonstrates the importance of incorporating behavioural responses to the presence of human activities into analyses of density and abundance. Earlier analyses of whales exposed to seismic operations are likely to have underestimated the numbers of potentially disturbed whales in areas ensonified by seismic operations by 25 to 64 %, implying that whales are not avoiding these areas on the large scales suggested in previous studies (e.g. Richardson et al. 1999). Studies that have reported avoidance of seismic operations by migrating bowhead whales in the Alaskan Beaufort Sea by up to 30 km based solely on aerial survey data have not accounted for the effects of variable whale behaviour on the sightability of whales around seismic operations. These studies compared distribution during periods without seismic operations to apparent distribution during seismic operations without incorporating corrections for changes in behaviour. My results suggest that the data from these earlier surveys should be re-examined taking account of changes in behaviour that likely occurred between experimental and control periods to determine whether the displacement by travelling whales is as great as has been suggested in the past. My corrected models suggest that feeding whales were widely distributed in the southern region of the study area, with higher densities of whales toward the southeast region despite the presence of air-gun activity, and therefore, avoidance on the previously reported large scales for travelling whales did not occur for feeding whales in 2008. Importantly my results also suggest that there was no obvious offshore displacement of whales away from the coast in 2008—something that has been a primary concern to the local hunters.

The lack of wide-scale avoidance or offshore displacement suggested by my results support recent acoustic evidence that whales continued to utilize areas of the Alaskan Beaufort Sea ensonified by seismic in 2008 (Funk et al. 2010). In 2008, bowhead whale calls were recorded on acoustic receivers throughout the study area (Funk et al. 2010). Blackwell et al. (2013) investigated bowhead calling behaviour in the same region in 2007 and found a statistically significant drop in the detected number of bowhead calls at the onset of seismic airguns in areas where received levels were 116–129 dB re 1μPa, but no change or a slight increase when received levels near the whales were <108 dB re 1μPa. However, deflection was thought to be an unlikely explanation for the drop in calling rates, partly because the whales would not have been able to move out of the area fast enough to account for the changes in calling rates due to their slow swim speeds (Blackwell et al. 2013). Whales may reduce their calling rate and cease to call altogether at the onset of seismic, though the distance or received sound level at which they do this is still under investigation (S. Blackwell pers. Comm.).

Study caveats and considerations for future research.

Aerial surveys were flown to monitor and help mitigate exposure to seismic survey operations in the southern Beaufort Sea in 2006–2008 and in 2010. However I only analyzed data collected in 2008. The 2008 survey season provided the greatest coverage of the survey area as well as the greatest number of sightings. However, limited sightings and variable effort in the other years did not allow me to incorporate yearly variation into my models. Whale distribution during the autumn migration in the southern Alaskan Beaufort Sea is subject to year-to-year variation in relation to ice conditions, prey distribution and availability and natural variation in migration timings (Moore & Reeves 1993, Quakenbush et al. 2013b). 2008 was considered a low ice year and little ice was encountered in the study area when the surveys were flown. As a result, ice presence was not included in my models and all of the whales seen during the 2008 surveys were in open water. Prey data were also not included in the models because data on zooplankton abundance were not available to me. The inclusion of zooplankton data may have helped to further explain why some parts of the study area were apparently more important to feeding whales than others. Presumably, the presence or absence of feeding by bowheads was related to the presence of prey and could thus be considered a surrogate for prey.

I examined the DASAR data (Appendix B1) and determined that seismic sounds would have been audible on all but two of the usable surveys available to me from the 2008 industry aerial surveys. I was therefore unable to investigate how whale distribution and density might differ in the absence of air-gun sounds compared to their distribution in the presence of air-gun sounds. Instead I only used those 22 surveys during which whales were presumed to be exposed to seismic sounds, and evaluated bowhead density when the study area was ensonified. My model would have been strengthened by incorporating estimated received sound levels near the whales and investigating the distribution and density of whales in relation to varying sound levels. Including estimated received sound levels would also help to address the lack of control data to validate that whale distribution did not change appreciably in the presence of low and moderate levels of seismic sounds.

Future analyses of these types of aerial survey data would benefit from including covariates that estimate levels of seismic sounds near the whales, biotic variables related to prey presence, other industry activities, and subsistence hunting activities. These covariates would strengthen the predictions provided by the models by incorporating yearly variation and might also help explain why whales occurred in higher densities in the southeast of the study area, but in much lower densities in the central-southwest during 2008.

Future studies investigating the impacts of seismic survey operations on bowhead distribution and relative abundance in areas ensonified by seismic sounds would also benefit from incorporating specific behavioural response studies. My analysis incorporated availability correction factors specific to bowhead whales observed in the presence of seismic operations that had their own limitations. The availability correction factors presented in Chapter 3 were calculated using fine-scale behaviour data comprised of surfacing, respiration and dive cycles. These behavioural data were mostly collected opportunistically– particularly behavioural observations of whales near seismic operations. There was little control over where and when observations of whales exposed to seismic occurred, resulting in only approximate information on the highly variable seismic sound levels to which the whales were likely exposed (Chapter 2). The correction factors therefore only account for how whale behaviour varies when seismic is present compared to when it is absent. In all likelihood, the level of response exhibited by whales to seismic sounds is related to both received sound level as well distance to the sound source. Understanding how whales vary their behaviour under different circumstances will enable the distribution and density of whales in areas ensonified by seismic sounds to be better investigated.

Finally, my analyses did not address local fine-scale deflections related to seismic survey operations –which can only be addressed with a larger sample size (currently unavailable), and a finer spatial resolution (which could not be used with the limited data). However, I was able to show that there was no large scale offshore deflection of non-calf bowhead whales in areas of the southern Beaufort Sea with active seismic operations in 2008. In addition, my analysis provided further support for the hypothesis that feeding whales are more tolerant of seismic operations than whales engaged in other activities such as travelling.

Combining bowhead behavioural studies with line-transect aerial survey data and spatial modelling shows how difference in behaviour affects estimates of whale abundance in areas ensonified by seismic sounds. Such information should improve the accuracy of future estimates of abundance and distribution of bowhead whales exposed to seismic operations.

Chapter 5: Conclusions

The main goal of my research was to investigate the influence of seismic operations on dive and surface-respiration behaviour of bowhead whales. I also set out to determine whether behavioural variation influences density analyses of bowhead whales in the Beaufort Sea.

I addressed the question of how exposure to seismic influences whale behaviour by analyzing fine-scale bowhead behaviour data collected in the presence and absence of seismic operations during 1980-2000. I evaluated the question of whether behaviour influences density predictions by applying density surface models, corrected for behavioural variations of whales exposed to seismic operations—and I used bowhead sighting and effort data collected during an industry monitoring aerial survey program for seismic operations conducted in the Southern Alaskan Beaufort Sea in 2008. This approach incorporated standard distance sampling methods into spatial models which provided an effective means of assessing both relative density and distribution of whales in areas ensonified by seismic sounds.

As outlined below, my findings are based on a combination of non-parametric statistics, advanced modeling techniques and distance sampling methodologies—each of which had a number of caveats. My research has relied on a combination of archival behavioural data, experimental survey related data, and industry monitoring aerial survey sighting and effort data. My analysis of bowhead behaviour data using mixed effects models resulted in new insights into the factors that influence bowhead behavioural reactions to seismic operations. Similarly, addressing whale behavioural variation within density analyses provided new insights into how fine-scale behaviour can influence our understanding of habitat use and distribution of whales in areas ensonified by seismic sounds. Throughout my research, I have highlighted the importance of understanding animal behaviour to address questions about the ways in which anthropogenic activities impact bowhead whales. My research leads to new questions needing further study to be answered.

Summary of Findings

In Chapter 2, I used a combination of non-parametric univariate tests and linear mixed effects (LME) models to investigate the effects of seismic survey operations on the dive and surface-respiration (SRD) behaviour of bowhead whales in the Beaufort Sea. In general, I found that the duration of surfacing decreased in the presence of seismic operations—especially for travelling and socializing non-calf whales. The LME models also indicated that dive durations were affected by the presence of seismic operations, but that the effects also depended on such variables as season, activity state and group size. My results highlight the contextual nature of behavioural variations exhibited by bowhead whales in the presence of seismic operations—and draw particular attention to the fact that seismic-induced changes in bowhead SRD behaviour may affect the availability of the whales for visual detection.

In Chapter 3, I assessed the effects of exposure to seismic survey operations on the probability of a bowhead whale being available for visual detection. I did so by calculating availability bias correction factors following methods outlined by Laake et al.(1997), and found that non-calf whales were less likely to be available for detection then other whales while travelling, and that their availability further declined in the presence of seismic operations. I also found that non-calves were also less available to observers during autumn when exposed to seismic operations than when not exposed, regardless of activity. This is the first study to investigate and quantify availability bias of bowhead whales exposed to seismic sounds.

In Chapter 4, I evaluated the influence of behavioural variability on density predictions of bowhead whales. I used an approach that combined distance sampling and spatial modeling methods to fit density surface models, corrected for availability bias. To determine the sensitivity of density estimates to variable availability of bowhead whales related to the presence of seismic operations, I compared predicted densities corrected for differences in behaviour associated with the presence or absence of seismic operations. The model results indicated that bowhead whales occurred in the shallower, nearshore waters—with few if any whales in the deeper slope waters. They also indicated that spatial segregation was related to whale activity in the Southern Alaskan Beaufort Sea in 2008, with higher densities of feeding whales occurring towards Camden Bay, while travelling whales were predicted in much lower densities from Prudhoe Bay into Harrison Bay. Density estimates that accounted for variations in whale behaviour due to seismic operations were as much as 64 % higher than estimates that only accounted for variable behaviour of undisturbed whales. This is the first study to highlight the influence of whale behaviour on predicted densities of bowhead whales in the vicinity of seismic operations—and is the first to suggest that the numbers of whales exposed to different received levels of seismic sound have been underestimated in previous analyses.

Evaluations of Research Hypotheses

My thesis addressed three hypotheses related to the effects of seismic operations on bowhead whale behaviour.

Hypothesis 1: Exposure to seismic operations causes bowhead whales to change their dive and surface-respiration behaviours.

Hypothesis 1 is supported by the results of Chapter 2. This was particularly evident in the results of the LME models, which proved to be a more powerful tool to assess the effects of exposure to seismic operations on bowhead whale behaviour than the univariate statistical tests. While the univariate tests were able to determine that the presence of seismic activities did have significant subtle effects on the surfacing and respiration behaviour of bowhead whales, the LME models determined that there was also an effect of seismic sound on the dive behaviour of whales. As discussed in Chapter 2, the LME models showed that the degree of behavioural change depended on factors such as season, activity states and the number of whales in an observed area. The LME models also accounted for the effects of repeated observations of individual whales and for the confounding effects of other key variables.

Hypothesis 2: The availability of bowhead whales for visual detection during aerial surveys changes when whales are exposed to seismic operations.

Hypothesis 2 is supported by the results of Chapters 2 and 3. In Chapter 2, my analysis of bowhead surface and dive behaviour showed that whales varied their behaviour when exposed to seismic operations. The trend for shorter surface durations and fewer respirations per surfacing, especially in the autumn and for travelling non-calf whales alters an observers' ability to sight whales—as whales can only be seen when they are at the surface. In Chapter 3, I incorporated the mean surface and dive durations of whales (both in the presence and absence of seismic operations) into equations to calculate the probability of whales being at the surface and available to be sighted by visual aerial observers. In most circumstances I found that this probability for whales that were exposed to seismic operations was lower than for whales that were presumed to be undisturbed. For example, it was 0.18 for non-calf whales when undisturbed, but dropped to 0.16 in the presence of seismic activity. There was little effect of seismic activity in summer, but seismic activity during autumn decreased the probability of a whale being at the surface and available to be seen from 0.18 to 0.11. Not accounting for this would have led to underestimating the relative abundance of bowhead whales in the affected area by 64 %. The subtle changes in dive and surface-respiration behaviours (Chapter 2) led to whales exposed to seismic survey activity being generally less available for visual detection during aerial surveys.

Hypothesis 3: Variable availability of bowhead whales due to seismic operations biases density predictions

Hypothesis 3 is supported by the results of Chapters 3 and 4. In Chapter 3, I found that whales were generally less available for detection when exposed to seismic survey operations. The resultant correction factors (Chapter 3) allowed me to assess the effects of variable availability on predicted densities of bowhead whales. I calculated simple percentage changes to evaluate the effect of applying availability correction factors to bowhead whale sighting data collected in the presence of seismic operations. This exercise determined that abundance estimates of whales exposed to seismic operations were up to 64 % higher after correcting for the variable availability of whales exposed to seismic operations.

An analysis of relative density and abundance using aerial survey sighting and effort data collected in the Southern Beaufort Sea was performed in Chapter 4, where I followed distance sampling methods that incorporated spatial modeling using a Generalized Additive Model (GAM) framework, and performed a density analysis for non-calf bowhead whales in an area ensonified by seismic operations in 2008. I found that estimates of density and relative abundance that corrected for the variable availability of whales increased between ~25 % and 64 % compared to those estimates that only accounted for variable behaviour of undisturbed whales.

Importantly, the models revealed that bowhead whales did not appear to be deflected offshore during the autumn of 2008—a concern that has been raised by local subsistence whalers. Instead, whales displayed a nearshore distribution with activity state explaining some of the observed spatial patterns, despite the exposure to seismic operations. Much higher densities of feeding whales were predicted for the Camden Bay area—an area that has been important to feeding whales in the past, while much lower densities of travelling whales were predicted for the central southwestern region of the study area—suggesting that the whales were not lingering in this area but transiting through instead. The analysis (Chapter 4) clearly highlights the influence of whale behaviour on predicted densities of bowhead whales in the vicinity of seismic operations and suggests that the numbers of whales exposed to different levels of seismic sound have been underestimated in previous analyses.

Potential Caveats

In Chapter 2, I combined non-parametric univariate statistical tests with Linear Mixed Effects (LME) models. The univariate Mann-Whitney U test and Kruskal-Wallis test assume independent samples; however, individual whales were often observed more than once during a behavioural observation session. I partly addressed this by acknowledging that the calculated significance levels of the univariate tests were nominal, and I also placed little emphasis on differences with nominal significance levels of $q > 0.01$. My application of LME models to the behaviour data did address the independence issue by including the individual whale as a random factor, but the models may still have overstated the statistical significance to some extent because it was often hard to know whether a whale observed for one or more surfacings was involved in a previously observed surfacing. Future analyses of behaviour data collected from aerial platforms should consider using the behavioural observation session—rather than the individual whale as the random effect. This would ensure that the assumption of statistical independence is more robust, and would also help to address any issues of synchronicity in the behaviours of whales observed in close proximity during the same observation session—something that I was unable to address in Chapter 2.

The LME models explained < 40 % of the variation in the data, due in part to the limitations of the data available to me. I chose to categorize both water depth and group size which may have reduced statistical power; however depth was selected as a significant explanatory variable in all SRD models indicating that I was still able to determine the importance of water depth to explaining variation in bowhead whale SRD behaviours.

The greatest limitation to my evaluation of the effects of seismic survey operations on bowhead whale SRD behaviours stemmed from the limited amount of data available for whales observed in the presence of seismic operations. Often seismic operations were only confirmed with either the observed presence of an active seismic ship near the whales or through the deployment of sonobouys during observation sessions. This resulted in a frequent lack of sound exposure information, which in turn meant that I was unable to incorporate either distance to the sound source or an estimated received level of sound into my analyses. I was therefore restricted to performing a relatively simple analysis based on only whether seismic sounds were present or absent. Despite this limitation, the presence of seismic was a significant explanatory factor in all four SRD models.

The approach that I took to calculate the availability correction factors for bowhead whales exposed to seismic operations was subject to limitations. Environmental, observer, and whale related variables inevitably influence both the time-in-view as well as the overall availability of a bowhead whale for visual detection by an aerial observer. The sampling design of my time-in-view experiment was performed in an opportunistic manner on the return of the aircraft from monitoring surveys during an industry aerial survey monitoring program in 2012. I was only able to collect data if time and fuel allowed. The highly visible nature of the sighting object meant that my field of view estimates likely represent the maximum potential detectability, and therefore the maximum time-in-view. Also, the linear model approach that I used to estimate the time forward and time aft likely suffered from correlated errors because the time measure t_2—recorded when the sighting object was perpendicular to the plane was used in the calculations of both time-forward, t_{f} and time-aft, t_{a}. Future analysis of data collected under such a sampling design should consider the use of a joint-regression where the errors of t_1 and t_3 are independent, but the error in t_2 is the same for each calculation of t_{f} and t_{a}.

I was also unable to investigate the influence of environmental variables (e.g., sea state, sea ice coverage and glare) on the boundaries of the search area. During high sea states, for instance, observers will reduce their search area because more time is taken to decide whether a potential sighting is, or is not, a marine mammal. The presence of ice also influences the whales diving behaviour, as was highlighted by the LME models in Chapter 2—which in turn affects the whales' availability for visual detection. Whale group size and activity also influence overall availability. Groups of two or more whales tend to be more detectable to observers, while groups of socializing or surface feeding bowhead whales tend to increase disturbance of the surface waters and thus lead to higher probabilities of detection, as has been evident with North Atlantic right whales (e.g., Hain et al. 1999). Observer scanning behaviour and individual variation are also known to influence the duration of detectability. Because my time-in-view measures stemmed from a single observer I was not able to account for individual variation into the time-in-view estimates. Future studies could use a mixed-effects modeling framework to account for variation due to observer scanning behaviour, which would lead to better estimates of variance around the correction factors. Despite these caveats, the correction factors that I have calculated can be considered the best available for bowhead whales in the Beaufort Sea, both in presumably undisturbed conditions and for areas with seismic survey operations.

Aerial surveys were flown to monitor and help mitigate seismic survey operations in the Southern Beaufort Sea in 2006-2008 and in 2010; however I chose to only use those data collected in 2008. The 2008 survey season provided the greatest coverage of the survey area as well as the greatest number of sightings. But, this meant that I was not able to incorporate yearly variation into my models. Whale distribution during the autumn migration in the southern Alaskan Beaufort Sea is subject to yearly variation in relation to ice conditions, prey distribution and availability and natural variation in migration timings (Moore & Reeves 1993, Quakenbush et al. 2013a). 2008 was considered a low ice year and there was essentially no ice in the study area during the period that surveys were flown. This meant that I could not include ice presence in the models because all of the whales seen during the 2008 surveys were in open water. I was also unable to include prey data in my models as data on zooplankton abundance were not available to me. The inclusion of zooplankton data would help to further explain why some parts of the study area were apparently more important to feeding whales than others.

I also determined through examination of DASAR data that seismic sounds would have been audible on all but two of the usable surveys available to me from the 2008 industry aerial surveys. For this reason, I could not investigate the effects of seismic survey operations on bowhead whale density in the study area. Instead I chose to only use those 22 surveys during which whales would have been exposed to seismic sounds and evaluate bowhead density in the study area when it was ensonified by seismic sounds. Future analyses of these types of aerial survey data would benefit from the inclusion of covariates that include biotic variables related to prey presence, other industrial activities and also subsistence hunting activities. Incorporating these covariates and the yearly variations strengthen the predictions provided by the models and may also help to explain why whales occur in higher densities in the southeast of the study area, but in much lower densities in the central-southwest highlighting why there is an apparent hole in their use of the southern Beaufort Sea.

Finally, my analyses failed to address the issue of local fine-scale deflections related to seismic survey operations because of insufficient observations. However, I was able to show that there was no large scale offshore deflection of non-calf bowhead whales in areas of the Southern Beaufort Sea with active seismic operations in 2008. In addition, my analysis also provided further evidence supporting the hypothesis that feeding whales are more tolerant of seismic operations than whales engaged in other activities such as travelling.

Future Research

Bowhead whale numbers in the Western Arctic have been steadily increasing over the past 30 years with the latest population estimate (2011) indicating there are as many as 17,000 whales. A large proportion of this Bering-Chukchi-Beaufort Sea population feeds in the Canadian Beaufort Sea during the summer, and passes through the southern Alaskan Beaufort Sea on their westward migration in the autumn. The whales are exposed in these areas to human activities related to the energy industry, and increasingly to shipping. Yet much remains to be learned regarding the impacts of industry on whale behaviour, lending favour to the need for renewed field studies that focus on bowhead diving behaviour and especially behavioural reactions to different industrial operations. Controlled-exposure experiments conducted under conditions in which distances to sound sources and received sound levels are known should be performed under a variety of circumstances to build on studies begun in the 1980s—studies which often suffered from small smaple sizes. Such field efforts would benefit from directed behavioural observation studies conducted in conjunction with directed tagging studies. Inclusion of innovative tag technology, such as DTAGs (acoustic dive recording tags) would allow fine scale surface and dive behaviours to be investigated in conjunction with calling behaviour. These tags also provide valuable data on the received sound levels—particularly the cumulative sound levels received by whales as they spend time or pass through areas subject to varying levels of human activity. Such studies would demand collaboration between industry, government and subsistence groups—but would provide rich insights into the impacts of different human activities under a variety of circumstances that would aid in developing improved management measures that allow for industry to safely develop as well as allow the bowhead whale population to flourish.

Increasingly there is a move toward using drones, or unmanned aerial vehicles (UAVs) to collect data on marine mammals (Koski et al. 2011), and there is great potential for using UAVs to monitor and mitigate human activities (Koski et al. 2013). These technologies could provide a more flexible and cost efficient means of collecting behaviour data, not to mention a safer means to monitor marine mammals in remote regions—such as the Beaufort Sea. Experiments would need to be designed to estimate field of view specific to UAV platforms, and could build on the methods that I followed in Chapter 3. These experiments, as with those for standard manned aerial surveys should aim to investigate the effects of environmental, animal and observer-related covariates on the field of view—particularly variability related to sea states, ice-coverage, glare and group size. Consideration of observer behaviour-related variability will be most important for manned aerial surveys as UAVs cover sea surface areas of known size. Field of view estimates that incorporate such variability would allow for greater accuracy in overall estimates of availability bias, and would therefore continue to improve analysis of whale sighting data in affected areas.

There is even potential to use satellite imagery to count whales in areas subject to human activities —such as seismic survey operations. A recently published study has described an innovative method of identifying and counting whales using high resolution satellite imagery (Fretwell et al. 2014). While this approach would not be effective for real-time mitigation (particularly in the Arctic), it could provide useful baseline data on the presence of large whales in coastal areas where human activities occur. Availability correction factors (as calculated in Chapter 3) could also be adapted for such methods. Counting whales from space essentially advances aerial survey techniques into the next stratosphere.

My research has demonstrated how the behavioural reactions of whales to seismic survey operations can be accounted for in the analyses of whale sighting data collected from aerial platforms. The scope of my density and relative abundance analysis presented in Chapter 4 can be expanded to include variability related to year, migration timing, ice conditions and prey distribution and availability. I look forward to the opportunity to incorporate data for zooplankton concentrations into these models allowing me to investigate why specific areas of the southern Alaskan Beaufort Sea appear to be more important to feeding whales than other parts—and particularly whether these areas vary from one year to the next.

I am also keen to investigate why bowhead whale density in the central Alaskan Beaufort Sea is consistently low, both in previous studies (e.g. Givens 2009) and in Chapter 4. Important questions to address include assessing whether the presence of the apparent hole is related to differing levels of industrial activity; whether prey availability is limiting potential feeding opportunities in the area; or whether the local subsistence whaling activities influence how whales are using the area. This could be achieved by expanding on the analyses that I performed in Chapter 4. One method would involve assessing whale density in relation to prey distribution and availability, industrial activities, ice presence and variation in migration timings before, during and after the whaling season at Cross Island. While this study is much more tangible than the more extensive behaviour and controlled-exposure experiments that I suggested be undertaken, it would still require collaboration between industry, government and the local subsistence whaling groups.

In conclusion, my research has expanded earlier bowhead whale behaviour studies to widen understanding of how bowhead whales react to seismic survey operations in the Beaufort Sea. It has resulted in the first availability bias correction factors for whales exposed to seismic surveys that in turn have shown how the subtle behavioural reactions of whales to seismic operations affect density assessments in areas ensonified by seismic sounds. As a result, my research will lead to more accurate estimates of numbers of whales exposed to differing received levels of seismic sounds. It will also result in better estimates of numbers potentially disturbed during their annual westward migration. Finally, my research methodologies and findings are also likely to be applicable to bowhead whale populations outside of the Western Arctic, as well as to other species of whales that may react to human activities in similar ways as bowhead whales.

References

ADFG (2012) Satellite Tracking of Western Arctic Bowhead Whales. Alaska Dept. of Fish and Game, Juneau, AK. Available at www.adfg.gov/index.cfm?adfg=marinemammalprogram.bowhead (accessed 9 Aug 2012).

Andrewartha HG, Birch CL (1984) The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago

Angliss RP, Outlaw RB (2006) Bowhead whale (*Balaena mysticetus*): Western Arctic Stock, Alaska Marine Mammal Stock Assessments 2006, NOAA Tech Memo. NOAA-TM-AFSC-168. p 181–187

Beale CM (2007) The behavioral ecology of disturbance responses. Int J Comp Psychol 20:111−120

Beale CM, Monaghan P (2004a) Behavioural responses to human disturbance: a matter of choice? Anim Behav 68:1065−1069

Beale CM, Monaghan P (2004b) Human disturbance: people as predation-free predators? Ecology 41:335–343

Bejder L, Samuels A, Whitehead H, Finn H, Allen S (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar Ecol Prog Ser 395:177−185

Bejder L, Samuels A, Whitehead H, Gales N (2006) Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour 72:1149–1158

Bisson LN, Reider HJ, Patterson HM, Austin M, Brandon JR, Thomas TA, Bourdon ML (2013) Marine mammal monitoring and mitigation during exploratory drilling by Shell in the Alaskan Chukchi and Beaufort Seas, July–November 2012: Draft 90-Day Report. Editors: D.W. Funk, C.M. Reiser and W.R. Koski. LGL Rep. P1272D-1. Rep. from LGL Alaska Research Associates Inc., Anchorage, AK, USA, and JASCO Applied Sciences, Victoria, BC, Canada, for Shell Offshore Inc, Housten, TX, USA, Nat. Mar. Fish. Serv., Silver Spring, MD, USA and U.S. Fish and Wild. Serv., Anchorage, AK, USA. 266p + appendices. (available at: http://www.nmfs.noaa.gov/pr/pdfs/permits/shell_90dayreport_draft2012.pdf).

Blackwell SB (2014) Personal Communication, Santa Barbara, CA

Blackwell SB, Nations CS, McDonald TL, Greene Jr. CR, Thode AM, Guerra M, Macrander AM (2013) Effects of airgun sounds on bowhead whale calling rates in the Alaskan Beaufort Sea. Mar Mamm Sci DOI: 10.1111/mms.12001

Blackwell SB, Nations CS, McDonald TL, Thode A, Kim KH, Greene Jr. CR, Macrander AM (2010) Effects of seismic exploration activities on bowhead whale calling distribution in the Alaskan Beaufort Sea. J Acoust Soc Am 127:1756–1756

Blackwell SB, Richardson WJ, Greene Jr. CR, Streever B (2007) Bowhead whale (*Balaena mysticetus*) migration and calling behaviour in the Alaskan Beaufort Sea, autumn 2001–04: An acoustic localization study. Arctic 60:255–270

Bourlière F (1954) The Natural History of Mammals, Translated from the French by H.M. Parshley

Knopf, New York

Brandon JR, Thomas TA, Bourdon M (2011) Beaufort Sea aerial monitoring program, Chapter 7. In. D.W. Funk, C.M. Reiser, D.S. Ireland, R. Rodrigues, and W.R. Koski (eds) Joint Monitoring Program in the Chukchi and Beaufort Seas, 2006-2011, LGL Alaska Draft Report P1213-1, Report from LGL Alaska Research Associates Inc. LGL Ltd, Greeneridge Sciences Inc. and JASCO Research Ltd., for Shell Offshore Inc. and Other Industry Contributors, and National Marine Fisheries Services, U.S. Fish and Wildlife Service. 592p

Brandon JR, Wade PR (2007) Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using Bayesian model averaging. J Cetacean Res Manage 8:225–240

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press, Oxford

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York

Caldwell J, Dragoset W (2000) A brief overview of seismic air-gun arrays. The Leading Edge 19:898–902

Canty A, Ripley B (2011) boot: Bootstrap R (S-Plus) Functions. R package Version 1.3-1

Caughley G (1974) Bias in aerial survey. J Wildl Manage 38:921–933

Citta JJ, Quakenbush LT, Okkonen SR, Druckenmiller ML, Maslowski W, Clement Kinney J, George JC, Brower H, Small RJ, Ashjian CJ, Harwood LA, Heide-Jørgensen MP (in press) Ecological characteristics of core areas used by western Arctic bowhead whales, 2006–2012.

Clark CW, Johnson JH (1984) The sounds of the bowhead whale, *Balaena mysticetus,* during the spring migrations of 1979 and 1980. Can J Zool 62:1436–1441.

COSEWIC (2005) COSEWIC assessment and update status report on the bowhead whale (*Balaena mysticetus)* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii + 51p. Available at www.sararegistry.gc.ca/status/status_e.cfm

Davis RA, Koski WR, Richardson WJ, Evans CR, Alliston WG (1982) Distribution, numbers and productivity of the Western Arctic stock of bowhead whales in the eastern Beaufort Sea and Amundsen Gulf, summer 1981. Rep. from LGL Ltd., Toronto, Ont., for Sohio Alaska Petrol. Co. [now BP Alaska], Anchorage, AK, and Dome Petrol. Ltd., Calgary, Alb. (co-managers). Summarized as SC/34/PS20 presented to the IWC Scientific Committee, June 1982. 18p

Diggle PJ, Heagerty P, Liang K, Zeger SL (2002) Analysis of longitudinal data. Oxford University Press, Oxford, UK

Dorsey EM, Richardson WJ, Würsig B (1989) Factors affecting surfacing, respiration, and dive behaviour of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea. Can J Zool 67:1801–1815

Dunlop RA, Noad MJ, Cato DH, Kniest E, Miller PJO, Smith JN, Stokes MD (2013) Multivariate analysis of behavioural response experiments in humpback whales (*Megaptera novaeangliae*). J Exp Biol 216:759–770

Dunn KP, Smyth GK (1996) Randomized quantile residuals. Journal Comput Graph Stat 5:236–244

Dunphy-Daly MM, Heithaus MR, Wirsing AJ, Mardon JSF, Burkholder DA (2010) Predation risk influences the diving behavior of a marine mesopredator. Open Ecol J 3:8–15

Edwards HH, Pollock KH, Ackerman BB, Reynolds JE, Powell JA (2007) Estimation of detection probability in manatee aerial surveys at a winter aggregation site. J Wildl Manage 71:2052–2060

Ellison WT, Southall BL, Clark CW, Frankel AS (2012) A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conserv Biol 26:21–28

Elton C (1950) The Ecology of Animals 3rd Ed. Methuen's monographs on biological subjects. Methuen, London

ESRI (2008) Arcview Verison 9.3. Earth Science Research Institute, Redlands, CA.

Evans TJ, Fischbach A, Schliebe S, Manly B, Kalxdorff S, York G (2003) Polar bear aerial survey in the Eastern Chukchi Sea: A pilot study. Arctic 56:359–366

Faul F, Erdfelder E, Lang A, Buchner A (2007) G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods 39:175–191

Forcada J, Gazo M, Aguilar A, Gonzalvo J, Fernández-Contreras M (2004) Bottlenose dolphin abundances in the NW Mediterranean: addressing heterogeneity in distribution. Mar Ecol Prog Ser 275:275–287

Ford JKB, Reeves RR (2008) Fight or flight: antipredator strategies of baleen whales. Mamm Rev 38:50–86

Fraker MA, Ljungblad DK, Richardson WJ, Schoik DRV (1985) Bowhead whale behaviour in relation to seismic exploration, Alaskan Beaufort Sea, Autumn 1981. Rep. from LGL Ltd, Sidney, BC, LGL Ltd. King City, Ont, Naval Ocean Systems Center, San Diego, CA and SEACO Inc, San Diego, CA., for U.S. Minerals Management Service [now Bureau of Ocean Energy Management], Reston, VA. 40p.

Frankel AS, Clark CW (1998) Results of low-frequency playback of M-sequence noise to humpback whales, *Megaptera novaeangliae*, in Hawai`i. Can J Zool 76:521–535

Fretwell PT, Staniland IJ, Forcada J (2014) Whales from space: counting southern right whales by satellite. PLoS ONE 9:e88655

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol 6:11

Frid A, Heithaus MR, Dill LM (2007) Dangerous dive cycles and the proverbial ostrich. Oikos 116:893–902

Funk DW, Ireland DS, Rodrigues R, Koski WR (2010) Joint monitoring program in the Chukchi and Beaufort seas, open water seasons, 2006–2008. LGL Alaska Report P1050–2, Report from LGL Alaska Research Associates, Inc., LGL Ltd., Greeneridge Sciences, Inc., and JASCO Research, Ltd., for Shell Offshore Inc. and other industry contributors, and Nationals Marine Fisheries Service, U.S. Fish and Wildlife Service, 506p + appendices.

Gailey G, Würsig B, McDonald TL (2007) Abundance, behavior, and movement patterns of western gray whales in relation to a 3-D seismic survey, Northeast Sakhalin Island, Russia. Environ Monit Assess 134:75–91

GEBCO (2003) General Bathymetric Chart of the Oceans, UK. Available at: http://www.gebco.net/

Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265–268

Gill JA, Sutherland WJ (2000) Predicting the consequences of human disturbance from behavioural decisions, Chap. 4. In: Gosling LM, Sutherland WJ (eds) Behaviour and Conservation, Conserv Biol Series 2, Cambridge University Press, Cambridge, p 51–64

Givens GH (2009) Spatio-temporal modeling of relative animal density using a long time series of line transect surveys with clustering and censoring. Paper SC/61/BRG1 presented to the IWC Scientific Committee, June 2009. 31p (available at: http://iwcoffice.co.uk/_documents/sci_com/SC61docs/SC-61-BRG1.pdf)

Givens GH, Edmondson SL, George JC, Suydam R, Charif RA, Rahaman A, Hawthorne D, Tudor B, DeLong RA, Clark CW (2013) Estimate of 2011 abundance of the Bering-Chukchi-Beaufort Seas bowhead whale population. Paper SC/65a/BRG01 presented to the IWC Scientific Committee, June 2013. 30p. (available at: https://events.iwc.int/index.php/scientific/SC65a/paper/viewFile/199/239/SC-65a-BRG01).

Givens GH, Hoeting JA, Beri L (2010) Factors that influence aerial line transect detection of Bering-Chukchi-Beaufort Seas bowhead whales. J Cetacean Res Manage 11:9–16

Goold JC, Coates RFW (2006) Near source, high frequency air-gun signatures, Paper SC/58/E30 presented to the IWC Scientific Committee, June 2006. 7p.

Greene Jr. CR, Altman NS, Richardson WJ (1999) The influence of seismic survey sounds on bowhead whale calling rates. J Acoust Soc Am 106:2280

Greene Jr. CR, Richardson WJ (1988) Characteristics of marine seismic survey sounds in the Beaufort Sea. J Acoust Soc Am 83:2246–2254

Hain JHW, Ellis SL, Kenney RD, Slay CK (1999) Sightability of right whales in coastal waters of the southeastern United States with implications for the aerial monitoring program. In: Garner GW, Amstrup SC, Laake JL, Manley BFJ, McDonald LL, Robertson DG (eds) Marine Mammal Survey and Assessment Methods, A.A. Balkerna, Rotterdam, p 191–207

Harwood LA, Auld J, Joynt A, Moore SE (2010) Distribution of bowhead whales in the SE Beaufort Sea during late summer, 2007–2009. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/111. iv + 22p. (available at: http://www.dfo-mpo.gc.ca/csas).

Harwood LA, Joynt A, Kennedy D, Pitt R, Moore SE (2009) Spatial restrictions and temporal planning as measure to mitigate potential effects of seismic noise on cetaceans: a working example from the Canadian Beaufort Sea, 2007–2008. DFO Can. Sci. Advis. Sec. Res. Doc 2009/040. iv + 14p. (available at: http://www.dfo-mpo.gc.ca/csas).

Harwood LA, Joynt A, Moore SE (2008) Bowhead whale feeding aggregations in the Canadian Beaufort Sea and their role in the mitigation of effects of seismic underwater noise. Working Paper /Presentation at the Review of Scientific Information on the Impacts of Seismic Sound on Fish, Invertebrates, and Marine Mammals, Workshop II, March 26–28, 2008, Ottawa, Ontario. 6p.

Hastie GD (2012) Tracking marine mammals around marine renewable energy devices using active sonar. SMRU Ltd report number SMRUL–DEC–2012–002 to the Department of Energy and Climate Change. March 2012. (unpublished). 99p (available at: http://mhk.pnnl.gov/wiki/images/a/a8/SMRU_2012.pdf).

Hastie T, Tibshirani R (1990) Generalized Additive Models. Chapman and Hall, London

Hedley SL, Buckland ST (2004) Spatial Models for Line Transect Sampling. Journal of Agricultural, Biological & Environmental Statistics 9:181-199

Heithaus MR, Frid A (2003) Optimal diving under the risk of predation. J Theor Biol 223:79–92

Huber HR, Jeffries SJ, Brown RF, DeLong RL, VanBlaricom G (2001) Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Mar Mamm Sci 17:276–293

Johnson DH (1999) The insignificance of statistical significance testing J Wildl Manage 63:763–772

Johnson SR, Richardson WJ, Yazvenko SB, Blokhin SA, Gailey G, Jenkerson MR, Meier SK, Melton HR, Newcomer MW, Perlov AS, Rutenko SA, Wursig B, Martin CR, Egging DG (2007) A western gray whale mitigation and monitoring program for a 3-D seismic survey, Sakhalin Island, Russia. Environ Monit Assess 134:1–19

Jolles CZ, ed. (1995) Speaking of whaling: a transcript of the Alaskan Eskimo Whaling Commission panel presentation on native whaling. p. 315-337. In: A. P. McCartney [ed] Hunting the largest animals, native whaling in the Western Arctic and Subarctic. Studies in Whaling No. 3, Circumpolar Inst, University of Alberta, Edmonton. , University of Alberta, Edmonton, Alb

Jørgensen B (1987) Exponential dispersion models. JR Statist Soc B 49:127–162

Koski WR, Abgrall P, Yazvenko S (2011) An inventory and evaluation of unmanned aerial systems for offshore surveys of marine mammals. J Cetacean Res Manage 11:239–247

Koski WR, Funk DW, Ireland DS, Lyons C, Christie K, Macrander AM, Blackwell SB (2009) An update on feeding by bowhead whales near an offshore seismic survey in the central Beaufort Sea, Paper SC/61/BRG3 presented to the IWC Scientific Committee, June 2009. 24p (available at: http://iwcoffice.co.uk/_documents/sci_com/SC61docs/SC-61-BRG3rev.pdf)

Koski WR, Funk DW, Ireland DS, Lyons C, Macrander AM, Voparil I (2008) Feeding by bowhead whales near an offshore seismic survey in the Beaufort Sea. Paper SC/60/E14 presented to the IWC Scientific Committee, June 2008.14p

Koski WR, George JC, Sheffield G, Galginaitis MS (2005) Subsistence harvests of bowhead whales (*Balaenoptera mysticetus*) at Kaktovik, Alaska (1973–2000). J Cetacean Res Manage 7:33–37

Koski WR, Johnson SR (1987) Responses of bowhead whales to an offshore drilling operation in the Alaskan Beaufort Sea, Autumn 1986: Behavioral studies and aerial photogrammetry. LGL Ltd., King City Ont, for Shell Western E&P Inc. 601 West Fifth Avenue, Anchorage, Alaska. vii + 124p

Koski WR, Miller GW (2009) Habitat use by different size classes of bowhead whales in the central Beaufort Sea during late summer and autumn. Arctic 62:137–150

Koski WR, Thomas TA, Funk D, Macrander AM (2013) Marine mammal sightings by analysts of digital imagery versus aerial surveyors: a preliminary comparison. Journal of Unmanned Systems 1:1–16

Kramer M (2005) R^2 statistics for mixed models Conference on Applied Statistics in Agriculture. Kansas State University, Manhattan, KS., p 148–160

Laake JL, Borchers DL (2004) Methods for incomplete detection at distance zero. Chapter 6. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced Distance Sampling: Estimating abundance of biological populations, Oxford University Press, Oxford, p 108–189

Laake JL, Calambokidis J, Osmek SD, Rugh DJ (1997) Probability of detecting harbor porpoise from aerial surveys: Estimating *g*(0). J Wildl Manage 61:63–75

Laist DW, Reynolds JE (2005) Influence of power plants and other warm-water refuges on Florida manatees. Mar, Mam, Sci 21:739–764

Landino SW, Treacy SD, Zerwick SA, Dunlap JB (1994) A large aggregation of bowhead whales (*Balaena mysticetus*) feeding near Point Barrow, Alaska, in late October 1992. Arctic 47:232–235

Liu H, Zheng Y, Shen J (2008) Goodness-of-fit measures of R^2 for repeated measures mixed effect models. J Appl Stat 35:1081–1092

Ljungblad DK, Moore SE, Clarke JT (1986) Assessment of bowhead whale (*Balaena mysticetus*) feeding patterns in the Alaskan Beaufort and Northeastern Chukchi Seas via aerial surveys, fall 1979–84. Rep Int Whal Commn 36:265–272

Ljungblad DK, Würsig B, Swartz SL, Keene JM (1988) Observations on the behavioral responses of bowhead whales (*Balaena mysticetus*) to active geophysical vessels in the Alaskan Beaufort Sea. Arctic 41:183–194

Madsen PT, Møhl B (2000) Sperm whales (*Physeter catodon L.* 1758) do not react to sounds from detonators. J Acoust Soc Am 107:668–671

Madsen PT, Møhl B, Nielsen BK, Wahlberg M (2002) Male sperm whale behaviour during exposures to distant seismic survey pluses. Aquat Mamm 28:231–240

Maj A (2011) lmmfit: Goodness-of-fit-measures for linear mixed models with one-level-grouping. R package, Version 1.0

Malme CI, Miles PR, Clark CW, Tyack P, Bird JE (1984) Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. Phase II: January 1984 migration. Prepared by Bolt Beranek and Newman Inc, Cambridge, MA. *For* U.S. Department of the Interior Minerals Management Service, Alaska OCS Office, Anchorage, AK. . Report No. PB-86-218377/XAB;BBN-5586

Manly BFJ, Moulton VD, Elliott RE, Miller GW, Richardson WJ (2007) Analysis of covariance of fall migrations of bowhead whales in relation to human activities and environmental factors, Alaskan Beaufort Sea: Phase I, 1996-1998. OCS Study 2005–033; LGL Rep. TA2799–3. Rep. from LGL Ltd., King City, Ont., and WEST Inc., Cheyenne, WY, *For* U.S. Minerals Management Service, Anchorage, AK. 128p

Marques FFC, Buckland ST (2004) Covariate models for the detection function, Chapter 3. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced Distance Sampling, Oxford University Press, Oxford, p 31–47

Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J Wildl Manage 53:1017–1024

McLaren IA (1961) Methods of determining the numbers and availability of ringed seals in the eastern Canadian Arctic. Arctic 14:162–175

Miller DL (2013) distance: A simple way to fit detection functions to distance sampling data and calculate abundance/density for biological populations. R package Version 0.7.3

Miller DL, Burt ML, Rexstad EA, Thomas L (2013a) Spatial models for distance sampling data: recent developments and future directions. Methods Ecol Evol 4:1001–1010

Miller DL, Rexstad EA, Burt L, Bravington MV, Hedley S (2013b) dsm: Density surface modelling of distance sampling data. R package version 2.0.1

Miller GW, Davis RA (2002) Marine mammal and acoustical monitoring for Anderson Explorations Ltd's open water seismic program in the southeastern Beaufort Sea 2001. Final report from LGL Ltd., King City, Ont., and JASCO Research Ltd, Victoria, BC. For: Devon Canada Corporation, Calgary, AB. 199p

Miller GW, Elliot RE, Thomas TA, Moulton VD, Koski WR (2002) Distribution and numbers of bowhead whales in the eastern Alaskan Beaufort Sea during late summer and autumn, 1979–2000. Chap 9 In: W.J. Richardson and D.H. Thomson[eds.], Bowhead whale feeding in the eastern Alaskan Beaufort Sea: update of scientific and traditional information, Vol.1. OCS Study MMS 2002-012; LGL Rep. TA2196-7. Rep. from LGL Ltd., King City, Ont., for U.S. Minerals Management Service, Anchorage, AK and Herndon, V.A.

Miller GW, Moulton VD, Davis RA, Holst M, Millman P, MacGillivray A, Hannay D (2005) Monitoring seismic effects on marine mammals--southeastern Beaufort Sea, 2001–2002. In: Armsworthy SL, Cranford PJ, Lee K (eds) Offshore oil and gas environmental effects monitoring/Approaches and technologies, Battelle Press, Columbus, OH, p 511–542

Miller PJO, Johnson MP, Madsen PT, Biassoni N, Quero M, Tyack PL (2009) Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico. Deep-Sea Res Part 1 56:1168–1181

MMPA (1972) The marine mammal protection act of 1972 as amended 2007. Compiled and annotated by the Marine Mammal Commission. 4340 East-West Highway, Bethesda, MD 20814. Updated for 2004 and 2007 Amendments by NOAA's National Marine Fisheries Service 1315 East-West Highway Silver Spring, MD 20910. 113p.

Moore SE (2000) Variability of cetacean distribution and habitat selection in the Alaskan Arctic, Autumn 1982–91. Arctic 53:448–460

Moore SE, Clarke JT (1993) Bowhead whale autumn distribution and relative abundance in relation to oil and gas lease areas in the northeastern Chukchi Sea. Polar Record 29:209–214

Moore SE, Clarke JT, Ljungblad DK (1989) Bowhead whale (*Balaena mysticetus*) spatial and temporal distribution in the central Beaufort Sea during late summer and early fall 1979–1986. Rep Int Whal Comm 39:283–290

Moore SE, DeMaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic 53:432–447

Moore SE, George JC, Sheffield G, Bacon J, Ashjian CJ (2010) Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005–06. Arctic 63:195–205

Moore SE, Laidre KL (2006) Trends in sea ice cover within habitats used by bowhead whales in the Western Arctic. Ecol Appl 16:932–944

Moore SE, Reeves RR (1993) Distribution and Movement. In: Burns JJ, Montague JJ, Cowles CJ (eds) The bowhead whale, Special publication No. 2. The Society for Marine Mammalogy. Allen Press, Lawrence, KS, p 313–386

Moore SE, Reeves RR, Southall BL, Ragen TJ, Suydam RS, Clark CW (2012) A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing Arctic. BioScience 62:289–295

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13

Patenaude NJ, Richardson WJ, Smultea MA, Koski WR, Miller GW, Würsig B, Greene Jr. CR (2002) Aircraft sound and disturbance to bowhead and beluga whales during spring migration in the Alaskan Beaufort Sea. Mar Mamm Sci 18:309–335

Pinheiro J, Bates D, DebRoy S, Sarkar D (2011) nlme: Linear and Nonlinear Mixed Effects Models, R package version 3.1–101, R Development Core Team

Pollock KH, Kendall WL (1987) Visibility bias in aerial surveys: A review of estimation procedures. J Wildl Manage 51:502–510

Pollock KH, Marsh HD, Lawler IR, Alldredge MW (2006) Estimating animal abundance in heterogeneous environments: An application to aerial surveys for dugongs. J Wildl Manage 70:255–262

Potter JR, Thillet M, Chitre MA, Doborzynski Z, Seekings PJ (2007) Visual and passive acoustic marine mammal observations and high-frequency seismic source characteristics recorded during a seismic survey. IEEE J Oceanic Eng 32:469–483

QGIS (2004) QGIS 1.8: A free and open source geographic information system, http://www.qgis.org/. QGIS Development Team 2004–2013

Quakenbush LT, Citta JJ, George JC, Small RJ, Heide-Jørgensen MP (2010) Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. Arctic 63:289–307

Quakenbush LT, Small RJ, Citta JJ (2013a) Satellite tracking of bowhead whales: movements and analysis from 2006–2012. U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Alaska Outer Continental Shelf Region, Anchorage, AK. OCS Study BOEM 2013-01110. 60p + appendices.

Quakenbush LT, Small RJ, Citta JJ (2013b) Satellite tracking of bowhead whales: movements and analysis from 2006 to 2012. U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Alaska Outer Continental Shelf Region, Anchorage, AK. OCS Study BOEM 2013-01110. 60 pp + appendices.

R (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org

Reeves R, Rosa C, George JC, Sheffield G, Moore M (2012) Implications of Arctic industrial growth and strategies to mitigate future vessel and fishing gear impacts on bowhead whales. Mar Policy 36:454–462

Reeves RR, Berger J, Clapham PJ (2006) Killer whales as predators of large baleen whales and sperm whales, Chapter 14. In: Estes JA, Demaster DP, Doak DF, Williams TM, Brownell Jr. RL (eds) Whales, Whaling, and Ocean Ecosystems, University of California Press, Berkeley. , p 174–190

Reeves RR, Ewins PJ, Agbayani S, Heide-Jørgensen MP, Kovacs KM, Lydersen C, Suydam R, Elliott W, Polet G, van Dijk Y, Blijleven R (2014) Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. Marine Policy 44:375–389

Richard PR, Laake JL, Hobbs RC, Heide-Jørgensen MP, Asselin NC, Cleator H (2010) Baffin Bay narwhal population distribution and numbers: Aerial surveys in the Canadian High Arctic, 2002-04. Arctic 63:85–99

Richardson WJ, Davis RA, Evans CR, Ljungblad DK, Norton P (1987) Summer distribution of bowhead whales, *Balaena mysticetus,* relative to oil industry activities in the Canadian Beaufort Sea, 1980–84. Arctic 40:93–104

Richardson WJ, Finley KJ, Miller GW, Davis RA, Koski WR (1995a) Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea - regions with different amounts of human activity. Mar Mamm Sci 11:1–45

Richardson WJ, Fraker MA, Würsig B, Wells RS (1985) Behaviour of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities. Biol Conserv 32:195–230

Richardson WJ, Greene Jr. CR, Malme CI, Thomson DH (1995b) Marine Mammals and Noise. Academic Press, San Diego, CA

Richardson WJ, Malme CI (1993) Man-made noise and behavioral responses. In: Burns JJ, Montague JJ, Cowles CJ (eds) The Bowhead Whale - special publication No 2: The Society for Marine Mammalogy, p 631–700

Richardson WJ, Miller GW, Greene Jr. CR (1999) Displacement of migrating bowhead whales by sounds from seismic surveys in shallow waters of the Beaufort Sea. J Acoust Soc Am 106:2281

Richardson WJ, Thomson DH (2002) Bowhead whale feeding in the eastern Alaskan Beaufort Sea: update of scientific and traditional information. OCS study MMS 2002–012; LGL Rep. TA2196–7. Rep from LGL Ltd., King City, Ont., for U.S. Minerals Management Service, Anchorage, AK, and Herndon, VA 744p

Richardson WJ, Würsig B, Greene Jr. CR (1986) Reactions of bowhead whales, *Balaena mysticetus*, to seismic exploration in the Canadian Beaufort Sea. J Acoust Soc Am 79:1117–1128

Robertson FC, Koski WR, Thomas TA, Richardson WJ, Würsig B, Trites AW (2013) Seismic operations have variable effects on dive-cycle behavior of bowhead whales in the Beaufort Sea. Endang Species Res 21:143−160

Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ, Nowacek DP, Wasser SK, Kraus SD (2012) Evidence that ship noise increases stress in right whales. Proc R Soc B 279:2363–2368

Samuel MD, Pollock KH (1981) Correction of visibility bias in aerial surveys where animals occur in groups. J Wildl Manage 45:993–997

Scott M (2009) Sea Ice, Earth Observatory. earthobservatory.nasa.gov/Features/SeaIce/ (accessed 31 Jan 2014)

Shono H (2008) Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fisheries Research 93:154–162

Smyth GK, Hu Y, Dunn KP, Phipson B, Chen Y (2013) statmod: Statistical modeling, R package version 1.4.18

Southall BL, Bowles AE, Ellison WT, Finneran JJ, Gentry RL, Greene Jr. CR, Kastak D, Ketten DR, Miller JH, Nachtigall PE, Richardson WJ, Thomas JA, Tyack PL (2007) Marine mammal noise exposure criteria: Initial scientific recommendations. Aquat Mamm 33:411−522

Southwell C, Borchers DL, Paxton CGM, Burt L, Mare Wdl (2007) Estimation of detection probability in aerial surveys of Antarctic pack-ice seals. J Agr Biol Environ Stat 12:1−14

Steinhorst RK, Samuel MD (1989) Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425

Storey JD (2002) A direct approach to false discovery rates. J R Stat Soc Series B 64:479–498

Sutherland WJ (1996) From Individual behaviour to population ecology. Oxford University Press

Suydam R, George JC (2012) Preliminary analysis of subsistence harvest data concerning bowhead whales (*Balaena mysticetus*) taken by Alaskan Natives, 1974-2011, Paper SC/64/AWMP8 presented to the IWC Scientific Committee, June 2012. 13p.

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5−14

Thomas TA, Koski WR, Richardson WJ (2002a) Correction factors to calculate bowhead whale numbers from aerial surveys of the Beaufort Sea, Chap 15 In: W.J. Richardson and D.H. Thomson (eds.) Bowhead whale feeding in the eastern Alaskan Beaufort Sea: update of scientific and traditional information, Vol.1. OCS Study MMS 2002-012; LGL Rep. TA2196-7. Rep. from LGL Ltd., King City, Ont., for U.S. Minerals Management Service, Anchorage, AK and Herndon, V.A.

Thomas TA, Richardson WJ, W.R K, Wursig B (2002b) Surfacing, respiration and dive cycles of bowhead whales in the Beaufort Sea: calves, subadults and adults. Chap 14 In: W.J. Richardson and D.H. Thomson[eds.], Bowhead whale feeding in the eastern Alaskan Beaufort Sea: update of scientific and traditional information, Vol.1. OCS Study MMS 2002-012; LGL Rep. TA2196-7. Rep. from LGL Ltd., King City, Ont., for U.S. Minerals Management Service, Anchorage, AK and Herndon, V.A.

Thomson DH, Fissel DB, Marko JR, Davis RA, Borstad GA (1986) Distribution of bowhead whales in relation to hydrometeorological events in the Beaufort Sea. Environmental Studies Revolving Funds Report No. 028. Ottawa. 119p.

Todd S, Stevick P, Lien J, Marques F, Ketten D (1996) Behavioural effects of exposure to underwater explosions in humpback whales (*Megaptera novaeangliae*). Can J Zool 74:1661–1672

Treacy SD, Gleason JS, Cowles CJ (2006) Offshore distances of bowhead whales (*Balaena mysticetus*) observed during fall in the Beaufort Sea, 1982–2000: An alternative interpretation. Arctic 59:83–90

Tregenza T (1995) Building on the ideal free distribution. Advances in Ecological Research 26:253–307

Vonesh EF, Chinchilli VM, Pu K (1996) Goodness-of-fit in Generalized Nonlinear Mixed-Effects Models. Biometrics 52:572–587

Vos DK, Ryder RA, Graul WD (1985) Response of breeding Great Blue herons to human disturbance in Northcentral Colorado. Colonial Waterbirds 8:13–22

Williams R, Hedley SL, Branch TA, Bravington MV, Zerbini AN, Findlay KP (2011) Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. Conserv Biol 25:526–535

Wirsing AJ, Heithaus MR, Dill LM (2011) Predator-induced modifications to diving behavior vary with foraging mode. Oikos 120:1005–1012

Wood SN (2006) Generalized Additive Models: An Introduction with R. Chapman and Hall, Boca Ratonm FL

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc B 73:3–36

Würsig B, Clark CW (1993) Behaviour, Chapter 5. In: Burns JJ, Montague JJ, Cowles CJ (eds) The bowhead whale, Society for Marine Mammalogy, Special Publication No 2, Allan Press, p 157–199

Würsig B, Dorsey EM, Fraker MA, Payne RS, Richardson WJ (1985) Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: A description. Fish Bull 83:357–377

Würsig B, Dorsey EM, Fraker MA, Payne RS, Richardson WJ, Wells RS (1984) Behavior of bowhead whales, *Balaena mysticetus,* summering in the Beaufort Sea: surfacing, respiration, and dive characteristics. Can J Zool 62:1910–1921

Würsig B, Dorsey EM, Richardson WJ, Wells RS (1989) Feeding, aerial, and play behavior of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. Aquat Mamm 15:27–37

Würsig B, Koski WR, Thomas TA, Richardson WJ (2002) Activities and behavior of bowhead whales in the eastern Alaskan Beaufort Sea during late summer and autumn, Chapter 12, In: W.J. Richardson and D.H. Thomson (eds.) Bowhead whale feeding in the eastern Alaskan Beaufort Sea: update of scientific and traditional information, Vol.1. OCS Study MMS 2002–012; LGL Rep. TA2196–7. Rep. from LGL Ltd. King City, Ont., for U.S. Minerals Management Service, Anchorage, AK and Herndon, VA

Yazvenko SB, McDonald TL, Blokhin SA, Johnson SR, Melton HR, Newcomer MW, Nielson R, Wainwright PW (2007) Feeding of western gray whales during a seismic survey near Sakhalin Island, Russia. Environ Monit Assess 134:93–106

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York

Appendices

Appendix A

Supplementary tables summarizing the results of the retrospective sensitivity analysis that was performed in Chapter 2 for each Linear Mixed Effects (LME) model investigating the effect of seismic sounds on bowhead whale behaviour. The LME models were fit to successively smaller cohorts of behaviour data to investigate the variation in selection and significance of explanatory variables.

Table A1 Summary table of results for the retrospective sensitivity analysis for the number of blows per surfacing of bowhead whales. • $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Model Covariates & Interaction terms		Full Model	1980-1999	1980-1998	1980-1986	1980-1985	1980-1984	1980-1983	1980-1982	1980-1981
Season	autumn†									
	summer	***	***	***	***	***	***	***	***	***
Depth	< 10 m†									
	10–19 m									
	20–49 m									
	50–199 m					*	*	***		
	> 200 m	**	*	**	**	**	**	***		
Ice %	< 5%†									
	> 5 %	***	***	**	**	*			*	**
Seismic	**undisturbed†**									
	present	**	**	**	**			*		***
Activity	forage†									
	social			•	***	**	**	***	**	
	travel			•		•	*	*		
Log(whales in 1km)					**	**	**			***
Group size	1–2†									
	2–3					*	*	*	***	
	> 4									
Motion	none†									
	fast	**	**	**	**	**	*	*		
	moderate	•								•
	slow									
	changing	**	**	**	**	**	**	***	**	**
Seismic × forage†										
	seismic × social	•	•	*	**	**	**			
	seismic × travel	*	**	**	*	*	*			
Seismic × autumn†										
	seismic × summer							*		
Seismic ×log(whales in 1km)		**	**	**					***	
R^2 coefficient based on likelihood ratio.		0.135	0.1521	0.145	0.181	0.1403	0.1147	0.2106	0.3502	0.394

† Delineates the category of each variable against which all other categories within that variable were compared

Table A2 Summary table of results for the retrospective sensitivity analysis for the median blow interval of bowhead whales. • $p \leq 0.1$,* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Model Covariates & Interaction terms		Full Model	1980-1999	1980-1998	1980-1986	1980-1985	1980-1984	1980-1983	1980-1982	1980-1981
Season	autumn†									
	summer	*	**	**				•		
Depth	< 10 m†									
	10–19 m	**	**	**	**	*				
	20–49 m	***	***	**	**	*				
	50–199 m	**	**	**	**				•	
	> 200 m	*	*	*	*					
Ice %	< 5%†									
	> 5 %							*		**
Seismic	**undisturbed†**									
	present	***	***	***	***					***
Whale State	non-calf†									
	mother	***	***	***	**	**			•	
Activity	forage†									
	social						**	•		
	travel	***	***	***	***	***	***	*		
Log(whales in 1km)			•	*		*		*		
Group size	1–2†									
	2–3	***	***	***	***	***	***	***		
	> 4				*	*				
Aerial	none†									
	present	**	*	***	***	***	***	***		
Motion	none†									
	fast									•
	moderate					•	*			
	slow									
	changing									
Seismic × atumn†										
	seismic × summer	***	***	***	***	*				
Seismic × < 10 m										
	seismic × 10–19 m	***	***	***	***			-		-
	seismic × 20–49 m	***	***	***	***			-		-
	seismic × 50–199 m							-		-
	seismic × > 200 m	*	**	*	**			-		-
Seismic × forage†										
	seismic × social					•			*	***
	seismic × travel	*	**	**	**	**			*	**
Seismic × no aerial†										

Model Covariates & Interaction terms	Full Model	1980-1999	1980-1998	1980-1986	1980-1985	1980-1984	1980-1983	1980-1982	1980-1981
seismic × aerial	**	**	*						
Seismic × log(whales in 1km)								*	
Seismic × none/mill									
seismic × fast									
seismic × moderate									•
seismic × slow									
seismic × changing									***
R^2 coefficient based on likelihood ratio.	0.127	0.141	0.147	0.136	0.073	0.087	0.063	0.084	0.127

† Delineates the category of each variable against which all other categories within that variable were compared

– Indicates that this variable was not included in the model.

Table A3 Summary table of results for the retrospective sensitivity analysis for the surface duration of bowhead whales. • $p \leq 0.1$,* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Model Covariates &	**Interaction terms**	Full Model	1980-1999	1980-1998	1980-1986	1980-1985	1980-1984	1980-1983	1980-1982	1980-1981
Season	autumn†									
	summer	*	**	**	***	**	***	***	*	***
Depth	< 10 m†									
	10–19 m									
	20–49 m								–	–
	50–199 m	*	**	**	**	***	***	***	*	*
	> 200 m	***	***	***	***	***	***	***	***	–
Ice %	< 5%†									
	> 5 %	**	**	*	*					
Seismic	**undisturbed†**									
	present	*	•	*	*					*
Whale Status	non-calf†									
	mother	**		*	**					*
Activity	forage†									
	social		•	*	**	**	***	***	•	*
	travel	**		*	**	***	***	**		
Log(whales in 1km)			•	•	*	*	**	**	*	
Group size	1–2†									
	2–3								**	*
	> 4								•	
Motion	none†									
	fast	***	***	***	***	***	***	***	***	***
	moderate	***	***	***	***	***	***	***	•	•
	slow	***	***	***	***	***	***	**	*	**
Seismic × autumn†										
	seismic × summer					*				
Seismic × non-calf										
	seismic × mother								*	•
Seismic × < 10 m										
	seismic × 10–19 m									
	seismic × 20–49 m									
	seismic × 50–199 m			•						
	seismic × > 200 m			**			**			
Seismic × forage†										
	seismic × social				•			**	*	
	seismic × travel	***	***	***	***	***	**	**	**	
Seismic × log(whales in 1km)		*	•		•					
R^2 coefficient based on likelihood ratio.		0.239	0.266	0.279	0.319	0.288	0.268	0.323	0.552	0.541

† Delineates the category of each variable against which all other categories within that variable were compared

– Indicates that this variable was not included in the model.

Table A4 Summary table of results for the retrospective sensitivity analysis for the dive duration of bowhead whales. • $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Model Covariates & Interaction terms		Full Model	1980-1999	1980-1998	1980-1986	1980-1985	1980-1984	1980-1983	1980-1982	1980-1981
Season	autumn†								•	**
	summer					•				
Depth	< 10 m†									
	10–19 m							*		
	20–49 m	•	*					*		
	50–199 m						*	***		
	> 200 m	*	*			*	**	***		
Ice %	< 5%†									
	> 5 %	*	•	**	**	**	*			
Seismic	undisturbed†									
	present	**	**	***	**	**				
Whale Status	non-calf†									
	mother	**	**	**	**				**	***
Activity	forage†									
	social	*	•							**
	travel									**
Log(whales in 1km)		*	**	**	**					•
Group size	1–2†									
	2–3	*	*	*	*				***	
	> 4					•			**	*
Seismic × autumn†										
	seismic × summer	*	*	**	*	***		*	–	–
Seismic × forage†										–
	seismic × social	*	**	*	*					–
	seismic × travel	*	*	*	*	*			*	–
Seismic × Group size (1–2)										
	seismic × 2–3						**	***		
	seismic × > 4									
Seismic × log(whales in 1km)		*	*	*	*					
R^2 coefficient based on likelihood ratio.		0.386	0.405	0.413	0.424	0.312	0.311	0.353	0.493	0.462

† Delineates the category of each variable against which all other categories within that variable were compared

– Indicates that this variable was not included in the model.

Appendix B

Supplementary figure detailing the deployment locations of the DASAR arrays in 2008. This figure was produced and published by Blackwell et al. (Chapter 9 in, Funk et al. 2010) and is used with permission

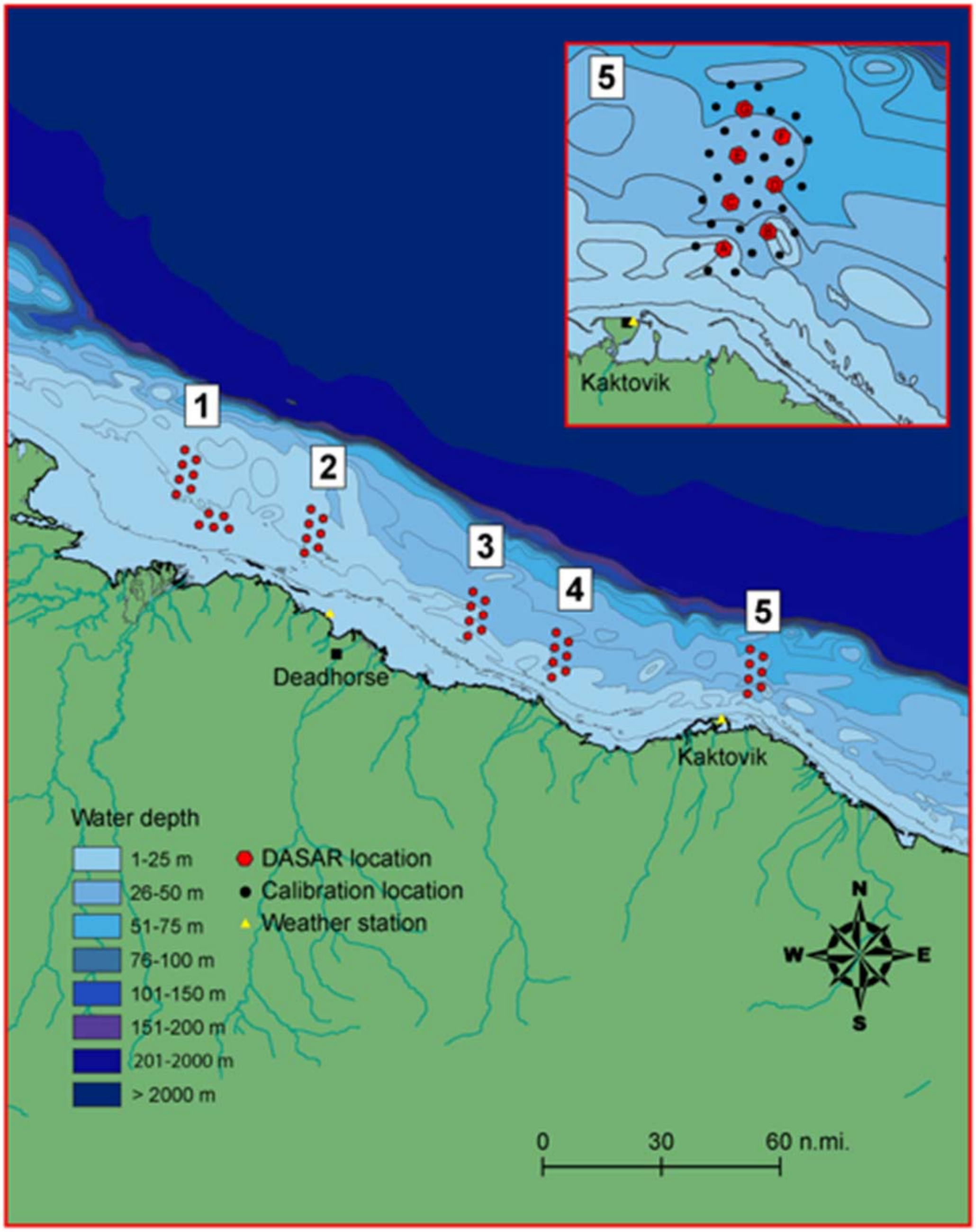

Figure B1 DASAR deployment locations in the central Alaskan Beaufort Sea 2008. The five main seven-DASAR arrays are detailed as red circles and labelled 1-5 from west to east. Within each array the DASARs are labelled A-G from south to north (as shown in inset). An additional DASAR array was also deployed in 2008. This array was deployed to the southeast of array 1. (Plot used with permission. S. Blackwell (pers. Comm.) & Funk et al. 2010).

Appendix C

Supplementary figures of the randomized quantile residual diagnostic plots generated for the density surface model fit to sighting data for all non-calf whales as for the density surface models fit to the sighting data for feeding and travelling non-calf whales.

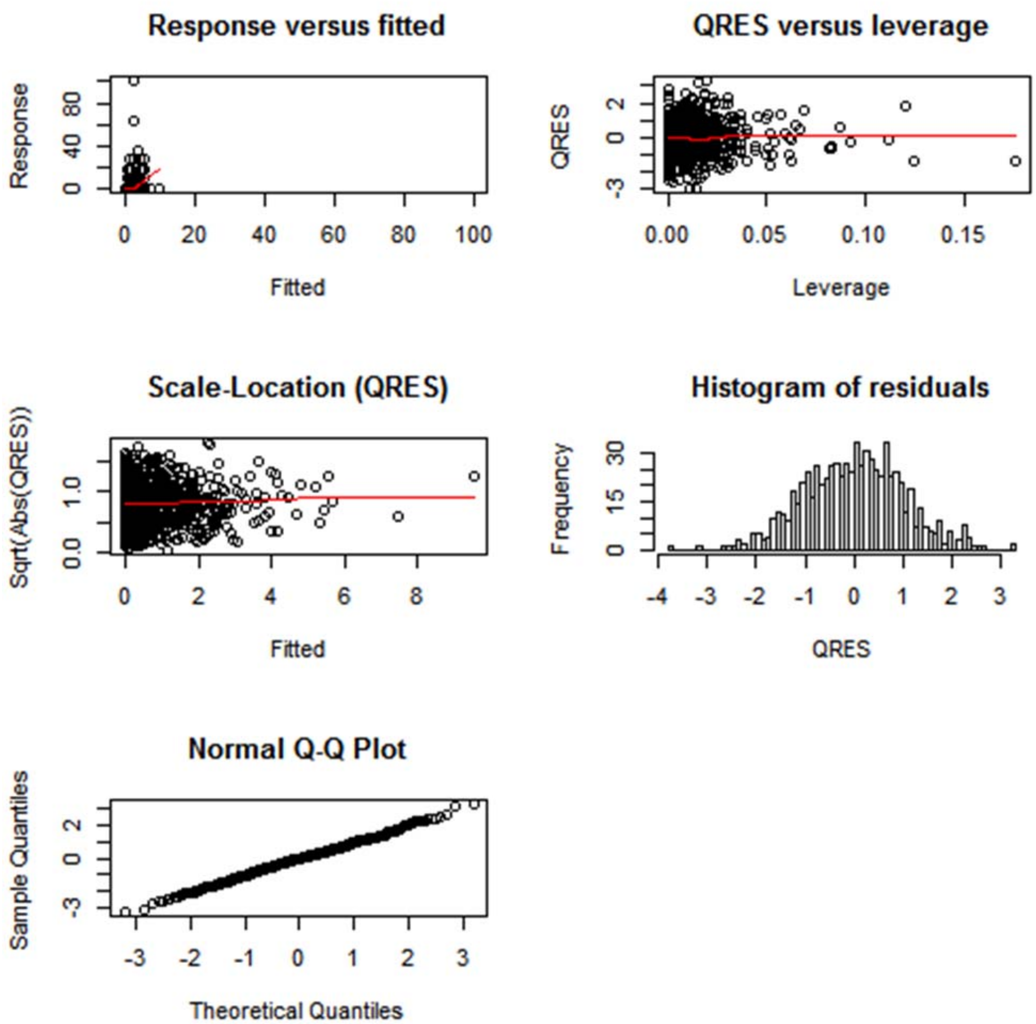

Figure C1 Randomized quantile residual diagnostic plots of the density surface model fit to sighting data of non-calf bowhead whales in the southern Beaufort Sea. Model fit and the value of the Tweedie parameter (θ) was assessed using these diagnostic plots. The flattest fit of the square root of the absolute value of the residuals versus the fitted values determined which value of θ was chosen and resulted in $\theta = 1.2$.

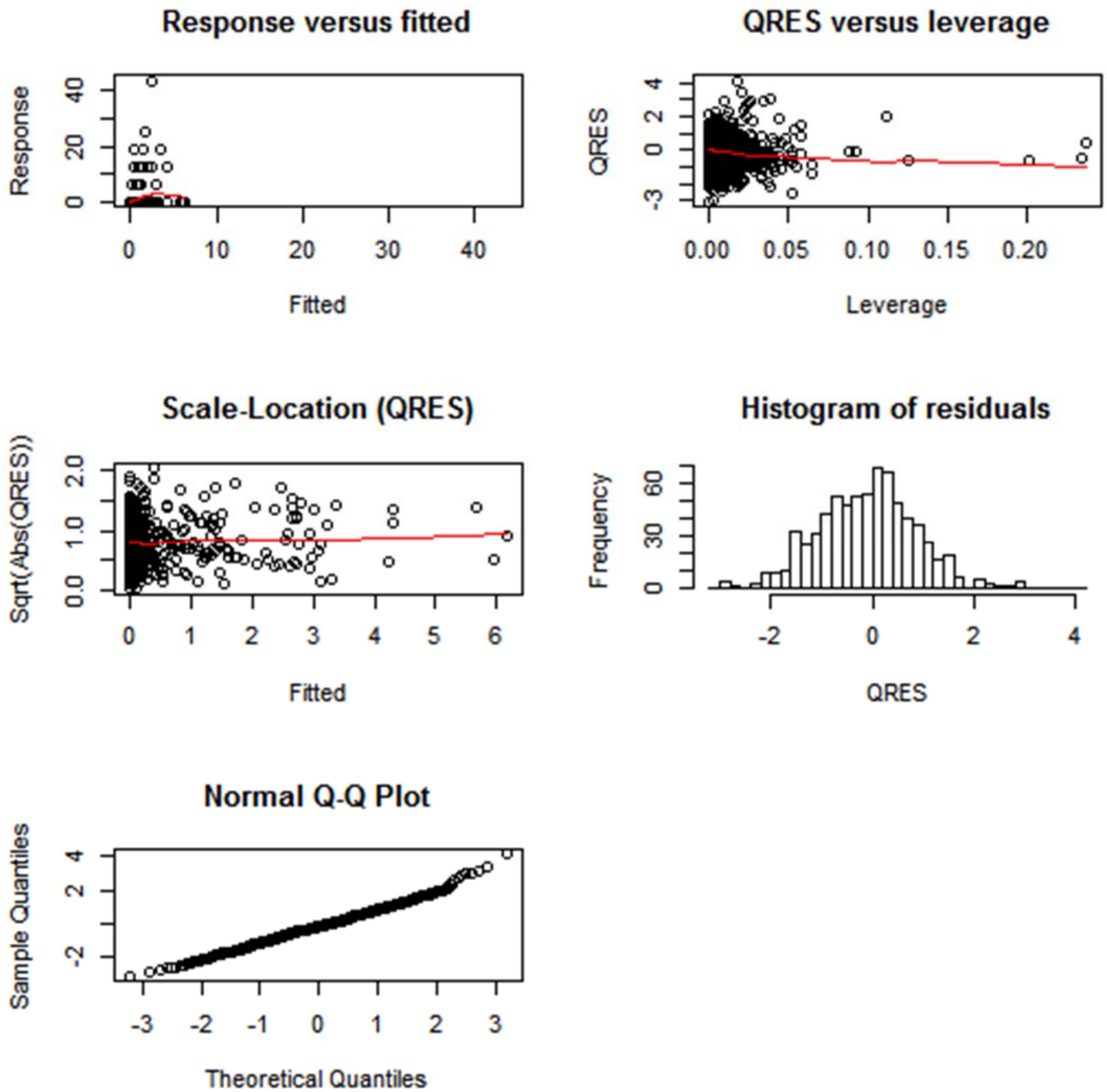

Figure C2 Randomized quantile residual diagnostic plots of the density surface model fit to sighting data of feeding non-calf bowhead whales in the southern Beaufort Sea**.** Model fit and the value of the Tweedie parameter (θ) was assessed using these diagnostic plots. The flattest fit of the square root of the absolute value of the residuals versus the fitted values determined which value of θ was chosen and resulted in $\theta = 1.2$.

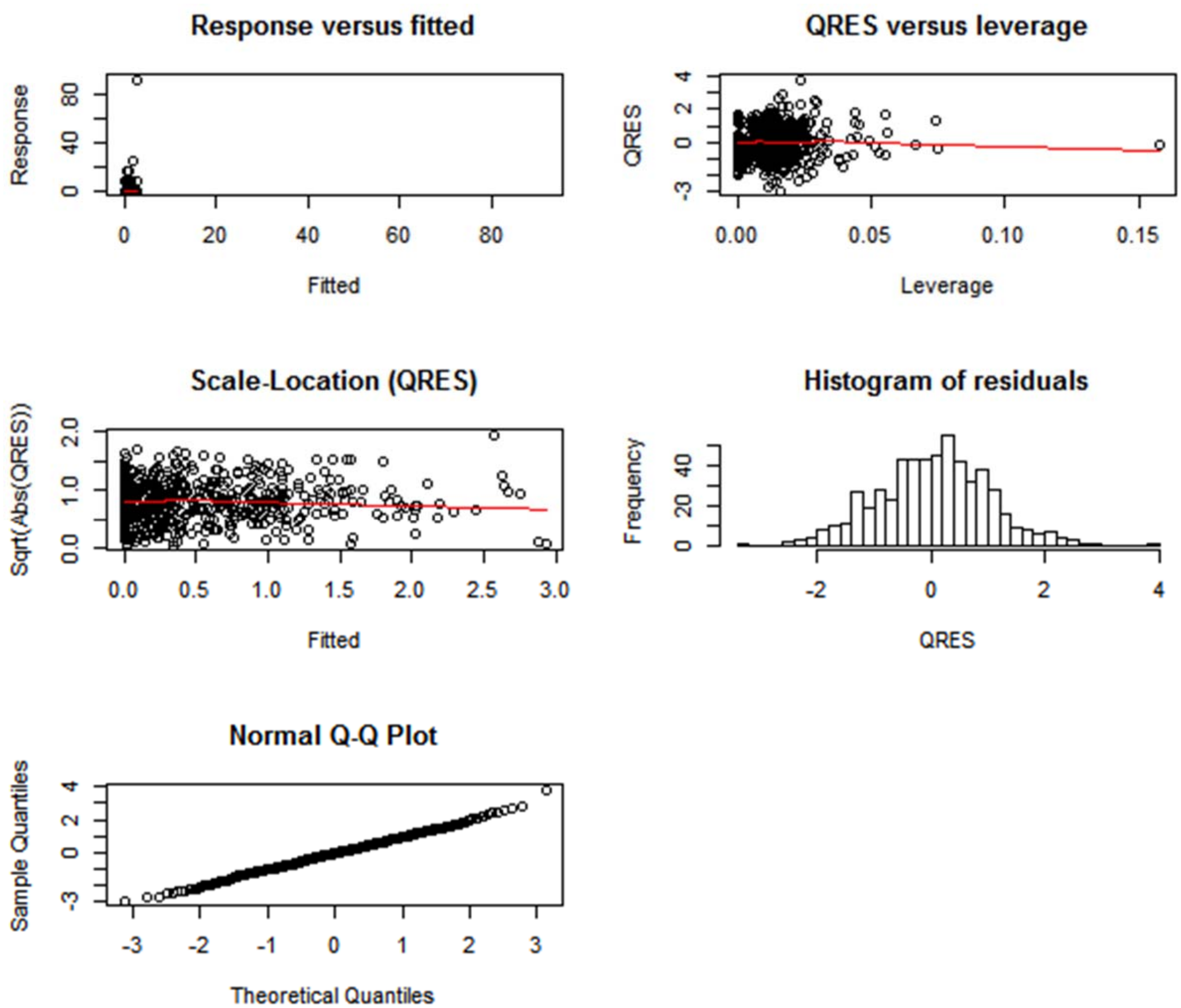

Figure C3 Randomized quantile residual diagnostic plots of the density surface model fit to sighting data of travelling non-calf bowhead whales in the southern Beaufort Sea. Model fit and the value of the Tweedie parameter (θ) was assessed using these diagnostic plots. The flattest fit of the square root of the absolute value of the residuals versus the fitted values determined which value of θ was chosen and resulted in $\theta = 1.3$.